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N. Serizawa · S. Nasuda · F. Shi · T.R. Endo
S. Prodanovic · I. Schubert · G. Künzel

Deletion-based physical mapping of barley chromosome 7H

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Abstract Chromosomal mutations in barley (*Hordeum vulgare*, 2n=2*x*=14, HH) chromosome 7H added to the common wheat (*Triticum aestivum*, 2n=6*x*=42, AABBDD) cultivar Chinese Spring were induced genetically by the gametocidal activity of certain alien chromosomes derived from wild species of the genus *Aegilops*. The rearranged barley chromosomes were characterized by C-banding, FISH and GISH. Twenty two deletion or translocation chromosomes in a hemizygous condition were selected for deletion mapping of 17 AFLP and 28 STS markers that are specific to 7H. Of the 22 breakpoints in chromosome 7H, seven involved the short arm (7HS), 12 the long arm (7HL) and three were in the centromeric region. The seven 7HS breakpoints separated all four 7HS-specific AFLP markers and split the 21 STS markers into six groups. One breakpoint occurred between two STS markers formerly occupying the same position in the genetic map. All seven 7HS breakpoints were separated from each other by either the AFLP or STS markers. The 12 breakpoints in 7HL divided the 13 7HL-specific AFLP markers into seven groups, and the seven STS markers into three groups. On the other hand, the 12 breakpoints in 7HL were divided into six groups by the AFLP markers and into two groups by the STS markers. This deletion-based map was in accordance with previously published genetic and physical maps using the same STS markers. The breakpoints, AFLP markers and STS markers were arrayed in a consistent order.

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N. Serizawa · S. Nasuda · F. Shi · T.R. Endo (✉)
Laboratory of Plant Genetics, Graduate School of Agriculture, Kyoto University, 606-8502 Kyoto, Japan, and CREST, JST (Japan Science and Technology Corporation), Japan
e-mail: endo@kais.kyoto-u.ac.jp
Tel.: +81-75-753-6137, Fax: +81-75-753-6486

S. Prodanovic · I. Schubert · G. Künzel
Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK), D-06466 Gatersleben, Germany

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Introduction

Different types of molecular markers, such as RFLP (restriction fragment length polymorphism) AFLP (amplified fragment length polymorphism) and microsatellites, have been used to construct barley linkage maps (Graner et al. 1991; Kleinhofs et al. 1993; Becker et al. 1995; Ramsay et al. 2000). However, even high-density molecular linkage maps can not reveal actual physical distances between genes because crossing-over events are not distributed randomly along chromosomes. Cytogenetically integrated linkage maps provide a tool for estimating the actual physical chromosomal locations of DNA markers and genes, thus enhancing the utility of genetic linkage maps for map-based cloning (Harper and Cande 2000). Künzel et al. (2000) constructed such maps for barley chromosomes by PCR analyses of 240 different microdissected reciprocal translocation chromosomes, using 301 STS (sequence-tagged site) markers that were derived from genetically mapped RFLP probes. They found most recombination events within a few relatively small areas spaced by large segments in which recombination was severely suppressed. In these maps, the translocation breakpoints (T-breakpoints) separated some of the STS markers of identical map positions, but many of them were still not separated. On the other hand, some of the T-breakpoints were not separated by the STS markers. Therefore, integration of more physical landmarks and DNA markers are expected to provide more precise maps of barley chromosomes.

Endo (1988) found that an alien chromosome (chromosome 2C) derived from *Aegilops cylindrica*, a wild species related to wheat, causes chromosome breakage in common wheat. When chromosome 2C is present in common wheat in a monosomic condition, chromosome mutations occur in gametes lacking it. Such chromosome mutations were used to establish deletion stocks (Endo

and Gill 1996) that have been used extensively for the deletion mapping of common wheat (Werner et al. 1992; Gill et al. 1993a, b, 1996a, b; Delaney et al. 1995a, b; Mickelson-Young et al. 1995; Faris et al. 2000). Shi and Endo (1997, 1999) introduced chromosome 2C into barley addition lines of common wheat and demonstrated that chromosome 2C can also induce chromosome mutations in barley chromosomes. By an efficient screening of structural changes in barley chromosomes added to wheat (Schubert et al. 1998), Shi and Endo (2000) initiated the production of deletion stocks of barley chromosome 7H added to wheat. Some of the barley deletions and barley-wheat translocations from that study were obtained in a hemizygous condition and are suitable for deletion mapping of DNA markers. The breakpoints of such terminal deletions and wheat-barley translocations (D-breakpoints) provide new physical landmarks for barley chromosomes.

In this study we conducted deletion mapping, employing the same STS markers as used by Künzel et al. (2000) to incorporate the D-breakpoints into the physically integrated map of barley chromosome 7H. In addition, AFLP markers were used to enrich the sample of DNA markers. We expected to find D-breakpoints positioned between those STS markers that were not separated by T-breakpoints. Also, the distribution of D- and T-breakpoints and of STS and AFLP markers along chromosome 7H were compared.

Materials and methods

Plant materials

We used 22 lines of common wheat (*Triticum aestivum* cv Chinese Spring, 2n=6*x*=42), genomes AABBDD) with either deletions (7 lines) or translocations (15 lines) involving chromosome 7H derived from barley (*Hordeum vulgare* cv Betzes, 2n=2*x*=14, HH). We also employed euploid Chinese Spring, and disomic addition lines of 7H, 7HS (short arm) and 7HL (long arm) to Chinese Spring (Islam 1983). The structural changes of chromosome 7H were found among the progeny of wheat plants carrying a pair of 7H chromosomes and the gametocidal chromosome 2C derived from *Ae. cylindrica* (Shi and Endo 1997, 1999, 2000) or another gametocidal chromosome from *Aegilops triuncialis* [which was different from chromosome 3C reported by Endo (1990)]. The aberrant 7H chromosomes were enumerated in the order of their isolation; 'A' and 'B' followed the number when two different 7H aberrations were found in the same individual. Only 7H aberrations in a hemizygous condition were used in this study. The aberrant chromosomes 7H-29, 7H-30, 7H-31 and 7H-32 were obtained among the progeny of the line carrying the *Ae. triuncialis* chromosome; the other aberrant chromosomes were obtained from the line carrying chromosome 2C.

Cytological screening and characterization of aberrant 7H chromosomes

7H aberrations were selected by simultaneous FISH and GISH using the probes of the subtelomeric sequence HvT01 and total genomic DNA of barley. The HvT01 is a 118-bp satellite DNA repeated in tandem (Belostotsky and Ananiev 1990) and is localized in the terminal regions of all barley chromosomes (Schubert et al. 1998; Shi and Endo 1999). Both probes were labelled with digoxigenine separately and then mixed in appropriate concentrations for the combined FISH and GISH. The breakpoints of the deletions and translocations were analyzed by C-banding prior to the combined FISH and GISH on identical metaphases. This analysis enabled us to determine the chromosome arms in which the chromosome breaks occurred. A sample of five or more chromosomes for each of the 7H aberrations was measured to calculate the approximate fraction length (FL) of their remaining chromosome arms (see Fig. 2): FLs were calculated in relation to the intact arm of the same chromosome using the standard arm ratio, L/S=0.92, of the normal 7H chromosome of Betzes (7HL is physically shorter than 7HS). Whole-arm translocations were analyzed by FISH using a biotin-labelled probe of the 192-bp repeat that hybridizes to the centromeres of all wheat chromosomes but not to barley chromosomes (Ito et al. unpublished). This probe was mixed in appropriate concentration with the combined FISH and GISH probe.

DNA extraction, AFLP markers, fluorescence AFLP analysis, and STS analysis

The genomic DNA was extracted from young leaves using the CTAB (cetyltrimethylammonium bromide) method (Saghai-Maroof et al. 1984). The concentration of DNA samples was adjusted to 100 ng/µl for digestion with restriction enzymes.

Seventeen AFLP markers previously assigned to chromosome 7H (Serizawa et al. 2001) were used. Four of them are specific to 7HS and 13 to 7L. The AFLP markers are described in this paper with their fragment size in bp prefixed by 'A' (e.g. A166). The details of adapters and primers are described in Serizawa et al. (2001): The AFLPs are described by a combination of the selective nucleotides and fragment size (e.g. AT/CAT166=A166).

The AFLP Analysis System I from Gibco-BRL (Rockville, Md.) was used, with modifications that radioactive primer-labelling and autoradiography were substituted by the fluorescence labelling and detection technique (Zhang et al. 2000). Restriction digestion, adapter ligation and pre-amplification were as described by Vos et al. (1995). To avoid ambiguity in scoring, all AFLP markers were tested at least twice.

Of 93 RFLP clones localized in chromosome 7H on the Igri/Franka genetic map, 66 RFLP markers had previously been converted into locus-specific STS markers suitable for translocation mapping (Künzel et al. 2000). These STS markers were tested for PCR fragment polymorphisms between Betzes barley and Chinese Spring wheat, checking simultaneously the arm specifity of their PCR products with DNAs of wheat-barley telosome addition lines. A total of 28 markers covering 136.3 of the 200.1 centimorgan length of the entire linkage map of chromosome 7H differentiated between barley and wheat. Of these 28 markers used for deletion mapping (see Fig. 4), three detected a barley/wheat fragment polymorphism: MWG530 (178 bp/400 bp), MWG807 (337/140) and MWG2072 (194/330). The remaining markers gave no PCR products in wheat. All primer sequences, PCR conditions and fragment lengths amplified in barley are available online at http://wheat.pw.usda.gov/ggpages/Barley_physical/STS.html.

Results

Cytological characterization of aberrant 7H chromosomes

Images of the sequential C-banding and FISH/GISH of the 22 aberrant 7H chromosomes are shown in Fig. 1. Of the seven deletions, two had breakpoints in the short arm (7H-24 and -31) and five in the long arm (7H-7, -16A, -29, -30, and -33). Of the 15 translocation chromosomes, ten possessed the centromere of chromosome 7H and carried an acentric wheat segment (wheat-to-barley

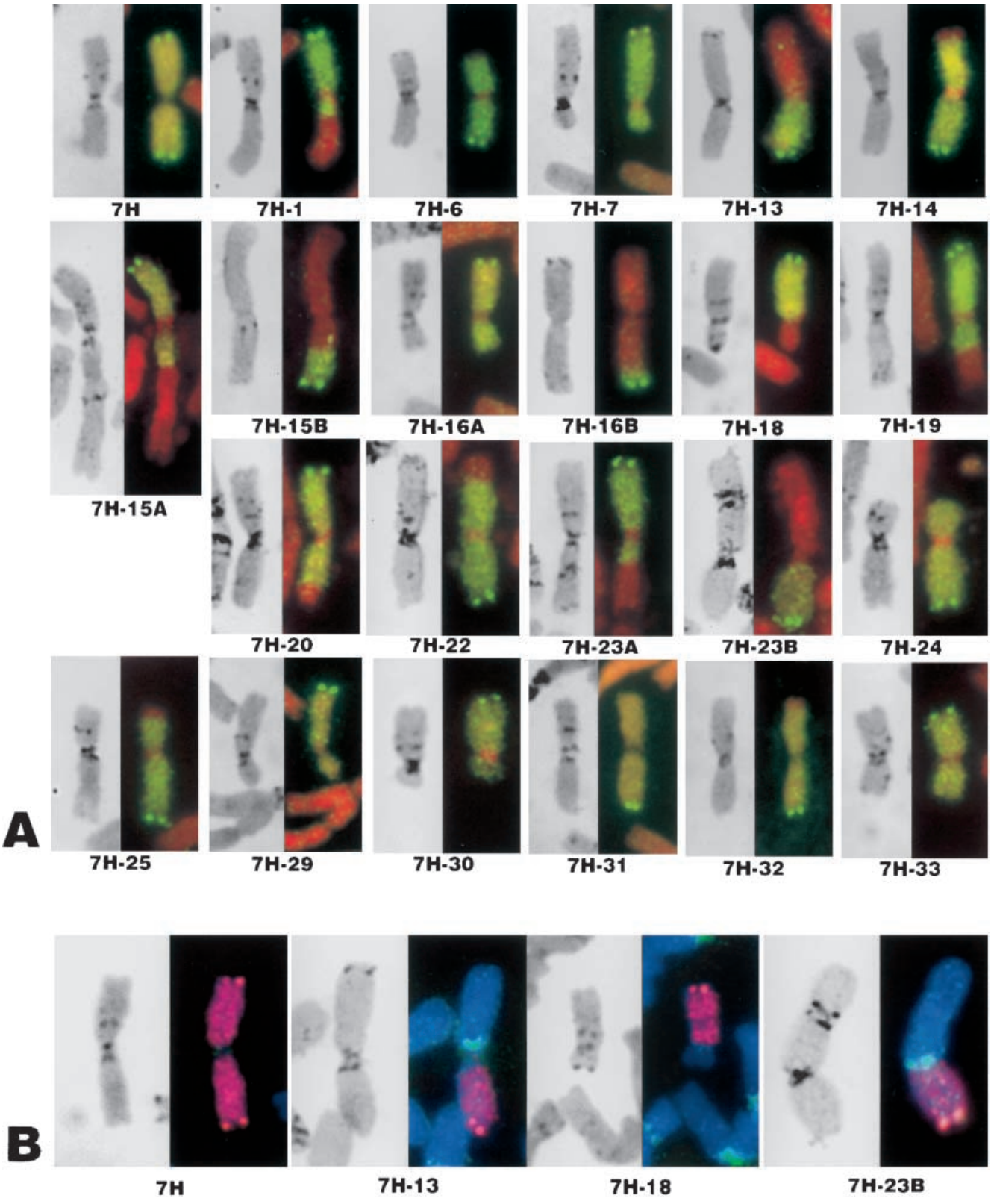

Fig. 1A, B Sequential C-banding (*left*) and combined GISH/FISH (*right*) of normal and aberrant 7H chromosomes. **A** Barley chromosomal segments are shown by yellowish green GISH/FISH signals detected with anti-digoxigenic FITC (fluorescein isothiocyanate); wheat chromosomes were counterstained with PI. Stronger FISH signals at barley chromosome termini indicate the subtelomeric repeat HvT01. **B** The centromeric 192-bp probe and the combined FISH/GISH probe were detected with anti-digoxigenine FITC and streptavidine-rhodamine, respectively; wheat chromosomes were counterstained with DAPI. Note the absence of FISH signals in the centromeric regions of 7H and 7H-18

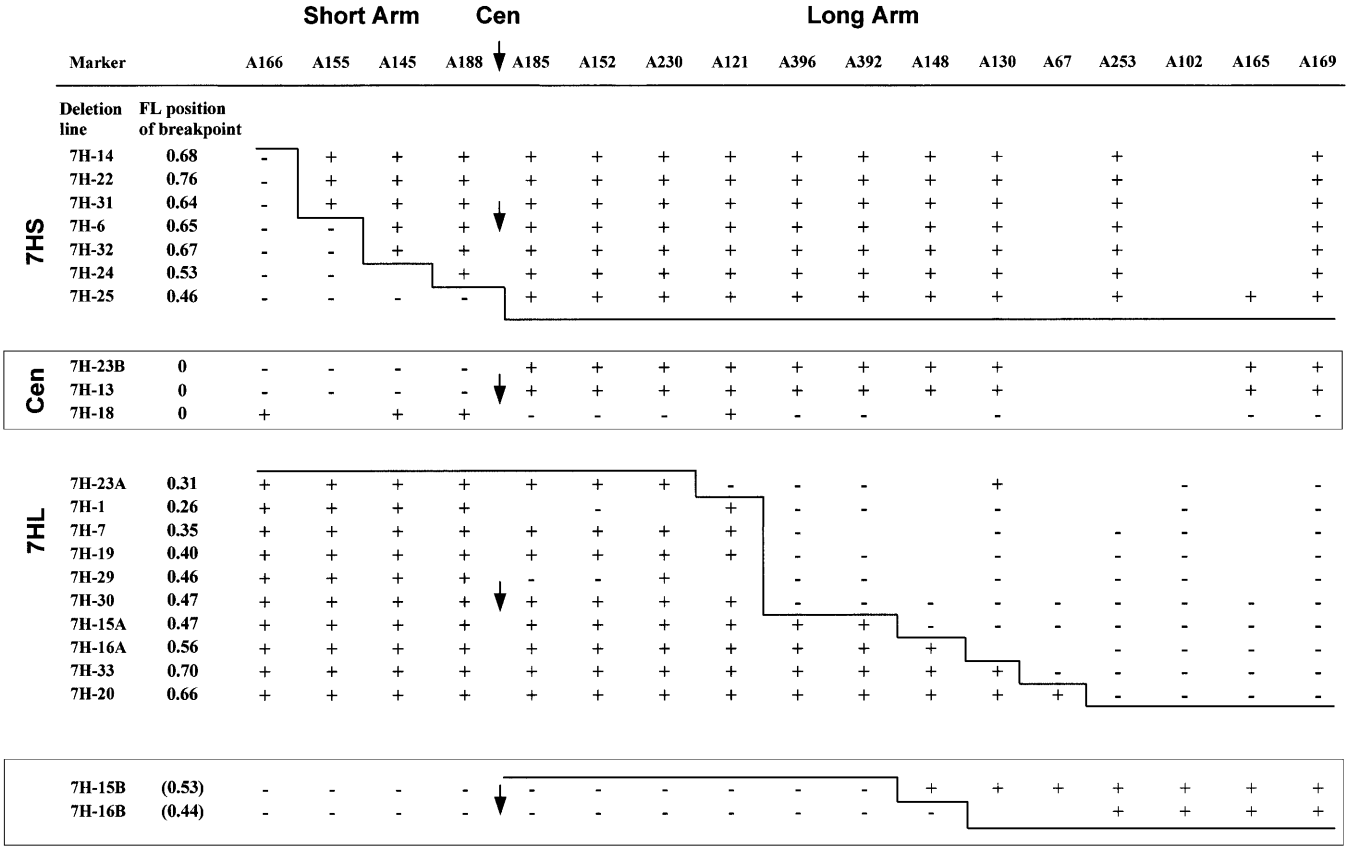

Fig. 2 Presence (+) and absence (–) of the 22 AFLP markers in the 7HS and 7HL deletions. Blanks represent ambiguous results of the AFLP analyses

type). Five of them had breakpoints in the short arm (7H-6, -14, -22, -25 and -32) and five in the long arm (7H-1, -15A, -19, -20 and -23A). None of the involved wheat segments was identifiable as to its chromosomal origin. Three of the translocations were whole-arm translocations: 7H-13 between 7HL and the short arm of wheat chromosome 7A, 7H-23B between 7HL and the long arm of wheat chromosome 5B, and 7H-18 between 7HS and an unidentified wheat chromosomal segment. 7H-13 and 7H-23B showed the FISH signals of the 192-bp wheat centromeric repeat sequence but 7H-18 did not (Fig. 1B). The remaining two translocations, 7H-15B and 7H-16B, are of wheat chromosomes carrying acentric 7H segments (barley-to-wheat type). According to C-banding patterns, 7H-15B is a wheat chromosome 3A carrying a barley segment in the short arm and 7H-16B is a wheat chromosome 7A carrying a barley segment in the long arm. The translocation chromosomes 7H-15A and 7H-16A were found in the same plants and appeared to represent the complementary translocation products to 7H-15B and 7H-16B because the acentric barley segments on wheat chromosomes corresponded in size to the deleted ones. This was confirmed by deletion mapping (Figs. 2 and 3). In contrast, 7H-23A and 7H-23B, which occurred in the same plant, probably arose independently in the male and female parental gametes because the breakpoint of 7H-23A was in 7HL and that of 7H-23B was in the centromeric region. In this paper both true deletions and translocations involving chromosome 7H were defined as ‘7HS deletions’ or ‘7HL deletions’ according to the corresponding chromosome arm from which the barley chromosomal segments were lost.

Deletion mapping of AFLP markers

The 22 deletions and translocations of chromosome 7H were investigated as to the presence or absence of the 17 AFLP markers (Fig. 2). The four 7HS AFLP markers were present in all 7HL deletions and divided the 7HS deletions into four groups. The breakpoints of the 7HS deletions, ranging from 46% to 76% of the length of 7HS from the centromere, separated the four AFLP markers from each other. There was no AFLP marker between 7H-22, 7H-14 and 7H-31, nor between 7H-6 and 7H-32.

The 13 AFLP markers specific to 7HS were present in all 7HL deletions and fell into seven intervals marked by the 12 breakpoints of the 7HL deletions (Fig. 2). None of the breakpoints occurred within the groups of markers A185, A152 and A230; A396 and A392; A253, A102, A165 and A169. The AFLP markers, in turn, divided the 7HL deletions into six groups. 7H-15A possessed all the markers that were missing in 7H-15B, and vice versa. 7H-16A and 7H-16B had no AFLP markers in common (although AFLP data of A130 and A67 were unclear). 7H-23A and 7H-23B shared the three most-proximal

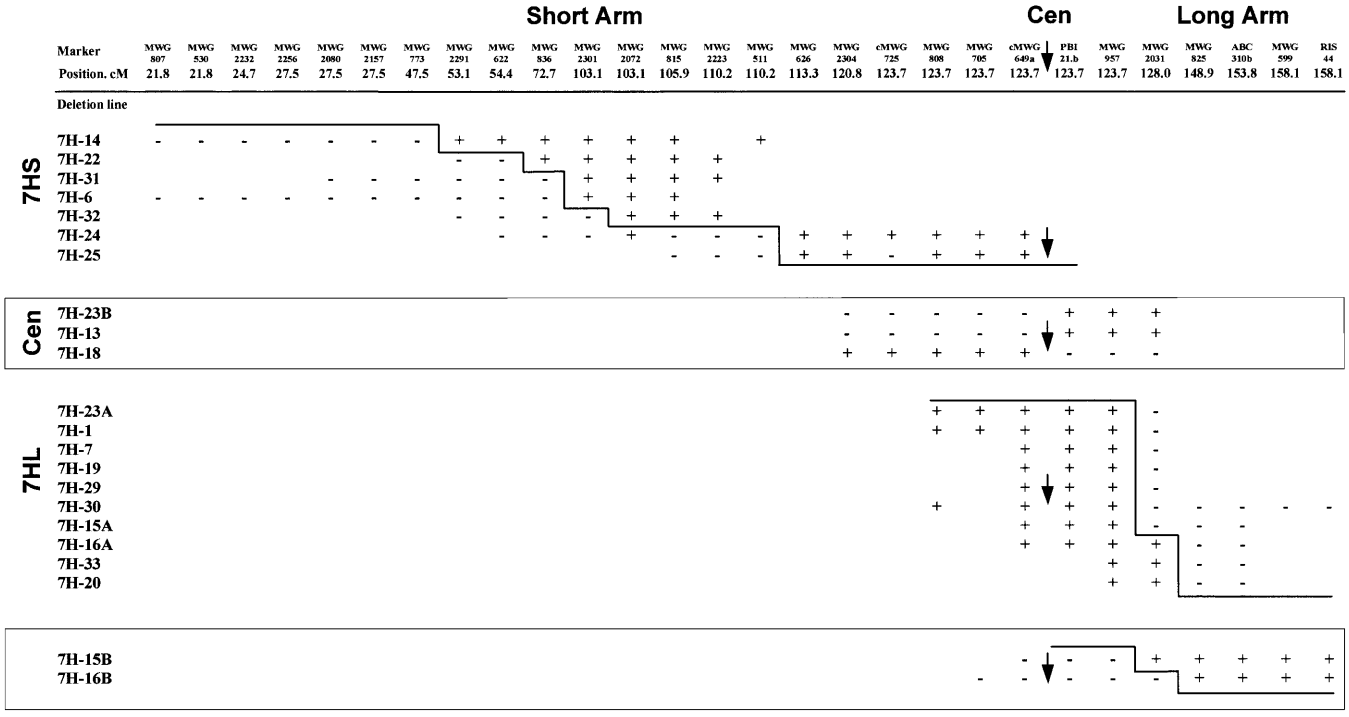

Fig. 3 Presence (+) and absence (–) of 28 STS markers of the 'Igri'×'Franka' map in the 7HS and 7HL deletions. Blanks represent unchecked combinations

7HL AFLP markers. Five 7HL deletions, 7H-1, 7H-7, 7H-19, 7H-29 and 7H-30, were not separated by any AFLP markers.

The optimal arrangement of the breakpoints and AFLP markers shown in Fig. 2 still contains a few minor contradictions. 7H-1 and 7H-29 lacked one and two 7HL markers, respectively, although they had the distal markers A121 and A230, respectively. 7H-18 and 7H-23A had the markers A121 and A130, respectively, but lacked the flanking markers. The presence of additional interstitial deletions or insertions of small amounts of barley chromatin could explain these contradictions.

Deletion mapping of STS markers

Based on the results of deletion mapping, the breakpoints of the 7H deletions were ordered against the 28 STS-markers that are arranged according to their genetic distances (Fig. 3, Künzel et al. 2000). The breakpoints of the seven deletions in 7HS were positioned between 47.5 cM and 110.2 cM from the centromere within the Igri/Franka RFLP linkage map and divided the 21 STS markers of 7HS into six groups. The order of these groups was consistent with the genetic distances of the STS markers comprising the groups. 7H-32 separated the two STS markers MWG2301 and MWG2072, which shared the same genetic position (103.1 cM). 7H-24 had the marker MWG2072 in spite of the absence of flanking markers and 7H-25 lacked cMWG725 in spite of the presence of flanking markers (Fig. 3). This suggests the occurrence of small interstitial insertions or deletions within 7H-24 and 7H-25.

The seven 7HL STS markers fell into three intervals divided by the 12 breakpoints, ranging from 123.7 cM to 148.9 cM. As expected from the AFLP analysis, 7H-15A and 7H-16A contained all markers that were absent from 7H-15B and 7H-16B, respectively, and vice versa. 7H-23A and 7H-23B shared two of the most-proximal 7HL markers. The deletion mapping data and the genetic distances of the STS markers are in accordance.

Discussion

Deletion mapping of an alien chromosome added to wheat

Hexaploid common wheat tolerates the addition of alien chromosomes, enabling the addition of sigle alien chromosomes to the genome. When added to wheat, gametocidal chromosomes from *Ae. cylindrica* and *Ae. triuncialis* induce frequent structural chromosomal alterations in barley (Shi et al. 2000) and rye chromosomes (Endo et al. 1994). In the present study, the combination of C-banding, FISH and GISH allowed us to identify reliably the 7H structural aberrations including wheat-barley translocations. Such translocations could be used in deletion mapping in the same way as terminal deletions. In deletion mapping using barley specific markers, the wheat genomic background is advantageous because barley deletion chromosomes can be easily detected by GISH and used in a hemizygous condition for deletion mapping with DNA markers.

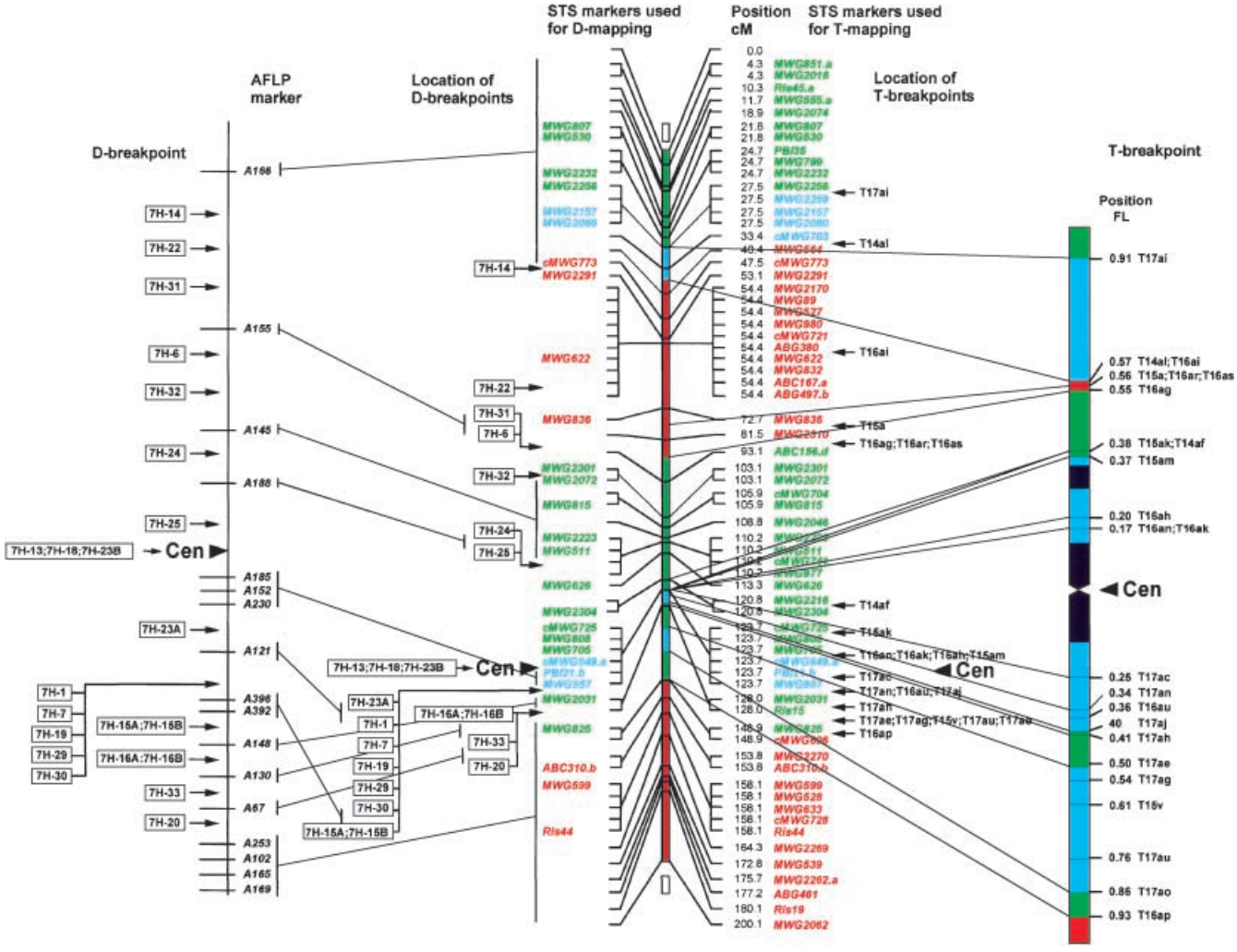

Fig. 4 Incorporation of the AFLP markers and D-breakpoints into the physically integrated linkage map of chromosome 7H (1) according to Künzel et al. (2000). Short arms are at the top. *Left* AFLP markers ordered by inserted D-breakpoints (*boxed*). *Middle* 'Igri'×'Franka' linkage map showing the map positions of D-breakpoints (*left*) and T-breakpoints (*right*). *Right* Physical map indicating the FL positions of the 24 T-breakpoints (*FL*=length of the non-translocated arm segment relative to the whole arm). Subregions of similar recombination rates identified by translocation mapping are shown in the *same color. Blue* indicates low (>4.4 megabases/centimorgan), *green* middle (1.0–4.4) and *red* high (=1 Mb/cM) recombination. *Black regions* of the physical map mark Giemsa N bands

This study was refined the arrangement of the D-breakpoints and the DNA markers. The DNA markers separated the D-breakpoints of similar FL values, and the D-breakpoints separated STS markers with identical genetic distances. The 7H arm of the D-breakpoints of two barley-to-wheat translocations, 7H-15B and 7H-16B, were not determined by the cytological analyses. However, the DNA marker analyses identified the 7H arms involved and also confirmed that the two barley to wheat translocations were complementary to 7H-15A and 7H-16A, respectively. Two whole-arm translocations, 7H-13 and 7H-23B, showing the FISH signals of the wheat centromeric repeats, revealed all AFLP and STS markers of 7HL and lacked all markers of 7HS (Figs. 1B, 2 and 3). This suggests that these translocations probably originated by centric fusion of 7HL and the wheat chromosome arms.

Integration of AFLP and STS markers

The D-breakpoints provided additional cytological markers for the map of chromosome 7H that was previously constructed by the integration of the breakpoints of reciprocal translocations (T-breakpoints) to the linkage map (Künzel et al. 2000) (Fig. 4). The same sequences of the D-breakpoints were obtained by AFLP and by STS analyses, confirming the accuracy of the results and the usefulness of the D-breakpoints as landmarks for physical mapping of barley chromosomes. A comparison of the relative positions of the D-breakpoints and the T-breakpoints based on the STS markers yielded interesting results. There were seven T-breakpoints and seven D-breakpoints distal to MWG626 (113.3 cM), whereas six T-breakpoints were present between MWG626 and the centromere but no D-breakpoint occurred in that re-

gion. Conversely, some of the D-breakpoints were found in narrow regions free of T-breakpoints, e.g. 7H-14 between T14al and T16ai; 7H-22 between T16ai and T15a; 7H-32, 7H-24 and 7H-25 between T16ag and T14af. Moreover, these D-breakpoints occurred between the STS markers that were not previously separated by T-breakpoints. The breakpoint of 7H-14 fell between cMWG773 and MWG2291, and that of 7H-22 fell between MWG622 and MWG836. There are four STS markers, including MWG622, positioned at the same genetic distance (54.4 cM) between T16ai and T15a. Preliminary PCR analysis localized MWG832 distal to the D-breakpoint of 7H-22 (data not shown). 7H-32 separated the two markers MWG2301 and MWG2071 with the same genetic distance (103.1 cM), arranging the former distal to the latter. 7H-24 and 7H-25 separated MWG511 and MWG626. Thus, the D-breakpoints could further resolve the STS marker clusters that were not separated by the T-breakpoints. The other D-breakpoints of 7HS and all of 7HL were located in regions where three or more T-breakpoints exist.

The FL values of D- and T-breakpoints gave no conflicting results for 7HL, but were somewhat contradictory for 7HS. For example, the D-breakpoint of 7H-22 (FL=0.76) was between MWG622 and MWG836 that are located between the two T-breakpoints, T16ai (FL=0.57) and T15a (FL=0.56). Such discrepancies can be attributed to the difficulty in estimating FL values of D-breakpoints. The seven D-breakpoints in 7HS were divided into four groups by the AFLP markers and into five groups by the STS markers, and were perfectly separated from each other by both markers. The 12 D-breakpoints in 7HL were divided into six groups by the AFLP markers, but no further subdivision was possible using the STS markers.

The distribution patterns of the AFLP and STS markers along chromosome 7H can be compared on the basis of the D-breakpoints (Fig. 4). There are more AFLP markers on 7HL than on 7HS (Serizawa et al. 2001) and more STS markers on 7HS than on 7HL (Künzel et al. 2000). Apparently, both types of markers were more or less uniformly distributed along 7HL. Although the STS markers were distributed along the entire 7HS arm, all four AFLP markers were located in the distal half. The other AFLP markers were located in regions flanked either by two STS markers or by one STS marker and the centromere to the telomere. Also, there are only two 7HL STS markers in the region proximal to MWG2031, but six AFLP markers were found in that region; at least three of them (A121, A396, A392) were located between MWG957 and MWG2031 where no other STS markers were found. Thus the additional AFLP markers further refined the physical and the genetic maps of chromosome 7H.

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References

Becker J, Vos P, Kuiper M, Salamini F, Heun M (1995) Combined mapping of AFLP and RFLP markers in barley. Mol Gen Genet 249:65–73

Belostotsky DA, Ananiev EV (1990) Characterization of relic DNA from barley genome. Theor Appl Genet 80:374–380

Delaney DE, Nasuda S, Endo TR, Gill BS, Hulbert SH (1995a) Cytologically based physical maps of the group-2 chromosomes of wheat. Theor Appl Genet 91:568–573

Delaney DE, Nasuda S, Endo TR, Gill BS, Hulbert SH (1995b) Cytologically based physical maps of the group-3 chromosomes of wheat. Theor Appl Genet 91:780–782

Endo TR (1988) Induction of chromosomal structural changes by a chromosome of *Aegilops cylindrica* L. in common wheat. J Hered 79:366–370

Endo TR (1990) Gametocidal chromosomes and their induction of chromosome mutations in wheat. Jpn J Genet 65:135–152

Endo TR, Gill BS (1996) The deletion stocks of common wheat. J Hered 87:295–307

Endo TR, Yamamoto M, Mukai Y (1994) Structural changes of rye chromosome 1R induced by a gametocidal chromosome. Jpn J Genet 69:13–19

Faris DJ, Haen KM, Gill BS (2000) Saturation mapping of a gene-rich recombination hot spot region in wheat. Genetics 154: 823–835

Gill Ks, Gill BS, Endo TR (1993a) A chromosome region-specific mapping strategy reveals gene-rich telomeric ends in wheat. Chromosoma 102:374–381

Gill KS, Gill BS, Endo TR, Mukai Y (1993b) Fine physical mapping of *Ph1*, a chromosome pairing regulator gene in polyploid wheat. Genetics 134:1231–1236

Gill KS, Gill BS, Endo TR, Boyko EV (1996a) Identification and high-density mapping of gene-rich regions in chromosome group 5 of wheat. Genetics 143:1001–1012

Gill KS, Gill BS, Endo TR, Taylor T (1996b) Identification and high-density mapping of gene-rich regions in chromosome group 1 of wheat. Genetics 144:1883–1891

Graner A, Jahoor A, Schondelmaier J, Siedler H, Pillen K, Fischbeck G, Wenzel G, Herrmann RG (1991) Construction of an RFLP map of barley. Theor Appl Genet 83:250–256

Graner A, Bauer E, Kellermann A, Kirchner S, Muraya JK, Jahoor A, Wenzel G (1994) Progress of RFLP-map construction in winter barley. Barley Genet Newslett 23:53–59

Harper LC, Cande WZ (2000) Mapping a new frontier; development of integrated cytogenetic maps in plants. Funct Integr Genomics 1:89–98

Islam AKMR (1983) Ditelosomic additions of barley chromosomes to wheat. In: Sakamoto S (ed) Proc 6th Int Wheat Symp. Kyoto Univ Press, Kyoto, pp 233–238

Kleinhofs A, Kilian WZ, Saghai Maroof MA, Biyashew RM, Hayes P, Chen FQ, Lapitan N, Fenwick A, Blake TK, Kanazin V, Ananiev E, Dahleen L, Kudrna D, Bollinger J, Knapp SJ, Liu B, Sorrells M, Heun M, Franckowiak M, hoffman D, Skadsen R, Steffenson BJ (1993) A molecular, isozyme and morphological map of the barley (*Hordeum vulgare*) genome. Theor Appl Genet 86:705–712

Künzel G, Korzun L, Meister A (2000) Cytologically integrated physical restriction fragment length polymorphism maps for the barley genome based on translocation breakpoints. Genome 154:397–412

Mickelson-Young L, Endo TR, Gill BS (1995) A cytogenetic ladder-map of the wheat homoeologous group-4 chromosomes. Theor Appl Genet 90:1007–1011

Ramsay L, Macaulay M, Ivanissevich S, MacLean K, Cardle L, Fuller J, Edwards KJ, Tuvesson S, Morgante M, Massari A, Maestri E, Marmiroli N, Sjakste T, Ganal M, Powell W, Waugh R (2000) A simple sequence repeat-based linkage map of barley. Genetics 156:1997–2005

Saghai-Maroof MA, Soilman KM, Jorgensen RA, Allard RW (1984) Ribosomal DNA spacer-length plymorphisms in barley: Mendelian inheritance, chromosomal location, and

population dynamics. Proc Natl Acad Sci USA 81:8014–8018

Schubert I, Shi F, Fuchs J, Endo TR (1998) An efficient screening for terminal deletions and translocations of barley chromosomes added to common wheat. Plant J 14:489–495

Serizawa N, Nasuda S, Endo TR (2001) Barley chromosome addition lines of wheat for screening of AFLP markers on barley chromosomes. Genes Genet Syst 76:107–110

Shi F, Endo TR (1997) Production of wheat-barley disomic addition lines possessing an *Aegilops cylindrica* gametocidal chromosome. Genes Genet Syst 72:243–248

Shi F, Endo TR (1999) Genetic induction of structural changes in barley chromosomes added to common wheat by a gametocidal chromosome derived from *Aegilops cylindrica*. Genes Genet Syst 74:49–54

Shi F, Endo TR (2000) Genetic induction of chromosomal rearrangements in barley chromosome 7H added to common wheat. Chromosoma 109:358–363

Vos P, Hogers R, Bleeker M, Reijans M, Lee TVD, Hornes M, Frijters A, Pot J, Peleman J, Kuiper M, Zabeau M (1995) AFLP: a new technique for DNA fingerprinting. Nucleic Acids Res 23:4407–4414

Werner JE, Endo TR, Gill BS (1992) Toward a cytogenetically based physical map of the wheat genome. Proc Natl Acad Sci USA 89:11307–11311

Zhang et al. (2000) Identification of AFLP markers on the satellite region of chromosome 1BS in wheat. Genome 43:729–735