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S.L. Fox · E.N. Jellen · S.F. Kianian · H.W. Rines
R.L. Phillips

Assignment of RFLP linkage groups to chromosomes using monosomic F_1 analysis in hexaploid oat

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Abstract The availability of molecular genetic maps in oat (*Avena* spp.) and improved identification of chromosomes by C-banding are two recent developments that have made locating linkage groups to chromosomes possible in cultivated hexaploid oat, 2n=6x=42. Monosomic series derived from *Avena byzantina* C. Koch cv Kanota and from *Avena sativa* L. cv Sun II were used as maternal plants in crosses with the parents, Kanota-1 and Ogle-C, of the oat RFLP mapping population. Monosomic F_1 plants were identified by root-tip cell chromosome counts. For marker analysis, DNAs of eight F_2 plants from a monosomic F_1 were combined to provide a larger source of DNA that mimicked that of the monosomic F_1 plant. Absence of maternal alleles in monosomic F_1s served to associate linkage groups with individual chromosomes. Twenty two linkage groups were associated with 16 chromosomes. In seven instances, linkage groups that were independent of each other in recombination analyses were associated with the same chromosome. Five linkage groups were shown to be associated with translocation differences among oat lines. Additionally, the results better-characterized the oat monosomic series through the detection of duplicates and translocation differences among the various monosomic lines. The F_1 monosomic series represents a powerful cytogenetic tool with the potential to greatly improve understanding of the oat genome.

Keywords *Avena* · Aneuploid · Monosomic analysis · Linkage group · Simulated F_1

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S.L. Fox (✉) · S.F. Kianian · R.L. Phillips
Department of Agronomy and Plant Genetics,
and Plant Molecular Genetics Institute, University of Minnesota,
St. Paul, MN 55108, USA

E.N. Jellen
Department of Agronomy and Horticulture,
Brigham Young University, 275 WIDB, Provo, UT 84602, USA

H.W. Rines
Plant Science Research Unit, U.S. Department of Agriculture,
Agriculture Research Service
and Department of Agronomy and Plant Genetics,
University of Minnesota, St. Paul, MN 55108, USA

Present addresses:
S.L. Fox (✉), Crop Development Centre,
University of Saskatchewan,
51 Campus Drive, Saskatoon, SK S7N 5A8, Canada
e-mail: foxs@sask.usask.ca
Fax: +1-306-966 5015

S.F. Kianian, Department of Plant Sciences,
North Dakota State University, Loftsgard Hall, Fargo, ND 58105,
USA

Introduction

The initial molecular linkage map of hexaploid oat was produced using a recombinant inbred-line population derived from a cross of the facultative winter-type oat *Avena byzantina* C. Koch cv Kanota and the spring-type *Avena sativa* L. cv Ogle (O'Donoughue et al. 1995). The map consisted of 561 loci arranged in 38 linkage groups with 29 unlinked loci. The number of linkage groups exceeded the expected haploid chromosome number of 21 for hexaploid oat (2n=6*x*=42). Additional loci have been added to the map reducing the number of linkage groups to 32 (Kianian et al. 1999). The assignment of linkage groups to chromosomes through the analysis of aneuploids should serve to effectively reduce the number of linkage groups to 21.

Aneuploid lines of hexaploid oat have been isolated mainly from two sources. Twenty monosomic lines (K1–K20) and one fertile nullisomic (K21) were isolated from *A. byzantina* cv Kanota (Morikawa 1985). Eighteen monosomic lines (SI–SXVIII) were isolated from *A. sativa* cv Sun II (Riley and Kimber 1961; Hacker and Riley 1963). SVII and SXIV can be maintained as fertile nullisomics, and sterile nullisomics can be obtained for SI, SIV, SVIII, SIX, SX, SXI and SXII (Kianian et al. 1997). Additional monosomic lines were isolated from Sun II haploid plants obtained from oat/maize hybridizations (Rines and Dahleen 1990; Davis and Rines 1991)

and have been characterized using chromosome C-banding (Jellen et al. 1997).

Jellen et al. (1993a) employed C-banding to distinguish all oat chromosomes in the cultivar Kanota. C-banding combined with RFLP marker data was used to show that the Kanota monosomic series represented 12 of the possible 21 chromosomes (Jellen et al. 1993b). In the Sun II monosomic series ten different monosomic chromosomes were identified in the SI–SXVIII set using RFLPs (Mendu et al. 1993), genomic in situ hybridization (Leggett and Markland 1995) and C-banding (Jellen et al. 1997). From 27 Sun II monosomics obtained from haploids, six new monosomics were identified by C-banding that were not found in either of the other series (Jellen et al. 1997). If confirmed, these lines collectively would represent a complete monosomic series.

The Kanota monosomics have been used by Rooney et al. (1994) to assign RFLP loci to chromosomes by dosage analysis. However, the number of loci for which this technique can be used is limited due to problems in reliably detecting signal-strength differences in species with large genomes. Using a variation of monosomic analysis (Sears 1944; Heyne and Livers 1953), Helentjaris et al. (1986) demonstrated an alternative approach by detecting the loss of the monosomic parent allele in monosomic F_1 maize plants. In a euploid F_1 plant, both the maternal and paternal alleles of a polymorphic RFLP locus can be observed. In a monosomic F_1 plant produced from crossing a monosomic maternal plant with a euploid paternal plant, only the paternal allele can be detected for a locus on the critical chromosome. Thus, an association is made between the linkage group where a locus is mapped and the chromosome. With the use of appropriate parents, a series of F_1s monosomic for different chromosomes provides a means of assigning any polymorphic locus to a chromosome.

The objective of the present study was to assign molecular linkage groups to individual chromosomes. Two or more linkage groups were assigned to the same chromosome in seven instances. Duplicate monosomic lines which were missing the same chromosome were identified. Lines were characterized for translocation differences, and homoeologous chromosomal regions were identified. In this paper, the generic chromosome nomenclature of Jellen et al. (1993a) is used, and the names of monosomic lines are used to indicate specific versions of a chromosome.

Materials and methods

Generation of the F_1 monosomic series

The F_1 monosomic series was developed by crossing each available monosomic line, used as a maternal parent, with one or both of the oat mapping population parents, Kanota-1 and Ogle-C, or another selection, Ogle-1 (Table 1). The latter three parents represent single-plant selections from their namesake cultivars. Kanota monosomics obtained from T. Morikawa (Osaka Prefecture University, Sakai, Osaka, Japan) were crossed to Ogle-1. Additional Kanota monosomics were obtained from A. Fominaya (University of Alcalá, Madrid, Spain) and were crossed to Ogle-C. Sun II monosomics SI–SXVIII were obtained from Dr. H. Thomas, Welsh Plant Breeding Station, Aberystwyth, UK, and Dr. T. Aung, Agriculture and Agri-Food, Winnipeg, Manitoba, Canada. These Sun II monosomics were crossed to both mapping population parents, Ogle-C and Kanota-1, to allow chromosome assignment of any locus from the oat RFLP map that has an allele detectable in Sun II. The Sun II monosomics (Sn-lines) derived from oat/maize hybrids were crossed only to Ogle-C.

Chromosome numbers of monosomic parents and F_1s were determined from root tips to confirm monosomy, following the protocol of Riera-Lizarazu et al. (1992).

RFLPs

Leaf tissue for DNA extraction was collected from Kanota-1, Ogle-C, Ogle-1, monosomic parents, F_1 and F_2 plants. Tissue was

Table 1 Crosses made between Kanota (K1–K21) and Sun II (SI–SXVII and Sn) monosomic lines and Ogle-1, Ogle-C and Kanota-1 euploid lines to develop F_1 monosomics for analysis of polymorphic markers

Line	Ogle-1 TM[a]	Ogle-C AF[a]	Line	Ogle-C		Kanota-1		Line	Ogle-C HR[a]
				HT[a]	TA[a]	HT	TA		
K1	×		SI	×	×		×	Sn1a 2–5	×
K2	×	×	SII	×	×	×	×	Sn1a 3–3	×
K3	×	×	SIII					Sn1a 4–4	×
K4			SIV	×				Sn5 1–3	×
K5	×		SV	×	×		×	Sn10–2 1–5	×
K6			SVI	×		×		Sn1e	×
K7	×		SVII	×	×	×	×	Sn3b R2 7–10	×
K8	×		SVIII	×	×	×	×	Sn1a 3–1	×
K9			SIX	×		×	×	Sn11 2–2	×
K10	×	×	SX	×	×		×	Sn10–2 3–3	×
K11	×	×	SXI	×	×	×	×	Sn8–2 4–1	×
K12	×		SXII	×	×	×	×	Sn10–2 3–3	×
K13	×	×	SXIII	×	×	×	×	Sn10–2 1–5	×
K14	×	×	SXIV	×	×	×	×	Sn8–1 1–1	×
K15	×	×	SXV	×	×	×		Sn11 4–3	×
K16	×	×	SXVI		×		×	Sn276C R2 4–13	
K17		×	SXVII		×	×	×		
K18	×	×	SXVIII			×	×		
K19		×							
K20	×	×							
K21	×								

[a] Indicates maternal parent source: TM=Dr. T. Morikawa, AF=Dr. A. Fominaya, HT=Dr. H. Thomas, TA=Dr. T. Aung, HR=Dr. H. Rines

immediately frozen at –20°C and lyophilized. DNA extractions were performed using a protocol modified from Kim et al. (1990). RNA was removed from DNA using the method of Sambrook et al. (1989). The DNA was re-suspended and volumes adjusted to achieve a final concentration of 2 µg of DNA/µl.

DNA digestions, Southern blotting and hybridizations were performed as described in Kianian and Quiros (1992). Probes used in this study were selected from UMN, BCD and CDO libraries based on linkage-group association and linkage distance within a linkage group (O'Donoughue et al. 1995) and on the presence of detectable alleles in the maternal monosomics as determined from parental screening blots.

Simulated F_1s

Simulated F_1s were developed by combining equal amounts of dry leaf tissue from eight random F_2 plants derived from each monosomic F_1 plant before extracting genomic DNA. Once the monosomic condition of the F_1 plant was confirmed, all progenies of it could be assumed to lack the critical monosome from the maternal monosomic parent. Thus, alleles of markers on the critical maternal monosome would be absent whereas both alleles of polymorphic markers on non-critical chromosomes should be represented. A minimum of four F_2 plants should ensure that each allele on a noncritical chromosome would be represented at least once $\{1-[P(\text{all AA})+P(\text{all aa})]=1-[1/4^n+1/4^n]=0.99, n=4\}$; however, the use of eight plants was considered to provide increased balance in ^{32}P signal strength on a hybridization blot for the alleles of markers on non-critical chromosomes. Parental line and F_1 panicles were bagged to prevent outcrossing; although, Sun II materials suffered reduced seed set as a result. Simulated F_1s considerably extend the amount of DNA that is available for marker analyses without having to produce additional F_1 plants or do additional cytology.

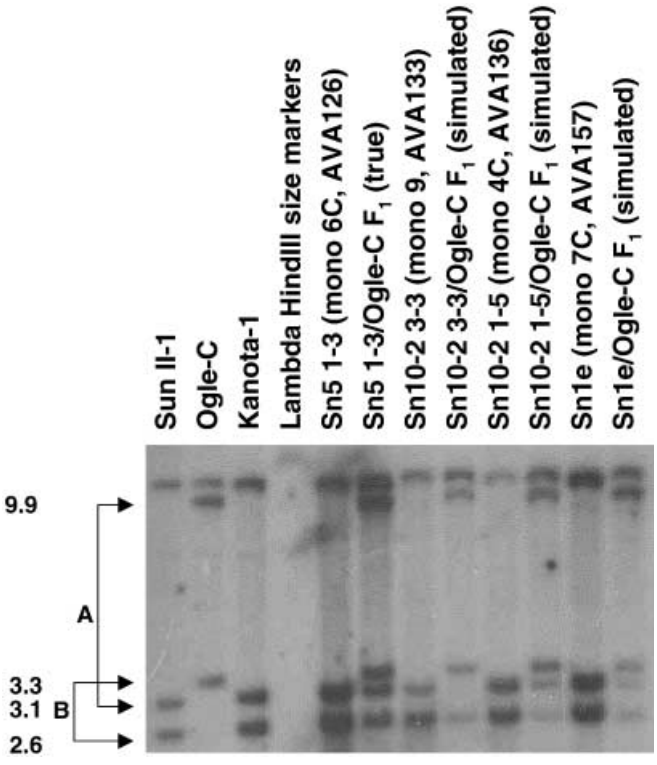

Fig. 1 Autoradiogram of the radiolabelled clone CDO1467 hybridized to a filter containing the *DraI* enzyme-digested DNA of Sun II monosomic lines and F_1s. In parentheses, either the monosomic chromosome and AVA source number are shown or it is indicated whether the monosomic F_1 is a true F_1 or a simulated F_1 developed from the DNAs of eight F_2 progeny. Note the reduction in signal strength of the 3.1-kb band in the Sn10-2 3-3 line and the absence of the band in the simulated F_1 Sn10-2 3-3/Ogle-C

Results and discussion

Ninety six F_1 monosomics were developed for this study (Table 1). Monosomic plants of lines K4, SIII, and Sn 276 C R2 4–13 were not available for crossing and only euploid plants were recovered from crosses with K6 and K9. Seed was not obtained from crosses SIV/Kanota-1 and SXVIII/Ogle-C, and only crosses by Ogle-C were available for the Sn-lines. F_2 populations to make simulated F_1 DNA preparations were developed for the Kanota monosomics/Ogle-1 or Ogle-C crosses and the Sun II monosomics/Ogle-C crosses. Simulated F_1 DNA prepared by extracting from combined leaf tissues of eight F_2 plants satisfactorily mimicked true F_1 DNA (Fig. 1).

Linkage group assignment to chromosome

Twenty two linkage groups were associated with 16 chromosomes by absence in an F_1 monosomic plant of a DNA fragment that was present in the maternal monosomic plant used to develop the F_1 (Table 2). The absence of a DNA fragment indicated that the allele was located on the maternal monosome that was not transmitted to the monosomic F_1 (Fig. 1). Knowing that the missing DNA fragment mapped to a particular linkage group allowed the association of the linkage group with a particular chromosome. Except when few loci were present, two or more loci from the same linkage group were used to make an association to a chromosome. A locus could not be used when an allele could not be scored in the monosomic parent. The F_1 monosomic was compared to its maternal monosomic parent to confirm that the parent did have the allele being scored and to show that the parent was homozygous at that locus. When the same DNA fragment-loss event occurred in different F_1s, it served to indicate that the maternal parents used to create them had the same monosome. For example, K1 and K2 are monosomic for chromosome 1C (Table 2). Table 2 lists the grouping of monosomic lines based on similar DNA fragment-loss events in their associated monosomic F_1s. These groupings of duplicates among monosomic lines are in agreement with ones determined independently using C-banding (Jellen et al. 1993b, 1997). Also, previous RFLP locus assignments to chromosomes 1C, 2C, 13 and 19, made by Rooney et al. (1994) and Jellen et al. (1993b), were corroborated in this study. Our conclusions regarding chromosomes 5C, 8, 11, 15, 16 and 18 could not be confirmed as the loci identified by probes used by previous authors were monomorphic between Kanota and Ogle.

Seven chromosomes were each shown to have two or more genetically independent linkage groups that were

Table 2 Loci from RFLP linkage groups (O'Donoughue et al. 1995) associated to specific chromosomes based on the analysis of F_1 monosomics. No associations were found for chromosomes 3C, 4C, 6C, 10 and 20

Monosomic chromosome	Aneuploid[a] (AVA #[b])	Linkage group	Enzyme	Locus
1C	K1 (192), K2 (193, TM)	21	*Eco*RI	*Xumn441B, Xbcd1250*
		31	*Dra*I	*Xumn442B, Xbcd1230B*
2C	K3 (195, 196), Sun II 8–1 1–1 (142)	15	*Eco*RV	*Xbcd1127A*
	K3 (195, 196, 197)		*Dra*I	*Xumn430, Xumn44, Xcdo54, Xcdo1385A*
5C	K8 (200), SIV (67)	5	*Dra*I	*Xbcd1230A*
	K8 (200)		*Dra*I	*Xumn442A*
			*Eco*RI	*Xcdo1319B*
			*Eco*RV	*Xcdo370*
7C	SVII (7, 172), SXIV (14, 179)	3	*Eco*RV	*Xbcd1735*
8	SXVI (352), SXVII (325, 326, 353, 354), SXVIII (327, 328, 355, 356)	23	*Eco*RV	*Xbcd1632C, Xcdo1090D*
9	Sn10–2 3–3 (133)	17	*Dra*I	*Xcdo1467A*
11	SI (1, 168), K19 (219)	13	*Dra*I	*Xcdo1174B*
			*Hin*dIII	*Xog49*
	K19 (219)		*Eco*RI	*Xumn107B*
			*Dra*I	*Xcdo549B*
12	SV (170)	2	*Eco*RI	*Xumn388, Xbcd342A*
			*Eco*RV	*Xcdo1158*
			*Dra*I	*Xbcd1829A*
13	K16 (214)	6	*Dra*I	*Xcdo82, Xcdo1467B*
		9	*Eco*RI	*Xcdo1445A*
14	K7 (199), K13 (208, TM)	16	*Eco*RI	*Xumn13, Xcdo1509C, Xbcd1265*
	K7 (199)	23	*Eco*RV	*Xcdo1090D, Xbcd1632C*
	K13 (208, TM)	38[c]	*Eco*RV	*Xog41A, Xcdo1449*
15	K10 (202, 203), K20 (220, 221), SXV (15, HT)	7	*Hin*dIII	*Xumn464B*
	K10 (202, 203), K20 (220, 221)		*Dra*I	*Xcdo1385C*
			*Eco*RI	*Xcdo1461*
	K10 (202, 203), K20 (220, 221), SXV (180, TA)	10	*Eco*RI	*Xbcd1950A*
	K10 (202, 203), K20 (220, 221)		*Eco*RI	*Xbcd1856*
	K20 (220, 221)	28	*Eco*RI	*Xcdo1168B*
16	K18 (218, AF)	20	*Dra*I	*Xumn364A*
17	K11 (204, 205), K17 (216)	3	*Eco*RI	*Xumn433, Xcdo216, Xbcd342B, Xcdo395B*
			*Dra*I	*Xcdo346A, Xcdo1385D, Xcdo1261B*
			*Eco*RV	*Xog41B*[b]
	K17 (216)	24	*Dra*I	*Xcdo348A*
18	K21 (222)	33	*Hin*dIII	*Xumn202*
19	K12 (206, TM), K14 (210, TM), SXII (12, 177)	22	*Hin*dIII	*Xumn589B*
			*Eco*RI	*Xumn28, Xumn575*
	SXII (12, 177)		*Eco*RV	*Xbcd1968C*
21	SVIII (8, 173), SIX (9, 174), SX (10, 175)	4	*Hin*dIII	*Xumn341B*
			*Eco*RI	*Xcdo220*
		12	*Dra*I	*Xcdo1174A*

[a] K refers to aneuploids derived from the cultivar Kanota. S refers to aneuploids derived from the cultivar Sun II

[b] AVA numbers are seed source numbers and were assigned to each monosomic line derived from a single plant shown to be deficient for a chromosome: TM refers to Kanota aneuploids obtained from Dr. T. Morikawa; AF refers to Kanota aneuploids obtained from Dr. A. Fominaya, HT refers to Sun II aneuploids obtained from Dr. H. Thomas, TA refers to Sun II aneuploids obtained from Dr. T. Aung

[c] Requires re-mapping of loci for confirmation of linkage group

physically associated to the same chromosome (Tables 2 and 3). These associations do not orient the linkage groups with respect to each other. The association between chromosome 18 and linkage group 33 (LG33) here was based on only one probe, UMN202. However, supporting this linkage group association, Kianian et al. (1997) showed that marker locus *Xcdo1428B*, located on LG33, is absent in aneuploid stocks K21, SII and SXIII, all of which are nullisomic for chromosome 18.

No linkage group associations were found for chromosomes 3C, 4C, 6C, 10 and 20. Putative monosomic lines for these chromosomes originated from Sun II haploids derived from oat x maize crosses (Jellen et al. 1997) and were not available until later in this study. Only F_1 monosomics from crosses to Ogle-C were made for these and the other Sn monosomic lines, and these F_1s were analysed for marker loci representing only 7 of the 38 linkage groups. Monosomic F_1s from the K1–K21 and SI–SXVIII monosomic sets were tested with markers representing 32 and 16 linkage groups, respectively. Six of the thirty eight linkage groups were not represented in this study because of lack of suitable or reliable polymorphisms in the markers tested; most of these six consisted of only a few markers each.

Differences in RFLP patterns were observed between Ogle-C and Ogle-1 in 10 out of 66 instances where probe

Table 3 Association of genetically independent oat RFLP linkage groups with oat chromosomes

Chromosome	Associated linkage groups
1C	21+31
13	6+9
14	16+23, 16+38
15	7+10+28
16	6+20[a]
17	3+24+34+30[b]
21	4+12

[a] Kianian et al. (1997)
[b] The association of linkage group 30 with chromosome 17 is by the 6.6-kb fragment of the locus *Xumn207B* (Jellen et al. 1993b; O'Donoughue 1995)

banding patterns were compared, demonstrating genetic variability in the original cultivar Ogle. RFLP differences were also observed among the various monosomic lines derived from Kanota and Sun II. Some loci could not be scored because a monosomic line sometimes carried alleles not present in the euploid Kanota-1 or Sun II-1 lines. To check if duplicates or allele differences among monosomic lines might be due to monosomic shifts or other variations in stocks, the K1–K21 and SI–SXVIII sets were each obtained from two different laboratories and compared. No significant linkage group associations could be attributed to differences in the monosomic-line source (Table 2).

False associations between linkage groups and chromosomes were avoided by running a DNA lane from the maternal parent control alongside that of its associated F_1, ensuring that the maternal parent had the allele being scored. Five monosomic lines (K10, K20, SVIII, SIX and SX) had alternate alleles at certain loci, and heterozygous loci on disomic chromosomes were detected in one line (K2, obtained from A. Fominaya). In both cases, absence of specific DNA fragments in the monosomic F_1 would not be due to absence of the critical monosome. A chromosomal region involving LG 27 could not be reliably assessed with the Kanota-derived monosomic F_1s. The loci *Xcdo58B* and *Xumn856B*, both from LG27, were observed to contain either one or the other allele, or both alleles, at each of these loci in several of the Kanota monosomic lines.

Marker assignments reflecting potential translocation differences

For monosomes 14 (K7, K13), 15 (K5, K10, K15,K20), 17 (K11, K17) and 19 (K12, K14), Jellen et al. (1993b) demonstrated RFLP polymorphism between the lines that were monosomic for the same chromosome. This variability was also observed in the present study (Table 2), except for monosomics K12 and K14, and reflects either genetic heterogeneity in the Kanota cultivar when monosomic lines were isolated or structural variation generated during the recovery or maintenance of monosomic lines.

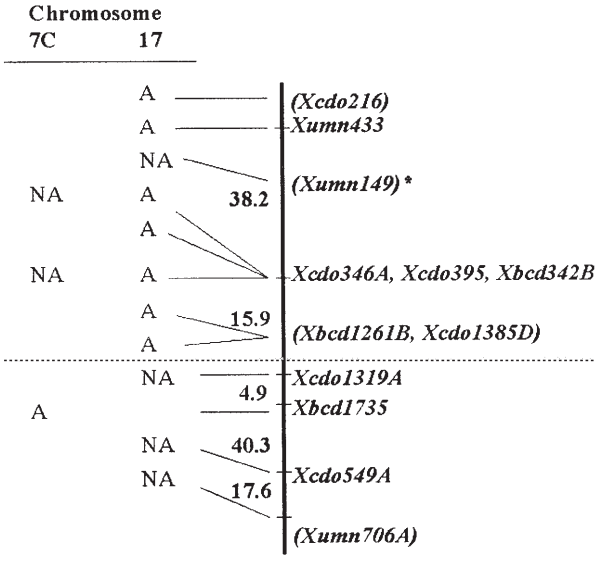

Fig. 2 Linkage group 3 (O'Donoughue et al. 1995) showing distances between selected loci that are associated (*A*) or not associated (*NA*) with chromosome 7C or 17. *Parentheses* around a locus name indicates a best-fit position for the locus. The *dotted line* is the suggested region where a translocation break would exist that separates the upper chromosome 17 portion from the lower chromosome 7C portion of this linkage group. The *asterisk* (*) indicates an anomalous association

The majority of the linkage groups were associated to chromosomes in a consistent manner; however, there were also several anomalies where linkage groups were found associated to more than one chromosome or to one but not another among monosomic lines thought to be lacking the same monosome (Table 2). Translocation differences have been frequently detected cytologically between oat cultivars, among members of monosomic sets, and may account for many of these anomalies. For example, the mapping parents Kanota and Ogle were found by genomic in situ hybridization to differ by at least three A-D/C translocations (Jellen et al. 1994). Also, a translocation involving chromosomes 7C and 14 was found in five of the 21 Kanota monosomic lines (Jellen et al. 1993b) and a reciprocal translocation involving chromosomes 3C and 14 was found in 15 of the 18 lines in the SI–SXVIII monosomic set (Leggett and Markhand 1995; Jellen et al. 1997).

Clustering of loci in linkage groups 3, 6, 11, 17, 23 and 30 suggests areas of reduced recombination (O'Donoughue et al. 1995) and may be due to proximity to the centromere or to translocation breakpoints. Linkage group 3 appears to involve a translocation between chromosomes 7C and 17. As shown in Fig. 2, seven loci between *Xcdo216* and *Xcdo1385D* appeared to be associated with chromosome 17 (represented by K11 and K17), but *Xumn149* was an exception. Four probes between *Xcdo1319A* and *Xumn706A* were not associated with chromosome 17. The opposite situation was observed for chromosome 7C (represented by SVII and SXIV) where *Xbcd1735* was associated with chromo-

some 7C but *Xcdo346A* and *Xbcd342B* were not. The 7C-17 translocation is particularly interesting as its presence in the *A. sativa* and absence in the *A. byzantina* taxonomic forms suggest separate paths of domestication from *Avena sterilis* progenitors (Zhou et al. 1999).

Linkage group 23 was associated with chromosomes 14 (represented by K7) and 8 (represented by SXVI, SXVII, and SXVIII). However, LG23 was clearly not associated with the K13 form of monosome 14 (Jellen et al. 1993b). Chromosome C-banding had shown that K7 represents the "normal" chromosome 14, and K13 a translocated chromosome 14 (Jellen et al. 1993b). It is possible that LG23 is part of this translocated segment of chromosome 14. Another translocation difference between K7 and K13 involves LG38.

A translocation difference not associated with clustered loci was observed between K11 and K17, both monosomic for chromosome 17. Linkage group 24 was associated with monosome 17 in monosomic K17 but not in monosomic K11. C-banding (Jellen et al. 1997) suggests that chromosome 17 is quite polymorphic, so large differences between different sources of monosome 17 might be expected.

Linkage-group associations to chromosomes made by analysis of nullisomic oat lines (Kianian et al. 1997) were the same as were found in this study for chromosomes 5C, 11 and 21. An exception was LG6, which was associated with chromosome 16 using nullisomic SVI (Kianian et al. 1997), but this linkage group was shown to be associated to chromosome 13 via the K16/Ogle monosomic F_1 in this study and by Jellen et al. (1993b). Thus, the linkage group was associated with two different chromosomes depending on the source of the aneuploid line employed.

Homoeologous relationships

Through inspection of probes that detected multiple polymorphic loci, it was possible to discern certain homoeologous linkage groups and thus homoeologous chromosomal regions. Chromosome 19 (LG22) was homoeologous with chromosome 17 (LG24) and chromosome 15 (LG28). Although the association of LG28 with chromosome 15 is based only on one locus, further mapping by Kianian et al. (1999) suggested that LG28 was associated with LG7 and LG10 which are also located on chromosome 15. Chromosome 15 (LG7) is homoeologous with chromosomes 13 (LG9) and 9 (LG17). Another region of chromosome 13 (LG6) is also homoeologous with chromosome 9 (LG17). Chromosome 21 (LG4) is homoeologous with chromosome 13 (LG6) and chromosome 5C (LG5). Linkage group 3 appears to be composed of regions of two chromosomes (7C and 17, Fig. 2) but also has loci that are homoeologous to linkage groups 14, 15, 17 and 24+34. Chromosome 14 (LG23) shows two blocks of homoeology: one block (about 18 cM) homoeologous to LG27 and a second block (about 17 cM) to chromosome 16 (LG20), LG14, and LG32. The second block occurs in four homoeologous regions suggesting that one of these regions is paralogous. Rooney et al. (1994) and Jellen et al. (1995) reported chromosomes 1C, 14 and 17 to be homoeologous and chromosomes 8 and 13 to be homoeologous. In the present study, there was very little evidence to support these conclusions largely because chromosomes 1C, 8 and 14 are poorly represented in the oat map by having few probes that recognize multiple polymorphic loci. Rooney et al. (1994) and this study detected homoeology between chromosomes 2C and 11 and between chromosomes 16 and 18.

Further work will be required to identify linkage-group associations for chromosomes 3C, 4C, 6C, 10 and 20. A more-saturated oat map will be required to fully investigate the translocations that have been identified in this study. The complexity encountered in assigning linkage groups to chromosomes in monosomics derived from different oat lines confirms the extensive amount of chromosomal rearrangement present in and among cultivated hexaploid oat lines and also points out the need for an oat monosomic set in a uniform genetic background.

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