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# The Mechanism of the Mixed Inheritance of Chloroplast Genes in *Pelargonium*

## Evidence from Gene Frequency Distributions Among the Progeny of Crosses

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**Summary.** The distributions are given of gene frequencies among embryos after G × W and W × G plastid crosses within and between eight *Pelargonium* cultivars and some of their inbred or hybrid derivatives.

Two distinct segregation patterns are recognized. Homozygous type I female parents ($Pr_1Pr_1$) have a high frequency of progeny with only maternal alleles, are intermediate for biparental and low for paternal offspring. Heterozygous type II female plants ($Pr_1Pr_2$) have an equally high frequency of maternal and paternal offspring and a generally low biparental frequency. These correspond to L-shaped and U-shaped gene frequency distributions respectively in which the only modes are at 0 per cent (maternal embryos) and 100 per cent (paternal embryos), with no mode corresponding to the population mean and no sign of a Gaussian distribution.

The extremely variable plastid gene frequencies are strongly influenced by the maternal nuclear genotype and by the plastid genotype in which the wild-type allele is always more successful than the mutant in strict comparisons.

The relative frequencies of maternal and paternal zygotes, and the mean gene frequency among all the zygotes in a cross, are explicable in terms of the input frequencies of genes from the two parents, their degree of mixing, and by some form of selective replication of plastids. This selection is controlled by nuclear and plastid genotypes which may act in the same direction, to increase the frequency of either the maternal or the paternal alleles, or in opposition. But selection alone is inadequate to explain the shapes of the gene frequency distributions. Instead, a model is proposed in which the segregation or replication of plastids appears to have a strong random element, which results in random drift of gene frequencies within a heteroplasmic zygote or embryo.

**Key words:** *Pelargonium* – Plastids – Inheritance – Gene frequencies – Random drift

## Introduction

In a recent classification of flowering plants according to whether their plastids are regularly transmitted at fertilization by the maternal parent alone or by both parents, Tilney-Bassett and Abdel-Wahab (1979) listed 37 maternal and 14 biparental genera. More detailed lists (Hagemann 1979; Kirk and Tilney-Bassett 1978; Sears 1980) include a few additional genera for which, besides or instead of genetical evidence, there is electronmicroscopical observation that the plastids are not transmitted by the male parent owing to their exclusion from the generative cell or from the male gamete. Cases of purely maternal inheritance may be largely accounted for by a simple pre-fertilization control so that at no time do the plastids of the two parents ever meet. By contrast, with biparental plastid inheritance, plastids from the two parents are regularly brought together inside the zygote. Within this mixed cell there are therefore two groups of plastids of different parental origin, of different frequency, often of different genotype, and probably, at least initially, occupying different zones within the zygote. With so many variables, the analysis of what happens to this complex intracellular population is thwart with difficulty. Nevertheless, considerable progress has been made in the genus *Pelargonium*, which is one of the best-studied examples.

Matings between *Pelargonium* plants with green or mutant white plastids in the germ line produce 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

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the zygotes develop. Depending on the direction of the cross, G X W or W X G, these embryos are pure green, variegated green and white, and pure white. A cross can be characterized partly by the mean frequency of the maternal allele (G or W) among the progeny (Table 1), which varies from 100 to 0 per cent maternal (within the limits of sample sizes), and partly by the proportions of maternal, biparental and paternal zygotes. Extensive genetical studies have demonstrated that both these parameters are controlled predominantly by the nuclear genotype of the female parent, irrespective of the direction of the plastid cross, and are modified by the poorer transmission of the mutant plastids than the normal ones; the effect of the male, if any, is a minor factor (Kirk and Tilney-Bassett 1978).

The recognition of the importance of the female nuclear genotype in the control of plastid inheritance still leaves unresolved the precise mechanism(s) through which the control acts. The classical 'sorting-out' hypothesis for plastids during successive rounds of cell division was extensively developed by Michaelis (1955). This in fact follows the hypergeometric distribution and after approximately 10N divisions, where N is the number of plastids per cell before doubling to 2N and the cell dividing into two cells each with N plastids, we obtain fine U- or L-shaped distributions according to whether the ratio of the two plastid types is equal or very unequal respectively. This might be regarded as a kind of random drift in which certain restrictions are imposed. Now, when we looked at the sorting-out of variegated plants during shoot growth, this kind of distribution accounted for the behaviour of plastids quite well (Kirk and Tilney-Bassett 1978). With 10 plastids per cell we could get complete sorting-out in about 100 divisions. But when we looked at *Pelargonium* embryos we found the same kind of distributions of green and white plastids after only one or two divisions. This was much too quick and so the sorting-out hypothesis had to be rejected. Moreover, when the G : W plastid ratio was 1:1, after some G X W plastid crosses, there was no mode corresponding to the mean at 50 per cent variegated, instead the variegated embryos were mostly almost all green or almost all white. This was not expected with the hypergeometric distribution.

These factors, plus the demonstration of a genetic control, and the extremely wide variation between crosses in the ratio of maternal : biparental : paternal progeny, led Tilney-Bassett (1970b) to discount the importance of random sorting-out of plastids, or of differences in the numerical plastid contribution of different cultivars, or of the position of the plastids in the zygote in determining the genotypes of the progeny of a cross. Instead, a model was proposed in which, of the two types of plastids in mixed zygotes, only one is replicated, except in a proportion of zygotes which give rise to the variegated embryos. This was an early precursor of the belief that the plastid population within the zygote might undergo considerable change prior to cell division so that the output at division might retain only a distant relationship with the input at fertilization. Within *Pelargonium* support for this idea already existed in the observation that in many crosses the normal green plastids were always more successful on average than the mutant even when they came from the male in which their number was likely to be less than the female contribution. The observation of differences in replication rates of different plastid genotypes has recently been extended to $W_1 \times W_2$ crosses in which one white mutant has an advantage over the other (Tilney-Bassett and Abdel-Wahab 1979).

Other more sophisticated, molecular and statistical studies with more amenable lower organisms have similarly provided evidence that the zygote is not a static receptacle for and distributor of organelles, but is rather a lush environment for the rapid replication and turnover of organelle DNA and, in yeast and *Chlamydomonas*, for recombination too. And from out of these findings has come the realisation that the study of organelles and organelle DNA in zygotes, and indeed other mixed cells, is a problem of intracellular population genetics (Birky 1976, 1978).

The zygote can be considered as having a population of plastids and cpDNA molecules and the frequency of each type of plastid within the zygote, whether of maternal or paternal origin, normal or mutant genotype, as the plastid gene frequency. The existence of three classes of progeny suggests that each zygote receives plastids from both parents and hence is initially heteroplasmic. The starting gene frequency might be about 50 per cent, or more likely there are fewer paternal than maternal plastids. It is estimated that in *Oenothera* the egg contributes up to 32 plastids and the male gamete 8-13 plastids to the zygote (Meyer and Stubbe 1974). Subsequent events in the zygote, or early embryo, shift the plastid gene frequency in some zygotes to 0 (MZ) or 100 per cent (PZ) or vice versa, and in other zygotes to a wide range of intermediate frequencies (BPZ). The problem is: What is the mechanism behind these changes in plastid gene frequencies?

We have examined the problem by considering each embryo from a cross as a population of plastids with a particular gene frequency. Ignoring rare mixed cells, which are hard to find in *Pelargonium* (Khera 1975), we can assume that each cell, and each plastid, is homoplasmic for one allele or the other, and hence the per cent of tissue in an embryo with the maternal or paternal phenotype (G or W) is an estimate of the frequency of the corresponding allele in the entire embryo. The different embryos from a cross, classified according to their allelic frequencies, then constitute an ensemble of populations. We can look at the varying shapes of these ensembles by plotting the frequency distributions of their constituant embryos. These frequency distributions have been used previously to estimate the mean output of green plastids after G X W and W X G crosses (Tilney-Bassett 1976), but in this paper we wish to present for interpretation the patterns themselves. We shall see that the distributions resemble those which result from random drift of gene frequencies in small Mendelian populations, coupled in some cases with selection. The random drift could result from the segregation of incompletely mixed populations of paternal and maternal plastids at the first and second zygotic divisions, or from random replication or even random recombination events. The selection may be for different plastid genotypes, and also for plastids of maternal origin.

## Materials and Methods

As sources of mutant white plastids (W), the parental cultivars are cv. 'Foster's Seedling' (FOS), cv. 'Flower of Spring' (FS), cv. 'J.C. Mapping' (JCM), cv. 'Hills of Snow' (HS), cv. 'Dolly Varden' (DV), cv. 'Lass O'Gowrie' (LG), cv. 'Miss Burdette-Coutts' (MBC), and cv.

'Frank Headley' (FH). All eight cultivars are white-over-green mesochimeras, with the layer structure L I green, L II white, L III green, in which the germ line that transmits the plastids is formed in the white L II layer. As sources of green plastids (G), isogenic (nuclear) green bud variants are derived from each of the chimera cultivars following rare layer changes in which the white germ layer is displaced by a green germ layer (GWG-GGW-GGG). In addition, many green $F_1$ hybrids of some of the parental cultivars and their $F_2$ progeny are used as sources of green plastids and some variegated hybrids as sources of white plastids.

In order to convert varying numbers of maternal, biparental and paternal embryos into effective plastid gene frequencies from the two parents after the G X W and W X G plastid crosses, it is necessary to take account of the intermediate state of biparental embryos as well as the extreme states of maternal and paternal ones. This is done by classifying the biparental – variegated – embryos into ten percentage groups according to their relative proportions of paternal plastid tissue. The classification is made, by eye, according to the percentage area covered by the paternal plastids in which a maximum of 30 per cent is allotted to the radicle and 35 per cent to each cotyledon. An eleventh group is of white embryos in which the extreme tip of the radicle – the suspensor haustorium – contains green chloroplasts; this latter class is at the paternal end of the scale after G X W crosses and at the maternal end after W X G crosses. The total score for each class of embryo is converted into the proportions of maternal and paternal plastid genes by an appropriate multiplication factor; the mean plastid gene frequencies for the whole cross – the ensemble of populations – are then estimated from the sum of the individual populations (Table 1). The mean plastid gene frequencies among the biparental progeny are estimated after excluding the uniparental embryos.

The extensive data surveyed are divided into G X W (Tables 2-4) and W X G (Tables 5-6) plastid crosses. In each case we have further divided the data into crosses in which the female parent is homozygous for the nuclear genotype $Pr_1 Pr_1$, which gives rise to the type I segregation pattern, or heterozygous $Pr_1 Pr_2$, which gives rise to the type II segregation pattern (see Results). In addition, we have been able to restrict the data to specific male plants for the G X W crosses, but not for the W X G crosses for which a number of different males were used; however, as noted earlier, different males have little effect on the segregation pattern. Within each Table we have been able to amalgamate families with the same percentage range of maternal plastid gene frequencies as these invariably possess very similar segregation patterns. We have varied the width of the ranges to suit the number of families available and to take account of the narrower or broader spread for each of the five groups of crosses. Finally, we have estimated the maternal plastid gene frequencies among the biparental progeny for each range, whether of a single family or an average of two or more amalgamated families. A few individual crosses, without amalgamation, are illustrated by histograms. In contrast to the tables, the green-tipped white embryos ($W^G$) are included with the 95 (90-100) per cent or 5 (0-10) per cent category after G X W and W X G crosses respectively.

## Results

The distributions of maternal, biparental and paternal embryos after G X W plastid crosses are shown in Tables 2-4. The Tables are divided into the results from type I plants

**Table 1.** Method of estimating the mean maternal allele frequency for the ensemble of populations sampled by a plastid cross. The example is from the G X W cross (DV W X G FS/5)G X W FS included in Table 2 and illustrated in Figure 1 B

| Classification of individual populations (embryos) % paternal plastids | Frequency of populations (embryos) in each class | Multiplication factors | | Proportion of plastid genes contributed to population ensemble | |
|---|---|---|---|---|---|
| | | Maternal allele | Paternal allele | Maternal[a] | Paternal |
| 0 – Pure maternal | 161 | x 12 | x 0 | 1932 | 0 |
| 5 ( 0 – 10) | 21 | x 11 | x 1 | 231 | 21 |
| 15 (10 – 20) | 10 | x 10 | x 2 | 100 | 20 |
| 25 (20 – 30) | 1 | x 9 | x 3 | 9 | 3 |
| 35 (30 – 40) | 5 | x 8 | x 4 | 40 | 20 |
| 45 (40 – 50) | 4 | x 7 | x 5 | 28 | 20 |
| 55 (50 – 60) | 0 | x 6 | x 6 | 0 | 0 |
| 65 (60 – 70) | 4 | x 5 | x 7 | 20 | 28 |
| 75 (70 – 80) | 1 | x 4 | x 8 | 4 | 8 |
| 85 (80 – 90) | 1 | x 3 | x 9 | 3 | 9 |
| 95 (90 – 100) | 8 | x 2 | x 10 | 16 | 80 |
| $W^G$ – White green-tip | 2 | x 1 | x 11 | 2 | 22 |
| 100 – Pure paternal | 12 | x 0 | x 12 | 0 | 144 |
| Sum | | | | 2385 | 375 |
| Mean plastid gene frequency overall | | | | 86.4% | 13.6% |
| Mean plastid gene frequency among biparentals | | | | 66.2% | 33.8% |

[a] The maternal allele corresponds to the green allele frequency after G X W crosses and to the white allele frequency after W X G crosses

**Table 2.** The percentage maternal, biparental (expressed as the percentage paternal) and paternal allelic frequencies among the progeny of G X W plastid crosses. All G females have the type I nuclear genotype; the W male is 'Flower of Spring'

| Range maternal allelic frequency | No. families within range | Mean maternal frequency among biparentals | Pure maternal % | Classification of biparentals % paternal alleles | | | | | | | | | | | Pure paternal | Total embryos |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 5 | 15 | 25 | 35 | 45 | 55 | 65 | 75 | 85 | 95 | $W^G$ | % | |
| 100 | 16 | – | 100.0 | – | – | – | – | – | – | – | – | – | – | – | – | 977 |
| 100-99 | 24 | 86.5 | 97.7 | 1.5 | 0.4 | 0.2 | < 0.1 | – | < 0.1 | – | < 0.1 | – | – | – | < 0.1 | 3251 |
| 99-98 | 4 | 77.2 | 93.2 | 3.6 | 1.0 | 0.4 | 0.6 | 0.2 | 0.4 | 0.1 | – | – | 0.1 | 0.4 | 0.1 | 836 |
| 98-96 | 10 | 74.7 | 93.3 | 2.8 | 1.0 | 0.4 | < 0.1 | 0.3 | 0.4 | 0.1 | < 0.1 | < 0.1 | 0.2 | 0.5 | 0.8 | 1836 |
| 96-94 | 4 | 73.0 | 83.7 | 7.0 | 2.8 | 1.4 | 0.6 | 0.5 | 0.3 | 0.3 | 0.5 | 0.1 | 0.7 | 1.1 | 0.8 | 952 |
| 94-92 | 2 | 74.2 | 79.0 | 8.5 | 3.2 | 1.3 | 1.1 | 1.3 | 0.8 | 0.8 | 0.3 | 0.5 | 0.3 | 0.8 | 2.1 | 377 |
| 92-90 | 2 | 71.0 | 77.0 | 8.9 | 4.2 | 0.5 | 0.5 | 1.4 | – | 0.9 | – | 0.9 | – | 2.3 | 3.3 | 213 |
| *88-86 | 1 | 66.2 | 70.0 | 9.1 | 4.3 | 0.4 | 2.2 | 1.7 | – | 1.7 | 0.4 | 0.4 | 3.5 | 0.9 | 5.2 | 230 |
| 86-84 | 3 | 62.5 | 68.6 | 9.0 | 3.0 | 2.3 | 1.3 | 1.4 | 1.0 | 1.0 | 1.2 | 1.0 | 1.4 | 3.3 | 5.4 | 690 |
| *82-80 | 1 | 62.8 | 55.7 | 12.7 | 4.2 | 3.8 | 1.4 | 1.9 | 1.9 | 3.3 | 2.8 | 2.4 | 2.8 | 1.9 | 5.2 | 212 |
| *78-76 | 1 | 55.2 | 63.4 | 6.9 | 2.8 | 2.8 | 0.7 | 1.4 | – | 0.7 | – | 3.4 | 4.8 | 2.1 | 11.0 | 145 |
| *72-70 | 1 | 55.6 | 62.5 | 1.1 | 2.3 | 1.1 | 1.1 | 1.1 | 2.3 | 1.1 | 1.1 | – | 2.3 | – | 23.9 | 88 |

* Note gaps in range above these positions

**Table 3.** The percentage maternal, biparental (expressed as the percentage paternal) and paternal allelic frequencies among the progeny of G X W plastid crosses. All G females have the type I nuclear genotype; the W male is 'Dolly Varden'

| Range maternal allelic frequency % | No. families within range | Mean maternal frequency among biparentals | Pure maternal % | Classification of biparentals % paternal alleles | | | | | | | | | | | Pure paternal | Total embryos |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 5 | 15 | 25 | 35 | 45 | 55 | 65 | 75 | 85 | 95 | $W^G$ | % | |
| 100-99 | 2 | 90.9 | 97.6 | 2.2 | 0.2 | – | – | – | – | – | – | – | – | – | – | 458 |
| 99-98 | 2 | 87.2 | 88.9 | 8.0 | 1.9 | – | 0.4 | – | – | – | 0.4 | – | – | – | 0.4 | 262 |
| 98-96 | 6 | 83.0 | 81.6 | 12.1 | 2.2 | 1.4 | 1.0 | 0.5 | < 0.1 | < 0.1 | 0.2 | 0.2 | 0.4 | 0.2 | < 0.1 | 1258 |
| 96-94 | 5 | 79.9 | 80.6 | 10.5 | 3.2 | 1.8 | 0.8 | 0.5 | 0.8 | 0.5 | 0.4 | 0.2 | 0.2 | 0.2 | 0.4 | 849 |
| 94-92 | 5 | 73.9 | 76.7 | 10.1 | 4.1 | 1.4 | 1.5 | 1.1 | 0.6 | 0.5 | 0.6 | 0.6 | 1.0 | 0.9 | 1.1 | 1037 |
| 92-90 | 1 | 69.4 | 71.9 | 13.5 | 3.4 | 2.2 | 1.1 | 0.4 | – | 0.7 | – | 1.1 | 4.5 | 0.7 | 0.4 | 267 |
| 90-88 | 5 | 73.5 | 61.2 | 15.0 | 8.3 | 4.2 | 1.2 | 1.9 | 1.3 | 0.9 | 0.9 | 1.4 | 1.3 | 1.4 | 1.1 | 1010 |
| 88-86 | 1 | 64.1 | 69.6 | 9.6 | 3.8 | 1.7 | 0.8 | 1.2 | 1.7 | 1.7 | 0.8 | 1.2 | 2.1 | 2.1 | 3.8 | 240 |
| *84-82 | 5 | 68.0 | 56.3 | 13.1 | 8.3 | 3.4 | 2.7 | 1.2 | 1.3 | 0.9 | 1.4 | 2.0 | 3.3 | 1.6 | 4.6 | 1002 |
| *80-78 | 2 | 61.8 | 57.8 | 10.6 | 4.2 | 3.8 | 1.8 | 2.6 | 1.8 | 1.5 | 1.3 | 2.0 | 3.3 | 2.7 | 6.6 | 547 |
| 78-76 | 2 | 62.6 | 50.9 | 12.4 | 6.8 | 3.4 | 2.4 | 2.2 | 1.4 | 2.0 | 2.9 | 2.5 | 4.2 | 2.0 | 6.8 | 589 |
| *74-72 | 1 | 49.7 | 55.1 | 7.9 | 3.7 | 4.7 | 1.4 | 2.8 | 2.8 | 2.3 | 0.9 | 2.3 | 8.9 | 3.3 | 7.9 | 214 |
| 72-70 | 1 | 55.0 | 54.5 | 9.0 | 1.4 | 3.4 | 1.4 | 0.7 | – | 2.8 | 2.8 | 3.4 | 4.1 | 2.1 | 14.5 | 145 |
| *68-66 | 1 | 60.6 | 34.1 | 15.9 | 7.4 | 5.0 | 3.5 | 2.7 | 0.8 | 1.6 | 2.3 | 1.6 | 8.9 | 3.9 | 12.4 | 258 |
| *64-62 | 1 | 51.4 | 40.7 | 7.1 | 2.7 | 1.8 | 3.5 | 3.5 | 5.3 | 3.5 | 2.7 | 1.8 | 8.0 | 1.8 | 17.7 | 113 |

* Note gap in range above these positions

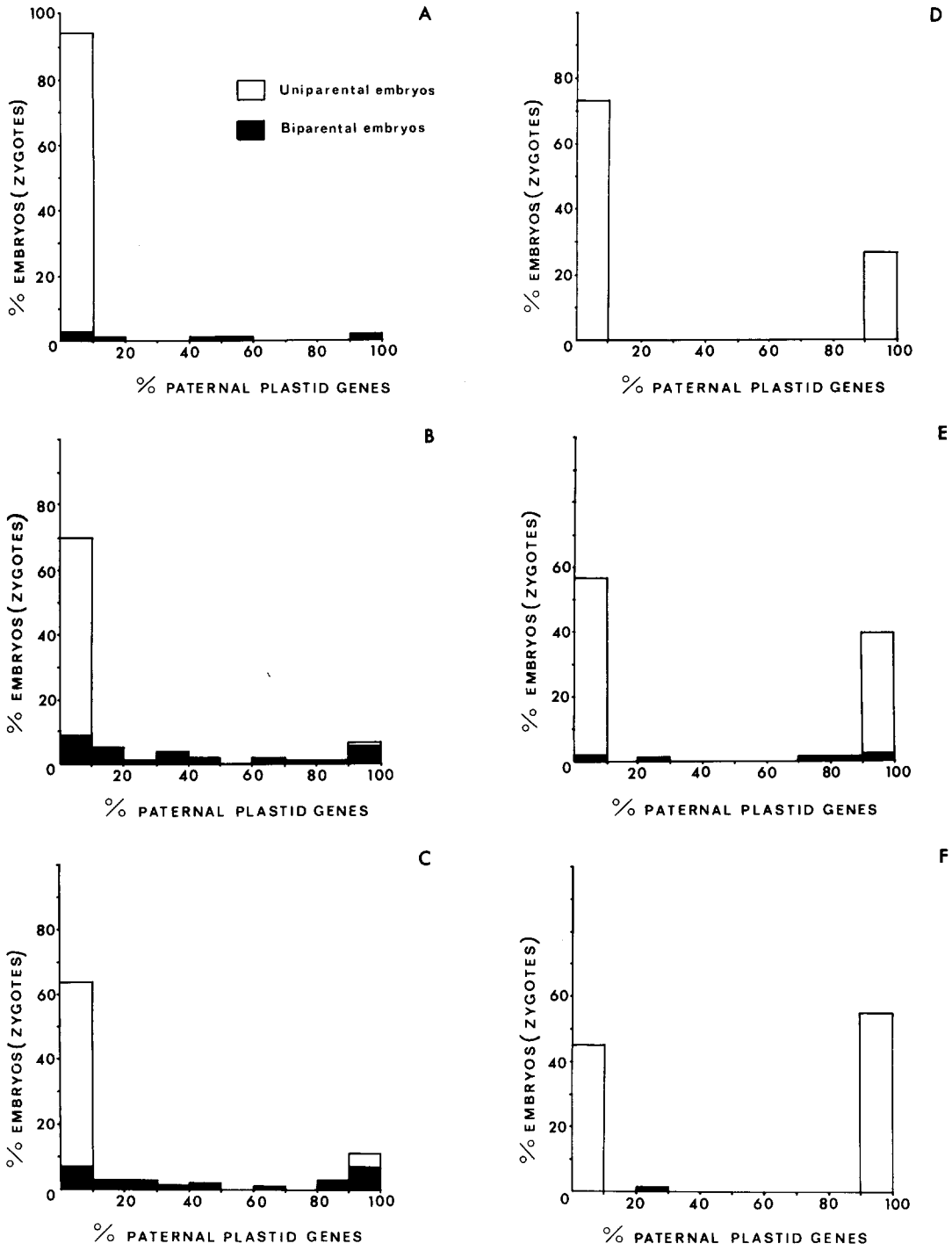


Fig. 1A-F. Series of histograms from G X W plastid crosses illustrating the transition from a predominantly maternal to a predominantly paternal allelic transmission while maintaining a low frequency of biparental progeny; all six plants are sibs. A-C L-shaped distributions with transitions from strongly maternal to weakly maternal among type I plants. D-F U-shaped distributions with transitions from maternal to paternal among type II plants.

A (DV W X G FS/22) G X W FS, 243 Embryos, 98-97% Maternal; among biparentals 62.1%
B (DV W X G FS/5 ) G X W FS, 230 Embryos, 87-86% Maternal; among biparentals 66.2%
C (DV W X G FS/7 ) G X W FS, 145 Embryos, 78-77% Maternal; among biparentals 55.2%
D (DV W X G FS/18) G X W FS, 223 Embryos, 74-73% Maternal; among biparentals None
E (DV W X G FS/36) G X W FS, 273 Embryos, 60-59% Maternal; among biparentals 56.8%
F (DV W X G FS/30) G X W FS, 110 Embryos, 46-45% Maternal; among biparentals Few

(Tables 2 and 3), in which the female parent is homozygous $Pr_1Pr_1$, and type II plants (Table 4), in which the female parent is heterozygous $Pr_1Pr_2$. These genotypes separate the segregation into two distinct patterns – type I (M > B > P), in which maternal transmission is strong, biparental usually intermediate and paternal weak, and type II (M > B < P), in which maternal and paternal transmissions are approximately equally strong and biparental weak (Tilney-Bassett 1976). The overall plastid gene frequency ranges from 100 to 62 per cent maternal for type I plants, and from 76 to 42 per cent maternal for type II plants.

Among the type I crosses the differences between 'Flower of Spring' (Table 2) and 'Dolly Varden' (Table 3) as sources of white plastids are minor. The pattern of segregation is the same for both males, but there appears to be a greater variance and rather more biparental progeny, for comparable maternal allelic frequencies, with 'Dolly Varden' than with 'Flower of Spring'. The tables show that with a slight drop in maternal gene frequency from 100 to 98 per cent, there is an increase in biparental progeny covering the whole range of plastid ratios and an almost simultaneous occurrence of some paternal progeny. It does not seem necessary, therefore, to have a significant build up of biparental progeny prior to the occurrence of purely paternal ones. In fact, as the histograms clearly indicate (Figs. 1A-C), the centre range of biparental classes remains rather flat while the build up of biparental progeny at the paternal end of the scale follows a little way behind the build up at the maternal end. Where the maternals are considerably more frequent than the paternal, there also appears to be a bias in favour of the maternal allele among the biparental plants. As maternal transmission decreases the initial L-shaped curves become increasingly U-shaped. The only modes are at 0 per cent (uniparental, maternal embryos) and 100 per cent (uniparental, paternal embryos). There is no mode corresponding to the population mean and no sign of a Gaussian distribution. The U-shaped curve is highly characteristic of the type II plants (Table 4) in which the histograms (Figs. 1D-F) illustrate the swing from a higher maternal to a higher paternal gene frequency with no change in the extraordinarily low biparental frequencies.

The W × G crosses (Tables 5, 6) cover the continuous range from 75 to 1 per cent maternal gene frequency, in which type I plants have the stronger maternal and type II plants the stronger paternal tendency, although with a clear zone of overlap. In all the families included in the survey the classification of variegated females as type I or type II after W × G plastid crosses was determined independently by testing their isogenic green clones in standard G × W crosses. Through most of the range the frequency of biparental progeny swings from a bias towards maternal to a bias towards paternal, as seen in the L-shaped histograms (Figs. 2G-H), in line with the total change. Never-

**Table 4.** The percentage maternal, biparental (expressed as the percentage paternal) and paternal allelic frequencies among the progeny of G × W plastid crosses. All G females have the type II nuclear genotype; the W male is 'Flower of Spring'

| Range maternal allelic frequency % | No. families within range | Mean maternal frequency among biparentals | Pure maternal % | Classification of biparentals % paternal alleles | | | | | | | | | | | Pure paternal | Total embryos |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 5 | 15 | 25 | 35 | 45 | 55 | 65 | 75 | 85 | 95 | $W^G$ | | |
| 76-74 | 1 | – | 75.4 | – | – | – | – | – | – | – | – | – | – | – | 24.6 | 57 |
| 74-72 | 1 | – | 73.1 | – | – | – | – | – | – | – | – | – | – | – | 26.9 | 223 |
| 72-70 | 2 | + | 70.8 | – | – | – | – | – | – | – | – | – | – | 0.9 | 28.3 | 113 |
| 70-68 | 3 | 42.9 | 66.7 | 1.5 | – | 0.8 | – | – | – | – | – | – | 0.8 | 2.3 | 28.0 | 132 |
| 68-66 | 2 | 66.7 | 63.9 | 2.1 | 0.5 | – | – | – | – | – | – | – | – | 1.0 | 32.5 | 191 |
| 66-64 | 4 | 59.3 | 59.3 | 3.1 | 2.1 | – | 0.3 | 0.3 | 0.8 | 0.5 | 1.8 | 0.3 | – | 1.5 | 30.2 | 388 |
| 64-62 | 3 | 70.1 | 55.9 | 3.8 | 2.4 | 0.6 | 0.8 | 0.4 | 0.4 | 0.2 | 0.8 | 0.2 | 0.6 | 0.4 | 33.5 | 499 |
| 62-60 | 4 | 61.3 | 56.2 | 2.3 | 1.6 | – | 0.5 | 0.2 | – | 0.2 | – | 0.4 | 0.4 | 1.4 | 36.8 | 555 |
| 60-58 | 5 | 50.7 | 56.4 | 1.6 | 0.4 | 0.4 | 0.1 | 0.1 | 0.4 | 0.1 | 0.1 | 0.2 | 1.1 | 1.0 | 38.0 | 803 |
| 58-56 | 4 | 59.3 | 54.7 | 1.4 | 0.2 | 0.5 | 0.2 | – | 0.2 | – | – | 0.7 | 0.2 | 0.5 | 41.2 | 422 |
| 56-54 | 10 | 67.2 | 52.7 | 1.7 | 0.6 | 0.1 | – | 0.1 | – | 0.2 | – | 0.3 | 0.3 | 0.2 | 43.8 | 909 |
| 54-52 | 6 | 40.8 | 51.8 | 0.7 | – | – | – | – | 0.2 | – | – | – | 0.9 | 0.5 | 45.9 | 434 |
| 52-50 | 2 | + | 51.8 | – | – | – | – | – | – | – | – | – | – | 0.7 | 47.5 | 141 |
| 50-48 | 1 | + | 44.8 | 3.4 | – | – | – | – | – | – | – | – | – | 3.4 | 48.3 | 29 |
| *46-44 | 1 | + | 44.5 | – | – | 0.9 | – | – | – | – | – | – | – | – | 54.5 | 110 |
| 44-42 | 3 | 61.9 | 40.3 | 0.9 | 0.9 | – | – | – | – | 0.5 | – | 0.5 | 0.5 | – | 56.4 | 211 |

**Table 5.** The percentage maternal, biparental (expressed as the percentage paternal) and paternal allelic frequencies among the progeny of W X G plastid crosses. All W females have the type I nuclear genotype; the G males are mixed

| Range maternal allelic frequency % | No. families within range | Mean maternal frequency among biparentals | Pure maternal % | Classification of biparentals % paternal alleles | | | | | | | | | | | Pure paternal | Total embryos |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | $W^G$ | 5 | 15 | 25 | 35 | 45 | 55 | 65 | 75 | 85 | 95 | % | |
| 75-70 | 1 | 67.8 | 23.1 | 13.1 | 22.5 | 4.4 | 6.2 | 7.5 | 6.2 | 3.1 | 1.3 | 2.5 | 3.1 | 1.9 | 5.0 | 160 |
| 70-65 | 2 | 56.4 | 25.8 | 1.3 | 14.1 | 8.3 | 8.3 | 8.5 | 8.3 | 6.7 | 4.5 | 4.7 | 2.7 | 3.6 | 3.1 | 446 |
| 65-60 | 1 | 50.8 | 28.7 | 2.0 | 16.0 | 2.7 | 5.3 | 7.3 | 4.0 | 4.7 | 6.7 | 12.0 | 4.0 | 4.7 | 2.0 | 150 |
| 60-55 | 1 | 51.8 | 14.3 | 9.1 | 10.8 | 6.1 | 6.7 | 7.0 | 6.1 | 8.5 | 10.8 | 7.3 | 7.3 | 5.6 | 0.3 | 342 |
| 55-50 | 1 | 54.8 | 9.3 | 3.4 | 24.4 | 5.4 | 4.4 | 5.9 | 3.9 | 8.8 | 8.3 | 7.3 | 2.9 | 7.8 | 8.3 | 205 |
| 50-45 | 3 | 49.1 | 12.8 | 3.8 | 11.9 | 6.5 | 5.5 | 3.8 | 3.7 | 4.4 | 7.1 | 7.5 | 7.1 | 7.8 | 17.9 | 704 |
| *40-35 | 3 | 42.2 | 6.1 | 5.0 | 6.3 | 3.8 | 4.0 | 3.3 | 4.5 | 7.1 | 8.1 | 10.3 | 9.6 | 9.5 | 22.3 | 602 |
| 35-30 | 6 | 52.6 | 7.3 | 4.0 | 6.9 | 5.0 | 4.1 | 3.6 | 3.0 | 3.7 | 2.9 | 3.4 | 4.0 | 4.8 | 47.3 | 1124 |
| 30-25 | 4 | 41.8 | 6.7 | 3.7 | 5.5 | 2.1 | 2.2 | 4.6 | 2.6 | 2.9 | 3.7 | 4.6 | 6.0 | 11.1 | 44.5 | 766 |
| 25-20 | 2 | 46.8 | 2.8 | 5.0 | 1.9 | 2.5 | 2.5 | 3.8 | 3.2 | 3.0 | 3.6 | 4.3 | 4.5 | 4.5 | 58.4 | 2921 |
| 20-15 | 2 | 28.0 | 2.6 | 2.0 | 0.7 | 2.0 | 2.0 | 0.7 | 2.6 | 1.3 | 3.3 | 10.5 | 13.7 | 13.1 | 45.8 | 153 |
| 15-10 | 3 | 27.4 | 1.1 | 2.0 | 1.4 | 0.3 | 1.7 | 1.1 | 0.8 | 2.0 | 2.8 | 4.2 | 7.3 | 15.5 | 59.6 | 354 |
| * 5- 1 | 2 | 20.5 | 1.9 | – | 0.2 | – | – | – | 0.4 | – | 1.2 | 0.8 | 1.9 | 3.1 | 90.5 | 483 |

* Note gap in range above this position

N.B. In contrast to G X W crosses (Tables 2-4), the green-tipped white embryos ($W^G$) are now at the left-hand end of the biparental progeny. Similarly, increasing paternal alleles corresponds to increasing green in contrast to decreasing green for the G X W crosses

**Table 6.** The percentage maternal, biparental (expressed as the percentage paternal) and paternal allelic frequencies among the progeny of W X G plastid crosses. All W females have the type II nuclear genotype; the G males are mixed

| Range maternal allelic frequency % | No. families within range | Mean maternal frequency among biparentals | Pure maternal % | Classification of biparentals % paternal alleles | | | | | | | | | | | Pure paternal | Total embryos |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | $W^G$ | 5 | 15 | 25 | 35 | 45 | 55 | 65 | 75 | 85 | 95 | % | |
| 32.5-30.0 | 1 | 45.6 | 12.6 | 3.2 | 7.4 | 3.2 | 2.1 | – | 1.1 | 4.2 | 1.1 | 5.3 | 5.3 | 7.4 | 47.4 | 95 |
| *22.5-20.0 | 3 | 37.0 | 6.4 | 4.5 | 0.8 | 1.4 | 1.6 | 2.6 | 1.8 | 3.4 | 1.9 | 4.6 | 8.1 | 8.6 | 54.3 | 626 |
| 20.0-17.5 | 3 | 36.3 | 3.1 | 4.3 | 2.1 | 0.8 | 1.9 | 1.6 | 1.9 | 3.1 | 3.7 | 3.9 | 8.2 | 10.3 | 55.1 | 486 |
| *15.0-12.5 | 1 | 36.6 | 4.6 | 2.6 | 0.7 | 2.0 | – | 0.7 | 2.0 | 1.3 | 2.0 | 3.9 | 5.2 | 5.9 | 69.3 | 153 |
| 12.5-10.0 | 2 | 33.8 | 3.6 | 1.0 | 1.1 | 0.7 | 1.0 | 1.6 | 1.4 | 1.0 | 2.3 | 4.3 | 3.6 | 5.7 | 72.6 | 1170 |
| 10.0- 7.5 | 9 | 27.5 | 2.7 | 1.2 | 0.6 | 0.2 | 0.3 | 0.9 | 1.0 | 0.8 | 2.2 | 3.5 | 4.5 | 7.8 | 74.3 | 1811 |
| 7.5- 5.0 | 1 | 20.6 | 2.1 | 0.5 | – | – | 0.2 | 0.2 | 0.2 | 0.2 | 1.2 | 4.3 | 4.5 | 6.6 | 79.9 | 422 |
| 5.0- 2.5 | 1 | 24.6 | 2.5 | – | – | – | 0.4 | – | 0.4 | 0.4 | 1.7 | 1.7 | 1.3 | 2.5 | 89.1 | 239 |
| 2.5- 1.0 | 1 | 20.1 | – | – | – | – | – | 0.9 | – | – | 1.4 | 0.9 | 2.7 | 4.1 | 90.0 | 221 |

* Note gap in range above these positions

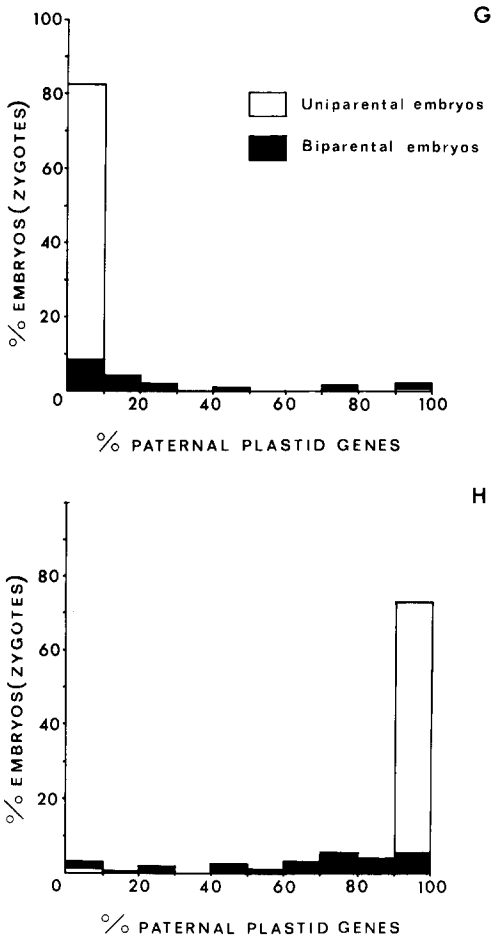


Fig. 2G-H. Two L-shaped histograms from W X G crosses illustrating the transition from moderately maternal (Type I) to moderately paternal (type II) allelic transmission with a rather flat distribution of biparental allelic ratios.
G MBC W X G FS, 288 Embryos, 67-66% Maternal; among biparentals 55.2%
H JCM W X G FS, 285 Embryos, 21-20% Maternal; among biparentals 44.4%

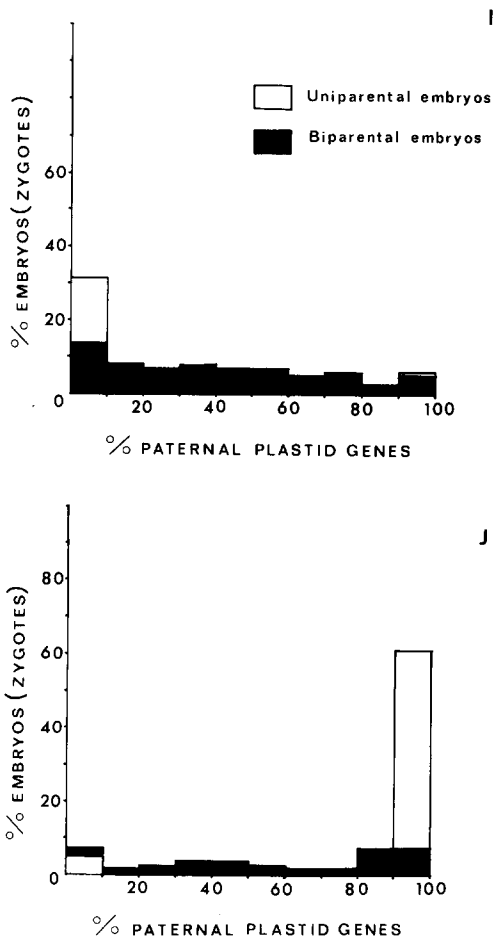


Fig. 3I-J. Two histograms illustrating the swing from a strongly maternal to a strongly paternal allelic ratio corresponding to the G X W and W X G reciprocal crosses respectively.
I (FS G X W DV/1) G X W FS, 273 Embryos, 96-95% Maternal; among biparentals 73.8%
J FS W X G (FS G X W DV/1), 349 Embryos, 10-9% Maternal; among biparentals 32.5%

theless, the bias is not strong and the frequencies for each class of biparental progeny are similar with no mode corresponding to the population mean and no sign of a Gaussian distribution.

The histograms (Figs. 3I-J) illustrate the remarkable swing from a strongly maternal to a strongly paternal gene frequency corresponding to the change from a G X W cross to the reciprocal W X G. This is an example of the general rule, to which 'Miss Burdette-Coutts' is the exception, that the green plastids are transmitted more successfully than the white irrespective of the direction of the cross, although the contrast is not always as vivid as in this case.

The data for the mean maternal allelic frequencies among biparental progeny are rather revealing for, as the overall gene frequency tends towards 100 per cent, or zero per cent, maternal allelic frequency, the maternal gene frequency among biparentals tends towards 80 per cent (Tables 2, 3), or 20 per cent (Tables 5, 6), respectively. This rather suggests that the mean ratio of maternal : paternal plastid genes within biparentals varies from 8:2 to 2:8, that is from 4:1 to 1:4, and only exceeds this ratio when there are very few biparentals and only one significant (> 0.5%) uniparental class.

Early in embryo development, possibly immediately after the first zygotic division, the terminal cell is cut off from a lower cell that eventually gives rise to the suspensor haustorium at the tip of the radicle. In this early division, which is marked by the white embryo with a green tip ($W^G$), we see the effect of a mixed cell dividing into an upper daughter cell with only mutant plastids and a lower daughter cell with mixed or only green plastids. Among biparentals within the range of 40 to 60 per cent paternal

allelic frequency, that is with a mean of 1:1, these $W^G$ embryos average nearly 10 per cent. On the assumption of a random sorting-out of plastids at this stage of development such a high frequency is only compatible with a small number of plastids, or segregating units.

## Discussion

Apart from technical differences in the method of scoring cell phenotypes, the estimation of the allelic frequency from a single *Pelargonium* embryo is analogous to that of estimating the allelic frequency from a single zygote colony in *Chlamydomonas* or yeast, and similarly for the estimation of their population means. Hence it is legitimate to compare the behaviour of cytoplasmic genes in all three organisms, and to seek common mechanisms.

Cytological proof that the *Pelargonium* zygote always receives plastid genes from both parents is lacking. Nevertheless, it seems safe to make this assumption. The extensive genetical data obtained from G × W and W × G plastid crosses between interbreeding cultivars reveals an extremely wide spectrum from less common crosses in which the plastids of all embryos are purely maternal in origin or, very rarely, purely paternal, to those more common crosses in which there are various ratios of maternal : biparental : paternal embryos among the ensemble (Kirk and Tilney-Bassett 1978). Moreover, wide differences are frequently found between sibs. It is easier to envisage these extremely variable outputs as arising from changes in gene frequencies within the zygote than as variance in the plastid inputs. For example, in the cross MBC G × W FS the ratio of G : W plastid genes among the progeny is approximately 99 : 1, and in the cross FS G × W FS approximately 1 : 1 even though an identical male is used for both (Tilney-Bassett 1976). It is hardly likely that one female has so many more plastids in its egg cells than the other.

Electron microscope studies show that the generative and sperm cells of *Pelargonium* contain numerous plastids (Lombardo and Gerola 1968; Hagemann 1979). It is unlikely that sometimes none of these enter the egg, to account for maternal zygotes, and yet sometimes so many do so that the maternal plastids are undetectable (paternal zygotes). Furthermore, an analysis of variance of the crosses shows the male cultivars to behave very similarly and the major differences to be on the female side. We shall therefore pursue our discussion on the basis of the generally accepted assumption (Sager 1972; Gillham 1978; Kirk and Tilney-Bassett 1978; Hagemann 1979) that like *Chlamydomonas* and yeast, the *Pelargonium* zygote is a mixed cell receiving cytoplasmic genes from both parental gametes.

The extremely variable plastid allelic frequencies among *Pelargonium* crosses are strongly influenced by the maternal nuclear genotype and by the plastid genotypes in which the wild-type allele is always more successful than the mutant in strict comparisons, that is to say that if we compare the crosses G♀ × W♂ and W♀ × G♂ then G♀ > W♀ and G♂ > W♂. Depending on their nuclear genotype, the following six cultivars have been arranged in a series progressing from very strongly transmitting females to very weak ones, as judged by the plastid output after G × W or W × G crosses with various cultivars (Tilney-Bassett 1976):

$$\text{MBC} > \text{LG} > \text{DV} > \text{JCM} > \text{FS} \approx \text{FOS}$$

The first three cultivars have the type I genotype, $Pr_1Pr_1$, and the second three the type II genotype $Pr_1Pr_2$. The nuclear gene was symbolized as Pr as it appears to control alternative patterns of plastid replication, and hence presumably has an effect on the replication of plastid DNA (Tilney-Bassett 1973). These effects are very interesting. After G × W crosses, the majority of the progeny of type I plants contain only maternal alleles, whereas the progeny of type II plants contain maternal or paternal alleles in about equal frequency. Hence it appears as if $Pr_1Pr_1$ homozygotes preferentially select the maternal plastid for replication. The strength of this selection is further modified by other genes. For example, with 'Dolly Varden' as the female parent there are many biparental and paternal progeny, but with 'Miss Burdette-Coutts' the paternal allele is almost completely eliminated. By contrast, in the environment created by the $Pr_1Pr_2$ heterozygote selection in favour of the maternal allele is relaxed and the paternal allele is now equally successful, although its transmission frequency is also affected by modifying genes. After W × G crosses, the six cultivars fall into the same order as for G × W crosses but the allelic frequencies are shifted towards the paternal, owing to selection for the wild-type plastid, which now comes from the male, being in opposition to, and apparently usually stronger than, the postulated selection for the maternal allele. On our selection model, we can now account for the crossing results in terms of whether nuclear and plastid genotypes are acting in the same direction, both selecting for maternal or paternal alleles, or in opposition. For example, in the cross MBC G × W FS the strong female plus the green plastids both select for the maternal allele (99.6% maternal), whereas in the reciprocal cross FS W × G MBC the weak female and white plastids both select against the maternal (8.4% maternal). Examples of nuclear genotype and plastids being in opposition are the crosses MBC W × G FS – strong female, white plastids (64.1% maternal) – and FS G × W MBC – weak female, green plastids (55.6% maternal).

Although it has been convenient to talk of selection exercising its effect on plastid replication, this should not be taken too literally. The effect could be on the replication of the organelle, or on the cpDNA molecules therein; alternatively, a preferential degradation might be occurring. We may also be observing the outward expression of exten-

sive gene conversion, possibly biased in favour of wild-type alleles by a mechanism akin to recombinational polarity in yeast (reviewed by Gillham 1978) or in favour of alleles from strongly transmitting females by methylation of cpDNA. It would also be naive to assume that selection alone is sufficient to account for the organelle behaviour. The present analysis looks at the distribution of allelic frequencies among the progeny of a cross. These are L-shaped, as previously observed by Hagemann and Scholz (1974) or U-shaped and without modes or peaks, except at the ends of distributions (Figs. 1-3, Tables 2-6). The input allelic frequencies into the zygote at the moment of fertilization are unknown, but it is reasonable to assume that there is some variation in numbers of plastids and of cpDNA molecules among the eggs and male gametes, so the input frequency distribution is probably Gaussian. In *Pelargonium*, the high frequencies of biparental and paternal progeny as well as maternal do not persuade us of the existence of the strong maternal bias such as is found in *Oenothera* in which paternal progeny do not normally occur (Schötz 1974, 1975; Kirk and Tilney-Bassett 1978). Hence the peak of the input distribution may be at 50 per cent or with a slight bias in favour of one parent or the other. The problem is to explain why we have fixation of one allele or the other in uniparental plants, and why the expected Gaussian distribution disappears to be replaced by an approximately linear distribution among the biparental zygotes. The concept of selection is of a directional force driving any change in gene frequency one way, towards maternal or paternal. This might be considered adequate for some typical type I G × W crosses (G > V > W), but the typical type II G × W cross (G > V < W) makes the unlikely demand for the selective forces to work separately and in opposite directions in different zygotes in the same cross. Furthermore, it is probable that a directional force would not eliminate completely the mode in the input Gaussian distribution, but would only shift it in one direction or the other. We are therefore of the opinion that neither selection nor gene-conversion give a complete insight into the causes at the molecular level for the changes in gene frequencies.

The frequency distributions strongly resemble those seen in random drift of finite populations in Mendelian population genetics. They also resemble those seen for chloroplast genes in *Chlamydomonas* and for mitochondrial genes in yeast (*Saccharomyces* and *Schizosaccharomyces*) where there is direct evidence from delayed division experiments for random drift of organelle gene frequencies (Van Winkle-Swift 1978; Sears 1979; Matagne and Hermesse 1980; Wolf et al. 1979; Thrailkill et al. 1980). The distributions suggest that there is some repeated stochastic event or events occurring in zygotes and early embryos which change gene frequencies. Such events would contribute to uniparental inheritance by fixing one allele or the other in some embryos, and would also eliminate the Gaussian distribution. Among possible mechanisms to be considered are the following:

(1) The argument that there might be a strong preferential survival of some embryos has been dismissed by careful genetical analysis of embryo frequencies at different stages of embryo development (Tilney-Bassett 1970a), and the stability of green and white cells in the readily formed periclinal chimeras (Tilney-Bassett 1963; Hagemann and Scholz 1974) suggests that there is little competition between pure cells. Explanations must therefore be sought in the behaviour of plastids in the zygote and its first divisions. As the existence of green-tipped white embryos shows, embryos have to become pure after very few divisions, probably as few as one or two, if plastids of the other colour are to be totally excluded; unless, perhaps, there is a mechanism for singling out one kind of plastid for subsequent degradation, or of inhibiting its multiplication, well into embryo development.

(2) A random element in the segregation of plastids at the first division of the zygote which separates the embryo from the basal cell and at the second division to separate the embryo from the future suspensor haustorium, might explain the high frequencies of uniparental zygotes and of green-tipped white embryos. However, this would necessitate the maternal and paternal plastids often segregating as single elements with little mixing between the two, as if there was only one maternal and one paternal plastid. The problem here is that there are crosses that produce high frequencies of biparental progeny with extremely high variance of gene frequencies for which we must accept a high degree of mixing of several plastids. It is difficult to imagine that conditions within the zygote are so variable as to virtually exclude all mixing in some cases and for it to be so thorough in others especially when comparing isogenic crosses as, for example, MBC G × W FS (3.2 per cent biparental) and MBC W × G FS (69.2 per cent biparental), and these are not the most extreme cases. Nevertheless, the shapes of the gene frequency distributions, in which there is no mode corresponding to the mean and in which the end classes among the biparentals (0-20% or/and 80-100%) show a rise in frequency, is inconsistent with a thorough mixing of the plastids from the two parents. Rather, it suggests that after fertilization, the two groups of plastids, from the male and female parent respectively, become mixed gradually and rarely completely by a migration of plastids between the two groups. Hence, irrespective of what other changes may influence the frequency of biparentals within the zygote population, each sample of plastids that enters the terminal cell at zygote division, if it contains both types of plastid, invariably retains the bias towards one or other parent.

(3) The possibility of repeated recombination events, including gene conversion, between G and W cpDNA molecules exists (Sager 1972; Birky and Skavaril 1976), but at

the moment there is no evidence for or against recombination of plastid genes in *Pelargonium* zygotes. Attempts to find wild-type recombinants from crossing different plastid mutants in *Pelargonium* and *Oenothera* (Kirk and Tilney-Bassett 1978) have failed, but this negative result is not conclusive evidence against recombination.

(4) A random element in the replication or degradation of plastids or cpDNA molecules is a possibility meriting serious consideration. There might, for instance, be turnover of plastids; if the plastids selected for degradation and replication were selected randomly, this would cause the frequencies of green and white plastids to drift. We propose that the selection of a plastid or plastid genotype for replication in the zygote and in the initial mixed cells of biparental embryos is by chance. This chance has a certain probability attached to it as determined by the nuclear controlled cytoplasmic environment and by the plastid genotype and initial frequencies, but there is still a stochastic choice. When the probability of selecting a plastid is weighted in favour of one genotype (usually G), or in favour of plastids from one parent (usually maternal), this introduces the element of selection discussed earlier.

Of course the drift and selection that we propose may have elements of several different mechanisms. The important principle is that, in contrast to the behaviour of chromosomes, the segregation and or replication of plastids appears to have a strong random element which results in random drift of gene frequencies within single cells and or clones. This, coupled with selection, leads to a fixation of alleles in some plants giving uniparental – maternal or paternal – inheritance and extremely high variance of gene frequencies among others.

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