DEVELOPMENTAL GENETICS AND CROP YIELD

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SUMMARY

On the basis of consideration of the patterns of seed differentiation in plants and recent results of developmental genetics in Drosophila, a program is outlined for the production of crops with improved seed characteristics. Tissue-specific mutations, modifying the size or quantity of seed components (embryo, aleurone, seed coat etc.), are expected to increase yield or render better quality by altering embryo-endosperm or endosperm-aleurone etc. ratios. The induction, isolation and utilization of tissue-specific mutations for plant breeding do not require techniques not already familiar to the breeder.

FACTORS OF YIELD

The fruit or grain of a crop plant is a differentiated organ, and as such is the endpoint of an integrated developmental process. Because of its agricultural and economic importance, analysis of the fruit has centered on characterizing yield. Yield is a quantitative expression of the formation of an end product, and does not usually consider or evaluate the developmental mechanisms involved in its maturation (1-3). The developmental geneticist views the process of fruit production and yield from a different perspective. This approach involves a description and analysis of the processes and events whereby a fertilized egg gives rise to a complex of several differentiated cell types. The focus is on dissecting the sequence and timing of the developmental events involved in generating the final phenotype. The developmental geneticist views yield as the summation of all of these separate, but integrated biological processes.

When an agronomist or plant breeder discusses yield, he is referring to the property of a community. The variability expressed both within and among populations of individual organisms constitute higher order fluctuations which the developmental biologist is not equipped to analyze. Hence, in this discussion we will deal with yield as a developmental phenomenon of the individual plant, and with its possible genetic manipulation. We will attempt to gain insight into how yield can be subjected to a developmental genetic analysis by analogy with other more characterized systems.

Yield is a character which is potentially limited by the fluctuations of numerous physical, chemical and biological factors. Besides such environmental parameters as climate, soil structure, nutrient levels, light quality and intensity which may be rate limiting, and the influence of such managerial practices as the density and spacing of planting, irrigation, fertilization and pest control (1-4), the developmental and physiological characteristics of the whole plant play a major role in determining the actual and theoretical yield capacity. General characters which are important in the growth and metabolism of the whole plant such as photosynthetic efficiency or nutrient utilization are crucial factors in determing yield (1, 3-5). The morphology of the entire plant is also an important component determing yield as is demonstrated by the effect of characters like dwarf growth habit or leaf shape and attitude (6-9). Basic physiological decisions such as partitioning of the plant's available resources between reproductive and vegetative structures certainly affect yield (2, 10). However, yield is also dependent on characters which are specific to the seed, and which constitute its unique genetically determined developmental and physiological composition. These characters, such as the final size of the seed, the seed's ability to mobilize nutrients, or the spectrum of macromolecules held in storage have not been well characterized. In most breeding programs seed development and its regulation is taken as given. Since a significant fraction of the carbohydrates, amino acids and other metabolites required by the seed are derived from vegetative tissues (2, 11, 12), it is assumed that more robust plants will produce a greater quantity of fruit and will, therefore, yield more. This discussion will take the opposite approach, and will attempt to view the seed as the endpoint of a developmental sequence which can be modified genetically for the purpose of increasing yield. That is, in a situation where all other parameters are optimal, what are the rate limiting factors affecting yield which are inherent in the seed itself? Which biochemical or developmental processes might be modified genetically to release this limitation? What kind of developmental genetic system is represented by the seed, and what analogies exist which demonstrate the kinds of genetic perturbations which are permissible? Some aspects of plant development and their relationship to yield have been described (12). In this discussion we have not attempted to review the available literature, but rather to explore the possibility that modifications of seed develop-

ment could increase the yield capacity of the major crop species. Because of their agricultural importance much of the discussion and many examples refer to the cereals.

Since we will be discussing the developmental genetics of yield, and since the mature seed is the developmental endpoint of interest, it is appropriate to consider the mechanisms involved in seed development. Although seed development of the *Gramineae* has been well studied (13), it has been difficult to characterize the developmental sequence in terms of other well-known angiosperms (14). In the absence of a uniform developmental pattern for the cereals, we will outline the principle processes involved in very general terms.

Subsequently we will examine other comparable developmental systems. This discussion will rely heavily on *Drosophila* for the following reasons: The level of biological complexity is similar, there are several examples of tissue interactions analogous to those observed in the developing seed, and the genetic analysis of *Drosophila* development has been very productive. The conceptual framework and developmental insights that have evolved in this system should be instructive to a discussion of possible genetic modifications of seed development.

SEED DEVELOPMENT

The mature seed is a mosaic structure, composed of several differentiated tissue types and two genetically distinct clones of cells (15, 16). At fertilization the female gametophyte contains seven cells derived from three divisions of the haploid macrospore: the egg cell and two synergids lie at the micropylar end while the three antipodal cells lie at the opposite pole. All of these cells are haploid. A large central cell which is the progenitor of the endosperm contains the remaining two haploid nuclei. Four layers of diploid maternal tissue, the nucellus, two integuments and the ovule wall, surround the gametophyte and complete the structure of the ovule. All of these tissues are involved in the formation of the seed. In the *Gramineae* as in other angiosperms a double fertilization occurs (15). Two sperm nuclei enter the embryo sac; one of the nuclei fuses with the female pronucleus in the egg cell to form the diploid zygote, and the other enters the central cell, fuses with the two polar nuclei, and forms the primary triploid endosperm nucleus. The synergids and the antipodal cells remain haploid.

Pollination and fertilization stimulate seed development (15, 17). Initial activity is most intense in the maternal tissues, the diploid integuments, nucellus and ovary wall, and the haploid antipodal cells. The nucellus surrounds the embryo sac and provides a pathway for the movement of nutrients to the embryo and endosperm. Enlargement of the nucellus, which varies in extent with different species, begins soon after pollination and appears to involve both cell divi-

sion and cell enlargement (15, 17). The integumentary layers generally undergo extensive enlargement early in development spurred by growth of the nucellus and endosperm. As the ovule matures into a seed these layers differentiate to form the hard, protective coverings of the seed coat. However, in some species such as maize the integuments have only a minor role (18), and instead the ovary wall differentiates the pericarp to serve the same function. In some cases the antipodal cells begin to divide after pollination, and 24 or more are present by fertilization (18, 19). The prominent development of these cells is characteristic of the *Gramineae*. Activity is also seen in the endosperm shortly after fertilization. The primary endosperm nucleus undergoes synchronous divisions within a syncytium to approximately the 128 to 500 n stage (18, 20, 21), depending on the species. The triploid nuclei then move to the periphery of the central cell where individual endosperm cells are formed. The antipodal cells become quite large and polyploid as the endosperm develops, but they soon become disorganized and by the time the endosperm has become cellular they have usually disappeared (18, 22). Early growth of the endosperm appears to be at the expense of the nucellus since the endosperm digests away the nucellus as it expands (18). Midway through development, cells in the center of the endosperm cease division and grow by cell enlargement; their ploidy level increases by endomitosis (23). Cells on the periphery continue to divide, and late in development they differentiate to form the aleurone layer (15). The endosperm acts as a buffer between the developing embryo and the maternal tissue, and it supplies nutrients for the embryo. In the Gramineae the endosperm also serves as a storage tissue and is involved in the synthesis of a unique spectrum of protein, carbohydrate, and lipid storage molecules.

The embryo is the final component of the seed to begin development. The initial cleavage divisions are slow, so that development of the embryo lags well behind the endosperm. Embryogenesis conforms to the Asterad type (13, 15), since each of the first generation blastomeres contributes to development of the embryo and the second cleavage division is longitudinal. Following the early morphogenetic events, the embryo grows rapidly to maturity drawing nutrients from the surrounding endosperm tissue.

This description of seed development highlights the fact that the seed is primarily composed of two very distinct developmental systems, the embryo and the endosperm, which arise from separate fertilization events and which are derived from different clones of cells. These two components follow independent and autonomous developmental sequences, and interaction between the two systems is not a prerequisite for their normal formation. The embryo, for example, can be excised at an early stage and cultured on a simple defined medium (24, 25). In cases where the development of the endosperm is genetically blocked (e.g. interspecific hybrids), the embryo can often be cultured *in vitro* and a mature plant

can be recovered (26). In fact, a process analogous to embryogenesis can proceed *in vitro* on chemically defined media from pollen (27) or somatic cells (28) in the complete absence of any endosperm function. Though an endosperm is most often required for normal embryo development, it does not appear to play any unique function or role in the development of the embryo beyond providing a nutritional milieu. Hence, modification of the endosperm is not limited by constraints imposed by any special requirements of the embryo. The endosperm is also able to develop and mature in the absence of an embryo (29). Seeds containing only the endosperm, or only the embryo have been found in capsules that have developed from incompatible interspecific *Datura* crosses (30). Since no correlation could be established between the size of the seed and the presence of an embryo in some species crosses, it appears that endosperm maturation required no specific information from the embryo. Thus each tissue proceeds as if its developmental fate were determined at an early stage. No inductive interactions or other significant exchanges of developmental information are apparent. Besides being the product of an independent fertilization event, and having a different ploidy level, the endosperm displays a unique spectrum of gene products which are not expressed in the embryo or the whole plant (31, 32). The literature is full of examples of tissue specific genetic characters expressed only in the triploid tissue of the seed (33, 34). Examples include defined enzymatic proteins, genes determining pigment production, morphological features, and gross protein, carbohydrate, and lipid molecules.

The triploid tissue of the seed is an excellent material for the developmental geneticist. It is a complex assemblage of tissues whose developmental sequence is distinct, temporally defined, and genetically controlled by a number of loci which are tissue specific. As a single organ, its developmental process is more simply manipulated experimentally and intellectually than that of the whole plant. The triploid tissues are organized into a very plastic organ. A wide spectrum of biochemical and morphological alterations have no effect on its development or its function of supplying nutrients for the growing embryo (33). It is, in the final analysis, a largely expendable organ under laboratory conditions since the embryo can be rescued using *in vitro* culture methods. In several instances experimental systems displaying similar attributes have permitted the recovery and characterization of a wide range of genetic variants. The quality of being an expendable component permits the isolation and analysis of a number of absolute and conditional mutant types, since the lack of functioning does result in an immediate lethal event and since many genetic loci are expressed only in that component. By these criteria the chloroplast in *Chlamydomonas reinhardi* can be considered an expendable organelle, since the organism can live at the expense of an exogenous carbon source in the absence of chloroplast function. The experimental utilization of this fact has permitted an extensive molecular genetic analysis of its organization and

functioning (35). In Drosophila a similar relationship exists in the larval stage between the larval tissues and the imaginal discs. This relationship, which is described in detail below, has been exploited to examine the genetic control of disc development.

DEVELOPMENT OF DROSOPHILA

The developmental genetics of Drosophila is an active field of research utilizing what appears in many ways to be a parallel genetic system. Since both the genetics and development of *Drosophila melanogaster* have been extensively characterized, it is proving to be a useful organism in which to investigate several fundamental developmental problems. Principally, these are the role of the egg cytoplasm in programming embryonic and subsequent development, and the process of cell determination. Numerous types of mutants have been induced and recovered in Drosophila. These mutants may be utilized by analogy and extrapolation to suggest the type of variants which can be expected to occur in the seed of higher plants. A juxtaposition of the two developmental systems may provide insights into seed biology, and some hints as to how a developmental geneticist could approach the character of yield.

The Drosophila life cycle consists of two distinct stages, the larval and the adult. During the intervening stages of pupation and metamorphosis, most of the larval structures are histolyzed and a new form of the organism, the adult fly or imago, is constructed from clusters of undifferentiated cells in the larva, called imaginal cells (36). The imaginal cells ar set aside early in embryogenesis, perhaps as early as the blastoderm stage (37). The imaginal discs contain the cells which will form the epidermal structures of the adult. Each disc is characterized by its position in the larva and by the part of the adult which it forms (38). The discs attain their final size and characteristic shape during the extended period of larval growth. Mature discs consist of undifferentiated, essentially embryonic cells, whose fate is rigorously determined, awaiting the hormonal signal to begin differentiation (38). The early onset of determination and the temporal separation between the determination of imaginal cells and their subsequent differentiation make Drosophila an appropriate organism in which to study the process of cellular determination and the possible early involvement of the egg cytoplasm.

Developmentally, the relationship between the Drosophila larva and the imaginal discs is very similar to that between the endosperm and the embryo in the seed. Although the imaginal discs originate from a relatively large number of cells, the divergence of larval and imaginal cells occurs early in embryogenesis and the subsequent development of each clone follows a distinct and independent pathway. Growth of the larval tissues occurs by an increase in cell size and effective ploidy level through polytenization (36), as occurs in the endosperm of many plant species. In both the larva and

the endosperm, the final number of cells is fixed at an early stage. The mode of differentiation increases the synthetic capacity in those cells for the output of specialized products required later in development: these cells have no function beyond this life stage. The imaginal discs, however, fulfill the same role as the plant embryo, that is they are the embryonic form of the following life stage. Cells of both the plant embryo and the imaginal discs remain rather quiescent until development of the host tissue reaches an advanced stage. Both remain diploid and divide normally during the process of determination and elaboration of the progenitors for different adult structures. As early as the imaginal discs can be recognized, they can be surgically removed from the larva, and grown to maturity by culturing them *in vivo* in the abdomen of an adult female (39). Mature discs differentiate normally when they are removed from their normal location in the larva (or recovered from the abdomen of an adult female) and injected into the abdominal cavity of a host larva prior to metamorphosis (40). Differentiation of mature discs has also been observed under controlled conditions *in vitro* (41). Most recently it has been demonstrated that normal imaginal structures can be recovered from one or a few cells that have been removed from their normal environment at the earliest cellular stage of embryogenesis (the blastoderm stage in Drosophila), and allowed to complete development under *in vivo* culture conditions (37). Each of these results shows that the imaginal cells have the capacity for autonomous development; there is no evidence for developmental information coming from the larvae. Thus, like the interaction between the plant embryo and endosperm, the demands of the discs on the larva are principally nutritional.

DEVELOPMENTAL MUTATIONS IN DROSOPHILA

In Drosophila, the analysis of developmental mutants has contributed significantly to our understanding of the relationship between the larval and imaginal cell types. Each mature imaginal disc has a characteristic size and morphology, and contains a wide variety of determined cell types (38). Several classes of mutants are known which block or modify the development of one or more discs without altering the larval tissues (42, 43). The most severe phenotype is that of the "discless" mutants in which formation of all of the discs is blocked, while the structure and function of the larval tissues is normal (42). A second large group of mutants includes those in which the imaginal discs are present, but one or more are abnormal. The variety of abnormalities includes discs that are too small or too large, discs with a different shape or texture, and discs that are unable to differentiate. Another class of mutants, the homeotic mutants, affect the determination process directly, since a portion of one disc is altered and gives rise to a structure normally formed by a different imaginal disc (38). Only a few mutants are known which specifically affect the other half of this system, the larval tissues. However, many will certainly be found among the late embryonic and larval lethal mutants now being isolated.

All of these mutants, with tissue specific and stage specific defects, help to resolve this complex developmental process into its individual steps, just as biochemical lesions helped in the reconstruction of biochemical pathways. These mutants emphasize the fact that critical decisions related to the developmental capacity of a tissue, as well as its final size and morphology, are under precise genetic control.

However, many of the morphological variants found in *D. melanogaster* are not developmental mutants of the type discussed above, but result instead from the secondary effects of mutions which alter general metabolic processes. Thus, it is appropriate to consider the features expected of developmental mutants, and examine procedures that have been successfully utilized to recover them. The autonomous development of a tissue requires the precise, sequential activation of many genetic functions, including general metabolic processes as well as tissue-specific developmental information. These two genetic components are integrated into the final biological product. Mutations that modify the regulatory processes defining the unique characteristics of a tissue ought to be found among the class of mutants in which the primary defect can be localized to a given stage and tissue. Since the general functions are required by all tissues, a lesion in the structural locus encoding for that information will alter the final phenotype of a number of tissue types. For example, alleles of the *rudimentary* locus, which have a defect in pyrimidine metabolism, can produce an abnormal wing phenotype and reduce female fertility (44). Alleles of the *rosy* locus, which alter a subunit of xanthine dehydrogenase, produce both color and morphological abnormalities in the larval Malpighian tubules and in the adult eye (45). In both cases a metabolic block leads to alterations in several tissues at different stages. Although these mutations are of genetic and biochemical interest, they do not provide new information relevant to the development of the tissues they affect. These mutations provide no insight into the regulatory mechanisms essential to the development of a given tissue. To a developmental geneticist, mutants which are defective in general metabolic processes and their associated pleiotropic effects constitute developmental noise. They modify developmental events, but are not directly involved in defining the unique characteristics of individual tissue types. Their effects can only be secondary and indirect.

There are instances in Drosophila, however, of mutants with unique tissue-specific, developmental effects. These include mutants that specifically alter the imaginal discs, such as the mutants described above and certain maternal effect mutants, like *grandchildless* in *D. subobscura*. Adult females homozygous for the *grandchildless* mutant produce defective eggs that develop normally except that the pole cells, which include the primordial germ cells, do not form (46). Hence, the defective eggs produce morphologically normal adult progeny that are sterile (and thus childless) because they possess no germ cells. Thus, the mutation blocks the development of a very specific cell type. Recent attempts to isolate

additional mutant types with tissue-specific defects emphasize the need for stringent selective conditions which account for the role of a given tissue in the biology of the organism. For example, several criteria were applied in sequence to select for imaginal disc-specific mutants in *D. melanogaster* (42, 43). To recover these mutants several investigators concentrated first on the analysis of lethal mutants (since few viable mutants with disc-specific abnormalities are known) that die late in development, after the larval stage and before emergence of the adult. Normal functioning of the imaginal discs is essential to the organism during this interval. It had previously been shown that the late lethal mutant, *lethal giant larvae* produces fully grown larvae having severely defective discs (47), suggesting that the discs might not be essential structures during the larval stage. Thus, the first requirement for a prospective disc-specific mutant was that development be arrested during the stage when the imaginal discs become essential for formation of the adult fly, and that prior development, when the discs are apparently dispensable structures, produce fully grown larvae. Only the late lethal mutants were subsequently examined for evidence of abnormal disc development. Mutant larvae were dissected and examined microscopically for missing discs, or discs with an abnormal morphology. If present, the discs were tested for their developmental capacities using the *in vivo* or an *in vitro* assay system to induce differentiation. The late lethal criterion significantly reduced the number of mutants to be analyzed by the second more difficult set of procedures, thus improving the efficiency of the overall selection process. The approach has been remarkably successful. Large numbers of mutants with defective imaginal disc development have been isolated, including many with phenotypes not previously observed (42). This class of mutants appears to provide the best means of dissecting imaginal disc development, the process of cell determination, into its component parts.

The same rigorous approach has been utilized to recover additional maternal effect mutants for examining the extent to which the egg cytoplasm is involved in the initial determination of different cell types (48, 49). In Drosophila the meiotic divisions occur at the end of oogenesis, so that oocyte differentiation is controlled by the diploid maternal genome. The fact that divergence of the larval and imaginal cell lines may begin as early as the blastoderm stage, prior to detectable zygotic gene activity, suggests that some component of the egg cytoplasm, presumably part of the egg cortex, is involved in the determination process (48). Any dependence of this process on localized ooplasmic substances should be reflected in a class of maternal effect mutants with tissue-specific defects, such as *grandchildless*. For example, if the distinction between larval and imaginal cells has been programmed into the egg, then there should be a class of maternal effect late larval lethal mutants. The problem has important theoretical and practical applications to seed development where the divergence of clonal seed components clearly occurs within the embryo sac prior to fertilization,

and thus under the direction of the maternal genome; and portions of the seed (seed coats) are actually derived from maternal tissues. The protocol to search for this mutant type follows. The first step was to isolate female-sterile *(fs)* mutants, that is, mutants where homozygous mutant females are unable to produce viable adult progeny. Many *fs* mutants were isolated using standard genetic manipulations. Since reduced female fertility is a phenotype that is part of the pleiotropic syndrome of many morphological mutants, the *fs* mutants were carefully examined for morphological variants, reduced viability during development of homozygotes, and reduced male fertility. Mutants with any abnormality other than female sterility were excluded from further consideration. The determinative events occur at or following the blastoma stage. Thus, the final selective criterion applied was that the early cleavage events should be normal; this eliminates mutants where the eggs are not fertilized as well as those that are unable to initiate or maintain cleavage divisions. The approach was quite successful. Utilization of these sequential selective steps allowed the recovery of six interesting mutants from nearly 4300 homozygous mutagenized stocks examined (48). Each of the mutants has a remarkably uniform phenotype. Although none of the new maternal effect mutants is a late larval lethal, each has a novel phenotype that is certain to improve our understanding of the role of egg components in zygotic development.

PROSPECTS OF SEED DEVELOPMENT MUTANTS IN CROP PLANTS

Our understanding of seed biology would benefit greatly from the same type of developmental genetic analysis. Several possible mutant types can be predicted based on the developmental and genetic analogies between the seed and the Drosophila larva. There should be mutants that specifically block formation of either the embryo or the endosperm; mutants that alter the size or morphology of the embryo or the endosperm; mutants that alter the spectrum of storage molecules in the endosperm; and mutants that block or alter formation of the seed coats. In short, there should be mutants that block or modify each process required to form the seed. Since each of the suggested variants affects the morphology or the composition of the seed, screening procedures to isolate the mutants should be straightforward. It bears repeating, however, that care should be taken to select mutants with tissue-specific defects rather than those with pleiotropic phenotypes. The distinct genetic differences between some components of the seed should facilitate the isolation of different mutant classes: the embryo has a diploid hybrid genome, the endosperm is a triploid hybrid, and the nucellus, integuments and ovary wall have a diploid maternal genotype. The analysis of developmental mutants will be essential to understanding the different processes involved in seed development, how the separate processes are regulated, which processes are limiting in terms of yield, and to what extent the genetic controls can be modified. This background is essential if an informed approach for modifying the yield characteristics of the seed

is to be attempted.

Reduced to its simplest terms the goal of the developmental geneticist interested in increasing quantitative yield is either to increase the total number of seeds produced by a plant, to increase the average size of the seeds produced, or both. The number of florets and their average fertility are the factors that contribute to determing the number of seeds produced by each plant. Several physiological parameters affect the average fertility of the florets (2, 50). The important developmental character appears to be the duration of the flowering stage. If this stage could be lengthened, then more flowers should be produced, unless the number of potential florets is a fixed genetically determined trait. [Number of rows of kernels in corn is genetically determined (51)] Whichever process limits the output of each plant, and it may vary with different crop species, modification of the regulatory elements for that developmental process may relieve the genetic constraints and improve the yield capacity of the species. Alternatively, mutants which hasten the onset of flowering, perhaps analogous to homeotic mutants, would increase the proportion of growth directed towards reproduction. Under good filling conditions, the size of the seed is limited by the size of the seed coat in some species (52). The maternally derived integuments produce the seed coats; each is a two-celled layer which increases in size by restricting cell division to a single plane. Thus a fixed size suggests that a fixed number of cell divisions occur. If so, this number is likely to be a genetically controlled and modifiable trait. However, in some varieties of wheat the 1000-grain weight has a yearly variation of as much as 50 percent (52) indicating that it is not the capacity of the seed that is limiting, but the ability to fill the seed. Many physiological factors influence this process, but one, the ability to function as a metabolic sink and to mobilize nutrients, appears to be inherent in the seed (11). Since the physiology of this process is not well understood, it is difficult to suggest mechanisms for possible modifications. But variants that draw resources from a larger area, or for a longer time should attain the maximum size more frequently.

If the concern is for increasing the qualitative aspect of yield, by increasing the protein content of the seed for example, then several developmental options are open. Since the proteins in the embryo are nutritionally superior to those in the endosperm (53), one possibility is to attempt to increase the size of the embryo, thereby altering the embryo to endosperm ratio. The existence of the mutant *lethal giant discs* in *D. melanogaster*, in which the imaginal discs of the mature larva are approximately 50 percent larger than normal (54), promotes the feasibility of this approach in the seed. An alternative method of changing the distribution of proteins within the seed would be to find a variant with a multilayered aleurone, since the aleurone also has a more nutritional protein spectrum (53). Without more information on the role of the aleurone during seed development, it is difficult to eva-

luate this approach. Finally, the geneticist may attempt to alter the spectrum of proteins (or other storage molecules) found in the endosperm itself by selecting for variants such as *opaque*-2 in corn or the new high lysine strains of sorghum (55, 56). The sorghum strains were recovered from among several thousand naturally occurring strains examined for the floury endosperm phenotype. Identification of this trait, which is also associated with the *opaque*-2 mutation, required processing longitudinal sections of several kernals from each strain. Recent results suggest that the scanning electron microscope may provide a more rapid means of examining samples (57). The effectiveness of any approach to modifying the nutritional character of the endosperm depends on finding more rapid and efficient methods to screen large numbers of potentially mutant seed.

In contemplating the variety of possible genetic modifications of seed development, it is important to realize that modern agricultural species have been released from many of the environmental pressures that resulted in the evolution of their present form. Efforts in mutation breeding should emphasize the importance of the seed as an end product over its reproductive function. Areas of conflict between man's needs and the plant's needs can be circumvented through the use of seed stocks or conditional mutants.

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