

MAIZE SUSCEPTIBILITY TO DROUGHT AT FLOWERING: A NEW APPROACH TO OVERCOME THE PROBLEM

SUSCETIBILIDADE DO MILHO À ESTIAGEM NA FLORAÇÃO: UMA NOVA ALTERNATIVA PARA SUPERAR O PROBLEMA

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- REVISÃO BIBLIOGRÁFICA -

SUMMARY

Among the agronomically important grasses, maize is the most susceptible to drought at flowering. Drought stimulates a protandrous pattern of development, increasing the anthesis-silking interval. Because maize has a short period of flowering and pollen remains viable for only a short period of time, each day of delay between pollen shed and silk emergence will reduce the rate of sexual fertilization and increase barrenness. The purpose of this article is to present an ideotype of maize designed to overcome this problem. The biological model described here can reduce sensitivity to water deficiency through morphological and anatomical modifications, such as the transference of the ear from the axil of a leaf to the apex of the plant; condensation of the upper stem internodes; and a reduction of plant height and leaf number. Genetic diversity was found for all traits of interest. It was possible to identify and select mutants that exhibited the proposed alterations in a single phenotype. However, associated with those mutants there were several undesirable characteristics, such as lack of vigor and disease susceptibility. To gain an agronomically acceptable phenotype with adaptation to a hot and dry environment further improvement is needed.

Key words: *Zea mays*, water deficiency, ideotype.

RESUMO

Entre as gramíneas de importância econômica, o milho é a que apresenta maior susceptibilidade à estiagem no florescimento. A seca estimula um comportamento protândrico da planta, o qual aumenta a duração do subperíodo antese-espigamento. Como o milho tem um período de floração curto e definido, e o pólen permanece viável por um intervalo reduzido, cada dia de defasagem entre antese e espigamento se reflete

numa redução da fertilização e aumento da esterilidade. O objetivo desta revisão é o de apresentar um ideotipo de milho concebido para superar este problema. Pretende-se com este modelo biológico reduzir a susceptibilidade da planta ao déficit hídrico, através de uma série de alterações anatômicas e morfológicas, entre as quais podem ser citadas: transferência do local de produção de grãos da axila de uma folha para o ápice da planta; condensação dos entrenós superiores do colmo; redução da estatura de planta e número de folhas produzidas. Encontrou-se variabilidade genética para todas as características desejadas. Os caracteres propostos também foram expressos num único fenótipo. Por outro lado, algumas características indesejáveis, tais como falta de vigor e susceptibilidade a doenças, também estiveram associadas aos mutantes mais promissores, indicando que os mesmos necessitam ser incrementados para que um fenótipo, agronomicamente aceitável, possa ser produzido e comparado às cultivares de milho disponíveis, em termos de adaptação a ambientes quentes e secos.

Palavras-chave: *Zea mays*, deficiência hídrica, ideotipo

INTRODUCTION

Water is the earth's most abundant compound and the major factor limiting crop productivity in the world (KRAMER, 1988). Approximately one-third of the earth's surface is subjected to permanent drought. Even many of the humid temperate regions, which produce a considerable fraction of the world's food, are frequently submitted to periods of severe water limitations.

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Soil water deficiency, specially when accompanied by excessively high temperatures, is the most common corn yield limiting factor around the world (JENSEN & CALAVERI, 1983; BECK *et al.*, 1996). In the developing world, where more than 60% of the world's maize is grown, annual losses due to drought may reach 24 million tons, which represents nearly 17% of an annual US corn year's production (EDMEADES *et al.*, 1993).

Maize is very susceptible to drought stress at flowering and early seed development (SINCLAIR *et al.*, 1990; WESTGATE, 1994/1997). This is partially because male and female flowers are separated by 30-100cm, silks must extend by up to 30cm to escape the husk, and a delicate stigmatic tissue and pollen grains are exposed to a desiccating environment. Drought at flowering favors development of the male inflorescence of the plant, which assures pollen production and dispersion, but inhibits ear and silk development (SANGOI, 1996). Therefore, one of the main causes of maize susceptibility to drought at flowering is the potential lack of synchrony between silk emergence and pollen shed, which reduces the rate of sexual fertilization and decreases kernel set (WESTGATE & BASSETI, 1990; BOLAÑOS & EDMEADES, 1996). Since maize has a short and definite period of flowering and pollen remains viable for only a brief period of time, each day of delay between pollen shed and ear pollination leads to a delay of sexual fertilization, an increase in barren plants and a significant yield reduction (BOLAÑOS & EDMEADES, 1993; BECK *et al.*, 1996; SANGOI & SALVADOR, 1996).

The purpose of this article is to present an alternative approach to overcome the problem of maize susceptibility to drought at flowering. It describes a maize ideotype designed to cope with high temperature and low moisture environments.

1. TRADITIONAL BREEDING STRATEGIES TO IMPROVE MAIZE TOLERANCE TO DROUGHT STRESS

Almost all commercial hybrid yield test programs emphasize yield as the main criterion for advancement. Much of the improvement observed in drought resistance of populations and inbreds results from selfing procedures in nurseries stressed by mid-summer drought or by high plant density (EDMEADES *et al.*, 1993). Selfing relies on a short anthesis-silking interval (ASI) for success. Poorly synchronized plants are automatically eliminated, so a great deal of selection for reduced ASI has taken place in routine breeding nurseries.

Therefore, selection against silk delay has been the most effective method of breeding for drought tolerance (TROYER, 1983; EDMEADES *et al.*, 1993; BOLAÑOS & EDMEADES, 1996). Plants with little silk delay use water more effectively. Silk delay is highly heritable (BOLAÑOS & EDMEADES, 1996), being therefore a good selection criterion against barrenness. Since corn plants grown at high plant populations show silk delay like plants grown under drought stress, high plant density stress has provided opportunity to breed for drought tolerance in non-drought environments (CASTLEBERRY *et al.*, 1984).

This conventional selection procedure against barrenness has been successful in creating drought resistant (CASTLEBERRY *et al.*, 1984; EDMEADES *et al.*, 1993) and high population tolerant (DUVICK, 1994; RUSSELL, 1991; TOLLENAAR, *et al.*, 1994) hybrids over the last 35 years. Other traits which are associated with stress tolerance are: increased ear growth rate prior to anthesis, rapid silk growth, reduced growth of the tassel, reduced ASI, initiation of a lower number of spikelets but with a greater proportion of those successfully forming grains, increases in the number of ears per plant, and increase in harvest index (BECK *et al.*, 1996; EDMEADES *et al.*, 1997).

Even though considerable progress has been made in terms of increasing maize tolerance to drought stress, losses in grain yield due to drought are still significant. The traditional approach of reducing anthesis-silking interval has not eliminated the problem of barrenness. Corn silks have a high water content and depend largely on a favorable water status to grow and emerge from the husks. At drought silks will not elongate and pollination will not succeed, even if the plant has genes that favor a brief ASI.

2. AN IDEOTYPE OF MAIZE FOR CONDITIONS OF HIGH TEMPERATURE AND LOW MOISTURE

An alternative approach for improving grain yield was proposed by DONALD (1968). He postulated that instead of breeding exclusively for grain yield, breeders should define an ideal plant type for a specific environment and then breed for this "ideotype".

The ideotype presented in this paper aims to reduce sensitivity to drought stress by transferring the site of grain production from the axyl of a leaf to the apex of the plant. This should remove the susceptibility of the ear to apical dominance. Besides changing the site of grain production, a

condensation of the upper internodes of the main stem to retract the apical inflorescence into the sheaths of the last few leaves in the culm and a significant reduction in plant height and leaf number are proposed to optimize the yield stability of the resulting plant under hot and dry conditions.

The change in the site of grain production

Maize is a monoecious diclinous species where individuals have separate staminate and pistillate flowers and produce gametes of both sexes in physically separated parts of the same plant (IRISH & NELSON, 1989/1993). The terminal inflorescence, or tassel, which develops from the shoot apical meristem, bears staminate flowers. Pistillate florets are born on lateral inflorescences, or ears, which develop from axillary buds.

Despite the significant morphological differences between tassel and ears at maturity, the physiology of early flower formation is quite similar. Both ear and tassel florets are bisexual and morphologically equal during primary developmental stages (CHENG *et al.*, 1983). The transition from immature bisexual primordia to mature unisexual floret is accomplished through the arrest and abortion of organ primordia of the inappropriate sex (DELLAPORTA & CALDERON-URREA, 1994).

Sex determination in maize is a complex and dynamic process involving a correlation between genes, environment and hormones (IRISH & NELSON, 1989).

The ambivalence observed in developing inflorescences of maize over a wide range of circumstances provides evidence that the switch from male to female or vice-versa is not a rare occurrence (VEIT *et al.*, 1993). With that in mind, a feasible way to reduce maize susceptibility to drought stress may be by transferring the site of grain production from the axyl of a leaf to the apex of the plant. This would be accomplished by taking advantage of the monopodial branching habit of maize, and the fact that, as originally differentiated, maize inflorescences have the potential to form perfect flowers and therefore to be sexually reversed (ROOD & SPRAGUE 1980; CHENG *et al.*, 1983; CHENG & PAREDY, 1994). The hypothesis is that the position of the female inflorescence at the apex of the plant would break apical dominance and with this decrease the dependence of conventional maize on favorable water conditions at flowering.

There are two possibilities to produce grains in the apical inflorescence. The first is by using mutants that have specific genes affecting the production of staminate flowers in the tassel (the

tassel-seeds). Such mutant plants produce functional pistillate flowers in the tassel that, after pollination, form viable seeds in the male inflorescence (NICKERSON & DALE, 1955). There are at least five tassel-seed mutations, dominant (Ts) and recessive (ts), that have been mapped to unlinked loci (COE *et al.*, 1988).

A second alternative involves a selection for condensation of the upper internodes in the main stem, associated with sex reversal, in order to retract the apical inflorescence into the sheaths of the last few leaves of the culm. This strategy would provide protection and mechanical strength for the apical inflorescence. Genetic variability for this trait has been previously reported by MATHEWS *et al.* (1974) and VEIT *et al.* (1993) who studied a mutant called terminal ear (te1). They observed that the pronounced elongation of the primary plant axis that occurs when the tassel begins to form was reduced in te1 plants, particularly in the upper internodes. This caused upper leaves to encompass the apical inflorescence. GALINAT (1992), using different allelic states of the gene ts2 (tassel-seed 2), was able to induce different degrees of feminization and observed that this trait was closely associated with the level of internode inhibition in the stalk and consequently with stalk height. The greater the percentage of female flowers in the apical inflorescence, the lower was the average internode length.

Plant height and leaf traits

The present ideotype is being proposed for an intensive grain production environment, with plant populations over 100,000 plants ha⁻¹, where water availability is the only limiting factor. In order to increase the leaf area index and to provide maximum crop growth rates, it is proposed to reduce plant height and leaf number. Selection will be for reduced internode length and number, and for erect leaves. The goal is to obtain a plant of approximately 1.5 meter high with around 15 leaves.

With smaller and less leafy plants, competition among plants will be reduced, allowing higher plant densities (SANGOI & SALVADOR, 1997a). Less vegetative biomass will be produced and light utilization efficiency will increase, resulting in greater resource availability for grain production (SANGOI, 1996).

There is also evidence in the literature that reduction in plant height and leaf number may be advantageous traits for the plant to deal with drought stress. MUENCHRATH (1995) attributed reduced barrenness and greater harvest index of a maize variety adapted to the desert of the US, to its shorter

plant stature and fewer leaves. Similarly, ACKERSON (1983) observed, in a comparison of two contrasting maize hybrids, that the more drought resistant material was shorter and produced fewer, smaller and shorter leaves. KRIEDEMANN & BARES (1983) noticed that the ratio of potential evapotranspiration to potential photosynthesis increases with plant height in high insolation and windy environments. Although smaller leaf area results in a lower amount of photosynthetic surface, it also reduces transpirational area (MUENCHRATH, 1995). The smaller leaf area of the ideotype may contribute to the maintenance of leaf temperatures conducive to normal photosynthesis under drought stress.

There are two main ways by which plant height and leaf number can be affected through plant breeding. The first is by using specific genes that promote reduction in internode length and, consequently, plant height. A number of dwarf and semi-dwarf mutants are known in maize and the trait is simply inherited (NEUFFER *et al.*, 1968). A second approach is through selection for earliness. There is a strong positive correlation between the duration of the life cycle, plant height and number of leaves produced by the plant. Precocious materials are usually shorter and less leafy than late genotypes in a particular environment (JOHNSON *et al.*, 1986).

Ear and grain characteristics: the problem of pollination

An ideotype as described here would result in a plant with no male inflorescence. Besides being an essential reproductive organ, the tassel is an important energy sink during its development and a potential source of shading (LAMBERT & JOHNSON, 1978; SANGOI & SALVADOR, 1997b). There are three main alternatives to overcome the lack of a tassel:

a) Male-sterility:

One alternative will be to employ cytoplasmic male-sterile-pollen restorer techniques as used to produce maize seed in the 60's. The seed would have to be produced under the crossing conditions used to produce hybrid seeds. Assuming that the character apical ear (*ape*) is controlled by a single pair of recessive alleles (*ape ape*), these genes would be present in the nucleus of the cells of both male and female inbred lines. However, the male line would have a cytoplasmic gene that would restore its ability of producing a viable tassel (as with Rf). Since the cytoplasm of the progeny tends to be inherited from the mother, the restoring genes

of the male progenitor would have very little influence on the phenotype of the F1 generation (POHELMAN, 1987). Therefore, this procedure would allow generation of almost 100% F1 seeds of *ape* plants. However, if the producer plants 100% of these seeds, there would be no pollen to fertilize the plants. A way to circumvent this problem would be to mix 5-10% of seeds of the same hybrid with a restorer cytoplasmic gene (SANGOI, 1996).

b) Parthenocarpic kernels:

Another possibility would be production of parthenogenic maize ovules. Some parthenogenic mutants ("lethals") are known in maize and other cereals (KHAN *et al.*, 1973) and the trait has been commercially used with great success in other species such as orange and grapes (HANNA, 1995). One potential concern with the use of parthenocarphy would be that the kernel would have no embryo and therefore could not be used as a seed in future generations. However, the majority of maize grain is not produced for seed purposes. Furthermore, for industries interested in extracting starch, the presence of the germ in maize kernels is a disadvantage because it creates the need for expensive refining steps to remove this oil-containing structure.

c) Apomixis

A third alternative to commercially produce this ideotype would be through apomixis. In apomitic reproduction, an embryo is formed from a mitotically unreduced megaspore mother cell or from a somatic cell of the nucleus or ovule. Apomixis makes vegetative reproduction or cloning through the seed possible. It fixes hybrid vigor by allowing a plant to clone itself indefinitely through seed. In crops such as maize, it could help to simplify hybrid seed production and also make hybrids readily available and/or affordable in developing countries (HANNA *et al.*, 1995).

The introduction of apomixis in maize has been attempted by using *Tripsacum dactyloides*, a wild perennial grass closely related to corn, as the source for the trait. This approach has problems such as a high degree of sterility in the progeny and a facultative apomitic behavior (SAVIDAN *et al.*, 1993). The great amount of sterility observed in crosses between maize and *Tripsacum* is due to the fact that these species have a different number of chromosomes and it is difficult to have a perfect pairing during meiosis. Besides this, several other undesirable traits are transferred from *Tripsacum* to the host.

Molecular methods may help to transfer genes controlling apomixis. This would require isolation of stable genes (preferably dominant) controlling obligate apomixis, insertion of the gene(s) into the genome of a target species, expression of obligate apomixis in the target species, and replication of the gene(s) controlling apomixis in the genome of the target species.

Initial steps in the selection process toward the ideotype

The search for the ideotype depicted schematically on Figure 1 began in Ames, Iowa, US, by screening the Neuffer/Wright Nursery Field in September of 1992, looking for mutant materials exhibiting variability for the desired traits: dwarfness, erect leaves, condensed peduncle, apical ear and tassel seeds.

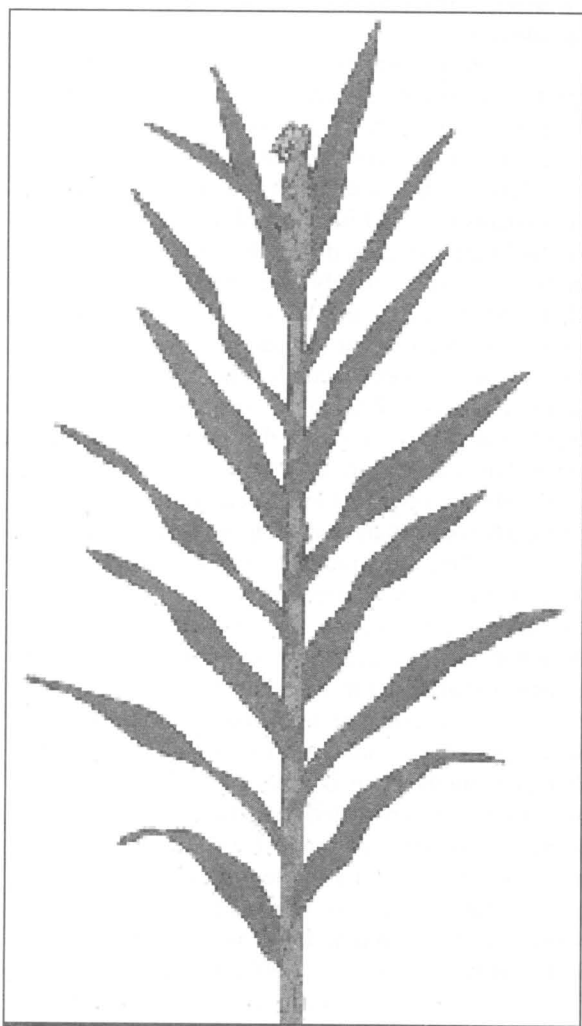


Figure 1 - An ideotype of maize for conditions of high temperature and low moisture.

Ethyl methanesulfonate (EMS), was used to induce the genetic variability as described by NEUFFER (1994). The pollen of three inbred lines was treated: Mo17, A632, and B73. Three different treatments were performed: a) treated pollen from Mo17 was used to pollinate ears of A632; b) treated pollen from B73 was used to self the same plant; c) treated pollen from A632 was used to self itself.

In all three cases, the kernels harvested in the ears of treated plants were called M1 which had one treated (from male) and one untreated (from female) genome. M1 kernels were sown in the field to observe the impact of the treatment and to generate M2 seeds. All normal M1 plants were selfed to produce M1 ears with M2 seeds. When selfing was not possible, M1 plants were outcrossed to a normal standard from the same inbred. Nearly 20 kernels of each selfed M1 ear were planted in the field in the following year. The M2 plants started showing segregation for the different mutations induced by the EMS treatment. The plants that showed traits of interest were selfed or crossed to a standard stock, producing, in either cases, M3 seeds. The M2 plants (M3 seeds) of Neuffer/Wright mutant nursery fields constituted the initial source of genetic material for the development of this ideotype.

In order to increase the genetic base, seeds of dwarf mutants were requested. 32 entries from the Maize Genetics Cooperative Stock Center (Urbana, Illinois) were received. The genetic background of these mutants was a mixture of the inbreds W23, M13, and L317.

Each M2 ear was sampled randomly and 30 kernels were separated and sown in the field on May 15, 1993. Kernels of each material were planted manually in individual 15m rows, one kernel per hill, in a row spacing of 75cm and a hill spacing of 50cm.

All plants within a row were selfed. In the case of plants with tassel-seeds or apical ears, pollen from neighbor plants within the same family (row) was taken and used to pollinate the *ts* or *ape* individuals. When there was some pollen shed in the tassel-seed inflorescence, selfing was performed. Some crosses among plants within the same row were also performed in the Stock Center dwarves due to the lack of synchrony between pollen shed and silk emergence in the same plant.

Two different procedures were used to harvest the Neuffer/Wright mutants: in rows where no plant showed at least one desired trait for the ideotype a random sample of five ears was collected. In rows where plants expressed a desired phenotype (either tassel-seeds, retractile-peduncle, apical ear or dwarfness), all ears were harvested. In the case of

the Stock Center dwarves, all grain-bearing ears were harvested.

Ten of the best mutants were selected to continue the evaluation process during the growing seasons of 1994 and 1995. Selection traits were: apical ear, retractile tassel, dwarfness, and tassel-seeds. For each one of these 10 mutants, 10 ears were chosen at random. From each ear, 30 kernels were randomly picked and sown individually in 15m rows. The spacing between seeds, rows and the other cultural practices, were as described previously.

Within each row, plants were selfed or sibcrossed. Whenever possible, pollen from plants of the same row was used to pollinate tassel-seeds and apical ears. Sometimes, pollen from adjacent rows within the same family (same original entry) had to be used to make sib-crosses. At harvest time, only ears of plants that had tassel-seeds or apical ears were harvested.

Preliminary results

After three years of field evaluation, five among all the mutants originally selected from the Neuffer/Wright nursery and Maize Genetics Stock Center consistently expressed desired traits for the ideotype. Three of them generated a considerable number of tassel-seeds. The other two produced an apical ear. Grains of tassel-seed mutants had no husk protection and thus were susceptible to fungal infection and bird damage. This resulted in a strong infection with *Ustilago maydis* in almost every tassel-seed inflorescence. The combined effect of kernel weight and a significant mass of smut spores exerted a strong pressure that usually exceeded the mechanical strength of peduncle, resulting in lodging of the seed head.

The apical ear mutants (*ape*) expressed three characteristics that are being proposed in the ideotype: apical ear, condensation of the upper internodes in the main stem and dwarfness (Figure 2). It was possible to identify genetic variability for most of the desired traits, which is an essential starting step in any kind of breeding program.

These mutants also developed several undesirable phenotypic characteristics such as lack of stable ear expression. Some plants produced a small but almost perfect apical ear (Figure 2). Other individuals showed intermediate forms ranging from a tassel to something in between a tassel and an ear.

Another undesirable trait observed in *ape* mutants was an excessive number of leaves, which were spaced closely on the main stem. In spite of their short height, these mutants produced and



Figura 2 - Apical ear mutant growing in the field, Ames, Iowa, 1994.

retained over 20 leaves per plant. In addition, plants were also susceptible to smut infections.

Causes for the problems presented by the apical ear mutants:

Three factors can partially explain the agronomic defects associated with *ape* plants. First, the genetic diversity of the source population from which the initial screening was performed was not very broad. The Neuffer/Wright nursery field and the mutants received from the Maize Genetics Stock Center were composed mostly by plants derived from only six relatively old inbreds: A632, B73 Mo13, Mo17, L317 and W23. It is possible that the narrow genetic base of the parental material limited the amount of new recombinations in subsequent generations, contributing to increased inbreeding depression. A second factor that probably facilitated inbreeding depression and lack of vigor was the small number of plants evaluated and selfed or sibcrossed for each mutant at each cycle of evaluation.

The third factor to mention is related to the technique used to generate genetic variability for the traits of interest. The use of chemical mutagens increases the frequency of mutations and expands genetic variability. On the other hand, even though chemical mutagens are less drastic in their effects than, for instance, ionizing radiation, it is possible that they might have produced small chromosome disruptions or unwanted mutations in genes not related to the traits of interest. Unfortunately, clean mutations that correct a single plant character are not easily obtained, nor as frequently as it was once supposed. More often, they are accompanied by undesirable pleiotropic effects (POEHLMAN, 1987). For traits controlled by several genes, the probability of success with induced mutation breeding is even harder. In those cases, the mutants

usually also present several agronomic defects linked to the traits the breeder is looking for. Therefore, it is possible that some of the problems presented by *ape* plants are side-effects of the procedure used to generate genetic variability.

CONCLUSION

It was possible to identify and select mutants that presented three of the desired traits in a single phenotype: i.e. apical ear, condensed upper internodes and dwarfness. The traits were also expressed in subsequent generations which supports a continuation of the project, as it indicates a genetic diversity for the traits of interest. The traits can be combined in one model plant and transmitted to the progeny. The mutants found had also undesirable characteristics that need further improvement before an agronomically acceptable phenotype is available. The expression of an apical ear is not stable, the plants bear too many leaves, their vigor is low and they are susceptible to smut infection.

The complete process of developing this novel phenotype is a three-step task. At first, a plant that consistently expresses the desired traits for the proposed environment must be found. Secondly, these plants must be tested for their superiority over current varieties in terms of adaptation to drought stress, high plant population and barrenness. Finally, the most fundamental step is to design an effective way to produce seeds economically for a plant that has no tassel, so that the ideotype can be incorporated into production systems. Mechanisms such as apomixis have only been tested experimentally in maize (SAVIDAN *et al.*, 1993) and a great effort will be required to use them efficiently in this crop.

Three cycles of field evaluation identified sources of genetic variability for the traits of interest, increasing their frequency in subsequent generations. It is important to know what genes are involved in the expression of the character *ape*, where these genes are located, and what kind of linkage or pleiotropic effects they do have with genes that control other important characteristics of the plant. Such information will be necessary to define future breeding strategies. Modern molecular techniques for identifying, mapping, extracting and inserting the genes, or gene blocks, will be needed to pursue.

Besides improving the mutants available so far, it will be important to look for additional natural sources of genetic variability for the traits of interest. Natural mutants may also overcome some of the undesirable pleiotropic effects that might have

been generated by the use of chemical mutagens to induce genetic variability.

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