

Lecture 7, January 28, 1954

Continuation of transposition of Ac; and its relation to somatic sectoring and to controls of mutation of mutable genes.

I. Review of previous discussion:

1. In all major respects, Ac is inherited as a mendelian unit:

a). Expected statistical ratio in  $F_2$ ,  $\frac{3}{4}$  Ac :  $\frac{1}{4}$  ac; found.

b). Expected  $\frac{1}{4}$  " in b.c. of Ac/ac: 1 : 3; found.

2. When homozygote, Ac/Ac, backcrossed by ac, some unexpected events revealed:

a). Not all of the plants carry Ac -- few with no Ac

b). Others, 2 Ac factors, independently located : Ac + Ac

c). Alteration in action of Ac discovered:

(1) Dosage action of single Ac double that of original Ac =  $\widehat{Ac} \widehat{Ac}$

(2) Dosage action of single Ac increased over that of original Ac but not double that of it.

(3) Dosage action decreased. Ds breaks occur earlier in development of tissue than those occurring when original was present.

3. The changes in Ac occur late in development of the sporogenous tissues:

(1) This shown by the scattered kernels on ear that carry the changed Ac factors. *Ear -*

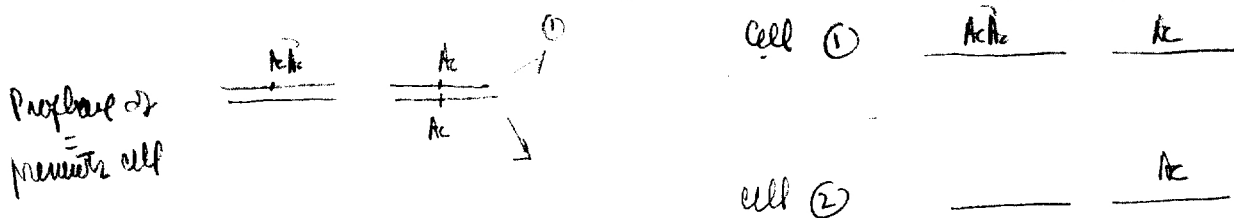
(2) In case presented, these changes occurred in only a few of the ovules produced by the female plants.

II. What is the mechanism responsible for these changes of Ac?

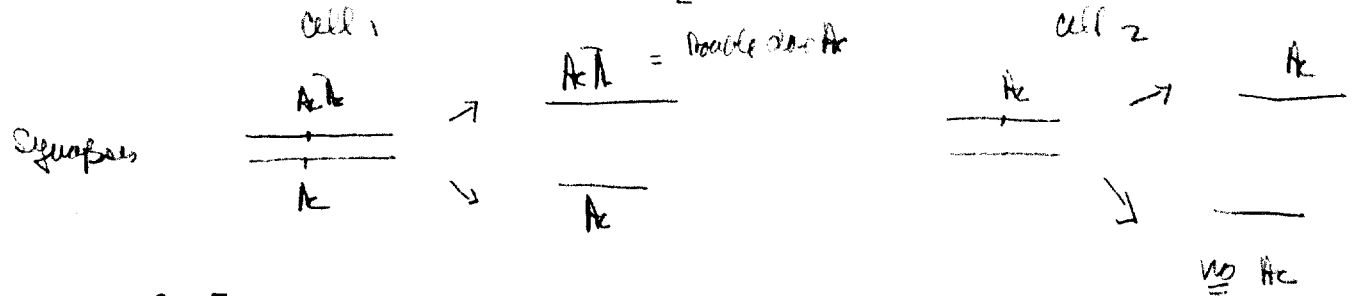
1. If one Ac transposed from one chromosome to another in sporogenous cell, before meiosis, could get either no Ac or 2 Ac in the resulting spore or gamete:



2. If one Ac in one chromosome remains in one chromosome after chromosome reduplication, can get double-dose Ac or no Ac:



In development of the megaspore, either of these two cells recovered but not both: Only one cell develops into the megaspore, and only one of spores produces the female gametophyte:



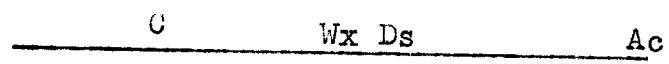
3. In either case, would expect to find a 1 : 1 ratio of kernels with no Ac to those with either 2 Ac or double-dose Ac.

Observed: 19 with no Ac to 23 with either 2 Ac or  $\widehat{Ac}Ac$ .

4. In addition, Ac was found to change in action-- to increase its dosage action or to decrease it. How does this occur?  
 If it is transposed, does its position affect its action?  
 If changes occur of this type, without change in position, is Ac composed of a number of sub-units? Or, is its efficiency in some manner altered?

III. What evidence have we that Ac does move from one position to another in the chromosomal complement? To study, should know the position of Ac in the chromosome complement and study its changes at this position and its removal from this position. This was done because of appearance of Ac in chromosome 9, which is well marked.

1. The first discovered case of Ac appearance in chromosome 9:
  - a). In <sup>c</sup>cross of ac/ac plant by Ac/ac plant, no evidence found for any linkage of Ac with markers in chromosome 9.
  - b). The  $F_1$  <sup>plants</sup> carrying Ac grown. 9 plants crossed to plants not carrying Ac. Both chromosomes 9 in male parents with Ac carried genetic markers in chromosome 9.
  - c). 8 plants showed that Ac was not linked to factors in chromosome 9.
  - d). 1 plant; the Ac in this plant linked to markers in chr. 9.
  - e). Its position tested. Found to be located to right of Wx:



f). Type of data obtained in test of linked and non-linked Ac:

C sh bz wx ds, ac female by I:  $\frac{I \ Sh \ Bz \ Wx \ Ds \ Ac}{C \ Sh \ Bz \ wx \ Ds \ ac}$  male

II:  $\frac{I \ Sh \ Bz \ Wx \ Ds}{C \ Sh \ Bz \ wx \ Ds}$   $\frac{Ac}{ac}$

Table 1, page 23, Symposium paper.

2. Later, other cases of appearance of Ac in chromosome 9 found. One of them, Ac in short arm, just to left of Wx:

    C        Ac Wx Ds

a). Example of how such a case discovered:

Number of plants in a culture came from one in which Ac had not been located in chromosome 9. These plants tested for Ac. One among them may now show Ac in chromosome 9:

The test type: *Example*

Female:  $\frac{c \ Wx}{c \ wx} \quad \frac{Ac}{ac} \quad x \quad C \ wx \ Ds, \ ac \ male:$

Kernels on resulting ear: *would expect*

1 C Wx, non-variegated : 1 ~~C~~ Wx, with areas of c wx  
*no Ac* *Ac*

1 C wx, non-variegated : 1 C wx, with areas of c  
*no Ac* *Ac*

If female were  $\frac{c \ Ac \ Wx}{c \ ac \ wx} \quad x \quad C \ wx \ Ds \ ac,$  then, modified

ratios of variegated to non-variegated expected in Wx and wx classes: The extent of deviation from 1 : 1 would depend upon how close Ac were to Wx. And, the frequency of transposition of Ac from chromosome 9 position, as indicated, to another position.

Example in one test:

<u>C Wx class</u>		<u>C wx class</u>	
Non-var.	CWx-cwx var	Non-var.	Cwx with c areas
19	207	164	14

b). Ac obviously closely linked to Wx. The order could be:

(1) or (2)

$\frac{c \ Ac \ Wx}{c \ ac \ wx}$

$\frac{c \ Wx \ Ac}{c \ wx \ ac}$

c). In usually genetic test, it would be simple to locate factor by a three-point test:

$\frac{C \ Ac \ Wx}{c \ ac \ wx}$

$\frac{C \ Wx \ Ac}{c \ wx \ ac}$

*can* determine the position and crossover frequencies readily in most genetic tests. This not easy in the case of Ac. This is because of transpositions.

- d). A number of different tests conducted with this case. It took nearly three years before location and cross-over frequencies could be stated with some certainty.
- e). Tests are tedious to describe and not easy to follow because of number of genetic markers used; and the many types of tests made.
- f). To avoid such descriptions, a relatively simple type of test can be used to illustrate what happens: The cross:

	female		male
(1)	$\frac{c \text{ ac } (wx) \text{ ds}}{c \text{ ac } (wx) \text{ ds}}$	/	$\frac{C \text{ ac } (wx) \text{ Ds}}{C \text{ Ac } (wx) \text{ ds}}$

(2) Type of kernels on the resulting ear:

	their constitutions as expected:	
	non-crossovers	cross-over
478 Colored, non-variegated :	$\frac{C \text{ ac } Ds}{c \text{ as } ds}$ or $\frac{C \text{ Ac } ds}{c \text{ ac } ds}$	$\frac{C \text{ ac } Ds}{c \text{ ac } ds}$
17 Colored with c areas		$\frac{C \text{ Ac } Ds}{c \text{ ac } ds}$

(3) 17 "crossover" carrying kernels selected from ear. Plants grown from them. 16 plants tested; one died.

Each plant crossed by I  $\frac{Wx \text{ Ds } ac}{c \text{ wx } ds \text{ ac}}$

The results: 13 plants of 16 only, as records of other 3 not here:

6 plants were crossover types:  $\frac{C \text{ Ac } (wx) \text{ Ds}}{c \text{ ac } (wx) \text{ ds}}$

6 plants had Ac, but not in chromosome 9 short arm

$$\frac{C \text{ ac } (wx) \text{ Ds}}{c \text{ ac } (wx) \text{ ds}} \quad \frac{Ac}{ac}$$

1 plant had no Ac. [*transposition in mitosis producing form in a mosaic (eliminated)*]

(4). This test shows that only half of the apparent crossovers are true crossovers. The rest carry an Ac, not in chromosome 9 short arm.

4. Other cases of appearance of Ac in short arm of chromosome 9:



a). Changes in Ac that were observed:

Disappearance from short arm coincident with appearance elsewhere.  
 Change in dosage action: Increased or decreased, either with or without change in location.

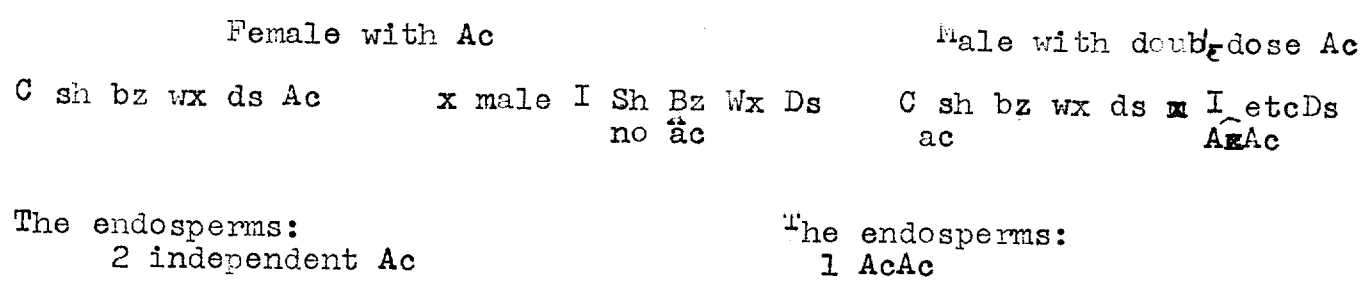
*... kernel ...*

5. A correlation noted between changes in location, and/or action of Ac and changes occurring at Ds. The coincidence rate is high.

a). This has made it possible for ready selections of changes in location of Ac in kernels carrying them. Will be discussed later, where this will be strikingly apparent.

IV. With evidence of changes that occur to Ac in mind, it is possible to evaluate the patterns produced in kernels carrying Ds and Ac.

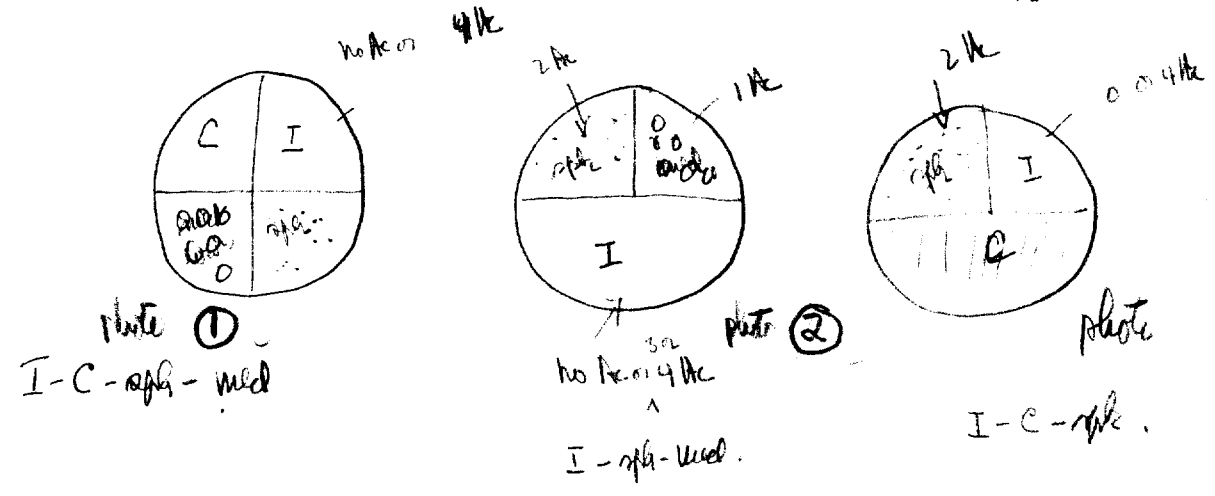
1. The "early sectorials". Changes of Ac occur very early in development of kernel. Result in sectors showing different types of Ac action: These appear in kernels carrying two Ac or a double-dose Ac.



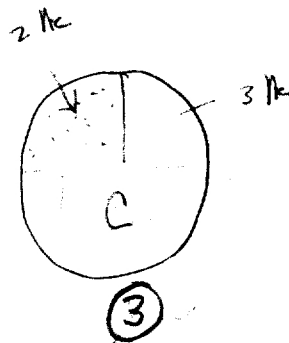
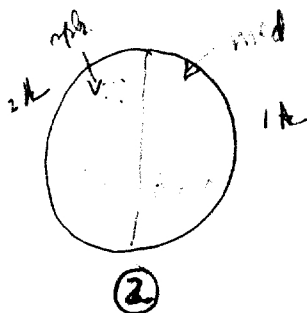
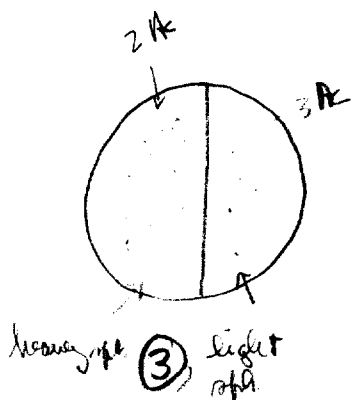
2. One of the AcAc males (homozygous and allelic positions) crossed to various tester plants as females. 90 - 95 % of kernels were early sectorials:

*C/C ♀ + I/I ♂*

The 3 most frequent types:



The infrequent types:



3. Other cases, from crosses with female introducing Ac. Some isolates give sectoring later in development: Examples: ~~Photo~~ (4)

amp. ← 4. With this in mind, can attempt to evaluate the patterns observed when 1 Ac present. Examples:

a). The kernels are mosaics of different Ac constitutions:

No Ac -- not Ds breaks; sectors not showing breaks

Photo (5)

2 Ac - sectors produced with late occurring Ds breaks

sub  
within them, /sectors produced with no Ds breaks or later occurring Ds breaks.

b). Pattern of variegation in the kernels receiving 1 Ac reflects the changes occurring to Ac and the time of these changes. It is not a "chance" pattern of Ds breaks.

amp. - c) ↓ Different isolates of Ac can show quite different patterns in 1 dose.

(1) With some, changes in Ac commence early in the development of the endosperm.

(2) With others, these occur much later.

(3) The consequence:

Various types of patterns produced by different Ac isolates. These different actions reflect differences in the Ac factors. These differences have been designated different "states" of Ac.

V. The bearing of the Ac investigation on the problem of what is operating to control the mutations at the locus of the mutable genes.

1. In the first discussion of this series, the reasons for undertaking the study of mutable loci were emphasized.

2. It was emphasized that in all examined cases, and there were many, -- a controlling system was present. This system controlled the time of occurrence of mutations during the development of a tissue and the cells in which it would occur.

(5). Where did this Ac come from? If we assume transposition from short arm of chromosome 9 to another chromosome, this situation could be explained:

Sporogenous cell

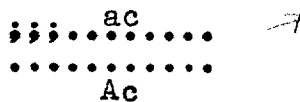
a).  $\frac{C \text{ Ac } ds}{\text{homologues}}$   $\frac{C \text{ ac } Ds}{\text{homologues of another chromosome}}$  .....

b). Ac transposed in this cell to ..... chromosome:

$\frac{C \text{ ac } ds}{\text{.....}}$   $\frac{C \text{ ac } Ds}{\text{.....}}$  ..Ac.....

c). Meiotic segregations:  
Synapsis:

$\frac{C \text{ ac } ds}{C \text{ ac } Ds}$



Segregations:

$\frac{C \text{ ac } ds}{\text{.....ac.....}}$

$\frac{C \text{ ac } Ds}{\text{.....Ac.....}}$

(6). In the described test, in selecting for supposed crossovers, we are also selecting for transpositions of Ds. Such were present in approximately one-half of the supposedly cross-over class.

mp, → 3. We can also test for the removal of Ac from chromosome 9 short arm:

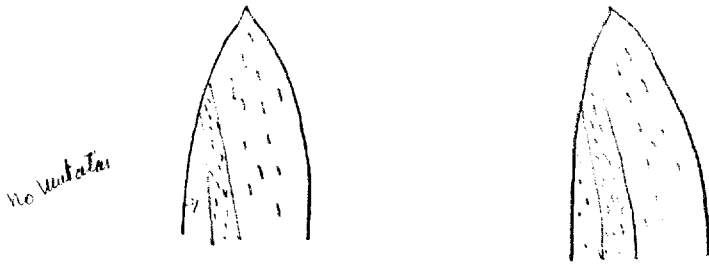
a). Example of the type of test:

Female  $\frac{c \text{ Ac}}{c \text{ Ac}}$  × Male  $\frac{C \text{ Ds } ac}{C \text{ Ds } ac}$

Types of kernels on ear from one such test: (Most of tests not here)

6 C, non-variegated: { 3 kernels did not germinate  
3 remaining plants tested:  
168 C with c areas: { 2 had no Ac  
2 kernels with very late speckled pattern of losses. { 1 had AcAc but no change in location  
Plant grown from one of two kernels:  
Ac not in chromosome 9. Plant was:  $\frac{C \text{ Ds}}{c \text{ ds}}$   $\frac{Ac}{ac}$   
Ac action altered from that shown when in chr. 9.

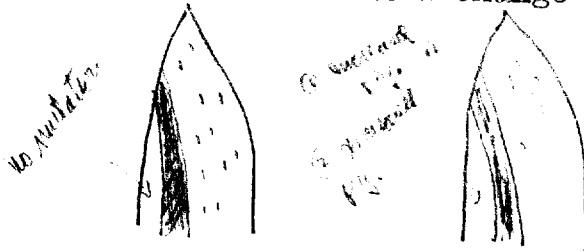
3. The observations for these conclusions came from the appearance of "twin sectors". They were:



4. These relationships within the twin suggested that one cell received something that the other cell lost, and this something was associated with the control of mutations in future development -- in the cells arising from those where the changes occurred.

5. Since twin sectors appear to come from sister cells, the event appeared to be associated with the mitotic process.

6. Also, the mutation process itself appeared to occur during a mitosis, and this often correlated with a change in the controlling system:

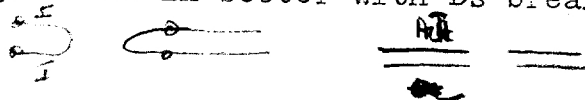


7. Ac controls the occurrence of breaks at Ds. If these events at Ds are compared to the mutations at mutable loci, then parallels may be drawn: Ac is the controlling system controlling the "mutations" in this case.

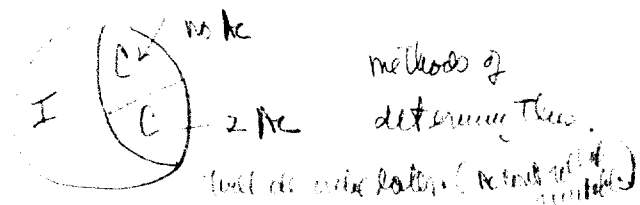
a). Segregations of Ac occur at somatic mitosis. One cell can gain an Ac that the other cell loses. Result is an altered time of occurrence or the absence of occurrence of Ds breaks in the progeny of the two resulting cells:

b). The coincident changes at both Ac and Ds: these frequent. Result in sister cells, one of which may have altered Ac:

Change in Ac in sector with Ds break



Resulting sector:





c). The parallel regarding controlling systems is striking. This would suggest that the mutable genes also have controlling units that are responsible for the patterns of mutations. These units either at the locus concerned or are separate - as with Ac.

VI. In next discussion, would like to consider Ds again and show that it, also, transposes from one location to another and that there are very striking consequences produced as a result of this: It is the cause of the appearance of some of the mutable genes.