

THE RESULT OF SELECTING FLUCTUATING VARIATIONS  
DATA FROM THE ILLINOIS CORN BREEDING EXPERIMENTS<sup>1</sup>

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There are few biological problems which are attracting more attention at the present time than that regarding the effect of selecting small, fluctuating variations. Until recently the effectiveness of such selection has been accepted almost without question. However, the recent work of Johannsen, Jennings and others has caused many biologists to entertain serious doubts as to the real evolutionary significance of so-called fluctuating variations. If one searches through the literature for clear cut cases in which plants or animals have been modified by the gradual accumulation of small variations he is surprised at the small number which are supported by adequate data. Of these few cases there is one which has been referred to frequently as a classic example, of what can be done by simple selection. I refer to the work of breeding corn (maize) for chemical constitution carried out by the Illinois Agricultural Experiment Station.

Over two years ago while engaged in some corn breeding work at the Maine Experiment Station, the writer had occasion to work out the pedigree tables which are given in the present paper. (cf. pp. 225-229). When displayed in this way, the results of these extensive experiments appeared suggestive of the results which actually come from an attempt to select fluctuating variations. The writer is well aware that no definite conclusions of far reaching importance can be drawn from this data alone. It was for this reason and with the hope of accumulating more definite data that publication has been delayed so long. In view of the interest manifested in this subject at the present time it has seemed worth while to publish these tables together with a brief discussion.

In 1908 the Illinois Experiment Station published<sup>2</sup> the detailed evidence of very careful and long continued experiments in selecting corn with reference to the chemical constitution of the grain. Four definite experiments were carried out simultaneously, viz: (1) Selecting to increase the protein content; (2) Selecting to decrease the protein content; (3) To increase the oil content and (4) to decrease the oil content. For the details of these experiments the reader must be referred to the bulletin mentioned and others by the same Station. For the present discussion it will be sufficient to mention only a few of the more important points regarding the methods used in these experiments.

After some preliminary work there were selected in 1896 one hundred and sixty-three ears from a standard variety of white dent corn. Chemical analyses were made from samples of these ears, showing the protein and oil content of each. From these one hundred and sixty-three ears the twenty-four showing

1. Communication faite à la seconde séance de la Conférence.

2. Ten Generations of Corn Breeding, by Louis H. Sauer. III. *Agr. Exper. Station Bull.*, No. 128.

the highest per cent. of protein were selected for starting the " high-protein " plot. In a like manner the twenty-four ears showing the highest per cent of oil were chosen for the " high-oil " plot. Similarly the twelve ears having the lowest protein content and the twelve ears having the lowest oil content were selected for starting the " low-protein " and the " low oil " plots respectively. In each case the plots were planted on the ear-to-the-row system. In the following year there were analyzed a number of ears from each of the twenty-four rows, say of the high-protein plot, and from these ears the twenty-four showing the highest per cent of protein, regardless of pedigree, were selected for planting in the " high-protein " plot the following year. Similar methods were employed in the succeeding years and in the other plots. The important point for consideration here is that in each year those ears from a given plot which showed the greatest deviation in the desired direction were chosen to continue that experiment. Thus it was an experiment in selecting fluctuating variations.

The success of the experiment in accomplishing the desired results are most marked. Thus starting with an average protein content, in the original one hundred and sixty-three ears, of 10.92 per cent they were able in ten years to increase the average per cent of protein to 14.26. On the other hand in the low protein plots the percentage was reduced to 8.64. Similar results were accomplished with the high and low oil plots. The yearly fluctuations in the different plots are shown in tables 1 and 2 which are taken from tables 5 and 6 of the Illinois bulletin No 128.

TABLE 1.  
*Average per cent. of Protein in the Crops harvested.*

YEAR.	HIGH PROTEIN PLOT.	LOW PROTEIN PLOT.
1896.	10.92	10.92
1897.	11.10	10.55
1898.	11.05	10.55
1899.	11.46	9.86
1900.	12.52	9.54
1901.	13.12	10.04
1902.	12.54	8.22
1903.	15.04	8.62
1904.	15.05	9.27
1905.	14.72	8.57
1906.	14.26	8.64

TABLE 2.  
*Average Per cent. of Oil in the Crops harvested.*

YEAR.	HIGH-OIL PLOT.	LOW-OIL PLOT.
1896.	4.70	4.70
1897.	4.75	4.06
1898.	5.15	5.99
1899.	5.64	5.82
1900.	6.12	5.57
1901.	6.09	5.45
1902.	6.41	5.02
1903.	6.50	2.97
1904.	6.97	2.89
1905.	7.29	2.58
1906.	7.57	2.66

That the striking results shown in these tables were not due to the effect of environmental circumstances is clearly shown by the analyses from the so-called "mixed protein" and "mixed-oil" plots. In these plots kernels from the high and the low strains were planted in the same hills. Subsequent analyses showed that under these conditions the various strains maintained their respective chemical characteristics. Thus there cannot be the least doubt but that certain characters were fixed<sup>1</sup> in these various strains by the selection practiced.

At the time that the selections were made a careful record of the pedigree of each ear was kept. These pedigrees are, of course, for the maternal side only, since hand pollination was not practiced. In the appendix to bulletin No. 128 all the analyses for the ten years are given and arranged in such a way that it is possible to trace out the pedigree of each individual ear. It is from this data that the following pedigree tables (Tables, 5, 4, 3, and 6) have been constructed. In the following discussion it will be advantageous to take each plot separately. This may be done in the order in which they occur in the bulletin.

#### *High Protein Corn.*

As stated above twenty-four ears containing the highest per cent of protein were selected from the one hundred and sixty-three ears analysed in 1896. These were given registry numbers from 101 to 124 inclusive as shown in column one of table 5<sup>2</sup>.

The next season four sound ears were analysed from each of the twenty-four rows. From these ninety-six ears, the twenty-four again having the highest per cent of protein were selected for planting. The distribution of these selected ears among the twenty-four original ears is shown in column two of table 5. For example it is seen that ear No 124 produced two ears (nos 216 and 209) which were among the first twenty-four as regards protein content. Ear No. 125 on the other hand failed to produce any ear (so far as the ears analysed showed) sufficiently rich in protein to be included among the first twenty-four. In this way it is seen at once that eight of the twenty-four original ears fail to be represented in the second generation while eight other ears contribute two ears each for planting in the following year. Exactly the same selection was practiced in the second year and the resulting selected ears are shown in the third column of table 5. Of the sixteen original ears represented in the second generation, only one, viz: No. 116, was dropped out in the third generation. In the next generation there is a very significant dropping out of some of the original lines. Thus in this fourth generation, only 9 of the original twenty-four ears are represented by progeny. Five of the original lines contribute twenty of the twenty-four ears, or 80 per cent in this generation while two lines, viz: 106 and 112 contribute fourteen ears or nearly sixty per cent. Thus at the end of the fourth generation it is clear that certain of the original lines have a much greater tendency to produce ears with a high per cent of protein. By simply selecting on the basis of the protein content of the individual ear, for four years, 70 per cent of the original lines have been dropped.

1. This point is also brought out in a recent paper by L. B. SWINN, "Increasing Protein and Fat in Corn", *American Breeders' Assoc. Report.*, vol. VI, pp. 5-11, 1911.

2. For convenience these ears will be called the first generation of high-protein corn.











In the next or fifth generation three more of these original lines were dropped<sup>1</sup>. Here again one finds that two of the original lines, viz: 112 and 121, contribute eleven of the fifteen selected ears or over 75 per cent. Line No. 106 which had six ears in the fourth generation failed to produce more than one ear good enough to come inside the first fifteen.

Passing to the sixth generation one finds that three more of the original lines are dropped from the contest. There are only three of the original twenty-four ears represented by progeny in this, the sixth generation, and one of these (No. 124) contributed only a single ear.

In the seventh generation these same three lines are represented. However, the superiority of line No. 121 to produce ears high in protein is clearly evident. Nineteen of the twenty-two ears, or over 86 per cent, come from this one line.

In the eighth generation there is practically no change in the relationship of these lines. Twenty of the twenty-two ears are furnished by line No. 121. In the ninth generation line No. 112 drops out and line No. 124 fails to secure a place in the tenth generation. *It thus happens that in the tenth and eleventh generations all of the high protein corn is the offspring of a single ear viz: No. 121.*

It is to be remembered that this condition has been brought about simply by selecting each year those individual ears which showed the highest per cent. of protein. Everyone who has had any experience with selection of this kind knows that many of the original lines are always dropped out as the work proceeds. But it is rather surprising to find so striking an example of the superiority of a single line<sup>2</sup>.

Before considering the other experiments it will be well to examine the pedigree of this line a little more closely. In the first four generations there is nothing remarkable in its history. Up to that time there are several other lines which give more promise of producing high protein ears than this one.

Line No. 112 has eight ears in the fourth generation and line No. 106 has six ears, while No. 121 has but two. One of these ears (No. 445) however, had within it the ability to produce ears high in protein content. In the fifth generation this ear produced five of the fifteen ears planted. This is a larger number of ears high enough in protein to be selected, than had been produced by any one ear up to this time. So far as can be learned from the published records there are no special cultural reasons why the progeny of this ear should have been higher in protein than the progeny of other ears.

In the sixth generation of line 121, ear No. 512 produced two ears and ear No. 507 produced six ears out of a total of fourteen planted. It should be stated here that in this year (1901) a severe drought injured the corn very much and had considerable influence on the resulting selection. The following quotation from the Illinois Bulletin No. 128 will make this plain: (page 469).

" In the case of the high-protein plot the damaging effect of this drought was so pronounced as to render the crop almost a total failure. The yield of ear corn amounted to only about six bushels per acre and consisted mostly of

1. It should be mentioned here that for the fifth generation only fifteen ears were selected and for the sixth generation only fourteen ears. For the years following the number of ears selected ranged from twenty-two to twenty-five.

2. In the tenth and eleventh generations the plan of detasseling alternate rows and saving seed from these only was put into effect. Also in these years a much larger number of ears were analyzed from each mother row. This change in method could not have effected the results brought out here, because, line No. 121 had demonstrated its superiority several generations before this change was made.

mere nubbins. On account of the scarcity of ears, it was impossible to follow the regular system of sampling, so the entire product from each plot-row was collected and all of the sound ears and even many nubbins were selected for analyses in order to obtain the results of the year and the sort of seed with which to maintain the experiment. The low protein plot did not suffer so badly from the drought, so that here the sampling and selection were made as usual.

Ears No. 507 and 515 were planted in the "Special High-Protein Plot" and all the ears selected from these two lines were from this plot. In the appendix of the bulletin mentioned, the analyses of twenty-seven ears from No. 507 (line 121) are given. Of these, six were selected. Similarly from ear No. 515 (line 112), the analysis of forty-five ears are given but only three were selected. None of these three ears were able to get progeny in the next generation while in striking contrast *every one* of the six ears from No. 507 produced ears good enough to be selected the following year. Further these latter ears produced practically *all* of the High-protein corn from this time on.

Certainly ears No. 507 and 515 at least had the same opportunity to produce high protein ears. The results as shown above however are strikingly different.

Looking at the pedigree of line 121 alone it may be said to fall into two parts. The first of these, covering the first four generations is characterized by mediocrity in protein productions. The second part i. e., after the fourth generation, is characterized by the production of a large number of ears with high protein content.

Evidently something happened to ear No. 415, or perhaps to ear No. 507 which produced a propotency towards high protein production. What this something may have been, can only be conjectured. It may have been of the nature of a mutation. This is perhaps the first suggestion that occurs to one. In this case there are certain possible contributory factors which may have been operative. The chief of these are to be found in either selective fertilization or in the proper amount of inbreeding. At this time the larger amount of pollen in the field was coming from two or three lines. These, of course, had been crossed with other lines but nevertheless they were pure bred on one side. We know too little of the effect of such inbreeding to make more than a suggestion.

The suggestion is certainly close at hand that in the third or fourth generation of line No. 121 a particularly happy combination or germinal plasma occurred. As a result of this combination a line which was previously only mediocre in its protein producing ability suddenly acquired a marked increase in this direction. This ability to produce a large number of high protein ears has evidently been transmitted to later generations.

The phenomena of propotency which it seems to me is displayed in this instance is one which has been discredited largely by scientific breeders in recent years. Pearl<sup>1</sup> however, has recently shown that in poultry the offspring of certain matings transmit for several generations at least, the ability to produce either a high or low degree of egg production as the case may be.

One more point must be considered here. From table 1 (page 225) it is seen that starting with a protein content of 10.92 per cent. at the end of the

1. Inheritance of Fecundity in the « Domestic Fowl », *Amer. Nat.*, vol. XLV, June 1911.

third year the protein content was only 11.46 per cent. or a gain of .54 per cent. in four years. However, the next year the protein content jumped to 12.52 per cent., or a gain of .86 per cent. in one year. Now referring back to table 5 it is seen that it is just at the end of the third years selection that there is a great reduction in the number of lines represented. Thus only six of the original twenty four lines are represented in the fifth generation. Also it is just here that line No. 121 begins to show its prepotency. The next year (1901) there is a very much larger increase in the average per cent. of protein, viz : 1.80 per cent. for the year. It has already been stated that climatic conditions caused an exceptionally high per cent of protein in this year. The next year (1902) the protein content fell back again and then rose with some irregularities.

The most interesting feature here, however, is that so long as a comparatively large number of lines are represented in the pedigree the average protein content remains almost stationary. When the number of the lines begins to be diminished the average protein content begins to be increased much more rapidly. This may of course, be a coincidence but it is a point which needs more analytical study.

Before discussing this question further it will be well to examine very briefly the remaining three experiments. In no one of these are the results so striking as in the high protein plots. However, in a general way they point to the same conclusions.

#### *Low Protein Plots.*

Table 4 shows the various lines of the low protein plots arranged in the same way as the high protein pedigrees. It will not be necessary to enter into the details of these tables. They present many interesting things to anyone who cares to study them. Only a few of the more important conclusions are pointed out here.

In the first place, it is seen that starting with twelve original lines there are only two of these represented in the last generation. Only three lines persist beyond the sixth generation. Of the two lines which have progeny in the last generation, one is much superior to the other in its ability, to produce ears low in protein. This has not been true of its whole history. In the first seven years, line No. 106 produced only a moderate number of ears low enough to be selected. After the seventh generation, however, this faculty appears to have increased very greatly.

Comparing this table with column 5 of table 1, it is seen that it was not until 1902, or the seventh generation, that any very great or permanent decrease in the per cent. of protein was brought about. Here again the most marked improvement in the direction sought occurs only after the number of lines has been very materially reduced.

The results of the low protein experiment while not quite so striking as those of high protein plot are nevertheless along the same general lines and tend to confirm the conclusions drawn from it.

#### *High Oil Plots.*

Table 5 gives the pedigrees for the high oil plots. From this table one may briefly note the following points :

1. Of the twenty-four ears used to start this experiment in 1896 only eight are represented by progeny in the third generation;

2. At the end of the sixth generation all but three of the original lines have been dropped;

3. These three lines are maintained to the end of the experiment. The number of selected ears in the later generation are not, however, equally divided between these three lines. Line No. 111 is by far the most prolific producer of ears with high oil content;

4. Again certain apparently crucial points in the history of these lines are noted. Thus in Line No. 111, ear No. 609 produced an exceptionally large number of ears with a high oil content. Similarly in line No. 118, ear No. 710 produced four good ears while seven other ears from the same line in the same generation failed to produce any which were good enough to be selected.

#### *Low Oil Plots.*

As shown in table 6, twelve ears were selected for starting the experiment in decreasing the oil content. From this table we note:

1. That only three of the original lines are represented in the seventh generation:

2. Of these three only two, viz: 106 and 110, are represented in the eleventh generation. Line No. 108 is maintained up to the eleventh generation and then dropped;

3. Of these two lines, No. 106 is by far the better, and contributed sixteen of the twenty-four ears to the last generation;

4. Again it is noted that certain ears have a marked tendency to produce a large number of ears with a low oil content. Examples of this are seen in the seventh generation in ears No. 722, 720, and 719.

#### *Discussions and Conclusion.*

Taking into consideration the results of all four experiments as displayed here it is clearly seen that one of the most striking effects of the selection practiced has been to reduce the number of lines. Two of the experiments (Tables 5 and 5<sup>b</sup>) were started with twenty-four ears each. At the end of five years the high-protein corn shows progeny from only three of the original ears, and the high-oil from four of the original ears. At the end of ten years the high-protein corn showed progeny from only one of the original ears and the high-oil from three of the original ears. So far the results are in accord with the genotype conception of Johanssen as applied to non-self-fertilized organisms. However, if nothing but the isolation of favorable genotypes had taken place the extremes of protein production would not have been greatly changed. This, however, did take place here. In the later years we find many individual ears with a per cent. of protein far beyond anything which occurred in the earlier years. In this respect these results parallel the classical case of de Vries's selection of buttereups. In this latter case the extreme was moved far beyond what it was before the selection. Unfortunately in the case of de Vries's work pedigree data is not available.

Table 7 shows for each year the maximum and minimum per cent. of protein in the ears which were selected for planting the high-protein plots.

TABLE 7.

Table showing the maximum and minimum per cent. of protein in the ears selected for planting in the high-protein plots.

YEAR.	MAXIMUM.	MINIMUM.
1896. . . . .	15.87	11.89
1897. . . . .	15.62	11.89
1898. . . . .	14.92	12.55
1899. . . . .	14.78	15.19
1900. . . . .	15.71	14.01
1901. . . . .	16.12	14.95
1902. . . . .	15.01	15.68
1905. . . . .	17.55	14.60
1904. . . . .	17.79	15.85
1905. . . . .	17.59	15.52
1906. . . . .	17.67	15.16

From this table it is clear that the maximum has been moved permanently in the direction of the selection. To obtain a more reliable basis for comparison we may average the maximum per cent. of protein in the first three years, and in the last three years. These averages are 14.14 per cent. and 17.62 per cent., respectively, or a difference of 5.48 per cent. Further it is seen that in the last four years the minimum per cent. of protein in the selected ears is greater than the maximum during the first two years.

Clearly we are dealing here not merely with the isolation of a genotype but with a definite evolutionary change. The whole variation polygon has been moved definitely in the direction of the selection<sup>1</sup>.

Yet I think that no one can study table 5 and still maintain that it was the simple selection of fluctuating variations that brought about the change in protein production. Certainly something was acting in line No. 121 which was not affecting the other lines.

The recent interesting experiments of Shall and East in dealing with homozygous strains of corn may have some bearing in this connection. These authors have shown<sup>2</sup> that when two strains of corn which have been inbred for several generations are then crossed the resulting progeny are far superior to either parent in yield. It is quite possible that a somewhat similar explanation would account for the great development of line No. 121, after the fourth generation.

It is of interest to note here the similarity between these experiments and the selection work with poultry at the Maine Agricultural Experiment Station. It has been shown<sup>3</sup> that after nine years of intensive selection of poultry for increased egg production the average production of the flock was not changed. A possible explanation of the different result reached by these two similar experiments may be in the fact that the corn plot was started with only twenty-four individual ears, while in the poultry experiments, seventy birds were used in the first year's breeding. In the succeeding years a very much larger number of

1. This question as to the amount of shifting of the entire variation polygon was studied to some extent, but it was deemed that the published data was not sufficient to draw trustworthy conclusions.

2. SHALL (G.-H.). A pure line method in corn breeding, *Rpt. Amer. Breeders Assoc.*, vol. V, pp. 51-59 — EVANS (E.-M.). *Amer. Nat.* Vol. XLIII p. 175-182, 1909.

3. PENN (R.) and SHAWCE. F. M., U. S. Dept. Agr., Bur. Anim. Ind. Bul. 110, pt. 1, 1909, *Zeit. f. Induct. Abst.-u.-Zererb.-Lehre.*, Bd. 2, 1909, pp. 257-275.

birds were used, while in the corn experiments there were never more than twenty-five ears planted in one plot. It would have been a much more difficult task to have isolated the high genotypes if such existed among the poultry.

In conclusion it should be said that too much credit cannot be given to the Illinois Experiment Station for the careful manner in which these experiments have been carried out. The experiments were begun with the practical object of finding out whether the chemical composition of corn could be modified by selection. The results showed unmistakably that it could. Whether the theoretical conclusions were correct or not, the fact remains that the methods used were such as to obtain the desired results.

## RÉSULTATS D'UNE SÉLECTION PARMI DES VARIATIONS FLUCTUANTES

### RÉSUMÉ

En 1908, la station expérimentale agricole de l'Illinois a publié<sup>1</sup> le compte rendu d'une longue expérience de sélection sur le Maïs, avec des références sur la composition chimique du grain. Quatre expériences importantes furent continuées pendant une période de dix années. Ces expériences furent faites dans le but :

- 1<sup>o</sup> D'essayer d'augmenter le contenu du grain en protéine;
- 2<sup>o</sup> D'essayer de diminuer ce même contenu;
- 3<sup>o</sup> D'essayer d'augmenter la proportion d'huile contenue dans le grain;
- 4<sup>o</sup> D'essayer de diminuer cette même proportion.

La méthode employée était la suivante : choisir chaque année, dans un lot donné, les épis qui montraient la plus grande déviation dans la direction désirée. C'était, par suite, une simple expérience de sélection parmi des variations fluctuantes.

Le succès de ces expériences, dans l'obtention du résultat désiré, fut très marqué; ainsi, dans le lot riche en protéine, la moyenne du pourcentage de protéine dans la récolte s'éleva de 10,92 pour 100 en 1896 à 14,26 pour 100 en 1906. De l'autre côté, dans le lot faible en protéine, la moyenne tomba de 10,92 pour 100 en 1896 à 8,64 pour 100 en 1906.

Ce résultat offre un intérêt tout particulier en raison des importants et récents travaux de Johannsen et autres sur le même sujet. Il semblerait que, dans ce cas, la sélection parmi des variations fluctuantes ait été couronnée de succès.

Dans le même Bulletin, la station expérimentale de l'Illinois a donné le "pedigree" détaillé (du côté maternel) de chaque épi examiné durant les dix années de l'expérience. De ce "pedigree", des tables ont été construites qui montrent la généalogie maternelle de chaque épi. En examinant ces tables, on voit que, dans les dernières années, les épis plantés ne sont pas distribués au hasard parmi la descendance de ceux qui avaient été choisis au début.

Au contraire, certaines lignées originales montrent une tendance marquée à produire, de préférence, des épis ayant le caractère désiré; ainsi dans le lot

1. Ten Generations of Corn-breeding, par Louis H. Smith; Illinois Agric. Exp. Stat. Bull. n. 128 (1908).

ayant un pourcentage élevé de protéine, *tous les épis plantés après la neuvième génération sont la descendance d'un même épi original.*

La présentation de ces résultats sous forme de tables "pedigree" montre, au moins, d'une façon très suggestive, de quelle manière la sélection peut agir. Elle démontre que, bien qu'ayant une égale opportunité, toutes les "lignes" ne produisent pas également de bons résultats. Tout au moins dans le cas qui nous occupe, la sélection parmi les variations fluctuantes s'est, en réalité, traduite par une sélection de diverses lignes possédant une puissance plus grande pour la production du résultat cherché.

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