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Irregular Segregation at the *Pr* Locus Controlling Plastid Inheritance in *Pelargonium*: Gametophytic Lethal or Incompatibility System?

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Summary. Two distinct segregation patterns are recognized after G×W plastid crosses in *Pelargonium*. Type I parents produce offspring in which maternal zygotes are frequent, biparental intermediate, and paternal zygotes rare (MZ > BPZ > PZ), as defined by the presence or absence of green or white plastids in the young embryos into which the zygotes develop. Type II parents produce offspring in which maternal and paternal zygotes are frequent with biparental zygotes the least frequent class (MZ > BPZ < PZ).

Type I plants, which breed true, are regarded as homozygotes – Pr_1Pr_1. Type II plants, which do not breed true, are regarded as heterozygotes – Pr_1Pr_2. The nuclear gene is symbolized as *Pr* as it is presumed to control alternative patterns of plastid segregation through an effect on plastid replication.

Selfs and intercrosses of heterozygous plants segregate in an "unexpected" 1 : 1 ratio and not the expected 3 : 1 (1 : 2 : 1). The alternative homozygote – Pr_2Pr_2 – could not be detected. Reciprocal crosses between heterozygotes (Pr_1Pr_2) and homozygotes (Pr_1Pr_1) give the expected 1 : 1 ratio when the Pr_2 allele is derived from the male, whereas there is often, but not always, a highly significant deviation from 1 : 1 when the Pr_2 allele is derived from the female.

A simple explanation, which is not wholly satisfactory, is to assume that Pr_2 is a gametophytic lethal on the female side. An alternative, or additional, explanation is that an incompatibility mechanism is involved in which Pr_1 is a self-compatible allele, Pr_2 a self-incompatible allele, and Pr_1–Pr_2 cross-compatible alleles. Successful fertilization is then determined by sporophytic control on the male side and gametophytic control on the female side.

Key words: *Pelargonium* – Plastid inheritance – Gametophytic lethal – Incompatibility

Introduction

The inheritance of plastids in zonal Pelargoniums (*Pelargonium* × *Hortorum* Bailey) is of the biparental pattern (Gillham 1978; Hagemann 1979; Kirk and Tilney-Bassett 1978; Sears 1980). Crosses between cultivars, in which the plastids carry either the normal wild-type allele – green phenotype (G) – or a mutant allele – white phenotype (W) – in their germ cells, produce progeny with a mixture of maternal zygotes (MZ), biparental zygotes (BPZ), and paternal zygotes (PZ) as defined by the presence or absence of green or white plastids in the young embryos into which the zygotes develop. The segregation pattern of this mixture is scored after G×W crosses in which the maternal zygotes are green and the paternal zygotes white, or vice versa after W×G crosses, and the biparental zygotes variegated. Two distinct segregation patterns are recognized. The type I pattern is found in cv. 'Dolly Varden', which breeds true and is therefore assumed to be homozygous (Pr_1Pr_1), and the type II pattern is found in 'Flower of Spring', which does not breed true and is therefore assumed to be heterozygous (Pr_1Pr_2). The nuclear gene is symbolized as *Pr* as it appears to control alternative patterns of plastid segregation, and hence presumably has an effect on the replication of plastid DNA (Tilney-Bassett 1973). After G×W crosses, the type I female nuclear genotype confers a characteristic segregation pattern among the progeny in which the maternal zygotes are frequent, biparental intermediate, and paternal zygotes rare (MZ > BPZ > PZ). This contrasts strongly with the type II female nuclear genotye which confers the characteristic segregation pattern of frequent maternal and paternal zygotes with biparental zygotes the least frequent class (MZ > BPZ < PZ). Hence it appears as if the Pr_1Pr_1 homozygotes preferentially select the maternal plastid for replication whereas in the cellular environment cre-

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ated by the Pr_1Pr_2 genotype selection in favour of the paternal plastid allele is now equally successful. Modifying genes account for differences between cultivars within the alternative patterns (Tilney-Bassett 1976). After W×G crosses, the six cultivars fall into the same order as for G×W crosses, except that the allelic frequencies are shifted towards the paternal owing to selection for the wild-type allele which now comes from the male. The reader is referred to the paper by Tilney-Bassett and Birky (1981) for a detailed discussion of the role of selection and random drift as factors in the determination of the behaviour of plastids in mixed zygotes.

A limited study of the progeny of selfs and hybrids within and between the type I and type II cultivars produced some rather unexpected results (Tilney-Bassett 1973, 1975; Kirk and Tilney-Bassett 1978). When the heterozygotes were selfed, instead of segregating into type II and type I progeny in a Mendelian 3:1 ratio (or 1:2:1), they segregated in a 1:1 ratio. Furthermore, when heterozygote and homozygote were crossed, the expected 1:1 ratio was only approached after the $Pr_1Pr_1 \times Pr_1Pr_2$ cross whereas after the reciprocal $Pr_1Pr_2 \times Pr_1Pr_1$ cross all but one of the progeny were of the type I phenotype. It thus appeared as if the Pr_2 allele was behaving as a gametophytic lethal on the female side, and "possibly" slightly lethal on the male side. The alternative possibility of zygotic selection was ruled out by the finding that the mean fertilization and embryo survival was the same for families of homozygotes and heterozygotes, and by the fact that embryo death was insufficient to swing the ratio from 3:1 to 1:1 (Tilney-Bassett 1974).

The conclusion that Pr_2 eggs were behaving as gametophytic lethals and were not being fertilized meant that all fertilized eggs were of the Pr_1 genotype. Hence, the huge difference between type I females ($Pr_1Pr_1 - Pr_1$ eggs) and type II females ($Pr_1Pr_2 - Pr_1$ eggs) could not be accounted for by differences in the genotype of haploid eggs, but must be predetermined by the female parent at or before meiosis when still diploid. Moreover, as there was no association in the behaviour either of flowers within an influorescence or of ovules within a flower, the female nuclear genotype activates the reaction sometime during the development of each ovule and not within the flower or influorescence as a whole (Tilney-Bassett and Abdel-Wahab 1979).

In order to increase our understanding of the properties of the Pr_2 allele, we have now incorporated a number of other type I or type II cultivars into our crossing programme, examined the effects of reciprocal plastid crosses, and greatly increased the numbers of progeny scored. At the same time we have looked at the question of whether our suggestions for the behaviour of the Pr_1/Pr_2 gene are compatible with our improved knowledge of fertilization, embryo survival and the disposition of embryos within the flower (Kubba and Tilney-Bassett 1980, 1981 a, b, c).

Materials and Methods

The six cultivars used in our crossing programme are 'Foster's Seedling' (FOS), 'Flower of Spring' (FS), 'J. C. Mapping' (JCM), 'Dolly Varden' (DV), 'Lass O'Gowrie' (LG) and 'Miss Burdette-Coutts' (MBC). All are white-over-green mesochimeras with the layer structure L I green, L II white, L III green, in which the germ layer transmits mutant white plastids (W) at fertilization. Derived from them are six isogenic bud variants which transmit normal green plastids (G) at fertilization.

The six green and variegated cultivars are selfed or intercrossed, as G×W or W×G plastid crosses, to produce inbred or hybrid families. A sample of the green progeny among these families, and of the variegated progeny that develop green flowering shoots, are then tested. Testing is achieved by growing these progeny to maturity and crossing them, as G×W plastid crosses, with the variegated 'Flower of Spring' or, rarely, 'Dolly Varden' as a source of white plastids. A fairly large sample of embryos (generally over 50) is scored to determine the segregation pattern of each plant. As, in these experiments, we are interested in the type of segregation and not in the precise ratio of maternal: biparental: paternal zygotes, we score each plant simply as giving the type I or the type II segregation pattern. Some of the complete segregation data has, however, been published elsewhere (Tilney-Bassett 1973, 1974; Abdel-Wahab 1980).

In order to allow for the small size of most segregating families, the goodness of fit with Mendelian 1:1 ratios has been tested throughout only after applying the Yates correction – subtracting 0.5 from the absolute values of the deviations.

Results

After selfing or intercrossing the three type I cultivars – 'Miss Burdette-Coutts,', 'Lass O'Gowrie' and 'Dolly Varden' – all 36 progeny behaved according to the type I pattern, confirming the true-breeding, homozygous, nature of their parents (Table 1). The heterozygous nature of the three type II cultivars – 'Foster's

Table 1. Segregation into type I progeny after selfing and intercrossing type I (Pr_1Pr_1) plants. The original plastid crosses are G×W or W×G

Parental selfs or crosses	Source male white 'test' plastids	Numbers of progeny		
		Type I[a] (G > V > W)	Type II[a] (G > V < W)	Total
G×W crosses				
DV G×W DV	DV	10	0	10
LG G×W DV	FS	9	0	9
MBC G×W DV	FS	1	0	1
MBC G×W LG	FS	9	0	9
W×G crosses				
DV W×G DV	DV	7	0	7
Pooled		36	0	36

[a] As the phenotype of all progeny is tested by G×W plastid crosses, the embryos scored have the relationship G > V > W, corresponding to MZ > BPZ > PZ, for type I progeny, and G > V < W, corresponding to MZ > BPZ < PZ, for type II progeny

Table 2. Segregation into type I and type II progeny after selfing or intercrossing type II (Pr_1Pr_2) plants, or from second (F_2) and third (F_3) generation type II progeny of type I × type II crosses. The original plastid crosses are G × W or W × G; F_2 and F_3 generations are derived from these original plastid crosses by G × G selfs

Parental selfs or crosses	Source male white 'test' plastids	Numbers of progeny			Test: 1 : 1 ratio		
		Type I (G > V > W)	Type II (G > V < W)	Total	χ^2	d. f.	P
G × G crosses							
F_2 of FS W × G MBC	FS	17	20	37			
F_2 of DV W × G FS	FS	22	20	42			
F_3 of DV W × G FS	FS	25	29	54			
F_2 of DV G × W FS	FS	0	1	1			
F_2 of LG G × W FS	FS	14	18	32			
G × W crosses							
FS G × W FOS	FS	0	2	2			
JCM G × W FOS	FS	1	1	2			
JCM G × W FS	FS	6	3	9			
W × G crosses							
FS W × G FS	FS	14	11	25			
Total					1.684	9	
Pooled		99	105	204	0.122	1	> 0.5
Heterogeneity					1.562	8	> 0.9

Table 3. Segregation into type I and type II progeny after intercrosses between type I female (Pr_1Pr_1) and type II male (Pr_1Pr_2) plants. The original plastid crosses are G × W or W × G

Parental crosses	Source male white 'test' plastids	Numbers of progeny			Test: 1 : 1 ratio		
		Type I (G > V > W)	Type II (G > V < W)	Total	χ^2	d. f.	P
G × W crosses							
DV G × W FOS	FS	3	4	7			
DV G × W FS	DV	9	3	12			
DV G × W JCM	FS	5	5	10			
LG G × W FOS	FS	3	2	5			
LG G × W FS	FS	12	25	37			
MBC G × W FOS	FS	3	3	6			
MBC G × W FS	FS	19	11	30			
MBC G × W JCM	FS	1	8	9			
W × G crosses							
DV W × G FS	FS	20	15	35			
LG W × G FS	FS	6	7	13			
MBC W × G FS	FS	10	4	14			
Total					13.851	11	
Pooled		91	87	178	0.051	1	> 0.5
Heterogeneity					13.800	10	> 0.1

Seedling', 'Flower of Spring' and 'J. C. Mapping' – was confirmed by the mixed segregation patterns of their 204 progeny; these were derived either from selfs or crosses within and between the parents, or from second and third generation type II progeny of type I × type II crosses (Table 2). Approximately half the progeny tested exhibited the type I and half the type II segregation pattern in excellent agreement with the "unexpected" 1 : 1 ratio, and with no significant heterogeneity between them.

The results of reciprocal crosses between representatives of the two pattern types are considered separately. The 178 progeny of type I × type II crosses were divided almost equally into the two groups in excellent

Table 4. Segregation into type I and type II progeny after intercrosses between type II female (Pr_1Pr_2) and type I male Pr_1Pr_1 plants. The original plastid crosses are G×W or W×G

Parental crosses	Source male white 'test' plastids	Numbers of progeny			Test: 1 : 1 ratio		
		Type I (G > V > W)	Type II (G > V < W)	Total	χ^2	d. f.	P
G×W crosses							
FS G×W DV	FS	15	1	16			
FS G×W LG	FS	4	0	4			
FS G×W MBC	FS	6	0	6			
W×G crosses							
FS W×G DV	DV	12	0	12			
FS W×G LG	FS	14	16	30			
FS W×G MBC	FS	9	7	16			
Total					27.157	6	
Pooled		60	24	84	14.583	1	< 0.001
Heterogeneity					12.574	5	< 0.05

Table 5. Test of goodness of fit between observed and expected frequencies of embryos per flower for the heterozygous cultivar flower of spring. The expected frequencies of embryos per flower are based on the binomial distribution of Pr_1 eggs confounded by the probability of their occurrence within upper ovules

Numbers of embryos per flower	Numbers of flowers scored	Relative expected frequency	Absolute expected frequency	Excess flowers	Excess embryos
5+	166	0.052	103.844	62.156	310.780
4	361	0.173	345.481	15.519	62.076
3	487	0.275	549.175	–	–
2	502	0.275	549.175	–	–
1	481	0.173	345.481	135.519	135.519
0	0	0.052	103.844	–	–
Totals	1,997	1.000	1,997.000	213.194	508.375

Chi-square goodness of fit = 205.995, hence $P \ll 0.001$. Total number of embryos scored = 5,220. Excess embryos that cannot be accounted for on the assumption that they are both derived from Pr_1 eggs and found in upper ovules may be estimated as

$$= \frac{508.375}{5{,}220} \times 100$$

$$= 9.74\%$$

After three rounds of reiteration, the number of flowers with zero embryos that most closely corresponds to the new expected frequency is estimated as 110. The goodness of fit test now gives $\chi^2 = 91.421$ and $P \ll 0.001$. The excess of embryos is estimated as 398.669 = 7.64%

[a] The frequency of flowers with 6 or more embryos, which is approximately 1.5% (Kubba and Tilney-Bassett 1980), is ignored in these calculations

agreement with the expected mendelian 1 : 1 ratio, and with no significant heterogeneity (Table 3). Moreover, the pooled results showed no significant differences between type I female parents with green or with white plastids ($P = 0.5$–0.1). Contrary to the behaviour so far, the data from the 84 progeny of type II × type I crosses is extremely heterogeneous even though, in these crosses, we used only one cultivar as the heterozygous parent (Table 4). When the female parental plastids were green (G×W crosses), we obtained only a single type II offspring indicating a highly significant deviation from the expected 1 : 1 ratio. Yet when the female parental plastids were white (W×G crosses), the pooled result had a reasonable fit with a 1 : 1 ratio. Nevertheless, there was a notable absence of any type II progeny from the W×G cross between 'Flower of Spring' and 'Dolly Varden'.

The "unexpected" 1 : 1 ratio, instead of a 3 : 1 ratio, after selfing and intercrossing heterozygous plants, confirms our previous experience for which we suggested

that the Pr_2 allele was behaving as a gametophytic lethal on the female side. If this was indeed the case we should not expect to find any Pr_2Pr_2 homozygotes. On the assumption that, if we had obtained any Pr_2Pr_2 homozygotes, they would be found among the type II progeny, we have selected, inbred and tested the progeny of 18 green type II plants; not one of these has bred true – all have again segregated into type I and type II – proving that there is at very least a significant deficit of Pr_2Pr_2 homozygotes ($P < 0.01$) and probably a complete absence.

Although the concept of the Pr_2 allele behaving as a gametophytic lethal on the female side provides an adequate explanation for our type II × type I crosses, and for our type II × type II selfs and intercrosses, we should note that this was when the female plastids were green, whereas when the female plastids were white, after type II × type I crosses, the Pr_2 allele was not lethal (Table 4). We will consider the further implications of this observation in the discussion. Meanwhile, in crosses in which the Pr_2 allele does appear lethal on the female side, it is worthwhile seeking additional support for this hypothesis from other evidence.

Each *Pelargonium* flower consists of 5 carpels each with two ovules localised one above the other to give a maximum of ten ovules per flower. On average, however, for the type II cultivar 'Flower of Spring', only 26% of these ovules are fertilized (Kubba and Tilney-Bassett 1981 b) and, after allowing for the early death of some embryos, the total fertility is down to 22% at the time the embryos are scored (Kubba and Tilney-Bassett 1981 c). Of these embryos, approximately 80% are found developing in the upper position and 20% in the lower position (Kubba and Tilney-Bassett 1981 a). Could these developing embryos all have arisen from Pr_1 eggs? To answer this question we can assume that, within a large population of flowers scored, the frequency of Pr_1 eggs per flower follows a binomial distribution and that this is confounded by the probability of these eggs occurring in the upper ovule of each carpel. Hence we can determine the goodness of fit between the observed and expected frequencies of upper Pr_1 embryos for flowers with any number of embryos (Table 5). The very poor fit ($P \ll 0.001$) is clearly caused by an excess of flowers with 1, 4 or 5+ embryos per flower. If these embryos were all in the upper position, they could not all have developed from Pr_1 eggs but, in fact, as approximately 20% of all embryos develop in lower ovules these can more than cover for the 9.7% excess of Pr_1 eggs not catered for by upper ovules. The binomial distribution also indicates that there should be some flowers with no upper Pr_1 embryos. These were probably included among uncounted flowers that drop off the inflorescences whenever they contain no developing embryos at all. We can, however, make an estimate of how many of these there should be, which for the data of Table 5 is approximately 110, and then re-calculate the excess of upper embryos; this is now limited to flowers with 1 and 5+ embryos with a total excess of 7.6%, which does not affect the earlier conclusion.

Discussion

The excellent fit with the expected 1 : 1 ratio, and without significant heterogeneity, after $Pr_1Pr_1 \times Pr_1Pr_2$ crosses (Table 3), provides no support for the suggestion of a partial lethality of Pr_2 on the male side. By contrast, the poor transmission of the Pr_2 allele, after G × W $Pr_1Pr_2 \times Pr_1Pr_1$ crosses (Table 4), does support the idea of the lethality of Pr_2 on the female side. Nevertheless, the clear evidence for the viability of Pr_2, after the reciprocal W × G $Pr_1Pr_2 \times Pr_1Pr_1$ crosses (Table 4) using the same- isogenic- female cultivar, makes it seem very doubtful that "lethality" is the right term. It is more probable that the Pr_2 ovules are always potentially capable of being fertilized but that in particular circumstances they are avoided. The rather limited data so far available suggests that the fertilization of the Pr_1 allele in preference to Pr_2 is stronger when the female parent contains normal rather than mutant plastids (Table 4). The enhancement of Pr_2 transmission in the presence of mutant plastids is, however, rather delicately balanced. On the one hand, there is a difference between successfully transmitting Pr_2 when 'Miss Burdette-Coutts' and 'Lass O'Gowrie' were male parents but not when 'Dolly Varden' was a male parent (Table 4). On the other hand, the W × G 'Flower of Spring' self – $Pr_1Pr_2 \times Pr_1Pr_2$ – (Table 2) which gave an "unexpected" 1 : 1 ratio suggests that Pr_2 was transmitted by only one parent even though in particular crosses there was proven transmission of Pr_2 by the female and by the male. Hence in these selfs and crosses, and others like them, it seems probable that the Pr_2 allele is not transmitted by the female parent even when, with an appropiate male, it is potentially capable of fertilization and subsequent transmission. It therefore appears that there is a mechanism by which Pr_2-containing ovules in the female are recognized by the male and, if appropriate, avoided.

We suggest that a suitable mechanism for avoiding particular matings is most likely to be found in the behaviour of incompatibility alleles (Lewis 1979; Linskens and Kroh 1967; Nettancourt 1977). We propose that Pr_2 behaves like a self-incompatible allele with oppositional inhibition between male and female germ cells carrying the same Pr_2 allele so that Pr_2Pr_2 homozygotes are not formed. By contrast Pr_1 is behaving like a self compatible allele so that Pr_1Pr_1 homozy-

gotes are formed and are self-fertile. We also obtain Pr_1Pr_2 heterozygotes showing that a match between the two alternative alleles is also possible. However, on the basis of this simple relationship, we would expect the self $Pr_1Pr_2 \times Pr_1Pr_2$ to give a ratio of 1 Pr_1Pr_2 : 2 Pr_1Pr_2 among the progeny, and what we actually obtain is a 1 : 1 ratio. The simple relationship based on a purely gametophytic control of the interaction between the alleles is therefore inadequate (Table 6 a).

A slightly more complicated mechanism, but nonetheless realistic, is to assume a sporophytic control in which the Pr_2 allele is dominant to Pr_1. There are then three alternative models each with predictable effects on the segregation ratio:

(i) There is sporophytic control on both the male and female sides so that all gametes behave as if they contain the Pr_2 allele. This model is untenable because all matings would be rejected and there would be no progeny (Table 6 b).

(ii) There is sporophytic control on the female side and gametophytic control on the male side so that the pollen grains carrying the Pr_2 allele are inhibited by the female styles. This model gives a 1 : 1 ratio among the progeny in which the Pr_2 allele is derived from the female parent (Table 6 c).

(iii) There is sporophytic control on the male side and gametophytic control on the female side. With this model all pollen grains have the Pr_2 phenotype and are therefore acceptable to Pr_1 eggs, but are rejected by Pr_2 eggs. The model therefore gives a 1 : 1 ratio among the progeny in which the Pr_2 allele is derived solely from the male side (Table 6 d).

The advantage of the third over the second model is that it is in accord with the regular transmission of Pr_2 by the male and its irregular transmission by the female, but neither model can be totally excluded.

The analysis of fertilization and the disposition of developing embryos between upper and lower ovules has shown that all Pr_2 eggs could be left unfertilized, but it does not prove that they are. The growth of pollen shows that the majority of germinating grains grow only a little way into the stigma, but that an average of less than eight grow into the style (Kubba and Tilney-Bassett 1981 b). There are therefore too few pollen tubes to fertilize all ten ovules, yet more than enough to account for those that are fertilized. Hence there is evidence of inhibition on both male and female sides which does not help us to exclude either of the sporophytic-gametophytic models.

It is, of course, still conceivable that the Pr_2 allele is behaving as a gametophytic lethal on the female side so that we do not need to invoke an incompatibility mechanism. However, we have already argued against this as the sole mechanism on the grounds that in particular crosses Pr_2 is transmitted by the female. It is also unlikely on the basis of our examination of serial sections at the time of pollination in which all ten ovules appear to be well developed, although the rapid shrivelling of unfertilized ovules is extremely clear two

Table 6. Models showing the expected progeny after selfing or intercrossing type II (Pr_1Pr_2) plants on the basis of different relationships between the two alleles assuming that Pr_1 is a self-compatible allele, Pr_2 is a self-incompatible allele, and the two alleles cross compatible. A + equals successful mating, a – equals no mating. $Pr_1(Pr_2)$ implies that the Pr_1 allele behaves as though recessive to Pr_2

		♂	
(a) There is gametophytic control in both sexes so that all matings are possible except between two self-incompatible Pr_2 alleles. The progeny ratio is 1 Pr_1Pr_1 : 2 Pr_1Pr_2		Pr_1	Pr_2
	Pr_1	+	+
♀	Pr_2	+	–
(b) There is sporophytic control in both sexes so that all Pr_1 alleles behave as if they are Pr_2, hence no matings occur and there are no progeny		$Pr_1(Pr_2)$	Pr_2
	$Pr_1(Pr_2)$	–	–
♀	Pr_2	–	–
(c) There is sporophytic control on the female side and gametophytic control on the male side. Hence the female style behaves as if it was Pr_2 and rejects all Pr_2 pollen tubes, while Pr_1 tubes are accepted. The progeny ratio is 1 Pr_1Pr_1 : 1 Pr_1Pr_2 in which the Pr_2 allele is derived from the female parent		Pr_1	Pr_2
	$Pr_1(Pr_2)$	+	–
♀	Pr_2	+	–
(d) There is sporophytic control on the male side and gametophytic control on the female side. Hence all pollen grains behave as if they are Pr_2 and are therefore accepted by Pr_1 eggs and opposed by Pr_2 eggs. The progeny ratio is 1 Pr_1Pr_1 : 1 Pr_1Pr_2 in which the Pr_2 allele is derived from the male parent		$Pr_1(Pr_2)$	Pr_2
	Pr_1	+	+
♀	Pr_2	–	–

to three days after pollination (Kubba and Tilney-Bassett 1981 c).

In respect of all these observations comparative studies are not very helpful because such differences as have been observed between type I and type II plants appear to be of only a minor nature. It therefore seems that the proposed selection against Pr_2 eggs in Pr_1Pr_2 heterozygotes is not reflected in any major difference in pollen tube growth, fertilization, embryo survival or distribution of developing embryos between upper and lower ovules. This is in accord with the impression that all ovules are potentially capable of being fertilized but, as only about one quarter of them are, there is ample flexibility to choose between ovules without affecting the total frequency of developing seeds.

In some respects the concept of incompatibility appears to be a nonsense when all the six cultivars under investigation regularly set seed after hand self and cross pollinations. We are, however, discussing cultivars of a horticultural plant that is a hybrid of several species and which has been continuously bred for over a century. Any original, outward expression of incompatibility has been bred out of the cultigen during selection for self-fertilization. Hence the behaviour that we have found is probably a derived and not a natural condition. Moreover, the behaviour would not have been detected at all had we not been carefully monitoring the Mendelian inheritance of quite another character – that of the control of plastid segregation in which there is sporophytic control on the female side (Tilney-Bassett 1976). Whether the lethality and incompatibility aspects of the Pr_1/Pr_2 gene are truly related to the effects on plastid segregation, or whether these are the quite different effects of two linked genes, are questions that must remain open.

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