

Chromosome Association in Allotetraploid Interspecific Hybrid Ryegrass and Parental Species

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Abstract: This study was carried out in glasshouse conditions in summer 2000. Metaphase I (MI) chromosome association and numbers of chromosome arms bound were studied in autotetraploid perennial (*Lolium perenne* L.) and annual ryegrass (*Lolium multiflorum* Lam.) and their interspecific hybrid plants (*Lolium hybridum*). In addition, the relationships among different cytological characteristics with respect to meiotic regularity were determined. Chromosome associations at MI were often regular in the parent species and hybrid ryegrass plants however different pairing irregularities were found to be higher in perennial and especially in hybrid ryegrass plants than in the annual ryegrass plant genotypes. Total bivalent pairing at MI were 5.820, 6.324 and 7.009 per cell and total quadrivalent pairings were 4.082, 3.825 and 3.339 in perennial, annual and hybrid ryegrasses, respectively. The difference was significant between annual ryegrass and hybrid ryegrass in terms of the frequency of ring quadrivalents at MI. All other types of chromosome associations showed no difference statistically between the parent species and hybrid ryegrass. In each ryegrass species, there were negative and significant correlations among the frequency of total quadrivalents and those of total and rod bivalents. The number of chromosome arms bound was lower in the allotetraploid hybrid ryegrass than in the parent species. The difference was significant between hybrid ryegrass and the parent species in terms of the same characteristic. On the other hand, there were positive and significant correlations among the number of chromosome arms bound and the frequency of ring quadrivalents, whereas negative and significant correlations were found among the former and those of rod bivalents in each ryegrass species, too. The allotetraploid interspecific hybrids of perennial and annual ryegrass are easily produced and also fertile. Again, sufficient cytological stability in the hybrid plants conserves the integrity of the constituent genomes, resulting in regular chromosome association.

Key Words: Interspecific hybrid, Hybrid ryegrass, Chromosome association

Allotetraploid Türlerarası Melez Çim ve Ebeveyn Türlerinde Kromozom Eşleşmesi

Özet: Bu araştırma sera koşullarında 2000 yılı yazında yürütülmüştür. Araştırmada, autotetraploid çok yıllık çim (*L. perenne* L.), tek yıllık çim (*L. multiflorum* Lam.) ve bunların türlerarası melez (*L. hybridum*) bitkilerinde MI kromozom eşleşmesi ve kromozom kol bağlantı sayısı incelenmiştir. Ayrıca, meiotik düzenlilik yönünden farklı hücrel özellikler arasındaki ilişkiler belirlenmiştir. Ebeveyn tür ve melez çim bitkilerinde MI kromozom eşleşmesi sıklıkla düzenli olmakla birlikte farklı eşleşme düzensizlikleri çok yıllık ve özellikle melez çim bitkilerinde tek yıllık çim bitki genotiplerinden daha yüksek bulunmuştur. Çokyıllık, tekyıllık ve melez çimde MI'de hücre başına toplam bivalent eşleşmeler sırasıyla 5.820, 6.324 ve 7.009 ve toplam quadrivalent eşleşmeler 4.082, 3.825 ve 3.339 olmuştur. MI'deki halka quadrivalentlerin sıklığı yönünden tek yıllık çim ve melez çim arasındaki fark önemli olmuştur. Kromozom eşleşmelerinin diğer tüm tipleri ebeveyn türler ve melez çim arasında istatistiksel olarak farklılık göstermemiştir. Her üç çim türünde, toplam quadrivalentlerin sıklığı ile toplam ve çubuk bivalentlerin sıklıkları arasındaki ilişki olumsuz ve önemli olmuştur. Kromozom kol bağlantı sayısı allotetraploid melez çimde ebeveyn türlerdekinden daha düşük olmuştur. Bu özellik yönünden melez çim ve ebeveyn türler arasındaki fark önemli olmuştur. Diğer taraftan, kromozom kol bağlantı sayısı ve halka quadrivalentlerin sıklıkları arasındaki ilişki her üç çim türünde de olumlu ve önemli olmasına karşın önceki özellik ve çubuk bivalentlerin sıklığı arasındaki ilişki olumsuz ve önemli bulunmuştur. Çok yıllık ve tek yıllık çimin allotetraploid türlerarası melezleri hem döllek ve hem de kolaylıkla üretilmektedir. Yine melez bitkilerdeki yeterli hücrel kararlılık düzenli meiosis doğuran öge genomların bütünlüğünü korumaktadır.

Anahtar Sözcükler: Türlerarası melez, Melez çim, Kromozom eşleşmesi

Introduction

The role of interspecific hybridization in plant evolution is well known (Stebbins, 1950). The origin of several domesticated crop species is based on interspecific hybrids combined with polyploidy. These species owe their importance to the successful combination of desirable features from two or more progenitors. As plant breeders have exhausted the variability in a species, or as they have sought some character not present in it, they have turned to crosses between species. Where the parental species have been widely different, the achievement of a hybrid has been an exciting event. In this process, it was not until sex was recognized in plants that any planned and significant progress was made in exploring the possibilities of interspecific hybrids (Briggs and Knowles, 1967).

Tetraploid hybrids are used on the assumption that corresponding diploid hybrids, although fertile, would show extensive transgressive segregation in advanced generations and could therefore not be managed as commercial varieties. It is argued that allotetraploid hybrids would be genetically more stable on account of their tetrasomic inheritance, reinforced by some preferential pairing of homologous chromosomes (Breese et al., 1981).

The diploid interspecific hybrids have chromosome pairing almost as good as that of the parental species (Jauhar, 1975). Homoeologous chromosome pairing in diploid F1 hybrids is normally complete, univalents being rarely seen at MI (Jauhar, 1975; Breese et al., 1981; Aung and Evans, 1985). Chiasmate association of homoeologous chromosomes must also occur in the tetraploids, in view of the substantial number of quadrivalents and trivalents that are readily seen at MI (Evans and Macefield, 1974; Clarke and Thomas, 1976; Lewis, 1980). However, there is evidence of some preferential pairing of homologous chromosomes (Breese and Thomas, 1977).

In common with many other synthetic allopolyploids, tetraploid hybrids between perennial and annual ryegrass (*L. perenne*, *L. multiflorum*) show some multivalent association at meiosis, indicating the occurrence of homoeologous as well as homologous chromosome pairing. Further homoeologous pairing must also occur in the form of heterogenetic bivalents (Lewis, 1980). Moreover, as homoeologous chromosome pairing results in recombination between the two *Lolium* species

genomes, there must be a gradual dissipation of interspecific hybridity through consecutive seed generations. The extent to which this occurs is clearly of great significance in a breeding context since the very desirable combination of agronomic features obtainable in the initial hybrids (Breese and Davies, 1975; Lewis, 1980) is based on several contrasting parental characteristics (Lewis, 1980).

Tetraploid interspecific hybrids were found to have significantly higher levels of bivalent frequency, and lower levels of multivalent frequency at MI. In addition, it is suggested that the differences in chromosome associations between the tetraploid hybrid and tetraploid perennial ryegrass must therefore reflect differences in chiasma distribution, and the results indicate a significant degree of preferential bivalent pairing in the hybrids (Lewis, 1980).

The material described in this paper is an allotetraploid hybrid between autotetraploid annual and perennial ryegrass, which are two important forage species of temperate grassland, each possessing distinctive agronomic features. The chromosome pairing and the number of chromosome arms bound at MI are discussed in allotetraploid hybrids and in parental species. In addition, the relationships were determined among different cytological characteristics with respect to meiotic regularity.

Material and Methods

Material

The study was carried out in the glasshouse of the Agronomy Department, Agricultural Faculty, Atatürk University, in summer 2000. Commercial cultivars of induced autotetraploid perennial ryegrass (*Lolium perenne* L. cv peramo, $2n=28$) and annual ryegrass (*Lolium multiflorum* Lam. cv Multimo, $2n=28$) and their allotetraploid interspecific hybrid ryegrass (*Lolium hybridum*, F1s, $2n=28$) were used. The seeds of parent cultivars were obtained from Ulusoy Seed Co. in the 1990's, and the hybrids (*L. perenne* x *L. multiflorum*) were obtained in summer 1997.

Methods

Both the parent and tetraploid hybrid plants were grown from seeds in wooden boxes, and the seedlings were transplanted into small earthen pots ($\varnothing 15$ cm) one

by one. They were placed in pots full of mould and then allowed to grow to a proper size for mitotic chromosome counting.

The eutetraploid plants of parent species and their interspecific hybrids which were used in the study of meiotic behaviour were grown in earthen pots of larger size (Ø20 cm). From each group, 65 plants were grown and kept under glasshouse conditions. Subsequent confirmation and detailed meiotic information were obtained from microsporocytes, and inflorescence samples were randomly taken from 15 plants in each group. The samples were picked at about the beginning of emergence from the flag leaf sheath, and pickled in Carnoy solution for fixation. Then the samples were kept in 70% ethanol in a refrigerator for several months (Deniz, 1992). Slides were made by the aceto-orceine squash method. One of anthers was squashed and mounted in 2% aceto-orceine (Hazarika and Rees, 1967). Chromosome behaviour at MI was determined in 25 pollen mother cells (PMCs) in each plant.

Experimental Design and Analysis of Data

This experiment had a completely randomized design (Yıldız and Bircan, 1991). Three species and 15 replications (plant genotypes) in each plant species were used in the study. Data of the interspecific hybrid and parent species were subjected to variance analysis according to the experimental design. The significant differences among the mean values were compared by using the LSD test (Yıldız and Bircan, 1991). The relationships among some cytological characteristics were determined according to simple linear correlation analysis.

Results and Discussion

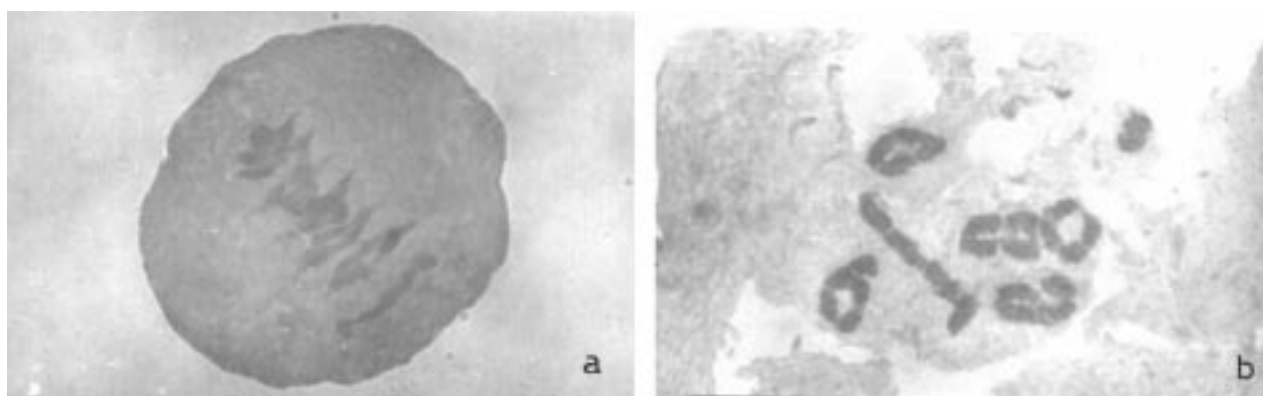
Mitotic Chromosome Numbers In Ryegrass Species

The somatic chromosomes of the plants of the parents were counted at the beginning of mitotic metaphase of the root-tip cells, and then were used in interspecific hybridization. The mitotic chromosomes of all plants from the three ryegrass species used in the meiotic study, were also initially counted. Both the parents and the hybrid plants were eutetraploid and had the expected $2n=28$ chromosomes.

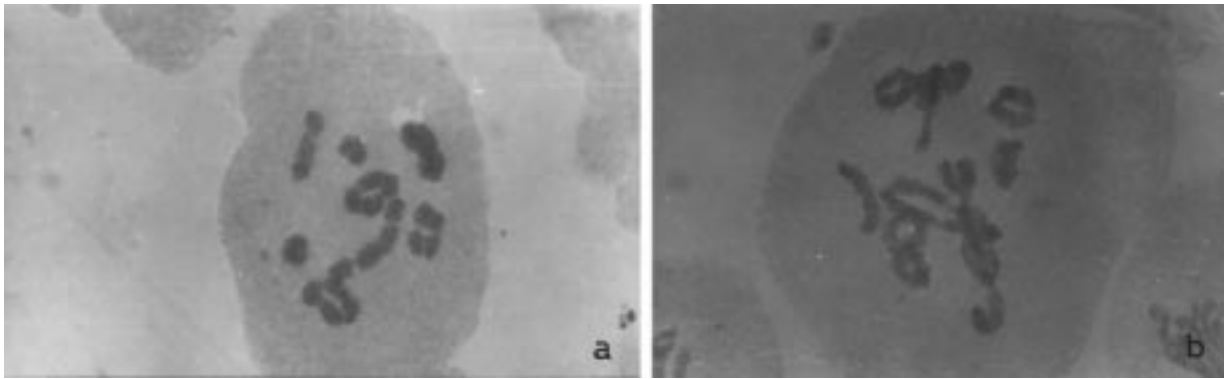
Chromosome Associations at MI in Ryegrass Species

Quadrivalent Frequency

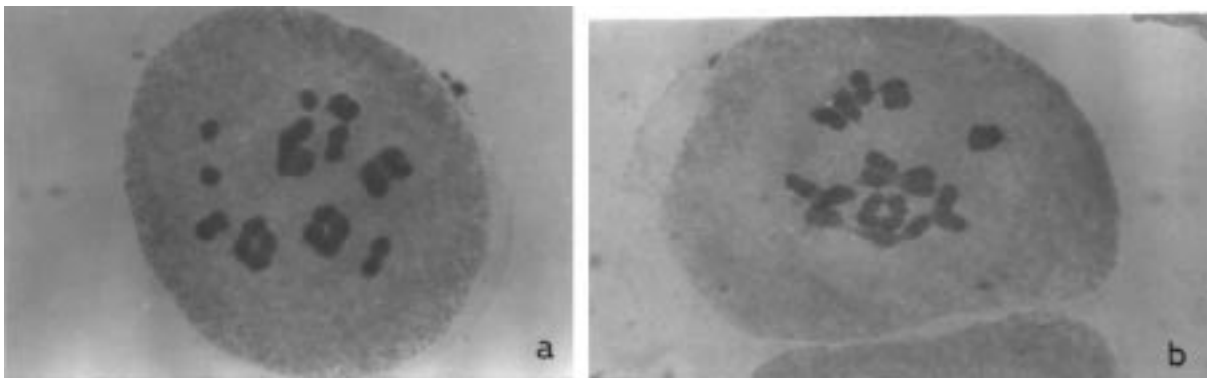
The mean frequencies of total and open quadrivalents ([IV]) showed no difference in the three *Lolium* species. Most of the chromosomes paired as quadrivalents at MI in the parental species (Figs. 1a, 2a). The average numbers of total quadrivalents were 4.087 and 3.825 per cell in perennial and annual ryegrass species, respectively. However, there were significant differences among the species in the mean frequency of ring quadrivalents (Table 1). Thus, the mean frequency of ring quadrivalents (ⓈIV) was highly reduced in the hybrid ryegrass, and the difference between it and the annual ryegrass was found to be significant (Table 1; Figs. 3a, b). A reduction in ring quadrivalent frequencies in the hybrid ryegrass with a parallel increase in rod bivalents indicates that the hybrid ryegrass formed rod bivalent associations at the expense of ring quadrivalents at MI (Tables 1 and 2). Similar results



Figs. 1 a, b. Chromosome associations (a: 6 ⓈIV + 1 IV , b: 3 ⓈIV + 2 IV + 1 II + 1 VI) showing two frying-pan and one linear open quadrivalents) at MI of meiosis in the PMCs of autotetraploid perennial ryegrass (Enl.: 1000x).



Figs. 2 a. b. Chromosome associations (a: 4 (IV) + 2 (IV) + 2 (II) , b: 2 (IV) + 7 (II) + 3 (III) showing three ring bivalents and one ring and one chain quadrivalents) at MI of meiosis in the PMCs of autotetraploid annual ryegrass (Enl.: 1000x).



Figs. 3 a.b. Chromosome associations (a: 4 (IV) + 5 (II) + 2 (IV) , b: 1 (IV) + 4 (II) + 8 (III) showing two compose ring and five compose rod bivalents) at MI of meiosis in the PMCs of interspecific hybrid ryegrass (Enl.: 1000x).

Table 1. The Frequencies of Chromosome Pairing (Mean and Range) and Chromosome Arms Bound at MI Per PMC in Autotetraploid Perennial and Annual Ryegrass and Allotetraploid Hybrid Ryegrass.

Species	Chromosome Associations									No. Arms Bound
	Quadrivalent			Bivalent			Univ.	Triv.	Hexav.	
	(IV)	(IV)	Total	(II)	(III)	Total	I	III	VI	
<i>L. perenne</i>	2.299 ab*	1.783	4.082	3.432	2.388	5.820	0.045	0.027	0.005	23.813 a*
	(2-4)	(1-3)	(2-6)	(2-7)	(0-5)	(3-10)	(0-2)	(0-1)	(0-1)	(21.2-26.0)
<i>L. multifl.</i>	2.368 a	1.457	3.825	3.717	2.607	6.324	0.005	0.005	0.005	23.912 a
	(2-5)	(0-3)	(2-7)	(2-7)	(0-4)	(3-9)	(0-2)	(0-1)	(0-1)	(21.3-26.2)
<i>L. hybridum</i>	1.783 b	1.556	3.339	3.972	3.037	7.009	0.059	0.037	0.015	23.131 b
	(2-5)	(0-4)	(1-4)	(2-10)	(0-7)	(6-12)	(0-1)	(0-1)	(0-1)	(20.6-26.0)
Gen.Mean	2.150	1.599	3.773	3.707	2.677	6.365	0.036	0.023	0.008	23.619

*Means with the same letter are not statistically different according to LSD test at P ≤ 0.01.

Correlations	n	r	P ≤
Frequency of total quadrivalents at MI with:			
frequency of ring quadrivalents	15	0.677	0.01
frequency of open quadrivalents	15	0.476	N.S.
frequency of rod bivalents	15	-0.719	0.01
frequency of total bivalents	15	-0.964	0.01
frequency of univalents	15	-0.086	N.S.
frequency of hexavalents	15	-0.465	N.S.
Frequency of rod bivalents at MI with:			
frequency of ring bivalents	15	-0.451	N.S.
frequency of total bivalents	15	0.717	0.01
frequency of open quadrivalents	15	-0.012	N.S.
frequency of ring quadrivalents	15	-0.782	0.01
Frequency of univalents at MI with:			
frequency of trivalents	15	0.747	0.01
Frequency of ring quadrivalents at MI with:			
frequency of open quadrivalents	15	-0.322	N.S.
Number of chromosome arms bound with:			
frequency of total quadrivalents	15	0.607	0.05
frequency of ring quadrivalents	15	0.774	0.01
frequency of open quadrivalents	15	-0.164	N.S.
frequency of ring bivalents	15	0.712	0.01
frequency of rod bivalents	15	-0.878	0.01
frequency of total bivalents	15	-0.524	0.05
frequency of hexavalents	15	0.104	N.S.

Table 2. Correlations Among Some Cytological Characteristics at MI in Autotetraploid Perennial Ryegrass.

Correlations	n	r	P ≤
Frequency of total quadrivalents at MI with:			
frequency of ring quadrivalents	15	0.943	0.01
frequency of open quadrivalents	15	0.872	0.01
frequency of ring bivalents	15	-0.871	0.01
frequency of rod bivalents	15	-0.841	0.01
frequency of total bivalents	15	-0.947	0.01
frequency of univalents	15	-0.513	N.S.
frequency of trivalents	15	-0.513	N.S.
frequency of hexavalents	15	0.392	N.S.
Frequency of rod bivalents at MI with:			
frequency of ring bivalents	15	0.614	0.05
frequency of total bivalents	15	0.808	0.01
frequency of open quadrivalents	15	-0.595	0.05
frequency of ring quadrivalents	15	0.841	0.01
Frequency of univalents at MI with:			
frequency of trivalents	15	1.000	0.01
Frequency of ring quadrivalents at MI with:			
frequency of open quadrivalents	15	0.659	0.01
frequency of ring bivalents	15	-0.871	0.01
Number of chromosome arms bound with:			
frequency of total quadrivalents	15	0.365	N.S.
frequency of ring quadrivalents	15	0.552	0.05
frequency of open quadrivalents	15	0.011	N.S.
frequency of ring bivalents	15	-0.106	N.S.
frequency of rod bivalents	15	-0.808	0.01
frequency of total bivalents	15	-0.377	N.S.
frequency of hexavalents	15	0.459	N.S.
frequency of trivalents	15	0.447	N.S.

Table 3. Correlations Among Some Cytological Characteristics at MI in Autotetraploid Annual Ryegrass.

were found in autotetraploid perennial ryegrass (Myers, 1941, 1945; Crowley and Rees, 1968; De Roo, 1968; Sağsöz, 1976; Breese et al., 1981).

Bivalent Frequency

Chromosome association at MI frequently occurred in bivalent pairing type in these ryegrass species, and there were no differences among all the three in the mean frequencies of various bivalent configurations (Table 1; Figs. 1b, 2b). It appears, therefore, that the various species differed in terms of chromosome associations at MI. In almost all hybrid ryegrass, cells with an average of 7.009 bivalents were observed, and generally more ring (Ⓐ) bivalents than rod (Ⓒ) ones were seen in some hybrids, or vice versa (Figs. 3a, b). Thus, the highest mean frequencies of ring and rod bivalents were found in the hybrid ryegrass, 3.972 and 3.037, respectively (Table 1). The variance analysis showed no significant difference between the mean frequencies of all bivalent types in three ryegrass species (Table 1). Thus, an increase in total bivalent frequency in hybrid ryegrass with a parallel reduction in total quadrivalent frequency

indicates that the hybrid ryegrass formed bivalent configurations at the expense of quadrivalent associations (Tables 1,4). There are two reasons for this relationship: First, the increase in the frequencies of bivalent configuration at the expense of quadrivalent formations primarily accounted for the number of homologous chromosomes in the allotetraploid hybrid ryegrass. Second, as a result of the reduction in chiasma frequency between homoeologous chromosomes originating from different ryegrass species, there were more preferential bivalent formations than allosyndetic quadrivalent configurations. These results are in agreement with the findings reported earlier for allotetraploid hybrids and the parent ryegrass materials (De Roo, 1968; Sağsöz, 1976; Lewis, 1980; Breese and Lewis, 1981; Kleijer, 1984; Aung and Evans, 1985).

Univalent, Trivalent and Hexavalent Frequencies

The mean frequencies of univalents, trivalents and hexavalents showed differences between the ryegrass species, but variance analysis showed no significant difference between the three species (Table 1). On the

Correlations	n	r	P ≤
Frequency of total quadrivalents at MI with:			
frequency of ring quadrivalents	15	0.622	0.01
frequency of open quadrivalents	15	0.777	0.01
frequency of rod bivalents	15	-0.662	0.01
frequency of total bivalents	15	-0.991	0.01
frequency of univalents	15	-0.167	N.S.
Frequency of total bivalents at MI with:			
frequency of ring bivalents	15	0.716	0.01
frequency of open quadrivalents	15	-0.570	0.05
frequency of ring quadrivalents	15	-0.805	0.01
Frequency of univalents at MI with:			
frequency of trivalents	15	0.725	0.01
Frequency of ring bivalents at MI with:			
frequency of open quadrivalents	15	-0.892	0.01
Number of chromosome arms bound with:			
frequency of total quadrivalents	15	0.196	N.S.
frequency of ring quadrivalents	15	0.801	0.01
frequency of open quadrivalents	15	-0.326	N.S.
frequency of ring bivalents	15	0.545	0.05
frequency of rod bivalents	15	-0.791	0.01
frequency of total bivalents	15	-0.138	N.S.
frequency of hexavalents	15	0.319	N.S.
frequency of trivalents	15	-0.340	N.S.

Table 4. Correlations Among Some Cytological Characteristics at MI in Autotetraploid Hybrid Ryegrass.

other hand, the three types of irregularities at MI appeared to be higher in interspecific tetraploid ryegrass, and these univalents and multivalents were found to be lower in autotetraploid annual ryegrass than in autotetraploid perennial ryegrass (Table 1). It appears that an increase in either of the frequencies of univalent and trivalent configurations would be associated with decreased chromosome arms bound. The situation was thus the same as in those found in allotetraploid hybrid ryegrass and the parent species (De Roo, 1968; Jauhar, 1975; Sağsöz, 1976; Lewis, 1980; Kleijer, 1984).

Chromosome Arms Bound

The mean number of chromosome arms bound was higher in the parent species than in the allotetraploid hybrid ryegrass. Therefore, there were significant differences in the mean number of arms bound among the parent species and interspecific hybrid ryegrass (Table 1). The significant differences for the mean number of arms bound in different ryegrass species suggest that the genotypes of different *Lolium* species differ in their chromosome homology in the homologous chromosomes. It is not inconceivable, therefore, that the high homology inducing synapsis in homologous chromosomes also directly promotes high chiasma frequencies and chromosome arms bound. Thus, concerning the mechanism by which this effect is produced, it is worth noting that there is a well established relationship between chromosome homology and the number of chromosome arms bound. Similar results have been found in the first meiotic division in different species (Kleijer, 1984; Kleijer and Morel, 1987; Deniz and Tufan, 1997).

Relationships Among Meiotic Characteristics

In perennial ryegrass, there were negative and significant correlations ($r = -0.964$; $r = -0.719$) among the frequency of total quadrivalents and those of total and rod bivalents, and the coefficients of correlations were highly significant (Table 2). Positive and significant correlations ($r = 0.607$; $r = 0.774$) were found among the number of chromosome arms bound and those of total and ring quadrivalents. On the other hand, there was a positive and significant correlation ($r = 0.712$) between the number of arms bound and the frequency of ring bivalents but negative and significant correlations ($r = -0.524$; $r = -0.878$) were found among the former and

those of total and rod bivalents (Table 2). These relationships indicate that MI cells with ring bivalents and quadrivalents produce regular meiosis in that process. In contrast, univalent and multivalent configurations cause irregular meiosis, lowering the number of arms bound. Therefore, there was a positive and significant correlation ($r = 0.747$) between the frequency of univalents and that of trivalents at MI (Table 2). Some researchers (Kleijer, 1984, 1987; Kleijer and Morel, 1987; Deniz, 1997; Deniz and Tufan, 1997) have reported similar relationships between some cytological characteristics at the first meiotic division.

In annual ryegrass, negative and significant correlations ($r = -0.871$; $r = -0.841$; $r = -0.947$) were found among the frequency of total quadrivalent types and those of all bivalent types (Table 3). On the other hand, there was a positive and significant correlation ($r = 0.801$) between the number of chromosome arms bound and the frequency of ring quadrivalents, whereas there was a negative and significant correlation ($r = -0.791$) between the former and that of rod bivalents (Table 3). Thus, the expected increase in the frequency of ring bivalents parallel with the decrease in the frequency of cells with ring quadrivalents at MI was evident, while the increase in the number of chromosome arms bound with the decrease in that of rod bivalents at MI was ascertained. The findings are in agreement with those reported previously by some researchers (Kleijer, 1984, 1987; Kleijer and Morel, 1987; Deniz and Tufan, 1997).

In interspecific hybrid ryegrass, negative and significant correlations ($r = -0.662$; $r = -0.991$) were found among the frequency of total quadrivalents and those of rod and total bivalents (Table 4). On the other hand, there were positive and significant correlations ($r = 0.545$; $r = 0.801$) among the number of chromosome arms bound and the frequencies of ring bivalents and quadrivalents, while a negative and significant correlation ($r = -0.791$) was found between the former and that of rod bivalents (Table 4). These relationships indicate, therefore, that chromosome associations at MI are not independent of one another. The situation was thus the same as findings reported by other researchers in several species and intergeneric and hybrid ryegrass (Kleijer, 1984, 1987; Kleijer and Morel, 1987; Deniz, 1997; Deniz and Tufan, 1998).

Conclusion

The pattern of chromosome pairing at metaphase would, of course, depend upon the effectiveness of chromosome pairing at pachytene and subsequently upon chiasma formation. Thus metaphase I chromosome associations were generally regular and most chromosomes showed predominantly ring bivalent and quadrivalent configurations at that stage of first meiotic division in three ryegrass species. Similar results were found in the number of chromosome arms bound in these ryegrass species, but the differences were significant between the hybrid ryegrass and the parent species in terms of the number of arms bound (Table 1). Thus, it is possible that the regularity of chromosome associations and cytological stability were higher in the parent species, especially in annual ryegrass, than in the allotetraploid interspecific ryegrasses. It is clear that regular chromosome pairing and cytological stability were

realised at MI with an increase in the frequencies of bivalents and quadrivalents, especially ring ones, in spite of the decrease in the frequencies of univalents and multivalents.

All natural allopolyploids have achieved regular meiosis, in which chromosome pairing is confined to identical pairs. It is reported, however, that sufficient stability for commercial seed multiplication is achieved in some hybrids through tetrasomic inheritance reinforced by preferential pairing between corresponding chromosomes (Thomas and Humphreys, 1991). Thus meiotic regularity conserves the integrity of the constituent genomes, resulting in diploid-like chromosome pairing and disomic inheritance. Consequently, these two species are closely related phylogenetically, having possibly evolved from a common progenitor (Jauhar, 1975). This is also further borne out by their complete inter-fertility.

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