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Conversions for earliness in maize inbreds

Numerous studies have shown earliness to be a completely inherited quantitative trait when a large range of difference in parents is considered. However, such studies do not usually address the ordinary problems which confront the practical plant breeder, since he is more often concerned with smaller differences, which if brought under precise control, can have large economic significance. If, among all the factors controlling earliness, there are a few major genes, each of which produces a recognizable phenotypic effect when heterozygous, then the backcrossing procedure itself becomes an efficient means to both detect and transfer such major genes if these exist. The plant breeder could then make discreet conversions for this quantitative trait, in the same manner as many other conversions are handled in plant breeding.

In 1956, the inbred parents of hybrid U. S. 13 were selected (Wf9, Hy2, Oh41 and 38-11, hereafter designated 9, Hy, 41 and 38 respectively), and crossed to the very early variety, "Gaspe Flint." Then, ten uninterrupted backcrosses were made to each of the four inbreds. In each backcross recovery progeny, the sole selection criterion of fewest days to anthesis was used to select 4 to 6 plants for further backcrossing from a minimum population of 64. After completion of the 10 straight backcrosses, 2 generations of sibbing, then two of selfing were completed. After the last selfing generation, a single ear progeny was selected as the final modified version of each inbred, and these $BC_{10}S_4$ recoveries were designated "9E," "HyE," "41E" and "38E." In the summer of 1971 all possible inbred and parental single cross combinations were grown out in 5 rep. experiments; the data collected are in Table 1. Total leaf numbers were determined by marking the 5th leaf while the first leaf was still present, and by marking the 10th leaf while the 5th was still present.

Little difficulty was encountered during the 10 backcrosses in identifying markedly earlier segregates, indicating that major earliness genes were being "dragged" (controlled). The completed early recoveries appear to be precise recoveries of the original lines, indicating that the major Gaspe genes are not linked to any easily recognizable phenotypic trait.

Days to Anthesis was markedly shortened in the 4 inbred lines, by 12.6, 6.84, 2.0, and 6.56 days in 9, Hy, 41 and 38, respectively. Factors producing this modification are partially dominant as seen by the fact that the crosses between original and modified "E" versions are earlier by 8.68, 6.20, -2.00 and 4.98 days respectively. (The exceptional result for inb. 41 will be discussed later). The degree of modification produced by E versions of inbreds when used in single crosses is proportional to the degree in which the inbred itself is modified. For example, inbred 9 was most modified by the earliness conversion, and 9E is more prepotent in single cross combination than any other E version. This indicates that different major Gaspe genes have about the same degree of dominance. Since there was never any visual evidence in backcross progenies that the earliest class of plants among the 4 inbreds (except for inb. 41) was more numerous in one than another, it is believed that the same number of loci was being transferred in each line, but that these differed from line to line, presumably because a given inbred may already have been isogenic for a given Gaspe gene, while another inbred may have been isogenic for another. If this is so, then the differing degrees of earliness modification among the 4 lines are due to the differing potencies of the Gaspe genes to which a given line was susceptible to modification.

Table 1. Inbreds, early recoveries, and their F_1s.

Pedigree	Days to Anthesis	Total Leaf No.	Height Top Ligule	Height EPN*	Ear Length	Kernel Row No.	Tillers Per Plant	Ears Per Plant	Grams Per Kernel	Yield lb/A
9	95.18	20.00	58.0	24.4	6.27	16.27	.000	0.967	.239	3,588
9E	82.58	15.50	39.9	12.9	5.99	13.87	.017	1.000	.235	2,377
9 x 9E	86.50	17.76	52.5	21.1	6.50	15.60	.000	1.000	.261	4,273
Hy	94.06	18.90	47.6	24.4	5.07	14.93	.017	.983	.223	2,256
HyE	87.22	15.72	37.0	15.6	5.13	16.43	.018	1.018	.160	2,008
Hy x HyE	87.86	17.48	43.4	20.4	6.21	16.27	.078	.961	.173	2,318
41	101.20	19.32	55.5	26.7	7.04	12.27	.180	1.016	.189	2,513
41E	99.20	18.98	52.0	24.9	6.42	12.13	.133	0.967	.213	2,665
41 x 41E	103.20	19.70	56.0	27.0	6.88	12.27	.098	0.984	.221	2,976
38	103.10	20.96	65.6	35.0	7.65	15.34	.180	1.000	.213	3,018
38E	96.54	19.20	60.2	26.8	7.71	13.63	.491	1.018	.238	2,985
38 x 38E	98.12	19.76	64.3	32.5	8.24	14.43	.441	1.017	.235	3,842
9 x Hy	86.07	20.11	74.8	40.7	7.24	18.40	.580	0.992	.255	7,301
9E x Hy	83.48	18.09	66.8	33.6	6.78	17.53	.680	1.000	.282	6,948
9 x HyE	84.17	18.52	67.6	30.7	6.83	18.69	.538	1.000	.251	6,696
9E x HyE	81.01	16.62	58.5	24.1	6.46	18.20	.683	1.008	.267	6,386
41 x 38	94.55	20.51	78.9	47.2	8.16	13.67	1.442	1.033	.286	6,810
41E x 38	92.73	19.88	75.2	42.9	8.18	13.93	1.303	.992	.268	6,510
41 x 38E	91.38	19.85	76.7	43.3	8.23	13.54	1.467	1.025	.318	7,220
41E x 38E	89.56	19.17	74.2	40.6	8.42	13.50	1.393	1.016	.246	6,955

*Ear Placement Node

Leaf number was reduced in the early conversions by 4.50, 3.18, 0.34 and 1.76 leaves respectively, in proportion to the degree of chronological modifications. Plant height to the top ligule and height of the ear placement node were reduced in proportion, and these relationships are carried into the single cross hybrids.

Effects upon ear length, kernel row number, tillers and ears per plant, and individual kernel weight were inconsistent.

Yielding ability of inbred lines was generally reduced by the earliness conversion, but the cross between a line and its "E" counterpart always showed heterosis for yield, presumably because of heterozygosity for the transferred chromosome segments. An increase in yield for these extremely close sister crosses of an average of 508 pounds per acre is rather surprising, and tells why the seed industry is rapidly abandoning the marginally economic pure single cross hybrid in favor of modified singles. In spite of their superior yielding ability, these sister crosses looked identical, except for traits directly related to earliness, to their unmodified counterparts. Heterosis in these narrow sister crosses was accompanied by increased ear length, so this study agrees with the general finding that ear length is the yield component most clearly associated with heterosis.

Yielding ability of 9 x Hy single crosses was reduced by insertion of E line conversions into the pedigree. It is difficult to say how real this reduction is, since only one population was used, and it can be expected that the smaller plants of the E versions would yield relatively better at higher populations. On the other hand, if the reduction is real, it is explainable on the basis that if conversion of both 9 and Hy "dragged" the same Gaspe locus, then their single cross hybrid would be homozygous for this segment and therefore less heterotic.

Yielding ability of the 41 x 38 single crosses was not altered by the insertion of E versions, and it is worth noting that leaf number and plant stature was least altered also. The several ways in which the 41 derivatives behaved differently seem unexplainable. The 41E line is earlier than 41 and has fewer leaves, but is prepotent for lateness and greater leaf number when combined with inb. 41; these data are consistent throughout the 50 individual data of 5 reps. In combination with inb. 38, it is prepotent for earliness and reduced leaf number. During the extended backcrosses by which 41E was derived, there seemed to be only 2 classes of plants, half the population being only slightly earlier than the other half, in marked contrast to the usual situation where each generation presents a very few plants really much earlier than the general population. Nevertheless, we are unable to devise a plausible genetic model to explain the erratic Oh41 data.

The finding in this research that earliness is always associated with a reduction in leaf number (and plant stature) is consistent with the generally accepted idea that earliness is determined by a signal which "tells" the apical meristem when to stop cutting off leaves, and when to produce the apical inflorescence (tassel). Our transferred loci from Gaspe always worked their effects by this means. Since the backcrossing process was just as effective when conducted during the very short days of wintertime in Hawaii, it is clear that the loci are independent of day-length effects, and operate to control the number of plastichrons to be completed by the apical meristem. Since ear placement is also always lower in early-converted entities, it is apparent that control is exercised by the transferred loci during the whole period of morphogenesis, since the ear inflorescence, as well as the tassel, was cut off after fewer plastichrons. The clarity of the relationship between earliness and leaf number makes it tempting to suppose that leaf number is the primary (or only) criterion of earliness. The data in Table 2 were derived from those in Table 1 by dividing days to anthesis by leaf number plus one (to account for the tassel) and are intended to show the time required by each genotype to complete one unit (plastichron) of development.

Table 2. Plastichron indices (time to anthesis divided by leaf number plus one).

Non-heterotic Pedigree	Index	Heterotic Pedigree	Index
9	4.53	9 x Hy	4.08
9E	5.00	9E x Hy	4.37
9 x 9E	4.61	9 x HyE	4.31
		9E x HyE	4.60
Hy	4.73	41 x 38	4.40
HyE	5.22	41E x 38	4.44
Hy x HyE	4.75	41 x 38E	4.38
41	4.98	41E x 38E	4.44
41E	4.96		
41 x 41E	4.99		
38	4.69		
38E	4.78		
38 x 38E	4.73		
Overall Mean	4.83	Overall mean	4.38
Mean of normals	4.73	Mean of normal x normal	4.24
Mean of earlies	4.99	Mean of normal x early	4.39
Mean of normal x early	4.77	Mean of early x early	4.52

Data in Table 2 show a remarkable consistency in overall number of days required per plastichron in all genotypes, but it is notable that heterotic entities (even the very narrow sister crosses) are always a little faster, and hence leaf number, while an overwhelmingly important factor, is not the sole determiner of earliness.

Very surprising is the fact that in both heterotic and non heterotic pedigrees, the "E" conversions in every case required more time to complete a plastichron than did normal counterparts. This strengthens the role played by leaf number in earliness, and indeed the transferred loci produced earliness solely by this means, even having to swamp the delay of a slower plastichron cycle to do so.

Since doing the original work on the U. S. 12 inbreds reported here, we have made earliness conversions of numerous other inbred lines. No other cases of anomalous behavior besides Oh41 have been observed, although the degree to which individual inbred lines are susceptible to earliness modification does vary. Often the recurrent parent is switched to a related line, or a finished "E" conversion is used as a source of major earliness loci, rather than Gaspe itself. In some cases our material is removed from Gaspe by 15 straight backcrosses, and it is still perfectly easy to "control" the earliness genes. As in the classical Nilsson-Ehle experiment, repeated attempts to quantitate numbers of genes controlling earliness in our experiments by scoring individual plants in the backcross progenies and then erecting frequency distributions result only in normal-appearing population curves. Nevertheless, the ease with which we continue to control transferred loci for extended backcrosses using only relatively small populations leads us to suggest that we are controlling only two major loci, or at most three.

The practical significance of earliness conversions is vast: A valuable inbred line can be moved widely across maturity zones without losing the attributes from which its value derives. A "pure" singlecross hybrid can be made to have an extended pollen/silking period by the insertion of, say, B73 x B73E as one parent. Field crosses can be made which would otherwise require split planting. Availability of germ plasm for a given maturity zone can be greatly expanded. Late exotics can be made amenable to maintenance in temperate zone breeding stations.

Attempts have been made to extend the oligometric approach outlined here to modify other quantitative traits such as shuck number, shuck texture, shank length, ear number, kernel row number, and internode length. All these endeavors have been successful, although not with the ease associated with the earliness conversion.

The research pursuant to this paper was conducted at the University of Illinois, at Indiana University, at Brookhaven National Laboratory, and at Cornnuts Research Department. More detailed data and statistical treatments are available on request.

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