

NOTES AND COMMENTS

FERTILITY AND SELECTION IN HYACINTH

I. GAMETIC SELECTION

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1. INTRODUCTION

TRISOMIC organisms are expected to produce 50 per cent. unbalanced gametes each with an extra chromosome. But all of them are not effective in fertilisation. Thus, in crosses with diploids, transmission of the extra chromosome to the progenies varies with sex and the trisome involved (Darlington, 1965, table 50). Buchholz and Blakeslee (1922) showed that the extra chromosome of a trisomic *Datura* retards the growth of the pollen tube in the style of a diploid. In the reciprocal cross, however, transmission of the extra chromosome to the progeny is greater, so evidently it has differential effects on the vitality of the pollen and the embryo sac. These results are based on the chromosome numbers of the seedling progenies. Consequently, they do not differentiate the effects of gametic and zygotic selection. I have attempted to make this separation in the present experiments with *Hyacinthus orientalis*.

2. MATERIALS AND METHODS

Crossing. The garden hyacinth var. Rosalie (R), trisomic for the nucleolar chromosome, has been used in crosses with three diploids, Pink Pearl (P.P.), Prince Henry (P.H.) and Salmoneta (S).

The bulbs were potted in late September in John Innes No. 1 potting compost mixed with an equal amount of peat. The pots were kept buried about three inches under soil till late December, and then were kept in the cold frame. The potted bulbs were transferred to the green house kept at 25° C. only for a fortnight before pollination. The flowers were allowed to mature in the normal time as forcing results in poor pollen production and bad stigmatic receptivity.

Flowers were emasculated two days before crossing and the following observations were made:

1. Proportion of ovules fertilised and seeds produced per fruit.
2. Proportion of plump and thin, shrivelled seeds per fruit. The latter are essentially inviable and represent zygotic elimination during embryo development.
3. Seed viability and seedling mortality.

Thus, the developing ovules per capsule were recorded two weeks after pollination. On maturity the seeds were collected with an arbitrary differentiation between plump and shrivelled seeds.

Seeds were sown in John Innes seed compost. Eight weeks' cold treatment to dry seeds at freezing temperature and keeping the seed pans tightly covered in a hot greenhouse gave good germination in eight to ten weeks.

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For chromosome counts, two-weeks-old developing embryos and endosperms, and root tips from young seedlings were squashed after Feulgen staining (Darlington and La Cour, 1962).

3. SEED SET AND VIABILITY

Hyacinth Rosalie was crossed with diploids Pink Pearl, Salmoneta and Prince Henry (table 1). Seed set varies in different crosses. The variation in fertility of different crosses involving the same hyacinth trisomic and different diploid varieties is analogous to that in unilateral crosses between a diploid and different trisomics of *Nicotiana* (Goodspeed and Avery, 1939) and maize (Einset, 1943).

TABLE 1

Seed set and viability in diploid-trisomic crosses of garden hyacinth

Cross	Total fruits	Seeds				Ovules per fruit	Proportion of ovules giving viable seedlings
		Shrivelled	Plump	Ripened and sown	Viable		
$\frac{(2x+1) \times 2x}{R \times P.P.}$	38	156	504	660	133	26	0.135
$\frac{2x \times (2x+1)}{P.P. \times R}$	33	142	175	317	88	28	0.095
S × R	12	0	68	68	...	22	...
P.H. × R	2	2	0	2	0	18	0

In reciprocal crosses between Rosalie and Pink Pearl, the former gives better fertility as seed parent (table 1). This is due to a higher proportion of fertilisation and seed ripening in $(2x+1) \times 2x$ cross than its reciprocal. In both cases all germinated seeds produced viable seedlings. However, the proportion of the plump and shrivelled seeds produced does suggest that the diploid as female parent induces greater seed abortion than the trisomic. This is different from the earlier results on barley (Tsuchiya, 1960) and *Collinsia* (Dhillon and Garber, 1960) where reciprocal crosses are equally fertile. This, however, has been inferred only from seed germination which does not permit any estimate of elimination during seed development.

4. CHROMOSOMAL SELECTION

In crosses involving the diploid and the trisomic, the extra chromosome of the latter is transmitted more often through the egg (fig. 1). The chromosome numbers of the young embryos (fig. 1) suggest that chromosomal selection mainly occurs before fertilisation. However, during the later stages of seed development zygotic selection does occur. But counts from the embryos and the seedlings suggest that it is indiscriminative with respect to chromosome numbers. Greater transmission of the extra chromosome through the egg is also known in several other cases (table 2, and Darlington, 1965, table 50). The earliest known case is that of *Datura* (Blakeslee, 1921) where pollen tubes from balanced and unbalanced grain show competition

in which the former is at advantage. The same explanation has been suggested for the results in *Solanum* (Lesley, 1928), *Nicotiana* (Goodspeed and Avery, 1939), *Collinsia* (Dhillon and Garber, 1960) and *Hordeum* (Tsuchiya,

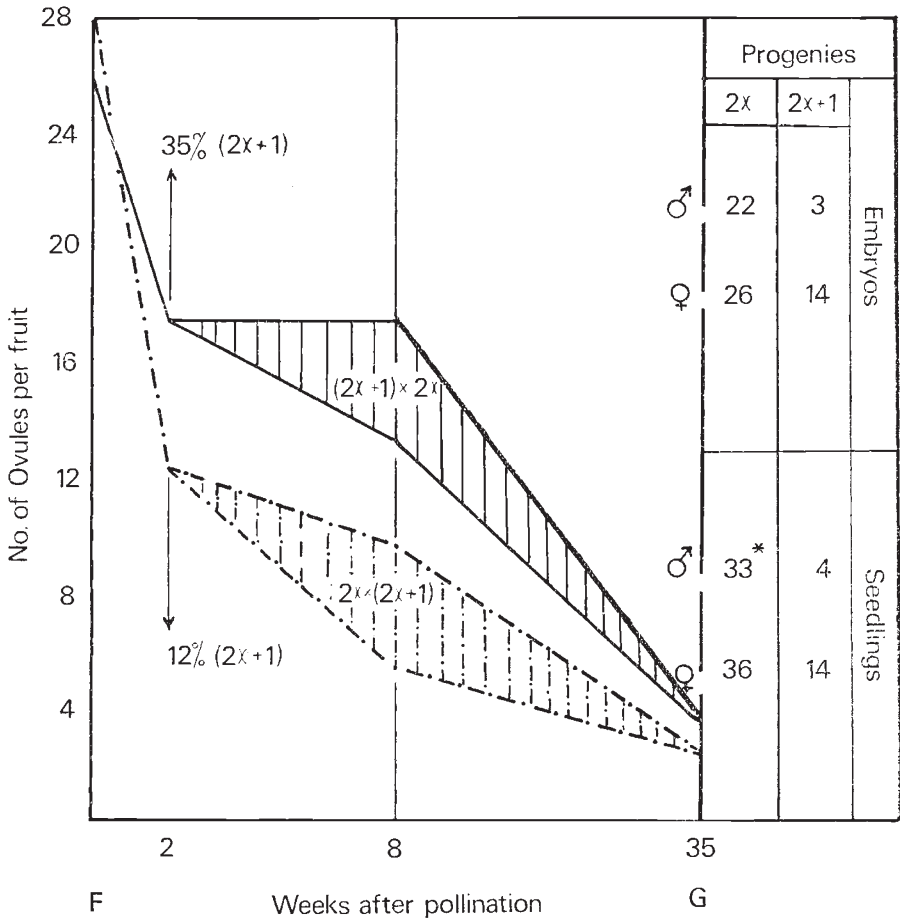


FIG. 1.—Graph showing fertility and chromosomal selection during seed development and germination in reciprocal crosses between diploid (Pink Pearl) and trisomic (Rosalie) hyacinths. The upper and lower points of each quadrangle at eight weeks after pollination denote the total number of seeds and the number of plump seeds produced at the time of fruit ripening in each cross. Thus, the distance between those two points represents the number of shrivelled seeds produced. Side table in the figure shows pollen and egg transmission of the extra chromosomes to the progenies.

* Includes one triploid.
 F = fertilisation, G = germination.

1960). *Antirrhinum majus* (Rudrof-Lauritzen, 1958) and *Spinacia oleracea* (Janick *et. al.*, 1959) are extreme cases where there is no transmission of the extra chromosome through the pollen.

Collinsia heterophylla is unusual in showing greater transmission of the extra chromosome through the pollen (Dhillon and Garber, 1860). But, the data do not indicate whether this is due to the better viability of the pollen than the egg or to selection operating during seed development and germination.

In *Clarkia* the extra chromosome behaves in a peculiar way. From crosses between eight diploids and six trisomics, Vasek (1961, table 2) raised nine families in all. One diploid (5-5) and three trisomics (1-13, 4-6, 7-4) were used both as male and female parents but only one trisomic (7-4) showed transmission of the extra chromosome. Female transmission produced only diploids and tetrasomics. Vasek has suggested that the extra chromosome of *Clarkia* trisomics is either eliminated or duplicated by non disjunction in the female cells. The fact that only one trisomic out of six shows transmission of the extra chromosome, indicates that the trisomics

TABLE 2

Percentage transmission of the extra chromosome of trisomics to their progenies in reciprocal crosses with diploids

Species	Pollen	Eggs	Reference
<i>Datura stramonium</i> "Globe"	3.0	26.0	Blakeslee, 1921
<i>Nicotiana sylvestris</i> "Recurved"	0	16.3	Goodspeed and Avery, 1939
"Compact"	1.9	18.2	
"Broad"	8.3	22.0	
"Pointed"	34.1	28.8	Rudrof-Lauritzen, 1958
<i>Antirrhinum majus</i>	0	5.0-20.0	
<i>Spinacea oleracea</i>	0	3.9-34.5	Janick <i>et. al.</i> , 1959
<i>Collinsia heterophylla</i>	43.6	39.2	Dhillon and Garber, 1960
<i>Hordeum spontaneum</i>	0	9.8-27.5	Tsuchiya, 1960
<i>Clarkia unguiculata</i>	12.5	6.4	Vasek, 1961
<i>Hyacinthus orientalis</i>	10.8	28.0	Ved Brat

are of two types. Possibly, they carry different chromosomes of the complement. There is, however, no size differentiation of chromosomes in *Clarkia*. Thus, differential behaviour of the extra chromosomes in different plants does not arise from the variation in the size of the chromosome involved. Instead, it could be achieved through a genotypically controlled cytoplasmic gradient in the sex cells.

The transmission rate of the extra chromosome however, varies in different species (table 2) and also amongst different trisomes of the same species (Darlington, 1965, table 50). Chromosome size affects the transmission rate in maize where larger chromosomes are transmitted more often owing, perhaps, to the higher rate of loss of small chromosomes during meiosis.

Present results on hyacinth resemble most of the known cases in showing greater transmission of the extra chromosome through the egg than the pollen. From similar studies Brock (1955) reports:

- (a) Inversion hybridity in hyacinth Rosalie ($2x+1$).
- (b) No loss of the extra chromosome during meiosis.
- (c) Only 16.5 per cent. pollen grains with the extra chromosome in early dividing anthers.

Brock has rightly suggested that his pollen grain data could be spurious due to sampling error as no such correlation exists during pollen grain

mitosis in triploid hyacinth where early and late dividing pollen samples are similar for chromosome numbers (Darlington and Mather, 1944). From his observations on chromosome behaviour in endosperm, he has also suggested that selective elimination of the trisomic embryos occurs during seed development when the extra chromosome of the trisomic induces very high chromosome breakage in $3x+1$ endosperm. This conclusion is, however, based on a singular observation. The present data on chromosome numbers in embryos and seedlings (fig. 1) do not suggest any elimination of this type. Instead, they show that the selection occurs mainly before fertilisation.

Unlike *Datura*, the diploid and the trisomic seeds of hyacinth germinate simultaneously. There is also no seedling mortality or any conspicuous difference in growth and vigour of the seedlings.

5. SUMMARY

1. In reciprocal crosses with diploids, a trisomic of *Hyacinthus orientalis*, gives a higher proportion of fertilised ovules and viable seeds when used as female parent.

2. The extra chromosome is transmitted more often through the embryo sac than the pollen. Selection against the genotypes which carry the extra chromosome occurs before fertilisation.

3. There is no difference in the time of germination and vigour of the diploid and the trisomic seedlings.

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