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Full Length Research Paper

C-banding analysis of chromosome translocations in doubled haploid wheats

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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 denaturation-reassociation 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 (Iordansky 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.

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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 *Yr16*to 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	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Avocet S
DH-2	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-3	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-4	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-5	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-6	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-8	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-10	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-11	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-12	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-13	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-14	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-15	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-17	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-18	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-19	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-20	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-21	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-22	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-23	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-25	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-26	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-27	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet

Table 1. Contd.

DH-28	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-29	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-30	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-40	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-41	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-50	F_4: *Yr16-2* {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-51	F_4: *Yr16-2* {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-52	F_4: *Yr16-2* {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-53	F_4: *Yr16-2* {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-54	F_4: *Yr16-2* {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-56	F_4: *Yr16-2* {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-57	F_4: *Yr16-2* {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-58	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-59	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-60	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-61	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-62	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-63	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-65	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #2/Avocet S
DH-66	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-67	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-69	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-70	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-71	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-73	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-74	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-75	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-76	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-77	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-78	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #2/Palmiet
DH-133	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Avocet S
DH-134	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-135	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-136	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-137	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-140	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-141	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-142	F_3: *Yr16-1* {[F_2:98SGI1(CD/Palmiet)}ex Row 1283 Greytown} #2/Palmiet
DH-145	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown} #1/Avocet S
DH-147	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-148	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-149	F_4: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-7 Resist Greytown} #1/Palmiet
DH-156	F_3: *Yr16*-2 {[F_2:98SGI1(CD/Palmiet)}ex Row 1284-8 Resist Greytown}
Palmiet	SG1-W43
Cappelle - Desprez ex Tony Worland	SG1-W47

[a]DH= 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
Seed germination	• Seeds were surface sterilized in 70% Ethanol for 1 min and 30% JIK for 5 min followed by rinsing three times in distilled water • Petri dishes containing two layers of filter papers were sterilized by immersing in boiled distilled water and removed after about 10 min • 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 ºC; petri dishes were sheathed using clean plastic bags to retain the moisture content of the filter paper
Collecting root tips and squashing	• 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 • Root tips were fixed in 45% acetic acid for 3 hr at 4 ºC and stored in 70% Ethanol until analyzed • 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
Staining	• 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 ºC • The slides were rinsed once in distilled water • Slides were directly transferred in a saturated barium oxide solution in staining dishes using slide rack (at room temperature and for 7 min) • Slides 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 ºC • 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 • Permanent slides were made after soaking dried slides in xylene for 10-15 min and mounted in DPX • Banding pattern were analyzed and recorded two days after mounting
Note	❖ 0.2 N/M HCl: [2 N HCl stock solution was prepared by mixing 86 ml concentrated HCl 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 {$Ba(OH)_2$} 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 {$Na_3C_6H_5O_7.2H_2O$} and 173.3 g of sodium chloride {NaCl} both dissolved in 1 liter distilled water. The solution was diluted 1:9 with distilled water before use 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 preparations: PART I: 9.47 g sodium phosphate dibasic {Na_2HPO_4} was dissolved to 1 l distilled water PART II: 9.07 g potassium dihydrogen phosphate {KH_2PO_4} was dissolved to another 1 l 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).

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.

Line [a]	5BS/7BS and 5BL/7BL	Line	5BS/7BS and 5BL/7BL	Line	5BS/7BS and 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	+		

[a]DH=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).

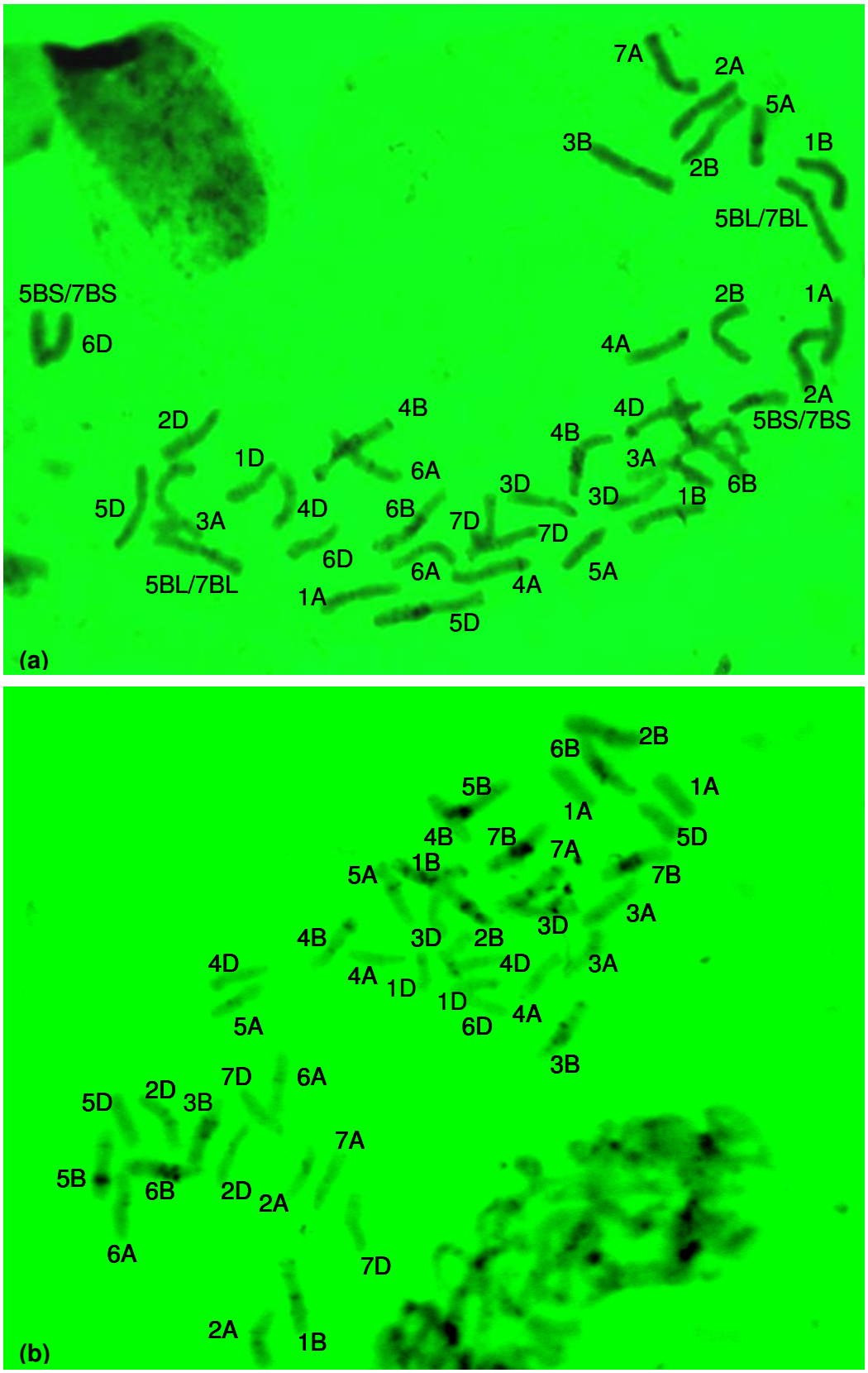

Figure 1. Karyotypes representing T*riticum aestivum* cultivar Cappelle-Desprez (**a**) and *Triticum aestivum* cultivar Palmiet (**b**) after the C-banding technique.

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.

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