THE CONNECTICUT

AGRICULTURAL EXPERIMENT STATION

NEW HAVEN, CONN.

BULLETIN 167, APRIL, 1911.

INHERITANCE IN MAIZE.

BY E. M. EAST AND H. K. HAYES.

The Bulletins of this Station are mailed free to citizens of Connecticut who apply for them, and to others as far as the limited edition permit.

Connecticut Agricultural Experiment Station.

OFFICERS AND STAFF

BOARD OF CONTROL.

His Excellency, Simeon E. Baldwin, *Ex Officio*, *President*.

Prof. H. W. Conn, *Vice President*	Middletown.
George A. Hopson, *Secretary*	Wallingford.
E. H. Jenkins, *Director and Treasurer*	New Haven.
J. W. Alsop	Avon.
Charles M. Jarvis	Berlin.
Frank H. Stadtmueller	Elmwood.
James H. Webb	Hamden.

STATION STAFF.

Administration	E. H. Jenkins, Ph. D., *Director and Treasurer.* Miss V. E. Cole, *Librarian and Stenographer.* Miss L. M. Brautlecht, *Bookkeeper and Stenographer.*
Chemistry.	
Analytical Laboratory,	John Philips Street, M. S., *Chemist in Charge.* E. Monroe Bailey, Ph. D., C. B. Morrison, B. S., R. B. Roe, A. B., C. E. Shepard, *Assistants.* Hugo Lange, *Laboratory Helper.* V. L. Churchill, *Sampling Agent.*
Proteid Research,	T. B. Osborne, Ph. D., *Chemist in Charge.* Miss E. L. Ferry, A. B., *Assistant.* Miss Luva Francis, *Stenographer.*
Botany.	G. P. Clinton, S. D., *Botanist.* E. M. Stoddard, B. Agr., *Assistant.* Miss M. H. Jagger, *Seed Analyst.* Miss E. B. Whittlesey, *Herbarium Assistant.*
Entomology.	W. E. Britton, Ph. D., *Entomologist; also State Entomologist* B. H. Walden, B. Agr., D. J. Caffrey, B. Agr., A. B. Champlain, *Assistants.* Miss E. B. Whittlesey, *Stenographer.*
Forestry.	Samuel N. Spring, M. F., *Forester; also State Forester and State Forest Fire Warden* W. O. Filley, *Assistant.* Miss E. L. Avery, *Stenographer.*
Plant Breeding.	H. K. Hayes, B. S., *Plant Breeder.* C. D. Hubbell, *Assistant.*
Buildings and Grounds.	William Veitch, *In Charge.*

TABLE OF CONTENTS.

Page.

PART IV.—PLANT CHARACTERS.

PART V.—PLANT ABNORMALITIES.

INHERITANCE IN MAIZE.

BY

E. M. East and H. K. Hayes.

INTRODUCTION.

The investigations reported in this paper were begun in the spring of the year 1906. During the first four years the work was conducted at the Connecticut Agricultural Experiment Station. Since the fall of 1909, it has been carried on both there and at the Bussey Institution of Harvard University. Strictly speaking the researches comprise more than five years' work, for several of the pure varieties used as parent stocks had been selfed for the two previous years, so that a number of crosses were made in 1905 with full assurance that as far as most of the visible characters were concerned, the parent strains were pure. There was some further advantage gained in that the writers have been interested in experimental maize breeding since 1900, for without this experience the probable error of the results would be greatly increased.

Genetic research during the past decade has been very fruitful of results; nevertheless one could scarcely say that the field has been thoroughly surveyed, much less that any part of it has been completely investigated. The rediscovery of Mendel's law in 1900 opened up a new era in the search for the principles

---

*"Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University, No. 9."

of heredity. Mendel's chief discovery — segregation of potential characters in the germ-cells of hybrids and their fortuitous recombination — was one of the really great achievements in biology, but even so, it may be questioned whether his chief legacy is not his method of work. As has already been stated by Bateson, previous investigators even including the biometricians dealt with facts *en masse*, and the seeming order of the mathematical formulas deduced served rather to conceal than to reveal the individual facts. Mendel's method of individual analysis by the study of simple characters in carefully controlled pedigree cultures, however, has yielded and will continue to yield results of great value to science. Still, since we are dealing, as yet, with the simplest elements of the science of genetics, the subject matter of an investigation may be expected to yield results (other things being equal) somewhat in the proportion in which it fulfills the following technical requirements.

1. The genus or species under investigation should be variable. There should be a goodly list of types which are differentiated by definite characters easy of determination. That is, the differences should be largely qualitative and not quantitative.

2. The different types should be freely fertile *inter se*, unless an investigation of the causes of sterility is contemplated.

3. The flower structure should be such that the technique of crossing and selfing is simple and accurate.

4. Since the accuracy of an analysis of the manner in which characters are inherited increases — generally speaking — as the square root of the number involved, the subjects should return a large number of seed per operation (selfing or crossing).

5. The flowering branches should be numerous. This is necessary for three reasons. If one is dealing with flower characters he must be able to determine the character of the plant from a mature flower while immature blossoms still remain for the production of the controlled seed. Obviously, it is also an advantage when dealing with plant characters,

to have more than one opportunity to secure a desired union. Further, it is advantageous to be able to make several different crosses upon one plant.

6. Seed should be viable for several years in order that different generations may be compared at the same time. This enables one to reduce to a minimum the physiological fluctuation due to varying environment which many characters undergo in a marked degree.

7. The subject material should be "workable" cytologically in order that it may be attacked from both standpoints.

It might be remarked here that some botanists consider that genetic research can throw no new light upon evolution and upon the meaning of species, unless the subject material is an uncultivated genus or species. This criticism is apparently no more pertinent than the one the chemists had to meet years ago when they were told that synthetic compounds could not possibly be the same as those produced by nature. The fact of physiological fluctuation due to varying environment is admitted, but it is *not admitted* that the *mechanism* of hereditary transmission of the character in question is affected by these fluctuations.

Some idea as to the effectiveness of an inquiry concerning inheritance in maize from the standpoint of science may be gained then by examining the degree in which the plant fulfils the above requirements.

Although the forms of maize are regarded by botanists as belonging to the one species *Zea mays* L., there is probably no species of the flowering plants — if horticultural color varieties are excepted — that appears under such varied forms. These forms are perfectly fertile *inter se*, moreover, so that the first and second of our requirements are fulfilled perfectly. The third requirement, that of an easy technique and accurate control of desired matings, is met very imperfectly. The plant is monœcious. Ordinarily, this type of flowering habit is desirable in pedigree culture work because accidental selfing is usually much more easy to prevent than it is in hermaphroditic plants. In the case of maize, however, there is such an enormous production of pollen that it is continually present in the air of the maize field. In spite of all precautions, therefore, seeds of unknown paternal ancestry do creep into the cultures. The general error due to this source has been determined in cases which are described later, but the determination of a probable error in a mass of data is not sufficient in genetic work. An actual error in which a single seed of unknown paternity becomes the ancestor of a pedigreed line, is sufficient to upset all inductions drawn from the data. For this reason the cultures have had to be larger than would otherwise have been necessary.

The requirement of a large number of seeds from one union to reduce the probable error of chance fertilization among gametes differing in character is quite satisfactory in maize as from two hundred and fifty to twelve hundred seeds are produced on the cobs of the various races. The small number of flowering branches, however, is a serious objection. In some cases there are two or even three and four ears upon each plant; but in most cases, especially in the large races, there is but one ear. And even where there is an extra ear one gains but little advantage. The ears mature about the same time and it is impossible to find out what seed characters the plant possesses before pollinating the ear which is to have its place in the controlled culture. The disadvantage of this fact to the investigator is apparent if one remembers that when studying ear abnormalities sometimes twenty to twenty-five cobs must be selfed by hand to be reasonably certain that one selfed ear with the desired characters is obtained.

Maize seed is rather delicate and must be carefully dried in a place where there is a good circulation of air. When dried until the moisture content is only about ten per cent, it remains in fairly good condition for three seasons. Seed older than this is almost worthless. In fact, there is a possibility of obtaining distorted results even in the second year. Ninety-eight to one hundred per cent of properly dried seed should germinate the next spring after harvesting, but this percentage falls to about ninety the year following. If, therefore, seeds of any particular gametic structure should lose their vitality first, incorrect results would be obtained.

The chromosomes of maize are small and difficult to study and scarcely anything is known of their behavior during the maturation divisions.

This discussion should give some idea of the advantages and disadvantages that maize presents as subject material for a genetic investigation from the standpoint of pure science. The plant, however, even if not as perfect as some others from this point of view, has another claim which ought not to be disregarded. The fact that maize is the basis of the agricultural wealth of the country makes it eminently desirable that every fact about the inheritance of its characters, should be learned as soon as possible. It is only through the application of such knowledge that the present arbitrary, and, in a way, unscientific methods of its improvement as an economic crop will be placed upon a definite and orderly basis.

PART I.

THE MATERIAL AND THE PROBLEM.

The Plant and its Origin.

Although there is no absolute information as to the origin of maize, most botanists agree that its original home is Mexico (Harshberger '93) or the region to the south of there. As to how it originated there has been much speculation, and various views are held by different writers. We think it not out of place to give here a synopsis of the most important theories, because in our opinion, the results from the pedigree culture work on the inheritance of plant characters described in Parts IV and V throw considerable light on the subject.

The Tribe Maydeæ of the order Gramineæ comprises but seven genera and only sixteen or seventeen species. The two genera which interest the maize student are Zea and Euchlæna both of which are monotypic. The especial distinctions between the two are given by Lamson-Scribner (: 00) in his key to the genera of Maydeæ as follows:

"**Euchlæna,** pistillate spikes axillary fasciculate, distinct, axis of each articulate."

"**Zea,** pistillate spikes axillary, grown together, forming a compound spike with a much thickened, continuous axis."

His complete descriptions are:

"*Euchlæna* Schrad. Ind. Sem. Hort. Gœtt. 1832. Spikelets unisexual, monœcious; the staminate 2-flowered, in pairs, one sessile the other pedicellate, arranged in terminal paniculate racemes; the pistillate 1-flowered, sessile and solitary at each joint of an obliquely articulate rhacis of a simple spike; the spikes fasciculate in the leaf axils and each more or less enveloped by a foliaceous bract. Glumes in the staminate spikelets 4, acute, the first two membranaceous, empty; flowering glumes smaller and like their paleas, hyaline. Stamens 3. Glumes of the pistillate spikelets 4, the outer one broad and boat-shaped, smooth, soon becoming hard, surrounding the inner glumes and narrow rhacis, second glume empty coriaceous, third glume hyaline with a palea but no flower; fourth or flowering glume with its palea hyaline. Styles very long, filiform, shortly bifid at the apex.

Tall annuals with long and broad leaves, closely resembling Indian corn in habit. Species one with several varieties in Mexico and Central America."

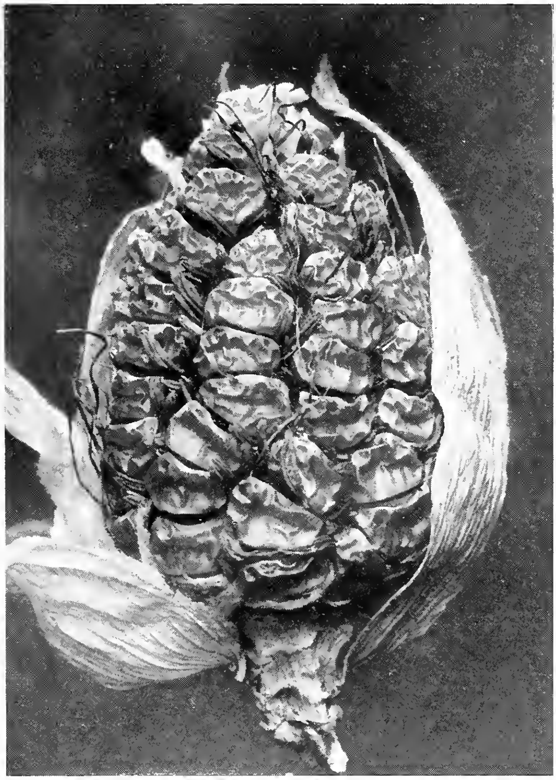
"*Zea* Linn. Sp. Pl. 971. 1753. Spikelets unisexual, monoecious; the staminate 2-flowered in pairs, one sessile the other pedicellate, along the numerous branches of a terminal panicle; the pistillate 1-flowered, sessile, crowded in several rows, along a much thickened continuous axis arising from the lower leaf-axils and closely enveloped by numerous large foliaceous bracts. Glumes four, awnless; those of the staminate spikelet acute; those of the pistillate very broad and obtuse or emarginate. Grain hard, only partially inclosed by the fruiting glumes. A well-known tall and striking annual grass with erect stems and broad leaves. The terminal staminate inflorescence forms the "spindle" [tassel], and the long projecting styles of the pistillate flowers constitute the "silk." The cob is formed by the union of the axes of several female spikes into a much thickened body. Species one or two, of American origin, presenting many varieties in cultivation known as corn, Indian corn or maize."

From these descriptions of the two monotypic genera, it is seen that *Euchlæna mexicana* Schrad., the common teosinte, is not greatly different from *Zea mays* L., our ordinary maize. Indeed to one who has grown and followed the extraordinary variability of both, it does not seem a greater step from teosinte to the maize most similar to it — the short many branched pop or flint types — than it does from the small dwarf pop maize to the giant dent forms. Teosinte is perfectly fertile with maize, which fact has led to some confusion, for Watson ('91) thinking that hybrids between the two constituted a pure wild species, named it *Zea canina* Watson. Segura (Harshberger, '96), however, by remaking the crosses and growing them near the region where the "Zea canina" was found, clearly proved the true nature of the latter. Harshberger ('93) first fell into the same error as Watson but later (Harshberger '96) discovering the true state of affairs suggested that maize originated either from (1) a cross between teosinte and some extinct but closely related plant, which by variation under a better environment finally produced a plant with larger maize-like ears; or that it came from (2) a cross between teosinte and a race of the latter that had varied under long continued cultivation. The basis of Harshberger's argument that teosinte must have been crossed by another form is his idea that only in the progeny from a cross would sufficient variability have appeared to have produced the more vigorous plant — the aboriginal maize.

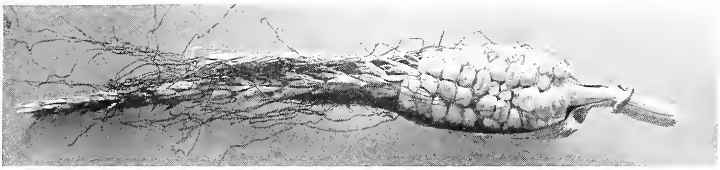
More recently Montgomery [: 06] has advanced the theory that teosinte and maize are both descended from an unknown many-branched grass whose branches terminated in a panicle of spikelets bearing hermaphrodite flowers. He says: "As evolution progressed, the central tassel came to produce only staminate flowers, these being higher and in a better position to fertilize the flowers on the lower branches. At the same time, the lateral branches came to produce only pistillate flowers, their position not being favorable as pollen producers, while, on the contrary, they were favorably placed to receive pollen. This differentiation in the flowers was accompanied by a shortening of the internodes of the lateral branches until they were entirely enclosed in the leaf sheaths [the husks]." The especial difference between the evolution of teosinte and of maize was thought to have been in the development of the ear of the first from the lateral branches of the tassel-like panicle and the ear of the second from its central spike. This argument of Montgomery is directly opposed to the old theory that the cob of modern maize is the result of a fusion of a number of two-rowed pistillate spikelets such as are found upon teosinte. His theory then, emphasizes the nature of the changes that took place; Harshberger's theory, the way they were transmitted.

In addition to these views it seems only necessary to mention that since maize is the only grass with a naked seed, the podded variety *Z. mays tunicata* Sturt. is by many considered to be an earlier stage in maize development.

Our own views on the subject have resulted from a consideration of the behavior of the characters of the various races of



a Ear with hermaphrodite flowers from the dwarf plant which appeared in Stowell's Evergreen sugar maize.



b. Mature seeds on male spike of plant heterozygous for starchiness, showing segregation. A common physiological fluctuation.

ABNORMALITIES

maize when crossed, the data on which they are based being given later. The matter is largely speculation and should be considered as such. It is merely the simplest manner of interpreting the known facts, by connecting maize with the other Maydeæ by a short series of changes that involve characters that mendelize. On the whole it does not differ greatly from Montgomery's theory.

Since we now believe that the essential rôle of hybridization is to recombine the characters possessed by the parent plants in definite ratios without actually producing anything new, [new combinations may produce characters formerly unknown], there is no necessity of postulating hybridization of teosinte with a more maize-like variety. It is known that when teosinte is cultivated in rich soil it sometimes produces ears having an irregular development of four rows. This is only an expression of one of the commonest modes of variation, repetition of parts or meristic variation. This variation in the ear has taken place again and again in maize and is inherited although sometimes obscured by physiological fluctuation. The ear of maize then is a meristic variation produced from the central spike of the tassel of the lateral branches of teosinte or of a teosinte-like plant, and not a fusion of the lateral spikelets. Lateral spikelets still appear in maize, apparently as if variation ran in grooves or paths of least resistance. This character has been found to segregate in a manner essentially Mendelian. The podded character also mendelizes and is allelomorphic to its absence. If then progressive meristic variations occurred in the central spikes of the side branches of the teosinte-like ancestor, followed by retrogressive variations affecting both the lateral spikes of the lateral branches and the pod character, a plant would have originated bearing naked hermophroditic ears. Further change might easily have come about, as Montgomery suggests, by a shortening of the side branches producing the modern husk, and finally the origination of the monœcious character. The latter occurrence is not at all hard to picture for the change of the staminate inflorescence to an hermaphroditic or even a pistillate one, is something which is exceedingly common in all or almost all strains of maize. It is a physiological fluctuation produced by excessive rainfall and fertile soil. The appearance of stamens on the modern maize ear is much more rare but that it does occur is shown by the ear pictured in Plate I. In fact one of our sterile dwarf mutations had nothing but hermaphroditic flowers.

The Varieties of Maize.

Although all of the varied forms of maize are regarded by modern taxonomists as sub-divisions of the species *Zea mays* L., many varieties have at various times been given specific rank. The Index Kewensis gives the six following types as species. The original sources have been consulted but the descriptions have been shortened to include only essential facts.

Z. Curagua, Molina, J. I. Saggio sulla storia naturale del Chili. pp. 306, Bologna, 1810. = *Z. mays.*

This variety is distinguished by its serrate leaf-edge. It has never been cultivated in the United States, but appears to be a flint type, *Z. mays indurata.* Syn. *Z. Caragua*, Stend. Nom. ed II, ii. 797.

Z. erythrolepsis, Bonafous, M. Histoire naturelle, agricole et économique du Maïs. Folio, pp. 181, Plates 19, Paris, 1836, = *Z. mays.*

"*Glumis rubris, seminibus compressis.*" "Le Maïs à rafle rouge cultivé sur les rives du Missouri, se distinque par l'aplatissement de ses grains, et surtout par le coleur rouge des écailles et corallines de l'epi femelle. La constance de ce caractère tend à lui mériter le titre d'espèce."

This form could hardly be considered a variety as it is a common variation in all of the commonly recognized varieties.

Z. hirta, Bonafous, M. Note sur une nouvelle espèce de Maïs. Ann, Sci. Nat. Ser. I v.17; 156-158. 1829. = *Z. mays.* "*Foliis hirtis et dependentibus; spiculis masculis sessilibus, diandris triandrisve; antheris subaureis.*"

A good variety, originally sent to Bonafous from Balbis of the Jardin des Plantes de Lyon. It varies into a series of flint, pop and dent types.

Z. japonica, Van Houtte, Fl. des Serres, XVI (1865-67), 121. t. 1673-74. 1867. = *Z. mays.* Syn. *Z. vittata*, Hort. and *Z. variegata*, Hort.

A small variety with leaves variously striped with white. A small flint type is the one chiefly cultivated for ornament, but the variety occurs again and again in fields of all of our common maize strains. It could undoubtedly be isolated pure by careful selection of these individuals.

Zea macrosperma Klotzsch. Bot. Zeitung 9; 718. 1851. In der Sitzung des Ges. naturf. Freunde zu Berlin. = *Z. mays*. Seed received by Humboldt from Cuzco. It is simply a large seeded dented starchy type.

Zea rostrata, Bonafous, M. Ann. Soc. Agr. Lyon. v. (1842), 197. = *Z. mays*. Simply a hook-seeded form of pop maize, somewhat similar to our common rice pop.

Of these types *Z. mays Curagua* Molina and *Z. mays hirta* Bonafous might be considered as good varieties. The four remaining names and also the varieties of *Z. mays* listed in the Index Kewensis might well be placed under the classification porposed by Sturtevant ('99), leaving out his *Zea mays amyleasaccharata* because the latter is a type which is probably identical with the "flinty" sweet corns with which canners have so much trouble. The three ears from the San Padro Indian collection sent to Sturtevant by Palmer, and upon which he based the variety, failed to yield a mature crop in Geneva, New York. It is therefore unknown whether this type would really prove true. Sturtevant's classification follows although I have added the word *mays* and have listed them as varieties instead of species. It is not strictly correct to give him as the authority for the names, as he used them specifically, but since they have come into general use in the United States it seems more convenient to keep them. Sturtevant himself based his claim for separate species principally upon the fact that intermediates were either absent or rare. This fact comes about, as will be shown later, from the alternative manner in which the distinguishing characters are inherited. In reality many other characters are inherited in the same manner, and it is only because the chief characters of these five varieties are striking to the eye that it is advantageous to keep them in use.

Zea mays tunicata, the pod corns. Sturtevant, Bul. Torr. Bot. Club 1894, p. 355 (Also St. Hil., Ann. Sci. Nat. 16; p. 143, fide De Candolle). A form in which each kernel is enclosed in husks (usually four) besides the foliaceous bracts that enclose the ear.

This form was first described by C. Bauhin in 1623, and has been the basis of a long list of synonyms since that time. It is probable that the prototype of the species possessed this character for it would thus be linked closer to the other Maydeæ. The strains now obtainable under this name have been hybridized until ears can be found whose kernels run the whole gamut of the other four kinds. The tendency of plants to form anew characters once possessed that have been lost, is well illustrated here. We have come across several ears of our ordinary varieties in which a few of the kernels at the base have been podded. Sturtevant gives two authentic cases where fully podded ears have appeared in other varieties under such conditions that it is very improbable that it was the result of hybridization.

Zea mays everta, the pop corns. Sturtevant, Bul. Torr. Bot. Club, 1894, p. 324.

"This [species] group is characterized by the excessive proportion of the corneous [starch in the] endosperm and the small size of the kernels and ear. The best varieties have a corneous endosperm throughout. This gives the property of popping, which is the complete eversion or turning inside out of the kernel through the explosion of the contained moisture on the application of heat."

Strains of the pop maizes are the smallest of our cultivated corns, and although there are varieties that reach a height of nine feet when cultivated on fertile soil, plants comparable in size to the average dent or starchy maize are never found. There appears to be a distinct correlation between size of seed and size of plant; therefore, since one never obtains large size seeds without a development of soft starchy matter, pop kernels much larger than those now grown are not likely to be produced through selection or hybridization.

Two forms of seed are known in the pop corns; one is simply a small seed with rounded crown similar in shape to the small flints; the other, characteristic only of pop corns, is peaked at the point where the style or "silk" was attached.

Other variations such as purple colored aleurone cells, yellow endosperm, red silks, and red and variegated pericarps characterize the pop maizes in common with the flint, sweet, dent and starchy corns. The modal number of rows also varies in different varieties from eight to sixteen. In this, pop maize is similar to dent, sweet and starchy, but different from flint maize. It is doubtful whether any true flint maize exists with a mode for number of rows higher than twelve.

Zea mays indurata, the flint corns. Sturtevant, Bul. Torr. Bot. Club, 1894, p. 327.

This group is characterized by the seeds having a corneous starchy endosperm, surrounding a soft starchy center immediately behind or partially surrounding the embryo. The strains in common cultivation are considerably larger than the pop corns, but varieties do exist which form a definite series from pop to dent differing only by the amount and extent to which soft starch replaces corneous starch in the endosperm. The same color varieties that were described for pop corns occur.

Zea mays indentata, the dent corns. Sturtevant, Bul. Torr. Bot. Club, 1894, p. 329.

A group characterized by the extension of the soft starch until it completely covers the summit of the seed. Corneous starch, however remains at the sides of the kernel and acts as a frame work to support the drying seed. The soft starchy portion shrinking in drying to a much greater extent than the other forms a characteristic indentation. Dent varieties occur averaging from five feet to twenty feet (reported) in height, with from eight to twenty-four rows as the modes (extremes to thirty-six rows). The usual color varieties occur.

Zea mays amylacea, the soft or flour corns. Sturtevant, Bul. Torr. Bot. Club, 1894, p. 331.

A group characterized by entire absence of corneous starch in the endosperm. Uniform shrinkage in drying usually gives a seed with no indentation. The mummy corns of Peru, Mexico and the southern United States appear to belong to this group, but this is not absolutely certain. The specimens that we have examined belonging to the New York Botanical Garden might have been flint corns which owe their floury appearance to partial decomposition.

This group marks the final disappearance of corneous starch in the endosperm. It is the end of a series beginning with the pop corns and coming up through the flints and dents. For this reason one might expect them to possess the largest seeds, as the length of time necessary for maturing the seed undoubtedly has something to do with the amount of soft starch formed. The plants are indeed large, but seeds occur varying from the size of the smaller flints to that of the larger dents. The origin of the starchy corns is not due simply to their correlation with the general plant structure and therefore a simultaneous origin with large varieties, but is dependent upon a separate character or group of characters. The usual color varieties occur.

Zea mays saccharata, the sweet corns. Sturtevant, Bul. Torr. Bot. Club, 1894, p. 333.

"A well defined group characterized by the translucent horny appearance of the kernels and their more or less crinkled, wrinkled or shriveled condition." The sweet corns are simply pop, flint and dent varieties (East : 09) that have lost their ability to mature starch normally. Some few starch grains are produced but they are generally small, angular and abortive. The reserve material of the endosperm seems to undergo a decomposition to cane sugar and the various hexoses. There is apparently something more than a simple non-development of starch, for the sweet corns in the "milk" state contain greater percentages of sugar than do the starchy varieties in a similar stage of ripeness. The same color varieties occur.

The Problem and its Treatment.

It is apparent that maize furnishes an admirable series of types which are perfectly fertile among themselves. The primary object of our work is to obtain pure forms of these diverse types by inbreeding, then to test the mechanism of inheritance of each separate character by controlled matings and an analysis of the resulting progeny. In doing this we simply follow Mendel's method of the individual analysis of pedigree cultures.

The specific questions attacked are numerous. Our principal object is to find whether the different characters under observation all obey the same law of heredity or whether separate principles are involved, and whether characters apparently inherited independently are not sometimes correlated with each other. The question of dominance of a character in the first generation of a cross has also interested us. Some characters are perfectly dominant, other characters imperfectly dominant, while still others form heterozygous combinations differing from either of the parents. There are even cases in which dominance appears to be reversible. If such a thing is possible, an explanation is desirable. The study of the phenomenon of Xenia, which has already formed the basal object of Correns' (: 01) fine monograph, throws some light on these questions.

Another object we have kept in mind is the problem of the purity of extracted homozygotes. It is a matter of common knowledge that characters that have been lost through retrogressive variations — characters that behave as mono-hybrids in inheritance — often reappear. The reverse of this phenomenon is also true. Is it because there is a phylogenetic "path" in which these changes run, so that the same variation appears again and again, or is there no absolute purity of the germ-cells but only a comparative purity as indicated by Morgan (: 10)?

The idea of prepotency has been held with great tenacity up to the present time. We hope these researches will throw some light upon this subject of so much importance to practical breeders. If there are individuals whose constitution is such that chance production of zygotes is interfered with, the fact brings many complications into the study of inheritance; but such complications must not interfere with the facts. Various other questions will be discussed in the proper places and for this reason will not be considered further here.

It may be well to mention that although these questions smack of the technical, it is maintained that in just so far as one contributes toward their solution, that far is the broad practical problem of better methods for the production of new economic maize types solved. The questions of purity of homozygotes, inheritance of size and number of ear-rows in the different sub-species are easily seen to be of practical agricultural importance. Other questions may seem of less importance or even of no importance from this point of view, but this is fallacious as is easily shown by illustrations from the science of chemistry where abstruse theoretical researches have continually proved to be the most practical in the end.

In certain quarters there has been a marked reaction against the continued Mendelian interpretation which has been given to every paper published since the year nineteen hundred in which actual experimental studies concerning the mechanism of inheritance have been reported. This reaction has taken the form of a philosophical query as to whether the characters of the organic complex of which living organisms are composed can in any sense be dissected and analyzed into the "units" of heredity which are the basis of Mendelian inheritance. Further it has been questioned whether there is any justification for the increasing complexity with which Mendelian formulæ are involved. It has been argued that with a multiplicity of "factors" any particular case can be interpreted as segregating according to the Mendelian hypothesis. For these reasons the writers wish to have their position in reporting the following investigations distinctly understood at the beginning.

It is fully understood that there is danger in improper analysis of complex ratios from pedigree cultures. This is inevitable. Yet it is not a more pertinent criticism to condemn complexity in biological facts than it is to frown upon the intricacies of modern organic chemistry because it is so different from the simple chemistry of Liebig. The answer is that the facts of heredity are complex.

In regard to the question of the ultimate nature of unit characters or the possibility of absolute segregation of characters in the germ-cells so that in the recessive there is actual absence of the character (gene) in question, we must await more results from the different points of view of the breeder, the cytologist, the physiologist and the physiological chemist. The facts reported in genetic investigations remain indelible. The interpretation of these facts may or may not be correct; they simply arbitrarily represent the facts in a convenient system of notation much as the facts of chemistry are represented by structural formulæ. This is the idea in the minds of the authors in the following report. It is thought moreover to represent the attitude of most genetic investigators and the excuse for making the above statements lies in the fact that unfortunately one often finds no appreciation of this attitude by biologists not actually engaged in genetic research.

We have, then, used the ordinary Mendelian notation, with allelomorphic pairs interpreted as presence and absence of characters not because we know that there is actual absence but because this interpretation fits our present knowledge. We have interpreted complex characters such as height which we are not able to analyze completely, as segregating characters. The conclusion that there is a segregation in the second hybrid generation very much in excess of the sum of the non-inherited fluctuation and of other variation due to the heterozygous condition of the pure (?) forms used and also of their combination in the first hybrid generation, is justified by the data. This is the essence of Mendelian theory; and, whether absolutely correct or not, it is an interpretation that cannot fail to be valuable to the commercial plant breeder. It gives him some knowledge of what may be expected in his endeavors to produce new types of maize by hybridization.

It might also be mentioned that following Johannsen, the word "gene" has been used to signify that substance present in the germ-cell which represents potentially the "unit character" or whatever it may be called that acts as an entity in heredity.

Previous Work on Inheritance in Maize.

Before describing in detail the material used in these experiments it may be well to give a short summation of the previous work in the field.

The early hybridists, Camerarius, Logan, Pontedera and Henschel, each made a desultory study of maize crosses, but obtained no results of present interest. Hardly more satisfactory are the papers of Dudley (1724), Sageret ('26), Puvis ('37), Gärtner ('49), Naudin ('63), Hildebrand ('67, '68), Vilmorin ('67) and Focke ('81), although these researches — representing work of the principal students of hybridization of the period — each gives several observations concerning the immediate effect of pollen upon the endosperm, — that phenomenon called Xenia by Focke ('81). These observations, however, can hardly be compared with those made since the cause of Xenia was discovered for the obvious reason that the facts concerning the changes in the endosperm were almost lost to sight in the search for effect of cross-pollination on the tissues of the maternal parent.

In the work of a slightly later period particularly in the United States (Kellerman and Swingle '89, '90; McCluer '92; Morrow and Gardner '92) a great improvement was made in the methods of investigation employed. The parental stock was often inbred to establish its purity, crosses were made by hand upon protected flowers, and the resulting progeny were studied with great care. Many facts of inheritance are unconsciously reported in their papers which are confirmed in the post-Mendelian work which gives them a meaning For example one finds these data in Kellerman and Swingle ('91). A *chance hybrid evidently produced by the pollination of a white maize with pollen from a variety with purple aleurone cells was inbred. A hand-pollinated ear contained 370 seeds, of which 206 were blue, 71 pink, 71 orange-yellow and 22 pure white. One wonders how the essential facts of dominance and segregation remained unnoticed in the face of such ratios as this. But even if it is interesting to reread these papers and consider them from a more modern viewpoint, it is hardly profitable to discuss them further here. The work previous to 1900 was in the wrong epoch, and since that time three valuable contributions to the subject in hand have been made. (De Vries 1899 and 1900, Correns 1899, 1900 and 1901, and Lock 1906.)

It is interesting at least, to note that in the cases of both De Vries and of Correns the studies of maize hybrids in which presence and absence of yellow and presence and absence of starch in the endosperm were concerned, contributed largely to their independent discoveries of dominance and segregation in hybrids, which they both unselfishly credited entirely to Mendel after their discovery of his previous paper. Thus *Zea mays* shares with *Pisum sativum* the honor of being the subject material in the establishment of Mendel's laws.

Correns' (:01) beautiful monograph was written with the especial idea of furnishing an explanation of the phenomenon of Xenia, but it naturally contributed a large amount of data upon the mechanism of inheritance of the characters with which he worked.

Correns' technique was as follows. The seeds were planted first in pots, allowed to attain a healthy start, and finally transplanted to the field. In the first year (1894) the plants to be used as "mothers" were planted together in his experiment field, castrated at the right time and the silks protected between

---

* The immediate parents were thought to have been white, but this was probably an error.

pollinations with paper bags. The individuals that furnished the pollen were planted together in places apart from the proposed mother plants and from them pieces of the male panicles (tassels) were carried in glass bottles to the mother plants. Slight changes in the plan of planting were made in 1895 and 1896, but I cannot find in any case that either the male flowers were protected from foreign pollen during their maturation or that special care was taken to have pollen for a cross furnished by an individual plant. Furthermore in handling the hybrids individuals were not selfed but bred *inter se*. Some of the families were given to gardeners who were growing no other maize, while others were detasseled and naturally pollinated *en masse* with the pollen of a pure race. The first method predominated. We can see then that the methods in use furnished correct results only when the characters in question were simple and of such nature that the races could be kept pure by inspection. Complex ratios such as are furnished when maize with purple aleurone cells is crossed with various white maizes differing in gametic structure, could not possibly be analyzed correctly.

Correns reached conclusions regarding the mode of inheritance of the following characters but it must be borne in mind that these results came from the study of data more or less massed, and not the study of individual crosses in as precise a manner as that outlined by Mendel.

Yellow endosperm was found to be dominant to its absence, and starchiness dominant to absence of starchiness (sweet). Both of these characters behaved as Mendelian mono-hybrids. It cannot be definitely stated, however, that crosses between all races of maize where presence and absence of these characters are concerned would give the same results. Long aleurone cells also proved dominant to short aleurone cells, and red pericarp to absence of red, but Correns was not entirely satisfied that these characters behaved as simple Mendelian monohybrids although he supposed this to be the case.

Purple aleurone cells appeared to form an allellomorphic pair with absence of purple, but he found that the heterozygotes when bred *inter se* did not give the normal number of whites. What he took to be heterozygotes of the same character were either pure purple, partial purple, or pure white when the purple was used as the male parent. In the reverse cross the purple appeared to be fully dominant. Correns (:01) endeavors to explain this phenomenon by the fact that in the formation of the hybrid endosperm two nuclei come from the female and but one from the male parent. He supposes that in some cases this may cause a dominance of the female characters. This purple character seemed to interfere with normal inheritance in still another case (Correns :02), where a blue sweet corn was crossed with a non blue pop. Here the second generation yielded only about 15½% of sweet kernels out of a total of over 8,000. Pollinated with the recessive parent there appeared nearly 50% of sweet kernels so that the female germ-cells seemed to have segregated normally. Correns suggested that in this case the four possible combinations of characters in the germ-cells did not take place with equal facility.

Our own data shows the error in the first case to be due to the fact that white races differ in their gametic structure in characters which affect the purple color. The observations in the second case have not been confirmed, but were probably due to improper classification of the heterozygous dominants and the recessives. (See starchy and non-starchy crosses.)

The shape and size of seed and relative weight of embryo and endosperm Correns thought behaved in a non-Mendelian manner, although he was not prepared to say in exactly what manner these characters were inherited.

Lock (:06) carried out a much more extended series of maize crosses at Peradeniya, Ceylon, from 1902 to 1906. His technique in certain cases was a considerable improvement on that of Correns in that both the male and female inflorescences were enclosed in bags and thus crosses were made between single individuals. Unfortunately his method was later changed and cross pollination was accomplished by planting the two races in alternate rows on an isolated plot of ground, and detasseling all plants of the race which it was proposed to use as the female parent. This method of course gave no chance to make a proper analysis of complex characters for could not be known just what gametic composition was possessed by the male parent. This criticism was anticipated by Lock himself but the method was used because he desired to have a large amount of data from which to establish the mathematical accuracy of Mendel's hypothesis of definite segregation and chance mating. In the cases of starchy and non-starchy, and yellow and non-yellow endosperm Lock's results were in accord with those of Correns. Furthermore he showed definitely that red pericarp behaved as a Mendelian character, allelomorphic to absence of red. Lock also crossed indented and non-indented races and remarks that in the F_2 generation a high degree of variability appeared, but without making crosses between individual plants and studying the progeny he could not decide whether or not Mendel's Law was followed. No data is reported on inheritance of height of plants but a number of crosses were made between F_1 plants and the shorter of the parental races, and he states that no segregation into short and intermediate plants took place. The plants on the contrary were remarkably uniform in height and he believed blended inheritance to be the rule for this character.

Lock's results in crossing races with purple aleurone cells with races with non-purple aleurone cells is so seriously complicated from the fact that he followed out no individual crosses that it is impossible to criticize his data. From the fact that individual ears showed such different ratios as 3 : 1, 9 : 7 and 1 : 3 we may suspect that he was dealing with white races of varying composition such as are described in our work on this character.

These short abstracts from the work of Correns and of Lock do not give an adequate idea of the large amount of painstaking investigation for which each should be credited however, and anyone interested in the subject should therefore consult the original papers.

The Material Used.

The types of maize which furnished the parental stock with which crosses were made for this series of studies were in most cases inbred by hand for at least two generations before any hybrids were actually made. When this procedure was impossible the parental ears were obtained from various commercial growers who made a specialty of the types which they furnished. From the maize obtained from them single ears were selected and planted. The plants forming the immediate progeny of these ears were used in part as the parents of crosses and in part to inbreed. When any of the seeds from the original ear were found to be heterozygous in any characters the fact is noted when the crosses are described. In this manner we were able to determine the purity of the parental stock used, for all of the grosser characters. Of course new variations were continually isolated and these were given numbers which show their origin. For example, the original stock of Longfellow corn is No. 15; if, however, new variations appeared in the Longfellow progeny they were numbered 15-1, 15-2, etc.

The following descriptions, then, comprise only original material; that is, single ears of various commercial varieties.

Zea mays tunicata. The podded corns.

21. Podded maize.

A fourteen-rowed ear with four husks around each kernel in addition to the usual paleas. The seeds looked like rice pop; they were small but showed a considerable amount of white starchy matter.

Zea mays everta. The pop corns.

20. A flint-like 8-row purple pop.

A pop with purple aleurone cells, showing a small amount of white starchy matter immediately behind the embryo, sufficient to keep the seeds from popping well. Ear 15 cm. long, 11 cm. in cir. Seeds .9 x .9 cm., white endosperm. Cob white.

60. Tom Thumb pop.

A dwarf true pop. Ear 7.5 cm. long, 8 cm. in cir., 12-rowed; pericarp colorless. Seeds rounded, true pop, .5 x .4 cm., endosperm yellow. Cob white.

23. White rice pop.

A white true pop. Ear 15.5 cm. long, 10 cm. in cir., 16-rowed. Seeds white, .9 x .5 cm., hooked. Cob white.

26. A white, flint-like pop.

A white true pop with rounded flint-like seeds. Ear 17 cm. long, 9 cm. in cir., 8-rowed. Seeds .8 x .9 cm. rounded. Cob white.

27. Red rice pop.

A true rice pop with red pericarp. Used only for inheritance of pericarp color.

28. White rice pop.

A true rice pop with white or colorless pericarp. Used only in cross with No. 27.

Zea mays indurata. The flint corns.

4. Benton maize.

An eight-rowed race intermediate between the flint and the dent corns. Ear 34 cm. long, 14 cm. in cir., 8-rowed, pericarp red becoming colorless at summit. Seeds 1.1 x 1.4 cm., some very slightly dented; endosperm yellow, slightly more starchy than a true flint. Cob white.

5. Watson flint.

A true flint with a pericarp rose red when developing in full sunlight, the seeds at the tip usually showing simply red striations beginning at point of attachment of the silk. Ear 27 cm. long, 13 cm. in cir., 8-rowed. Seeds 1.0 x 1.2 cm., endosperm colorless. Cob white.

11. Sturges' flint.

A twelve-rowed yellow flint race. Ear 20 cm. long, 14 cm. in cir., 12-rowed, pericarp colorless. Seeds 1.0 x 1.0 cm., endosperm yellow. Cob white.

13. Sanford flint.

An eight-rowed race. Ear 30 cm. long, 13 cm. in cir., 8-rowed; pericarp colorless. Seeds 1.0 x 1.3 cm.; endosperm colorless. Cob white.

15. Longfellow yellow flint.

An eight-rowed yellow race. Ear 27 cm. long, 11.5 cm. in cir.; 8-rowed; pericarp colorless. Seeds .9 x 1.2 cm.; endosperm bright yellow. Cob white.

17. Palmer's red-nosed yellow flint.

An eight-rowed yellow race. Ear 22 cm. long, 12 cm. in cir.; 8-rowed; pericarp a dirty red at the sides of seed becoming almost colorless at summit. Color not deep as in common red maize. Seeds 1.0 x 1.4 cm.; endosperm yellow. Cob white.

24. Rhode Island white cap.

An eight-rowed flint race. Ear 29 cm. long, 12 cm. in cir.; 8-rowed; pericarp colorless except for a slight pink tinge of rose similar to No. 5 but less in amount. Seeds .9 x 1.2 cm.; endosperm colorless. Cob white.

25. Brindle flint.

A common flint race not breeding true to the character from which it derives its name, — a mosaic pericarp formed by slashes of dark red extending irregularly from the point of the attachment of the silk. Eight-rowed true flint.

Zea mays indentata. The dent corns.

2. Illinois low protein dent.

A white dent selected for low proteid content at the Illinois Agricultural Experiment Station for eight generations. Protein content 8.30 per cent. Ear 19 cm. long, 18 cm. in cir.; 16-rowed; pericarp colorless. Seeds 1.5 x .8 cm.; endosperm colorless; white starchy matter largely increased in summit over usual dent type. Cob white.

8. Illinois high protein dent.

A white dent selected for high proteid content at the Illinois Agricultural Experiment Station for eight generations. Proteid content 15.46 per cent. Ear 20 cm. long, 14 cm. in cir.; 14-rowed; pericarp colorless. Seed 1.1 x .9 cm.; endosperm colorless; white starchy matter decreased from amount usual in dent types but summit still well dented. Cob white.

3. Leaming dent.

A yellow dent race. Ear 21 cm. long, 16 cm. in cir.; 20-rowed; pericarp colorless but sometimes very slightly tinted with dirty brick red at sides of seeds. Seeds 1.3 x .7 cm.; endosperm dark yellow; considerable soft starch at summit; well dented. Cob dark red.

6. Leaming dent.

Same race as No. 3 but of different ancestry. Ear, 19.5 cm. long, 18.5 cm. in cir.; 18-rowed.

7. Leaming dent.

Same race as No. 3 but of different ancestry. Ear 18 cm. long, 17 cm. in cir.; 20-rowed.

9. Leaming dent.

Same race as No. 3 but of different ancestry. Ear 18.5 cm. long, 16.5 cm. in cir.; 16-rowed.

12. Leaming dent.

Same race as No. 3 but of different ancestry. Ear 19 cm. long, 17 cm. in cir.; 18-rowed.

16. Leaming dent.

Same race as No. 3 but of different ancestry. This ear was 18-rowed and perfectly formed. It was surrounded by five lateral branches each having either four or eight rows of seeds.

1. Missouri cob pipe dent.

A very large dent race characterized by large cob. Ear 28 cm. long‘ 22.5 cm. in cir.; cob 14 cm. in cir.; 20-rowed; pericarp colorless. Seeds 1.5 x .9 cm.; endosperm white. Red cob.

22. Mosaic red dent.

A dent characterized by dark intense red pericarp. Used only for study of that character.

Zea mays amylacea. The flour corns.

10. White floury.

A thoroughly floury race, showing absolutely no corneous starch. Ear 22 cm. long, 14.5 in cir.; 14-rowed; pericarp colorless. Seeds 1.2 x 1.0 cm.; endosperm colorless. Cob white.

Zea mays saccharata. The sweet corns.

19. Stowell's evergreen.

A large-eared extremely wrinkled-seeded late sugar corn. Ear 16 cm. long, 15.5 cm. in cir.; 14-rowed; pericarp colorless. Seeds 1.4 x .7 cm.; endosperm colorless. Cob white.

18. Early Crosby.

A twelve-rowed sugar corn. Ear 14.5 cm. long, 14 cm. in cir.; 12-rowed; pericarp colorless. Seeds .9 x .9 cm.; decidedly wrinkled but thick full seeds; endosperm colorless. Cob white.

54. Black Mexican.

An eight-rowed sugar corn characterized by purple aleurone cells. Ear 13.5 cm. long, 12 cm. in cir.; 8-rowed; pericarp colorless. Seeds .9 x 1.1 cm.; aleurone cells purple; endosperm colorless.

Methods Used.

In carrying out the large amount of tedious routine work necessary in the collection of data from the crosses of the above types, a great effort was made to reduce experimental errors to a minimum. No part of the work was left to farm workmen except the preparation of the breeding plots and their cultivation. The planting, labeling of families, crossing, selfing, harvesting, filing of seed and collection and reduction of data were done by the authors. The senior author alone is responsible for the details of the work until 1909. In 1909 and 1910 the senior and junior authors both shared in the labor. Since 1907 efficient aid in harvesting, filing seed, etc., has been given by Mr. C. D. Hubbell of the Conn. Agr. Exp. Station. In 1910 Mr. D. W. Davis and Mr. O. E. White, graduate students at Harvard University, aided in selfing ears of various selections.

The ears have always been shelled and seeds classified and filed in seed envelopes. Where there has been the least question about classification the work has been duplicated by two observers. If then there has been a doubt concerning the characters borne by particular seeds, those in question have been grown for another generation. The planting has been done from the seed envelopes directly to the field. There they were planted in hills three and one-half feet apart each way, four seeds to the hill. It was not considered necessary to start the seeds in the greenhouse in sterilized soil as is done with smaller seeds. Maize seed very seldom germinates after remaining in the ground over the winter in this climate. Furthermore the corn which was not hand pollinated was not husked directly on the field so that there was but little chance that any seeds should remain upon the ground. Great care was taken not to drop seeds at planting time in other than the hills marked out. These were covered carefully and after the young plants appeared above the surface, any individuals not exactly in the hill were removed. No plants have ever given evidence that they were misplaced and there is every reason to believe that the work is accurate in this regard.

The different families were marked in the field by heavy stakes to which wired tree labels were attached. As an additional precaution against mis-labeling or misplacement of labels, however, a planting plan was always kept on file showing the exact location of every plant in the field. With this safeguard every field stake might have been removed without making the least confusion.

All crossing and selfing were done by hand. Individual plants were used as the male parent in nearly every case. If possible the male parent of a cross was also selfed with its own pollen so that selfed seed of that individual was accessible if necessary. If for any reason it was particularly desirable to have the progeny of a plant where through an accident none of its own pollen was available, it was pollinated from a sister plant. This fact was always noted, however, and the male parent selfed if possible.

Heavy manila paper bags were used to protect both male and female inflorescences from foreign pollen. These were found much more desirable than paraffined bags as the latter were likely to become inverted and filled with water during a rain storm. The manila bags stood up well in the rain, dried out quickly, and seldom failed to furnish dry viable pollen. The tassels were bagged about three days before any pollen was ripe. Of course here there was a slight chance of enclosing foreign pollen. This pollen, however, would have been three or more days older than the pollen coming from the bagged flowers, and therefore much less viable. Even disregarding this fact, however, the immense amount of pollen furnished by the bagged infloresence would so dilute any foreign pollen that the ratio would be at least 10,000 to 1 in favor of the former.

The female flowers were always bagged of course before any of the silks were showing, and any bracts or leaves showing foreign pollen were carefully removed. Here again, however, is a slight chance of enclosing foreign pollen. This error has been determined by bagging 53 ears and allowing them to remain in the bags. Forty-four ears formed no seeds, six ears formed one seed each, two ears formed two seeds each and one ear formed four seeds. There are over five chances to one then that no viable foreign pollen enters in this way.

The pollination is accomplished by removing the bag from the tassel, shaking out the empty anthers and dusting the pollen over the silks of the proposed mother plant. The bag covering the silks is not entirely removed but is held so that its opening is horizontal with the silks resting inside. The pollen is then shaken in at the opening as quickly as possible, taking care not to let the silks touch the hands or clothing of the operator or the leaves or stem of the plant. It is sometimes impossible to keep from touching the silks with the fingers, as it may be necessary to rearrange them in the bag. To guard against contamination from this source the hands are carefully cleaned with 95 per cent. alcohol after each pollination.

The silks at the base of the ear mature first; those at the tip of the ear last. For this reason, if one is to be absolutely certain of a well filled ear, it is necessary to pollinate two or three times with fresh pollen. This procedure has the disadvantages of increasing the error, however, not to speak of the difficulty of obtaining pollen, so that in this work but one pollination was made in each case. When pollinated about five days after bagging, fairly well filled ears were generally obtained, particularly with the small races.

Immediately after pollination the ear is rebagged and tagged. From this time until the ears are mature they are inspected every little while to see that the bags are not too tight for the maturing seeds. The bags remain on until the ears are harvested. They are then picked, husked, tagged with wired tree labels and dried. Boards through which wire nails have been driven are hung from the ceiling of the drying room to prevent the depredations of mice. The ears are impaled upon these nails and thus dry surrounded by a current of air.

Experimental Error.

The manipulation during pollination is undoubtedly productive of an experimental error which even the most careful work cannot entirely prevent. This error was determined as follows. Twenty-five ears were bagged and allowed to remain in this condition for five days. The bags were then opened and given the manipulation that was necessary for hand-pollination, except that no pollen was applied. The ears were then rebagged and remained so until harvest time. No seed were formed on sixteen ears; three ears produced one seed each; four ears produced two seeds each; while one ear produced four seeds and one ear produced five seeds.

There is a possibility then of an experimental error of five or six seeds out of the two hundred to eight hundred produced per ear. This is to be considered as a maximum error and not the probable error, the latter being less than one seed per ear.

PART II.

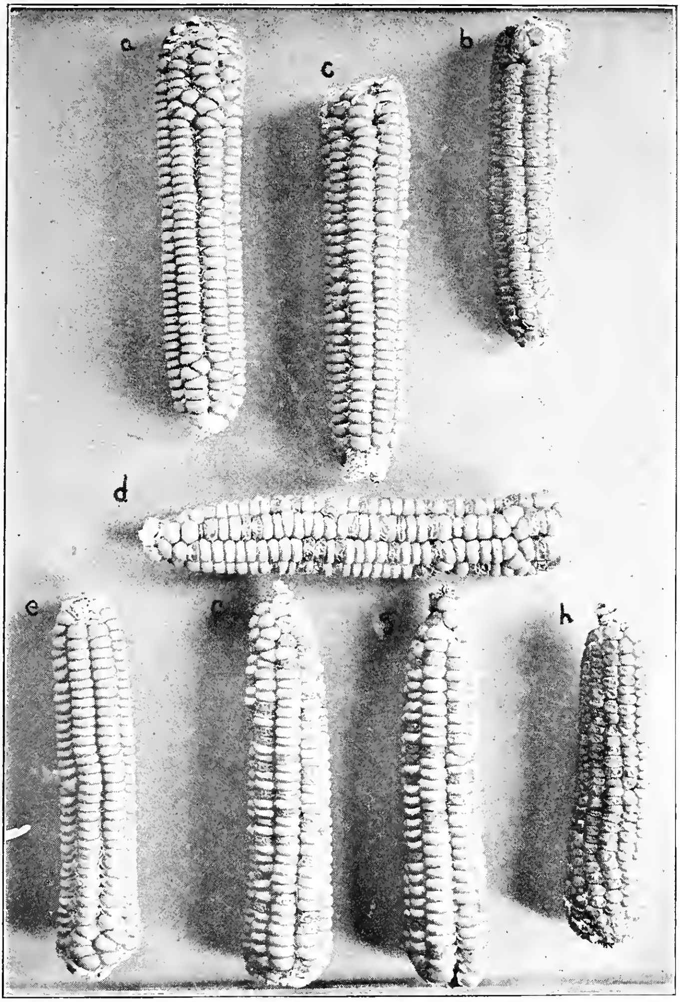
ENDOSPERM CHARACTERS.

These hybridization studies are all reported under the headings of the different characters investigated, as this seems to be the method calculated to show the data with the least confusion. The female parent is written first, using the variety number given under the description of the material under investigation. For example 7 x 54 represents a cross of Leaming yellow dent female with Black Mexican sweet male. When this cross is grown and hand-pollinated selfed ears are obtained, they are numbered (7 x 54)-1, (7 x 54)-2, (7 x 54)-3, etc. Should ear number 2 be grown for still another generation, the crop obtained is numbered (7 x 54)-2-1, (7 x 54)-2-2, etc., thus the exact generation of a particular ear is always shown. The characters under consideration are known by letters; '*S*', for example means presence of starchy character and '*s*', absence of starchy character: '*P*', represents presence of purple aleurone cells; '*p*', its absence. An ear numbered (7 x 54)-2-1 P S represents an ear of the third or F_3 generation from which purple starchy seeds have been selected for planting.

Starchiness and Non-starchiness.

Starchiness is the condition of the endosperm of all of Sturtevant's maize varieties except *Zea mays saccharata*, regardless of the physical condition — corneous starch or soft starch — in which it appears. The starch grains are fully developed and possess a shape characteristic of the species *Zea mays*. The sugar maize does not have the ability to develop these starch grains to maturity. Some starch is formed but it remains small, angular and abortive, hence the seeds ripen from the stage of maturity called the "milk" without much change, giving the seed a wrinkled translucent appearance. The difference in size of the starch grains in the two races is shown in Table 10. This difference in the size of starch grains however,

PLATE II.



a. No. 24 Rhode Island white cap (starchy parent); *b.* No. 53 Crosby non-starchy parent); *c.* result of cross 24x53 showing heterozygous seeds in which starchiness is completely dominant. *d*, an ear with F2 seeds showing mono-hybrid segregation. Lower row daughters of *d*. *E*, *f* and *g*, results from planting starchy seeds. One ear out of three is pure starchy. *h*, result from planting non-starchy seeds.

Segregation of Starchiness and Non-starchiness.

is not the whole difference between starchy and non-starchy races. As the starchy races ripen, starch formation goes on at a steady rate, while in the non-starchy races there is an actual breaking down of endosperm materials into cane sugar and various hexoses. This is shown by determinations we have made of reducing sugars in both starchy and non-starchy races when both were at the "milk" stage of maturity. The non-starchy races contained from one and one-fourth to two and one-half as much reducing sugar as the starchy races.

Correns (:01) has already shown that starchiness behaves as a Mendelian dominant allelomorphic to its absence. Dominance was complete, and segregation generally * exact and inheritance discontinuous. It is not to confirm his work that the matter is taken up here, but to consider other questions to which the data are relevant. These questions relate chiefly to the mathematical hypothesis of Mendelism, to prepotency of individuals, and to gametic purity. The data from which the problems are discussed are not selected, but the figures

---

* The one exception was the pop and sugar cross mentioned later.

TABLE 1.

NO. 15 FLINT STARCHY X NO. 54 NON-STARCHY.

Ear No.	S	*s*	Total	Ratio per 4	Dev.	P. E.
(15 x 54)–1	135	48	183	2.9508 : 1.0492	0.0492	0.0864
(")–2	253	85	338	2.9944 : 1.0056	0.0056	0.0635
(")–3	150	42	192	3.1248 : 0.8752	0.1248	0.0843
(")–4	238	96	334	2.8504 : 1.1496	0.1496	0.0639
(")–6	190	72	262	2.9008 : 1.0992	0.0992	0.0722
(")–8	302	96	398	3.0352 : 0.9648	0.0352	0.0586
(")–11	242	105	347	2.7896 : 1.2104	0.2104	0.0627
(")–15	236	79	315	2.9968 : 1.0032	0.0032	0.0658
(15 x 54)–2–1	235	70	305	3.0820 : 0.9180	0.0820	0.0669
(")–2–2	242	79	321	3.0156 : 0.9844	0.0156	0.0652
(")–2–3	248	66	314	3.1592 : 0.8408	0.1592	0.0659
(")–2–4	227	68	295	3.0780 : 0.9220	0.0780	0.0680
(")–2–5	200	59	259	3.0888 : 0.9112	0.0888	0.0726
(")–2–6	182	74	256	2.8436 : 1.1564	0.1564	0.0730
(")–2–7	238	91	329	2.8936 : 1.1064	0.1064	0.0644
(")–2–8	195	58	253	3.0832 : 0.9168	0.0832	0.0734
(")–2–9	162	38	200	3.2400 : 0.7600	0.2400	0.0826
(")–2–10	131	53	184	2.8476 : 1.1524	0.1524	0.0861
(")–2–11	132	40	172	3.0696 : 0.9304	0.0696	0.0891
(")–2–12	101	32	133	3.0376 : 0.9624	0.0376	0.1013

include only about one-fourth of the hand-pollinated ears at our disposal, belonging to the starchy and non-starchy cross. This number seemed sufficient for our purpose, and the segregating kernels were not counted on the remaining ears. It should be mentioned however, that any wide departures from the normal on any of the four hundred selfed heterozygous ears of this cross would have been noted and reported if such had occurred.

Dominance was found to be complete. In no case was there the slightest difference between the homozygous and the heterozygous seeds in either outward appearance or in the character of the starch cells when examined microscopically. Whatever it is that is brought in by the starchy parent to cause starch formation is sufficiently active to bring about complete change when present in one "dose" (that is from one parent). As in all endosperm characters, when S is the male parent the starchiness appears in the current generation so called, giving the most perfect illustration of Xenia there is known. As a matter of fact, one is not dealing with the current generation but with the F_1 generation, the endosperm being a younger generation than the plant which bears the ear. In no case, in an experience with several thousand seeds, did an F_1 seed showing Xenia fail to show a heterozygous condition; nor did extracted recessives (sugar seeds) of the F_2 generation ever show a heterzoygous condition. From this, one may conclude that the second male nucleus that fertilizes the endosperm nucleus always bears the same characters as the first male nucleus that fertilizes the embryo nucleus or egg. Several heterozygous seeds have been found, however, that were not completely starchy, but had developed bilaterally into half starchy and half nonstarchy. There was not a gradual change from the one condition to the other, but a distinct line of demarkation, with one side as absolutely distinct from the other as are the pure races of each kind. None of these seeds were homozygous starchy, and Correns' interpretation of similar phenomena as cases in which the second male nucleus did not fuse with the endosperm nucleus but each developed separately, seems well founded. Attention is called to the matter for this reason. It is an hypothesis generally received with quiescence if not with acquiescence, that starchiness (and other "presence" characters) is due to presence of an enzyme not possessed by the allelomorph. Now if this is true, the enzyme must be a colloid with such large molecules that there is absolutely no dialysis, otherwise it seems as if it would diffuse through the unripe seed sufficiently to act as a catalyser throughout the entire endosperm. No matter what is the correct interpretation, there is certainly a definite chain of hereditary transmission of characters from cell to cell during development, and each original cell follows an inertia of its own with little influence on others.

TABLE 2.

NO. 24, FLINT STARCHY X NO. 54, NON-STARCHY.

Ear No.	S	*s*	Total	Ratio per 4	Dev.	P. E.
(24 x 54)-1	274	94	368	2.9784 : 1.0216	0.0216	0.0609
(")-2	219	73	292	3.0000 : 1.0000	0.0000	0.0684
(")-6	256	89	345	2.9680 : 1.0320	0.0320	0.0629
(")-8	200	64	264	3.0304 : 0.9696	0.0304	0.0719
(")-9	155	69	224	2.7680 : 1.2320	0.2320	0.0781
(")-10	212	59	271	3.1292 : 0.8708	0.1292	0.0710
(")-11	213	77	290	2.9380 : 1.0620	0.0620	0.0686
(")-12	268	80	348	3.0804 : 0.9196	0.0804	0.0626
(")-13	264	106	370	2.8540 : 1.1460	0.1460	0.0607
(")-14	227	90	317	2.8644 : 1.1356	0.1356	0.0656
(24 x 54)-1-2	207	68	275	3.0108 : 0.9892	0.0108	0.0704
(")-1-6	223	75	298	2.9932 : 1.0068	0.0068	0.0677
(")-1-8	235	90	325	2.8924 : 1.1076	0.1076	0.0648
(")-1-9	106	36	142	2.9860 : 1.0140	0.0140	0.0980

We have said that dominance appears to be complete; segregation also appears to be complete. It is seldom necessary to subject extracted recessives to proof by growing them a further generation. Some strains of non-starchy maize, No. 18 for example, are much less wrinkled than others; and when such a strain is crossed with a flint type there is less difference between dominants and recessives in appearance than when certain other types are crossed. But in no case is there the least difficulty in separating the segregates correctly. Whether this apparent segregation is as complete as it appears, we shall discuss presently. It should further be mentioned that the seeds can also be classified with absolute exactness by microscopical examination.

Tables 1-9 contain the proportion of the starchy and non-starchy seeds obtained as progeny when heterozygous seeds were planted; although, as was stated before, only a few ears from each family were counted. One object in view is to show the behavior of starchy and non-starchy in several races.

TABLE 3.

NO. 5, FLINT STARCHY X NO. 18, NON-STARCHY.

Ear No.	S	s	Total	Ratio per 4	Dev.	P. E.
(5 x 18)–4	181	68	249	2.9176 : 1.0924	0.0924	0.0740
(“)–8	172	66	238	2.9908 : 1.1092	0.1092	0.0757
(“)–10	215	68	283	3.0388 : 0.9612	0.0388	0.0694
(“)–16	225	69	294	3.0612 : 0.9388	0.0612	0.0681
(“)–18	186	61	247	3.0120 : 0.9880	0.0120	0.0743
(“)–21	136	42	178	3.0560 : 0.9440	0.0560	0.0876
(“)–25	176	50	226	3.1152 : 0.8848	0.1152	0.0777
(“)–30	218	68	286	3.0488 : 0.9512	0.0488	0.0691

There is reason to believe that different races can be identical in appearance, but may have such different gametic composition that they may affect a character possessed by a race with which they may be crossed, in very different manners. (See purple aleurone cells and non-purple.) Examination of the tables shows this not to be the case with starchy and non-starchy. All of the starchy and non-starchy races with which crosses have been made behave in exactly the same manner. There is no difference in appearance in heterozygotes from different races that is not accounted for by the different shaped seeds possessed by the parents, and wide variations in shape occur only in generations later than F_1. In the F_1 generation the shape is intermediate between that of the two parents.

TABLE 4.

NO. 11, FLINT STARCHY X NO. 18, NON-STARCHY.

Ear No.	S	s	Total	Ratio per 4	Dev.	P. E.
(11 x 18)–7	220	74	294	2.9932 : 1.0068	0.0068	0.0681
(“)–14	218	81	299	2.9164 : 1.0836	0.0836	0.0676
(“)–15	200	77	277	2.8880 : 1.1120	0.1120	0.0702
(“)–22	235	87	322	2.9192 : 1.0808	0.0808	0.0651

If one examines the tables carefully however, he sees at once that there is quite a difference in the ratios obtained. They vary from a ratio of 2.7896 : 1.2104 in ear (15 x 54)-11, Table 1 to a ratio of 3.2020 : 0.7980 in ear (19 x 7)-2, Table 7. This brings up an important question. Does this discrepancy represent an expected probable error in chance matings; or, is there a prepotency in certain families through which excessive numbers of dominants or of recessives tend constantly to reappear? Correns did indeed find in one family such an excess of starchy seeds, but it is not known whether this apparent prepotency was transmitted in further generations.

Tables 1-9 show several cases where ears with a ratio deviating from the expected 3 : 1 of Mendelian hypothesis have been grown for another generation. For example, ear (8 x 54)-1 of Table 6 has a ratio of 2.9420 : 1.0580 while ear (8 x 54)-5 of the same table has a ratio of 3.0780 : 0.9220; yet the progeny of these ears average just about the 3 : 1 ratio of theory. There are even more ears with an excess of recessives from the ear that had the excess of dominants and *vice versa*. Other deviants have been grown for several generations, and while the exact ratios have not been recorded it may be stated with confidence that wide deviations occurring in considerable numbers would have been noticed while making other records. It may be concluded then that no prepotency or tendency to aberrant ratios is a constant characteristic of any of our families. How then can the discrepancies from theoretical ratios be explained?

To study this question the probable errors of all of the ratios have been calculated. The method used has been that of Johannsen (: 09, p. 405), except that the mean error has been reduced to the probable error by multiplying by the factor 0.6745. The standard deviation of a Mendelian proportion is $\pm\frac{\sqrt{p \times q}}{p+q}$ where *p* and *q* are the Mendelian terms, in this case case 3 and 1. Then $\text{S. D.} = \pm\frac{\sqrt{3 \times 1}}{4} = \pm\frac{1.7321}{4} = \pm 0.4330$. The probable error, $E = \pm 0.6745\frac{\text{S. D.}}{\sqrt{n}}$ where *n* is the total number of variates.

To find out whether the different ratios given in Tables 1-9 are what should reasonably be expected if the Mendelian theory of chance matings of equal numbers of gametes *S* and *s* in both male and female germ-cells is correct, it should be understood just what is meant by probable error in the law of error. Plus errors and minus errors should occur with equal frequency, small errors should occur more frequently than large errors, and very large errors should not occur. Determined as above the probable error means that the chances are:

1 to 1 that the true value lies within ± E
4.5 to 1 that the true value lies within ± 2E
21 to 1 that the true value lies within ± 3E
142 to 1 that the true value lies within ± 4E

The theory of error also provides for errors of any size in their proper frequency or rather infrequency, but as a matter of fact in practice if errors greater than ± 4E occur they are probably due to experimental errors or avoidable mistakes.

We may consider each ear given in Tables 1-9 as a determination and its probable error as the probable error of a single determination. With this in mind we find that in the 94 ears tabled there are 49 plus errors and 45 minus errors. Further we find that the theoretical mode or 0 error is almost 3 : 1, being in fact very slightly greater. The errors are distributed as follows:

Within ± E 47.8% — Theory 50.0%
Within ± 2 E 83.0% — Theory 82.3%
Within ± 3 E 96.8% — Theory 95.7%
Within ± 4 E 100.0% — Theory 99.3%

The sum total of these segregates is 23529 to 7811, a ratio of 3.0031 : 0.9969 ± .0066.

It should be mentioned simply in order to suppress no data that one ear was found with a probable error somewhat in excess of ± 4 E. It was found by growing this ear for another generation however that this was due to an experimental error. There was a great excess of sugar seeds, but in the starchy seeds there proved to be about 4 heterozygotes to 1 homozygote. Since no other ear like this has ever been obtained, and since it is known that during the progress of this experiment several ears were first selfed with pollen killed by rain and afterward pollinated with pollen from a sugar plant to get material for another purpose, it seems highly probable that this ear was of a similar mixed parentage and that its explanatory label had been lost.

As to whether these data support the Mendelian hypothesis or not there may be slight grounds for a difference in opinion. Our own opinion is that when we take into consideration the chance for experimental error, the ratios are well within the limits of probable error. One thing at least is brought out clearly, the behavior of segregates in more than one generation and a variety of matings are necessary, if one is to draw conclusions as to the exact mode of inheritance of character pairs from small numbers.

One further point remains for discussion. Do the extracted homozygotes breed true? In other words, is segregation an absolute separation of a gene from its absence? or, is there only a relative segregation? Morgan (:10) has suggested that relative segregation may explain Mendelian facts, if one presupposes that when the amount of the gene falls below a certain limit the dominant fails to develop. This idea while interpreting the facts in the F_2 generation is inadequate to explain the apparent purity of further generations of extracted recessives, for if this hypothesis were true many recessives would show the dominant character when crossed.

In Table 9 is shown the segregation of extracted dominant starchy seeds. The ratio is as nearly the expected 2 heterozygotes to 1 homozygote as could well be expected. Several

---

TABLE 5.

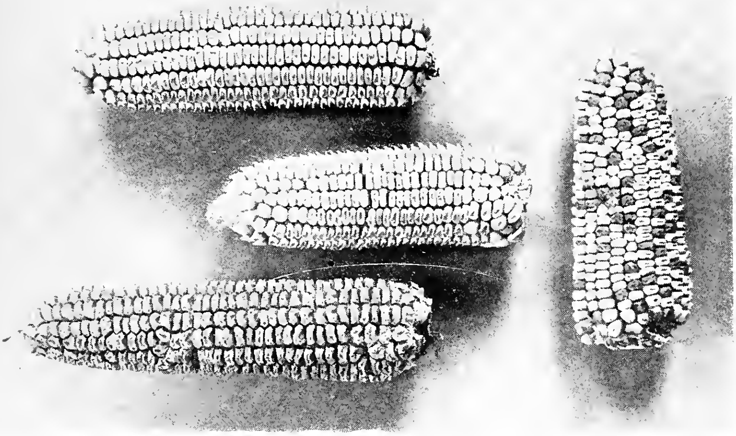
NO. 17, FLINT STARCHY X NO. 54, NON-STARCHY; NO. 18, NON-STARCHY X NO. 58, FLINT STARCHY; AND NO. 7, DENT STARCHY X NO. 54, NON-STARCHY.

Ear No.	S	*s*	Total	Ratio per 4	Dev.	P. E.
(17 x 54)–1	328	102	430	3.0512 : 0.9488	0.0512	0.0563
(18 x 58)–1	332	102	434	3.0600 : 0.9400	0.0600	0.0561
(7 x 54)–1	379	137	516	2.9380 : 1.0620	0.0620	0.0514
(")–2	493	131	624	3.1604 : 0.8396	0.1604	0.0467

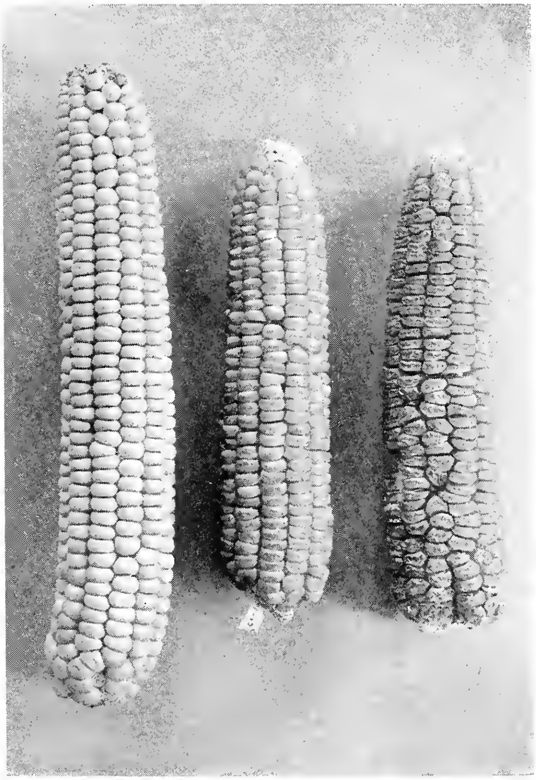
thousand dominant homozygotes have been bred for further generations and these have all bred true to the starchy character. This is, in general, the case with the extracted non-starchy seeds. Furthermore, there are in commercial use many sugar corns that are extracted recessives. Golden Bantam, Late Egyptian and many others are examples of races that have originated from crosses with starchy varieties. The wrinkled seeds have been selected and have bred true. Out of the many million seeds that are annually grown for the canning factories, however, there does appear an occasional ear with semi-starchy seeds. These ears transmit the character and give the canners no end of trouble. There is no way to find out whether these ears appear only on varieties which somewhere in their ancestry had a starchy parent. One can only say that they do appear in ratios not exceeding one ear in ten thousand. By some lucky chance some of these ears made their appearance in our controlled cultures. All of our extracted recessives have proved true to non-starchiness (*) except from the progeny of ear (8 x 54)-1-6. The majority of the progeny of this ear were also non-starchy, but three ears appeared which were decidedly semi-starchy, one of which is shown in Plate III, fig. b. There was no possibility that these ears could have grown from a normal heterozygous seed. They were not plump seeds like a true heterozygote nor did they segregate into starchy and non-starchy in the next generation. The entire ear was rather uniformly semi-starchy and quite different from the true starchy ears. Microscopical examination showed definitely that starch grains had been developed normally to a size intermediate between the true starchy and the true sweet seeds of the same family. This fact is shown in Table 10.

---

* There are other cases where some apparent starchiness is always developed, namely when pop races are crossed with non-starchy races. We interpret this as being due to the small size of the resulting F_2 seeds borne on intermediate F_1 ears. When the seeds are small the endosperm material more nearly fills the pericarp than when they are large. The wrinkled condition is therefore less apparent. If one has had considerable experience in classifying starchy and non-starchy seeds, such crosses are seen to show normal segregation. If, however, careful classification is not made and the seeds are not tested in further generations pop and non-starchy crosses always appear to show an excess of starchy seeds. It is suggested that this is the explanation of Corren's failure to obtain normal ratios in a similar cross. These cases are not real exceptions to the statement made above, however, for recessives extracted from pop crosses are never grown commercially as sugar corns.



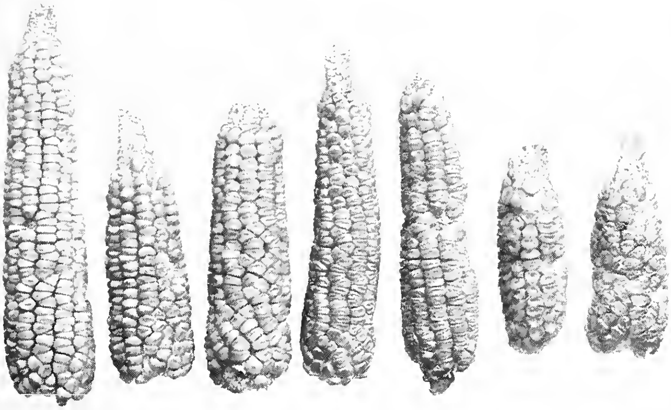
a. P2, F1, and F2 seeds from cross between No. 19 Stowell's Evergreen sugar and No. 2 Illinois low protein dent maize.



b. Middle ear is a semi-starchy ear No. (8x54)-1-6, progeny of an extracted recessive (wrinkled) seed. On the left is an extracted dominant (starchy) ear of the same cross. On the right is a well wrinkled ear, sister of No. (8x54)-1-6.

SEGREGATION OF STARCHINESS AND NON-STARCHINESS.

a Random sample of progeny of starchiest seeds of semi-starchy ear shown in PLATE III.



b. Random sample of progeny of most wrinkled seeds of semi-starchy ear shown in PLATE III.

GAMETIC PURITY.

TABLE 6.

NO. 8, DENT STARCHY X NO. 54, NON-STARCHY.

Ear No.	S	s	Total	Ratio per 4	Dev.	P. E.
(8 x 54)–1	381	137	518	2.9420 : 1.0580	0.0580	0.0513
(")–2	340	137	477	2.8512 : 1.1488	0.1488	0.0535
(")–3	400	141	541	2.9576 : 1.0424	0.0424	0.0502
(")–5	384	115	499	3.0780 : 0.9220	0.0780	0.0523
(8 x 54)–1–3PC	243	64	307	3.1660 : 0.8340	0.1660	0.0667
(")–1–4PC	302	105	407	2.9680 : 1.0320	0.0320	0.0579
(")–1–6PC	231	81	312	2.9616 : 1.0384	0.0384	0.0672
(")–1–8PC	321	117	438	2.9316 : 1.0684	0.0684	0.0558
(")–1–14PC	238	66	304	3.1316 : 0.8684	0.1316	0.0670
(")–1–6P	145	40	185	3.1356 : 0.8644	0.1356	0.0859
(")–1–11P	268	78	346	3.0984 : 0.9016	0.0984	0.0628
(")–1–13P	320	107	427	2.9976 : 1.0024	0.0024	0.0565
(")–1–15P	293	96	389	3.0128 : 0.9872	0.0128	0.0592
(")–1–1	237	88	325	2.9168 : 1.0832	0.0832	0.0648
(")–1–2	236	88	324	2.9136 : 1.0864	0.0864	0.0649
(")–1–4	176	60	236	2.9832 : 1.0168	0.0168	0.0760
(")–1–10	242	80	322	3.0064 : 0.9936	0.0064	0.0651
(")–1–29	272	93	365	2.9808 : 1.0192	0.0192	0.0611
(8 x 54)–5–2	236	90	326	2.8956 : 1.1044	0.1044	0.0647
(")–5–3	294	99	393	2.9924 : 1.0076	0.0076	0.0589
(")–5–4	147	61	208	2.8268 : 1.1732	0.1732	0.0810
(")–5–5	277	72	349	3.1748 : 0.8252	0.1748	0.0625
(")–5–6	357	123	480	2.9748 : 1.0252	0.0252	0.0533
(")–5–8	324	109	433	2.9932 : 1.0068	0.0068	0.0651
(")–5–10	306	85	391	3.1304 : 0.8696	0.1304	0.0591
(")–5–11	249	86	355	2.9732 : 1.0268	0.0268	0.0638

Seeds from the ear shown in Plate III, fig. b, were divided into two classes, those most nearly starchy and those most nearly non-starchy, and planted. A number of selfed ears were obtained from each class. Those resulting from the seeds most nearly non-starchy were in part what would immediately be classified as non-starchy and in part as starchy in appearance as the parent ear. The ears resulting from the seeds most nearly starchy were all as starchy as the parents and certain of them even more so. This fact is shown in Plate IV. Microscopical examination of the most starchy seeds of this generation showed that the starch grains were most of them developed to normal size. The ears were not uniform nor was there uniform starchiness among the seeds of a single ear. Seeds could be selected which formed a series running from true sweet to true starchy, yet those most nearly starchy had a rough appear-

TABLE 7.

NO. 19, NON-STARCHY X NO. 7, DENT STARCHY AND NO. 19, NON-STARCHY X NO. 8, DENT STARCHY.

Ear No.	S	*s*	Total	Ratio per 4	Dev.	P. E.
(19 x 7)–2	297	74	371	3.2020 : 0.7980	0.2020	0.0607
(“)–5	486	156	642	3.0280 : 0.9720	0.0280	0.0461
(19 x 7)–5–1	304	109	413	2.9444 : 1.0556	0.0556	0.0575
(19 x 8)–1	183	64	247	2.9636 : 1.0364	0.0364	0.0743
(“)–2	464	152	616	3.0128 : 0.9872	0.0128	0.0471
(“)–3	449	151	600	2.9932 : 1.0068	0.0068	0.0477
(“)–4	303	96	399	3.0376 : 0.9624	0.0376	0.0585
(“)–5	414	139	553	2.9948 : 1.0052	0.0052	0.0507

ance very different from the well-filled pericarp of the true starchy seeds of the same family. These seeds will be selected for starchiness and if uniform ears are finally obtained, will be crossed with non-starchy again to see if their behavior is the same as normal starchy maize. Provisionally one is forced to one of two conclusions. *Either homozygous recessives (and likewise dominants) are not complete segregates, but products of a partial quantitative separation of genes allowing traces of the dominant character to remain, traces which may sometimes accumulate sufficiently to bring out the dominant character: or, progressive variations are constantly taking place in small numbers, most often along paths that have been passed before.*

TABLE 8.

NO. 60, POP STARCHY X NO. 54, NON-STARCHY.

Ear No.	S	*s*	Total	Ratio per 4	Dev.	P. E.
(60–5 x 54)–2	274	82	356	3.0788 : 0.9212	0.0788	0.0619
(“)–6	273	102	375	2.9120 : 1.0880	0.0880	0.0603
(“)–8	163	53	216	3.0184 : 0.9816	0.0184	0.0795
(“)–11	191	58	249	3.0684 : 0.9316	0.0684	0.0740
(“)–12	249	84	333	2.9908 : 1.0092	1.0092	0.0640
(60–3 x 54)–1	296	87	383	3.0912 : 0.9088	0.0912	0.0597
(“)–5	260	107	367	2.8336 : 1.1664	0.1664	0.0610
(“)–6	243	73	316	3.0760 : 0.9240	0.0760	0.0657
(60–8 x 54)–1	227	67	294	3.0884 : 0.9116	0.0884	0.0681
(“)–8	224	71	295	3.0372 : 0.9628	0.0372	0.0680

It is our opinion that dominant starchiness — if it is the same dominant starchiness — has been formed anew. It occurs too rarely to support a partial segregation theory such as Morgan's (: 10). If it is asked why starchiness is the character that arises anew rather than another variation, it is suggested that the peculiar chemical structure of the germ cell of maize may be such that a molecular readjustment is much more likely to bring about starchiness than any other variation. Such a path of least resistance for variations might account for the many cases in animals and plants where the same variation has apparently occurred again and again.

Conclusion.

These starchy and non-starchy crosses represent a much larger number of individuals than have ever before been studied in accurately controlled pedigree cultures. Taking them as a whole they show that the mechanism by which the members of an allelomorphic pair are distributed among the gametes, is accurate. The aberrant ratios sometimes obtained are what should be expected by the Law of Error. They are not inherited, and we believe this to show that there is no such thing as prepotency *per se* which would cause abnormal ratios. We might extend this conclusion further and say that there is no conclusive evidence of a failure of segregation of male gametes or of selective fertilization (Lock : 06), or of partial gametic coupling that presupposes gametes bearing opposite genes to be formed in unequal numbers (Bateson and Punnett : 08). Disbelief in prepotency of the kind described above does not indicate disbelief in different "potencies" as described by Davenport (: 10). Different potencies, that is various degrees of manifestation of the same character due to its modification during development by the action of *other developing* genes possessed by the individual, is a different thing and is entirely logical. In prepotency or potency of this kind segregations are perfectly normal, and modifications which occur in characters are due to the gametic constitution of the individual.

The aberrant ratios obtained by Correns in the pop-sugar cross referred to above, may have been due to modification by other unknown characters possessed by the parents, but it seems more likely that they were due to improper classification of dominants and recessives for the reason that recessives in such crosses although hyaline and easily classified microscopically often do fill the pericarp with endosperm material owing to the small size of the seed.

If then, in cases of simple mono-hybrids where there are no complications, a ratio of 3.0031 : 0.9969 ± .0066 is obtained; are we not compelled to take the view that segregation occurs at the reduction division? Could any less exact division give the distribution of genes necessary for such exact recombinations? Of course it has long been suspected that this was the time of segregation, but Bateson (: 09 p. 271) has felt that obstacles were in the way of interpreting the chromosomes as such important bearers of hereditary qualities. These obstacles were three in number; first, it is objected that no correspondence has been shown between visible differences of type (except sex) and chromosome differences; second, that no correspondence between complexity of type and chromosome numbers has been shown; and third, that bud sports are somatic segregates. There are, it seems to us, no real obstacles here. One should expect that the quality of the chromosome and not shape or number, is the important fact. It is even likely that most of the important morphological characters are carried by all of the chromosomes, hence a doubling of chromosome number as has occurred in *Oenothera gigas* may be relatively unimportant. The case of bud sports is also fairly clear since Winkler (: 09) has shown that a graft hybrid between the black night shade and the tomato proved to have the sum of the haploid numbers of the two parents and not the sum of the diploid numbers. The somatic cell then has a regulatory apparatus of its own. What might be called the normal bud sport (other sports probably occur from abnormal cell divisions) is probably due to the fusion of two somatic cells of a heterozygote, followed by a reduction, in which one of the homozygote forms appears. It must be not understood however that because Bateson's objections are considered surmountable, we therefore believe it to be *proved* that the chromosomes are the sole bearers of hereditary characters and that the *reduction division* is the time of Mendelian segregation. Judgment must still be suspended on these matters.

TABLE 9.

EARS FROM F_2 GENERATION PLANTS OF STARCHY AND NON-STARCHY CROSSES.

Starchy Seeds Planted.

Selection	Heterozygous S	Homozygous S
(8 x 54)–1	6	4
(")–2	4	5
(")–3	30	17
(")–5	75	31
(")–1–1	67	32
(")–1–2	44	25
(")–4	71	38
(")–10	48	28
(15 x 54)–2	46	13
(")–3	25	17
(24 x 54)–1	28	14
Total	444	224
Ratio	1.93	1

TABLE 10.

RANDOM COMPARISON OF DIAMETER OF STARCH GRAINS.

Extracted Starchy Seeds from (8 x 54)–1 and Semi-Starchy and Non-Starchy from (8 x 54)–1–6.

Diam. in mm.	.009	.017	.034	.052	.069	.086	.103	.12	.138	.155	Total
No. variates from starchy seeds	..	1	9	23	34	66	36	16	12	3	198
No. variates from semi-starchy seeds	..	17	52	57	48	17	11	5	..	..	227
No. variates from non-starchy seeds	34	94	52	13	..	..	..	..	..	..	193

Yellow and Non-yellow Endosperm.

Correns (:01) and Lock (:06) each found a yellow color in the endosperm which behaved with its absence as a single allelomorphic pair. We have found *two* * yellow colors in the endosperm each behaving when crossed with its absence, as an independent allelomorphic pair. A part of the experiments with these characters has been described in a previous paper (East :10). In this paper some further data are presented.

Both of these yellow colors, although they behave in inheritance as separate entities are either identical or very similar in composition. They are insoluble in water, somewhat soluble in alcohol and easily soluble in ether, chloroform, benzine, benzol and carbon bisulphide. They occur in rhombic plates in the starch cells and possibly also in the chromoplasts although this is not certain. From these facts it might be supposed that they were hydrocarbons with compositions similar to carotin. They do not give the general reactions however which the fatty pigments or lipochromes — of which carotin is an example — give with sulphuric acid or iodine dissolved in aqueous potassium iodide. Independent of their solubility reactions, this would class them with the anthochlorins (Courchet '88).

Considering the importance to Mendelian theory of the discovery that two similar and possibly identical characters may each act with its own absence as an independent allelomorphic pair, further chemical investigations are being made which will be reported in a separate paper. It may simply be stated here that as far as is known these colors are indistinguishable, but as they behave differently in crosses they will be known as Y_1 and Y_2.

A number of crosses were made between yellow and non-yellow which gave only 3 : 1 ratios. The remaining crosses shown in Tables 11-16 each showed one or more ears with dihybrid ratios.

---

* Lock mentioned that light yellow seeds appeared in his crosses, but he classed them as whites which vitiates his study of Mendelian numerical proportions.

TABLE 11.

F_2 SEEDS FROM CROSS OF NO. 1 WHITE DENT X NO. 7 YELLOW DENT.

Ear No.	Y	*y*	Ratio Approx.
(1 x 7)–1	587	212	3 : 1
(1 x 7)–2	127	30	3 : 1

Table 11 gives the results from two selfed ears of No. 1 white dent crossed with No. 7 yellow dent. They approximate 3 to 1 ratios although ear No. 1 has an excess of non-yellow and ear No. 2 an excess of yellow seeds. This cross proved to be too late for the Connecticut climate and the resulting F_3 seeds were immature and difficult to classify. Yellow was dominant and appeared as Xenia in the F_1 seeds but the F_2 seeds varied in different ears in a peculiar manner. Where there was sufficient soft starchy matter in the caps of the seeds the heterozygotes were considerably lighter colored at the cap than when the seeds possessed more corneous starch. The same phenomenon occurred in reciprocal crosses; so that when there was sufficient soft starchy matter the heterozygotes could be distinguished from the homozygotes either way the cross was made. (See cross of floury yellow with non-yellow.)

Ear (1 x 7)-1Y gave only one selfed ear with 126 yellows of various shades, 14 white, and 3 doubtful seeds. The mother seed was probably Y_1 Y_2 y_1 y_2. Several open field ears from yellows with white caps all proved to be heterozygous, thus proving the above statement regarding Xenia. The crop from the white seeds proved pure for non-yellow.

TABLE 11A.

F_3 SEEDS OF EAR NO. 2 OF CROSS SHOWN IN TABLE 11.

Yellow Seeds Planted.

Ear No.	Y	y	Ratio Approx.
(1 x 7)–2–3	423	108	3 : 1
(")–2–7	351	108	3 : 1
(")–2–8	375	120	3 : 1
(")–2–12	343	111	3 : 1
(")–2–14	577	...	Pure yellow
(")–2–17	286	58	3 : 1
(")–2–18	209	87	3 : 1
(")–2–19	360	135	3 : 1
(")–2–20	341	105	3 : 1
(")–2–22	319	92	3 : 1
(")–2–23	408	168	3 : 1
(")–2–25	633	40	15 : 1

Table 11a shows the results from planting (1 x 7)-2 Y seeds. Ears Nos. 3 and 17 have an excess of yellow seeds. Possibly they were 15 : 1 ratios in which the yellows were very light and could only have been classified with certainty by growing the supposed whites another generation. The remaining ears all showed 3 : 1 ratios except ear No. 25. This ear was clearly a 15 : 1 ratio. The crop from (1 x 7)-2y (extracted whites) gave 12 pure white ears, showing that the classification of the F_2 seeds was correct.

A cross between No. 5 white flint and No. 6 yellow dent (Tables 12 and 12a) showed in all cases complete dominance of yellow. In the F_1 seeds which were of course flinty like the mother, there was no soft starch in the cap and the heterozygotes were exactly like pure yellow flint seeds. In the F_1 plants the F_2 homogygous and heterozygous yellow seeds were also indistinguishable. It was necessary to grow them to distinguish heterozygous yellow from homozygous yellow. In the F_2 plants with F_3 seeds, however, there was a considerable segregation of dented ears from flint ears. Here as in the cross of (1 x 7) it was fairly easy to distinguish heterozygous yellows from homozygous yellows when the seeds of the former had a well developed soft starchy zone in the cap.

Although as has been stated the F_1 seeds were all exactly like pure yellow flint seeds, they nevertheless belonged to two classes. The Xenia seeds (F_1 seeds) of the hybrid ear contained 159 seeds which were dark yellow and 145 seeds which were a considerably lighter yellow. This striking phenomenon was not understood until another generation was grown from the seeds. Table 12 showing the selfed ears resulting from the dark seeds, and Table 12a showing the selfed ears resulting from the light seeds make this matter plain. Excluding ear (5 x 6)-9 from Table 12 because it evidently came from a pure yellow seed grown in this family through an error, and ear (5 x 6)-11a from Table 12a which evidently grew from a self-pollinated seed of the mother No. 5, it is clear that the No. 6 plant furnishing the pollen for the cross was homozygous for one yellow and heterozygous for the other. The classification into light and dark yellows was somewhat arbitrary and therefore some ears in Table 12 gave ratios of 3 : 1 and some ears in Table 12a gave ratios of 15 : 1 but the fact that about one-half of the F_1 seeds had a gametic formula of $Y_1\ y_1\ Y_2\ y_2$ and one-half the formula $Y_1\ y_1$, or $Y_2\ y_2$, is certain. Ear (5 x 6)-7a is the only ratio in doubt. It is probably 15 : 1 as the yellows were very light and difficult to classify, and some were probably placed with the non-yellows.

TABLE 12.

F_2 SEEDS FROM CROSS OF NO. 5 WHITE FLINT X NO. 6 YELLOW DENT.

Dark Yellow Seeds Planted.

Ear No.	Y	y	Ratio Approx.
(5 x 6)–1	326	29	15 : 1
(")–2	316	27	15 : 1
(")–3	313	28	15 : 1
(")–7	354	122	3 : 1
(")–8	331	109	3 : 1
(")–9	307	...	Pure yellow
(")–10	475	25	15 : 1
(")–11	298	113	3 : 1
(")–12	368	19	15 : 1
(")–13	363	35	15 : 1
(")–14	489	29	15 : 1
(")–15	427	118	3 : 1

TABLE 12A.

F$_2$ SEEDS FROM SAME CROSS AS SHOWN IN TABLE 12.

Light Yellow Seeds Planted.

Ear No.	Y	*y*	Ratio Approx.
(5 x 6)–1a	359	117	3 : 1
(")–2a	144	54	3 : 1
(")–3a	173	63	3 : 1
(")–4a	433	136	3 : 1
(")–5a	557	35	15 : 1
(")–6a	316	120	3 : 1
(")–7a	450	49	10 : 1
(")–8a	229	86	3 : 1
(")–9a	325	115	3 : 1
(")–10a	227	87	3 : 1
(")–11a	. . .	434	Pure white
(")–12a	318	118	3 : 1
(")–13a	256	93	3 : 1

Tables 13, 13a, b, c, d, show results from an opposite cross. No. 11, yellow flint was the female parent and No. 8, white dent was the male parent. There was no effect of Xenia, as the F$_1$ hybrid seeds were as yellow as the pure No. 11. Table 13 shows the results from the F$_1$ hybrid seeds. Every ear approximates a 3 : 1 ratio except ears (11 x 8)-7 and (11 x 8)-8. Ear (11 x 8)-7 is shown afterwards by Tables 13b and c to have been in reality a 15 : 1 ratio. In other words it was a $Y_1 y_1 Y_2 y_2$

TABLE 13.

F$_2$ SEEDS FROM CROSS OF NO. 11, YELLOW FLINT X NO. 8, WHITE DENT

Yellow Seeds Planted.

Ear No.	Y	*y*	Ratio Approx.
(11 x 8)–1	358	154	3 : 1
(")–2	124	41	3 : 1
(")–3	389	127	3 : 1
(")–4	340	96	3 : 1
(")–6	252	83	3 : 1
(")–7	454	145*	3 : 1
(")–8	204	70**	3 : 1

---

* ** Proved to be a mixture of Y y and y, with preponderance of Y y.

ear. Ear (11 x 8)-8 probably was also of the same character as about half of the seeds classed as white proved to be heterozygous. Table 13d shows only two ears out of eight to have been other than white but an inspection of the open field crop showed such a large proportion of apparently heterozygous ears, that this ratio is probably not the real one.

Ear (11 x 8)-2 proved to be $Y_1 y_1$ or $Y_2 y_2$ as is shown in Table 13a. There is a ratio of about 2 heterozygous to 1 homozygous ears.

TABLE 13A.

F_3 SEEDS OF EAR NO. 2 OF CROSS SHOWN IN TABLE 13.

Yellow Seeds Planted.

Ear No.	Y	*y*	Ratio Approx.
(11 x 8)–2–1	275	. .	Pure yellow
(")–2–3	237	75	3 : 1
(")–2–5	244	71	3 : 1
(")–2–7	374	. .	Pure yellow
(")–2–8	344	113	3 : 1
(")–2–9	280	. .	Pure yellow
(")–2–10	99	31	3 : 1
(")–2–11	173	38	3 : 1
(")–2–15	274	75	3 : 1

Ear (11 x 8)-7 was evidently wrongly classified as is shown in Tables 13b and 13c. Ear (11 x 8)-7-1 is probably a 15 : 1 ratio. If this is true then there were 2 ears with gametic formula $Y_1 y_1 Y_2 y_2$, 2 ears with gametic formulæ $Y_1 y_1$ or $Y_2 y_2$, 1 ear with formula $Y_1 Y_1 Y_2 Y_2$ [Ear (11 x 8)-7-9], and 3 ears with formulæ $y_1 y_2$. The apparently white seeds from this ear were not all non-yellow, but partly pure and partly heterozygous light yellows. That is, they were $Y_1 Y_1$ or $Y_2 Y_2$ or $Y_1 y_1$ or $Y_2 y_2$.

TABLE 13B.

F_3 SEEDS OF EAR NO. 7 OF CROSS SHOWN IN TABLE 13.

Yellow Seeds Planted.

Ear No.	Y	y	Ratio Approx.
(11 x 8)–7–1	207	25	8 : 1
(")–7–4	253	68	3 : 1
(")–7–6	193	73	3 : 1
(")–7–8	163	79	3 : 1
(")–7–9	456	. .	Pure yellow
(")–7–11	108	35	3 : 1
(")–7–14	88	5	15 : 1

TABLE 13C.

F_3 SEEDS OF EAR NO. 7 OF CROSS SHOWN IN TABLE 13.

Apparently White Seeds Planted.

Ear No.	Y	y	Ratio Approx.
(11 x 8)–7–1a	. . .	504	Pure non-yellow
(")–7–2a	271	. . .	Pure light yellow
(")–7–3a	. . .	330	Pure non-yellow
(")–7–4a	323	117	3 : 1
(")–7–5a	. . .	300	Pure non-yellow

TABLE 13D.

F_3 SEEDS OF EAR NO. 8 OF CROSS SHOWN IN TABLE 13.

White Seeds Planted.

Ear No.	Y	y	Ratio Approx.
(11 x 8)–8–1	406	194	3 : 1
(")–8–3	. . .	394	Pure non-yellow
(")–8–6	. . .	560	"
(")–8–7	. . .	348	"
(")–8–9	. . .	490	"
(")–8–11	. . .	360	"
(")–8–12	. . .	360	"
(")–8–13	442	. . .	Pure yellow

TABLE 14.

F_2 SEEDS FROM CROSS OF NO. 11 STURGES' YELLOW FLINT X NO. 24 SANFORD'S WHITE FLINT.

Yellow Seeds Planted.

Ear No.	Y	y	Ratio Approx.
(11 x 24)–3	467	164	3 : 1
(")–4	320	137	3 : 1
(")–5	499	142	3 : 1
(")–6	356	116	3 : 1

Table 14 shows the results from selfing the F_1 seeds of a cross between No. 11, yellow flint and No. 24 white flint. There was no effect of Xenia. The ears gave 3 : 1 ratios and the extracted non-yellows proved to be pure in the F_3 generation.

TABLE 15.

F_2 SEEDS FROM CROSS OF NO. 15 LONGFELLOW FLINT X NO. 8 WHITE DENT.

Yellow Seeds Planted.

Ear No.	Y	y	Ratio Approx.
(15 x 8)–1	305	73	3 : 1
(")–2	166	12	15 : 1
(")–3	246	85	3 : 1
(")–4	428	142	3 : 1
(")–5	393	124	3 : 1
(")–6	353	106	3 : 1
(")–7	480	140	3 : 1

Table 15 gives the results from selfing the F_1 seeds of a cross between No. 15, Longfellow yellow flint and No. 8, white dent. There was no appearance of Xenia in the F_1 seeds. The F_2 seeds segregated in 3 : 1 ratios with the exception of ear (15 x 8)-2. This ear was originally classified as bearing 128 yellow and 50 non-yellow seeds. The F_3 seeds produced by the supposed whites, however, showed the correct ratio to have been 166 yellow and 12 non-yellow. The whites proved true in three other ears. The white seeds from ear (15 x 8)-1 were not grown, and therefore the large excess of yellow seeds cannot be explained. It is possible of course that this ear as well as one or two others that were not planted really had light yellows classified as whites. If this were true one might consider that the original mother plant was homozygous for one yellow and heterozygous for the second. It seems not improbable that this was the case, for the same results were obtained in two other instances.

TABLE 16.

F_2 SEEDS FROM CROSS OF NO. 19 WHITE SWEET X NO. 7 YELLOW DENT.

Yellow Seeds Planted.

Ear No.	Y	*y*	Ratio Approx.
(19 x 7)–2	277	77	3 : 1
(")–5	599	43	15 : 1

One other cross, No. 19 non-yellow sweet and No. 7 yellow dent (Table 16), gave di-hybrid ratios. The hybrid seeds were yellow starchy varying somewhat in shade. Only two selfed ears were obtained from the F_1 seeds. As shown in Table 16 one is a 3 : 1 ratio and one is a 15 : 1 ratio. Here again is evidence that the male parent was homozygous for one yellow and heterozygous for the second yellow. To be sure there is a slight excess of non-yellows in ear (19 x 7)-5, but this is accounted for in the F_3 generation. The supposed non-yellows gave one heterozygous yellow to seventeen non-yellows. The true ratio

TABLE 16A.

F_3 SEEDS OF EAR 5 OF CROSS SHOWN IN TABLE 16.

Dark Yellow Starchy Seeds Planted.

Ear No.	Y	*y*	Ratio Approx.
(19 x 7)–5–1	315	98	3 : 1
(")–5–6	320	97	3 : 1
(")–5–9	19	1	15 : 1
(")–5–12	203	14	15 : 1
(")–5–13	440	25	15 : 1

then is 601 : 41 which is very close to theoretical expectancy. The results from planting the yellow starchy seeds of (19 x 7)-5 are shown in Table 16a. Unfortunately the admixture of segregates with wrinkled endosperm made these a little difficult to classify, but there is scarcely a doubt that 2 ears were mono-hybrids and three ears di-hybrids, although no dependence can be placed on ear (19 x 7)-5-9 with only 20 seeds. No pure yellows were obtained from these seeds unless ear (19 x 7)-5-9 were of this class. The deficiency of these data was supplied by the crop of the yellow sweet F_2 seeds of the same ear. Twelve selfed ears were obtained. They are not given in a table because we were not able to prove the classification by growing for another generation, and it is difficult to make *exact* visible classifications of yellow and non-yellow sugar seeds. There is scarcely any doubt however that two ears were pure for both yellows (seeds all dark yellow), two pure for light yellow, (seeds all light yellow) three heterozygous for one yellow (seeds light yellow and white), one at least and probably two heterozygous for two yellows (seeds dark yellow, light yellow and white) and the rest homozyous for one yellow and heterozygous for one yellow (seeds dark yellow and light yellow).

This family gave by far the best demonstration of two yellows as far as the eye is concerned. The ears homozygous for two yellows would never have been classed as the same variety with those homozygous for one yellow. Nearly all the seeds were absolutely distinct, and yet when they were arranged in a series there would always be a number that were difficult to place.

Table 17 gives the F_2 segregates of a mono-hybrid cross between No. 10 white flour and No. 6 yellow dent. There seems to be no question of a di-hybrid ratio, but the cross is interesting for another reason. The heterozygous seeds are lighter than the homozygous so that the effect of Xenia is shown either way the cross is made; that is, Xenia is shown both where *white flour* is crossed with yellow, and where *yellow flour* is crossed with white. The effect is the same as that shown when light starchy caps are formed when a starchy yellow dent is pollinated by a non-yellow, but as in this case the whole seed is floury, therefore it is all changed to lighter yellow.

It might be mentioned that No. 60 yellow pop crossed with No. 2 white, and No. 9 yellow dent crossed with No. 10 flour also show Xenia. The hybrid seeds become so much whiter that there is no difficulty in distinguishing the greater part of them from homozygous yellows.

TABLE 17.

F_2 SEEDS FROM CROSS OF NO. 10 WHITE FLOUR AND NO. 6 YELLOW DENT.

Yellow Seeds Planted.

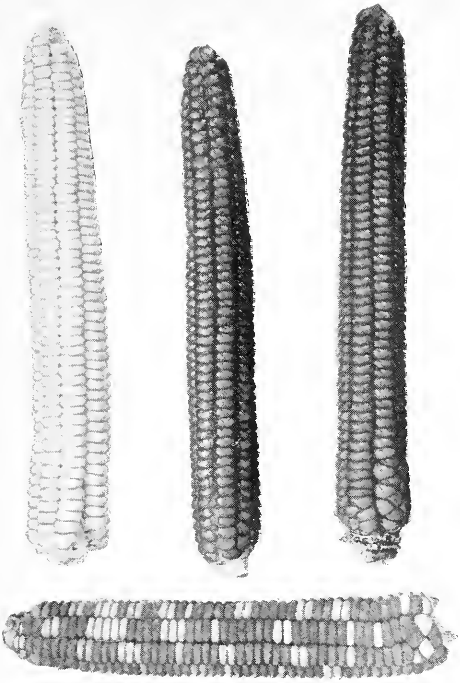
Ear No.	Dark Y	Light Y	Total Y	*y*	Ratio Approx.
(10 x 6)–1	162	357	519	187	3 : 1
(")–2	141	242	383	119	3 : 1
(")–3	175	301	476	156	3 : 1
(")–4	131	243	374	127	3 : 1

Conclusions.

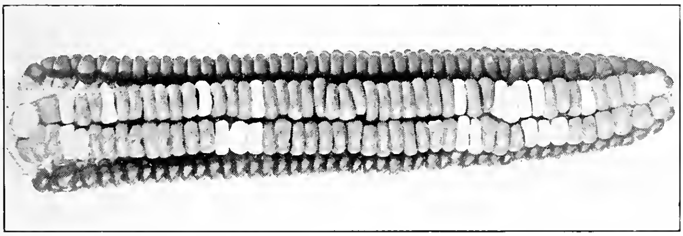
This completes the list of crosses in which new facts have been observed in regard to yellow endosperm. Other crosses might be described where simple mono-hybrid ratios were obtained, but these have already been described by Lock. The di-hybrid ratios have been described in greater detail because they belong to a class of facts having a very important theoretical bearing on the Mendelian hypothesis, which is discussed later in the paper.

It should perhaps be stated that Correns' other general facts have been corroborated. The pure extracted dominants of the F_3 generation have appeared in about the general ratio of 1 homozygote to 2 heterozygotes when dealing with mono-hybrids. There have been insufficient numbers to determine the exact ratio of extracted dominants when dealing with di-hybrids, but in both cases the F_4 generations have in every case bred true. This fact we hold to be more important than the ratio. It may look somewhat queer to say that the extracted F_2 non-yellows have always bred true, when a number of cases have been described in which the seeds that were thought to be non-yellows, proved to be heterozygous yellows. This

PLATE V.



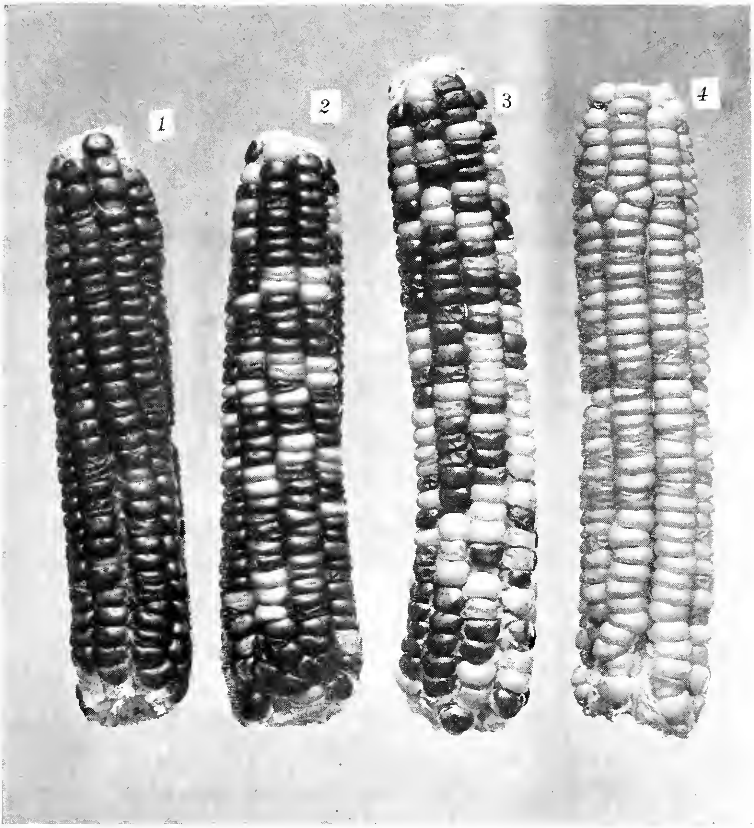
a. At left, No. 24 Rhode Island white cap (white endosperm), at right, No. 15 Longfellow (yellow endosperm). In center, hybrid showing dominance of yellow. Below, F2 seeds showing segregation.



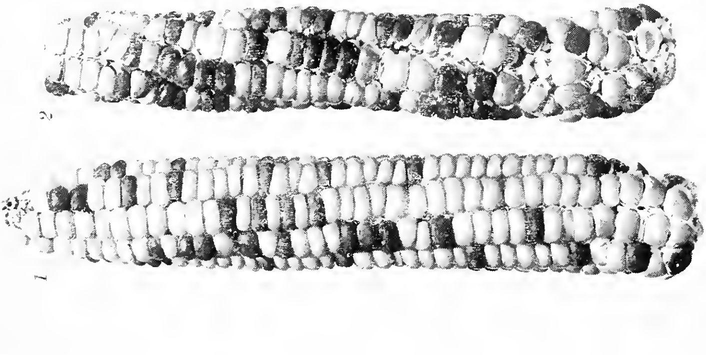
b. An ear showing dominance of red pericarp in F_1. The pericarp has been removed from two rows of seeds, showing mono-hybrid segregation of F2 endosperms beneath it into yellow and non-yellow.

Segregation of Yellow and Non-Yellow Endosperm.

PLATE VI.



a. Cross 24x54. 1. Ear (24x54)-12-5; a pure extracted purple. 2. Ear (24x54)-12-6; purples 208, non-purples 65, a 3:1 ratio. 3. Ear (24x5b)-12-4; purples 147, non-purples 117, a 9:7 ratio. 4. Ear (24x54)-12-3; a pure extracted non-purple.



b. Purple seeds produced by random crossing of non-purple seeds of ear (24x54)-12 shown in Table 18g. 1. Ear (24x54)-12-9x12x8; ratio 1 purple: 3 non-purple. 2. Ear (24x54) 12-11x12x10; ratio 1 purple: 1 non-purple.

Inheritance of Aleurone Color.

is due to the simple fact that the seeds with the gametic formula $Y_1\ y_1$ or $Y_2\ y_2$ vary in color intensity so that it is generally impossible to *classify correctly* from 1 to 5 seeds per ear. These F_2 seeds prove their gametic structure in the F_3 generation; and those that have behaved as pure extracted non-yellows in F_3 have never given anything but pure non-yellows in the F_4 generation.

The occurrence of the two yellow colors casts a further doubt upon the correctness of Lock's work since his main object was to show the truth of Mendel's mathematical conclusions when dealing with large numbers. Our results both here and in the case of the purple aleurone cells show the futility of not making crosses between individuals and of not selfing individual F_1 plants. This is a further excuse for presenting in detail the individual crosses between starchy and non-starchy races with the same object as Lock.

Purple and Non-purple aleurone cells.

The consideration of the inheritance of this character includes also that of a hypostatic red color which appears in crosses between the various purple and non-purple families. The pigments are both fairly easily soluble in water. They are seen first in the aleurone cells of the maturing seeds a few days after fertilization. When the seed is mature the red color becomes an intense dark rose madder, and the purple becomes almost black. Several tests of each pigment were made by macerating the aleurone cells in 50% alcohol and testing the filtrate. With lead subacetate both turned green and a green precipitate separated. The precipitate from the red seeds was somewhat darker and turned greenish brown on evaporation while that from the purple seeds remained a lighter green. Ferrous sulphate added to the red pigment produced but little if any change in color although a dirty precipitate separated on shaking. When added to the blue pigment, however, a dark blue precipitate separated leaving the liquid colorless. This precipitate left a blue residue on evaporation, while the residue from the red pigment was simply a slight discoloration, dark, but with no distinct color except possibly a redness at the edges. Ferric chloride however gave markedly different reactions in the two cases. Added to the red pigment an orange color was produced which became somewhat darker on evaporation. The precipitation was slight. Added to the blue pigment the color was first greenish with blue edges. This turned dark blue and a bluish precipitate separated which later turned green and remained so on evaporation. With ferric alum there was no change except that each pigment became more intense in color. Sodium hydroxide formed brownish green precipitates, darker with the purple. Acids gave red colorations which were lighter with the red pigment. The acid and alkali tests are evidently the usual reactions with vegetable color "indicators" and differ only through the various amounts of pigment present.

It is recognized that tests such as these are arbitrary in nature and cannot form the basis of conclusions as to the chemical composition of the pigments. It seems certain however that they differ somewhat in composition, although they are probably different stages of oxidation of the same color base.

It will be seen in the following pages that purple crossed with different strains of non-purple gave different results. This is clearly due to the various gametic formulæ possessed by the different whites. It may also be that the purples differ somewhat among themselves in unseen characters even though they were pure for purple when selfed. Our analysis of the large amount of data which follows shows that there is simple Mendelian segregation and recombination of several factors and that there is really no confusion of results such as led Correns and Lock to advance various supplementary hypotheses to account for the facts. The use of the color factor C, shows how Lock obtained his purples by crossing white seeds supposedly heterozygous for purple, with white; but it is impossible to analyze his data since individual pollinations were not made. A supplementary hypothesis of Correns should also be mentioned because, if it were true it would necessitate a very different conception of the interpretation of the inheritance of all endosperm characters. Correns supposed that purple × non-purple always gave purple while non-purple × purple sometimes gave non-purple and sometimes gave purple. He accounted for this by the supposition that since the endosperm nucleus is formed by the union of *two maternal* nuclei with *one paternal* nucleus, therefore the maternal endosperm characters would often dominate the paternal characters through the effect of the greater amount of maternal nuclear material. This is *never* the case and the fact is quite important. If Correns' supposition were true and the amount of nuclear matter determined the characters to be formed, no Mendelian segregation of endosperm characters and their recombination by chance matings could be demonstrated. Since all of our data shows it to be untrue, it follows that the *quality* and not the quantity of nuclear material is the important thing. The nucleus evidently regenerates or throws off material to come to its proper adjustment for the performance of its functions, and *always* in accordance with the *quality* of its structure.

In order to facilitate a consideration of the data, it will be presented in families. Each family comprises the progeny resulting from a particular cross. They are taken up in the order of increasing complexity.

Family (24 and 54)

This family includes all of the progeny of the cross of No. 24 white flint with No. 54 Black Mexican sweet, this being the variety with purple aleurone cells. The Black Mexican which furnished the pollen for this cross had proved true to the purple color for three generations, but pollen for the crosses of the different hybrid families came from several different ears. For this reason there is no certainty that the purple aleurone parent had the same gametic structure in each family. The data for the above family are reported in the sub-divisions of Tables 18 to 20. In these tables there is no correlation of the purple and starchy characters, there being a simple 3 : 1 relationship of starchy and non-starchy seeds in both the case where purples and non-purples were obtained in F_2 in the ratio of 3 : 1 and where they are obtained in the ratio of 9 : 7. We may therefore leave this character out of consideration and consider only the purple character.

The F_1 seeds formed in the hybrid ear were all purple. Upon growing these seeds nine selfed ears were obtained with the ratios of purples to non-purples shown in Table 18. The purple color of these segregates was of full depth and covered the entire seed with one or two exceptions. These exceptions were zygotic variations due to heterozygosis and were quite different from the partial or light purples obtained in other families. In the latter case it was due to a transmissible gametic factor which will be explained later. Table 18 shows the ratio of purples to non-purples to be 3 : 1 in the case of seven ears and 9 : 7 approximately in the case of two ears. This immediately suggests the mono-hybrid ratio in the first case and a di-hybrid ratio in the second case. That this is the true state of affairs is shown by the behavior of the seeds of these ears in later generations. The progeny of the purple seeds of ear (24 x 54)-1 (Table 18a) were either pure purples or heterozygous purples segregating in the ratio of 3 : 1. The non-purple seeds of the same ear (Table 18b) produced only non-purples. The same ratio was obtained from purple seeds of ear No. (24 x 54)-11 shown in Table 18c.

The fact that F_3 extracted non-purple seeds continued to breed true is shown by the results of the F_4 generation shown in Table 18d. Extracted purple starchy seeds were also planted from Ear No. (24 x 54)-1-4 and ten selfed ears proved pure. Twenty-six ears were also obtained from the open field crop which were also pure purple, six being pure starchy and twenty heterozygous starchy.

These continued 3 : 1 ratios with purity of the extracted homozygote are what should be expected from the progeny of the mono-hybrid ears of Table 18. If the 9 : 7 ratios given by ears No. 9 and No. 12 of Table 18 are true di-hybrid ratios resulting from the interaction of two factors both of which are necessary for the production of the purple color, one should expect in the F_3 generation but one pure purple out of nine to occur and the remaining ears to be about 50% monohybrids with a 3 : 1 ratio and 50% di-hybrids with a 9 : 7 ratio. The progeny of ear No. (24 x 54)-12 (Tables 18e, 18f) shows how nearly these expectations are confirmed. Out of a total of nineteen selfed ears two were pure purple, ten were mono-hybrids and seven were di-hybrids. It must be concluded therefore that the purple color is due to the action of the factor P upon another color factor C, which is probably similar in nature to that which Bateson found in sweet peas. The gametic structure of No. 24, the non-purple variety, evidently differed in the ovules of the seeds of the original hybrid ear. Part of them lacked both P and C and gave a 9 : 7 ratio when crossed with the purple (C P), and part of them contained either P or C and therefore gave a mono-hybrid ratio when crossed with C P. If one supposes C to be contained by the non-purple in the first case then the result is as follows, Cp x C P = C C P p. The gametes formed differ only in presence or absence of P and a simple mono-hybrid ratio is obtained in the F_2 generation.

In the second case the cross is c p x C P = C c P p, and the F_2 populations have the formulae and ratios 9 C P : 3 C : 3 P : 1 c p, the first nine being purple and the last seven being white. This being the case the various non-purple seeds of F_2 should prove true non-purples when selfed but should sometimes give purples when crossed. The non-purples exist in the following ratios:

1 C C p p
2 C c p p
1 c c P P
2 c c P p
1 c c p p

When crossed at random there are 7 x 6 = 42 possible combinations of which 24 should give all non-purple and 18 some purples. Of these eighteen ears 2 should be pure purples, 8 purples and non-purples in the ratio 1 : 1, and 8 purples and non-purples in the ratio of 1 : 3. In Tables 18g and 18h besides the selfed non-purples seven combinations of different non-purples are shown, besides several reciprocal crosses. Of these one combination and its reciprocal gives a 1 : 1 ratio and one combination and its reciprocal gives a 1 : 3 ratio.

None of the F_2 seeds of the selfed ears of this cross showed any seeds with red aleurone cells. Among the open field ears containing F_2 seeds however, were noticed several seeds with aleurone cells of a peculiar blue color and several of the red color. Five selfed ears were obtained from the blue aleurone seeds (Table 19). Four of these ears gave 9 colored (P and R) seeds to 7 non-colored and one gave a simple mono-hybrid ratio in which no reds were found. The red seeds varied in shade until the darkest seemed to the eye to be purple. They could be separated accurately only by a microscopic examination of sections of the aleurone cells. The purples (the blue seeds proved to be exactly like ordinary purple seeds) occurred in greater numbers than the reds but the exact ratios were not determined in this family, because their parentage was not certain.

The red seeds found in the open field ears also proved to be heterozygous for red as shown by Table 20. They gave simple 3 : 1 ratios except ear No. 1 which proved to be pure red although heterozygous for starchiness. F_3 seeds were obtained from the red seeds of ear No. 8 as is shown in Tables 20a and 20b. It happened that in this small number five pure red ears were obtained and only three ears that were heterozygous and segregated in the ratio of 3 : 1.

Besides the ears shown in Table 20a, two ears from extracted red seeds were crossed with pure extracted non-purples (whites) of the F_3 generation of cross (24 x 54). Ear No. 1 gave 125 purples and 123 non-purples. Ear No. 2 gave 108 purples and 124 non-purples. The red ears, the maternal parents of the crosses, were evidently heterozygous and therefore a 1 : 1 ratio was obtained. The non-purple which furnished the pollen must have carried the P factor which oxidized the seeds which otherwise would have become red to the purple color. This fact proves the epistatic nature of P over R and is a further proof of the di-hybrid nature of the purple color. Another ear crossed with non-purples of the same family as above gave all purple seeds. This ear evidently was homozygous for red and all of its seeds were oxidized to purple. Two other of these red ears were crossed with extracted purples of the same cross from which came the extracted whites used above. The seeds of the resulting ears were all purple. (See Plate 8a.)

Several red non-starchy seeds from ear (24 x R)-16-8 (Table 20b) were also planted. Three selfed ears resulted in two pure for red and one giving 248 reds to 60 non-reds, a 3 : 1 ratio. One ear of this lot was crossed with the same extracted purples used in crossing the starchy red seeds resulting in an ear with all purple seeds. Another ear was crossed with one of the extracted non-purples used in crossing the red starchy seeds and resulted in an ear with 119 purple starchy and 124 non-purple starchy seeds. The results from the non-starchy seeds of this family were therefore the same as those from the starchy seeds.

The non-red seeds from (24 x R)-16-8 both starchy and non-starchy bred true to the non-red character. Four crosses between individual ears of this lot were made and the resulting seeds were all non-red. This is the result which should be expected from an ear giving a mono-hybrid ratio as did ear (24 x R)-8 and shows that the purples resulting from the crosses between the non-purples coming from the 9 : 7 ratios were not accidental.

TABLE 18.

F_2 SEEDS FROM CROSS OF NO. 24 WHITE FLINT X NO. 54 PURPLE ALEURONE NON-STARCHY.

Purple Aleurone Starchy (*PS*) *Seeds Planted.*

Ear No.	PS	Ps	pS	ps	Total P	Total p	Ratio Approx.
(24 x 54)–1	207	67	67	27	274	94	3 : 1
(")–2	170	54	49	19	224	68	3 : 1
(")–6	197	65	59	24	262	83	3 : 1
(")–9	83	44	72	25	127	97	9 : 7
(")–10	166	40	46	19	206	65	3 : 1
(")–12	153	40	115	40	193	155	9 : 7
(")–8	159	41	41	23	200	64	3 : 1
(")–11	166	55	47	22	221	84	3 : 1
*(")–13	205	81	59	25	286	84	3 : 1

---

* All purple seeds were full dark purples except a few splashed purples from this ear.

TABLE 18A.

F_3 SEEDS OF EAR 1 OF SAME CROSS AS TABLE 18.

Purple Aleurone Starchy (*PS*) *Seeds Planted.*

Ear No.	PS	Ps	pS	ps	Total P	Total p	Ratio Approx.
(24 x 54)–1–3	. . .	. .	. .	. .	144	. .	Pure P
(")–1–4	. . .	. .	. .	. .	384	. .	Pure P
(")–1–5	. . .	. .	. .	. .	96	. .	Pure P
(")–1–11	. . .	. .	. .	. .	320	. .	Pure P
(24 x 54)–1–2	161	55	46	13	216	59	3 : 1
(")–1–6	171	56	52	19	227	71	3 : 1
(")–1–8	180	71	55	19	251	74	3 : 1
(")–1–9	79	29	27	7	108	34	3 : 1
(")–1–10	255	. .	91	. .	255	91	3 : 1
(")–1–14	195	. .	80	. .	195	80	3 : 1
Total	. . .	. .	. .	. .	1251	410	. . . .

TABLE 18B.

F_3 SEEDS OF EAR 1 OF SAME CROSS AS TABLE 18.

Non-Purple Aleurone Starchy (ps) Seeds Planted.

Ear No.	P	*p*	Ratio Approx.
(24 x 54)–1–4a	. .	208	Pure white
(“)–1–5a	. .	312	“
(“)–1–6a	. .	362	“
(“)–1–7a	. .	320	“
(“)–1–15a	. .	296	“

TABLE 18C.

F_3 SEEDS OF EAR 11 (TABLE 18A) OF SAME CROSS AS TABLE 18.

Purple Aleurone Non-Starchy (Ps) Seeds Planted.

Ear No.	Ps	ps	Ratio Approx.
(24 x 54)–11–2	312	. .	Pure P
(“)–11–3	368	. .	“
(“)–11–4	280	. .	“
(“)–11–1	240	82	3 : 1
(“)–11–5	197	78	3 : 1
(“)–11–6	205	52	3 : 1
(“)–11–11	40	12	3 : 1
Total Het.	682	224	. . . .

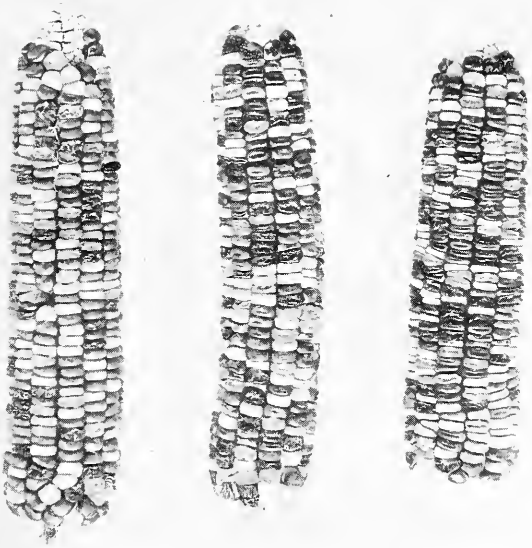
TABLE 18D.

F_4 SEEDS OF EAR (24 x 54)–1–6 (EXTRACTED PS, TABLE 18B) OF SAME CROSS AS TABLE 18.

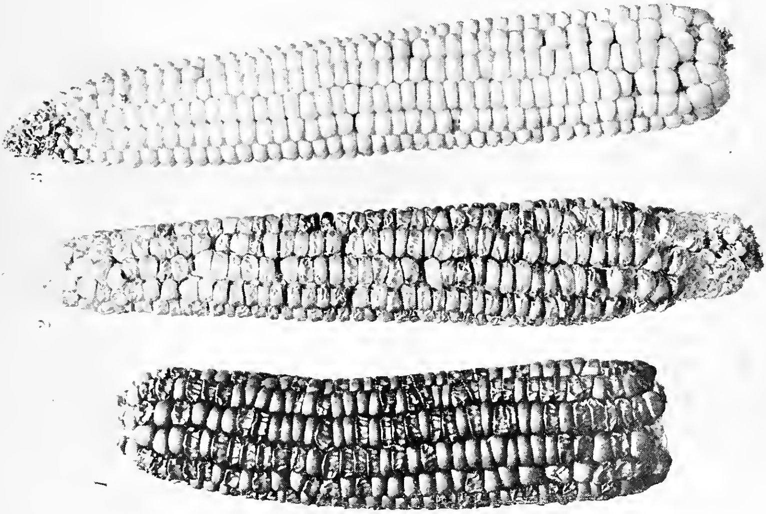
Non-Purple Starchy (ps) Seeds Planted.

Ear No.	ps	PS
(24 x 54)–1–6–1	All	
(“)–1–6–2	“	
(“)–1–6–5	“	
(“)–1–6–8	“	
(“)–1–6–1 x (24 x 54)–8–5 RS	. .	All
(“)–1–6–6 x (“)–8–8 RS	. .	“
(“)–1–6–12 x (“)–8–3 RS	. .	“
(“)–1–6–9 x (“)–8–10 RS	. .	“
(“)–1–6–10 x (“)–8–1 RS	. .	“

Open-field crop all white.



a. Flint and dent segregates from F2 of cross 8x54. Flint character carried by No. 54.



b. F3 types from cross 8x54. 1. Pure extracted purple (PPCC). 2. Pure extracted parti-colored ((PPcc). 3. Pure extracted non-purple (ppCC or ppcc).

INHERITANCE OF ALEURONE COLOR.

TABLE 18E.

F_3 SEEDS OF EAR (24 x 54)–12 OF SAME CROSS AS TABLE 18.

Purple Starchy (PS) Seeds Planted.

Ear No.	PS	p	SS or Ss	Ratio Approx.
(24 x 54)–12–1	280	. .	Ss	Pure
(")–12–2	147	40	Ss	3 : 1
(")–12–3	190	60	Ss	3 : 1
(")–12–4	147	117	Ss	9 : 7
(")–12–5	288	. .	Ss	Pure
(")–12–6	208	65	Ss	3 : 1
(")–12–7	188	115	Ss	9 : 7
(")–12–8	237	72	SS	3 : 1
(")–12–8$_1$	212	72	Ss	3 : 1
(")–12–9	159	120	SS	9 : 7
(")–12–10	145	56	Ss	3 : 1
(")–12–11	95	30	Ss	3 : 1
(")–12–12	179	59	Ss	3 : 1

TABLE 18F.

F_3 SEEDS OF EAR (24 x 54)–12 OF SAME CROSS AS TABLE 18.

Purple Non-Starchy (Ps) Seeds Planted.

Ear No.	P	p	Ratio Approx.
(24 x 54)–12–1a	160	53	3 : 1
(")–12–2a	186	64	3 : 1
(")–12–3a	137	115	9 : 7
(")–12–4a	97	65	9 : 7
(")–12–6a	109	80	9 : 7
(")–12–9a	123	120	9 : 7

TABLE 18G.

F_3 SEEDS OF EAR (24 x 54)–12 OF SAME CROSS AS TABLE 18.

Non-purple Starchy (pS) Seeds Planted.

Ear No.	P	p	Ratio Approx.
(24 x 54)–12–3b	. .	All	. . . .
(")–12–4b	. .	"	. . . .
(")–12–6b	. .	"	. . . .
(")–12–7b	. .	"	. . . .
(")–12–12b	. .	"	. . . .
(")–12–2b x 12–4b	. .	"	. . . .
(")–12–4b x 12–2b	. .	"	. . . .
(")–12–5b x 12–1b	. .	"	. . . .
(")–12–8b x 12–9b	13	62	1 : 3
(")–12–9b x 12–8b	81	226	1 : 3
(")–12–10b x 12–11b	79	86	1 : 1
(")–12–11b x 12–10b	93	99	1 : 1

TABLE 18H.

F_3 SEEDS OF EAR (24 x 54)–12 OF SAME CROSS AS TABLE 18.

Non-Purple Non-Starchy (ps) Seeds Planted.

Ear No.	P	p
(24 x 54)–12–2c	..	All
(")–12–3c	..	"
(")–12–5c	..	"
(")–12–9c	..	"
(")–12–10c	..	"
(")–12–12c	..	"
(")–12–13c	..	"
(")–12–1c x 12–4c	..	"
(")–12–4c x 12–1c	..	"
(")–12–7c x 12–3c	..	"
(")–12–3c x 12–7c	..	"
(")–12–6c x 12–8c	..	"
(")–12–8c x 12–6c	..	"

TABLE 19.

F_2 SEEDS FROM CROSS BETWEEN NO. 24, WHITE FLINT AND NO. XP PURPLE ALEURONE.

Purple Aleurone Starchy (PS) Seeds Planted.

Ear No.	P+R	p	Ratio Approx.	Notes
(24 x P)–16–2	287	192	9 : 7	SS: some seeds red
(")–16–5	141	117	9 : 7	ss: few P's strongly colored
(")–16–6	165	115	9 : 7	ss: few P's strongly colored
(")–16–7	278	89	3 : 1	Ss: 84 P's lighter at cap
(")–16–8	253	193	9 : 7	ss: 69 P's lighter at cap

TABLE 20.

F_2 SEEDS FROM CROSS BETWEEN NO. 24 WHITE FLINT AND NO. XR RED ALEURONE.

Red Aleurone Starchy (RS) Seeds Planted.

Ear No.	RS	Rs	rS	rs	Total R	Total r	Ratio Approx.
(24 x R)–16–1	160	52	..	..	212	..	Pure red
(")–16–4	26	12	13	3	38	16	3 : 1
(")–16–6	140	43	53	22	183	75	3 : 1
(")–16–8	195	73	41	19	268	60	3 : 1

TABLE 20A.

F_3 SEEDS OF EAR (24 x R)–16–8 OF SAME CROSS AS TABLE 20.

Red Aleurone Starchy (*RS*) *Seeds Planted.*

Ear No.	R	r	Ratio Approx.
(24 x R)–16–8–3	360	. .	Pure red
(")–16–8–4	161	65	3 : 1
(")–16–8–5	60	. .	Pure red
(")–16–8–6	172	53	3 : 1
(")–16–8–8	320	. .	Pure red

TABLE 20B.

F_3 SEEDS OF EAR (24 x R)–16–8 OF SAME CROSS AS TABLE 20.

Red Aleurone Non-Starchy (*Rs*) *Seeds Planted.*

Ear No.	R	r	Ratio Approx.
(24 x R)–16–8–1a	160	. .	Pure red
(")–16–8–2a	248	60	3 : 1
(")–16–8–3a	280	. .	Pure red

Family (8 x 54)

The F_1 Xenia seeds of the cross between No. 8 non-purple dent starchy and No. 54 purple non-starchy were all purple in color. Four selfed ears were obtained when these hybrid seeds were planted. The segregation of the F_2 seeds is shown in Table 21. A new phenomenon of peculiar interest appeared in this family. A certain number of seeds were solid dark purple, others were splashed dark purple, others were a very faint purple and have been called particolored, while still others were without the purple color. The splashed dark purples were seeds that had a break in the purple color; that is the purple color was dark but appeared in patches. These splashed purples are found in all of the purple-non-purple crosses except the family * just described. It seems evident then that they are due to the interaction of characters which

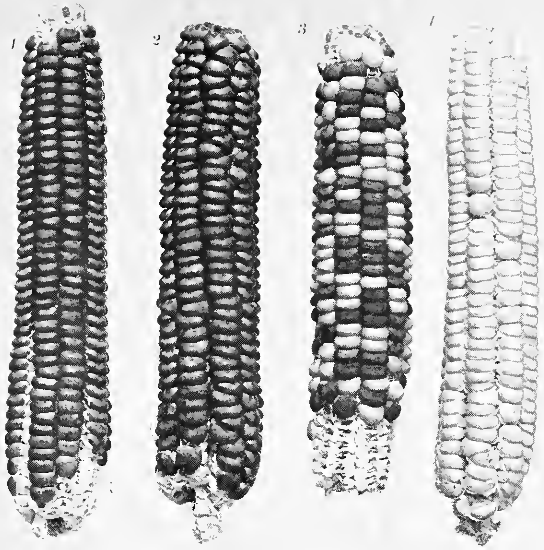
---

* Only one or two splashed purples were ever found in family (24 x 54).

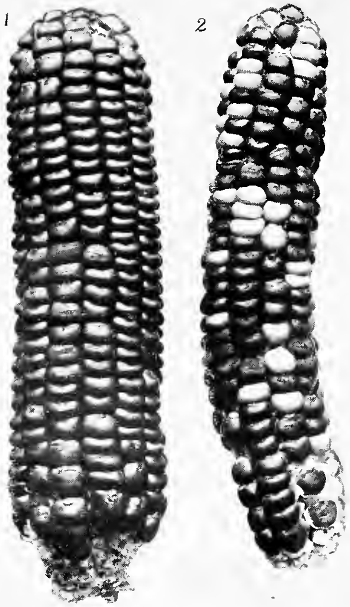
happen to be absent from the (24 x 54) family; but at the same time they are zygotic variations which are not inherited, for their progeny are exactly like the progeny of the dark purple seeds. Further, these patches are not in a regular pattern nor does the selection of seeds of this nature have the slightest tendency to fix the phenomenon as a separate character. There is reason for believing however that no homozygous purples (C C P P) are ever of this nature, and that the splashing is simply due to incomplete dominance, but caused by a factor or factors brought in by the non-purple parent.

The fact that particolored or very light purples which transmitted the character also appeared in this family made it seem probable that a new character had appeared, making the family a tri-hybrid. But this is not the simplest interpretation. We have seen in the other family that the behavior of purple is best interpreted as the interaction of two factors C and P. In this family the hypothesis that either Cp or cP seeds are not pure whites but very light purples is supported by all of the data. At first sight it seems more reasonable that they should have the formula Cp. If in accordance with older interpretations of color inheritance, the purple color is formed by an enzyme, P acting upon a chromogen C it is more reasonable to suppose that in the presence of the chromogen an exceedingly small amount of the enzyme might give rise to the particolored seeds, than it is to believe that the normal amount of enzyme would form the purple color with a trace of chromogen. The reason for this statement rests upon the well known fact that enzymes are organic catalysers and can accelerate reactions involving quantities very disproportionate to their own amount. There is an objection to this interpretation, however, for when particolored seeds are crossed with those having red aleurone cells and which therefore have the gametic formula R C, they invariably give purples. This proves that the gametic formula of the particolored seeds is c P and they are so designated in the tables.

The suggestive work of Miss Wheldale (: 09, : 09a, : 10) in correlating the results of biological chemistry with those of genetics, has made it very probable that a basic chromogen is present in all flowers which are able to form a sap color, and that the complexities of color inheritance may be referred to



a. 1. Pure purple aleurone resulting from crossing pure extracted red aleurone with pure purple. 2. Same result from crossing pure extracted red aleurone with colorless aleurone. 3. Seeds half purple resulting from crossing heterozygous red aleurone with colorless aleurone. 4. Result from selfing the male parent of 3.



b. 1. (24x54)8-3 pure extracted red aleurone. 2. (24x54)-8-6 heterozygous red aleurone. Cut does not show color value when compared with Fig *a*.

INHERITANCE OF ALEURONE COLOR.

the dual nature of the oxydases necessary for the formation of the color compounds. It is quite likely that the color in the aleurone cells of maize is similar in nature to flower color; and, as we fully agree with Miss Whedale's conclusions, none of our factors C, R and P are to be regarded as chromogens. The argument above is in agreement with this viewpoint. If one wishes to denote a chromogen, the addition of an X to represent it, common to both families, makes no difference in the interpretation of the results.

If we are dealing with a di-hybrid ratio, one pure purple ear out of every nine should be expected in the F_2 generation. Tables 21a and 21b show that one such ear was obtained out of seventeen ears. If the total purple seeds and the sum of the particolored and white seeds is considered in Tables 21, 21a and 21b a close approximation to a 9 : 7 ratio is obtained. If the particolored seeds could in every instance be distinguished from whites the ratio of purples to particoloreds to whites should be 9 : 3 : 4. It will be noticed however that in the ears from which this ratio should be expected there is generally an excess of whites. This is explained by the fact that particoloreds especially when non-starchy are not always distinguishable from whites. The last two ears shown in Table 21d are in fact ears grown from seeds which were originally classed as whites. If this hypothesis in regard to the particolored is true, one should expect the purple F_2 seeds to give in the F_3 generation, one ear pure purple, two ears showing segregates of purple and particolored in the ratio of 3 : 1, two ears showing segregates of purple and non-purple in the ratio of 3 : 1, and four ears showing purples, particolored and non-purples in the ratio 9 : 3 : 4. Among the ears received (Tables 21a, 21b) there were one of the first class, six of the second class, three of the third class and seven of the fourth class.

Tables 21c and 21d show the results from growing the particolored seeds of the same ear, No. (8 x 54)-1. One ear should be pure particolored to two showing segregates of particolored and non-purple in the ratio of 3 : 1. Out of the fifteen ears obtained three were evidently of the first class and twelve of the second class.

In all of these tables the progeny of hybrid starchy seeds segregated normally.

Seeds classified as non-purples were also planted from this same ear No. (8 x 54)-1. The thirteen selfed ears resulting as progeny of starchy seeds all proved to be non-purple. Two particolored ears, however, appeared in the eight selfed ears resulting from planting non-purple, non-starchy seeds. This showed that there was more difficulty in classifying the non-starchy non-purples than in classifying starchy non-purples. Non-purple seeds planted from ear No. (8 x 54)-5 also gave a few particolored progeny.

Four thousand seeds from tested whites of the F_3 seeds were planted in an isolated plot the next season and were allowed to inter-cross naturally. If we were dealing with di-hybrid non-purples in this case, such inter-crossing should give some purples, such as were obtained in the (24 x 54) family. The resulting crop of this large number of plants however were all true non-purples, proving that we were dealing with non-purples with formulæ either CC, Cc or cc. Further proof of the constitution of the particolored is shown in the following facts. No particoloreds ever gave full purples. Furthermore, pure extracted particoloreds (c c P P) from ear No. (8 x 54)-1-13b of Table 21c were grown for another generation and their gametic structure tested by various crosses. Several of these ears were selfed and all proved to be pure particoloreds (ccPP). Three different ears were crossed with pure extracted purples from progeny of ear No. (24 x 54)-1-4. As would be expected all of the seeds were purple. Two of the ears however had a decided reddish purple color while one was dark purple without the reddish tint. Four ears were crossed with extracted red seeds (RRCC)· All produced purple seeds. Nine ears were crossed with plants of the progeny of the non-purples of ear No. (24 x 54)-12. It will be remembered that this ear gave a ratio of nine purples to seven non-purples. The seven non-purples would have the following formulæ: 1 PPcc, 2 Ppcc, 1 ppCC, 2 ppCc, 1ppcc. Crossing the particoloreds at random with pollen of individual plants of this lot should give on the average one ear with all purple seeds when pollinated by ppCC, two ears with 50% purple and 50% particolored when pollinated by ppCc, four ears pure particolored when pollinated by PPcc, Ppcc or ppcc. Nine ears were obtained of which one had all purple seeds, three had 50% purple and 50% particolored with a total of 308 purple seeds to 294 particolored seeds and five were all particolored. It should be mentioned, however, that the particolored seeds obtained by crosses with the whites of this (24 x 54) family in which the (ccPP) seeds were not particolored, gave seeds which averaged much lighter in appearance than the pure particolored. In other words particoloreds crossed with whites of other families show imperfect dominance of particolored. Some gene common to both parents of the (8 x 54) family, therefore, accounts for the production of the color.

These two families differed in no other endosperm character except presence and absence of starchiness. No correlation of any kind was observed between these two allelomorphic pairs.

TABLE 21*.

F_2 SEEDS FROM CROSS BETWEEN NO. 8 NON-PURPLE DENT STARCHY AND NO. 54 PURPLE NON-STARCHY.

Purple Seeds Planted.

Ear No.	CP	cP	Cp or cp	Total Purple	Total Non-Purple
(8 x 54)–1	297	75	146	297	221
(")–2	230	75	172	230	247
(")–3	...	..	...	302	239
(")–5	...	..	...	270	229
Total	...	..	...	1099	936

---

* There were 1,514 starchy and 521 non-starchy seeds.

TABLE 21A*.

F3 SEEDS OF EAR NO. (8 x 54)–1 OF TABLE 21.

Purple Starchy (PCS) Seeds Planted.

Ear No.	CP	cP	Cp or cp	Total Purple	Total Non-Pur.	Starchiness
(8 x 54)–1–1	233	70	..	233	70	SS
(")–1–2	16	6	7	16	13	Ss
(")–1–3	238	69	..	238	69	Ss
(")–1–4	321	86	..	321	86	Ss
(")–1–6	...	..	..	312	..	Ss
(")–1–8	239	106	93	239	199	Ss
(")–1–9	223	65	95	223	160	SS
(")–1–12	285	..	66	285	66	SS
(")–1–14	160	33	111	160	144	Ss
(")–1–20	126	54	..	126	54	SS

---

* There were 1,362 starchy and 435 non-starchy seeds in the Ss ears.

TABLE 21B.

F3 SEEDS OF EAR NO. (8 x 54)–1 OF TABLE 21.

Purple Non-Starchy (PCs) Seeds Planted.

Ear No.	CP	cP	Cp or cp	Total Purple	Total Non-Purple
(8 x 54)–1–1a	229	..	79	229	79
(")–1–3a	236	44	116	236	160
(")–1–4a	295	..	93	295	93
(")–1–6a	260	86	..	260	86
(")–1–7a	86	20	38	86	58
(")–1–10a	239	89	..	239	89
(")–1–11a	223	55	88	223	143

TABLE 21C*.

F$_3$ SEEDS OF EAR NO. (8 x 54)–1 OF TABLE 21.

Particolored Starchy (cPS) Seeds Planted.

Ear No.	cP	Cp or cp	Starchiness
(8 x 54)–1–2b	322	99	SS
(")–1–5b	402	..	SS
(")–1–6b	115	70	Ss
(")–1–7b	150	64	SS
(")–1–10b	386	..	SS
(")–1–11b	254	92	Ss
(")–1–13b	427	..	Ss
(")–1–14b	262	112	SS
(")–1–15b	256	133	Ss

---

* There were 1,026 starchy and 321 non-starchy seeds in the Ss ears.

TABLE 21D.

F$_3$ SEEDS OF EAR NO. (8 x 54)–1 OF TABLE 21.

Particolored Non-Starchy (cPs) Seeds Planted.

Ear No.	cP	Cp or cp
(8 x 54)–1–2c	149	110
(")–1–3c	364	...
(")–1–4c	168	89
(")–1–5c	123	59
(")–1–1w	230	115
(")–1–12w	131	99

Family (15 x 54).

This family brings in a third allelomorphic pair namely presence and absence of yellow in the endosperm. No. 15 is Longfellow pure for the presence of starchiness and for a single yellow factor. This cross was made to find out whether there were further differences in the behavior of the purple factor when crossed with other non-purples, and it was thought that the yellow endosperm might prove a disturbing factor. This is not the case for the F_1 seeds were all purple with the exception that a few splashed purples, which behaved like the normal hybrid purples, also occurred in this family. Eight ears were obtained by growing the F_1 seeds, and starchiness and yellowness were found to segregate in a normal manner. There was a total of 1765 Y to 604 y and 1746 S to 623 s seeds.

There is only one fact of particular interest in this family. Table 22 shows the eight selfed F_1 ears grown from the purple-starchy hybrid seeds, containing the F_2 seeds. It will be noticed that in the table, six of the ears appear to show monohybrid segregation and two of them di-hybrid segregation. This is not really the case. All of the ears giving the 3 : 1 ratio were also di-hybrids. The figures in the column headed "Purple" contained purples, splashed purples and particoloreds. Some unknown cause produces many seeds in this cross that are heavily splashed with purple. These always behaved as heterozygous purples, although the heterozygous purples were not always splashed, but were generally full colored purples. The particoloreds are seeds containing the P factor but lacking the C factor as in cross (8 x 54). The difficulty here was to distinguish by sight *all* of the splashed purples (P C) from the particoloreds (Pc). They were all included in the table therefore as "Purples."

The ears (15 x 54)-2 and (15 x 54)-3 did not show particolored seeds, but that the same gametes were concerned is shown by the following data. Theoretically, if ear (15 x 54)-2 is a di-hybrid the purple seeds when selfed should give 1 ear with all purple seeds, 4 ears with 3 purple seeds to 1 non-purple seed and 4 ears with 9 purple seeds to 7 non-purple seeds. Twelve selfed ears were obtained in the next generation. One had all purple seeds. Seven had purple and non-purple seeds at the ratio of 9 : 7, there being a total of 1035 purple and 763 non-purple seeds. Four had purple and non-purple seeds at the ratio of 3 : 1, there being a total of 480 purple to 162 non-purple seeds. It should be remarked that in two of these ears a few very light particolored seeds were found, showing that the seemingly aberrant ear (15 x 54)-2 had a slight tendency to throw particoloreds like the other ears of the family. There is also some evidence that microscopical examination of the embryo stem would show particoloreds in the ordinary ratio.

The non-purples from this ear were also grown. Eighteen selfed ears were obtained. All of them were true to non-purple. Two of them had a few particolored seeds (6 in one case and 14 in another). These seeds might possibly have been produced by the contamination of a few grains of foreign pollen, but they might very well be white seeds of the formula Pc which were showing the racial tendency to a slight production of pigment (i. e. particoloreds).

Non-purples from the other aberrant ear No. (15 x 54)-3 were also grown and when selfed gave only non-purples. Three intercrosses and their reciprocals were made between different plants from this lot. It happened that no purple seeds were obtained as should be expected in a portion of the cases, as explained before. That the non-purples did differ in composition among themselves was shown however by crossing a pure particolored (PPcc) of the (8 x 54) family with pollen from one of our non-purples, ear No. (15 x 54)-3-10. The ear resulting from the cross had 179 purple seeds and 168 particolored seeds. This 1 : 1 ratio could only have been obtained from a non-purple heterozygous for C (Cc). As a non-purple with the formula Cc could only have been obtained from a di-hybrid cross, it is proved that all of the ears of this family were di-hybrids. The complete gametic structure of the hybrid seeds, speaking of endosperm characters only, is YySsCcPp.

TABLE 22.

F_2 SEEDS FROM CROSS BETWEEN NO. 15 NON-PURPLE YELLOW STARCHY AND NO. 54 PURPLE NON-STARCHY.

Purple Seeds Planted.

Ear No.	Purple*	Non-Purple	Ratio Approx.
(15 x 54)-1	138	45	9+3 : 3+1
(")-2	203	135	9 : 7
(")-3	109	83	9 : 7
(")-4	250	84	9+3 : 3+1
(")-6	201	61	9+3 : 3+1
(")-8	307	91	9+3 : 3+1
(")-11	254	93	9+3 : 3+1
(")-15	239	76	9+3 : 3+1

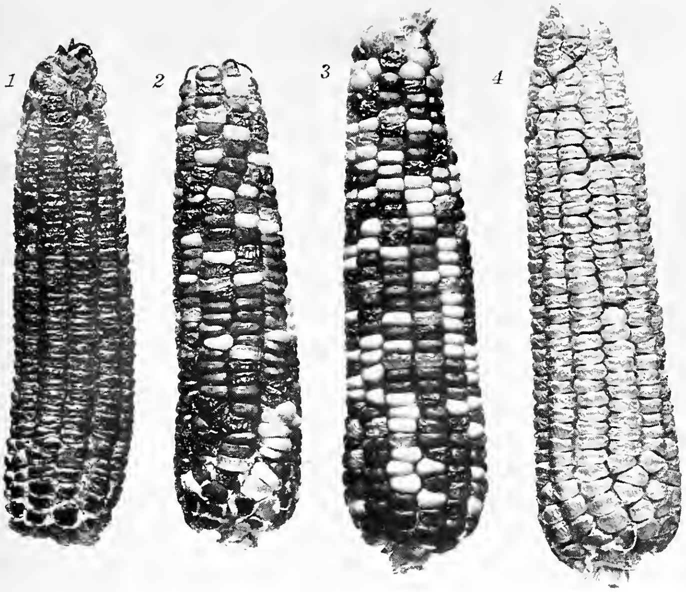
---

* Every ear except ears 2 and 3 contained splashed purples which act as heterozygous purples in inheritance and particoloreds which act as if they had the gametic formula (cP), but the intergradations were so gradual that it was impossible to make an accurate classification. The matter is not worth mentioning here except for the reason that persons who had not had experience with the behavior of purple and non-purple crosses in other families would be utterly at loss for a classification and it would be necessary for them to grow each individual seed for another generation to determine its gametic formula.

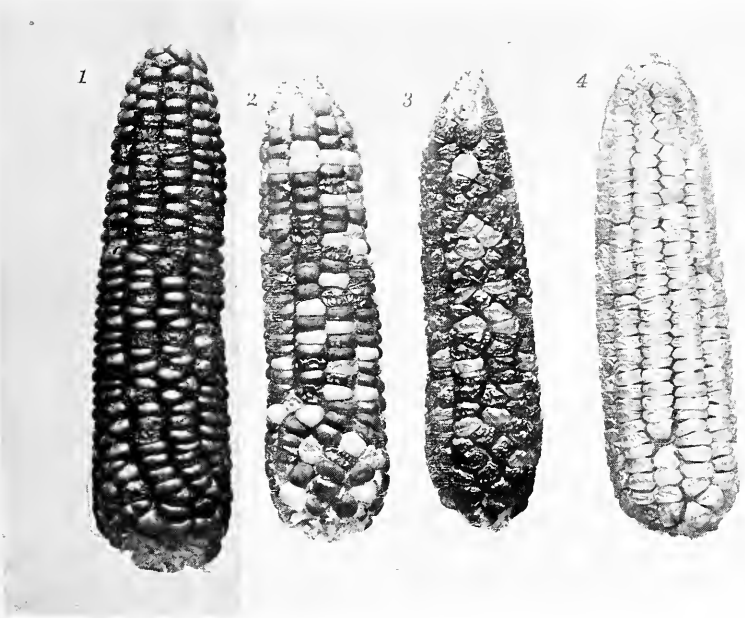
Family (18 x 58)

No. 18, the female parent of this cross is a small non-purple sugar maize which usually has twelve rows. The purple parent is a small eight-rowed flint. The F_1 seeds were purple. Only one selfed ear was obtained from the F_1 plants through an unfortunate loss of pollen. The segregation of F_2 seeds is shown in Table 23. The hybrid seeds have the gametic formula Pp RrCc. The seeds with the formula PR and probably also with the formula P give particoloreds or very light purples as they did in family 8 x 54. They were very light however and the 138 seeds classed as whites or non-purples contained some particoloreds as is shown in the F_3 generation. Theoretically in the F_2 generation there should be 36 purples (27 PRC+9 PC), 9 reds (RC), 12 particoloreds (9 PR+3 P) and 7 whites (3 C+3

PLATE IX.



a. F3 color segregates from cross (18x58). 1. Pure extracted purple. 2, 3. Ears from heterozygous plants. 4. Pure extracted non-purple.



b. F3 color segregates from cross (18x58). 1. Pure extracted red. 2, 3. Ears from heterozygous plants. 4. Pure extracted non-red. Proper color values are not shown.

Inheritance of Aleurone Color.

R+1 prc). There is an excess of whites because the particoloreds could not be classified easily, so it might be said that there should be 36 purples: 9 reds: 19 particoloreds and whites. In the one ear obtained there is still an excess of the last class, but the behavior of the seeds in the F_3 generation proves the gametic constitution of the parents. Tables 23a and 23b give the results from planting purple F_2 seeds. The last four ears shown in Table 23a were planted from splashed purples but they gave the same result as the full purples. We may conclude therefore that splashed purples behave the same as self-colored purples in inheritance. Theoretically the entire lot of purples should have the following gametic constitutions and proportions:

Class 1. 1 P P R R C C = Pure purple.
“ 2. 2 P p R R C C = 3 purple: 1 red.
“ 3. 2 P P R r C C = Pure purple.
“ 4. 2 P P R R C c = 3 purple: 1 white.
“ 5. 4 P p R r C C = 12 purple: 3 red: 1 white.
“ 6. 4 P p R R C c = 9 purple: 3 red: 4 white. 3 being particolored.
“ 7. 4 P P R r C c = 12 purples: 4 white. 3 being particolored.
“ 8. 8 P p R r C c = 36 purples: 9 reds: 19 whites. 12 being particolored.
“ 9. 1 P P C C = Pure purple.
“ 10. 2 P p C C }
“ 11. 2 P P C c } = 3 purples: 1 white.
“ 12. 4 P p C c = 9 purples: 7 whites and particoloreds.

These ears when selfed should give the proportions shown at the right of the above column. An examination of Tables 23a and 23b show that out of the 23 selfed ears obtained the expected ratios were followed rather well. There were two pure purple ears, Classes 1, 3 and 9; 2 ears of Class 2; 3 ears of Class 12; 4 ears of Classes 4, 7, 10 and 11 which collectively give 3 purples; 1 white; 3 ears of Class 8; 9 ears of Classes 5 and 6. The particolored seeds are very light in color and although they are classified as nearly as possible in the tables this classification should be considered only an approximation and not a reality.

Particoloreds and whites are considered together in determining the gametic constitution of the ears. The particolored seeds proved to be true particoloreds of the same nature as those of family (8 x 54). The selfed ears resulting from such seeds of ear No. (18 x 58)-1 of Table 23, gave no purples. Pure particoloreds ears and heterozygous particolored ears were obtained but no exact visual classification of the latter could be made and it was not considered worth while to determine their precise constitution by breeding.

The red segregates occurring in ear No. (18 x 58)-1 were also tested in the F_3 generation. Fifteen selfed ears were obtained and are shown in Table 23c. Among them were five pure red ears, six which threw reds and whites in the ratio of 9 : 7 and four which threw reds and whites in the ratio 3 : 1. The number of pure red ears obtained was slightly greater than should generally be expected but such a deviation should occur about once out of five times when dealing with lots of only fifteen ears. The selfed white segregates of ear No. (18 x 58)-1 of Table 23 yielded about one particolored ear either homozygous or heterozygous out of every four. This shows the error in trying to classify particolored and white seeds. There is no doubt however that when pure white segregates are planted they always breed true.

TABLE 23.

F_2 SEEDS OF CROSS BETWEEN NO. 18 NON-PURPLE NON-STARCHY AND NO. 58 PURPLE STARCHY.

Ear No.	Purple PCR+PC	Red RC	Particolored PR+P	Non-Purple + some P
(18 x 58)–1	191	56	42	138

TABLE 23A.

F_3 SEEDS OF EAR (18 x 58)–1 OF TABLE 23.

Purple Starchy Seeds Planted.

Ear No.	Purple	Red	* Parti-colored	Non-Purple
(18 x 58)–1–1	167	49	. .	84
(“)–1–2	18	4	. .	. .
(“)–1–3	41	13	. .	. .
(“)–1–6	211	72	. .	92
(“)–1–8	221	. .	66	96
(“)–1–8a	138	65	. .	83
(“)–1–11	80	. .	. .	. .
(“)–1–12	66	17	12	17
(“)–1–1s	240	. .	. .	78
(“)–1–2s	141	48	72	65
(“)–1–3s	121	38	. .	113
(“)–1–4s	93	21	15	60

---

s Planted splashed purples.

* Particolored classification is only approximate.

TABLE 23B.

F_3 SEEDS OF EAR (18 x 58)–1 OF TABLE 23.

Purple Non-Starchy Seeds Planted.

Ear No.	Purple	Red	* Parti-colored	Non-Purple
(18 x 58)–1–2	49	25	. .	26
(“)–1–3	68	20	5	66
(“)–1–4	183	61	. .	73
(“)–1–5	240	. .	61	. .
(“)–1–6	22	7	. .	8
(“)–1–7	207	. .	. .	147
(“)–1–8	184	. .	24	140
(“)–1–9	360	. .	. .	. .
(“)–1–10	186	. .	68	. .
(“)–1–11	99	22	41	. .
(“)–1–12	84	. .	. .	34

---

* Particolored classification is only approximate.

TABLE 23C.

F_3 SEEDS OF EAR (18 x 58)–1 OF TABLE 23.

Red Starchy Seeds Planted.

Ear No.	Purple	Red	Non-Purple	Ratio Approx.
(18 x 58)–1–1	...	222	162	9 : 7
(")–1–2	...	350	...	Pure
(")–1–3	...	222	80	3 : 1
(")–1–5	...	212	171	9 : 7
(")–1–6	...	195	115	9 : 7
(")–1–7	...	148	74	3 : 1
(")–1–12	...	187	102	9 : 7
(")–1–2s	...	300	...	Pure
(")–1–3s	...	350	...	Pure
(")–1–4s	...	276	...	Pure
(")–1–6s	...	209	63	3 : 1
(")–1–7s	...	44	35	9 : 7
(")–1–9s	...	237	141	9 : 7
(")–1–10s	...	361	...	Pure
(")–1–11s	...	206	61	3 : 1

---

s Red sugar (s) seeds planted.

Family (7 x 54)

This cross introduces a combination of yellow endosperm and a dent character, the Leaming parent having long dented yellow seeds usually with formulæ $Y_1Y_1Y_2Y_2$. The current effect of the cross gave purple seeds some of which were splashed as in the previous case where yellow flint was the non-purple parent. There was nothing of special interest in the F_2 generation as the ears segregated purple and non-purple seeds in di-hybrid ratios without the appearance of particolored (cP) seeds. The characters in which these parent varieties differed segregated absolutely independently of each other.

Family (17 x 54)

The yellow flint which is the non-purple parent in this family is similar to No. 15. The ear is shorter, however, and has present a red pericarp color described under pericarp color as R_4. The F_1 seeds were purple. They were sometimes splashed purples but more rarely than in the other crosses. The F_2 seeds gave a simple mono-hybrid ratio but they were not followed into further generations. The plant of No. 17 used as the parent was homozygous therefore for either C. or P.

No. 54. Black Mexican sugar and No. 60 Tom Thumb pop above. Below F_1 ears with F2 seeds. At left ear from the family without factor inhibiting the formation of color in aleurone cells. Other ears contain this inhibiting factor (heterozygous in mother plants).

INHERITANCE OF ALEURONE COLOR.

Family (19 x 54)

No. 19 the female parent of this cross is a large sugar corn comparable in size with the large dent varieties. The F_1 seeds were deep purple and the F_2 seeds segregated in ratios exceedingly close to the theoretic number for mono-hybrids.

Family (60 x 54)

No. 60 is a dwarf pop maize with a yellow endosperm, known as Tom Thumb. The individuals used as parents in the various crosses were pure Tom Thumbs but it is not certain that they were the product of a single selfed ear. They were grown from an ear which was self-pollinated, but because the silks appear in this variety while the young ear is entirely hidden in the axil of the leaf, it is less certain that foreign pollen was excluded from the bagged ears than it is in the case of our other crosses. The bags were slipped down into the leaf axil as firmly as possible but there was still some chance for cross pollination. This chance existed only among plants of the same variety, however, for no other pollen was mature at the same time. As several of these crosses were made upon different plants of variety No. 60 it is not strange therefore that one or two of the crosses acted as if parents with different gametic formulæ had been used. It does not follow that this was the case, for the Tom Thumb or the Black Mexican or both might have been heterozygous in some non-visible character.

The result of the immediate cross was different from our other crosses in which the purple aleurone cells were concerned; some of the seeds were dark purple, some were varying shades of light purple and some were white (i. e. non-purple). The behavior of the purple and non-purple hybrid seeds in the next generation showed conclusively that we were dealing neither with a reversal of dominance nor with a character in which the female gametes segregated normally and the male gametes abnormally as suggested by Correns, but with an entirely new dominant factor in which the Tom Thumb variety was probably heterozygous. This factor we take to be an actual inhibiting factor similar in action to the dominant white found in poultry. It is also analogous to the latter in that it does not always completely inhibit the development of color, in which case light purples similar in appearance to the particoloreds of earlier crosses develop. They are not like the particoloreds of family (8 x 54), however, for in the cross under consideration seeds with the gametic formula cP do not develop color. The light purples behave as if the inhibiting factor could vary zygotically so that in some cases light purples are developed while in others the color is completely inhibited, and also as if various amounts of color are developed in the presence of the inhibiting factor due to different combinations of other gametes. For example, it seems probable that more color may be developed in the presence of the inhibiting factor when the zygote is homozygous for the purple factor than when it is heterozygous. Further it seems less likely that any purple color develops when the inhibiting factor is homozygous than when it is heterozygous. This makes the segregating seeds of F_1 or F_2 ears very difficult to classify visually. The only accurate determination of the gametic structure of a seed is through its own further breeding.

Fifteen ears of Tom Thumb were crossed with the purple sugar corn, but only five crosses were selected from which to grow the F_2 generation. One of these, No. 60-5 x 54, had dark purple and non-purple seeds, while the other four crosses had only non-purple or very light purple seeds. It was a little unfortunate perhaps that this selection was made. The white seeds in cross 60-5 x 54 proved to be selfed Tom Thumbs, and the behavior of the purple hybrids showed that no inhibiting factor had been present in ear 60-5. The behavior of the crosses made on ears 60-2, 60-3, 60-8 and 60-11 showed that they had been homozygous in the inhibiting factor. No doubt a number of the other crosses would have shown that the maternal plants were heterozygous in the inhibiting factor.

For these reasons the data from cross 60-5 x 54, which may be called the purple family (without the inhibiting factor), have been listed in Table 24, while the other four crosses containing the inhibiting factor are shown in Table 25.

The resulting F_2 seeds obtained by selfing the purple F_1 seeds of cross 60-5 x 54 shown in Table 24 were purples, reds and non-purples. No light purples (particoloreds) appeared in this family. Splashed purples occurred as in other families, but as in other families all splashed purples were heterozygotes and not all heterozygotes were splashed purples, showing the phenomenon to be due — as before — to incomplete dominance *caused by other factors*. The only peculiar thing about this cross was the appearance and inheritance of the red color. The extracted reds bred true apparently and were hypostatic to purple as in other families, but they were purplish red (dark magenta) in appearance and not clear reds such as appear in other crosses. It is conceivable that this red is not the same red that appeared in the other crosses. It may be caused by something similar to what Wheldale (: 10) has suggested may occur in stocks; viz. that the blue oxygenase may act in conjunction with the red peroxydase or vice versa. The only difficulty in alining the results obtained with the ordinary behavior of the known factors, is the fact that almost none of the ears of the F_3 generation show the same ratios as the F_2 generation.

The ratio obtained in this generation, 1843 purples: 188 reds: 545 non-purples immediately suggests 12 : 1 : 3, which could be obtained from F_1 seeds with a formula Pp Xx CC RR where X is an inhibiting factor from the Tom Thumb which affects R but not P. Our failure to obtain ears in F_3 with segregates of 9 purple; 3 red; 1 non-purple caused this hypothesis to be discarded. The same ratio could be obtained by supposing that there is a partial gametic coupling between P and R similar to that obtained by Bateson and Punnet (: 08) between purple color and long pollen in the sweet pea. These authors suppose gametes to be produced after the general formula 7 AB: 1 Ab: 1 aB: 7 ab, from which result zygotes $3n^2$-(2n-1) AB: 2n-1 Ab: 2n-1 aB: n^2-(2n-1)ab. Such an interpretation, while it may represent Bateson's and Punnett's facts, throws no light on the mechanics of heredity for there is no reasonable way known at present for such a segregation to come about. In our own case * no such excess of purples was obtained in the F_3 generation. It seems better therefore to consider the results of the F_2 generation in the light of the breeding records of the F_3 generation. If this is done, the following interpretation fits the facts best. Tom Thumb, the female parent has the gametic formula pcR, and Black Mexican the male parent has

---

* Bateson and Punnett have never reported their F_3 generation of sweet peas, although they state that it gave *conflicting results*.

the formula PCR. The F_1 generation is therefore PpCcRR. If this is the true formula there is the following theoretical expectation in the F_2 and F_3 generations:

	F_2	gives in F_3
9 Purple	1 PPCCRR	Pure Purple.
	2 PpCCRR	3 Purple : 1 Red.
	2 PPCcRR	3 Purple : 1 Non-purple.
	4 PpCCRR	9 Purple : 3 Red : 4 Non-purple.
3 Red	1 CCRR	Pure Red.
	2 CcRR	3 Red : 1 Non-purple.
4 Non-purple	1 PPRR	Pure Non-purple.
	2 PpRR	Pure Non-purple.
	1 ppccRR	Pure Non-purple.

An examination of the F_3 segregates given in Tables 24a-e show how nearly the experimental results accord with the theory. First notice that out of 55 ears obtained by selfing purples of the F_2 generation, 20 segregated purples and non-purples without reds. This is more than our own theory calls for (theoretically 12 out of 55), so that here is clear evidence that we do not have to deal with partial gametic coupling of the kind described by Bateson and Punnett. But, since the deficiency of reds in the F_2 generation is too great to be due to chance and since there is a certain excess of purples in the F_3 generation, we must say frankly that we are dealing with something that we cannot yet explain.

The entire data from the 55 purple F_2 seeds from which selfed ears were obtained may be classified as follows: 8 ears pure purple; 20 ears segregating purples and non-purples in the ratio of 3 : 1; 9 ears segregating purples and reds in the ratio of 3 : 1; 1 ear each segregating purples and reds in ratios of 5 : 1, 6 : 1 and 12 : 1; 11 ears segregating purples, reds and non-purples in the ratio of 9 : 3 : 4; 3 ears segregating purples, reds and non-purples in the ratio of 48 : 3 : 13 or thereabouts.

From the red F_2 seeds 13 selfed ears were obtained. Out of these, 3 were pure red and 10 segregated reds and non-reds in about the ratio of 3 : 1. It should be remarked, however, that in three cases the heterozygous reds gave a greater excess of reds than usually should be expected with chance mating.

From the non-purple F_2 seeds 16 selfed ears were obtained: 15 were pure non-purple while one gave 12 purples to 49 non-purples. As this is a poor ear, the 12 seeds may be due to foreign pollen, or a chance pollen grain possessing the inhibiting factor may have produced the F_2 white seed from which the ear resulted.

With the plants resulting from non-purple F_2 seeds random intercrosses were also made. Of these 13 gave ears with all non-purple seeds and one gave an ear with 49 purples and reds and 140 non-purples.

These results generally follow our theory pretty closely, but there are abnormalities difficult to explain. We seem to be dealing with only two heterozygous factors — since 8 pure purples are obtained from 55 ears — yet tri-hybrids and tetrahybrids *are possible* which give such results. By our theory no whites should give purples when crossed at random. One such ear occurred. Was it an error? It is difficult to say. But if we were dealing with heterozygous red (Rr) we should expect more than one ear out of 14 to give purples on random crossing. Furthermore, it can be seen by inspection that there are many reasons why we cannot be dealing with simply a heterozygous red factor. It is not denied however that several other unknown factors *with* a heterozygous red factor might interpret the facts. It does not seem possible to explain the results by any reasonable system of gametic coupling or by selective mating. P and C certainly are present in an heterozygous condition. R is probably homozygous although it was not found in the Black Mexican in other crosses. But this is not peculiar since the Black Mexican used in the cross can only be said to be pure for purple. On the other hand, the red does not appear to the eye to be exactly the same red which appeared in the other crosses. It is more purplish in color, as if it were a modified purple. Nevertheless it always bred true after extraction.

Let us now turn to what may be called the white side of this family. As was stated before ears 60-2, 60-3, 60-8 and 60-11 gave no dark purples when crossed with No. 54. (Some seeds were afterwards found to be very slightly purple.) One may conclude therefore that they (the maternal plants) were either homozygous for a factor that inhibits the development of the purple color; or, that there is a reversal of dominance, which is improbable. There were other ears that gave both purple and non-purple seeds in crosses. These were either heterozygous for an inhibiting factor or exhibited dominance of both purple and non-purple on the same ear which is still more improbable. None of these ears were followed into the F_2 generation, but progeny of all four of the ears of the first type were grown.

The results of the F_2 generation from these ears are shown in Table 25. There is no reason why some of these families might not differ from others in invisible factors, for different plants of No. 60 were crossed with pollen from different plants of No. 54. They are placed in one table here but certain differences in their behavior in F_3 leads us to consider them separately. There is a total of 662 purples, 94 reds and 2838 light colored purples and non-purples. The reason for classing the light purples and non-purples together will be seen later.

The results of the F_3 generation as well as our experience with other crosses are such as exclude the possibility of a reversal of dominance. The purples did not breed true nor did the behavior of any of the classes indicate anything other than a normal Mendelian segregation involving several characters. Furthermore, a belief in reversal of dominance in our opinion strikes at the foundation stone of Mendelism. Not that dominance is an important part of Mendelism. It is not. Yet no analysis can be made of breeding records without following *every* individual for several generations if dominance is reversible. Of the thousands of extracted recessives that have bred true, many would have proved to be heterozygous dominants if dominance is reversible.

Taking the same F_1 gametic formula that served for the purple side of the family and adding an inhibiting factor I which comes from No. 60, gives the best interpretation of the data. This makes the F_1 formula PpCcIiRR. In F_2 the following classes would be expected:

27 P I C R	Color non-purple.
9 P I R	“ non-purple.
9 P C R	“ purple.
9 I C R	“ non-purple.
3 P R	“ non-purple.
3 I R	“ non-purple.
3 C R	“ red.
1 p c i r	“ non-purple.

The ratio is 9 purple : 3 red : 52 non-purple. The experimental results given in Table 25 show that here also there is a deficiency of reds. Many light purples also appeared, but these were classed as non-purples. This was done because in F_3 the light purples behaved as if they possessed the factor I in a heterozygous condition, the variation in color being due to the different combinations in which the factors P and C appeared.

With this theory the expectation in F_3 is 52 non-purples and light purples giving:

28 Producing all Non-purple seeds.
2 “ 1 Purple : 3 Non-purple.
4 “ 3 Purple : 13 Non-purple.
4 “ 3 Purple : 1 Red : 12 Non-purple.
8 “ 9 Purple : 3 Red : 52 Non-purple.
2 “ 1 Red : 3 Non-red.
4 “ 3 Red : 13 Non-red.

9 Purples giving:
1 Producing all Purple seeds.
2 “ 3 Purple : 1 Red.
2 “ 3 Purple : 1 Non-purple.
4 “ 9 Purple : 3 Red : 4 Non-purple.

3 Reds giving:
1 Producing all Red seeds.
2 “ 3 Reds : 1 Non-red.

Let us now examine Tables 25a-e which give the results from selfing the seeds of certain of the F_2 ears. Table 25a shows the progeny of ear (60-3x54)-1. This ear gave the smallest proportion of purple seeds in F_2, and such purples as were produced in F_2 were lighter in color than normal full purples. In F_3 the purples are again light in color. They are classed in with the non-purples in the last column, those showing some color being given first. The first two ears are progeny of the darkest purples; one has purple and non-purple seeds in the ratio of 3 : 1 and one is pure purple. The next two ears planted from lighter purples show a difference between themselves. One gives 3 light purples : 1 non-purple, the other gives 1 purple : 2 non-purple. The latter probably came from an ear heterozygous for the inhibiting factor and the former from a real purple. Of those ears resulting from white seeds, one has 33 red seeds dark enough to be classed as real reds and a number of very light reds classed with the non-purples — a total of probably near 25% reds, while another gives light purples (and possibly light reds) and non-purples. The remaining ears are non-purples. Five plants from non-purple F_2 seeds were also crossed, and gave all non-purple seeds. In reality, however, only two random crosses can be said to have been made, since the pollen of No. (60-3 x 54)-1-2 ES was used three times, while once the same plant was used as the mother. The progeny of ear (60-3 x 54)-1, therefore, behave like those of other ears of this family except that all of the progeny of purples are light in color. They give pure purples and purples segregating into 3 purples : 1 non-purple, but none are dark like normal purple ears. Some geneticists would probably interpret this as prepotency of the non-purple or rather lack of prepotency of the purple. But when one talks of prepotency he really confesses ignorance of the gametic constitution of his cultures. Is it not much more likely that the true reason for the production of these light purples lies in a fact more in keeping with what is known of hereditary phenomena? May not one say that here is a dominant purple character coming from the individual of unknown character of variety No. 54 which was used as the male parent? If the purple gene from the male parent was such as to give always a lighter purple in zygotic combinations where purple is visible then no dark purples would occur in the segregates resulting from crosees. Such results were obtained from four selfed plants. Two ears resulted from planting purples which were only slightly lighter than normal dark purples, such as the parents of ears (60-3 x 54)-1-1 and (60-3 x 54)-1-2, and two ears resulted from planting seeds quite light in color. (Table 25a).

Similar results were obtained from cross (60-8 x 54), of which the F_3 generation from ear (60-8 x 54)-8 are shown in Table 25e. Here eleven ears resulted from selfing seeds with the modified color if two red seeds are included. None of these ears had seeds dark in color, but the ratios are no doubt the same as those given in Tables 25 b-d. The general reduction of the amount of purple color, however, makes the error of classification too great for safe conclusions. There is even *some* doubt about the classification of the seeds from the F_2 generation of these two crosses (Table 25), but the results of the F_3 generation are such as to give us considerable faith in them.

Tables 25 b-d give a considerable number of F_3 progeny from F_2 seeds of three other ears. There seems to be no reason why they should not be considered together. From the purple F_2 seeds planted, twelve selfed ears were obtained. Three ears were pure purples of the normal shade. One ear gave a ratio of 3 purples : 1 red and two ears a ratio of 3 purples : 1 non-purple. The other six ears gave purple, red and non-purple segregates. Four of these ears were clearly of the ratio 9 : 3 : 4, but in the remaining two there was a considerable deficiency of red seeds. From the F_2 red seeds planted, only one selfed ear was obtained. This ear gave red and non-red segregates in the ratio of 3 : 1.

A large number of selfed ears were obtained from the F_2 light purple and non-purple seeds. Ears of each of the classes expected by the proposed theory were obtained, as will be seen by an examination of the Tables 25 b-d; but as the visual classification is arbitrary owing to the light color of most of the seeds, it could not be depended upon without further breeding. The light colored seeds are given first in the last column of the tables, followed by the seeds which were apparently non-purple. If one is a little charitable about the exactness of the classification the following conclusions can be drawn.

Both seeds which were apparently non-purple and seeds which were light purple in color in the F_2 generation gave light purple seeds among the F_3 segregates. This fact proves both the impossibility of exact classification and the gametic identity of seeds slightly different in their appearance.

Two plants from light red seeds (Table 25b) were selfed. One resultant ear showed a ratio of 1 dark red : 3 light red and non-red; the other ear showed only light red and non-red seeds which were classed together. Thirty-six plants from light purple and from non-purple F_2 seeds were selfed. Of these, fifteen ears resulted from planting seeds classified as non-purple in F_2. Only four of them threw dark purple segregates in F_2. On the other hand only two of the ears resulting from selfed plants which were progeny of seeds classified as light purples, threw no dark purple segregates. It seems to us that this shows a fair classification of seeds heterozygous for the inhibiting factor. A few seeds, however, were wrongly classified in the F_2 generation and proved their proper status in the F_3 generation.

Out of the total of 36 selfed ears from light purple and non-purple F_2 seeds, 23 threw dark purple segregates and 13 produced only light purple and non-purple seeds. Of those ears which threw purple segregates, none of them had ratios of purple to light purple plus non-purple greater than might reasonably be expected by chance mating. The different ratios expected in F_3 were followed rather well, although it is recognized that these ratios could not be determined accurately with such small numbers.

Conclusions.

There can be but little doubt that the factors I, C, P and R are concerned in this cross. Whether there is another factor which modifies the purple color or not, is a question that cannot yet be settled, because we have no data concerning the individual plant of No. 54 that formed the male parent; yet there seems to be no other way to account for the light purples in Table 25a and Table 25e. The ultimate analysis of the behavior of the R factor in this cross must also be left in abeyance. These unsettled questions however have no bearing upon two important conclusions which the evidence forces upon us. The first is that one should be exceedingly careful before he decides that the transmission of certain characters is an exception to the general law of Mendel. When a collection of white or non-purple aleurone strains are promiscuously crossed with a purple aleurone maize, the results seem almost impossible to bring into conformity with simple Mendelian results, yet this confusion is brought about simply by the gametic differences of the non-purple races. If such confusion can result in the case of a simple color inheritance, much more care must be taken to analyze the transmission of more complex characters before subsidiary hypotheses are submitted.

The second important fact is in regard to prepotency. It has been shown that certain families of purple and non-purple hybrids produce very light purples when P exists alone without C, while other families produce no color. No modification of the Mendelian ratio occurs, yet some transmissible difference in the two families gives this different result. Here is a probable explanation of prepotency. If these white families were mixed together, a mixture more easily imagined in the case of bisexual individuals, there would appear to be a difference in prepotency of the purple character. It therefore seems probable that prepotency is due only to a difference in gametic character which modifies somatic appearances and not to an actual modification of Mendelian chance ratios as others have suggested.

The behavior of the other families is so simple that we think there can now be no question but that the purple aleurone color behaves as a normal Mendelian character in inheritance.

TABLE 24.

F₂ SEEDS OF CROSS BETWEEN NO. 60–5 NON-PURPLE POP AND NO. 54 PURPLE SWEET.

Purple Seeds Planted.

Ear No.	Purple	Red	Non-Purple
(60–5 x 54)–2	271	28	57
(")–3	236	21	71
(")–4	92	11	33
(")–5	203	36	69
(")–6	272	33	71
(")–8	144	14	58
(")–10	198	21	55
(")–11	190	4	55
(")–12	237	20	76
Total	1843	188	545

TABLE 24A.

F₃ SEEDS OF EAR NO. (60–5 x 54)–2 OF TABLE 24.

Ear No.	Planted from	Purple	Red	Non-Purple
(60–5 x 54)–2–1	Purple S	277	23	. .
(")–2–2	" S	16	. .	5
(")–2–3	" S	176	45	69
(")–2–4	" S	233	48	92
(")–2–1	" s	209	49	72
(")–2–4	" s	396	. .	. .
(")–2–1	Red S	. . .	219	91
(")–2–5	" S	. . .	All	. .
(")–2–1	L. Purple S	194	27	71
(")–2–2	" S	167	56	80
(")–2–1	Non-Pur. S	. . .	. .	Pure
(")–2–2	" S	. . .	. .	"
(")–2–3	" S	. . .	. .	"
(")–2–4	" S	. . .	. .	"
(")–2–2 BS x 2–1	Red x Red S	. . .	380	. .
(")–2–3 AO x 2–2	Pur. x Pur. S	280	. .	98
(")–2–3 CS x 2–1	L. Pur. x L. Pur. S	152	37	54
(")–2–5 ES x 2–4	Non-Pur. x Non-Pur. S	. . .	. .	Pure
(")–2–2 EO x 2–1	Non-Pur. x Non-Pur. s	. . .	. .	"

TABLE 24B.

F₃ SEEDS OF EAR NO. (60–5 x 54)–6 OF TABLE 24.

Ear No.	Planted from	Purple	Red	Non-Purple
(60–5 x 54)–6–3	Purple S	87	24	38
(")–6–4	" S	204	. .	60
(")–6–6	" S	262	. .	80
(")–6–7	" S	318	58	. .
(")–6–4	" s	265	83	. .
(")–6–1	Red S	. . .	135	29
(")–6–2	" S	. . .	287	76
(")–6–3	" S	. . .	164	48
(")–6–1	" s	. . .	240	71
(")–6–1	Non-Pur. S	. . .	. .	Pure
(")–6–2 AS x 4	Pur. x Pur. S	384	. .	. .
(")–6–5 AS x 7	" S	420	. .	. .
(")–6–2 AO x 3	" s	200	. .	. .
(")–6–2 ES x 1	Non-Pur. x Non-Pur. S	. . .	. .	Pure
(")–6–4 ES x 5	"	. . .	. .	"

TABLE 24C.

F₃ SEEDS OF EAR NO. (60–5 x 54)–8 OF TABLE 24.

Ear No.	Planted from	Purple	Red	Non-Purple
(60–5 x 54)–8–1	Purple S	125	. .	. .
(")–8–2	" S	176	55	. .
(")–8–3	" S	212	60	. .
(")–8–4	" S	170	. .	. .
(")–8–6	" S	183	. .	60
(")–8–1	" s	180	28	65
(")–8–2	" s	182	35	. .
(")–8–5	" s	153	. .	35
(")–8–6	" s	217	. .	71
(")–8–7	" s	150	. .	. .
(")–8–1	Red S	. . .	176	34
(")–8–2	" S	. . .	182	. .
(")–8–2	" s	. . .	156	57
(")–8–1	Non-Pur. S	. . .	. .	180
(")–8–4	" S	12	. .	40
(")–8–5	" S	. . .	. .	250
(")–8–1	" s	. . .	. .	250
(")–8–2	" s	. . .	. .	220
(")–8–3	" s	. . .	. .	240
(60–5 x 54)–8–2 ES x4	Non-Pur. x Non-Pur. x	. . .	. .	400
(")–8–7 ES x6	Non-Pur. x Non-Pur. x	49	. .	140
(")–8–4 EO x 5	Non-Pur. x Non-Pur. x	. . .	. .	220

TABLE 24D.

F$_3$ SEEDS OF EAR NO. (60–5 x 54)–11 OF TABLE 24.

Ear No.	Planted from	Purple	Red	Non-Purple
(60–5 x 54)–11–3	Purple S	115	42	47
(“)–11–4	“ S	175	. .	49
(“)–11–5	“ S	175	65	. .
(“)–11–6	“ S	180	. .	62
(“)–11–8	“ S	209	69	. .
(“)–11–10	“ S	210	. .	67
(“)–11–11	“ S	101	. .	38
(“)–11–12	“ S	112	. .	39
(“)–11–2	“ s	46	. .	21
(“)–11–3	“ s	144	. .	46
(“)–11–4	“ s	178	. .	64
(“)–11–7	“ s	180	. .	. .
(*)–11–1	L. Purple S	116	25	49
(“)–11–3	“ S	204	41	75
(“)–11–5	“ S	124	. .	52
(“)–11–1	“ s	218	29	75
(“)–11–2	L. Red S	. . .	163	38
(“)–11–1	Non-Pur. S	. . .	. .	Pure
(“)–11–2	“ S	. . .	. .	“
(“)–11–5	“ S	. . .	. .	“
(“)–11–7	“ S	. . .	. .	“
(“)–11–1	“ s	. . .	. .	“
(“)–11–2	“ s	. . .	. .	“
(60 x 54–5)–11–7 AS x 11-6	Pur. x Pur. S	142 Pur. and Red		56
(“)–11–3 ES x 11-5	Non-Pur. x Non-Pur. S	. . .	. .	Pure
(“)–11–6 ES x 11-4	Non-Pur. x Non-Pur. S	. . .	. .	“
(“)–11–2 EO x 11-3	“	. . .	. .	“

TABLE 24E.

F_3 SEEDS OF EAR NO. (60–5 x 54)–12 OF TABLE 24.

Ear No.	Planted from	Purple	Red	Non-Purple
(60–5 x 54)–12–3	Purple S	206	78	80
(")–12–4	" S	201	44	67
(")–12–4a	" S	350	. .	. .
(")–12–5	" S	169	59	. .
(")–12–6	" S	245	65	. .
(")–12–7	" S	204	67	. .
(")–12–8	" S	191	49	88
(")–12–9	" S	187	. .	66
(")–12–10	" S	239	. .	66
(")–12–13	" S	248	. .	77
(")–12–14	" S	217	. .	77
(")–12–1	" s	240	. .	72
(")–12–3	" s	350	. .	. .
(")–12–4	" s	184	43	56
(")–12–5	" s	300	. .	. .
(")–12–7	" s	147	53	. .
(")–12–1	Red S	. . .	229	76
(")–12–3	" S	. . .	280	. .
(")–12–4	" S	. . .	172	56
(")–12–1	Non-Pur. S	. . .	. .	Pure
(")–12–8	" S	. . .	. .	"
(60–5 x 54)–12–2 AS x 3	Purple S	161	56	53
(")–12–11 As x 6	" S	175	. .	63
(")–12–2 AO x 1	" S	229	. .	74
(")–12–3 ES x 5	Non-Pur. S	. . .	. .	Pure
(")–12–4 ES x 5	" S	. . .	. .	"
(")–12–5 ES x 7	" S	. . .	. .	"
(")–12–7 ES x 5	" S	. . .	. .	"
(")–12–9 ES x 8	" S	. . .	. .	"

TABLE 25.

F₂ SEEDS OF CROSS BETWEEN NO. 60 NON-PURPLE POP AND NO. 54 PURPLE SWEET.

Very Light Colored and White Seeds Planted.

Ear No.	Purple	Red	L. Pur. + Non-Pur.
(60–8 x 54)–1	83	5	66 + 135 = 201
(")–7	19	7	44 + 150 = 194
(")–8	35	4	41 + 215 = 256
(60–11 x 54)–2	22	4	22 + 40 = 62
(60–2 x 54)–1	68	15	96 + 159 = 255
(")–7	86	7	99 + 150 = 249
(")–10	89	14	69 + 148 = 217
(60–3 x 54)–1	26	..	76 + 282 = 358
(")–3	46	7	87 + 140 = 227
(")–5	54	12	102 + 159 = 261
(")–6	65	6	113 + 144 = 257
(")–7	69	13	117 + 184 = 301
Total	662	94	2838

TABLE 25A.

F₃ SEEDS OF EAR NO. (60–3 x 54)–1 OF TABLE 25.

Ear No.	Planted from	Pur.	Red	L. Pur. + Non-Pur.
(60–3 x 54)–1–1	Purple S	..	..	235 + 76 = 311
(")–1–2	" S	..	..	245 = 245
(")–1–1	L. Purple S	..	..	217 + 69 = 286
(")–1–2	" S	..	..	39 + 72 = 111
(")–1–5	Non-Pur. S	..	..	0 + 384 = 384
(")–1–6	" S	..	..	105 + 204 = 309
(")–1–7	" S	..	33L	380*
(")–1–9	" S	..	..	0 + 390 = 390
(")–1–10	" S	..	..	0 + 280 = 280
(")–1–1	" s	..	..	0 + 448 = 448
(")–1–2	" s	..	..	0 + 200 = 200
(")–1–3	" s	..	..	0 + 152 = 152
(")–1–4	" s	..	..	0 + 280 = 280
(60–3 x 54)–1–1 ES x 1–2	Non-Pur. x Non-Pur.	..	..	0 + 250 = 250
(")–1–2 ES x 1–1	"	..	..	0 + 258 = 258
(")–1–3 ES x 1–2	"	..	..	0 + 110 = 110
(")–1–4 ES x 1–2	"	..	..	0 + 308 = 308
(")–1–8 ES x 1–6	"	..	..	0 + 352 = 352

---

* Light reds and non-reds.

TABLE 25B.

F3 SEEDS OF EAR NO. (60–3 x 54)–5 OF TABLE 25.

Ear No.	Planted from	Pur.	Red	L. Colored + Non-Colored
(60–3 x 54)–5–1	Purple S	165	47	0+66 =66
(")–5–2	" S	250	. .	. . . .
(")–5–3	" S	203	62	. . . .
(")–5–4	" S	300	. .	. . . .
(")–5–6	" s	273	. .	0+ 95= 95
(")–5–1	" s	176	13	0+ 69= 69
(")–5–1	Red S	. . .	190	0+ 71= 71
(")–5–1	L. Purple S	58	. .	136+110=246
(")–5–2	" S	90	49	115+ 96=211
(")–5–2a	" S	104	. .	78+152=230
(")–5–3	" S	59	. .	91+145=236
(")–5–5	" S	80	. .	58+ 97=155
(")–5–5a	" S	79	. .	65+ 54=119
(")–5–6	" S	. . .	. .	88+ 26=114
(")–5–4	L. Red S	. . .	62	78+ 95=173
(")–5–2	" s	. . .	. .	75+ 51=126
(")–5–2	Non-Pur. S	. . .	. .	0+352=352
(")–5–4	" S	. . .	. .	0+ 30= 30
(")–5–7	" S	67	. .	138+193=331
(")–5–8	" S	. . .	. .	0+380=380
(")–5–9	" S	. . .	. .	0+345=345
(")–5–2	" s	. . .	. .	0+390=390
(60–3 x 54)–5–1 ES x 5–7	Non-Pur. x Non-Pur.	. . .	. .	125+313=438
(")–5–2 ES x 5–4	"	47	. .	14+126=140
(")–5–5 ES x 5–4	"	. . .	. .	0+320=320
(")–5–10 ES x 5–9	"	. . .	. .	90+154=244
(")–5–11 ES x 5–9	"	. . .	. .	43+ 87=130
(")–5–17 ES x 5–7	"	. . .	. .	109+144=253
(")–5–1 ES x 5–5	"	. . .	. .	0+360=360
(")–5–3 ES x 5–4	"	. . .	. .	0+104=104
(")–5–4 ES x 5–3	"	. . .	. .	0+254=254
(")–5–7 ES x 5–5	"	. . .	. .	0+400=400

TABLE 25C.

F_3 SEEDS OF EAR NO. (60–3 x 54)–6 OF TABLE 25.

Ear No.	Planted from	Pur.	Red	L. Colored + Non-Colored
(60–3 x 54)–6–2	Purple S	180	. .	0 + 71 = 71
(“)–6–2a	“ S	175	9	0 + 64 = 64
(“)–6–5	“ S	138	20	0 + 40 = 40
(“)–6–1	L. Purple S	31	5	36 + 38 = 74
(“)–6–1a	“ S	49	. .	68 + 49 = 117
(“)–6–3	“ S	27	. .	53 + 48 = 101
(“)–6–4	“ S	66	13	63 + 61 = 124
(“)–6–6	“ S	36	. .	144 + 130 = 274
(“)–6–1	“ s	90	. .	108 + 142 = 250
(“)–6–1	Non-Pur. S	. .	. .	0 + 250 = 250
(“)–6–3	“ S	25	. .	70 + 106 = 176
(“)–6–5	“ s	21	3	45 + 62 = 107
(“)–6–6	“ s	. .	. .	0 + 152 = 152
(“)–6–7	“ s	69	. .	53 + 105 = 158
(60–3 x 54)–6–3 AS x 6–2	Pur. x Pur.	51	. .	88 + 80 = 168
(“)–6–1 AO x 6–2	“	132	57	. . . .
(“)–6–2 ES x 6–3	Non-Pur. x Non-Pur.	14	. .	15 + 31 = 46
(“)–6–3 ES x 6–5	“	. .	. .	0 + 380 = 380
(“)–6–5 ES x 6–6	“	. .	4	21 + 117 = 138
(“)–6–6 ES x 6–5	“	. .	17	78 + 122 = 200
(“)–6–7 ES x 6–3	“	. .	. .	37 + 170 = 207
(“)–6–8 ES x 6–6	“	. .	4	65 + 61 = 126
(“)–6–2 EO x 6–1	“	. .	. .	84 + 222 = 306
(“)–6–4 EO x 6–3	“	. .	. .	33 + 26 = 59
(“)–6–3 EO x 6–4	“	80	25	24 + 171 = 195

PLATE XI.

Cross 60-5x54. F_3 generation not including red segregates. The combinations possible when parents differ in presence and absence of purple aleurone cells and presence and absence of starchiness. First three resulted from planting non-purple, the remainder from purple seeds. Ears 1, 4, 5 resulted from planting non-starchy, the remainder from starchy seeds.

INHERITANCE OF ALEURONE COLOR.

TABLE 25D.

F_3 SEEDS OF EAR NO. (60–8 x 54)–1 OF TABLE 25.

Ear No.	Planted from	Pur.	Red	L. Colored + Non-Colored
(60–8 x 54)–1–6	Purple S	135	36	0 + 56 = 56
(")–1–7	" S	67	16	0 + 20 = 20
(")–1–3	" s	280	..	....
(")–1–1	L. Purple S	20	..	66 + 76 = 142
(")–1–1a	" S	51	17	63 + 164 = 227
(")–1–2	" S	35	1	31 + 84 = 115
(")–1–3	" S	40	20	67 + 124 = 291
(")–1–5	" S	20	16	27 + 21 = 48
(")–1–1	" s	74	..	101 + 115 = 216
(")–1–1	Very L. Pur. S	..	..	92 + 121 = 213
(")–1–2	" S	67	5	83 + 109 = 192
(")–1–4	Non-Pur. S	..	..	0 + 250 = 250
(")–1–5	" s	..	..	0 + 250 = 250
(")–1–6	" s	..	..	0 + 230 = 230
(")–1–7	" s	..	..	0 + 240 = 240
(60–8 x 54)–1–6 ES x 1–7	Non-Pur. x Non-Pur. S	..	..	0 + 100 = 100
(")–1–7 ES x 1–6	"	..	..	0 + 250 = 250
(")–1–8 ES x 1–9	"	..	..	43 + 66 = 109
(")–1–9 ES x 1–8	"	..	..	151 + 158 = 309
(")–1–10 ES x 1–9	"	..	68	0 + 161 = 161
(")–1–1 EO x 1–2	Non-Pur. x Non-Pur. s	..	..	0 + 240 = 240
(")–1–3 EO x 1–7	"	..	..	½[*] + ½ = 1

---

[*] Approximated.

TABLE 25E.

F$_3$ SEEDS OF EAR NO. (60–8 x 54)–8 OF TABLE 25.

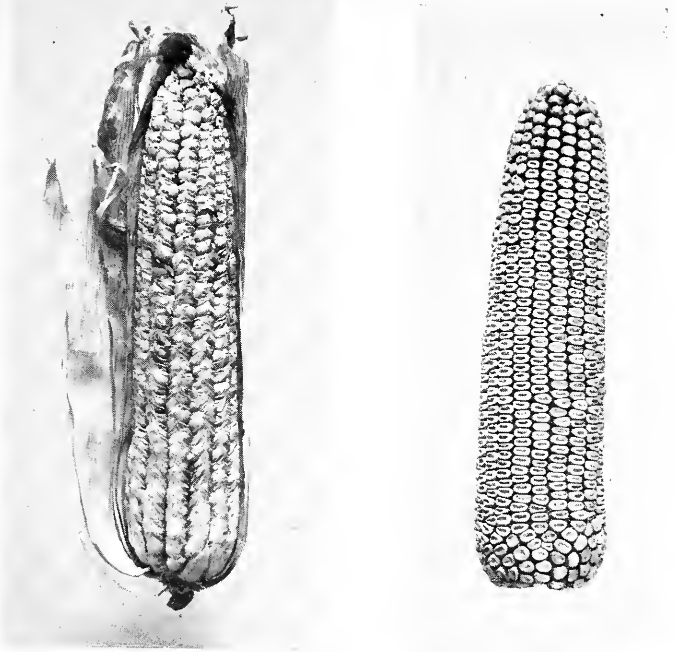
Ear No.	Planted from	Pur.	Red	L. Colored + Non-Colored
(60–8 x 54)–8–2	Purple S	..	†54L	236+100=336
(“)–8–5	“ S	..	..	212+ 0=212
(“)–8–1	Red S	..	200L	....
(“)–8–2	“ S	..	5L	26+ 8= 34
(“)–8–1	L. Purple S	..	..	110+104=214
(“)–8–2	“ S	..	..	224+123=347
(“)–8–5	“ S	..	..	50+148=198
(“)–8–7	“ S	..	62L	0+248=248
(“)–8–8	“ S	70L	..	84+164=248
(“)–8–1	“ s	..	..	90+202=292
(“)–8–1 lower ear	“ s	..	..	97+243=340
(“)–8–3	Non-Pur. S	..	..	80+294=374
(“)–8–9	“ S	..	..	80+216=296
(“)–8–2	“ s	..	37L	0+263=263
(60–8 x 54)–8–1 ES x 8–7	Non-Pur. x Non-Pur. S	..	..	0+300=300
(“)–8–2 ES x 8–3	“ S	..	..	39+260=299
(“)–8–4 ES x 8–9	“ S	..	..	49+214=263
(“)–8–5 ES x 8–17	“ S	..	..	0+200=200
(“)–8–6 ES x 8–9	“ S	..	..	0+300=300
(“)–8–7 ES x 8–17	“ S	..	..	24+270=294
(“)–8–1 EO x 8–2	“ s	..	..	88+174=262
(“)–8–5 EO x 8–3	“ s	..	..	48*+153=201

---

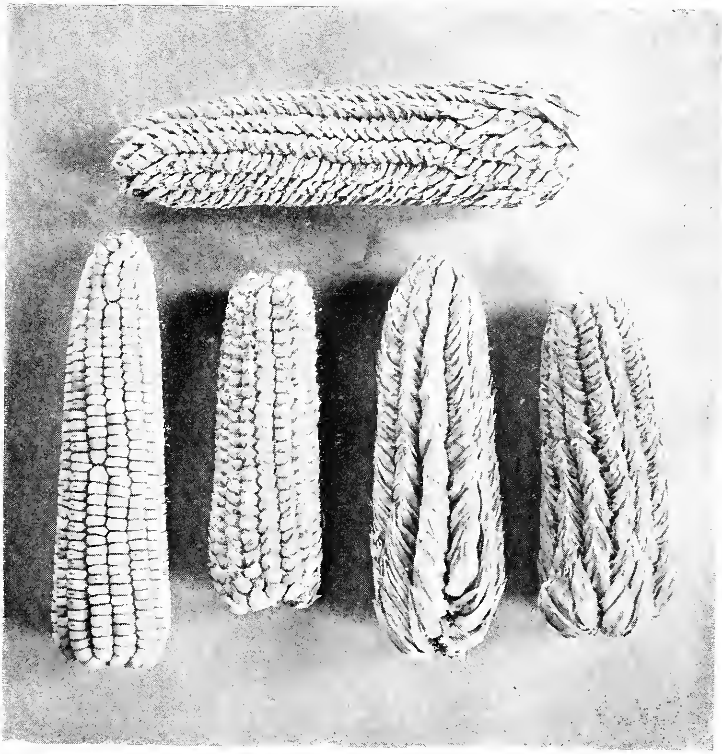
* Several seeds rather dark purple.

† Those marked L are light in color but not nearly as light as those given in the last column.

PLATE XII.



a. No. 21. Podded maize. *b*. No. 7, non-podded maize.



c. Cross 21x7. F_1 above; pod character fully dominant. F2 below; complete segregation in monohybrid ratio.

INHERITANCE OF "PODDED" CHARACTER.

PART III.

XENIA.

The appearance of the endosperm in the F_1 generation in the crosses discussed in Part II really include almost all of our observations of true Xenia, but the subject is sufficiently important to warrant a more systematic arrangement of the facts.

The word Xenia was proposed by Focke to denote the effect, if any, produced by the action of pollen upon the maternal tissue of the seed plant. The classical example of such effect was the endosperm of maize. After the discovery by Guignard ('99) and Nawaschin ('99) that the endosperm is in reality a part of the filial generation formed by the development of the endosperm nucleus after fusion with the second male nucleus of the pollen cell, De Vries ('99), Correns ('99) and Webber (: 00) saw in this the explanation of the phenomenon in maize. These facts took away the only authentic illustration of Xenia in its original use — the effect of foreign pollen on maternal tissue. In this older sense the word is therefore of no value, and it may be used solely to describe the visible effect of the second male nucleus on the endosperm. Unfortunately, botanists have not been so prompt in discarding belief in the original meaning of Xenia as the zoologists in discarding telegony. In the experience of Correns, of Lock and of ourselves the effect of the second male nucleus has never extended to maternal tissue. One of the present authors has made several experiments in which pollination without fertilization (between infertile species) has had an effect on maternal tissue, (parthenocarpie), but this effect was simply that of a chemical stimulus or irritant producing cell division in the carpels.

The visible effects of double fertilization have been found in the following cases, in all of which the parents have been selfed strains that precluded errors in the observations. Non-starchy seeded plants crossed with starchy seeded plants always show starchiness. Starchiness is completely dominant, therefore the reciprocal cross, bringing in the "opposing" character, never shows Xenia.

Yellow endosperm is also completely dominant in most cases. Non-yellow crossed with yellow endosperm therefore shows Xenia while the reciprocal shows no Xenia. Three exceptions to this rule were found, however. In the large races of dent maize where the zone of soft starch at the summit of the seed is extensive, the heterozygous yellow is somewhat lighter in color than the homozygous yellow, and Xenia appears when the cross is made either way. It shows as a cap of lighter color than the homozygous yellow. When floury yellow races are crossed with floury white races this lighter color of the heterozygote extends throughout the seed. In this case difference in color is always great enough to be noticed by a careful observer in either cross, but where the cap only is floury the color intergrades to that of the homozygous yellow. When dealing with races with corneous endosperms, such as the flint and pop varieties, there is so little difference in color that the homozygous yellow is generally indistinguishable from the heterozygous yellow; therefore Xenia occurs only when the white is the female parent. Even here, however, we have found two different cases where a few heterozygous yellows were distinguishable from homozygous yellows when the latter were used as the female.

Both the red and the purple colors in the aleurone cells behave in the same way as regards Xenia. When the two parents differ only in these characters, they are completely dominant and Xenia occurs only when they are possessed by the male parent. Even in the race in which a slight purple color appeared when the color factor was absent (P c instead of P C) the same slight color appeared when it was used as the male upon a race in which P and C were both absent. Furthermore when this race was crossed either way with a white race bearing the color factor (P c x p C or p C x P c), the full purple developed and appeared as Xenia. The red color undoubtedly behaves in the same way although we have made no original crosses dealing with these conditions. Again, two pure white races (P c and p C) which show not the slightest color may bring together the two factors P and C necessary for full development of the purple color, and Xenia results when either is the female parent.

The next and last case in which we have observed Xenia is that in which the white parent possesses a character that inhibits the development of red or purple aleurone cells. Correns and Lock probably used races containing this character but they did not distinguish it from a recessive white or simple absence of the purple character. They therefore concluded that when a white race was crossed with a purple, Xenia sometimes results and sometimes does not result, and that no change occurs when the purple is the female parent. The true state of affairs is just the opposite of this. When a white containing the inhibitor is the male parent, a white seed results, and while the same result is obtained in the reciprocal cross it is of course unnoticed when the white is the female parent. Sometimes the purple is not fully inhibited and then a light purple results no matter which parent is the mother.

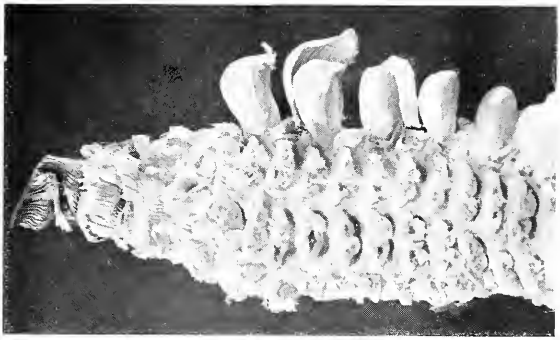
If one considers these observations as a whole, the following law regarding Xenia may be formulated:

When two races differ in a single visible endosperm character in which dominance is complete, Xenia occurs only when the dominant parent is the male; when they differ in a single visible endosperm character in which dominance is incomplete or in two characters both of which are necessary for the development of the visible difference, Xenia occurs when either is the male.

Correns observed that in every case where Xenia may be expected to occur, the seeds showing Xenia were always hybrids. This fact was assumed to prove that the second male nucleus always bears the same characters as the one that fuses with the egg cell to form the embryo. For this reason Mendelian segregation of the gametes must have occurred previous to the division of the pollen nucleus. Our observations are entirely in accord with those of Correns. The latter author and also Webber observed several cases where Xenia occurred in only one-half of the endosperm. These rare phenomena which are probably similar in nature to the gynandromorphs occurring in insects, they both interpreted as the independent development of the endosperm nucleus and the second male nucleus. We have observed many instances of this phenomenon and have grown a number of them to see if the tendency was inherited but without positive results. Correns' and Webber's explanation of the cause of these seeds is probably correct, yet the suspicion cannot be avoided that if the two nuclei can develop independently then the female nucleus ought sometimes to develop to the total exclusion of the male. If this were true a seed showing no Xenia where it is to be expected, should sometimes prove to be a hybrid. This has never occurred in our work, a fact in disagreement with the work of Webber. It may be possible then that the cause of these seeds is Mendelian segregation in somatic tissue, such as often occurs in bud sports. This could be proved if there occurred among the F_1 seeds of a cross in which the parents differed in two characters, an individual in which the characters were segregated differently: for example, if a white sweet maize were pollinated with a yellow starchy race, and a seed developed having one half yellow sweet and the other half white starchy. The matter is simply mentioned because it is important to biological theory, and it was thought that some experimentalist might happen upon such an individual.

It is thought that Webber's idea that seeds with splashed purple aleurone cells are due to mosaic development of cell descendants of the endosperm nucleus and of the second male nucleus, is incorrect. If this idea were true, in cases where the endosperm is heterozygous yellow, this character also should be mosaic. Such cases have never been reported. It therefore seems better to consider the splashed purples as cases of incomplete dominance caused by other factors as was explained in greater detail earlier in the paper.

PLATE XIII.



a. Podded maize. The four husks successively removed showing naked seed at right. The double rowed condition characteristic of all maize varieties is seen most clearly.

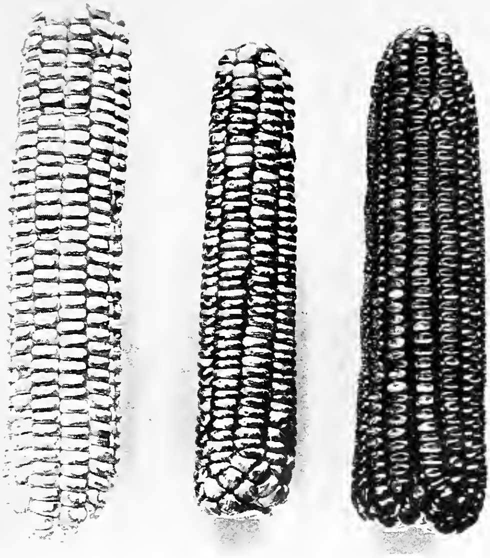
b.

c.

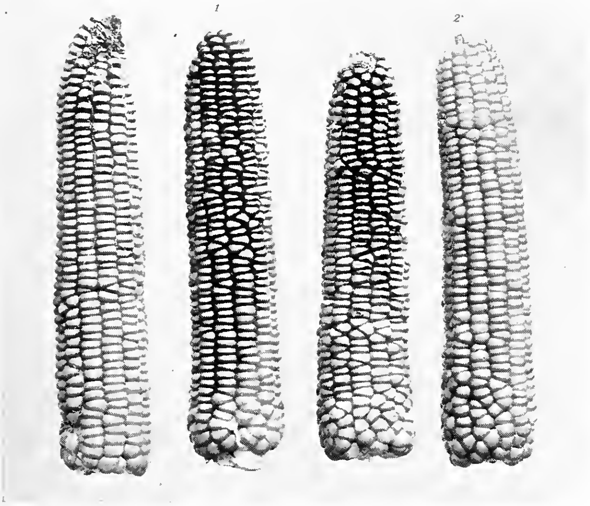
Male spikes (tassels) showing development of seeds. *b*, a dominant F2 plant; *c*, a recessive F2 plant. Segregation is persistent in this cross, 21x7.

INHERITANCE OF "PODDED" CHARACTER.

PLATE XIV.



a. At left, the color which develops in sunlight—R4; in center variegated or mosaic seeds—R2; at right, common red pericarp—R1.



b. Segregation of pericarp color R4 in F2 of cross 5x11. Amount of color developed is variable depending on light conditions during maturation.

Pericarp Colors.

PART IV.

PLANT CHARACTERS.

In this part of the paper the inheritance of normal plant characters is considered. These characters in general have no effect upon the endosperm — the new generation — and therefore do not show as Xenia in the daughter seeds of the ear that has been crossed.

Podded and Podless Maize.

The inheritance of the podded character is interesting because it is a shining example of a case where a gross morphological character behaves as a simple Mendelian mono-hybrid. No. 21 a podded maize was crossed with a common Leaming dent like No. 7, but not of the same stock. The F_1 generation was as perfectly podded as the podded parent. There was of course some variation in the length of the husks of the seeds, a variation apparently physiological in character depending upon the vigor of the mother plant, but this variation was no greater in the F_1 generation than it was in the pure podded maize. The F_2 generation yielded 64 podded and 21 non-podded individuals. The latter were without any trace of husk and were not distinguishable from ordinary non-podded corn which had never been crossed with a podded variety. (See Plate XII.)

The F_1 generation was also crossed back with the recessive — the non-podded variety — and in the next generation yielded 41 podded ears and 50 non-podded ears. In other words Hh x h gave 50% Hh and 50% hh as was to be expected. The character was again strictly discontinuous. The extracted recessives proved absolutely true.

Pericarp Color.

There are various red sap colors appearing in the pericarp, the cob, the husks, the silks, the glumes and the anthers of maize. We have not been able to make a chemical study of them and so cannot say if they are due to the same compound, but the comparatively small amount of data regarding their inheritance that we have obtained is particularly interesting on account of the number of different organs in which color occurs. It has long been thought that such colors that manifest themselves in different parts of a plant, are single units as regards heredity, but are produced in visible quantities only when developmental conditions are favorable or when certain transmissible limiting factors or extension factors which effect their development, are present or absent. Our especial problem was to find out whether these red colors occurred and were transmitted separately or whether they were linked together in genetic or in chemical relationships. This work is therefore simply a report of progress.

The first red pericarp, which we will call R_1 was found in No. 27, a rice pop maize. It was the ordinary dark red color of the varieties commonly known as red corns. It did not have a red cob or red silks, although the glumes of the male flowers were sometimes reddish. Crossed with number 28, a rice pop with white pericarp, white cob and silks, it gave 75 red and 22 white ears in F_2. The color was inherited absolutely discontinuously, the reds being all dark and the whites showing no trace of color.

The only other cross with apparently this same dark pericarp color, was a peculiar ear found in a field of dent maize of unknown parentage. This ear, as shown in Plate XV, fig. a, had seeds with red pericarp on one side and seeds which were sometimes white and sometimes striped with red on the other side. The ear appeared in a field of white maize in which only white maize was planted. It must have been produced therefore by a hybrid seed R_1 r_1. Furthermore since it was the only ear in the field showing red pericarp, it is likely that it was nearly all pollinated by white. One would expect its seeds therefore to be half R_1r_1 and half r_1r_1, and that they would give in the next generation 50% red ears, 50% white ears. In order to test any possible transmission of the variation which appeared in this ear however, both the red seeds and the seeds from the side which had white and striped kernels were planted. From the dark red seeds were obtained 22 dark red ears and 22 white ears; from the white and striped seeds were obtained 15 ears showing a few red striped seeds and 15 ears with only white seeds. No difference was observed between the progeny of white and of striped seeds. Both kinds of seeds from this side of the ear gave striped ears and white ears. A selfed red ear of this generation gave a simple mono-hybrid ratio in the next generation — 75 red ears and 26 white ears. The explanation of this phenomenon evidently is the same as that of the bud variations that sometimes occur in perennials. They occur in annuals but are usually unnoticed. The plant due to produce a red ear varied somatically so that one-half of the ears was red and one-half striped. This variation was transmitted by seeds, but at the same time the hybrid character of its seeds was unchanged as shown by their segregation into reds and whites in the next generation and the normal segregation of the hybrid dark reds in a further generation. This strain had red cobs, and there was perfect coupling between the two characters in the next generation.

Two other red pericarp colors seemingly independent of red in other parts of the plant have been found, which may be called R_2 and R_3. R_2 is a dark red that occurs as irregular red stripes radiating from the point where the silk was attached; R_3 is a dirty red color more abundant at the base of the seed and almost wanting at the summit. The dye occurs in small amounts. The latter red, which occurs in Palmer's red-nosed yellow appears to be completely coupled * with red silks. It is almost certain that this red forms an allelomorphic pair with its absence that is entirely independent of R_1, R_2 and R_4, but our numbers are too small to make a full report on the matter. The mosaic red (R_2) is also one that has not been subjected to sufficient genetic study. Thus far (2 generations) it has not bred true but has thrown a percentage of non-reds.

Two other red pericarps have occurred, however, which are interesting because they are the same in appearance but are not allelomorphic to each other. The first is a rose red (R_4) characteristic of No. 5. It develops only in presence of light, hence the ears with thick husks show the color but faintly. When the husks are stripped away and the ear matures in full sunlight, however, the color appears over the entire ear as a bright

---

* Coupling is proved by the fact that red silks occur *without* red pericarp in other combinations.

rose red. In numbers 2, 8 and 18 there appeared another red which we at first thought was the same as the above. It occurs in less amounts and on thick-husked ears can only be detected by careful examination. Since these two reds behave as separate allelomorphic pairs they are called R_4 and R_5.

The transmission of these two reds was shown by crossing No. 5 (R_4) with No. 18 (R_5). In F_1 all of the ears were red. In F_2 there were 131 red ears and 7 white ears. No. 5 (R_4) was also crossed with No. 2 (R_5) and gave similar results although the number of plants was small. In F_2 there were 52 red ears and 2 white ears.

It may be asked whether the red in No. 5 (R_4) acts as a simple mono-hybrid in crosses with strains having no red in the pericarp. We have only one cross of this kind in which data for pericarp color were taken. No. 11-2 (r_4) was crossed with No. 5 (R_4) and yielded 251 red ears and 91 white ears in F_2.

None of these varieties had the red color in other organs.

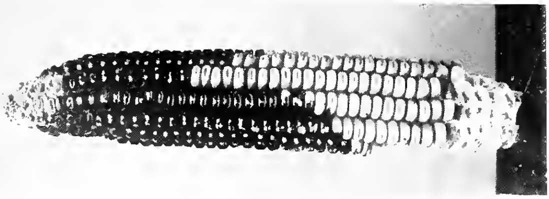
Cob Color.

Several crosses were made in which one parent had a red cob and one a white cob. None of the parents had dark red pericarps (R_1) but in one case R_4 was present (the light red pericarp developing in presence of light). In a cross between No. 5 and No. 6, F_2 yielded 277 ears, of which 212 had red cobs and 65 white cobs. It was strictly a mono-hybrid cross, and the character red-cob seemed not to be coupled with the pericarp color. This red we may call R_c.

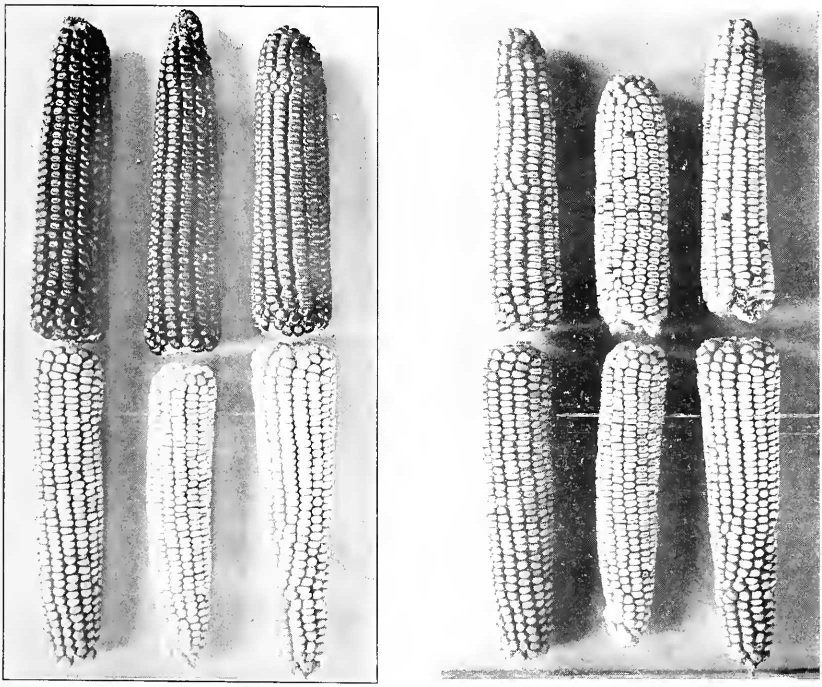
The parents in this case were tested for purity although there are strains of No. 6 in our possession that do not have red cobs. The results of the other crosses were similar and space will not be taken to report them in full. It must be noted however, that although no di-hybrid reds were found, it is not beyond probability that such might be found in an extensive series of crosses.

Silk Color.

Varieties are also obtained which have red silks although the red color is not manifested in other parts of the plant. In fact, No. 19, which has the darkest red silks of any variety in our pos-

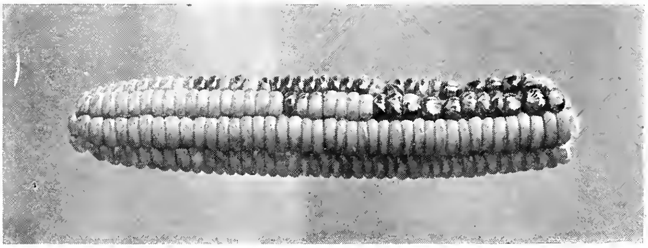


a. Somatic or bud variation from dark red seeds to slightly variegated seeds in ear whose seeds were supposed to be half R_1, r_1, and half r_1, r_1.



b. Progeny of red seeds of *a.* Half dark red, half white.

c. Progeny of slightly variegated seeds of *a.* Half slightly variegated, half white.



d. Similar bud variation in which R_2 is concerned.

PERICARP COLORS AND SOMATIC SEGREGATION.

session, has white cob and pericarp. It is not quite clear, however, how this character is transmitted. The facts are obscured by the action of the bag over the ear to be hand-pollinated, which prevents the full development of the red color by shutting out the light. For this reason one cannot be certain whether the F_1 plants which are selfed are full reds or only red-haired silks.

An illustration of what is obtained in a cross between red silk and non-red silk varieties is as follows. No. 12-2 which is pure for non-red silks was crossed with No. 9-2 which is pure for red silks. In F_1 there were 110 plants with red silks and 27 with greenish-white silks with red hairs. In F_2 the progeny of 3 F_1 plants were grown. The first ear gave 123 plants with red silks and 40 with white silks. The progeny of the other two ears were of three classes; reds, greenish-whites with red hairs and greenish-whites in the numbers 198 : 29 : 94. We will not attempt to analyze this ratio. It is simply mentioned to show that the silk color does mendelize without the production of color in other parts of the plant.

Glume Color.

No plant has yet been obtained which has red glumes and yet shows no red color in other parts of the plant. One has been found however that is pure for red glumes and shows no red in other parts with the exception of the silks.

General Consideration of Red Sap Color.

It is difficult to put aside the thought that all of these red colors are localizations of the same general pigment. If this were true, there should be a series of varieties in which increasing extension of color is found, until red appears in all the organs in which it ever occurs. This is not true. Varieties exist, for example, with red pericarp and red cob, with red pericarp and white cob and with white pericarp and red cob. If these formed a series with increasing extension of red one might find the color localized in the cob and not found in the pericarp, but the theory could not account for the existence of varieties with red pericarp and white cob. It seems as if these facts would drive us to one of two conclusions. We are dealing either with different color compounds each of which manifests itself in only one organ, or with identical genes held in the germ cells in such different combinations that they may be manifested differently. The latter interpretation is more probable, and the natural assumption is that identical genes held by different chromosomes in some way accounts for the different manifestations. Yet there is an obstacle to this assumption which though not necessarily insurmountable, is at least important. One cannot quite understand why a red color should be manifested in different organs simply because its gene is held by different chromosomes.

Since the first draft of this paper was written Emerson * has reported important data from many crosses where certain of these red colors of maize are sometimes absolutely coupled in their inheritance and sometimes show spurious allellomorphism. For example, if a plant with a red cob and a red pericarp is crossed with one in which these colors are absent, there is segregation in F_2, but the colors remain together. On the other hand, if a cross is made between a plant having a red cob and a white pericarp and one having a white cob and a red pericarp, the colors show spurious allelomorphism. The spurious allelomorphism is shown by the F_2 generation, in which is produced 1 red pericarp-white cob : 2 red pericarp-red cob : 1 white pericarp-red cob. His idea is that in the case first mentioned the colors are both carried in the same chromosome while in the second case they are carried in different but homologous chromosomes. As Emerson himself has stated, this theory assumes the inevitable pairing of the two chromosomes carrying the colors, which is probable but unproved. Our own data show no facts diametrically opposed to this hypothesis but the criticism regarding genes held by different chromosomes that was made above would also apply here.

Physical Transformations of Starchiness.

Although presence and absence of starchiness behaves as a Mendelian allelomorphic pair in heredity, the physical condition of the starch is a different matter. Starchiness acts as a filial or endosperm character and shows as Xenia in individual seeds.

---

* At meeting of Amer. Soc. Nat., Ithaca, N. Y., Dec. 29, 1910.

The physical condition of the starch behaves as a plant character affecting the entire ear. One may have ears which show a tendency towards the dented character in some seeds and a tendency towards the flint character in other seeds. Such ears are probably always heterozygous dent-flint combinations, and simply show zygotic variations. The different kinds of seeds give the same results in the next generation and show no tendency toward a real segregation of dent and flint characters in the individual seeds.

The difference in the appearance of the starch in the different races of maize has been described earlier in this paper. The immediate cause of these differences is the amount and location of the soft starch formed in proportion to that of corneous or translucent starch. In the pop corns there is total absence of soft starch or at most only a small amount immediately surrounding the top and back of the embryo. As this amount of soft starch increases, the starch cells of the seeds lose their ability to hold the steam formed by the moisture they contain when heated, and can no longer evert their entire contents as cooked starch. They may pop slightly but they can no longer be considered commercial pop corns. They have passed into the flint corn class. This class includes varieties with varying amounts of soft starch up to those in which it covers the cap. The latter are dent corns, for the dent is simply formed by the greater percentage of contraction which the soft starch undergoes in drying. The amount of dentness is in direct proportion to the thickness of the soft starchy layer at the cap. A few varieties are known in which the soft starch has replaced *almost all* the corneous starch. They are known as semi-starchy corns. They are not so well known however, as the floury corns in which the corneous starch is absent.

As all of these varieties are known in *Z. mays curagua*, *Z. mays hirta* and *Z. mays tunicata*, it is obvious that the proportions these two kinds of starch (in appearance at least) plays a great part in the commercial classification of maize. Also, since so many varieties are known in which every possible ratio of corneous starch to soft starch occurs, it is evident that the transmissible characters which cause these differences are relatively numerous and their interactions complex. For these reasons, it is perhaps too much to expect that the inheritance of this complex of characters will be cleared up until all possible combinations of these varieties have been made and studied. Our data serve only to establish certain general facts.

The first bit of evidence in the matter comes from a consideration of the behavior of the only class of maize varieties that apparently are beyond the scope of the subject in hand — the sugar varieties. When the latter are crossed with starchy varieties it is perfectly clear that starchiness is a separate character independent of the physical form in which it exists. Sugar varieties are found that are simply dents and flints which lack starchiness. We have also produced by crossing, sugar varieties that are characteristic pop corns lacking starch. No sugar varieties are known which would be soft starch varieties (Z. mays amylacea) if they contained the S factor, but it can hardly be doubted that such could be produced. The experimental evidence is as follows. When Black Mexican, Early Crosby and Golden Bantam are crossed with dent varieties, the Xenia starchy seeds, or F_1 generation are all flint-like in character. These when grown produce F_1 ears which have an appearance intermediate between dents and flints and give in F_2 ears which are characteristically flint in character. In the case of the cross between Black Mexican sugar No. 54 and Illinois High Protein dent No. 8, these flint segregates of F_2 were carried to the F_3 generation and bred true. Since pure dent varieties were the male parents of these crosses, the occurrence of flints in F_2 can only be accounted for by supposing that the sugar varieties that were used as the female parents of the crosses were latent flints. In the same way Stowell's Evergreen sugar and Late Egyptian sugar were proved to be latent dents by crossing them with starchy flint varieties. The Xenia seeds were dented and pure dents appeared in the F_2 generation. One peculiar thing occurred in the cross between Black Mexican sugar, No. 54 and Illinois High Protein dent, No. 8. In F_1 all of the ears were intermediate between dent and flint with a tendency toward dentness, except one. This ear was a pure flint in appearance. Only one of the intermediate ears was grown in the F_2 generation and it produced 91 dents and intermediates and 6 flints. The pure dents could not be separated from the intermediates but flints occurred in the ratio of one out of sixteen. The ear which was apparently flint in F_1 proved

PLATE XVI.

At left, No. 15, Longfellow flint. At right, No. 8 Illinois high protein dent. In center, F1 ears of cross 15x8, showing intermediate character of physical condition in which the starch is stored.

DENT-FLINT CROSSES.

to be an intermediate in F_2. Thirty-four ears were obtained, of which three were clearly dented, a number were intermediate, while from ten to twenty would ordinarily be classed as flints. Thirteen of the latter were grown in the F_3 generation and produced from 50 to 175 ears apiece. Nine out of the thirteen gave only flint ears in a total of 947 individuals. The other four ears produced a total of 264 ears of which between 10 and 20 were flints (i. e. ten were certainly flints and ten others were questionable). Therefore, since 9 out of 13 of the 20 ears classified as "probable flints" in F_2 proved to be true flints in F_3, we have 14 ears pure flint to 20 dents and intermediates in F_2. We do not know enough about this cross to say just what occurred here, but it is probable that one factor for dentness was missing in the pollen which produced the hybrid seed from which this lot F_2 ears came. In the other case a di-hybrid ratio appears.

Several other crosses were made between true dent and true flint races, that is, races in which the parents both were starchy. No. 15 Longfellow flint was crossed with No. 8 Illinois High Protein dent. The F_1 generation was intermediate in character. Through an unfortunate oversight data regarding the segregation in F_2 were taken on the progeny of only one ear of the three F_1 ears planted. This ear gave 33 dents and intermediates to 3 flints. About 200 ears were obtained from the other two F_1 ears planted and from our general field notes we can say that not less than 15 dents and intermediates to each flint ear were obtained. One flint ear gave a crop of 94 ears in F_3, all of which were flint. One dent ear grown in F_3 also proved to be pure. A better idea of these results is given by the photographs on Plates XVI and XVII, however, than can be given by written description.

Two crosses were made between No. 11, Sturgis' flint and No. 8, Illinois High Protein dent. Both were intermediate in F_1. In F_2, progeny of one F_1 ear of the first cross gave 44 dents and intermediates to 3 flints. In F_3, one ear from an intermediate of F_2 gave 23 dents and intermediates and 2 flints. Five F_1 ears of the other cross were grown in F_2 resulting in 175 dent and intermediate ears, and 17 flint ears. The ratio here is about 10 : 1, but if any error was made in the classification it certainly occurred by placing intermediates in the flint class.

Another cross of this kind was that of No. 5-5, Watson's flint with No. 2, Illinois Low Protein. The ears were intermediate in F_1. In F_2 there was segregation, for ears exactly like No. 2 were obtained. Out of the 101 ears obtained, however, no ears were produced that could be classed definitely as flints. One or two flint-like ears occurred which will be tested for purity this coming season. It is quite likely that we have here a tri-hybrid or possibly a tetra-hybrid.

The female parent of this cross, No. 5, was also crossed with No. 6, Leaming dent. F_1 generation was intermediate as before. Five F_1 ears were grown with the following results:

Dents and Inter.	Flints
98	16
71	17
51	5
42	7
Total, 262	45

These ears gave different ratios. Probably more ears were classed as flints than would prove to be such in the F_3 generation, yet they were classified similarly in each case and F_3 tests would probably only reduce the proportion of flints from each ear. Paradoxical as it may seem, however, different ratios are to be expected in F_2 if the general hypothesis concerning the applicability of Mendelian principles to cases where variation is apparently continuous, is true (East : 10). This is explained in the following paragraphs.

In the crosses described above three facts stand out definitely. The characters which give the flint or the dent appearance to maize are transmitted as plant characters to the entire ear and not as endosperm characters to the individual seed. They conform to the essential feature of Mendelism by showing segregation; and they are due to the action of more than one transmissible character. The question remains, can any or all of these characters be named?

Our experience suggests that the proportion of corneous starch to soft starch depends partially upon size and shape of the pericarp and upon the number of rows per ear. All of the races (pop corns) in which soft starch is absent have small seeds, and the full corneous starch character cannot be transferred to large seeds by recombination through hybridization. On the other hand, by crossing a pop maize with a dent maize dent seeds may be obtained which are much smaller than many races with flint seeds. Further, dent races are known which have much larger seeds than some races in which the corneous starch is entirely absent (the flour corns). There is also some relation between the size of the plant and the amount of soft starch in their seeds. The floury or semi-floury corns are in general larger than the corneous starchy corns. Here again, however, there is an overlapping, for we have produced dent races by crossing with dwarf pop races, which are much smaller in size than the large pop and flint races.

Relationship between the physical character of the starch and shape of pericarp is much more intimate than it is between the former and size characters. In the rice pops the pericarp is drawn to a point at the place where the silk is attached. This makes the rice pop races have rather long slender seeds, but it is probably due to a separate character or characters. Leaving this complication out of consideration one may say that the pop corns have small seeds which are almost as broad as they are long. As the seeds become larger, if the ratio of length to breadth remains about unity or less, flint races are formed. If, instead, the ratio of length to breadth increases, dent races are formed. On the other hand, medium large to large seeded races may have almost any ratio of length to breadth and be either flint, dent or floury varieties.

Of course the shape of the pericarp depends somewhat on the number of rows, as the greater this number the more the seeds are crowded together and thus lengthened. Small-seeded pop and flint races exist with as high as 20 rows, but when the seeds are medium in size flint races are usually 8-rowed and 12-rowed, and never — in our experience — over 16 rowed. Dent races, on the other hand, seldom occur with less than 12 rows, but when large seeded they do exist with as few as eight rows. Floury races we have never seen with less than 10 rows, but they reach as high as 24 rows.

These relationships may simply be correlations and not direct causes of the proportion of corneous starch to soft starch that exists in various strains of corn. But even if they were directly concerned, they could not account for the large number of differences in varieties, for none of the correlations are sufficiently high. Many other characters, the exact nature of which is unknown, must be concerned in the matter. The simplest interpretation of the matter seems to be the interaction of independent allalomorphic pairs of the nature reported by Nillson-Ehle (: 10) and East (: 10) in earlier papers. If this interpretation be granted, one should expect that greatest difference in character pairs would exist in the case of pop and starchy races. Flint and dent races with about the same size seeds and small differences in number of rows should differ by fewer pairs of characters.

We have seen that in two of such crosses the evidence points to the existence of two allelomorphic pairs giving pure flints and pure dents in the F_2 generation once in every sixteen individuals. In another cross (5-5 x 2) at least three character pairs are concerned. It happened that in two of these cases the male parents were Illinois High Protein and Illinois Low Protein dent races, which gives us some idea as to why there was a di-hybrid ratio in one case and a higher ratio in the other case. These two strains were both isolated by selection from a commercial variety known as Burr's White. This variety, as are most commercial varieties, is a mixture of complex hybrids. By continued selection of ears high in protein and of ears low in protein with close interbreeding of the progeny these two strains were isolated. The high proteid race is characterized by a high percentage of corneous starch, bringing it into closer relationship to the flint corns. The low proteid race is characterized by a high percentage of soft starch, bringing it into closer relationship with the flour corns. It was the high proteid strain, that is, the one nearer the flint varieties, that gave the di-hybrid ratio when crossed with a flint race; while the low proteid strain, — the one nearer the flour corns, — gave the higher ratio.

This result is what one should expect, but can the 6 : 1 ratio obtained in the cross between No. 5 and No. 6 be explained so easily? We believe it presents no difficulties if the complex gametic constitution of No. 6 is properly appreciated. The individual which furnished the No. 6 pollen came from a selfed daughter ear of the original No. 6. Its sister ears varied in number of rows from 12 to 20 with the mode at 16. The individual furnishing the pollen in cross 5 x 6 was in all probability therefore a complex hybrid itself, and the cross instead of being simple was really a collection of crosses. There is no doubt that many intermediate ears were classed as flint in the table given above. If they could all be grown for another generation it is quite likely that a series of mono-di-tri and higher hybrids would be found. It may be asked why, if this is the case, were not the other crosses complex? The answer is that they undoubtedly were more complex than they seemed. For example, if a large number of F_1 ears were grown it is likely that *some* would give ratios other than those found. It was simply chance that gave us fairly good di-hybrid ratios from a *few* F_1 ears in two instances. The most important reason why the cross with No. 6 was likely to be more variable than the others, however, lies in the fact that *all* of the other strains had been inbred for much longer periods.

Size Characters.

The remainder of Part IV will be devoted to a discussion of the inheritance of size characters, — variations that have been considered to be and to casual observation are, continuous. Our studies have been concerned with the number of rows per ear, height of plant, length of ear and size of seed.

It is perfectly obvious to one familiar with the maize plant that it is almost impossible to work out in detail the inheritance of the complex factors that interact to cause the transmissible differences in the size of its organs. That size characters are complex in themselves is shown by the numerous varieties grown commercially. They each vary from their own means, but different variety means in height are found all the way from two and one-half to fourteen feet with but little actual difference between the most similar strains. Further to complicate matters, all size characters respond to environmental stimuli, and these non-inherited fluctuations obscure the analysis of pedigree cultures in a still greater degree. *For these reasons we do not attempt to analyze our results further* *than to say that they do show segregation in every case.* And segregation is held to be the important and essential feature of Mendelism. Therefore we believe that size characters mendelize.*

Let us now consider the hypothesis by which segregation in characters apparently continuous in their variation, could come about. Nillson-Ehle (: 09) has shown that black glumes in oats when crossed with their absence behave sometimes as monohybrids and sometimes as di-hybrids, and that presence and absence of red pericarp color in wheat sometimes behaves as a tri-hybrid. He further showed, although not quite so conclusively, that presence and absence of ligule in oats behaves as a tetra-hybrid. In this and in a former paper (East : 10) it has been shown that yellow endosperm, red pericarp and dented seeds (as opposed to flinty seeds) behave as di-hybrids, with so many data that the facts can hardly be questioned. We have also shown although less conclusively that other red pericarped varieties and other varieties which differ in their ratios of soft to corneous starch behave as higher hybrids.

TABLE 26.

INHERITANCE OF ROWS IN CROSS (5 X 6).

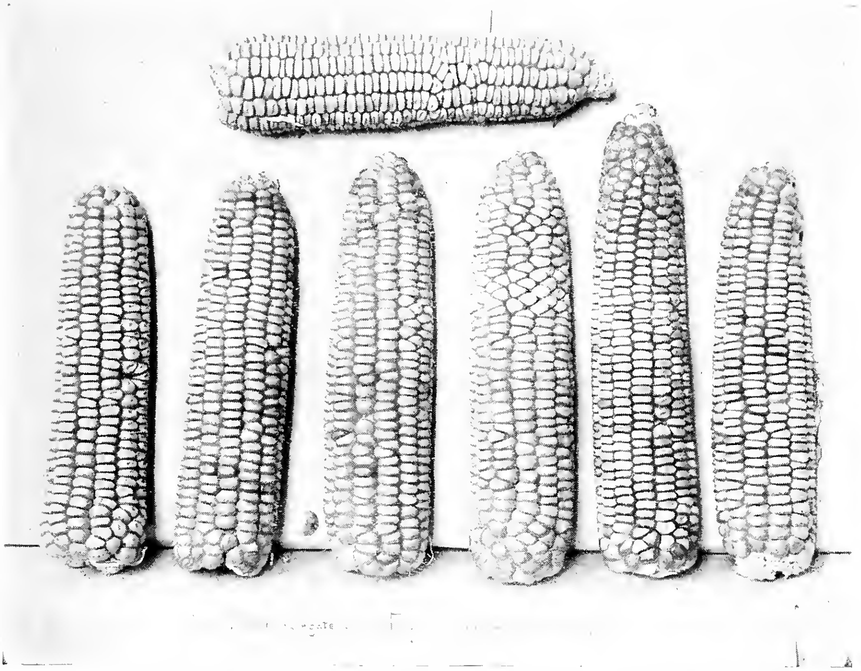
No.	Gen.	Rows of Parents	Row Classes								
			8	10	12	14	16	18	20	22	24
No. 5 flint (2 yrs.)	P	8	289	2	2						
No. 6 dent	P	18	. .	. .	6	31	51	18	4		
No. 5 x 6	F_1	8	13	36	53	10					
(5 x 6)–1	F_2	12	12	48	35	9	1				
(5 x 6)–2	F_2	10	7	22	15	2					
(5 x 6)–22	F_2	10	8	45	31	1					
(5 x 6)–23	F_2	12	4	25	60	18	4	2	1		

It should be clearly understood what this means to Mendelian theory. *Several genes for the same character may exist in the germ cells of one organism, the number being limited possibly by the number of chromosomes.* The limited number of cases thus

---

* It is probable that the number of internodes per plant is one of the factors directly concerned in the inheritance of height of plant.

PLATE XVII.



a. F2 dent segregate above (frequency about 1 in 10). Random sample of its F3 progeny below.

b. F2 flint segregate above (frequency about 1 in 16). Random sample of its F3 progeny below.

Dent-Flint Crosses.

far found presumably is due to the fact that few size characters have been investigated, for nowhere would these phenomena be so likely to occur as in quantitative characters.

It is fortunate for us that it has been possible to prove the presence of several independent allelomorphic pairs due to produce the same somatic character, for characters like color where dominance is relatively perfect. Beginning with this as a basis, one can extend the theoretical possibilities of such facts to other cases and thus be better prepared for the paradoxical complexities that occur in actual pedigree cultures. When in a cross there is simple presence dominant to absence of one gene for a certain character, the ratio in F_2 is 3 dominant to 1 recessive; when two independent allelomorphic pairs producing the same character are concerned, the ratio in F_2 is 15 dominants to 1 recessive. In general then if n allelomorphic pairs are concerned, in F_2 there will be a ratio of 4^n-1 dominants to 1 recessive. It is not likely however that dominance is ever perfect in these complex hybrids. For example, in the case of the two yellow colors in the maize endosperm, the intensity of the yellow decreases in the following order $Y_1Y_1Y_2Y_2$, $Y_1y_1Y_2Y_2$ or $Y_1Y_1Y_2y_2$, Y_1Y_1 or Y_2Y_2, Y_1y_1 or Y_2y_2 and $y_1y_1y_2y_2$. In size characters dominance is probably very incomplete or absent. A heterozygous combination presumably produces half the effect of a homozygous combination. Then as dominance becomes less and less evident the Mendelian classes vary more and more from the formula $(3+1)^n$ and approach the normal curve of error $(\frac{1}{2}+\frac{1}{2})^n$. When there is no dominance

TABLE 27.

INHERITANCE OF ROWS IN CROSS (5 x 2).

No.	Gen.	Rows of Parents	Row Classes								
			8	10	12	14	16	18	20	22	24
No. 5 flint (2 yrs.)	P	8	289	2	2						
No. 2 dent	P	16	..	..	2	14	56	42	20	1	1
No. 5 x 2	F_1	8	1	9	20	4					
(5 x 2)–6	F_2	10	4	18	61	14	3	1			

and open fertilization, a state is reached in which the curve of variation simulates the fluctuation curve, with the difference that the gradations are heritable. The heritable variations are always more or less obscured, however, by the ever present fluctuation.

The experimental results may now be considered—remembering only that fluctuations are present and that in maize many genotypes are often present in one parent. In Table 26 are shown the results from a cross between a race practically pure to the eight rowed type, No. 5, and a dent No. 6, which varies from twelve to twenty rows with the mode at sixteen rows. The F_1 generation is intermediate and furnished four inbred ears that were grown in the F_2 generation. Now three of these four F_2 families show no greater range of variation than F_1, yet it is a noticeable fact that they vary in different ways. Ear (5 x 6)-1 shows a modal condition at ten rows. It may be considered that the crossed seed from which the F_1 ear that produced this crop came, contained the genes for lower numbers of rows from the varying parent, No. 6. Ear (5 x 6)-23, on the other hand, evidently contains genes from No. 6 that were due to produce higher numbers of rows.

TABLE 28.

INHERITANCE OF ROWS IN CROSS (11 x 5).

No.	Gen.	Rows of Parents	Row Classes								
			8	10	12	14	16	18	20	22	24
No. 11 flint	P	12	1	4	387	7	1				
No. 5 flint	P	8	289	2	2						
No. 11 x 5	F_1	12	2	11	26	2					
(11 x 5)–8	F_2	12	10	38	107	23	8				
(11 x 5)–18	F_2	10	19	33	100	5					

Table 27 shows a slightly higher variability in F_2 than in F_1.

Table 28 is interesting because it shows the results of a cross between two varieties that have been selected for many years until they are relatively true to the 12-rowed and 8-rowed

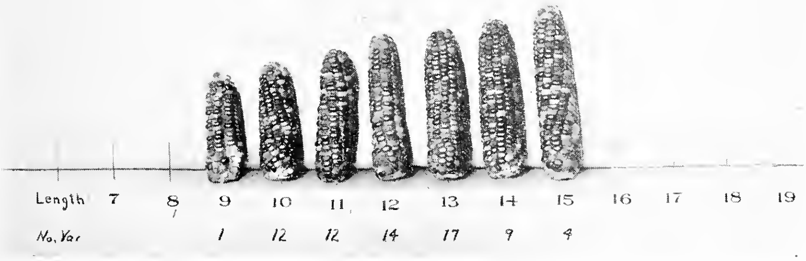
PLATE XVIII.

a. No. 60, Tom Thumb maize, showing variation in length of ear. Class centers are even centimeters $({}^{1}{}_{6})$.

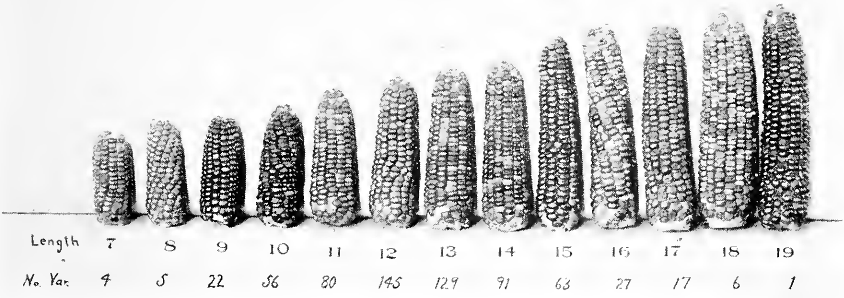
b. No. 54. Black Mexican sugar maize, showing variation in length of ear $({}^{1}{}_{6})$.

INHERITANCE OF LENGTH OF EAR.

PLATE XIX.



a. Variation in length of ear of F1, generation of cross between No. 60 and No. 54 ($\frac{1}{6}$).



b. Variation in length of ear of F2 generation of cross between No. 60 and No. 54. Family (60-5x54) ($\frac{1}{6}$).

INHERITANCE OF LENGTH OF EARS.

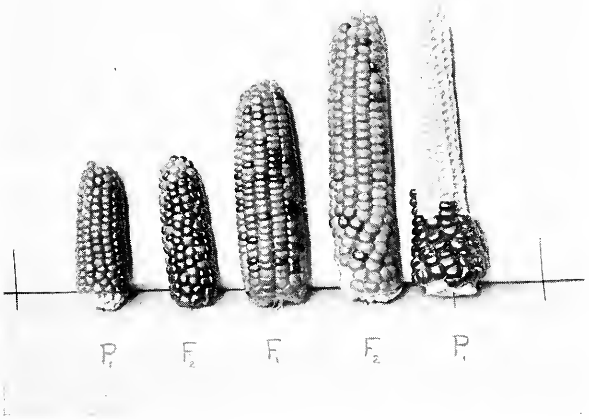
PLATE XX.

a. Variation in length of ear of F_2 generation of cross between No. 60 and No. 54. Family (60-3x54) ($\frac{1}{6}$).

b. Variation in length of ear of F_2 generation of cross between No. 60 and No. 54. Family (60-8x54) ($\frac{1}{6}$).

INHERITANCE OF LENGTH OF EARS.

a. Average size of seeds of No. 60 (upper left) and No. 54 (lower left) and the F1 generation of the cross between them. Extremes of the F2 generation at right.



b. Average ears of No. 60 (left) and No. 58 (right) with average of F1 generation in center. Extremes of F2 generation shown.

SIZE INHERITANCE.

TABLE 29.

INHERITANCE OF ROWS IN CROSS (11 x 18).

No.	Gen.	Rows of Parents	Row Classes 8	10	12	14	16	18	20	22	24
No. 11 flint	P	12	1	4	387	7	1				
No. 18 sugar (2 yrs.)	P	12	13	32	51	4					
No. 11 x 18	F_1	12	2	10	24	1	1				
(11 x 18)–4	F_2	12	1	9	78	10					
(11 x 18)–10	F_2	10	8	13	62	13					

conditions, respectively. F_2 shows a distinctly higher variability than F_1. It is expected that 8-rowed F_2 plants may breed relatively true.

Table 29 is given simply to show that a cross between two 12-rowed varieties does not show an extension of the row classes. Such a condition should sometimes be possible if our general hypothesis is true, yet it might not occur in more than one cross in hundreds.

Table 30 shows the results from a cross between another variety true to the eight rowed condition and a variety which varies from ten to eighteen rows with the modal condition at twelve. Unfortunately only a few plants matured in the F_1 generation and no conclusions can be drawn regarding its variability. The F_2 generation apparently shows a marked segregation. The

TABLE 30.

INHERITANCE OF ROWS IN CROSS (15 x 8).

No.	Gen.	Rows of Parents	Row Classes 8	10	12	14	16	18	20	22	24
No. 15 flint	P	8	100	1							
No. 8 dent	P	14	. .	3	54	36	12	2			
No. 15 x 18	F_1	8	. .	2	5						
(15 x 8)–2	F_2	10	14	15	28	9	1				
(15 x 8)–3	F_2	12	4	13	25	6	3				
(15 x 8)–2–10	F_3	14	. .	1	8	14	6	1	1		
(15 x 8)–2–1	F_3	8	32	35	23	4					
(15x 8)–2–5	F_3	12	4	41	116	15	3	1			

results in the F_3 generation are the most interesting, however, for the progeny of an eight rowed F_2 show a distinct tendency toward an 8-rowed condition, while progeny of F_2 ears having twelve and fourteen rows respectively, though highly variable, show a transmission of their parental qualities.

Our largest pedigree series for number of rows is shown in Table 31. The male parent is the same as was used in the previous cross. The female parent is an eight-rowed type but is not so pure for this condition as the eight-rowed varieties previously used. The general crop in F_1 was discarded before the data was taken upon the number of rows. This oversight is partially rectified by the records from 21 hand-pollinated ears, but the true variability is presumably somewhat greater. Two F_1 ears were grown in the F_2 generation, one having the moda condition at ten rows and the other at twelve rows. Nine ears from the F_2 progeny from (8 x 54)-1 produced F_3 crops. This table should be examined in order to appreciate the significance of the results of this generation. There is a marked tendency in different ears to segregate into twelve-row and eight-row types. Two of the ears have modal conditions at ten rows,

TABLE 31.

INHERITANCE OF ROWS IN CROSS (8 x 54).

No.	Gen.	Rows of Parents	Row Classes								
			8	10	12	14	16	18	20	22	24
No. 8 dent	P	12	..	3	54	36	12	2			
No. 54 sugar	P	8	89	25	7						
No. 8 x 54	F_1	12	1	6	14						
(8 x 54)-1	F_2	12	9	22	16	1					
(")-5	F_2	12	1	3	16	1					
(")-1-1	F_3	10	..	15	87	4					
(")-1-2	F_3	8	20	38	50						
(")-1-2a	F_3	10	61	48	54						
(")-1-3	F_3	10	32	75	15						
(")-1-3a	F_3	8	5	20	27	1					
(")-1-5	F_3	12	..	33	158	26	3				
(")-1-6	F_3	12	4	36	109	8	2				
(")-1-10	F_3	8	Very irregular, mostly 8-rowed								
(")-1-13	F_3	10	96	43	8						

but their variability is so great that the presumption is that this represents simply the continuance of the heterozygous condition. In our opinion there is no question about segregation of number of rows but we are perfectly aware that the believer in selection would be justified in the criticism that that is the cause of the results obtained.

Table 32 shows the frequency distribution of the heights of two varieties Nos. 5 and 6, and the F_1 and F_2 generations of the resulting cross. A good idea of the possible segregation in the F_2 generation of such crosses as this, is obtained by the comparative size of the coefficient of variation of the F_1 and the F_2 generations. In every case it is at least 50% higher in the F_2 generation than in the F_1 generation. The F_1 generation is not intermediate between the two parents but is nearly as high as the taller parent. This fact is not to be regarded as in any way connected with dominance. It is due to the increased vigor which comes from crossing in maize as shown in a previous paper (East : 09). The total results of the F_2 generations show segregation from the lowest class range of the shorter parent to the highest class range of the taller parent. It must not be thought however that these segregates are regarded as pure types. Their behavior in further generations is still problematical. Continued selection of shorter or taller segregates presumably will give an approach toward the selected condition. The criticism that any such results would be due to selection and not segregation is not valid in this case, however, for segregates of extreme types that never appear in either of the parents alone have occurred here in the F_2 generation.

Table 33 shows similar segregation in heights of plants in another cross, No. (54 x 60). The frequency distribution of the heights in No. 54 was obtained from plants grown during the season and on the same soil upon which the F_2 generation was grown. The exact distribution of heights of No. 60 and of the F_1 ears was not taken because at that time another object was in view. The range of distribution as shown by the black lines, is correct. From notes recorded at the time we know that the F_1 generation was quite uniform, the measurements being distributed around classes 67 to 73. Here again the effect of crossing is observed in the relatively tall plants of this generation. The lowest plants in the F_2 generation reach the upper range of No. 60 while the highest plants are practically the height of the highest plants of No. 54. The reason that no plants were obtained in the lower range of No. 60 is due no doubt to their continued heterozygous condition in some of their characters and therefore an increased vigor.

Table 34 shows that the lengths of ears in the above cross segregate in a similar manner. The F_1 generation is not forced toward the long-eared parent as it is in the heights of the plants. In other words ear length does not show the increased vigor due to heterozygosis that is seen in the heights of plants. There can be scarcely a doubt that the greatly increased variability in F_2 is the direct result of segregation.

The segregations of weights of seeds in the above cross is shown in Table 35. The Black Mexican parent No. 54 shows somewhat distorted variation in this character as there are four classes of large sized seeds containing only six ears in all. No F_2 segregates occurred of this size. The reason is that the ears of No. 54 which produced this crop were commercial seed of which only three individuals were used in crossing. The F_1 generation in both Tables 34 and 35 were recorded from only one cross although three crosses were made. To be strictly fair, therefore, the F_2 generation of cross No. (60-5 x 54) is the only one that can be directly compared with the F_1 generation given. We have records, however, of a sufficient number of ears of the other two crosses to know that they differ but slightly if any from the one recorded in the tables. But even if we should be conservative and leave out of consideration the F_2 generations of crosses (60-8 x 54) and (60-3 x 54), there is still no question but that segregation has occurred.

TABLE 32*.

FREQUENCY DISTRIBUTION OF HEIGHTS OF PLANTS IN CROSS (5 x 6).

No.	Class Centers in Inches for Heights of Plants																					A.	S. D.	C. V.
	51	54	57	60	63	66	69	72	75	78	81	84	87	90	93	96	99	102	105	108	111			
5	3	2	4	5	11	17	17	18	10	6	4	..	..	..	..	..	..	..	..	..	..	68.22± .406	6.49± .324	9.51± .421
6	..	..	..	..	..	..	..	..	..	..	..	..	1	2	2	13	14	16	14	8	3	101.18± .400	5.07± .283	5.01± .279
(5 x 6) F_1	..	..	..	..	..	..	..	..	..	..	5	4	3	9	9	6	5	4	4	7	..	94.53± .740	8.21± .519	8.68± .553
(5 x 6)–1 F_2	2	1	3	6	3	5	10	10	22	16	10	7	11	13	6	10	8	4	4	2	..	81.00± .685	12.76± .486	15.75± .684
(5 x 6)–2 F_2	..	..	..	2	..	2	4	2	6	5	12	8	12	6	5	8	3	10	8	2	2	88.33± .802	11.78± .567	13.34± .675
(5 x 6)–8 F_2	2	..	..	..	4	4	12	7	9	13	12	15	10	8	8	1	1	1	..	..	..	79.46± .621	9.55± .438	12.02± .559
(5 x 6)–14 F_2	..	1	2	4	2	7	8	17	21	11	27	24	16	9	11	10	5	4	2	..	..	81.24± .513	10.28± .364	12.65± .450

* Grown side by side in same season.

TABLE 33*.

FREQUENCY DISTRIBUTION OF HEIGHTS OF PLANTS IN CROSS (54 x 60).

No.	Class Centers in Inches for Heights of Plants																								Total
	22	25	28	31	34	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	
No. 54	..	..	..	..	..	..	..	..	..	..	..	..	2	6	10	17	24	26	21	14	14	7	3	1	145
No. 60	<—	—	—	—	—	—	—>[1]	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	100
(60–5 x 54) F_1	..	..	..	..	..	..	..	..	..	..	..	..	..	<—	—	—	—	—	—	—	—	—>[2]	..	..	55
(60–8 x 54) F_1	..	..	..	..	..	..	..	..	..	..	<—	—	—	—	—	—	—	—	—	—	—	—>[3]	..	..	26
(60–3 x 54) F_1	..	..	..	..	..	..	..	..	..	..	..	<—	—	—	—	—	—	—	—	—	—	—	—>[4]	..	30
[5](60–5 x 54) F_2	..	..	..	..	..	2	2	1	8	18	26	44	95	117	126	92	59	31	22	3	3	..	..	..	649
[6](60–8 x 54) F_2	..	..	..	..	..	1	..	1	5	6	13	13	35	29	36	27	21	20	9	6	4	1	1	..	228
[7](60–3 x 54) F_2	..	..	..	..	..	5	15	13	32	31	68	60	72	34	47	14	13	5	..	..	..	..	..	..	409

* Distributions giving figures grown side by side in same season.

[1] [2] [3] [4] Extremes were measured and number of plants counted. All strongly convergent around the central classes.

[5] Grown from five different ears.

[6] Grown from two different ears.

[7] Grown from three different ears.

TABLE 34*.

FREQUENCY DISTRIBUTION OF LENGTHS OF EARS IN CROSS (60 x 54).

No.	Class Centers in Cm. for Lengths of Ears.																	A.	S. D.	C. V
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21			
No. 60	4	21	24	8	..	..	..	..	..	..	..	..	..	..	..	..	..	6.6± .073	.81± .051	12.27± .783
No. 54	..	..	..	..	..	..	..	..	3	11	12	15	26	15	10	7	2	16.8± .121	1.87± .088	11.13± .531
(60–5 x 54) F_1	..	..	..	..	1	12	12	14	17	9	4	..	..	..	..	..	..	12.1± .121	1.51± .088	12.48± .722
[1](60–5 x 54) F_2	..	..	4	5	22	56	80	145	129	91	63	27	17	6	1	..	..	12.7± .058	1.99± .037	15.67± .296
[2](60–8 x 54) F_2	..	..	1	10	19	26	47	73	68	68	39	25	15	9	1	..	..	12.9± .076	2.25± .053	17.44± .413
[3](60–3 x 54) F_2	..	..	2	5	17	33	33	33	27	21	13	10	11	12	1	2	1	12.6± .128	2.81± .087	22.30± .744

* No. 60 and F_1 gen. grown in 1909, F_2 gen. in 1910.

[1] Grown from five ears.

[2] Grown from two ears.

[3] Grown from three ears.

TABLE 35.

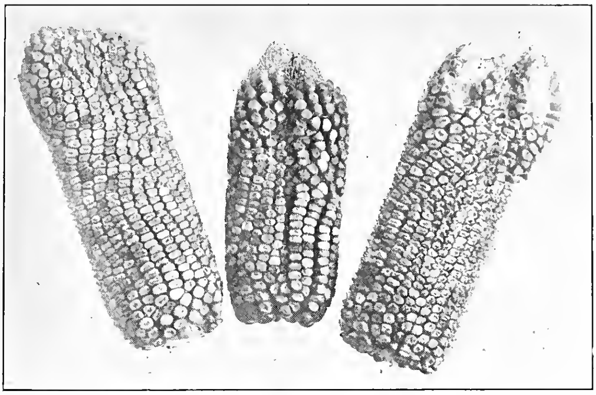
FREQUENCY DISTRIBUTION OF WEIGHTS OF SEEDS OF CROSS (60 x 54).

No.	Class Centers in Grams for Weights of 25 Seeds.																				A.	S. D.	C. V
	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5			
60	7	22	28	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2.7± .034	.39± .024	14.44± .899
54	..	..	..	..	..	..	..	..	2	2	5	7	14	10	5	4	1	2	1	2	8.3± .107	1.21± .074	14.54± .963
(60–5 x 54) F_1	..	..	..	5	12	13	17	4	3	..	..	..	..	..	..	..	..	..	..	..	4.6± .059	.64± .041	13.91± .912
[1](60–5 x 54) F_2	..	1	7	17	49	98	113	83	69	43	27	13	8	1	..	1	..	..	..	..	5.3± .032	1.09± .022	20.56± .442
[2](60–8 x 54) F_2	..	..	..	1	3	15	16	17	23	23	18	12	8	9	1	1	..	..	..	..	6.2± .067	1.23± .047	19.84± .799
[3](60–3 x 54) F_2	..	..	..	4	10	24	41	53	40	52	21	19	9	8	2	3	..	..	..	..	6.0± .047	1.17± .033	19.50± .563

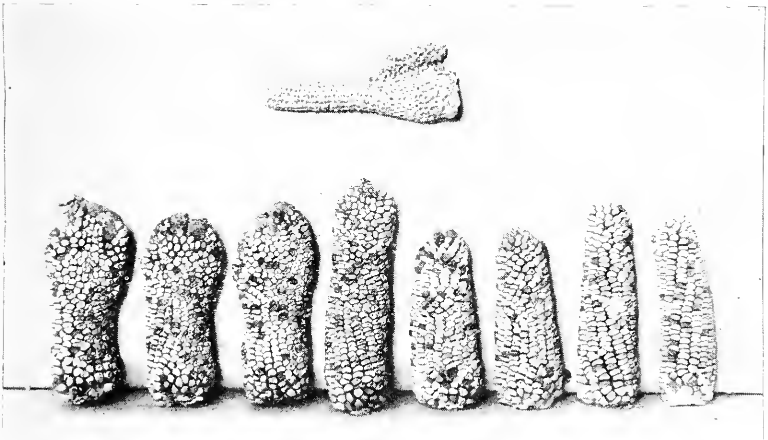
[1] Grown from five ears.

[2] Grown from two ears.

[3] Grown from three ears.



a. Fasciated ears. F2 generation of cross with normal showing dominants and heterozygotes.



b. F2 cob of heterozygote above; sample of F3 progeny below. From left to right first six show the abnormality in different degrees. Last two ears are normal.

INHERITANCE OF EAR FASCIATIONS.

PART V.

PLANT ABNORMALITIES.

A few abnormalities have appeared in the maize varieties under observation during the progress of these investigations. They have been studied with two objects in view. The first object was to see whether the manner of transmission of heritable monstrous characters gives any clue to the reason why monstrosities have seldom obtained a foothold in nature when in competition with normal types. The second object was commercial. If teratological specimens appear in commercial varieties of maize, it is desirable to know the easiest method to destroy them.

Dwarf Forms.

The first dwarf form appeared in the 1908 culture of No. 6 Leaming dent. This strain had been selfed for the two previous years without producing dwarfs. In the third generation, however, in a culture of 100 plants 5 dwarfs appeared. The plants were normal in appearance, having all parts correlated as in the full sized plants, as is shown in Plate XXV. They were from two to three feet in height and contrasted strangely with the other plants of the variety which were from nine to eleven feet in height. The female flowers seemed to be normal. At least cobs were formed and silks appeared. The pollen however was completely sterile. The dwarf plants were pollinated first with their own pollen and when no seeds formed were pollinated with pollen from normal-sized plants. A few seeds formed on two ears, which were planted the next season. From one ear which had been borne on a plant eighteen inches high only two plants resulted, one being a dwarf and the other of normal height. From the other ear which came from a plant three feet six inches high, seventeen individuals resulted, one of which was a dwarf. The dwarfs, as in the former year, had a normal correlation of parts. The leaves were opposite and the ear appeared in the axil of the sixth leaf from the top as in the normal plants. The pollen appeared to contain some normal grains this year and both of the plants were selfed. No seed set, however, and when pollinated with pollen from normal plants it was found that the silks had passed the receptive stage. This delay lost the strain. Seeds from the old ear of No. 6 had again been planted and had given two dwarfs out of sixty plants, but these had been lost in the same manner.

No. 69-5 a flint with a mosaic red pericarp also gave similar dwarfs with a ratio of 48 normal to 14 dwarf plants. The ear from which they came was a selfed ear from a commercial strain obtained the year before. The commercial strain had given no dwarfs but as only about 100 plants had been grown it is uncertain whether or not they had ever appeared before.

A different kind of dwarf plant appeared in a commercial strain of Stowell's Evergreen sugar corn in 1908. It was very short (18 inches) and had short leaves of the normal breadth. The joints were very close together and the whole appearance of the plant suggested a normal plant that had been pushed together like a telescope. An attempt to self this plant failed, but four days afterward it was pollinated with pollen from a normal strain of Stowell's Evergreen. A fairly good ear resulted which was planted in 1909. One dwarf like the maternal parent appeared out of thirty-seven plants. It was completely sterile, but a selfed normal plant from the same lot gave two dwarfs out of seventy-six plants in 1910. (See Plate XXIV.)

It is a matter of conjecture what occurred in these cases. In the first instance, at least, controlled cultures that had produced no dwarf plants, suddenly threw dwarfs. It was a much more definite occurrence than De Vries' Oenothera mutations for these were mutating when De Vries found them. If the normal type were completely dominant, one must conclude that one seed had been selfed in the case where the dwarf was pollinated with pollen from normal Stowell's Evergreen. In the other two cases the cross-pollination was made with pollen from plants of the same strain, and as only a small number of individuals were produced in the next generation, production of dwarfs was probably continued through the pollen gametes.

The variation was transmitted by plants normal in character, and whether one believes it to be a case of Mendelian dominance of normals or not, there was nevertheless definite segregation.

The fact that segregates appeared in ratios of less than one abnormal to three normal, may have been due to any one of several causes. Abnormal zygotes may have been formed and not have been able to develop, for the germinating power of the seeds formed on the dwarf plants was very low. On the other hand, it may be that this result was due to the same fact that probably gives rise to higher ratios in crosses that have been studied thoroughly; namely, more than one chromosome possesses the necessary material for normal height. There is also the possibility that many abnormalities, particularly those which show great latitude in their development, are due not to regular Mendelian segregation, but to some abnormal chromosome reduction. If some reductions took place normally and some abnormally through some disturbance of the plant's normal physiology, abnormal and normal plants might be produced without definite and constant ratios.

Regularity of Rows of Seeds on Cob.

The great majority of maize ears have rows of seeds running in straight regular rows from butt to tip. Sometimes two rows or even four rows may be dropped in going from the butt to the tip but even then a sufficient amount of regularity exists to call them straight-rowed ears. A varying percentage of ears in each variety, however, have the rows quite irregular, — the seeds often being squeezed together in such a hit and miss manner that the number of rows can only be counted by making cross sections of the cob. Experience with maize cultures shows that there are two distinct kinds of irregularity, one a physiological fluctuation which is not inherited, and one a definitely inherited character or possibly a set of characters. The non-inherited fluctuations are always present while the inherited irregularity may be present or absent. The latter kind has been isolated in several varieties, the most conspicuous being the Country Gentleman sugar corn.

Since the inherited irregularity can only be distinguished from the fluctuation by breeding and then with difficulty owing to the obscuring effect of the latter, it is difficult to come to any conclusion regarding the method of its transmission when dealing with mixed strains. It could undoubtedly be determined by careful work with a cross of which Country Gentleman formed one of the parents. We have not made such a cross, but observations of large commercial cultures of Country Gentleman lead us to believe that irregularity is a Mendelian dominant, although it may not act as a simple mono-hybrid.

Ears with irregular rows appearing in our cultures have been planted several times, but have proved to have been due to physiological fluctuation in all but one instance. An ear of strain 29-2 produced some ears with irregular rows, one of which happened to have been inbred. This ear gave 33 normal progeny and 12 with irregular rows in the next generation. One of these irregular ears gave 33 normal and 15 irregular ears in a further generation, while one of the regular rowed ears gave 125 normal and 5 irregular ears. One of these 5 irregular ears was selfed and will be tested next year. This is about the percentage of irregular ears that the variety gives in the commercial field, however, so the idea suggests itself, that these five ears were fluctuations. If we regard this as the true interpretation of the regular ears giving irregular ears, and reduce the number of irregularities in the progeny of the irregular ears in the same proportion, a ratio of 66 normal to 23 irregular ears is obtained. This looks like a case of monohybridism with reversed dominance. It is suggested, however, if this is a case of twice planting a heterozygous mono-hybrid; that it is an example of fluctuating dominance in which some apparently normal ears are really heterozygotes. One cannot even say that only homozygotes show dominance, for it was an irregular ear in each case that threw normals. There is no *a priori* reason why this hypothesis should not be true, but it seems probable that a more complex set of conditions exists. The one fact that stands out clearly is that if the percentage of irregular ears increases much over four percent in a commercial progeny row culture, the whole culture must be discarded to eliminate the undesirable "blood."

Bifurcated Ears.

Occasionally there is found among the eight rowed flint corns ears which have only four rows. Their cobs are grooved so that they appear to be almost splitting. One of these individuals appeared in a culture of No. 17 (Palmer's Red-nosed yellow) that had been selfed for three generations. It was grown with the special object of finding out whether the four rowed condition is a final recessive condition as to number of rows. This proved not to be the case. The condition is a secondary effect of a heritable abnormality which causes the cob to show various conditions of splitting into two rowed sections at the base. The variations in this feature are shown in Plate XXIII, fig. a. From this ear, 34 ears abnormal in varying degrees and 12 normal ears were obtained. This ratio suggests the progeny of an ear heterozygous for presence and absence of the abnormality. It will be tested further.

A bifurcation of a different kind appeared in the progeny of No. 7 Leaming dent that had been selfed for four years. In its extreme form the tip of the growing ear becomes monstrously fasciate; but it may vary toward the normal to such a degree that the abnormality is shown only as a slight flattening of the ear when observed in cross-section. The ear in which this abnormality appeared was only slightly flattened; its progeny, however, showed 11 with divided tip and about 20 flattened ears out of 44. (See Plate XXII.)

The normal-eared grand parent of No. 7 had been crossed with No. 19, and from an extracted starchy ear of the F_2 generation there resulted the same abnormality. This ear, No. (19 x 7)-5-7 had a divided fasciate tip. It produced 29 ears with divided tip, 33 ears abnormally flattened and 23 normal ears, — a ratio of 62: 23. The illustration of this sort of fasciation shown in Plate XXII, fig. b, gives an idea of how gradually the abnormal ears intergrade with the normal ears. Yet this is a dominant character alternatively inherited. It is difficult to tell the pure normal ears by inspection but they appear to breed true when isolated.

Ears with Lateral Branches.

An illustration of an ear with lateral branches which is probably nearer the ancestral type of maize appeared in the original culture of No. 17. It is figured in Plate XXIII, fig. b. The ear was not hand pollinated and of course no conclusion can be drawn from the ratio in which the abnormality appeared in the next generation. As a matter of fact 4 ears out of 25 progeny were so affected. One of these happened to have been selfed, but it produced only a few seeds. Ten plants resulted from this poor individual, two of which were abnormal.

The only valid conclusion from these data is that the character does segregate. Normals and abnormals are produced; which fact suggests — as stated earlier in the paper — that the loss of the lateral branching character of maize occurred as a retrogressive mutation.

Plants with Striped Leaves.

Zea mays japonica is a race which produces leaves with longitudinal stripes with and without chlorophyll formation. In other words, the leaves are green with white stripes. Several races of this kind exist where the striping is apparently homozygous and the race breeds true. What experience we have had with striped races has been with another type of striping. The phenomenon has appeared several times in our cultures, and is clearly the same thing that Baur (: 09) obtained in pelargoniums. The full green type is dominant, the striped type is heterozygous, while the homozygous recessives are sometimes formed but cannot live because they lack assimilating organs. Crosses between the striped plants and normal green plants always gave all green progeny. Planting, in two cases, from plants that were striped when very young, 274 normal and 27 striped plants were obtained. This result might seem to indicate a more complex condition than Baur obtained. It is not necessarily so, however, for the plants were first examined for striping when about 18 inches high. This may have been too late to give them the proper classification, since it was found that many of the 27 striped plants became greener as they aged. Several plants without chlorophyll died when only a few inches high. These were probably homozygous recessives.

Hermaphrodite Flowers.

Perhaps it should be mentioned in passing that the immature sex organs, so called, of maize seem endowed with the power of becoming either stamens or carpels. One often finds a normal ear ending in stamens, and nearly every plant produces lateral branches which have carpels and stamens mixed together indiscriminately.

A number of cases have also been observed where a few of the ovules of an ear were surrounded by three stamens as in a perfect flower. The only instance we have seen where all of the ovules had three stamens within the glumes of the flower that is usually aborted, was that of the dwarfs with wide leaves mentioned under the heading "Dwarf forms." It might be supposed that this was an atavistic type representing some of the characters, at least, of the ancestral maize. We should prefer to believe, however, that this development of stamens is merely an accompaniment of the dwarfing due to an endeavor to retain physiologic balance. That is, this type is really a healthy luxuriant form producing very large ears for such a small plant. There may have been developmental energy present which when unable through inner limitations to produce a tall plant, manifested itself in producing stamens.

Considered together, these various abnormalities present several interesting features. It would be rash to make any dogmatic statements in regard to their inheritance, yet it is fair to say that if dominance shows progressive — and recessiveness retrogressive — variations, both types are present. Some of them are evidently simple in character — as far as inheritance goes — while others are complex. It may be that the same apparent type of variation will be found to be simple in some races and complex in others. By this it is meant that both 3 : 1 and higher ratios will be found affecting characters which to the eye are the same.

It does not seem probable that abnormal and degenerate types are always or even commonly extracted recessives in which absence of characters is concerned, as Davenport (: 08) has suggested. This statement has little basis from the data presented here, but the senior author has worked out certain dominant abnormal types in the genus Nicotiana which adds to our experience. The presumption is that they are more often dominant like most of the abnormalities found in man.

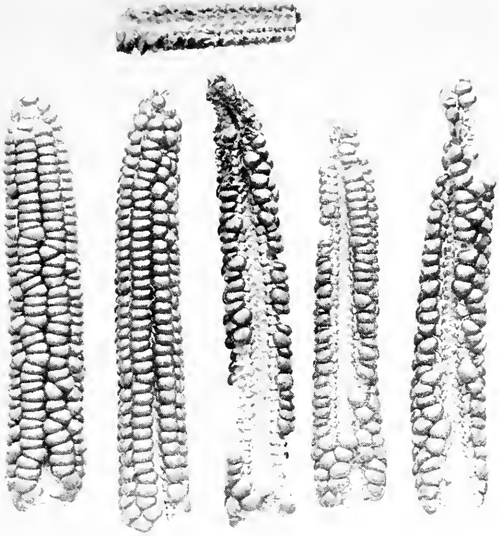
Perhaps the fact of prime importance from these data is the variable dominance of characters and their obscuration by physiological fluctuation. As stated once before, this shows the extreme importance of pedigree cultures to the commercial breeder, for some of these complex abnormalities cannot be distinguished from normal plants by gross inspection. It is possible that histological study might show points of difference but these methods are not at the command of the commercial grower.

It will be noticed that several monstrous variations occurred in strains that had been selfed for several generations. The effects of inbreeding in maize will form the subject matter of another paper, but it might be well to suggest here a possible cause for their production. Inbreeding in maize gives the same effect as lack of nutrients, while cross-breeding gives the opposite effect. There is retardation or acceleration of cell division, respectively. Now such monstrosities as ears with divided tips, occur more frequently either in cross-bred plants that are over supplied with fertility, or in inbred plants. Perhaps the first case represents fluctuation only, and is uninherited; as to this point we have no data. But disregarding this possibility, might not abnormal distribution of chromatin produce these variations in both cases. The first kind could be caused by abnormally accelerated division and the second kind by abnormally retarded division.

General Conclusions.

The various points of genetic theory discussed in this paper are not sufficiently connected to make possible a short and at the same time intelligible recapitulation. We simply desire to mention our conclusions regarding the central problem of all genetic investigations, that of laws of heredity.

When Mendel's Law of Heredity was rediscovered in 1900, it was the general belief that it covered only a few isolated cases. Many apparent exceptions were cited. One by one, however, these exceptions have been found to yield to interpretation by simple extensions of the Mendelian notation when fully understood. In our experience as reported here, no exceptions to Mendelian interpretation have been found. Such exceptions may exist, yet it seems as unwise to say that Mendel's Law is not general as to conclude at once that it can be made to cover every possible case. One may say that Mendel's Law has



a. Heterozygous bifurcated cob above; dominant and heterozygous progeny below showing imperfect dominance.

b. Multiple ear. An imperfectly dominant character. Aboriginal maize probably possessed a similar character.

ABNORMALITIES.

A plant of the dwarf mutation appearing in Stowell's evergreen sugar maize compared with a normal ear of the latter.

Dwarf Forms.

A dwarf type which appeared in Leaming dent maize compared with a normal ear of that variety.

DWARF FORMS.

covered so many cases that its generality is rendered highly probable, although insufficient genetic investigation has been accomplished to place it on equal terms with any of the great laws of physics and chemistry. Yet some of the great laws of chemistry were accepted when surrounded by seeming exceptions. Some of these exceptions have been cleared up by such recent advances as the Ionic Theory and the Phase Rule; some still remain.

Is it not probable that other like generalities will be found in biology, which, although they may entirely change our general conception of the fundamental action of Mendel's Laws, will nevertheless leave the facts upon which it was based as useful and practicable as have been left the facts of chemical recombination in definite and multiple proportions in the light of the Electron Theory?

LITERATURE CITED.

BATESON, W. and PUNNETT, R. C.

:08 Reports to the Evolution Committee 4 : 1-60.

BATESON, W.

:09 Mendel's Principles of Heredity. Cambridge University Press. pp. 1-396.

BAUR, E.

:09 Das Wesen und die Erblichkeitsverhältnisse der "Varietates Albomarginatae Hort." von Pelargonium Zonale. Zeitschrift für induktive Abstammungs- und Vererbungslehre 1 : 330-351.

CORRENS, C.

'99 Untersuchungen über die Xenien bei Zea Mays. Ber. d. Deutsch. Bot. Ges. 17 : 410-417.

:00 G. Mendel's Regel über das Verhalten der Nachkommenschaft der Rassenbastarde. Ber. d. Deutsch. Bot. Ges. 18 : 158.

:01 Bastarde zwischen Maisrassen mit besonderer Berücksichtigung der Xenien. Bibliotheca Botanica. 53 : 1-161.

:02 Scheinbare Ausnahmen von der Mendels'schen Spaltungsregel fur Bastarde. Ber. Deutsch. Bot. Ges. 20 : 159.

COURCHET.

'88 Recherches sur les chromoleucites. Ann. Sci. Nat. Bot. Ser. 8. 7 : 263.

DAVENPORT, C. B.

:08 Degeneration, albinism and inbreeding. Science N. S. 28 : 454, 455.

:09 Inheritance of characteristics in domestic fowl. Carnegie Institution of Washington Publication 121 : 1-100.

:10 Imperfections of dominance and some of its consequences. Amer. Nat. 44 : 129-135.

DE VRIES, H.

'99 Sur la fécondation hybride de l'albumen. Comptes rend. l'Acad. Sci. 129 : 973-975.

:00 Das Spaltungsgesetz der Bastarde. (Vorläufige Mittheilung.) Ber. Deutsch. Bot. Ges. 18 : 83.

DUDLEY, P.

1724 An observation on Indian corn. Philosophical Transactions 6 : 204-205.

EAST, E. M.

:09 A note concerning inheritance in sweet corn. Science, N. S. 29 : 465-467.

:10 A Mendelian interpretation of variation that is apparently continuous. Amer. Nat. 44 : 65-82.

FOCKE. W. O.

'81 Die Pflanzenmischlinge. Borntraeger. Berlin. pp. 569.

GÄRTNER, C. F.

'49 Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. Hering, Stuttgart. pp. 791.

GUIGNARD, L.

'99 Sur les anthérozoides et la double copulation sexuelle chez les végétaux angiospermes. Rev. génér. d. Bot. 11 : 129-135. Also Comptes rend. l'Acad. Sci. 128 : 869.

HARSHBERGER, J. W.

'93 Maize : a botanical and economic study. Con. Bot. Lab. Uni. Pennsylvania 1 : 75-202.

'96 Fertile crosses of Teosinthe and Maize. Garden and Forest. 9 : 522-523.

HILDEBRAND, F.

'67 Unmittelbarer Einfluss der Pflanzenbastardirung auf die durch dieselbe erzeugte Frucht. Verh. des naturh. Ver. d. Rheinl. u. Westf. 24 : 101 *et seq.*

'68 Einige Experimente und Beobachtungen über . . . . (2) den directen Einfluss des fremden Pollens auf die Beschaffenheit der durch ihn erzeugten Frucht. Botan. Zeitg. 26 : 325 *et seq.*

JOHANNSEN, W.

: 09 Elemente der exakten Erblichkeitslehre. Jena. Fischer pp. 1-515.

KELLERMAN, W. A. and SWINGLE, W. T.

'89 Experiments in cross-fertilization of corn. Ann. Rep. Kan. Exp. Station 1 : 316-337.

'90 Experiments in crossing varieties of corn. Ann. Rep. Kan. Exp. Station 2 : 288-334.

'90a Crossed corn the second year. Ann. Rep. Kan. Exp. Station 2 : 334-346.

'90b Bibliography of cross-fertilization of varieties of corn. Ann. Rep. Kan. Exp. Station 2 : 346-353.

'90c Preliminary study of the receptivity of corn silk. Ann. Rep. Kan. Exp. Station 2 : 353-355.

'91 Crossed varieties of corn the third year. Kan. Exp. Sta. Bull. 27 : 139-158.

LAMSON-SCRIBNER, E.

: 00 American Grasses — III. U. S. Dept. Agr., Div. Agrostology Bull. 20 : 10-12.

LOCK, R. H.

:06 Studies in plant breeding in the tropics. III — Annals of the Royal Botanic Gardens, Peradeniya. 3 : 95-184.

MC CLUER, G. W.

'92 Corn crossing. Ill. Agr. Exp. Sta. Bull. 21 : 82-101.

MONTGOMERY, E. G.

:06 What is an ear of corn? Pop. Sci. Mon. 68 : 55-62.

MORGAN, T. H.

:10 The chromosomes in heredity. Amer. Nat. 44 : 449-496.

MORROW, G. E. and GARDNER, F. D.

'92 Field experiments with corn. Ill. Agr. Exp. Sta. Bull. 25 : 173-203.

NAUDIN, CH.

'63 Nouvelles recherches sur l'hybridité dans les végétaux. Nouvelles Archives du Muséum. Tome 1.

NAWASCHIN, S.

'99 Resultate einer Revision des Befruchtungsvorgangs bei Lilium Martagon und Fritillaria tenelle. Bull. d. l'Acad. Imp. d. Sciences de St. Petersbourg, 9 : Nr. 4.

NILLSON-EHLE, H.

:09 Kreuzungsuntersuchungen an Hafer und Weizen. Lunds Universitets Årsskrift, N. F. Afd. 2., Bd. 5, Nr. 2. 1-122.

PUVIS, A.

'37 De la dégénération et de l'extinction des variétés de végétaux propagés par les greffes, boutures, tubercules, etc., et de la création des variétés nouvelles par les croisemens et les semis. Paris.

SARGERET, E.

'26 Considérations sur la production des hybrides, des variantes et des variétés en général, et sur celles de la famille des Cucurbitacées en particulier. Ann. d. Sci. Nat. T. 8.

STURTEVANT, E. L.

'99 Varieties of corn. U. S. Dept. Agr., Office Exp. Sta. Bull. 57 : 7-103.

DE VILMORIN, HENRI.

'67 Sur la fecondation du Maïs. Bull. Soc. Botan. de France. Tome 14 : 246.

WATSON, S.

'91 Proc. Amer. Acad. Arts and Sci. 26 : 158.

WEBBER, H. J.

:00 Xenia, or the immediate effect of pollen in Maize. U. S. Dept. Agr. Division of Vegetable Physiology and Pathology. Bull. 22 : 1-44.

WHELDALE, M.

:09 The colors and pigments of flowers, with special reference to genetics. Proceedings Royal Society, B. 81 : 44-60.

:09 On the nature of anthocyan. Proceedings Cambridge Philosophical Society 15 : Pt. 2, 137-168.

:10 Plant oxydases and the chemical inter-relationships of color-varieties. Progressus Rei Botanicae 3 : 457-494.

WINKLER, H.

:09 Uber die Nachkommenschaft der Solanum-Propfbastarde und die Chromosomenzahlen ihrer Keimzellen. Zeitschr. f. Botanik 2 : 1-38.