THE INFLUENCE OF GENOTYPE AND ENVIRONMENT ON UNIVALENT TRANSMISSION IN TWO MONOSOMICS OF *AVENA SATIVA* L.

BY

CHYI CHYANG LIN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

AND RESEARCH IN PARTIAL FULFILMENT

OF THE DEGREE OF

MASTER OF SCIENCE

UNIVERSITY OF MANITOBA

1964

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Dr. R.C. McGinnis, Department of Plant Science, for suggesting the problem, providing the materials, and for his guidance and encouragement throughout the investigation and the writing of the manuscript; to Dr. L.E. Evans and Dr. S.B. Helgason for their suggestions in the preparation of the manuscript. Sincere thanks are also extended to the National Research Council of Canada for financial support.

ABSTRACT

The influence of genotype and environment on univalent transmission was studied in two monosomics, 15 and 21, of Avena sativa.

The effect of variety and four temperature levels on the univalent transmission rate of three monosomics for chromosome 21 was measured. The transmission rates were quite close for all three monosomics under the lowest temperature (50°F) but the two Garry monosomics had a comparatively higher transmission rate than Taylor's monosomic at 60, 70 and 80°F. Taylor's monosomic was quite tolerant to all temperature treatments.

The effect on the univalent transmission of temperature level at meiosis only, compared with its effect on both meiosis and flowering was also studied on Taylor's monosomic. It showed that there is no significant difference between these two treatments. In general, the monosomic transmission rate is high under high temperatures and low under low temperatures.

The influence of seed source and variety on monosomic transmission rate was studied on three monosomics for chromosome 15 and five monosomics for chromosome 21 grown under similar environments. The two monosomic-15 lines obtained from X-irradiation showed a higher

transmission rate than that found in the monosomic obtained spontaneously.

The univalent transmission rates determined for five different monosomic lines of chromosome 21 were not consistent. Monosomics from the same variety as well as from different varieties may have similar or quite different transmission rates. Thus this characteristic cannot be used safely in the identification of different monosomics in producing a series.

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INTRODUCTION

During the last decade phenomenal progress has been achieved in the field of plant aneuploidy. Apart from the value of aneuploids as a genetic tool, the use in practical plant breeding is being explored. The production of aneuploid series, especially monosomics, in polyploid species of economic crops, has resulted in major advances in simplifying the analysis of polyploid inheritance, in locating genes on specific chromosomes and in analyzing chromosome translocations.

The production and maintenance of monosomic lines largely depend on the behaviour of the univalent chromosomes. If the univalent transmission rate for each chromosome is found to be specific in a species, it would provide an additional tool in the identification of different monosomics in a series. It would be especially advantageous if the univalent transmission is unaffected by changes in the environment.

Recently several monosomics have been produced in common oats, Avena sativa L., and identified from karyotype studies (McGinnis 1962). The present study has been carried out on two of them, 15 and 21, to determine the effect of genotype and environment on univalent transmission. Several

sources of both monosomics were available making possible genotypic comparisons.

LITERATURE REVIEW

Following the discovery of monosomics in wheat in 1924 by Kihara (11), monosomics have been produced in a number of other crops including tobacco, cotton and oats. The review of literature concerning transmission rates in monosomics of these crops will be presented separately.

I. WHEAT (*Triticum aestivum* L.)

In 1924, Kihara (11) was first to discover monosomics in this species. He also studied the meiotic behaviour of the univalent. Since that time many monosomics have been produced by various workers.

Nishiyama (16) studied the transmission rate in a monosomic. The transmission of n = 20 and n = 21 gametes was found to be respectively 11 and 89% in the pollen and 73 and 27% in ovules.

Sears in 1944 (24) studied the transmission rates of male and female n - 1 gametes in monosomics. He observed that the transmission rates through the ovules was about 75% regardless of the chromosome involved and through pollen it varied from 1 to 15% depending on the chromosome concerned. He attributed the greater frequency of n - 1 female gametes to the frequent failure of the univalent chromosome to be included in the gamete, whereas the low

percentage of n - 1 male gametes was due to their inability to compete with normal n gametes. No evidence was found of preferential selection in favour of normal male gametes by the ovules. The same author in 1952 (25) compared the transmission rates of mono-telosomic, mono-isosomic and normal monosomic plants. He did not find differences among them in female gametes, but on the male side, differences were quite evident with the mono-isosomics. He also reported that where the monosomic was an isochromosome, 26.4% of functioning male gametes were n - 1, 30.0% were 20 + telo and 43.6% were 20 + iso.

Morrison (15) from the study of meiotic behaviour of monosomics concluded that 97% of the P.M.C.'s showed 20 bivalents and pollen grains with 20 chromosomes were twice as numerous as those with 21 chromosomes, but the pollen grains with 20 chromosomes were 30 times less effective in competition with pollen grains having 21 chromosomes.

II. TOBACCO (*Nicotiana*, spp.)

Clausen and Goodspeed in 1926 attributed the fluted and corrugated characters in *N. tabacum* to the monosomic condition (5), the first aneuploids to be studied in this crop.

Lammerts (12) studied the inheritance of monosomics in *N. rustica*. He reported the percent of functional female *n-1* gametes (with 23 chromosomes) ranged between 31 and 75%. In only 3 of 7 monosomics studied were *n-1* gametes transmitted with an appreciable frequency through the male.

Olmo (19) reported that in *N. tabacum* 45.6 to 83.2% of the female gametes were *n-1*, whereas the transmission of *n-1* male gametes ranged between 0 and 7.3%, and averaged 2%.

Greenleaf (9) suggested that the frequency of univalent elimination was the same in both male and female gametogenesis in *N. tabacum* and that about 80% of all megaspores were *n-1* regardless of the chromosome concerned.

Clausen (3) isolated twenty or more monosomics of *N. tabacum* and found the monosomic transmissions differed from one another. He mentioned the value of monosomic analysis in this amphidiploid species for associating a gene or gene complex with a specific chromosome and also

for analyzing chromosomal translocations.

In 1944, Clausen and Cameron (4) completed the monosomic series comprising 24 monosomics. They observed that all were identifiable on the basis of the behaviour of the monosome in meiosis, of pollen characteristics, of ovular abortion, of seed production and of n-1 gamete transmission ratios. Each monosomic was characterized by a specific transmission rate, the range being 5-80%.

III. COTTON (*Gossypium hirsutum* L.)

Endrizzi (7), in 1963, conducted genetic analysis of six primary monosomics and one tertiary monosome of cotton. He based his classification on cytological data and was thus able to classify six different monosomes which were found to be quite stable. The n-1 gametes were transmitted with a high frequency through the egg but very rarely through the pollen. Endrizzi, *et al.*(8), advocated the use of monosomics as a tool for developing better cotton.

Brown and Endrizzi (1), in 1964, studied the origin, fertility, and transmission of monosomics. The percentage of monosomic plants from the progeny of selfed monosomics ranged between 20.7 and 40.4, most being close to 36%. They also reported data on two monosomics (MI and MII) regarding monosome transmission through the male and female.

In 24 plants of MI x G. hirsutum ♂ were monosomics (about 67% n gametes and 33% n-1 gametes on female side). In the reciprocal cross only 1 monosomic plant was found among 97 (about 1% n-1 gametes in the pollen). In MII, 2 of 24 plants from the cross with G. hirsutum pollen were monosomics. In the reciprocal cross, out of 108 plants studied, no monosomics were detected. It showed that the transmission of n-1 gametes in pollen is extremely low.

IV. OATS (Avena sativa L.)

Huskins (10), in 1927, was the first to observe monosomics in heterozygous fatuoid plants in oats. He also reported the selective elimination of fatuoid male gametes.

Nishiyama (17) studied the origin of fatuoid oats and also observed the behaviour of the univalent chromosome in the monosomic plants. For the calculation of univalent transmission he employed the number of micronuclei in tetrads and he compared these findings with the actual transmission rates. From the presence and absence of the micronuclei in tetrads he calculated the proportion of n-1 and n pollen grains to be 6:1. He suggested that the same ratio of 6:1 may be applied to the n-1 and n gametes in the female giving the frequency of zygotes as 36(2n-2), 12(2n-1) and 1(2n). He also observed that the average sterility of 41 chromosome plants was 57.24%. He

assumed that the sterility was caused entirely by the death of 40-chromosomes zygotes. The ratio of plants surviving was therefore converted to 8(2n-2), 12(2n-1), 1(2n), which showed a fair agreement with his observed data. Nishiyama also reported another plant with 20^{II} plus telocentric (17, 18). This $20^{II} + 1^{telo}$ plant was morphologically different being tall and fertile compared to the heterozygous fatuoid. Thus he associated the fatuoid gene or genes with the short arm of the C-chromosome.

Philp (20), in 1935, reported a monosomic for a submedian chromosome which carried a gene for normal chlorophyll production. He extensively studied its behaviour and reported that the monosomic transmission rate was about 10% from the selfed monosomic plant. Further he showed that the odd chromosome is transmitted in about 7% through male side and 20% through female side although this difference was found to be not significant. Philp (21) reported another monosomic which carried the gene or genes for broad leaves. The chromosome involved was also submedian but shorter than the one mentioned above. He reported that this chromosome was included in the pollen nucleus and presumably also in the egg nucleus in the range of 4.25 - 7.75% with an average of about 6%. Some variation observed in the ratio was probably caused by the influence of the environment, resulting in the death of 40-chromosome zygotes or by

certation.

Costa Rodrigues (6) produced 20 monosomics in Missouri 04047, by exposing pre-flowering panicles to X - irradiation. Progenies of five of these monosomics were studied and the frequency of nullisomic plants was found to vary from 2.1 to 46.0%.

Chang (2) reported on six monosomics which were produced by X - irradiation in the variety Cherokee. He studied the progenies of selfed monosomics and reported that the frequencies of disomics ranged from 3.1 to 15.4%, monosomics from 84.3 to 95.4% and nullisomics from 0 to 6.1%. The transmission rate of 21- and 20-chromosome pollen of different monosomics was calculated to be 75.0 to 100% and 0 to 25.0%, respectively and the transmission rate of 21- and 20-chromosome egg to be 1.3 to 11.5% and 88.5 to 98.7% respectively. Chang suggested that the low frequency of nullisomics may be due to a varietal effect or to deleterious effects of X-rays.

Rajhathy and Morrison (23) and Rajhathy (22) determined the karyotype for Avena sativa. With the aid of their idiograms, McGinnis and Taylor (14), in 1961, identified an essential chromosome for chlorophyll production namely chromosome 21. They reported that the univalent always divided at anaphase I as reported by Nishiyama (17) and Philp (20), and that the univalent

transmission through the pollen was 16.8%. The n-1 pollen competed quite favourably in fertilization with the result that 63.9% nullisomics were obtained from a selfed monosomic plant.

McGinnis and Andrews (13) found a second chromosome, 15, involved in chlorophyll production. They found that 64.1% of the progeny of this monosomic were nullisomic, 32.6% monosomics and 3.3% disomics. Their data again showed that certation was not a factor in univalent transmission.

No authentic information as to the effect of environment on the transmission rate of monosomics is available.

MATERIALS AND METHODS

Three different monosomics for chromosome 15 and five for chromosome 21 were selected for this study. A description of the material employed is listed in Table 1.

TABLE 1

Source and Identity of Monosomics used in Study of Transmission Rate

Monosomic	Chromosome Identity	Origin
Garry 18-81	15	spontaneous (McGinnis, 1962)
Garry R_2-524	15	x-irradiation (McGinnis and Andrews,1963)
Garry R_2-263	15	x-irradiation (McGinnis and Andrews,1963)
Garry 3-12	21	spontaneous (McGinnis,1962)
Garry 21-390	21	spontaneous (McGinnis, 1962)
Sun II	21	spontaneous (Riley and Kimber, 1962)
Condor	21	spontaneous (Holden, 1962)
R. L. 1574 X Ripon[x]	21	spontaneous (Taylor, 1961)

[x]hereafter referred to as Taylor's monosomic.

I. THE EFFECT OF VARIETY AND TEMPERATURE ON THE UNIVALENT TRANSMISSION

Three lines of monosomic-21 namely Garry 3-12, Garry 21-390 and Taylor's were grown in 6-inch pots in the greenhouse. At 2-3 weeks before the onset of meiosis, 3-6 pots of each were transferred from the green-house to 4 growth cabinets run at 50, 60, 70 and 80°F respectively. The intensity and duration of light (1600 foot candles and 16 hours) were maintained the same in all four growth cabinets. A panicle from each plant was collected (Plate I. Figure 3.) and fixed in Carnoy's Fluid (6:3:1, alcohol, chloroform and acetic acid) for the study of the meiotic behaviour of the univalent chromosome and for counting micronuclei in the tetrads. The anthers were squashed in aceto-carmine.

To study the effect of treatment on fertility and univalent transmission, 3 to 5 panicles were retained on each plant. After the panicles had completed fertilization (the dehiscence of the anthers on the basal florets was checked, Plate I, Figure 2), the plants were transferred to the greenhouse. The fertility was calculated by counting the total number of florets on each panicle and the seeds obtained. For studying the univalent transmission rate the harvested seeds were treated with Arason and put in vermiculate saturated with water and kept at 0 - 2°C for two

PLATE I. Stages of development of monosomic oat panicles used for temperature studies.

Figure 1. All florets have completed meiosis.

Figure 2. All florets have completed fertilization.

Figure 3. The stage for collecting P.M.C.'s.

Figure 4. Three panicles retained on each plant for treatment.

1

2

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4

days to break dormancy. The germination boxes were then left at room temperature until the roots were 2 to 3 cm. long. Root tips about 1 cm. in length were collected in ice water and pre-treated at 0 - 2°C for 24 hours, then fixed in Farmer's Fixative (3:1, alcohol and acetic acid). Staining was accomplished with Feulgen after hydrolyzing in 1 N HCl at 60°C for 8-11 minutes. Root tips were then squashed in aceto-carmine and chromosome counts made on mitotic metaphase (Plate II, Figs. 1-4).

II. THE EFFECT ON THE UNIVALENT TRANSMISSION OF TEMPERATURE LEVELS AT MEIOSIS ONLY COMPARED WITH ITS EFFECT ON BOTH MEIOSIS AND FLOWERING

Taylor's monosomic was employed in this experiment. All the nullisomics were albino and could be classified visually, thus greatly reducing the cytological work. Only the green seedlings had to be examined cytologically. Taylor's monosomic was exposed to the four temperature levels (50, 60, 70 and 80°F) in growth cabinets about two weeks before the plants underwent meiosis. In order to exclude the effect of temperature on univalent behaviour at fertilization 9-10 plants from each growth cabinet were transferred to the greenhouse at the stage when the basal florets had completed meiosis while the florets on the distal part of the panicle were just at pre-flowering (Plate I, Fig. 1.).

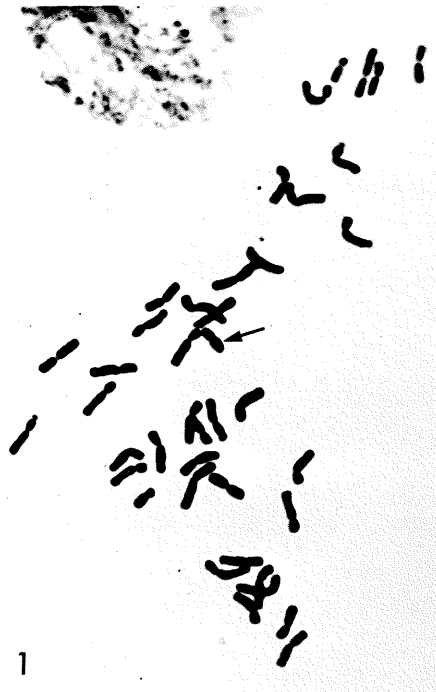
PLATE II. Root tip chromosomes of monosomic and nullisomic oats.

Figure 1. Metaphase of monosomic-15 with 41^{I} chromosomes.

Figure 2. Metaphase of nullisomic-15 with 40^{I} chromosomes.

Figure 3. Metaphase of monosomic-21 with 41^{I} chromosomes.

Figure 4. Metaphase of nullisomic-21 with 40^{I} chromosomes.



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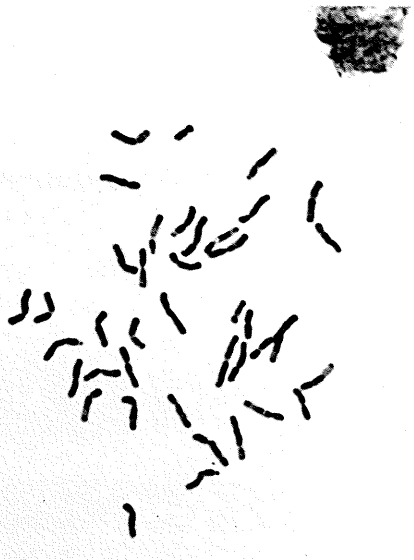

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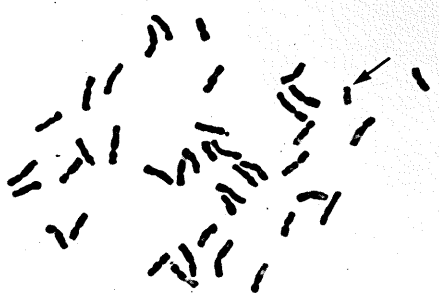

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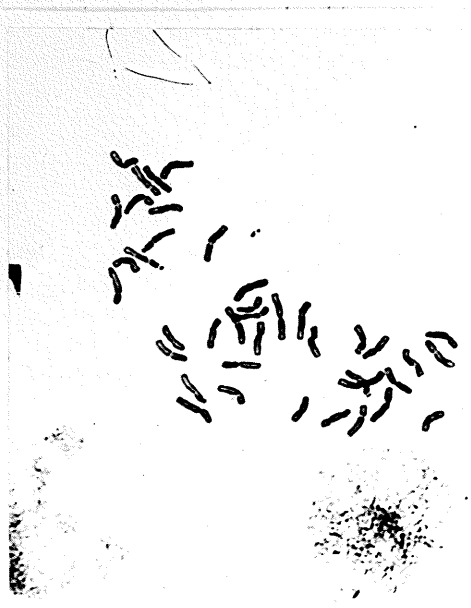

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One panicle was collected for P.M.C. studies and three other panicles of approximately the same age (Plate I, Fig. 4) were maintained on each plant under treatment for fertility and transmission rate calculations. Root tips from a total of 3,720 progeny of these plants were examined in this study.

To determine the effect of temperature at both meiosis and flowering stage on univalent behaviour 5-7 plants were left in each growth cabinet until all the florets on the panicle had completed flowering. They were then transferred to a greenhouse until maturity. Fertility was calculated and transmission rate was studied by germinating these seeds and counting the chromosome number in each seedling.

III. A COMPARISON OF TRANSMISSION RATE OF MONOSOMIC-15 AND MONOSOMIC-21 FROM DIFFERENT SEED SOURCES OR VARIETIES (Listed in TABLE 1.)

In order to further compare the transmission rate of the same monosomic from a different source or variety, progeny from three monosomic lines of chromosome 15 from different seed sources, grown in the field were analyzed cytologically. Similarly 5 different monosomic lines for chromosome 21 were grown in a greenhouse and chromosome counts made on their progeny.

RESULTS

I. THE EFFECT OF VARIETY AND TEMPERATURE ON THE UNIVALENT TRANSMISSION

The effect of four levels of temperature on univalent transmission was studied in Garry 3-12, Garry 21-390 and Taylor's monosomic, all of which are deficient for chromosome 21. The data concerning this is presented in Table 2. It showed that there was a marked difference in fertility between the Garry monosomics and Taylor's under each level of temperature. Taylor's monosomic invariably showed the highest fertility under all four levels of temperature. It had a maximum fertility (87.6%) at 60°F followed by 70°F (84.7%), 50°F (74.6%) and 80°F (25.6%). Garry 3-12 and Garry 21-390 showed the highest fertility at 70°F of 45.5% and 33.1% respectively, and the lowest fertility at 80°F (4.9 and 4.4% respectively). The fertility of normal Garry and Taylor's was 80.9 and 90.1% respectively under greenhouse conditions.

The monosomic transmission rate was quite similar for all the three monosomics under 50°F. At this temperature Garry 3-12, Garry 21-390 and Taylor's monosomic showed transmission rates of 37.0, 39.2 and 37.0% respectively. However there were marked differences at 60, 70 and 80°F. The transmission rate for Garry 3-12, Garry 21-390 and Taylor's was 67.4, 74.8 and 34.6%

TABLE 2. The effect of 4 temperature levels on the fertility and transmission rate of 3 lines of monosomic-21.

Temp.	Monosomic	Number of Plants	Number of Florets	Number of Seeds	Fertility (%)	Number of Progeny with 42 Chromosomes	41	40	Percentage of Progeny with 42 Chromosomes	41	40
50°F	Garry 3-12	5	944	102	10.8	1	37	62	1.0	37.0	62.0
	Garry 21-390	5	880	129	14.7	7	38	52	7.2	39.2	53.6
	Taylor's	3	950	709	74.6	0	47	80	0.0	37.0	63.0
60°F	Garry 3-12	3	824	292	35.4	4	62	26	4.4	67.4	28.2
	Garry 21-390	3	788	138	17.5	3	74	22	3.0	74.8	22.2
	Taylor's	5	1,472	1,289	87.6	10	122	221	2.8	34.6	62.6
70°F	Garry 3-12	3	982	447	45.5	1	54	41	1.0	56.3	42.7
	Garry 21-390	3	596	197	33.1	1	63	30	1.0	67.0	31.9
	Taylor's	3	1,290	1,092	84.7	1	38	61	1.0	38.0	61.0
80°F	Garry 3-12	6	2,168	107	4.9	6	66	22	6.4	70.2	23.4
	Garry 21-390	6	1,672	73	4.4	1	41	29	1.4	57.8	40.8
	Taylor's	3	798	204	25.6	1	47	73	0.8	38.9	60.3

Fertility of Garry disomic = 80.9%
Fertility of Taylor's disomic = 90.1%
(grown under greenhouse conditions)

respectively at 60°F; 56.3, 67.0 and 38.0% respectively at 70°F; and 70.2, 57.8 and 38.9% respectively at 80°F. Thus Taylor's monosomic showed a considerably lower transmission rate at the temperature levels of 60, 70 and 80°F as compared with the Garry monosomics which generally had a high transmission rate except at the low temperature of 50°F.

The theoretical univalent transmission rates calculated from the presence of micronuclei in tetrads (Plate III and Plate IV, Fig. 9) are shown in Table 3. Assuming the frequency of n=21 and n=20 gametes to be the same in both the male and female, the expected segregation of 42-, 41- and 40-chromosome progeny from a selfed monosomic plant was calculated for each monosomic line and is shown in Table 4. This calculated segregation seemed to approximate the actual segregation obtained from chromosome counts only at the 50°F level for the three monosomic lines, but at all temperature levels for Taylor's monosomic. As indicated in Table 4, the actual monosomic transmission rate for Garry 3-12, Garry 21-390 and Taylor's at 50°F is 37.0, 39.2 and 37.0% respectively, whereas the expected transmission rate is 31.0, 26.8 and 22.9 respectively. Taylor's monosomic showed the actual transmission rate of 37.0, 34.6, 38.0 and 38.9% at 50, 60, 70 and 80°F respectively, whereas the expected transmission rate was 22.9, 24.0, 23.3 and 27.5% respectively for the 4

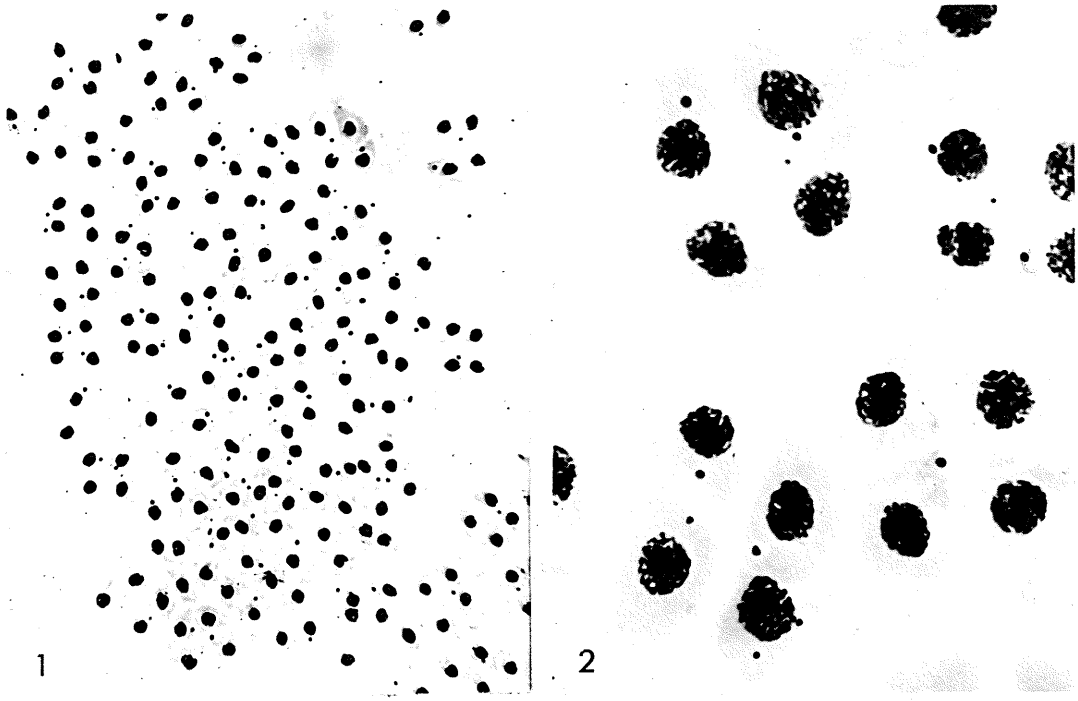


PLATE III. Tetrad stage showing micronuclei in monosomic-21 plants.

Figure 1. High percentage of tetrads with one or more micronuclei.

Figure 2. Higher magnification of Figure 1.

PLATE IV. Meiotic stages in monosomic-21 plants.

Figure 1. Late diakineses showing $20^{II}+1^{I}$.

Figure 2. Anaphase I showing lagging univalent.

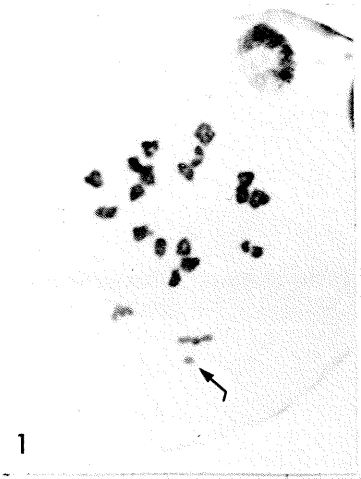
Figure 3-5. The univalent chromosome dividing and daughter chromosomes going to each pole.

Figure 6. Two daughter chromosomes not included in nuclei.

Figure 7. One daughter chromosome not included in nucleus.

Figure 8. More than two daughter chromosomes not included in nuclei.

Figure 9. Tetrad stage showing micronuclei.



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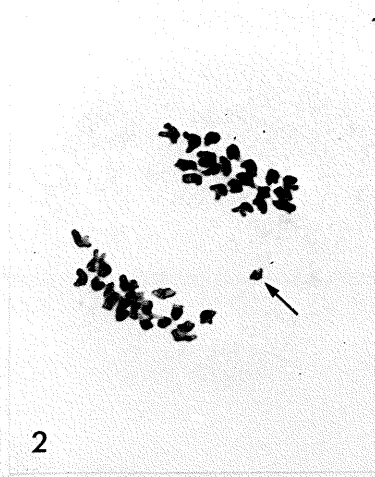

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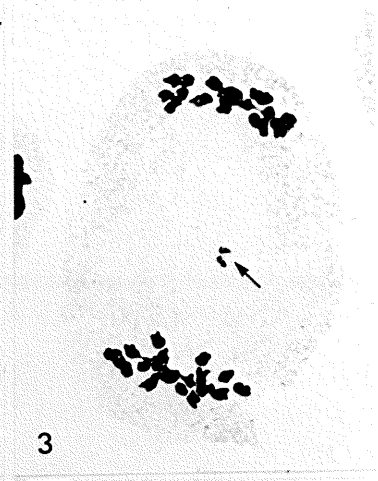

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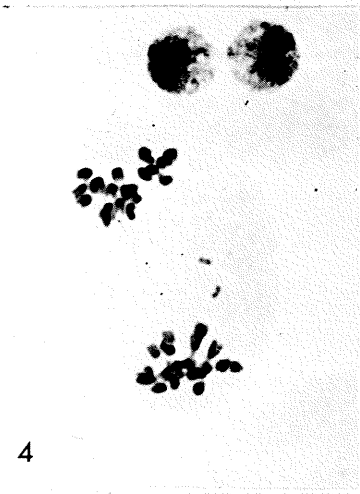

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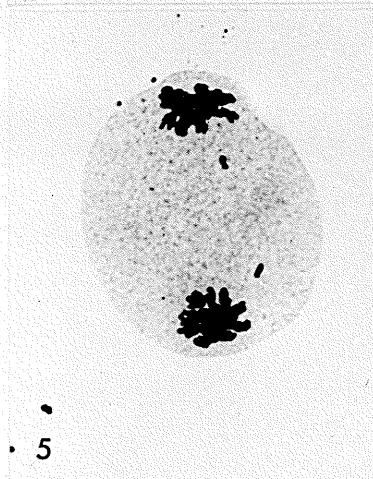

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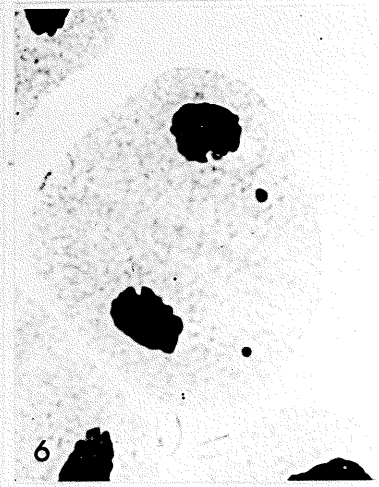

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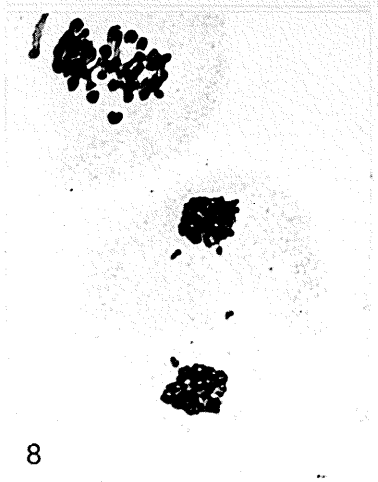

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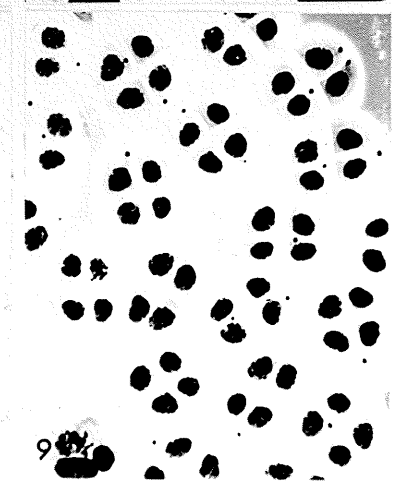

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TABLE 3. Number of micronuclei in tetrad of three monosomics under 4 temperature levels and calculation of univalent transmission frequency.

Temp.	Monosomic	Number of Micronuclei per Tetrad	Number of Tetrads	Number of Gametes	Total Gametes with n=21	Per Cent Gametes with n=21
50°F	Garry 3-12	0	80	320	160	50
		1	191	764	191	25
		2	198	792	0	-
		3	26	104	0	-
		4	16	64	0	-
	Total		511	2,044	351	19.2
	Garry 21-390	0	91	364	182	50
		1	242	968	242	25
		2	266	1,064	0	-
		3	35	140	0	-
		4	31	124	0	-
	Total		665	2,660	424	15.9
	Taylor's	0	62	248	124	50
		1	187	748	187	25
		2	247	988	0	-
		3	32	128	0	-
		4	8	32	0	-
	Total		536	2,144	311	14.9

TABLE 3. (Continued)

Temp.	Monosomic	Number of Micronuclei per Tetrad	Number of Tetrads	Number of Gametes	Total Gametes with n=21	Per Cent Gametes with n=21
60°F	Garry 3-12	0	102	408	204	50
		1	182	728	182	25
		2	161	644	0	-
		3	21	84	0	-
		4	16	64	0	-
	Total		482	1,928	386	20.0
	Garry 21-390	0	102	408	204	50
		1	171	684	171	25
		2	153	612	0	-
		3	15	60	0	-
		4	12	48	0	-
	Total		453	1,812	375	20.7
	Taylor's	0	86	344	172	50
		1	240	960	240	25
		2	287	1,148	0	-
		3	26	104	0	-
		4	10	40	0	-
	Total		649	2,596	412	15.9

TABLE 3. (Continued)

Temp.	Monosomic	Number of Micronuclei per Tetrad	Number of Tetrads	Number of Gametes	Total Gametes with n=21	Per Cent Gametes with n=21
70°F	Garry 3-12	0	80	320	160	50
		1	140	560	140	25
		2	118	472	0	-
		3	11	44	0	-
		4	3	12	0	-
	Total		352	1,408	300	21.3
	Garry 21-390	0	42	168	84	50
		1	140	560	140	25
		2	100	400	0	-
		3	18	72	0	-
		4	4	16	0	-
	Total		304	1,216	224	18.4
	Taylor's	0	32	128	64	50
		1	110	440	110	25
		2	150	600	0	-
		3	19	76	0	-
		4	12	48	0	-
	Total		323	1,292	174	13.5

TABLE 3. (Continued)

Temp.	Monosomic	Number of Micronuclei per Tetrad	Number of Tetrads	Number of Gametes	Total Gametes with n=21	Per Cent Gametes with n=21
80°F	Garry 3-12	0	92	368	184	50
		1	139	556	139	25
		2	98	392	0	-
		3	14	56	0	-
		4	4	16	0	-
	Total		347	1,388	323	23.3
	Garry 21-390	0	66	264	132	50
		1	159	636	159	25
		2	182	728	0	-
		3	22	88	0	-
		4	9	36	0	-
	Total		438	1,752	291	16.6
	Taylor's	0	58	232	116	50
		1	135	540	135	25
		2	164	656	0	-
		3	17	68	0	-
		4	7	28	0	-
	Total		381	1,524	251	16.5

TABLE 4. A comparison of expected and actual segregation of 42-, 41- and 40- chromosome progeny from 3 sources of monosomic-21, (Garry 3-12, 21-390 and Taylor's) based on data compiled in Table 2 and 3.

Temp.	Monosomic	Univalent Transmission Rate (Table 3)	Expected Percentage of Progeny with 42 Chromosomes	41	40	Actual Percentage of Progeny (Table 2) with 42 Chromosomes	41	40	x^2	P
	Garry 3-12	19.2	3.7	31.0	65.3	1.0	37.0	62.0	3.1	.20
50°F	Garry 21-390	15.9	2.5	26.8	70.7	7.2	39.2	53.6	12.4	<.01
	Taylor's	14.9	1.7	22.9	75.4	0.0	37.0	63.0	3.8	.15
	Garry 3-12	20.0	4.0	32.0	64.0	4.4	67.4	28.2	20.9	<.01
60°F	Garry 21-390	20.7	4.3	32.8	62.9	3.0	74.8	22.2	29.5	<.01
	Taylor's	15.9	1.9	24.0	74.1	2.8	34.6	62.6	2.7	.30
	Garry 3-12	21.3	4.5	33.6	61.9	1.0	56.3	42.3	10.9	<.01
70°F	Garry 21-390	18.4	3.4	30.1	66.6	1.1	67.0	31.9	23.5	<.01
	Taylor's	13.5	1.9	23.3	74.8	1.0	38.0	61.0	4.7	.10
	Garry 3-12	23.3	5.4	35.7	58.9	6.4	70.2	23.4	20.1	<.01
80°F	Garry 21-390	16.6	2.8	27.7	69.5	1.4	57.8	40.8	15.5	<.01
	Taylor's	16.5	2.7	27.5	69.8	0.8	38.9	60.3	4.2	.10

temperature levels. However there were obvious discrepancies for Garry monosomics at temperature levels of 60, 70 and 80°F. Data showed Garry 3-12 had the actual transmission rate of 67.4, 56.3 and 70.2% respectively for 60, 70 and 80°F whereas the expected transmission rate was 32.0, 33.6 and 35.7% respectively for these 3 temperature levels; Garry 21-390 showed the actual transmission rate of 74.8, 67.0 and 57.8% respectively for 60, 70 and 80°F whereas the expected transmission rate was 32.8, 30.1 and 27.7% respectively for the 3 temperature levels.

II. THE EFFECT ON THE UNIVALENT TRANSMISSION OF TEMPERATURE LEVELS AT MEIOSIS ONLY COMPARED WITH ITS EFFECT ON BOTH MEIOSIS AND FLOWERING

The data regarding the effect of temperature level at meiosis only on univalent transmission rates compared with its effect on both meiosis and flowering were tabulated in Table 5. Taylor's monosomic was employed. By comparing the data using the sample mean t-test it was possible to show that there was no significant difference in fertility between the two treatments at any of the four temperatures studied. Fertility was not affected by continuing the temperature level until after fertilization in this monosomic. Similarly, although the level of monosomic transmission was generally higher when the temperature treatment was continued to post-fertilization, it was not

TABLE 5. The effect on the univalent transmission of temperature levels at meiosis only compared with its effect on both meiosis and flowering in Taylor's monosomic.

Temp.	Number of Plants	Number of Florets	Number of Seeds	Fertility (%)	t	Number of Progeny with 42 41 40 Chromosomes			x^2	P	Percentage of Progeny with 42 41 40 Chromosomes		
50°F	9[a]	3,496	2,727	78.0	1.90	1	251	620	10.97	.01	1.0	28.5	70.5
	7[b]	2,174	1,548	71.2		6	132	275			1.5	31.9	66.6
60°F	10[a]	4,570	4,012	85.1	0.86	10	265	733	16.10	.01	1.0	26.3	72.7
	5[b]	1,472	1,298	87.6		10	122	221			2.8	34.6	62.6
70°F	10[a]	4,076	3,415	83.8	0.85	14	305	690	8.99	.02	1.4	30.2	68.4
	6[b]	1,746	1,421	81.4		5	139	214			1.4	38.8	59.8
80°F	10[a]	3,548	1,199	33.8	1.11	10	241	472	3.22	.20	1.4	33.3	65.3
	5[b]	1,082	271	25.1		3	74	107			1.6	40.2	58.2

$$t^{0.05}_{(df.=13)} = 2.16$$
$$t^{0.05}_{(df.=14)} = 2.15$$

a Temperature treatment only affected at meiosis.
b Temperature treatment affected at both meiosis and flowering.

significantly so over the data obtained for the treatment involving meiosis only. Monosomic transmission rate varied between 26.3 and 33.3% at the different levels of temperature at meiosis only and from 31.9 to 40.2% for the second treatment. The range is comparatively narrow in both cases. By using the x^2-test of independence it showed the two treatments to be similar in effect on the transmission rate at 50, 60 and 70°F. However it seems different at the highest temperature level (80°F) where some certation effect is suspected. The two treatments also exhibited a similar trend in monosomic transmission rate, that is under low temperature the transmission rate is low and under high temperature, it is high.

The P.M.C. material from the four levels of temperature treatment were collected and studied. It was found that the behaviour of the univalent during meiosis was not much different in the P.M.C. material collected from different temperature levels. The univalent chromosome always lagged at anaphase I, split, and the halves passed to the opposite poles (Plate III, Figs. 1-5). One or both of the daughter univalents were often excluded from the nuclei at telophase (Plate III, Figs. 6-7) and they lagged behind the other chromosomes at anaphase II, eventually passing toward the poles at random. They were seldom

incorporated in the nuclei and thus formed micronuclei in the tetrads (Plate III, Fig. 9). Occasionally, 4 or more micronuclei were observed (Plate IV, Fig. 2), probably the result of asynapsis of another pair of chromosomes or from misdivision of the daughter univalents at anaphase II.

By counting the number of micronuclei in tetrads the theoretical percentage of gametes with n=21 and n=20 were also calculated. The data concerning these was presented in Table 6. The percentage of gametes with n=21 varied from 13.9 (60°F) to 21.5 (80°F) and those with n=20 gametes varied from 86.1 (60°F) to 78.5 (80°F). At 60°F the percentage of n=20 gametes was highest. The expected segregation frequencies calculated by using the univalent transmission data listed in Table 6 are presented in Table 7. These data were found to fit the segregations actually observed in the progeny of those monosomics, treated at the meiosis stage only in all temperature levels. The expected monosomic transmission rates were 26.7% for 50°F, 24.0% for 60°F, 31.8% for 70° and 33.7% for 80°F whereas the actual transmission rates were 28.5, 26.3, 30.2 and 33.3% for the 4 temperature levels.

TABLE 6. Number of micronuclei in tetrads of monosomic-21 (Taylor's) under 4 temperature levels and calculated univalent transmission frequency.

Temp.	Number of Micronuclei per Tetrad	Number of Tetrads	Number of Gametes	Total Gametes with n=21	Per Cent Gametes with n=21
50°F	0	86	344	172	50
	1	240	960	240	25
	2	287	1,148	0	-
	3	26	104	0	-
	4	10	40	0	-
Total		649	2,596	412	15.9
60°F	0	181	724	362	50
	1	597	2,388	597	25
	2	815	3,260	0	-
	3	73	290	0	-
	4	56	224	0	-
Total		1,722	6,886	959	13.9
70°F	0	310	1,240	620	50
	1	528	2,110	528	25
	2	552	2,208	0	-
	3	47	188	0	-
	4	12	48	0	-
Total		1,449	5,794	1,148	19.8
80°F	0	440	1,760	880	50
	1	668	2,672	668	25
	2	652	2,608	0	-
	3	54	216	0	-
	4	32	128	0	-
Total		1,846	7,384	1,548	21.5

TABLE 7. Expected segregation of 42-, 41- and 40- chromosome progeny from selfed monosomic-21 (Taylor's), under 4 temperature levels calculated from the univalent transmission frequency listed in Table 6, and compared with the actual segregation frequency from the plants under temperature treatment at meiosis only.

Temp.	Univalent Transmission Frequency (Table 6)	Expected Percentage of Progeny with 42 Chromosomes			Actual Percentage of Progeny with 42 Chromosomes			x^2	P
		42	41	40	42	41	40		
50°F	15.8	2.5	26.7	70.8	1.0	28.5	70.5	0.4	.8
60°F	13.9	1.9	24.0	74.1	1.0	26.3	72.7	0.7	.7
70°F	19.8	3.9	31.8	64.3	1.4	30.2	68.4	1.8	.5
80°F	21.5	4.6	33.7	61.7	1.4	33.3	65.3	2.6	.3

III. COMPARISON OF TRANSMISSION RATES OF MONOSOMIC-15 AND MONOSOMIC-21 FROM DIFFERENT SEED SOURCES OR VARIETIES

The influence of seed source on the monosomic transmission rates in 3 monosomic lines all deficient for chromosome 15 was studied. The data showed that both Garry R_2-524 and Garry R_2-263 produced from x-irradiation had higher monosomic transmission rates of 87.0 and 78.1% respectively, as compared with 33.0% in Garry 18-81 which was obtained spontaneously (Table 8).

The influence of variety on the monosomic transmission was determined on 5 different monosomic lines of chromosome 21, all of which were obtained spontaneously. The data reported in Table 9 showed that monosomics of Sun II and Condor both have a relatively higher transmission rate (79.0 and 80.0% respectively) than Garry 3-12 (54.0%), Garry 21-390 (66.0%) and Taylor's (37.6%). Taylor's monosomic had the lowest transmission rate in the group. It appeared that Garry 3-12 and Garry 21-390 had a somewhat different transmission rate, but the difference was found to be not significant. Sun II and Condor (different varieties) have a very similar transmission rate.

TABLE 8. The influence of seed source on the frequency of progeny types in monosomic-15 grown in the field.

Monosomics	Segregation of Progeny with 42	41 Chromosomes	40	Total Plants Screened	Percentage of Progeny with 42	41 Chromosomes	40
Garry 18-81	2[x]	141	284	427	0.5	33.0	66.5
Garry R_2-524	5	74	6	85	5.9	87.0	7.1
Garry R_2-263	9	75	12	96	9.4	78.1	12.5

x One plant had 41 chromosomes plus a centric fragment

TABLE 9. The influence of variety on the frequency of progeny type from monosomic-21 grown under greenhouse conditions.

Monosomics	Number of Progeny with 42 Chromosomes	41 Chromosomes	40 Chromosomes	t	Total Plants	Percentage of Progeny with 42 Chromosomes	41 Chromosomes	40 Chromosomes
Garry 3-12	0	54	46	2.2	100	0.0	54.0	46.0
Garry 21-390	1	66	33		100	1.0	66.0	33.0
Sun II	6	79	15		100	6.0	79.0	15.0
Condor	11	80	9		100	11.0	80.0	9.0
Taylor's	3	70	113		186	1.6	37.6	60.8

$t\ (^{.05}_{df.=2}) = 4.3$

DISCUSSION AND CONCLUSIONS

Under the lowest temperature level (50°F) the influence of seed source and variety on the univalent transmission rate of three monosomics deficient for chromosome 21 was not evident, but at the other temperature levels (60, 70 and 80°F) the transmission rate was quite different among them. The difference was especially marked at 80°F between Garry 3-12 with a monosomic transmission of 70.2% and Taylor's with 38.9%.

The high monosomic transmission rate that occurred in both Garry monosomics indicates that either the percentage of n-1 male gametes was lower than the n gametes which is improbable on the basis of micronuclei studies, or that the n-1 pollen competed less favourably than n pollen in fertilization (certation effect) at the higher temperatures. At 50°F more nullisomic plants were obtained in the progeny and the monosomic frequency was reduced. It seems reasonable to assume that these oat monosomics also have the same tendency to produce a high frequency of n-1 female gametes as reported in wheat and tobacco monosomics and under low temperature, the percentage of functional n-1 male gametes is increased thus resulting in a high percentage of nullisomics. Taylor's monosomic showed comparatively

greater tolerance to temperature on the univalent transmission rate. The percentage of functional n-1 male gametes was almost the same for all temperature levels.

In other species such as tobacco, univalent behaviour is quite specific for each monosomic (7) and thus can be used in identifying the different monosomics. This study makes obvious the fact that a similar precise behaviour is not present in the oat monosomics. The data indicates that transmission rates in some varieties are particularly responsive to the temperature while others tend to be more tolerant suggesting genotypic control as well.

There are no significant differences between the temperature treatments affecting the univalent transmission rate at meiosis only and its effect on both meiosis and flowering in the study with Taylor's monosomic at 50, 60 and 70°F. Thus there is no certation effect imposed by these 3 temperature levels in this monosomic. Both the observed and calculated transmission rates are similar. The assumption made earlier by Nishiyama (17), Philp (20) and McGinnis and Taylor (14) that the univalent chromosome is transmitted with equal frequency on male and female side was found to be correct insofar as Taylor's monosomic was concerned.

The influence of seed source on the monosomic transmission rate in three monosomic lines of chromosome 15

was noticeable. The monosomics produced from x-irradiation gave higher transmission rate than the monosomic obtained spontaneously. Perhaps many of the nullisomic zygotes are lethal because of other deleterious mutations caused by x-irradiation.

The study of 5 different monosomic lines of chromosome 21 again clearly indicated that the univalent transmission varies considerably between varieties. Although there also appeared to be a difference between lines within the same variety, this difference was found to be not significant by statistical analysis (paired t-test). This method of analysis however requires a large difference to reach the minimum level of significance. The transmission rates are quite similar in the two varieties Sun II and Condor, both having a high monosomic frequency (79 and 80% respectively). The Garry lines were much below this frequency of monosomic transmission. The Taylor's monosomic had the lowest transmission rate. The effect of genotype and its response to various environments must be an important factor in determining univalent transmission.

Oats appears to be a crop that is quite sensitive to minor variations of either environment or genotype. This could be additional evidence of considerable diploidization

in the species. Certainly the use of univalent transmission rates for indentifying different monosomics is unsafe by itself and at the best can be used only as a guide in identification.

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