5. Summary

1. Chiasmata formed in a pericentric inversion loop in an acrocentric bivalent give rise to the production at AII of long and short metacentric chromatids which have one segment duplicated and one missing, also to acrocentrics which may or may not contain the inversion.

2. The metacentrics superficially resemble iso-chromosomes, but genetically they are not, the arms being homologous only in the distal regions. Observations of Giles (1943), who proposed iso-chromosome formation at meiosis by a process of centromere misdivision and reunion are more readily interpreted as being due to a pericentric inversion.

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BREEDING SYSTEMS IN *PLANTAGO*

M. D. ROSS

Department of Biology, Dalhousie University, Halifax, Nova Scotia

1. Introduction

PALIWAL AND HYDE (1959) reported an association between the presence of an accessory or B chromosome and male sterility in a strain of *Plantago coronopus*. All the male steriles studied in their material had a single B chromosome, while all the hermaphrodites lacked B chromosomes. During a study of breeding systems in this genus, I obtained data which are difficult to reconcile with such an association. These data are given here, together with a brief survey of some of the breeding mechanisms found in this genus.

2. The situation in *Plantago coronopus*

Paliwal and Hyde's strain of *P. coronopus* (supplied by Professor Hyde) showed two types of male sterile, here called MS and Intermediate MS. The first type has minute anthers which are not exserted, or has small, slightly exserted indehiscent anthers. The Intermediate MS type has small exserted anthers producing very little or no pollen. This type is probably functionally male sterile. A minority of plants are intermediate between the male steriles and the hermaphrodites. The anthers are exserted, but produce

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only a little pollen compared with normal hermaphrodites. Normal herma-
phrodites have large exserted anthers, and produce abundant pollen.

Table 1 gives the F_1 results obtained from crossing and selfing this strain of
P. coronopus. Male steriles on crossing to hermaphrodites yielded mostly or
exclusively male-sterile offspring, while hermaphrodites segregated both
types on selfing. There is no simple genetic interpretation of these results.
They are difficult to reconcile with the association between male sterility and
the presence of a B chromosome postulated by Paliwal and Hyde (1959),
since the hermaphrodites, lacking B chromosomes themselves, would be
expected to leave only hermaphrodite offspring. This expectation was not

TABLE 1

F_1 *from crossing three male steriles of* Plantago coronopus *with three hermaphrodites, and from selfing
the hermaphrodites*

Cross or selfing	Offspring				
	MS	Inter MS	Inter	H	% MS*
MS1 × H1	131	1	0	2	99
MS1 × H2	68	2	0	16	81
MS1 × H3	92	0	0	7	93
MS2 × H1	101	1	0	2	98
MS2 × H2	9	0	0	0	100
MS2 × H3	40	0	1	0	98
MS3 × H1	54	0	0	5	92
MS3 × H2	104	0	0	6	95
MS3 × H3	45	1	0	0	100
H1 selfed	29	15	4	6	81
H2 selfed	7	17	13	62	24
H3 selfed	3	6	0	14	39

MS = Male sterile; Inter MS = Intermediate male sterile;
Inter = Intermediate; H = Hermaphrodite.
* Includes intermediate male steriles. For further details see text.

fulfilled (table 1). Paliwal and Hyde (*loc. cit.*) noted that small numbers of
B chromosomes do not usually have marked effects on plants, and that their
report was probably the first to associate complete male sterility with a
single B chromosome. Working with the related species, *P. serraria*, Fröst
(1959) concluded that the B chromosomes of that species were independent
of the male sterility that also occurred. It is clear that further studies are
required before the mode of inheritance of male sterility is understood in
P. coronopus.

Paliwal and Hyde (*loc. cit.*) also reported that male-sterile *P. coronopus* set
seed apomictically after pollination with *P. amplexicaulis*, which belongs to a
different section of the genus. No seed was set when I crossed male-sterile
P. coronopus with *P. alpina* and with *P. serraria*, which belong to the same
section of the genus, and with *P. lanceolata* from a different section of the
genus.

3. Breeding systems in *Plantago*

The genus *Plantago* contains both outbreeding and inbreeding species.
Outbreeding is favoured in some species because of protogyny, self-incom-
patibility and male sterility. The male sterility leads to outbreeding because

male-sterile (*i.e.* female) plants must be pollinated by the hermaphrodites (Mather, 1940). Species which consist of male steriles and hermaphrodites are said to be gynodioecious (Darwin, 1889).

Table 2 presents conclusions on the breeding systems of 11 species of *Plantago*. Some of these will now be briefly considered.

TABLE 2

Breeding systems in Plantago

Species		Breeding systems		Author
P. coronopus		SC	MS	Present author, Paliwal and Hyde (1959)
P. serraria		SI	MS	Fröst (1959)
P. maritima (Europe)		SI	G	Gregor (1939), Knuth (1909)
P. maritima (N. America)		SC	H	Gregor (1939), present author
P. lanceolata		SI	G	Baker (1963)
P. media	prob. SI		G	Rahn (1957), present author, Fröst (1959)
P. major		SC	G(1)	Rahn (1957), Knuth (1909)
P. ovata	prob. SC		G	Present author
P. lagopus			G	Knuth (1909)
P. aristata		SC†		Fernald (1950)
P. rhodosperma		SC†		Chandler (1954)
P. wrightiana		SC†		Chandler (1954)

SC = self-compatible; SI = self-incompatible; G = gynodioecious; G(1) = gynodioecious, at least locally; MS = male steriles occur, but the presence of gynodioecy is not established in natural populations; H = only hermaphrodites have been recorded.

† These species are assumed here to be self-compatible because of the presence of cleisto-gamous flowers (*P. aristata* and *P. rhodosperma*), or because of the occurrence of fertilisation before expansion of the corolla (*P. wrightiana*).

P. coronopus

It is not clear whether male steriles are found in natural populations of this species. However, the breeding data (table 1) are quite similar to data obtained from gynodioecious species, and are not compatible with monogenic recessive inheritance, which is the usual mode of inheritance for male-sterile mutants in non-gynodioecious plants. This species is taken as self-compatible since 5 inflorescences from 4 plants yielded on selfing an estimated 66, 84, 88, 88 and 100 per cent. seed set, respectively.

P. maritima

The taxonomy of *P. maritima* and its close allies is confused. Fernald (1950) treated populations from eastern North America under the names *P. juncoides* and *P. oliganthos*, while Pilger (1937) regarded *P. juncoides* as a variety of *P. maritima*, but retained *P. oliganthos* as a separate species. Gregor (1939) crossed diploid sea plantains from western and eastern North America with European diploid *P. maritima*, and obtained good seed set in nearly all crosses. He found that plants from North America and Greenland produced 4 seeds per capsule and were self-compatible, while plants from Europe had 2 seeds per capsule and were self-incompatible. Gregor and Lang (1950) found greater variability in European than in North American sea plantains. Knuth (1909) recorded gynomonoecy and gynodioecy in European material with usually 5-10 per cent. of male steriles, and I had no difficulty in finding

male steriles in a small population in North Wales. By contrast 600 plants from two populations in Nova Scotia failed to reveal a single male sterile. Hence this species or species-complex appears to be self-incompatible and gynodioecious in Europe, but self-compatible and hermaphrodite in North America.

P. lanceolata

Male sterility is inherited digenically, but other factors are present, such that the overall mode of inheritance is not simple (Ross, 1969).

P. media

Rahn (1957) stated that this species was probably self-incompatible. My material appears to be weakly self-incompatible since four crosses set about twice as many seeds per cross as two selfings.

P. major

Knuth (1909) reported that this species was gynodioecious and gyno-monoecious. I found 5 male steriles among 140 plants grown from seed obtained from Kiev Botanic Garden. A sample of 100 plants from a natural population in Nova Scotia consisted of 7 male steriles, 74 hermaphrodites and 19 gynomonoecious plants.

P. ovata

Chandler (1954) raised more than 1300 plants from seed derived from a strain cultivated in India, and found 65 per cent. male steriles. Such a high proportion of male steriles suggests that the species is gynodioecious, even though counts on natural populations are lacking.

P. lagopus

Ten male steriles among 106 plants raised from seed from Mainz Botanic Garden, and 2 male steriles among 36 plants raised from seed from Stockholm Botanic Garden help to confirm Knuth's report (Knuth, 1909) of gynodioecy in this species. Gynomonoecious plants are also present.

4. DISCUSSION: SELF-INCOMPATIBILITY AND GYNODIOECY

Baker (1963) posed the question of why both self-incompatibility and male sterility should be present in *P. lanceolata*. The self-incompatibility appeared to render the male sterility superfluous as an outbreeding mechanism, since not only the male steriles but also the hermaphrodites must be cross fertilised. This survey does not answer Baker's question, but adds two (or three if we include *P. serraria*) other species in which both outbreeding mechanisms probably occur (table 2). The most striking situation occurs in *P. maritima* in which self-incompatibility is associated with gynodioecy in Europe, while self-compatibility is associated with apparent absence of gynodioecy in related North American populations.

5. SUMMARY

1. The occurrence of male sterility in *Plantago coronopus* has been associated with the presence of a single B chromosome. Breeding evidence presented here does not support such an association.

2. A survey of breeding systems in the genus *Plantago* has established that there are several species which are both self-incompatible and gynodioecious.

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A TEST FOR " AFFINITY " IN MAIZE

KENNETH E. MICHEL

Department of Biology, Slippery Rock State College, Pennsylvania, U.S.A.

1. INTRODUCTION

THE non-random assortment of non-homologous chromosomes has been demonstrated in the " normal " diploid house mouse. Michie (1953, 1955) and Wallace (1953) have offered the hypothesis of affinity to account for the loose genetic association of unlinked genetic markers in this organism. The hypothesis states that at the first meiotic division in hybrids there is a tendency for non-homologous centromeres of the same ancestral origin to segregate to the same pole of the cell. The hypothesis is expanded by Michie (1955) into the possibilities of polar affinity, the centromeres being acted upon independently by some polar force, and mutual affinity, an attraction for each other of centromeres of like origin. The point to be made here is that the centromere is either the controlling force or the structure acted upon. In either case, centromere markers on independent chromosomes would give

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