Standard karyotype and nomenclature system for description of chromosome bands and structural aberrations in wheat (*Triticum aestivum*)[1]

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A standard karyotype based on N-banding, C-banding, and modified C-banding has been constructed for *Triticum aestivum* L. 'Chinese Spring'. An idiogram and a nomenclature system have been developed for the description of individual bands. Nomenclatural rules have been proposed for the description of chromosomal structural aberrations and polymorphic bands in other wheat cultivars. As a rule each short arm (S) and a long arm (L) consists of a series of dark bands (C-bands) and light bands (mainly euchromatic) and by definition there are no interbands. In some cases, each arm has been subdivided into two or more regions. The description of a band requires designation of a chromosome number, arm (S or L), region, and band. The region number is separated from the band number by a decimal point. Except for arms 1AS, 3AL, 4AS, and 6AS, all wheat chromosome arms have one or more intercalary C-bands and are divisible into three or more bands. It is hoped that the proposed karyotype and nomenclature system will be widely adopted and lay the foundation of definitive chromosome analysis in wheat.

Key words: C-banding, N-banding, common wheat, heterochromatin, idiogram.

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Un caryotype standard a été établi pour le *Triticum aestivum* L. cv. Chinese Spring, d'après les bandes N, les bandes C et les bandes C modifiées. Un idiogramme et un système de nomenclature ont été développés pour la description des bandes individuelles. Des règles nomenclaturales ont été proposées pour la description des aberrations structurales des chromosomes et celle des bandes polymorphes chez d'autres cultivars de blé. En général, chacun des bras courts (S) et des bras longs (L) comporte une série de bandes foncées (les bandes C) et des bandes claires (principalement euchromatique) et, par définition, il n'existe pas d'entre-bandes. Dans certains cas, chaque bras a été subdivisé en deux régions ou plus. La description d'une bande nécessite une désignation de numéro de chromosome, de bras (S ou L), d'une région et de la bande. Le numéro de la région est séparé du numéro de la bande par un point décimal. À l'exception des bras 1AS, 3AL, 4AS et 6AS, tous les bras des chromosomes du blé ont une ou plus d'une bande C intercalaire et sont divisibles en trois bandes ou davantage. Il est à espérer que la description caryotypique proposée et le système de nomenclature avancé seront largement adoptés et serviront de base pour l'analyse définitive des chromosomes du blé.

Mots clés : bandes C, bandes N, blé tendre, hétérochromatine, idiogramme.

[Traduit par la rédaction]

Introduction

Following the first reports on chromosome identification by C-banding (Gill and Kimber 1974*a*; Natarajan and Sarma 1974; Zurabishvili et al. 1974) and N-banding (Gerlach 1977; Jewell 1979; Endo and Gill 1984), there has been widespread use of chromosome banding methods in various aspects of wheat cytogenetics research (for a review see Gill and Sears, 1988). In particular, polymorphic banding patterns among cultivars (Iordansky et al. 1978; Seal 1982; Endo and Gill 1984; Friebe and Heun 1988; Friebe et al. 1988) and numerous structural aberrations have been described in wheat (Endo 1988; Kota and Dvořák 1988). These advances have opened many possibilities for the genetic mapping of polymorphic C-bands (Jampates and Dvořák 1986; Curtis and Lukaszewski 1991) and the physical mapping of genes to specific bands on individual metaphase chromosome maps of wheat (Dvořák et al. 1984; Kota and Dvořák 1986; Mukai et al. 1990, 1991). Thus, there is an urgent need for a standard karyotype and a generalized nomenclature system for description of chromosome bands, banding polymorphisms, and various structural aberrations in wheat.

Gill and Kimber (1974*a*) and later Lukaszewski and Gustafson (1983) presented idiograms of the 21 C-banded wheat chromosomes based on standard genetic nomenclature of wheat. However, no attempt was made to develop a nomenclature system for the description of bands. Iordansky et al. (1978) proposed the Generalized Cytological Nomenclature for Cereal Chromosomes (GCNCC) after the Paris Conference (Anonymous 1972) on standardization in human cytogenetics. Under the GCNCC system, chromosomes were numbered on the basis of their length rather than the existing genetic nomenclature. Van Niekerk and Pienaar (1983) and Gill (1987) took initial steps in combining the genetic and GCNCC nomenclature and made proposals for a standard nomenclature system for the description of chromosome bands in wheat.

The chromosome banding nomenclature proposals were discussed at the First North American Wheat Cytogenetics Workshop held in Columbia, Missouri, in 1986 (Gill 1986). At the 7th International Wheat Genetics Symposium (IWGS), Cambridge, England, an international chromosome banding nomenclature committee was formed, which met at the site of the 7th IWGS and reached a consensus

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on nomenclature and designation of chromosome bands in *Triticum aestivum* L. 'Chinese Spring' wheat.

Following the instructions and in consultation with the committee, we undertook the construction of a standard karyotype and nomenclature system for the description of the chromosomes of 'Chinese Spring' wheat. Furthermore, we propose nomenclature for the description of polymorphic bands and frequently observed chromosome aberrations in wheat. It is hoped that this nomenclature system will be widely adopted by wheat cytogeneticists. Based on the experience of many cytogeneticists, further changes and refinements may be necessary and these can be incorporated in due course.

Materials and methods

Seed of 'Chinese Spring' wheat used in the construction of the standard karyotype was obtained from E.R. Sears, University of Missouri. The original C-banding technique, henceforth simply referred to as the C-banding technique, used in cereal chromosomes was reported independently from several laboratories (Merker 1973; Sarma and Natarajan 1973; Gill and Kimber 1974*b*, 1974*c*; Natarajan and Sarma 1974; Shchapova 1974; Verma and Rees 1974; Zurabishvili et al. 1974). In the present study, a more recent version of these techniques reported by Giraldez et al. (1979) was used with some modifications. The N-banding procedure was originally reported by Gerlach (1977) and an improved N-banding technique reported by Endo and Gill (1984) was used here. A modified C-banding technique, which combines parts of the protocols of N-banding and C-banding procedures, was reported by Endo (1986) and was used in the present study. It is important that various workers should be able to obtain reproducible results similar to the banded karyotypes illustrated here; to this end, details of the protocols used are given below.

Seeds were germinated in Petri dishes on moist filter paper. Root tips (1.5–2.5 cm long) were treated with cold water for 24 h for N-banding and modified C-banding procedures and with 0.05% colchicine for 3 h for the C-banding procedure. Pretreated root tips were fixed in ethanol (99%) – glacial acetic acid (3:1). For the N-banding and C-banding procedures, root tips were fixed for up to 3 days at room temperature before banding and may be fixed for months in a refrigerator. For the modified C-banding procedure, root tips were fixed for 1 day and then used for banding. Further steps for each method are described separately.

N-banding (N)

Root tips were stained in 1% acetocarmine solution for 1–2 h at room temperature and then squashed in 45% acetic acid. The cover slip was removed by freezing and the preparation was treated with 45% acetic acid at 50°C for 5–10 min and air dried overnight. The preparations were incubated in hot phosphate buffer (1 M NaH_2PO_4) at 94°C for 2 min, rinsed in tap water, and air dried. Next the preparation was stained in Banco Giemsa stain (1 drop per millilitre Sorenson's phosphate buffer) for 15–20 min, rinsed briefly in tap water, and air dried.

Modified C-banding (MC)

Initially, the preparations were handled similar to the N-banding procedure. Next, the preparations were treated in a saturated barium hydroxide solution at ca. 50°C for 2.5 min, rinsed in tap water, immersed in 2× SSC (0.3 M sodium chloride plus 0.03 M trisodium citrate) at 50°C for 3–10 min, and rinsed in tap water, and the wet slides were stained in Wright or Leishman Banco Giemsa staining solution (one drop per millilitre Sorenson's phosphate buffer) for an appropriate time (ca. 20 min), rinsed in water, and air dried.

C-banding (C)

The root tips were transferred to 45% acetic acid for 2–3 min, followed by squash preparation and removal of the cover slip by freezing. The slides were transferred to 99% ethanol overnight and then air dried for a few minutes. Next, the preparations were incubated in 0.2 M HCl at 60°C for 2 min (in a water bath), washed in distilled water, incubated in saturated barium hydroxide solution at room temperature for 7 min, rinsed in distilled water, and incubated in 2× SSC at 60°C for 1 h. The slides were directly transferred to 1–5% Giemsa staining solution (Fisher) in phosphate buffer for up to 30 min. The staining of chromosomes was monitored until optimal staining was observed. After washing, air-dried slides were placed in xylene and mounted in Permount for observation.

Other well-established C-banding techniques have been described by Badaev et al. (1985) and Lukaszewski and Gustafson (1983). Detailed protocols may be requested from the authors.

Results and discussion

Cultivar selection

The karyotype is based on 'Chinese Spring', which is a standard cultivar for cytogenetic analysis in wheat. Fortunately, there is no apparent C-banding polymorphism within the variety except in chromosome 7A, which occasionally showed a terminal C-band polymorphism (Seal 1982).

It is also assumed that 'Chinese Spring' possesses a primitive karyotype with respect to gross structural aberrations. However, Endo and Gill (1984) found that chromosome 4B (new designation) of 'Chinese Spring' has a different morphology (arm ratio 1.1) as compared with its morphology (arm ratio 1.5) in most other 6*x* and 4*x* wheats. Apparently, in 'Chinese Spring' chromosome 4B may have suffered a pericentric inversion. This implies either that 'Chinese Spring' has a separate lineage from most other 6*x* wheats or that it is derived from other 6*x* wheats.

Evidence has also been presented for the occurrence of a cyclical translocation involving chromosomes 4A, 5A, and 7B (Gill and Chen 1987; Naranjo et al. 1987). It is believed that a 4A–5A translocation occurred in *Triticum monococcum* L. (Naranjo et al. 1987). The 4A/5A chromosome was involved in another translocation with 7B during the origin of tetraploid wheats to produce translocation chromosomes 4A/7B and 7B/4A. Presumably, all tetraploid and hexaploid wheats contain ancient translocated chromosomes 4A/7B, 5A/4A, and 7B/5A. Thus, the occurrence of this cyclical translocation should have no effect on the designation of 'Chinese Spring' as having the standard karyotype.

The designation of 'Chinese Spring' with a standard karyotype implies that karyotypic variants in other cultivars including banding polymorphisms and structural aberrations must be described with respect to the 'Chinese Spring' standard karyotype.

Genome allocation for chromosomes 4A and 4B

Dvořák (1983), on the basis of similarity of the C-banding pattern of chromosome 4A (old designation) of polyploid wheat to a similar chromosome in *Aegilops speltoides*, proposed the genome reallocation of chromosomes 4A and 4B. Further evidence based on banding analysis of meiotic configurations in *Triticum turgidum* × *Ae. speltoides* hybrids (Chen and Gill 1984) and *in situ* hybridization (Rayburn and Gill 1985; Dvořák et al. 1990) supported genome reallocation of chromosome 4A to 4B. Initially, chromosome 4B (old designation) did not appear to be an A-genome chromosome because of its lack of pairing with any *T. monococcum* chromosome (Dvořák 1976); more recent evidence indicates that the old 4B may in fact be an A-genome chromosome and its anomalous pairing behavior may be due to the structural aberrations that it suffered

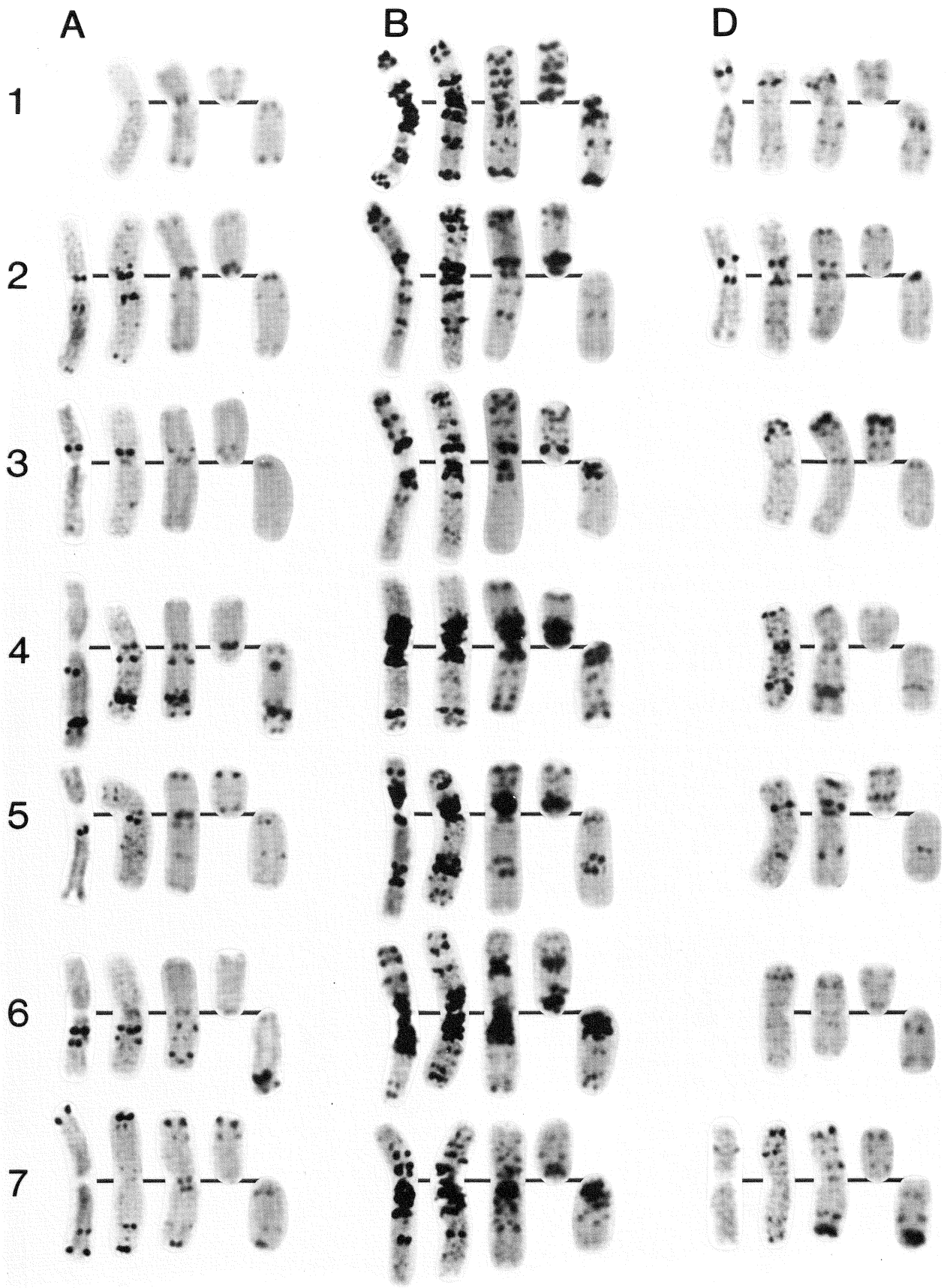

FIG. 1. A banded karyotype of 'Chinese Spring' wheat. Each panel of chromosomes was stained (from left to right) by N-banding, modified C-banding, and C-banding (whole and telosomic chromosomes). Because chromosomes 1A and 3D to 6D do not show any N-bands, they were not identified.

during the origin of wheat (Naranjo et al. 1988). In view of these considerations, the participants at the 7th IWGS unanimously voted to reallocate chromosomes 4A and 4B. Thus old 4A now has been allocated to the B genome and is designated chromosome 4B. The old 4B has been allocated to the A genome and is now designated as chromosome 4A. These new designations have been adopted in the construction of a standard karyotype.

Arm designations

In accordance with the resolution of the 7th IWGS, the short arm will be designated by the letter S and the long arm by the letter L. In those cases where both arms are of similar length, the designation of S and L has been based on homoeologous relationships. Thus, for almost metacentric chromosomes 6A, 7A, 4B, and 7D, arm designations have been based on homoeology rather than length.

Relationship among heterochromatin bands revealed by different staining techniques and staining solutions

Because three different techniques, namely, N-banding, modified C-banding, and C-banding, have been used in the construction of the wheat karyotype, it is important to understand the relationship among heterochromatin bands revealed by the three staining procedures. First of all, N-banding and modified C-banding do not always reveal new bands not observed by C-banding, although certain bands may be stained more intensely. Therefore, C-banding should be considered as a technique that stains all constitutive heterochromatin (C-bands), whereas N-banding and modified C-banding are specialized staining techniques.

As shown by Endo and Gill (1984), N-bands are only observed on 16 pairs of chromosomes in 'Chinese Spring' wheat. Chromosome 1A and chromosomes 3D through 6D do not show N-bands and are not shown in Fig. 1. It is also clear, in comparison with other techniques, that for each N-band there is a corresponding C-band (C^+N^+), but for many C-bands, there are no corresponding N-bands (C^+N^-). Additional details between C-banded and N-banded heterochromatin have been discussed by Gill (1987).

Differences between the modified C-banding and C-banding technique pertain only to minor bands. One should note C-bands in terminal position in 4AL, terminal and subterminal positions in 6AL, proximal to centromere in 7AL, among others, that are not intensely stained by the modified C-banding technique. However, there are many faint C-bands that are intensely stained by the modified C-banding technique. Especially note several C-bands in distal position in the 5BL arm that can be clearly observed by the modified C-banding technique. Those bands that are not consistently stained by the two C-banding techniques have been indicated by hatch marks and were not named in the idiogram. Different brand stains may also lead to observable differences in C-bands as was shown by Seal and Bennett (1982).

G-banding

Recently several reports have appeared on G-banding of cereal chromosomes (Yang and Zhang 1988). These authors have reported up to 20 G-bands per chromosome in several plants. Unfortunately, at present, no reproducible method is available for G-banding analysis. Thus, by necessity, the wheat chromosome band nomenclature system will be based on C-bands, unlike the human banding nomenclature, which was based on G-banding patterns of individual chromosomes (Anonymous 1972).

Chromosome band nomenclature

The designation of chromosome bands is in part based on the recommendations of the 1971 Paris Conference on standardization in human cytogenetics (Rowley 1974). Each arm may or may not have "landmark" bands. A chromosome landmark is defined as a "consistent and distinct morphologic feature that is an important diagnostic aid in identifying a chromosome." Diagnostic bands are prominent C-bands observable with many different banding techniques. The fraction length (FL) of the diagnostic bands from the centromere has been calculated and is indicated on each chromosome map.

A region is defined as any area of a chromosome lying between two adjacent landmarks.

A band is defined as a "part of a chromosome clearly distinguishable from adjacent parts by virtue of its lighter or darker staining ability." Each arm consists of a continuous series of dark bands and light bands; by definition, there are no "interbands." Regions and bands are numbered consecutively from the centromere outwards along each chromosome arm (Anonymous 1972).

Each chromosome has a distinct centromere, and the heterochromatin bisected by the centromere is considered as two bands, each being labeled as band 1, in region 1, of each arm. A band used as a landmark is considered as belonging entirely to the region distal to the landmark and is accorded the number 1 of that region.

Five items are required in designating a particular band: the chromosome number, the genome designation, the arm symbol, the region number, and the band number within that region. The region number is separated from the band number by a decimal point.

Nomenclature rules on the subdivision of existing landmark bands state that "in the event that a band serving as a landmark requires subdivision, all sub-bands derived from it should retain the original region and band number of that landmark." This rule is to be followed even if subdivision should cause one or more sub-bands to lie in an adjacent region. The sub-bands are numbered sequentially from the centromere outward. For example, if the original band 1L1.1 was subdivided into three equal or unequal sub-bands, the sub-bands would be labeled 1L1.11, 1L1.12, and 1L1.13, with sub-band 1.11 being proximal and 1.13 distal to the centromere. Finally, if a sub-band is to be subdivided, additional digits without punctuation should be used; e.g., sub-band 1L.11 might be further subdivided into 1L1.111, 1L1.112, etc.

It can be seen that the proposed nomenclature provides the necessary accuracy and flexibility for describing banded chromosomes and any future additions to the bands. In common wheat, an attempt has been made to label each arm as region 1 so that band numbers could be named consecutively from the centromere outwards. However, all B-genome chromosomes with heavy proximal C-bands have been designated into separate regions. Also if band numbers exceeded more than nine, then the arm was subdivided into two regions. For chromosomes 1B and 6B, the nucleolus

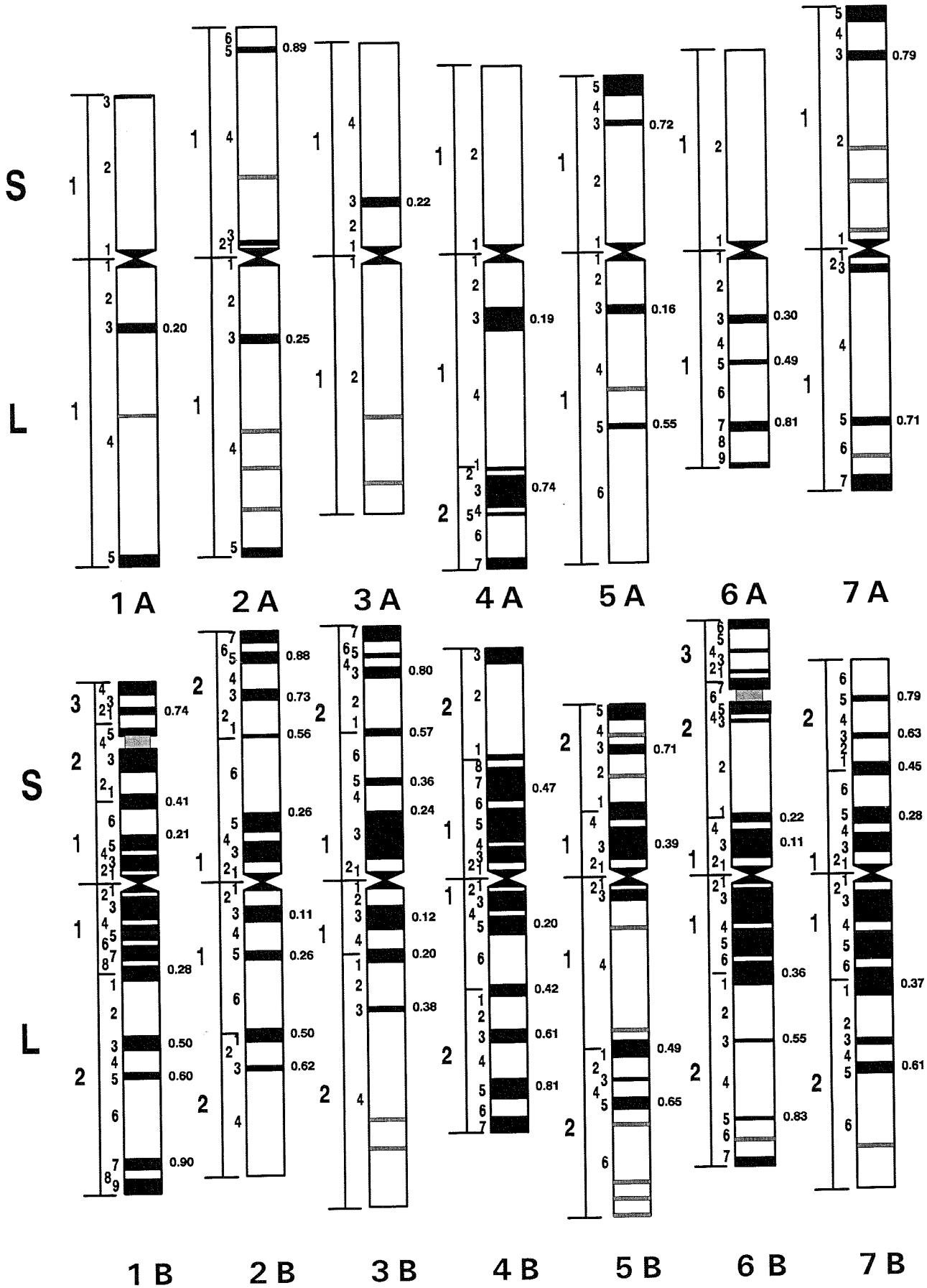

FIG. 2. Idiogram of banded chromosomes of 'Chinese Spring' wheat. Band numbers are indicated on the left and FL positions on the right of each chromosome. The hatched bands were not numbered, as they were not consistently observed.

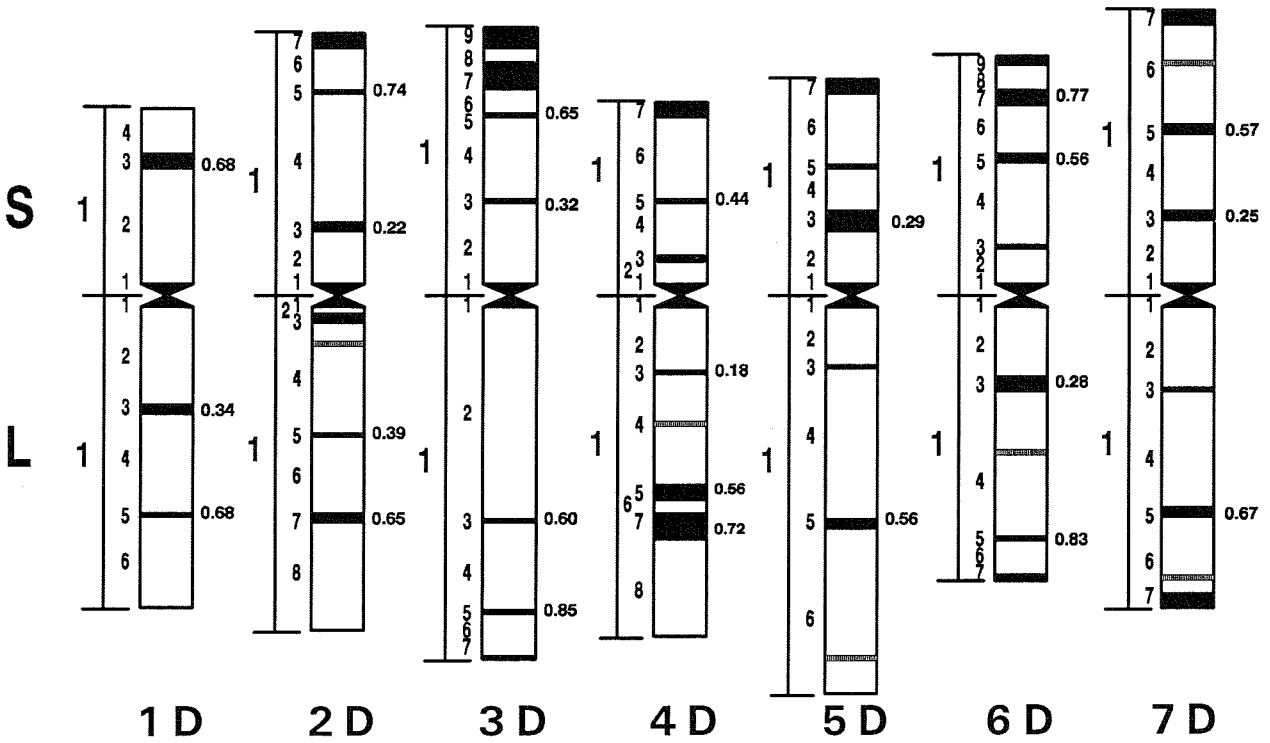

FIG. 2 *(concluded).*

organizer (NO) arms have been divided into three regions because of difficulties associated with the interpretation of the bands in the NO region.

Description of individual chromosomes

The karyotype was constructed by N-banding, modified C-banding, and C-banding analysis of individual chromosomes, and C-banding of individual ditelosomic chromosomes of 'Chinese Spring' wheat (Fig. 1). An idiogram of the banded chromosome is shown in Fig. 2. In designating bands, some special situations have been considered. Centromeric heterochromatin may not be observed in all chromosomes in a metaphase cell, but the first band in each arm of all chromosomes belongs to centromeric heterochromatin. Telomeric bands may or may not be observed on all chromosomes; only those telomeric bands have been designated that are prominent. Similarly, more bands may be revealed by one technique but not another. Thus, a $N^+MC^+C^+$ designation will be given to those bands that are stained by the N-banding (N), modified C-banding (MC), and C-banding (C) technique. Designation $N^-MC^+C^+$ would mean that a specific band is not revealed by N-banding but is seen with MC-banding or C-banding only. The following is a brief description of each of the 21 chromosomes of 'Chinese Spring' wheat.

Chromosome 1A

Chromosome 1A has mostly faint C-bands. The short arm shows only a faint terminal C-band in a few preparations. A faint proximal band, L1.3, at FL.20 in 1AL is useful for identification but may not always be visible. Note the prominent terminal $N^-MC^-C^+$ band in 1AL.

Chromosome 2A

It is a highly diagnostic chromosome as a result of prominent centromeric heterochromatin and diagnostic band L1.3 at FL.25, which is $N^+MC^+C^+$. Note the series of faint bands in both arms of 2A with the MC technique.

Chromosome 3A

The diagnostic band S1.3 at FL.22, which is $N^+MC^+C^+$, is most useful for the identification of this chromosome.

Chromosome 4A

Chromosome 4A is structurally anomalous. It may have undergone a pericentric inversion, as its short arm shows homoeology to 4BL and 4DL arms and vice versa (Hart and Gale 1990). In addition, the distal region of 4AL may be derived from 7BS because of its homoeology to 7AS and 7DS arms (Gill and Chen 1987; Naranjo et al. 1987). No such chromosome with this morphology was observed in *T. monococcum* (Friebe et al. 1990). Note that the 4AS telosome is acrocentric. The short arm is devoid of C-bands. Diagnostic bands L1.3 at FL.19 and L2.4 at FL.74 are prominent and $N^+MC^+C^+$. Note that L2.1 is $N^-MC^+C^+$ and L2.7 is $N^-MC^-C^+$.

Chromosome 5A

Diagnostic band L1.3 at FL.16 is $N^+MC^+C^+$ and critical for the identification of the 5A chromosome. Diagnostic band L1.5 is $N^-MC^+C^+$. Note the prominent centromeric and terminal bands in 5AS. Band S1.3 is best observed with the MC technique.

Chromosome 6A

The 6AS arm is unmarked, although a series of faint bands can be seen with the MC technique. The long arm is well marked. The diagnostic bands L1.3 at FL.30 and L1.5 at FL.49 are $N^+MC^+C^+$. The bands L1.7 at FL.81 and L1.9 are $N^-MC^-C^+$. Note absence of bands <1.3 and <1.5 in the 6AL telosome, indicating its origin from a different wheat cultivar.

Chromosome 7A

This chromosome can be easily identified because of diagnostic bands S1.3 ($N^-MC^+C^+$) at FL.79 and L1.5 ($N^+MC^+C^+$) at FL.71, along with prominent telomeric

bands in each arm. It is a metacentric chromosome, but the long arm can be distinguished on the basis of the greater size of the subtelomeric band L1.6 as compared with subtelomeric band S1.4. Note that band L1.3 is $N^-MC^-C^+$.

Chromosome 1B

Note centromeric C-bands along with a prominent satellite in the short arm and prominent interstitial and terminal dark bands in 1BL. The subdivision of the secondary constriction region of 1BS has been difficult, as bands S2.3 and S2.5, which flank the region, most often stain as a single dark band. In longer chromosomes, S2.3 is more prominent than S2.5 and both are joined by a faintly staining thread-like band, designated S2.4. These bands are seen only with the C-banding technique; both N- and MC-banding techniques do not stain this region.

Mukai et al. (1991) have shown by *in situ* hybridization analysis that bands S2.3, S2.4, and S2.5 represent the 18S.26S rDNA domain and lie within the secondary constriction region. Moreover, S2.3 and S2.5 lie in regions of inactive condensed rDNA and only the more diffuse S2.4 band is active in organizing a nucleolus.

Chromosome 2B

The distal three C-bands and proximal C-bands in the short arm and a series of moderate-size C-bands in the long arm make this chromosome easy to distinguish from the remaining chromosomes of wheat. Note that S2.3 and L2.3 stain more prominently with the N- and MC-banding than the C-banding technique.

Chromosome 3B

It is similar to 2B except short arm bands are more evenly spaced along the length of the arm and there are fewer C-bands in the long arm. Note differences in the intensity of staining of some bands with the three techniques. S2.7 is $N^-MC^-C^+$, whereas S2.5 is stained more prominently by N and MC techniques.

Chromosome 4B

In 'Chinese Spring' 4B is almost a metacentric chromosome, with almost 50% of the proximal short arm consisting of a compound heterochromatic block and a terminal C-band. In most other wheats, the compound heterochromatic block is located in the long arm and the arm ratio (L/S) is close to 1.5. The long arm, in addition to proximal bands, contains four dark bands, including a terminal C-band, that mark the entire arm. Note that bands S2.3, L2.1, and L2.4 are essentially $N^-MC^-C^+$. Band L2.6 is stained more intensely with N- and MC-banding techniques.

Chromosome 5B

5BL is the longest among the long arms in the chromosome complement of wheat. Furthermore, prominent proximal C-bands in the short arm and interstitial C-bands in the long arm make it a highly diagnostic chromosome for easy identification. Note that band S2.5 is $N^-MC^+C^+$. Note four small C-bands in the 5BL arm that are $N^-MC^+C^-$, which may be used to subdivide band L2.6.

Chromosome 6B

It is the second satellited chromosome of the wheat complement. Because of its longer satellite and different arm ratio, it can be easily distinguished from satellited chromosome 1B. The short arm contains bands S2.3 and S3.2 (staining prominently with N- and MC-banding techniques), which are separated from the bands S2.5 to S2.7 (lying within the secondary constriction region and stained only by the C-banding technique) by intervening lighter bands, S2.4 and S3.2. Note that band S3.4 is $N^-MC^-C^+$. Mukai et al. (1991) have reported on the more detailed analysis of the NO region using deletions. The long arm can be conveniently divided into proximal heterochromatic region 1 and mostly euchromatic distal region 2. In the long arm, L2.3 is $N^-MC^+C^+$ and some other bands also show differential staining with the three techniques.

Chromosome 7B

In 'Chinese Spring', 7B can be distinguished from other heavily banded B-genome chromosomes by the absence of terminal C-bands. The C-bands are most prominent in the centromeric region, with faint C-bands in the distal region in each arm. Note that L2.3 is $N^-MC^-C^+$.

Chromosome 1D

S1.3 at FL.68 is $N^+MC^+C^+$ and highly diagnostic for identification.

Chromosome 2D

Band S1.3 at FL.22 and L1.3 are $N^+MC^+C^+$ and diagnostic for the identity of this chromosome. This chromosome may be confused with 5A, from which it can be distinguished by the presence of band S1.3, where there is no such band at that position in 5A.

Chromosome 3D

Prominent C-bands at the distal end of the short arm are highly diagnostic for its identification.

Chromosome 4D

Prominent interstitial C-bands L1.5 and L1.7 in 4DL are highly diagnostic for its identification. Note the numerous thin C-bands seen with the MC technique.

Chromosome 5D

Bands S1.3, S1.7 in the short arm, and L1.5 in the long arm are diagnostic for identification.

Chromosome 6D

Bands S1.7 and L1.3 are diagnostic for its identification. This chromosome can be distinguished from 1D because of its size and arm ratio.

Chromosome 7D

Bands S1.3, S1.5, and S1.7 in the short arm and prominent long arm bands L1.5 and L1.7 are diagnostic for its identification. Note that S1.5 is $N^+MC^+C^+$. Recent data from restriction fragment length polymorphism (RFLP) analysis indicated that 7DL chromosome arm, not 7DS, is homoeologous to 7AS and 7BS (unpublished results).

Nomenclature of chromosomal aberrations

Kimber and Sears (1970) proposed a nomenclature system for the description of aneuploids in the Triticinae. At that time, chromosome pairing provided the exclusive means of chromosome identification and, therefore, all identifications were denoted in terms of pairing configurations. With the advent of banding techniques, rapid and direct identification of somatic chromosomes, including chromosomal structural aberrations, has become feasible. Thus, it is now possible to detect the exact position (as to arm and band number) of chromosome breakpoints in deletions and interchange points in translocations. The Paris Conference (see Rowley

1974) proposed a nomenclature for the description of chromosomal structural changes and this system has been adapted in wheat. Certain aspects of nomenclature for translocated chromosomes described by Koebner and Miller (1986) have been adapted. The following is a description of each structural change, followed by a formula to denote the change and a description of the change.

Terminal deletion (del)

42, del(1B) (L2.5:0.40), $2n = 42$, breakpoint in 1BL arm band L2.5 at 0.60 FL with concomitant loss of the distal 0.40 FL of the chromosome segment.

Interstitial deletion

42, del(1B) (S2.1::S2.3), an interstitial deletion with breakpoints at S2.1 and S2.3 with concomitant deletion of the intervening segment and union of broken ends.

Double terminal deletion

42, del(1B) (S3.2:0.26, L2.5:0.40), a terminal deletion in 1B at each end with a 0.26-FL segment deleted distal to the breakpoint at FL 0.74 in band S3.2 and a 0.40-FL segment deleted distal to the breakpoint at FL 0.60 in L2.5.

Inversions (inv)

42, inv(4B) (S1.7L1.5), a pericentric inversion in chromosome 4B with breaks in band 1.7 in the short arm and band 1.5 in the long arm, with inversion of and reunion of the interstitial segment with the distal segments.

Translocations (T)

42, Trcp (2B,5B) (L2.1;L2.2), a balanced reciprocal translocation between chromosomes 2B and 5B, with breakpoints at band L2.1 in 2B and L2.2 in 5B, giving rise to chromosomes T2BS·L2.1::5BL2.2→ter (terminal) and T5BS·L2.2::2BL2.1→ter. If the exact breakpoint position is not known, the translocation chromosome may be described as T2BS·2BL-5BL, for centromeric breakpoints T2BS·5BL.

Ti,4AS·L1.2::6RL::L1.2→ter or Ti,4AS·L-6RL-L, an intercalary translocation of a piece of 6RL at the L1.2 band of 4A.

Following Koebner and Miller (1986) for translocations within the Triticeae, the chromosomes in the lower homeoelogous group should be indicated first, and in interspecific translocations, the host chromosome should precede the alien chromosome segment.

Isochromosomes (i)

41,i(1BL), if analyzed by banding of somatic cells or 20 II + i I (1BL) if analyzed by meiotic pairing, a plant containing an isochromosome 1BL, in addition to the remaining chromosome complement.

Telochromosomes (t)

41,t(1BL) for somatic cells or 20 II + t I (1BL) for meiotic cells, monotelosomic 1BL; 42,tt(1BL) or 20 II + t II (1BL), ditelosomic 1BL; 44,tttt(1BL,1BS) or 20 II + t II (1BL) + t II (1BS), double ditelosomic 1BL and 1BS.

Ring chromosomes (r)

41,r(6B) (S2.2L2.3), a centric ring chromosome, with deletion of both terminal segments, the broken ends having joined to form a ring.

Dicentric chromosomes (dic)

41,dic(1B) (L2.1) or Ster→L2.1::L2.1→Ster, a dicentric 1B chromosome with a break at band L2.1, breakage and union have occurred at band L2.1 on sister chromatids to form a dicentric 1B chromosome.

Concluding remarks

The banding techniques have provided a powerful tool for the analysis of the cytogenetic structure and manipulation of the genome of wheat. It is unfortunate that even after almost two decades of banding analysis, no universal nomenclature system has been developed in wheat. The present proposal has been put forth after consultation with numerous colleagues and especially the members of the Wheat Chromosome Banding Nomenclature Committee. As a result, this nomenclature system should find widespread acceptance and use.

The present proposal is different from previous proposals in several key points. The number of regions into which an arm can be subdivided has been kept to a minimum. The following criteria were used in subdividing an arm into two or more regions: (*i*) a number of bands that exceeded a single-digit number (i.e., chromosome 4AL arm); (*ii*) a chromosome that contained a series of proximal bands where the exact number of bands was difficult to determine (This is true for all the B-genome chromosomes and in every case each arm has been subdivided into proximal and distal regions); (*iii*) special situations such as NO regions of 1BS and 6B where exact numbers of bands are hard to determine.

The band number has been separated from the region number by a decimal point. Thus for most arms, bands can be counted consecutively from the centromere outwards. This adds an element of simplicity to the nomenclature.

Only dark-staining, reproducible C-bands have been indicated by dark bands. Many other faint C-bands are observed with one or more techniques; these either have not been labeled or are indicated by hatched lines. For a more detailed study of such a region with faint bands, an investigator can freely subdivide each band into sub-bands according to the rules of nomenclature proposed here.

All dark C-bands should be considered as landmark bands which are diagnostic in the identification of individual chromosomes. They also subdivide each arm into easily recognizable light-staining bands. The C-bands are abundant enough that all of the chromosome arms belonging to B and D genomes and most in the A genome can be divided into at least three or more bands. Furthermore, many more faint C-bands are observed so that most arms are divisible into 1–2 μm size bands. It is only arms 1AS, 3AL, 4AS, and 6AS that remain unmarked and special efforts should be made to mark these arms.

Further possibilities of linear differentiation are offered by preliminary reports of G-banding in cereals, which reveal up to 20 bands per arm (Yang and Zhang 1988). The G-bands can further be used to subdivide the existing bands based on the rules of nomenclature proposed here. This subdivision of bands can be easily accomplished by the use of hundreds of deletion stocks that are now available in 'Chinese Spring' wheat (Endo 1988; Kota and Dvořák 1988).

The *in situ* hybridization (ISH) technique in conjunction with repeated DNA probes which result in multiple ISH sites offer another option for the subdivision of existing bands. In the near future, we can look forward to cytogenetically analyzing ca. 1 μm length of chromatin or even smaller sections at a time in wheat. Undoubtedly, such a capability will vastly expand our ability to cytogenetically analyze and

TABLE 1. Somatic metaphase chromosome size (μm) and arm ratio (AR) of the 21 chromosomes of *T. aestivum* 'Chinese Spring' (data from Gill 1987)

Chromosome	Size (AR)	Chromosome	Size (AR)	Chromosome	Size (AR)
1A	11.1(1.9)	1B	11.8(1.7)	1D	8.4(1.7)
2A	12.5(1.3)	2B	12.9(1.2)	2D	10.1(1.3)
3A	11.5(1.3)	3B	13.8(1.3)	3D	10.7(1.4)
4A	11.9(1.7)	4B	11.4(1.1)	4D	9.0(1.8)
5A	11.5(1.8)	5B	12.1(2.0)	5D	10.4(1.9)
6A	9.8(1.1)	6B	12.7(1.2)	6D	9.9(1.2)
7A	11.3(1.0)	7B	12.5(1.5)	7D	10.1(1.1)

NOTE: The measurements were made on acetocarmine-stained chromosomes, which were identified following C-banding.

manipulate the genome of wheat with unprecedented precision and efficiency.

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