The Location of Genes Governing Long First Internode of Corn

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ABSTRACT

Knowing breeding behavior and cytological location of traits helps breeders. My objective was to locate dominant genes for long first internode of corn (*Zea mays* L.). I determined that Hopi Indian corn PI213733 (variety Komona) displayed the trait and grew well in the U.S. Corn Belt. I crossed PI213733 to 26 translocation tester stocks in Minnesota inbred A188 background, backcrossed semi-sterile plants carrying the translocation to A188 the next generation, and grew the segregating generation planted in trenches 15 cm deep with ridges of dirt 10 cm high one year, in trenches 25 cm deep the other year and also at normal (6 cm) depth. Emerged plants were classified for semi-sterility or for normal pollen. I concluded from multiple testers for each chromosome arm that dominant genes for long first internode are located (chromosome and region) on *3S*, on *6* near the centromere, and on *9S*; spurious associations occurred for two testers. Measurement of cell lengths indicated that PI213733 had more cells than A188 both in upper and in lower mesocotyl sections and that lower, older cells elongated sooner. I found a normal-sized kernel with twin embryos that developed two long first internode seedlings indicating that the amount of endosperm did not limit mesocotyl growth.

THE mesocotyl or first internode of the corn plant is the structure that compensates for depth of planting of the kernel. The mesocotyl continues to grow until emergence of the coleoptile after which mesocotyl growth is inhibited. Further growth of the seedling plant is due to the development of successive leaves previously enveloped by the coleoptile (see Figure 1).

Corn grown in the U.S. Corn Belt is commonly planted ~6 cm deep. In the arid southwestern region of the United States and parts of western Mexico, Indians plant their local varieties of corn at a depth of 30 cm or more in an attempt to reach soil moisture. These Indian varieties emerge from great depths of planting due to their inherent capacity to develop long mesocotyls (see Figure 2).

The long mesocotyl characteristic might be of value in U.S. Corn Belt hybrids. It could contribute to increased seedling stands where the seeds were intentionally planted deeper than normal to reach soil moisture or to avoid damage from surface application of harmful chemicals, where the seeds were accidentally planted deeper than normal due to poor planter adjustment, or where the seeds were planted at normal depth, but greater seedling emergence force was required because of surface-crust formation.

A knowledge of the mode of inheritance of agronomic characteristics is of value to the plant breeder. The primary objective of the present study was to determine which chromosome arms contain a dominant gene or genes normally governing the ability of a certain Hopi Indian corn variety to emerge from deep depths of planting.

WALLACE *et al.* (1949) state that in deeply planted corn the length of the mesocotyl varies greatly among varieties. In varieties from the American southwest and from western Mexico the mesocotyl may be 30 cm or even more in length if the corn has been planted deeply. DUNGAN (1950) compared a strain of Indian corn with hybrid U.S. 13. In plantings at 5-cm intervals from 5 to 30 cm deep, the Indian corn emerged from the 30-cm depth while U.S. 13 failed to emerge from depths of planting >20 cm. He observed that the kernels of U.S. 13 were 20% larger, but a lower proportion of the food reserves was used during germination than for the Indian corn. BROWN *et al.* (1952) described the cultural practices of Hopi Indian corn growing. Because lack of water is always a problem, the corn fields are located where soil moisture is likely. The fields are not plowed, but the weeds are removed; then the sand is scraped away from an area 30 cm or so in diameter and a hole is dug in moist soil for receiving the kernels. Eight to 12 kernels are placed in each opening and are then covered carefully by hand, using first the moist soil and then sand. The hole may be 6 to 10 cm deep in the soil, but 30 cm or even 46 cm below the surface of the sand. The hills are spaced three steps apart in the row and rows are likewise three steps apart, and after emergence, the plants are thinned to five or six per hill. ANDREW (1953) reported a sweet corn inbred

This paper is dedicated to Dr. Charles R. Burnham, pioneer corn cytogeneticist, enthusiast, teacher, fisherman, and good friend, who died April 19, 1995. Dr. Burnham participated in all facets of this study including revision of the first draft of this paper.

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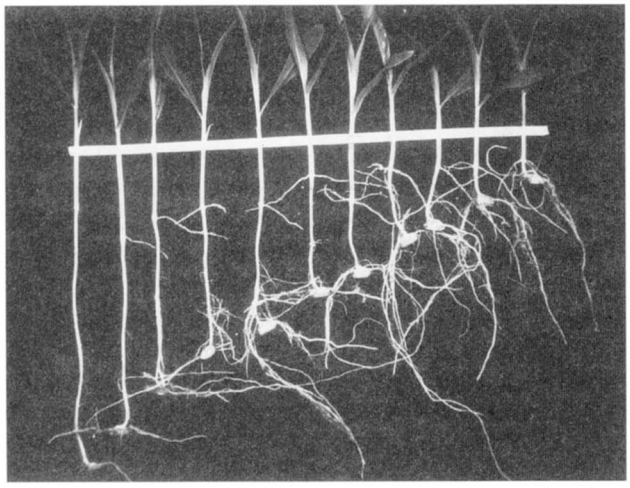

FIGURE 1.—Normal response of mesocotyls of hybrid U.S. 13 to a series of depths of planting (white tape represents soil line, first nodes can be detected by secondary roots or swellings.

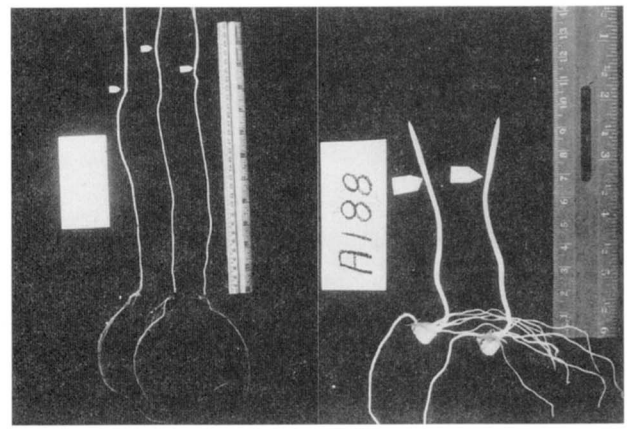

FIGURE 2.—Length of mesocotyls of PI213733 (variety Komona), which averages ~24 cm maximum, and Minnesota inbred A188, which averages ~7 cm maximum (arrows denote first nodes).

line (5002) exhibiting an unusually short mesocotyl. In all but two of 25 F_2 families a satisfactory fit to a three long to one short ratio occurred. The total of the segregates equaled 1667:544 where 1658:553 were expected. He concluded that the character was inherited as a simple recessive and suggested the designation *sft* (short first internode).

A brief account of reciprocal translocation early history follows. BARBARA MCCLINTOCK (1930) determined that *semi-sterile 2* was a reciprocal translocation involving the second and third smallest chromosomes. Her method involved the cytological examination of crosses of *semi-sterile 2* with known trisomics. ANDERSON (1935) showed that in heterozygous interchange (semi-sterile) plants, the distribution of chromosomes is such that one-half of the spores receive a normal and an interchange chromosome, one-fourth receive both normal, and one-fourth receive both interchange chromosomes. The last two classes have all parts of both chromosomes represented and are viable. The spores that receive a normal and an interchange chromosome are deficient for a portion of one chromosome and duplicated for a portion of another. These fail to form normal pollen and appear as empty or starch-free, abortive grains. The elimination of these types of spores make the interchange appear to be transmitted as a single unit. Crossing over may occur between an interchange chromosome and its normal homologue at any point. The interchange may thus be followed in linkage tests by means of the semi-sterility, which behaves in outcrosses like a dominant gene at the locus of the interchange in both linkage maps. ANDERSON (1938) first suggested the use of reciprocal translocations in linkage tests. Reciprocal translocations are particularly useful genetic tools because they have little effect upon the plant other than semi-sterility of the pollen and ovules. ANDERSON's method is especially useful for unmarked portions of the chromosomes and for determining the number of genes controlling quantitative traits. An excellent chapter in *Maize for Biological Research* provides a more extensive review (BURNHAM 1982).

Translocation marker techniques have been successfully utilized to locate factors for the following characteristics: smut susceptibility and resistance (BURNHAM and CARTLEDGE 1939); reaction to smut and firing (SABOE and HAYES 1941); husk length, ear length, and days to silking (FREEMAN 1946); resistance to *Helminthosporium carbonum* (ULLSTRUP and BRUNSON 1947); kernel row number (MANN 1950); oil content of the kernels (MILLER 1951); resistance to European corn borer (IBRAHIM 1954); pericarp tenderness (MOHAMED 1954); pollen restoration (LINDEN 1956; (DUVICK *et al.* 1961); resistance to *H. turcicum* (JENKINS *et al.* 1957); and resistance to *Puccinia sorghi* (RUSSELL and HOOKER 1962).

MATERIALS AND METHODS

I obtained four different Hopi Indian corns (PI213732, PI213733, PI213734, and PI213735) from the Regional Plant Introduction Station at Ames, Iowa. In a preliminary test PI213733 and PI213735 displayed lengths >24 cm from germ face to coleoptilar node. The ears of PI213735 often rotted under bags subsequent to hand pollination, so I concentrated work on PI213733 (variety Kokoma). I crossed PI213733 to a set of 26 translocation tester stocks (see Table 1) that had been part of a backcrossing program that placed the translocations in a near-uniform Minnesota inbred A188 background. The next season I classified fresh pollen of the crosses with the aid of a pocket microscope (30× magnification) and a bakelite jar cap and tagged plants showing semi-sterility typical of translocation heterozygotes. I classified the pollen on two or more dates of all semi-sterile plants subsequently pollinated with pollen from PI213733. I harvested two or more semi-sterile ears from each translocation stock.

I grew two ears of each heterozygous translocation × PI213733 cross at University Farm, St. Paul; classified each plant's pollen on two or more dates; and pollinated all semi-sterile plants with pollen from A188. I inspected all hand pollinated ears to insure they displayed the semi-sterility typical of translocation heterozygotes and harvested one such

ear from each ear row. The plants from resulting seed of translocation heterozygote × PI213733)A188 would be expected to segregate for semi-sterility and for long mesocotyl where the genes for long mesocotyl expressed dominance over their alleles in A188.

I conducted a separate study to compare the mesocotyl cell lengths of PI213733 with Minnesota inbred A188. I planted 50 kernels each of PI213733 and of A188 4 cm deep germ face up in a sand bench in a completely randomized field plot design, allowed the plants to grow to the three leaf stage, and then uprooted and examined the plants. I chose 18 plants of each seedlot with nearly identical mesocotyl lengths, divided them according to seedlot, excised the mesocotyls, and then transversely cut them in half. I kept the upper regions (near leaves) separate from the lower regions (near roots) within each seedlot. I made fresh radial hand sections of each specimen and determined the length of >250 cortical cells by use of an ocular micrometer.

I grew the segregating populations, translocation heterozygote × PI213733)A188, on a farm near Mankato, Minnesota. I delayed planting until the latter part of June when soil temperature was warmer. I dug trenches 15 cm deep, first with a tractor cultivator, then with a tile crumber to form a smooth, even surface and drove wooden stakes at each end of the trenches for taut strings attached 25 cm above the level of the bottom of the trenches. I planted 100 kernels along the bottom of the trenches germ face up at 18-cm intervals from each of two ears from each backcross progeny except for four ears where <100 kernels were available. I shoveled soil back into the trenches and added soil to form a ridge up to the level of the strings.

The next year I grew the segregating populations on the same farm again delaying planting until the latter part of June. I dug trenches 25 cm deep with a Davis T-66 Self-propelled Utility Trencher, manufactured by Davis Mfg., Inc. of Wichita, Kansas. I planted 50 kernels germ face up at 14-cm intervals with double spaces between seedlots from each of two ears from each backcross progeny except for five ears that were short of seed. I then filled the trenches to original ground level and refilled them after settling.

The following year I grew the segregating populations on the same farm and again delayed planting until the middle of June. I planted up to 50 kernels for each ear of each backcross progeny with a hand planter at an approximate depth of 6 cm. Each seedlot germinated in excess of 90%.

During flowering I classified pollen, tagged plants for pollen type, and recorded number of normal and semi-sterile plants for each seedlot each year.

RESULTS AND DISCUSSION

Locating genes for long mesocotyl: As previously stated, the backcross populations were expected to segregate for semi-sterility and for the long mesocotyl condition. Linkage of a gene or genes conditioning the long mesocotyl character with a chromosome or chromosomes involved in a specific translocation tester would result in an excess of normal plants over semi-sterile plants in the population that survived the deep plantings. I applied the chi-square test for goodness of fit to the expected 1:1 frequency. The results of the deep planting experiments are summarized in Tables 1 and 2.

As previously indicated each linkage association may be with either or both chromosomes involved in the translocation. For example, the significant association for tester stock *1-3(5883-1)* in itself might indicate a gene or genes conditioning mesocotyl length on the short arm of chromosome *1*, on the short arm of chromosome *3*, or genes located on both of these arms. To determine which arm or arms are involved, it is necessary to observe the results for other tester stocks testing the same arms to determine whether the association is consistent in each test involving that region. Testers *3-4(5156-9)* and *3-6c*, both of which test the short arm of chromosome *3*, show significant associations with long mesocotyl as indicated by the excess of emerged plants with normal pollen thus indicating a dominant gene or genes conditioning long mesocotyl length located on the short arm of chromosome *3*. The excess of emerged plants with normal pollen in *6-9(5454-4)* and *6-9d* indicate a dominant gene or genes for long mesocotyl length located near the centromere of chromosome *6*. The excess of emerged plants with normal pollen in the cultures segregating for *2-9c* and *6-9(5454-4)* indicate a dominant gene or genes for long mesocotyl length located on the short arm of chromosome *9*. No explanation is offered for the significant associations obtained between normal pollen and long mesocotyl for testers *2-7c*, which is persistent but inconclusive, and *5-10(6760-1)*, which is spurious.

The above results indicate a minimum of three dominant genes controlling the long mesocotyl characteristic: one located centrally on the short arm of chromosome *3*, one located near the centromere on either the short or long arm of chromosome *6*, and one located centrally on the short arm of chromosome *9* (Table 2).

Approximately 20% of the deep planted population survived the first year planting while only ~10% survived the second year planting. The reason for the difference between the 2 years is unknown but at least two possible causes are suspected. Three-year-old seed is generally considered more susceptible to fungal attack than 2-year-old seed. Also the planting under ridges represented a depth of planting 15 cm below the original soil line, while the planting in trenches resulted in a depth of planting 25 cm below the original soil line; the soil temperature at seed level was probably cooler in the latter case.

The 20% emergence of the first planting is near that expected for a backcross population where two genes are necessary for emergence (one-half squared equals 25%); the 10% emergence of the second planting is more similar to that expected where three dominant genes are necessary for emergence (one-half cubed equals 12.5%). Both of these expected ratios are based upon the assumption that 100% of the plants heterozygous for all three (or two) of the genes for long mesocotyl survived the deep planting.

To observe the segregation of semi-sterility among both short and long mesocotyl types and to detect any factor or factors other than deep planting that might be affecting the expected 1:1 ratio of semi-sterile to

TABLE 1

Segregation of normal and semi-sterile pollen among survivors of seed stocks segregating for long mesocotyl planted 25 cm deep

Translocation			First year				Second year			
Designation	Break points		N	SS	χ^2	P	N	SS	χ^2	P
1-3 (5982-1)	1S.77	3L.66	28	28	0.000		3	3	0.000	
1-3 (5883-1)	1S.88	3S.60	15	5	5.000	0.05	9	2	4.455	0.05
1-8b	1L.59	8L.82	32	43	1.613		5	0	5.000	0.05
1-8 (6766-2)	1L.54	8L.77	39	34	0.342		5	6	0.091	
1-9b	1L.50	9L.60	33	39	0.500		5	9	1.143	
2-4L	2L.59	4S.40	23	19	0.381		3	0	3.000	0.10
2-4b	2L.81	4L.53	27	14	4.122	0.05	0	1	1.000	
2-6d	2L.41	6L.45	7	8	0.067		5	3	0.500	
2-7c	2L.47	7S.34	30	14	5.818	0.02	10	5	1.667	
2-9c	2S.49	9S.33	13	4	4.765	0.05	6	0	6.000	0.02
2-10 (6061-4)	2S.60	10L.57	14	14	0.000		10	13	0.391	
3-4 (5156-9)	3S.47	4L.67	29	14	5.233	0.05	16	10	1.385	
3-6c	3S.56	6L.54	43	29	2.722	0.10	11	3	4.571	0.05
3-7c	3L.46	7L.45	19	27	1.391		9	4	1.923	
4-6e	4S.62	6L.56	29	22	0.961		15	18	0.273	
4-7 (7108)	4S.17	7S.45	11	8	0.474					
4-9f	4L.55	9L.18	11	17	1.286		8	5	0.692	
5-7e	5S.40	7S.18	19	20	0.026		3	1	1.000	
5-7 (5179)	5L.55	7L.73	15	14	0.034		4	6	0.400	
5-9e	5L.46	9L.74	32	28	0.267		19	17	0.111	
5-10 (6760-1)	5S.78	10S.40	23	11	4.235	0.05	8	6	0.286	
5-10 (X57-16)	5S.42	10L42	26	25	0.020		11	8	0.474	
5-10 (5688-9)	5L.78	10L53	24	18	0.857		9	19	3.571	0.10
6-9 (5454-4)	6S.00	9S.75	29	13	6.095	0.02	15	0	15.000	0.01
6-9d	6S.73	9L.82	35	6	20.512	0.01	6	0	6.000	0.02
8-10 (6488-2)	8L.14	10S.34	30	32	0.065		21	15	1.000	

N, normal; SS, semi-sterile.

normal plants, the last planting of the segregating seedstocks was made at a normal depth. The results on normal planting in Table 3 indicate that the ratios obtained all fit the expected 1:1 ratio. It seems probable then that the cause for significant deviations from one normal to one semi-sterile among the deep planted testcross progenies was due to the advantage of the long mesocotyl segregates under deep planting conditions.

If the genes discovered in the present study differ in their relative effects, such differences might be determined by using a series of planting depths in the screening process. Future studies might start with a minimum depth of 25 cm and add greater depths in an effort to partition the effects of the genes involved. At the maximum depth only the seedlings carrying the gene with the greatest effect would be expected to survive. The proper translocation stock would provide segregates affording a direct linkage test for the gene displaying the greatest effect with semi-sterility; all survivors from the maximum depth with normal pollen would belong to the parental class while survivors with semi-sterile pollen would represent crossovers. In this manner the gene with the greatest effect could be more accurately located.

By the same token, the use of depths of planting <25 cm might allow the detection of genes for long mesocotyl with less effect than those found in the present study. All in all, the use of a series of depths of planting seems a desirable method of obtaining more information on the expression of characters involved in the inheritance of long mesocotyl.

In the present study attempts were made to develop a satisfactory laboratory method of growing corn seedlings with maximum mesocotyl lengths. All attempts failed. A satisfactory method should meet the following requirements. The seedlings must be grown in the dark because light on the coleoptile inhibits mesocotyl growth through an auxin destruction process (INGE and LOOMIS 1937). The container for growth media should be designed to allow manipulation of the seedlings without damage or loss of identity at harvest. The container and growth media must be such that they allow the establishment and maintenance of proper environmental growth conditions. Because the amount of endosperm may be a critical factor in maximum mesocotyl elongation (DUNGAN 1950), growth media should be chosen that supply a minimum of nutrients that might augment the food reserves in the endosperm.

In one of the attempts to develop a laboratory growth method, a kernel of long mesocotyl origin developed

TABLE 2

Segregation of normal and semi-sterile pollen among survivors of seed stocks segregating for long mesocotyl planted 25 cm deep and at normal depth

Translocation			Deep 2 year				Normal depth			
Designation	Break points		N	SS	χ^2	P	N	SS	χ^2	P
1-3 (5982-1)	1S.77	3L.66	31	31	0.000		15	10	1.000	
1-3 (5883-1)	1S.88	3S.60	24	7	9.323	0.01	22	18	0.400	
1-8b	1L.59	8L.82	37	43	0.450		18	15	0.273	
1-8 (6766-2)	1L.54	8L.77	44	40	0.190		17	16	0.030	
1-9b	1L.50	9L.60	38	48	1.163		12	14	0.154	
2-4L	2L.59	4S.40	26	19	1.089		14	20	1.059	
2-4b	2L.81	4L.53	27	15	3.429	0.10	19	14	0.758	
2-6d	2L.41	6L.45	12	11	0.043		23	26	0.184	
2-7c	2L.47	7S.34	40	19	7.475	0.01	23	27	0.320	
2-9c	2S.49	9S.33	19	4	9.783	0.01	25	18	1.140	
2-10 (6061-4)	2S.60	10L.57	24	27	0.176		7	10	0.529	
3-4 (5156-9)	3S.47	4L.67	44	24	5.882	0.02	23	20	0.209	
3-6c	3S.56	6L.54	54	32	5.628	0.02	15	18	0.273	
3-7c	3L.46	7L.45	28	31	0.153		22	27	0.510	
4-6e	4S.62	6L.56	44	40	0.190		26	23	0.184	
4-7 (7108)	4S.17	7S.45	11	8	0.474					
4-9f	4L.55	9L.18	19	22	0.220		13	16	0.310	
5-7e	5S.40	7S.18	22	21	0.023		13	14	0.037	
5-7 (5179)	5L.55	7L.73	19	20	0.026		24	19	0.581	
5-9e	5L.46	9L.74	51	45	0.375		16	17	0.030	
5-10 (6760-1)	5S.78	10S.40	31	17	4.083		11	12	0.043	
5-10 (x57-16)	5S.42	10L42	37	33	0.229		18	23	0.610	
5-10 (5688-9)	5L.78	10L53	33	37	0.057		23	16	1.256	
6-9 (5454-4)	6S.00	9S.75	44	13	16.860	0.01	25	16	1.976	
6-9d	6S.73	9L.82	41	6	26.064	0.01	27	16	2.814	0.10
8-10 (6488-2)	8L.14	10S.34	51	47	0.163		10	8	0.222	

N, normal; SS, semi-sterile.

twin seedlings with each mesocotyl measuring >18 cm in length (see Figure 3). The seedlings resulted from twin embryos under a single germ face in a single caryopsis of normal size. The fact that an average amount of endosperm reserves supported a total mesocotyl length of >36 cm suggests endosperm reserves did not limit mesocotyl length.

The development of a satisfactory laboratory technique for evaluating mesocotyl elongation would aid in the study of the inheritance of long mesocotyl. Some applications are as follows. Proper translocation seed stocks segregating for long mesocotyl and semi-sterility could be first evaluated for mesocotyl length in the laboratory and then be transplanted in the field. This procedure would differ from the present study in that both long and short mesocotyl plants could be classified for semi-sterility. Because mesocotyl elongation is a seedling characteristic, use of a laboratory method of evaluating mesocotyl length would facilitate the application of the gene marker translocation technique (ANDERSON 1938). In this method the kernels would be

TABLE 3

Average cell lengths in microns of the upper and lower region of the mesocotyls of PI213733 and Minnesota inbred A188 planted 4 cm deep

	Upper region (near leaves)	Lower region (near seed)	Mean[a]
A188	159.4	229.9	194.6
PI213733	95.9	176.2	136.1
Mean[a]	127.7	203.0	

[a] Means differ at $P < 0.01$.

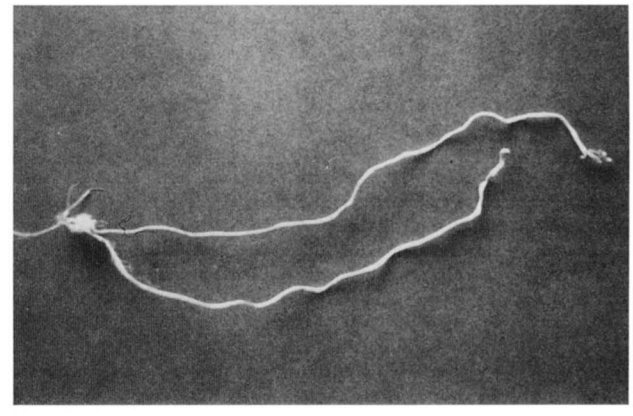

FIGURE 3.—Twin seedling of long mesocotyl origin (~0.3×). An average amount of endosperm reserves supported >36 cm of mesocotyl growth.

first classified for the gene marker (which denotes presence or absence of the translocation) then grown in paired rows and evaluated for long mesocotyl. Significant differences in mesocotyl length between rows would be due to a gene or genes for long mesocotyl associated with that particular tester stock.

Transferring long mesocotyl genes to Corn Belt hybrids: Because the source of the long mesocotyl characteristic used in the present study (PI213733) is adapted to the southwestern United States and lacks adaptation to the U.S. Corn Belt, the backcross method probably represents the best breeding technique available for transferring genes for long mesocotyl to corn belt material. This method involves the use of a recurrent parent to which desired plants in segregating progenies are crossed back; after a suitable number of backcrosses, a new line is evolved that is very similar to the original recurrent parent except that the desired characteristic has been added.

As previously indicated the genes discovered in the present study express some degree of dominance over the normal alleles of A188. For this reason, it should not be necessary to convert all the lines in a hybrid made up of two or more inbreds.

In the case of long mesocotyl, selection in segregating populations could be enforced by use of the deep planting screening as used in the present study; survivors would carry the long mesocotyl gene or genes to be crossed back to the recurrent parent. However, use of the deep planting screening technique would seriously limit the maturity of inbreds that could be handled because of the delay in planting necessary to insure favorable soil temperatures at the lower depth. The deep planting technique also requires special machinery and considerable extra work in comparison with normal planting. For the aforementioned reasons the use of a laboratory method of screening long mesocotyl plants would greatly help the backcross program.

Comparison of mesocotyl cell lengths: I was interested in the developmental morphology of long mesocotyl. The lengths of mesocotyl cells of PI213733 averaged 30% shorter than those of A188 (Table 3). As previously mentioned, all plants used for cell measurement were selected to have nearly identical mesocotyl lengths; therefore, PI213733, with the shorter cell lengths probably has a higher total number of cells per comparable length of mesocotyl than does A188.

The cell lengths of the upper region of the mesocotyls were 38% shorter than the lower region (Table 3). This probably indicates that older cells in the lower region of the mesocotyl entered the elongation stage of cell growth before the younger cells in the upper region of the mesocotyl. The varieties × positions source of variance was practically nonexistent indicating more cells per comparable length of mesocotyl in both the upper and lower regions of PI213733 than in A188. The lack of interaction also indicates that the general pattern of cell growth subsequent to initiation was similar in both the normal and long mesocotyl materials studied (analyses not shown).

The mechanism of mesocotyl elongation is not well known. The data obtained in the present study fit the hypotheses that mesocotyl elongation is dependent upon cell elongation that begins in the lower, older cells of the mesocotyl and progresses upward to the coleoptilar node; PI213733, with a greater number of cells per unit length of mesocotyl, has the potential to produce longer mesocotyls.

I thank the communicating editor and anonymous reviewers for helpful suggestions.

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