Meiotic pairing in autohexaploid *Lathyrus*: a mathematical model

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A mathematical meiotic pairing and chiasma model is described for a hexaploid. It estimates, on the basis of observations on chromosome associations at metaphase I of meiosis, the frequencies of initial hexavalent, quadrivalent and bivalent pairing, as well as the frequency of chiasmate association of the two chromosome arms, both after multivalent and after bivalent pairing. These estimates use all nine degrees of freedom available (10 configuration types distinguished). Although potential complications like multiple pairing partner exchange and interstitial chiasma formation are not accommodated by the model, a very close fit is found between the configuration frequencies observed in *Lathyrus palustris* ($2n = 6x = 42$) and those reconstructed on the basis of the model. This does not necessarily imply that the model fully represents biological reality, but at least it shows that the arms are significantly different in respect of chiasma formation and that chiasma frequencies may differ between multivalent and bivalent pairing. The hexavalent pairing frequency, as estimated by correcting metaphase frequencies for failure of chiasma formation, was only slightly lower than theoretically expected for an autohexaploid. However, the pairing of the six homologous chromosomes as a quadrivalent + a bivalent was considerably lower than with random pairing. The frequency of pairing as three bivalents was correspondingly higher.

Keywords: autohexaploid, *Lathyrus palustris*, mathematical model, meiosis, multivalent.

Introduction

True natural autohexaploids are rare. There is still some doubt about the well-known example *Phleum pratense* (Nordenskiöld, 1949, 1953; Sybenga, 1992). A few more species may be autohexaploids (Mosquin, 1967), but there is usually insufficient certainty, and meiosis tends to show very low multivalent frequencies. Natural and artificial apomictic autohexaploid grasses have been reported (see, for instance, Kindiger & Dewald, 1994) but these do not reproduce generatively, and details of their meiosis have not been published.

In a previous paper (Khawaja *et al.*, 1995) the meiotic behaviour of *Lathyrus palustris* L. ($2n = 6x = 42$) was described, and it was concluded to be an autohexaploid. Comparison of the observed meiotic metaphase I configuration frequencies with those predicted by the model of Jackson & Casey (1982), although not contradicting this conclusion, showed large differences. That model is based on a frequency of hexavalent pairing of 8/15, a frequency

of quadrivalent + bivalent pairing of 6/15 and a frequency of pairing as three bivalents of 1/15. This is a reasonable assumption when pairing is random and synaptic initiation is concentrated at the ends of the chromosomes. It results in a star-like pairing configuration when all six chromosomes are completely paired and the points of partner exchange are located in the middle of the chromosomes (Fig. 1a). The chiasmate association frequency of all arms (*c*) was assumed to be equal and readily derived from the observed configurations' frequencies. It may vary between 0 and 1.

A multivalent frequency lower than predicted on the basis of a random pairing model is often interpreted to result from low pairing affinity between some or all of the constituent genomes. The group of Kimber in Missouri has developed sets of models for polyploid hybrids with varying genome combinations. The set constructed for pentaploids by Espinasse & Kimber (1981) and an amended version by Chapman & Kimber (1992) are close to what is needed for hexaploids. In these models, like in that

Fig. 1 (a) One example of hexavalent pairing with one pairing partner switch at the middle of the chromosomes, an idealized situation; chromosomes numbered 1–6; chromosome arms A and B, the latter being shorter. Pairing is between A1 and A6, B1 and B2, A2 and A3, B3 and B4, A4 and A5, B5 and B6. One of the 225 possible combinations, 120 of which are hexavalents. (b) One example of quadrivalent with bivalent pairing; the quadrivalent has one partner switch: one of the 225 combinations, 90 of which are quadrivalent + bivalent. The remaining 15 are sets of three bivalents, not shown here.

of Jackson & Casey (1982), the average arm association frequency c is used, and is considered to be a measure of overall pairing affinity. It is combined with a factor x , measuring relative affinity between the most related two genomes in a polyploid hybrid, and varying between 0.5 and 1. It is derived from the relative multivalent frequencies. If c is high and $x = 0.5$, the conclusion is that the plant concerned is an autopolyploid. The assumptions on which these models are based are not identical to those of Jackson & Casey (1982) and the model presented here. The limitations and relative merits of such models have been discussed by Sybenga (1992, 1995).

It has appeared that triploid and tetraploid models, when designed both for polyploid hybrids and for autopolyploids, can be considerably improved by estimating separate chiasmate association frequencies for the two arms, and also for multivalent and bivalent pairing, instead of simply using a single arm association factor c (Sybenga 1975a,b, 1992, 1994, 1995). Therefore, it is of interest to develop a model for hexaploids in which arm association frequencies are similarly estimated separately. Although the present model has not been designed for hexaploid hybrids, it may be reasonable to conclude that when the multivalent frequencies are low some or all of the genomes are less closely related than in an autohexaploid. However, as there are also other factors that reduce multivalent frequencies, this conclusion is not necessarily always justified. The present model, therefore, does not go

as far as directly estimating preferential pairing or pairing affinity between the constituent genomes. Satisfactory models that can do this at the hexaploid level would be rather difficult to develop.

Results

The model

One set of six homologous chromosomes is considered. It is assumed that long-distance attraction determining which chromosome segments will ultimately be able to pair and form chiasmata precedes chiasma formation, and that it is concentrated near the ends of the chromosomes. This implies that in this model at most one pairing partner switch will occur. Each chromosome may pair with each one of five partners such that there are $(5 \times 6)/2 = 15$ different pairing combinations for each arm. Assuming the arms to pair independently there is a total of $15 \times 15 = 225$ different combinations. When analysing the different combinations, it is seen that with random pairing 120 or $8/15 = 0.53333$ result in hexavalents, 90 or $6/15 = 0.4$ result in quadrivalents with a bivalent (Fig. 1) and $1/15 = 0.06667$ result in three bivalents. The multivalents have one partner switch per chromosome. This approach is similar to that of Sybenga (1975a,b, 1994) for tetraploids and that of Jackson & Casey (1982) for a range of polyploids, including hexaploids, but different from that of Driscoll *et al.* (1979) and Espinasse & Kimber (1981) for polyploids in general. The importance of the difference is discussed by Sybenga (1992, 1995). With preferential pairing between specific chromosomes, the multivalent frequencies are lower than those given above. As mentioned above, factors other than affinity may reduce multivalent pairing and there also are several factors increasing multivalent frequencies. Such effects have been discussed by Sybenga (1995).

In the following the unit of calculation is one chromosome, and the frequency or probability expressions relate to what happens or may happen to a single chromosome.

Assuming that all chromosomes actually pair, the frequency of a chromosome being involved in hexavalent pairing can be given as fh , in quadrivalent with bivalent pairing as fq and in pairing as three bivalents as fb , the sum equalling 1.

Each chromosome has two arms, arm A and arm B (Fig. 1), with chiasmate association frequencies a and b , respectively. If chiasma formation is not identical after bivalent and multivalent pairing, for which there are sound reasons (Sybenga 1992, 1995), chias-

mate association of arm A may be designated as *ah* after hexavalent pairing, as *aq* after quadrivalent pairing, and as *ab* after bivalent pairing. Similarly, *bh*, *bq* and *bb*, respectively, apply for arm B. It is assumed that there is no interference across the centromere and/or the point of partner switch. Using the general chiasmate association factors *a* and *b*, after bivalent pairing a ring bivalent is formed with a frequency of *a.b*, an open bivalent with a frequency $(1-a).b + (1-b).a$, and two univalents $(1-a).(1-b)$. For multivalents, similar relations can be given. A chromosome being involved in a ring hexavalent, for instance has a frequency $a^3.b^3$, in a chain hexavalent a frequency $3.(1-a).a^2.b^3 + 3.(1-b).b^2.a^3$, etc. This is also the frequency of occurrence of these configurations.

All together the relations in Table 1 can be derived. Note that single univalents are combined with the configurations with uneven chromosome numbers (quivalent, trivalent). The remaining univalents are treated as pairs.

In meiotic diakinesis/metaphase preparations the frequencies of 10 different configurations can be determined: ring hexavalents, chain hexavalents, quivalents with univalent, pairs of trivalents (no univalents), ring quadrivalents, chain quadrivalents, trivalents with univalent, ring bivalents, open bivalents and pairs of univalents. Hexavalents, quivalents and a pair of trivalents are unique for hexavalent pairing, ring quadrivalents are unique for quadrivalent pairing, but all other configurations have more than one origin. Chain quadrivalents and trivalents with univalent are derived from hexavalent pairing and quadrivalent+bivalent pairing. Ring bivalents are derived from quadrivalent+bivalent pairing and from three-bivalent pairing, and open bivalents and pairs of univalents are derived from all three pairing categories. In the case where two trivalents with two univalents occur in the same cell, there are two possibilities: (i) the two univalents originate from a potential bivalent and the two trivalents are a trivalent+trivalent combination derived

Table 1 Formula for frequencies of meiotic pairing configurations in an autohexaploid

Configuration	Formula
<i>After hexavalent pairing:</i>	
Ring hexavalent	$fh.ah^3.bh^3$
Chain hexavalent	$3fh.\{ah^2.(1-ah).bh^3 + ah^3.bh^2.(1-bh)\}$
Quivalent + univalent	$6fh.ah^2(1-ah).bh^2.(1-bh)$
Two trivalents	$3fh.ah^2(1-ah).bh^2.(1-bh)$
Quadrivalent + open bivalent	$3fh.\{ah.(1-ah)^2.bh^3 + ah^3.bh.(1-bh)^2\}$
Quadrivalent + two univalents	$3fh.\{ah.(1-ah)^2.bh^2.(1-bh) + ah^2.(1-ah).bh.(1-bh)^2\}$
Trivalent + open bivalent + univalent	$6fh.\{ah.(1-ah)^2.bh^2.(1-bh) + ah^2.(1-ah).bh.(1-bh)^2\}$
Trivalent + three univalents	$6fh.ah.(1-ah)^2.bh.(1-bh)^2$
Three open bivalents	$fh.\{ah^3.(1-bh)^3 + (1-ah)^3.bh^3\}$
Two open bivalents + 2 univalents	$3fh.\{ah.(1-ah)^2.bh.(1-bh)^2 + ah^2.(1-ah).(1-bh)^3 + (1-ah)^3.bh^2.(1-bh)\}$
Open bivalent + four univalents	$3fh.\{ah.(1-ah)^2.(1-bh)^3 + (1-ah)^3.bh.(1-bh)^2\}$
Six univalents	$fh.(1-ah)^3.(1-bh)^3$
<i>After quadrivalent with bivalent pairing:</i>	
Ring quadrivalent	$fq.aq^2.bq^2$
Chain quadrivalent	$2fq.\{aq^2.bq.(1-bq) + aq.(1-aq).bq^2\}$
Trivalent + univalent	$4fq.aq(1-aq).bq.(1-bq)$
Two open bivalents	$fq.\{aq^2.(1-bq)^2 + (1-aq)^2.bq^2\}$
Open bivalent + two univalents	$2fq.\{aq.(1-aq).(1-bq)^2 + (1-aq)^2.bq.(1-bq)\}$
Four univalents	$fq.(1-aq)^2.(1-bq)^2$
Ring bivalent	$fq.ab.bb$
Open bivalent	$fq.\{ab.(1-bb) + (1-ab).bb\}$
Two univalents	$fq.(1-ab).(1-bb)$
<i>After three-bivalent pairing:</i>	
Ring bivalent	$3fb.ab.bb$
Open bivalent	$3fb.\{ab.(1-bb) + (1-ab).bb\}$
Two univalents	$3fb.(1-ab).(1-bb)$

See text for definitions.

from hexavalent pairing; and (ii) the two univalents are each associated with a trivalent, and there are two trivalent+univalent combinations. In the present example this did not occur. If it does, the trivalent+trivalent frequency, theoretically equalling one half the quinquivalent frequency (see Table 1) can be estimated separately and this value should be subtracted from the two-trivalent+univalent frequency to obtain the value for the trivalent+univalent frequency for this particular class of cells.

The nine degrees of freedom in the 10 classes of observations are theoretically sufficient to estimate three pairing parameters (fh , fq and fb) and six chiasma parameters (ah , bh , aq , bq , ab , bb), but it depends on the construction of the model whether each parameter has an appropriate degree of freedom. In a first simple test it may suffice to assume that $fh = 8/15 = 0.53333$, $fq = 6/15 = 0.4$ and $bq = 1/15 = 0.06667$ and that chiasmate association frequencies are independent of the pairing system. Then only an average a and b are estimated, and seven degrees of freedom remain unused and available for a test. Estimates for a and b are derived as follows.

The frequency of chromosomes with both arms bound by one or more chiasmata, the frequency of those with one arm bound, the other not bound, and the frequency of chromosomes with neither arm bound, are determined. In ring hexavalents all six chromosomes have both arms bound. In chain hexavalents four chromosomes have both arms bound whereas two have either arm A or arm B not bound. In quinquivalents with univalent three chromosomes have both arms bound, two have one arm bound, the other not, and one chromosome (the univalent) has neither arm bound, etc. The overall frequency of chromosomes with both arms bound can be expressed as $a.b$, the frequency of chromosomes with one arm bound and the other not, by $\{a.(1-b) + (1-a).b\}$. Chromosomes with neither arm bound have a frequency of $(1-a).(1-b)$. As these three formulae add to unity, there are only two degrees of freedom, sufficient for estimating the parameters a and b .

$$m = (6rhex + 4chex + 3quin + 2triv/triv + 4rquad + 2cquad + triv + 2rbiv)/total = a.b$$

$$n = (2chex + 2quin + 4triv/triv + 2cquad + 2triv + 2obiv)/total = a.(1-b) + (1-a)b = a + b - 2ab$$

$$\text{neither arm associated: } (quin + triv + univ)/total = (1-a).(1-b) = 1 - a - b + ab,$$

where m and n are auxiliary parameters used to simplify the calculations, $rhex$ equals the number of chromosomes associated into ring hexavalents, $chex$

those in chain hexavalents, $quin$ those in quinquivalents with the accompanying univalent, $triv/triv$ those in the combination of two trivalents, $rquad$ those in ring quadrivalents, $cquad$ those in chain quadrivalents, $triv$ those in trivalents with accompanying univalent, $rbiv$ those in ring bivalents, $obiv$ those in open bivalents and $univ$ those in univalents not accompanying quinquivalents and trivalents; $total$ equals all chromosomes in all cells scored.

As $b = m/a$ and thus $n = a + m/a - 2m$, or $a + m/a - (n + 2m) = 0$, a quadratic equation can be derived: $a^2 - (n + 2m).a + m = 0$. The same applies to b , and thus two roots can be derived:

$$a = \{n + 2m + \sqrt{((n + 2m)^2 - 4m)}\}/2$$

and

$$b = \{n + 2m - \sqrt{((n + 2m)^2 - 4m)}\}/2.$$

If it is suspected that the chromosomes do not pair according to the simple 'random' system, specific multivalent and bivalent pairing factors can be estimated. Firstly, the hexavalent pairing frequency (fh) will be considered. The four configurations specific for hexavalent pairing are ring hexavalents, chain hexavalents, quinquivalents with univalent and a pair of trivalents. The frequency formulae for the latter two differ only by a factor of 2 (see Table 1) and they can be combined or either one of the two can be taken to represent both. Thus there are three independent equations (the fourth is the sum of all configurations minus these three), with three degrees of freedom, sufficient for estimating three parameters: fh , ah and bh . The equations (see Table 1) can be reduced to:

$$rhex = fh.ah^3.bh^3$$

$$chex = 3fh.(ah^3.bh^2 + ah^2.bh^3 - 2ah^3.bh^3)$$

$$quin = 6fh.(ah^2.bh^2 - ah^3.bh^2 - ah^2.bh^3 + ah^3.bh^3)$$

which, introducing auxiliary parameters eh and dh , via:

$$eh = ah + bh = \frac{12rhex + 2chex}{6rhex + 2chex + quin}$$

and

$$dh = ah.bh = \frac{6rhex}{6rhex + 2chex + quin}$$

leads to:

$$ah = (eh + \sqrt{eh^2 - 4dh})/2$$

$$bh = (eh - \sqrt{eh^2 - 4dh})/2$$

and

$$fh = rhex/(ah^3.bh^3).$$

The frequency of hexavalent pairing (fh) can also be derived from ($rhex + chex + quin + triv/triv$) divided by an appropriate function based on ah and bh , and this may give slightly different results. For simplicity, only the formula shown above has been applied, which is theoretically sufficient.

A similar approach is possible for estimating quadrivalent + bivalent pairing (fq) and aq and bq . However, here only one specific configuration is available: the ring quadrivalent ($rquad$). Chain quadrivalents ($cquad$) and trivalents with univalent ($triv$) can also form after hexavalent pairing. It is necessary, then, first to estimate the frequencies of these two configurations after hexavalent pairing from ah , bh and fh . This is simply carried out using the formulae from Table 1. What remains after subtraction from the observed frequencies are $cquadq$ and $trivq$ to be ascribed to quadrivalent + bivalent pairing. We now have:

$$\begin{aligned} rquad &= fq.aq^2.bq^2 \\ cquadq &= 2fq.(aq^2.bq + aq.bq^2 - 2aq^2.bq^2) \\ trivq &= 4fq.(aq.bq - aq^2.bq - aq.bq^2 + aq^2.bq^2) \end{aligned}$$

and (see Sybenga 1975a,b)

$$fq = \frac{4rquad + 2cquadq + trivq}{16rquad}.$$

Via

$$dq = aq.bq = \frac{4rquad}{4rquad + 2cquadq + trivq}$$

and

$$eq = aq + bq = \frac{8rquad + 2cquadq}{4rquad + 2cquadq + trivq}$$

estimates of aq and bq are obtained from dq and eq :

$$aq = (eq + \sqrt{eq^2 - 4dq})/2$$

$$bq = (eq - \sqrt{eq^2 - 4dq})/2$$

in parallel to ah and bh from dh and eh for hexavalent pairing.

The three-bivalent pairing frequency fb is estimated as $(1 - fh - fq)$. More indirect are the estimates of the arm association factors ab and bb . They apply to three-bivalent pairing, but also to the bivalent of quadrivalent + bivalent pairing. When the average a and b are known, as well as ah , bh , aq and bq , the

values of ab and bb can be derived from:

$$\begin{aligned} a &= fh.ah + 2fq.aq/3 + fq.ab/3 + fb.ab \\ &= fh.ah + 2fq.aq/3 + (fq/3 + fb).ab \end{aligned}$$

or:

$$ab = \frac{a - fh.ah - 2fq.aq/3}{fq/3 + fb}$$

and

$$bb = \frac{b - fh.bh - 2fq.bq/3}{fq/3 + fb}.$$

In practice, especially when some critical configurations are rare, or when interference operates, the estimated configuration frequencies for hexavalent and quadrivalent pairing that have to be subtracted from the observed frequencies may be high, and then negative values may remain. Clearly, the more derived the estimates are the more liable they are to statistical error.

Application to observations

In Table 2 the derived and assumed pairing parameters fh , fq and fb and chiasma parameters a , b , ah , bh , aq , bq , ab and bb are shown. They have been derived from observations that are given in column

Table 2 *Lathyrus palustris* L., $2n = 6x = 42$. Estimates of pairing parameters (fh , fq , fb) and chiasma parameters (ah , bh , aq , bq , ab , bb)

C	D	F
$a = 0.989755$	0.989755	0.989755
$b = 0.581673$	0.581673	0.581673
$fh = 0.533333$	0.521285	0.521285
$ah = 0.989755$	0.987348	0.987348
$bh = 0.581673$	0.662225	0.662225
$fq = 0.4$	0.249275	0.251364
$aq = 0.989755$	1.000781	0.987303
$bq = 0.581673$	0.684982	0.691443
$fb = 0.066667$	0.229440	0.227351
$ab = 0.989755$	0.997839	0.995108
$bb = 0.581673$	0.311144	0.387595

C: Pairing random, all chiasma parameters equal to average a and b . D: All parameters as estimated from the observations using the formulae in Table 1. F: Like D, but two trivalents with univalent assumed instead of the observed one. For the original observations see column A of Table 3.

See Khawaja *et al.* (1995).

Table 3 *Lathyrus palustris* L. $2n = 6x = 42$; 50 cells at metaphase I of meiosis

	A	B	C	D	E	F	G
<i>rhex</i>	51	0.1457	35.62	51.00	51.00	51.00	43.9
<i>chex</i>	80	0.2286	77.96	80.00	80.00	80.00	71.9
<i>quin</i>	2	0.0057	1.59	2.00	2.00	2.00	19.6
<i>triv/triv</i>	0	0	0.80	1.00	1.00	1.00	—
<i>rquad</i>	41	0.0781	46.40	41	37.30	41	50.9
<i>cquad</i>	78	0.1486	123.57	78	79.36	78	81.9
<i>triv</i>	1	0.0019	2.55	1.00	2.00	2.00	51.9
<i>rbiv</i>	128	0.1219	120.90	127.21	131.81	126.01	125.2
<i>obiv</i>	280	0.2667	233.74	277.59	276.98	277.99	144.8
<i>univ</i> (pair)	3	0.0029	2.43	3.21	2.47	2.01	80.0

Total 2100 chromosomes

A: Observed numbers of configurations. B: Relative frequencies derived from A by multiplying the observed numbers of configurations by the number of chromosomes involved in the configuration concerned (six for hexavalents, etc.) and dividing by the total number of chromosomes (2100). C: Numbers expected on the basis of random pairing; $fh = 0.53333$, $fq = 0.4$, $fb = 0.066666$, average a and b as given in Table 2. D: All parameters as estimated. E: Expected numbers with fh , fq and fb as estimated, ah and bh as estimated, $aq = ah$ and $bq = bh$ and ab and bb derived from average a and b in combination with ah and bh . F: Like D, but two trivalents with univalent assumed instead of the observed one. G: Expected according to Jackson & Casey (1982), partly random chiasma distribution, $P = c = 0.785$.

Data from Khawaja *et al.* (1995).

A of Table 3. The different columns of Table 2 represent different combinations of estimated and assumed parameter values, and these have been used to calculate the numbers of configurations presented in columns C–F of Table 3. In Table 3, as noted above, column A gives the observed numbers in 50 cells of hexaploid *Lathyrus palustris*, $2n = 6x = 42$ (Khawaja *et al.*, 1995). The configurations actually observed were occasionally more complex than suggested by the terms ‘ring hexavalent’, ‘chain hexavalent’, etc. Interstitial chiasmata were not rare and some large configurations were hard to interpret. However, as explained by Sybenga (1975a,b), in these models arm association frequencies and not chiasma frequencies are dealt with and interstitial chiasmata can usually be assigned to specific arms. For instance, a typical ‘frying pan’ multivalent has one free arm, which lacks a chiasma, whereas two homologous arms can have a chiasma-containing segment and a chiasma-free segment, together constituting one chiasma-free and one chiasma-containing arm. Thus the configuration is assigned to the class ‘chain multivalent’. True ‘figure 8’ multivalents are equivalent to ring multivalents. ‘Bird cage’ multivalents result from interstitial chiasmata combined with more than one point of pairing partner switch (Darlington, 1965) and, for the

present purpose, are also assumed to be equivalent to ring multivalents, although the situation may be more complex. ‘Bird cages’ were not with certainty observed in the present material, but in some cases there was some doubt.

In column B of Table 3 the relative frequencies are given, expressed as the probability that a chromosome is involved in a specific configuration. For column C the estimated average arm association frequencies a and b were used for all pairing configurations, and combined with the random pairing factors 8/15, 6/15 and 1/15 (Table 2). For column D all parameters were applied as estimated, and the same is true for E, except that in this case it is assumed that the chiasma factors are the same for hexavalent and quadrivalent pairing ($aq = ah$ and $bq = bh$). The difference is small. In Table 2 column D it is seen that the chiasmate association estimate aq for the long arm after quadrivalent pairing is larger than 1, which is unacceptable. In fact, intermediate steps in the calculation showed negative values for some configuration frequencies, which is just as unacceptable. It appeared that adding one trivalent with univalent and subtracting a ring bivalent and an open bivalent in the observations gave an almost exact fit (column F). Column E shows the case where the chiasmate association frequencies are

made equal for the two types of multivalent. The effect is negligible.

Finally, the partly random model of Jackson & Casey (1982), as in Khawaja *et al.* (1995), was applied for column G. As expected, the completely random model of Jackson & Casey (1982) gives exactly the same result as with the present model when for all chiasmate association frequencies the average c between a and b is used, in addition to the random pairing factor. The difference with column G is small.

Discussion

The very low frequency of configurations with simultaneous chiasma failure in both A and B arms (quivalent with univalent, pair of trivalents, trivalent with univalent, univalent pairs) suggests that one arm has a very high chiasma frequency. As there are many configurations where one or two of the same arm type do not have chiasmata (chain hexavalent, chain quadrivalent, open bivalent), the other arm must have a much lower chiasma frequency. This is borne out by the chiasmate association estimates for all pairing types. Although the low frequencies of the critical configurations (quivalent, a pair of trivalents, trivalent with univalent, a pair of univalents) introduce a relatively large error, the fact that all of them are low makes the estimates reliable. The difference between ab and bb for bivalent pairing may be expected to reflect the differences between the physical arm lengths, as observed in the somatic karyotype (Khawaja *et al.*, 1995). It is greater than the difference between ah and bh and between aq and bq for multivalent pairing. This may reflect a real difference between pairing systems or it may merely be coincidental, for instance the consequence of the very indirect estimate of the two chiasma parameters for bivalents. On the other hand, there is a fundamental difference between multivalents and bivalents in as far as in multivalents the point(s) of pairing partner switch and the centromere both determine the difference between the 'arms'. The pairing partner switch may be expected to be, on the average, nearer the middle of the chromosome. In bivalents only the centromeres determine relative arm lengths. However, it would be expected that if partner switch would cause the arms to be more equal in multivalents this would be the result of a reduction of the chiasmate association frequency of the longer 'arm'. This was not observed here.

A valid question is whether pooling of all seven groups of six chromosomes distorts the estimates. It

has been shown (Sybenga, 1992, 1994) that when arm association frequencies do not differ excessively among the chromosomes pooling gives a good representation of the average. The karyotype of *L. palustris* (Khawaja *et al.*, 1995) looks sufficiently homogeneous.

If the arm chiasma frequencies are assumed to be equal, as in the partly random model of Jackson & Casey (1982) (Table 3, column G), very much higher frequencies of simultaneous absence of chiasmata in A and B arms (quivalent, a pair of trivalents, trivalent with univalent, univalent) are expected. This is clearly not the case and that model is clearly not realistic for *L. palustris*.

Substituting the average arm association frequencies (a and b) and the random pairing factors ($fh = 8/15$, $fq = 6/15$ and $fb = 1/15$) in the formulae (Table 3, column C) gives reasonable correspondence between predicted and observed values for the hexavalent pairing-derived configuration frequencies. In particular, however, the expected chain quadrivalent frequency, is too high and, consequently, the open bivalent frequency is too low. This is reflected in the low estimate of fq (Table 2, column C). The reasons are not known. The estimate is rather indirect, but not seriously so. It is affected by the frequency of the rare trivalent with univalent, but this effect is not large, as shown by the small change in fq when the trivalent with univalent frequency is increased by a factor of two (column F of Table 2). Apparently, the excess of bivalent pairing is caused only by the low quadrivalent pairing frequency and not by a reduction of hexavalent pairing. Any effect of partner switch on reducing quadrivalent frequencies by interfering with chiasma formation (Sybenga, 1992), assumed to cause high bivalent frequencies in autotetraploids, would also affect hexavalent pairing estimates and can not play a role here.

Although it should be possible, in principle, to deduce a relative affinity factor from fh and fq , similar to x of Kimber and coworkers, or a preferential pairing factor p (Sybenga, 1994), this may not be realistic because, apart from disturbing factors as mentioned above and the complexity of the relations, hexavalent and quadrivalent pairing apparently follow different patterns even in an autohexaploid. It is not clear how this could be accommodated in a preferential pairing or affinity model.

The overall conclusions are as follows.

- 1 It is possible to design mathematical models for autohexaploids which can be used to estimate several reasonably realistic pairing and chiasma

parameters with reasonable precision.

- 2 *Lathyrus palustris* is a true autohexaploid with hexavalent formation approaching random pairing, but reduced quadrivalent pairing and correspondingly higher bivalent pairing.
- 3 The two 'arms' of the average chromosome differ considerably in chiasmate association frequency, both when true arms and when segments distal of points of pairing partner switch are concerned.

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