

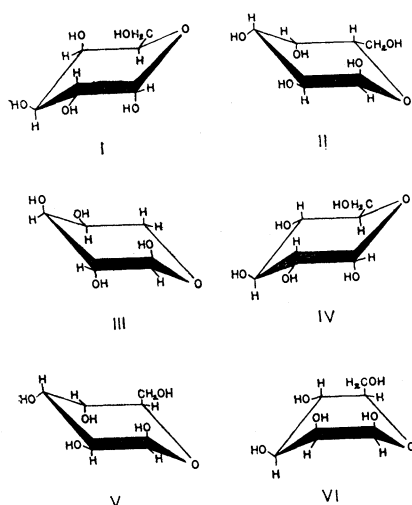


Fig. 1. Some conformations of pyranoid sugars.

reference and (ii) specification of conformations in terms which refer to the α -anomers only. Both systems are, we believe, preferable to two previously suggested (2, 3). By Reeves' system (2), enantiomorphs received different symbols. This situation was avoided by Isbell (3), but his system applies only to chair forms of aldohexopyranoses, ketoheptopyranoses, and the higher sugars.

In our system, a symbol describing the kind of pyranoid ring is used; thus, *C* denotes the chair, and *B*₁, *B*₂, and *B*₃ specify the three boats (4). If the reference group (5) at carbon atom 1 of the α -anomer (*D* or *L* series) is axial, the symbol *A* is added to the ring symbol; if the reference group is equatorial, the symbol *E* is added. Thus, eight symbols (*CA*, *B*₁*A*, *B*₂*A*, *B*₃*A*, *CE*, *B*₁*E*, *B*₂*E*, and *B*₃*E*) are obtained which, appended to the systematic names, unambiguously describe all the chair and boat conformations of all the pyranoid sugars and their derivatives (6).

Table 1. Names of conformations of pyranoid sugars IV, V, and VI by the previous and the present systems.

Formula	Name	Reference
IV	α -D-Glucose-C1	(2)
	α -D-Glucose-C'1	(3)
	α (<i>Ca</i>)-D-Glucose	(1)
	[α (<i>Ca</i>) conformation]	*
V	β -D-Altrose-1C	(2)
	β -D-Altrose-C'2	(3)
	β (<i>Ca</i>)-D-Altrose [α (<i>Ce</i>) conformation]	(1)
	β -D-Altrose- <i>CE</i>	*
VI	β -D-Mannose-3B	(2)
		(3)
	β (<i>B</i> ₃ <i>a</i>)-D-Mannose	
	[α (<i>B</i> ₃ <i>e</i>) conformation]	1
	β -D-Mannose- <i>B</i> ₃ <i>E</i>	*

* Present authors.

The compounds having formulas I, II, and III are thus named α -D-galactopyranose-*CA*, α -L-galactopyranose-*CA*, and α -L-arabinopyranose-*CA* (Fig. 1). Table 1 gives the names for compounds IV, V, and VI by the previous systems and the present one (7).

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4. The three boats are those in which carbon atoms 1 (and 4), 2 (and 5), and 3 (and the oxygen atom), respectively, lie (*cis*) outside the plane of four other atoms of the ring.
5. A reference group at asymmetric carbon atom 1 (the "glycosidic" or anomeric carbon atom) is regarded as being any atom other than a hydrogen atom, or any group other than an alkyl or polyhydroxyalkyl (including hydroxymethyl) group.
6. This system is applicable, in conjunction with suitable symbols for the respective rings, to all pyranoid conformations having an axial-equatorial arrangement of exocyclic bonds at carbon atom 1.
7. For added clarity, the appropriate symbol (*a* or *e*) may, if desired, be inserted in parentheses after the anomeric symbol. Thus, II is α (*a*)-L-galactopyranose-*CA*; V is β (*a*)-D-altropyranose-*CE*; and VI is β (*a*)-D-mannopyranose-*B*₃*E*.

26 March 1959

Intracistron Recombination in the *Wx/wx* Region in Maize

Abstract. Five independently occurring waxy (*wx*) mutants produce low frequencies of standard type (*Wx*) pollen grains (0.3 to 3.8×10^{-5}). In crosses between these mutants, frequencies of *Wx* pollen grains range from 1.4 to 88×10^{-5} , depending on the cross. Data from the crosses allow the ordering of the mutants within the region. Functional complementation between the different mutants does not occur.

Genetic resolution can be enhanced greatly by using microorganisms and selective techniques for the detection of recombinants. The results obtained by Benzer with phage (1) and Pritchard with *Aspergillus* (2) have profound genetic implications, pointing as they do to the delineation of different mutational sites within a single functional region. Pontecorvo (3) has discussed the impact of these findings on modern genetical theory. It would be most desirable to be able to make similar studies in higher organisms, but it is difficult to handle populations of sufficient size to do more than hint at the existence of such a phenomenon.

A system in maize has been described

(4) which makes it possible to deal easily with numbers giving a resolving power comparable to that obtained with some microorganisms. The technique uses the haploid pollen grain as the unit of observation and relies on the fact that the staining reaction of a pollen grain with a KI and I₂ solution depends on its genotype at the *Wx/wx* region. The standard type (*Wx*) pollen grains stain black, owing to the presence of amylose with amylopectin in the starch granules. The waxy mutant (*wx*) pollen grains, which contain only amylopectin, stain light brown. Thus the millions of microspores produced by a maize plant are available for analysis. Standard preparations containing about 50,000 pollen grains can be made and scored within a relatively short time.

If two independently occurring *wx* mutants are crossed, recombination may be detected in the pollen grains produced by the F₁ cross between the two mutants. One product of recombination would be a functional (*Wx*) region, and pollen grains carrying such regions would stain black in contrast to the brown-staining pollen grains of either of the parental types. Then, if the frequency of black-staining (*Wx*) pollen grains in the population from an F₁ cross between two mutants is significantly higher than the frequency in either parental stock this would indicate that the two mutations occupy different sites within the region.

To make such tests, five independently occurring, spontaneous *wx* mutants were crossed in all possible combinations (5). These mutants were *a*, *B*, *C*, *H21*, and *90*. All occurred in stocks of different genetic background. Only the *a* mutant allows the formation of measurable quantities of amylose. Plants homozygous for *a* have 2 to 5 percent amylose in the starch of the endosperm, in contrast to *Wx/Wx* plants, which have about 25 percent amylose. Tassel samples were collected just before pollen shedding and stored in 70-percent alcohol. Subsequently, each type was scored for the frequency of black-staining (*Wx*) pollen grains. The plants sampled were grown in the field in 1958, except for the *a* crosses, which were grown in 1957. The results are presented in Table 1.

Table 1 shows that for the parental stocks there are low but measurable frequencies of *Wx* pollen grains. The figure for any mutant would include back-mutations, suppressor mutations, and contamination arising from a wind-blown pollen grain lodging in one of the glumes to be sampled. For the crosses it may be seen that the frequencies range from no higher than the parental stocks to many-fold higher.

The data in Table 1 are derived from preparations in which 24 anthers (three anthers from each of eight glumes) were combined. For most crosses with a high

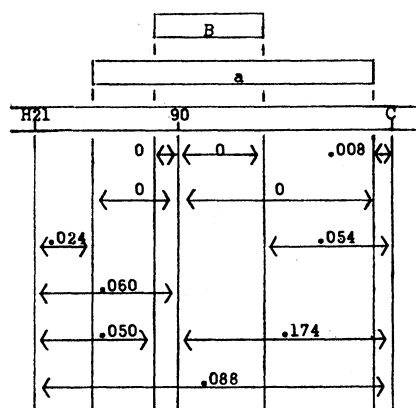


Fig. 1. Preliminary map of the Wx/wx locus constructed from the data in Table 1. The value for any cross is corrected for the frequency of Wx microspores appearing in the parental stocks and doubled for the purpose of map construction.

incidence of Wx pollen grains, a large number of single anther preparations have been scored. In each instance, the distribution of numbers of Wx pollen grains per anther showed good agreement with a Poisson distribution. There was no indication of bursts of Wx pollen grains in a particular anther, or glume, or tassel sector, such as might result from somatic crossing-over or premeiotic mutation.

Where more than one cross between two mutants was made, the progeny from each cross was sampled. In each cross, there was good agreement between the different progenies. In some cases, reciprocal crosses were available. The data again showed good agreement.

A small population (nine plants) from

Table 1. Estimates of incidences of Wx microspores in the mutant strains and in the crosses between them. The means shown in column 3 have been calculated from preparations each containing about 50×10^3 pollen grains.

Strain	Estimated No. of microspores sampled (in thousands)	$\bar{x}$ No. $Wx \times 10^{-6} \pm s\bar{x}$
<i>a</i>	522	1.4 ± 0.4
<i>B</i>	472	3.8 ± 1.2
<i>C</i>	444	0.7 ± 0.4
<i>H21</i>	559	2.7 ± 0.8
<i>90</i>	353	0.3 ± 0.4
<i>H21</i> $\times$ <i>B</i>	987	28.1 ± 2.2
<i>H21</i> $\times$ <i>90</i>	1168	31.8 ± 2.7
<i>C</i> $\times$ <i>H21</i>	1218	46.0 ± 2.7
<i>90</i> $\times$ <i>B</i>	717	1.4 ± 0.6
<i>90</i> $\times$ <i>C</i>	596	88.0 ± 5.7
<i>C</i> $\times$ <i>B</i>	1077	29.5 ± 2.9
<i>Rec. C</i> $\times$ <i>C</i> (6)	252	1.3 ± 0.9
<i>C</i> $\times$ <i>a</i>	575	5.5 ± 0.9
<i>a</i> $\times$ <i>H21</i>	533	13.6 ± 1.9
<i>a</i> $\times$ <i>90</i>	646	0.9 ± 0.5

the backcross progeny $(90 \times C) \times C$ has been sampled in 1959 in the greenhouse. Five of the plants had frequencies of Wx pollen grains which were no higher than the parental stocks. Four plants had high frequencies of Wx pollen grains, with a mean of 63×10^{-5} . Under greenhouse conditions, the F_1 plants $(90 \times C)$ had 75×10^{-5} Wx pollen grains. Such a segregation into approximately equal numbers of plants with high and low frequencies of Wx pollen grains would be expected if heterozygosity at the Wx/wx region were a prerequisite for the appearance of high frequencies of Wx pollen grains.

Considering the above data, one is forced to conclude that each mutant tested differs from every other mutant and that there is a characteristic, reproducible frequency of Wx pollen grains for the cross between any two wx mutants. Heterosis, per se, cannot account for the Wx microspores, as witness the frequencies in $90 \times B$ and *Rec. C* $\times$ *C* (6). A logical corollary of these conclusions is that the Wx pollen grains arising in the crosses are the result of recombination within the *waxy* region. If so, it should be possible to establish a linear order for the mutants within the region. This can be done, since only one arrangement will satisfy the data. This arrangement is given in Fig. 1. It is necessary to assume that two mutants, *B* and *a*, occupy considerable portions of the region. Note further that the additivity of distances is not good. This may be a consequence of the occurrence of these five mutants in quite different genetic backgrounds. To investigate genetic fine structure it would seem essential that the mutants be induced in the same strain. This is now being attempted.

The size which it is necessary to assume for mutants *B* and *a* may also be a consequence of the heterogeneous backgrounds for the mutants. Alternatively, it may be real. One possibility for *B* is a deficiency of the genetic material for the area which the mutant is indicated as occupying. For *a* this is less probable, since *a* is a functionally intermediate allele allowing the synthesis of 10 to 20 percent of the amount of amylose found in Wx starch. If the genesis of a mutant were functional region plus "gene-controlling element" within the region, as McClintock (7) has shown to be possible, then the mutant would appear as a block in studies of this type, assuming that recombination to reconstitute a functional region would have to take place outside the area of the "gene-controlling element." A *waxy* mutant which is known to have had such an origin is being studied presently.

The Wx/wx region also governs the type of starch produced in the triploid cells of the endosperm. If functional complementation occurs, it should be de-

tected in the endosperm of seeds produced by a cross of two mutants. Analyses (8) of amylose in the crosses do not reveal large increases over the mutant stocks. Therefore the mutants would appear to be located in a single cistron (9, 10).

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27 April 1959

Time-Lapse Motion Picture Technique Applied to the Study of Geological Processes

Abstract. Light-weight, battery-operated timers were built and coupled to 16-mm motion-picture cameras having apertures controlled by photoelectric cells. The cameras were placed adjacent to Emmons Glacier on Mount Rainier. The film obtained confirms the view that exterior time-lapse photography can be applied to the study of slow-acting geologic processes.

The usefulness of time-lapse motion-picture photography for certain purposes is well known. For the most part the technique has been restricted to interior installations with controlled light facilities. Recent developments in photographic equipment have made possible the application of fully automatic time-lapse photography in natural settings.

A 16-mm motion-picture camera that has automatic aperture control coupled to a photoelectric cell appeared on the market in 1957. With the addition of timing and shutter-tripping mechanisms, such a camera can take single-frame exposures at regular preselected intervals over long periods. The possibility that such equipment might be installed in remote areas without requiring continual care suggested that the time-lapse technique might be adapted for use in the study of extremely slow-acting geologic processes. In order to determine the usefulness of this equipment in such