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Review Articles

Arrangement of Chromosomes in the Interphase Nucleus of Plants*

Lydia Avivi and Moshe Feldman

[1]Sackler Medical School, Tel-Aviv University, Ramat-Aviv, Israel
[2]Department of Plant Genetics, The Weizmann Institute of Science, Rehovot, Israel

Abstract. Chromosomal arrangement in the interphase nucleus has two main aspects: (1) arrangement of chromosomes with respect to nuclear polarity and to other nuclear components, and (2) arrangement of chromosomes with respect to one another. The latter aspect consists of two main types of spatial relationships; (a) relationships between different members of one chromosomal set, (b) relationships between different chromosomal sets. Data concerning various aspects of chromosomal arrangement in the interphase nucleus are presented and discussed and the genetic control as well as subcellular mechanisms which are involvled in nuclear organization, are elucidated. Evidence is presented indicating that, in common wheat, the gene system that determines the specific pattern of chromosomal arrangement in the nucleus is operating via the microtubular elements of the spindle system. The significance of ordered arrangement of chromosomes in the nucleus for the regularity of genetic activity and chromosomal behavior, is pointed out.

Introduction

Chromosomal arrangement in the interphase nucleus has two main aspects (1) arrangement of chromosomes with respect to nuclear polarity and to various nuclear components, and (2) arrangement of chromosomes with respect to one another (Comings 1968; Feldman and Avivi 1973a, 1973b; Vogel and Schroeder 1974; Mosolov 1974). Classical and more recent cytological studies (Beams 1948; Vanderlyn 1948; Pusa 1963, 1966; Engelhardt and Pusa 1972; Lafontaine and Lord 1969; Beams and Muller 1970; Franke 1974) have shown that in plants, as in animals, interphase chromosomes are always attached to the nuclear membrane. This attachment is via specific chromosomal segments such as centromeres (Heitz 1932; Vanderlyn 1948; Feldman et al. 1966; Avivi et al. 1969; Avivi and Feldman 1973b; Wagenaar 1969; Oakley and Dodge 1974; Fussel 1975), telomeres (Vanderlyn 1948; Sved 1966; Wagenaar 1969) and possibly other regions. Centromere attachment followed by telomere attachment to the newly formed nuclear membrane at telophase, significantly restricts chromosomal movement in the regenerating nucleus. Consequently, throughout the stationary phase of each cell cycle, namely, telophase, interphase and prophase, the telophase chromosomal arrangement is maintained and chromosomes do not lose their late anaphase grouping and so reappear at prophase in the same position.

Chromosomes are arranged in a polarized manner in the nucleus with centromeres clumped together and attached to a limited area at the polar side of the nuclear membrane while the telomeres are attached to the membrane at the opposite side. The telomeres are more scattered and separated from one another than the centromeres. The chromosomal arms radiate in a meridional manner from the centromere attachment area and are aligned parallel to each other, mainly on the periphery of the nucleus. In this polarized arrangement, chromatin occupies peripheral positions in the nucleus, leaving the inner space for the nucleolus or nucleoli. Further studies of chromatin organization in the interphase nucleus reveal that the heterochromatin tends to occupy a more peripheral position than the euchromatin. This arrangement led Hsu (1975) to suggest that the outer heterochromatin may act as a

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Offprint requests to: L. Avivi (address see above)

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bodyguard protecting the inner euchromatin from mutagens, clastogens and viruses.

The polarized arrangement of chromosomes is just one aspect of chromosomal organization in the interphase nucleus. Another aspect, representing a higher level of organization, is the non-random distribution of chromosomes with respect to one another. The genetic complement of an organism is composed of one or more chromosomal sets depending on the ploidy level of the organism. If, in the interphase nucleus, chromosomes are organized in sets, then the arrangement of chromosomes with respect to one another may be considered as comprising of two main types of spatial relationships:

1. Spatial relationships within one set of chromosomes, i.e. between different members of the same set.
2. Spatial relationships between two or more sets of chromosomes. The latter consists of the following:

A. Spatial relationships between the two homologous sets in diploid or allopolyploid plants.

B. Spatial relationships between the three or more homologous sets in autopolyploid plants.

C. Spatial relationships between the homoeologous (partially homologous) sets in segmental or genomic allopolyploid plants.

The literature describing each type of spatial chromosomal relationships will be reviewed and discussed.

Spatial Relationships Within One Set of Chromosomes

Direct observations of telophase and prophase nuclei provided evidence for specific order within one chromosomal set. In 1926, Sharp stated that "in some plants, mitotic prophase chromosomes seem to be arranged end-to-end in a more or less continuous spireme, which later, at metaphase, breaks up into independent chromosomes". Such end-to-end associations, in two parallel "tracks", each track representing one chromosomal set, were described in certain fungi (Ramirez and Miller 1962; Namboodiri and Lowry 1967). Wagenaar and his co-workers (Wagenaar 1969; Ashley and Wagenaar 1972, 1974) reported on such end-to-end associations in several higher plants too. From these observations at telophase or prophase of sporophytic and gametophytic nuclei, it was inferred that chromosomes of one set form a chain-like or a ring-like chromosome association at interphase as well. The arrangement of non-homologues in this end-to-end association at interphase is highly specific and their sequence is maintained throughout the life cycle of the plant (Ashley and Wagenaar 1974). Telomeric connections and definite arrangement of members of one chromosomal set in somatic cells were also observed by other cytologists in several additional higher plants (Gerassimova 1933; Shchapova 1971; Stack and Clarke 1973; Godin and Stack 1975; Kihara 1979).

Unfortunately, in many plants, these telomeric connections and chromosomal spatial relationships are not clearly observable at metaphase. Moreover, chromosomes at metaphase may be arranged on the spindle fibers in a pattern different from that at interphase, on the nuclear membrane. In order to retain, as far as possible, interphase chromosomal arrangement in metaphase cells, spindle formation was suppressed by cold pretreatement. Indeed, studies of the distribution of distances between pairs of non-homologous chromosomes in cold treated metaphase cells, revealed that chromosomes are arranged non-randomly with respect to one another; some or these distributions deviated significantly from one another as well as from that expected of two randomly arranged chromosomes. Such studies were made in common wheat (Darvey and Driscoll 1972; Feldman and Avivi 1973a, 1973b), in *Triticum umbellulatum* (Kushnir 1977) and in maize (Horn 1970, 1975; Horn and Walden 1978). Since the homologous chromosomal sets are normally closely associated in the interphase nucleus (s. next chapter), evidence indicating non-random distribution of non-homologous chromosomes reveal, in fact, specific spatial relationships within one chromosomal set.

Additional and more direct evidence for a specific order within one chromosomal set in the interphase nucleus came from studies of the distribution of radiation-induced chromosomal exchanges in several plants. These studies indicated that the non-homologous chromosomes are arranged non-randomly in the interphase nucleus (Sax 1940; Evans and Bigger 1961; Kumar and Natarajan 1966; Kaina et al. 1979) (Table 1). Similarly, data from spontaneous chromosomal exchanges in maize (Jancey and Walden 1972; Jancey 1975; Walden and Jancey 1976) implied that, at interphase, non-homologous chromosomes are arranged in a definable spatial distribution with respect to one another. Similar observations were reported by Werry et al. (1977) who studied the relative position of interphase chromosomes in *Haplopappus gracilis*. In this study, a specific pattern of interphase chromosomal arrangement was inferred from the frequency of induced interchanges between chromosomes, following irradiation during G_1 phase. Moreover, the inferred relative position of interphase chromosomes was found to be consistent in *H. gracilis* with the pattern of non-random chromosomal distribution that was observed at metaphase (Werry et al. 1977). In conclusion, the above data indicate that members of one chromosomal set are arranged non-randomly with respect to each other and occupy definite positions in the interphase nucleus of plants.

Table 1. Occurrence of non-random arrangement of non-homologous chromosomes in higher plants

Species	Type of cells[a]	Reference
Dicotyledons		
Nigella arvensis (Ranunculaceae)	Root tips (1)	Wagenaar 1969
Vicia faba (Papilionaceae)	Root tips (6)	Evans and Bigger 1961
Callitriche hermaphroditica (Callitrichaceae)	Root tips (1)	Wagenaar 1969
Crespis capillaris (Compositae)	Root tips (1)	Wagenaar 1969
Crespis neglecta (Compositae)	Root tips (1)	Wagenaar 1969
Crespis conizyfolia (Compositae)	Root tips (1)	Wagenaar 1969
Crespis sibiria (Compositae)	Root tips (1)	Wagenaar 1969
Haplopappus gracilis (Compositae)	Root tips (1) (6)	Werry et al. 1977
Monocotyledons		
Allium cepa (Liliaceae)	Root tips (1)	Wagenaar 1969
Ornithogalum virens (Liliaceae)	Root tips (1), pollen grains (1)	Ashley and Wagenaar 1972, 1974
Ornithogalum virens (Liliaceae)	Root tips (1), pollen grains (1)	Ashley 1976
Ornithogalum virens (Liliaceae)	Root tips (1)	Godin and Stack 1976
Hordeum vulgare (Gramineae)	Root tips (6)	Kumar and Natarajan 1966
Triticum aestivum (Gramineae)	Root tips (3)	Darvey and Driscoll 1972
Triticum aestivum (Gramineae)	Root tips (3)	Feldman and Avivi 1973a, 1973b
Triticum umbellulatum (Gramineae)	Root tips (3)	Kushnir 1977
Secale cereale (Gramineae)	Root tips (1)	Wagenaar 1969
Zea mays (Gramineae)	Root tips (3)	Horn 1970, 1975
Zea mays (Gramineae)	Meiocytes (6)	Jancey and Walden 1972
Zea mays (Gramineae)	Meiocytes (6)	Jancey 1975
Zea mays (Gramineae)	Meiocytes (6)	Walden and Jancey 1976
Zea mays (Gramineae)	Root tips (3)	Horn and Walden 1978

[a] The numbers in brackets indicate the method of pretreatment and observation:

1. Observation in untreated prophase, metaphase or anaphase cells.
2. Observation in pretreated metaphase cells.
3. Measurements of distances between cytologically marked homologous or non-homologous chromosomes in pretreated metaphase cells.
4. Observation in interphase nuclei.
5. Measurement of distances between homologous segments in interphase nuclei.
6. Concluded from frequency of interphase induced exchanges between homologous or non-homologous chromosomes

Spatial Relationships Between Sets of Chromosomes

A. Spatial Relationships Between the Two Homologous Sets in Diploid or Allopolyploid Plants

Already at the dawn of the century there were reports referring to association of homologous chromosomes during the mitotic cycle (Table 2). Classical plant cytologists such as Strasburger (1904, 1905, 1907, 1910), Sykes (1908), Overton (1909, 1022), Stomps (1910), Nemec (1910), Tahara (1910), Muller (1912), Gates (1912), Lawrence (1931) and Watkins (1935), who studied the distribution of chromosomes in sectioned cells, noticed that homologous chromosomes tend to associate with each other in somatic metaphases. In fact, these associations actually reflect the association of the two chromosomal sets in these cells. More recent investigations of squashed mitotic cells which were either pretreated to arrest metaphase or untreated, corroborated the tendency for homologous chromosomes to lie close to each other, so indicating the close association of the two homologous sets. This tendency was found in a large number of higher plants representing both dicotyledon as well as monocotyledon families (Table 2). These investigations were carried out by Hiraoka (1958a, 1958b) Mitra and Steward (1961), Kitani (1963), Steinitz-Sears (1963), Reitberger (1964), Butterfass (1967), Brown and Stack (1968), Stack and Brown (1969a, 1969b), Wagenaar (1969), Ashley and Wagenaar (1972, 1974), Chauhan (1973), Werry et al. (1977) and others. These observations were recently substantiated in several more critical cytological studies. These studies took into account that, at metaphase, chromosomes may be arranged on the spindle in a pattern that differs from that at telophase, interphase and prophase, and that pretreatment with chemicals which prevents spindle formation and causes shorten-

Table 2. Occurrence of somatic association of homologous chromosomes in higher plants (in phylogenetic order)

Species	Type of cells[a]	Reference
Dicotyledons		
Morus alba (Moraceae)	Root tips (1)	Tahara 1910
Morus indica (Moraceae)	Root tips (1)	Tahara 1910
Cannabis sativa (Moraceae)	Root tips (1)	Strasburger 1910
Melandrium rubrum (Caryophyllaceae)	Root tips (1)	Strasburger 1910
Lychnis dioica (Caryophyllaceae)	Root tips (1)	Sykes 1908
Spinacia oleracea (Chenopodiacea)	Root tips (1)	Stomps 1911
Beta vulgaris (Chenopodiaceae)	Stem tips (2)	Butterfass 1967
Nigella arvensis (Ranunculaceae)	Root tips (1)	Wagenaar 1969
Padophyllum peltatum (Berberidaceae)	Root tips (1)	Overton 1922
Arabidopsis thaliana (Cruciferae)	Sporogenous anther tissue (1)	Steinitz-Sears 1963
Calycanthus floridus (Calycanthaceae)	Root tips (1)	Overton 1909
Pisum sativum (Papilionaceae)	Root tips (1)	Strasburger 1907
Trifolium pratense (Papilionaceae)	Root tips, leaves (4)	Reitberger 1964
Trifolium hybridum (Papilionaceae)	Root tips, leaves (4)	Reitberger 1964
Vicia faba (Papilionaceae)	Root tips (6)	Revell 1953
Vicia faba (Papilionaceae)	Root tips (6)	Mcleish 1953
Vicia faba (Papilionaceae)	Root tips (6)	Rao and Natarajan 1967
Vicia faba (Papilionaceae)	Root tips (6)	Michaelis and Rieger 1968
Vicia faba (Papilionaceae)	Root tips (6)	Rieger et al. 1973
Impatiens balsamina (Balsaminaceae)	Sporogenous anther tissue (1), root tips (4)	Chauhan and Abel 1968
Ricinus communis (Euphorbiaceae)	Root tips (1)	Nemec 1910
Mercurialis annua (Euphorbiaceae)	Root tips (1)	Strasburger 1910
Mouriria anomala (Melastomaceae)	Root tips (1)	Ruys 1924
Daphne odora (Thymelaeaceae)	Leaves, tapetum (1)	Hiraoka 1958a
Oenothera lata (Onagraceae)	Nucellus (1)	Gates 1912
Callitriche hermaphroditica (Callitrichaceae)	Root tips (1)	Wagenaar 1969
Salvia nemorosa (Labiatae)	Sporogenous anther tissue (4)	Chauhan and Abel 1968
Nicandra physaloides (Solanaceae)	Root tips (1)	Janaki-Ammal 1932
Plantago lanceolata (Plantaginaceae)	Root tips (1)	Nemec 1910
Plantago ovata (Plantaginaceae)	Sporogenous anther tissue (4), tapetum (4)	Stack and Brown 1969b
Sambucus elbulus (Caprifoliaceae)	Pistil tissue (1)	Battaglia 1947
Bryonia dioica (Cucurbitaceae)	Root tips (1)	Sykes 1908
Dahlia coronata (Compositae)	Root tips (1)	Ishikawa 1911
Dahlia sp. (Compositae)	Root tips (1)	Lawrence 1931
Crepis capillaris (Compositae)	Root tips (1)	Kitani 1963
Crepis capillaris (Compositae)	Root tips (1)	Wagenaar 1969
Crepis capillaris (Compositae)	Root tips (3)	Ferrer and Lacadena 1977
Crepis neglecta (Compositae)	Root tips (1)	Wagenaar 1969
Crepis conizyfolia (Compositae)	Root tips (1)	Wagenaar 1969
Crepis sibirica (Compositae)	Root tips (1)	Wagenaar 1969
Crepis taraxifolia (Compositae)	Root tips (3)	Ferrer and Lacadena 1977
Crepis rubra (Compositae)	Root tips (3)	Ferrer and Lacadena 1977
Haplopappus gracilis (Compositae)	Tissue and cell culture (1)	Mitra and Steward 1961
Haplopappus gracilis (Compositae)	Sporogenous anther tissue (1)	Brown and Stack 1968
Haplopappus gracilis (Compositae)	Root tips (1) (6)	Werry et al. 1977

Table 2 (continued)

Species	Type of cells[a]	Reference
Monocotyledons		
Hydrocharis morsus-ranae (Hydrocharitaceae)	Root tips (1)	Sykes 1908
Najas marina (Najadaceae)	Root tips (1)	Müller 1912
Galtonia candicans (Liliaceae)	Embryo, root tips (1)	Strasburger 1905
Galtonia candicans (Liliaceae)	Root tips (1)	Digby 1910
Yucca draconis (Liliaceae)	Root tips (1)	Müller 1909
Yucca guatemalensis (Liliaceae)	Root tips (1)	Müller 1909
Yucca aloifolia (Liliaceae)	Root tips (1)	Müller 1909
Yucca rupicola (Liliaceae)	Root tips, embryo (1)	Watkins 1935
Albuca fastigiata (Liliaceae)	Root tips (1)	Müller 1912
Aloe hanburyana (Liliaceae)	Root tips (1)	Müller 1912
Euconis bicolor (Liliaceae)	Root tips (1)	Müller 1912
Bulbine annua (Liliaceae)	Root tips (1)	Müller 1912
Muscari botryoides (Liliaceae)	Root tips (1)	Müller 1912
Scilla bifolia (Liliaceae)	Root tips (1)	Müller 1912
Chionodoxa luciliae (Liliaceae)	Root tips (1)	Müller 1912
Hyacinthus orientalis (Liliaceae)	Root tips (1)	Müller 1912
Ornithogalum virens (Liliaceae)	Root tips (1)	Therman 1951
Ornithogalum virens (Liliaceae)	Root tips (1)	Chauhan 1973
Ornithogalum virens (Liliaceae)	Root tips (1)	Ashley and Wagenaar 1974
Ornithogalum virens (Liliaceae)	Root tips (1)	Godin and Stack 1976
Ornithogalum graminifolium (Liliaceae)	Root tips (1)	Therman 1951
Ornithogalum caudatum (Liliaceae)	Root tips (1)	Therman 1951
Allium cepa (Liliaceae)	Root tips (2)	Berger and Witkus 1948
Allium cepa (Liliaceae)	Root tips (1)	Wagenaar 1969
Funkia sieboldiana (Amaryllidaceae)	Embryo, root tips (1)	Strasburger 1905
Funkia sieboldiana (Amaryllidaceae)	Root tips (1)	Sykes 1908
Funkia sieboldiana (Amaryllidaceae)	Root tips (1)	Müller 1912
Funkia ovata (Amaryllidaceae)	Root tips (1)	Sykes 1908
Nerine rosea (Amaryllidaceae)	Root tips (1)	Müller 1912
Beschorneria superba (Amaryllidaceae)	Root tips (1)	Müller 1912
Rhoeo discolor (Commelinaceae)	Sporogenous anther tissue (1)	Brown and Stack 1968
Oryza sativa (Gramineae)	Root tips (1)	Kuwada 1910
Sorghum halepense (Gramineae)	Root tips (1)	Huskins and Smith 1932
Avena strigosa (Gramineae)	Root tips (3)	Sadasivaiah et al. 1969
Avena sativa (Gramineae)	Root tips (3)	Sadasivaiah et al. 1969
Avena sativa (Gramineae)	Root tips (3)	Dubuc and McGinnis 1970
Avena sativa (Gramineae)	Root tips (3)	Thomas 1973
Hordeum vulgare (Gramineae)	Root tips (6)	Kumar and Natarajan 1966
Hordeum vulgare (Gramineae)	Root tips (3)	Fedak and Helgason 1970
Hordeum vulgare (Gramineae)	Root tips (3)	Yoshida et al. 1972
Hordeum vulgare (Gramineae)	Root tips (3)	Yoshida and Yamaguchi 1973
Triticum aestivum (Gramineae)	Root tips (2)	Schulz-Schaeffer and Haun 1961
Triticum aestivum (Gramineae)	Root tips (3)	Feldman et al. 1966
Triticum aestivum (Gramineae)	Root tips (3)	Feldman 1968
Triticum aestivum (Gramineae)	Root tips (3)	Mello-Sampayo 1968, 1973
Triticum aestivum (Gramineae)	Root tips (3)	Avivi et al. 1969
Triticum aestivum (Gramineae)	Root tips (3)	Feldman et al. 1972
Triticum aestivum (Gramineae)	Root tips (3)	Singh and Joshi 1972
Triticum aestivum (Gramineae)	Root tips (3)	Feldman and Avivi 1973b
Triticum aestivum (Gramineae)	Root tips (5)	Singh et al. 1976
Triticum tauschii (Gramineae)	Endosperm (1)	Kitani 1963
Triticum umbellulatum (Gramineae)	Root tips (3)	Kushnir 1977

Table 2 (continued)

Species	Type of cells[a]	Reference
Triticum kotschyi (Gramineae)	Root tips (3)	Kushnir 1977
Secale cereale (Gramineae)	Root tips (1)	Wagenaar 1969
Secale cereale (Gramineae)	Root tips (2)	Yoshida et al. 1974
Zea mays (Gramineae)	Sporogenous anther tissue (4), root tips (4)	Maguire 1967, 1972
Zea mays (Gramineae)	Root tips (3)	Miles 1968
Zea mays (Gramineae)	Root tips (3)	Horn 1970, 1971, 1973, 1975
Zea mays (Gramineae)	Root tips (3)	Horn and Walden 1978
Listera ovata (Orchidaceae)	Root tips (1)	Müller 1912

[a] The numbers in brackets indicate the method of pretreatment and observation:
1. Observations in untreated prophase, metaphase or anaphase cells.
2. Observations in pretreated metaphase cells.
3. Measurements of distances between homologous chromosomes in pretreated metaphase cells.
4. Observations in interphase nuclei.
5. Measurements of distances between homologous segments in interphase nuclei.
6. Concluded from frequency of exchanges between homologous chromosomes.

ing of chromosomes, may also disrupt chromosomal arrangement which is dependent on the intact nuclear membrane. Thus, in order to minimize disruption and preserve, as much as possible, interphase chromosomal distribution, cells were pretreated with cold water. Such physical treatment suppresses spindle formation but, unlike colchicine and other antitubulins it hardly affects interphase chromosomal arrangement. Following the cold treatment, the distance between cytologically marked homologues was measured in a large population of cells and analyzed statistically. These studies were carried out in common wheat (Feldman et al. 1966; Feldman 1968; Avivi et al. 1969; Feldman et al. 1972; Feldman and Avivi 1973a, 1973b; Singh and Joshi 1972; Mello-Sampayo 1973), in oats (Sadasivaiah et al. 1969; Dubuc and McGinnis 1970; Thomas 1973), in barley (Fedak and Helgason 1970; Yoshida et al. 1972; Yoshida and Yamaguchi 1973), in two wild species of *Triticum* (Kushnir 1977), in rye (Yoshida et al. 1974), in maize (Horn 1970, 1971, 1973, 1975; Horn and Walden 1978), and in several species of *Crepis* (Ferrer and Lacadena 1977). All these investigations show clearly that the mean distance between homologues in somatic cells is significantly shorter than that expected for random distribution, thus verifying previous cytological observations that homologous chromosomal sets are indeed associated in somatic nuclei.

Close association between homologous sets was reported in plant cells in various tissues and developmental stages, i.e. embryos, endosperms, root-tips, shoot-tips, leaves, petals, tapeta and sporogenous tissues (Table 2). This may indicate that the phenomenon is a common feature of all somatic cells throughout

Table 3. Occurrence of somatic crossing-over in fungi

Species	Reference
Myxomycetes	
Dictyostelium discoideum	Katz and Sussmann 1972
Dictyostelium discoideum	Gingold and Ashworth 1974
Ascomycetes	
Saccharomyces cerevisiae	Roman 1956
Saccharomyces cerevisiae	Holliday 1964
Saccharomyces cerevisiae	Hurst and Vogel 1964
Saccharomyces cerevisiae	Yost et al. 1967
Aspergillus nidulans	Pontecorvo and Roper 1952
Aspergillus nidulans	Käfer 1960, 1961, 1963
Aspergillus nidulans	Morpurgo 1962
Aspergillus nidulans	Wood and Käfer 1967
Aspergillus niger	Pontecorvo et al. 1953
Aspergillus sojae	Ishitani et al. 1956
Penicillium chrysogenum	Pontecorvo and Sermonti 1954
Fusarium oxysporum	Buxton 1956
Neurospora crassa	Mitchell 1963
Neurospora crassa	Pittenger and Coyle 1963
Verticillium albo-atrum	Hastie 1967
Basidiomycetes	
Ustilago maydis	Holliday 1961, 1964, 1965, 1967
Puccinia graminis	Ellingboe 1961
Schizophyllum commune	Ellingboe and Raper 1962

Table 4. Occurrence of somatic crossing-over in higher plants

Species	Reference
Dicotyledons	
Portulaca grandiflora (Portulacaceae)	Imai and Kanna 1935
Arabidopsis thaliana (Cruciferae)	Hirono and Redei 1965
Pisum sativum (Papilionaceae)	Blixt 1972
Glycine max (Papilionaceae)	Vig 1971, 1973a, 1973b, 1974, 1975, 1977
Glycine max (Papilionaceae)	Vig and Zimmermann 1977
Glycine max (Papilionaceae)	Ashley 1978
Gossypium hirsutum (Malvaceae)	Barrow et al. 1973
Gossypium hirsutum (Malvaceae)	Barrow and Dunford 1974
Salvia splendens (Labiatae)	Hendrychova-Tomkova 1964
Nicotiana tabacum (Solanaceae)	Carlson 1974
Nicotiana tabacum (Solanaceae)	Dulieu 1975
Lycopersicum esculentum (Solanaceae)	Ross and Holm 1960
Antirrhinum majus (Scrophulariaceae)	Harrison and Carpenter 1977
Crepis capillaris (Compositae)	Dubinin and Nemtseva 1969
Monocotyledons	
Tradescantia hirsuticaulis (Commelinaceae)	Christianson 1975
Tradescantia hirsuticaulis (Commelinaceae)	Mericle and Mericle 1967
Zea mays (Gramineae)	Jones 1936, 1937
Zea mays (Gramineae)	Brink and Nilan 1952
Zea mays (Gramineae)	Greenblatt and Brink 1962

the life cycle of the plant. Indeed, as was found by Strasburger (1905, 1907, 1910) and Watkins (1935), the association of homologous chromosomes commences immediately after fertilization and terminates at first anaphase of meiosis, as the homologues segregate to opposite poles. Several cytologists (Brown and Stack 1968; Stack and Brown 1969a, 1969b) claim that the degree of association between homologous sets is increased in premeiotic cells, but this observation requires further investigation. In our opinion, the degree of homologous association should be the same in all the somatic nuclei.

As was found in Diptera (Metz 1916), in plants too, the association of homologous sets is most intimate at the stationary phase, (telophase, interphase and prophase), and relaxes at the mobile phase (metaphase and anaphase) of the cell cycle (Avivi et al. 1969; Avivi and Feldman 1973b). Homologous chromosomes become more intimately associated while moving to the poles at anaphase. At telophase they become attached to the same or to close sites on the newly formed nuclear membrane thus maintaining intimate somatic association throughout interphase and prophase (Feldman et al. 1966; Avivi and Feldman 1973b). At the end of prophase, after the breakdown of the nuclear membrane, the homologues move somewhat apart which enables them to maneuver, divide and separate with the least interruption. The supposition that association of homologous sets is more intimate at the stationary phase of the cell cycle is evidenced from direct studies of chromosomal distribution at interphase. Intimate associations of homologous blocks of heterochromatin during somatic interphase were reported by classical cytologists (Strasburger 1904, 1905, 1907, 1910; Overton 1922; Janaki-Ammal 1932). Such close associations were recently confirmed in several additional plants (Maguire 1967; Chauhan and Abel 1968; Stack and Brown 1969b). Moreover, Singh et al. (1976) measured the distances between homologous heterochromatic segments in interphase nuclei of common wheat and established that they were intimately associated and lying much closer to each other than homologues usually lie at metaphase. The conclusions of analyses of radiation — or chemically-induced interchanges at interphase are in full accord with these observations. Such studies show that irradiation induces a significantly greater proportion of homologous exchanges than is expected by chance alone (Evans and Bigger 1961; Kumar and Natarajan 1966; Michaelis and Rieger 1968; Rieger et al. 1973; Werry et al. 1977). Similar results were observed after treatment with alkylating agents (Revell 1953; Mcleish 1953) or with mytomycin

C (Rao and Natarajan 1967). Likewise, the finding of occasional somatic crossing-over in a number of fungi (Table 3) and higher plants (Table 4) which takes place during the S-phase or G_2, implies that somatic association between the two sets of homologous chromosomes definitely occurs at interphase.

The idea of somatic association of homologous chromosomes was rejected by several classical cytologists (for details see Tischler 1951) who considered it merely as a random association of chromosomes of similar size during somatic metaphase. Rejection of the phenomenon was also expressed by Westergaard (1964) who suggested that, "primitively, homologous chromosomes synapsed at each cell division and that this ability has been lost without recurrence in most diplonts, because of selection against somatic crossing-over and somatic reduction". Westergaard's point of view was supported by several recent studies (Person 1959; Walters 1970; Palmer 1971; Burns 1972; Darvey and Driscoll 1972; Dvorak and Knott 1973; Therman and Sarto 1977) which failed to find evidence for somatic association. These views, however, are in contrast to the abundance of information presented above (Table 2). The universality of somatic association of homologous chromosomes is evidenced by its occurrence in a large number of species representing a wide spectrum of the plant kingdom. In contrast to Westergaard's view, multicellular organisms apparently evolved different ways of suppressing somatic crossing-over and somatic reduction yet maintained somatic association which is presumably necessary for many aspects of chromosomal behavior and genetic activity.

B. Spatial Relationships Between the Three or More Homologous Sets in Autopolyploid Plants

In many autopolyploids, where more than two homologous sets of chromosomes are present in each somatic cell, multiple associations were observed. Thus, Strasburger (1907) and Ruys (1924, 1925) found in several polyploid plants distinct association of groups of chromosomes in which the number of chromosomes in each group corresponded to the level of ploidy. Similarly, Lawrence (1931) found that more than two homologues were attracted to one another in polyploid *Dahlia* and Ashley and Wagenaar (1972, 1974) observed associations of four homologues in an autotetraploid line of *Ornithogalum virens*. These data show clearly that in these autopolyploid plants there is a complete association of all the homologous chromosomal sets.

On the other hand, in some autopolyploid plants, in spite of the fact that more than two homologous sets exist in every somatic cell, the associations are always in pairs only. Ishikawa (1911) found such association of pairs in *Dahlia coronata*, a species with a tetraploid chromosome number. Similar associations in pairs were found by Berger and Witkus (1948) in an autotetraploid line of onion. These data indicate that in some autopolyploids the chromosomal sets are arranged in pairs rather than grouped all together and that the various pairs are spatially separated from each other in the nucleus.

C. Spatial Relationships Between the Homoeologous Sets in Allopolyploid Plants

In genomic and segmental allopopyploid plants there are homoeologous (partially homologous) as well as homologous sets of chromosomes. The spatial relationships of the homoeologous chromosomal sets represent another phenomenon superimposed on the intragenomic chromosomal arrangement. Although the information on these relationships is very scanty, it was found in common wheat (Feldman and Avivi 1973a, 1973b) that chromosomes of each genome, both homologues and non-homologues, tend to lie significantly closer to each other than to chromosomes of different genomes. These data show that while homologous sets are associated homoeologous sets are separated and tend to occupy different regions of the common wheat nucleus.

Satellite Association

One aspect of the non-random chromosomal distribution in the nucleus is the so-called satellite association or association of nucleolar organizer regions (NOR's). This association can occur between NOR's of both homologous and non-homologous chromosomes. Associations of homologous NOR's were reported by Ghosh and Roy (1977) in interphase of *Allium cepa* while Darvey and Driscoll (1972) observed association of non-homologous NOR's in common wheat. In contrast to the finding in common wheat, Sadasiviah et al. (1969) did not detect association of non-homologous NOR's in *Avena strigosa*.

The persistent attachment of nucleolar organizers to the nucleolus throughout interphase and prophase results in close associations of the chromosomes involved also at metaphase. Such association of the homologous SAT-chromosomes was found by Horn and Walden (1978) in cold treated maize somatic metaphase. Moreover, it was found (Horn and Walden 1978) that this type of association is insensitive to colchicine treatment. These findings are in full accord with data in man where satellite association was studied very intensively (Galperin 1968; Back and Zang 1969; Nankin 1970; Cooke 1972; Sele et al. 1977).

Genetic Control and Sub-Cellular Mechanisms of Chromosomal Arrangement at Interphase

The two types of chromosomal spatial relationships, namely, within a chromosomal set and between chromosomal sets, are apparently regulated by different genetic factors and sub-cellular mechanisms. This is supported by Ashley and Wagenaar (1974) who noticed that associations betwen homologous sets seem to be more easily disrupted by fixation and squashing than those between members of one chromosomal set. At present, no information is available on gene systems and sub-cellular mechanisms that determine the pattern of chromosomal arrrangement within one chromosomal set. Yet, there are two main views relating to the maintenance of this order throughout the life cycle of the plant. Several plant and animal cytologists suggested (DuPraw 1970; Costello 1970; Boss 1972; Ashley and Wagenaar 1974; Godin and Stack 1976) that spatial relationships between members of one chromosomal set are maintained by end-to-end or centromere-to-centromere connections, either of chromatin or of protein nature. These connections are permanent, do not break in mitosis and are maintained throughout the organism's life cycle. According to this view, members of one chromosomal set become attached to each other at the end of the first meiotic anaphase and separate from each other, to form new chromosomal combinations, only in the following meiosis.

An alternative and more plausible possibility is that the connections between members of one chromosomal set are not permanent and exist only at the stationary phase of the cell cycle, i.e., telophase, interphase and prophase. These connections are indirect and result from specific attachments of centromeres and telomeres of every chromosome to definite sites on the nuclear membrane. In those stages lacking intact nuclear membrane, i.e. metaphase and anaphase, chromosomes are disconnected from one another in order to facilitate free chromosomal movement.

As to the mechanisms involved in determining the specific pattern of arrangement within a given set, it is assumed that particular spindle polar sites are arranged in a constant distinctive order which is similar in every cell of a given organism. Assuming a highly specific affinity between any centromere and a given polar site, the arrangement of the latter determines the relative position of the different centromeres with respect to one another at the end of each anaphase movement.

In contrast to the situation regarding arrangement of chromosomes within one set, some information is available on gene systems controlling spatial relationships between two or more chromosomal sets. Such a genetic effect was found in common wheat and related species (Feldman 1966, 1968; Feldman and Avivi 1973b), in oat (Thomas 1973), in maize (Miles 1968) and in *Pennisetum* (Singh 1978). The effect of these genes on the degree of association between chromosomal sets is presented in Fig. 1.

The best known of these genes is the Ph or the 5BL gene of common wheat. Feldman and Avivi (1973b) found that this gene affects the pattern of chromosomal

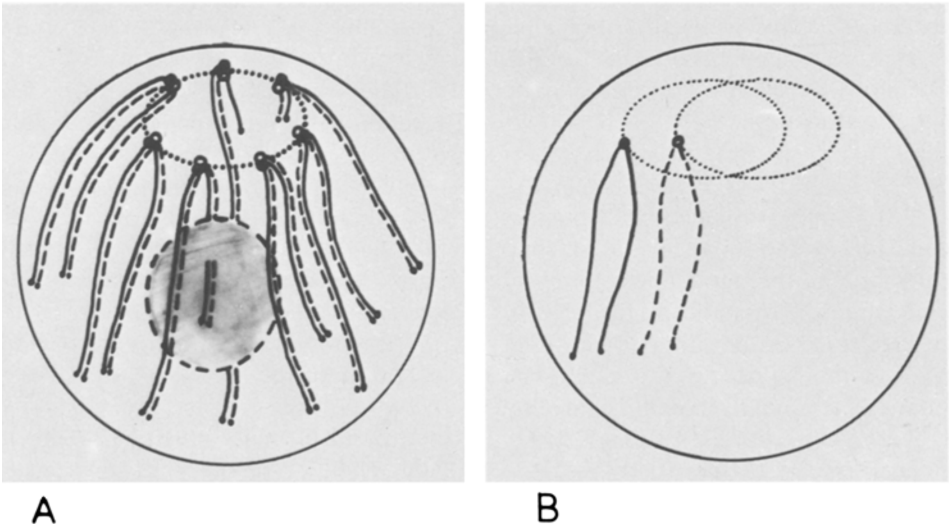

Fig. 1. Genetic effect on somatic association between homologous chromosomal sets; **A** Polarized arrangement of chromosomes in the interphase nucleus with complete association between the two homologous sets; **B** Separation of homologous chromosomal sets (only one pair of chromosomes is drawn)

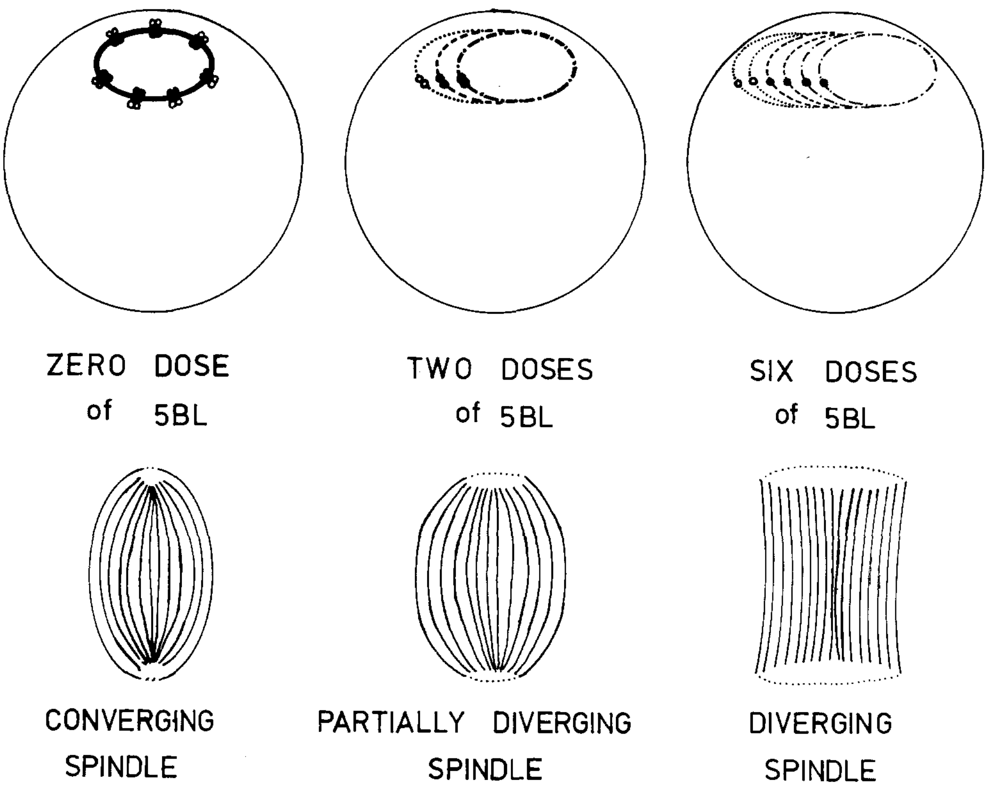

Fig. 2. Effect of different doses of the 5BL gene on the association of homologous and homoeologous chromosomal sets (*upper drawings*; only centromeres are drawn) and on the structure of the spindle *(lower drawings)* in hexaploid wheat

distribution in the nuclei of common wheat. Figure 2 demonstrates the pattern of centromere arrangement in nuclei of plants with different doses of 5BL. In plants deficient for this gene, as in nullisomics for chromosome 5B, all chromosomal sets, homologous as well as homoeologous, are intimately associated in somatic cells. In plants with the normal two doses of this gene, homologous sets are associated with eath other while homoeologous sets are separated. Six doses of the 5BL gene, as in tri-isosomic 5BL plants, induce the separation of homologous sets as well.

As to the mechanisms involved in association of chromosomal sets, Feldman et al. (1966) and Mello-Sampayo (1968, 1973) adduced evidence indicating that the centromere is the chromosomal region which is responsible for positioning the homologous chromosomes close to one another. This indicates the involvement of the achromatic part of the mitotic apparatus in the association of homologous chromosomal sets. Evidence supporting this assumption was obtained by Avivi et al. (1969) and Avivi and Feldman (1973b).

From the evidence that the 5BL gene modifies some of the characteristics of the spindle system (Avivi et al. 1970a, 1970b), Avivi and Feldman (1973a, 1973b) argued that this gene affects somatic association of chromosomal sets via its effect on the spindle system. Evidence was obtained (Feldman and Avivi, in preparation) that the 5BL gene induces divergent or split spindle. Thus the effect of this gene at the subcellular level can be visualized by assuming that it modifies the structure of the spindle and primarily that of the spindle poles (Fig. 2). In plants deficient for the 5BL gene, the spindle is a converging one. Such a spindle brings the centromeres of all chromosomal sets to the same polar region. In plants with two doses of 5BL the spindle is partially divergent or parallel. This leads to a partial separation of the homoeologous chromosomal sets from one another. Such modification of the spindle, though separating homoeologous sets, is insufficient to separate homologous sets. In plants with six doses of 5BL the spindle is divergent or split. Such a spindle causes the separation of all chromosomal sets, homologous as well as homoeologous.

Genes affecting the structure of the spindle are known in various plants. A recessive gene modifying the normal converging spindle to a diverging one was discovered in maize by Clark (1940). Genetic effects inducing split spindle were reported in several plant species and hybrids, diploids as well as polyploids (Darlington and Thomas 1937; Vasek 1962; Tai 1970).

It is only reasonable to assume that all those polyploid plants in which the association of chromosomal sets is limited to pairs only (s. previous chapters), contain genes similar to the 5BL gene of common wheat. Such genes determine a pattern of chromosomal distribution in somatic and premeiotic cells that lead to bivalent pairing at meiosis of polyploid organisms which otherwise would exhibit multivalent configurations (Avivi 1976a, 1976b).

It was suggested (Feldman and Avivi 1973a, 1973b) that the ordered arrangement of chromosomes in the interphase nucleus is significant for the regularity of many aspects of chromosomal behavior such as meiotic pairing, replication and condensation, as well as for genetic activity.

For a better understanding of interphase chromosomal arrangement and its biological significance, more information is needed on this phenomenon, its genetic control and the sub-cellular mechanisms involved.

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