whence, using equations (1), (2) and (3), $\sigma - 1 = \chi_{n-1}^2/2N$. Further, each equation may be written $a_i = \sigma' t_i^p / e s_i^{p-1}$, where $\sigma = \log \sigma'$. Summing over all i gives

$$\chi_{n-1}^2/2N = \sigma - 1 = -\log e/\sigma' = -\log \Sigma t_i^p / s_i^{p-1}. \quad (4)$$

Finally, substituting for a_i in (1),

$$\Sigma t_i^p / s_i^{p-1} \log t_i / s_i = 0. \quad (5)$$

APPLICATION

In many genetical situations there will only be a few classes, with the result that equation (5) may be solved for p without difficulty. The substitution of this value in (4) then leads to the required number N . In some cases it will be possible to derive an expression for N directly.

For example, consider the case in which two loci are known to be linked with recombination fraction $p = 1 - q$; we wish to test whether a double heterozygote has the dominant alleles in coupling or repulsion. On backcrossing to the double recessive, the segregation of the four phenotypes amongst the progeny will be either $p/2 : q/2 : q/2 : p/2$ or $q/2 : p/2 : p/2 : q/2$. Substitution of these values in (5) shows that, independently of p , $p = \frac{1}{2}$, and substituting in (4) then gives $\chi_{3/2}^2/2N = -\log 2\sqrt{pq}$, whence

$$N = -\chi_{3/2}^2 / \log 4pq.$$

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Note added in proof: see BAILEY. 1961. *Introduction to the Mathematical Theory of Genetic Linkage*, Oxford: Clarendon Press, p. 30; for the case of two classes and a recommendation that the χ^2 value should be "one-tailed".

POPULATION STRUCTURE, BREEDING SYSTEM, INTER-SPECIFIC HYBRIDISATION AND ALLOPOLYPLOIDY

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1. INTRODUCTION

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Inter-specific hybridisation in higher plants has three common results when sexual reproduction is retained in the hybrid population. A hybrid swarm may be produced; the hybrids may back-cross to the parent species, and so their hybrid origin may be obscured; or they may produce allopolyploid derivatives reproductively isolated from the parent species. Introgression is more likely to occur in cross-fertilisers than in self-fertilisers (Baker, 1953), while Grant (1956) has argued that since the union of un-reduced gametes is more likely to occur in rare self-fertilising hybrids than in rare cross-fertilising hybrids, allopolyploids are more likely to arise in self-fertilisers, and cites the high coincidence of polyploidy and self-fertility in some

annual plant groups as evidence of this tendency. Baker (1959) quotes further similar evidence for this view.

However, the frequency of production of allopolyploids depends not only on the frequency of union of un-reduced gametes, but also on the frequency of inter-specific hybridisation, which is expected to be higher in cross-fertilisers, especially on or near geographical boundaries between species, where one of the species may be rare and so have little opportunity to be fertilised with compatible pollen from other plants of the same species (Baker, 1953).

In addition, self-fertilising allopolyploids are known to have arisen from hybrids between cross-fertilising or self-incompatible species. *Galeopsis tetrahit* is a self-fertilising allopolyploid derived from hybrids between the two cross-fertilising species *G. pubescens* and *G. speciosa* (Müntzing, 1930). In *Brassica*, the self-fertilising allopolyploids *B. napus*, *B. juncea* and *B. carinata* have arisen from hybrids among the self-sterile species *B. campestris*, *B. oleracea* and *B. nigra* (U, 1935; Ramanujam and Srinivasachar, 1943; Mizushima and Katsuo, 1953). Newly synthesised *Brassica* allopolyploids vary from self-incompatible to self-compatible. Olsson (1953) considers that in *B. napus* cross-fertilising forms have been lost by back-crossing to the parent species, and this seems a likely explanation for the selection of self-fertility in these allopolyploid.

Self-fertility may then be a derived condition in allopolyploids and it may reasonably arise by selection. Baker (1959), however, has suggested that allopolyploidy, not self-fertility, may isolate allopolyploids from their parent species.

There are thus a number of factors which affect the chances of producing allopolyploids. They include variations in population density and breeding systems as they affect inter-specific hybridisation; variations in self-fertility of hybrids, which may not be related to the breeding system of the parents, and the degree of reproductive isolation conferred on hybrids by allopolyploidy.

The effect of polyploidy, breeding system and population composition and density on the frequency of inter-specific hybridisation has been investigated using *Brassica campestris*, a self-incompatible annual or biennial, and *B. napus*, a self-fertile allopolyploid annual or biennial originally derived from hybrids between *B. campestris* and *B. oleracea*. Both species are pollinated by a variety of insects, of which honey bees (*Apis mellifera*) are the most important.

2. MATERIAL AND METHODS

Swedes and rape (*B. napus*) and turnips and wild turnips (*B. campestris*) were allowed to flower together in groups of various sizes in the field. These groups were:

1. Yellow-fleshed swedes separated from one another by at least 10 metres in a crop of white-fleshed turnips. Hybrids are distinguishable from swedes by their white flesh, by the production of hybrid nodules, by their relative infertility, and by their slightly more hairy and greener leaves.
2. Turnips and wild turnips were similarly isolated in a rape crop. Hybrids are easily distinguished from turnips by the rape-like leaf colour and surface.
3. Groups of one swede and one turnip plant were grown together, separated by 100 metres or more from other swedes or turnips.
4. Groups of four turnips and four swedes were grown together, separated by 100 metres or more from other swedes or turnips.

Plants in each group flowered together. Seeds were harvested from each plant, and the number of plants from each resembling parents and hybrids was counted.

The self-fertility of some swede and turnip plants was tested by bagging flowers before they opened. Emasculated flowers of both species were pollinated with pollen from the other species to test inter-specific fertility. Some un-emasculated flowers were self-pollinated and crossed with the other species at the same time.

3. RESULTS

Self-fertility. One hundred swede flowers on 13 plants produced 81 pods and 976 seeds. Seven flowers on one plant produced no seed, and four flowers on another only seven. This failure may not be connected with self-incompatibility. Four hundred and forty flowers on 24 turnip plants gave 29 pods and 80 seeds. Only seven plants set seed, and these only 0.5 seeds per flower. These seeds may have come from selfings, or from pollen contamination. The turnips were much less self-fertile than the swedes.

Inter-specific cross-fertility. *B. napus* ♀ × *B. campestris* ♂ set 226 seeds from 61 emasculated flowers on eight plants. These produced 165 plants, 160 of which were hybrids, and five *B. napus*. *B. campestris* ♀ × *B. napus* ♂ set 278 seeds from 70 flowers on 10 plants. These gave 122 hybrids and one *B. campestris*. There were thus no strong barriers to crossing between the two species.

The 69 un-emasculated turnip flowers on ten plants which were selfed and crossed with swedes produced 660 seeds, which gave 297 hybrids and 7 *B. campestris*, but the 42 flowers on seven swede plants treated in this way produced only 41 hybrids and 292 *B. napus* from 483 seeds. This result may be related to the self-fertility of the two species; *B. campestris* being self-sterile, and the self-incompatibility barrier to its own pollen being greater than the inter-specific compatibility barrier, while in the self-fertile *B. napus* self-pollen is not inhibited and is more compatible than *B. campestris* pollen.

One *B. napus* plant produced 31 hybrids and 10 *B. napus* when selfed and crossed with *B. campestris*. Some of its sister plants also produced unusually high proportions of hybrids (table 1), and these results will be discussed later.

Open pollinations. Results from open pollinations are given in table 1.

Turnips grown in groups of four with four swedes produced about 10 per cent. of hybrid seedlings. A good supply of compatible turnip and swede pollen should have been available to pollinate these plants. There was some variation in the proportion of hybrids produced by different turnip plants.

Turnip plants grown singly with one swede plant produced about 58 per cent. of hybrid seedlings, with considerable variations in the proportion of hybrids produced by different plants. These plants would have been pollinated by a good supply of self-incompatible pollen, and perhaps by a poor supply of swede pollen. Contamination with pollen from outside the small group may have been of importance in these insect pollinated plants.

The turnips grown in the rape crop, where a good supply of self-incompatible pollen and also a plentiful supply of rape pollen would have been available, produced about 88 per cent. of hybrid seedlings.

These results show clearly the effects of variations in population composition on the frequency of inter-specific hybridisation in this self-sterile species.

The swedes grown singly with one turnip plant produced about 0.3 per

TABLE 1
Results from open pollination of Brassica napus and B. campestris

	<i>B. napus</i>			<i>B. campestris</i>		
	Plant	<i>B. napus</i>	Hybrids	Plant	<i>B. campestris</i>	Hybrids
Group 1	1	63	11	1	391	16
	2	434	14	2	124	43
	3	134	14	*	...	...
	4	297	14	*	...	...
	Totals	928	53	Totals	515	59
Group 2	5	61	6	5	251	20
	6	112	2	6	119	33
	7	70	3	7	376	40
	8	95	0	8	212	13
	Total	338	11	Totals	958	106
Group 3	9	336	1	9	6	66
Group 4	10	80	0	10	33	106
Group 5	11	108	0	11	209	191
Group 6	12	53	1	12	81	98
	Totals	577	2	Totals	329	461
Grown in crop of <i>B. campestris</i>				Grown in crop of <i>B. napus</i>		
	13	483	1	13	10	176
	14	157	0	14	14	180
	15	333	7	15	17	133
	16	153	101	16	17	188
	17	237	106	17	30	159
	18	242	7	18	30	120
	19	319	14	19	24	117
	20	67	6	20	29	174
	Totals	1991	242	Totals	171	1247

* These *B. campestris* plants died after flowering and before seed ripened.

cent. of hybrids. These plants would be pollinated by an adequate supply of their own pollen, and possibly by an inadequate supply of turnip pollen.

The swedes grown in groups of four with four turnip plants produced about 5 per cent. of hybrids. Turnip plants in the same groups produced about 10 per cent. of hybrids, so that when adequate supplies of compatible pollen of both species were available, the proportions of hybrids given by both species were not greatly different.

Six of the eight swede plants grown in the turnip crop produced about 2 per cent. of hybrids, which is significantly and unaccountably lower than from the swedes grown in groups with four turnip plants. The other two swedes, however, produced 30 and 40 per cent. of hybrids. These two plants, 16 and 17, with plants 3, 4, 9 and 12, were the selfed progeny of one plant. Their sister plants in the other open-pollinated groups gave an average proportion of hybrids. One sister plant, 9, gave a high proportion of hybrids when pollinated with its own and turnip pollen (31 hybrids: 10 *B. napus*), but few hybrids when grown with one turnip. Some members of the family may have been unusually compatible with turnips, or some cryptic self-sterility system of the type found by Bateman (1956) in *Cheiranthus cheiri* may exist in these swedes.

Apart from these three aberrant plants, the swede plants produced few hybrids in any circumstances. Variations in population composition did not greatly affect the incidence of inter-specific hybridisation of this self-fertile species.

4. DISCUSSION

B. napus and *B. campestris* cross readily when either is the male or female parent. *B. napus* is self-fertile, *B. campestris* self-sterile, and the results obtained from open pollination of different groups of the two species may be explained in terms of the variations in amounts of compatible pollen from each species available for fertilisation. The self-fertile *B. napus* produced few hybrids, but the self-sterile *B. campestris* produced many hybrid progeny when compatible pollen from other *B. campestris* was not available, and few when it was. Calder (1937) and Baumgart (1960) also obtained few hybrids from *B. napus* grown with *B. campestris*, and many from *B. campestris* grown with *B. napus*.

In areas where species meet one may often be much commoner than the other, and if the less common species is also self-incompatible it may, like *B. campestris*, hybridise freely with the other species; but if it is self-compatible, like *B. napus*, it will be less likely to hybridise. These results support the conclusion of Baker (1953) that cross-fertilising species are more likely to hybridise in these circumstances.

B. napus may be protected from hybridising with *B. campestris* by its self-fertility, and not by its allopolyploidy. Some advantage to pollen of the same species coupled with facultative self-fertilisation may then be an efficient isolating mechanism even under conditions otherwise highly favourable to inter-specific crossing.

Inter-species hybridisation is a usual prelude to the production of allopolyploids, and is more likely to occur in cross-fertilisers than in self-fertilisers.

Self-fertilising allopolyploids have arisen from hybrids between out-breeding species, so self-fertility may be a derived condition in allopolyploids. It may effectively isolate the allopolyploid from its diploid parents, and so may arise by selection as Olsson (1953) suggests.

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