The gene markers previously used to identify chromosome aberrations in the endosperm of the maize seed produce cell areas with well-defined boundaries when dominant genes are removed from the cell allowing their recessive alleles to operate. These tissue alterations are brought about during development by any process that removes chromosomes in whole or in part from the cell. The change occurs in the nucleus but the effect is visible in the cytoplasm. Isolated single cells show these changes. Obviously something passes through the nuclear membrane, either from the nucleus to the cytoplasm or in the reverse direction, but does not go beyond the cell membrane since no cell division has occurred in the single cell alterations to liberate nuclear products into the cytoplasm or the reverse.

Where the effects of the gene products are confined within the cell such genes may be considered as cell-limited. Genes of this type in maize aleurone are C, R, Pr and I. For illustration of this type of gene action see figure 1 and Jones1, 2 and Clark and Copeland.3

In marked contrast to these cell-limited genes are the cell-diffusible genes where the gene products pass through the cell wall and affect adjoining cells over a considerable area. The A1, A2 and Y color genes in maize are of this type. The A series of anthocyanin genes are necessary to produce color in all parts of the plant. In the recessive condition the aleurone is colorless, the cob and pericarp are brown and the other parts of the plant are green or brown, depending upon other genes present. The dominant allele produces anthocyanin in the leaves, silks, glumes, anthers, aleurone and scutellum when the complementary genes are present. When A is removed from the aleurone by the loss of the locus containing this gene that part of the seed is colorless. However, there is a gradual diminution in color from the pigmented to the unpigmented area extending over an area of several cells so that the border is not distinct as it is in other color changes involving C, R, Pr and I. Evidently something diffuses through
the cell walls from the pigmented cells into the unpigmented cells for a considerable distance. The colored cells bordering the uncolored area are also darker over a distance of about ten cells adjoining the uncolored area.

**FIGURE 1**

**FIGURE 2**

Figure 1. A change from colorless to colored aleurone cells in a maize seed resulting from the removal of a dominant color inhibitor, a cell-limited gene.

Figure 2. A change from colored to colorless aleurone cells in a maize seed resulting from the removal of the dominant color producer, A₁, a cell-diffusible gene. Note the gradation in color from dark to light areas and the darker border areas between the colored and colorless areas.

The colorless cells produce something that is not used but diffuses into the cells containing the dominant allele and forms a band of darker colored cells. See figure 2. This is an interaction between different alleles at the same locus producing an effect that is greater than that produced by either allele alone and is analogous to heterosis which is normally effected within the cell.

Other cell-diffusible genes of this type are the Y endosperm color genes. In these cases there is no darkening of the border cells containing the dominant allele, only a gradual diminution of color from yellow to colorless. Some of the chlorophyll-controlling genes of the zebra pattern type are probably cell-diffusible. The margins of these bands of lighter green chlorophyll running across the leaf are usually indistinct. However, these have not been observed in areas where the dominant gene has been removed in somatic tissue. Many of the chlorophyll genes are cell-limited as shown by the well-defined stripes of green and white tissue in the leaves running lengthwise. These differently colored areas are produced normally
in the recessive condition but there are also cases where the colorless areas result from the removal of the dominant allele by chromosome aberration or by mutation and the margins are usually distinct.

The pericarp \((P)\) and the plant color factor \((B)\) are also cell-limited genes. Endosperm genes controlling the reserve food formation such as sugary \((su)\), waxy \((wx)\) and brittle \((bt)\) are cell-limited. Adjoining cells show clear-cut effects of the dominant or recessive allele with no gradation either way. The shrunken \((sh)\) condition does not appear in small recessive areas and this may be a cell-diffusible gene. Dull, floury, mealy, opaque and many defective genes have not been observed in adjoining dominant and recessive areas. Many seeds heterozygous for miniature and other defective genes have been examined and no recessive areas have been found. Either these genes are cell-diffusible or cell-lethal.

Cell-diffusible genes of the \(A\) type furnish an excellent example of a gene-substrate interaction. Since the gene products are transferred from cell to cell they are capable of extraction and analysis as shown by Sando and others.\(^4\) Working with purple husked maize, the purple color dependent upon the presence of the dominant \(A\) gene, they obtained evidence for the conversion of flavanols to anthocyanidins by reduction of their corresponding glucosides.

It has been shown by Clark\(^5\) that the genes controlling the development of the male gametophyte in maize operate normally when separated in the cell into a number of small nuclei, provided a full complement of chromosomes is present. This evidence, together with the facts reported here, shows that gene products are effective outside the nucleus and that the interaction between different genes and different alleles of the same gene takes place in the cytoplasm in some cases.