IONIZING RADIATION FOR THE CONTROL OF PLANT PATHOGENS

A REVIEW[1]

R. S. Willison[2]

Since conventional methods for controlling post-harvest rots in fruits often leave much to be desired, supplementary measures that do not add to the residue problem would be welcome. Accordingly, in the summer of 1962, an investigation of the control of brown rot and black mold of stone fruits by gamma radiation was proposed as a joint project involving Atomic Energy of Canada Ltd. , the Ontario Horticultural Experiment Station, Vineland, and the Research Laboratory of the Canada Department of Agriculture, Vineland, Ontario. The literature was searched as a preliminary step in the project, Although studies of the reactions of micro-organisms to radiation began soon after the discovery of radioactivity (18), information on the adaptation of ionizing radiation to plant pathology is not yet voluminous. However, it was soon evident that investigations on the effects of such radiation on numerous micro-organisms, both in vivo and ~~in vitro~~, were well beyond the preliminary exploratory stage. The present paper reviews various aspects'of the application of ionizing radiation to the direct control of diseases in growing plants and of decays in harvested fruits and vegetables,

Types of radiation.

It may be useful to first review briefly the various types of radiation and their suitability for our purposes, as well as to define the units used in their measurements.

The ionizing effect is produced by the release of electrons and the formation of ionic pairs. Also, some of the energy lost by the radiation on impact is taken up by the surrounding atoms or molecules, induces structural changes of various degrees of magnitude, and produces heat. Ionizing radiation occurs in various forms in two categories: particulate rays, and high frequency or high energy electromagnetic waves, The main particulate radiations are:

(i) beta rays, **or** fast moving electrons with **a** negative charge.
(ii) protons, or positively charged hydrogen nuclei.
(iii) neutrons, or uncharged particles, each of the same mass as a proton.
(iv) deuterons, each composed of a neutron and a proton, therefore carrying one positive charge.
(v) alpha particles, or helium nuclei, each equivalent to a pair of deuterons and having a double positive charge.

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2 Plant Pathalogist.

The electromagnetic waves are similar to one another in type and effect, but differ in origin and often in frequency and wave-length. Gamma rays are high energy waves accompanying the emission of particles during the disintegration of certain radio-active substances. For example, Co^{60} emits both beta particles and gamma rays. X-rays are produced by a sudden change in the velocity of a stream of electrons (cathode ray) on impact with a target in a vacuum tube. They are caused by the resulting changes in the atoms of the target. X-rays are usually of longer wave-length or lower frequency than gamma rays, though modern machines are capable of producing high energy X-rays approximating the frequencies of gamma rays. X-rays and gamma rays range in wave-length from 0.01 to 1.4Å.

Ultraviolet light, with wave lengths of 2,000 to 4,000 Å, has not enough energy to be ionizing, but excites atoms by rearranging the orbits of their electrons. Ultraviolet light is useful for some types of surface sterilization, or asepsis, because many micro-organisms as well as viruses are sensitive to it. The behaviour of micro-organisms under ultraviolet light is however, different from that under ionizing radiation (21), and is outside the scope of the present review.

The alpha and beta particles are not deeply penetrating, but, as they have very high energy, cause surface burns and are particularly dangerous to humans if substances emitting them are ingested or inhaled. Gamma rays, X-rays, and neutrons, on the other hand, penetrate very deeply and even small doses, particularly of neutrons, can be very dangerous to human health. Beta radiation has been used by some plant pathologists for surface sterilization (9, 10, 17), but the more penetrating and pervasive types of radiation appear to be more suitable for most phytopathological purposes.

Units of measurement.

Several different units have been used by different workers to designate the amounts of radiation or dosages applied during irradiation. This variation in usage appears to have been due to the evolution of new concepts and a shift in emphasis, at least as far as radiation biology is concerned, from the radiations *per se* to the energy changes in the irradiated specimens.

The curie, "c", (10, 29) is the amount of radioactive material equivalent in activity to 1 gm of radium, in which 3.7×10^{10} atoms disintegrate per second, regardless of the products of the disintegration. For example, 1 c of cobalt 60, which yields gamma radiation, is equivalent in energy to only 2×10^{-4}c of polonium 210, which yields alpha particles.

The roentgen, "r" (10, 12, 14, 15, 26, 29, 30, 31) was originally applied to the measurement of the activity of X-rays, but more recently to gamma radiation also. The roentgen is defined as the amount of radiation that will produce 2.1×10^9 ion pairs in 1 cc of dry air at standard temperature and pressure. Exposure to a roentgen of X or gamma radiation, however, results in the uptake of almost 100 ergs per grarn of irradiated water or tissue, The kilo-roentgen, 10^3 r or "kr" is used by some authors (19, 20, 31).

The roentgen - equivalent - physical, "rep" (2, 3, 4, 5, 17), derived directly from the roentgen, is the amount of energy that a roentgen of radiation delivers to a gram of wet tissue. The rep is defined as the amount of radiation that will produce an uptake of 93 ergs of energy by a gram of wet tissue.

The rad (6, 7, 8) and its multiple the Kilorad, "k rad" (1), are similar to, but more convenient than, the rep. The rad is a measure of absorbed energy induced by radiation and is equivalent to 100 ergs per gram of irradiated material, usually wet tissue. Since the rad indicates the amount of energy absorbed by a unit weight, it is independent of the type of radiation used. For practical purposes, the roentgen, rep, and rad represent approximately equivalent amounts of energy abgorption.

Effects of radiation on pathogenic micro-organisms in vitro,

The sensitivity of plant-pathogenic micro-organisms to radiation in vitro appears to be highly complex, not only varying widely between organisms and between different stages of development and different functions of the same organism, but also being affected by substrate and growing conditions,

Some bacteria have been found to be more susceptible than others. According to Hellmers (14), Pectobacterium parthenii var. dianthicola (? Erwinia chrysanthemi) and P. carotovorum (E. carotovora), pathogenic to carnation, withstood gamma radiation at dosages of 1×10^5 r but not at 3×10^5 r. On the other hand, Dimond (12) and Waggoner and Dimond (29) found that cultures of Agrobacterium tumefaciens subjected to 5×10^4 r of gamma radiation at the rate of 80 r per hour were still capable of producing normal galls on non-irradiated plants, though 63 per cent of the bacteria were inactivated at 3×10^3 r and more than 90 per cent were killed at 1×10^4 r. It was therefore argued that the pathogenicity factor of A. tumefaciens was less susceptible to radiation effects than the survival factor.

Wide differences in the sensitivity of actively growing hyphae to radiation have been reported for different fungi, in some cases within the same genus (Table 1). Moreover, some species are resistant to many times the dosage lethal for others pathogenic to the same host: for example, Phytophthora infestans and Alternaria solani, isolated from potato (Table 1), and Phomopsis citri and Diplodia natalensis, from citrus fruits (Tables 1 and 2). Variations in resistance occurring within a species may be partly due to the age of the culture at the time of irradiation,: since Kljajic (15) reported that the actively growing mycelium of several fungi was most sensitive in cultures 24 hours old. The nature of the medium in which the mycelium is growing is also an important factor. According to Stapleton (25), a medium containing organic complexes, such as proteins, exercised a greater protective effect on some organisms than one containing simple, chemically defined, ingredients, Sommer, Eckert, and Creasy (23) also obtained evidence of protective action when spores of Penicillium digitatum were irradiated, either in orange juice or in inoculated citrus fruits. A similar effect would also account for the different responses to irradiation

Table 1. Some plant pathogens grouped according to dosage of gamma radiation lethal to actively growing mycelium.

Dosage range*	Organism
Less than 1×10^5	Phomopsis citri, Phytophthora infestans (8).**
1×10^5 to 2.5×10^5	Botrytis allii, B. cinerea***, Monilinia fructicola, Pellicularia rolfsii, Penicillium digitatum, P. expansum, P. italicum, Phoma sp. (from blueberry,) Pythium debaryanum, Sclerotinia sclerotiorum (8); Alternaria solani,*** Ascochyta pisi,***, Aspergillus niger, Trichothecium roseum (15).
2.5×10^5 to 5×10^5	Alternaria citri, A. tenuis, Cladosporium sp. (from lemon), Gloeosporium musarum, Gloeosporium sp. (from blueberry), Rhizopus nigricans (from peach and sweet potato), Stemphylium radicinum (8).
5×10^5 to 7.5×10^5	Diplodia natalensis*** (8); Alternaria dianthi (14); Alternaria solani***, Ascochyta pisi*** (15).
7.5×10^5 to 1×10^6	Diplodia natalensis*** (8); Fusarium culmorum (14); Alternaria solani***, Ascochyta pisi***, Fusarium oxysporum f. vasinfectum (15), Botrytis cinerea*** (15) (17); F. oxysporum f. lycopersici (30).

* Dosage in rads, reference (8); in roentgens, references (14, 15, 30) in reps beta radiation, reference (17).

** Numbers in brackets indicate references.

*** Organisms in more than one category were variable in sensitivity, possibly at different stages of growth.

in Tochinai's and in Czapek's media exhibited by both conidia and hyphae of Monilinia fructicola, the peach brown rot fungus (5), and of the Penicillium species from citrus fruits (4) (Table 2). Tascher (26) found that seed-borne pathogens, Such as Diplodia zeae and Gibberella saubinetti were much less sensitive to X-rays in dormant infected seed than they were in vitro on potato dextrose agar. The effect of substrate on the sensitivity of different fungi to irradiation is, however, far from uniform and varies greatly from one organism to another, as indicated by the investigations of Beraha and his colleagues (8), (see also Table 3).

In many but not all fungi, higher dosages of radiation were required to prevent germination of spores than to suppress growth of mycelium (Table 2). According to Kljajic (15), the conidia of Helminthosporium turcicum from corn, and Penicillium expansum from apple, were less susceptible than the mycelium, while the reverse was true for Botrytis cinerea from grape, and Fusarium oxysporum f. vasinfectum from cotton. In Aspergillus niger from grape, Ascochyta pisi from pea, Alternaria solani from potato, and Trichothecium roseum from plum, conidia and hyphae were equally resistant (or susceptible). Schwinghamer (21), reported that the calculated sensitivity to X-radiation of the mycelium of the flax rust, Melampsora lini, was ten times that of the uredospores irradiated at a comparable level of hydration. However, the uredospores of M. lini, Puccinia graminis f. sp. tritici, P. graminis f. sp. avenae, and P. coronata f. sp. avenae became increasingly sensitive to X-rays, gamma rays, and neutron:'; when their moisture content exceeded 45 per cent.

Sommer et al (23) investigated the response of spores of various fungi to gamma radiation and found that germination that occurred after irradiation commonly resulted in abnormal germ tubes capable of limited elongation only. They concluded that survival, as indicated by potential for unlimited growth, was generally more sensitive than the germination process. They also demonstrated that irradiated, abnormally germinating sporangiospores of Rhizopus stolonifer, though incapable of forming a colony, were able to hydrolyse pectin nearly as rapidly as similar, but non-irradiated spores, Castellani, Matta, and Guerzoni (10) regarded as signs of a true radiation disease the modifications in shape and structure of the germ tubes of spores of Gloesporium musarum that became more frequent with increases in dosage above 5×10^4 r (see also Table 2). On the other hand, at dosages well below the lethal level, ionizing radiation, whether gamma rays or neutrons, may stimulate germination of conidia and growth of cultures as reported by Vasudeva and colleagues (28) for Colletotrichum falcatum (Glomerella tacumanensis) and Ustilago nuda.

Effects of radiation on the host,

In peaches, abnormalities in texture and colour, such as softening of the flesh or browning of the skin, resulted from irradiation with gamma rays at doses greater than 4×10^5 rep but not at 3×10^5 rep (5). Beraha and his associates (5) considered that more subtle changes, such as an increase in ripening rate or an alteration in flavour, may occur at doses that cause no obvious injury.

Table 2. Dosage of radiation required for suppression of gerrnination of conidia and growth of hyphae of various plant pathogens in vitro.

Organism	Host and Disease	Type of radiation	Dosages and Effect	Ref.
Botrytis cinerea	Grape and strawberry fruit rot	beta	1×10^5 rep. - growth delayed. 4×10^5 rep. - growth more or less suppressed. 8×10^5 rep. - cultures killed.	17
Diplodia natalensis Phomopsis citri	Orange - stem end rots	gamma	4.7×10^5 to 8.9×10^5 rad - hyphae killed. 4.6×10^4 to 9×10^4 rad - hyphae killed.	6
Gloeosporium musarum	Banana - anthracnose	beta	5×10^4r - affect shape and structure of germ tube 3×10^5r - germ'n. of conidia inhibited.	10
Monilinia fructicola	Peach - brown rot	gamma	2×10^5 rep - limit for hyphal growth 1×10^6 rep - 50% germ'n. of conidia*.	5
Rhizopus nigricans	Peach - black mold	gamma	4×10^5 rep - limit for hyphal growth 5×10^5 rep - 50% germ'n. of conidia.	5
Penicillium digitatum P. italicum	Citrus - fruit rots	gamma	1.03×10^5 rep - suppressed colonies** $1,57 \times 10^5$ rep - lethal to young hyphae** 4.7×10^5 rep - lethal to conidia**	4
Phytophthora infestans	Potato - late blight	gamma	2.3×10^4 rad - limit for hyphal growth 20 Kr - almost suppressed growth 100 Kr - lethal to hyphae	7 19

* In complex medium (Tochinai's, 25); in simple medium (Czapek's). 2×10^5 rep reduced germination to 30% (cf. Table 3).

** In Tochinai's medium; lower dosages required in Czapek's.

Table 3, Effect of culture medium* on resistance to gamma radiation of young actively growing mycelium of various fungi (8).

Rating order of media**	Organism
C=T	Botrytis cinerea (from blueberry), Gloeosporiurn sp. (from blueberry), Gloeosporium rnusarum (from banana).
C=H=T	Alternaria citri (from lemon), Alternaria tenuis (from tomato) Phytophthora infestans (from potato).
C=H>T	Penicillium expansum (from apple).
C>T>H	Rhizopus nfgricans (from peach). (see H>C>T)
H=T>C	Monilinia fructicola (from peach).
H>C=T	Botrytis allii (from onion), B. cinerea (from grape and strawberry), Cladosporium sp. (Erom lemon), Phomopsis citri (from orange), Sclerotinia sclerotiorum (from bean), Stemphylium radicinum (from carrot).
H>C>T	Rhizopus nigricans (from sweet potato).
H>T>C	Penicillium digitatum (from lemon), P. italicum (from orange).
T>C	Pellicularia rolfsii (from watermelon)), Phoma sp. (from blueberry).
T>C=H	Diplodia natalensis (from peach),
T>H>C	Pythium debaryanum (from potato).

* Czapek's (c), Tochinai's (T), and host (H).

** =, equally sensitive (or resistant) in both media; >, more resistant in the first than in the second medium of a pair.

The threshold for visible injury in oranges was slightly lower than that for peaches, about 2.75×10^5 rad of gamma radiation, whereas severe injury occurred at 4.5×10^5 rad and textural changes in the pulp at doses above 9×10^5 rad (6).

Nelson, Maxie, and Eukel (17) reported the grape varieties Tokay and Emperor to be somewhat less sensitive to beta radiation than the Thompson variety, for which the threshold of injury was at 2×10^5 rep. The latter variety became slightly brown and developed a cooked flavour in about 3 days at 3 to 4°C after exposure to 4×10^5 rep. At 8×105 rep injury was more severe, appeared earlier, and included cracking of the skin. The same authors (17) observed no injury in strawberries, variety Shasta, irradiated at a dose of 2×10^5 rep. Irradiation at 4×10^5 rep induced water-soaking, a "cooked" odour, and off flavors, and, at 8×10^5 rep, immediate exudation of juice followed by collapse in a few days,

Slight softening of potato tubers, variety Red Pontiac, occurred after irradiation at 1.37×10^5 rad. At higher doses, discoloration and softening became more pronounced (7). According to Rubin and colleagues (19) irradiation of tubers at doses of 10 kr (1×10^4 r) had no depressing effect on peroxidase activity, suberin formation, or wound biosynthesis of ascorbic acid. Periderm formation, however, was noticeably depressed, at least temporarily. Irradiation may therefore have an inhibitory effect on cell-division.

In Tascher's experiments with seed-borne diseases (26), dormant seeds of corn, wheat and barley were damaged by irradiation with X-rays at dosages between 1'and 2×10^4 r. Either the percentage of germination was reduced or the seedling plants were stunted or otherwise injured. As might be expected, germinating seed was even more sensitive than dormant seed.

Dimond (12) observed that young tomato plants irradiated with 3×10^4 r of gamma radiation at the rate of 80 r per hour had slow terminal growth, poorly developed leaf laminae, very poor root development, and the new growth lacked central parenchyma, These effects are interpreted as the result of impairment of the ability of the plant to undergo chromosomal and cell division and cell enlargement. Skoog (22) and later workers showed that exposure of plants to low doses of ionizing radiation caused temporary suppression of auxin production. At higher doses, this effect on auxins may become permanent. The interference with growth cell division observed in irradiated tomato plants (12, 29, 30, 31) is probably associated with lowered auxin levels.

Inhibition of growth in irradiated carnation cuttings was reported by Hellmers (14). Cuttings irradiated at 3×10^3 r rooted almost normally and the resulting plants grew well and produced good bloom, but after irradiation with dosages of 7×10^3 r or more, root formation was suppressed and the cuttings failed to grow. Wheat seedlings were somewhat more sensitive; Schwinghamer (20) noted that a 0.5 kr (5×10^2 r) dose of X-rays initiated inhibition of leaf development and a 1.5 kr dose caused stunting of roots and the formation of root-tip nodules.

Effects of radiation on host-pathogen relationships.

Changes effected through the host: Dimond (12) and Waggoner and Dimond (29) suppressed crown-gall formation completely on three hosts by exposing whole young plants to a dose of 3×10^4 r of continuous gamma radiation (chronic) at a rate of 1 to 2×10^3 r per day. X-rays in excess of 4×10^3 r at a rate of 1 to 5 r per second delayed the onset of gall formation in tomato for periods varying with the total dosage applied (Table 4). Irradiation also inhibited further growth of galls already present on the plants, Radiation was equally effective whether applied before or after inoculation with Agrobacterium tumefaciens, but bacteria capable of producing galls on non-irradiated plants could be isolated from galls suppressed by doses of 8 to 16×10^3 r. The authors therefare concluded that radiation suppressed the galls by affecting the host rather than the pathogen and that the formation of hyperplastic tissue was inhibited because auxins were at low levels.

Changes in the resistance of tomato to Fusarium oxysporum f. lycopersici were also observed by Waggoner and Dimond. Plants exposed to chronic gamma radiation at the time of inoculation or later were more susceptible than nag-irradiated controls (30). On the other hand, irradiation with 21 kr of X-rays five to ten days before inoculation increased resistance markedly (31). When irradiation was restricted to certain parts of the plant, increased resistance was associated with treatment of the root before inoculation and, to a lesser extent, with treatment at the time of inoculation, Conversely, irradiation of the shoot at any time lowered resistance to some extent. Since F. oxysporum (Table 2) is resistant to levels of radiation much higher than the tomato plant can tolerate, it was concluded that this reduction in infection was also due to an effect on the host, It is generally accepted that root and shoot play different roles in auxin synthesis and use, Moreover, increases in the resistance of tomato to Fusarium wilt were accompanied by stunting of the plant. Furthermore, Davis and Dimond (11), working with the same host and fungus, showed that preinoculation treatments with plant growth regulators also reduced growth and increased resistance. Waggoner and Dimond (31) suggested, therefore, that, in the Fusarium - tomato interaction, radiation changes the resistance of the host by lowering its auxin level. The mechanism by which resistance is changedin this case is evidently different from that operative in the suppression of crown gall in the same host since the formatian of hypertrophied tissue is not involved in the wilt disease.

In experiments with rust fungi and their specific hosts, Schwinghamer (20) used chronic doses of gamma radiation administered at the rate of 1 kr per day and acute single doses of X-rays at higher dosage rates. Chronic doses of 10 kr had no effect on the reaction of 16 varieties of flax resistant to Melampsora lini whether inoculation preceded or followed irradiation. In susceptable flax varieties, however, irradiation after inoculation caused a temporary delay in infection, In this case, the radiation was considered to have affected the rust, not the resistance of the host, since a 10 kr acute dose of X-radiation proved lethal to more than 90 per cent of day-old infections. In cereals, on the other hand, the host reacted to irradiation;

both acute and chronic irradiation before inoculation changed the reaction type of some varieties, but not of others. Any changes that occurred were invariably towards increased susceptibility. Chronic irradiation begun one day after inoculation was less effective in breaking resistance. Changes in host response were distinct at 5 kr doses of chronic radiation, but were initiated by as little as 1.5 kr of acute X-ray treatment and reached a maximum at approximately 3 kr. Changes in reaction type may be associated with specific physiological changes, since the reactions of a given variety to different races of rust changed to different degrees. For example, in wheat varieties normally resistant to races 15B and 111 of Puccinia graminis f. sp. tritici, irradiation induced a much greater shift towards susceptibility to race 15B than towards susceptibility to race 111. Irradiation of the crown or shoot apex of cereal seedlings affected both rust development and stunting of leaves much more than irradiation of either roots or leaves alone, In Schwinghamer's opinian, the association of rust reaction with a process initiated in the shoot apex and affecting growth of leaves suggests that growth-regulating substances may be involved directly or indirectly in the mechanisms governing the resistance or susceptibility of cereals to rust fungi. If so, the type of resistance encountered here differs from the examples cited in the preceding paragraphs, since the shift was towards increased susceptibility, rather than towards increased resistance,

Changes effected through the pathogen: Since Brasch and Huber (9) demonstrated the possibility of using beta rays to prevent deterioration of foodstuffs in storage, considerable work has been done on the use of radiation in the post-harvest control of pathogens causing rots, decays, or molds in fruits and vegetables. In almost every case, the dosage required either for surface sterilization or to kill the pathogen in existing infections is well above the level tolerated by the host tissue. Thus, as Hannan (13) pointed out, it is not practicable to control decays in most fruits and vegetables by using radiation as a sterilant. However, as already intimated, radiation effects start to occur in germ tubes'and growing hyphae at dosages below the lethal level (10, 23). Treatment at appropriate dosages of radiation, then, could'be expected to bring fungistasis into play (2, 17), so that decays or rots could be checked indefinitely or at least long enough to prevent wastage of perishable products during distribution and sale (Table 4).

Some complications may arise from the fact that low doses of radiation may stimulate fungal growth (28). For example, Beraha et al (6) reported that Diplodia natalensis induced more and faster rotting in inoculated oranges irradiated at dosages of 2×10^5 rad or less (Table 4). Also, Mathie and Marais (16) found that low doses of X-radiation increased the rate of apple decay by Penicillium expansum, and Rubin et al (19), (also Table 4) showed that 10 kr of gamma radiation stimulated Phytophthor rot of potato tubers. Beraha and colleagues (4) described an even more involved interaction, in that irradiation at dosage levels preventing decay of oranges and lemons by radiation-sensitive fungi, such as Penicillium digitatum and P. italicum, may expose the fruit to decay by organisms that do not ordinarily attack it.

Table 4. Effects of ionizing radiation on infection.

Organism	Host and Disease	Rad'n.	Dosage and Effect	Ref.
Agrobacterium tumefaciens	Tomato crown gall	X-ray	4 x 103r delayed galls 3 or 4 days	12
		X-ray	6 x 10^3r delayed galls 3 weeks,	29
		gamma	3 x 104r suppressed gall form'n.	
Erwinia carotovora	Potato soft rot	gamma	4.8 x 10^5 rad did not suppress rot in tubers	7
Phytophthora infestans	late blight	gamma	10 kr stimulated tuber decay	19
			4.5 x 10^4 rad prevented decay (+ 1 x 10^5 rad)8	7
Botrytis cinerea	Strawberry rot	gamma	2 x 105 rep checked inf'n.	3
		beta	1 to 2 x 10^5 rep, reduced rot	17
Rhizopus nigricans	mold	gamma	2 x 105 rep checked inf'n. (2 x 4 x 10^5 rep)	3
B. cinerea	Grape rot	gamma	5 x 105 rep delayed inf'n. 10 days	3
		beta	1 to 2 x 10^5 rep. reduced inf'n. (2 to 4 x 10^5 rep)	17
Diplodia natalensis	Citrus stem-end rots	gamma	2 x 10^5 rad stimulated inf'n.	6
			2. 75 x 10^5 rad checked inf'n.	
Phomopsis citri		gamma	9 x 10^4 rad checked inf'n.	6
			1. 15 x 10^5 rad stopped inf'n.	
Penicillium spp.	fruit rots	gamma	1. 5 to 2 x 105 rep stopped rot** (a) for 12 days at 75°F. (b) for 17 days at 55°F. checks rotted in 3 days at 75°F. (2.75 x 10^5 rad)	4
Penicillium expansum	Apple fruit rot	gamma	1 x 105 rep suppressed rot 6 days at 70-75°F.	3
			2 x 10^5 rep suppressed rot 10 days at 70-75°F.	
Monilinia fructicola	Peach brown rot	gamma	2 x 10^5 rep delayed rot 10 days at 80-85°F.	5
Rhizopus nigricans	mold	gamma	2. 5 x 10^5 rep delayed inf'n. 10 days at 80-85°F. (3 to 4 x 10^5 rep)	5

** In brackets, threshold dose for injury to host.
Higher doses required for established than for incipient infections.

In the instance cited, Alternaria citri developed and caused rot in irradiated fruit, but not in the lion-irradiated controls.

The flux of radiation, or dose-rate, is also an important factor, since it determines the effective total dose required. Dimond (12) stated that the extent of crown-gall suppression in tomato decreased as the dose-rate decreased, so that total doses that prevented gall formation when delivered at a flux of 80 r per hour had no effect when delivered at 5 r per hour. According to Beraha et al. (7), doses of 1.37×10^5 r or more of gamma radiation gave complete control of Pythium debaryanum in potato tubers when administered at 7×10^3 r per minute, but not when administered at 3×10^3 r per minute. Beraha (1) also demonstrated that blue mold (Penicillium italicum) was not completely controlled in inoculated oranges held 12 days at 75°F after irradiation with 182 k rad of gamma radiation at 3 k rad per minute whereas at 20 k rad per minute a dose of 157 to 182 k rad was effective, as was a dose of 125 to 137 k rad at 40 k rad per minute. Somewhat similar results were obtained with green mold (P. digitaturn) in the same host, Similarly, 125 to 150 k rad total dose delivered at 25 k rad per minute almost completely suppressed brown rat (Monilinia fructicola) in peaches and gray mold (Botrytis cinerea) in pears for 17 days, but 210 k rad at 2. 5 k rad per minute did not control decay (1).

Host response is also affected by dose rate (1). It is inferred from several reports that this response is not necessarily of the same magnitude as that of the pathogen, though there is no explicit statement to that effect. The optimum flux and total dose would have to be determined experimentally for each host-pathogen complex.

Discussion and Summary.

The information presented above leaves no doubt that micro-organisms, generally, can survive larger doses of ionizing radiation than higher plants can tolerate. The direct control of diseases in growing plants by the fungicidal action of radiation, therefore, is not likely to be feasible and, indeed, has not often been attempted, Hellmers' results are typical (14) (see also Table 1). He showed that,, whereas bacterial and fungal pathogens of carnation were not seriously affected by gamma radiation at dosages of 1×10^5 r or lower, carnation cuttings were prevented from rooting by irradiation at 7×10^3 r.

Irradiation of seeds for the control of seed-borne diseases seems equally impracticable, Tascher (26) found that X-rays, in dosages great enough to inhibit the pathogens, in most cases either impaired germination or injured the young seedlings.

Controlling disease by altering the resistance of a host to its pathogen is no more promising than the more direct approach. Dimond (12) and Waggoner and Dimond (29 and 31) used gamma radiation to suppress crown gall development and to increase resistance to Fusarium wilt in tomato plants, but control of the disease was counterbalanced by deleterious effects on the treated plants. In Schwinghamer's experiments (2), irradiation not only induced abnormalities in wheat plants, but lowered their resistance to

certain strains of stem rust.

The disappointing results of irradiating plants during their growth and development are no doubt due to the cell nucleus being the principal site of damage, particularly during mitosis and meiosis. Sparrow and Woodwell (24) have correlated the sensitivity of higher plants with chromosomal and nuclear characteristics. Plants with large nuclei and low chromosome numbers arc much more sensitive than polyploids and plants with small nuclei and high chromosome numbers. Plants vary so greatly in these respects that differences in sensitivity between species may be as much as 500-fold (24). As micso-organisms also vary widely in sensitivity, control of some diseases may be possible, if not practical.

Because of the sensitivity of dividing nuclei, mature tissues, in which cell division has virtually ceased, should not be subject to as wide a range of radiation damage as immature growing tissue. Irradiation for the control of wastage in harvested fruits and vegetables may therefore be feasible, but the working margin would depend on the host–pathogen combination. The effective range of treatment is determined, on one side, by the critical minimum for injury to the host and, on the other, by the critical maximum dose for stimulation of the pathogen (6, *14).* In some cases, these two limits may be too close for practical purposes; for example, in the control of Diplodia stem rot of citrus fruit and Botrytis rot of grape (Table 4). In others, they overlap completely and control is not possible, as with soft rot of potato (Table 4). In still others, e.g. Phytophthora rot of potato, Phomopsis and Penicillium rots of citrus fruits, Botrytis rot and Rhizopus mold of strawberry, and Monilinia rot and Rhiaopus mold of peach (Table 4), the critical points are far enough apart to offer some promise of practical application,

It should be remembered that, in almost all the experimental work with fruits and vegetables, the samples under test were artificially inoculated, usually in wounds, so that incipient infections were present before irradiation was undertaken, It is for this reason that the radiation is considered to act on the fungus, not on the host, in these cases, at least so far as control is concerned. The data presented in Table 4, therefore, represent tests made under more exacting conditions than would normally occur in properly handled commercial packs. It seems reasonable to expect more satisfactory control of wastage in sound fruit than in injured fruit in which infections have already started, since the germination of irradiated fungal spores is usually abnormal (23).

The favorable results already obtained experimentally with peaches (3, 5) warrant continuation of the proposed project to control brown rot and mold by gamma radiation. Logically, future work should proceed mainly along practical lines on a semi-commercial scale with uninjured fruit packed in the usual way in commercial containera. Experimentation should be planned to determine the effects of irradiation on the shelf life of the fruit under a variety of conditions both before and after treatment. Before the method can be put into commercial practice, the economic and mechanical aspects of the problem will also have to be considered. It is expected that safety requirements and the exacting nature of the operation will necessitate treatment at central locations under the supervision of trained personnel.

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RESEARCH LABORATORY, CANADA AGRICULTURE,
VINELAND STATION, ONT.