HOMOLOGIES OF THE EAR AND TASSEL IN *ZEA MAYS*

EDGAR ANDERSON

Geneticist to the Missouri Botanical Garden
Engelmann Professor in the Henry Shaw School of Botany of Washington University

The exact correspondence between the variation of the male and female inflorescence of *Zea Mays* is a problem which has attracted a number of minds and has produced several theories, none of which completely satisfied the existing data. The morphological facts have been assembled by Weatherwax ('23, '35), and he, Collins ('19) and Kempton ('19) have reviewed the pertinent literature. After surveying all the existing evidence Collins' final conclusion was that, though he had used the hypothesis of a shortened and twisted central spike to explain the results in crosses between *Zea* and *Euchlaena*, "facts of other kinds are more easily interpreted by the theories of fasciation and reduction of branches . . . . There are also facts that do not seem to accord with any of the theories yet proposed. Until the apparently contradictory evidence can be reconciled, it seems best to keep the several possibilities in mind and await additional evidence before attempting a complete interpretation." Though the facts reported below shed further light on the problem, Collins' words of caution are still in order and the complete solution, while perhaps not far distant, is still to be awaited. Though he disagreed rather completely with Collins on other points, Weatherwax's final conclusions ('23) concerning the ear were very similar. "The last word has not yet been said on the evolution of the ear of corn, and it cannot be said until further researches have corrected, amplified, and evaluated the data now at hand, and woven the results into a harmonious theory." [loc. cit. pp. 112-113].

Earlier workers were interested in the problem of ear and tassel relationships chiefly from theoretical considerations. With the development of large-scale scientific maize breeding in the U. S. cornbelt, it is now a problem of considerable economic importance as well. If a corn breeder could size up the potentialities of the ear, merely by examining the tassel, he could take many short cuts, both in the creation of new inbred lines and in maintaining their desirable characters.

Methods.—The general method of work is discussed in some detail since in the author's opinion it is of even greater significance than the results themselves (though, as will be demonstrated below, useful correlations have already been established by these methods). In beginning the work, a few tassels were examined in great detail, with particular reference to the structures considered significant by systematists: glumes, spikelets, pedicels, secondary and tertiary branches, etc. With these facts thoroughly in mind, as many kinds of maize as possible were grown and examined. A particular effort was made to secure rare and unusual varieties, especially those from Central America and South America.

The work was begun in 1941. By 1944 the general pattern of variation in tassel morphology was apparent. Then, for the first time, a serious effort was made to compare tassel and ear morphology in segregating families and in inbred lines of maize. A preliminary study of various inbreds from the U. S. Department of Agriculture and several agricultural experiment stations had indicated that this might be a fruitful method of investigation. Among the old well-established inbred lines used in modern hybrid corn breeding, there are many with extreme tassel types and ear types. Furthermore, they are practically pure breeding and they can be compared when planted in different soils, at different times of year and in different places. Through the kindness of the Pioneer Hi-Bred Corn Company, the inbred plots and breeding records of this company were put at my disposal in the summer of 1944. By a fortunate circumstance their breeding farm is not far distant from the Iowa Agricultural Experiment Station at Ames, where a further set of highly significant inbreds and hybrids was obtained from Professors E. W. Lindstrom and J. C. Eldredge. I am very much indebted to these individuals and institutions who have allowed me to study tassel morphology in their own experiments, most particularly to Mr. Raymond Baker of the Pioneer Hi-Bred Corn Company. His encouragement and cooperation have made possible this preliminary report though he is in no way responsible for its shortcomings.

The general method of work was to select either F_2 segregates or a series of inbreds with some outstanding characteristic of the tassel and then to examine the ears for possible correlations. When one was suspected, more material was examined to see if the correlation still held. The customary procedure in such cases was to walk rapidly through the breeding plots, keeping an eye out for tassels which were very extreme for the character under observation, and then to study the ears on these plants. When an ear-tassel correlation was at length apprehended, various methods of recording it were tried out. It was then measured precisely in a series of inbred lines, and the figures so obtained were compared not only with the actual ears borne by these inbreds but also with their progeny in controlled crosses. For instance, it was suspected that the length of the upper tassel branches was an important factor in ear length; Lindstrom's LA inbred line of maize was found to be an outstanding inbred line in the length of its upper tassel branches. Not only did it prove to have a long ear for an inbred; a reference to breeding records showed that on the average it had transmitted longer ears to its progeny than any of the other inbreds with which it was being compared. To summarize: tassel variation was studied in a general way for three years before precise correlations of ear and tassel were attempted. Even then, they were first run to earth by quick qualitative methods before they were submitted to statistical treatment.

It is unfortunate that much of the so-called quantitative investigation in this country is done in exactly the opposite fashion. In many laboratories measurements are taken by the hundred and are then submitted to mathematical analysis in the hopes that useful results will emerge. This is putting the cart before the horse. It is a fundamental principle, too often ignored, that before a biological phenomenon is to be investigated on the mathematical level it must first be thoroughly analyzed on the biological level. One must first understand in at least a general sort of way what is happening in the material under investigation before he can set up an efficient measure of that particular phenomenon. The ear-tassel correlation problem is an instructive example. In terms of what one human being can accomplish in a life time, the numbers of features of maize ears and tassels which might be measured are almost infinite. It is scarcely to be wondered, therefore, that few significant results were obtained by those who studied ear-tassel correlation with an electric computing machine (Collins, '16; Kempton, '26). Statistical analysis has a useful place in biology but it must be preceded by biological analysis.

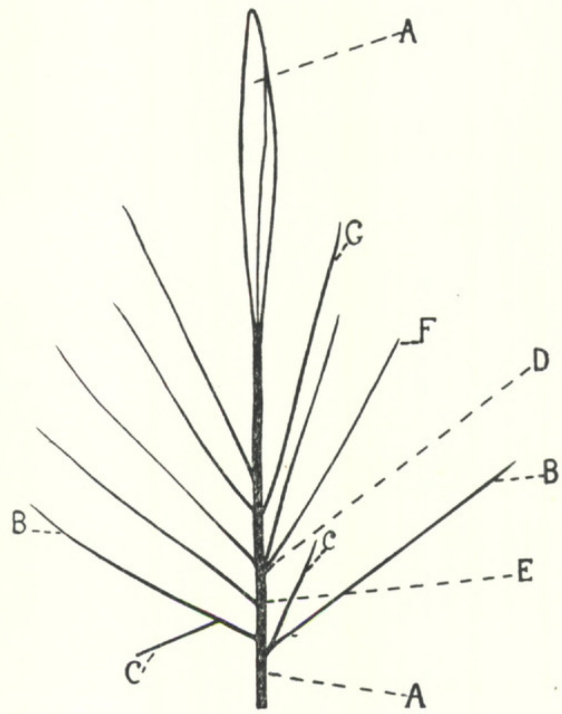

Fig. 1. Diagram showing main features of male inflorescence ("tassel") of *Zea Mays.* Further explanation in text.

Tassel Morphology in Zea Mays.—In order to grasp the following discussion it will be necessary to have the fundamental ground-plan of the male inflorescence of maize (the tassel in common speech) thoroughly in mind. Its branching system is illustrated diagramatically in fig. 1; certain variations in the arrangements of the spikelets are shown in fig. 2. The tassel always consists of a primary axis (AA), fig. 1, usually with a certain number of secondary branches (B, F, G, etc.). The lower secondaries may themselves branch at the base giving rise to

Fig. 2. Diagram showing variation in spikelet arrangement on secondary tassel branches in North American strains of *Zea Mays*. 'A' shows very slight condensation of internodes; 'B' shows higher condensation; 'C', the extreme of a common North American tendency, the shortening of the pedicel in the pedicellate spikelet. Further explanation in text.

tertiary branches (C). The primary axis is terminated by the central spike (A). The secondaries may all arise separately from the primary axis or a part of them may be whorled (D) or, in rare cases, they may all be in whorls of 2 or 3. The number of secondaries varies widely even under the same cultural conditions and is usually quite constant in inbred lines. There are occasionally only 1 or 2 (in rare cases none), or there may be up to 40 or more in each tassel. The length of the secondaries varies greatly as well as their comparative lengths along the tassel.

Figure 2 diagrams the manner in which the spikelets are arranged upon the branches of the inflorescence. The maize of the American corn belt is highly variable for this character, as will be discussed below. 'A', in fig. 2, diagrams the simplest arrangement and one which is, from a technical agrostological point of view, the normal one for *Zea Mays.* The spikelets are arranged in pairs, one spikelet in each pair being sessile and one pedicellate. In North American maize there is great variation in the length of the pedicel and in some inbred lines the condition may be like that illustrated at 'C' where the spikelets are in pairs but the members of each pair are practically indistinguishable in pedicel length.

All North American dent corn has a considerable number of condensed or telescoped internodes as illustrated in 'B'. Sometimes the condition is no more extreme than illustrated at 'A'. The fifth node from the apex is really two nodes and bears two pairs of spikelets instead of one. The example shown at 'B' is by no means extreme, and there are many inbred lines and Mexican varieties which show twice as much condensation as this. The tassel branch segment in 'B' has exactly as many spikelet pairs as 'A' and 'C' but many of the internodes are condensed. From the apex to the base the number of spikelet pairs at each apparently single node are 3, 3, 1, 2, 2, and 1. Technically, of course, there are 3 fused nodes at the first, each with its own pairs of spikelets, 3 at the second, and so on down the stalk.

Inbred lines of maize vary in the angle at which the secondaries leave the primary axis and the angle is usually surprisingly constant for each inbred line. In certain inbreds it is sometimes constantly under 10 degrees; in other inbreds it may even exceed a right angle.

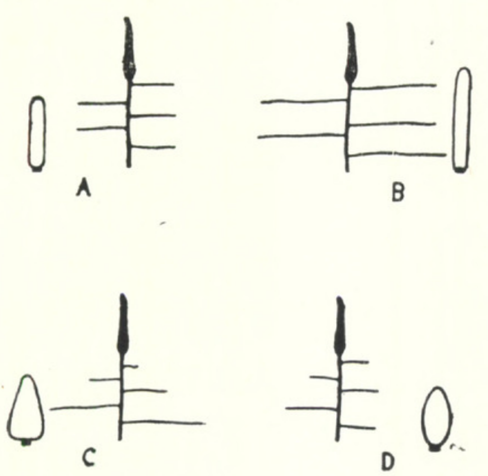

Fig. 3. Relation between tassel shape and ear shape in *Zea Mays;* highly diagrammatic. Further explanation in text.

Maize from different parts of the New World, as well as inbred lines, varies greatly in the position at which the lowest spikelet pair is set on the secondary. In some Mexican varieties and certain commercial inbreds it is so close to the base of the secondary that it almost seems to arise from the primary axis. In most high-altitude South American varieties, the secondary has a long basal internode below the first spikelet pair. In our notes, this is referred to as the "sterile zone" and is usually measured on the third secondary from the base of the tassel.

Correlations.—It may make the discussion easier if we anticipate the general conclusions from the data before presenting the results in detail. The correlations between tassel and ear are those which would result *if* the ear *were* composed of branches fused spirally about a central cylinder (see fig. 3). The actual correlations are a fact. Their interpretation is quite another matter and is discussed briefly on page 338. Figure 3 demonstrates, for several extreme tassel types, the fairly precise correspondence between the "profile" of the tassel branches and the shape and size of the ear. However, all of these patterns are affected by the degree of condensation which varies independently of the number of tassel branches and their absolute and relative lengths. It will, therefore, be necessary, first of all, to discuss ear-tassel correlations for condensed internodes.

Condensation.—As has previously been explained, the internodes of North American maize tassels may frequently be condensed or telescoped. Sometimes an internode is extremely shortened but is still visible as a separate internode. More frequently 2, 3 or even 4 internodes are so foreshortened that they give the appearance of a single node bearing 2, 3, or 4 pairs of spikelets. It is, in other words, a kind of controlled fasciation which operates throughout the plant. In the ear, it is one of the factors controlling row number. As will be demonstrated below, there is in North American maize a surprisingly close correlation between the condensation of the tassel and the degree to which row number is increased above 8 or 10 rows. For several reasons, condensation can be studied much more effectively in the tassel. In the first place, the tassel is apparently much more sensitive, and a low degree of condensation which will not reach a threshold of expression as to row number can be exactly measured there. In the second place, the ear is a highly complex organ in which it is difficult to detect the individual effects of various developmental factors. The tassel is much more simple and in it the effects of condensation can be studied independently of other factors. In the tassel, for instance, one may study condensation, the development of secondary and tertiary branches, and whorled branches vs. alternate or spiral branching, and all three can be followed as independent variables. In the ear they all affect row number in one way or another.

The genetic background of condensation is obscure. It seems to be a kind of fasciation due either to a single mutant gene and a large number of minus modifiers or to a large number of genes which produce the same general effect. It has a pronounced geographical distribution which is exactly that of denting. Though dented kernels and condensation are different things genetically they are both found in an exaggerated degree in the Mexico City-Toluca neighborhood (Anderson, unpublished) and seem to radiate from there in all directions. From archeological evidence we know they have been there for at least a thousand years and that it is apparently the center to which all our North American dent corns can be traced back.

The number of spikelet pairs per internode (and therefore the degree of condensation) varies within very wide limits, and these extreme types are characteristic of two widely separated areas in the New World. The varieties of high altitudes in South America have little or no condensation in the secondaries. A specimen tassel grown in the United States from Peruvian seed had the following number of spikelet pairs per node on its lowest secondary branch (scored from base to the tip, node by node): 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 1, 1, 1, 1, 1, 1, 1, 1. The opposite extreme is found in the dent and pop corns with sharply tapering ears ("Mexican Pyramidal" of Anderson and Cutler, '42) which are the typical maize of the region around Mexico City. Popcorns similar, if not identical, are grown in the United States under the name of "Japanese Hull-less" (a misleading name since they are apparently no more Japanese than they are hull-less). The lowest secondary branch from one of these pop corns scored as follows: 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 2, 2, 4, 4, 4, 4, 5, 3, 3, 4, 4, 4, 3, 3, 3, 1, 1, 1. In order to facilitate exact quantitative comparisons between tassel condensation and ear row number, these raw data need to be converted into a single score. This is a little difficult since sometimes the basal portion of the tassel will be most condensed, sometimes the entire tassel, and sometimes merely the terminal portion. Average condensation per node is not too significant since few tassels are highly condensed for their whole length and the great majority have at least a basal or terminal portion which is quite uncondensed. After comparing a great variety of condensation patterns the following procedure was worked out and gives a fair and objective index for making exact comparisons. The apparent number of nodes is counted and the central three-quarters are selected for computation. If there are 36 nodes, for instance, the central 27 are used. The quarter which are discarded are the least condensed nodes at the base, or at the tip, or both. However, they are consecutive nodes at each of these points. If the tassel in question had had no condensation for 10 or so nodes at its base, then all the discarded nodes would have been basal; if it had had such an area at the apex, then all the discarded nodes would have been from that area; if it had had four uncondensed nodes at the base then the basal 4 would have been eliminated from the computations as well as 5 from the tip to make up the 9 nodes. For the central three-quarters of the tassel, the total number of spikelet pairs in that portion is divided by the number of nodes. This gives an index running from 1.0 to 4.0, or even a little higher. This condensation index can be defined precisely as "the average number of spikelet pairs per apparent node in the most condensed central three-quarters of the basal-most secondary branch of the male inflorescence." All of which sounds very much more complicated than it actually is. In common speech it could be rendered as, "a precise measure of how thickly the male flowers are set together in the lower part of a corn tassel." Most of the South American maize which has been examined scores 1.0 on the Condensation Index and the maize of western Mexico is 1.0 to 1.4. Maize of the Mexico City-Toluca area scored from 1.5 to 4.2. In the U. S. corn belt one open-pollinated field of Reid's Yellow Dent scored from 1.0 to 2.2. Forty of the commoner inbreds used in hybrid corn breeding had indices from 1.0 to 3.0, the average (median) being at 1.6.

For North American maize the Condensation index, as calculated above, proves to be a fairly precise measure, not only of tassel condensation, but of potential ear row numbers. We may anticipate the evidence given below and state that for

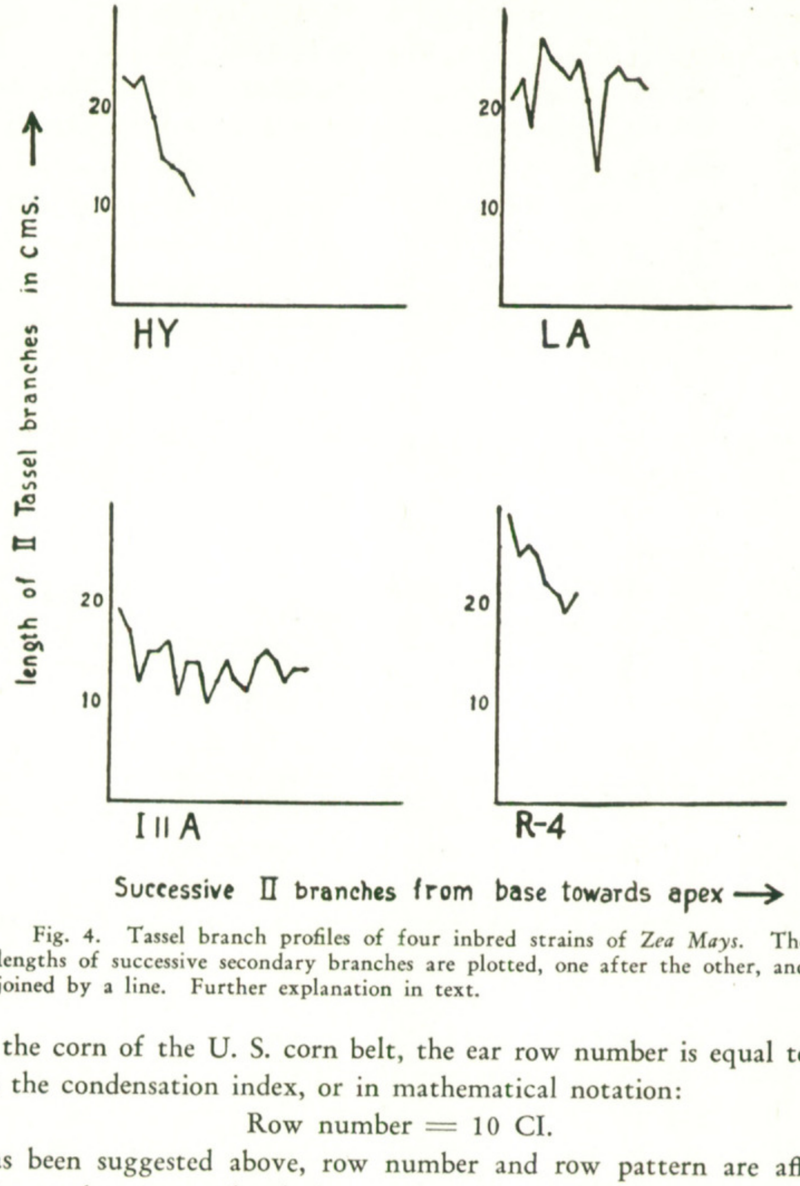

Fig. 4. Tassel branch profiles of four inbred strains of *Zea Mays*. The lengths of successive secondary branches are plotted, one after the other, and joined by a line. Further explanation in text.

much of the corn of the U. S. corn belt, the ear row number is equal to roughly ten times the condensation index, or in mathematical notation:

Row number = 10 CI.

As has been suggested above, row number and row pattern are affected by various factors but in much of the maize of the United States, condensation is the chief variable. For all practical purposes we can assume that North American maize has a "fundamental" row number of 8 or 10 and that any increase above this number will be directly proportional to the Condensation Index as calculated from the tassel. This is not just a theory; it has been experimentally verified in a wide variety of inbred, hybrid, and open-pollinated material. Before discussing it, it will be necessary to review the evidence for variability in row number. This character, as might be expected, is influenced not only by inherent capacity for many or few rows, but by the vigor of the plant and by environmental influences. Even highly homozygous inbreds and first-generation hybrids may vary considerably in row number. The latter, as is well known, is always an even number since the fundamental variable is the number of alicoles, each one of which gives rise to two rows (Collins, '16). A hybrid which is characterized by 14 rows may bear a good many ears with 12 and with 16 rows. A weak inbred which averages only 14 ears may behave in crosses as though it averaged 16, etc.

One of the most precise tests for the exact correspondence between row number and the Condensation Index was afforded by Lindstrom's PR inbred and its remarkable mutant PR-M. As Lindstrom has stated ('40), the former is potentially 20-rowed and the mutant is potentially 16-rowed. Fifteen tassels of each were examined. The average Condensation Index for the PR tassels was 2.2; for the PR-M tassels 1.7. If we assume that the row number divided by the Condensation Index will give us what the rowing would have been without condensation, we may divide 20 by 2.2 for PR and 16 by 1.7 for PR-M. The answer to the nearest round number is 10 for each. In other words, the higher degree of condensation in the tassel of PR as compared to PR-M is exactly proportional to the increase in ear row number.

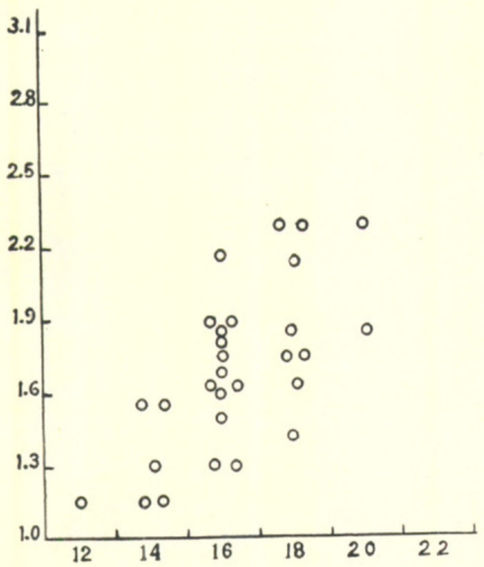

Fig. 5. Scatter diagram showing the correlation between tassel-node condensation and ear row number in a group of F_1 crosses between inbred lines of commercial corn. Vertical scale, *average* condensation index of the two parental inbred tassels. Horizontal scale, number of rows of kernels on the ears of the F_1 hybrid plants.

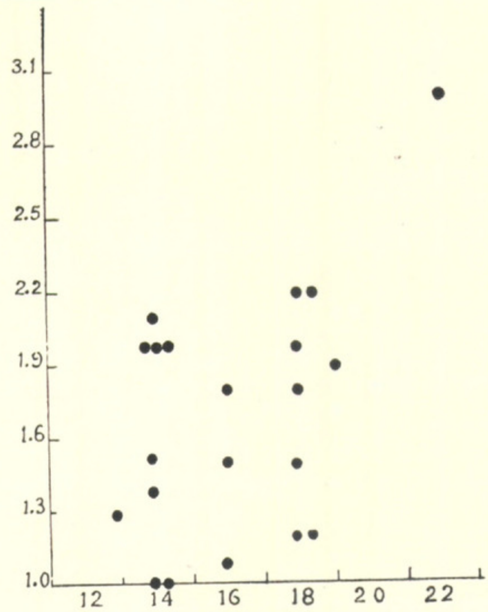

Fig. 6. Scatter diagram showing correlation between tassel-node condensation and ear row number among 21 plants of a back-cross between two inbred lines of yellow dent corn. Each dot represents a single plant. Vertical scale, condensation index of the tassel; horizontal scale, number of rows of kernels on the ear.

Another precise test was afforded by a series of standard commercial inbred lines of maize and their F_1 hybrids, selected from breeding plots of the Pioneer Hi-Bred Corn Company. The inbreds were being grown in short rows for observation. After a quick inspection, a single representative tassel was chosen from each inbred, and the Condensation Index was calculated in the manner described above. The average Condensation Index for any two inbreds was then calculated and compared with the actual row number obtained in a hybrid between these two inbred lines. Here again, only one plant was examined. No conscious selection was made other than to see that the ear was obtained from a healthy plant with no obvious malformations. The correlation between tassel condensation and ear row number is presented in fig. 5. Considering the variability of row number this is a remarkably high correlation, especially when one considers that neither tassel condensation nor ear row number was an average value, but was merely a single selected individual. It will be noted that for lower values of the Condensation Index the row numbers are on the average about 10 times the Index but that for higher values these potentialities are not realized. It may be that, under the conditions of the experiment (the plants were being grown three to a hill), the plants with high condensation were not able to reach their full potentialities. It is also possible that in corn-belt maize there has been a strong selection of modifying factors which would keep the high degrees of condensation under control. It is certainly true in Japanese Hull-less popcorn, where these "bearpaw" ears have not been selected against, that highly condensed tassels are accompanied by equally highly condensed ears. One tassel selected because it was highly condensed along its whole length, with an average condensation of 3.3, had 32 rows of kernels; a much less condensed tassel, with an Index of Condensation of 2.1, had 24 rows of kernels.

Figure 6 shows the same kind of scatter diagram in a population where the effects of environment are much more severe and a less close correlation would be expected. A hybrid between two inbred lines was back-crossed to one of the parents, and these were planted three to a hill in a large plot. In the previous example, while the hybrids were subject to this same crowding, they were all planted with individuals of their own genetic constitution, and interaction between plants was relatively constant throughout the experiment. In this back-cross the plants varied in their general vigor. A strong plant which happened to be in the same hill with two quite weak siblings had an excellent opportunity to reach its full potentialities; a weak plant in the same hill with two very strong ones could not have been expected to do so.

Finally, fig. 7 diagrams a larger population in which the interaction between the three plants in each hill is somewhat less extreme. In this case ear-to-row tests were being made of an open-pollinated strain of a long-eared yellow dent. One healthy, vigorous plant was selected in each row and its row number and Condensation Index were obtained.

There is even a correspondence between the condensation *pattern* of the basal-most secondary branch of the tassel and the flattening of the ear. If the tassel branch is highly condensed along its entire length, then the ear will be a true "bearpaw." If the tassel branch is highly condensed at the tip but much less so below, then the ear will be more or less circular in cross-section with a flaring, usually two-pointed apex. If the tassel branch is highly condensed at the base but runs out into a long uncondensed portion, then the ear will be broadly elliptic at the base but with a normal apex. No exceptions to this generalization have been noted in all the material which has been examined. Plate 17 shows three very different ears of maize with very different degrees of condensation and different condensation pattern. In all three, if the actual row number is divided by the Condensation Index calculated for the tassel, 10 is indicated as the "fundamental" row number.

The pattern of condensation in the lowest tassel branches of the three ears is as follows (in each case the figures indicate the number of pairs of spikelets at each apparent node, beginning from the base):

Mexican "Bearpaw" dent—2, 3, 3, 2, 2, 2, 4, 4, 5, 3, 4, 3, 3, 3, 3, 4, 2, 4, 2, 3, 3, 3, 3, 2, 1, 3, 3, 3, 3, 5, 4, 3, 4, 4, 3, 3, 4, 2, 3, 3, 3, 4, 2, 2, 4, 3, 4, 4, 3, 2, 3, 2, 4, 3, 2.

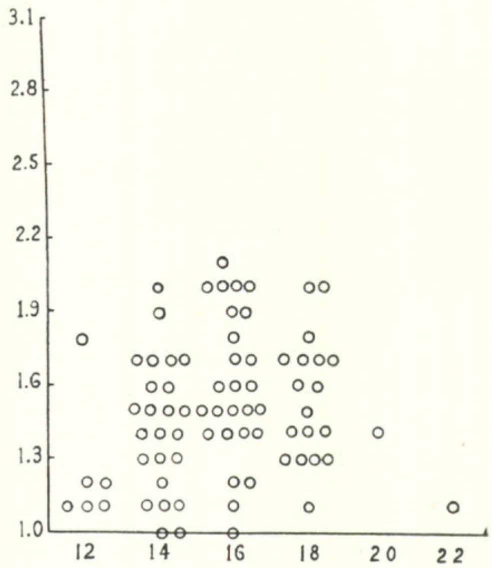

Fig. 7. Correlation between condensation of the tassel and row number of the ear in an ear-to-row plot of long-eared yellow dent. Scales as in figs. 5 and 6. Further explanation on p. 334.

Open-pollinated long-ear Reid—1, 1, 1, 1, 1, 2, 2, 2, 1, 2, 2, 2, 1, 3, 3, 1, 1, 2, 3, 3, 3, 4, 3, 5, 4, 5, 4, 5, 4, 5, 4, 4, 4, 1, 3, 1, 3, 2, 3, 1, 2, 2.

Inbred Os 420—1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 3, 1, 1, 2, 1, 1, 1, 1, 1, 2, 1, 1, 2, 1, 1, 1.

There is a close correspondence between these patterns and the ears. The tassel of the "Bearpaw" dent is highly condensed along its whole length; so is the ear. The tassel of the open-pollinated yellow dent is slightly condensed below but very heavily condensed towards the apex; the ear has 18 rows at the base but is fasciated at the apex with approximately 22 rows. OS 420 has only a light degree of condensation throughout its tassel and it has an ear with 14 rows.

Tassel profile and ear shape.—As shown schematically in fig. 3, there is a surprisingly close correspondence between tassel branch length and ear length and between the relative lengths of successive tassel branches and the shape of the ear. If the tassel branches are all long, as in fig. 3, 'B', then the ear is long and cylindrical; if they are all short (fig. 3, 'A'), then the ear is short but still cylindrical. If the branches get successively shorter towards the apex, then the ear tapers sharply and regularly (fig. 3, 'C'). If they are short both at the base and the apex and longest in between (fig. 3, 'D'), then the ears have a kind of "hand grenade" shape as in certain sorts from South America.

This correlation is more than a general one between different races of maize; if used in conjunction with the other correlations reported in this paper it may even be used to judge between related inbreds. It apparently is highly correlated not only with the actual shape of the inbred ear but also with the behavior of the inbred in crosses. Tassel branch diagrams are presented in fig. 4, using a modification of the simple method recently described by Anderson and Schregardus ('44). It will be seen that the "profile" of the tassel established in fig. 4 is an excellent reflection of the known behavior of these inbreds. Inbred LA is known to produce long cylindrical ears in single crosses with other inbreds while inbred HY is also notorious as producing sharply tapering ears in crosses with other inbreds. Preliminary indications are that the tassel profile may even be a better indication of ear-shape potency than the actual ear of the inbred itself. Some 40 inbreds were carefully examined and their tassel profiles were compared with the ears. All agreed in a general sort of way though there were a few exceptions. These exceptional profiles agreed better with the breeding records than the ears themselves. Figure 4 shows a case in point, the profiles of inbreds Ill. A and R-4. The profile of the former suggests a short, nearly cylindrical ear. The profile of R-4 suggests a long ear, tapering pretty sharply, though not as extreme as HY. The actual ears of these inbreds are somewhat as indicated, but when compared with each other they are very much alike; much more so than the tassel profiles. However, both of these inbreds are widely used commercially. It is well known that in hybrids, R-4 produces a much longer but more tapered ear than does Ill. A.

In the material which has been investigated there is even some indication that if the first one or two tassel branches are markedly longer than the rest there will be a tendency for the basal portion of the ear to be somewhat larger. This correlation rests on scattered observations and needs to be carefully tested with lines which are reasonably constant for other characters but differ in the basal enlargement of the ear or the length of the lowest one or two tassel branches.

Tertiary tassel branches and irregular rowing.—The kernels of an ear of maize may be spaced either evenly or unevenly. A little examination will show that the unevenness is due to two quite different factors. The rows may be regular but the kernels set crookedly in the row, or the rows themselves may be irregular in spite of the fact that the kernels are set straight in the rows. This latter condition is, among other things, correlated with the number of tertiary branches on the lower secondary branches of the tassel. Here again, the two extreme conditions have marked geographical distributions. The common dent varieties of the American corn belt have an intermediate condition between these two extremes, and ordinarily have 1 or 2 of the lower secondaries which bear tertiary branches, usually not more than 1 or 2 tertiaries arising from each. In the Peruvian area 6 or more of the basal secondaries may bear tertiaries. There are frequently 5 tertiaries on the basal-most secondary, and the larger tertiaries may themselves give rise to short branches of the fourth order. Similar tassels are also to be found in Guatemala. The other extreme is found most highly developed in Mexico where in spite of the fact that the tassels are often very large, tertiary branches are few or none.

If the ear were formed *as if* the tassels were wrapped spirally about a central core, then one might expect these short tertiary branches to upset the rowing. Such is probably the case. As with the factor for condensation, there is apparently a lower threshold for expression in the tassel than on the cob. A tassel with one or two tertiaries is not always accompanied by irregular rowing. However, inbred lines characterized by highly irregular rows have a high degree of tertiary branching in the tassel. There even seems to be a rough correspondence between the comparative length of the tertiaries and the place on the ear where the irregularities appear. These may take two forms. Ordinarily, they show as a place where the row runs out. Sometimes, however, they merely appear as an extra grain inserted between two adjacent rows.

Further correlations are suspected but will require detailed examination of critical material to establish. These are as follows: (1) a positive correlation between the size of the primary axis at the base and the size of the shank and cob, (2) a positive correlation between the number of tassel branches and the comparative size of the pith zone in the center of the cob, (3) a negative correlation between the angle made by the primary axis and the secondary branches of the tassel and the brittle-stiffness[1] of the main stalk of the corn plant, (4) a correlation between very large, rough, pointed spikelets and long, more-or-less pointed kernels.

Discussion.—The correlations outlined above are definite enough to be of some use in practical maize breeding. This does not necessarily mean that they are decisive evidence in the old controversy as to whether the ear of corn is homologous with the central spike of the tassel or whether it is homologous with an entire tassel of fused branches. When we come to understand the tassel and the ear not merely as end products but in terms of the actual forces which mould them as they are, we may find that both of these concepts have their place. It is quite possible that, in so far as some forces are concerned, an entire ear is like the central

[1] No one English word expresses this quality.

spike of the tassel, but that in terms of other forces it is more exactly homologous with tassel branches fused spirally side by side. An extension of the general method described in the introduction should make it possible to settle such questions fairly definitely.

The observations reported above do provide fairly clear evidence with regard to the old controversy as to whether or not the ear of maize is fasciated. The "condensation" reported above is a kind of regular, controlled fasciation which only occasionally becomes so extreme as to produce elliptical axes and multiple growing-points. The new evidence also suggests quite as clearly that fasciation is only one of several forces and that in North American maize it operates only in ears of more than 8 or 10 rows. The whole history of the maize ear is much too complex to discuss here even in a preliminary fashion. Understanding that the condensation of North American maize is a special feature and that it apparently traces back to the Mexico City-Toluca area and is tied up with the history of dents and "bearpaw" popcorns should enable us to approach the larger problem more intelligently. Apparently, primitive South American maize had a whorled tassel and a short, ovate or top-shaped ear with regularly disposed kernels but no straight rows, as we know them in modern maize. Some unexplained agent, perhaps *Tripsacum* (Mangelsdorf and Reeves, '39), introduced long straight rowing and alternate or spiral tassel branches. The extremely simple 8-rowed flints are not among the older prehistoric remains either in South America or in the American Southwest. The straight 8-rowed ear is apparently a highly derived rather than a primitive condition in *Zea Mays* (if we consider that remarkable aggregation of forms *as a whole* and not merely from the point of view of the American corn belt). Increase in row number in South American varieties is accompanied by an increase of condensation in the central spike but apparently not in the tassel branches. This is one of many points concerning condensation that needs further investigation.

Little has been said concerning the genetics of any of the characters described above. They are all apparently multiple-factorial. Preliminary evidence suggests that the factors are not scattered at random through the chromosomes. An extension of the methods of analysis outlined above should make it possible to begin the exact genetic study of quantitative characters in maize. Emerson and his co-workers have already assembled a series of marker genes and an effective cooperation between different laboratories. Unfortunately, however, the chief character (ear row number) which has so far been investigated (Emerson, '32) is one which does not lend itself well to exact analysis. Since the difference between an easily recorded character and an easily analyzed character does not seem to be generally understood it may be well to amplify this *dictum*.

Ear row number is a good example of a quantitative character which is easy to record exactly but difficult to analyze. Any ordinary ear of maize has just so many rows and there is no quibble about it. However, we are not interested as geneticists in the number of rows; we want to find out something about the forces which go to make low row number or high row number. As has been demonstrated above, these forces are of various kinds, *each one a quantitative multiple factor character in itself*. Before we can analyze the genetics of row number we must, first of all, break it down into its component forces. The section on "Condensation" presents data which suggest that condensation is *one* of these components. With the method of tassel scoring outlined above, it should be possible to study the genetics of this primary multiple factor character and learn where the genes for condensation are and how many there are and how they interact. The other factors affecting row number will then be easier to analyze, but serious genetic analysis must again be preceded by morphological detective work.

Just as the early work on the genetics of eye-color mutants and wing mutants in *Drosophila* was based upon long hours of study and scrutiny by such gifted observers as the late Calvin Bridges, so any serious attempt to study the genetics of quantitative characters must be preceded by explorative observation. It is generally admitted that the genetics of quantitative characters is much more difficult than that of single factor mutations. After a decade of work, I am convinced that the preliminary observational analysis of quantitative characters presents unsuspected difficulties; difficulties, furthermore, of a higher order of complexity. It is indeed a research field in its own right. Although plant material is apparently easier to analyze morphologically than either vertebrate or insect material, it will require long and coöperative preliminary research if problems concerning quantitative characters are to be brought to the level where they are ready for genetic analysis. A series of apparently unrelated papers which have emanated from this laboratory in the past decade (Anderson and de Winton, '35; Anderson, '39; Anderson and Ownbey, '39; Anderson and Hubricht, '43; Anderson, '44; and Anderson and Schregardus, '44) are all connected in one way or another with this problem. While some of them have so little apparent connection with plant genetics that they could not have been published in a journal devoted to that subject, they are all concerned with multiple factor genetics. They represent various attempts to work out methods for analyzing quantitative characters on a morphological level. In this paper I have attempted to demonstrate how such techniques might be applied to practical maize-breeding problems.

SUMMARY

1. The methods used in this study are described. The necessity of analyzing the material on a biological level before statistical methods are applied is stressed and illustrated by examples.

2. Variation in the tassel (the male inflorescence of *Zea Mays*) is described, character by character, and methods of recording it exactly are outlined.

3. Evidence for the following ear-tassel correlations is presented:
   a. Tassel internode condensation and increase in row number.
   b. Tassel branch length and ear length.

c. Tassel branch pattern and ear shape.

d. Tertiary branches and irregular rowing.

4. In North American corn, the relation between tassel condensation and row number is surprisingly exact. In general, it is close to the following equation:

$$\text{Condensation Index} = \text{row number} / 10.$$

5. The geographical distribution of tassel condensation is discussed. It reaches its highest development in the Mexico City-Toluca area which is also the center for extreme denting.

6. The problem of homologies between tassel and ear is briefly discussed. It is tentatively concluded that in so far as the actual forces are concerned *both* the fused tassel branch hypothesis and the central spike hypothesis may be essentially true.

7. The application of these facts to the genetics of quantitative characters is discussed briefly. Using condensation as an example, a distinction is made between multiple factor characters which can be recorded exactly and those which can be analyzed exactly.

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Explanation of Plate

PLATE 17

Three ears which illustrate the correspondence between the condensation of nodes in the tassel and the increase in row number of the ear: Left, inbred yellow dent Os 420; center, "bearpaw" dent from Mexico; right, open-pollinated yellow dent from Iowa. (N. B. This ear *is* right side up; the feature at the apex is the expanded tip of the cob.)

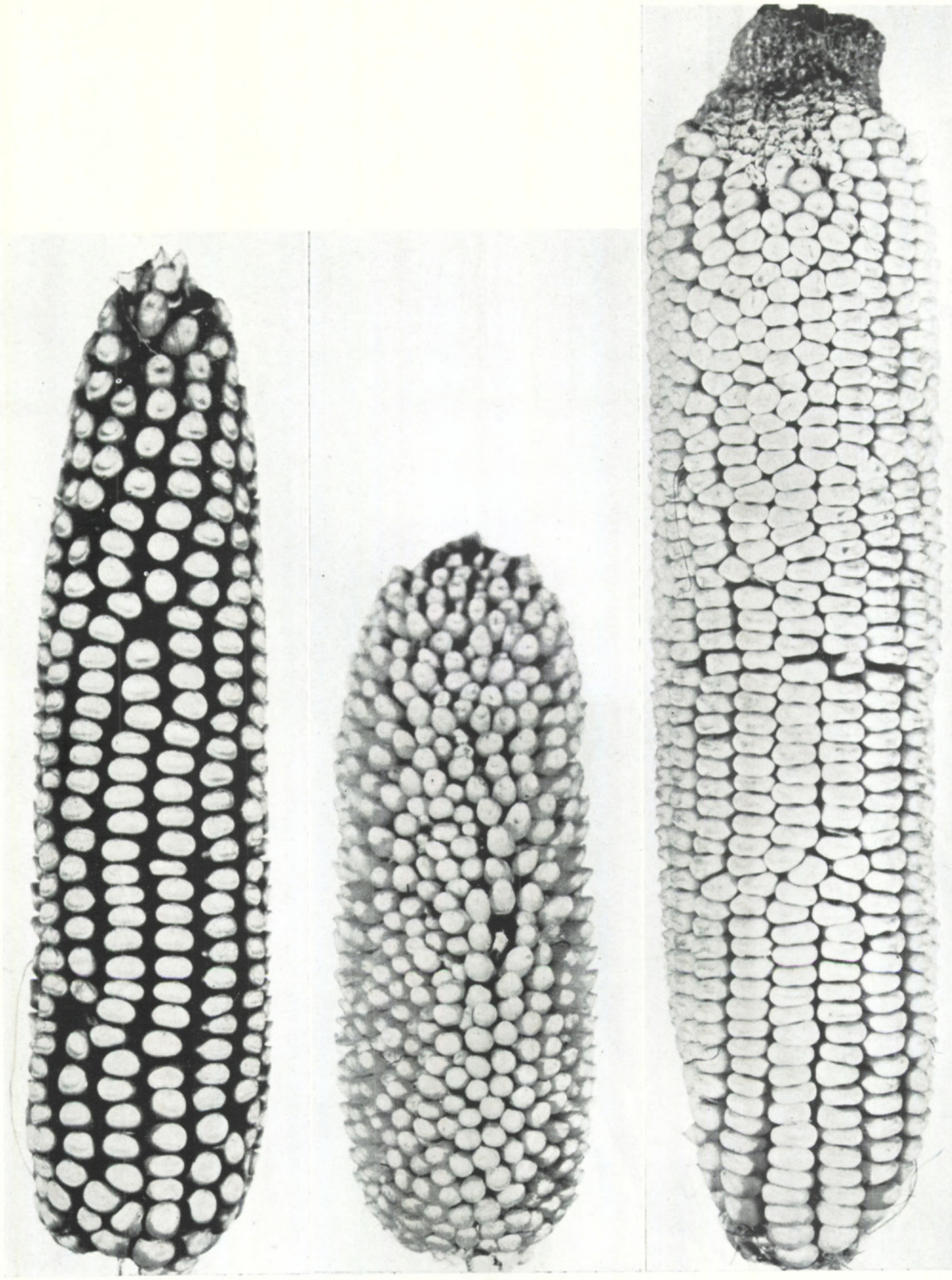
Condensation indices and condensation patterns for these ears are as follows, the figures representing the number of spikelet pairs per node beginning at the base of the lowermost tassel branch:

Inbred Os 420
C. I. = 1.4
1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 3, 1, 1, 2, 1, 1, 1, 1, 1, 2, 1, 1, 2, 1, 1, 1

"Bearpaw" dent
C. I. = 3.2
2, 3, 3, 2, 2, 2, 4, 4, 5, 3, 4, 3, 3, 3, 3, 4, 2, 4, 2, 3, 3, 3, 3, 2, 1, 3, 3, 3, 3, 5, 4, 3, 4, 4, 3, 3, 4, 2, 3, 3, 3, 4, 2, 2, 4, 3, 4, 4, 3, 2, 3, 2, 4, 3, 2

Open-pollinated yellow dent
C. I. = 2.9
1, 1, 1, 1, 1, 2, 2, 2, 1, 2, 2, 2, 1, 3, 3, 1, 1, 2, 3, 3, 3, 4, 3, 5, 4, 5, 4, 5, 4, 5, 4, 4, 4, 1, 3, 1, 3, 2, 3, 1, 2, 2

Further explanation in the text.



ANDERSON—EAR-TASSEL HOMOLOGIES