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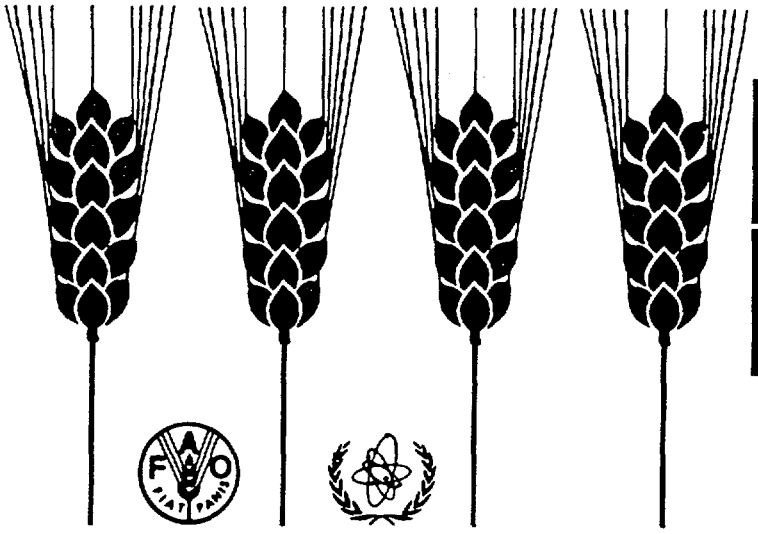

Mutation Breeding Review

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MUTATION BREEDING OF PEARL MILLET AND SORGHUM

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Abstract

Pearl millet and sorghum are important food and feed crops grown mostly in semi-arid regions of the world. Although there exists a large amount of genetic variability in both species, it does not always satisfy the needs of plant breeders in improving varieties with regard to yield, quality, resistance or environmental adaptation. Plant breeders interested in using induced mutations for variety improvement will find in this review information about the techniques used by others.

Introduction

Pearl millet, Pennisetum americanum (L.) Leeke and sorghum, Sorghum bicolor (L.) Moench, belong to the Gramineae family. It is believed that both originated in Africa. Both species are important world food crops and are more tolerant of droughty

growing conditions and soils low in nutrients than most other grain crops. Even though there are basic differences between the two species, both respond in similar ways to mutagens. Therefore, this discussion will include both species.

PEARL MILLET - Pearl millet is a robust annual bunchgrass. It has a history of species name changes with some of the more recent, previous names being P. glaucum (L.) R. Br. and P. typhoides (Burm.) Stapf. et C. E. Hubbard. Pearl millet also has many common names, such as 'Bajra' in India, 'Souna' and 'Sanio' in Senegal, and 'babala' in East Africa, 'mil a chandelles' in West/North Africa and 'dukhn' in Arabic.

It is a diploid, sexual species with large chromosomes (2n = 14). Its bisexual flowers and protogynous habit of flowering (stigmas exerted before anthers) make it a plant which is readily self- or cross-pollinated. Pearl millet is easily maintained in a highly inbred condition. Heterosis is pronounced with the best hybrids yielding nearly twice as much grain as adapted open-pollinated varieties. Pearl millet is a highly variable species with much diversity in plant and seed characteristics.

Pearl millet is grown on about 31 million hectares in the world, primarily in India, Africa, United States, and Australia. It is estimated that pearl millet occupies 46% of the total millet area and represents about 40% of the total millet production in the world (Rachie and Majmudar - 1980). The grain is used as food in India and Africa. The remainder of the plant is used as fodder, fuel, and in building. It is used as a forage crop in the United States and Australia. Since it is considered to be more drought and heat tolerant than sorghum and maize, it is usually grown in dry areas. Pearl millet grows best on light-textured, well-drained soils.

The reader interested in more details about taxonomy, distribution, utilization, and botanical and genetic characteristics should consult the excellent reviews by Burton and Powell (1968), Rachie and Majmudar (1980), and Jauhar (1981).

SORGHUM - Sorghum is a diploid, 2n = 20, perennial (usually cultivated as an annual), sexually reproducing species. It is mainly a self-pollinated crop, however, some of the grassy sorghums such as sudangrass have been reported to have as much as 34% natural cross-pollination.

It is believed that sorghum originated some 5000 to 7000 years ago in eastern Africa. Like many other grasses, it has taxonomically undergone a number of name changes (at one time called S. vulgare), however, S. bicolor (L.) Moench is now the universally accepted name. Common names of sorghum include 'Jowar', 'Jonna', 'Cholam', and 'Jawa'.

Sorghum is usually ranked fifth in acreage among the grain crops of the world. The United States and Asia each produce about one-third and Africa about one-fourth of the total world grain production. Sorghum grain is used for food in Africa and Asia. In the United States, South America, and Australia, it is a major feed grain and forage crop. Other uses in various countries include construction, alcoholic beverages, fuel, basketry material, brooms, and molasses.

Sorghum is grown on all six continents where summer temperatures exceed 20°C and the frost-free days are 125 days or more. It is mainly cultivated in the hot and dry areas because of its tolerance to drought and hot temperatures.

Large amounts of natural genetic variability exist within the species as evidenced by height (40 to 600 cm), panicle size and shape, grain characteristics, maturity and other morphological characteristics. This genetic variability has been utilized in hybrid production since the mid 1950's and along with fertility and management practices has increased sorghum production and yields over 350% in the United States.

The reader interested in more information on all aspects of sorghum from taxonomy and genetics to cultural and management practices and utilization should consult Rooney et al (1980) and the books Sorghum Production and Utilization (1970) and Sorghum in Seventies (1972).

Mutation Research

Research related to mutation breeding in pearl millet and sorghum has been limited. One of the main reasons for this has been the tremendous amount of unexploited natural variation present in these species. The evaluation and utilization of some of this variation has taken place in the past 20 years. No attempt was made here to do an exhaustive search of the literature. A few papers were selected for discussion. The reader interested in more information can refer to literature cited.

Mutagens, Doses, and Mutation Rates

M_1 seedling characteristics, seed set and the frequencies of chlorophyll-deficient mutants are usually used as indicators of the effectiveness of mutagens and for determining doses.

PEARL MILLET - Burton and Powell (1966) treated air-dry seeds of 10 pearl millet inbreds with 5.67×10^{12}, 1.14×10^{13} and 1.70×10^{13} (total doses of flux x time) thermal-neutrons (TN) or for four hours with 0.2, 0.4, and 0.6% ethyl methane sulfonate (EMS) in an unbuffered water solution. Significant inbred x treatment interactions were observed for 5 of 13 characteristics studied. All treatments delayed seedling emergence and days to maturity, and reduced seedling height, plant height, leaves per culm, and selfed and sibbed seed set. EMS reduced percent emergence and plants per plot to reach maturity. The 1.70×10^{13} TN and 0.4% EMS treatments increased the average chlorophyll-deficient seedling mutation rate 5-fold. More chromosomal interchanges were induced with the low TN treatment than with the high EMS treatment.

Burton, Powell, and Hanna (1974) studied the effects of 3 cycles of recurrent seed treatment with TN (6.68×10^{12} and 1.52×10^{13}), EMS (3-hour soaks in 0.2 and 0.4% water solution at 35°C), and diethyl sulfate (DS) in 0.1 and 0.2% water solutions at 35°C on 5 inbreds. TN gave the highest percentage of M_1 striped plants, the lowest percentage of M_1 selfed seed set and the highest frequency of M_2 chlorophyll-deficient seedlings. Either TN treatment plus a low dose of EMS or DS usually increased these effects. High EMS treatments gave more M_2

mutants than low EMS or DS treatments. However, DS was equal or tended to be better than EMS when combined with TN. DS had no effect on yield of M_1 selfed seed per head. High EMS treatment reduced it only 10% while the low TN treatment reduced selfed seed 40%. The second cycle of mutagen treatments increased the average number of M_2 mutant plants by 74%. Only a small increase in number of mutant plants was observed after the third cycle of treatments.

Vijendra Das (1978) irradiated dry seeds of two genotypes, HB3 (an F_1 hybrid) and MS 7625, with 40, 50, 60, 70, 80, and 90 kR of X-rays (50 kVp) and 10, 20, 30, and 40 kR of ^{60}Co gamma rays. The approximate M_1 LD_{50} was 60 kR for X-rays and 20 kR for gamma rays. Gamma rays produced more M_1 lethality, growth reduction, pollen sterility, and a higher M_2 mutant frequency than X-rays. Gamma rays also showed the higher mutagenic efficiency for the genotypes studied.

Tara Mohan (1973) soaked seeds of two inbreds in 0.005, 0.10, and 0.20% aqueous solutions of N-nitroso-N-methyl urea (NMH) for 4 hours after a 9-hour water pre-soak. The 0.20% dose was almost lethal. Two-thirds and one-third of the M_1 plants produced M_2 chlorophyll-deficient mutant segregating progenies at the 0.005 and 0.10% doses, respectively.

Burton and Hanna (1976, 1982) soaked inbred 'Tift $23DB_1$' (fertile maintainer for A_1 sterile cytoplasm) seeds in water solutions of 200 and 500 ppm streptomycin (STY), 50 ppm mitomycin (MIT) and 250 and 1000 ppm ethidium bromide (EB) at 5°C for 40 hours for the purpose of inducing cytoplasmic male sterile mutants. The 250 and 1000 ppm EB doses increased male sterile mutant frequencies by over 50- and 100-fold, respectively, over the control. However, by the M_3 generation, most of the male sterile mutants had reverted to fertile pollen shedders. One percent of 402 M_2 progenies of M_1 selfed plants segregated for chlorophyll deficient plants indicating that EB may also be considered a nuclear mutagenic agent. The 200 and 500 ppm STY and 50 ppm MIT treatments increased the frequencies of stable cytoplasmic male sterile mutants by 2.9, 3.6, and 6.2 times, respectively, over the control. Appropriate crosses with maintainer and restorer inbreds indicated that the induced mutants had similar sterility maintainer and fertility restorer requirements as did the A_1 cytoplasm.

Hanna and Young (1974) irradiated pollen of three inbreds with ^{60}Co gamma rays at 0.2, 0.6, 1.2, 3.0, 5.0, 8.0, 12.0, and 16 kR. Seed set resulting from irradiated pollen was reduced by about 50% at doses between 1.2 and 3 kR. Pollen lethality resulted from doses between 12 and 16 kR. Pollen irradiation produced M_1 plants that did not sector, which increased the chances of recovering mutations without having to self every head on a plant.

Other reports on this subject are by Kumar and Joshi (1939), Joshi (1968), and Singh, et al. (1978).

SORGHUM - Harris et al. (1965) treated seed (about 15% moisture) of 'Redbine 60' and 'Shallu' with 10, 20, 30, 40, and 50 kR of ^{60}Cobalt gamma radiation. The critical dose (50% M_1 sterility) was between 20 and 30 kR for Redbine 60 and between 40 and 50 kR for Shallu. Variety x dosage interactions were present for a number of seedling and seed characteristics.

Higher doses resulted in significantly higher mutation frequencies expressed as lower seedling survival and increased sterility in the M_2 generation. Reddy and Smith (1975) also found that gamma rays caused a differential M_1 plant response and M_2 mutation frequency for two sorghum varieties.

Mohan and Axtell (1975) successfully induced opaque endosperm mutants (high lysine) in a vitreous endosperm line from seed soaked in a 0.1% diethyl sulfate (DES) solution for three hours. The seeds were thoroughly rinsed immediately after treatment to prevent hydrolysis to ethyl sulfinic acid which is toxic to seed and reduces germination (Guiragossian et al - 1979). Over 500 putative opaque mutants were isolated from M_3 seed produced on approximately 23,000 M_2 heads. One of the mutants 'P-721' had a desirable plant type as well as both higher protein and lysine.

Goud (1972) treated six sorghum varieties with 10, 20, 30, and 40 kR gamma rays. The highest average percent of chlorophyll mutants in M_2 plants was induced in the 20 to 30 kR range. There was a genotype x dose interaction for M_2 mutant frequency. M_1 sectors for various chlorophyll and morphological chimeras were observed.

Kapoor (1967) used 0.45, 0.30, and 0.15% ethyl methane sulfonate (EMS) solutions to treat 8 hour presoaked seeds at three pH levels (3.5, 7.0, and 9.2) and three temperatures (2°C, 14°C, and 26°C) for 12 hours. M_1 seedling survival decreased with lower pH and higher doses. The frequency of chlorophyll-deficient M_1 chimeras was highest at higher temperature and higher doses. M_1 seed set was highest at low temperatures and low doses. The author suggested that 0.3% EMS treatments for 12 hours at 14°C or higher would yield high frequencies of chlorophyll and viable mutations.

Malinovskii et al (1975) soaked air-dried seeds of five varieties for 20 hours in N-nitrosomethylurea (NMH) at 0.003, 0.006, 0.01, and 0.012%, ethyleneimine (EI) at 0.008, 0.01, 0.02, and 0.03%, and 1,4-bis-diazoacetyl-butane (DAB) at 0.0875 and 0.175% concentrations for the purpose of inducing cytoplasmic male sterility. They observed from 0.3 to 9.8% sterile (both male and female) M_1 plants depending on mutagen and concentration. In M_2 generation from 0 to 20% of the families segregated for male sterility. Appropriate crosses showed that this sterility was cytoplasmic in nature. The most effective mutagens were EI at 0.02 and 0.03% and NMU at 0.003 and 0.006%. DAB was ineffective in their study for inducing male sterility.

Patil and Goud (1979) studied M_3 and M_4 progenies after 20, 30, and 40 kR gamma rays or 0.05, 0.075, or 0.1% EMS. Frequency of chlorophyll mutations decreased from the M_2 to M_4 generation. EMS treatments showed the highest frequency and broadest spectrum of chlorophyll mutations. Differential sensitivity of varieties to mutagens was observed.

Sree Ramulu (1970) treated three varieties with gamma rays (10 to 30 kR), X-rays (10 to 90 kR), EMS (0.05, 0.10, and 0.15%), DES (0.001 and 0.003%), and methyl methane sulfonate (MMS), and N-nitrosoethyl urea (NEH) each at 0.005 and 0.01% for 8 hours. EMS and DES appeared to be the most effective for inducing

mutations. A saturation effect was obtained at higher doses where no increase in mutations occurred.

Porter et al. (1978) treated seeds with 0.1 and 0.2% DES to induce brown midrib (bmr) mutants with reduced lignin which were identified in segregating M_3 head rows.

Ross (1965) recovered true breeding and non-true breeding M_1 plants after colchicine (0.5% in melted lanolin applied to coleoptiles) treatment of seedlings. The true breeding plants resulted from somatic chromosome reduction followed by doubling to restore the original chromosome number. The production of true breeding M_1 mutants appeared to be genotype specific for 'Experimental 3'.

The reader interested in more information on this subject in sorghum should also refer to a brief discussion on a number of sorghum mutagen research experiments summarized by Sree Ramulu (1975).

Quantitative Genetic changes

Few studies with pearl millet and sorghum have been concerned with using mutagens to induce quantitative genetic variability or genetic combining ability.

Burton and Powell (1969) and Burton et al. (1974) used three cycles of recurrent TN and EMS seed treatments on six pearl millet inbreds (refer to previous section for doses) to study the effects of mutagens on specific yield genes and to determine if these mutagens could be used to enhance genetic variance for yield. Seed for each cycle was produced by sibbing within each inbred treatment. Design II singlecrosses (Comstock and Robinson - 1952) were produced from selfed progenies of normal M_1 plants from the second recurrent seed treatment. Singlecrosses were made between two different inbreds receiving the same treatment because within-inbred matings resulted in poor seed and weak hybrids. The results showed that TN and EMS did not affect forage yields and suggested that pearl millet has many specific yield genes, each with a small effect. The authors suggested that several cycles of recurrent selection would probably be needed along with the mutagen treatments to improve combining ability of pearl millet inbreds.

Harris et al (1965) did not find significant gains in genetic combining ability for sorghum grain yields after gamma irradiation. Barabas (1965) isolated a mutant from colchicine treated sorghum seedlings that yielded an average of 27% more dry matter over a period of four years. Ross (1965) lists five hybrids, three restorer lines, and one variety that were developed as a result of colchicin induced genetic variation.

Qualitative Genetic changes

Qualitative or relatively simply inherited mutant characters have been most frequently induced, isolated and described in mutagenic studies. Some of the reasons for this is that (A) they are relatively easily recognized due to prominent phenotypic characteristics, (B) the probability of mutating one or a few genes is greater than many genes without selection and recurrent mutagen treatments, and (C) simply inherited

recessive characteristics can be recovered more easily with smaller populations in the early (M_2 and M_3) generations than complexly inherited characters. Although most induced mutations are undesirable, some agronomically valuable mutations have been induced.

PEARL MILLET - Qualitatively inherited characters reported have included chlorophyll-deficient mutants (Hanna et al.- 1978, Chandola et al.- 1963), dwarfs (Joshi - 1968, Venkateswarlu and Mani - 1973) and early mutations (Hanna and Burton - 1978). The dwarfs and early mutations could have direct practical application to plant breeding. Mutations that affect reproductive behavior have also been reported. Among these are female sterility with aposporous apomictic development (Hanna and Powell - 1974), facultative apomixis (Hanna and Powell - 1973), male sterility (Krishnaswamy and Ayyangar - 1942) and cytoplasmic male sterility (Burton and Hanna - 1976, 1982). Rabson et al. (1978, 1979) described methods for identifying and isolating genotypes with improved grain protein and lysine content.

Murty (1980), Raut et al.(1974), and scientists at ICRISAT (1978-79 annual report, page 59) were able to induce downy mildew resistance by treating seed with ^{60}Co gamma rays. These mutants have resulted in the release of a number of downy mildew resistant inbreds and hybrids (Mutation Breeding Newsletter no.3,6,11).

Burton, Hanna and Powell (1980) reported that three induced mutants (orange node in T13, early in T18, and stubby head in T23) after three cycles of recurrent mutagen treatment increased forage yields 21.7 to 38.2% when crossed with their normal counterparts. Either the loci controlling these mutants induced heterotic effects or other loci were modified that did not alter the normal appearance of these mutants.

SORGHUM - The DES induced high lysine - high protein mutant, 'P-721', reported by Mohan and Axtell (1975) has exciting potential for improving grain quality. The lysine and protein content were 3.09 and 13.9% for P-721 compared to 2.09 and 12.9% for the normal, respectively.

Porter et al. (1978) showed that brown midrib (bmr) mutants induced with DES had significantly lower lignin which resulted in higher dry matter digestibility of mature forage than the normals. Hanna et al (1981) reported that lower lignin-higher digestibility was already expressed in forage at one month after planting which emphasizes the potential of the bmr genes in improving quality of forage sorghums used for pasture, hay, and silage.

Cytoplasmic male sterility has been induced with chemical mutagens in the M_2 generation by Malinovskii et al (1975) and Erichsen and Ross (1963) and in the M_1 generation by Chen and Ross (1963).

Many types of early, dwarf, head, seed, and morphological mutations have been reported - Goud (1972), Harris et al (1965), Kapoor (1967), Sree Ramulu (1975), Patil and Goud (1979) and Barabas (1962).

Induced Chromosomal Changes

The physical mutagens have been most effective in breaking chromosomes and producing various chromosomal aberrations. Chromosomal rearrangements have been induced in pearl millet with a number of chemical and physical mutagens (Pantulu - 1967; Burton and Powell - 1966; Hanna and Young - 1974; Jauhar - 1974, 1981; Tyagi - 1976; and Lal - 1979). Burton and Powell (1966) reported that TN doses of 1.70×10^{13} (flux x time) produced 4 times as many plants (28%) with chromosomal interchanges as 0.6% EMS treatments. Seeds are usually treated in most experiments but the treatment of pollen should be considered because it eliminates sectoring and many lethal characteristics (Hanna and Young - 1974; Schertz - 1970).

Schertz (1970) irradiated sorghum pollen with 3 to 10 kr of ^{60}Cobalt gamma rays to develop a translocation tester stock series. Other reports of mutagen effects on cytological changes are briefly summarized by Sree Ramulu (1975).

Low dose stimulation

Burton et al (1971, 1975) treated pearl millet hybrid seeds with gamma ray dosages of 0 to 25.6 kR. They found no radiation induced stimulation on forage yield from 0.15 to 9.60 kR but a significant reduction in forage yields at higher doses. Seed irradiation did not adversely affect forage quality.

Conclusions and Recommendations

Pearl millet and sorghum have a tremendous amount of natural variation that is yet to be exploited. Usually, a search for a gene(s) should begin here. If not found in the available populations then use mutagens.

A clear objective(s) is needed before beginning a mutation breeding program (e.g. pest or disease resistance, dwarfs, male sterility, etc.). The objective will not be important to select mutagens or doses but screening techniques to accomplish the goal in the shortest time period.

The number of seeds to treat will depend on factors such as expected no. of genes, mutagens, screening techniques, manpower and available plot area. Generally M_1 populations should be as large as possible. Estimates range from 5000 to 50000 M_1 plants as a minimum (ref. Manual on Mutation Breeding, IAEA, Vienna 1977).

Most mutagen studies with pearl millet and sorghum have used air-dry seeds. Some studies with chemical mutagens have used a 4 to 9 hour presoak before treatment or low temperatures (5°C) during treatment. The presoak allows for better survival especially with more toxic chemical mutagens. The low temperature slows down seed germination and allows the mutagen to penetrate the growing point at the youngest possible stage which should result in larger M_1 mutant sectors. Researchers must recognize that treated seeds usually result in sectored M_1 plants. A mutation can be selected in the M_1 if it is dominant and phenotypically recognizable, or if the treated plant is heterozygous for that locus. The selected mutant sector can be selfed and reselected for true breeding plants in the M_2 generation. If a mutation is recessive, it becomes necessary to self

all heads on all M_1 plants to recover mutations in M_2. The M_2 plants are screened for the desired characteristic and true breeding plants are selected in the M_3. It must be remembered that along with the desired characteristic(s) there are undesirable changes such as lethals, chromosome breakage and undesirable mutations which need to be separated from the desirable characteristics in the breeding process. Simply inherited recessive mutants are usually easy to recover in the M_2 generation. Later generations may need to be studied to recover more complex mutations.

Treatment of pollen with mutagens has not been frequently used in pearl millet and sorghum and is probably an important, but overlooked technique especially in pearl millet since it has a protogynous habit of flowering and can be easily cross-pollinated. M_1 plants from seeds produced from normal x irradiated pollen crosses do not sector for mutations. Therefore, it is necessary to self and progeny test only one M_1 head per plant in the M_2. Also many lethals and gross chromosomal aberrations are eliminated, because the treated pollen grains with these induced undesirable characteristics are non-functional (Hanna and Young - 1974). The seed is probably more resistant to these gross abnormalities than the pollen. The treatment of pollen is presently limited to physical mutagens. Procedures for treating pollen with chemical mutagens need to be developed. Pollen treatment with any mutagen would be effective for nuclear mutations but not for cytoplasmic mutations.

Most of the mutagens used on pearl millet and sorghum have been effective in inducing mutations. However, some mutagens such as ethidium bromide, streptomycin, and mitomycin have been more effective for cytoplasmic mutations (based on studies to induce cytoplasmic male sterility) and thermal neutrons and gamma rays more effective for inducing chromosomal breaks. Gamma rays, ethyl methane sulfonate, and diethyl sulfate appear to be three of the most effective mutagens for inducing a wide array of mutations in both pearl millet and sorghum. Combination treatments of physical and chemical mutagens have generally been more effective for mutation induction than either mutagen by itself. Reports in the literature indicate that pearl millet and sorghum lines show differential genotypic response to the various mutagens and doses. Therefore, no specific recommendations can be made for untested genotypes but ranges of doses for initial studies can be suggested. Also F_1 hybrids (probably due to their heterozygosity and vigor) tolerate higher mutagen doses and produce more mutants than inbreds at a specific dose. It is generally recommended that at least two mutagen doses be used : low (60% M_1 plant survival) and high (40% M_1 plant survival). This rule may not be helpful when using TN since M_1 seedling vigor and plant survival are not greatly affected. Recommended mutagens and dose ranges for seed treatments (except where noted) follow:

Mutagens	Doses
Thermal neutrons	5.67×10^{12} to 1.70×10^{13} (flux x time)
Gamma rays	
Seed	10 to 30 kR
Pollen	2 to 5 kR
X-rays (50 kV)	40 to 70 kR
Ethyl methane sulfonate	0.2 to 0.4% (4-12 hours)

Methyl methane sulfonate	0.005 to 0.01 (8 hours)
Diethyl sulfate	0.1 to 0.2% (3 hours)
Streptomycin	200 to 500 ppm (5°C for 40 hours)
Mitomycin	50 ppm (5°C for 40 hours)
Ethidium bromide	250 to 1000 ppm (5°C for 40 hours)
N-nitroso-N-methyl urea	0.005 to 0.10% (4-12 hours)
Colchicine	0.1 to 0.5%

Research on inducing quantitative variation has been limited in both pearl millet and sorghum. However, the studies that have been conducted indicate that for mutation breeding to be successful with quantitatively inherited characters, several cycles of recurrent selection may be needed after mutagen treatment (Burton et al.- 1969, 1974).

The researcher interested in other aspects of mutation breeding should consult the Manual on Mutation Breeding (2nd Ed.), Tech. Report 119, IAEA, Vienna, 1977, for helpful information on mutagens, doses, and breeding procedures.

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