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Recombination and genome size

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Summary. *Within* complements the chiasma frequency per chromosome, which directly reflects the amount of recombination, is generally closely correlated with chromosome length, i.e. the chromosomal DNA content. The correlation does not apply when comparisons are made *between* the complements of different species. Analyses of results from three Angiosperm genera show a progressive decrease in the chiasma frequency per picogram of DNA with increase in nuclear DNA amount.

Key words: Genome size – Chiasma frequency – Recombination – DNA content

Introduction

The amount of DNA in the chromosomes of eukaryotes is more, often much more than is required for transcription. There is disagreement about what the "excess" DNA does or does not do.

Some maintain it is junk or selfish (Doolittle and Sapienza 1980; Orgel and Crick 1980), others that is functional and, by implication, of adaptive significance (Cavalier-Smith 1978). The differing opinions are part and parcel of the long-standing controversy over the C-value paradox. There are, of course, well-established correlations between genome size, a measure and reflection of the nuclear DNA amount, and a number of phenotypic characters among both plants and animal species (Cavalier-Smith 1985). Leaving aside the question of how one should interpret these correlations, whether as causes or consequences, it is surprising that the evidence, to date, shows no relation between the DNA variation between species and the amount of recombination at meiosis; surprising because one would have expected change in the overall chromosome length and their constituent DNA molecules to influence directly the amount of recombination. What evidence there is shows that recombination varies quite independently of DNA amount (Cavalier-Smith 1985). On the strength of this the only generalisation which can be made is that the amount of recombination per unit length of DNA must, on average, decrease with increasing genome size (Cavalier-Smith 1985). The present results confirm the negative correlation but, in addition, demonstrate that the correlation is of a well-defined, consistent pattern.

As will be explained, to reveal the pattern one needs to take account of (1) the amount of recombination per unit of DNA rather than the total DNA and (2) the chromosome number.

Lathyrus

In Table 1 are the chromosomal DNA amounts in 12 *Lathyrus* species, along with the average chiasma frequencies at first metaphase of meiosis in pollen mother cells. The obvious way to find out if the chiasma frequencies, a direct index of recombination, are correlated with the DNA amount is to plot one against the other. They are not (Fig. 1 a), as is confirmed by a regression analysis of variance ($P = > 0.10$). On the face of it the chiasma frequency bears no relation to the DNA amount.

There is an alternative approach to interpreting these results, namely to compare the chiasma frequency *per picogram of DNA* with the total DNA amount for each species (Fig. 1 b). The rationale of this comparison, and its justification, are as follows. Assume first, as a null hypothesis, that the chiasma frequency increases proportionally with increasing DNA amount, that is to say, the chiasma frequency doubles with doubling of the DNA quantity; second, that the DNA amount is constant within the species scored. With regard to the

Table 1. DNA amounts and the mean chiasma frequencies in pollen mother cells of diploid species of *Lathyrus, Lolium* and *Petunia.* All the data are from colleagues or ex-colleagues to whom we express thanks. The DNA value for *Lathyrus montanus* along with the chiasma frequencies of all *Lathyrus* species, are from Hazarika (1966). The remaining *Lathyrus* DNA values are from Narayan (1982). Chiasma frequencies and DNA values for the *Lolium* species are from Jones (1966) and Hutchinson, Rees and Seal (1979) respectively, the *Petunia* data from White (1984). Chiasma frequencies per pollen mother cell in each species are derived from scoring 20 cells in an average of 6 plants. The DNA values from populations of each species are the means of an average of 5 plants

	n	DNA amount (2C)	Chiasma frequency	Chiasma frequency / DNA amount	Chiasma frequency-*n* / DNA amount
Lathyrus					
L. angulatus	7	10.76	17.45	1.62	0.97
L. annuus	7	14.95	15.34	1.02	0.57
L. articulatus	7	12.15	16.16	1.33	0.75
L. cicera	7	14.64	15.84	1.08	0.60
L. hirsutus	7	20.51	17.75	0.87	0.52
L. sativus	7	16.78	12.79	0.76	0.35
L. tingitanus	7	22.08	14.41	0.65	0.34
L. nisssolia	7	12.92	15.83	1.23	0.68
L. latifolius	7	24.78	14.99	0.60	0.32
L. maritimus	7	13.15	14.20	1.08	0.55
L. montanus	7	20.30	14.06	0.68	0.34
L. sylvestris	7	24.65	14.63	0.59	0.31
Lolium					
L. perenne	7	4.16	12.41	2.98	1.30
L. multiflorum	7	4.31	12.77	2.96	1.34
L. rigidum	7	4.33	12.61	2.91	1.30
L. temulentum	7	6.23	14.24	2.29	1.16
L. remotum	7	6.04	14.12	2.34	1.18
L. loliaceum	7	5.49	13.99	2.55	1.27
Petunia					
P. parodii	7	3.00	10.34	3.45	1.11
P. axillaris	7	2.81	11.67	4.15	1.66
P. hybrida	7	2.73	11.96	4.38	1.82
P. inflata	7	2.41	11.77	4.88	1.98
P. parviflora	9	1.73	16.48	3.82	4.32

first assumption, comparisons *within* complements of a wide range of species (Mather 1937) have confirmed directly the proportionality between the chiasma frequency and chromosome length (in modern parlance the chromosomal DNA amount). Such proportionality is demonstrated in Fig. 2, which is derived from the detailed results of Shaw and Knowles (1976). There are it is true exceptions, notably species whose chromosomes display a large disparity in length and which include very small chromosomes with a disproportionately high chiasma frequency. We shall return to this particular phenomenon later. As for the second assumption, it is widely accepted that the DNA amount is remarkably constant within populations. Indeed, with few exceptions, and in the absence of gross numerical or structural change, there is a remarkable constancy in the DNA amount not only within but between populations of the same species. Moreover, it can be estimated with reasonable accuracy and the DNA values taken as fixed values. Given these assumptions one should expect on plotting the chiasma frequency per picogram of DNA against the total DNA amount for each species a straight line with a slope of O. In *Lathyrus* what one finds, in contrast, is a negative regression, significant at the 1 per cent level (Fig. 1 b). The conclusion is that the chiasma frequency per unit of DNA decreases with increasing DNA amount, that is to say with genome size.

Lolium

In Fig. 1 c the chiasma frequencies from 6 *Lolium* species are plotted against the total chromosomal DNA amounts (from Table 1). Here there is a positive and highly significant correlation between them, a situation

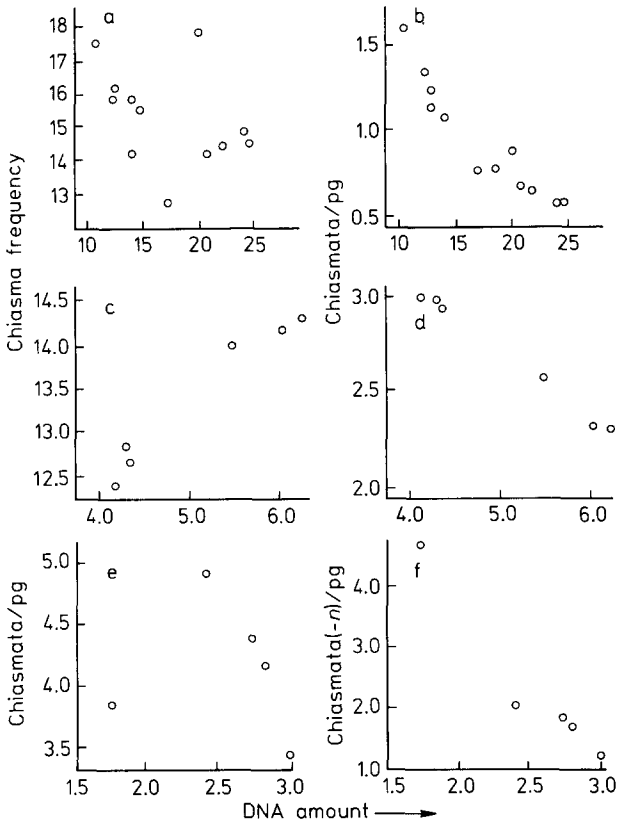

Fig. 1. **a** The mean chiasma frequency per pollen mother cell in *Lathyrus* species plotted against the nuclear DNA amount. **b** The mean chiasma frequency per picogram of DNA plotted against the nuclear DNA amount. **c** The mean chiasma frequency per pollen mother cell in 6 *Lolium* species plotted against the nuclear DNA amount and the mean frequency per picogram plotted against the DNA amount **d.** In **e** are the mean chiasma frequencies per picogram of DNA plotted against the nuclear DNA amount in 5 *Petunia* species; in **f** the chiasma frequency per picogram minus *n* is plotted against the nuclear DNA amount. All DNA values are in picograms per 2C nucleus

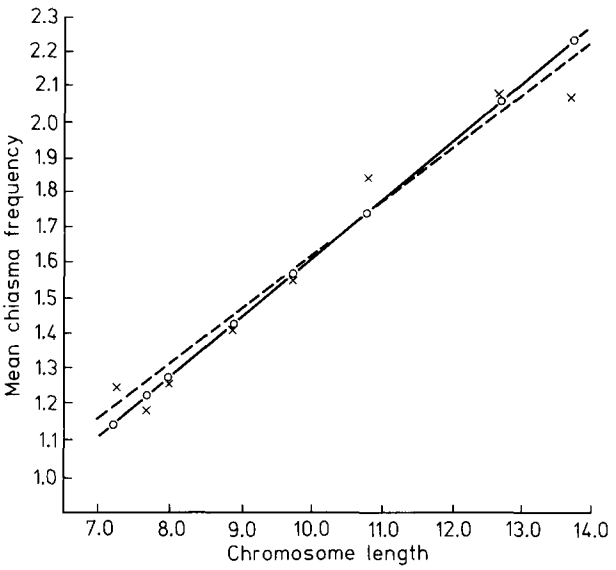

Fig. 2. The mean chiasma frequency of the eight largest autosomes in spermatocytes of *Caledia* species *nova 1* plotted against the mitotic chromosome length (from the data of Shaw and Knowles with their permission). *Solid line and open circles,* the values expected assuming the chiasma frequency, is directly proportional to length; *crossess (and dotted line)* from the values observed

that would appear to bear no relation to that in *Lathyrus.* When, however, the number of chiasmata per picogram of DNA is plotted against the total DNA amount (Fig. 1d) the relation between the two parameters corresponds precisely with that in *Lathyrus* in showing a negative regression (significant at the 0.1% level), a decrease in chiasma frequency per unit length with increase in genome size.

Petunia

Adopting the same procedure of plotting the number of chiasmata per picogram of DNA against the total DNA (from Table 1) does not reveal the same neat pattern as in *Lathyrus* and *Lolium* (Fig. 1e). The results, it seems, are completely different and out of step. The difference is more apparent than real.

It will be seen from Table 1 that the *Petunia* species have different chromosome numbers. One has 9, the others 7. There are good reasons for taking account of this difference. Each bivalent within a complement acquires at least one chiasma independently of its length and, consequently, DNA content. This was recognised and appreciated some 50 years ago, in particular by Mather (1937). The 'd' and 'i' model of chiasma distribution which he derived from his observations allocates to each and every bivalent an "obligatory" chiasma quite independently of its length, in sharp contrast to the subsequent chiasmata which are directly dependent upon length. It is this obligatory chiasma which accounts for the disproportionally high chiasma frequency in very small chromosomes. Mather's observations and interpretation are as valid now as then. This obligatory chiasma is catered for in the *Petunia* data by plotting the chiasma frequency *minus n* (the basic number) per picogram of DNA against the total DNA (Fig. 1f). This figure shows a negative relationship such as was established for *Lathyrus* and *Lolium.* The regression is significant ($P = < 0.01$).

Conclusion

The analyses above show, for species within these Angiosperm genera, a remarkably consistent negative correlation between the capacity for chiasma formation and genome size, given that one takes account of the chiasma frequency per picogram of DNA (or other standard unit) and, also, of the chromosome number. It is true that no account was taken of chromosome number in *Lathyrus* or *Lolium*. That the correlation was not obscured in these genera is understandable because the chromosome number is constant among species. Using the same "formula" applied to *Petunia* namely

$$\frac{\text{chiasma frequency } (\textit{minus } n) \text{ per picogram of DNA}}{\text{total nuclear DNA amount,}}$$

and plotting the results for all three genera together one may extend the comparison to embrace not only species within but, also, between genera (Fig. 3). The points fall on a relatively smooth curvilinear regression line but one which shows a particularly rapid change up to about 6 pg.

Whether this curve will accommodate the results from a wider range of genera and species remains to be seen. It is certain that it will not accommodate all. By virtue of genotypic control and of chromosome structural change meiosis in many species is anomalous. In *Drosophila* species for example meiosis, albeit in one sex, is achiasmate. A single gene can reduce the chiasma frequency to nil (Rees 1961). Differentiation may also profoundly influence the chiasma frequency with the result that the frequency varies substantially between "male" and "female" meiosis within the same individual (John and Lewis 1965). It is obvious therefore that no claim could be made on the basis of the results we present that genome size is the only factor affecting the amount of recombination. Nevertheless, in a crude sense, there is a convincing argument that it is an important one. The same conclusion may be drawn from a different yet comparable analysis by von Wettstein et al. (1984).

From the standpoint of the causal relationship between chromosomal DNA and chiasma frequency it is worth emphasising the contrast between the situation which applies within chromosome complements of a species and that which applies between the chromosome complements of different species. As mentioned earlier the chiasma frequency variation within the complement is generally closely and positively correlated with chromosome length and DNA content. Between complements our results confirm that they are not; further, that the chiasma frequency decreases progressively per unit length with increase in DNA amount. We shall consider the possible causes for this contrast in a later paper. In the meantime it is worth recalling that change in DNA amount is accompanied by change in DNA composition, for example an increase in the proportion of repetitive DNA with increase in amount (Narayan 1982). In at least some of the repetitive segments, such as those located in heterochromatin, there is no chiasma formation. Equally important, perhaps, these highly repetitive sequences may supress recombination in their vicinity (John and King 1980). This is but one of many possible explanations for the results. In so far as the explanation is valid it is predictable that change in recombination with genome size in particular genera will reflect the particular nature of change in DNA composition which accompanies the change in amount.

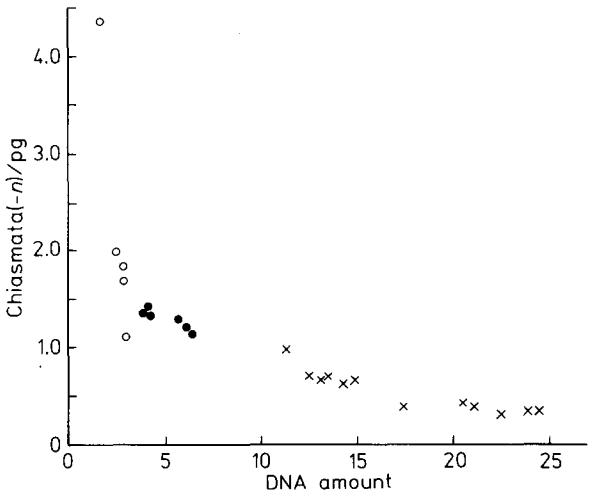

Fig. 3. The mean chiasma frequency minus *n* per picogram of DNA plotted against the 2C nuclear DNA amount in species of *Petunia* (open circles), *Lolium* (*closed circles*) and *Lathyrus* (*crosses*)

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