Radiation-induced plant mutations* - A Review

by

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Introduction: Radiation may be considered as the movement of energy through space, in either corpuscular or electromagnetic form. Corpuscular radiation consists of streams of atomic or subatomic particles which can transfer their kinetic energy to any matter with which they collide. The particles may be negatively charged such as the electrons in beta rays, positively charged as the helium nuclei of alpha rays, or electrically neutral as the neutrons. Electro-magnetic radiation, on the other hand, may behave as a self-propagating stream of particles, called photons, which cause electric and magnetic disturbances affecting the internal structure of matter and thus dissipate their energy. Radio waves, visible light, x-and gammarays are fundamentally similar classes of electromagnetic radiation.

An electron which had been excited to a sufficiently high level of energy leaves the atom or molecule to which it belongs. This process is called "ionization" because it results in an outright separation of electric charges. Lower radiation frequencies like radio waves and visible light are not able to knock out electrons. High energy radiations like X-rays have a greater potency which is not only capable of ejecting electrons from all kinds of atoms - i. e., of forming ions - but also of initiating chemical changes. Such radiations are called ionizing radiations. During the process of ionization by radiation the ejected electrons get attached to the atoms of the substance, forming pairs of positive and negative ions, The means by which different radiations cause changes in biological materials is still not clearly understood. Energy from radiation may be dissipated by a process of ionization in which electrons are ejected from atoms or molecules, and through excitations which raise the electrons of a molecule to higher energy levels (10, 13).

Radiations that have been used most extensively to induce mutations are ultraviolet rays, X-rays, alpha, beta, and gamma rays from radioactive nuclides, and fast and slow neutrons.

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Which are relatively inexpensive. They are non-ionizing and limited in their tissue penetrating ability. Ultra violet ray is capable of producing biological effects only through excitation and photochemical reactions. On an energy basis it is far less efficient in producing structural aberrations in chromosomes than are the ionizing radiations. It is selectively absorbed by the nucleo-proteins of the chromosomes, more by nucleic acid than by protein. In genetic experiments on plants its use is restricted to spores or pollen grains. So far as is known, no mutants of economic interest have been obtained in higher plants with ultra-violet radiation.

X-rays and gamma rays: Have identical properties and differ only in their mode of origin. They are electromagnetic shortwave radiations. They interact with matter by photoelectric effect, Compton Scattering and pair production. Gamma rays from natural or artificial radioisotopes such as Co. 60 have a shorter wave-length and possess more energy than X-rays. X-rays are generally produced in a broad range of energies. Soft X-rays of longer wave-length (10 to 1A°) are less penetrating but more densely ionizing than the shorter wave-length (0·1 to 0·05 A°) hard X-rays. In the energy range used for most biological experiments X-rays and gamma rays transfer their energy to tissue through ionization and through excitations of atoms or molecules. They have relatively sparse ion density. Genetic alterations may be effected through direct change in the molecules of the games or indirectly through other chemical changes in the cell.

Beta rays: Such as those from P³³ and S³⁵, produce nearly the same effects in the tissue as x- or gamma rays (21). They are high speed electrons emitted from the nucleus of an unstable atom. They have a lower specific ionization and greater penetrating power than alpha rays. Their special characteristic is that the source may be incorporated directly in the cell molecules giving a somewhat greater localization of the site of action. Though beta rays seldom penetrate more than a few hundred microns of tissue, for genetic purposes a beta-emitting isotope may be absorbed into or near the chromosome.

Neutrons: They are electrically neutral particles which are obtained mostly from nuclear fission reactions in an atomic pile. The more energetic fast neutrons cause ionization, indirectly releasing their energy in elastic collisions with nuclei of atoms present in the

tissue, particularly with hydrogen, producing densely ionizing protons from it. Slow or thermal neutrons cause transmutation of certain specific atomic nuclei with a consequent release of alpha, beta or gamma rays or protons. The principal nuclear transmutations by thermal neutrons in tissue are those with nitrogen which ejects a proton, with an isotope of boron which ejects an alpha particle, and with hydrogen which emits a gamma ray. The linear energy transferred per unit length of track in tissue is greater for alpha particles than protons, and greater for protons than electrons. This is one of the most important physical factors influencing the biological effect of an ionizing radiation (15, 23).

Doses of x-. alpha, beta and gamma rays are commonly measured in roentgen (r) units. Beta rays, which are streams of electrons, are measured in terms of "rep" (roentgen equivalent physical), with one rep being the unit of energy absorption equal to 93 ergs gram of tissue. Several energy units have been employed to measure neutron doses. In America the n-unit has been commonly used and it is equivalent to 2.5 r units of X-rays or gamma rays $(1 \text{ r} = 1.61 \times 10^{12} \text{ ion pairs/gm (air)})$. Since 1953 'rad' is used as the unit of absorbed dose of radiation at the site of interest and 1 rad is equal to 100 ergs/gram.

Wilhelm Conrad Roentgen discovered x-radiation in 1895. Investigations were immediately begun about its injurious effects on plants. In 1896, Henri Becquerel discovered natural radioactivity. The discovery gave further impetus to investigations concerning the biological effects of ionizing radiations. A few years later, in 1898, Marie Curie discovered radioactivity in radium and polonium, which were isolated in 1904 from a uranium mineral, pitchblende. Such naturally radioactive elements, particularly radium, were also employed by many early investigators. Gager published a book of 278 pages on the effects of ionizing radiation on plants as early as 1908 (7). There was a rapid rise in the number of investigations on the subject in nineteen-twenties and another period of rapid work began about 1945 (31).

Radioactive isotopes of some heavy as well as lighter elements are known to ocaur naturally, but the major contribution to biological research has resulted from the advent and general availability of artificial radio isotopes. By products of the nuclear age, such as kilocurie sources of radiation or high intensity nuclear radiations in or near reactors, have also helped to stimulate experiemental work

on various plants. In fact, artificial radioactivity was discovered in 1934. Before the advent of the nuclear reactor various radioisotopes were made through the use of cyclotrons and other sources
of high speed sub-atomic particles. The nuclear reactor, in which
uranium-235 is fissioned through a chain reaction process, is a source
of radioisotopes in quantities millions of times greater than available
previously, with much greater variety of radiations and at greatly
reduced cost. Radioisotopes are used (1) as sources of ionizing
radiations in much the same way as radium and X-rays and (2) as
tracer atoms. The useful radiations from radioisotopes are alpha
particles, beta particles, gamma rays and positrons (similar to beta
particles but positively charged). As tracer atoms these isotopes
serve to follow the complicated course of individual batches of atoms
in physical transfer or chemical or biological reactions (34).

There are several kinds of radioisotopes now available. Hundreds of isotope-labeled compounds have been prepared by synthesis. Some of the commonly employed radioisotopes are P³², Ca⁴⁵, C¹⁴. H³ Tritium, Co⁶⁰, Cu⁶⁴, Fe⁵⁹, S³⁵, Cr⁵¹, Cs¹³⁷, I¹³¹, Rb⁸⁶, K⁴², Sr⁹⁰, and Na²⁴. Of these, the first nine are used as important tracers in agricultural research. In radiation genetics P³². S³⁵, H³, Co⁶⁰ and Co¹⁸⁷ are commonly used. Important radiation properties of a few radioisotopes are given below (4):

Carbon¹⁴ emits beta rays of 0.155 Mev strength. Its halflife is 5568 years (half-life is the period during which the element loses half of its radiation energy periodically).

Phosphorus 32 emits beta particles of strength 1.712 Mev with a half-life of 14 days.

Sulphur 35 emits beta rays of strength 0.166 Mev and its half-life is 87 days.

Cobalt 60 emits beta particles of strength 0.31 Mev and gamma rays of 1.17 Mev and 1.33 Mev strengths. Its half-life is 5.3 years.

Calcium 45 emits beta rays of strength 0.254 Mev and its half-life is 152 days.

Hydrogen 3 (Tritium) emits beta rays of strength 0.01795 Mev and its half-life is 12.46 years.

Ionizations caused by radiations from the nuclides are revealed either by electrical effects or by recombination effects of the ions. The radiations are detected and counted most commonly with sensitive electronic Gieger scalers and Scintillation Counters. Photographic visualization of tracer distribution is obtained from autoradiograms, and in the estimation of minute quantities of the substance, paper chromatography with autoradiography or electronic counting is employed.

Genetic effects of ionizing radiations on plants: The first discovery that hereditary changes similar to those occuring naturally could be induced in animals and plants by man-made radiations was made by American Scientists. Dr. H. J. Muller (19, 1927) and Dr. L. J. Stadler (32, 1928), but two Swedish Scientists, Dr. Herman Nilsson-Ehle and Dr. Ake Gustafsson were the first to put the idea to practical use in crop breeding (1929). Muller x-rayed male fruit-flies and obtained a wide variety of sports. Stadler got the same results with barley and corn. Since most of his new plants were distorted and inferior, Stadler then concluded that no radiation-spurred mutant could be of practical value. The two Swedish Scientists began shooting x-rays at barley seeds in almost lethal doses and in a few years found that they could step up nature's mutation rate as much as a thousand fold (17, 29). A few geneticists and plant breeders in Germany and Russia also recognized early that this method might be used to increase variability in crop plants.

In U. S. A. until the 1950's there was little research or confidence in the potentialities of radiation-induced mutations for agriculture, as many geneticists believed that radiation caused only destructive changes. The persistent, successful efforts of European workers in producing useful plant mutations (36), the greater availability of radiation sources and an interest in finding peaceful uses for atomic energy, the generally increased knowledge of hereditary materials and the production at a number of laboratories of mutants having special significance to practical plant breeders, have been the causes for the recent more optimistic attitude toward the use of radiations for plant improvement (14).

With better radiation sources, radiation genetics is under study from two different points of view. The first approach is designed to give a better understanding of the science of radiation genetics and consequently of genetics itself. The second is a much more practical approach to the use of radiation for the solution of specific agricultural problems. By means of fundamental studies, plant scientists have been able to difine to a certain extent the way in which radiation should be given to plant, the biological conditions which must be fulfilled, the type of radiation to use and the results that may be expected as well as a great many other factors necessary for an intelligent approach to the problem. The genetic effects of ionizing radiations on plants may be briefly reviewed under general effects of radiation on cells, effect of ionizing radiations on chromosemes, radiation-induced gene and somatic mutations, and modifying factors.

Side by side with the frequence of aberrations, radiation causes certain amount of damage also to cells. Some of such damages are - depression of mitotic activity, depression in the synthesis of desoxyribonucleic acid, and the stickiness of metaphase and anaphase chromosomes. The depression of mitotic activity by radiations has been studied in a variety of organisms. of radiation employed and the sensitivity of cells of different species are the important factors here. Inhibition of mitosis has been observed with even low doses of x-rays and ultraviolet rays of certain wavelengths. With x-rays there seems to be a compensatory effect in cell-division following the depression, but with ultraviolet radiation, no compensatory rise is observed. UV of certain wave-lengths is absorbed strongly in the nucleic acids of the cell, and this is of significance in determining its genetic effects. Pollen grains of many species of plants are found to be effectively treated with ultraviolet radiation. Even low doses of x-rays inhibit the synthesis of DNA, as observed in Vicia root tips, and thus cause mitotic delay. Another general effect of radiation on dividing cells is the appearance of clumped chromosomes at metaphase and an irregular separation at anaphase. The chromosomes appear to be pycnotic or sticky as a primary effect of radiation (13, 33).

It has long been known that ionizing radiation causes chromosome aberrations. Depending on the stage of nuclear development at the time of irradiation three general classes of aberrations are produced (16, 24).

(a) Irradiation at the resting stage results in chromosomes aberrations. At this stage of the nuclear cycle, the chromosomes respond to irradiation as if they were single strands and at metaphase anaphase the induced aberrations are seen to involve both of the two sister chromatids. The chromosomes aberrations include dot deletions, rod deletions dicentric chromosomes, and ring chromosomes. Though it is difficult to detect them, inversions and free translocations are also produced.

- (b) Irradiation at prophase results in chromatid aberrations. At this stage, the chromosomes have divided into sister chromatids, and the irradiation may break both or only one of the two sister chromatids at any given locus. The chromatid aberrations include deletions of one of the two chromatids, deletion of both chromatids to form iso-chromated aberrations, breakes and reunions in the chromatids of different chromosomes followed by illegitimate reunions to form chromatid dicentrics or chromatid exchanges, and breaks and reunions of chromatids of the same chromosome to form chromatid rings or exchanges. The chromatid exchanges or translocations can usually be detected only at metaphase, but the chromatid deletions, isochromatids dicentrics and rings can be recognized at either metaphase or anaphase.
- (c) Irradiation in very late prophase or prometaphase produces half chromatid or sub-chromatid aberrations. These include half chromated exchanges between sister chromatids, and more rarely, half chromatid exchanges between chromatids of different chromosomes. They can be detected only at anaphase as a rule, and even at that stage the existence of half chromatids is inferred from the nature of the aberration.

The inhibition of cell-division by ionizing radiation is important in studies of radiation sensitivity at various stages of cell cycle. Chromosomes show great variation in their sensitivity to ionizing radiation at different periods in their nuclear cycle of mitosis and meiosis. It has been noticed that meiotic chromosomes are more sensitive than mitotic chromosomes and that chromosomes at the time of nuclear division are much more sensitive than they are during the resting stage (work on Tradescantia microspores and the meiotic chromosomes of Trillium). Cytological studies of chromosome breakage induced by ionizing radiation at various stages of nuclear development have provided evidence regarding the time of chromosome duplication and the nature of chromosome breakage and reunion (work on Tradescantia microspores). The above mentioned aberrations constitute chromosomal alterations including changes in structure, delections, duplications, inversion and translocations of genetic loci.

Effects of radiation may frequently cause changes in the chromosome number also. This class includes types with increases or decreases in the number of whole chromosomes or sets of chromosomes aneuploids and polyploids and other genetic changes. Polyploidy is often induced as a result of inhibition of mitosis by radiation. It is

commonly observed that ionizing radiation causes abnormal distribution of chromatids to the daughter nuclei, both at mitotic and meiotic divisions, bringing about an euploid condition, which sometimes has a lethal effect on the individual. Ionizing radiation also affects the frequency of crossing-over altering transmission of genes (13).

Each type of aberration bears a particular relation to the doses of radiation and exhibits a quantitative relation to the intensity of the radiation, the relation depending largely on whether one break or two breaks are necessary to produce that type of aberration. Earlier studies on the comparative efficiencies of various ionizing radiations indicated that there was but little difference between the gamma rays and the hard and medium x-rays. Increased efficiency was observed in soft x-rays. Neutrons and alpha particles are considerably more effective per unit of energy dissipated in tissue than electromagnetic radiations. Utilizing the neutron-x-ray comparisons, Lea and Catcheside (1942) attempted to determine the approximate under of ionizations required to produce a chromosome Their conclusion was that seventeen ionizations, on the average, are required for a breakage to occur (16). Ultraviolet is the only non-ionizing radiation capable of fragmenting chromosomes. On the energy basis, UV is by far less efficient compared to x-rays. Kev beta rays are essentially similar in effectiveness to gamma rays emanating from Co60. P32 and C14 both producing beta rays, when absorbed by the cut stems of inflorescences of Tradescantia, were found to produce chromosome aberrations similar to those produced by x-rays (8, 9 Giles 1947; Giles and Bolomey 1948).

There are some gene mutations induced by radiations, which are genetic changes characterized by the absence of cytologically visible alterations in the chromosomes (sometimes, these have been called "point mutations"). Radiation is the first highly effective means discovered for producing gene mutations in quantity. Stadler produced such mutations in maize and barley employing x-rays. Different kinds of radiations were used by different workers to produce the same effect in different kinds of material. Experimental facts indicate one-hit event for the production of gene mutation and gene mutation shows a linear dose dependence (37). An important application of radiation has been its use for the production of mutations at many loci, making possibile the construction of chromosome maps, better understanding of the action and interaction of many genes, and confirmation of the general similarity of the biochemical processes under genetic control found in lower and higher organisms.

Effects of ionizing radiations in the production of cytoplasmic mutations (maternally inherited changes also deserve attention. The most striking effect of this kind is the segregating of chlorophyll mutants in the progenies of irradiated plants like barley found by Stadler, Gustafsson and many others. A wide range of types of chlorophyll mutations has been defined and described. X-irradiation, and chronic gamma-irradiation from Co⁶⁰ have been employed in this line. Mutation rates increased with the radiation dose. In some cases, maternally inherited gigas mutants with greater yield are obtained (5, 35).

Plants are irradiated in the early flowering stages in order to affect the developing gametes. Somatic mutations are first induced in seeds by irradiation. Such affected cells may subsequently give rise to germinal tissue which transmits the mutations to later generations. Vegetative cuttings and fruit trees have also been exposed to gamma radiation from Co⁶⁰. Many economically important somatic mutations have been induced by radiation in plants like carnations, antirrhiuums and dahlias etc. (28).

Many external and internal factors have been found to modify the genetic effects of radiation (37). According to early hypotheses, the machanism by which radiations induced structural aberrations was based largely on physical consideration. The principal factors were considered to be the type, does and intensity of radiation (16). Later work has indicated that some environmental factors like moisture, oxygen, storage and temperature have also much influence on the genetic effects of radiation (x-rays and gamma rays). On the other hand, the genotype age of the tissue, stage of the chromosome number of an organism have been found as important internal factors. influencing its radiosensitivity. It has also been noted that an increase or decrease in the yield of aberrations can be brought about by supplementary environmental treatments like fractionated dosage, centrifugation of the cells during irradiation, irradiation with infrared before or after x-irradiation, anoxia, irradiation in an atmosphere of Co or Co, and treating the cells with various chemical agents. (13, 14).

The interplay between the effects of moisture, oxygen, storage and temperature are found to be complex, particularly with radiations of sparse ion density (20). Major experimental conclusions show that there is a pronounced effect of oxygen is increasing the frequency of of x-ray induced aberrations of all types. Moisture content in the

embryo of irradiated seeds influences the radiation response in resulting seedings. The highest total number of mutations is observed from high radiation does to seeds in their dormant condition. The oxygen effect and the temperature effect seem to be closely interrelated. So is the effect of storage of seeds after irradiation and before hydration. In the case of neutron irradiation these factors do not seem to influence the effects (20).

Differences in response to irradiation have been noticed among species, varieties and genetic strains within a variety.

Regarding the stage of life cycle for getting more mutations by irradiation, the following general inferences has been made from the experimental results. Aged seeds show greater frequency of induced mutations than fresh seeds. Young plants are more radiosensitive than mature plants. Meiotic cells have been found to be more radiosensitive to radiation than mitotic cells (23, 29). Chromosome aberrations are relatively more frequent when pollen is irradiated than when seeds are irradiated. Pollen irradiation has an advantage over seed irradiation because a change induced in a single cell will be represented in every cell of the progeny, if it fertilizes an egg. In bud and seed irradiation a desired change may be seen in one or a few cells which produce only a small sector of the mature plant. There is also a possibility of the neighbouring cells outgrowing the altered cells and change may be imperceivable. Polyploids are in general more resistant to radiation than related diploids.

Radiations in plant breeding: The use of radiations in plant breeding is very promising. What is more important is not the induction of mutations, but the survival of the induced mutations through cell division. An ionizing radiation causes a change in the fundamental hereditary material at a molecular level. It is then taken up by the self-reproducing chromosome units in the cell. Recombination takes place with the residual genotype. There is the reaction of the genotype with the environment. Then the plant breeder selects those genotypes which are suitable to his particular needs. Thus, it is a series of events from the induction of mutation to the growing of a new variety of plant in an area. In other words, one has to get a useful and viable mutation induced in a cell and that single cell, uncontaminated by other cells, has to pass down a cell lineage to make a new plant. After the mutation has been artificially induced, the techniques of selection and testing are the same as those employed in conventional breeding methods.

Dr. Ditervon Wettstein, one of the Swedish workers in the field of radition genetics says, "We have found that by radition we can get almost anything out of plants we really want. Most food plants of today are rather old-fashioned, and their variations have exhausted by many years of inbreeding. They need to be reconstructed to suits the needs of modern agriculture, with its emphasis on high yield and mechanization. We now have an instrument with which we can rebuild all the food plants in the world". This is a very optimistic view! "We have only made a start in creating useful new plant varieties. Now we are trying to learn how to control the mutation process - to discover the conditions under which we can produce at will the plants the world needs. We get the widest variety of mutations from some plants by irradiating them for short periods at certain times; others seem to do better if exposed for a whole season. Many new practical developments are on the way. For instance, we expect to develop grains that will mature earlier, which will be very important not only in Sweden, but in all northern countries. Even a few days' earliness will make a great difference in world production by anticipating frost and storm. We already have the early strains, but their yield is not high enough. We are confident that we can get both qualities" (17).

Ake Gustafsson and Olof Tedin conclude (12), "However well-founded the scepticism against the value of irradiation experiments in plant breeding may once have appeared, it is by now evident that induced mutations can increase the yielding capacity of a variety, or on the other hand leave its production capacity in tact and improve special qualities of importance in modern agriculture, such as stiffness of straw, earliness, protein content, baking quality, fibre strength, grain size-in cereals as well as in peas, lupines, flax, tomatoes, etc. This series of papers goes to indicate that mutation research is indispensable for the progress of plant breeding. Artificial mutation implies a means of augmenting variability. Some mutants directly increase agricultural fitness. Others are useful in recombination work. We are now able, to some scant degree, to influence and to control the sum total of the mutation process, as well as to direct the mutation of individual loci".

Disease resistance is the most outstanding contribution of radiation to plant breeding. There are some special uses of radiation as a tool in plant breeding such as those pioneered by Sears (27) and and Elliott (6) in transferring a small useful piece of chromosome from Aegilops and Agropyron respectively to wheat to get the disease resistance to wheat. With reference to crop improvement the following achievements are so far made in various parts of the world by causing desirable mutations by radiation (14, 22).

	Plant	Improvement
1. 2.	Barley	Stiff straw, earliness, dense spike, increased yield of seed and straw, higher protein content, improved malting quality, disease. resistance. Stem rest resistance, earliness, short straw,
		stiff straw, increased test-weight, improved quality.
3.	Wheat	Short and stiff straw, earliness, increased yield, improved baking quality, stem and stripe rust resistances.
4.	Peanuts (Ground nuts)	Increased yield and oil production, disease resistance, size and shape, better adopted to mechanical harvesting.
5.	Soybeans	Earliness, increased yield.
6.	Vetch	Greater vitality.
7.	Beans	Increased yield, disease resistance, earliness and bush habit.
8.	Mustard	Increased yield and oil production.
9.	Peas	Gigas mutant form with higher yield.
10.	Sesame	Higher yield (3).
11.	Jute	Taller plants (2).
12,	Tomato	Increased yield.
13.	Apple	Red fruit.
14.		Striped fruit.
15.	African violet	Self-fertile varieties.
16.	Carnations	Flower color sports (25).
17.	. African violet	Leaf shape and flower color variants.
	Rice	New dwarf type which may substantially reduce loss due to lodging.
19	. Peaches	Early varieties.

Of these varieties, the Primex White mustard Svalof the "Stralart" of Weibullsholm, and the "Schafers Universal" in Phaseolous were released into the market in Sweden. Numerous mutants in barley, wheat, peas, lupine, being rather promising, await their final large-scale testing (12). In the U.S. A. the Michigan Experimental Station has released a new bean variety, Sanilae (Phaseolus vulgaris, L.,), with its earliness and bush habit. As a result of the efforts of Gregory (11) an improved peanut variety was released in North Carolina State in January 1959. A large number of irradiated crops comprising cereals, forage grasses, legumes, vegetables, fruit trees, oil and fibre crops of economic importance are at present under observation regarding the beneficial mutations they may be showing (22). Regarding the potential uses of radiation in plant breeding, the following points may be mentioned:

- 1. It is useful in inducing variability.
- It may be used in breaking extremely close linkages by which may things can be achieved.
- In the realm of interspecific and intergeneric hybrids, parts
 of non-pairing chromosomes may be transferred with the
 help of radiation to stable synapsing chromosomes.
- 4. It may be practical to have a crop with "induced heterosis" by irradiation of pollen.

Conclusion: It is beyond dispute that beneficial mutations can be produced by irradiation. Radiation does not produce ready-made varieties but it increases variability with a greater frequency than that occuring in nature through spontaneous mutations. The plant breeder has a very large scope to make selections. He has to grow large progenies and make effective screening to get what is needed. The good features of a mutation can be recombined with other outstanding characteristics through conventional methods of hybridization and selection. When the induced mutation process is controlled and directed to give the desired mutations, by decreasing the chromosome aberrations, physiological injury and sterility, ionizing radiation will be a very usful tool in plant breeding. Mutation induction, as a technique of plant breeding will then be a profitable supplement to the convenitonal methods of selection and hybridization.

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