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Nucleolar Organizing Chromosomes of *Ricinus**

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Summary. Pachytene chromosome morphology was compared in nine races of *Ricinus communis* L. (2n = 20), using pollen mother cells (PMCs) and light microscopy. Of the ten bivalents, only the two possessing nucleolar organizing regions (NORs), chromosomes 2 and 7, exhibit structural variations among the races. The NORs are located in the short arms of these two chromosomes. Most of the observed structural variations affect these short arms, which are similar morphologically and consist largely of heterochromatic segments. The PMCs contain a single nucleolus and this is associated with the NOR of each of the two chromosomes at a particular frequency in each race. In eight races, a nucleolar constriction (NC) is present in either chromosome 2 or chromosome 7. In these races, the nucleolus is associated with the chromosome possessing an NC at a frequency of 100% and with the chromosome lacking an NC at a frequency ranging between 5.6 and 100%, depending upon the race. No microscopically visible NC is present in the ninth race. In this race, the nucleolus is associated with both chromosomes 2 and 7 at a frequency of 100%. The association of the nucleolus with a chromosome possessing an NC is at the NC and with a chromosome lacking an NC is at the terminal heterochromatic segment of the short arm. Several interpretations are offered to account for the variations in frequency of association between the nucleolus and each of the nucleolar organizing chromosomes. It is suggested that the two non-linked NORs have evolved through some intragenomic changes rather than polyploidy, that this species is highly intolerant to structural variations other than those occurring in or near the NORs, and that structural variations in the nucleolar organizing chromosomes are not associated with racial variations in plant phenotype.

Key words: *Ricinus communis* L. – Pachytene – Nucleolar organizing chromosomes – Structural variations – nucleolus association frequency

Introduction

Ricinus communis L., the castor plant, is the sole species of the genus *Ricinus*. This species is distributed in many of the warmer regions of the world. And it consists of numerous races, naturalized and cultivated (Mueller 1866; Norton 1941).

Previous reports (Jakob 1956; Jelenkovic and Harrington 1973; Paris et al. 1978) have shown that the ten pachytene bivalents are clearly distinguished morphologically. A notable feature of the castor karyotype is the relatively large heterochromatic segments in each bivalent. This feature is useful not only for identification of individual chromosomes but also for studies of chromosome alterations. Another feature is the presence of a single nucleolus and two nucleolar organizing chromosomes at pachytene. The NORs are located in the highly heterochromatic short arms of these two chromosomes. Each of these short arms contains five easily recognizable heterochromatic segments.

The highly polytypic nature of *Ricinus communis* and the fact that it provides favorable material for cytological investigations has prompted us to explore the possible existence of karyotypic variations in this species. We report here that (1) structural variations among nine races are confined to the two nucleolar organizing chromosomes, particularly in or near their NORs, and (2) races differ also in frequency at which each of these chromosomes is associated with the nucleolus.

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Table 1. Some distinguishing characteristics of nine castor races[a]

Race	Plant size	Habit[b]	Number of nodes to the first inflorescence[c]	Internode length	Maturity	Leaf size	Maximum number of leaf lobes	Waxy 'bloom'	Color of leaves and stems	Style color	Capsule surface	Seed size	Seed color
A39	Medium	I	10	Medium	Second early	Medium	9	Absent	Tinged[d] green	Red	Spiny	Large	Dark brown
AF-3	Medium	P	17	Very short	Late	Medium	9	Present	Tinged green	Red	Spiny	Small	Light brown
EA	Medium	P	30	Very short	Very late	Medium	10	Present	Tinged green	Red	Spiny	Very small	Light brown
ES	Small	A	7	Long	Very early	Small	8	Present	Mahogany	Red	Spineless	Medium	light brown
G	Very small	A	7	Short	Early	Small	8	Absent	Tinged green	Red	Spineless	Medium	Brown
K	Medium	I	12	Medium	Second early	Medium	10	Absent	Mahogany	Red	Spiny	Large	Reddish brown
L	Extra large	P	40	Long	Very late	Large	10	Absent	Mahogany	Red	Spiny	Large	Dark brown
Z-1	Large	P	25	Medium	Late	Extra large	11	Absent	Tinged green	Red	Spiny	Extra large	Black
Z-2	Large	P	25	Medium	Late	Extra large	11	Absent	Pure green	Green	Spiny	Extra large	Speckled red

[a] *The nine races differed in the mechanism governing dehiscence and indehiscence of capsules but these differences are not shown here*

[b] A = annual, P = perennial, and I = intermediate tendency

[c] Average number, based on data obtained under greenhouse conditions in New Jersey, USA

[d] Tinged green is lower in anthocyanin than mahogany

Materials and Methods

Plant Material

One to six plants of each of nine monoecious races were studied. Unless otherwise stated, these races were collected or developed by one of us (OS). Phenotypic characteristics of the nine races are given in Table 1. The genes conditioning some of these characteristics are known (for genetics of different characteristics see reviews by Zimmerman, 1958; Creech and Kramer 1959; also Stein 1961, 1967). The list of races follows.

'A39' was represented by two plants. This race was developed from a cross between R7, a sex-reversal mutant of 'Gamadon' (see below) and M3, an inbred of cultivar US3/415-9. A39 is distinguished by its strong male expression, due to the presence of *id* genes (George and Shifriss 1967) and extreme genetic instability (Shifriss 1960) that generates 3 to 20% sex mutants depending upon the environment in which this inbred is grown. – 'Afruri-3' (AF-3) was represented by one plant. Open pollinated seeds of this race were gathered from a population found along the banks of a river near the town of Elvanli, Turkey in 1966. No other populations or races or distinct deviants were found in the same area. The plant that was studied resulted from one generation of self-pollination. This race breeds true for a unique syndrome of growth characteristics, small seed size, high oil content, and dormancy of freshly harvested seed. It may also be tolerant to cold. – 'East Africa' (EA) was represented by six plants grown from seeds provided by Dr. Hava Stein of the Weizmann Institute of Science, Rehovot, Israel. EA probably produces the smallest seeds in this species. – 'Early Spineless' (ES) (Syn. 'Mautner') was represented by one plant of an advanced inbred. ES is distinguished by its rapid growth, earliness, and slender morphological structures. – 'Gamadon' (G) was represented by one plant of an advanced inbred. G is a selection from a Manchurian cultivar and is distinguished by its small plant size. It is highly unstable genetically with respect to sex expression. – 'Karsiyaka' (K) was represented by one plant. Open pollinated seeds of this race were gathered from a tree found growing in a park in Karsiyaka, Turkey in 1966. The plant studied resulted from one generation of self-pollination. K proved to be true breeding and is practically identical to the ornamental cultivar known in the seed trade as 'Sanguineus'. – 'Lakeland' (L) was represented by two plants grown from open pollinated seeds obtained from a tree five meters tall that flourished on a rubbish heap in Lakeland, Florida in 1967. L represents a distinct population that is well adapted to growing along irrigation canals in southern Florida. – 'Zanzibarensis-1' (Z-1) was represented by three plants grown from commercial seed samples provided by Joseph Harris Seed Company of Rochester, New York, and George W. Park Seed Company of Greenwood, South Carolina. Z-1 is distinguished by its huge leaves, large capsules, and large seeds that are black in color and square in shape. – 'Zanzibarensis-2' (Z-2) was represented by a clone obtained from a plant grown in a garden in Sturbridge, Massachusetts, in 1974. This race is similar to Z-1 except that its plant color is pure green and seed color is red.

The races were grown in pots or barrels in the greenhouse. Clonal plants, when needed, were obtained from shoot cuttings that rooted under mist in a propagation bed. Rooting was stimulated by treatment with 'Hormo-Root "B" ' (Hortus Products Co., Newfoundland, New Jersey), which includes indolebutyric acid.

The term race refers here to a population of plants that differs from other populations of the same species at one or more gene loci. The above listed races were selected for our study because they represent fairly well the wide range of genetic variation in this species. Most of the races probably differ from one another at many loci. An exception is the difference between races Z-1 and Z-2. These are found in the open pollinated cultivar known in the seed trade as 'Zanzibarensis'. Z-1 and Z-2 may differ at relatively few loci, perhaps at two loci only (see Stein 1967).

Cytological Techniques

Collection, fixation, enzyme treatment, staining, phase contract microscopy, and photomicrography were the same as described previously (Paris et al. 1978).

Nucleolus-chromosome Association

The nucleolus and the pachytene chromosomes are spread in the flattened PMC. Therefore, any chromosome region is likely, by chance, to be in contact with the nucleolus in a certain percentage of PMCs. Preliminary data showed that the frequency of contact between the nucleolus and all chromosome regions, excluding the regions of the short arms of chromosomes 2 and 7, is less than 2% in all races. In contrast, the frequency of contact between the nucleolus and the distal regions of the short arms of chromosomes 2 and 7 is greater than 5% in all races. On this basis, chromosomes 2 and 7 were deemed to be functionally associated with the nucleolus and to contain NORs. The frequency of association between the nucleolus and the NOR of a particular chromosome in any given race is here termed nucleolus association frequency (NAF). The NAF was determined from pachytene figures only. Synizesis was excluded because the chromosomes are not distinguishable from each other at this stage. For the purpose of determining NAF, cells in which the short arms of chromosomes 2 and 7 were so clumped with other chromosomes as to preclude their identification were considered to be in synizesis. Diplotene was also excluded because the nucleolar organizing chromosomes dissociate from the nucleolus during this stage.

Nucleolar Constriction (NC)

This term refers to a microscopically visible chromosomal constriction associated with nucleolar organization. An uncoiled chromosome segment followed distally by two unpaired satellites, it is synonymous with the term 'secondary constriction' used in its strict sense, i.e. the chromosomal constriction associated with the nucleolus, as distinguished from other (tertiary) constrictions that may be present in the chromosome complement. The short arm of either chromosome 2 or chromosome 7 exhibits an NC in most races.

Results

Chromosome Morphology

The only chromosomes which differ structurally between the races are the two nucleolar organizing bivalents, chromosomes 2 and 7. There are four distinct forms of chromosome 2 and five distinct forms of chromosome 7. And the races exhibit a total of six different combinations of these forms (Fig. 1). Chromosomes 2 and 7 of each of the races are described below, A39 being used as a standard for comparison (Paris et al. 1978).

Race A39

Chromosome 2 (Fig. 2a a′) has a long heterochromatic segment in the long arm and five heterochromatic segments in the short arm. The fifth (terminal) segment of the short arm is separated from the rest of the chromosome by an NC and is unpaired (seen as two satellites). Chromosome 7 (Fig. 2b b′) also has a heterochromatic segment in the long arm and five heterochromatic segments in the short arm. These five segments form a progression in size, the smallest being adjacent to the centromere.

Race K

Chromosomes 2 (Fig. 2c c′) and 7 (Fig. 2d d′) are the same as in A39.

Race G

The fifth segment (satellites) of the short arm of chromosome 2 (Fig. 2e e′) is smaller than that of A39 and K. Chromosome 7 (Fig. 2f f′) is the same as in A39 and K.

Race ES

Chromosome 2 (Fig. 2g g′) is the same as in A39 and K. The fourth segment from the centromere in the short arm of chromosome 7 (Fig. 2g g′) is euchromatic, except for a small dot of heterochromatin in the central portion of the segment. With regard to this segment, ES is unique among the nine races.

Race Z-2

The fifth heterochromatic segment of the short arm of chromosome 2 is in direct contact with the fourth seg-

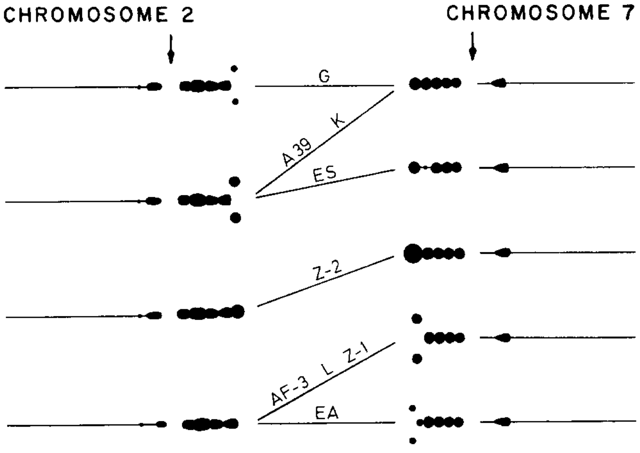

Fig. 1. Schematic representation of forms of the two nucleolar organizing chromosomes and their combinations exhibited by nine castor races. Four forms of chromosome 2 at left, five forms of chromosome 7 at right. Thickened portions of lines represent heterochromatic regions, unthickened portions of lines euchromatic regions, and gaps in the lines centromeres and NCs; centromeres are lined up by arrows. Six combinations and the races exhibiting each are indicated in center, see text

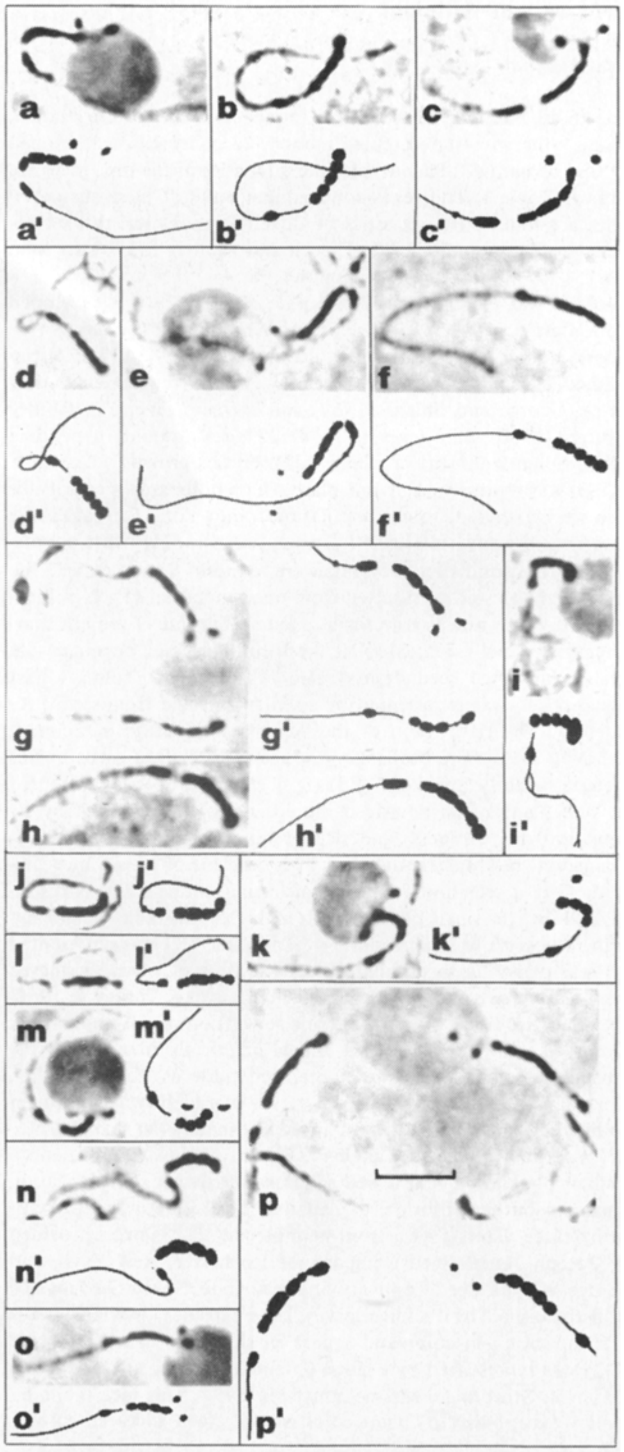

Fig. 2. Photomicrographs and interpretive drawings of chromosomes 2 and 7 in nine castor races (entire long arm not shown in all cases). a a′ – Chromosome 2 of A39. b b′ – Chromosome 7 of A39. c c′ – Chromosome 2 of K. d d′ – Chromosome 7 of K. e e′ – Chromosome 2 of G. f f′ – Chromosome 7 of G. g g′ – Chromosome 2 (top) and Chromosome 7 (bottom) of ES. h h′ – Chromosome 2 of Z-2. i i′ – Chromosome 7 of Z-2. j j′ – Chromosome 2 of AF-3. k k′ – Chromosome 7 of AF-3. l l′ – Chromosome 2 of L. m m′ – Chromosome 7 of L. n n′ – Chromosome 2 of Z-1. o o′ – Chromosome 7 of Z-1. p p′ – Chromosome 2 (left) and Chromosome 7 (right) of EA. Magnification bar represents 5 μm

ment and is paired (not seen as satellites) (Fig. 2h h′). The fifth heterochromatic segment of the short arm of chromosome 7 is also paired and is extremely large (Fig. 2i i′), two or three times the size of that in A39, K, G, and ES. The unique feature of Z-2 is that no NC was observed in either chromosome 2 or chromosome 7. Of the nine races, Z-2 possesses the largest amount of heterochromatin.

Race AF-3

Chromosome 2 (Fig. 2j j′) lacks the fifth segment of the short arm. Also, the proximal heterochromatic segment of the long arm is shorter than in A39, K, G, ES, and Z-2. The fifth heterochromatic segment of the short arm of chromosome 7 (Fig. 2k k′) is separated from the rest of the chromosome by an NC and is unpaired (seen as two satellites). The size of the segment constituted by the satellites is uncertain, due to its being unpaired and apparent size variability between cells, but is probably intermediate between that of A39, K, G, and ES on one hand and Z-2 on the other.

Race L

Chromosomes 2 (Fig. 2l l′) and 7 (Fig. 2m m′) are the same as in AF-3.

Race Z-1

Chromosomes 2 (Fig. 2n n′) and 7 (Fig. 2o o′) are the same as in AF-3 and L.

Race EA

Chromosome 2 (Fig. 2p p′) is the same as in AF-3, L, and Z-1. The fifth heterochromatic segment of the short arm of chromosome 7 (Fig. 2p p′) is separated into two parts. The proximal part is paired; the distal part is separated from the proximal by an NC and is unpaired (seen as two small satellites). The total size of the parts composing the segment appears to equal that of A39, K, G, and ES.

Table 2. Classification of nine castor races into three groups according to the NAFs of chromosomes 2 and 7. The NAFs were based on observation of 250 pachytene figures per race

		Nucleolar Association Frequency (%)		
Group	Race	Chromosme 2[a]	Chromosome 7[a]	Chromosome possessing a nucleolar constriction
1	A39	100.0	5.6	2
	G	100.0	6.0	2
	K	100.0	19.2	2
2	ES	100.0	100.0	2
	Z-2	100.0	100.0	None
	EA	88.8	100.0	7
3	AF-3	14.4	100.0	7
	Z-1	11.6	100.0	7
	L	10.8	100.0	7

[a] Refers to the short arm of this chromosome

Nucleolus Association Frequency (NAF)

The NAFs of both chromosome 2 and chromosome 7 are subject to great variability between races (Table 2), ranging from 10.8 to 100% in chromosome 2 and 5.6 to 100% in chromosome 7. Based on the NAFs of both chromosomes, the races can be classified into three groups:

In group 1, consisting of A39, G, and K, the NAF of chromosome 2 is high and the NAF of chromosome 7 is low.

In group 2, consisting of ES, Z-2, and EA, the NAFs of both chromosomes are high.

In group 3, consisting of AF-3, Z-1, and L, the NAF of chromosome 2 is low and the NAF of chromosome 7 is high.

Discussion

Intraspecific Chromosome Variations

Races of some plant species can be distinguished from one another by structural differences in their chromosomes. For example, races of *Zea mays* (maize) may differ in number, size, and position of their chromosome knobs (Longley and Kato 1965). And races of *Lycopersicon esculentum* (tomato) may differ in chromosome length, number of chromomeres, and structure of the short arm of the nucleolar organizing chromosome (Lesley 1938; Gottschalk 1954). Among races of maize, knob variation is most common and this variation can occur in any chromosome of the complement. But among races of tomato, the most common variations affect the short arm of the nucleolar organizing chromosome.

The present pachytene study of nine castor races has shown that microscopically visible structural changes in these races are limited exclusively to the two nucleolar organizing chromosomes and particularly in or near to their NORs (Fig. 1). Thus, unlike in maize, structural variations in tomato and castor races are confined largely or only to their nucleolar organizing chromosomes.

The above cited intraspecific chromosome variations in maize, tomato, and castor are not associated with any striking phenotypic changes at the organismal level, nor do they impair reproduction or modify the mating system. Whatever may be their biological significance, most of these variations affect heterochromatic segments. Maize has a dispersed heterochromatin whereas tomato and castor have a differentiated heterochromatin (see idiograms of maize, tomato, and castor in Neuffer et al. (1968), Khush and Rick (1968) and Paris et al. (1978), respectively). It is therefore tempting to suggest that the degree of tolerance of heterochromatin to structural changes is somehow related to the mode of its organization. This means that large heterochromatic blocks located mainly near centromeres are less tolerant to changes than interspersed segments. However, the nature of vulnerability of the heterochromatin to structural changes is not known.

A survey of spontaneously occurring and radiation induced chromosome mutants in castor has shown that these mutants are highly or completely sterile (Jelenkovic and Shifriss, unpublished). This fact together with our present results suggest that castor is very intolerant to reproduction of chromosome variants other than those associated with structural changes near or in their NORs.

NORs in Two Linkage Groups

The visual evidence for the location of the NORs in the short arms of chromosomes 2 and 7 in all races studied is the greater than 5% frequency of association between the nucleolus and each of these short arms in each of these races (see Materials and Methods, also Table 2). The presence of two or more NORs in different linkage groups is common in plants (see review by Gates 1942). In some genera, e.g. *Brassica*, this condition has been attributed to polyploid evolution (Kamala 1976). There have been suggestions that *Ricinus* is of polyploid origin (Richharia 1937; Jakob 1957, Narain and Singh 1968). These suggestions were based on the observation of meiotic 'secondary associations' in diploid races as well as in a haploid mutant. It was assumed that such associations reflect pairing between homologous chromosome parts. However, a recent meiotic study of a haploid castor seriously questions the validity of this assumption (Jelenkovic et al. in press). We favor the hypothesis that the NORs in castor have evolved through some intragenomic chromosome changes and that two non-linked NORs have a selective advantage over one NOR.

Location of Castor NORs

The short arms of chromosomes 2 and 7 are highly heterochromatic and structurally similar, each possessing up to five distinct segments. However, as Figure 1 illustrates, there exist racial variations in the structure of the short arms of both chromosomes. For example, the short arm of each chromosome may or may not possess an NC.

The association of the nucleolus with a chromosome possessing an NC is at the NC. The NC is located between the distal end of the fourth segment and proximal end of the fifth (satellites) (Fig. 1, and 2a c e g k m o) in seven races. In race EA, the NC is located within the fifth segment, resulting in a proximal paired portion and a distal unpaired portion appearing as two small satellites (Fig. 1 and 2p). The association of the nucleolus with a chromosome lacking an NC is at the terminal heterochromatic segment of the short arm, i.e., at the fifth segment or at the distal end of the fourth if the fifth is deficient (Fig. 1, and 2g h i p). Thus, the NOR of each short arm is located at one or more of several potential sites between the distal end of the fourth segment and the distal end of the fifth segment. A more precise localization of the NORs in castor would require critical mapping of rRNA genes as well as other genes which play a role in nucleolus organization (see review by Phillips 1978, for the use of special chromosome mutants and molecular hybridization in studies of the NOR in maize).

Variability in the NAF Value

In pachytene nuclei of castor, the two nucleolar organizing chromosomes, 2 and 7, are associated with a single nucleolus (for similar cases in other plant species see review by Jelenkovic and Harrington 1972). But the frequency of association of each of the two chromosomes with the nucleolus, the NAF value, depends on the race. In this respect, there are three groups of races. In group 1, the NAF of chromosome 2 is high and the NAF of chromosome 7 is low. In group 2, the NAFs of both chromosomes are high. And in group 3, the NAF of chromosome 7 is high and the NAF of chromosome 2 is low (Table 2).

In eight of the nine races, one of the nucleolar organizing chromosomes possesses an NC and the other lacks an NC (Fig. 1). In these races, the NAF of the chromosome possessing an NC is consistently 100% and the NAF of the chromosome lacking an NC is variable, 5.6 to 19.2% in six races (A39, G, K, AF-3, Z-1, L) and 88.8 to 100% in two races (EA and ES) (Table 2). It is evident that in seven of these eight races the chromosome lacking an NC is less prone to participate in nucleolar organization than the chromosome possessing an NC. But it is also clear that the absence or presence of an NC is not the only factor which affects such participation. Note that in race ES the NAFs of both chromosomes are 100%.

Race ES is of particular interest for another reason. A rare pachytene nucleus of ES contained two nucleoli, one of which was four times larger in size than the other. The large nucleolus was associated with chromosome 2 possessing an NC and the small nucleolus was associated with chromosome 7 lacking an NC.

Race Z-2 lacks an NC altogether but it forms a normal nucleolus and the NAF of each of its nucleolar organizing chromosomes is 100% (Fig. 1 and 2h i, Table 2).

Doerschug (1976) and Givens and Phillips (1976) suggested that in maize the NC represents the active site of nucleolar organization although this site contains relatively few rRNA cistrons as compared to the adjacent heterochromatin. The NC in both castor and maize may be the most active site of transcription. But the findings in races ES and Z-2 show that in castor a heterochromatic segment of the NOR is capable of organizing a nucleolus, that heterochromatic segments of 2 NORs are adequate for normal nucleolar organization, and that presence of an NC is not essential for nucleolar organization. These findings are compatible with the view that degree of chromosome transcriptional activity is related to extent of chromosome loop formation and is not necessarily related to degree of chromosome coiling (Monesi 1965; LaCour 1966).

Based on available literature on other aspects of the NOR we suggest here three interpretations, which are not mutually exclusive, to account for the racial variations in NAF values between the two nucleolar chromosomes.

First, the NAF value of each of the two nucleolar organizing chromosomes depends on the number of rRNA genes it carries; the higher the number the higher is the NAF value. In cases in which the NAF values of both chromosomes are 100%, each chromosome carries at least the minimum number of rRNA genes required for 100% association. But the two chromosomes may still differ in number of rRNA genes above that minimum. This interpretation implies that both frequency of association and relative contribution of each of these chromosomes to nucleolar organization are positively correlated with the number of the rRNA genes in the NOR. It has been known for some time that the number of rRNA genes is subject to wide variations within a species (Ritossa et al. 1966; Miller and Brown 1969). Also, there is a general, though not invariable, correlation between number of rRNA genes in an NOR and nucleolus size (see Flavell and O'Dell 1979).

Second, the two independent NORs have a functional relationship which affects their relative activity, including NAF. In the hybrid *Xenopus laevis* x *X. mulleri*, the dominance of the *X. laevis* NOR over the *X. mulleri* NOR has been attributed to such a relationship (Honjo and Reeder 1973).

Third, the NAF values of the two nucleolar organizing chromosomes are regulated by genes outside the NORs. A type of control of rRNA genes at a locus adjacent to the NOR has been reported in *Drosophila melanogaster* (Procunier and Tartof 1978). Also, in the hybrid *D. melanogaster* x *D. simulans*, the dominance of the *D. melanogaster* NOR (including NC) over the *D. simulans* NOR has been attributed to a heterochromatic segment located close to but outside the *D. melanogaster* NOR (Durica and Krider 1978). In wheat, it has been suggested that nucleolus formation by individual NORs is under complex genetic control (Flavell and O'Dell 1979).

Chromosome Morphology and Plant Phenotype

The nine races can be classified under two alternative groups of associated characteristics which we tentatively designate as syndrome-1 and syndrome-2. Each syndrome affects the structure and behavior of the nucleolar organizing chromosomes. Races A39, G, K, ES, and Z-2 (Fig. 1, Table 2) belong to syndrome-1. This syndrome consists of the following characteristics: (i) a relatively long heterochromatic segment at the proximal end of the long arm of chromosome 2, (ii) the presence of the fifth heterochromatic segment in the short arm of chromosome 2, (iii) 100% NAF for chromosome 2, and (iv) absence of an NC in chromosome 7. Races AF-3, L, Z-1, and EA (Fig. 1, Table 2) belong to syndrome-2. This syndrome consists of the following alternative characteristics: (i) a shorter heterochromatic segment at the proximal end of the long arm of chromosome 2, (ii) absence of the fifth heterochromatic segment in the short arm of chromosome 2, (iii) 11 to 89% NAF for chromosome 2, and (iv) the presence of an NC in chromosome 7.

It has not been established experimentally that the two alternative groups of associated characteristics are syndromes in the sense that each of them is inherited as a unit. If they are syndromes in this sense, there must be a mechanism which brings about simultaneous changes in amount of heterochromatin at two different sites in chromosome 2.

Z-1 and Z-2 are the two most closely related races, being indistinguishable except for differences in pigmentation and derived from the same cultivar. However, Z-1 exhibits syndrome-2 and Z-2 exhibits syndrome-1. It is therefore evident that these syndromes are not indicators of taxonomic affinities.

No consistent relationship exists between structural variations in the heterochromatin of the nucleolar organizing chromosomes and racial variations in plant phenotype. For example, races AF-3 and Z-1 differ distinctly in plant phenotype as well as in geographical origin and adaptation but they have morphologically identical nucleolar organizing chromosomes. By contrast, Z-1 and Z-2 are very closely related races and they exhibit great divergence in structure of their nucleolar organizing chromosomes (Fig. 1). Therefore, the variations in the heterochromatin of the nucleolar organizing chromosomes may affect either biochemical processes the consequences of which are not easily detected at the organismal level or functions unrelated to nuclear control of plant development.

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