

The Effects of Phosphate Treatments on Chromosome Pairing in Diploid and Autotetraploid Meadow Fescue (*Festuca pratensis* Huds.)

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Abstract: This study was carried out under greenhouse conditions in 1994-1995. The influence of phosphate treatments (0, 1, 2, 3 and 4g P₂O₅/pot) on meiotic chromosome pairing and the number of arms bound at the first metaphase (MI) in plants of diploid Senu variety of meadow fescue (*Festuca pratensis* Huds.) and its advanced generation (C₆) autotetraploid (Tetra Senu) were studied.

In diploids, quadrivalents and univalents frequencies showed no difference with changes in phosphate treatments. Total bivalent frequency per cell remained stable with phosphate changes in spite of a significant increase in the number of arms bound. With phosphate effect, however, a reduction in rod bivalent frequency and a parallel increase in ring bivalent frequency were observed. On the other hand, negative and significant correlation was found between ring bivalent frequency and univalent and quadrivalent frequencies whereas positive and significant correlation was found between the last two properties.

There was significant difference in ring bivalent frequency per cell between phosphate treatments in autotetraploids. In addition, positive and significant correlation was found between ring bivalent frequency and the number of arms bound whereas negative and insignificant association was found between the latter and quadrivalent frequency. Therefore, negative and significant correlation was found between ring bivalent frequency and quadrivalent frequency.

Diploid ve Autotetraploid Çayır Yumağında Kromozom Eşlenmesi Üzerine Fosfat Uygulamalarının etkisi

Özet: Bu araştırma 1994-1995 yıllarında sera koşullarında yürütülmüştür. Çayır yumağı (*F. pratensis* Huds.)'nin diploid Senu çeşidi ve onun ileri generasyonuna (C₆) ait autotetraploid bitkilerde metafaz I (MI)'deki kromozom eşlenmesi ve kol bağlantı sayısı üzerine fosfat uygulamalarının (0, 1, 2, 3 ve 4 g/saksı P₂O₅) etkisi incelenmiştir.

Diploidlerde, fosfat uygulamasındaki değişme ile birlikte quadrivalent ve univalent sıklıkları herhangi bir değişme göstermemiştir. Fosfat miktarındaki değişmelere bağlı olarak kromozom kol bağlantı sayısında önemli bir artış olmasına karşın hücre başına total bivalent sıklığı değişmemiştir. Bununla birlikte, fosfat miktarındaki artışa paralel olarak halka bivalent sıklığı artarken çubuk bivalent sıklığında bir azalma gözlenmiştir. Diğer taraftan, halka bivalent sıklığı ile univalent ve quadrivalent sıklıkları arasında olumsuz ve önemli ilişki olmasına karşın son iki özellik arasında olumlu ve önemli ilişki bulunmuştur.

Autotetraploidlerde, hücre başına halka bivalent sıklıkları yönünden fosfat uygulamaları arasında önemli farklılık olmuştur. Ayrıca, halka bivalentlerin sıklığı ve kromozom kol bağlantı sayısı arasında olumlu ve önemli ilişki bulunmasına karşın kromozom kol bağlantı sayısı ve quadrivalent sıklığı arasında olumsuz ve önemli ilişki bulunmuştur. Bu yüzden, halka bivalent sıklığı ile quadrivalent sıklığı arasında olumsuz ve önemli ilişki bulunmuştur.

Introduction

The development of the colchicine treatment as a means of producing polyploids has resulted in an increased interest in autotetraploid fodder cultivars during the past fifty years. One of the major breeding problems has been that of increasing the seed fertility in autotetraploid plants. Several attempts have been made to investigate the relationship between the seed fertility and the regularity of the meiosis in different crop species (1, 2, 3).

It is well known that chiasma frequency at meiosis varies in different environments (4) and there is a condirable literature describing the influence upon chiasma frequency of temperature changes (5), chemical treatments (6) and ionizing radiation treatments on chiasma formation (7). Again, it is shown that there is an influence of changes in mineral treatments upon chiasma frequencies and chiasma distributions with changes in levels of mineral elements in other researches (8, 9). Similarly, large induced changes in chromosome volume

and nuclear dry mass are demonstrated in root tip meristems of rye (10). Since there is always a certain variation in frequency of chromosome configurations per cell, it is interesting to note the effect of phosphate treatment on the between-cell variance. Any observed differences in the variance could be attributed solely to the treatment effects since all cells within a plant are genetically identical, so the variance would not be heritable (4). On the other hand, control of chiasma frequency can also be genetically determined as shown in barley (11). For all of these reasons, the extent of variation in chiasma frequency between cells within plants is determined in part by the genotype of the plant but also by environmental factors (5, 12).

Recent studies have shown that the average chiasma frequencies found in pollen mother cells of meadow fescue and rye plants are subject to the control of the genotype (3, 13, 14). It has also been reported that chiasma formation is not always independent in different bivalents, but may be correlated (12). On the other hand, high levels of phosphate increased chiasma frequency in two strains of diploid rye (9). It was considered worthwhile, therefore, to investigate the similar effects of phosphate treatments on chromosome pairing and the number of chromosome arms bound at MI in the advanced generation of autotetraploid meadow fescue and its representative diploid cultivar.

Material and Methods

The Characters of Experimental Soil

The soil mixture used in the research was prepared by mixing homogenously some and with the field soil taken from 0-20 cm depth. The samples taken from this soil mixture at random in 3 replications, were analyzed in Erzurum Village Services Research Institute.

The soil samples were analyzed with the following methods: for K 1N ammonium acetate, for P Sodium bicarbonate, for the amount of N Kjeldahl and for mechanical analyses Bouyoucos hydrometric method was used. Thus, the texture of trial soil was sandy-loam and is average pH 7.92 and N content 0.065% while available P_2O_5 amounted to 0.059 g/kg, available K_2O was 1.161 g/kg and proportion of lime was 3.07%.

Material

This study was carried out in the greenhouse of Agronomy Department of Agricultural Faculty, Atatürk University in 1994-1995. In this study, the Danish diploid cultivar Senu of meadow fescue (*Festuca pratensis* Huds.) and its advanced generation (C_6) of artificial autotetraploid (Tetra-Senu) plants were used (15).

For this study, clay pots were used and each pot was filled with air dried soil of about 4.600 g. Ammonium sulphate with 21% N and triple superphosphate with 42-44% P_2O_5 content were used as chemical fertilizers.

Methods

Experimental Treatments

Plants used in the trial were primarily grown in the wooden growth boxes. Then a single seedling was raised in each pot and one plant was randomly taken from in each ploidy level. Since it was intended to establish clones of individual genotype in the two ploidy levels, the plants were raised in the greenhouse for a longer period for vegetative growth and tillering. After reaching certain size, clones taken from the parent plants were transplanted into the pots one by one on March 28, 1994. Each clone had sufficient root system to establish itself when transplanted into individual pots. Clones of a large number of genotype were raised in this way for use in the experiment. In the first year, same amounts of N and P_2O_5 (3.0 and 2.3 g/pot respectively) were applied to all the plants and the whole phosphorus and the half of nitrogen were mixed with the soil in the pots during transplantation process. The remaining half of the nitrogen was applied at mid-summer, namely on August, 5, 1994. In the second year; in addition to 3.0 g N/pot year standart application, 0.0, 1.0, 2.0, 3.0 and 4.0 g/pot year P_2O_5 doses were in turn applied to all plants at random. The whole of P_2O_5 doses and the half of N were applied on March, 3, 1995. The remaining half of the N was applied in the beginning of anthesis period on May, 10, 1995. The plants were appropriately irrigated with tap water to keep the soil steadily at the field capacity level. Necessary attention was paid to the irrigation in order to prevent loss of water caused by drainage.

Cytological Observations

In each ploidy level, 20 clone plants which were taken from the same single genotype were grown under greenhouse conditions. The plants were kept in heated greenhouse in autumn and winter (from 10 October-1 March) and unheated ones under natural conditions for the rest of the year. Suitable inflorescences for meiotic studies were collected from each plant in each treatment and pickled in Carnoy solution for fixation for about two days. Then the inflorescence samples were transferred into 70% ethanol and kept in refrigerator until the time of study (4, 16). Following the fixation of the samples, slides were made by aceto-orceine squash method. One of the anthers was squashed and mounted in aceto-orceine solution of 2% (16, 17). Configurations of chromosome pairing and number of chromosome arms bound at MI

were determined from at least 20 pollen mother cells (PMC) in each plant (18).

Experimental Design and Analysis of Data

This experiment was arranged in a completely randomized design with 4 replications (19). The cytological investigations were made on samples which were taken from the plants in the second year of experiment. Data of diploid and tetraploid plants were separately analyzed according to the experimental design. The comparison of the mean values were made using Duncan test (19).

Results and Discussion

Chromosome Pairing In Diploid Meadow Fescue Quadrivalent and Univalent Frequencies

The mean frequencies of quadrivalents and univalents showed no difference with increasing phosphate levels

(Fig. 1 a,b). But, there was negative and insignificant correlation between the number of arms bound and quadrivalent frequency (Table 3). Therefore, it appears that the number of arms bound was not essentially correlated with quadrivalent frequency in diploid meadow fescue. Hossain (18) stated that chiasma frequency is not essentially correlated with quadrivalent frequency in autotetraploid rye. On the other hand, positive and significant correlation was observed between the number of arms bound and quadrivalent frequency (Table 3; $P < 0.05$).

Bivalent Frequency

There were no significant differences between the mean frequency of total bivalents under different phosphate treatments (Table 1) whereas there were significant differences in the mean frequency of ring bivalents (II) per cell between phosphate treatments (Table 1; $P < 0.05$, Fig. 1 c). Although the mean frequencies of rod bivalents (III) were highly reduced

P ₂ O ₅ Treat.	Plant Num.	Chromosome Configurations				Uni. I	No. Arms Bound**
		Quadri. IV	II *	III *	Total		
Cont.	1	–	5.20	1.80	7.00	–	12.20
	2	0.25	4.00	2.20	6.20	0.60	11.20
	3	–	4.60	2.40	7.00	–	11.60
	4	0.45	4.00	2.00	6.00	0.20	11.75
	Mean	0.18	4.45b	2.10a	6.55	0.20	11.69b
1	5	0.05	6.09	0.90	7.00	–	13.10
	6	–	6.00	1.00	7.00	–	13.00
	7	–	5.60	1.40	7.00	–	12.60
	8	0.50	3.95	2.00	5.95	0.10	11.85
	Mean	0.14	5.41ab	1.33ab	6.74	0.03	12.64ab
2	9	0.45	5.40	0.70	6.10	–	13.32
	10	–	5.90	1.10	7.00	–	12.90
	11	0.40	5.30	0.80	6.10	0.20	13.00
	12	–	5.70	1.30	7.00	–	12.70
	Mean	0.21	5.58ab	0.98b	6.55	0.05	12.98a
3	13	–	6.10	0.90	7.00	–	13.10
	14	–	5.50	1.50	7.00	–	12.50
	15	–	5.75	1.25	7.00	–	12.75
	16	–	6.85	0.15	7.00	–	13.85
	Mean	–	6.05a	0.95b	7.00	–	13.05a
4	17	0.30	5.60	0.70	6.30	0.20	12.95
	18	–	5.45	1.55	7.00	–	12.45
	19	0.05	6.09	0.90	6.99	–	13.10
	20	–	5.35	1.65	7.00	–	12.35
	Mean	0.09	5.62ab	1.20ab	6.82	0.05	12.71a

Table 1. Effects of Phosphate Treatments on Meiotic Features in Diploid Meadow Fescue Plants.

*, **: Indicate significance at the 0.05 and 0.01 level, respectively. Mean values within a column are not significantly different based on Duncan test.

under the phosphate treatments, the differences with the control were found to be significant (Table 1; $P < 0.05$). A reduction in rod bivalent and quadrivalent frequencies under the phosphate treatments with a parallel increase in ring bivalent indicates that phosphate treatments favoured ring bivalent formations at the expense of rod bivalents and quadrivalents (Fig. 1 d). According to this, negative and highly significant correlation was found, as expected, between frequencies of ring and rod bivalents. Again, there was negative and significant correlation between the frequency of total bivalents and those of quadrivalents and univalents (Table 2) and also between the frequencies of ring bivalents and the last two (Table 2). On the other hand, there was positive and insignificant correlation between rod bivalent frequency and quadrivalent and univalent frequencies (Table 2). A similar relationship between ring bivalent frequency and rod bivalent and univalent frequencies at MI cells in diploid barley in response to phosphate treatments was reported (4).

Chromosome Arms Bound

There were highly significant differences between the numbers of arms bound under the phosphate treatments

in diploid plants (Table 1; $P < 0.01$), the mean number of arms bound for the control being the lowest, as expected. It is noted that an increase in the phosphate available to the plant is accompanied by an increase in mean chiasma frequency in PMC in both diploid rye and barley materials, (9, 4). Again, concerning the mechanism by which this effect is produced, it is worth noting that there is a well established relationship between chromosome length and the number of chiasmata (20). It is not inconceivable, therefore, that the treatments inducing large chromosome size also directly promote high chiasma frequencies (9).

In diploid meadow fescue, there were more ring bivalent with two bounds instead of rod bivalents with one bound as a result of the increasing in chiasma frequency. A test in this regard showed that negative and highly significant correlation was found, as expected, between the frequencies of ring bivalents and rod bivalents and again between the former and quadrivalent frequencies at MI cells (Table 2; $P < 0.01$, $P < 0.01$). It was reported that similar relationships were found between cytological characteristics at first meiotic division in diploid barley (4).

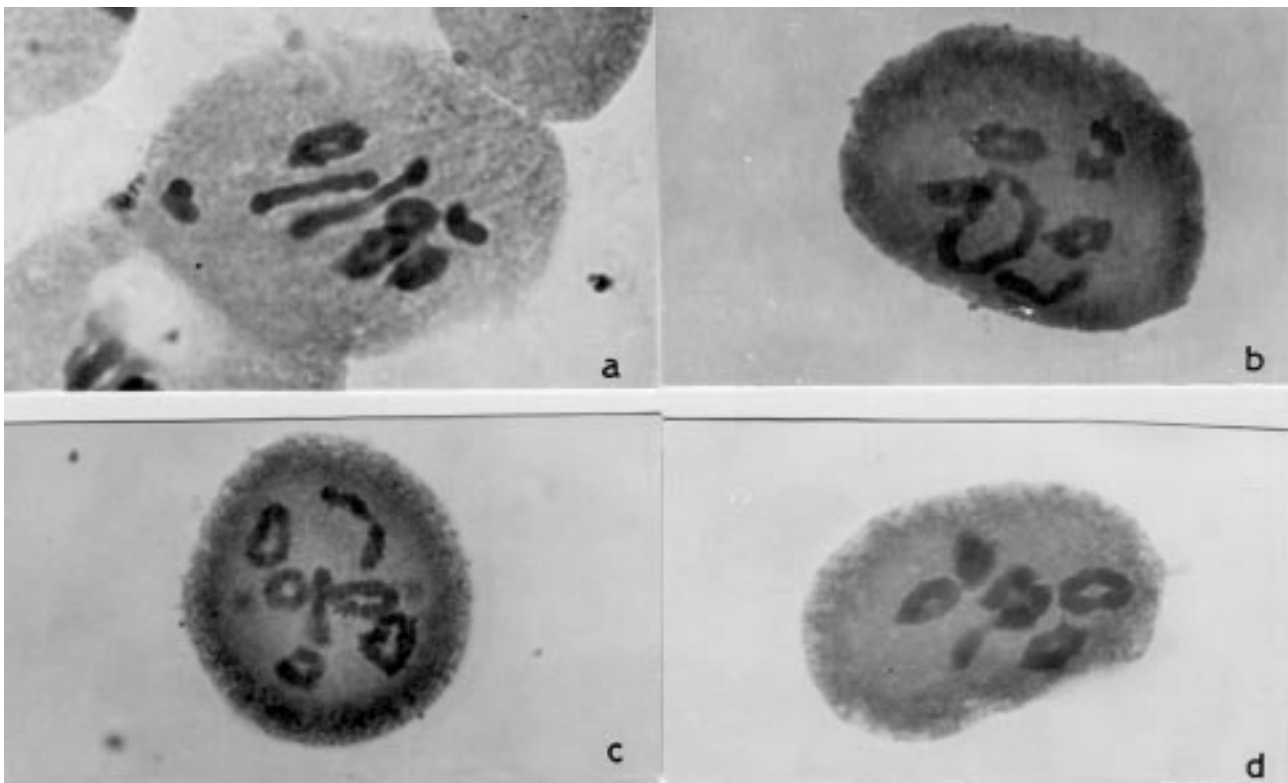


Figure 1. a, b, c, d. Chromosome pairings (a: $6_{II} + 2I$, b: $1_{IV} + 5_{II}$, c: 7_{II} showing 2 rod bivalents, d: 7_{II}) at MI of meiosis in the pollen mother cells of diploid meadow fescue (Enl.: 1000x).

Correlations	n	r	P \leq
Frequency of quadrivalents at MI cells with:			
frequency of ring bivalents	20	-0.609	0.01
frequency of rod bivalents	20	0.085	N.S.
frequency of total bivalents	20	-0.986	0.01
frequency of univalents	20	0.519	0.05
Number of chromosome arms bound with:			
frequency of quadrivalents at MI cells	20	-2.218	N.S.
frequency of ring bivalents at MI cells	20	0.901	0.01
frequency of rod bivalents at MI cells	20	-0.971	0.01
frequency of total bivalents at MI cells	20	0.303	N.S.
Frequency of univalents at MI cells with:			
frequency of ring bivalents	20	-0.598	0.01
frequency of rod bivalents	20	0.321	N.S.
frequency of total bivalents	20	-0.643	0.01
Frequency of ring bivalents at MI cells with:			
frequency of rod bivalents	20	-0.837	0.01
frequency of total bivalents	20	0.664	0.01

Table 2. Coefficients of Correlation Between Some Cytological Characteristics at MI in Diploid Meadow Fescue.

Chromosome Pairing In Eutetraploid Meadow Fescue

Quadrivalent Frequency

The mean frequency of quadrivalents showed no increase with increasing phosphate levels and variance analysis showed no significant difference between treatments (Table 3, Fig 2 a). The results further showed that under the control, the frequencies of total and rod bivalents increased significantly at the expense of quadrivalents. Again, negative and significant correlation was found between quadrivalent frequency and ring and total bivalent frequencies (Table 4; $P < 0.01$). On the other hand, there was negative and insignificant association between the number of arms bound and quadrivalent frequency (Table 4; $r = -0.255$). Similar results were found in diploid rye (9). Hossain (18) also reported that chiasma frequency is not essentially correlated with quadrivalent frequency in autotetraploid rye. The mean frequency of quadrivalents in individual genotypes within the same treatment group was, however, highly different (Table 3). It appears, therefore, that various genotypes differed in their response to phosphate treatments.

Bivalent Frequency

In eutetraploid plants, chromosome pairings mostly occurred in bivalent form and also there were changes in the mean frequencies of all bivalent configurations within the phosphate levels used (Table 3). It appears, therefore, that the various genotypes differed in their response to phosphate treatments. On the other hand, there were no

significant differences between the mean frequencies of total and also rod bivalents under the different phosphate treatments (Table 3) whereas there were significant differences in the mean frequency of ring bivalents per cell between phosphate treatment with a parallel reduction in quadrivalents indicates that phosphate treatment favoured ring bivalent formations at the expense of quadrivalents (Table 3; $P < 0.05$; Fig. 2 b). Therefore, there was negative and significant correlation between ring bivalent frequency and quadrivalent frequency (Table 4; $P < 0.01$). Again, negative and insignificant correlations were found between quadrivalent and rod bivalent frequencies and also between the latter and ring bivalent frequencies (Table 4; $r = -0.383$, $r = -0.114$). Consequently, there are two reasons for this correlation: First, the increase in quadrivalent frequency at the expense of rod bivalents primarily accounted for the increase in chiasma frequency. Second, as a result of the increase in chiasma frequency under the phosphate treatments, there were more ring bivalents with two bounds instead of rod bivalents with one bound. These results are in agreement with the findings reported earlier for both diploid barley and tetraploid rye materials (4, 18).

Univalent, Trivalent and Hexavalent Frequencies

The mean frequencies of univalents, trivalents and hexavalents showed no difference with increasing phosphate levels (Table 3). There was positive and significant correlation between frequency of univalents and trivalents (Table 4; $P < 0.01$, Fig. 2 c) whereas no

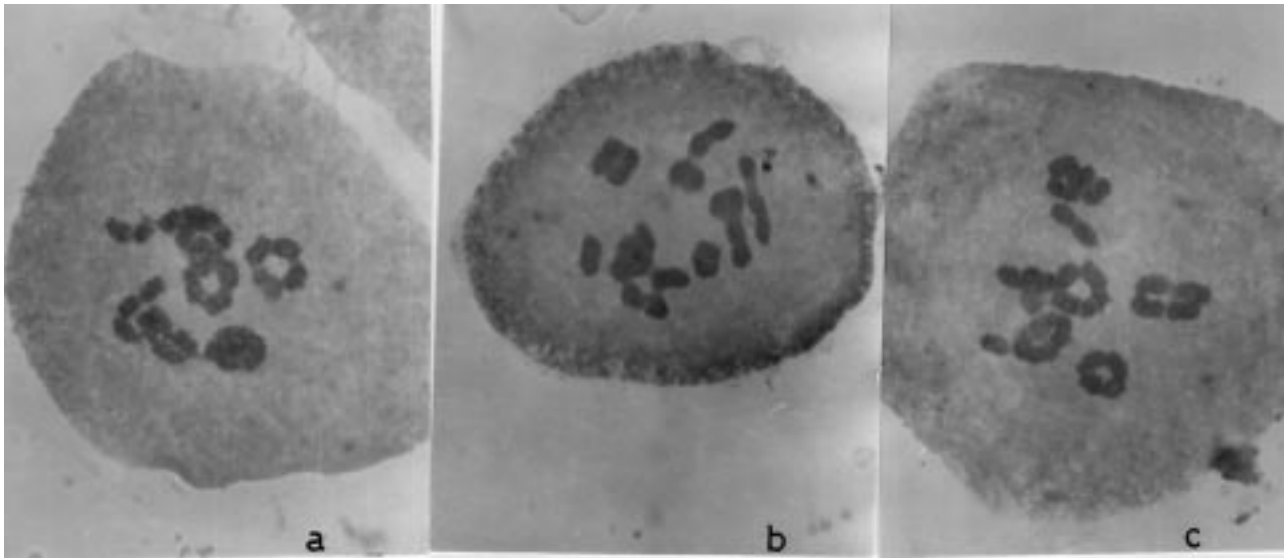


Figure 2. a, b, c. Chromosome pairings (a: 7_{IV}, b: 2_{IV} + 10_{II} showing 2 composite bivalents, c: 5_{IV} + 3_{II} + 2_I) at MI of meiosis in the pollen mother cells of tetraploid meadow fescue (Enl.: 1000x).

P ₂ O ₅ Treat.	Plant Num.	Chromosome Configurations							No.Arms Bound**
		Quadri. IV	Bivalent $\textcircled{\text{II}}^*$	Bivalent 	Total	Uni. I	Tri. III	Hexa. VI	
Cont.	1	2.35	5.30	4.00	9.30	-	-	-	22.80
	2	2.65	3.45	4.50	7.95	-	-	0.25	22.15
	3	2.50	5.00	4.00	9.00	-	-	-	22.00
	4	3.50	4.60	2.40	7.00	-	-	-	23.60
	Mean	2.75	4.59b	3.73	8.31	-	-	0.06	22.64b
1	5	4.35	3.30	1.30	4.60	0.35	0.35	-	21.65
	6	3.70	4.10	2.30	6.40	0.10	0.10	-	24.80
	7	3.15	3.90	2.80	7.70	-	-	-	24.15
	8	1.20	7.80	3.80	11.60	-	-	-	23.80
	Mean	3.100	5.03ab	2.55	7.58	0.11	0.11	-	23.60ab
2	9	1.65	6.45	4.25	10.70	-	-	-	23.50
	10	3.00	4.35	3.65	8.00	-	-	-	24.30
	11	3.75	3.35	3.15	6.50	-	-	-	23.60
	12	1.45	7.90	3.20	11.10	-	-	-	24.40
	Mean	2.46	5.46ab	3.56	9.08	-	-	-	23.95ab
3	13	2.60	5.80	1.80	7.60	-	-	0.40	26.60
	14	2.35	6.10	3.20	9.30	-	-	-	24.10
	15	3.20	4.80	2.80	7.60	-	-	-	24.40
	16	2.60	5.75	2.25	8.00	0.25	0.25	0.10	25.25
	Mean	2.69	5.61ab	2.51	8.13	0.06	0.06	0.13	25.09a
4	17	2.50	4.90	3.50	8.40	0.30	-	0.15	24.20
	18	1.25	8.40	2.90	11.30	0.25	0.05	-	24.70
	19	2.00	8.50	1.40	9.90	0.20	-	-	26.00
	20	2.50	7.00	2.00	9.00	-	-	-	25.50
	Mean	2.06	7.20a	2.45	9.65	0.19	0.01	0.04	25.10a

*, **: Indicate significance at the 0.05 and 0.01 level, respectively. Mean values within a column are not significantly different based on Duncan test.

Table 3. Effects of Phosphate Treatments on Meiotic Features in Autotetraploid Meadow Fescue Plants.

correlation was found between these and hexavalent frequency (Table 4). On the other hand, there was negative and insignificant correlation between the number of arms bound and trivalent frequency, but there was positive and insignificant correlation between the former and hexavalent frequency (Table 4; $r=0.258$). It appears that the numbers of arms bound were not essentially correlated with trivalent and hexavalent frequencies in autotetraploid meadow fescue. Similar relationship was found in autotetraploid rye (18).

Chromosome Arms Bound

The differences between phosphate treatments were highly significant (Table 3; $P<0.01$). However, the number of chromosome arms bound under the control treatment and first two phosphate levels were statistically similar (Table 3) but the mean number of arms bound for the control was slightly lower. The last two phosphate levels, as expected, increased the mean number of arms bound significantly than those of the other three treatments (Table; $P<0.01$). It is noticed that an increase in the phosphate available to the plant is accompanied by an increase in mean chiasma frequency in PMC in both diploid rye and barley materials (4, 9). Again, concerning the mechanism by which this effect is produced, it is worth noting that there is a well-established relationship between chromosome length and the number of chiasmata (20). It is not inconceivable, therefore, that the treatments inducing large chromosome size also directly promote high chiasma frequencies (9). The significant differences for the mean number of arms bound in the

different genotypes suggest that the genotypes differ in their response to phosphate treatments (Table 3). Similarly, it is reported that the genotypes differ in their response to nitrogen treatments in autotetraploid rye (18).

Conclusion

The results showed an effect on the numbers of arms bound and bivalent frequencies due to different phosphate treatments at both ploidy levels. The numbers of arms bound in the C_6 generation were lower than twice those of the diploids and the situation was thus the same as that found in several species by other researchers (2, 3, 17, 21). Most of the chromosomes showed bivalent pairings, especially ring ones, and quadrivalents at two ploidy levels (Tables 1, 3). It is important to note that the variation in the numbers of arms bound as a result of the different mineral treatments is normal. On the other hand, the frequency of bivalents per cell in the C_6 generation was higher than C_3 and especially C_0 generations (15, 16). It is clearly seen that this meiotic improvement was realised in MI with increase in bivalent frequency in spite of the decrease in quadrivalent and all other types of associations. Because, it is suggested that both bivalents and quadrivalents appear to be realistic alternatives for balanced gamet formations in so far as the chiasma frequency (18) or the number of arms bound remains unaffected. Meiotic improvement and thus an improvement in fertility of autotetraploids can be achieved

Correlations	n	r	P≤
Frequency of quadrivalents at MI cells with:			
frequency of ring bivalents	20	-0.852	0.01
frequency of rod bivalents	20	-0.383	N.S.
frequency of total bivalents	20	-0.980	0.01
frequency of univalents	20	0.110	N.S.
frequency of trivalents	20	0.423	N.S.
Number of chromosome arms bound with:			
frequency of quadrivalents at MI cells	20	-2.255	N.S.
frequency of ring bivalents at MI cells	20	0.526	0.05
frequency of rod bivalents at MI cells	20	-0.512	0.05
frequency of total bivalents at MI cells	20	0.209	N.S.
frequency of hexavalents at MI cells	20	0.258	N.S.
frequency of trivalents at MI cells	20	-0.197	N.S.
Frequency of ring bivalents at MI cells with:			
frequency of rod bivalents	20	-0.114	N.S.
frequency of total bivalents	20	0.852	0.01
Frequency of univalents at MI cells with:			
frequency of trivalents	20	0.700	0.01

Table 4. Coefficients of Correlation Between Some Cytological Characteristics at MI in Autotetraploid Meadow Fescue.

by increased frequency of bivalents or quadrivalents (2, 3, 17) However, it is suggested that quadrivalents are not associated with increased fertility, on the contrary bivalent frequency is related with fertility (18, 22, 23, 24). In addition, a bivalent formation is more easily and efficiently accomplished than the formation of a quadrivalent. Again, bivalents are less sensitive to environmental changes than quadrivalents, because environmental stress can reduce chiasma frequency in the PMC which affects quadrivalents (18).

It is not unreasonable to suggest that plant breeders should take advantage of the effects of minerals in altering chiasma frequencies and, hence, genetic recombination (4, 9). Although chiasma frequency was not determined in this study, it might be assumed that the increased numbers of arms bound observed were the result of increased chiasma frequencies induced by mineral treatments. It is suggested that through the use of mineral treatments, presumably chiasma frequency and also recombination can be altered markedly in autotetraploid meadow fescue genotypes.

References

1. Moore, K., The Influence of Climate on A Population Tetraploid Spring Rye, *Hereditas*, 49, 269-305, 1963.
2. Simonsen, Ø., Cytogenetic Investigations in Diploid and Autotetraploid Populations of *L. perenne* L., *Hereditas*, 70, 157-188, 1973.
3. Simonsen, Ø., Cytogenetic Investigations in Diploid and Autotetraploid Populations of *F. pratensis* Huds., *Hereditas*, 79, 73-108, 1975.
4. Fedak, G., Increased Chiasma Frequency in Desynaptic Barley in Response to Phosphate Treatments, *Can. J. Genet. Cytol.*, 15, 647-649, 1973.
5. Dowrick, G.J., The Influence of Temperature on Meiosis, *Heredity*, 11, 37-49, 1957.
6. Barber, H.N., The Suppression of Meiosis and The Origin of Diplochromosomes, *Proc. Roy. Soc. (London)* B128, 170-185, 1940.
7. Lawrence, C.W., The Effect of The Irradiation of Different Stages in Microsporogenesis on Chiasma Frequency, *Heredity*, 16, 83-89, 1961.
8. Law, C.N., Effects of Potassium on Chiasma Frequency and Recombination, *Genetica*, 33, 313-329, 1963.
9. Bennett, M.D. and Rees, H., Induced Variation in Chiasma Frequency in Rye in Response to Phosphate Treatments, *Genet. Res. Camb.*, 16, 325-331, 1970.
10. Bennett, M.D. and Rees, H., Induced and Development Variation in Chromosomes of Meristematic Cells, *Chromosoma*, 27, 226-244, 1969.
11. Enns, H. and Larter, E.N., Note on The Inheritance of ds: a Gene Governing Meiotic Chromosome Behavior in Barley, *Can. J. Plant Sic.*, 40, 570-571, 1960.
12. Elliott, C.G., Environmental Effects on The Distribution of Chiasmata Among Nuclei and Bivalents and Correlation Between Bivalents, *Heredity*, 12, 429-439, 1958.
13. Rees, H., Genotypic Control of Chromosome Behaviour in Rye. I. Inbred Lines, *Heredity*, 9, 93-116, 1955.
14. Rees, H. and Thompson, J.B., Genotypic Control of Chromosome Behaviour in Rye. III. Chiasma Frequency in Homozygotes and Heterozygotes, *Heredity*, 10, 409-424, 1956.
15. Deniz, B., Inducing Artificial Tetraploids From Diploid Meadow Fescue (*Festuca pratensis* Huds.) Varieties and The Investigation of Some Meiotic Characteristics of Them. *Plant Aging. Basic and Applied Approaches. Series A: Life Sciences*, Vol.: 186, Plenum, 411-415, 1990.
16. Deniz, B., Investigation of Meiotic Behaviour in Diploid and Eutetraploid Meadow Fescue. NATO ASI Seminar on Plant Morphogenesis. Molecular Approaches, Paper Abstracts, P.117, held in Heraklio, Crete, Greece, 5-17 September 1992.
17. Hazarika, M.H., and Rees, H., Genotypic Control of Chromosome Behaviour in Rye. X Chromosome Pairing and Fertility in Autotetraploids, *Heredity*, 22, 317-332, 1967.
18. Hossain, M. Gul, Effects of External Environmental Factors on Chromosome Pairing In Autotetraploid Rye, *Cytologia*, 43, 21-34, 1978.
19. Yıldız, N. and Bircan, H., Araştırma ve Deneme Metodları, Ders Kitabı, Atatürk üniversitesi Ziraat Fakültesi Yayınları No: 305, 277, Erzurum, 1991.
20. Mather, K., Crossing Over, *Biological Reviews*, 13, 252-292, 1938.
21. Deniz, B., Meiotic Regularity in Diploid and Eutetraploid Meadow Fescue, *Tr. J. of Agriculture and Forestry*, 21, 565-572, 1997.
22. Hilpert, G., effects of Selection for Meiotic Behaviour in Autotetraploid Rye, *Hereditas*, 43, 318-321, 1957.
23. McCollum, G.D., Comparative Studies of Chromosome Pairing in Natural and Induced Tetraploid *Dactylis*, *Chromosoma (Berl.)*, 9, 571-605, 1958.
24. Aastveit, K., Variation and Selection for Seed-Set in Tetraploid Rye, *Hereditas*, 60, 294-315, 1968.