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Identification of the 21 monosomic lines in *Avena byzantina* C. Koch cv. 'Kanota'

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Summary. All of the 21 possible monosomic lines have been screened and confirmed from 33 monosomic stocks of *Avena byzantina* C. Koch cv. 'Kanota'. All of them, except Mono-21 which was a progeny of monosomic 'Cherokee' (*A. sativa*) repeatedly backcrossed with 'Kanota', were obtained in the progenies of haploid (2n = 3x), aneuploid (2n = 6X ±) and autotriploid (2n = 9X) partners of twins. Identification of the monosomics was carried out by means of the double monosomic method, monosomic analysis on marker genes, leaf peroxidase isozyme analysis, karyotype analysis and nullisomic analysis. The monosomic lines were numbered from Mono-1 through to Mono-21, mainly in the order of monosome length from the longest to the shortest. Most monosomic lines were hardly distinguishable by morphological characteristics from each other or from normal disomics. In the selfed progenies of four monosomic lines, Mono-8, -9, -17 and -19, segregation of nulli-, mono- and disomics was observed, but no nullisomics were found in the other lines. In most cases the frequency of monosomics ranging from 35.5 to 97.8% was, compared to those of nulli- and disomics, highest in the selfed progeny of monosomics. The monosomic lines were easily maintained and can be used for genetic analysis because of their good seed fertility and high monosome transmission rate. They have the near isogenic background of 'Kanota'.

Key words: Oats – Monosomic series – Nullisomics – *Avena byzantina* – Chromosome identification

Introduction

Cultivated oats, *Avena byzantina* and *A. sativa*, are hexaploid species which have 42 chromosomes in each somatic cell. Because their mono- and nullisomics are viable, it should be possible to produce the different monosomic and nullisomic series in these oats. The complete aneuploid series should be invaluable for conducting genetic and cytogenetic analyses of oats.

In wheat, spectacular results were obtained with the use of aneuploid lines produced by Sears (1954). The production of monosomic oats has been carried out with various cultivars by many authors (Huskins 1927; Nishiyama 1931, 1933; McGinnis 1962a, b; Hacker and Riley 1963, 1965; Rajhathy and Dyck 1964; Chang and Sadanaga 1964a, b; Andrews and McGinnis 1964; Lafever and Patterson 1964a, b; Hacker 1965; Maneephong and Sadanaga 1967; Singh and Wallace 1967a, b). However, a complete series of 21 monosomic lines which has a near isogenic background in a single cultivar has not yet been established. Nishiyama and his coworkers isolated 33 monosomic families from a single varietal population (Nishiyama et al. 1968; Nishiyama 1970). However, they did not make a critical identification of 21 kinds of monosomic lines.

Since 1973, the present author has identified monosomic lines with this material by means of double monosomic analysis (Morikawa 1977, 1982) and leaf peroxidase isozyme analysis (Morikawa 1978). In addition, the successive backcrosses to the two lines, i.e., M34 and Mk-24 which had different genetic backgrounds, have been made in order to obtain a near isogenic monosomic series of 'Kanota'.

In the present investigation, chromosome numbers and pairings were observed in each successive backcross generation and the identification of 21 monosomic lines was made by morphological comparison, karyotype analysis and comparison of the monosome's transmission rates. Both the current and previous results will be reported and discussed.

Materials and methods

Twenty monosomic lines of *Avena byzantina* C. Koch cv. 'Kanota', one monosomic line of *A. sativa* L. cv. 'Cherokee'

and their disomic line were used in the present study. The first 20 monosomic lines were supplied by Nishiyama and tentatively designated as Mk-1 to 4, 6 to 9, 11, 13, 15, 18 to 20 and 22 to 27 (Nishiyama 1970). A monosomic line for the shortest chromosome was produced by Sadanaga and designated M 34. The 'Kanota' monosomic lines were derived from the progenies of haploid (2n=3x) (Nishiyama and Tabata 1964), aneuploid (2n=6X±) and autotriploid (2n=9X) partners of twins. The cultivars 'Kanota' produced twin plants at a higher frequency than other cultivars (Nishiyama et al. 1968). This is the reason why 'Kanota' was used as the genetic background of the monosomic lines. Since 'Kanota' monosomic lines were isolated from a single varietal population, any difference observed among monosomics could be attributed to the difference in their monosomes. M 34 was derived from the progeny of the X-irradiated 'Cherokee' population, Maneephong and Sadanaga 1967).

The karyotype analysis was done as follows: seeds of each monosomic line were germinated on moist filter paper in petri dishes, and were kept in darkness at 22 °C. After 3 or 4 days the root tips were collected from the germinated seeds and pretreated with cold water (about 0 °C) for 24 h, then fixed with a 3:1 alcohol-acetic acid solution and stored in 70% alcohol. The root tips were hydrolyzed in 1N HCl at 60 °C for 9 min, stained with Feulgen's reagent and squashed in aceto-carmine. Three good metaphase plates per monosomic line were selected for taking photomicrographs using a ×100 oil immersion lens and enlarged at a magnification of ×2,000. For meiotic observations, microsporocyte samples were fixed in a 3:1 alcohol-acetic acid solution and stored in 70% alcohol. Slides were prepared using the aceto-carmine squash method.

For field observation of plant characters, all the lines were seeded in the seed beds at the end of October, and one month after germination all the seedlings were transplanted to the experimental field at 20 cm intervals in 60 cm rows. Seed fertility was determined by calculating the percentage of the first and second florets which set seed. Peroxidase isozyme separation and detection were performed using the method of Morikawa (1978).

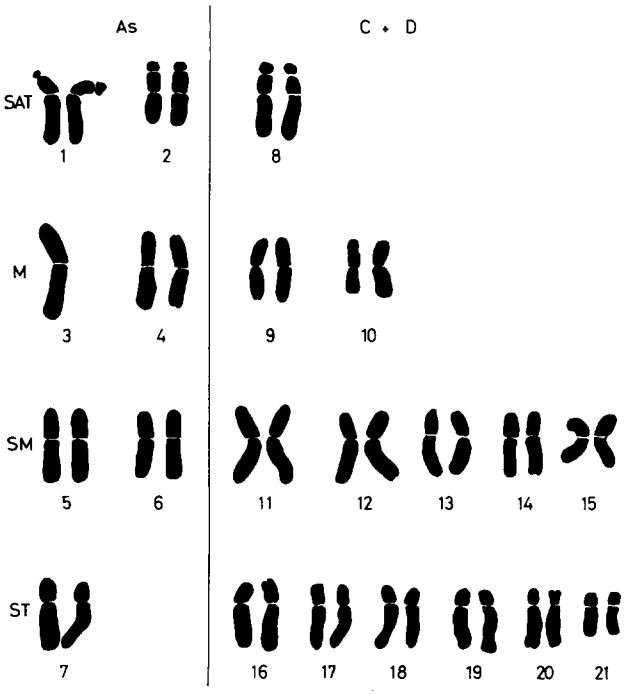

Fig. 1. The karyotype of Mono-1 (2n=41) of *Avena byzantina* cv. 'Kanota' that is deficient for the largest chromosome (M 3)

Table 1. The previous and revised numbering of the 21 monosomic lines in *Avena byzantina* C. Koch cv. 'Kanota'

Revised no.	Previous no. (Nishiyama 1970)	Monosome[a] (Rajhathy 1963)
Mono-1	Mk-1	M 3
2	2	SAT 1
3	3	SAT 8
4	4	SM 11
5	6	ST 7
6	7	M 4
7	8	ST
8	9	SM
9	11	ST
10	13	SM
11	15	SM
12	18	SM
13	19	SAT 2
14	20	ST
15	22	SM
16	23	M 9
17	24	SM 15
18	25	ST 19
19	26	M 10
20	27	ST 20
21	M 34	ST 21

[a] Monosomes not numbered are those which could not be identified among the chromosomes of the same group

Results

The standard karyotype of the hexaploids was proposed by Rajhathy (1963). This karyotype is consistent with all four hexaploid species, *A. fatua, A. sterilis, A. sativa* and *A. byzantina*. 'Kanota' oats (*A. byzantina*) had three pairs of satellite chromosomes (SAT), four pairs of metacentric chromosomes (M), seven pairs of submetacentric chromosomes (SM) and seven pairs of subterminal chromosomes (ST). Figure 1 shows the idiogram of the karyotype of Mono-1 of 'Kanota', in which one of the longest metacentric chromosomes is missing. Chromosome arms formed by the location of the centromere can be easily measured. All chromosomes of the SAT and M groups were easily identified by the distinctive differences in the size of their satellite or arm ratio but it was difficult to distinguish the members of both the SM and ST groups because of their similar chromosome size. In both the SM and ST group, only the longest and shortest chromosomes were identified. The second and third shortest chromosomes of the ST group were also identified.

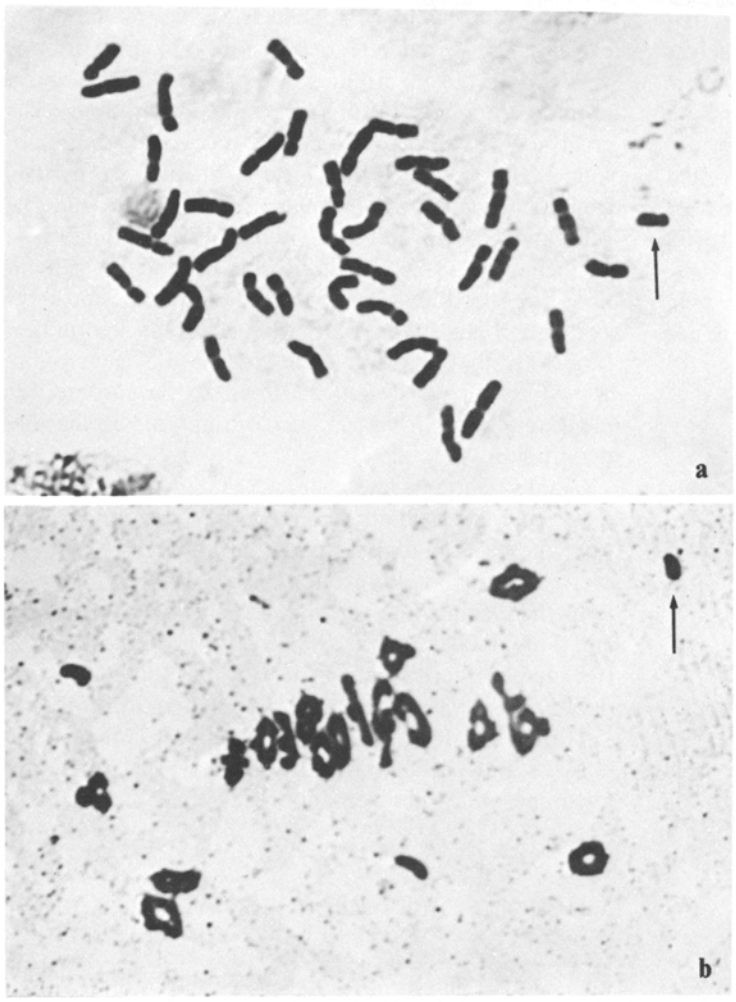

Fig. 2 a, b. The somatic and meiotic chromosomes of the F1 hybrid between 'Kanota' disomic and 'Cherokee' mono-M 34: **a** Somatic chromosomes of a root tip cell at metaphase. **b** Meiotic chromosomes of a PMC at metaphase I forming 19 bivalents and 3 univalents. The *arrow* indicates the shortest chromosome (ST 21)

Table 1 shows a revision of the previous numbering (Nishiyama 1970) of the 21 monosomic lines in 'Kanota' oats. The revised numbering system from Mono-1 to -21 is mainly based on the size of their monosomes, from the longest to the shortest. Of the 21 monosomes, it was possible to identify 13 based on the standard karyotype of Rajhathy (1963) but the remaining eight monosomes, which are not numbered on the karyotype designation in Table 1, are difficult to identify by karyotype analysis. Monosome-2, -3 and -13 which possess a satellite on their short arm, were SAT 1, SAT 8 and SAT 2, respectively. Monosome-1, -6, -16 and -19 of the M group were M 3, M 4, M 9 and M 10, respectively. Monosome-4 and -17 of the SM group were SM 11 and SM 15, respectively. Monosome-5, -18, -20 and -21 of the ST group were ST 7, ST 19, ST 20 and ST 21, respectively.

The original mono-M 34, redesignated Mono-21, was derived from cv. 'Cherokee' that was backcrossed six times with 'Kanota', and its genetic background became similar to 'Kanota'. Table 2 shows the chromosome numbers of the backcrossed progenies of the monosomic hybrids. In the F1, 'Kanota' × M 34, one monosomic and six disomic plants were obtained. Figure 2 shows the somatic chromosomes of the F1 hybrid that was deficient in one shortest chromosome (indicated by arrow). This result indicates that the 20-chromosome male gamete of M 34 was involved in fertilization. In the B1 and B2, 26 monosomics and six unexpected double monosomics ($2n=40$) were obtained in total. Occurrence of the unexpected 40-chromosome plants in these early backcross generations seemed to be due to the irregular meiotic chromosome pairing, as shown in Fig. 2 b that reveals $19II+3I$ at metaphase I of the F1 hybrid. One shortest chromosome (indicated by arrow) was included among the three univalents. In the B3–B5 generation three disomic and 21 monosomic plants were found. No 40-chromo-

some plants were produced. These facts indicate that chromosome pairing became stable in later backcross generations. Segregation of morphological characters was scarcely observed in the selfed progeny of the B6 generation.

Both disomics and monosomics found in the selfed progeny of Mk-24 that was the original monosomic for Mono-17 showed gigas appearance (Nishiyama 1970). Such a great alteration of plant morphology was assumed to be induced by a structural change of a chromosome. Therefore, in order to obtain the monosomics with a standard genetic background, successive backcrosses were made between Mk-24 and disomic 'Kanota' as the recurrent parent. Table 3 shows chromosome numbers in the backcross generations. The great majority of the backcrossed offspring were monosomic. This indicates that most of them were derived from 20-chromosome female gametes. In the B1 generation, 40-chromosome plants were obtained at a frequency of 28.6%. Plants in the B3 and B4 generations produced unilateral panicles and did not show any sign of gigas type. Thus, the genetic background of Mono-17, that was renamed in the B5 generation, appeared to have become normal. Its monosome was identified to be SM 15, according to Rajhathy's designation.

Table 4 shows some characteristics of the 21 monosomic lines. Ten plants were examined per monosomic line. The heading time is divided into three periods, i.e., early, intermediate and late. Under fall-sowing conditions the disomic line usually heads between April 20th and 24th at Sakai, Osaka, Japan. This heading time was considered intermediate. There was about a 2-week difference between early and late heading. Mono-1, -2, -5, -10, -17 and -20 showed early heading. Mono-4, -9, -16, -18 and -21 showed late heading. The remaining ten monosomic lines were intermediate.

Table 2. Chromosome numbers of the F1 hybrid, disomic 'Kanota' × monosomic 'Cherokee' (M 34), and its backcrossed progenies[a]

Generation	No. of plants with 2n =			Total plants examined
	40	41	42	
P1 (disomic 'Kanota')	0	0	10 (100)[b]	10
P2 (M 34 'Cherokee')	0	8 (100)	0	8
F1	0	1 (14.3)	6 (85.7)	7
B1	3 (25.0)	9 (75.0)	0	12
B2	3 (15.0)	17 (85.0)	0	20
B3	0	9 (90.0)	1 (10.0)	10
B4	0	5 (71.4)	2 (28.6)	7
B5	0	7 (100)	0	7
B6	0	4 (66.7)	2 (33.3)	6

[a] Backcrosses were made between monosomic hybrids and P1 as the recurrent male parent
[b] Percent

Table 3. Chromosome numbers of the F1 hybrid, monosomic Mk-24 × disomic 'Kanota', and its backcrossed progenies[a]

Generation	No. of plants with 2n =			Total plants examined
	40	41	42	
P1 (monosomic Mk-24)	0	4 (44.4)[b]	5 (55.6)	9
P2 (disomic 'Kanota')	0	0	9 (100)	9
F1	0	9 (100)	0	9
B1	4 (28.6)	9 (64.3)	1 (7.1)	14
B2	0	10 (100)	0	10
B3	0	6 (100)	0	6
B4	0	7 (100)	0	7
B5	0	7 (100)	0	7

[a] Backcrosses were made between monosomic hybrids and P2 as the recurrent male parent
[b] Percent

Table 4. Characteristics of the 21 monosomic lines in 'Kanota' oats

Monosomic line	Heading time	Plant height (cm)	Awn[c]	Seed set (%)
Mono-1	early	116.7 (4.4)[b]	−(+)	78.3
2	early	106.8 (1.4)	−(+)	81.0
3	intermediate[a]	123.3 (2.7)	−(+)	94.0
4	late	125.0 (2.8)	−(+)	97.5
5	early	102.4 (1.5)	+(−)	88.8
6	intermediate	115.0 (1.1)	−(+)	91.2
7	intermediate	118.0 (1.6)	−	93.8
8	intermediate	108.4 (1.9)	+	93.8
9	late	88.8 (2.4)	−(+)	87.1
10	early	109.2 (0.8)	+(−)	78.1
11	intermediate	105.2 (1.3)	−(+)	96.3
12	intermediate	101.2 (2.1)	+(−)	97.6
13	intermediate	102.0 (1.3)	−(+)	92.8
14	intermediate	107.6 (1.5)	− +	78.8
15	intermediate	110.0 (2.0)	+(−)	88.0
16	late	95.8 (1.3)	+(−)	91.3
17	early	106.0 (3.1)	+(−)	93.9
18	late	97.6 (1.9)	+(−)	98.4
19	intermediate	102.5 (2.5)	−	99.4
20	early	101.9 (1.6)	+(−)	87.9
21	late	122.6 (1.2)	−(+)	69.1
Disomic	intermediate	115.6 (5.7)	−(+)	99.4

[a] From April 20–24
[b] SE in parentheses
[c] + = awned; − = awnless; ( ) = minor

Table 5. Frequencies of nulli-, mono- and disomics in the selfed progeny of the 21 monosomic lines of 'Kanota' oats (1973–1981)

Monosomic line	No. of plants examined	Percent			
		Nullisomic (20II)	Monosomic (20II + 1I)	Disomic (21II)	Monotelosomic (20II + 1t)
Mono-1	49	0	91.8	4.1	4.1
2	49	0	87.8	10.2	2.0
3	44	0	90.9	9.1	0
4	36	0	97.2	2.8	0
5	45	0	97.8	2.2	0
6	59	0	83.1	16.9	0
7	66	0	90.9	9.1	0
8	152	42.1	53.3	3.9	0.7
9	73	2.7	88.9	9.3	0
10	49	0	89.8	8.1	2.0
11	50	0	90.0	10.0	0
12	76	0	35.5	64.5	0
13	30	0	86.7	13.3	0
14	37	0	86.5	13.5	0
15	36	0	97.2	2.7	0
16	32	0	65.6	34.4	0
17	36	2.8	75.0	22.2	0
18	50	0	40.0	60.0	0
19	34	41.2	50.0	5.8	0
20	36	0	94.4	5.6	0
21	34	0	97.1	2.9	0

Plant height of the disomic lines was 115.6 ± 5.7 cm. Mono-9, -16 and -18 were 88.8 ± 2.4, 95.8 ± 1.3 and 97.6 ± 1.9 cm high, respectively, being semidwarf. However, Mono-3, -4, -7 and -21 were taller than the disomic lines. The remaining 14 lines had nearly the same height as that of the disomic.

'Kanota' oats usually have awnless or weakly awned first florets. Mono-8, the so-called monosomic fatuoid, was clearly distinguishable from the disomics by the well developed awn on all the first florets. In contrast, Mono-7 and -19 were completely awnless.

Except for Mono-1, -10, -14 and -21, which were weakly sterile, disomics and most of monosomic lines showed good seed set. Accordingly, maintenance of all monosomic lines is easy.

Table 5 shows the frequencies of nulli-, mono-, di- and monotelosomics in the selfed progenies of monosomic lines on selfing in which the results from 1973–1981 were pooled. It is remarkable that the expected nullisomics were not found in the 17 monosomic lines, even though the total number of plants examined was small (34–152 per line). In 14 lines the frequency of monosomics was higher than 80% with 3–17% disomics. Mono-12 and -18 produced only 35.5 and 40.0% monosomics, respectively. Nullisomics were obtained in the progeny of four monosomic lines. Mono-8 and -19 gave about 40% nullisomics and Mono-9 and -17 only about 3%. Four kinds of monotelocentrics were obtained in the progenies of four monosomic lines, Mono-1, -2, -8 and -10, though their frequencies were quite low. All these monotelocentrics were fertile. Their deficient chromosome arms have not yet been identified, though they are assumed to have originated from misdivision of the monosomes formed in the monosomic 'Kanota'.

Table 6 shows the characteristics of four nullisomic lines. Nulli-8, that was derived from the selfed progeny of Mono-8, showed strong desynapsis, complete sterility and fatuoid character. The primary and secondary florets had distinct awns and each floret had a distinct sucker mouth. Nulli-9 was extremely weak, often dying before flowering, produced many tillering and was self-sterile. Nulli-17 was very weak and grass-like with comparatively large florets and was self-sterile. Nulli-19 was shorter in height with virescent appearance in some environments and was sterile.

Table 7 shows the keys for identifying the 21 monosomic lines which allowed them to be distinguished from each other or from disomics. The monosomic analysis of the marker genes of hexaploid oats has already been carried out by utilizing the present monosomic series (Morikawa 1980). The structural genes controlling leaf peroxidase, *Px9-a* and *Px0-a*, were located on chromosome 6 and 18, respectively. The gene for awn development, *A* was located on chromosome 7. The gene inhibiting the expression of fatuoid

Table 6. Characteristics of four nullisomic lines obtained in the selfed progeny of monosomic lines in 'Kanota' oats

Nullisomic line	Morphology	Main chromosome configuration
Nulli-8	Nullisomic fatuoid, primary and secondary florets have distinct awn and each floret has a distinct sucker mouth.	5II + 30I
9	The nullisomic is extremely weak often dies before flowering with high tillering.	20II
17	The nullisomic is very weak-grasslike with comparatively large florets.	20II
19	The nullisomic is shorter with virescens appearance in some environments.	20II

Note: all four nullisomics are completely self-sterile

Table 7. Keys for identifying the 21 monosomic lines of 'Kanota' oats

Monosomic line	Morphology	Marker gene	Seed fertility[a] of double mono	Monosome
Mono-1	Large flowering glume		Low	M 3 (longest)
2			Low	SAT 1
3			Intermediate	SAT 8
4	High mono. frequency		High	SM 11
5			Sterile	ST 7
6		*Px9-a*	Intermediate	M 4
7	Awnless	*A*	Intermediate	ST
8	Fatuoid	*I-Ft-1*	Sterile	SM
9	Semidwarf, weeping panicle		Intermediate	ST
10	Awned		Sterile	SM
11	Creeping culm		Intermediate	SM
12	Slender culm, low mono. frequ.		High	SM
13	Low germination rate		High	SAT 2
14	Small flowering glume		Intermediate	ST
15	Awned		Low	SM
16	Semidwarf, weeping panicle		Intermediate	M 9
17	Unilateral panicle	*Cm*	Low	SM 15
18	Low mono. frequ. semidwarf	*Px0-a*	High	ST 19
19	High nulli. frequency	*cdv*	High	M 10
20	Unilateral panicle		Low	ST 20
21			–	ST 21 (shortest)

[a] Seed fertility of double monosomics for chromosome 8 and another chromosome that corresponds to the monosome in the respective monosomic line (after Morikawa 1982)

character, *I-Ft-1* was located on chromosome 8. The gene for compact panicle *Cm* was located on chromosome 17. The gene conditioning chlorophyll deficiency-virescens, *cvd* was located on chromosome 19.

A comparative observation of various characters of 19 double monosomics commonly lacking a chromosome 8 has been made (Morikawa 1982). Their selfed seed fertility varied significantly and they were divisible into the three seed fertility groups: low, intermediate and high. Double monosomics belonging to the low seed fertility group showed great differences in their panicle morphology. These characteristics can also be used as a key for identification of the monosomics.

Discussion

All monosomic lines except Mono-21 were originally derived from several chromosome aberrants of a single cultivar (Nishiyama et al. 1968; Nishiyama 1970). Accordingly, the genetic background of those monosomic lines was believed, with the exception of Mono-17, to be uniform. The original line (Mk-24) of Mono-17 had a gigas morphology that was probably caused by a mutation independent of the aneuploid condition as both monosomic and disomic progeny had that gigas phenotype. This abnormality was eliminated by successive backcrosses with a 'Kanota' disomic line as the

recurrent parent. Mono-21 was produced in a 'Cherokee' (*A. sativa* cultivar) background that was also replaced by the 'Kanota' background through repeated backcrosses. Thus, a complete set of 21 monosomic lines with the same genetic background is now available for hexaploid oats. A new numbering system for 21 monosomic lines is proposed here, based on the length of individual monosomes, as suggested by Nishiyama (1970). In both the B1 and B2 generations of 'Cherokee' M 34, 40-chromosome plants were frequently obtained. Similarly, in the B1 generation of Mk-24, four 40-chromosome plants were produced. Hafiz and Thomas (1978) reported that the chance for univalent shift occurring is greater in earlier than in later backcross generations. The 40-chromosome plants obtained here appeared to be double monosomics. Since the F1 hybrids showed 19II + 3I in most PMC's at metaphase I, both M 34 and Mk-24 had, at least, one chromosome possessing different pairing affinity with that of 'Kanota'. The F1 hybrids had a chance to produce 19-chromosome gametes, from which double monosomics were derived.

The standard karyotype proposed by Rajhathy (1963) was used for various cytological studies in oats. However, the differences in length among the chromosomes and chromosome arms were not sufficient to distinguish all the monosomes. In the present investigation, only 13 monosomes could be identified by their morphology. As a method for classification of oat monosomics, the karyotype analysis has only a limited value.

Hacker and Riley (1963) screened aneuploid in *A. sativa* cv. 'Sun II' by checking the somatic chromosome number of young seedlings, from which they obtained 40 monosomic plants. These monosomics were classified into 13 classes based largely on nullisomic phenotypes (Hacker and Riley 1965). Thomas (personal communication) has isolated an additional two monosomic classes from the same cultivar, making 15 monosomic classes in total. The 'Sun II' monosomics were numbered in the order that they were found. Mutual checking of the corresponding lines between the two monosomic collections has not yet been done.

The identification of 21 monosomics is a most difficult and important cytogenetical work. McGinnis (1966) reviewed several methods used for this purpose, and concluded that chromosome size measurements could not provide a conclusive clue, but that the intercross between different monosomics to produce 40-chromosome hybrids was a promising approach. Morikawa (1977) made such intercrosses among 20 monosomic lines which have similar characters and observed morphological and cytogenetical characters of the 40-chromosome hybrids produced. Based on the results 11 monosomic lines, i.e., Mono-1, 2, 3, 4, 5, 7, 8, 10, 11, 14 and 15 could be identified. However, it was impossible to obtain 40-chromosome hybrids in some cross combinations. Because the production of this type of plants requires both the gametes from which the hybrids will arise to be deficient in a chromosome, the double monosomic method is applicable only to those monosomic lines which produce nullisomics at a fairly high frequency in their selfed progeny.

Most of the oat monosomics differ little morphologically from each other or from the disomics (Hacker and Riley 1965; McGinnis 1966; Sing and Wallace 1967b; Nishiyama 1970). However, some 'Kanota' monosomic lines showed visible characteristics, as described in Table 6, though their identification can not be totally based on these characteristics. The characters of nullisomics were far more distinct than those of the monosomics and were stably expressed in different genetic backgrounds. Nullisomics, namely, Nulli-8, -9, -17 and -19, obtained by screening a small size selfed progeny of 'Kanota' monosomics showed definite morphological characteristics that could be utilized for distinguishing the deficient chromosomes. Failure to produce nullisomic progeny from a number of monosomic lines was probably due to the small numbers of progeny whose chromosomes were observed.

In fact, in common wheat that is also hexaploid like the present material, nullisomic analysis was effectively employed for identification of the missing chromosome of the nullisomics (Sears 1953). The frequency of nullisomics in the selfed progeny of monosomics in 'Chinese Spring' wheat ranged from 0.9–7.7% in Missouri, USA (Sears 1954) and 1.1–13% in Sasayama, Japan (Mochizuki and Shigenaga 1964). The overall frequency of nullisomics in the selfed progeny of 'Kanota' monosomics was 4.2%, with a range from 0% in most monosomics to 42% in Mono-8. These figures are almost comparable to those reported in common wheat. Hacker and Riley (1965) isolated nullisomics from 10 monosomic classes in *A. sativa* cv. 'Sun II' and the mean frequency was 17.3%, ranging from 0%–77% in the field in Cambridge, England. The most of these nullisomics were self-sterile though four of them were highly fertile. All four nullisomics of 'Kanota' oats were completely self-sterile. It is interesting to note that there are significant differences between two oat cultivars in both frequency and fertility of nullisomics. The same is true for common wheat nullisomics, that is, some of them are fertile, whereas some others are completely sterile (Sears 1954).

Most monosomic lines produced monosomics in the selfed progeny at a high frequency ranging from 35.5–97.8%. The frequencies of nullisomics and monosomics are determined by the frequency of functional 20-chromosome gametes. Due to univalent elimination taking place in meiotic divisions, 20-chromosome gametes are produced at a much higher frequency than normal, 21-chromosome gametes. By making reciprocal crosses between six 'Kanota' monosomics and disomics, Fukunishi (1977) estimated that more than 90% of female gametes participating in fertilization were the 20-chromosome type in all monosomics examined, whereas on the male side 24.1% of the gametes ranging from 0 to 81.7% were the chromosome deficient type. As a result, frequency of nullisomics in the selfed

progeny of the monosomics became quite variable among the six monosomic lines tested.

The 21 monosomic lines are easily maintained because of their good seed fertility and high monosome transmission rate, and they have the near isogenic background of 'Kanota'. Accordingly, these lines are worth utilizing for genetic analysis or for materials for chromosome engineering. Monosomic analysis of the marker genes derived from different cultivars or species has already been done by using these lines. They will contribute greatly to oat improvement.

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