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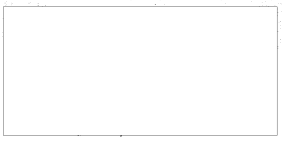

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PLANTS AND X-RAYS

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INTRODUCTION

When Roentgen made his great discovery in 1895 he could hardly have suspected the full scope of its application. Only now, 50 years after the discovery, can we appreciate its significance. Examining only the biological effect of these rays, which possess stimulating and generative qualities, one can only marvel at the power and significance of this new tool which has been placed at the disposal of experimental science.

During these 50 years a vast amount of experiments and observations have been performed demonstrating the effect of X-rays on animal and plant life. During this period the interest which biologists have shown in these rays has fluctuated. Although the expectations of the first investigators in the field of medicine have, in general, been realized, after the first brilliant success a period of disillusion set in before the successful use of these rays was conclusively established for diagnosis and cure of numerous diseases.

Similar fluctuations in attitude can be noted in the evaluation of the biological effects of X-rays, depending on the success or failure of the experiments performed.

Interest in the effects of short waves appeared shortly after their discovery, but the peak of interest was reached in 1927 when Muller made his announcement about the multifold increase in the number of mutations obtained by the use of these rays on fruit flies. Certain of our biologists responded quickly to Muller's discovery. It seemed that a method had been

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found by which it was possible to induce an outburst of mutations in any kind of plant or animal life and that among these many mutations it would be easy to select those which would be useful to agriculture and industry in one way or another. By selecting certain changes and by fixing them by heredity it was possible to expect to obtain new forms and even new species. In short, X-rays appeared to open wide horizons for experimental generation of new forms of life. After a short while, however, assertions were made on all sides to the effect that X-rays have not only failed to produce, but that they cannot produce, the changes which first investigators expected. A few more years passed and X-rays assumed what we believed to be their proper place in the field of biology. Of course, X-rays are not omnipotent; they have not produced new families, or even new genera. But from the changes which have been produced by radiation, it is possible to obtain not only radical deviations, but forms which are very desirable to the experimenters. This will be demonstrated later by many examples. Certain works in this area are destined to become classics while others, which held great promise, but which were superficial or insufficiently checked, will be forgotten.

The same may be said in relation to phenomena of stimulation due to exposure to X-rays. At first a great interest was taken in this type of experiments. In that period the majority of authors noted that X-rays had a positive effect on the energy with which plants germinated, sprouted, and developed. Then a series of works appeared denying that X-rays have any positive

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action. As a result a sceptical attitude developed in relation to the possibility of stimulating plant growth by radiation of seeds or sprouts. Only in the last few years have works begun to appear (in the United States as well as in the USSR) which indicate that with appropriate dosages of these rays it is possible not only to stimulate the growth and development of agricultural crops, but even to increase their yield.

We feel that our sketch should be prefaced by a short explanation of the physics of these rays. But first of all it is imperative to say a few words about the nomenclature of the rays.

Roentgen called them X-rays since he didn't understand their properties clearly. But in due time their name became so closely associated with his that they quite properly received the name of Roentgen rays. This is particularly fortunate since it is most convenient for the coining of such new terms as roentgenbiology, roentgenmutation, etc. However, on certain occasions we will resort to the term X-ray for brevity, as many contemporary authors do. [sic] [In this English translation, however, the term X-ray will be used exclusively.]

THE PHYSICS OF X-RAYS

Investigators in recent years have shown that atoms, which were considered indivisible, are actually complex structures consisting of a central nucleus and an outer shell, composed of the smallest existing particles of matter, carrying negative charges. These particles are called electrons. In order to

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obtain X-rays it is necessary to have, not only electrons from the outer shell of the atoms, but also electrons separated from atoms or "free electrons". The process of formation of X-rays takes place in a vacuum tube, filled with rarified gas, where by application of high voltage across the tube free electrons are split off (from individual atoms) and directed at a very high speed toward the anode, thus forming a beam of "cathode rays". The electrons are propelled along their path at a speed approaching that of light. In order to impart such speed to electrons it is necessary to expend a large amount of energy which is derived from a special source of current. If a metal plate is placed in the path of the electrons, they will strike it with tremendous force, their speed diminishes abruptly and at that instant X-rays are formed. This plate has to be made from a metal with a very high melting point since electronic bombardment generates a large amount of heat. Such a plate is called the anode of the tube while the tube itself is called an X-ray tube. The most prevalent type of electronic tube is the so-called Coolidge tube which was first made in the United States in 1913. The X-ray tube is, essentially, a container from which air has been pumped out. Inside the container are two electrodes; one is connected to the anode, the other to the cathode, which constitutes the source of electrons (fig. 1. X-ray apparatus in action). X-rays are short wave radiations ranging in wave length from 0.02 to 100 angstrom units; a unit of length which is equivalent to 1/10,000 μ or 1/10 milli μ . The energy radiated by the tube is not uniform, consisting of both short and long wave radiation. The qualitative composition of the radia-

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tion depends on the intensity of the voltage: the greater the voltage the greater is the quantity of short wave rays produced.

X-rays are invisible and can only be detected by their action. Three basic means are used to detect rays: (1) fluorescence, (2) photography, and (3) ionization. The first method is based upon the ability of X-rays to cause visible luminescence in certain substances. If a screen is made from such substances it will light up every time that X-rays touch it (fluoroscopic examination is based upon this principle). The photographic action of X-rays is similar to fluorescence but more pronounced. It is possible, for example, to obtain photographic prints by means of X-rays. These prints can be retained as documentary evidence for an indefinite period. At the present time Kostov (1943) has had great success in photographing ears of wheat by means of X-rays; a method which enables him to obtain not only the external morphological appearance of the ears, but even the extent of development of the kernels inside the ear, due to the penetrating action of X-rays. Such photographs, produced by the action of X-rays, are known as radiograms.

The ionization method is based on the ability of X-rays to cause air and other gases to become conductors by imparting positive or negative charges to ions of neutral gas molecules. The amount of current passing through the ionized gas, with a given difference in potential is proportional to the intensity of the X-rays which cause the ionization. Special ionizing chambers which are used in order to measure the degree of ionization of the gas, can serve as dosage meters, for quan-

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titative measurement of X-rays.

In their optical properties X-rays show all of the characteristics of light rays. They can be refracted and reflected. They exhibit the phenomena of polarization and diffraction. The ability of X-rays to penetrate deep into the tissues and to induce various changes there is of particular significance in biology. It should be noted that only rays which are absorbed exert any effect. Rays which penetrate feebly or those which are completely reflected have no action. The ability to penetrate increases as the wave length is shortened.

During the very first year of discovery of X-rays people working with them experienced serious inflammations of the skin accompanied by loss of hair. It soon became apparent that the action of the rays is not limited to their effect on the skin, but that all of the internal organs of men and animals are affected if the amounts of exposure are sufficiently great. Radiation therapy is based upon this phenomenon.

In 1903 Heinecke amazed everyone by his discovery that mice and guinea pigs can be killed by X-rays. Autopsy of animals killed in this manner showed that their spleens were small and dark; while a histological examination revealed an extraordinary increase in the amount of pigment, and the disappearance of follicles and cellular elements of the spleen. Similar changes took place in the lymph nodes, in bone marrow, etc. In cases of sub-lethal dosage a regeneration of lymphatic tissues commences after several days. However, a discussion of this as-

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pect of X-ray action is outside the scope of this book; those interested in this phenomenon are referred to the book written by Nemenov in 1926.

THE MEASUREMENT OF ENERGY

Before proceeding further with our account some concept of the units of measurement of X-rays should be established. This is particularly imperative in view of the fact that the use of various units of measurement by the numerous workers in this field increases the difficulty of comparing the results obtained in the radiation of various plants and animals.

The most widespread unit of measurement, up to recent years, was a dosage bearing the abbreviation HED (High-Erythema-Dose). This dose is equivalent to that amount of rays which results in a reddening and peeling of the skin in man, ten days after exposure to radiation. But this measure, as most biological units, is too inaccurate since the indicated signs of action vary, depending on the age and condition of the given patient, and on the pigmentation of the skin. Clark, who examined many patients in numerous clinics, has shown that the erythemic dose varies from 400 r to 1200 r (roentgen units), depending on individual differences, and that the average dose equals about 850 roentgen units.

Many German and French investigators used the Holtzknecht unit (H), which is equal to about 1/5 of the erythemic dose, to measure X-rays.

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This latter unit was abandoned in favor of a new international unit r (roentgen unit) which corresponds to the amount of energy required to produce, as a result of complete ionization in air, at zero degrees centigrade and normal atmospheric pressure, charges of one electrostatic unit per cubic centimeter of the irradiated object.

Dosage meters used for quantitative determination of X-rays give the measurement in roentgen units. The majority of investigators, however, are not content to indicate the amount of X-rays in roentgen units; they also indicate the source of radiation, the voltage, the amperage, the distance of the object from the tube, the duration of exposure, and the quality (or absence) of filters.

Filters are very thin plates (of aluminum, copper, etc.) and serve to disperse the X-rays of specific wave lengths. This makes it possible to achieve some uniformity (of wave lengths) in the beam which irradiates the object.

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CHAPTER 1

PHYSIOLOGICAL CHANGES PRODUCED BY X-RAYS

As has been stated above, cellular reactions to various irritants depend on the power of the irritating agent. At first normal cellular activity is accelerated; exposures of longer duration to stronger doses produce depression; prolonged exposures result in death. This thesis has found confirmation in the works of the most recent investigators and was most precisely formulated by Arndt: "Weak irritants stimulate activity; medium irritants depress them; strong ones halt them." This formularization has been extended by Schultze to include all processes of animal and plant cells, of diseased, as well as of healthy organisms. This generalization has become accepted in literature as a basic biological law.

Since X-rays have an irritating effect on the activity of organisms, it was necessary to determine to what extent they conform to the Arndt-Schultze law. There was little objection on the part of the majority of investigators to that part of the law which states that strong doses of radiation tend to suppress normal activity. Numerous experiments testify to the depression of the development of organisms or tissues which have been subjected to strong or prolonged doses of radiation. Concerning the other part of the law, however, opinion is sharply divided. While some point out the stimulating effect of weak doses, others deny this effect altogether, or else they acknowledge it only as a temporary spurt of activity which is followed by normal, or even depressed, development. For example,

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in 1923 Holtzknecht wrote: "We have no basis for assuming that because a substance is harmful that, in some amount or other, it may be beneficial. Consequently, since X-rays fatigue and kill cells, we cannot conclude that doses exist which stimulate or accelerate cellular development. Fifteen years of roentgenology have established only the depressing effects of X-rays on cellular activity."

It should be noted that the term "stimulation" is ambiguous since stimulation includes negative, as well as positive, responses to stimuli. Undoubtedly certain differences of opinion stem directly from the use of this word. In order to avoid this type of misunderstanding the term "stimulation" will be used in its more generally accepted sense, i. e., to indicate the positive reaction.

The dose of X-rays which stimulates the life processes of plants is commonly referred to as an "irritating dose". From the numerous investigations of various authors it is evident that some of them have succeeded in establishing irritating dosages for the subjects of their experiments, while others deny the possibility of the existence of such dosages.

One of the earliest investigators of the biological effects of X-rays was Schober, who in 1896 set out to study the nature of X-rays in order to determine whether they were identical with light rays or not. Schober selected sprouting oats as the most light sensitive object he could find. Having sprouted oat seeds in darkness, he selected the most vigorous specimens (1-2 centimeters high) and planted them, five to a

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cup, in four small cups. He then placed the cups in a darkened box and subjected them to the action of X-rays for one hour, with the source of the rays being one centimeter away from the box. Careful observation of these plants did not reveal in them any evidences of (heliotropic) bending. But when the box with the cups was placed on the window sill and a diffused light was permitted to enter through a narrow slit, after an hour it was possible to observe a bending of the sprouts in the direction of the light. After 2 and 4 hours this bending was even more pronounced. On the basis of this experiment the author concluded that X-rays were not identical with light rays.

In 1897, Atkinson set up experiments in order to determine the effect of prolonged irradiations on plants. Having established, by preliminary experiments, that radiations of 1 to 10 hours on leaves of Caladium, on flowers of Begonia, and on various sprouts, do not produce any visible signs of injury; he set up an experiment with prolonged irradiations (45-hour exposures). This experiment was conducted in darkness. The irradiated plants behaved identically with the controls, which had been grown together with them in a dark room. When the irradiated and control plants were placed in light both groups exhibited pale green color. The difference lay in the fact that the plants which had been exposed to X-rays attained full color more slowly than the plants which had not been subjected to radiation. This observation forced the author to assume that X-rays exert a certain detrimental effect on plastids. The author did not succeed in establishing any other differences in the plants despite the prolonged exposure.

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Lopriore in his experiments in 1897 found indications of the irritating effect of X-rays. By subjecting parts of plants of Vallisneria spiralis to X-rays, the author discovered an acceleration of the movement of plasma in the cells. By subjecting to the action of X-rays sprouting pollen tubules of two plants (Genista and Darlingtonia) he succeeded in slowing down the process of sprouting.

Maldiney and Thouvenin who, in 1898, were the first to perform experiments with irradiation of seeds (they used seeds of Convolvulvus arvensis, Lepidum sativum, and Panicum miliaceum), came to the conclusion that X-rays accelerate the germination of seeds. In addition they observed that X-rays do not affect the formation of chlorophyll since the sprouts come up from the ground with the characteristic pale green coloring. Unfortunately the amounts of seeds used (only 3 in each experiment and in each control) was not significant. The question of stimulation by exposure to X-rays consequently remained unsettled as a result of insufficient evidence. However, by comparison with previous experiments, this is a step forward since the authors noted the amperage and the distance from the source of radiation.

In 1904, Perthes studied the effects of X-rays on the seeds of Vicia faba which have since become the favorite subject for experiments with radiation. By measuring the length of roots in exposed and control plants this author established the retardation of growth in irradiated plants. In this way his experiments demonstrated the depressing (inhibitive) action of

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X-rays. As a counterpoise to this, the experiments of Evller in 1906 showed that the irradiated seeds of beans, radishes, lettuce, squash, and cucumbers exhibited a greater energy in sprouting, a more powerful development, and earlier bloom than the control plants.

In his first comprehensive experiments in 1904-1905, Koernicke used the seeds of Vicia faba, Vicia sativa, and Brassica napus in large numbers. His experiments were distinguished by being more thoroughly set up and controlled than those of his predecessors. In the first place, he investigated the effects of radiation on seeds in various states: dry, turgid, and sprouting. Secondly, the X-rays were used in definite, and ever increasing, dosages expressed in Holtzknecht units (H), in the following quantities: 16, 20, and 26 Holtzknecht units. With small dosages Koernicke observed temporary arrest of growth; with more powerful doses, total cessation of growth. In the following experiments a dosage of 20 Holtzknecht units produced a small acceleration in Vicia faba and a significant one in Brassia napus, The difference between the irradiated plants and the control was striking; from 100 irradiated seeds of Brassica napus 50 sprouted; from the same number of control seeds, only one. In due time, however, the differences between the irradiated and control plants disappeared entirely.

In 1907 Guilleminot used for his experiments seeds of the gillyflower (Mathiola) in batches of 20. Sixteen batches were subjected to proportionately increasing dosages of X-rays from 10 to 20,000 roentgen units. Sixteen other batches re-

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ceived various exposures to radium and four were retained for control. Two control batches were left under normal conditions, one at maximum dryness, and the last batch under enforced humidity. From his experiments he concluded that retardation of growth is characteristic for irradiated plants, provided the dosage is sufficiently great. Acceleration of growth was observed when the plants were exposed to dosages between 5000 and 7000 roentgen units, but the results were too small to be significant.

By the time Schmidt set up his experiment in 1910 it had become customary to express dosages of radiation in HED (High-Erythema-Dose). This investigator exposed peas, which had previously been soaked in water for 6 hours, to various doses of X-rays (1/20, 1/10, 1/4, 1/2, and 1 High Erythema Doses). The plants raised from the irradiated plants possessed unusual size (45 to 50 centimeters), their leaves and pods were twice the size of normal (unirradiated) plants, and contained from four to five peas per pod, while normal plants contained only two or three. The experiments of this investigator brought him to the following conclusion: "It appears to me most probable that this fact should have practical significance for horticulture and fructiculture." Thus his experiments brought him to confirm the existence of irritating doses while the experiments of Wetterer, in 1911, brought the latter to diametrically opposite conclusions. A group of turgid seeds of sunflowers was divided into five equal parts. The first part was retained for control, the second received 5 H (5 Holtzknecht units), the third received 10 H, the fourth -- 20 H, and the fifth -- 40 H. Then the control and

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irradiated seeds were planted in a soil which had been enriched with nutritious substances. Observations revealed that seeds receiving doses of 5 and 10 Holtzknecht units came up simultaneously with the control seeds; those which received 20 units came up considerably later, and those which received 40 units never came up at all. Further observations of their development showed that while the control plants developed very fully the irradiated plants showed progressively poorer developments proportionately to the increase of their exposure to radiation.

The experiments of Promsy and Drevon in 1912 are interesting because the effect of temperature on sensitivity to X-rays was investigated, and also because the rays were used in fractional doses. Seeds of lentils, rye, beans, white lupine and kidney-beans were used. These experiments brought them to the following conclusions. Under normal conditions (15 degrees centigrade) the sprouting of seeds exposed to X-rays was sometimes accelerated and sometimes retarded. When the temperature was raised to 35-40 degrees (centigrade) the results became more exact. The doses of X-rays applied by the authors under the higher temperature invariably exerted a beneficial influence on the sprouting and development of the seeds.

In 1913, Schwarz used broad beans (Vicia faba) in his investigations. They were subjected to 30, 60, 90, and 150 second-exposures. The 150-second exposure produced the most favorable results; plants receiving this dose exhibited the tallest and most vigorous development. Irradiations of five minutes greatly retarded the growth of the plant, however this retardation did not show up immediately; such plants came up at the

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same time as the others, but eventually their growth stopped altogether, although the plants remained green for a long time. The author did not observe any sports or atypical development. In order to avoid any kind of discrepancies due to occurrence of unusually vigorous specimens, in his second experiment, Schwarz selected the most vigorous plants for his control, those next in vigor of development for the weakest dose, etc. Measurements of the plants three weeks after irradiation revealed that the length of the stems in the control plants was 25 centimeters, a 60-second exposure to X-rays gave 40 centimeters, a 90-second exposure produced 42.5-centimeter stems, and greater dosages produced 37-centimeter stems. Thus Schwarz's experiments produced a typical graph curve for growth due to stimulation.

In the experiments of Miège and Coupé in 1914 a clearly defined stimulating action of X-rays showed up in work with Raphanus and Lepidium. The irradiated plants exhibited a more vigorous development by comparison with the controls. This showed up in a 45% increase in the weight of the leaves, and a 59% increase in the total weight of the green part of the plants.

In the same year Koernicke once more took up his experiments and from 1914 to 1920 he produced several works in which he pointed out that during the 10-year period since the performance of his first experiments, a series of authors demonstrated the stimulating action of X-rays. For this reason Koernicke once more set up experiments with the seeds of Vicia faba, Phaseolus multiflora, Phaseolus vulgaris, Lupinus albus, Sinapis

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arvensis, Papaver somniferum, Zea Mays, Triticum vulgare, Avena savita, and Brassica. He deliberately selected plants whose seeds showed morphological and physiological differences. For each experiment he used from 220-300 plants, employing, as formerly, various doses of rays. In summarizing his observations he gives us a brilliant example of the Arndt-Schultze law. Turgid seeds behaved in the same manner: those which had begun to sprout accelerate their development under mild exposure, and show retardation with strong exposures. Besides, having on hand data from experiments with seeds of various species, it was possible for him to establish the variable sensitivity of plants to X-rays. It turned out that the most sensitive (to X-rays) were the broad beans (vicia faba).

In 1917 Yamada soaked grains of rice in salt water for seven days before irradiation with doses of 3, 5, 7, and 10 Holtzknecht units, after which he soaked them again and only after that planted them in soil. He did not observe any acceleration of sprouting and the size of the irradiated plants was, at first, smaller than the controls. Eventually, however, the plants which had received a dose of 3 Holtzknecht units showed the finest development; they had a greater number of stems per bush and their yield exceeded the controls by 40%. Doses of 7 and 10 Holtzknecht units lowered the yield by 2.4 and 5.4%, which the author ascribed to injury of the plants by insects and fungi.

In 1918 Nakamura gave a brief description of his experiments with Oryza sativa ("Sinriki"), the seeds of which were subjected to 5, 10, and 15 minute exposures, after a brief soak-

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ing in water. He points out that plants which had been irradiated for five minutes showed an increase in yield.

Komuro, in 1919, also established that irradiated seeds of Oryza sativa ("Sekiyama") show accelerated germination and that seeds in an air-dry state were less affected by X-rays than plants which had been soaked for 12 hours. Optimum doses were 5 to 10 Holtzknecht units.

During a five-year period, from 1917 to 1921, Komuro set up experiments with irradiation of seeds and sprouts of rice.

On the basis of these experiments Komuro came to the following conclusions: 1. X-rays exert a harmful effect on seeds proportionately to the water content of the seeds. 2. The seeds of some plants accelerate their development; seeds of other plants retard theirs. 3. Moderate dosages act as positive stimuli on the seeds. 4. Young plants exhibit a variable sensitivity to X-rays.

In 1920 Jungling irradiated sprouts of Vicia faba and then placed them in special boxes with glass sides. The length of the roots was noted on the walls every 24 hours. The reaction to X-rays was judged according to the growth (in length) of the roots and the appearance of side branches. Jungling observed various injuries depending on the size of the dose. The cessation of growth, in length, and cessation of appearance of new side roots he considered as a maximum injury. The dose capable of producing this he called a "full dose" ("Volldosis"). With a smaller dose slow growth would continue for two more days after

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which the rate of growth would accelerate and side branches would begin to appear. This was the "medium dose" ("Mittel-dosis"). Reversing the process he judged doses on the basis of length of time it took for side branches (roots) to appear. If the side roots appear two days later than the control plants, it means that 35% of "full dose" was given. A delay of one day indicates 25% of a "full dose". However, if 10% of a "full dose" was applied, the appearance of the side roots was accelerated (see Chapter 4). These observations indicate that Jungling was seeking a biological dose meter by his experiments.

In 1922, three other authors, Schwarz, Czepa, and Schindler, were more categorical in their denial of the stimulating action of X-rays. Having set up experiments with 12 different species of plants (wheat, barley, oats, peas, beans, broad beans, mustard, lettuce, Onobrychis and three field grasses), they did not succeed in establishing irritating doses. They believed that the major error of the majority of X-ray biologists lay in the fact that they used insufficient numbers of samples in their experiments, which made it impossible for them to do away with individual differences. However, they were able to confirm the depressing effect of large doses of radiation on plant growth.

In 1922, Sierp and Robberts attempted to introduce a new factor into X-ray research by examining the growth of separate organs and in that manner were able to analyze their action in detail. They used sprouts of Avena sativa, whose coleoptyles are extremely sensitive. These experiments indicated how correct

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they were in considering detailed examinations imperative. For example, the sheathing of sprouts of graminae turned out to be extremely sensitive, but it is difficult to detect, if only the overall growth is observed; but it shows up clearly if separated stages of development are followed through. After a certain acceleration of growth the authors observed its retardation which became more pronounced as the lengths of exposure were increased.

In 1922, Lalleman limited her observations to the biological effects of X-rays on the first stages of development of the seeds of Panicum miliaceum, Lepidium sativum, Brassica napus, Triticum sativum, Lens esculata, Phaseolus vulgaris and onion bulbs. The growth of plants was measured on the 14th day after irradiation. This time was selected on the basis of the following considerations: in the first place, the injurious effects of X-rays on plants do not become immediately apparent, they become more pronounced with passage of time after exposure; and secondly, plants cannot be cultivated on water indefinitely without affecting plant development. Roots, stems, side roots, leaves, and hypocotyls were subjected to measurement.

Lalleman divided her investigations into two parts: one group of plants were subjected to weak doses of X-rays, and others, to medium and strong ones. Seeds of the first group included: Phaseolus vulgaris, Lepidium savitum, Brassica napus, Panicum miliaceum, and Lens esculenta. The seeds designated for the experiment were divided into 16 samples. 8 served as control and 8 others were irradiated by X-rays in, 1/12, 1/4, 1/3, 1/2,

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5, 10, and 20 Holtzknecht units, which, with the apparatus she was using, corresponded to 5, 15, and 30 seconds and 1, 3, 5, 10, and 20 minutes. The number of seeds varied depending on the species of plant being irradiated. After irradiation the plants were placed between two layers of cotton in Petri dishes, and at given intervals the sprouting seeds were counted. These experiments showed that the most diverse doses of X-rays failed to have a baleful influence on either dry or soaked seeds. In order to test the effect of X-rays on rate of growth, experiments were set up with seeds of lentils, wheat, and dried kidney beans. From these experiments the author concluded that the weakest doses of X-rays do not stimulate plant growth. In relation to the second part of the experiment, i. e., the action of medium and strong doses of X-rays, Lalleman set out to clarify two questions: (1) do very strong doses of X-rays destroy the ability of seeds to germinate and (2) do medium doses delay the time of appearance of sprouts. Experiments were set up with various types of beans and lentils. In her experiments the author did not succeed in establishing the inhibition or retardation of sprouting. In exposing 1000 germinated lentil seeds to various doses of X-rays and then measuring the lengths of stems, roots, and side roots it turned out that decrease in size is directly proportional to increase of dosage received by the seeds.

The experiments of Altmann, Rochlin, and Gleichgewicht were set up with unusual thoroughness for their time (1923). In the first place they used seeds of a pure strain of Vicia faba from a single crop and of identical weight (which was determined

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on torsion scales). In addition they triple-checked their experiments and irradiated seeds in various states (dry, soaked, and germinating). The sprouting and development of young plants were most carefully and minutely observed: the appearance of side roots and first leaflets was noted; the length of roots, stems, and size of leaves were measured. These observations brought the authors to the following conclusions: (1) by gradually increasing dosages it is possible to obtain a transient acceleration of development, which carries within itself the seeds of a depression of development, which depression is inversely proportional to the brevity of the acceleration; (2) the "irritating dose" changes depending on the stage of development (for dry beans it was between 6 and 12 Holtzknecht units, for germinating ones, between 1 and 3 Holtzknecht units).

Investigating the problem of the accelerating and retarding effect of X-rays on the development of plants, Czepa, in 1924, irradiated seeds of Vicia faba, Vicia savita, Phaseolus vulgaris, and lettuce with various doses of rays, ranging from 1/2 to 25 Holtzknecht units. Only in one experiment did he observe acceleration of growth in the plants used by him. In all the others he noted neither acceleration nor retardation of development; consequently, he assumed that the one exception was due to chance and didn't attach any significance to it. In further experiments in which Czepa used stronger dosages (150 and 300 Holtzknecht units) the energy of the sprouting of seeds didn't diminish at all, while plants which had received 150 Holtzknecht units actually exceeded the controls. Czepa did not continue or intensify his investigations, although his results show

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that stimulating doses reside somewhere between 25 and 150 Holtzknecht unit doses of the rays. On the contrary, as a result of his experiments he came to the conclusion that stimulating doses do not exist for Vicia faba, Vicia sativa, Phaseolus vulgaris, and lettuce.

Martius, in 1924, also failed to find a stimulating dose in his experiments in which he was trying to ascertain the dependence of the action of the rays on their intensity. Using filtered rays of high intensity (130 kilovolts, 4 milliamperes) he observed, that radiations of only 1.9 seconds with a focal distance of 10 centimeters were sufficient in order to halt development.

In 1924, Geller posed the question of the constancy of the effect of X-rays on young plants, at a definite dosage, and came up with negative conclusions. Comparing the data of previous investigators he formulated the following conclusions: (1) X-rays either depress or accelerate plant development; (2) their action depends: (a) on the dose, (b) on the species and X-ray sensitivity, (c) on its internal and external states (plants in normal growth are more sensitive than slowly growing ones or quiescent seeds; and the more favorable the external environment the greater will be the effect of the rays), (d) on the place or area which is being irradiated; (3) since the action depends on various factors, absolute doses for either depression or acceleration of the rates of growth do not exist, there are only relative doses; (4) the author believes that the permanence of effect is very limited; (5) the initial ac-

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celeration of development is sometimes followed by depression; (6) with moderately large doses (those which retard development but which do not kill the plant) microscopic examination does not reveal any particularly obvious injuries of the cells but only retardation of action, and when the doses are small, acceleration of action.

In 1925, Gambarov, who tried to hedge his experiments with the most thorough precautions, also came to the conclusion that irritating doses do not exist. From a huge number of seeds of Vicia faba equina he selected several hundred which were identical in weight and outward appearance. After soaking the seeds for 36 hours in water he transferred them to a specially constructed box with sawdust. The bottom and two narrow sides of this box were made from zinc, while the wide sides were of glass. The length of the roots of the irradiated and the control plants was measured through the glass with a millimeter rule for 12 days. In addition the appearance of side roots was noted. Despite the fact that Gambarov used the so-called "irritating" doses, i. e., 1, 2, 3, 4, 5, and 10 HED (High-Erythema-Dose), not only did he fail to observe acceleration of growth, but he actually obtained the contrary effect due to the fact that the development of the plants was retarded by these dosages.

In 1925 Iven's detailed and reliable book on the action of X-rays was published. In it he presents the results of his experiments with seeds of Vicia faba in dry and turgid conditions. The irradiation was conducted with ever increasing dosages of

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X-rays expressed in HED (High-Erythema-Dose), ranging as follows: 1/250, 1/100, 1/10, 1.5, 10, 18, and 22. When doses of 1/250 to 1/2 HED (High-Erythema-Dose) were used on dry seeds, acceleration of germination was noted. On a graph curve, it was possible to observe first a gentle and then a sharp rise (from 1/20 to 1/2 High Erythema Doses). Beginning with 1/2 High Erythema Dose the graph curve begins to decline. Consequently, Iven's experiments confirm that the irritating effect of X-rays on the first stages of plant development follows the Arndt-Schutze law. Ten or twenty days later, however, depending on the intensity of growth and external conditions, the difference between the irradiated plants and controls tends to disappear. On the other hand, those plants which exhibited a retardation of growth, due to action of larger doses of rays, were unable in the course of their development to catch up with the controls: the retarding effect of rays is retained.

When Iven used turgid seeds, the maximum rise of the graph curve occurred at 1/100 HED (High-Erythema-Dose). By these parallel experiments with dry and turgid seeds Iven demonstrated the significance of the condition of the plant on its sensitivity to X-rays.

As for the action of X-rays on developmental processes, it became apparent (in Iven's experiments) after a definite interval of time. Differences between the irradiated and control plants showed up in the growth of stems and in the time of appearance of the first leaf. With stimulating doses the first leaf appeared earlier than in controls, while larger doses re-

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tarded the appearance of leaves. What is most interesting is that the retardation was proportional to the dosages. Finally, when dry seeds received doses of 22 HED (High-Erythema-Dose), no leaves appeared at all, stems and roots were shorter, and the latter showed black pigmentation. In addition they lacked side roots. When Iven exposed turgid seeds to X-rays all of these phenomena appeared with smaller doses than were required for dry seeds.

Between 1924 and 1926 Ancel published a series of works in which she attempted to clarify the question of the existence of irritating doses of X-rays for certain plants of the bean family, especially Phaseolus and Lens esculenta. In the first experiment (in 1924) the differences in the energy of germination among individual seeds (both control and irradiated ones) were so great that the author refused to ascribe any effect to the X-rays. Besides, Ancel repeated the experiments of Maldiney and Thouvenin with the seeds that they had used (Convolvulus and Lepidum) and likewise obtained negative results. In the next experiment (1925-a) she demonstrated the importance of the role played by temperature at which the plants develop after being irradiated. A lower temperature (10-14 degrees -- centigrade, of course) increases the injuries due to strong doses of X-rays; a higher temperature (20-25 degrees) lowers them. In her third work (1925-b) she raised the question of the significance of the time interval from the moment of exposure to the moment of the appearance of injuries due to X-rays. All of the experiments performed by her indicate that the intensity of injuries due to X-rays are functions of the time from the moment

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of irradiation: the longer the time interval, the more pronounced is the appearance of injury. In her fourth work (1926) Ancel examined in detail the effects of irradiation on separate parts of plants (in this case of lentils and beans). In one of the numerous (but identical as far as results were concerned) experiments dry lentil seeds were exposed to doses of 40, 70, 100, and 150 Holtzknecht units. In the measurement of individual parts of the plants, on the 14th day after irradiation, it became apparent that injuries due to X-rays were not identical for various parts of the plants. On the basis of this data we have set up the following table in order to facilitate comparison.

Table 1

(based on Ancel's data, 1927)

Dosages in Holtzknecht units	Percentages of Injuries		
	Main root	Stem	Side roots
40	15.79	9.10	23.8
70	31.71	21.95	31.57
100	37.24	32.81	65.94
150	69.14	56.21	83.69

This table indicates that side roots are most susceptible to injury, then comes the main root, and, finally, the stem. Similar results were obtained in studying the percentages of injuries in beans. Finally, in experiments devoted to determination of irritating doses of X-rays for dormant buds of lentils (1926), the author argues against the experiments of Weber, who had established the stimulation (by irradiation) of such

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buds in lilacs. She subjected 16 sprouts of lentils (whose stems ranged from 8-10 centimeters and whose roots were protected by plates of leaded rubber) to doses of 8 Holtzknecht units. On the fifth day after irradiation two dormant buds (located on the sides of the main stem) began to develop. On the tenth day after irradiation the stems had reached the length of 46 millimeters, and the buds supplied additional stems with an average length of 16 millimeters; while on the control plants the buds showed no development whatsoever. This experiment provided the basis for believing that stimulating doses of X-rays exist. However, if the stem is cut off, after it reaches 100 millimeters in height, the buds will produce additional shoots. This fact caused Ancel to believe that in the X-ray experiment it was the injury of the stem by the rays, and not the effect of irradiation, which caused the buds to grow. In order to find out if injury of the stem by X-rays will produce the same effect as cutting, she irradiated the stem with doses of 20 and 40 Holtzknecht units; the dormant buds began to develop as they had after the stem was removed. In other experiments when the whole plant (except for the roots) was subjected to radiation, the stem ceased to develop, but the buds remained dormant: apparently the dose was so great that it injured the buds as well. From her experiments Ancel comes to the conclusion that the development of buds in her experiments with X-rays is due to the phenomenon of compensation resulting from injury to the stem, and not from the stimulating action of X-rays on the buds.

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In 1925 A. V. and L. I. Kol'tsov set up experiments with irradiation of pea and wheat seeds. They exposed dry and sprouted seeds of Triticum vulgare lutescens to various doses of X-rays, but they did not note differences in the onset of various phases. In individual cases an increase of total weight was observed in irradiated plants, but it was not possible to arrive at any kind of definite conclusions. Experiments with peas gave more definite results as far as acceleration of development was concerned. For example, the plants bloomed 3-4 days earlier than the controls. However, the total weights varied to such an extent in their experiments that the authors were unable to establish any rule to which irradiated peas conformed.

In 1926 Bersa attempted to approach the work of previous investigators critically. For example, he considered that the work of Schwarz, Czepa, and Schindler (mentioned previously) suffered from many shortcomings, but that their merit lies in the fact that they were the first to point out the many sources of errors due to the inconstancy of vegetative (plant) objects. By his investigations Bersa was trying to show how careful one has to be in the interpretation of the results of experiments. The first condition to be observed is to have a sufficiently large number of test-objects. In sprouts of Vicia faba the author measured the lengths of the stems, from the ring where the root begins to the apex of growth and the length of the root from the ring to the tip. With doses of 0.05 Holtzknecht units an increase in length of the root of 26 percent was observed, but the author did not attach any significance to this since only 10

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roots were examined. The measurement of control and irradiated roots of Sinapis alba did not reveal any significant differences, while a measurement of their hypocotyls showed an incontestable acceleration. The following experiments gave less significant or negative results. For instance, although an acceleration of the growth of hypocotyls takes place, this growth depends not on cell division but on expansion of the cells, i. e., the cells of the hypocotyl enlarge greatly as an aftermath of taking water. In general the cells of the hypocotyl are less sensitive than the cells of the root. If the root is seriously injured the stoppage of access of water affects the hypocotyl. Weak irradiations, however, do not affect the water supply of the stem; substances from the stem reach the abnormally slowly growing root; this results in the overfeeding of the hypocotyl, which accelerates its rate of growth at the expense of the root. Consequently, the irradiation of sprouts by weak doses does not always result in an acceleration of growth, but it is always indicative of the disruption of the balance between the shoot and the root. On the basis of the fact that even in medical and zoological experiments flawless results do not exist, Bersa concludes that X-rays are not capable of producing real irritating effects.

Beginning in 1928 Johnson began publishing a series of works dealing with the irradiation of plants, but since her investigations are being continued up to the present, we feel that it would be more appropriate to describe them later.

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In 1929 Doroshenko set up experiments with three plants (Avena byzantina, millet, and winter rye). The conditions of irradiation were identical in all experiments, only the length of exposures were varied (5, 10, and 20 minutes). The effects of irradiation became apparent in Avena byzantina from the first stages of development, especially with the 20-minute exposure. When the plants which had received this dose had already given complete shoots, the controls showed only individual sprouts. In the course of its development the stimulating effects became more pronounced; tufts appeared two days earlier than in the controls, stems elongated four days earlier, ears were formed two weeks earlier, and since the planting took place very late in the season, the control plants never blossomed. The irradiated plants, on the other hand, which had gotten ahead of the controls, bloomed lustily. Doroshenko's experiments demonstrated the stimulating effect (of radiation) on the development of the reproductive as well as on the vegetative organs of the plants. However, when Doroshenko attempted to increase the exposures (to 20, 30, and 40 minutes), she found that exposures of 40 minutes fall beyond the optimum, although still within the threshold of physiological stimulation. Still greater exposures (1 hour, 1 hour and 15 minutes, and 1 hour and 20 minutes), however, already had a depressing (retarding) effect. The application of a second exposure showed that it had a stronger stimulating effect on development than single doses. All of these favorable data apply to Avena byzantina. As for Toulouse millet, the author did not succeed in finding a stimulating dose for it. The same was true for flax (of both the curly and the long-fiber

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varieties). On the other hand, winter rye, as a result of irradiation, not only developed vigorously but changed its form as well.

The first experiments on irradiation of potato tubers were performed by Sprague and Lenz in 1929. For their experiments they selected the tubers of two family varieties: "Irish Cobbler" and "Green Mountain". Half of the tubers were irradiated; the other half were left for control. The tubers were subjected to radiation just after sprouts began to appear on them. One part (experiment 1) of them was subjected to doses of 2 HED (High-Erythema-Dose); the other part (experiment 2) was subjected to 1 HED. The first leaves in experiment 1 had an abnormal appearance; eventually, however, only normal leaves developed, and they remained green for several days longer than those of the control plants. As for the yield of the potatoes in number of tubers, it was 84.4 percent of the controls for experiment 1, and 104.7 percent for experiment 2. But in both irradiated groups, the weight of the average tuber was above average (of the control). So we can see that even heavy irradiation, which injured the leaves and decreased the number of tubers did not diminish the total crop.

Patten and Wigoder in their experiments in 1929 once more returned to the classical objects of roentgenology: the seeds of beans, mustard, and barley. In their opinion the effects of X-rays on growth and development may be studied most easily on plants where cell division takes place so quickly that the progress of sprouts may be observed daily. Giving the seeds

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a dose of 3 HED (High-Erythema-Dose) they observed various reactions which were dependent on the species of plants (since other factors were constant). The most sensitive, in their experiments, were the seeds of large beans, especially if they were irradiated from 48 to 72 hours after growth had begun. In mustard sprouts the smallest doses (about 1/20 High-Erythema-Dose) caused the most rapid growth, while irradiated barley lagged behind the controls.

The value of Chekhov's contribution (1930-1931) lies in the fact that in radiating seeds of dry and sprouting plants of various sorts (barley, rye, lentils, and oats) he paid particular care to the condition of the plants at the moment of irradiation, a condition which varies with different times of the year, and even of the month. He demonstrated that weak doses of rays had a stimulating effect on both germination and on further development. In experiments with dry seeds when strong doses were used, which have a depressing effect, the graph curve of their growth does not fall evenly; these doses do not depress germination and the force of sprouting, but after sprouting a certain percentage of the developing plants dies. As doses are increased, the number of plants which die increases also and the time of onset of death becomes shortened. Very strong doses have the effect that only 1/10 as many irradiated plants come up as (compared to) control plants.

In 1931 Cattel demonstrated that the growing parts of wheat sprouts are relatively sensitive to X-rays. His experiments are remarkable for the fact that he performed them on 200,000 samples and kept repeating them for a period of three years. Dry

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seeds were thoroughly washed in distilled water, then they were soaked in it for 3½ hours and placed in humid chambers; the chambers were then placed in thermostats at a temperature of 26 degrees (centigrade). After 24 hours the coleoptyle, leaf, and two side roots were 2 millimeters long, the primary root was 5 millimeters in length. At this time sprouts were selected for irradiation (they had to be of equal size and completely healthy). After irradiation the sprouts were once more placed in humid chambers which were placed in thermostats for 48 hours, after which the sprouts of both the control and irradiated plants were measured. These measurements showed that each of the four growing parts (coleoptyle, leaflets, side, and primary roots) was affected to a different degree. These changes could be observed after only a few hours. Equal doses of radiation produced equal changes. Sprouts which had received large doses showed various irregularities in their development; roots thickened, thickenings appeared in cells, etc.

In 1933 Chull and Mitchel set up their experiments with extreme care both biologically and physically. As far as the physical aspect of the experiment is concerned, the authors subjected seeds to irradiations which were both quantitatively and qualitatively identical (100 kilovolts, 5 milliamperes, at a distance of 30 centimeters). They used an aluminum filter 1 millimeter thick. As for the biological aspect of the experiment, the authors used for their experiments seeds of corn, oats, and sunflowers, placed them in humidifying chambers on a layer of cotton, soaked in distilled water, and kept it at 22 degrees (centigrade). After 24 hours the seeds of all three plants began

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to sprout. Twenty seeds (and sometimes more) were selected from the mass, whenever possible on an identical level of development and were divided into two parts. One part was retained for control and the other was placed on fresh damp cotton and irradiated. The optimum irradiation for sunflowers turned out to be 3 minutes (i. e., 144 roentgen units); for corn and certain varieties of wheat, the optimum dose was 2 minutes. For other varieties (of wheat) exposures of 30, 45, or 60 seconds were sufficient. As soon as the irradiations were concluded, the plants (and controls) were planted in soil, sand, or on cotton in the humidifying chamber. Experiments demonstrated that a variety of hard wheat ("Minhardi") was less sensitive to X-rays than "Trumball" which in turn was less sensitive than a variety known as "Marquis" (Markiz). From this the authors concluded that just as there exist varieties which are more resistant to cold, so there are those which are more resistant to radiation. The most interesting data were obtained with corn, a variety called "Madison Jellow Dent" [translator's note: "Madison Yellow Tooth" -- ?]. Turgid kernels of corn were divided into three parts; the first was irradiated with an aluminum filter, the second without one, and the third part was used as a control. Determinations of raw and dry weight of the coleoptyles showed that irradiated seeds are from 5 to 26 percent heavier in the raw and from 3 to 16 percent heavier in a desiccated condition. It is possible to ascribe this increase in the weight of the coleoptyles to a faster utilization of the endosperm reserves of the irradiated cells. Several weeks after irradiation plants, which had received 1-3 minute doses, had thicker stems

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than the controls or those which had received 5-minute doses. The weight of the green part of the plant was greater in the irradiated plants.

Oats (when irradiated) grew to above average height. A comparison of controls and irradiated seeds of sunflowers gave a good graph curve for their development. A group of plants which had been irradiated for three minutes was the first to blossom. These experiments indicate that when experiments are carefully set up, and the proper dosages are used [redacted] favorable results can be obtained. Unfortunately, the authors did not follow through their experiments until the crops could be harvested and, unfortunately, they did not repeat their experiments even one more time.

The experiments of Benedict and Karsten are interesting because they used in their experiments rays which were practically monochromatic. They placed grains of wheat in special dishes [containers] in such a manner that all of the buds pointed in the direction of the (X-ray) tube, at a distance of 1 centimeter from the aperture, in such a manner that it was possible to insert a lead screen (filter) between the seeds and the aperture. After irradiation the seeds were treated with fungicide and allowed to sprout; then their diastatic activity, their (reduced) sugar content, their respiration, and their water contents were determined. Sprouts, which had been exposed to radiation for 5 seconds, showed an increase in their diastatic activity and their sugar content. If the dosage was increased, however, it was possible to observe a decrease in one or the other

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of these elements. The amount of substance used for respiration did not increase by comparison with the controls, but neither did it diminish with large doses of radiation. These results indicate that under the conditions of this experiment irradiated seeds cannot convert their reserve starches into sugars as easily as normal cells, and also they cannot use their sugar for growth as rapidly as the control cells.

The effects of radiation on seeds of citrus fruit were observed by Haskins and Moore in 1935. They observed a curious phenomenon of premature flowering of two grapefruit plants grown from seeds which had been exposed to doses of 300 and 1300 roentgen units. One of the plants was an albino and, consequently, was non-viable; the other developed more or less normally, despite its dwarf size, and after a few months exhibited a second blossoming.

The experiments of Long and Karsten, in 1936, were set up with soya under field conditions. The irradiated and control seeds produced, all told, 12,751 plants. When the first beans were formed, the plants were cut off, at ground level, and weighed. The weight of the green part of the plant was greater in the irradiated plants. Since the experiment was conducted with large numbers which had been allowed to grow under normal conditions, and since the average increase of weight of the irradiated plants, as compared with controls, exceeded the standard deviations three times over, the authors came to the conclusion that this indicates a true stimulating action of the rays, although this should not be taken as absolute proof of it.

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In 1935 Frolov used for his investigations three plants, namely, soy, wheat, and flax, which had been used for radiation experiments by many other authors. The irradiation of wheat grains not only accelerated development, but resulted in a 60 percent increase in yield as compared with controls. The experiments in 1936 gave somewhat lower results. X-rays have a stimulating effect on flax only in the first stages of development; after that a depressing effect sets in. The irradiation of soya seeds produced negative results, in contradiction to the experiments of Long and Karsten.

In 1934 Tushnyakova and Vasilevskiy set up experiments with sedge (Cyperus esculentus), soya, blue lupine, tomatoes, and melons. The sedge was treated with X-rays for the purpose of shortening its growing season and causing it to multiply vegitatively. The tubers were irradiated in dry and soaked conditions for 5, 10, 15, and 20 minute periods. At first the irradiated tubers lagged behind in their development, but eventually those which had received 15-minute irradiations moved ahead. Two months after exposure the difference between the controls and the irradiated plants was striking. The authors pointed out the differences produced by irradiation which were due to the condition of the materials and the experiment. In 1933, 1934, and 1935 experiments were conducted in the field, and although there was no difference in the time of development, the plants which had been irradiated for 35 minutes stood out sharply because of their height and vigor of development. They had a high productivity and a shorter growing season.

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In experiments with soya a shortening of the period of ripening (in comparison with controls) was observed. The same thing was observed with blue lupine where the irradiated plants ripened 12 days earlier than the controls. The experiment with melons was not concluded, but it showed that plants which had received 200 roentgen units ripened earlier than the controls. Irradiated Mexican tomatoes ripened more intensively than the controls and the number of fruit and their weight was greater.

The experiments of these authors should be considered as preliminary, despite the fact that the experiments with sedge were repeated over a period of several years. The small number of samples used in these experiments and the lack of concentration (i. e., the data were scattered too widely) of the data prevent us from considering these experiments completely conclusive.

In 1935 Tsuryupa irradiated seeds of hard wheat Triticum durum variety melanopus, and also those of oats and cotton. After irradiation the seeds were planted in growing dishes and their development was minutely observed. The discrepancy between the development of the vegetative part of the plants and their productivity in Tsuryupa's experiments indicates how different the effects of X-rays can be in their application to different plants. In experiments with wheat it was observed that X-rays have a greater effect on the development of the reproductive organs than on vegetative ones. On the other hand when oats were used, the effects were just the opposite. Although X-rays do not increase the germination of

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wheat, they increase their sprouting power. As far as yield is concerned, positive effects were obtained in some cases, exceeding the controls by 60 percent. In addition, the growing season was shortened so that the irradiated plants ripened ten days earlier. In the case of flax the author observed the activization of the initial stages of development, which were followed by depression, while irradiation of soya seeds caused development to be retarded from the very beginning.

A whole series of works were performed by Johnson (1926, 1928, two in 1931, 1933, and two in 1936). In fact, her investigations are being carried on right up to the present. The wide variety of objects, the thoroughness of details, and the multiplicity of aspects which this author investigated place her in the first ranks of roentgen-biologists. In her very first work, devoted to research on sunflowers (1926 and 1928), she compared the effects of doses from 5 to 10 HED (High-Erythema-Dose) on dry and soaked seeds. She studied the relationship between amounts of exposure and growth; she investigated the effects produced by radiation on catalysis, oxidation, and on respiration. Not satisfied with these physiological investigations, she turned her attention to phenological observations, which gave most significant results with doses of 10 HED (High-Erythema-Dose). Her experiments showed that germination of seeds is not accelerated by irradiation, while sprouting is slightly retarded. Soaked seeds which were irradiated with medium doses came to a complete halt in their development in the first three weeks; after that, there was a temporary acceleration. The depression of growth during the first

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three weeks (as a result of irradiation) is approximately proportional to the dosages. Plants which had been soaked previous to irradiation did not attain the size of the control plants, but they bloomed earlier. In her next work (1931) the author presents the results obtained from irradiation of two thistles, several Solanaceae and Vicia faba. In order to give stimulation a chance to show its effects, Johnson permitted her plants to grow for 25 days (since previous experiments demonstrated that the effects of radiation tend to vanish three weeks after irradiation unless a second dose is administered). Comparative examination of fresh and dried weights of the irradiated and control plants revealed that only one plant, "sunberry", had increased its weight due to stimulation with weak doses of X-ray. Since one weak dose, in Johnson's experiments, did not produce stimulation, she gave a second dose after a certain interval. It is interesting that in these experiments Johnson used the same dose for Vicia faba as Patten and Wigoder, who pointed to the increase in size of the plant as a result of irradiation. Despite the fact that identical conditions were maintained for irradiation (seeds were used after being allowed to germinate for 40 hours in water), Johnson failed to observe any stimulation in the roots or tubers. In irradiation of tulip bulbs it was observed that the length of leaves was increased, but the formation of flowers was unaffected. In this work the author presents her observations concerning the increase of growth of plants by irradiation of bulbs and tubers of certain plants. She points out that when these experiments were set up under, more or less, working conditions, [redacted] they did not ex-

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hibit the effects of stimulation. The irradiation of wild potatoes from Colorado gave favorable results in the preliminary experiments. However, this experiment was given up when the author discovered that upon repetition with a large number of samples, this reaction could not be obtained.

Finally, Johnson wrote a large article in Duggar's book ("The Biological Effect of Radiation") in which she summarizes the results obtained by her, and others, and comes to the conclusion that strong and medium doses of rays have a harmful effect on the development of plants. As for weak doses, she considers that in those cases when they produced results, the authors did not give sufficient consideration to the individual variability of plants.

In 1937, Zankevich and Brunst were studying the effects of X-radiation on individual developments of tobacco (Nicotiana rustica), poppies, flax, and rhubarb. Increasing doses of radiation were used (250, 500, 750, 1500, 3000, 6000, and 10,000 roentgen units). Doses of 500 and 750 roentgen units had a stimulating effect on tobacco and flax. In tobacco the increase in size was of transitory nature, but in flax a certain amount of stimulation was retained until the end of the growing season. Medium doses of rays resulted in a retardation of growth, which was (in degree) directly proportional to the dosage. Large doses had a lethal effect. The authors make an interesting observation to the effect that the "latent period" of plants is of different duration: in poppies and flax it lasts 7 to 10 days, while in tobacco and rhubarb it is of short duration or entirely absent.

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Zaurov in 1927 [sic, 1937-?] used various doses of X-rays on the seeds of Indian hemp. He observed an insignificant increase in the length of stems with a dose of 500 roentgen units in the first measurement (experiment) and a similar increase with a dose of 2000 roentgen units in a second experiment. Depression set in starting with doses of 4000 roentgen units. Small doses of X-rays (125-1000 roentgen units) produce an increase in bushiness; larger doses depress bushiness.

In 1938 Breslavets and Sinitskaya, who were interested in changing of forms of decorative plants, set out to study the effects of X-rays on these plants. They irradiated dry seeds, despite indications from literature that irradiation of sprouting seeds is more effective. This was done for a definite purpose: "If the effect of some dose of X-rays on dry seeds were to result in the change of shape or coloring of the leaves, or of the flowers, or of both, it would then be possible to send the dry irradiated seeds to various horticultural state farms (sovkhoz), and to amateurs, while sprouted seeds could only be used by us." Summarizing the results of action of X-rays on five kinds of decorative plants the authors come to the conclusion that not in a single case was it possible to obtain the correct biological graph-curve for germination and sprouting-power of the plants. But it is interesting to note that the experiments brought out a variable sensitivity to X-rays of these plants. This result, however, should have been expected since the five plants belong to completely unrelated families. The most sensitive (to X-rays) turned out to be sweet pea, which could have been foreseen on the basis of available data, which

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point out that the bean group is particularly sensitive to X-rays. Asters also proved to be quite sensitive in this respect, while carnations and gillyflowers (stock) were so insensitive that doses of 8000 and 16,000 roentgen units have (within limits) a stimulating effect on them. Tobacco occupies an intermediate position as far as radiosensitivity is concerned.

If we carefully scrutinize the voluminous data obtained by the various authors in their experiments on the physiological action of the rays, we will see that they lead to completely diverse conclusions. Some authors indicate the existence of stimulating doses; others deny their existence. This would be understandable if it were a question of different varieties, since numerous investigators have established that plants are variable in their sensitivity to X-rays. However, contradictory results are reported even when the same species of plant is being investigated. As has already been pointed out, the seeds of Vicia faba are a favorite object in X-ray research. Let's take a look at how various authors evaluate the results of irradiation of this plant. Perthes found only a depressing effect, Koernicke observed a temporary cessation of growth, Schwarz obtained a typical biological curve of development, i. e., he found that weak doses of X-rays stimulate plant development, that stronger ones retard it, and that still stronger ones stop development altogether. In the experiments of Altmann, Rochlin, and Gleichgewicht a temporary acceleration of development was observed; this was followed by an developing-off to the rate characteristic of the controls. Gambarov failed to find the stimulating dose for Vicia faba equina, which had been established in Iven's experiments. And, finally,

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Johnson, repeating the experiments of Patten and Wigoder, was unable to confirm the stimulating effect of X-rays which Patten and Wigoder had observed, despite the most careful reproduction of their experiment.

Besides, as Rochlin and Gleichgewicht pointed out in 1925, Vicia faba is not an appropriate object for the study of the stimulating effects of X-rays because its threshold of stimulation is too low. It is so radiosensitive that the weakest doses of radiation cause a retardation of growth and thus complicate experiments.

Naturally the question comes up of why experiments dealing with the irradiation of one/ and the same/ plant produce such different results. This is not easy to answer. But if we carefully analyze all of the experiments we will see that in the main the discrepancies can be explained by an insufficiently accurate measurement of doses (this applies particularly to that period when doses were measured in erythemas). The sensitivity of people to X-rays varies considerably, and to equate an erythema dose to 600 roentgen units, as some authors do, is completely inaccurate. In general, it is only in the last few years that we have learned to measure X-ray dosages with any great degree of accuracy. Besides this chief shortcoming, we have to take others into consideration. In experiments with Vicia faba, which is the subject of investigations of many authors, it is amazing what small numbers of seeds were used for irradiation. The reason for this lies in the large size of the seeds, which constitutes a substantial barrier for performing the

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experiment within the restrictions imposed by the Coolidge tube, which has limited area of action. The desire for great accuracy forces the investigators to irradiate the seeds simultaneously with several dosages, removing from the field of action of the rays Petri dishes (which contain seeds) at various intervals of time, in order to secure the most uniform voltage and amperage. It is small wonder then that some authors limited their experiments to 5-10 seeds of this plant. Despite all attempts to match the seeds in size and weight, it was still necessary to take into consideration the individual variations, which could only have been overcome by using large numbers of plants. Consequently, the criticism of those authors (Schwarz, et. al.) who point out that individual variability of the seeds completely overshadows the effects of the rays, is entirely justifiable. Only experiments where the numbers of plants used is sufficiently great to permit biometric analysis, can establish whether changes in size and development result from irradiation. But it is most interesting to note that the very same authors (mentioned above) who categorized the experiments of their predecessors as inconclusive on the basis of insufficient numbers of test-objects, used only 20 seeds in their experiments.

A third source of errors in the experiments is found in the small variation of dosages. Most authors are content to vary the time of exposure or the distance from the tube, both of which are selected at random. It is very characteristic of authors of this type of experiment, who obtain changes from random doses of X-rays, to jump to conclusions concerning the existence or absence of stimulating doses.

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Experiments which undertake the investigation of the effects of X-rays on plants have still another shortcoming: most of them are incomplete. The majority of investigators either note only the first phases of development of the irradiated plants and compare them with the controls, or else cut them down as soon as the first fruit appears and judge the effect of X-rays on this or that plant on the basis of the weight of the fresh (green) or dried mass, ignoring the fact that Doroshenko (in 1929) and Tsuryupa (in 1934) accurately pointed out that X-rays can affect reproductive organs, as well as vegetative ones, and that their effect is even more pronounced on the former.

However, the most serious defect of experiments with irradiation of plants, as of all experiments with stimulation, is the preconceived notion in the mind of the investigator. If the latter, on the basis of theoretical considerations, refuses to acknowledge the action of this physical factor on the development of plants, then, upon getting positive results he ascribes them to chance. That is what Seide does in his experiments (1929) with the ova of Ascaris megalocephala. Observing in one experiment an increase of 26 percent (as compared to the control) in dividing irradiated ova, and failing to obtain similar results upon repetition of the experiment, he calmly proceeded to chalk off the first experiment as "due to chance", instead of determining why the second experiment didn't succeed. Johnson acted in the same way. Observing the increase in weight of the fresh (green) mass of the plant as a result of irradiation of "sunberry" seeds, she assumed that it was due to chance and deleted

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it from her count. On the other hand, those investigators who are prejudiced in favor of stimulation of X-rays are even more guilty, for they sometimes contrive their experiments in such a manner as to include basic contradictions.

Nevertheless, the great bulk of the experiments and observations of plants which had been exposed to the action of X-rays constitutes a unique body of biological data, which are most interesting, both in their theoretical and their practical aspects.

INVESTIGATIONS PERFORMED IN THE ELECTROBIOLOGICAL LABORATORY

We were guided by the above considerations when we decided, by a series of systematic experiments on the effects of radiation on plants of various species, including agriculturally significant ones, to answer the question posed by our predecessors as to whether irritating, and consequently stimulating, doses of X-rays exist. But we expanded the question of stimulation to include the question of yield, and consequently not only brought the plants up to the fruit-bearing stage of their development, but we analyzed the yield as well.

The experiments were first conducted in a laboratory for the biontization of seeds which in 1935 became part of the All-Union Institute on Fertilizers, Soils, and Agricultural Engineering, and later of the All-Union Institute for Electrification of Agriculture, and upon liquidation of the latter, of the Timiryazev Agricultural Academy.

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Our experiments began in 1931, and our first subject was rye. This was a very happy choice for, as we shall see later, rye turned out to be very sensitive to X-rays.

Rye. In order to find out the regularity of the process we systematically increased dosages for each succeeding experiment in the following order: 250, 500, 750, 1000, 2000, 4000, and 8000 roentgen units. Not content with varying the X-rays quantitatively, we also tried qualtitative variations in our experiments, i. e., we used hard and soft rays. Seeds which had been soaked for twelve hours as well as sprouted ones were irradiated. We present the findings of these experiments separately.

Rye sprouts (investigations of Breslavets, Afanasyeva, and Medvedyeva). For irradiation we used freshly sprouted seeds of rye, but since we hadn't selected the sprouts for irradiation with sufficient care, some of them had attained 1/2 centimeter in size. We believe that this difference in size is largely responsible for the uneven manner in which the irradiated sprouts came up. Immediately after irradiation the sprouts were planted in flower pots, several per pot. The plants developed in them for 27 days; after that they were planted, one at a time, in a heavily fertilized plot of ground. When the plants were still in the pots, before planting out, they were photographed. On this photograph differences in their development (depending on the dosages they had received) were clearly apparent. Doses of 250 roentgen units already have a depressing effect on the development of rye; doses of 500 roentgen units

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produce approximately the same effect. But when the dose is increased to 750 roentgen units, part of the plants develop poorly while the remainder die. A dose of 1000 roentgen units has such a depressing effect on the plants that they barely reach a height of 2-3 centimeters. With doses of 2000 roentgen units only a few sprouts survived; with a dose of 4000 only one survived; while a dose of 8000 roentgen units was completely lethal, not a single plant surviving.

However, we did not limit ourselves to a single optical evaluation. On the 27th day after irradiation, i. e., just before planting out into the field, we carefully measured the plants, the controls and those which had received various dosages of the rays. The results of these measurements can be seen in Table 2.

Table 2

(based on the data of Breslavets, Afanasyeva and Medvedyeva, 1932)

Dose	Average Height in Centimeters	Average Bushiness (Number of Stems per Plant)	Dose	Average Height in Centimeters	Average Bushiness (Number of Stems per Plant)
Control	14.50	2.00	1000 h. r.	3.36	1.10
250 h. r. (hard rays)	11.14	2.06	1000 s. r.	6.90	1.60
250 s. r. (soft rays)	13.50	2.40	2000 h. r.	1.53	1.00
500 h. r.	7.60	1.70	2000 s. r.	1.25	1.00
500 s. r.	8.50	2.02	4000 h. r.	1.46	1.00
750 h. r.	4.50	1.30	4000 s. r.	1.27	1.00
750 s. r.	4.14	1.20			

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A careful examination of this table will reveal that a dose of 250 roentgen units is already sufficient to depress the average height of the plants, but the average bushiness (number of stems per plant) is still somewhat higher than in the controls. Besides, the differences between the effects of soft and hard rays begin to show up here: the soft rays have a less drastic effect on the plants. This difference also shows up in other doses with the exception of the 750 roentgen unit dose, where the soft rays produce smaller size and lesser bushiness than the hard rays. But, in general, the difference of the effects of soft and hard rays in our experiments was so slight that in future presentation of data, we will deal only with hard rays, since they were used in the majority of experiments.

The phenological observations conducted by us in the spring and summer of 1932 have demonstrated that the average irradiated plant grew its ear, flowered, and ripened at about the same time as the controls. However, individual variations for some plants were 3-4 days. These individual differences are frequently encountered among irradiated plants, as we shall see when we turn our attention to the study of other aspects.

We should note that only during flowering did some of the irradiated plants attract attention by their unusual development. Such plants could be encountered only with dosages of up to 1000 roentgen units. Starting with doses of 2000 roentgen units obviously degenerate forms with smaller ears began to show up. When the rye was ripe, it was collected by individual

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plants and the weight and contents were subjected to analysis. The number of ears was counted, the total weight of seeds was obtained, the total number of grains, and also the number of healthy and injured seeds. These results are presented in Table 3.

Table 3

(based on the data of Breslavets, Afanasyeva, and Medvedyeva, 1932)

Dose in r.	Number of ears	Number of Seeds			Weight of seeds
		Normal Seeds	Underdeveloped and diseased	Total	
Control	3.7	111.7	35	146.7	5.36
250	10.0	255	85	340	12.52
500	7.0	122	59	181	6.94
750	4.5	82	37	119	4.57
1000	3.5	80	13	93	3.18

All these data refer to a single plant. In analyzing this table it turns out that a dose of 250 roentgen units more than doubles the number of ears, and the number and weight of seeds. A dose of 500 roentgen units has a much weaker effect, although the number of ears, and the weight and number of seeds still show a significant gain over the controls. A dose of 750 roentgen units already depresses the development of ears and seeds, while a dose of 1000 roentgen units gives a still more pronounced depressing effect. Plants which had received doses of 2000, and 4000 roentgen units perished early in the spring.

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If we were to project line graphs on the basis of these data, we would see first a sharp rise of all quantitative factors and then their gradual falling off. This points up our mistake in setting up the experiment, since for irradiation of sprouts we took too large an initial dose.

Apparently we should have begun with smaller doses, perhaps as small as 50 roentgen units. It is possible that smaller doses than the one we used would have also produced increases in yield and we would have obtained a less lopsided curve (i. e., a more normal curve).

Our experiments with the irradiation of rye sprouts indicate how wrong it would have been for us to limit our observations to the initial stages of development (as the majority of authors did with various plants) or take them only as far as ear formation (as Long and Karsten did). Comparing the two tables we can see how much the number of stems per plant has increased with benevolent dosages with the course of development. With a dose of 250 roentgen units the number of stems per plant is not much greater than that of the controls, while the number of ears at harvest time is almost triple that of the controls, and this does not include the number of underdeveloped (those which had failed to catch up) ears of the same stems.

If we had not carried our experiments through harvest time, we would have had to agree with those authors who point to the small irritating effect of X-rays, or to their total absence of irritating effect.

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The seeds (investigations of Breslavets and Afanasyeva) received the same doses of X-rays as the sprouts, but these doses produced a different effect on the development of the plants. Just as had been done with the irradiated sprouts, the soaked irradiated seeds were planted in flower pots and on 27th day transferred to field plots. When we set out the flower pots according to dosages, we saw a very vivid example of the curve of the Arndt-Schultze law. (Fig. 2. Differences in development of rye depending on the dosages of X-rays they had received.)

In order to check by means of figures our direct observation, we measured all of the plants on the 27th day after planting. As may be seen from Table 4, the numerical data coincide with the visual evaluation.

Table 4

(based on data of Breslavets and Afansyeva, 1932)

Dose r.	Average Length in Centimeters	Average Bushiness (Number of Stems per Plant)	Dose r.	Average Length in Centimeters	Average Bushiness (Number of Stems per Plant)
Control	12.5	2.0	1000	23.0	3.2
250	20.0	2.6	2000	17.9	2.0
500	23.9	3.1	4000	17.7	2.6
750	22.8	3.1	8000	10.8	1.6

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If we carefully examine our irradiated plants and compare them with the controls when both are in the process of growing additional stems, some interesting details can be brought to light. The first thing that attracts attention is the increased size of the leaves; their breadth and coloring are directly related to the dosages. With doses of 250 roentgen units it was not possible to find any obvious differences with the controls, but with doses of 500 roentgen units the width of the leaves and their darker (more intense) green coloring were immediately apparent. Doses of 750 roentgen units intensify these characteristics still more. The climax is reached with doses of 1000 roentgen units when the width of the leaves is nearly double that of the controls. Beginning with 2000 roentgen units the size of the leaves first approaches that of the controls, and then becomes considerably narrower. It was likewise obvious at a glance that plants which had received "benevolent" doses had larger roots than the controls. We also measured 50 roots from each dose by means of an ocularmicrometric ruler and then transposed the results into microns (these measurements were performed by Lipayeva). Measurements were always made from the same spot on the root, namely, where the root begins to differentiate into the plerome and the periblem (Table 5) (fig. 3).

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Table 5

The Average Diameter of the Root, Expressed in Microns

(based on the data of Ereslavets and

Afanasyeva, 1932)

Control	250 r	500 r	750 r	1000 r	2000 r	4000 r	8000 r
303.8	362.9	387.4	393.2	358.6	326.4	316.8	305.23

By using the average size of diameters of the roots it was possible to obtain the same kind of a graph curve that it was possible to do by using the length of the stems. With a dose of 250 roentgen units the curve rises sharply; a dose of 500 roentgen units continues the rise; with 750 roentgen units the curve reaches its apex, after which a gradual falling off begins; and at 8000 roentgen units the average diameter of the root equals the diameter of the control plants.

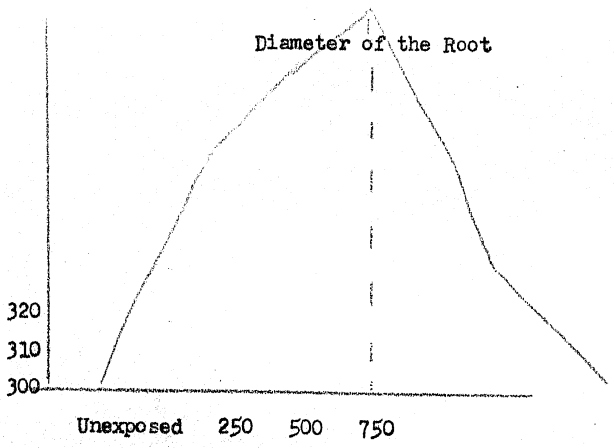

Fig. 3. Curve representing the changes of diameter of roots depending on their exposure to various doses of X-rays

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During the spring and summer phenological observations were carried on, which showed, just as with the irradiation of sprouts, that there aren't any particular differences in the onset of the various phases of ear formation, flowering, and ripening between the irradiated plants and the controls. Individual plants, however, ripened from 8-10 days earlier than the controls. This is a point that will bear looking into, in the future.

Upon ripening, the ears of certain of the irradiated plants were nearly one-and-a-half times as large as the ears of normal plants in our experiment, which, in turn, were considerably larger than plants which are grown under ordinary field conditions. These ears in turn (i. e., those of irradiated plants) sometimes exceeded normal size by one-and-a-half times. (Fig. 4, comparative sizes of ears of control and irradiated rye: a - control, b - irradiated.) But especially amazing was the size of the grains which by their size approached the size of Polish wheat. In order to compare the weight of the initial material with the weight of seeds obtained from irradiated plants we determined their weight on torsion scales, weighing each seed separately. On the basis of these facts, two variable graph curves were constructed. By examining the left curve we can see that in the initial material seeds weighing 15.5 milligrams were most common and that they varied from 9.5 to 33.5 milligrams, while in the right curve (weights of seeds obtained from irradiated material) a weight of 39.5 milligrams was predominant, a weight which doesn't even occur in the initial

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material. The weight of the experimental seeds varies from 21.5 to 51.5 milligrams. A comparison of these two curves points up the large size and uniformity of the irradiated grain, which from the point of view of agriculture gives it a great advantage over the initial material. (Fig. 5. Comparison of two line graphs based on the weight of normal and irradiated seeds. Note: dark solid line is control; broken line is for seeds exposed to 750 roentgen units.)

An analysis of the identical factors in the yield (just as analysis of the yield of the irradiated shoots) shows that all graph curves based on individual factors tend to shift to the right.

From Table 6 we can see that the average number of ears on a control plant is 4.5, while plants which have been exposed to 250 roentgen units have on the average nearly 12 ears. Then as the doses of X-rays are increased, the number of ears tends to diminish; however, it does not approach the control until a dose of 2000 roentgen units is reached.

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Table 6

(based on data of Breslavets, Afanasyeva, and Medvedyeva, 1932)

Dose in r.	Number of ears	Number of seeds per plant: Normal seeds	Underdeveloped and diseased	Total	Weight of seeds
Control	4.5	87.0	48.0	135.0	5.29
250	11.7	382.8	63.7	446.5	15.96
500	8.7	292.5	52.0	344.5	13.43
750	8.0	297.0	61.0	358.0	14.08
1000	7.0	230.5	70.0	300.5	10.74
2000	4.5	131.0	20.5	151.5	5.58
4000	3.0	90.0	38.0	328.0	3.66
8000	3.0	57.0	59.0	86.0	3.21

Only doses of 4000 and 8000 roentgen units, which have to be considered strong doses, cut down the average number of ears per plant to three, i. e., they give a number which is smaller than the control (Fig. 6.).

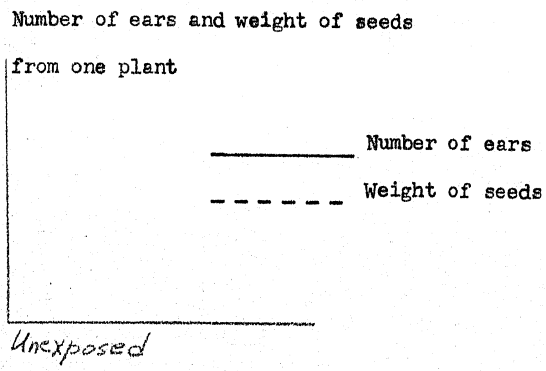

Fig. 6. Number of ears and weight of seeds per single plant in controls, and in irradiated rye

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If we analyze the column with the number of seeds, we shall see a similar picture: the number of seeds triples with a dose of 250 roentgen units, then it begins to go down gradually, and just as for the number of ears, the number falls below that of the controls with doses of 4000 and 8000 roentgen units (Fig. 7.).

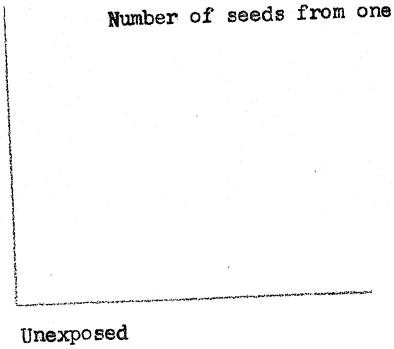

Fig. 7. The change in the number of seeds depending on exposure to various doses of X-rays

The diminution of the number of underdeveloped and diseased seeds in plants which have been irradiated by beneficial doses of rays, as compared with the controls, should also be noted. In controls 48 out of 135 seeds were underdeveloped or diseased, that is 35.5 percent, while in plants which had received 250 roentgen units only 63.7 out of 446.5 seeds were diseased, that is 14.3 percent. This indicates an increase not only in quantity of the yield, but also in quality. If we add to this what we know concerning the increase of the weight of the seeds, than the full significance to agriculture of the proper use of X-rays becomes evident.

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If we now turn our attention to the total weight of the seeds, we shall see that 250 roentgen units triple the weight, that exposures of 500 and 750 roentgen units keep it on the same level, and that only beginning with 1000 roentgen units does the weight begin to regress (with 4000 and 8000 roentgen units it is nearly twice as small as that of the controls). Thus a dose of 8000 roentgen units has a strongly depressing effect on the number of ears, the weight and number of seeds, and, in addition, it increases the number of underdeveloped and diseased seeds (Fig. 6.).

Looking over the data for every specific plant, for each of the doses, we find great individual variations. So, for example, the number of ears can vary from 2 to 24; the number of normal seeds, from 17 to 930; the total weight for any one plant, from 1.06 to 36.26 grams. This great variability is characteristic not only of rye, but of all other plants which are subjected to the action of X-rays, as can be seen from literature. If we turn our attention to the variability of the number of ears, the first thing that strikes our attention is the large number of secondary stems on irradiated plants, which did not have time to come to maturity. These secondary stems, in turn, increase the number of underdeveloped seeds and thus lower the <u>total</u> seed weight for a single plant. [The word "total" is probably incorrect; the author probably meant "average" weight.] If we are not in a position to answer, at the present moment, why irradiated plants have so many secondary stems which do not reach maturity, we can at least venture a conjecture. Apparently, X-rays, by stimulating development in plants, open up possibilities which

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in normal plants never reach beyond the potential stage. However, these possibilities never reach full development because something is missing from the environment, and this results in the incomplete development of stems and ears. What is missing (nourishing elements in the soil, or light, or heat, or all of these elements) we cannot tell at this time.

From our preliminary data it is quite obvious that X-rays act as stimulants on the development of rye. If we compare all of the curves by which the growth, development, and productivity of the irradiated plants are reflected, we shall see that they coincide. The initial height of the plants, the diameter of roots, the number of stems, the number and weight of the seeds, all act in a similar manner under irradiation. Radiations of 250 roentgen units send the curves up steeply; 500 and 700 roentgen units continue this tendency; and with doses of 1000 roentgen units the curves begin to drop.

At this point it seems proper to point out once more the necessity of carrying through the experiments with irradiation of seeds, or sprouts, to the point of the ripening of the seeds; otherwise, it is possible to obtain an incorrect impression of the effects of X-rays. If we had carried our experiments only up to the point where plants were beginning to send secondary stems, from the graphs of their development we might have come to the conclusion that doses of 1000 roentgen units were most conducive towards increases in yields. But by the time the seeds of the irradiated plants ripen, doses of 250, 500, and 750 roentgen units outstrip the 1000 roentgen unit dose, which by this time

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is exhibiting effects which are to a certain extent depressing, since it is with this dose that signs of decline begin to show up. However, even this dose cannot be excluded from determination of effects of X-rays on other plants, for there are times (depending on the problem we want to solve) when it becomes important to obtain a greater initial development.

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The advantages of X-irradiation are not limited by an increase of yield of the irradiated plants; the advantages can be transmitted to the offspring of the plants. These data were obtained by us as a result of planting, in the fall of 1932, seeds produced from plants which were irradiated in 1931. For planting we selected seeds of the plants which gave the greatest yields. For control we used the offspring of the control plants of 1932, from which we similarly selected the best plants, hence the best indicators of the control plants of 1932, by comparison with 1931. During the growing season phenological observations of the irradiated and control plants were conducted, and no appreciable difference in the length of various phases [of development] was observed. The ripened plants were subjected to the same detailed analysis as in 1932, i.e., the number of ears and the number and weight of grains were determined. The obtained data are compared in Table 7.

Table 7

Average data per single plant

(based on data of Breslavets and Afnasyeva, 1932 and 1933)

Dose	Number of ears		Total weight of seeds		Number of seeds	
r	1932	1933	1932	1933	1932	1933
Control	4.5	7.3	5.29	7.74	135.0	222.2
250	11.7	4.7	15.96	4.93	446.0	168.2
500	8.7	6.8	13.43	9.17	343.5	279.2
750	8.0	7.8	14.03	10.04	358.0	306.5
1000	7.0	7.2	10.74	8.78	300.5	277.6
2000	4.5	5.5	5.58	7.42	151.5	215.7
4000	3.0	7.1	3.66	9.44	128.0	283.8
8000	3.0	7.2	3.21	8.18	86.0	306.6

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An examination of this table indicates an obvious secondary action which shows up in the increased yields with certain doses of X-rays. Although we see that the 1933 yield is less than that of 1932, nevertheless the increase is evident in the total weight of the seeds as well as in their number. In order to facilitate the comparison of the effect of direct irradiation and of its secondary action we have drawn up Table 8, where results are given in percentages, using the controls as index of 100.

Table 8

(based on data of Breslavets and Afnasyeva, 1932 and 1933)

Doses r	Number of ears		Total weight of seeds		Number of seeds	
	1932	1933	1932	1933	1932	1933
Control	100.0	100.0	100.0	100.0	100.0	100.0
250	260.0	64.4	301.7	63.7	330.7	75.7
500	193.3	93.1	253.6	118.7	254.4	125.7
750	177.7	106.8	266.1	129.7	265.2	137.9
1000	155.5	98.6	203.0	113.6	222.6	124.9
2000	100.0	75.3	105.5	95.8	112.2	97.0
4000	66.6	97.2	69.1	121.9	94.8	127.7
8000	66.6	98.6	60.7	106.7	63.7	137.9

From the data of this table it is possible to arrive at the very definite conclusion that a dose of 750 roentgen units not only increases the weight of seeds by 166 percent as a result of direct X-radiation, but that it retains an increase of nearly 30 percent in next year's yield, as a secondary action. Doses of 250 roentgen units which produce such sharp increases (21 percent), by comparison

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with control, during the year of irradiation, here give strongly negative indications. We will return to this question later (see Chapter 3). Doses of 1000 and 2000 roentgen units reveal in their secondary action a gradual diminution [of yield] which takes place more slowly than under the direct effect of X-rays. The secondary action is distinguished by the fact that strong doses (4000 and 8000 roentgen units) which depress the development of the plant in the first year (as a result of direct irradiation) give a positive effect eventually. Probably the explanation of this phenomenon lies in the fact that those plants upon which the rays had the most depressing effect had perished.

Peas (investigations of Breslavets and Atabekova). (This work, started jointly, was transferred on the following year to Atabekova alone). This plant was selected as an object for investigation chiefly because it is well known in literature for its sensitivity to X-rays. Besides, this was felt to be a useful object for genetic investigations because it is self pollinating.

Taking into account the sensitivity of peas to X-rays we used weaker doses for them, i.e., we began with 50 roentgen units. Pea seeds which were irradiated under air-dry conditions were planted in vegetating dishes on the day after irradiation. When the irradiated and control plants formed pods, they were photographed. 350 roentgen units should be considered the most beneficial dose since at this dose the plant showed the most vigorous development and gave the greatest number of pods (Fig. 8. Differences in the development of peas depending on application of various dosages of X-rays).

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In this experiment the yield could be judged only by the number of pods which were counted on the controls as well as on all of the irradiated plants. The average number of pods per plant with its probable error is shown in Table 9.

Table 9

Peas. Average number of pods per single plant

(data of Atabekova, 1933)

Dose in r	Number of pods	Dose in r	Number of pods
Control	2.33 ± 0.32	450	3.57 ± 0.33
50	2.54 ± 0.35	550	3.38 ± 0.39
100	2.56 ± 0.35	650	3.25 ± 0.39
200	2.57 ± 0.39	750	3.38 ± 0.35
250	3.63 ± 0.71	1000	2.64 ± 0.44
350	4.63 ± 0.38		

From this table it can be seen that a very weak dose (250 roentgen units) makes the difference between the controls and the irradiated plants reliable [i.e., greater than the probable error], while a dose of 350 roentgen units significantly increases the number of pods. Beginning with 450 roentgen units the curve begins to drop and with 1000 roentgen units the number of pods evens out with the number of pods in the control plants. These facts indicate the stimulating effect of X-rays, which shows up in the increase of the number of pods per plant. For a more accurate evaluation of the quality of the obtained yield of peas, the irradiated and control peas were weighed on a torsion scale in batches of 525.

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In 1935 [this date should probably be 1933 to correspond with the table below, or vice versa] the irradiated pea seeds were planted out on plots of the Timiryazev Academy with a quadruple repetition of the experiments. As the action of X-rays indicates, we selected the average weight of seeds, collected from a single plant. This data is compared in the following table.

Table 10

Peas. The weight of seeds from one plant

(based on data of Atabekova, 1938)

Dose in r	Weight of seeds, gr.	Dose in r	Weight of seeds, gr.
Control	3.66 ± 0.28	550	3.56 ± 0.29
250	4.29 ± 0.32	650	3.89 ± 0.33
350	5.07 ± 0.37	750	4.22 ± 0.39
450	4.26 ± 0.30		

From this table we can see that as far as the increase of the weight of the seeds is concerned the dose of 350 roentgen units has a particularly beneficial effect. From this we can deduce that for peas, just as for rye, an irradiation of the seeds before planting leads to an increase in yield (Fig 9).

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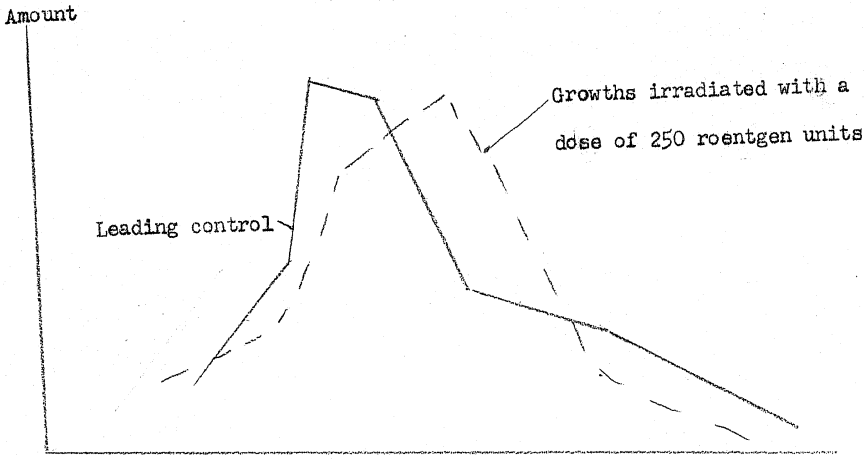

Fig 9 Comparison of the weights of pea seeds in controls and in plants which had received 250 roentgen units

Five years of experimentation with the effects of radiation on plants permit us to express our convictions concerning the significance of this factor in stimulation of growth, development and yields of plants. Negative results which were obtained by many investigators we explain by insufficient work on the dosages, which are specific for every species and variety of plant. Let us take an example from our own experience. Despite three years of experience with spring wheat we still have been unable to obtain stimulating doses for it. We don't draw pessimistic conclusions from this that stimulating doses don't exist for wheat, but we consider that we have not discovered them as yet. Nevertheless our experiments with this plant are rather interesting.

Wheat (investigations of Afanasyeva). For our experiments we used a pure line of soft wheat whose seeds were irradiated in air-dry conditions, soaked, and, finally, in the form of sprouts. The

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air-dry seed was discovered to be not radiosensitive; it didn't react in any way on exposure to small and medium doses of X-rays, while exposures to heavy doses produced a depressing effect on the first phases of development of the plant. In order to study the effects of X-radiation on soaked seeds they were planted in the laboratory and in field plots. This last experiment was performed under quadruple repetition using hand planting by row. The seeds which had been planted under laboratory conditions all came up at the same time (regardless of dosage) as the controls. The percentage of irradiated seeds which came up in no way differed from the controls. During further development obvious depressing effects were noted with a dose of 16,000 roentgen units (just as in the previous experiment). Under field conditions it was possible to observe that as the dosages increased, the viability of the plants went down. The dose of 16,000 roentgen units, which under laboratory conditions came up in the same amounts as the other dosages and the controls, under field conditions made a 50 percent lower showing. This is explained by the loss of a certain percentage of the developing plants during the entire growing season of the plant. Not a single one of the dosages of X-rays used showed a stimulating effect and only doses of 8,000 and 16,000 roentgen units exerted a depressing effect on the growth and development of the plants. This depressing effect lowered the yield by 30 percent for a dose of 8,000 roentgen units, and by 63 percent for a dose of 16,000 roentgen units.

For neither the dry nor the soaked seeds of wheat were we able to find stimulating doses of X-rays. Since many authors point out that sprouts are more sensitive than seeds, either dry or wet, it

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became necessary for us to try out the effect of the rays on sprouts. Seeds of wheat were allowed to germinate on wet filter paper; of the germinating seeds we picked out those which had just begun to show the sprout. After irradiation with doses from 50 to 8000 roentgen units, the seeds were planted under laboratory conditions in three groups, 100 seeds per group. Shoots appeared simultaneously in all dosages and in the control. Further observations of the development of the plants and periodic measurements showed that doses of 50, 100, and 200 roentgen units do not affect the growth and development of the plants, whose size remains equal to that of the controls. With doses of 5000 [this is a mistake, it should read 500] roentgen units it is possible to observe weak depressive effect. With dosages of 1000, 2000, 8000 and especially 16,000 roentgen units it was possible to observe a strong depression of development. Plants irradiated by other doses developed identically with the controls. Phenological observations have shown that plants which had received a dose of 1000 roentgen units begin sending secondary stalks 4 days later than the controls, and that they begin to ripen ten days later. By harvest time far from all of the plants which had been exposed to this dose had ripened; the ears were small and many of the seeds were underdeveloped. At the time of harvest the height of the plants was measured, and the number of ears were counted for every plant for each of the doses. Threshed grain was weighted separately for each plant. The obtained average data (height of plants at harvest time, the number of ears and weight of seeds, are counted per single plant) are presented in Table 11.

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Table 11

(Based on data of Afanasyeva, 1934)

Dose in r	Height of Plants cm.	Number of ears	Weight of grain gr.	Dose in r	Height of Plants cm.	Number of ears	Weight of grain gr.
Water							
Control	93	3	2.44	1000	93	3	2.39
Dry	93	3	2.20	2000	94	3	2.50
125	92	3	2.26	4000	92	3	2.19
250	91	3	1.14	8000	88	3	1.78
500	93	3	2.54	16000	75	2	0.91
750	93	3	2.33				

Analyzing this table, we can see that the height of the plants remains unchanged despite the action of rather strong doses of X-rays (only doses of 8000 and 16000 roentgen units decrease the height). Similarly only the strongest of all applied dosages, i.e., 16000 roentgen units, brings the number of ears down to 2 from 3, which is the number found on the controls and on all the plants which had received smaller dosages. The weight of the grain per single plant began to become smaller with the application of 4000 roentgen units and fell to nearly a third when 16000 roentgen units were used.

In comparing the action of radiation on dry, soaked, and sprouted seeds of wheat it was established that the latter are the most sensitive, for doses of 1000 roentgen units had strong depressive effects on them. Summarizing the investigations of the effects

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of X-rays on seeds of wheat we can see that for this plant, in Afanasyeva's experiments, stimulating dosages have not yet been found. This does not mean, however, that we should stop trying to find them. It is possible that by changing external conditions (for example, temperature) it will be possible to achieve success.

In any case, of the three plants subjected to the action of X-rays, our small laboratory obtained a significant increase of yield with peas, and a very large increase of yield with rye. Besides continuing to work with the irradiation of rye we have already planted with experimental seeds half a hectaire of rye at one of the kolkhoz of the Moscow Oblast. The results of these experiments will be described in another article. We shall only point out that on both the initial development and yield X-rays exerted a most beneficial ~~development~~ effect.

The investigations which were conducted in our laboratory on changes in the development of plants due to irradiation of seeds of rye, wheat, and peas, were set up with the idea of avoiding the mistakes of our predecessors.

1. The seeds irradiated in our experiments received exact doses of X-rays carefully measured by means of dosemeters by expert physicists. 2. The amounts of radiant energy were gradually increased in order to obtain the full curve due to irritating dosages (i.e., according to the Arndt-Schultze law). 3. A sufficiently large number of seeds were used in the experiments so that results wouldn't be affected by individual fluctuations. 4. Whenever possible similar conditions of temperature and humidity were maintained

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both during irradiation and while the plants were growing. 5. Thorough phenological observations were carried on during the course of the entire development of the plant from the moment it came up from the ground to the complete ripening of the seeds. The crop was carefully gathered and analyzed. These observations showed that stimulation during the first stages of development does not coincide with the increase of yield, at least for the most thoroughly investigated object, i.e., spring wheat. 6. Measurements were carried on. There were measurements of the main root of the sprouts, measurements of the plants on the twenty-seventh day after planting, and measurements of ears and stems at harvest time. 7. The seeds were weighed in such a manner that the weights of healthy and of diseased seeds could be obtained as well as the total weight. In addition all of the seeds of a single plant, selected for the exceptionally large size of seeds, were weighed, grain by grain.

As far as separate cultures are concerned, our investigations have shown that rye is sufficiently sensitive to X-rays that experiments can be set up with it and a whole series of questions which are of interest to radiation biologists can be answered. These experiments: 1. showed the incontestable application of the Arndt-Schultze law to the action of X-rays on plants, at least on rye, since the measurement of young plants on the twenty-seventh day after planting gave a splendid growth curve; a small dose (250 roentgen units) stimulated development, 500 and 750 roentgen units produced still further development in the same direction, until at 1000 roentgen units maximum stimulation was achieved, after that the curve began to drop; 2. confirmed the variable sensitivity of soaked seeds

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and sprouts; 3, showed that differences do not depend on the quality of the rays, i.e., hard or soft rays; 4, the effects of radiation showed up in different ways depending on the individuality of various plants, which affected the number and weight of seeds, the length of the stems and ears, the time of ripening, etc.

Besides these purely technical conclusions we were also able to establish the stimulating effect of X-rays on rye. Plants which had received beneficial doses developed more quickly, had broader leaves, and exhibited a deeper green color than the control plants. The average diameter of the roots followed the same curve of growth as the other parts of the plants. With a dose of 750 roentgen units it increased by 30 percent, gradually diminishing its size as the doses increased. Analysis of the yield indicates that the number of ears increases nearly three times, while the number and weight of seeds per plant does the same thing. The advantages of irradiation are not limited to the increase of yield of the directly irradiated plant, they are also transmitted to the descendants of the irradiated plant. Seeds collected from irradiated plants gave an increased yield on the following year. With a dose of 750 roentgen units the increase was 37.99 percent.

Since pea seeds are known to be extremely radiosensitive the weakest possible doses of X-rays were used for their irradiation. In the first experiment the number of pods per single plant doubled (in comparison with controls) when a dose of 450 roentgen units was used. In an experiment of another year a dose of 350 roentgen units raised the weight of seeds per single plant from 3.66 grams (weight of the control) to 5.07 grams.

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The irradiation of the seeds and sprouts of spring wheat produced neither stimulation of development nor an increase in yield. Only high doses of X-rays (8000 and 16000 roentgen units) clearly showed the depressing effect.

Summarizing the results of our five years experiments with three plants we can draw the conclusion that an exposure of rye and peas to X-rays before they are planted results in the stimulation of their development and an increase of yield. For wheat we have so far been successful in finding doses which produce one or the other of the above results.

Ryegrass (investigations of Breslavets). Several years have passed since the end of our experiments with the action of X-rays on agricultural crop plants, and the question of application of these rays to meadow grasses came up. One of these was the Westerval'd rye-grass, picked out as the most rapidly growing one. Doses of 200, 300, 400, 500, 750, 1000, 2000, 4000 and 8000 roentgen units were selected for this plant as well as a control. They were planted on February 24, 1942 in quadruple. First of all the time of appearance of seeds with the various dosages was noted (Table 12).

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Table 12

(Based on data of Breslavets, 1942)

Dose in r	28 February	2 March	4 March	6 March
Control	53	66	71	76
200	39	58	78	97
300	45	49	84	100
400	46	68	89	100
500	32	81	94	97
750	37	75	83	97
1000	40	70	85	96
2000	29	85	95	100
4000	18	39	84	91
8000	2	15	61	73

These data show that doses of 300, 400, 500 and 2000 roentgen units cause all seeds to grow through, while in the controls only 76 percent came up. We have come across this type of phenomenon more than once in our experiments with X-rays on the seeds of many other species of plants. These facts should be noted since they show that an amount of the valuable seeding material can be saved by application of radiation.

By the end of March the plants had developed to such a point that it was no longer possible to leave them in boxes. They were removed from the ground and the number of roots for each of the plants for each dosage was counted. In addition the lengths of roots and stems, and the weight of the stems were recorded (Table 13).

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Table 13

(Based on data of Breslavets, 1942)

Dose in r	Number of roots	Length of stems	Length of roots	Weight of stems
Control	100	100	100	100
200	200	123	100	113
300	230	150	102	112
400	230	110	102	112
500	200	118	126	125
750	290	119	125	176
1000	120	90	98	80
2000	150	107	100	87
4000	127	127	93	102
8000	95	88	48	300

As can be seen from this table, a dose of 750 roentgen units nearly tripled the number of roots, increased the length of stems by 19 percent, increased the length of the roots by 25 percent, and increased the weight of the stems by 76 percent. The above dose obviously stimulates the growth of the plants, while a dose of 8000 roentgen units which depresses plant development can be used to create the impression of the unevenness of the soil due to the uneven development of the plants.

For the number of roots we can see the typical biological curve of the Arndt-Schultze law: a gradual rise up to and including 750 roentgen units and then a gradual falling off to the dose of

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8000 roentgen units. The same may be observed for length of stems and roots, and weight of stems. From this we may draw the conclusion that Vesterval'd's ryegrass is a radiosensitive plant.

Meadow grasses (investigation of Afanasyeva). The seeds of the following meadow grasses were subjected to X-rays: bottom grasses; red fescue, red top grass (Agrostis) and Kentucky blue grass (Poa pratensis); top grasses, fescue, timothy, brome grass, and American couch or quack grass. Doses of 750, 1500, and 3000 roentgen units were used for irradiation. The irradiated and control seeds were planted in boxes in quadruple. The boxes were located in the greenhouse of the botanical garden. Sprouts of the irradiated seeds appeared at the same time as the sprouts of the controls. The doses used had practically no effect on the percentage of plants which came up, since we didn't attach any significance to a small rise in the percentage (3-6 percent). Then the appearance of the second and third leaves were counted but no differences were observed here either. When the plants were removed from the ground the number of leaves and roots of each plant were counted, measurements of their length and weight and circumference of their root system were made. This was done for red fescue, for meadow fescue, brome grass, and for American couch or quick grass. The obtained data failed to show any differences, by any of the above signs, between the irradiated and unirradiated plants. The doses of X-rays which were used failed to show either a stimulating or a depressing effect.

Data for the second accounting, at the time of appearance of the third leaf, were obtained for brome grass and fescue. These data

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show that separate doses increase, by this moment, the percentage of plants which have developed three or more roots. This can be seen from the following table (Table 14).

Table 14

Percentage of plants which after 35 days have developed from 1-5 roots

(based on the data of Afanasyeva, 1943)

Name of kind (of Plant)	Control		750 r		1500 r		3000 r	
	No of roots		No of roots		No of roots		No of roots	
	1& 2	3	1& 2	3	1 &2	3	1& 2	3
Red fescue	61.1	35.9	55.9	43.1	49.1	50.9	29.8	70.2
Brome grass	43.5	56.4	32.1	67.9	25.6	74.4	41.8	58.1

From this table we can see that with a dose of 3000 roentgen units the percentage of plants of red fescue having three or more roots is nearly double that of the controls, namely: 70.2 percent of the plants (as against 35.9 percent) have from 3-5 roots; while a dose of 1500 roentgen units with brome grass increases the number of roots by 18 percent over the controls.

These data give us some background for selection of doses which are capable of developing root systems.

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CHAPTER 2

CHANGES OF MORPHOLOGICAL CHARACTERISTICS

From a theoretical, as well as from a practical, point of view the morphological changes caused by X-rays are no less important than the physiological ones.

Of particular interest are the hereditary changes, i.e., mutations. However we should also not overlook such changes as show up for only one or two generations, i.e., variations or modifications, since the application of X-rays is not unthinkable as a procedure [method] in agricultural engineering, by means of which definite changes can be obtained. We shall say a few words about terminology in order not to have to come back to that question later on.

The process which causes hereditary changes to arise as a result of the action of X-rays we are going to call X-ray mutation (roentgeno-mutation); the mutated individual we shall call the X-ray mutant (roentgeno-mutant); the individual whose changes are not of a hereditary nature we shall call X-ray variant (roentgeno-variant). Besides, it should be pointed out that contemporary genetics distinguishes between two types of mutations: 1, chromosomatic aberrations and 2, gene-mutations.

The study of mutations on objects that have been most thoroughly investigated (corn and snapdragons) has shown that all of the organs of the plant, as well as their properties, can be changed under the influence of X-rays.

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The scope and great range of the changes can be seen from the survey of literature that follows. These changes range from great interruptions of development and even appearance or disappearance of structures to insignificant changes which cannot be seen with the naked eye. And of course there are gradations. The greatest changes which are produced by irradiation are lethal ones, i.e., the kind where death sets in during one of the stages of ontogenesis. These are followed by sublethal mutations. These two groups of mutations are deviations from the norm, and since they are very obvious, they have given rise to the popular notion that irradiation produces monstrous, defective, anomalous, or pathological changes. This popular opinion points to the weakening of the general constitution which shows up in the disharmony of the development of the organs, the shortening of the life span, the decrease of fertility, and in the loss of resistance to the environment. However, by the present time, enough facts have been accumulated which point to the existance of mutations which raise the viability of plants on the one hand and which create new, and more valuable, forms of plants, on the other. In general as the methodology of induction of mutations has improved it turned out that often such mutations appear, in our case such X-ray mutations, which cannot by any stretch of the imagination be considered to be anomolies or monsters. It is a different matter, however, with the establishment of the mutation changes, since the smaller the deviation from the norm the more difficult it is to detect. Starting with a definite boundary, we can speak of small mutants (Baur, 1933), which occur much more frequently than great mutants, which (just as the former) change the morphological

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characteristics and the physiological properties of the plants. The occurrence of these changes often leads even to an increase of viability of the mutants.

From what has been described, the tendency of contemporary experimenters to look for factors which would guarantee the appearance of mutants, should be understandable. With this aim in mind, various chemical and physical factors were tried out. By far the most brilliant achievement in this direction were Muller's experiments, the results of which were reported at the International Congress of Geneticists in 1927. Muller showed that the frequency of mutations in Drosophila melanogaster increases manyfold when exposed to X-rays. The year 1927 can be considered to mark the beginning of radio-genetics and of exact investigation of mutations. It is rare in the history of science to see any branch of the natural sciences seized upon by so many investigators, and developed as systematically as was the area of experimental investigations of mutations induced by shortwave rays. In his first experiments Muller showed the existence of a definite relationship between the dose and the frequency of mutations and was able to draw general conclusions concerning the mechanism of the action of X-rays.

Muller's first results were quickly confirmed because quite independently from him Gager and Blakeslee working on thorn apple in 1928, Stadler working on corn and barley in the same year, and Goodspeed and Olsen working on tobacco [also in 1928] all obtained increases in the frequency of gene-mutations and chromosomic aberrations.

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Even earlier, however, in 1926, Linsbauer's substantial experiments on the action of X-rays on mosses and ferns were published. The author selected these plants because, first, their structures are not highly differentiated, and secondly, because of their high regenerative and reproductive properties. He was also influenced by the fact that cell division in them can be observed in vivo. Linsbauer considered that experiments on radiation of these plants could throw light on the physiological basis of the effect of X-rays on organisms on the one hand, and could serve for investigation of the mechanism of development on the other. From among mosses he selected: Lunularia cruciata, Fegatella cruciata, Fegatella conica, and Riccia fluitans. From ferns he selected: Lycedium japonicus and Gymnogramme chrysophila. He measured the rays in H [Holtzknecht units]. We are going to leave aside his experiments on the action of X-rays on the sprouting and growth of these mosses and ferns since in the current article we are only interested in their formative action.

Normally in liverworts [i.e., hepatic mosses] gemmae develop in such a manner that both points of growth grow into the widened top of the thallus which bears at its invaginated end an infinetly growing point of growth. When the thallus is several weeks old it reveals a disklike central part, which is the remainder of the gemma, and issuing from it is a young ribbonlike thallus with dichotomous branching.

When the gemmae were irradiated by high doses of X-rays (from 10 to 40 Holtzknecht units) they began to show irregularities in their development, forming thalli with three, four, and more lobes. Sometimes the irradiation can induce true proliferation. Linsbauer

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sees the explanation for such formations in that the irradiation disrupts the development of the embryonic tissue of the point of growth and although the primary thallus continues to grow for some time, this growth is due only to the expansion of cells which are already formed at the moment of irradiation. Eventually the normal point of growth ceases to function, and this gives an impetus for its replacement. Sometimes proliferation is not observed, but the plant remains abnormal, as long as the point of growth does not develop and the cells formed around it grow into one or several thalli. Plants which have deviated to a lesser degree from the norm which had received a dose of 10 Holtknecht units produce gemmae, while those which have received 20 Holtzknecht units have thalli which show deformations. When doses of 40 Holtzknecht units were used substitutions were obtained after 8 days. It is remarkable that even such a high doses of X-rays does not lead either to necrosis of the individuals cells nor to a dying-off of the thallus.

Irradiation of fern prothallia which had not had a chance to develop very far by the time of their irradiation make it possible to observe that some cells do not multiply at all while the peripheral ones give a considerable number of offspring. Two cells (the eighth and the tenth) in the observed irradiated prothallium produced outgrowths consisting of several cells. From these outgrowths, in place of the original prothallium, there develops the replacement for the prothallium, the "regenerator", which continues to develop further. The extreme variant of such changes is a prothallium upon which develop three stalks with embryos of auxiliary prothallia. In addition it is possible to observe the formation of additional prothallia on the basal cells of the filament of prothallia.

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So, instead of a normal and gradual peripheral growth, the irradiated thallus gives rise in various places to numerous divisions of cells which give rise to additional prothallia. Eventually the center of cell formation is displaced as a result of which separate lobes arise. Further development of the prothallia proceeds normally up to the development of completely normal sexual organs. In general the irradiation of prothallia of ferns leads to the disruption of the harmonious development of the plant since exposure to irradiation inactivates the cells.

The experiments of Gager and Blakeslee, published in 1927, were the continuation of experiments reported on at the meeting of the American Botanical Society in 1922. Consequently these works should really be considered the first which were set up with higher plants with the specific aim of increasing the number of mutations. However a technical point which disqualifies these experiments is the fact that the investigators used radium rays rather than X-rays. However the authors used radium which was enclosed in a tube of lead-glass. As is well known radium emanations consist of a radioactive gas which yields alpha and beta particles and gamma rays. The latter obtain the same properties of penetration of tissues as X-rays, while alpha and beta particles are absorbed by the lead-glass; so that the effect of radium in this case was reduced to the action of gamma rays.

It should be noted at this point that as far back as 1906 Gager exposed the pollen and ova cells of Oenothera biennis to irradiation. However the changes produced by these rays had a somatic character.

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From the experiments of Gager and Blakeslee of particular interest is one which, for that time, produced remarkable results. Irradiation increased the frequency of mutations by 17.7 percent. These were chromosomatic aberrations as a consequence of which various morphological changes developed, which received specific names. In addition among the offspring of the irradiated plants two gene-mutations were observed: "albino" and "swollen". The latter had thick, swollen, shiny stems and stalks, thick leaves, and dwarf size.

A second investigator who had begun to experiment with the action of X-rays on plants and who confirmed Muller's results, was Stadler. In a whole series of works (1928, 1929, 1930, 1931, 1932 and 1933) he published interesting data which he obtained for corn and barley. In the first experiments he irradiated sprouted seeds. From 26 irradiated plants of barley which gave 66 ears in X_1 (first generation) three X-ray mutants of recessive type were obtained. They showed various degrees of albinism which led to the death of these plants. The fact that these mutants appeared only in a few ears, indicates that these X-ray mutants arise in the course of ontogenesis. The 1243 ears which were examined from X_2 (second generation) contained 14 mutants which were also albinos. Stadler immediately raised the question of the significance of the voltage. He irradiated seeds with high and low voltages. As his experiments showed (Table 15) voltage did not affect the frequency of mutations.

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Table 15

The effect of X-rays and radium on the frequency of mutations in sprouting barley seeds

(based on Stadler's data, 1928)

	Total number of investigated descendants	Number of descendants which are divided in relation to mutation of the sprouts
X-Rays		
High voltage		
Large doses	210	6
Small doses	259	1
Low voltage		
Large doses	494	6
Small doses	480	1
Total	1243	14
Irradiated by radium, all doses	1039	3
Not irradiated	1341	0

These experiments also permitted him to make an interesting comparison between the effects of X-rays and radium. The latter turned out to be less effective.

Stadler was also the first to combine the action of X-rays with the action of salts of heavy metals (barium, lead and uranium) for a period of 6 hours, 15 hours before irradiation. The author

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expected to increase the process of mutation on the assumption that the absorption of X-rays increases proportionately to the atomic weight of the substance used (Table 16).

Table 16

The combined action of X-rays and salts of heavy metals on frequency of mutation in sprouting seeds of barley

(based on Stadler's data, 1928)

Action		Number of	Number of
Irradiation	Chemicals	descendants	mutations
X-Rays	$Ba(NO_3)_2$	136	9
X-Rays	$Pb(NO_3)_2$	133	9
X-Rays	$UO_2(NO_3)_2$	194	11
X-Rays		72	2
Unirradiated		53	0
Unirradiated		76	0

As can be seen from this table, the soaking of the seeds in the metallic salts increased the number of mutations: one out of 16 ears showed mutations, while when X-rays were used alone there was only one mutation in 36 ears, i.e., the preliminary treatment increased the number of mutations by 50 percent.

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In another of his experiments in 1928 Stadler studied the influence of X-Rays on the frequency of crossovers and the appearance of a mosaic effect in the endosperm of corn. Irradiation increased the frequency of mutation in corn by 20 percent. Stadler attributes this increase partly to the intensification of the process of mutation in the genes and partially to chromosomatic aberration.

In his work in 1930 Stadler summarizes the results of the experiments with the genetic action of X-rays on barley and corn. Both dry and sprouting seeds were exposed to action. The appearance of mutations in barley was revealed during the growth of the self fertilized offspring of each ear.

In the first series of experiments 53 X-ray mutations were found from among 2800 plants. At the same time 1500 control plants failed to produce a single mutation. 60 percent of these mutants were true albinos, 5 per cent were white sprouts which gradually acquired green coloration in the course of their development, 15 percent were yellow (of various intensities of coloring), 10 percent were greenish yellow, and the remaining 10 percent had various kinds of multicolored leaves. The majority of these mutations were lethal and nearly all of them grew very badly. Not many of the mutants which reach maturity remain stable. When the mutants were crossed with the controls the changes were transmitted through the pollen, appearing as recessives in X_2. Stadler considers these mutations as changes of the dominant gene in the corresponding recessives in the somatic cells of the homozygotic plant.

As for the effect of X-rays on corn, the irradiation of the embryo produces chimeras at various stages of its development.

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In this work Stadler once more raises the question of the relationship between the frequency of mutations and the intensity and wave length of the X-rays. The wave length was obtained from unfiltered rays of 54 - 108 kilovolts. The doses were changed by varying the lengths of exposure from 2 to 30 minutes, with the other conditions of irradiation being held constant (108 kilovolts, 4 milliamperes, 18 centimeters from the tube, without filters). As the experiment shows (Table 18), the frequency of mutations increases proportionately to the dose.

Table 17

The relationship between doses and frequency of gene-mutations after irradiation of seeds

(based on Stadler's data, 1930)

Time of exposure in min.	No. of plants examined from X	Mutations X_2	% of Mutations X_2	Time of exposure in min.	No. of plants examined from X	Mutations X_2	% of Mutations X_2
2	156	0	-	18	144	6	4.16 ± 1.66
4	148	0	-	20	375	10	2.66 ± 0.83
6	152	0	-	22	135	9	6.66 ± 2.14
8	146	2	1.37 ± 0.96	24	167	5	2.99 ± 1.33
10	381	2	0.52 ± 0.36	26	113	9	7.96 ± 2.54
12	156	2	1.28 ± 0.90	28	178	11	6.17 ± 1.80
14	138	9	6.52 ± 2.10	30	177	9	5.08 ± 1.65
16	161	4	2.48 ± 1.22				

A wide variation of the wave length (40, 56, 81, 98 and 116 kilovolts) did not alter the frequency of mutations. The application of ultrasoft "border" rays (10 or even 7 kilovolts) also induced mutations.

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And, finally, it was Stadler who made the interesting observation that when oats and wheat are irradiated their frequency of mutations is considerably lower than that of barley. The probable reason for the low mutability of oats and wheat lies in the reduplication of their genes, and in the large number of chromosomes. If the dominant gene A is present in triplicate, then a recessive mutation will not show up. The coincidence of three homologous genes undergoing mutation at the same time is so rare that such occurences can be overlooked.

As for Goodspeed's works, they will be described in large part in the third chapter. Let us examine here only those experiments in which he indicates the formative action of X-rays. The irradiated seeds and sprouts of tobacco in their eventual development revealed a whole series of morphological changes in size of the plants and size and shape of the leaves. It should be noted that these variants were not always recessive in character. Crossing one of the offspring of the irradiated plant with normal plants, Goodspeed established that in X_2, five plants out of 50 revealed identical and significant changes in the form and coloring of the flowers, and, at the same time, one of the plants reestablished the parental [ancestral?] type. From the descendants of these plants a stable type ("127") developed. Cytological investigations have shown that by means of reorganization of the chromosome elements, or of the chromosomes themselves, a true selective type can arise which is completely different from the type from which it is derived. So, Goodspeed was one of the first investigators who was able to show that X-rays constitute a factor by means of which we can create new

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types of higher plants. For lower plants this had been demonstrated previously, specifically by Nadson's experiments with Saccharomyces cerevisiae.

The experiments of Stubbe were set up on an even greater scale. Beginning with 1928 he has been publishing his interesting works on the effects of X-rays on snapdragons. His experiments constitute the continuation of Baur's investigations of 1927, 1930 and 1932 which had been begun with the express purpose of obtaining mutations experimentally. The initial material in Baur's experiments was plant 50 (del), which was derived from a plant that had been obtained in 1907. From that time this family had been allowed to multiply by means of constant self-pollination. Consequently this was a homozygotic family. Investigators watched carefully for natural mutations to arise during this whole period. During the 20 years, 30,000 individual plants were obtained, among them only 16 individual cases of mutations were observed, which corresponds to a mutation frequency of 1.5 percent. By way of irritants Baur used various chemicals with and without the aid of centrifugation. He succeeded in raising the number of mutations to 2.1 percent. Stubbe's experiments were much more successful. He used shortwave rays. His works will be described later on since they were continued till 1940.

The experiments of McKay and Goodspeed in 1930 were performed with cotton, the flowers of which were castrated on the eve of blooming [opening], and the unopened pollen of which was placed in gelatine capsules. On the following morning the pollen was subjected to radiation after which it was placed on the stigma of the castrated flowers. The irradiation was performed in doses of 4, 8, 12,

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16, and 25 minutes (50 kilovolts, 5 milliamperes, 10 centimeters distance from the tube with an aluminum filter). From 17 ripe fruit 311 seeds were obtained, from which only 21 plants came up. The authors point out that the greater the dosage, the smaller was the number of seeds per fruit. The external morphology of the seeds was changed by comparison with the control plants. The authors observed: a rounding and a deformation of the stigmae, anastomosis of the veins of the leaves, special forms of leaves, fasciation and thickening of the stems, imperfect flowers, and, finally, dwarf size. From their experiment the authors came to the conclusion that by means of X-rays it was possible to induce quantitative and qualitative changes in the hereditary matter of cotton.

Sapegin, in 1930, presents in his article the results of experiments with wheat. The maximum effect was obtained from a dose at 130 kilovolts, 5 milliamperes, 30 centimeters from the tube, with 1 millimeter aluminum filter and exposures from 20 to 30 minutes (i.e., around 2500 roentgen units). 480 plants from several pure lines of winter and spring wheat were subjected to irradiation. As a consequence thousands of changed descendants were obtained. A large part of the descendants were chromosomic aberrants. Many of the X-ray mutants were defective, but strong fertile specimens, which were of practical interest, were also observed. Eventually (in 1934) Sapegin traced the offspring of the first generation of the X-ray mutants. He pointed out the variegation of this generation and the relative homogeneity of the second generation. The author established special characteristics of mutation for each biological type. Karyological analysis carried out for wheat, tobacco, and

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thorn apple showed that the X-ray mutants, for the most part are chromosomic aberrations. Abrupt anomalies of the chromosomes lead to significant changes of the phenotype, while small changes of the nucleus are conducive to small changes of the phenotype. The relationship between the phenotype and fertility is even closer. Sapegin explains the homogeneity of the second generation by low fertility. The X-ray mutations of winter varieties are very singular; they produce a large number of speltoids: "Zemka"-- 55 percent, "Ukrainka" -- 51 percent, "Saratovskaya" -- 39 percent, "Odesskaya Girka" -- 17 percent, "Kooperatorka" -- 16 percent, "Styephyachka" -- 12 percent. These experiments permit the author to conclude that with the aid of X-radiation it is possible to obtain a greater or lesser variety of chromosomatic aberrations, chiefly sterile ones, and a small number of gene mutations which retain their changes in future generations. From this the selective significance of this new method of creating new forms can be seen. From X_3 of winter wheat "Kooperatorka" a frost resisting X-ray mutation was obtained.

Chekhov in 1930 subjected to irradiation dry seeds of barley, lentils, wheat, and rye. By means of very thorough daily observations he was in a position not only to determine the stimulating or depressing effects of X-rays, but also [redacted] to catch the arising mutations in the early stages of their development. Despite larger doses of X-rays than were used by Stadler, Chekhov obtained only six X-ray mutants from barley. One of these, as a sprout had leaves with a yellow tint, eventually it became still more yellow, and, finally, it perished. Four were typical albinos, and they also perished. The sixth plant had at the beginning of its

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development leaves completely devoid of chlorophyll. Part of them never did turn green and wilted away; the other part turned green after several days, but the green coloring did not come in evenly: in some cases it came in from the tip of the leaves towards the sheath, covering the entire blade of the leaf, in other cases it proceeded from the sheath towards the tip of the leaf, and occasionally the green coloring came into isolated areas in the center of the leaf in the form of tongues, or else only the veins would turn green.

When all of the X-rayed barley seeds were planted at the zonal seed station only four specimens were found with chlorophyll deficiencies.

From among the collected plants grown from X-rayed seeds Chekhov observed in the barley "Chervonets" the following X-ray variations: (1) low growing forms, (2) changes in the distribution of rows in the ears, (3) more frequent occurrence of naked seeds in the ears.

In the winter wheat ("Durable") he observed: (1) low growing forms, (2) more vigorous and more friable ears, (3) ramose ears.

In irradiation of lentil seeds Chekhov observed two albinos, which at first developed on par with the controls, but eventually perished.

The experiments which Delaunay has been conducting since 1928 occupy a special place in the field of genetic effects of X-rays. These experiments were selected not only because they were performed with wheat, which happens to be the most important crop for the

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USSR (which in itself is a very important fact), but these experiments were selected chiefly because they have demonstrated how powerful a factor X-rays can be in creating new biological forms. The X-ray mutations obtained by Delaunay were complex in their phenotypical aspect. Delaunay saw the explanation for this not only in the pleiotropic action of individual genes, but also in the fact that the changes due to mutations depend on whole bundles of genes, as a result of the aberration of the chromosomes. As gene-mutations Delaunay considers in his experiments only certain bearded mutants, those with naked ears, and, probably, the "squarehead"; other X-ray mutants are chromosomatic aberrants. The profundity of the changes is such that taxonomers would not attribute certain of the mutants to the species from which they were derived.

The variety and profundity of the transformations Delaunay had obtained in his experiment presented a picture which reminded one of the development of new forms which can be observed in the descendants of hybrids between distant species. The variety of directions taken by the mutations was so great that among the 64 X-ray mutants very few similar forms are found. In his presentation Delaunay examines the transformations by individual characteristics. 1. Compactness of the ear. In a variety "Delphi" which Delaunay used the compactness of the ear was 3.1 while some of the X-ray mutants had a compactness of 4.4, and others of 1.8. The character of compactness of the ears was very diverse: there were "squareheads", "reverse squareheads", "compacts", and evenly compact ones with long ears. 2. Sizes and shapes of the covering scales. In length the covering scales vary from 5.5 to 10 millimeters; in width, from 2 to 4 millimeters. In

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shape the covering scales are extremely diverse, ranging from blunt and flat scales of speltoids to sharp and pear-shaped ones. 3-4. The beardedness and furriness of ears. These signs vary greatly, just as the length of the hairs does. In X_2 a completely naked [hairless?] X-ray mutant appeared. 5. The waxy layer is developed to different degrees. One X-ray mutant was completely devoid of the waxy layer. 6. Pigmentation of the ears (among the X-ray mutants white, red and black eared ones could be found). 7. Fertility. On the basis of fertility Delaunay divides his mutants into four groups: (a) completely fertile, (b) low fertility, (c) almost non-fertile, and (d) completely non-fertile. 8. Length of growing season. Prolonged growing season seems characteristic for certain of the mutants. 9. Height of plants. The height of stalks varies from 8 centimeters in dwarfs to 79 centimeters.

The changes due to mutations found expression in all aspects which could be observed without recourse to more refined methods of examination.

Delaunay points out the tremendous scope of variation among plants due to the influence of X-rays. He points out the variety of directions that the changes took and the profundity of transformations due to mutations. This permitted Delaunay to select a large amount of material for experiments in the creation of new forms. The new varieties of wheat which he obtained by means of X-rays are already being tested. His experiments are proof, par excellence, of the inaccuracy of the concept that X-rays produce only defective changes, since they show that forms appear which are completely

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viable, and which are in no way inferior, and sometimes superior, to the forms from which they are derived.

In 1931, Horlacher and Killough observed the effect of X-rays on somatic changes of cotton. Most frequently they were able to observe the appearance of dwarfs, then that of branching, and of fused cotyledons. Besides they noted the appearance of wrinkled leaves, whose form indicated that their various parts developed at different rates of speed. All of the plants which had received high dosages of rays (100 kilovolts, 5 milliamperes, with an exposure of 50 minutes, and a distance of 17 centimeters) showed variegation of color in some of their leaves. But plants which had received smaller doses of the rays also had variegated leaves. It would be approximately true to say that the number of variegated leaves was proportional to the dosage used. There were two types of variegated leaves: spotted ones, and those with yellow tissue [veining?] at the edges [corners?]. The first type were of three colors: green, yellow, and white. Such conditions of the tissues can result, according to the authors, either from cytoplasmic changes, or as a result of abnormal conduct of the chromosomes due to effect of X-rays, or of both. They consider the type of variegation which shows up in the corners, the chimera type, most interesting. In their opinion it indicates changes within the nucleus. One plant from the yellow line produced only green leaves; it was depressed in its development and lay prostrate on the ground. The authors consider it quite possible that all growing buds were killed except one which gave rise to the green shoot. Horlacher and Killough assume that their experiments

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indicate the possibility of progressive changes due to X-rays. They consider that the appearance of green leaves on a yellow line, or changes from forked leaves to normal ones are examples of such progressive changes. These facts also indicate that gene-mutations took place in the somatic tissues of the plants.

In 1933 De Mol irradiated flower bulbs of hyacinth, variety "Moreno" at the time when the flower clusters were forming. Having divided the bulbs into four groups he gave them doses of 50, 100, 200 and 300 roentgen units respectively. Among the plants that grew up 49 different anomalies were observed. Meiosis took place normally but the greater part of the pollen became sterile. Sterility increased proportionately with the dosages of irradiation.

Similar dosages were used with tulip bulbs, and in the mature plants 40 anomalies were observed. Chiefly, however, the anomalies were in the flowers themselves which were irradiated while in flower. Their cells were slowed down in the process of cell division, from which stems the disharmony of their development. Summarizing the color changes of the descendants De Mol came to the following conclusions: (1) changes of coloring are most pronounced in those tulips which were irradiated at a time when the process of cell division was at its maximum, (2) apparently the intensiveness of irradiation was related not to the qualitative changes of color but to the quantitative ones.

With various doses of X-rays and depending on the time of irradiation (nearer or further from the time of reduction-division) it was possible to find sometimes completely sterile pollen, sometimes all of the pollen seeds had diploid and tetraploid numbers of

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chromosomes, and sometimes the cells were double or quadruple.

In 1934, MacArtur set up experiments with seeds of tomatoes and spinach (also with hen's eggs), but only the tomatoes gave interesting results. Seeds (variety Vaughen Meerlina) were divided into seven samples, 1000 seeds per sample, one to be used as control and six for irradiation (110 roentgen units, 7 milliamperes, 25 centimeters from the tube, without a filter). The irradiation was performed in doses of 9, 18, 27, 36, 46½ and 60 minutes, the maximum dose was equal to 14½ erythema doses. About 600 control and 1200 irradiated seeds were planted. Among the latter were 8 yellow-white plants with chlorophyll deficiencies which perished without forming leaves. From 346 descendants 43 had clear mutational changes (12.4 percent). The number of mutations was proportional to the dosage: those which had been irradiated for 60 minutes gave 15.9 percent mutants, those irradiated for 46½ minutes gave 8.3 percent. It is possible that higher dosages would have still greater effects, since the lethal boundary had not yet been found. Changes showed up in the coloring of leaves and stem, the form of the leaves, height, branching, and rate of ~~speed~~ growth. The majority of mutations consisted of changes in the plastid mechanism: the cotyledons and first leaves had white or brown splotches or streaks, or they were dark reddish purple and shiny. Some underwent changes in the shape of the cotyledons; 25 percent of their descendants had polycotelydonous sprouts. The shape of the leaf of one of the X-ray mutants resembled a potato leaf, another one had curly leaves. There were also two ultradwarfs, but they had very different leaves. Several X-ray variants were noticeable only by their strongly retarded and squat size. The most

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interesting new forms were those whose top growth was affected. Further investigations showed that all mutations were recessive and single-factored, more than half of the mutations were lethal, some were semi-lethal. The author did not observe either giant, nor fast growing types, nor any which were of any particular value because of their flowers or their fruits, in short there were no superior types which had any economic significance.

Asseyeva and Blagovidova in 1935 used radiation in order to obtain artificial mutations in potatoes. Both soft (64 kilovolt) and hard (180 kilovolt) rays were used. Mutations were found both in the leaves and in the tubers. They noted an interesting peculiarity of the action of the rays on the tubers, specifically the significance of the variety [of potatoes] on the frequency of mutations (Table 18).

Table 18

Leaf mutations of potatoes

(based on the data of Asseyeva and Blagovidova, 1935)

Variety	Number of instances	Variety	Number of instances
"Vol'tman"	23	"Sviter"	7
"Model'"	10	"Epikur"	0

Tuber mutations were found only variety "Vol'tman" (five instances in 10 bushes). From their experiment they drew the following conclusions: (1) the number of mutations increases, generally, in proportion to the number of roentgen units; (2) the effect of short

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and long exposures is approximately equal; (3) soft and hard rays are equally effective; (4) irradiation with intervals or all at once does not seem to have any perceptible difference on the frequency of mutations.

Haskins and Moore in 1935 were observing changes of growth in citrus sprouts due to action of X-rays. Albinism often appears in citrus plants especially in the leaves of hybrids. Under irradiation however an abnormally high percentage evidenced a lack of chlorophyll. This condition varies within wide limits; from those in which all green pigment is absent, through variegated leaves, to full albinism. Besides the authors observed numerous instances of terminal and lateral fasciation, and of twisting of stems, and of duplication. The latter phenomenon was exhibited by the fact that the central veins of the leaves would split near the stem. In some cases, especially in grapefruit, the entire leaf would become double. In lemons this development often leads to the appearance of leaves with two or three leaflets on the same plant. In two grapefruit plants the appearance of cup shaped leaves was observed.

Krayevoy, in 1935, in irradiating a pure line of Pisum sativum vulgare with a dose of 1000 roentgen units, found that this dose was semi-lethal. Among the progeny there appeared plants which by their phenotype were completely distinct from normal ones. In another experiment, with the action of doses of 250, 500 and 750 roentgen units, aberrant karyotypes were found. They had unpaired chromosomes, which had not undergone secondary division, and which were abnormally thick. A certain number of aberrants remains in X_3

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and for that reason the author calls this type the delayed modification of the karyotype. He observed that as the dosage is increased, the percentage of aberrants increases (Table 19).

Table 19

(based on Krayevoy's data, 1935)

	X_1		X_2		X_3	
Dose r	No.	%	No.	%	No.	%
250	2	4	0	0.0	0	0
500	9	18	2	0.2	0	0
750	17	34	5	0.5	1	-

These plants differed in phenotype from the plant from which they were derived.

In his third article, devoted to the question of the effect of X-rays on plants, Krayevoy raises the question of whether it is possible to obtain useful types by the experimental method, and answers the question affirmatively. He points to the works of Sapegin, MacKay and Goodspeed, Horlacher and Killough, and also to the unpublished work of Giyyemino, who obtained two useful mutations from a pure strain of barley: (1) with reduced beards and (2) with a longer ear.

Ternovskiy [Ternovsky in bibliography] in 1935, was studying the character of mutations, due to X-rays, on male and female gametophytes in various stages of development. Flower buds of Nicotiana

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taliacum, Solanum melongena and S. annuum were subject to irradiation (65 kilovolts, 2-3 milliamperes, without filter, at a distance of 25-27 centimeters from the anticathode). Doses were varied depending on lengths of exposure from 1 to 30 minutes. All plants of S. melongena perished from all doses which were used. From S. annuum he succeeded in obtaining one fruit with a small number of seeds. In X_1, 18 plants came up and neither they, nor any of the plants of the succeeding generations, showed any deviations. The tobacco turned out to be least sensitive to X-rays and in all doses a certain number of seeds were obtained. The flower buds of tobacco behave variously in relation to X-rays. Young flower buds, i.e., before reduction-division and during it, were considerably more sensitive to irradiation than the more mature buds. Natural mutations in tobacco are quite rare (as Goodspeed points out) and in Ternovskiy's experiments from 36,000 control plants not a single mutation was located. Seeds from the irradiated buds exhibited low sprouting energy. As early as the sprouting stage a number of peculiarities were observed: narrow leaves, very furry ones, those retarded in growth, and ramose ones. In the adult stage he observed the most varied mutations, a fact which made the classification of deviations more difficult. The various mutations were encountered in various frequencies, but most often the narrow leafed form was encountered. In general, the number of mutations obtained was directly proportional to the doses. Ternovskiy set as one of his aims the determination of the significance of sex in his experiments. He used the following method: before irradiation the flower buds were measured and numbered. After irradiation each bud was castrated and the pollen was

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collected in separate little packages. This pollen was then used to pollinate castrated but unirradiated buds. The castrated and irradiated buds were pollinated with normal [unirradiated] pollen. In X_1 7,305 plants were examined. The total percentage of mutants from irradiated male sexual cells was significantly higher than from the irradiated female cells. As far as the character of mutations is concerned, the author did not establish any differences in the descendants of the male and female sexual cells. In contrast with this, differences in varieties acquire great significance: an experiment in 1932 showed that Dyubek Nikitskiy gave 44 various deviations, Dyubek Gaprinskiy gave only 2 deviations, which soon perished, and no deviations in X_2. The second generation of Dyubek Nikitskiy very characteristically showed deviations in the offspring of those plants which did not reveal any deviations in X_1. Then this experiment was expanded by the irradiation of four genotypes: Nicotiana tabacum var. macrophylla, var. chinensis, Dyubek Nikitskiy, and a Persian [Iranian] variety. All told 2,800 plants were used. The variety chinensis and the Persian variety gave a very insignificant number of deviations in leaf forms. The variety macrophylla did not give a single X-ray mutant, but in one family a haploid was found. Analysis of this material indicated that the penchant towards giving rise to hereditary deviations under the influence of X-rays is specific for the genotype.

In general the isolated mutants are heterozygotes which are split in X_2. This property of descendants is explained by the fact that under the influence of irradiation changed sexual cells arise alongside normal sexual cells. Various combinations of the two gave

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a checkered heterozygotic picture in X_1. Observations of X_2 and X_3 showed that extreme deviations: extremely narrow leaves, variegated leaves, and white color of stems were usually not hereditary, and their descendants returned to the original forms. Cytological investigations showed that these instances were due to chromosomatic aberrants, chiefly monosomatic ones. However, gene-mutations were also observed. In X_2 3.9 percent of X-ray mutants were found. However the percentage of mutants varied greatly, reaching 30-40 percent in some families. Biometric working over of X_3 has shown that as far as the shape of the leaves is concerned the investigated families have formed a new biometric series with a displacement in the direction of having more narrow leaves. On the other hand hereditary broadleafed forms have also been found. Examination of stable gene-mutations in X_3 and X_4 has shown that they have a normal number of chromosomes ($2n = 48$) and that their reduction-division is normal. Among the irradiated descendants of Dyubek Nikitsky and N. tabacum var. macrophylla in X_1, X_2, and X_3 five haploids were found. They were characterized by low stature, small flowers, and complete sterility. Ternovskiy approached the use of X-rays, as a means of obtaining mutations of practical value, with considerable circumspection. In any case, he felt that, at the present stage of development, X-radiation could not replace cross breeding, which leads to whole outbursts of new forms.

Lutkov published in 1937 several articles describing gene-mutations produced by the influence of X-rays in peas and barley. As source material he used in his experiment (1937 a) two strains of Pisum sativum. The first strain (D. S. 276) was obtained from a

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London horticultural institute from Pellew, the second (D. S. 228) was obtained from Wellensiek from Holland. Young flower buds were subjected to radiation, the doses varied from 300 to 2500 roentgen units. The percentage of fruit which would begin development as a result of fertilization by radiated pollen fell sharply as the doses were increased. A dose of 2500 roentgen units had a lethal effect on the pollen. The number of developing seeds in the pods was sharply cut down as the dosages of X-rays were increased. While a dose of 300 roentgen units gave from 4-6 seeds per pod, a dose of 1200 roentgen units cut this number down to 1-2. Very frequently despite the development of the fruit (i.e., the pods) there would be no seeds inside. In X_1 only 490 plants grew up, which differed from one another in the power of their development and in morphological changes. Cytological examination of the number of somatic chromosomes in plants of X_2 revealed, in one family, the appearance of trisomic forms with 15 chromosomes. The additional chromosome induces sharp morphological changes. So one plant was distinguished by very thin trailing stems, characteristically thin and wide, very large and stretched-out stipules with smooth edges. The leaf blades also had an elongated form, the flower stems were thin, the flowers were smaller than normal ones with a somewhat underdeveloped and narrowed middle petals. This trisomic plant, 60 percent of whose pollen was abortive, turned out to be completely sterile under self-pollination. Another trisomic plant had rough, leathery leaf blades, with a narrowing of the internodes, and it was partially fertile. A third trisomic plant stood out sharply first by its variegated leaves and by a diminution of the leaf blades. It was completely infertile.

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In addition, in one of the seeds of X_3, in one of the descendants of a partially sterile plant, a tetrasomic form turned up; it had 16 chromosomes instead of 14. It was entirely sterile.

As for gene-mutations, Lutkov found only two instances of chlorophyllic changes, an albino and one with a golden yellow color of leaves. Mutations of the fasciative type were more frequent. This type of mutational change (which along with the fasciation of the stem, induces a stemminess of the plant with the distribution of the flowers near the top of the plant in the form of an irregular umbrella) is definitely of interest from the agricultural point of view.

As for the second subject of Lutkov's experiments with X-rays (i.e., barley -- 1937 b), the author used doses of 400, 600, 800, 1000, 1200 and 1400 roentgen units. All told, 876 sprouts were irradiated. It became apparent that doses of 1200 roentgen units were sublethal and that stronger doses (1400 and 1600 roentgen units) caused all the plants to perish in the initial stages of development. In studying X_2 several chlorophyll mutations were found, and also an interesting form of barley which lacked ligules. Since the plants without ligules appeared among the descendants of a single ear, which only produced four seeds (another ear produced plants all of which had ligules), Lutkov expressed the supposition that in the given instance, as a result of X-radiation, a somatic mutation occurred in one of the cells which produced the single ear and stem. Final confirmation of the nature of the mutation of this plant was obtained from X_3. This form of barley without ligules turned out to be stable and produced in X_3 only liguleless plants.

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In another experiment (1937 c) the author used as his source material the Abyssinian barley Hordeum distichum var. Stendeli Körn., a typical spring plant. The plants were irradiated at the stage of ear formation, at a time when the already formed pollen grains were maturing. Doses of 500, 1000, 1500, 2000 and 2500 roentgen units were used. The 2500 roentgen unit dose was the maximum subletha1 dose. Analysis of 7 355 plants from X_2, which represented the descendants of 213 plants in X_1 (besides a whole series of chlorophyll mutations of the albino, pale cream, yellow and variegated types), produced a form of winter barley. These plants, which had been left out to vegetate under field conditions until the middle of September and which were then transferred to a greenhouse, retained their winter type, continuing to thicken (i.e., to produce additional stems). An anatomic examination of the points of growth showed that the cone of growth in these mutational forms of barley is of a characteristic winter type, i.e., in the cone of growth only the embryonic differentiation of leaves is found, but no differentiation of embryonic flowers. Consequently by both their general habits and by their anatomical structure these winter type plants must be considered to be true winter forms of barley. The character of the splitting in X_2, and also in X_3 and X_4, of the heterozygotic seeds indicates that this particular mutation is a recessive one, apparently produced by a transformation of gene S (spring type) into gene s (winter type).

In a third experiment (1937 d) with X-radiation sprouts, dry seeds, and ears were exposed. Analysis of X_1 of this experiment indicates that the basic type of deviations was the narrow leafed form of the plants, which varied greatly depending on the stage of its

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development. Side by side with almost needle-like forms it was possible to observe plants with insignificant deviations from the control. The narrow leafed forms had a low viability and complete sterility. A very small number of these plants reach the stage of ear formation; these ears, it should be noted, have nothing in common with the double rowed type of ear from which they are derived, rather they remind one of Aegilops. Other types of "X-ray morphs" were two eared forms with cylindrical ears (with a development of additional ear membranes at the base of the ear), then plants with a more compact type of ear, plants with less compact [i.e., looser] types of ears, etc. Analysis of subsequent generations demonstrated that all of the types of "X-ray morphs" enumerated above are not hereditary deviations and in X_2 produce normal looking plants. However an analysis of X_2 revealed many gene-mutations of the recessive type, which arose as a consequence of X-radiation and which were found in X_1 in a heterozygotic condition. The bulk of these changes consisted of various chlorophyll deviations. The frequency of mutations increased with the increases of the dosage (Table 20).

Table 20

(based on the data of Lutkov, 1937)

Dose r	Number of examined ears	No. of ears which are heterozygotic due to appearance of mutations	Percentage of mutations
400	201	2	0.99
600	160	3	1.87
800	163	3	1.84
1000	131	3	2.29
1200	139	4	2.87

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The percentage of mutations was determined by the relationship of the number of plants which are heterozygotic due to mutational changes of ears of X_1, to the total number of examined ears for each dosage, the hereditary character of the changes being checked in X_3.

The basic type of chlorophyllic mutations of the sprouts were mutations of the "albino" type. These were sprouts devoid of chlorophyll which would develop 2 to 3 leaves and then perish on the 12 to 15th day of their development. Then followed mutations of the virus type (white-yellow, yellow-green, and pale yellow mutations) characterized by lateral and longitudinal stripings of the leaves, etc. All of these chlorophyllic deviations which appeared in X_2 in a homozygotic condition are recessive mutational changes of a lethal type. An exception is formed by a single type which is characterized by a longitudinal striping of the leaves. This character varies in its expression at various stages of development of the plant. At the beginning of the growing season these mutational forms present the appearance of perfectly normal green plants, on the 20th to 25th day on the newly appearing leaves white stripes begin to appear, these stripes are narrow at first, then gradually they begin to cover greater and greater areas of the blades of the leaves. Finally, leaves appear which are nearly completely white, and only a small part of these mutational forms ever reach the stage of ear formation. The character of the splitting of the phenotypically normal plants of X_2 indicates that this mutation is of a recessive type.

In addition to the mutational changes of the chlorophyllic

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ligueless and winter types of barley, the X-radiation of dry seeds produced a hereditary type change of the ear which resembled the ears of Hordeum intermedium. The ears of this mutational form exhibited branching, forming at the base of the ear branch ears which were somewhat deformed in appearance. The number of grains in the ramose form of barley in some cases reached 25 to 28 while the two rowed ears of Hordeum distichum var. Stendeli the number of grains varies from 18 to 22. This mutational form remained stable even in X_4. The character of the splitting indicates that the given mutation is a recessive mutation of a single gene. Still more singular was the mutation which resulted in the almost complete deformation of the ear. It was characterized by the underdevelopment of individual ears along the length of the ear, by absence of flower membranes, ovaries, and anthers, and by distortion of the axis of the ear. When individual seeds of this mutational form were planted it proved to be completely stable in X_3.

In addition to all the above mutations, five dwarfs were found in X_2, they proved to be stable and fertile.

In 1940 Joung [This should be Young and not Joung. See bibliographical reference on page 95 of the book] observed the occurrance of a new mutation of from irradiated tomato seeds. This new character remained constant for two generations. Apparently this mutation is homozygotic. When the new X-ray mutant was crossed with the normal plants, which had yellow colored corollas the latter dominated in F_1, and a typical monohybrid splitting was observed in F_2.

In 1940 Gustafsson and Ewert obtained two mutations by ir-

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radiation of seeds of a pure strain of barley "Gullkorn". These mutations (one of them a double flowered mutation and the other with changed scales) are interesting from a selective point of view since they indicate that is is possible to obtain mutations which go beyond the limits of normal changes of cultivated crops which give a high yield.

We can now turn to a description of the works of Stubbe who investigated the effects of short wave rays on plants continuously from 1927 to 1940. The first work was taken up with the purpose of sounding out Baur's investigations (which were begun in 1927) on obtaining mutations experimentally. As source material he used the descendants of the same strain (A50) of snapdragons that had been used by Baur. This homozygotic family continued to multiply by way of self-pollination. Stubbe used a voltage of 5 to 10 kilovolts, 5 to 10 milliamperes, the distance from the anticathode was varied from 10 to 20 centimeters, and the exposures were varied from 5 minutes to 5 hours and 20 minutes. However an even greater number of experiments were carried out with a voltage of 20 to 70 kilovolts. Flower buds at various stages of development were subjected to radiation. This was quite possible to do with a single inflorescence, in view of the clusterlike shape of the inflorescence of Antirrhinum majus. The immediate consequence of X-radiation was that all of the buds which were undergoing reduction-division underwent a serious delay in development. This delay can be so marked that further development becomes impossible. Other buds develop into flowers but they become infertile, although the point of growth continues to develop. Sometimes he observed zones of depression of growth which affected up to 10 buds. After that normal flowers appeared again.

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In 1928 77 plants were irradiated and in 1929 4507 sprouts were selected from X_1, [redacted] of them 397 had clear indications of transformation. Stubbe found 30 dwarfs, 209 narrow leafed plants, 5 which resembled the radiomorphs described by Stein in 1937, 11 with variegated leaves, 9 with blue-green leaves, 4 with transmuted flowers, and 126 depressed plants.

In a second series of experiments, performed in 1929, from each of the transmuted plants (all of them were self-pollinated) seeds, from a single pod, were planted. The description of morphological changes, presented by Stubbe, indicates that the action of X-rays induces the appearance of an unusual variety of forms. At first Stubbe called them mutations only conditionally, but further experiments showed that a large part of these changes had a hereditary character. Stubbe divided these changes of form into five groups.

I. Dwarfs

Among them the most extreme deviations from the norm are represented by plants whose points of growth are absent. With age the storing up of nutritive substances in the leaves causes a puffing up of the epidermis in the region of the point of growth from which, eventually, new shoots issue bearing barrow leaves. The viability of such dwarfs is negligible. Other plants reached a height of 14 centimeters, these were semi-dwarfs. One of them had two flowers which were infertile (in the male parts), the tubules of the corolla were split as far as the calyx. A third type of dwarf plants displayed negligible growth with a strong inclination toward branching and plagiotropic direction of growth. The leaves of all of the dwarf plants are very narrow, small, and often possess needlelike points on their

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ends.

2. Narrow Leafed Forms

The width and length of leaves, the type of branching, the form of the flowers, and the fertility of these flowers vary within very wide limits. The narrow leafed forms are usually accompanied by splitting and other deformations of the flowers. The most extreme change which accompanied the narrow leafed type was represented by a single plant whose petals had a tendency to turn green, the anthers were absent, and, apparently, formed part of the gynecium, the style was funnel shaped, the upper and lower labia were shortened. Nearly all of the narrow leafed forms had their fertility disrupted. In the majority of the plants the anthers were quite brown, empty, or else they were filled with white empty pollen.

3. Plants Resembling Radiomorphs

These ~~which~~ had been described by Stein as resulting ~~which resulted~~ from exposure of snapdragons to radium. This type of mutants can be recognized very early since even in young plants dark streaks appear on the blades and the leaves become wrinkled. This wrinkling intensifies during the growth of the leaves and determines their deformation. In especially strongly transformed shoots the wrinkling of the leaves carries over into the flowers which causes the upper and lower lips to tear and round out. However the fertility of such plants is completely normal. Some shoots at first display these changes, after which the development assumes the normal course. When flowers of this changed branch (stain) are self-pollinated, among the descendants appear individuals with distorted flowers having irregular numerical relationships (of parts).

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4. Plants with Variegated Leaves of the Albi-Maculata Type

The hereditary characteristics are transmitted only by the maternal line. One X-ray mutant (basiflora) is of particular interest. Its sprouts are at first green, then, after several weeks, they become variegated. At the same time the young leaf blades are green only at their tips, the central part of the leaf is white and begins to turn green (starting at the central vein) only with age. Old leaves have the normal green coloring.

5. Depressed Plants

While remaining phenotypically normal these plants lag behind their age group in development and have an extremely lowered viability.

In further experiments in 1930 Stubbe worked out the methodology of the experiments more thoroughly. Seeds and sprouts were subjected to X-rays. The seeds had been previously soaked for 2 to 3 days in water. The sprouts were irradiated when they were 3 to 4 weeks old, at a time when the cotelydons had attained their full development and the first leaflets were beginning to appear. Only 20 to 50 percent of the seeds came up and after a day of retarded development, further development proceeded quite normally. From the irradiated seeds 8230 were selected and from among them 27.42 percent turned out to be mutants. The irradiated sprouts gave 29.17 percent mutants.

As has already been pointed out above Stubbe was dealing with and extraordinary object, since these snapdragons had for a great number of years been under Baur's care. The latter developed many

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pure strains of this plant, and had studied many genes which determined its characteristics and properties. Baur's long experiments revealed, incidentally, that each strain has its own coefficient of mutation. Strain "50", which Stubbe used for his experiments, had a relatively low coefficient of mutation, only 1 percent. By the use of high doses of X-rays this coefficient was raised up to 300 percent.

In these same experiments Stubbe established the dependence of the frequency of mutations on the size of the dose. The table presented below proves this since for all doses, the number of mutations increases as the dose is raised (table 21).

TABLE 21

The relationship between doses and the frequency of gene-mutations after irradiation of buds.

(based on data of Stubbe, 1930)

Dose, r.	Culture	Gene-mutations	Percent
100	202	7	3.46 ± 1.29
200	151	6	3.97 ± 1.59
400	241	3	1.24 ± 0.79
800	204	9	4.41 ± 1.44
1600	265	10	6.03 ± 1.46
3200	122	19	15.57 ± 3.28

In the following article Stubbe works on the question of which stage (of development) is most sensitive to X-rays. With this aim in mind he studied the X_3 generation and discovered that the majority

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of the gene-mutations occurs in those buds which at the time of irradiation had finished reduction-division. From 80 mutations 58 descended from such flower buds and only 22 from buds which were undergoing reduction division [at the time of irradiation] or had not yet undergone it.

Already in his first experiments Stubbe discovered that the frequency of mutations after irradiation is not identical for both sexes of snapdragons. This caused him, eventually (in 1933), to set up experiments with irradiation of mature male gonads. He considered that if this stage of male haplophase will show the same high X-ray sensitivity as immature gonads that the experimentor will obtain considerable advantages. In the first place, a desired uniformity in the stage of development for irradiation will be obtained. In the second place, it will not be necessary to worry about absorption of soft rays by somatic tissues. In the third place it will be possible to make an exact count of the frequency of gene-mutations.

The methodology of the experiments consists of the following: pollen from flowers which have just bloomed is placed in a thin layer on parchment paper, and, immediately after irradiation is transferred to the stigmae of castrated plants. For irradiation he used both soft (30, 50, and 70 kilovolts with filters) and hard (125 and 175 kilovolts with filters) rays. The results of this experiment were amazing: in both divisions of the experiment completely unexpected, but identical, curves for frequency of mutations were obtained. The curves rose up to 400 roentgen units, then fell to 1600 roentgen units, and after 3200 roentgen units rose again. From this it seems clear that even such great differences in voltage as 10 and 175 kilovolts do not have any effect on the

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frequency of mutation, everything depends on the quantity of roentgen units. These curves are the resultants of two completely independent biological processes. On the one hand this is the expression of relationship which exists between doses of irradiation and frequency of mutation, and on the other hand it is due to the gradual killing off of the pollen grains by increasing doses of X-rays.

The explanation of the drop in the curve between 400 and 3200 roentgen units, according to Stubbe, lies in the fact that the rays affect within the nucleus of the cell areas of different sensitivity, one of which gives mutations with low doses (up to 400 roentgen units), while other produce mutations only with doses of around 3200 roentgen units. This explanation of the author finds confirmation in the fact that in all of the fully investigated objects (Drosophila, corn, etc) labile loci were found. Consequently there is nothing surprising in that they should, under changes in external conditions, vary more frequently than other areas. Besides this hypothesis is bolstered by the fact that from the 18 mutations obtained by irradiation of 400 roentgen units, four are obtained many times and only four appeared at first. It is obvious that the 400 roentgen unit dose affects the more labile areas. If we call genes which change frequently, "labile genes", it will become clear that with the 400 roentgen unit dose the percentage of mutations of labile genes reaches 78 percent and then falls from dose to dose, and that with 3200 roentgen units it only equals 25 percent. On the other hand as doses increase the percentage of mutations of new genes, which appear for the first time, rises.

Besides, in his previous work in 1932 Stubbe established that genes which affect vegetative organs show an increase in the

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percentage of mutations with each increase of dosage, while genes which determine the shape and color of the flowers do not show any rise in the number of mutations (in comparison with irradiated plants). From these facts we can conclude that genes which determine the characteristics of generative organs are extremely stable or that the process of mutation is related to various stages of development.

The results of irradiation of Crepis Tectorum obtained by Gerasimova in 1940 are very interesting. Mature ovicells were subjected to X-radiation. The peripheral flowers were castrated and one half hour after irradiation (by 2800 X-ray units) were fertilized by normal pollen. In 1934 from 20 seedbuds of one inflorescence 8 sterile plants were obtained, 7 of them had normal chromosomes, one was a translocated one (i.e. an interchange of parts of the B and D, Chromosomes took place). This latter plant was non-fertile under self-pollination, but under free pollination it produced 972 seeds from which (in 1935) 200 plants were grown and subjected to analysis. It turned out that these descendants could be divided into three groups: (1) typically normal plants, (2) plants which repeated the conduct and external appearance of the original trisomic plant (based on the B - Chromosome), and (3) underdeveloped dwarfs. Cytological investigations revealed an extremely interesting phenomenon: the genetic specificity of parts of the chromosome. The distal end of chromosome B displaces the balance of the genes, and creating external effects; at the same time, the proximal end (of the B-chromosome) does not produce this effect. Besides, it turned out that if, at one of the stages of development, in the cells of the cone of growth a partial loss of the distal end of the B-chromosome should occur, then monstrous, dwarf, and generally abnormal forms will develop.

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CHANGE OF SEX DUE TO EFFECTS OF X-RAYS

In 1936, Knapp and Schreiber irradiated Sphaerocarpus Donnellii in three various stages: (1) shortly before reduction-division, (2) very young tetrads after reduction-division, and (3) mature spores. They used high dosages of X-rays (from 1000 to 15,000 X-ray units). The experiments showed the variable sensitivity of these stages, the young tetrads shortly after reduction-division turned out to be most sensitive, mature spores were the least sensitive. As is well known, sex in this is mostly determined on a strictly genetic basis. The diploid spore mother cells (with 14 + X + Y chromosomes) always develop into 2 female haploid spores (7 + X) and 2 male haploid spores (7 + Y).

When the control spores are planted they always produce 50 percent male and 50 percent female plants. When the spores are irradiated one always observes a predominance of male specimens. This predominance becomes more pronounced as the doses are increased. Analysis of the tetrads shows that this shift is due not only to selectivity, or a greater depression of the viability of the female plants, but also to a transformation of females into males. Cytological examinations confirm this premise. If the tetrads had 3 male spores then two of them had 7 + Y, and a third had 7 + an incomplete X chromosome or a fragment of it. Apparently, that piece of the chromosome is lost which carries the female determinant. The transformed male specimens showed little difference from normal male plants; they had normal anthers. In general however they were more robust and they developed more quickly. The authors explained this increase in size of cells and organs as due to the effect

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of an increased amount of chromatin. However the formation of spermatozoa in the transformed specimens was disrupted. The spermatozoa were feebly motile, and they were sterile.

INVESTIGATIONS PERFORMED IN THE ELECTROBIOLOGICAL LABORATORY

As has already been pointed out, in the first part of this book, our experiments were performed in a laboratory which can really be called an electrobiological laboratory and which while changing its location retained its purpose and program. The following personnel participated in the work:

Atabekova, Afanasyeva, Breslavets, Medvedyeva, and Tom

Rye

In our experiments with rye, among plants whose ears had a normal shape and size, we encountered X-ray mutants which differed in this respect. The most obvious ones were ears with branching, then those with short and compact ears (which reminded one of squarehead wheat by their shape), then those with triple flowered ears, and also wide and flat ones, spindle shaped ones, and abnormally thin ones. Consequently it was possible to obtain, by means of X-rays, several new forms, from which a selection could be made.

The most interesting, from an agricultural point of view, were two X-ray mutants: (1) with ears of the squarehead type and (2) with triple flowered ears.

When sprouts of rye (of variety "VYaTKA") were irradiated by a dose of 250 roentgen units two tetraploid plants turned up.

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Measurements indicated that the diameters of the roots and pollen grains, in the first year, showed a noticeable enlargement. However the general behavior of the plants wasn't any different than that of the normal controls. However on the following year the descendants of these plants (generation X_1) had ear scales of completely unique shape. They reminded one of the scales of single grain wheat. As a result of this the ears also had a different appearance from the ears of diploid plants.

Just as other investigators, we observed among irradiated plants many sprouts with variegated leaves and many albinos. The latter increased as the doses were increased. The variegation of leaves was most varied: most frequently these were plants which had yellow or pale yellow stripes on the leaves, which gradually disappeared with age, and the plant would finish its development with leaves which had normal green coloring. In some plants however this striped condition was retained till the plants were ripe. The more pronounced was the variegation of the leaves the more poorly did the plants develop and the smaller were their ears and grains.

It was also possible to establish a definite regularity in the action of X-rays on the behavior of rye. The higher the dosage, the greater was the number of dwarfs and depressed plants.

The changes produced by X-rays in hemp are extremely interesting. In hemp it was possible to observe the appearance of all of the variations which other investigators had described in other plants. Seeds of hemp (which had been soaked for 24 hours) were subjected to gradually increasing dosages of rays ranging from 1000 to 10,000 roentgen units, inclusive. Very soon after being planted

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the effects of heavy doses (beginning with 6000 X-ray units) began to tell on the development of young plants. They began to lag in size behind the control plants (and those which had received small doses). In addition these plants began to show various morphological changes.

Most frequently one observed a change in the typical bright green coloring of the hemp leaves. White spots of various sizes appeared on them. Sometimes the whole leaf blade would be covered by fine white dots. These variegated patterns sometimes had a sharp contrast between the white and green textures and sometimes they were washed out and not obvious. In rare cases half of the leaf would be entirely devoid of color (figure 10. Hemp leaves, half devoid of chlorophyll). If the plant reached full maturity the number of spots on it could be seen to diminish. In addition, these spots would become more colored with time, becoming yellow, or pale green. Plants which had received very large doses of X-rays exhibited a very interesting peculiarity in the development of their leaves: if the colorless area covered half of the leaf, or slightly less, then that part of the leaf would die off with age, but the green part of the leaves would remain viable as long as the plant remained alive. In rare instances real variegation of leaves would be retained during the whole course of development. These plants had a very handsome appearance. The fixation of such variegated forms for decorative purposes is worth consideration. The variegation of leaves which we observed was, apparently, caused by irradiation since among our controls we did not find a single variegated plant. It is very interesting to note that as doses of X-rays are increased

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the number of plants with variegated leaves increases, as can be seen from the Table below (table 22).

TABLE 22

The action of X-rays on Hemp Seeds

(based on data of Breslavets 1939)

Dose	Survival			% of change of male flowers into hermaphrodites	% of variegated leaves	% of deformation of leaves
r	Total	Male Plants	Female Plants			
Control	82	42.7	57.3	34.3	-	1.2
1000	82	41.0	59.0	58.4	13.4	19.5
2000	73	49.3	50.7	60.0	59.6	36.1
3000	62	51.6	41.1	75.0	68.2	53.9
4000	51	33.3	64.7	72.2	59.3	47.2
5000	51	31.6	65.4	64.7	61.2	63.2
6000	45	37.8	62.2	52.9	86.6	95.5
7000	29	31.6	68.4	50.0	75.0	85.7
8000	27	37.6	62.3	55.5	88.9	88.8
9000	11	-	-	-	100	100
10,000	13	-	-	-	100	100

Beginning with the 1000 roentgen unit dose the percentage of plants with variegated leaves invariably grows and only with 7000

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roentgen
[redacted] units does the number of variegated plants fall somewhat in comparison with the action of the 6000 roentgen [redacted] unit dose, thus giving the double humped curve which is typical for the action of X-rays. When the doses are raised to 9000 and 10,000 roentgen [redacted] units all of the plants at the beginning of their development have variegated leaves; the greater part of these plants, however, dies before reaching the blooming stage. On many plants, particularly on those which had received especially large doses of rays, it is possible to observe the appearance of deformed leaves. The deformation usually consists of the fact that the compound leaf of hemp becomes simple (fig 11. Deformation of leaves in young hemp plants.) or sometimes it comes to resemble fern leaves. The deformation of leaves becomes more frequent as the doses increase in size. With doses of 9000 and 10,000 roentgen [redacted] units all of the plants exhibit leaves which are deformed to a greater or lesser extent (Table 22). This phenomenon follows the same regularity that is found in the change of color. Measurements of two month old plants indicate that doses of rays up to 4000 roentgen [redacted] units, inclusively, stimulate the development of the plants. (table 23).

TABLE 23

(based on date of BRESLAVETs, 1939)

Dose, r	Length of stems	Difference	Dose, r	Length of stems	Difference
Control	30.9 ± 1.0	-	5000	24.9 ± 1.5	6.0 ± 1.8
1000	35.7 ± 0.9	4.8 ± 1.3	6000	22.5 ± 1.6	8.4 ± 1.9
2000	36.3 ± 1.4	5.4 ± 1.7	7000	21.9 ± 2.0	9.0 ± 2.2
3000	35.7 ± 1.8	4.8 ± 2.1	8000	24.3 ± 2.1	6.6 ± 2.3
4000	33.9 ± 2.1	3.0 ± 2.3			

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Apparently it is necessary to do some work within these limits with the irradiation of hemp seeds, since this experiment shows statistically significant increases in the length of stems with the action of definite doses of rays. Since these data present an interest for agriculture they should be considered with redoubled care. Beginning with 5000 roentgen units the depression of size sets in and in doses of 9000 and 10,000 roentgen units all plants are dwarfs (fig 12. a-dwarf, b-normal plant). Besides the number of surviving plants is too small to be compared with plants which have developed more or less normally: for that reason facts have been excluded from the table.

Besides these qualitative changes of stems, dichotomy was observed at various heights, sometimes near the top (fig 13. Dichotomy of the top of the stem in hemp.), and sometimes near the base of the plant. Another change in the stem is determined by the cessation of development of the top bud, which gives rise to monstrous forms. In some cases this change is accompanied by extreme deformation in the leaves which completely changes the behavior of hemp (fig 14. Cessation of development of the top bud and extreme deformation of leaves, in hemp).

As has already been pointed out in the survey of literature, sex can also be changed by the action of X-rays. The same could be expected in hemp which happens to be labile in relation to sex. However before turning our attention to the change of sex we should examine the variable survival of plants on the basis of sex (table 22). The total number of plants which reached the flowering stage was 82 in the control and it remained the same for the 1000 roentgen unit dose, however, beginning with 2000 roentgen units the

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number of surviving plants begins to fall, irrevocably, so that with the highest dosages we have only 11 to 13 plants surviving. If the effect of irradiation on male and female plants is examined separately it will be noted that the slight initial predominance of the female plants, in the controls, is supplanted by a two to one predominance of female plants over the male. This predominance of the female plants leads one to believe that they are very stable in relation to X-rays. The first of the specific changes of the male inflorescence are changes in the bract and perianth. The imitation of pistils is all the more complete in that their ends acquire a reddish tinge. All of the plants (controls as well as the irradiated plants) were subjected to identical conditions, i.e. during 11 days they were subjected to shortened days and only after that period did they receive additional light. As is well known under these conditions hemp changes its sex. Our plants did not avoid these changes; however, the observations of external changes were limited chiefly to the male plants, since the changes of sex can be observed more readily in them than in female plants. Observations of the control plants revealed that due to the influence of the shortened day 34.3 percent of the male plants changed their sex. Irradiation intensified this process which increased as the doses were increased (as can be seen from table 22). The number of male plants which changed sex under influence of irradiation increases up to 3000 roentgen [redacted] units, after that the process becomes somewhat disorderly. It would not be fair to expect an evenness of the process, since it is also affected by the factor of differential viability of the sexes. From this we may conclude that plants which have undergone the most profound changes, including sexual changes, are the first to perish. As a result of irradia-

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tion not only does the number of transformed plants increase but the changes are more profound than in the control plants. The changes produced by 2000 roentgen units were so great (fig 15. Change of sex in hemp due to action of X-rays. Male plant. Above are staminate flowers, in the middle nearly ripe seeds, below are some male plants which are partially transformed into female plants, stigmata can be seen.) that some of the male plants produced seeds which eventually grew up normally. One plant which at first developed as a pure female plant eventually produced a branch near the top which had only male flowers on it. In this way chimeric plants were produced. Another plant which at first was a typical female plant eventually produced male flowers which were distributed on various stages of the inflorescence. There was still another plant which was neither male nor female in character and which had female flowers alternating with male ones. There were also plants which a had male inflorescence but only female flowers.

These examples are completely sufficient to show the wide diversity of forms which arise from the simultaneous action of the shortened days and X-rays. These observations show that irradiation does not induce any new changes of sex, but it does intensify or accelerate these processes, the action becoming more marked as the doses of rays are increased.

Summarizing the experiments of numerous authors who studied the effects of X-rays it is possible to confirm the tremendous significance of X-rays as a stimulator of mutations. There are no aspects which cannot be changed by its influence.

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The most frequent change described is that of size. It is sufficient to point out that all of the authors note the appearance of dwarfs in the descendants of irradiated plants, and, occasionally, also of gigantic forms. Since these changes concern the most diverse plants, belonging to different species, we can conclude that with the help of X-rays we can create plants of desired size. From bast plants we require a high, even stem, since the height of the plants is correllated with the length of the fibers. By adjusting the appropriate dose of X-rays for action on the plants we can select from among the new forms that arise those which are useful, fix them by heredity and obtain new material for selection of bast plants. From among decorative plants we can easily obtain dwarf forms since they occur very frequently.

The general behavior (or characteristics) of the plants changes just as frequently. Many investigators succeeded in obtaining by irradiation forms with very little branching as well as forms which branched a great deal. Plants which don't branch much and which have few stems are very valuable among plants which produce bast fibers. On the other hand, in plants which are raised for the green mass, such as fodder grasses, having much branching and many stems is an asset.

The action of X-rays is capable of producing great changes in leaves, which affect their form, color, and structure. In plants where the size of the leaf is of prime importance (tobacco, tea, etc) from among the X-ray mutants it is possible to select those with large leaves. The wide range of leaf changes can be used for decorative purposes, using as source material some-

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times wide leaves and sometimes narrow, needlelike ones to create new forms which are so prized in horticulture. Changes in leaf structure can serve the same purpose. It is sufficient, for example, to produce a wrinkled appearance with certain parts of the leaf blade blown up in order to achieve the purpose. All these changes can only be welcomed by horticulturalists since they increase the variety of available plants. To this must be added the variegated coloring of the leaves which also arises quite frequently as a result of irradiation. Leaves lose their coloring either completely or partially, in which case the most curious distributions of white or yellow spots or stripes can be observed. What unusual decorative forms can be created by combining changes of form and coloring of leaves! Equally rich prospects open up before horticulturalists in relation to changes of form and color in the corolla, calyx, and fruit.

From what has been said, the tremendous significance of X-rays in the creation of new forms should be clear. Many of the changes which have arisen in plants deserve attention not only from the theoretical but also from the practical point of view. This does not mean, however, that is is easy to obtain desirable changes in plants. A great deal of labor is required, not only in order to find doses which will change the form of the plants, but particularly in order to see to it that these changes are desirable ones, and that is difficult and very time consuming. But no matter what difficulties beset the path of the experimentor they are well worth the success which is bound to crown the efforts of the persistant investigator, sooner with some plants and later with others.

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STAT

Chapter 3

INTRACELLULAR CHANGES

PLASMIC CHANGES

In 1897 Lopriore's article: "The Actions of X-Rays on the Protoplasm of Living Vegetative Cells" appeared. Lopriore's observations indicated that X-rays accelerate the flow of plasma (cytoplasm) in cells of Valloneria Spiralis. When the source of rays is removed the protoplasm of the cells regains its normal state. But if the irradiation was of an hour's duration harmful effects of X-rays manifested themselves. The protoplasm still continued to move, but it became granular, and numerous vacuoles appeared in it, and it acquired a yellow tinge. Several years later (in 1902) Sekt repeated the experiments of Lopriore on the stem hairs of Cucurbita Pepo, and also on the stamen hairs of Tradescantia virginica and on the leaf hairs of Tradescantia sellov. [redacted]

The hairs were irradiated in a humid chamber after being separated from the organs on which they appeared. Observing the movements of the plasma in the irradiated hairs Sekt determined that not only is the movement of the plasma accelerated due to the action of X-rays, but that the movement is retained for a longer period of time than in control hairs. Irradiation for periods of 1.5 hours however caused dying off, the beginning of plasmolysis and sometimes deformation of the entire cell. The cell could be returned to its normal condition by placing it into fresh water. Plasmolysis set in much more readily if the distance from the(X-ray) tube was diminished. This caused Sekt to assume that in these cases some other rays also affect the cells. He became convinced

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of this when he set up experiments with spirogyra cells which, in general, are characterized by acute sensitivity to electric currents. When the distance from the tube is great, spirogyra does not react to the rays, but when the distance is diminished to 10 to 20 centimeters plasmolysis sets in within the cells in 5 to 10 minutes. After an hour or two the threads of spirogyra die. Sekt also set up interesting experiments with irradiation of Mimosa pudica and Oxalis corniculata. At a distance of 25 - 30 centimeters from the tube after only 10 minutes the leaves were observed to begin folding. After 45 minutes all of the leaflets folded and the petioles arched. If the source of the rays was removed in 20 to 25 minutes the leaves would resume their normal position. Sekt explains this phenomenon by a lowering of the turgidity which, in turn, depends on the specific effect of X-rays on the protoplasm of the cells.

After a considerable interval Schmidt's work: "Experimental Investigation of the Action of Small and Large Doses of X-rays on Young Cells" appeared in 1910. However these investigations were concerned only with the irradiation of sprouts, and not with cells, as such.

Williams' experiments (1923) are very interesting. They point up the significance of selection of the proper objects for X-radiation. In order to obtain quantative data for this action it is essential to have identical materials, to irradiate cells at the same stage of development, to perform the experiments under conditions as identical as possible, and to use hemogeneous rays. As material for his experiments Williams used the skin from the upper surface of petioles of Saxifraga umbrosa where, as he knew

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from previous experiments, cells are all in a mature state and equal in size. Besides these cells are completely transparent and the circulation of the plasma is retained for a long time (48 hours in distilled water). Williams used special doses of X-rays in his experiments and in order to obtain more homogeneous rays, filtered them through an aluminum plate. In order to assure identical external conditions he conducted experiments in darkness and at identical temperatures. The skin was examined microscopically at definite intervals after irradiation. The examinations were carried out under high magnifications of ordinary microscopes and also with the aid of ultramicroscopes. The first change brought about by X-rays was the increase of speed of the circulation of the plasma, as could be ascertained by the accelerated movements of reflecting particles. If the time of exposure was increased the Brownian movement of the particles increased. Since temperature during the experiment was held constant and since the size and optical properties of the particles remained the same, the increase of the speed of movement of the latter indicated a change in the viscosity of the protoplasm. Still longer periods of irradiation cause a decrease in the speed of the movement and finally to its complete stop. If the action of X-rays is extended beyond the time required to accelerate movement, other changes in the plasma take place. The protoplasm begins to withdraw from the walls and, in addition, its pink color becomes less intense. It was possible to assume that the pigment was being broken down; however irradiation of aqueous solutions of the juice of red beets does not confirm this assumption. Apparently, the discoloration is due to acids which

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are liberated as a result of the change in viscosity. An additional factor is the passage of solutions from the cell thus diminishing the amount of cellular juices. When the time of irradiation was extended the speed of the circulation of the plasma was reduced, as has been pointed out earlier. The surface of the protoplasm became more and more irregular and some cells became strongly vacuolized. In order to determine whether this process is reversible Williams transferred the cells into distilled water. However, the process of contraction (wrinkling) of the protoplasm continued in the water, consequently this process was not reversible.

Actually the experiments of Lopriore, Sekt, and Williams establish the change of viscosity as a result of the effect of X-rays on various vegetable objects. In 1923 Weber set up special experiments for the measurement of viscosity in protoplasm of cells which had been exposed to the action of X-rays. The first experiments were set up with Spirogyra. The dosage used was 170 Holtzknecht units. After an hour the ability of the chlorophyll band (ribbon) to settle out under centrifugation was tested. After a five minute period of centrifugation the displacement was identical with that of the controls. Consequently, Weber did not succeed in determining a change in the cytoplasm as a result of the primary action of X-rays. However when the five minute centrifugation was performed 20 hours after irradiation a remarkable difference in the displacement of the chromatophores was observed. In the irradiated controls of spirogyra the displacement of chromatophores took place in 88 percent of the cells, while the X-rayed chromatophores were not displaced at all. Another experi-

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ment with identical irradiation of threads of spirogyra was performed 24 hours after irradiation. Only 15 percent of the cells showed displacement of the chromotophores while in controls 84 percent of the cells exhibited displacement. 48 hours after irradiated and unirradiated cells remained the same. From these experiments it follows that one hour after irradiation there is no change in the viscosity of the plasma, after 24 to 48 hours the viscosity of the irradiated cells increases. Consequently secondary action of X-rays is observed. With the dose of X-rays which was used no morphological changes in spirogyra were revealed and further experiments were not successful.

Weber selected for his second experiment shoots of Phaseolus multiflorus. When he irradiated them with a dose of 24 Holtzknecht units they did not manifest any changes in viscosity. Neither did Weber find any changes in the viscosity of the protoplasm in the roots of this plant, despite the fact that they are extremely sensitive to all kinds of radiation. From this Weber concludes that changes of viscosity do not take place in living vegetable cells as a result of primary action. Weber considers this quite understandable since the primary action affects not the cytoplasm but the karyoplasm, which carries a different electrical charge. He concludes that the viscosity of the nucleus changes from the fact that the nucleolus slips out of it under centrifugation.

The Japanese scientist Komuro published several works devoted to investigations of cellular changes induced by X-rays. Actually these were the first detailed cytological studies.

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In his work in 1922 in his investigations of the effects of this type of radiant energy on the root tips of Vicia faba he demonstrated changes which took place in them. Subsequent authors only carried these studies further and in more detail. Root cells raised from seeds which had received 50 Holtzknecht units manifested a multiplicity of nuclei, increase in size of the cells and nuclei, a vacuolization of the nucleolus and of the cytoplasm, an increase in the number of nucleoli, and a diminution of chromatin material. In the periblem some cells were found to be in a condition of Karyolysis and others in the state of pycnosis. In his following work (1924) Komuro investigated changes at various intervals after irradiation in the same object. These observations showed him the succession (i.e. order) of the phenomena which he described in his previous work. One and a half hours after irradiation, vacuolization of the cytoplasm, chromatolysis, and irregular mitosis were observed. After 6 hours degeneration of the nuclear membrane, pycnosis, karyolysis, and appearance of abnormal two-nucleied cells was observed in addition to previous symptoms. After 9 hours gigantic nuclei and nuclei with numerous nucleoli were observed in addition to the other symptoms. In his work Komuro calls attention to the similarity of these changes with those of malignant tumors. This similarity is brought out still more strongly in his following work, in 1925, in which Komuro investigated the effects of X-rays of various powers. Seeds of Vicia faba of the same variety "Hyogo" were soaked in water for 72 hours and after irradiation by doses of 20 to 40, and 50 Holtzknecht units were planted in sand. Their roots were fixed after 8 days. However he did not observe any significant differences in

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the action of these three doses. But he did describe in greater detail those changes which arise in cells as a result of irradiation. Among general changes the extreme rarity of mitosis and their multipolarity, or dispersion of chromosomes through the cytoplasm are characteristic. In addition, the withdrawal of the protoplasm from the cell wall (in which case the cytoplasm becomes condensed or roughly vacuolized) was also observed. The author used these objects to study the formation of cells with two nuclei and showed that they can arise by various means: 1) by constriction of the nucleous, 2) by budding of the nucleous, and 3) by asymmetrical mitosis. As for the formation of polynuclear cells (those with more than 3 nuclei) they arise as a result of inhibition (or depression) of the development of the cell wall in conjunction with one of the following processes: 1) tripolar mitosis, 2) a division of one of the cells in a tri-nuclear cell, 3) the exclusion of some of the chromosomes or parts of the chromosomes from the division of the nucleous in the telophase and 4) the improper distribution of chromosomes in the anaphase. Komuro explains the formation of bi - and polynuclear cells by a lowering of the viability (i.e. senility) of part of the protoplasm i.e. the inability of the protoplasm to increase sufficiently for normal division.

In addition to the above phenomena he observed an increase in the size of nuclei and nucleoli, eccentric placement (position) of nucleoli in the nuclei with the separation of the chromatin material from it, vacuolization of nucleoli, and also the slipping out of nucleoli from the nuclei. Occasionally gigantic nuclei arose which willed the entire cell: they took hemotoxylin pigmentation strongly and held several pale nucleoli. All of these

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phenomena were accompanied by pycnosis and karyolysis. The increase of the size of the cells' nuclei and nucleoli, the hyper - and hypochromatic condition of the nuclei, according to Komuro, all indicate a degenerative or senile condition of the tissues. Komuro thinks that all these phenomena remind one of the conditions found in the cells of malignant tumors. This resemblance of the changes he confirmed by his experiments of the actions of X-rays, on the one hand, and tar, on the other, on the roots of Vicia faba and Pisum sativum (1927). And, finally in his fourth article (1928) Komuro points out the appearance of tumors on the roots of Vicia faba due to irradiation. In the cells of the tumor one finds cells showing normal cell division as well as cells which are in a state of decomposition. This observation shows that until their death the cells of the tumor continue to grow. It is remarkable that side roots develop completely normally without forming any nodes.

In 1924 -1926 Strangeways and Oakley observed changes in the cellular tissues immediately after irradiation or else 80 minutes later. In the first series of experiments the first abnormality to be noted was the appearance of a granular condition of the chromosomes in the metaphase and anaphase. As the time of action of the X-rays was increased a greater number of cells showed this abnormality, the granular changes of the chromosomes became more distinct and finally some of the chromosomes underwent fragmentization. Under a more prolonged period of radiation (60 minutes) the cytoplasm also becomes granular and less dense. At the same time the outline of the cells changes and becomes abnormal, and the cytoplasm breaks up into separate parts. In other cells the nucleus and cytoplasm suddenly fall apart and a raylike structure

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appears. This raylike structure arises from small areas of the protoplasm and at the same time some of these areas contain large or small bits of nuclear material. Finally the cells become so disorganized that only shadows of dispersed fragments of the nucleus and cytoplasm remain. Sometimes even they vanish and all traces of the cell and the nucleus disappear. These experiments show with remarkable clarity the growth of changes as doses are increased. However these experiments fail to show whether the action of the rays takes effect immediately or whether there is a definite latent period. In order to clarify this question, the authors transferred the irradiated objects of the culture into an incubator for 80 minutes. An examination of these cultures revealed that a period of 15 to 20 minutes is essential in order to manifest the action of X-rays.

Koernicke after irradiating roots of Vicia faba observed the appearance of waviness on them which he ascribes to internal differences in tension. Koernicke traced this down to an enlargement of the transverse diameter of the cells in the parenchyma of the root wall (bark). The folds, which were observed in the external parts of the bark, changed the direction of growth of the cells. The cells of the epidermis which were caught in the corners of the fold were crushed. The author observed the presence of binuclear and polynuclear cells in the periblem and plerome. But Koernicke did not find any injury to the cytoplasm. So that the earliest X-ray biological experiments established that the destructive power of X-rays is proportional to the dosages used.

The majority of workers who investigated the effects of X-rays on cells performed their experiments in such a manner that primary

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effects of X-rays on the cells were not distinct from the indirect effects which depend on the reaction the organism as a whole. With this consideration in mind, Strangeways and Hopwood used the embryonic tissues of chicks in a drop of nutrient solution for their experiments in 1926. These cultures revealed a wide zone of cells with 20-100 mitotic figures. The division of the unirradiated cells requires under these conditions from 40 to 50 minutes. A whole series of experiments, performed by these authors, indicate that the diminution in the number of cells undergoing mitosis which is found 80 minutes after irradiation is not observed immediately after irradiation. When stronger doses of X-rays were used the authors observed fragmentation of the chromosomes, their separation (or delay) in the anaphase, and, sometimes, fragmentation of the cells. When the dosages are increased the number of abnormal cells increases and also the number of bipolar and multipolar cells, and then the number of fragmented cells increases. In order to establish the reason for the diminution of mitosis a whole series of experiments was subjected to detailed examination. This examination revealed that when the strongest of the doses used by these authors was applied, [redacted] cells which were already in a state of mitosis before irradiation (even if they were in the very early prophase) would complete their division. Consequently, these observations indicate that the diminution of the number of cells which undergo mitosis and the absence of cells in mitosis is due, not to the injury, death, or decomposition of the cells undergoing mitosis, but to the inhibition of development of those cells which had not yet entered or had just begun mitosis at the time of irradiation. This explains the apparent contradiction between the

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conditions of the cultures observed immediately after irradiation and those observed 80 minutes later.

In 1927 Bersa traced the action of X-rays on cellular elements with particular care. By means of a comprehensive series of experiments he established that the greatest number of pathological mutations can be observed after 36 and 48 hours. A careful examination of these mitoses leaves the impression that the chromatin has undergone substantial changes: the chromosomes tend to contract, to stick together, to fall apart. These signs indicate that the viscosity of the plasma has diminished and that the surface tension has increased. From this stems the tendency towards the stretching of the threads (the bridges that form), on the one hand, and the striving towards rounding out into drops, on the other.

In 1927 Pekarek approached this question very thoroughly in his article. He turned his attention to studying the effects of X-rays on mitosis, their numbers, and on chromosome changes. However, like Bersa, he considers that the primary effects of X-rays should be sought in changes of the colloidal condition of the plasma.

Nadson and Rochlin have performed important works in this area (1926 and 1933). They examined the cells of the irradiated epidermis of onion scales in a living condition immediately after irradiation, after a half hour, after an hour, and so on up to 48 hours. The first consequence of irradiation, that the authors were able to trace, was the increase in the rate of protoplasmic movement. However, a depression soon sets in, this is manifested by the slowing down of the movement of fat globules and chondrio-

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somes, and in the weakening of the Brownian movement. This, in turn, indicates an increase in the viscosity of the protoplasm. Finally, the movement of the protoplasm stops altogether, after an hour the threads of protoplasm disappear and the protoplasm collects in the corners of the cell. At the same time the protoplasm, which was originally fluid and homogeneous, becomes murky. This indicates a weakening of its dispersion. At this time the nucleus also begins to change, it's granular structure becomes more coarse, and the outlines of the nucleus and the nucleolus become more distinct. Then fat droplets appear in the protoplasm. Their appearance indicates the breakdown of the lipoproteids under the influence of X-rays. Lipophanerosis takes place. Approximately at the same time (i.e. 2 to 3 hours after irradiation) vacuoles appear. Twenty-four hours after irradiation the plasma becomes pale, completely transparent, and watery.

At the same time the vacuolization becomes more intense, the structure of the protoplasm becomes coarsely foamy, lipophanerosis continues. Finally the structure of the protoplasm becomes bubbly and on the surface of the bubbles numerous fat globules appear. Except for the lipophanerosis the same changes can be observed in the nucleus as in the protoplasm, i. e. coagulation, vacuolization, and karyolysis (the dissolution of the nuclear material). The nucleolus disappears. Frequently during degeneration, the outline of the nucleus become irregular and greatly transformed. The rate of changes depends first of all on the length of irradiation, but also on the physiological condition of the cell.

In his article, "The Changing of Hereditary Characteristics of Microorganisms by Experimental Means" Nadson (in 1935) devotes

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a separate chapter to changes which X-rays induce in protoplasm. It is extremely interesting that he associates these changes with the Arndt-Schultze law (see chapter 1 of this book) according to which small doses stimulate cellular activity, stronger doses depress it, and still stronger doses kill the cell. Nadson considers that he not only succeeded in confirming this law, but also that he discovered the regularity of its action, since cells under the influence of irradiation pass through definite phases, each of which has its distinctive morphological and physiological characteristics. The first phase is characterized by the fact that the cellular protoplasm becomes agitated (aroused) as can be seen from the quick and varied changes of the vacuoles. The protoplasm becomes swollen with water and its dispersion and penetrability increase. This is the phase of stimulation. This process is reversible. The second phase is the dispersive phase when life processes are slowed down. The protoplasm which was originally transparent and homogeneous in appearance, becomes somewhat turbid, then finely and delicately dispersed which indicates the lowering of dispersion. The protoplasm loses water, becomes less swollen, its penetrability diminishes. The vacuoles become larger. Almost at the same time the disintegration of the lipoprotein complex (lipophanerosis) takes place. These phenomena are still reversible if they have not gone too far. The third phase is a phase of still more profound, and clearly pathological changes, of disorganization and more or less quick process of drying off, of necrobiosis and, finally, death. This phase is characterized by the onset of coagulation of the protoplasm, the continuation of the processes of losing water, and the final dissolution of the lipoprotein complex. The penetrability of the protoplasm increases sharply, plasmolysis takes place, the

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vacuoles diminish in size. This phase is not reversible. In other cases the protoplasm of the cell is broken down by automatic processes, as a result of which all that remains are a few fat globules.

In order to determine the changes in the viscosity of the protoplasm under X-radiation Breslavets (1936) selected pollen grains as objects in which these changes can be most easily observed by means of centrifugation, for the reason that a large part of these individual cells, at a certain stage of their development, become filled with a large number of starch granules which can be displaced by centrifugation. In this respect the pollen grains of hyacinth are particularly convenient since the transparent integument of the grains permits microscopic observation of the entire thickness of the protoplasm. Preliminary experiments have shown that, depending on the time of irradiation, a greater or lesser displacement of the starch granules takes place. The following method was used for the determination of the viscosity of the protoplasm: The centrifuge tubes were filled with 5 cubic centimeters of 10 percent solution of cane sugar, into each of the four tubes a single anther (from the same flower) was placed, and the centrifuge was set in motion (2000 revolutions per minute). After 5 minutes an anther was removed from one of the tubes and placed on a microscopic slide with a drop of iodine in potassium iodide, while the centrifuge was set in motion once more. After 15 minutes a second anther was removed and placed on a cover glass (of a microscopic slide?), a third was removed after 30 minutes and a fourth, after 60 minutes. Due to the action of the iodine the starch granules became dark blue in color and

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their displacement (which depended on the time of centrifugation) within the pollen grain could be easily observed. A 5 minute action (of the centrifuge) cleared 1/6 of the space from starch granules; 15 minutes, 1/2; 30 minutes, 2/3; and 60 minutes, 3/4. Thus the displacement of starch granules is proportional to the time of action of the centrifugal force. Preliminary experiments have shown that the viscosity of young pollen grains is very great. It is precisely these young pollen grains which had to be used for the experiment since in them the starch granules reach their maximum size. For this reason experiments for the study of viscosity of the protoplasm were begun with large doses of X-rays. The conditions of irradiation were as follows: 220 kilovolts, 5 milliamperes, distance from the tube 70 millimeters, no filters (table 24).

TABLE 24

The effect of centrifugal force on the displacement of starch granules in pollen after irradiation after various time intervals.

(Based on data of Breslavets, 1936)

Dose, r	5 min.	10 min	20 min	30 min
Control	2/3	3/4 - 7/8	3/4 - 7/8	7/8
2000	2/3	3/4	7/8	-
4000	1/3	1/3	2/3	3/4
8000	1/3	3/4	3/4	7/8
16000	1/3	1/3	3/4	3/4
32000	1/3 - 1/2	1/2	1/2	3/4 - 7/8
48000	1/3 - 1/2	1/3 - 1/2	1/3 - 1/2	1/2 - 3/4

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These experiments indicate that the viscosity of the protoplasm begins to increase only with the action of 4000 roentgen units, and that it continues to grow up to a dose of 48000 roentgen units, inclusive. Apparently the centrifugation method is too coarse to distinguish finer differences in viscosity of the protoplasm due to action of X-radiation. It is interesting to note that pollen grains sprouted even after the action of such doses as 48000 roentgen units. Microscopic examinations (Breslavets, 1937) indicate that only doses of 16000 roentgen units begin to change the structure of protoplasm, making it more coarsely grained.

In 1936 Erdmann investigated the effect of loss of water contained in the protoplasm on the action of X-rays. The author points out that yeast is an object in which it is possible to measure the water content in living cells, and that it is possible in yeast to measure the effect of X-rays by the depression of their ability to multiply. The water extent was measured by: 1) hypertonic solution, 2) drying in a desiccator, 3) natural aging of the yeast cells.

It should be kept in mind that all vegetable cells, in addition to the water in the protoplasm, contain free water. By removing this water with hypertonic solutions it is possible to cause a shrinking of protoplasm (due to loss of water). The sensitivity to the rays is related to the water held by the living protoplasm. The criterion which indicates the loss of water from protoplasm is the growth of the cell. The ability to grow is related to a definite degree of turgidity of the protoplasm and it constitutes a very sensitive indicator of the loss of turgidity. The loss of water in Erdmann's experiments was produced by

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potassium chloride, or sodium chloride, or urea. These experiments showed that when the protoplasm lost its turgor the effect of X-rays was reduced by 25 to 30 percent, by comparison with cells whose protoplasm was in the normal state of turgidity. If cells from a hypertonic solution are transferred to top water then irradiation produces the same effect as it does on yeast cells which had not been forced to lose water. Desiccation, by causing the protoplasm to lose water, lowers the sensitivity of the cells to rays just as happens when water is removed by hypertonic solutions. The sensitivity of older cultures of yeast is reduced by 35 percent by comparison with normal ones. Actually the aging of yeast cells is also accompanied by loss of water which accounts for the reduction of sensitivity.

The article of Heilbrunn and Mazia, "The Effect of Irradiation on Living Protoplasm" (1937) forms a chapter in Duggar's book. In this chapter the authors develop the idea that if there is no doubt that irradiation affects the protoplasm and the protoplasts, that we cannot know whether this is the effect of the direct (primary) action of the rays on the organism because our knowledge in this area is still very limited. Even among experiments where cells are examined microscopically, the number of experiments devoted to the study of the direct (primary) effects of radiation on protoplasm is insignificant. The authors consider that our primary interest should be in primary action of irradiation on living protoplasm and in the study of this action by means of physico-chemical methods, namely; 1) permeability to water and soluable substances, 2) viscosity, 3) electrical charges and potentials, and

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4) chemical reactions.

Permeability, or rather, changes in permeability due to the action of visible and ultraviolet light and radium were studied in both animal and vegetable cells; while the investigation of the effects of X-rays was performed, chiefly, on animals only. Brummer has shown that on human skin and on erythrocytes irradiation diminishes permeability while Hassel and Hofman indicate to the contrary (i.e. that permeability increases). The data of Kretz and Kovacs are equally contradictory; the former comparing the speech of diffusion of chlorides through the normal skin of the frog and through skin which had been exposed to 10 to 30 HED (High Erythema Dose) demonstrated an increase of permeability (of the irradiated skin) of almost 200 percent. Kovacs, on the other hand, was unable to establish any differences (of permeability) due to X-radiation. And, finally, Seckt, in 1902, while observing changes of the stoma openings under irradiation established the increase in permeability due to irradiation on a plant organism (Tradescantia selloi).

Viscosity

Investigation of changes of viscosity of the protoplasm due to the action of waves of different wavelengths, ranging from the ultra violet to X-rays and radium, showed Heilbrunn that the main mass of the protoplasm (Plasmosol) first because liquid and them, as dosages were increased, more viscous. While the internal plasma became more viscous the external layer became diluted to 1/4 of its original state.

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Changes in the cytoplasm, after irradiation, are similar in various organisms, although they differ clearly in the degree of radiosensitivity of their tissues. Temporary stimulation of physiological processes is the first stage of the effects of X-rays. This is followed by a gradual diminution of activity and finally complete inactivity. A great many observations were performed on protoplasmic movements (Lopriore, Nadson, Rochlin, Williams), on motility of chromosomes, fat globules, etc., which indicate corresponding changes in viscosity and, also, the selective penetrability of protoplasm (Nadson). Protoplasmic currents enter the permeable cytoplasm and accumulate around the nucleous, or in some other place; the cytoplasm gradually becomes turbid as a result of formation of grainlike, small fat-globules, whose number and size gradually increase, and finally, first small and then large vacuoles appear (Nadson, and Rochlin, Heilbrunn and others). When these changes become irreversible, death sets in (Lopriore, Nadson). The vacuoles may increase in size or the plasma may disintegrate.

Irradiation induces changes which are similar to "long-term" modifications, this is particularly clearly demonstrated in Drosophila. These are cytoplasmic changes which in subsequent generations revert to the original state. Many such changes, for various features, were described by Stein (from 1922 to the present) in irradiated snapdragons.

Certain investigators noted also that even where reverse changes were induced the reversibility was often partial and that

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cytologically imperceptible changes can be retained and (later) manifest themselves by formation of new tissues and possess, in the final analysis, cytogenetic significance. Stubbe's experiments indicated that the genes of Epilobium hirsutun have a greater frequency of mutation when irradiated within the protoplasm of E. luteum than in their own protoplasm and he concluded that changes in interaction between the nucleus and the cytoplasm revealed themselves in various reactions, which are sometimes regulated by the nucleus and sometimes by the cytoplasm.

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CHANGES OF CHROMOSOMES AND PLASTIDS

Improved microscopic techniques created a new approach to the investigation of the effects of X-rays on cells. Nürnberg has particularly contributed to this area. Basing his work on the comparative investigation of normal and irradiated ova of white mice he came to the conclusion that X-rays can cause considerable injury to the body of the cell. The destructive action manifests itself in the bending and rolling of the chondriosomes into tangled balls and, consequently, disarranging them (i.e. knocking them out of line). For this reason Nürnberg considers chondriosomes to be extremely fine morphological indicators of the condition of the cell.

Nürnberg's assumption was confirmed by the work of Russian investigators (Nadson, Rochlin, Wail, and Frankel). On the basis of their investigations all of them came to the conclusion chondriosomes are the most sensitive (parts of the cell). In the experiments of Nadson and Rochlin the length of irradiation ranged from 2.5 minutes (1 High Erythema Dose) to 60 minutes (24 High Erythema Doses). In the cells of the epidermis of onion scales the chondriosomes are small granular structures in the form of elongated rods or straight threads. The first effect of X-rays manifests itself by an increase in the changeability of the forms of chondriosomes. When the action of irradiation is increased the chondriosomes puff up unevenly along their length, the irregularities of their contours increase, the threads become stumpy or assume the shape of tadpoles, spindles, and sometimes of fragments or triangles. In certain places in the cell the chondriosomes gather in very large

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numbers reminiscent of agglutination of chloroplasts. When the doses are increased still more the chondriosomes undergo still greater changes: vacuolization, dissociation of monoproteins, accompanied by an increase in lipophanerosis, dissolution of albuminous compounds, and, finally, the complete disappearance of the chondriosomes.

Wail and Frenkel (in 1925), studying the effects of X-rays on the cells of frogs livers, established that morphological changes first appear in the chondriosomes and later in the nucleus. Tschasownikow (in 1928) came to a similar conclusion for the same object. He fixed small pieces of irradiated frogs liver at intervals starting with 3 hours and ending with 6 days after irradiation, and he observed that the chondriosomes were the first to show effects of X-rays. However, Tschasownikow points out that in observing chondriosomes one has to be extremely careful in one's conclusions because, in the first place, chondriosomes can be injured traumatically since in the surface of sections they fall apart into grains, and, secondly, the effect of fixative agents on the surfaces has to be kept in mind. Consequently, Tschasownikow examined only such cells as could not have been injured traumatically. It is for this reason (he thinks) that he did not observe the phenomena described by Wail and Frenkel. In his materials the chondriosomes retain their normal structure and position for 12, 24, and even 48 hours. Only after 48 - 72 hours and more did Tschasownikow find truly degenerative changes in the chondriosomes. The changes consisted of disintegration of chondriosomes into granules which then swelled into lumps. At the same time changes took place in the plasma and nucleus. Sometimes he observed necrosis in the nucleus although

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the chondriosomes were unaffected. In other cases light (colored) vacuoles appeared in the plasma alongside of partially injured chondriosomes. In general we have very few facts about changes in chondriosomes due to influence of irradiation, and besides they are contradictory. Apparently, despite the detailed examinations of Nadson and Rochlin, this question has to be undertaken once more, especially since their observations have been performed with living cells, in which various destructive processes could take place quite independently of the action of X-rays. In this respect it seems sufficient to point out one particular danger, the possibility of carbon dioxide poisoning in the moistening chamber.

Plastids have likewise been insufficiently investigated in order to be able to come to definite conclusions about what effects X-rays have on them. In 1898 Lopriore, in the work mentioned above, described the lightening of chloroplasts in Valisneria spiralis which were induced by strong doses of X-rays. In 1936 Johnson made the observation that chloroplasts develop improperly. Tollendaar and Hudson in tobacco, Stubbe in snapdragons, Stadler in barley and corn, Lutkov in barley and others, all observed changes in the green parts of plants due to irradiation. Certain of these changes were hereditary (see Chapter Two).

In 1931, Knudson irradiating the spores of Polypodium aureum found gigantic, irregular, amoebalike plastids in the prothallia, especially in the peripheral cells. He assumed that they arose as a result of the fusion of small plastids. This explanation quite agrees with Schürhoff's findings. The latter established that under certain abnormal conditions the plastids swell, their edges become soft and gluey, and this can lead to the formation of

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abnormal forms.

In 1935 Hruby, while irradiating the spores of Polypodium aureum with various dosages, established that even the strongest doses did not depress (inhibit) their sprouting. A few irregularities were observed in the three strongest doses. Then he repeated his experiment using still stronger doses. The experiments indicated that abnormalities in the plastids increase proportionately to the doses. For example: with a dose of 2355 roentgen units the number of cells with abnormal plastids was 21.6 percent, while with 6800 roentgen units the percentage of such cells goes up to 46.5. Before any of the nuclei of the cells showed any changes in all of the plastids, even in the smallest, vacuoles appeared. To a certain extent Hruby confirms Knudson's observations concerning the adhesion of small plastids into large, shapeless forms. In the majority of cases, however, the union of the plastids is explained by the fact that plastids had begun to divide and that this division did not reach completion.

Later Knudson published a large article on the action of X-rays on fern chloroplasts.

He selected a fern because the latter forms spores which are tiny in size and simple in structure. Every effect induced by X-rays can be a primary instead of a secondary one as can happen when seeds are irradiated. The irradiation was performed with a Coolidge tube at a distance of 12.5 centimeters, at 78 - 80 kilovolts and 4 milliamperes, without a filter. The irradiation was performed intermittently. In one experiment the spores were exposed to the following dosages: 7000,10,000, 12,000, 15,000 and

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20,000 roentgen units. In another experiment dosages from 20,000 to 50,000 roentgen units were administered at intervals in "packets" of 5,000 roentgen units. Fifty-one prothallii were isolated.

The classification presented below is based on cells of medium age. In very young cells the plastids are small and undeveloped, in old cells they are likely to change shape due to age. Knudson divides the observable differences into eleven types:

Type A - Normal Plastids

In prothallii from unirradiated spores and nearly all of the irradiated ones the plastids are characteristically similar in size and shape. They are very small, flat or disklike in shape, and have a thickness of 1.5 μ. Their area ranges between 3 x 4.5 μ and 6 x 9 μ. Another characteristic sign of normal cells is the larger number of plastids per cell.

Type B - Grouped Plastids

The plastids congregate about the nucleus in groups. Prothallii with this type of plastids are characterized by thin walls, blue-green coloring, and slow growth.

Type C - Gigantic and Amoeboid Plastids

Plastids of this type of various sizes and shapes assume strange outlines. They are formed by the fusion of small plastids. Later small plastids arise from them by budding. When these (fused) plastids have a more or less regular shape they can be measured. Squarish plastids of this type were 50 x 60 μ. Occasionally ringlike forms occur.

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Type D - Thinner Plates of Irregular Shape

In cells of medium age plastids fuse into thin threads. The starch granules in them are large.

Type E - Very Large, Thin Plastids

Only one prothallium of this type was observed. It was of hefty build.

Type F - Irregular Thin Plastids

In cells of medium age they are linked by thin green processes. In some of the older cells the plastids fuse.

Type G - Thin Plates of Various Sizes, with Vacuoles

Type H - Large Plastids

This type occurs most commonly. Plastids of this type resemble normal ones but are/ at least/ twice as large.

Type I - Thin, Small Plates of Various Sizes

Some of them are connected by thin green processes, others are vacuolized. The surface of these plastids is irregular due to large starch granules.

Type J - Small Plastids, Variable in Shape, with a Tendency Toward Congregating in Groups and Vacuolizing

Nearly every cell shows a colorless, ringshaped structure of variable size.

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Type K - Vacuolized Plastids

This is an unusual type of plastids. In young cells the plastids are completely normal, only their contents appear more fluid and more finely grained. In slightly older cells the plastids begin to exhibit an irregular distribution of chlorophyll. Occasionally whole islands of tissue appear, devoid of chlorophyll. In older cells the plastids are almost devoid of starch. They are spherical in shape and the chlorophyll is in the shape of thin or thick interconnected stripes. Some plastids exhibit an equatorial band. Prothalii with plastids of this type grow very slowly.

These new plastid types were retained in culture for 6 years. Since with doses of less than 30,000 roentgen units changes of plastids were not observed, there can be no doubt that these changes could only have been induced by irradiation. In other experiments, performed with millions of prothallii, changes in plastids were not observed. As has been pointed out above, in Hruby's experiments a much higher occurence of abnormal plastids was observed than in Knudson's experiments. The latter explained the difference by the fact that spores of Polypodium contain less water, while the spores of Equisetum are, apparently, in a more active physiological state and contain a greater amount of water. As Knudson's detailed experiments have shown, sporophytes obtained from prothalii with B-type plastids (grouped plastids) all had plastids of this type. This grouped arrangement of plastids was maintained for 2 - 3 years, after which this grouping was lost. From young leaves spores were not obtained, and from mature ones only gametophytes with the normal type of plastids were obtained. Another type of plastids (the

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gigantic) is transmitted as a result of sexual reproduction to the sporophyte and to the subsequent gametophyte.

These data almost exhaust the observations of plastids in cells which had been subjected to X-rays. This is explained by the fact that the majority of investigators directed their attention to changes in the nuclei and in the chromosomes which arise as a result of irradiation. This is quite understandable since the majority of X-ray biologists were seeking to obtain inheritable changes and consequently paid more attention to the nucleus as the carrier of hereditary properties. Investigations devoted to changes of the nucleus and chromosomes are very numerous, especially in relation to zoological objects, due to the finely developed methodology of investigation of chromosomes in salivary glands. However, there are quite a number of these fine investigations performed with vegetable objects which had as their aim the solution of theoretical questions. These will be described below.

NUCLEAR CHANGES

Sakamura, in 1920, was one of the first to investigate the effects of X-rays on the nucleus and chromosomes of the vegetable cell. While investigating somatic mitosis in the roots of Vicia faba and Pisum sativum, Sakamura came up against certain questions concerning the structure of chromosomes and this caused him to turn to the experimental method. Sakamura set up broad experiments with the action of various chemical substances, and also with hot water, electrical fields, and X-rays. Of all of these effects we are interested (in this case) in the last one (X-rays). As Sakamura has

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demonstrated, when X-rays are used the first effects to be observed are the shortening and thickening of the chromosomes. The degree of shortening and thickening depends on the intensity or duration of action. In the same way chromosome changes are retained longer as the intensity or duration of the X-rays is increased. Sakamura also established that the maximum shortening of chromosomes does not take place immediately after stimulation, but that a certain amount of time must elapse in order for these changes to appear. If the action of the X-rays is too strong the chromosomes in the metaphase will bunch together into a single lump, surrounded by a light area. As soon as irradiation is over the lumps begin to unwind and the shortened chromosomes scatter in disorder throughout the entire protoplasm. Since during the formation of such lumps achromatic filaments were never observed Sakamura assumed that the hyaline (clear) area is associated with the general disorganization of the achromatic filaments. In general the shape and size of the chromosomes depends on the given environment. The chromosomes are capable of reacting to different conditions without changing their substance (qualities).

Iven, while irradiating seeds of Vicia faba, established the appearance of many nucleoli in the nucleus and also of extra-nuclear nucleoli. He also observed deviations from the normal division of nuclei, but not in all the cells.

Alberti and Politzer (1923, 1924, and 1934) performed their experiments with animals but their observations and conclusions are so interesting that we can include them as we have done with the experiments of many other zoologists. Alberti and Politzer exposed their materials to 3 + 12 HED (High Erythema Doses, first giving them 10 minute exposures and later 40 minutes). The objects were fixed

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after 2, 4, 7, and 10 hours, and then after 1, 2, 3, 4, 5, 6, 7, and 8 days. Observing internal changes they established that after 2 - 4 hours after irradiation the number of ongoing mitoses decreases and pathological forms appear. Ten hours after irradiation not a single mitotic figure was to be seen. On the fifth day mitotic figures reappeared in material which had been exposed to weak doses. On the basis of their observations Alberti and Politzer make a distinction in the action of X-rays: (1) the primary effect, which manifests itself in changes in the course of ongoing mitoses, (2) the intermediate period without mitoses, and (3) secondary effect, a reappearance of mitoses which are different from normal ones.

The primary effect manifests itself in pycnosis of the nucleus in the spireme stage, in an abnormal distribution of chromosomes, and in the formation of "hour-glass" figures which Alberti and Politzer call "pseudomitoses". After a ten minute period of irradiation the number of "pseudomitoses" reaches 8 percent; after 40 minutes, 25 percent. The completion of "pseudomitoses" can take place in two ways: by condensation of the "bridge" (spindle) and by appearance of asymmetrical danther nuclei. It is also possible to observe the flowing of the whole chromatin material from one cell to another (as a result of which one cell is left without a nucleus) and partial pycnosis (i.e. that is migration of the chromosomes to various poles and adhesion of some on the equator). The intermediate period is characterized by pycnosis and vacuolization of the nuclei. The abnormal divisions with the secondary effect (of the X-rays) are different than with the primary ones. The secondary effect is most frequently characterized by a lagging (retardation)

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of the chromosomes. The authors observed the greatest number of irregularities in the metaphase where the chromosomes were observed to turn, disintegrate (into fragments), and wander off to the poles. As a result of the irregular migrations of the chromosomes micronuclei form, whose number increases noticably on the fifth and eighth days after irradiation. Besides this the authors observed displacement of phases. One group of danther chromosomes could be in the telophase while another could be in the prophase. The duration of the primary effect does not depend on the dose, but the length of the period without mitoses is largely dependent on it (the dose). With 1/3 H (Holtzknecht unit) the mitosisless stages last about 12 hours; with 1H, a whole day; with 4H, 3 days; with 12H, 5 days; with 20H, 8 days. The secondary effect, however, is very clearly dependent on the dose. Although this question has not been solved by the authors [redacted] 30 days after exposure to 4H (Holtzknecht units) only normal mitoses were observed. The primary effect affects only those cells which were at the time of irradiation in a state of division or immediately prior to it. The processes of division were slowed down. The secondary effect affects those cells which at the time of irradiation were in the resting stage.

Kanti, Kemp, and Juel (1930) demonstrated that the number of mitoses diminishes at the time of irradiation, dropping to zero and then increasing once more. This slowing down is particularly marked in the last phases of division.

In 1926, Bersa in irradiating the roots of Zea Mays observed (several hours after irradiation) a strong depression (inhibition) of nuclear division which increased as the dosages were increased.

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The works of Pekarek (1927) occupy a unique place in the annals of X-radiology, both by their thoroughness and by their versatility. For his experiments he also used the seeds of Vicia faba, selecting for irradiation seeds of identical size. The seeds were planted in sawdust and were irradiated when they attained the length of 2 - 3 centimeters. On the 13th day after the beginning of the experiment the roots of the control plants begin to lengthen and branch out while the seeds of irradiated plants show no branching and are much shorter. Pekarek explains the retardation of growth of the irradiated plants by a halting of cell division. Pekarek (just as Körnicke) notes an unevenness of the surface of the root after irradiation. The folds spread through the epidermal, the sub-epidermal, and the deeper layers. Pekarek considers that the folds are the result of unequal growth of the bark and the plerome due to the fact that cells of the bark grow lengthwise and plerome cells, sidewise (in width).

The observations made by Schwarz as early as 1837, that nuclei tend to increase in size with age and then shrink when the cells become senile, were confirmed by Pekarek who measured nuclei on two diameters. These measurements showed him that with age (i.e. maturity) the mass of the nucleus doubles. The shape of the nucleus also changes; it becomes thinner and finally assumes the form of a disk. The length of the nucleus, then, increases with age, the width remains the same, and the thickness diminishes with age. Under the influence of X-rays the nucleus assumes an ellipsoidal shape (i.e. it behaves as do the nuclei of normal cells which are located much further away from the tip of the root). This change in the mass of the nucleus shows a tendency towards transformation

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of the meristem tissues into permanent ones under the influence of X-rays. In order to be able to judge concerning the frequency of cell division, Pekarek made counts in control and irradiated roots after 2, 5.5, 21, 28, 50, 72, 100, and 144 hours. The counts indicated that shortly after irradiation the number of divisions decreased almost to zero. Eventually the frequency of nuclear divisions increased, but did not equal that of normal cells. The diminution of frequency of divisions indicates that irradiation affects, not only the nuclei which were in the process of division, but also those in the resting stage. In addition new divisions do not commence for some time after irradiation.

Pekarek also distinguishes between the primary and the secondary effects of X-rays. He considers that primary effects are those which cause abnormalities in cell division in cells which at the moment of irradiation were in division. Secondary effects (which he calls anomalous) take place in nuclei which at the moment of irradiation were in the resting stage. Immediately after irradiation by small doses there are no observable changes; 2 hours later, however, alongside of normal (mitotic) figures, pathological ones appear. After 5.5 hours there are still fewer normal figures. The action of X-rays on Vicia faba manifests itself in that young cells lose their embryological character and exhibit signs of senility. Transformation into permanent tissues proceeds from the zone of elongation and, eventually, includes part of the root tip. The undulation and wrinkling of the surface of the root are related with the transformation of the periblem

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tissues into permanent ones. The premature transformation of the embryological cells into permanent components manifests itself in the enlargement of the nucleus. The variety of anomalies due to the primary effects are based on the fact that nuclei, at the time of exposure, are found in various stages of division.

The secondary effects show up in nuclei which commenced mitosis in an injured condition. The migration of chromosomes is irregular, not only in timing, but also in location. The unequal migration of chromosomes gives rise to dwarf nuclei. Furthermore as a result of the failure of the formation of new cell walls, binuclear and polynuclear cells arise. Chromosomes often carry additional spindle fibers and are clearly visible. Nuclei in the resting stage show premature senility which is manifested by the formation of "chromocenters" (chromatin nodules). At the same time various degenerative forms are encountered (karyorexis, pycnosis, karyolysis), whose number increases with the time interval after irradiation.

Tschasownikow (1928) considers that it is characteristic, in cell nuclei of normal liver cells, for basophyllic elements to dominate over acidophyllic ones. From 9 - 12 hours after irradiation the first changes appear in the nuclei which, in general, lead to the accumulation of basichromatin. The accumulation of basophyllic granules and lumps near the nuclear membrane can serve as the first indication of the degeneration of the nucleus. This phenomenon is known as hypermitosis of the nuclear membrane. As a result of these processes the number of basophyllic particles

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increases and, at the same time, the basophyllic substance begins to penetrate the nuclei by diffusion. These phenomena characterize the onset of pycnotic changes which lead to total degeneration. Blakeslee, Bergner, Satina, Avery, Cartledge, and Potter, in 1929, exposed to the action of X-rays plants which had been grown from two groups of seeds of Datura Stramonium, one group for 50 minutes and the second, for 65. Of the nine plants in the first group only one was normal; of the seven plants of the second group none was normal. Various types of chromosome configurations were observed in these plants, usually involving 4 or 6 chromosomes. There were two cases of simple translocation (chain), 5 - 7 cases of segmental interchange or fractional translocation (ring), and one case of fragmental adhesion. Fourteen of these plants had poor pollen.

Sapegin (1930) pointed out that when 480 plants of several pure strains of winter and spring wheat were irradiated, hundreds of changed descendants arose, the majority of which were chromosomal aberrants. The aberrations of the chromosomes were various: univalent, fragments, asynaptic, chromosomal adhesions, and trivalent and quadrivalent formations.

Delaunay (1930) subjected young ears of Triticum vulgare albidum and T. durum melanopus to irradiation. Experiments were eventually conducted only with the first of these plants. These experiments revealed, first of all, that the later the plants were irradiated the greater was the degree of infertility of the ears (Table 25).

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TABLE 25

The Infertility of the Ears with Various Periods of Irradiation

(Based on the data of Delaunay, 1930)

Ears,	irradiated	on	July	8	—	16.7	grains	per ear
"	"	"	"	13	—	21.0	"	" "
"	"	"	"	19	—	11.0	"	" "
"	"	"	"	22	—	7.0	"	" "
"	"	"	"	23	—	5.3	"	" "
"	"	"	"	30	—	0.0	"	" "

(Control ears gave on the average 26.4 grains per ear)

The 30th of July was the day of the full bloom.

The seeds which were gathered from the irradiated ears gave rise to numerous mutations (see Chapter II) among which were various chromosomal aberrants.

Mutation 2N - 1 + β . This mutation was represented in X_1 by one puny plant with a single ear. A cytological analysis revealed that this plant had in its cells only 41 chomosomes and that in place of the missing chromosome it had a tiny fragment. Probably this was a fragment of the 42nd chromosome. It divided evenly and was not lost in karyokinesis. The ear of this plant gave four well developed seeds from which four plants came up which differed from the (original) parent plant and from the X_1 plant. The fragment in the nuclear plate was not lost but it was greatly

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enlarged. Nevertheless this β fragment was approximately one fifth the length of an average chromosome of wheat. In another mutation two chromosomes in X_1 were shorter than normal ones. A third mutation (complex polysomic) had in its chromosome set 45 units, i.e. three more than is normal. It had 43 long chromosomes, one short fragment, and one round α. The formula for the karyotype of this plant can be written as follows: $2N + 1 + \frac{1}{2} + \alpha$. This is a complex instance of polysomy and chromosomal fragmentation. A fourth mutation (a simple monosomic one with a karyotype formula of $2N + 1$).

Plotnikowa (1931) also used soft wheat (Triticum vulgare var. ferrugineum) for her investigations. Ears which had been cut off the plant at the time that they were undergoing reduction-division were exposed to radiation. In the diakinesis or metaphase of the irradiated cells it is rarely possible to count 21 chromosomes, usually the chromatin material fuses into a ball. A small part of the chromatin material distributes itself throughout the plasma in the form of small drops. In the early anaphase the chromatin stretches out in the direction of the spindle fibers, forming threads, which are thickened in certain spots. In the late anaphase the two chromatin groups are connected by means of the chromatin threads. The second reduction division proceeds in the same manner as the first. The pollen tetrads are improperly formed: they may contain two normal sized cells, the third may be gigantic, and the fourth a dwarf. Besides this various other phenomena were observed: pentads, binuclear and mononuclear tetrad cells, multicellular tetrads, and nuclei of various sizes, having in each of the cells from one to several nuclei, sometimes

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of tiny size. The works of Goodspeed (1929 to 1939) occupy an important place in the annals of X-radiology. For a decade he studied the effects of X-rays, with his colleagues, on the genus Nicotiana. He began his experiments in 1927 with N. tabacum (1929). As a precaution all opened flowers and all buds were first removed from the inflorescence. From the seeds of the irradiated plants 1040 plants were obtained from which 40 were subjected to detailed cytological analysis. Two plants of the 40 showed a loose interconnection of the chromosomes in the diakinesis, and the number of microcytes in the tetrads was greater than the usual four. During interkinesis lagging chromosomes could always be observed and in the second division there were always less than 24 chromosomes participating. Four of the plants had in their metaphasal plate 23 bivalents and a single univalent; three plants had 24 bivalents and one univalent; the eighth one had 22 bivalents and one univalent or 23 bivalents. Consequently the last eight plants represent simple meiotic aberrants.

In five other plants chromosomal fragmentation was observed. In one of the plants an extra chromosome of small size appeared in the somatic plates. During reduction-division two of these plants had 22 bivalents and 23 bivalents plus a tiny body; a third had 23 bivalents and a single fragment. It is interesting that all of the fragments were identical in shape and size. Usually these fragments place themselves between the bivalents and divide during the second division. Sometimes they divide during the first (reduction) division and their halves migrate to opposite poles. It frequently happened that this division was unequal.

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In his joint work with Avery (Goodspeed and Avery, 1930) Goodspeed describes in detail the reorganization of chromosomes under the influence of irradiation. The somatic set of chromosomes consisted of 50 units and during the first division there were 24 or 25 units. The authors explain this difference by the alternating appearance of quadrivalents. The formation of rings is characteristic for irradiated tobacco since in normal tobacco this phenomenon is not observed. The quadrivalents arise due to the conjugation of two bivalents, which testifies to the homology of all four chromosomes. However one of these bivalents is simple while the other has a complex origin, actually being a trivalent, consisting of two large elements connected by a third, which is in the center. This small component arose from the division of a small segment of one of the partners of the bivalent which afterwards adhered to the other partner. In this fashion X-rays have induced a basic reorganization of the chromosomes. In another case in the mother cells of the pollen a very complex element (component) was observed. Apparently the opposite ends of a single, whole chromosome fused which led to the formation of a "bridge" in the anaphase and to the appearance of fragments. In a third case a new type of reorganization was observed: the permanent appearance of a tiny fragment. A genetic examination leads us to believe that this additional phenomenon is due to a translocated segment from a non-homogenous chromosome. The composition of the nucleus in this plant is complicated by the appearance of five complex configurations, one of which is obviously a trivalent. A fourth plant had 24 elements of which two were trivalent. In the chromosome set of the pollen mother cells there were 28 elements, 25 of them bivalent, two

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univalent, and one a fragment. One bivalent has very small dimensions and is weakly colored by hematoxylin, apparently it is formed from two homological fragments. All of these fragments can be traced (or followed) through two generations. A sixth plant had 22 bivalents, two more or less complex elements and one univalent. A sister plant had 22 bivalents, one trivalent, and one univalent. On the basis of these observations the conclusion was reached that certain changes in the external morphology of the chromosomes, due to the influence of X-rays, represent a structural reorganization (modification) of the chromosomes. In some plants these changes do not bring about a complete loss of viability, consequently it is possible to observe, in subsequent generations, the chief categories of structural changes of the chromosomes. The great increase in the amount of available data on the genetic effects of X-rays calls attention to [redacted] changes (reorganizations) which can have great significance for the evolutionary processes, especially since, at the present time, it has been established that such modifications often arise under natural conditions.

In their subsequent work Goodspeed and Avery (1932) describe 14 types of plants which arose from a single, irradiated sexual cell of Nicotinum tabacum. A cytological investigation of the parent (or source) plant showed a change in the reorganization of its chromosomes under the influence of X-rays. One of the derivatives of this plant had homological fragments which conjugated with each other. One plant (27.154 P001) had a configuration in the first reduction-division which can be characterized by the formula $21_{II} + 5I + 1 + 2f$ (f signifies fragment, II signifies bivalent, and I signifies univalent), one of the two fragments being joined

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to one of the bivalents. Configurations $22_{II} + 3_I + 1 + 2f$ or $22_{II} + 1_I + 1 + 2f$ were also observed. These configurations were responsible for the variations in the number of units found in the various pollen mother cells. From the unpaired chromosomes contained by this plant at least one represented structural change as can be deduced from its size. In this experiment at least five chromosomes of the haploid set underwent structural changes under the influence of X-rays. This was manifested by the appearance of fragments, small univalents (unpaired chromosomes), and abnormal bivalents (pairs). The authors traced these changes down to the sixth generation from the irradiated plant. These three works are sufficient to give an idea of the kind of chromosomal changes that were found by Goodspeed and his co-workers.

For the purpose of increasing the number of modifications M. Navashin (1931) exposed seeds of Crepis tectorum to X-rays for intervals ranging from 40 to 2200 seconds. He radiated with intervals and used 10 batches of seeds. All of these plants produced shoots, but the irradiated plants showed various abnormalities in the formation of the first leaves. The number of abnormalities increased proportionately to the dosages of X-rays. Cytological examination of the root tips, taken from the plants three months after sprouting, revealed an abnormally high percentage of modifications. All of the changes in the chromosomes were translocations. Observations revealed that parts (sections) of chromosomes, regardless of size, could be transposed to any of the other chromosomes. It is interesting to note from these observations that the equal division of the chromatin material ("centermeasure") displays an amazing stability. All of these chromosomal changes have

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not affected the viability of the cells or of the organs.

Levitskiy (1931) also describes fragmentation, loss of parts of chromosomes, and translocation of parts of some of the chromosomes to others. (The mutuality of the translocations was eventually established.) In Secale cereale two of the 14 chromosomes (which usually possess two well-developed processes) had only oval "heads" which apparently were parts of the processes. In one nuclear plate of Crepis capillaris chromosome A developed a second spindle fiber, chromosome D lost a large part of its large "shoulder" (process) and chromosome C, on the other hand, enlarged significantly, apparently at the expense of part of the translocation of the D chromosome. In another nuclear plate of the same species a tearing apart of the A chromosome at its very center ("middle mark") was observed. Both "shoulders" formed little "heads" and spindle fibers. A third nuclear plate showed that chromosome D enlarged its "head" but lost its "companion" (i.e. paired chromosome), while chromosome C lost part of its "head" and acquired a "companion". Afterwards, year after year, the examinations of the effects of X-rays appear in the works of Levitskiy and his co-workers, but since the results of these observations are summarized by the author in his 1940 article they will be presented in their proper place.

Nadson and Rochlin (1933), who devote their attention chiefly to the action of X-rays on the protoplasm and chondriosomes, also point out changes in the nuclei of living cells. These changes commence [redacted] with the contours of the nucleolus becoming more distinct while the texture of the chromatin becomes more coarse. Then coagulation and vacuolization appear in the nucleous, and

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finally karyolysis sets in. The nucleolus disappears. The outline of the nucleus becomes irregular and very variable, sometimes its size diminishes. The rate of changes depends, first of all, on the duration of exposure to irradiation (the dosage), and also on the physiological state of the cell.

Stone's experiments (1933) with nuclei of Tulipa silvestris and Rhoeo discolor in meiosis and with the somatic nuclei of Crosus Olivieri are interesting. Parallel observation of the two groups indicate that X-rays induce a physiological reaction which is sufficient to inhibit nuclear division, but not the process of division which has already begun. Apparently the intensity of the reaction gradually increases and when it reaches its maximum it begins to affect the nuclei which are in the resting stage. Many of them are in an abnormal condition. Stone did not observe any direct, visible effects of irradiation except for the rolling of the chromosomes into balls (knots) and their compression, which he ascribes to the delay between irradiation and fixation. In materials which were fixed 24 hours after irradiation stages up to the metaphase are relatively normal, although in some of the cells fragments are observed in the diakinesis and the metaphase. From the beginning of the first metaphase to the second telophase the behavior of the chromosomes is completely abnormal. These abnormalities consist of fusion and disintegration of the chromosomes.

If flower buds are irradiated when the mother cells are in early prophase then, naturally, the stages of meiosis are normal, except for the appearance of occasional fragments. If the irradiation is performed two or three months before the beginning of the first

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metaphase (while the tissues are going through somatic mitoses), then the reduction-divisions also proceed normally. These observations permit Stone to establish the main difference between the two divisions, which consists of differences in the time required to complete the cycle of division. Mitosis proceeds very quickly, lasting a few hours, while the [redacted] (extended) phases of meiosis require many hours or even days for their completion. Consequently, in mitosis the chromosomes have time to complete division before the induced physiological changes attain a high degree of intensity, while chromosomes in meiosis can be exposed to the induced changes at any stage of division. The ongoing division does not stop; the induced changes, in turn, affect not only the nucleus at rest, but also chromosomes in all phases. But only in the anaphase do these changes show up in the form of fragments or dissolution of the chromosomes. The division does not stop, but the rate may be slowed down. Stone explains the delay in the final stages of meiosis (in bulbs which had been irradiated a month before fixation) by a slowing down of the division. The fact that meiosis in bulbs exposed to X-rays 2 or 3 months before proceeds normally indicates that despite the fact that [redacted] abnormal inductions in the somatic tissues of the cells give rise to the pollen mother cells, the latter exist for a very short time and are displaced by normal tissues. This is confirmed by the quick reestablishment of normalcy in the morphological and physiological properties of tulips which had been exposed to the influence of irradiation. A comparison of the results obtained by Stone with those of Goodspeed shows a large disagreement between them. Goodspeed obtained abnormal final stages in meiosis due to the action of X-rays in cells of the

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archesporium (archegonium?) and the pollen mother cells. Their irradiation in Tulipa caused the final stages to be abnormal. /I believe that the last sentence should read: "Their irradiation in Tulipa did not lead to abnormalities in the final stages"/ But since the whole cycle of meiosis in Nicotiana Tabacum is considerably shorter than in Tulipa, Stone's hypothesis is applicable to the results obtained by Goodspeed.

Mather and Stone (1933) found that the application of X-rays as means of displacement of nuclear material has led to very interesting results, especially in Drosophila and Zea Mays. Definite types of regroupings were established; what was not established was why only these types of groupings should appear. They assume that their observations provide a cytological basis for the appearance of these regroupings and, in addition, they provide certain data concerning the evolution of chromosome sets. They used three species of Crocus for their experiments: C. Olivieri (2n = 6), C. Balansae (2n = 6), and C. biflorus (2n = 18). The bulbs were irradiated for 15 and 30 minutes; the roots were fixed after 30 minutes and after 7, 24, 48, and 72 hours. Then the bulbs were planted in pots and after three months the roots were fixed again. Cytological examinations of these roots permitted the authors to establish that the abnormalities which arise in the chromosomes due to the action of X-rays are represented, chiefly, by two phenomena: fragmentation and fusion of the chromosomes by their ends (tips). These processes lead to all sorts of irregularities: 1. Proximal fragments, which are parts of torn chromosomes and which contain the median points. These occur very frequently

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and exhibit perfectly normal behavior. 2. Distal fragments or parts of chromosomes without median points. These latter have lost their ability of migration in the anaphase and with each division of the cell there are fewer and fewer of them, and finally they disappear completely. 3. Translocations, which arise by fusion of distal segments with whole chromosomes and which are retained after all divisions. (Mutuality of translocations had not yet been established at that time.) 4. Double median points which result from the fusion of two whole chromosomes, or two proximal segments, or of one of these with a chromosome. With every division of the cell some of these are lost. 5. Ring chromosomes which are formed by the fusion of two ends of a single normal chromosome or of a proximal fragment. (Recently the appearance of ring chromosomes has found a different explanation.) From this we can see that the only chromosomal abnormalities which are capable of maintaining themselves through a series of cell divisions are translocations and proximal fragments. Having made these observations concerning the origin and survival of definite abnormalities Mather and Stone set out to solve one of the important cytological problems, namely: at what point in mitosis do the chromosomes split? Basing themselves on Stone's premise that irradiation does not affect chromosomes which are in division, they conclude that the abnormalities must arise during the resting stage, which has been retarded (or inhibited) by X-rays. If the chromosomes split in the metaphase or anaphase of the preceding division then unequal abnormalities should arise as a consequence of the existence of two elements (chromatids). The appearance of two unequal chromatids, however, has not been observed in any species. If, on the other hand,

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chromosomes arise (split) after the appearance of abnormalities then the chromatids which appear will be equally abnormal. Since Mather and Stone only observed the appearance of equally abnormal chromatids, they conclude that the chromosomes must divide in the early prophase. In other words, in the first case the X-rays affect chromatids and in the second case they affect the entire split chromosome.

In 1934 Mather compared the behavior of chromosomes in reduction-division after irradiation, in Vicia faba and Tradescantia bracteata, which differ from each other in that Vicia faba has a higher frequency of chiasmas and a lower terminalization than Tradescantia. The haploid chromosome set of Vicia faba consists of five short chromosomes with subterminal adhesions (m-chromosomes) and one chromosome with a submedian adhesion (the M chromosome), which is twice as long as each of the former. The average frequency of chiasmas in the M-bivalent (i.e. pair) is nearly double that of the m-bivalents. X-radiation causes the appearance of fragmentation and translocations in the first metaphase. The translocations give rise to various configurations. One such translocation consists of four chromosomes and apparently results from an exchange of segments, or mutual translocation, or else of an inversion of a segment in one of the chromosomes. Another configuration contains the m and M chromosomes. One form of break is more frequent than others and that is a break in the "loop" or "shoulder" which carries the median point. The latter is not clearly apparent in the early metaphase and here the break occurs more rarely. In the late metaphase, when the median points move toward the poles and the chromosomes are thinnest at this point, the break occurs more frequently. This indicates that the chromosomes are weakened by

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the action of X-rays and break easily. In the early metaphase the break occurs along the whole length of the chromosome, but in the anaphase and telophase several large chromosomal fragments are more frequently encountered. These fragments do not contain the median points and, consequently, are not able to migrate to the poles. They linger at the equator and form micronuclei in the interphase, and during the second division they lie apart from other chromosomes. The two median points of a single chromosome can go either to the same pole or to different ones. In the first case the double median point can be retained and in the second division it can give rise to a new chromosomal type of pollen grains. In the second case two danther nuclei will be connected by a stretched chromosome until it breaks. In Tradescantia from 4 to 7 days after irradiation almost all of the chromosomes in meiosis are fragmented. Many translocations are also observed. Cells in the telophase and interphase stages are frequently abnormal in the number and size of the chromosomes, which results from the presence of lingering chromosome fragments which eventually give rise to micronuclei. The abnormalities of the first division manifest themselves in the metaphase of the second division by formation of more than two (nuclear) plates, or by abnormal structure of the chromosomes, either forming rings (loops) or having from 2 - 4 median points ("centermeasures"). Sometimes chromosomes are observed in the second metaphase which are composed from identical chromatids. The tetrad stage is irregular. In the metaphase of the division of the primary nucleus of the pollen grain fragments are observed in various numbers. The chief difference in the behavior of the chromosomes of Vicia and Tradescantia lies in the

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fact that in the first plant fragmentation occurs up to the anaphase and in the second, up to the metaphase. Apparently the various stages at which fragmentation occurs are related to a certain difference in the behavior of normal chromosomes, which consists of the fact that Vicia has a low "terminalization" of chiasmas, while in Tradescantia "terminalization" is high. (The term "terminalization" was used by Darmington to refer to the movement of chiasmas away from the median points, caused by the repulsion of median points during the prophase.)

In 1935 Marshak studied the effects of X-rays on various stages of meiosis in Gasteria. This plant was selected because each flower bud on it contains six anthers each of which contains spore mother cells in the same stage of development. By this means Marshak avoided the usual difficulties encountered in work with the biological effects of X-rays which arise because of lack of uniformity in the cells. The effects of X-rays observed in the first anaphase were chromosomal fusion, fragmentation, and the appearance of achromatinic areas (spots). The number of chromosomal abnormalities in buds of various ages reaches its maximum from 1 - 5 days after irradiation. At the time of irradiation the nuclei in these buds were either in the pachytene stage or in the early premeiotic prophase. The chromosomal changes show a direct relationship to the dosages. This linear function signifies that the "photoelectrons" (photons?), which were formed during the absorption of X-rays by the tissues, act directly on the biological agents (or factors). This hypothesis of direct action explains the higher frequency of chromosomal aberrations in cells which were irradiated at certain

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(definite) stages of division. On the basis of his observations Marshak came to several important, theoretical conclusions: spore mother cells irradiated by small doses of X-rays at various stages (of division), manifest various frequencies of chromosomal abnormalities in the first anaphase. The maximum frequency of abnormalities were observed in buds which had been irradiated when the cells were in the pachytene stage or in premeiotic mitosis. This indicates that those parts of the chromosomes which are sensitive to X-rays are in close proximity in pairs in the pachytene stage and in the early prophase of mitosis. From the nature of the chromosomal configurations it is possible to conclude that the chromosomes consist of two parts when they form configurations, and that chromosomal division takes place between the pachytene stage and the anaphase in meiosis, and during the prophase in mitosis.

Krayevoy (1935) used X-rays on young sprouts (seedlings) of Pisum sativum var. glancospermum. During the entire growing season at regular intervals (of time) samples of the roots were taken from each of the plants. The karyotype of the aberrants (which resulted from the action of X-rays) has unpaired chromosomes and chromosomes whose secondary spindle fibers are missing. Besides, the chromosomes are somewhat thickened. A certain number of aberrants are retained till X_2 (the second generation of X-radiated plants) and for that reason the author calls this type of change "delayed modification of the karyotype". Krayevoy established a definite regularity in the appearance of aberrants. The higher the dosage the greater the number of aberrants. The number of the latter diminishes with each generation, reaching zero in X_3.

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Heeren, in his work in 1936, once more raises the question concerning the primary biological action of X-rays on living cells since, usually, this action manifests itself only after a definite, so-called "latent", period. Consequently, the determination of what is understood by the latent period is very important. Jungling proposes to define it as the actual delay of the beginning of the reaction. We can displace the beginning of the reaction by means of X-rays, if after irradiation of turgid beans we dry them out and by this means reduce them to a latent condition, and then soak them again and cause them to grow; then the action of the rays will manifest itself later. This definition of a latent condition was not accepted by everyone. What is usually understood by the latent period is the time which elapses between irradiation and the first visible cellular change. As the methods of investigation are refined this interval is shortened more and more. In his experiments Heeren set out to analyze in more detail the previously observed retardation of the growth of the plant. In this experiment seeds of Vicia faba were subjected to swelling in boiled water for 24 hours, after which they were placed in glass dishes filled with water soaked cotton. Alongside the sprouting seeds a glass plate with grooves was placed in order to observe the direct growth of the roots by Meissner's method (which is based on the interference of light waves of equal length). This method permitted the determination of lengths of 0.29 μ . Before irradiation (as measurements by Meissner's method showed) the roots grew very quickly: 0.29 μ in 15 seconds. When the sprouts were irradiated twice by doses of 9.5 roentgen units the effect of the rays did not become apparent. During the next two days the same dose was administered four times

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and each time immediately after irradiation the growth would cease, only to be followed by a sudden acceleration of growth. These observations show that immediately after irradiation the roots grow much faster than before irradiation. If the dose was increased to 11.5 ~~X-ray~~ roentgen units then the roots instead of lengthening, would shorten. The probable explanation of this phenomenon, according to Heeren, lies in the fact that at the time of irradiation the cells always shorten, but this effect is masked by the simultaneously ongoing growth. The contraction of the cells during irradiation is, apparently, the result of plasmolysis. The contraction of the protoplast is followed by the contraction of the cellular membrane and a shortening of the cells is observed. In order to eliminate the expansion of the root cells due to absorption of water, a paraffin oil was used which does not interfere with the growth of the roots. This experiment permits the differentiation of growth from expansion due to absorption of water, and it showed contraction due to the influence of irradiation. In addition Heeren's experiments lay a foundation for investigation of the effects of various agents on the action of X-rays. When a root was narcotized by water saturated with carbon dioxide, it ceased to grow and was incapable of reacting to X-rays. These experiments permit us to establish the following picture of the action of X-rays: first of all the protoplast contracts, it withdraws from the elastic cell wall, which follows the contracted protoplasm, and then the whole cell contracts (i.e. becomes shortened). The expansion of the cell by simple absorption of water goes on; X-rays have no effect on it. The absence of reaction to irradiation in narcotized cells confirms the fact that the active contraction of the protoplast sets in as a

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result of irritation caused by the rays.

In 1936 Sizova observed the structural transformation of chromosomes under the influence of X-radiation of physiologically changed cells. Preliminary experiments showed that a five hour sojourn of Crepis capillaris sprouts in a desiccator filled with carbon dioxide does not induce any structural changes. Roots which had been kept for five hours in carbon dioxide before irradiation showed (after irradiation) 50 percent of their plates changed. Those which had not been in carbon dioxide showed changes in only 26 percent of the plates. However the chromosomal changes were similar in character. Ammonia fumes also fail to produce chromosomal changes but the chromosomes become shorter and thicker. If, after being kept in ammonia fumes for six hours, the sprouts are irradiated then the number of changed plates reaches 44 percent. A preliminary cooling on ice before radiation has a similar effect. The number of plates with structural changes then goes up to 40 percent.

In 1937 Marshak investigated the frequency of appearance of abnormal chromosomes, under the influence of X-rays, in the anaphase. He performed his experiments on a wide variety of objects; sarcoma of mice, carcinoma of rats, and roots of Vicia faba, Pisum sativum, Allium lepa, and Lycopersicum esculentum. In all objects the frequency of chromosomal abnormalities (chiefly fragmentation and fusion of chromosomes) reaches its maximum two or three hours after irradiation and then gradually returns to normalcy after 48 hours. The curves which express the action of X-rays are identical for all objects. The curves of the retardation of mitoses are parallel to

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the curves of chromosomal abnormalities. According to Marshak's observations the retardation of mitoses is not related to the length of the chromosomes as some investigators had supposed. Three hours after irradiation by equal doses, frequency counts of changed anaphases showed 19 percent retardations in Allium, which has extremely long chromosomes, and 22 percent in Lycopersicum, whose chromosomes are among the shortest in the vegetable kingdom. Despite the great differences in the length of the chromosomes of the various objects investigated, the diameters (i.e. lengths) of their sensitive areas (zones) are surprisingly similar in their dimensions. This similarity causes us to suppose that this is a dimension of some physical structure in the chromosome which is identical in all of the objects investigated. The size of this diameter (i.e. dimension) coincides with the average size of polypeptid chains or the size of a molecule of simple proteins (10×10^{-8}). Similarly, the reaction to the action of ammonia and carbon dioxide before and during irradiation agrees with the hypothesis that the sensitive substance of the chromosomes belongs to the same category of protamins (simple proteins) and histones. The cyclical changes in the localization and distribution of the chromatin material indicate that this substance is negatively charged and, apparently, consists of nucleinic (or nucleic) acid. These changes in the distribution of the negatively charged substance are in accord with the observations of the changes in sensitivity to X-rays.

In 1938, Sax subjected the microspores of Tradescantia reflexa, which had six pairs of chromosomes and one pair of fragments, to irradiation. Several hours after irradiation by a dose of 25 roentgen

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units the meiotic chromosomes and also the chromosomes in the microspores gather in knots and the homplogical chromosomes fuse. Twenty-four hours after irradiation "bridges" and free fragments are observed in the anaphase. After 48 hours, Sax observed several breaks in the chromosomes, but four days after irradiation he no longer found any. The breaks liberate the distal ends of the arm of the chromosome and the broken off ends of sister chromosomes fuse at one end. Usually the first break of the chromosome is observed 6 hours after irradiation. When the torn chromosome divides in the anaphase its ends fuse forming a "bridge". The distal ends of the torn chromosomes always fuse, forming a single fragment. The size of the fragments can vary, but "bridges" never exist without fragments. The break in two chromosomes can be accompanied by a reciprocal interchange, or by fusion of the chromosomes when the fragment is liberated. It is very difficult to trace (follow through) such mutual interchanges. As has been already pointed out above the torn ends of each arm of a single chromosome can form chromosome rings. The irradiation of the chromosomes in the reduction-division can bring about a high rate of infertility (sterility) in the microspores; nevertheless some of the microspores develop, and they show very frequent breaks in their chromosomes. If the fragments are retained (i.e. not lost) the chromosomes from which they broke off develop normally. Sometimes, as a result of irradiation, diploid microspores develop, and frequently microspores with chromosomal aberrants appear (fragmentations, fusion of chromosomes, and, more rarely, unequal distribution between the poles, monocentric spindles, and inactivity of the median points). In contradiction to the opinion expressed by many cytologists that the "blow" delivered by X-rays can break only one chromosome in

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a given location Sax considers that his observations demonstrate breaks in chromosomes and in chromatids in the same divisional figure, and even in single chromosomes. Then he sets out to solve whether these breaks are localized or not. If the break and fusion of the chromosomes occur at every point in the chromosome from the "blow" received by the X-rays, then the break can occur at any point, by chance, along the whole length of the chromosome. But if secondary factors enter into the action (rotation of chromosomes, or the relative positions, or differential contraction) then the breaks must be localized. In order to solve this question Sax conducted an analysis of the position of the breaks in the cells, which had been irradiated when the chromosomes were in the resting stage. This analysis showed that 50 percent of the breaks of the chromosomes occur in the proximal third of the arm of the chromosome. They are less frequent in the central part of the arm and more frequent in the distal parts of the chromosomes. Then plants which had been irradiated with 150 roentgen units were analyzed in order to determine the types and frequencies of chromosomal aberrations in various stages of meiosis and mitosis. After 24 - 30 hours after irradiation the number of chromosomal aberrations was 11 percent, after 48 - 55 hours the number diminished, and between the third and the eleventh day it went down to 3 percent. At the same time the fertility of the pollen attained 80 percent. On the 12th day after irradiation a small increase in the number of chromosomal aberrations was observed, on the 14th day their number went up to 40 percent. At this time the infertility of the pollen rises sharply. Between the 15th and the 19th days the infertility of the pollen is so great that it is difficult to investigate the chromosomes. On the 9th day the fertility of the pollen increases up to 50 percent and remains such for 10 days.

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By the end of the fourth week the cycles of mitosis and meiosis approach completion and the fertility of the pollen becomes normal despite the irradiation of the premeiotic cells.

It turns out that chromosomes in meiosis are ten times as sensitive as chromosomes in the resting stage of the microspore. The prophase of mitosis is twice as sensitive to X-rays as the resting stage, but in the prophase half of the breaks occur in the chromatids, while resting nuclei show breaks only in the chromosomes.

In addition, by his experiments Sax confirmed the observations of many other investigators that X-ray mutations are independent of the temperature at time of irradiation.

In 1940, Savchenko irradiated young shoots of Crepis capillaris and fixed the roots immediately after irradiation. A cytological examination did not disclose any mutations. On the basis of this observation Savchenko comes to the conclusion that X-rays do not impede the process of mitosis which is already under way, but they do prevent the commencement of new mitoses. In order to be able to form an accurate concept of the nature of effect of X-rays on cell division, the cells were chilled in order to slow down their reaction rate. It turned out that the chromosomes simply become swollen; there were no other changes. Consequently, X-rays do not exert any direct effect on the formation of chromosomes. Under irradiation cells simply cease to divide and after irradiation is concluded they remain in the resting stage for some time. The duration of this condition differs: 12 hours after irradiation the author observed prophases and occasionally metaphases; 18 hours

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after irradiation he observed anaphases and telophases. In the first cellular division after irradiation fragments, chromosomal breaks and fusion of chromosomes were observed.

Immediately after Muller's communication was published in 1929 Levitskiy also set up experiments with the irradiation of Crepis capillaris, whose chromosome set consists of three pairs of distinctly differentiated chromosomes (A, C, and D). The transformations of the chromosomes were described in 1931 (Levitskiy and Araratyan). In the spring of 1932 shoots of this plant were irradiated once more and from the plants which developed 20 specimens which showed marked deviations were selected. From the seeds collected from these freely self-pollinated plants X_1 was obtained. This generation was subjected to that cytological examination which established the karyotype characteristics of numerous plants. These data were published in 1934 (Levitskiy, Shepeleva, and Titova). Of the 491 plants of X_1 that were examined 84, or 17 percent, showed modifications. The majority of them (74) were "structural" modifications of the chromosomes, either in pure form or in combination with triploid (4) or trisomatic (1) sports. There were only 10 pure numerical changes: 6 triploids, 1 tetraploid and 3 trisomes (of all the 3 possible types). The most frequent of the structural changes were translocations which previously (to 1934) were explained as a simple transfer of part of one chromosome to another. The same reasoning was applied to explain the regularity of transformations induced by X-rays (Levitskiy and Sizova, 1934). This reasoning, it appears, was confirmed by an examination of reduction division in karyotypic aberrants, performed by Petrov (1934) on Levitskiy's materials. Petrov described a chainlike

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linkage in diakinesis as typical for simple translocations. A detailed examination of bulk material showed that "X-ray aberrations in Crepis in the overwhelming majority of cases (and perhaps in all cases) are mutual" (Levitskiy and Sizova, 1934). On the other hand a reexamination of Petrov's material , performed on earlier stages, revealed in meiosis also the mutual character of the translocation which appears in the form of a ring, so rarely, apparently, due to the insignificant size of one of the parts of the chromosomes which participate in the exchange. From each of the irradiated parent plants several modified individuals were obtained; these modifications were of various types. In some cases several individuals with identical chromosomal changes arose from the same parent plant, indicating that they derived from a single modified cell of the parent plant which gave rise to a whole aberrant "sector" or part in the mother plant.

All of these changes were first obtained in a heterozygotic condition, and later in a homozygotic one. In addition to balanced (i.e. mutual) changes, duplications were obtained from whole chromosomes (all three types) and from the distal and proximal parts of the D-chromosome. The last of these changes was obtained in tetrasome condition. Some of the aberrants that were examined showed a depressed fertility. Usually this decrease of fertility was found in a heterozygotic state; sometimes it was found in a homozygotic one. In the first case, according to Levitskiy, this phenomenon is due to cytological causes. Among karyotypes of pollen grains of structurally heterozygotic aberrants the normal karyotypes are more numerous than balanced aberrant karyotypes. Two heterozygotic

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translocants had many pollen grains with karyotypes that had an additional chromosome or part of a chromosome. The gametophyte reaches a total of nine various types.

From Gerasimova's two experiments (1940a and 1940b) which are of exclusively genetic significance, for this part of our exposition of the effects of X-rays, we shall take only purely cytological data. Ripe ovicells of Crepis tectorum were exposed to X-rays (1940a) and then fertilized by normal pollen. From 20 ovules of a single plant 8 very infertile plants came up; seven of them had normal chromosomes, one was a translocant. The translocation occurred between B and D, the break in them took place along the partner of the D-chromosome not far from the proximal arm of the B-chromosome. In the translocation almost the entire distal arm of the B-chromosome transferred itself to the remnant of the partner (or pair) of the D-chromosome, becoming a gigantic partner, suspended by a long thread. Apparently, the D-chromosome gave up to the B-chromosome part of its partner (pair), but this part was so minute that it was not noticeable. Cytologists examined 189 descendants of these plants: 84 were normal, 59 turned out to be heterozygotic translocants, and one was a homozygotic translocant. In 34 of the plants only one chromosome was changed. In a work published in the same year the sizes of chromosome partners (pairs) are examined. As has already been pointed out, as a result of X-radiation of the ovicells of Crepis tectorum one plant arose whose D-chromosome had a gigantic partner. This partner consisted of the entire distal arm of the B-chromosome (of which only the short proximal arm was left). Among the descendants of this plant there were homozygotic specimens of this translocation. In some

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cells the gigantic partner would lose a small or large fragment of itself, sometimes disappearing entirely. Simultaneously with the metaphases, which were characterized by a partial or complete loss of the giant partner, cells were encountered with additional nuclei, chromatin spheres, etc., which were indicative of loss of fragments or whole chromosomes during cell division. It was natural to associate this with changes in the giant partner. An analysis of the figures indicated to Gerasimova that when a partner exceeds a certain size [redacted] it runs a great risk of being lost or diminished.

In order to conclude the literary survey of the action of X-rays on the nucleus and the chromosomes it is essential to have a look at the changes which arise in the two plants that have been most thoroughly studied in this respect, i.e. Nicotiana and Zea Mays. The radiation of Nicotiana tabacum by large doses of X-rays produces (in the sexual cells, seeds, and seedlings) an extreme degree of fragmentation and fusion of the chromosomes, accompanied by changes in the spindle mechanism. Cytological investigations reveal such an extreme and obvious destruction of the chromosome mechanism in mitosis and meiosis that the resulting lethal effect brings about a complete sterility in gametes and zygotes. Nevertheless, in some instances a small number of seeds did develop, and they gave rise to plants which showed extreme morphological modifications. In one case 48 descendants were obtained from a plant and only 2 of them were anywhere near normal, the rest exhibited a most extreme variety of external characteristics. However the offspring of one of the two outwardly normal plants showed a very great range of variations.

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The scope of chromosomal aberrations displayed by Nicotiana tabacum is partially due to the fact that this plant is of multiploid (polyploid) origin. Goodspeed observed two haploids in the genus Nicotiana: one of them from the variety purpurea which arose from irradiated seedlings, and the other from irradiated seeds which arose in the X_1. In addition, two haploids appeared in N. glutinosa in the X_3 generation. All told, Goodspeed observed the appearance of 11 haploids, the occurrence of which the author ascribes, not to the direct action of irradiation, but rather to the secondary effects of irradiation. Goodspeed assumes that a parthenogenetic development of the ovicells is possible. He also notes the appearance of numerous trisomes in the var. purpurea, although only three of them were traced (i.e. followed up) cytologically. Probably they sprang from parents with an unbalanced chromosome condition which is conducive to the formation of somatic gametes. One of the triploids arose from an induced trisome. A vigorous side shoot appeared on an abnormally puny plant of X_1 (of the Maryland Mammoth variety). It turned out to be tetraploid and arose from a sector (part) with tetraploid cells. This tetraploid shoot is, doubtless, a by-product of irradiation, since such shoots never appeared in unirradiated plants. High frequency radiation (in this case X-rays) by primary or secondary action increases the number of chromosomal injuries and inhibits conjugation. This constitutes a source of polysomites and monosomites, which appear as products of the primary action of irradiation, but also as by-products of the secondary action. These by-products include: (1) induced mutations, acting on the conjugation of chromosomes, and (2) induced chromosomal reorganizations; translocations,

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duplications, inversions, etc. The induced asynapsis in N.sylvestris can serve as an example of the first type. It showed up in X_2 and was traced down to X_3. Among the plants of X_2 and X_3 many trisomites turned up, several double trisomites, and four tetrasomites. The fusions of chromosomes, which are followed or preceded by fragmentation, are typical products (i.e. results) of irradiation. What happens to the fragments (i.e. their fate) is very important to the continuation of the existence of the plant. In some cases fragments are retained and become permanent parts of the chromosome set. One type of N. tabacum retained a pair of fragments for 4 or 5 generations. In some of the unestablished types Goodspeed observed many fragments. One of the consequences of induced fragmentation can be the insufficiency of chromatin material. In Nicotiana such insufficiencies result in various morphological types.

However, neither in Nicotiana, nor any of the other plants, have chromosomal reorganizations induced by radiation been as well investigated cytologically as they were in Zea Mays (Anderson, 1937). Anderson devoted a chapter in Duggar's book to: "Induced chromosomal alterations in Maize". This plant has 10 chromosomes but different varieties or strains have visible differences in their chromosomes: the presence or absence of bumps on their tips, different size and shape of the chromosomes, and also a different appearance of median points and bumps. These peculiarities permit the identification of each chromosome, as has been done for Drosophila. In addition to the normal diploid set of 10 pairs of chromosomes it is possible to encounter one or several B-type

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chromosomes. This aberrant type of chromosome behaves more abnormally in meiosis and does not seem to have any hereditary function. When maize (corn) cells are X-radiated the same types of changes appear in the nucleus as have already been described for other plants. In some strains of maize part of the chromosomes were in an inverted condition. These, so-called, inversions were observed in the short arm of the 8th chromosome. A short inversion was also found in the 4th; this latter included the median point. These inversions occur in the natural state. McClintock observed an inversion in the second chromosome; 2/3 of the chromosome were inverted. Long heterozygotic inversions produce, in the prophase of meiosis, loops which are typical for inversions. These loops form as a result of the fact that only homologous parts of the chromosomes conjugate. Sterility in the pollen and the ovicells were observed in long inversions, which resulted from a crossingover in the loop of the inversion. When the inversions are homozygotic the fertility is normal. In heterozygotic inversions partial sterility is observed. "Shortages" (losses of chromosome tips) crop up in maize cells after irradiation, but they are not transferred to the offspring. Zygotes containing chromosomes with "shortages" are viable and vigorous, but spores with a "shortage" in their haploid set do not come to life before it is time for them to function. Chromosomes with "shortages" pair up with homologous parts of the corresponding normal chromosome. As has already been pointed out above chromosomes in maize can be identified; consequently when the "shortages" were measured it was possible to establish the position of certain genes in certain limited locations of specific chromosomes.

The most noticeable, and apparently the most significant,

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changes produced by X-rays are those in chromosomes. The high sensitivity of the nucleus to X-rays (as compared with the less sensitive cytoplasm) has always been noted by investigators. However the reason for this has not been established. Uber and Goodspeed (1935) assume that the difference can be ascribed to a difference in the mineral salt contents. There can be no doubt, however, that other factors must play significant roles. According to the investigations of Marshak and Bolman (1936), the presence of elements with high atomic weights increases the absorption of X-rays, and it is due to this that they explain the increase in transformations. In relation to this Stadler established in 1928 that plants from seeds which had been soaked in salts of heavy metals before being irradiated showed a noticeable increase in the frequency of induced mutations. The relative weakness of the bonds which connect molecules of micelle (colloidal iron) or genes in chromosomes, which are broken by the impact of an electron may determine the great sensitivity to X-rays of the nucleus, as compared to the cytoplasm. Metz (1934) assumes that the isolating substance of the visible, gelatin-like envelope around the chromosome may be destroyed by irradiation and cause a tight contact between chromosomes which results in their fusion, fragmentation and similar other disorganizations in the nucleus and its contents. In nuclei which have received such doses one can clearly observe (from the metaphase to the telophase) pycnosis or contraction of the chromosomes into a darkly stained mass. This can be observed in meiosis as well as in mitosis. Kornicke, Komuro, Marshak, Pekarek, Stone, and Husted all observed this. The pycnosis may be preceded by a shortening and a thickening of the chromosomes previous to the metaphase (Riley) and breaks in the prophase threads (Sizova).

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Less drastic, but equally lethal or sublethal effects are described with all kinds of details by various investigators. The induced changes include: extremely aberrant and improperly distributed (i.e. arranged) chromosomes, reconstructed (i.e. rearranged) nuclei, cells with dwarf nuclei, multinuclear cells, chromatin plates between two or several danther cells, the formation of two or three spindles, etc. Increases in number and size of nucleoli, their vacuolization, and improper budding almost always accompany such nuclear changes.

All of these changes were observed by the following investigators: Delaunay, Goodspeed, Avery, Olson, Huskins and Hunter, Husted, Katayama, Kornicke, Komura, Krayevoy, Lewitsky, Araratyan, Shepeleva and Titova, Sizova, Marshak, Bolman, Mather, McClintock, Metz, Mol, Nadson, Rochlin, M. Navashin, Nebel, Nettling and Stubbe, Patten and Vigoder, Pekarek, Riley, Sax, Stone, Strangeways and Hopwood, Ternovskiy, Thompson, Jungling, and Langendorf.

By means of X-rays questions concerning the mechanism of chromosomal rearrangements, and conditions of chromosomes at various stages of the nuclear cycle were also studied. On the basis of numerous investigations of plant and animal organisms which had been subjected to the action of X-rays, it is possible to assume that the fact that chromosomal changes are due to direct action of X-rays (and not to the influence of cytoplasmal changes) has been established.

In addition to these changes Komuro, Patten, and Wigoder observed multinuclear cells in Vicia; and Huskins, in Trillium.

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CYTOLOGICAL INVESTIGATIONS PERFORMED IN THE ELECTRO-BIOLOGICAL LABORATORY

In the first part of our work we presented data on the physiological changes in rye, peas, and wheat, and on the increase in yield of the first two. In our cytological investigations we uncovered certain laws which relate these changes to the intracellular ones.

Rye -- Sprouts and Seeds (Investigation by Afanas'yeva, Breslavets, and Medvedyeva)

After having studied the morphology of the resting nucleus and the process of cellular division in normal rye we proceeded to investigate the nuclear changes due to the action of X-rays. With dosages of 250 roentgen units the most frequent changes observed by us were the appearance of cells with two nuclei, whose fate (future) differed, depending on how far apart from each other they were located. If they lie close together they soon fuse and give rise to tetraploid nuclei. If they lie at some distance from each other then the cell remains binuclear for some time. This condition, however, stimulates more rapid division, and cells with single nuclei result. This same dose results in the appearance of a doubled number of chromosomes and in the related increase in size of the nuclei. In addition to these changes which are conducive to the increase in the amount of nuclear material, which (in turn) leads to an increase in cellular activity and stimulation of the growth and development of the plant, other changes were observed which cannot be considered to be beneficial to the life of the cells and the development of the plant. These (latter) changes consist of a flowing out of the

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nucleoli from the nuclei and even the flowing out of the nuclear material itself. These changes are encountered in a dose of 250 roentgen units so rarely that they do not have much effect on the activity of the cells; they do, however, serve as a warning that it is dangerous to increase this dosage.

Figure 16. Intracellular changes with a dose of 750 roentgen units: 1 - an abnormally large cell with two nucleoli; 2 - the same with a single nucleolus; 3 - four nucleoli in the nucleus of a tetraploid cell; 4 - the fusion of two long nucleoli, each of which in turn was formed by the fusion of two nucleoli; 5 and 6 - complex shapes of fused nucleoli; 7 - nuclei passing from one cell to another (rye).

In addition, various irregularities appear in the prophase which imitate the figures of reduction division. The irregularities in the prophase lead, in the further development of the process of division, to irregularities in the metaphase such as fusion of the chromosomes into several or a single shapeless glob or (sometimes) their complete decomposition. With a dose of 250 roentgen units these abnormalities are few, but as doses are increased the number of abnormal figures, in both resting and dividing nuclei, increases. The greatest increase is in the number of cells whose nuclear material is completely disintegrated. This phenomenon reaches its maximum frequency with a dose of 8,000 roentgen units. Besides, the number of dividing nuclei decreases, beginning with a dose of 1,000 roentgen units. With doses of 4,000 roentgen units dividing nuclei are almost never encountered. If we remember (as has been pointed out in the first part of our work which is devoted to physiological changes induced

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by X-rays) that all plants which received doses of 4,000 and 8,000 roentgen units perished, then the reason for their death becomes quite clear. Strong doses of X-rays destroy the nuclei, and cells deprived of their nuclei, sooner or later, die off. If the injuries to the nucleus are not as great, then, nevertheless, it loses its ability to divide, or else, divides very slowly. The tips of the roots, not having any other means of increasing in size except by elongation of the cells, at first stop growing, and then slowly perish.

As has been pointed out in literature more than once, soaked seeds have a completely different sensitivity to X-rays than sprouts (seedlings). When a dose of 5,000 roentgen units is used on sprouts the growth and development of young plants is depressed (inhibited). The same dose when used on seeds stimulates their development and increases the yield. A dose of 750 roentgen units has a still greater effect in this direction. With this dose the maximum yield is produced. Parallel intracellular changes take place in the roots. When this dose was used two roots were found which consisted entirely of hexaploid cells, i.e. the number of chromosomes was triple that of normal diploid nuclei which have 14 chromosomes. Each nuclear plate had 42 chromosomes. In these two roots we never encountered cells with a diploid number of chromosomes. On the basis of these considerations we assumed that these roots belonged to one, or two, hexaploid plants. We do not know which because at that time we did not make individual fixations.

Figure 17. 1 - A shortening and thickening of chromosomes in the metaphase; 2 - a lobed nucleolus in the prophase; 3 - the formation

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of rings and figure 8's in a somatic metaphase; 4 - hexaploidal plate; 5 - the distribution of hexaploidal plates in roots (rye).

In all three doses (250, 500, and 750 roentgen units) we almost never found changes which could be considered detrimental to cellular activity. Such changes appear only with doses of 1,000 roentgen units, and then in very insignificant amounts. But as doses are increased the number of changes increases, reaching its maximum with 8,000 roentgen units.

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These observations, which are in agreement with the observations of other authors, indicate that X-rays induce intracellular changes. One of these changes, which is induced by weak doses of X-rays, is beneficial to cellular activity. It increases the intensity (i.e. rate) of cell division and stimulates a faster rate of growth and promotes a more vigorous development of the plant. Stronger doses are conducive to the appearance of changes which are injurious to cellular activity, they slow down the process of division and cause the process to proceed inproperly and even may cause the complete disintegration of the chromosomes. This, of course, is reflected in the yield, which diminishes as doses increase.

The increase in size of the diameters of the roots, depending on the dose of X-rays used, has already been pointed out. This increase can be conditioned by either the number of cells, or by their size. In order to determine this question we made cell counts and measured their sizes, in a certain layer of the root. Previous experience had shown us that with rye it was necessary to use the subepidermal layer of cells. For comparison we took average data from cell counts for 10 roots (10 roots for each of the 8 doses and for the control). For each root counts were made for five sections: the first, 3 to 4 sections above the place where the tissues begin to differentiate into the primary bark and the axial cylinder, the other four sections were taken 3 to 4 sections above that, along the root. In this fashion for each dose (of X-rays) 50 sections were counted and their arithmetical means calculated. As can be seen from the appended table, the number of cells increases beginning with a dose of 250 roentgen units, and

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and reaches it maximum at 750 roentgen units and then, beginning with 1000 roentgen units it begins to drop gradually.

TABLE 26

The average number of cells in the subepidermal layer.

(Based on the data of Breslavets and Afanas'yeva, 1932)

Control	250 r	500 r	750 r	1000 r	2000 r	4000 r	8000 r
40	56	61	68	57	39	40	35

If a graph is constructed on the basis of this data it will not differ in any respect from a curve which is characteristic for physiological changes in rye, induced by similar doses of X-rays (fig 18).

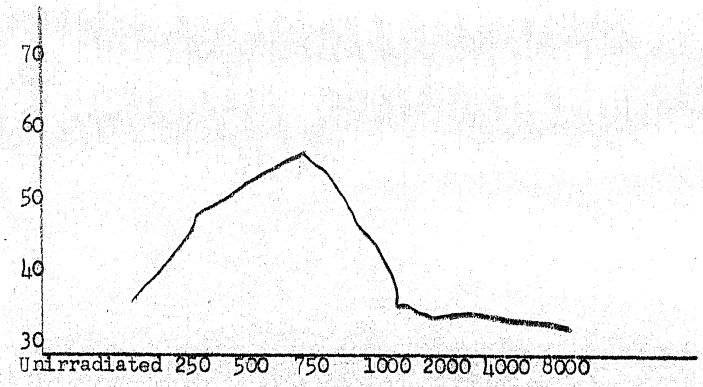

Figure 18. Changes in the number of cells in the second layer of the root depending on the applied doses of X-rays (rye)

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When the number of cells were counted in beneficial doses of X-rays the reason for their increase became obvious: it was due to the increase in the number of cell divisions (mitoses). In order to obtain data on this we counted all the mitoses that could be seen in a single section (magnification 800X), thus determining the number of cells whose nuclei were in any of the stages of mitosis. As table 27 indicates the number of mitoses at first increases, as doses of X-rays are increased, reaching its maximum at 750 roentgen units, after which the number drops (figs 19 and 20) (table 27).

(Figure 19. Changes in the number of mitoses per cross section of the root depending on the dose of X-rays used (rye). The caption above the graph reads: number of mitoses per cross section of root.)

(Figure 20. One third of the cells undergoing division (rye).)

TABLE 27

Number of mitoses per cross section of the root (based on the data of Breslavets and Afanasyeva 1932

Control	250 r	500 r	750 r	1000 r	2000 r	4000 r	8000 r
68	78	93	98	71	56	38	10

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Let us now turn our attention to the results obtained when sizes of the cells and the nuclei were measured (in cells we measured the length and width, in nuclei we measured 2 diameters at right angle to each other).

From table 28 we can see that the length and width of cells does not change from the action of X-rays, or rather that these changes are so small that they can be disregarded.

TABLE 28

Length and width of cells in microns

(based on data of Breslavets and Afanas'yewa, 1932)

	Control	250 r	500 r	750 r	1000 r	2000 r	4000 r	8000 r
Length	19.4	17.9	19.9	19.7	19.9	22.7	19.9	22.7
Width	18.7	20.9	22.3	22.3	19.8	21.8	20.3	20.2

Thus we can answer the question: on what the increase of root diameters depends. Our counts and measurements indicate that it depends on the increase in the number of cells, whose size remains almost unchanged.

Nuclei, however, shows a certain increase in their size. Thus, from table 29, we can see that with doses of 250, 500, 750 and 1000 roentgen units the nuclei increase in size. Since the sizes of the cells remain the same the relationship which exists in normal roots between the nucleus and the plasma is upset. And this explains the more intense (i.e. accelerated) cell division

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when these doses of X-rays are used.

TABLE 29

Average diameters of nuclei in microns

(based on the data of Breslavets and Afanas'yeva, 1932

Control	250	500	750	1000	2000	4000	8000
9.7	11.5	11.0	11.1	11.2	10.4	10.5	10.

Quantitative changes in flowers, just as the qualitative changes presented above, indicate that these changes parallel changes in yield. When soaked seeds are irradiated by doses of X-rays, up to and including 1000 roentgen units, the growth and development of plants is stimulated, thus increasing the number of ears and grains, and increasing the quality of the grains as far as their weight is concerned. Cytological examinations indicate that, with these dosages, first the diameters of the roots increase, and secondly, the number of cells increase due to a more rapid rate of division. Beginning with 2000 roentgen units, X-rays have a less beneficial effect on the yield, while doses of 4000 and 3000 roentgen units noticeably depress the development of the plants. We note a corresponding decrease in the diameters of the roots and a slowing down of the rate of division.

On the basis of these observations and measurements, in 1933 we formulated the following working hypothesis.: Certain doses of X-rays induce beneficial changes which include the appearance of

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binuclear and polyploid cells. These beneficial intracellular changes are related to increases in yield. Stronger doses of X-rays induce injurious cellular changes: the appearance of asymmetrical binuclear conditions, the destruction of the chromatin, and the reduction of the rate of division. These changes in the cells produce a decrease in the yield.

In the following year we resolved our experiments by the introduction of seeds which had been obtained from irradiated plants. In a previous section we have already pointed out the consequence of X-radiation, which results in an increase of yield when beneficial doses of X-rays are used. They(X-rays) have a similar effect on intracellular changes. In our investigations we used seeds of plants which in the previous year had received a dose of 750 roentgen units, since this dose exerted the most beneficial influence on the plants. We didn't find any abnormalities in the root cells of these plants: the resting and dividing nuclei behaved normally. But in contrast to normal cells (tissues) the number of cellular divisions was significantly greater. We consider that this increase in the intensity (rate) of division was reflected in the stimulation of the growth and development of the plants and that these, in turn, affected the yield, which was increased by about 30 percent above normal.

Peas (investigation of Atabekova)

The cytological investigation of peas can be regarded as a check on our hypothesis concerning the relationship between intracellular changes and the yield. The experiments with peas completely confirmed our hypothesis. These experiments were also begun by a

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study of normal roots of unirradiated peas, whose cells are distinguished by a rather large nucleus and a single nucleolus (which is as it should be). The process of division of cells and nuclei proceeds quite normally. In the metaphase stage (just as in rye) we can observe the 14 chromosomes which have clearly defined individualities. When the behavior of the nucleus, at rest and in division, was determined the roots of plants which had received doses of 250 roentgen units as seedlings, were examined. This dose was of interest to us because small experiments gave increased yields of seeds. The cytological investigations showed that the division of the nucleus, almost without exception, proceeded normally. In the root cells of only one plant were chromosomes observed to lag and form the characteristic "bridges". The most typical and constant characteristic of this dose was the appearance of "symmetrical binuclearity" (Figure 21. Symmetrical binuclear conditions in cells of irradiated peas (from the work of Atakekova).)

By this expression ("symmetrical binuclearity") we mean the existance of two nuclei of equal size in the cell itself. "Symmetrical binuclearity" in rye is accompanied by an increase in yield. The same is true of peas.

When dry pea seeds were exposed to the action of X-rays the most interesting results were obtained with doses of 1000, 8000, and 36000 roentgen units. When a dose of 1000 roentgen units was used, out of 30 examined roots, binuclear cells were found in 3 roots and tetraploid cells, in one. These phenomena were observed in plants which gave augmented yields. However even with this dose occasionally injurious deviations were observed: disintegration of chromosomes, numerical aberrations, and lagging chromosomes

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in the anaphase.

When a dose of 8000 roentgen units is used the process of nuclear division is disrupted abruptly, anomalies appear in all phases of karyokinesis. The number of binuclear, trinuclear, and polynuclear cells rises sharply. The binuclear cells are usually asymmetrical, sometimes the diameter of one nucleus is several times greater than that of the other (Figure 22. Asymmetrical "binuclearity" in cells of irradiated peas (from the work of Atabekova).) Adhesion and contraction of chromosomes and disruption of their normal form lead to their improper redistribution (Figure 23. Contraction (shortening) of chromosomes in root cells of irradiated peas (from the work of Atabekova).) Along with the increase of the number of chromosomes per cell their diminution was also observed. In general the action of this dose is characterized by endless numerical aberrations, and also by the appearance of cells with two protoplasts. The action of a dose of 36000 roentgen units was lethal to the plant under field conditions. Under laboratory conditions, however, a few seedlings were obtained whose roots were examined cytologically. These examinations revealed the disintegration of chromosomes into the most minute fragments, translocations, inversions, "shortages", and the formation of ringshaped chromosomes. In the anaphase part of the chromosome lags behind, others are ejected into the cytoplasm, sone are completely destroyed and from their remains shapeless or spherical bodies are formed. In individual cases giant cells with enormous nuclei were observed.

The appearance of "symmetrical binuclearity" and polyploidism were observed in plants obtained from seeds of plants which had been irradiated with "stimulating" doses of X-rays.

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Among the beneficial effects we must include the increase in the number (i.e. the frequency) of divisions. Measurements of the root diameters confirmed this supposition.

Stimulating doses of cells induced intensive cell division, which accounts for the increase in the diameters of the roots (since the size of the cells remained constant). Injurious doses of X-rays cause the appearance of chromosomal fragmentation, lagging in the anaphase, and asymmetrical "binuclearity". The slowing down of the rate of division of cells and nuclei are closely related in peas (as well as in rye) with a depression of development and a decline in the yield. From this we can conclude that the investigation of pea roots (irradiated by various dosages) completely confirms our hypothesis concerning the relationship between the intracellular changes and the yield.

Wheat (investigation of Afanas'yeva).

The first object selected for the investigation was a pure strain of spring wheat Triticum vulgare var. caesium. Air dry seeds of this plant were irradiated by various doses of X-rays (125, 250, 500, 750, 1000, 2000, 4000, 8000, and 16000 roentgen units). Exactly 24 hours after irradiation the seeds were planted in silica sand and the sprouts were subjected to observation. Not a single dose had a lethal effect on the seeds of wheat. Neither were any particular differences observed (between the various dosages and the control) in the number of shoots that came up, or in their sizes. The only exception was the 16000 roentgen unit dose which depressed the development of the seedlings. Before the investigation of the roots of irradiated plants were undertaken, the

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stages of resting and dividing nuclei were carefully studied. No deviations from the normal behavior of the chromosomes and the nucleus were observed. After that the roots of plants irradiated by each of the doses of X-rays were examined. With the action of the 125 roentgen unit dose division proceeds normally. With the 250 roentgen unit dose a root was found, a whole sector of which consisted of tetraploid cells. No changes were discovered when doses of 500 and 750 roentgen units were used. In the 1000 roentgen unit dose the chief deviation from the control was the appearance of various inclusions in the cytoplasm: they were small, shaped in chains, dots, or small knots, sometimes they were larger like globs of chromatin (Figure 24. Inclusions in the cytoplasm of cells of irradiated wheat (from the work of Afanas'yeva).) In the 2000 roentgen unit dose these inclusions were observed in considerably larger numbers. These inclusions are probably nuclear in origin. In addition in this dose one begins to find micronuclei (Figure 25. A micronucleus in the cell of irradiated wheat (from the work of Afanas'yeva).) The same inclusions, but in larger amounts, are encountered in the 4000 roentgen unit dose. In addition, fusion of tips of chromosomes in the center of the (nuclear) plate are observed. In the majority of cases, however, the plates were normal, only the chromosomes were small and thin. In a dose of 8000 roentgen units the number of cells with chromosomal inclusions is still greater, nuclei begin to bud, this gives rise to micronuclei, the number of abnormal nuclear plates increases. All of these are encountered still more frequently in the 16000 roentgen unit dose. In addition this dose is characterized by the formation of two or more protoplasts in a single cell.

The second object selected for investigation was hard wheat,

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Triticum durum var. melanopus. Dry seeds of this plant were subjected to the same doses of X-rays as were the seeds of soft wheat. The first cursory cytological examination revealed that the number of nuclear divisions in irradiated plants diminishes significantly by comparison with the controls. This was eventually confirmed by numerical data as can be seen from Table 30, where M is the relationship of the number of nuclei in division to the total number of nuclei, expressed as percentage of the total number of nuclei. Thus, the average percentage of nuclear divisions is the expression of the intensity of division. D. is the difference (i. e. the deviation) and m$_D$ is the probable error of the difference.

TABLE 30

Average percentage of nuclear divisions in different doses

(based on the data of Afans'yeva, 1936)

Dose	M±m	D ± m$_D$	Ratio
Control	5.67 ± 0.13		
125	4.53 ± 0.12	1.14 ± 0.18	6.33
250	4.67 ± 0.12	1.00 ± 0.18	5.56
500	4.58 ± 0.14	1.00 ± 0.19	5.74
750	4.57 ± 0.13	1.30 ± 0.16	8.12
1000	4.69 ± 0.13	0.08 ± 0.16	6.12
2000	3.90 ± 0.12	1.77 ± 0.18	9.83
4000	3.91 ± 0.12	1.76 ± 0.18	9.78
8000	3.20 ± 0.14	2.38 ± 0.19	12.52
16000	3.33 ± 0.12	2.34 ± 0.18	13.00

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From table 30 we can see that the highest percent of divisions is in the control. Even with doses of 125 roentgen units the percentage of division declines, while with doses of 8000 and 16000 roentgen units the intensity of division falls to one half. This decline in the intensity (frequency) is statistically significant since the difference exceeds the probable error by considerably more than three times.

The counts which were then performed for the various stages of division provided the figures for Table 31.

Table 31

Average percentages of various phases of division depending on the dose of X-rays

(based on the data of Afanas'yeva)

Dose, r	Percentage of all figures of division	Percentage of prophases	Percentage of metaphases, anaphases and telophases
Control	5.67	3.36	2.31
125	4.53	2.32	2.21
250	4.67	2.44	2.23
500	4.58	2.52	2.06
750	4.37	2.28	2.09
1000	4.69	2.25	2.44
2000	3.90	1.81	2.09
4000	3.91	1.97	1.94
8000	3.29	1.30	1.99
16000	3.33	1.29	2.04

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From the table it becomes clear that the high percentage of division of the nuclei in the control is due to the presence of a large number of prophases. This predominance points out that at the moment of fixation an extra large number of cells has begun mitosis. In irradiated plants, beginning with 125 roentgen units the percentage of prophases falling in relation to the control, is almost equal to the percentages of all of the other phases. In doses of 8000 and 16000 roentgen units the percentage of metaphases, anaphases, and telophases (taken together) predominates. Thus, under irradiation the number of mitoses decreases at the expense of the early stages (of division).

In parallel with the study of changes of intensity of nuclear division, the effect of X-rays on the intensity of growth were undertaken. As these experiments have shown, the only apparent effect of X-rays on wheat seeds was a retardation of growth. A comparison of the intensity of nuclear division and the decrease of growth indicates that the latter can be, at least partially, explained by the decrease in the intensity of nuclear division. In addition, those doses which have the most inhibitory effect on the growth of the plant also induces the greatest intracellular changes: formation of micronuclei, multinuclear cells, chromatin "bridges", inclusions in the cytoplasm, etc.

As has already been pointed out in the first chapter, stimulating doses of X-rays have not been established for wheat, neither were beneficial intracellular changes, resulting from radiation, established. This circumstance confirms the correctness of our hypothesis concerning the relationship between the

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intracellular changes and the stimulation of growth and development, and yield.

Polyploidism

One of the problems posed in our laboratory was how to obtain polyploid plants of rye, wheat, and peas. In our first works with the influence of X-rays on these plants we wrote: "The formation of tetraploid and octoploid sectors (in plants) cannot but reflect on the formation of sexual cells". And actually in the descendants of these plants we find seeds all of whose sprouts have either all polyploid cells (rye), or the cells have a mozaic structure consisting of diploid and tetraploid tissues (peas). In order to establish the distribution of polyploid cells, Atabekova carefully studied all of the successive sections of roots of peas in which she found polyploid cells. These cells were concentrated in a relatively small sector, the other parts of the root contained normal cells. The most interesting example encountered was a polyploid root obtained when the seedling was irradiated by a dose of 450 roentgen units. An examination of the meristem turned up diploid cells (2n = 14), tetraploid cells (4n = 28), hexaploid cells (6n = 42), and octoploid cells (8n = 56). A thorough study of 60 successive sections enabled us to determine the order (distribution) of these cells in the root. They are distributed in vertical rows and they retain this distribution as far as they can be traced along the whole fixed tip of the root (Figure 26. Distribution of polyploid cells in the cross section of a pea root (from the work of Stabekova).) This examination shows how mozaic (chimeral) tissues arise from diploid and poly-

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ploid cells. Unfortunately we did not succeed in obtaining a polyploid pea plant by means of X-rays.

With wheat in this relationship things were even worse. Afanas'yeva succeeded in finding tetraploid cells in only one plant.

With rye things were different; by means of individual examination of roots of separate plants not only was it possible to find two tetraploid plants (which arose due to the influence of X-rays) but also to trace their descendants down to the second generation (inclusive). Twelve seeds were obtained from one of these plants. From these seeds 4 plants were obtained by the following spring. Three of them grew up to form ears, and all three ears were distinguished by hard, compact scales which caused them to resemble the ears of einkorn (Triticum monococcum). The pollen grains of these plants as well as their elements (the two sperms and the vegetative nucleus) were distinguished by their extraordinary large size. From this tetraploid only four grains (seeds) were obtained, which (as examination revealed) were also tetraploid. In this fashion we had the opportunity of examining three generations of tetraploid rye and were able to trace their morphological characteristics. The questions which relate to the obtaining of new forms (types) which arise in connection with this plant will be left for another section of our book. However we can note certain interesting cytological details among which we should first note the changes in the size of the cells in three generations. (Table 32).

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TABLE 32

Changes in root diameters, cells, and nuclei of three generations of tetraploid rye (based on the data of Breslavets, 1939)

Generation	Diameter in microns		
	Roots	Cells	Nuclei
X	386	37.25	18.25
X_1	383	42.12	19.75
X_2	437	43.25	19.75

It is interesting to note that the average root diameter, which in general is enlarged in tetraploids as compared to normal diploids, remains the same in X and X_1 (i.e. in the generation which arose due to the direct influence of X-rays and in its offspring), while in X_2 a large increase in diameter is observed. When the diameter of cells and nuclei are compared in the three generations we note that while the nuclei achieve their maximum size in the second generation (X_1) the cells continue to increase in size. In other words, a restoration of the upset relationship between the nucleus and the plasma takes place: The large nuclei in the generation X almost fill the entire cell.

The facts presented indicate that in the area of intracellular changes due to X-rays, as well as in the area of physiological changes, our modest (in size) electrobiological laboratory succeeded in obtaining interesting results.

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Chapter 4

THE EFFECT OF THE QUANTITY AND QUALITY OF THE RAYS ON THE TRANSFORMATION OF PLANTS

a) Quantity of the Rays.

In this chapter we are not going to spend much time in considering the effect of the quantity of X-rays on physiological changes, since, actually, all of the experiments of this kind indicate a close relationship between the amounts of rays used and the changes that are produced. If the Arndt-Schultze law is not confirmed in all cases it can be ascribed to the fact that the experiments were improperly set up rather than to the nature of the action itself.

Here we shall examine those experiments which point to a direct relationship between the dosages and the morphological changes, both hereditary and non-hereditary. Although the results obtained with plants are not as clear but as those obtained with the fruit fly (Drosophila), nevertheless there can be no doubt, at the present time, that a direct, linear, relationship exists between the dosage and the frequency of mutations. How the frequency of mutations varies, in irradiated corn, as dosages are increased can be seen from table 33.

[See Table 33 on following page]

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TABLE 33

The Relationship Between Doses and Frequency of Gene-Mutations in corn seeds. (based on the data of Stadtler, 1931)

Duration of Irradiation in minutes	Number of cultures examined	Mutations	Percent of mutations	Duration of irradiation in minutes	Number of cultures examined	Mutations	Percent of mutations
2	156	0	-	18	144	6	4.16 ± 1.66
4	148	0	-	20	375	10	2.66 ± 0.83
6	152	0	-	22	135	9	6.66 ± 2.14
8	146	2	1.37±0.96	24	167	5	2.99 ± 1.31
10	381	2	0.52±0.36	26	113	9	7.90 ± 2.54
12	156	2	1.28±0.90	28	178	11	6.17 ± 1.80
14	138	9	0.52±2.10	30	177	9	5.08 ± 1.65
16	161	4	2.48 ± 1.22				

In Stubbe's (1933) article concerning the relationship between doses and frequency of gene-mutations, after irradiation of male gonads (which is presented in detail in the second chapter of this book), the results of irradiation, which were obtained under three different set-ups, are presented. These results show a regular rise in the frequency of mutations up to 400 roentgen units after which the frequency falls to 16000 roentgen units and then rises again.

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In another important experiment, in which only the mutations in sprouts were counted, a splendid, direct ratio was obtained between doses (of 3000 and 6000 roentgen units) and the number of mutations (Table 34)

TABLE 34

Increased frequencies of mutation in Antirrhinum Majus h. after irradiation of the male gonads by short-wave rays, independent of length of exposure of quality of the rays.
(based on the data of Stubbe, 1933)

Dose in r	Irradiated male gonads	Mutations	Percent of mutations resulting from irradiation
3000	7369	237	1.38 ± 0.136
6000	3616	176	2.78 ± 0.266

Our experiments on the change of sex in hemp obtained by irradiation with various doses of X-rays (see chapter two), and Lutkov's experiments with peas and barley (in the same chapter) can serve as good illustrations of this phenomenon (i.e. the direct relationship).

Up to the present time experiments for the purpose of investigating the relationship between the quantity of the rays and mutability have indicated that the frequency of mutations is directly pro-

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portional to the dosage.

b) Quality of the Rays

This question, as others, has its own history. Way back in 1898 only a year after Roentgen made his wonderful discovery Maldiney and Tovvenin broached the question of the quality of the rays in their experiments, in that they irradiated seeds of Convolvulus Sivensis and Lepidum sativum with and without filters. In other words they were trying to determine differences in the actions of hard rays (using the filter) and mixed rays.

Perthes (1904) on the basis of his experiments came to the conclusion that intensity of the rays is more significant than the length of exposure to radiation.

In 1919 Körnicke in his experiments with Vicia faba did not succeed in establishing any difference in the action of hard and soft rays or in filtered and unfiltered ones.

The experiments of Sierp and Robberts (1922) with the seedlings of oats, whose coleoptyles are most sensitive to rays, confirmed this (i.e. Körnickes findings).

In the same year (1922) Martius set out to determine what the biological effects of rays of various wave lengths have, when the energy is kept constant. On the basis of his experiments he came to the conclusion that when the amount of energy is kept constant and the wave length (hardness) of the rays is varied, that soft rays have a greater biological effect than hard rays. Iven

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is of the same opinion. Ancel (1928) was the first to experiment with the effects of "fractional" doses of X-rays on plants, in this case on lentils. In all 18 experiments "fractional" doses proved to be less harmful than doses given "all-at-once." Next she (Ancel) set up a very interesting experiment: 18 hours after sprouting, the seedlings of lentils which had roots 6 millimeters long were divided into two groups, Group I received a dose of 30 roentgen units and 3 hours later a dose of 450 roentgen units, Group II received 450 roentgen units directly. Measurements, performed 15 days later, showed that the length of the roots in Group I was 50 millimeters, while that of Group II was 40 millimeters. In the author's opinion this result indicates that the initial exposure to a weak dose (30 roentgen units) protected the roots from the action of the large dose and that this is a case of protection from X-rays by X-rays, i.e. that it is a case of X-rayphylaxis. This experiment was repeated 48 times and each time the same results were obtained.

The experiments of Glovker, Hayer, and Jungling were extremely interesting for their time (1929). From a theoretical point of view, write the authors, by analogy with the physical action of X-rays, it could be expected since soft and hard X-rays have identical effect on ionization of air that the biological effect would likewise be independent of the quality of the rays. The experiment was performed with seeds of the "notorious" Vicia faba equina. During the year 174 groups of 8 to 10 beans each were subjected to the action of hard and soft X-rays. The qualitative data for the entire series were identical: With small doses (up to 280 roentgen units) soft rays turned out to be more injurious, with larger doses the difference tended to diminish, so that with doses of 380 roentgen units

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the effect of hard and soft rays was identical. So that these experiments, in general, tended to confirm the "biological identity" of soft and hard rays.

Doroshenko (1929 - 1930) writes that when X-rays are used on seedlings, weak currents used in prolonged duration have the greatest stimulating effect. High voltage currants, even when used for a short period, have depressing (inhibiting) effects. Two small doses have a greater stimulating effect than a single large dose (which is equal to the two small ones).

Long and Karsten also point out that a greater stimulation is obtained when filters are used, than without them. The filters used in the experiment decrease the intensity of rays of all wave lengths, but especially that of the soft rays, so that if a stimulating effect is obtained it must be ascribed to the action of the longwave part of the spectrum, while the injurious effects, to short waves, or the stimulating effect can be ascribed to the lesser intensity and injury, to the greater, regardless of the wave length. Since the authors felt that experiments using soft rays on large amounts of dry seeds were wanting, they set up an experiment in which dry soya seeds were irradiated only by the soft part of the spectrum. Since soft rays are absorbed by air it was necessary to place the seeds close to the (X-ray) tube. For this reason the authors used the kind of apparatus which held the soya seeds under the X-ray machine for only 5 seconds after which they were ejected into vessels placed below and a second batch of seeds took their place, and so on. Larger doses were obtained by increasing the exposure time from 5 to 25 seconds. When the voltage increased, the

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intensity of the wavelength (and hence of the whole beam) increased proportionately to the square of the voltage used. The results of the experiments were rather inconclusive.

Stubbe (1937 and 1939) considers that the question of the relationship between the quantity of the rays and the frequency of mutations should be resolved into two questions: 1) what qualities of the rays can cause mutations, and 2) do equal amounts of rays of different qualities produce equal increases in the frequency of mutations.

Stadler's numerous experiments with the seeds of agricultural plants indicated that many mutations can be obtained by rays of medium hardness, as well as by hard rays of radium. His and Stubbe's experiments with soft rays (the so-called borderline rays), using 8 to 10 kilovolts, were equally successful.

Very hard rays (500 kilovolts) were successfully used on snapdragons by Noetling and Stubbe in their experiments in 1936. All of these experiments indicate that rays with voltages from 8 to 500 kilovolts (i. e. the entire range of the X-ray spectrum) induce numerous mutations.

The results of experiments which have attempted to establish the threshold of action on the ultraviolet end (of the spectrum) have been less clear cut. The negative results which were obtained in experiments with snapdragons and Drosophila have indicated that ultraviolet rays can be effective only when they are not absorbed by the surrounding tissues.

The results obtained by Noetling and Stubbe indicate that pollen grains of snapdragons are particularly suitable for the

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study of the effect of ultraviolet light (table 35).

TABLE 35

The relationship between dosages and frequency of gene-mutations after irradiation of the male gonads of Antirrhinum majus h. by rays of various qualities.

(based on the data of Noetling and Stubbe, 1934)

(1)	(2) dose in ℣	(3) culture	(4) mutation	(5) frequency of male gene mutations
	100	95	-	-
	200	92	2	1.67 ± 1.34
Borderline rays 0.015 and 0.019 mm A (filter)	400	93	8	3.10 ± 2.83
	800	95	4	3.71 ± 1.94
	1600	44	2	4.04 ± 2.97
	3200	44	3	6.31 ± 3.66
	100	118	2	0.93 ± 0.88
	200	101	2	1.48 ± 1.20
Soft X-rays 30-70 kv/ 0.05, 0.06, 0.08 mm Cu (filter)	400	140	5	3.07 ± 1.46
	800	127	4	2.65 ± 1.42
	1600	86	1	0.66 ± 0.87
	3200	91	2	1.70 ± 1.35

[Table 35 continued on following page]

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(1)	(2)	(3)	(4)	(5)
	100	93	2	1.65 ± 1.32
	200	97	2	1.56 ± 1.26
Hard X-rays 125-175 Kv/ 0.3 and 0.85 mm Cu (filter)	400	97	5	4.56 ± 2.14
	800	97	4	3.62 ± 1.90
	1600	49	1	1.63 ± 1.75
	3200	50	3	5.50 ± 3.22

In their experiment the authors divided the spectrum into the smallest parts possible. Pollen grains transmit a significant percentage of both visible and ultraviolet light and it can be stated with certainty that they also consume a definite percentage of the rays. In comparing the effects of unfiltered rays with monochromatic ultraviolet rays it was discovered that the frequency of mutations rises sharply when light from the 280 to 285 millimicron (spectral) line is used, while irradiation of pollen by rays of the 366 millimicron line has no effect in increasing the frequency of mutations. From this we can conclude that the threshold of action (which induces mutation in the pollen grains of snapdragons), in the ultraviolet area, lies in the vicinity of the 313 millimicron line, although it is not possible to establish any effect for the 265 millimicron line. In this fashion these experiments established the thresholds for action of ultraviolet rays (in both directions, that is for longer as well as for shorter rays) on the pollen grains of snapdragons.

In 1936, Stadler and Sprague showed that when they irradiated

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the pollen grains of corn by unfiltered ultraviolet rays, the frequency of mutations rose sharply.

At the same time we get an answer to the first question posed by Stubbe (see above) "concerning the threshold of wavelength at which mutations can be induced". The answer consists of the fact that the threshold is determined by the ability of the rays to penetrate (the tissues); and that in order to induce mutations any source of rays may be used, beginning with ultraviolet rays.

Stubbe considers that the second question concerning rays of different qualities is also answered, since in the region of X-rays, from softest to the hardest rays, when identical doses were used no statistically significant differences in results were obtained. In plants this was confirmed by experiments with snapdragons, in which equal doses of soft and hard X-rays (as well as gamma-rays of radium) induced identical frequencies of mutations. In other words, we can consider as established that the inductive action of X-rays does not depend on wave length. This conclusion is splendidly confirmed by the table taken from Stubbe (Table 36).

TABLE 36

The action of equal doses of rays of various qualities which induce mutations
(based on the data of Stubbe, 1934)

Kind of rays	Dose in r	Irradiated Male Gonads	Mutations	Percent of mutations resulting from irradiation.
(1)	(2)	(3)	(4)	(5)	(6)

[Table 36 continued on following page]

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(1)	(2)	(3)	(4)	(5)	(6)
Radium	-	3000	1083	31	1.03 ± 0.30
X-Rays	506 Kv	3000	1937	62	1.31 ± 0.25
X-Rays	180 Kv	3000	1536	47	1.22 ± 0.28
Radium		6000	1504	56	1.89 ± 0.35
X-Rays	506 Kv	6000	1171	60	3.29 ± 0.52
X-Rays	180 Kv	6000	1140	60	3.43 ± 0.53

From this table we can see that when equal doses of rays are used (3000 roentgen units in one case and 6000 roentgen units in the other) hard X-rays (506 kilovolts) and soft ones (180 kilovolts) produce equal increases in the number of mutations (as compared with the control). It should be noted that the number of mutations induced by the 6000 roentgen unit dose is nearly 3 times as great as that produced by 3000 roentgen units.

Now let us turn to the question raised in 1928 by Ancel as to whether administration of doses in fractions affects the appearance of mutations. The most clear cut experiment that was set up for the clarification of this point, was also that of Stubbe who tested the difference between the action of rays of different qualities in concentrated doses and in doses which had been divided into three (fractions) and administered at 24 hour intervals (table 37).

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TABLE 37

The action of concentrated and fractional (three fractions at 24 hour intervals) doses of rays of various qualities on the frequency of mutations in Antirrhinum majus h.

(based on the data of Stubbe, 1934)

Kind of irradiation and quality of the rays	Dose in r	Irradiated	mutations	Percent of mutations resulting from irradiation
180 Kv 3 fractions	3000	1209	49	2.22 ± 0.42
506 Kv 3 fractions	3000	1973	62	1.31 ± 0.25
180 Kv concentrated	3000	1536	47	1.22 ± 0.28
506 Kv concentrated	3000	1568	48	1.23 ± 0.27
180 Kv 3 fractions	6000	1140	60	3.43 ± 0.53
506 Kv 3 fractions	6000	1170	60	3.29 ± 0.52
180 Kv Concentrated	6000	1487	74	3.14 ± 0.45
506 Kv Concentrated	6000	1337	79	4.07 ± 0.54

All of these experiments indicate (despite the indications of earlier experiments to the contrary) that neither the quality of the rays, nor the fractioning of doses have any effect on the number of mutations but that the only significant factor is the size of the dose (i.e. the number of X-ray units).

This was confirmed by our experiments with rye. These experiments established that there is no difference between hard

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and soft rays in relation to stimulation or depression (Breslavets, Medvedeva, and Afanas'yeva, 1935).

One more interesting question remains. This is the question of the quality of gene-mutations obtained by experimental means. In his very first work, Muller noticed the identical quality of spontaneous mutations and those obtained by experimental means, This is confirmed for all of the objects examined. The numerous gene-mutations obtained through the action of X-rays in snapdragons, corn, and Drosophila had all been encountered previously among spontaneous mutations. They possess the same properties, affect all organs and all of the physiological properties of the organism, and are likewise usually recessive (few few being dominant).

The first indication of differences in the quality of spontaneous and experimentally obtained mutations crop up in Stubbe's experiments (1932 - 1933). In the first experiments it was found that after irradiation of the buds the percentage of gene-mutations in the vegetative cells rose sharply, in comparison with the controls, while the percentage of those mutations which determine changes in the shape of the flowers did not rise. In another experiment, under irradiation by soft and semi-hard rays, it was found that as the doses were increased the percentage of previously encountered mutations diminished while the number of new (not previously encountered) mutations increased. Stubbe explains this by the fact that the action of large doses shake up the structure of the genes to an extent which cannot occur under normal conditions, or with weak doses (of X-rays). As a consequence after strong doses, even genes which, in general, are distinguished by great stability, undergo

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mutation.

The majority of experiments in this area, however, indicate that experimentally obtained mutations do not, in any way, differ from spontaneous ones. If mutations induced by irradiation, which were not encountered previously, turn up it is, in all probability, due to the fact that none of the objects, with spontaneously arising mutations, were sufficiently observed to uncover all of the possible mutations. In addition, we know that in every more or less thoroughly investigated object spontaneous mutations, which had not been encountered in X-ray experiments, crop up from time to time.

The regularity of distribution of experimentally obtained chromosomal aberrations, confirms the assumption concerning the lack of specificity in the effects of short wave radiation, which should have been expected on the basis of the physical properties of the rays.

The following facts indicate that various sectors of the wave spectrum do not produce specific effects: 1) Stubbe's experiments which were set up with an isolated segment of ultraviolet rays; 2) the fact that as a consequence of irradiation the same kinds of mutations arise as are observed under natural conditions (Contemporary findings indicate that the action of ultraviolet rays does differ from the action of X-rays); 3) the appearance of reverse mutations due to action of short waves.

The significant factor in the increase of mutations is the amount of energy used (the number of roentgen units) and not the quality of the rays (voltage). The frequency of mutations rises in direct proportion to the dose.

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VARIABLE SENSITIVITY OF ORGANISMS TO X-RAYS

In the first chapter we have already pointed out that X-rays have a different effect, not only on different species and finer subdivisions of the classification system, but also, frequently, on organisms of a single species. Then we only broached the question, in this chapter we shall attempt to clarify it. The first premise expressed on this subject was that of BERGONIÉ and TRIBANDEAU in 1906. In their article they point out that according to the data of all the doctors, irradiation, which induces the death of neoplasm cells, leaves the immediately adjacent cells of the normal tissues, including those of the swelling, uninjured. In addition, experiments with living tissues have indicated that the rays have a selective action on healthy tissues. These authors have shown that while X-rays destroyed the seminal cells of rat ova they did not affect the interstitial glands. On the basis of this, the authors assumed that it was possible to formulate the following law (which is known as the BERGONIÉ-TRIBANDEAU law): "X-rays act with greater intensity on those cells which have a greater power of reproduction, on those which have a longer karyokinetic future, on those whose morphology and function are less

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definitely fixed." On the basis of this, they find it quite understandable why irradiation destroys tumors without affecting the healthy tissues.

In HERTVIG's experiments (in 1911) with the action of radium on unfertilized frogs eggs the particular sensitivity of reproductive cells (embryonic tissue, testicles, ovaries, skin) is likewise pointed out. The greater the demands placed by life on the cell (and especially on its nucleus), the greater are the changes in the nucleus and cytoplasm; and life places its greatest demands on embryonic tissues, whose cells grow, multiply, and differentiate into other tissues.

SCHWARZ (1913), in a similar fashion, raised the question concerning the stage of development at which irradiation must be given in order to have the most beneficial effect. His experiments have indicated that acceleration of growth is observed only when seeds (before sprouting), or very young shoots are irradiated, whereas in old tissues he was not able to induce this acceleration.

A survey of KÖRNICKE's experiments (1915) indicates that various species of plants display a variable sensitivity to X-rays. In addition to this, the more intense are the life processes of a plant, the more sensitive it is to irradiation. In order to clarify the reasons for the variable sensitivity of various species to X-rays, KÖRNICKE formulated the hypothesis that it is related to the number and size of the individual cells, which, in turn, are related to the amount of energy absorbed by them. His experiments

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indicate that Vicia faba are injured by doses of 100 roentgen units, Zea mays by doses of 250 roentgen units, but that even when doses of 500 roentgen units are used no traces of injury are observed in Papaver somniferum. In addition, the extreme resistance of bacteria to X-rays (where the cells, amounts of protoplasm, and water are minute) and the extreme sensitivity of large cells (which contain large amounts of protoplasm and water, as compared with vegetative cells) such as sexual forming cells, should indicate the direction in which the reasons for selective radio sensitivity should be sought.

NADSON (1920) also points out that radium does not have the same effect (in relation to both quantity and quality) on various species of yeasts, and even on individuals or cells of the same species. "The more intense and rapid are the life processes and development of yeasts, the more sensitive they are to the action of radium; for this reason young cultures are affected by radium more quickly, and to a greater extent."

PETRY (1921) considers that the experiments of KÖRNICKE and SCHWARZ show that resting (dry) seeds are not sensitive to X-rays, even if they are affected by doses 30 times greater than those which affect sprouts of the same species. This proves that the sensitivity of various parts of the cells to X-rays is determined by the physiological condition of the cell, which is based, according to PETRY, on chemical differences. However, the sprouting of seeds is not a simple chemical transformation, it consists of many various, particular processes which determine changes of composition

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and function of the seed. Conclusions concerning the action of the rays can be based on the insensitivity of resting seeds only on the condition that we know which of these processes is responsible for sensitivity to X-rays. The simple swelling of sprouting seeds may make them more sensitive to irradiation, just as the accompanying activization of proferments (Pro-enzymes) may, or the enzymatic breakdown of the high-molecular reserve substances, by increasing the number and kinds of molecules, or the diminution of the size of molecules which increases the ability of substances to ionize. The presence of oxygen as a result of soaking the seeds in water may have an even greater significance.

PETRY also studied the action of other factors in conjunction with irradiation, as for example: temperature, cyanide poisoning, absence of molecular oxygen, etc. Experiments showed that sensitivity to X-rays is not necessarily related to the energy of respiration and growth, and may be separated from them. By its low temperature coefficient the reaction of X-rays is not only considered to be an independent process, independent from the metabolic processes, but on the basis of this low coefficient PETRY classifies it as a reaction of light. Experiments involving cyanide have demonstrated that sensitivity to X-rays is not related to the depression (inhibition) of growth. From this it is possible to conclude that only the composition of the cells is responsible for their behavior towards the harmful influence of X-rays, and not the transformation of substances which takes place within the cell. From these experiments PETRY comes to the conclusion that the

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process of injury to the cells is a purely photochemical reaction. The absence of molecular oxygen does not inhibit sensitivity to X-rays. The final conclusion from PETRY's experiments is as follows: the reason for the sensitivity to X-rays during the time of sprouting, lies not in the changes in respiration, but in the commencing constitutional transformations. The question (13) whether the process of swelling of the seeds, as such, exerts an influence, or whether this swelling is a phenomenon with far-reaching consequences (which accompany sprouting) which forms a light-sensitive system. So, the X-ray reactions form an independent process, allied to the photochemical one, in all probability consisting of photochemical changes of the important components of the cell.

Although PERTHES' (1922) article was written in order to clarify other questions, it is directly related to the question of variable sensitivity to X-rays. His first question is: "do X-rays have a selective action?" All of the facts point to the variable sensitivity of various types of cells, but PERTHES assumes that all cells are sensitive to X-rays in some degree. Nevertheless, the selective action of these rays is the essential basis for the effect they have on tumors. PERTHES attaches a special significance to the latent action of irradiation, both for practical purposes and for theoretical investigation. The time after which the influence of irradiation begins to manifest itself is extremely variable: the higher the dose and the sensitivity of the irradiated cell, the shorter is the time interval. PERTHES explains the latent action by the fact that irradiation of the component parts of the cell, chiefly the nucleus, induces chemical

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changes which proceed slowly, and gradually increase the amount of harmful substances (probably insoluble products) which increases first their stimulating and later their harmful action. PERTHES considers that his hypothesis completely corresponds to the available data. In the first place it shows that not only latency, as such, but its duration is, to a certain extent, in invefse ratio to the intensity of irradiation. In the second place this hypothesis offers a good explanation for the fact that during the latent period (i.e. before the appearance of the main effects, the foremost of which are the abnormal processes of the cells) cellular reactions slow down, etc. It also explains why in some objects the stimulating effect becomes harmful and injurious to the cells and tissues. Observations indicate that the substance which affects the cell is, at first, found in a minimum amount which gradually increases because of the influence of irradiation.

ALBERTI and POLITZER (1924) in their first article, devoted to the action of X-rays on organisms, write that even the very first biological X-ray experiments showed that resting cells were more stable in relation to the action of X-rays than cells in mitosis, or any of the stages of mitosis. If the various stages of mitosis are projected on the X-axis (abscissa) and the sensitivity to X-rays (expressing, for example, the number of perishing ova of the horse ascaris) is projected on the Y-axis (ordinate), we will then get a curve at whose peak will be the metaphase. Consequently a small irradiation will disrupt only those mitoses which are in the metaphase, higher doses will destroy those stages which are nearest to the metaphase, both before and after. Finally

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there exist stages which will lead to the necrosis of all stages of mitosis. In order to kill the resting cells, greater doses than any of the previous ones are required.

GELLER's observations (1924) on irradiated beans, peas, wheat, and lilac buds permitted him to conclude that the action of rays is determined first by the species of the plant and secondly by their condition. Unsprouted seeds are more sensitive than sprouted ones, swollen seeds are more sensitive than dry seeds. The age of the seeds does not affect their sensitivity. Changes in external conditions (temperature, humidity of the air) show up under irradiation. JUNGLING's observation concerning the importance (significance) of the point of application of irradiation is very interesting. When the tip is irradiated growth in the tip slows down, when the whole root is irradiated the side roots cease their development.

In SEIDE's (1925) article we find a summarization of experiments with zoological objects which indicates that strong injuries occur in early stages of development with moderate doses of X-rays and radium, while older stages are completely unaffected by these doses. SEIDE's own experiments indicate an extreme sensitivity of the stages when chromosomes begin to form (prophase). Stages when the chromosomes are completely formed (metaphase) are considerably less sensitive. ROCHLIN and GLEICHGEWICHT (1925) compared the action of X-rayson sprouted seeds of Phaseolus vulgaris and Vicia faba. By irradiating them with identical dosages they estab-

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lished: (1) a variable sensitivity of these two plants and (2) a variable sensitivity among individuals. What is most interesting is that the authors discovered that the more sensitive the object the more quickly is stimulation followed by retardation. In Vicia faba equina retardation is induced by very small doses, for which reason this object is not suitable for investigation of the stimulating effects of X-rays. So to study this effect the authors used Phaseolus vulgaris instead. When the seedlings of the two plants were irradiated by identical doses (1½ High Erytheme Doses), two weeks later sprouts of Ph. vulgaris only slightly retarded their growth while sprouts of V. faba stopped growing altogether.

NEMENOV (1925 and 1926) considers that old cells are most sensitive to X-rays. The age of the cell, according to him, is determined by the relation of the already lived part of its life to the total life span of the given cell. The essence of the biological process in the X-irradiated cell, which leads to the aging of the cell, apparently consists of the disruption of metabolism and of the retention of the products of metabolism within the cell.

IVEN (1925) also takes note of the varied sensitivity of X-rays which varies chiefly with the species of the plant. Comparing the data of numerous experiments he comes to the conclusion that small seeds have a low sensitivity to X-rays and seeds of large size, high sensitivity. The most sensitive objects are the seeds of Vicia faba, which are the largest in size (of those objects which have been subjected to irradiation). He also notes the importance of the physiological condition of the seeds for

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successful irradiation, pointing out that turgid seeds react to irradiation to a considerably greater degree than dry seeds. Cytological examinations have revealed that nuclei of vegetative cels are more stable than those of sexual cells. The vegetative cells, in turn, manifest a difference of behavior: cells of the points of growth of the root and stem are more sensitive than the cells of the permanent tissues.

ANCEL (1927) finds shortcomings in the works of many authors, who point out the differences in the sensitivity of dry and sprouting seeds, in the fact that these authors failed to follow up their studies after the appearance of shoots. She finds it necessary to fill out their experiments in this direction by the study of changes in sensitivity of lentil seedlings from the moment that sprouting begins to the time the roots reach a length of 24 centimeters. Her observations showed that the sensitivity of lentil seeds continued to rise from the moment of the appearence of sprouts, that it reached its maximum when the roots were 10 millimeters long, after which it went down gradually to the time the roots were 24 millimeters. [Either this should be centimeters or else the previous measurement in this same paragraph, see above, should be "24 millimeters.] These results safeguard experimenters from mistakes, if they set up experiments with seedlings whose roots have different lengths.

STADLER (1928) was the first to show that with equal doses, 8 times as many mutations appear in sprouting seeds, as in resting seeds. Mutability in generative cells at the time of formation of

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sexual cells or gonads is studied in greater detail.

GOODSPEED (1929) pointed out that certain stages of reduction-division are particularly favorable for obtaining chromosomal aberrants, but whether the same can be said in relation to gene mutations has not yet been determined.

STUBBE (1932) showed that when snapdragon buds are irradiated by equal doses that more mutations occur if the irradiation takes place after reduction-division than if it takes place during or before it.

In the first chapter the results of experiments of BRESLAVETs and her co-workers concerning the variable sensitivity of turgid seeds and sprouts of rye were presented (BRESLAVETs, AFANAS'YeVA, and MEDVEDEVA, 1933) and also of dry and turgid (soaked) seeds of peas (ATABEKOVA, 1935).

JOHNSON performed many experiments for the purpose of clarifying physiological changes of plants due to the influence of X-rays. Two of her works have a direct bearing on our subject. In the first of these works (1933) the author investigated the effect of irradiation on three varieties of French spinach (Athriplex hortensis): (1) variety with pale, almost yellow leaves, the spinach which is most frequently used as food, (2) variety with dark red leaves which is cultivated as a decorative plant, and (3) green variety which exhibits the most luxuriant growth. Experiments with different varieties of the same species were set up in order to clarify whether or not the differences in

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their reactions to external factors (in this case, X-rays) stem from the physiological properties of the plants themselves. Specifically, whether or not the presence of the colored cell juice of hortensis can protect the protoplasm from the harmful effect of the rays. Comparative examination revealed that after exposure to X-rays all three varieties manifest a significantly smaller size at maturity and a certain retardation in flowering, but that these reactions are strongest in the red variety. In general, the red and pale varieties show greater injuries than the green variety. The pale plants (when irradiated) had a greater percentage of stem injuries and dichotomy of branches; the green variety had the greatest number of plants with abnormal leaves, rearrangement of leaf positions, and flat branches; the red variety, more frequently than the others, exhibited side branching. On the basis of this experiment the author concludes that not only families, genera, and species, but even varieties of a single species can differ in their physiological and morphological responses to irradiation.

In her 1936 work JOHNSON states that the ten-year investigation of the action of X-rays on various species of plants make it possible to divide the plants into groups according to their sensitivity to X-rays. She divides the plants which had been investigated into: (1) species which are not affected by the rays, (2) species on which irradiation has a weak effect, apparently only for a short time after irradiation, and (3) species which are sensitive to irradiation. Species of the second group manifest

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sensitivity to X-rays in the early stages of development, but as they mature they resume their normal characteristics. In this group are found: Chenopodium album, Spinacia oleracea, Cheiranthus, Matthiola bicornis, Calandrinis grandiflora, Quamoilit corcinea, Asperula orientalis, Portulaca. In the third group, a dose of 2500 roentgen units is lethal for seedlings of Nemophila insignis, Gaillardia picta, Phlox drummondii. For other plants of this group a dose of 2500 roentgen units diminishes the general size, but out of 39 plants, 9 plants increase their size. Dimorphoteca increases its general size, while for Clarkia this dose was lethal for many specimens, but those which survived are exceptionally strong and vigorous (it may be assumed that they were totally or partially polyploid. (our comment -- L. P.)) . The leaves have a tendency towards irregularity of shape and color. It is most interesting that species of this group show large differences in the duration of effects of irradiation. This is particularly evident in Caryophylaceae and in the following genera: Impatiens, Clarkia, Antirrhinum and others. The author concludes her article by the statement that although the reasons for stability or sensitivity of definite species are not known, nevertheless observations of many species establish the fact that the members of certain families (Chenopodiaceae, Potulacaceae and Brassicaceae) are in general stable, while members of other families (Solanaceae, Scrophulariaceae and Carduaceae) are injured more readily than most.

NADSON in her article: "at the International Radiological

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Congress," describes an interesting report of two French scientists GOL'VEN and LASKASAN [or possible HOLVEN and LASCAÇON] on the subject of how to explain the "individual" sensitivity of organisms, i.e. why two individuals of the same species which are, apparently, in completely identical conditions, react unequally to some external factor, as, for example, the action of visible or invisible radiation. On the basis of their experiments they propose the following explanation: cells have a certain sensitive zone, and the fate of the cells (and with them, of the whole organism) depends on what kind and how many quanta of radiant energy reach this sensitive zone, and this happens to vary with individuals.

In 1933, LAMBERT set up a series of important and detailed experiments for the purpose of finding out the relationship between the physiological state of the tissues and sensitivity of the plant to X-rays. His experiments showed that the boundaries of sensitivity of dry peas lie between 5000 and 10,000 roentgen units; for those which had been soaked in water 6-12 hours, not more than 10,000 roentgen units; and for those which had been soaked for 18-24 hours, between 2500 and 5000 roentgen units. LAMBERT considers that the appearance of sensitivity is not a function of the static state of the seed (which is represented by its chemical composition), but that it is determined only by the dynamic factors (introduced by swelling) which make the seed sensitive to X-rays.

GUSTAFSSON (1936 a and b) observed a very high sensitivity in cells when they were in meiosis or in division within the pollen grain, while resting seeds can take very strong doses without losing

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their ability to sprout. Some authors concluded that this is so because the root and the shoot in the seed are well protected. However the tetrads, or pollen mother cells, are also well protected by thick tissues of the petals and sepals and by the wall and lining cells, but nevertheless they are extremely sensitive to X-rays. On the basis of this GUSTAFSSON considers that chromosomes in the tetrads, or pollen mother cells, are in a more sensitive stage (this is probably the stage of their reproduction). As for the nuclei of resting seeds, their chromosomes are not ready for reproduction and for that reason they are not sensitive to radiation. In addition the author attaches great significance to the increase in the water content in dividing cells. A study of disruptions in dividing nuclei shows that the majority of them are found in nuclei which have just begun division. This demonstrates the differential action of X-rays on the one hand, and the cytological inequality of the nuclei on the other. It should be noted that this latter inequality may depend on the chromosomes themselves. The fact that nuclei can enter into division quickly shows that the chromosomes are ready for it, but that they are not able to commence without an external stimulus, i.e. without water. According to GUSTAFSSON the frequency of disruptions of divisions is related to the water content, and since nuclei which are the first to begin division show the highest frequency in the disruption of this process, the parallel between these two phenomena can only mean that nuclei which are the first to divide contain the greatest amount of water. This assumption is confirmed by the fact that by supplying the seeds with water it is possible to change rate of nuclear division.

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The final experiments of STUBBE and DÖRING (1940), who succeeded in demonstrating that changes in the physiology of the metabolism increase the frequency of mutations, were most interesting. This was demonstrated in experiments with malnutrition of snapdragons, the seedlings of which, when deprived of sufficient amounts of nitrogen, phosphorus, and sulphur, exhibited typical symptoms of malnutrition. However, plants which were raised in complete absence of nutrient substances had a similar percentage of mutations as the control. It is possible to conclude from this that the deciding factor in mutability is, not the lack of nutrient substances, but disharmony in the metabolism. Further experiments have shown that under other conditions the deciding factor (the one that brings on mutations) may fail to show up as a result of the fact that the transmuted cells may be ejected by the organism, or because they cannot continue their development due to excessive injuries. The authors consider that similar processes have taken place in other experiments, for example chemical ones, by which frequent failures can be explained. Numerous experiments have demonstrated that mutations induced by irradiation are determined by the physiological condition of the irradiated object. In order to find out if mineral deficiencies influence the frequency of mutations in irradiated objects, experiments were set up combining the influence of phosphorus deficiency and X-rays, i.e. pollen grains from normal plants and from plants which had been raised without sufficient phosphorus, were irradiated. As the experiments have shown, a shortage of phosphorus by itself did not raise the percentage of

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mutations but in conjunction with the action of X-rays (6000 roentgen units) the significance of the first factor shows up in the number of mutations (Table 38)

TABLE 38

Combined tables. Experiments with Antirrhinum majus L. (based on the data of STUBBE, 1934)

Type of Action	Cultures	Number of Mutations	Mutations per each 100 plants
Full diet (unirradiated)	498	5	1.004 ± 0.44
Phosphorus deficiency (unirradiated)	587	8	1.362 ± 0.47
Full diet (+6000 r)	543	44	7.099 ± 0.10
Phosphorus deficiency (+6000 r)	966	118	11.211 ± 1.01

So we see that changes in diet affect not only the frequency of spontaneous mutations but also change the action of short waves which induce mutations. However the mechanism of the action, upon which this fact is based, is completely unknown. Up to the present time Stubbe investigated the absence of those elements (nitrogen, phosphorus, and sulphur) which enter the composition of the chromosomes so that it is understandable that disruption in the metabolic function of these elements leads to irregularities in the structure of the substance of the genes, i.e. to mutations. A calcium deficiency does not increase the percentage of mutations, but then calcium is not an essential part of the substance of the gene.

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Stadler (1929) takes an extremely interesting point of view in his explanation of the diversity of the effects of X-rays and various species and genera of plants. He established that different species of the same genus manifest differences in their ability to undergo mutations. The irradiation of seeds of Avena sativa, A. bysantina, A. strigosa, and of Triticum monococcum, T. Dicoccum, T. durum, and T. vulgare by identical doses leads to different results. While species A. brevis and A. strigosa show increases in the percentage of mutations when subjected to irradiation, A. bysantina and A. sativa do not show any increase over unirradiated plants. Similarly in T. monococcum the percentage of mutations is very great and it falls gradually through dicoccum and durum to vulgarum which doesn't exhibit any mutations (Table 39).

TABLE 39

Frequency of mutations obtained by experimental means in various species of Avena and Triticum.

(based on Stadler's data, 1929)

Species	Number of Chromosomes	Frequency of mutations per unit	Species	Number of Chromosomes	Frequency of mutations per unit
Avena brevis	7	4.1 ± 1.2	Triticum monococcum	7	10.4 ± 3.4
A. sativa	7	2.6 ± 0.6	T. dicoccum	14	2.0 ± 1.3
A. bysantina	21	0	T. durum	14	1.9 ± 0.5
A. sativa	21	0	T. vulgare	21	0

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By comparing the data of this table we see that the frequency of observable mutations decreases as the number of chromosomes increases. In order to explain this phenomenon Stadler offers the following hypothesis. If we assume that in A. Bysantina and A. Sativa the same gene is present in each "genome" (allelomorph) in a dominant condition, then the formula for this "genome" will be $\frac{A_1\ A_2\ A_3}{A_1\ A_2\ A_3}$. If a mutation will occur from A to a it will lead to a heterozygotic condition $\frac{A_1\ A_2\ A_3}{a_1\ A_2\ A_3}$, which in time will lead to a homozygotic condition $\frac{a_1\ A_2\ A_3}{a_1\ A_2\ A_3}$. This plant will not show any change since the four dominant allelomorphs will mask (conceal) the two which had undergone mutation. In this way the multiplication of "genomes" (allelomorphs) prevents the phenotypical appearance of recessive mutations in polyploid forms, and it will be rarer as the number of identical "genomes" (allelomorphs) is greater in a plant. In other words the reason for the lesser mutability of A. bysantina, A. sativa, T. dicoccum, T. durum, and T. vulgare must be explained by their polyploid state.

It should be noted that the polyploid condition is significant, in this respect, only for gene mutations. With respect to chromatic aberrants, Goodspeed (1930) has demonstrated the reverse to be true: Nicotiana glutinosa and N. silvestris with 12 pairs of chromosomes are changed by equal doses of irradiation with much more difficulty than N. tabacum and N. rustica, each of which

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has 24 pairs. For chromosomal mutations the larger number of chromosomes increases the possibility of their occurrence and creates greater possibilities for their variations and survival. On the basis of this Delaunay (1930-1931) obtained many chromosomal mutations by irradiating ears of Triticum vulgare.

In species in which polyploidism does not interfe e with the appearance of dislocations however, variations in the mutability of the genes may be observed. Experiments with the irradiation of pollen grains of Antirrhinum majus in Stubbe's experiments (1929) showed a frequency of mutations of 4 percent with a dose of 3000 roentgen units. The irradiation of pollen of a self-pollinating strain A. Glutinosum from Opruba by a similar dose didn't produce any results. A similar stability toward X-rays is shown by A. Silicum.

If these facts can be substantiated for a large number of species it will be possible to assume that individual species of a genus are distinguished not only quantitatively, i.e. by the number of their genes or allelomorphs, but also qualitatively, i.e. by the stability of their allelomorphs. The reason for this must be sought in the process of selectivity, by means of which labile allelomorphs are gradually lost (ejected) by wild forms, the same being accomplished in cultured species by artificial selection. Although we should note that up to the present not a single case is known where the use of strong doses of irradiation has failed to increase the number of mutations. We have a right to speak of the totality of the genetic action of the rays, but we should keep in mind that the quantity of rays needed to obtain a definite per-

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centage of mutations differ for each species of a genus, and, perhaps, for each strain of a species.

In summarizing the facts about the variable sensitivity to X-rays the greatest importance must be attached to the ability of various forms to react to irradiation. Various genera, species, and subdivisions of species, and even individuals of the same species react differently to irradiation.

Seeds in various physiological stages (dry and soaked seeds) exhibit different sensitivity to X-rays. The greater the intensity of life processes in plants the greater is the effect that irradiation has on them. A definite relationship exists between the water content of the cells and sensitivity to X-rays, the percentage of mutations are increased when the plant is deprived of phosphorus, and plants have a greater sensitivity to X-rays in the early stages of their development.

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THE BIOLOGICAL DOSIMETER

As soon as the biological effects of X-rays were established the need for expressing their action in some kind of units immediately arose. Since the action of the rays on human skin soon became apparent (the skin of people who worked with X-ray apparati became reddened and peeled) the so-called erythema dose was proposed as a dosimeter. This dose had an international designation HED, a contraction of the words Haut-Erythema-Dosis (the dose which caused the irritation of the skin). However this reddening varies very greatly depending on the pigmentation of the skin (blonds are more sensitive to X-rays than brunettes), and the age and health of the patient. Consequently a real need arose for the precise determination of the dosage. This need arose chiefly due to the medical practice of applying X-rays for treatment of tumors and for diagnoses of ailments. We cannot linger on the history of this question, we can only point out that at the present time exact dosimeters exist based on the ionization of air by X-rays. The number of roentgen units (r) used in experiments is determined by means of dosimeters. These dosimeters have determined the extent of inaccuracy of measurement of roentgen units in HED's (High Erythema Doses). As Clarck's experiments, which were conducted on numerous patients in several clinics, have shown that, depending on the individuality of the patient and on his condition, the HED varies between 400 and 1200 roentgen units with the average lying around 849 roentgen units. If we will recall from our data the fact that a plant which is sensitive to X-rays,

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such as Pisum savitum, is stimulated by a dose of 350 roentgen units and depressed by a dose of 1000 roentgen units we shall understand that such a dosimeter (as the HED) is worthless.

In this manner an accuracy was attained in determination of the dose but that did not do away with the need for a biological dosimeter. In investigations of the effects of X-rays on plants it becomes necessary to feel out doses, which are capable of inducing desired changes, by a strictly trial and error method. Only by analogy can we judge concerning the effect that the rays will have on a certain plant, and then only approximately. The reason for this lies in the variable sensitivity of plants to X-rays and in their physiological condition. As we have pointed out previously (chapter 4, section B) sensitivity to X-rays varies greatly depending on the genus, species, and even variety of the plant. This clearly expressed property of plants of reacting variously to irradiation has forced (and is forcing) investigators to seek a biological dosimeter which will enable them to determine quickly the sensitivity (to X-rays) of a given plant.

In 1931 Packard proposed the use of Drosophila eggs as a biological dosimeter. This proposal opens the possibilities of a new biological method.

Johnson (1936) points out that two species of plants: Nemophila and Zinnia are also sensitive to X-rays. Although she does not point out that the plants can be used as dosimeters, nevertheless the extreme sensitivity of these species to irradiation

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is of theoretical interest because it permits the observer, who is experienced in the effects of radiation on plants, to judge the approximate dosage on the basis of the extent of the injury. The author herself points out that two considerations mitigate against the use of the plants as dosimeters: The changeability of the plants and the fact that the effects of irradiation do not show up immediately. Even if the plants are given lethal doses, they can continue to live for several weeks, while leaves (the most sensitive of the organs in respect to rays) can reveal abnormal developments a long time after the irradiation.

Preliminary experiments have indicated that for 11 day old sprouts of Nemophyla insignis a dose of 2500 roentgen units was lethal. In a second experiment 28 day old sprouts were irradiated by doses of 1000, 1500, and 2000 roentgen units, and this experiment showed that a direct relationship exists between dosage and the percentage of survival among the plants. On 110th day after sprouting, 70 percent of the control plants survived, 60 percent of the 1000 roentgen unit group, 27 percent of the 1500 roentgen unit group, and 6 percent of the 2000 roentgen unit group. So we see that the majority of plants which received a 2000 roentgen unit dose perishes while those which received a 1000 roentgen units show retardation and diminution of growth. A dose of 1500 roentgen units exhibits an intermediate development. Conversely, it is possible to estimate the dose of X-rays by the number of surviving plants.

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Preliminary experiments with Zinnia revealed its sensitivity to X-rays. The effect of the rays on the growth, the weight, the formation of abnormal leaves, and the diminution of branches all show a direct relationship between the injuries and the dosage. The size of the dose can be estimated by the extent of the injuries, just as in Nemophyla.

But as the author herself points out, the results require several weeks to show up (110 days for Nemophyla), and for that reason it is doubtful whether this method can be used as a biological dosimeter. We feel that this question should be broached on the cytological level. Promsy and Drevon (1912), Körnicke (1920), and others point out the increase in the diameter of the cells due to X-radiation, the irregular course of Karyokinesis, etc. This is also well demonstrated in our work with rye (Breslavets and Afanas'Yeva) with peas (Atabekova), and with wheat (Afanas'yeva). Let us take by way of an example the intracellular changes obtained from X-radiated seeds of rye (for a more detailed description and diagrams see Chapter 3). By irradiating seeds of rye with doses of 250, 500, 750, 1000, 2000, 4000, and 8000 roentgen units we can observe the following changes. With a dose of 250 roentgen units in 30 roots examined only one nuclear plate was found with a triploid number of chromosomes and one with greatly shortened and thickened chromosomes. In general the cells and the nuclei were completely normal in division as well as in the resting stage. With a dose of 500 roentgen units only in two roots were nuclei which migrated from one cell to another and fusion of cells observed. One tetraploid plate

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To these criteria another one may be added, which was proposed by Johnson, namely the speed of reaction. On the third or fourth day after the irradiation of seeds and on the second day after irradiation of sprouts we can already have our answer on how a certain plant reacts to a given dose of X-rays by its intracellular changes. In order to establish these changes by a worked out methodology, of crushing the roots and staining them with aceto-carmine, does not present any difficulties.

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THE RETENTION OF THE EFFECTS OF X-RAYS

In the great majority of experiments with irradiation of seeds, the latter are planted immediately after irradiation. Naturally the question of how long the action can be retained comes up. Very frequently for theoretical purposes and particularly for practical ones it is important to retain the action for a long time. Our laboratory has frequently received requests for irradiation of seeds from outlying places where good X-ray setups and dosimeters do not exist. If the action of X-rays is retained for only a short time it is obvious that it was impossible for us to accept such requests. Since the literature on this question is very contradictory it became necessary to set up our own experiments to clarify it.

Guilleminot (1910) writes: "The injurious action of irradiation is retained for two years in its original force."

Schwarz (1913) considers that the action of X-rays is re-

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versible, i.e. that irradiated seeds retain the irritation induced by X-rays for only a short time.

This opinion is seconded by Geller who concludes, on the basis of his experiments that the irritating action of X-rays is replaced in a few days by normal development, except when irritation is such that it leads to gradual death of the plant.

IVEN (1925) tries to prove, on the basis of the experiments of Guilleminot and Weber, that even after being stored for several months, irradiated seeds retain the full force of the primary effects of irradiation.

The data of Muller (1928) and Harris (1929) on this subject are very valuable. On the basis of their experiments they have pointed out that the frequency of lethal mutations was identical among sperm taken immediately after irradiation and in those taken several days afterwards.

Afanas'yeva (1936 and 1938) used a plant with which she had done a great deal of work, namely: spring wheat Triticum vulgare var. caesium 0111 (pure strain), the seeds of which were irradiated by a dose of 16000 roentgen units. The author was aware from previous experiments that this dose invariably produces the same changes in the cells. These changes include: inclusions in the cytoplasm, formation of micronuclei, occurrence of two and more protoplasts within single cells, changes in the number and shape of the chromosomes, irregular nuclear plates, and, finally, chromatin

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bridges. In the first experiment the seeds were planted at five different periods: one day after irradiation, after 1 month, after 3 months, after 6 months, and, finally, after a year. From table 40 we can see that all of the above described changes appeared after a day and also after all of the other periods including one year.

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TABLE 40

Frequency of cytological irregularities in the somatic cells of wheat

(based on Afanas'yeva's data, 1936)

Date of Planting	Time of planting after irradiation	Number of fixing of the roots (batch)	Number of micronuclei	Average number of micronuclei per root	Number of polynuclear cells	Inclusions in the cytoplasm	Metaphase with		Abnormal plates	Chromatin bridges	Formation of two or more protoplasts
							Changed number of chromosomes	Changed shape of chromosomes			
16 May 1934	After 1 day	I	500	12	38	many	+	+	+	+	+
16 Jun "	After 1 mo.	II		not counted		"	+	+	+	+	+
16 Aug "	After 3 mo.	III	590	25	34	"	+	+	+	-	+
16 Sep "	After 6 mo.	IV	629	31	33	"	+	+	+	+	+
16 May 1935	After 1 yr.	V	360	16	13	"	+	+	+	many	very frequently

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A weakening or vanishing of the effects of X-rays was not observed. On the contrary, a certain increase can be detected in the changes. For example, the number of micronuclei and multinuclear cells increases somewhat. Three months after irradiation the number of micronuclei was 25 per root instead of 12, six months afterwards it was 31, a year afterwards the number went down again close to the original one. It seemed interesting and important to determine whether the action of irradiation can be retained for even longer periods, say for 2 or 3 years. Simultaneously with the planting of the seeds which were irradiated in 1934, two controls were planted. The first control consisted of the unirradiated seeds of wheat of the 1933 crop which were kept in the same conditions as the irradiated ones. Seeds of the same pure strain of the 1935 crop served as the second control. In the second table (Table 41) data of the cytological examination of 1937 were compared with those of 1934.

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TABLE 41

Intracellular changes induced by the action of X-rays

(based on Afanas'yeva's data)

Date of Planting	Time of Planting After Irradiation	Number of changes for 20 roots					Percent of roots with the formation of cells with polyprotoplasts
		Micronuclei	Poly-nuclear cells	Chromosomes	Metaphase		
					Changed shape of chromosomes	Changed number of chromosomes	
16 May 1934	After 1 day	326	22	35	4	3	5
16 May 1937	After 3 days	486	9	65	3	18	100

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As can be seen from Table 41, the action of X-rays on cells is not lost for a long time. All intracellular changes induced by X-rays and observed in roots fixed several days after irradiation are also observed in roots which are fixed three years after irradiation. The number of observed changes, the number of micronuclei in particular, actually increased, as did the number of polyprotoplast cells. Examination of both control groups did not reveal any changes in the nuclei. Consequently the experiments indicate that the changes induced by X-rays are stable and do not disappear or weaken even when irradiated seeds are stored for three years.

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NATURAL RADIATION AND COSMIC RAYS

In 1928, Muller in his first works dealing with the increase of frequency of mutations induced by X-rays, expressed the premise that spontaneously arising mutations are possibly due to natural shortwave irradiation. This assumption was all the more probable since all of the experimentally obtained mutations did not differ in any way from natural mutations.

Olson and Lewis (1928) in their article: "Natural Radioactivity and the Origin of [redacted] Species," write that in nature all living creatures are constantly bombarded by gamma-rays of low intensity which are due to a wide distribution of radioactive substances. On the basis of materials obtained by Goodspeed the above authors have indicated that due to natural radiation two variants per thousand should occur in tobacco, i.e. exactly the percentage that was found to exist. They also set out to discover whether or not in areas of increased radioactivity there wasn't also an increased percentage of mutations in the fauna and flora. Similar ideas were expressed by Haldane (1929), and Dixon (1929) considers that from the works of Goodspeed and Olson it is possible to conclude that cosmic rays (which have the same properties that X-rays have)

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were a factor in the occurrence of changeability by direct action on the germ plasm. After such theoretical assumptions a series of experiments were begun for the purpose of proving the influence of radioactivity and cosmic rays on mutability of genes under natural conditions.

Babcock and Collins (1929) selected for their investigations one of the genetics laboratories in Berkley and also a small tunnel in San Francisco. The two locations were separated from each other by a distance of 15 miles. Electroscopic examinations revealed that the amount of ionizing radiation in the tunnel was twice as great as at the laboratory in Berkley. Except for this the conditions of the two experiments were identical, for all practical purposes. In Berkley 3481 experiments were performed; in the tunnel, 2500.

Average percentage of lethalities in the tunnel	0.526±0.074
Average percentage of lethalities in the laboratory	0.251±0.044
Difference	0.275±0.086

From this it is possible to conclude with certainty that the natural ionizing radiation on earth is an important controling factor in the frequency of occurrence of new hereditary characteristics in plants and animals. Although this does not prove that radiation is the direct cause of mutations, it does open the way for an experimental solution of this question.

Whether natural radiation on earth induces mutations or only affects their frequency is not important; what is obvious is

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that it plays a significant role in evolution. Radioactive substances are distributed in the earth's crust as well as on the surface. The greater part of the deposits of radioactive substances are located near the surface of the earth and acts as a source of ionizing radiation which affects the mutability of organisms in its vicinity.

Engelstad and Moxnes (1934) performed experiments with the action of cosmic rays on white mice. Silver mines to the west of Oslo were a suitable place for the work since 350 meters of ore provided protection against cosmic radiation. A building which was accessible to cosmic rays served as a control station. Experiments with the animals lasted more than 10 months, 438 specimens were used (they belonged to five generations, four of which were born during the course of the experiment). The experimented animals did not differ from the control animals either in behavior or in the skeletal structure. The only difference was that the animals living in the mine were heavier.

Thomas (1936) wrote two interesting articles in relation with this question. He points out that there can be no doubt about the occurrence of mutations, it is sufficient to point out the new species Spartina townsendis which arose and spread in our time. It is difficult to imagine that such changes can be spontaneous; we must seek some external cause for their appearance in the environment. In a survey of experiments on the obtaining of mutations by artificial means Timofeyev-Ressovskiy showed that the only effective method for inducing mutations is bombardment by shortwave rays or high-speed

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electrons. At the same time numerous experiments on the action of X-rays on the structure of the nucleus indicate that irradiation can also cause cytological changes which can be associated with specific differences. But since the time of Muller's discovery that the frequency of mutations can be raised by the action of X-rays, there has been little hope of proving that species in nature arise due to the influence of natural short wave radiation or radioactive particles. The consensus of investigators on this question is: "that the process of mutation can be induced by natural radiation is out of question since sufficient amounts of energy required for artificial induction of mutations are not available." Thomas considers that this is true in relation to the products of decomposition of radioactive substances, but contemporary discoveries of the nature and distribution of cosmic rays has changed the situation considerably. We now know that photons and high-energy charged particles reach the earth in large quantities. These particles by their properties and behavior are very similar to the radiation produced by X-rays and to the emanations of radioactive bodies; consequently there is no reason for assuming that their effect on nuclei will be any different. The difference consists of the fact that X-rays, under experimental conditions, fall in a constant and continuous beam upon the chromosomes while cosmic rays bombard them in a diffused fashion by separate and infinitely minute particles. If we will take as a measure of the activity of X-rays the amount of energy which was used for tobacco by Goodspeed and Olson (1938), we shall see that their action is more intense than that of cosmic rays at sea level. The majority of

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doses used in order to induce mutations is 1500 times stronger than the action of cosmic rays. However recent experiments have shown that the ionization produced by cosmic rays falls rapidly as it passes through the atmosphere of the Earth and that it increases with altitude. Thus at an altitude of 11,000 feet the intensity of radiation increases threefold; at an altitude of 22,000 feet, 10 fold; at the altitude of 62,000 feet the ionization is 83 times as great as at sea level. In the stratosphere the intensity of cosmic rays is 150 times as great. This radiation does not consist of a uniform stream of equally charged particles; their composition also changes with altitude. In addition, from the author's point of view, the phenomena which are known as "explosions" or "showers" of cosmic rays, are interesting in the respect that they represent beams of ionized particles which upon striking, say, a mass of sporocytes, can deliver direct blows to the various chromosomes. Compton and Bennet consider that the density of these beams increases with altitude more rapidly than the intensity of the whole beam of cosmic rays. Compton has demonstrated that "showers" on mount Evans (6900 feet at 50 degrees 58 minutes north latitude) liberate more than 3×10^8 ions. The same ionization on the same latitude was applied to tobacco by Goodspeed and Olson in their experiments. This brings us to the conclusion that if modifications of the nucleus and consequent mutations arise due to the action of cosmic rays that the frequency of their occurrence must change with the altitude and location. At sea level few mutations are observed, but their number rises with altitude. It should however be pointed out that in

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high altitudes the intensity of ionization is affected by the latitude: measurements performed at 22000 feet in Panama (20 degrees N) and in Peru (4 degrees S) are 29 percent lower than those made in California (41 degrees N) and 38 percent lower than in Washington (54 degrees N). On the other hand the altitude to which plants rise (at which they can live) falls rapidly as the latitude increases. Consequently, in order to clarify the question of the influence of the altitude above sea level on the changeability of species and the intensity of cosmic radiation observations must be made at various points on the earth's surface. Certain preliminary data permit us to believe that such an influence exists. Vavilov's data on the geographic distribution of varieties of the most important grain plants are particularly interesting in relation to this point. He established that the greatest variations in species and varieties are found in mountains of the tropics and moderately warm areas. Thus he found 60 varieties of Triticum vulgare in Afghanistan; 52/ in Persia; 46/ in Beludzhistan; but only 32/ in India; 31/ in Mongolia; and 12 in Italy. Vavilov determines seven or eight centers of origin of agricultural plants. Nearly all of these points are located in high mountains or plateaus, not more than 40 degrees from the equator. There can also be no doubt that the flora of mountain areas of the tropics and moderately warm countries is far more varied than in the lowlands. Standly points out that the flora of little Costa Rica has more than 6000 species of vascular plants, i.e. nearly as many as in the whole southwestern United States, although Costa Rica is only half the size of Florida and has many mountainous areas which have not yet been explored botanically. The

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mountains of Costa Rica rise to 11,000 feet and more than half of the country lies above 3,000 feet. Observations indicate that the plant-inhabitants of these tropical mountain areas are very variable, however the question remains to what extent the richness of varieties can be explained by this means. Costa Rica is an interesting example since it is a young mountainous area of the late Eocene and Oligocene periods, while a large percentage of its endemic flora is such that we cannot assume that it is due to the spread of species from the north.

The authors idea is very finely confirmed by the genus Primula. Although the order Vernales is widely distributed in Europe and in eastern Asia, chiefly in the lowlands, it comprises only 19 species; while numerous other orders, which inhabit mountainous areas, are much richer in species and endemic forms (i.e. Petiolares has 66 species, Nevales has 61, etc). All told there are some 330 species of mountain primules. Almost all of the alpine genera of Primulaceae are richer in species than the genera of the valleys.

Jepson considers as proven that the most copious formation of new varieties is related with gradual slopes of hills.

Thomas sees further proof for his idea that many important changes in fossil flora are definitely related to periods of mountain formation. For example, in the west of North America at the time of the Upper Cretaceous period mountains rose to a height of 20,000 feet. But since this was a warm period, with rich flora, the rise of the mountains did not destroy it and some species of plants survived and

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underwent mutations. Shortly after this in the fossil flora of the United States 83 genera and numerous species are encountered which were not encountered in Cretaceous flora. According to Thomas this indicates that the formation of new species is related to growth of plants in high altitudes where the intensity of cosmic rays is high. To arguments of several authors who point out that great variations in temperatures play an important role in the mountains Thomas replies that in lowland areas where variations are also great, such a multiplicity of forms is not encountered.

Muller, Timofeyev-Ressovskiy, Efroimson, and others are opposed to attaching significance to natural radiation as the cause for spontaneous mutability. They base their arguments on the following considerations. It is known that the frequency of mutations is proportionate to the dose of roentgen units (r). A single unit (1r) affects 2.1×10^9 ions. A dose of 3420 roentgen units (which affects 7.2×10^{12} ions) induces 15 lethal gene-mutations, related to sex, in Drosophila melanogaster. Since in the immediate environment of the fly natural radiation affects 30 ions per cubic centimeter per second, during the life span of the fly, which is around 14 days, she is affected by natural radiation equivalent to 3.6×10^7 ions. Since the natural frequency of mutations is 0.1 percent, or $\frac{1}{150}$ of the 15 percent which is induced by a dose of 3420 roentgen units, while the relation of ionization is ($3.6 \times 107 : 7.2 \times 10^{13}$) 1 : 200,000 the disproportion is $\frac{1}{150} : \frac{1}{200,000}$ which equals $\frac{1}{1333}$. In other words, natural radiation has to be 1333 times as great in order to explain spontaneous frequency of mutations related with sex.

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[sic]

Delbrück and Timoffeeff-Ressovsky (1936) consider that the more interesting facts presented by Thomas can be explained by contemporary concepts of evolution. The high altitudes of mountainous areas produce specific conditions and a great variety of local types which are conducive to isolation and selection of specially adapted varieties. Each of the free living populations usually have a large number of mutations which can serve as a basis for evolution.

The same issue of the magazine "Nature" which contained the article of the above authors also contained H. Thomas' answer. He pointed out that there is a difference between ionization induced by cosmic rays and the gamma rays of radium, and that it would be improper to conclude that with equal mean intensities their actions would be identical.

In 1933 Friesen had the idea of subjecting Drosophila flies to the action of cosmic rays in the stratosphere, but it was not till 1935 that he succeeded in raising the flies in a "stratostat" to an elevation of 15,900 meters. For two hours the flies were bombarded by cosmic rays whose intensity was 100 times greater than their intensity on the earth's surface. Friesen used the usual method for determination of lethal mutations in the X-chromosome. At the same time an experimental control was set up. In the 2724 fly chromosomes which had been raised into the stratosphere, 8 mutations were obtained, while in the 2445 control chromosomes 10 mutations were found. These negative results with cosmic rays of high intensity should make us careful about accepting the theory which considers cosmic rays to be an important factor in organic evolution. Stubbe,

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in 1932-1933, set up an interesting experiment for the purpose of investigating the influence of cosmic ultraradiation on the mutability of genes of the well-known strain of Antirrhinum majus. He also based himself on the works of Vavilov who pointed out that high mountainous areas constitute the so-called "genocenters" which produce the greatest varieties of species. A high mountain station on the Jungfrau was selected as the setting for these experiments. Eight week old plants were transported to the station and were left there for one or two growing seasons. However the mutability of the genes of the plants cultivated at the elevation of 3300 meters did not differ in any respect from those in the lowlands.

These experimental data of Friesen and Stubbe indicate that if cosmic ultraradiation plays only the most insignificant part, if any, in the formation of spontaneous mutations.

Since natural radiation and cosmic rays can account for only an insignificant part of the frequency of spontaneous mutations they cannot be considered the sole cause for the occurrence of such mutations.

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