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Agnes Hansen
University of Minnesota

Ernst C. Abbe
University of Minnesota

would not expect this lack of cross transport in view of the vascular anastomosing in the pulvinus and the crossing over of the lateral vascular traces at the primary leaf node as has been described by Harris, Sinnott et al, and by Doutt.

STRUCTURE AND GROWTH OF THE MESOCOTYL IN THE MUTANT OF MAIZE, DWARF-1 [1]

AGNES HANSEN AND ERNST C. ABBE
University of Minnesota

One of the mutants affecting stature of maize is known as dwarf–1. This work was undertaken because the manner in which this gene for dwarfism influences the structure of the mesocotyl of the seedling plant had not been studied. It is a seedling character readily differentiated even in the early stages of development (Fig. 1A), and is thus well adapted to a study of gene action in the early ontogeny of the plant.

Since the growth pattern of the mesocotyl is modified by temperature, humidity and light, the last factor acting as an inhibitor of the growth of the mesocotyl, the seedlings were grown in a dark room having a constant temperature of 24° C., and a relative humidity of 80%. A hygrothermograph provided a continuous record of the temperature and relative humidity.

The kernels used all came from a single ear which was produced as the result of selfing an F_1 obtained by back-crossing d_1d_1 to University of Minnesota inbred A188. The writers are indebted to the Division of Agronomy and Plant Breeding of the University of Minnesota for the space used in the preliminary breeding and for the opportunity of using its stock of inbreds.

The plants were grown in glass tubes containing sterilized cotton. A coarse, wire mesh screen, coated with paraffin was used to support the glass tubes. This screen with its cotton-filled tubes, each containing a single kernel, was placed over a glass tank of distilled water. The level of water in the tank was kept about an inch below the seed. Every twenty-four hours, the water in the containers was completely replaced with fresh water.

The plants were collected at twelve-hour intervals under red light having a wave length of 620 millimicra to which the mesocotyl is relatively insensitive. They were fixed in Chrom-acetic-formalin killing solution for twenty-four hours, then stored in 70% ethyl alcohol.

The length of each mesocotyl was measured with a steel milli-

[1] Supported in part by a grant in aid of research from the Graduate School of the University of Minnesota.

meter rule for the older plants, with a binocular dissecting microscope, equipped with an ocular micrometer for the younger plants. The width of the mesocotyl was measured with the ocular micrometer. The mesocotyl is the region between the point of attachment to the scutellum and the base of the coleoptile. (Fig. 1.)

In comparing the rate of growth in length of the mesocotyls of the dwarf plants with that of their normal-sized sisters, it was found that the mesocotyls of the dwarf plants grow much more slowly in length and are shorter at maturity (Fig. 2; see also Fig. 1A and Fig. 1B). Is this difference in growth patterns of the mesocotyls related to cell size or to cell number? Studies to resolve these questions were made at three developmental stages of the dwarf seedling plant,—61 hours, 122 hours, and 182 hours (maturity of mesocotyl). The dwarf-1 seedlings were compared age for age and length for length with the normal plant. Camera lucida drawings of the cells of the cortical region were made from paraffin embedded material which had been sectioned longtitudinally and stained with tannic acid-ferric chloride and basic fuchsin.

The data on cell size and number are summarized in the Table. Cell number along the length of the mesocotyl is, in each case, the mean of counts along eight vertical rows in the cortical parenchyma. Cell number across the mesocotyl is the mean of counts made at three levels (top, middle, bottom), the cells of the central vascular cylinder being excluded. Mean cell length was determined by dividing the length of the mesocotyl by the mean number of cells in that dimension. Mean cell width was determined by dividing the width of the parenchymatous portions of the mesocotyl by the mean number of parenchyma cells across the mesocotyl.

The size and shape of the cells of the mesocotyl of the young dwarf plant, 61 hours old, 0.8 mm. long and 1.7 mm. wide were compared with a normal plant of the same length, but 51 hours old, and 1.6 mm. wide, and with a normal plant of the same age as the dwarf but 1.6 mm. long and 1.5 mm. wide. It was found that the sizes and shapes of the cells of young mesocotyls of both dwarf-1 and normal plants were much alike (Fig. 3). The mean cell length of the 61-hour dwarf-1 mesocotyl was 16 μ, in its normal sib of the same age it was 19 μ, and in the normal sib of the same length (0.8 mm.) it was 13 μ. Mean cell width in the 61-hour dwarf-1 was 26 μ, just as in its normal sibs, one of the same age, the other of the same length (cf. Table). There is relatively little difference in length of cell and no essential difference in width of cell whether the mesocotyls of the normal sib are compared with those of the 61-hour dwarf-1, length for length or age for age.

The cells of a mature dwarf mesocotyl 7.0 mm. long, 2.3 mm. wide, 182 hours old were compared with those of its normal sister plants and are illustrated in Figure 4. On the left are the cells of a normal plant with a mesocotyl of the same length, 7.0 mm., but

1.7 mm. wide and only 86 hours old. On the right are cells from the mesocotyl of a normal plant of the same age, 182 hours, having a length of 31 mm. and a width of 1.9 mm. Mean cell length of the 182-hour dwarf-1 mesocotyl was 99 μ, in its normal sib of the same age was 186 μ, and in its normal sib of the same length was 59 μ. Mean cell width in the 182-hour dwarf-1 was 38 μ, in the normal sib of the same age was 29 μ and in its normal sib of the same length was 30 μ (cf. Table). The cells of the mature dwarf mesocotyl are not as long but are wider than those of the mature normal, while those of the normal mesocotyl of the same length are shorter and narrower.

It is evident from the Table and from Fig. 1A that the mesocotyl of the young dwarf-1 plant is essentially of the same width as is that of its young normal sib. Insofar as organ form and size, in this respect, are concerned, there is no evidence of difference in gene action at this ontogenetic level. However at maturity of the dwarf-1 mesocotyl, it is also clearly evident from Fig. 1B and the Table that the dwarf-1 mesocotyl is appreciably broader than is its normal sib. Is the wider mesocotyl of the mature dwarf-1 plant due to a greater number of cells across the mesocotyl or to greater width of the cell as compared with the normal plant? To answer this question the cortical parenchyma cells were counted across the top, middle, and bottom of each mesocotyl studied and the mean number recorded in the Table. The number of parenchyma cells across the mesocotyls of mature dwarf-1 and normal plants was essentially the same, (45 in dwarf-1 and 42 in its normal sib), the greater width of the dwarf-1 mesocotyl being directly correlated with wider and not more cells. Since the cells of the dwarf mesocotyl are wider than those of the normal sibs at later stages of development, we may conclude, that the gene combination d_1d_1 permitted greater lateral growth of the cell walls concerned as compared with gene combinations containing D.

A point of morphogenetic significance that may be mentioned here, is that throughout the seedling stages there is no essential change in the number of cells across the mesocotyl of either dwarf-1 or its normal sib. It is clear that lateral growth in each mesocotyl during this part of the seedling stage involves cell enlargement only. On the other hand, longitudinal growth of the mesocotyl involves both cell enlargement and cell multiplication. It is evident that the gene combination d_1d_1 does not affect the number of cell divisions contributing to the width of the mesocotyl.

A characteristic of the mesocotyl of dwarf-1 which is still more evident than its greater width (as compared with its normal sib) is its marked shortness (Figs. 1A, 1B, and 2) at all stages of development studied. Does a difference in cell number in the length of dwarf-1 and normal mesocotyls, as well as length of the cell contribute to the shortness of the dwarf mesocotyl? The parenchyma

TABLE

	Mesocotyl Length				Mesocotyl Width			
	Age [1] hours	Length of Mesocotyl mm.	Mean Cell No. Lengthwise [2]	Mean Cell Length in μ [3]	Width of Mesocotyl mm.	Width of Vascular tissues in mm.	Mean Cell No. across [4]	Mean Cell Width in μ [5]
Normal	51	0.8	60	13	1.6	0.4	43	26
Dwarf-1	61	0.8	49	16	1.7	0.6	41	26
Normal	61	1.5	81	19	1.6	0.5	44	26
Normal	86	7.0	118	59	1.7	0.5	40	30
Dwarf-1 (mature)	182	7.0	71	99	2.3	0.6	45	38
Normal (mature)	182	31.0	167	186	1.9	0.6	42	29

[1] hours from planting; at 24°C, 80% humidity
[2] mean of counts along 8 vertical rows in parenchyma
[3] length of mesocotyl/mean cell number lengthwise
[4] mean of counts in parenchyma at three levels (top, middle, bottom) in mesocotyl
[5] width of mesocotyl minus width of vascular tissue/mean cell number transversely

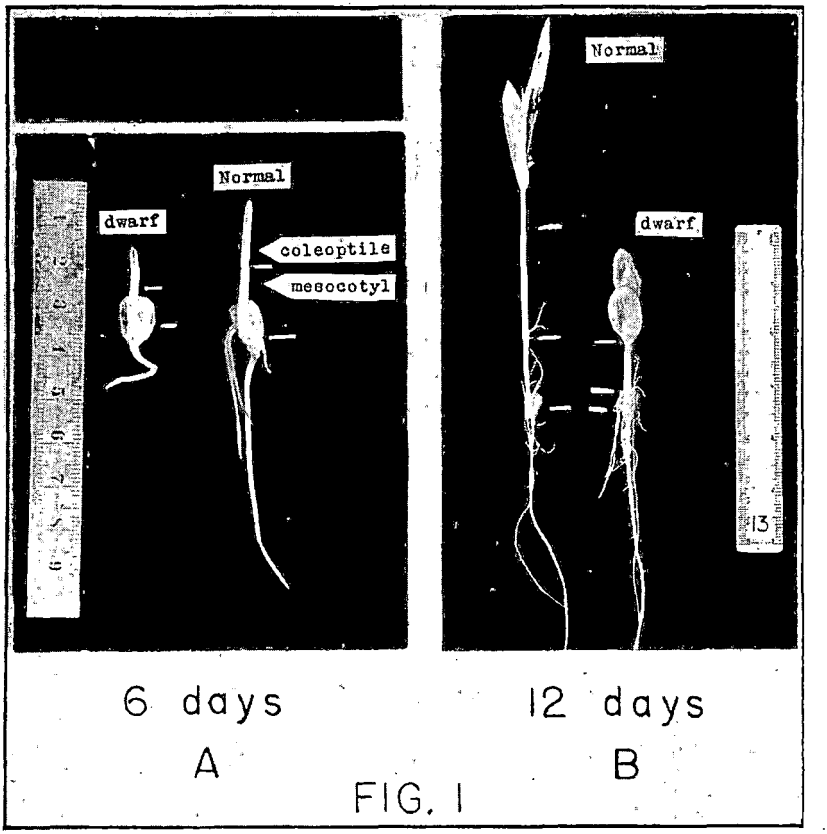


FIG. 1

cells were counted in eight vertical rows at more or less equal distances across the mesocotyl. The mean number of cells for each mesocotyl, lengthwise, is recorded in the Table. The mature normal mesocotyl (182 hrs. old) had more than twice as many cells contributing to its length (167 cells) as compared with the mature dwarf mesocotyl (71 cells). Also, the mature normal cell averaged about twice the length of the mature dwarf cell. It is evident that the gene combination d_1d_1 has inhibited the total number of cell divisions contributing to cell number along the longitudinal axis of the mesocotyl as compared with the normal.

In summary, there are several manifestations of the action of the gene d_1 during the development of the mesocotyl in maize. The mesocotyls of homozygous recessive dwarf-1 plants, as compared with their normal sibs have:

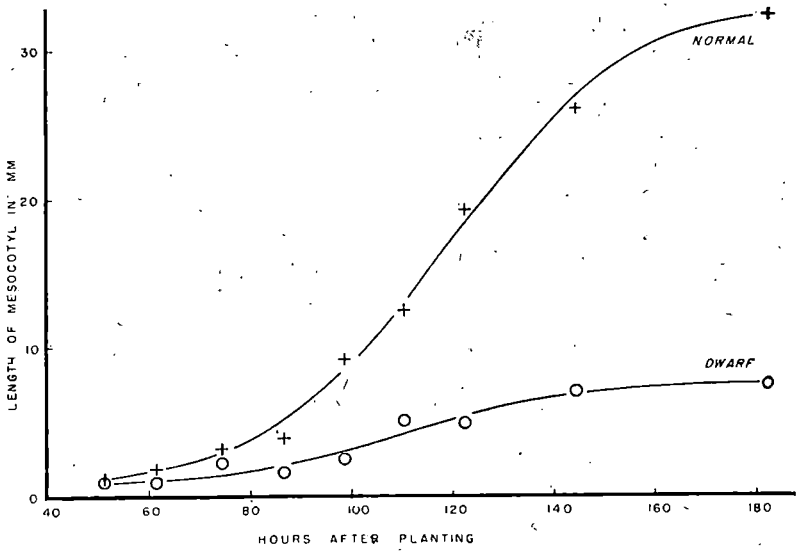
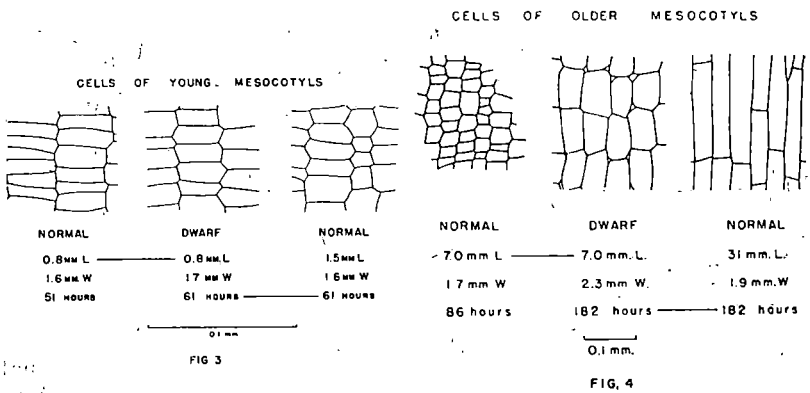


FIG.2



1. A depressed rate of growth in length and are shorter at maturity
2. Fewer and shorter parenchyma cells at maturity
3. Greater width at maturity
4. The same number of cells transversely; these cells are wider.

The processes of cytokinesis and cell enlargement as they contribute to the form of the mature dwarf-1 mesocotyl (as compared with its normal sibs) are directly affected so that there is:

1. A reduced rate and number of cell divisions along the axis of the mesocotyl

2. A reduced rate of cell elongation
3. No modification of cell divisions transverse to the mesocotyl
4. A greater amount of cell enlargement laterally.

The action of the gene d_1 in the homozygous recessive state, as evident from the growth of the mesocotyl, depresses the rate and reduces the number of cell divisions along the axis but does not affect the number transverse to the axis; inhibits cell enlargement along the axis and stimulates it transverse to the axis. The influence of the gene is not a simple one, but is complex, affecting both planes and rates of cell division and cell enlargement.

THE DEGREE OF EXTRAMEDIAL RESPONSE TO HYBRIDITY IN THE GROWTH RATES OF PLANT AND EAR IN A SERIES OF HYBRIDS IN MAIZE

ERNST C. ABBE
University of Minnesota
and
KWEI-WU WANG
Agricultural Institute of Shensi, China

Hybrid vigor in maize is a phenomenon not only of established economic importance but also of great scientific interest. Its existence has long been recognized, but its careful study began only relatively recently with the great developments in our knowledge of genetics and breeding. Hybrid vigor is commonly considered to be the increased development exhibited by a hybrid as compared with its parents. This often is also referred to as "heterosis." However, there is considerable ambiguity in the application of both the term "hybrid vigor" and of the term "heterosis," especially in quantitative studies. Because of this we will instead adopt the convention of referring the degree of expression of response to hybridity to the mean between the parents. This has elsewhere[1] been designated an extramedial response to hybridity.

The degree of extramedial response to hybridity is the extent by which the hybrid exceeds the mean between the parents. It may be expressed conveniently in the form of a quotient, the extramedial hybridity quotient, or med. H.Q., in which the quantitative feature of the hybrid is represented by AB, and in the parents by AA and BB:

$$\frac{AB}{\left(\frac{AA + BB}{2}\right)}$$

[1] Abbe, E. C. 1944. Heterosis, Hybrid Vigor, and Hybridity Quotients. (in press).