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Metabolic and biochemical changes caused by gamma irradiation in plants

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Abstract Applications involving radioisotopes and radiations reveal a great promise particularly for the welfare of the society. However, in the event of a nuclear accident, the direct and indirect effect of radionuclide and radiation transfers in soil–plant–air environment are envisaged on almost all the components of the food chain. It also assumes significance as we often overlook the fact that radiations, emitted by any radioisotope although cannot be seen or felt, interacts with matter and could alter its biochemical, biophysical and biological characteristics. The interaction of ionizing radiation with human body and consequent biological effects are well characterized and quantified using data derived from the radiation workers and/or the nuclear accidents around the world. However, radiation impact on agriculture viz a viz economic productivity are not well understood and available data is scanty, scattered and inconclusive. At the plant level the effects could be visualized at morphological, biochemical, physiological and/or biophysical levels, where the magnitude of the effected change depends heavily on the exposure dose, soil, farm management and other environmental variables. This review attempts to collate and critically analyze the available researches on how the ionizing radiation might interact with crops at the whole plant or tissue or cell level to affect economic yield under various edaphic variables where not only the productivity but also the quality of the agri-produce may become vulnerable.

Keywords Ionizing radiation · Radionuclide · Agriculture · Biochemistry and metabolism

Introduction

Use of radiations and isotopes for the benefit of mankind has become a way of life in most of the developed countries around the globe. Even in developing countries like India, utilization of nuclear techniques in the area of agriculture, defense, power generation has increased over last few decades. Applications involving radioisotopes and radiations reveal a great promise particularly for the welfare of the society. However, very often, inadvertently the policy makers and others overlook the safety issues involved in use of nuclear tools [1]. One often forgets that radiations, emitted by any radioisotope although cannot be seen or felt, interact with matter and could alter the chemical, physical and biological nature of the matter and that living beings, globally, are always under exposure of some level of natural radiation [2]. Presence of radionuclides has been reported in the fly ash generated from the Thermal Power plants [1] and in the sludge from waste water treatment plants [3] which can very easily intercepted by crop plants [4].

Natural presence of gamma emitting radionuclides in agricultural crops and radiation effect on soil and humic acids has been reported [5, 6]. In the present scenario, when malnutrition among humans is prevalent, improving quantity as well as the quality of produce is a matter of

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paramount importance [7]. Some developing countries overcome malnutrition by distributing supplements to the population and/or fortifying food with nutrients. Another approach could be to develop biofortified crops which could serve as a cheaper and sustainable alternative [8], which calls for crop improvement. Gamma irradiation has also been shown to inhibit microbial growth and is widely used for preservation of food such as rice, wheat flour, pulse, gram, dry fruits, dry fish etc. In the United States, the Food and Drug Administration (FDA) has approved irradiation for eliminating insects from wheat, potatoes, spices, fruits and vegetables [9].

Gamma rays and their interaction with the biological system

Gamma rays belong to ionizing radiation and are the most energetic form of such Electromagnetic Radiation, having the energy level from around 10 kilo electron volts (keV) to several hundred keV. Therefore, they are more penetrating than other types of radiation such as alpha and beta rays [10]. Gamma radiation can be useful for the alteration of physiological characters [11].

Gamma ray interaction at the whole plant, tissue and at the cellular level

The biological effect of gamma-rays is based on the interaction with atoms or molecules in the cell, particularly water, to produce free radicals [10]. These radicals can damage or modify important components of plant cells and have been reported to affect differentially the morphology, anatomy, biochemistry and physiology of plants depending on the radiation dose [12]. Since radio sensitivity is related to cellular and metabolic activity, some relationship might be expected to exist between radio sensitivity and nutritional status. Gamma irradiation was shown to alter the physicochemical properties of nutrients and improved utilization of proteins and phosphorus from wheat bran at 0.5–5 Mrad [13].

Very low dose of ionizing radiation in wheat triggered germination and yielded uniform crop performance under field condition thus, suggesting that crop response to low dose gamma occurs essentially at physiological than at genetic level. Experiments conducted at NRL, IARI, New Delhi clearly reveal that low dose of gamma radiation holds promise for physiological improvement in wheat. Seeds treated with low dose gamma radiation 0.01–0.10 kGy reduce plant height; improve plant vigor, flag leaf area, total number of EBT [14]. Shinonaga et al. [15] used multitracers to show direct elemental absorption of radionuclides from the atmosphere by the soybean plants. In addition numerous biological applications involving stable and radionuclides such as tracing the radiation emission viz a viz isotope decay function was useful for studying plant root development [16] and transport of trace elements [17] or isotope discrimination as function of carbon and nitrogen fixation [18].

The irradiation of seeds with high doses of gamma rays was shown to disturbs the synthesis of protein, hormone balance, leaf gas-exchange, water exchange and enzyme activity [19]. Effects of radiation at plant level could be visualized at morphological, biochemical and physiological levels, where magnitude of the affected change depends heavily on the exposure dose. Considering the above data present study is to determine the effects of radiation on physiological and biochemical characteristics. However, study of the effects of radiation on plants is a broad and complex field but in this review we focused on effect of gamma irradiation on physico-chemical parameters.

Gamma irradiation for crop improvement

Genetic variability is essential for any crop improvement programme; therefore creation and management of genetic variability becomes central to crop breeding. Mutations are one of the important sources of genetic variability, which is ultimately utilized in the plant improvement program. In a prospective mutation breeding programme, in cereal crop, particularly wheat, a few major characters of direct interest should be:

- Improvement of grain yield.
- Increase in the number of ovules and carpel.
- Increase in the number of flowers per spikelets.
- Increase in the size and quality of kernels.
- Early flowering and maturity.
- Erect and dwarf plant type [9].

The use of mutagens in crop improvement helps to understand the mechanism of mutation induction and to quantify the frequency as well as the pattern of changes in different selected plants by mutagens. Mutation breeding generates a knowledge base that guides future users of mutation technology for crop improvements. Gamma irradiation has been used successfully to develop radio mutants in flowering plants and abiotic stress tolerant legume species [20].

Physiological changes induced by gamma irradiation

Physiological symptoms in a large range of plants exposed to gamma rays have been described by many researchers [10, 21–23]. The symptoms frequently observed in the low or high dose irradiated plants are enhancement or inhibition of germination, seedling growth, and other biological responses [23, 24]. The growth of *Arabidopsis* seedlings exposed to low-dose gamma rays (1 or 2 Gy) was slightly increased compared with that of the control, while the seedling growth was noticeably decreased by the high-dose irradiation of 50 Gy. Although no conclusive explanations for the stimulatory effects of low-dose gamma radiation are available until now in accordance to the results obtained by [25].

Gamma irradiation, i.e. use of ionizing radiations, can be potentially important to improve grain production and quality in wheat. Different doses of gamma irradiation can be used to alter the physiology, morphology, biochemistry and yield characteristics of wheat crop. Poor seed set, poor tillering and uneven filling of grains along the spike reduce quantitative yield in wheat. To improve yield, it is imperative to increase number of tillers per ear, leaf or photosynthetic area, number of grains per ear, leaf mass, total vegetative mass, plant vigour, stem thickness, and number of spikelets per spike etc. [26]. Singh et al. [27] suggested that the positive effect of low dose of gamma radiation on wheat plant growth due to impact on gas exchange characteristics and mineral nutrient uptake and utilization.

The wheat seeds irradiated with gamma at doses of 1,000–15,000 R and wheat plants irradiated with same dose at the stage of spike formation were used to compare the following plant and yield characteristics at harvest i.e. the seed yield, plant height, length of central spike, number of seeds in the central spike, weight of the seeds in the central spike, and absolute weight of 1,000 seeds. A decrease in plant height and an increase in yield were observed at irradiation doses of 5,000–15,000 R. The results clearly proved that gamma irradiation even at higher dose of 1,000–15,000 R can be successfully used to develop yield efficient wheat plant types. Wheat grains from irradiated plants were also rich in proteins and essential amino acids [28].

Germination and survival percentage

Seeds irradiated with low dose gamma radiation induce positive effect or no effect but the higher doses induce negative effect in germination rate and survival percentage in almost all plants. Irfaq and Nawab [29] observed that wheat cultivars Pirsabak-91 (P-91), Khyber-87 (K-87) and Tarnab-78 (T-78) irradiated with dose range 0–40 kR slightly delayed the germination with increase in radiation intensity while the survival rate adversely affected at all the doses. The results coincide with those of Matsumura [30], Horvat [31], Muhammad [32] who observed delay in germination in wheat species after treatment with gamma rays and X-rays. The same findings by Matsumura [30], Masayuki [33], Khan and Bari [34] and Chaudary [35] who advocated that increase in the radiation intensity is associated with the decrease in survival. A reduction percentage of seedling survival with an increasing gamma-ray dose was observed in the sunflower varieties of USH-430 and SHSF-333 as depicted by Kumar and Ratnam [36]. This was also observed by Ratnam et al. [37], Ahmed [38]; Jambulkhar and Joshua [39] in sunflower, Swaminathan and Gupta [40] in *Brassica campestris*, Khan [41] in mung bean and Cheema and Atta [42] in rice.

Growth and yield of plants

The commonly reported expressions of these efforts were more vigorous vegetative growth [43], early maturity [44] and higher yield [45]. Gamma rays are known to influence plant growth and development by inducing cytological, genetical, biochemical, physiological and morphogenetic changes in cells and tissues [46]. Significant positive effect of gamma irradiation at 0.15 kGy have been reported on growth and development of okra [47]. Chauhan et al. [48] found five high yielding mutants of six rowed barley M2 generation using 25 krad doses while Siddiqi et al. [49] found inhibitory effect on yield and yield components of barley and triticales with higher dose of gamma rays. Subhan et al. [50] observed that irradiation had positive effect on grain yield of barley with maximum production at 10 krads of gamma rays with variable level of nitrogen. Stimulatory effects of low dose irradiation of seeds have been reported by many investigators. Al-Ouadat and Razzouk [51], Chang Kum [52] reported that low γ-irradiation doses caused an increase in plant height, stimulating effects on earliness and increased total plant yield in tomato hybrids. However, El-Sayed et al. [53] found that 10 krad γ-rays increased plant height, yield, chlorophyll *a* and *b* and carotenoids in tomato hybrids.

In a classic study, wheat grains were irradiated with 150, 250, 350 and 450 Gy gamma rays and radiation effects was studied on the second generation. The study indicated a significant increase in growth characters like plant height, number of tillers per plant and yield, by 150 Gy of gamma irradiation. Number of spikes per plant, 1000 grain weight, grain yield per plant was increased [54]. Investigation clearly suggest that low dose of gamma irradiation 0.03–0.07 kGy can help in cereal crop improvement program. However further research is required to study the abiotic stress adaptability response of irradiated plants particularly in terms of their capacity to produce higher grain yields under stressful conditions. The conclusion of the present investigation will go along way in recommending use of gamma irradiation technique for agricultural applications.

Gamma ray for improved yield–dose dependence of the relationship

The growth of *Arabidopsis* seedlings exposed to low-dose gamma rays (1 or 2 Gy) was slightly increased compared with that of the control, while the seedling growth was noticeably decreased by the high-dose irradiation of 50 Gy. Although no conclusive explanations for the stimulatory effects of low-dose gamma radiation are available until now, papers support a hypothesis that the low-dose irradiation will induce the growth stimulation by changing the hormonal signaling network in plant cells or by increasing the antioxidative capacity of the cells to easily overcome daily stress factors such as fluctuations of light intensity and temperature in the growth condition [21]. In contrast, the growth inhibition induced by the high-dose irradiation has been attributed to the cell cycle arrest at G2/M phase during somatic cell division and/or various damages in the entire genome [55].

Gamma irradiation and grain quality

Gamma irradiation has important effects on the quality of cereal grains. Khattak and Klopfenstein [56] found that nutritional quality of cereal grain in terms of amino acid profile is altered upon irradiation. A similar study conducted by Srinivas et al. [57] showed that a high degree of autolysis in irradiated wheat is due to an increased susceptibility of proteins to protease action. The result of Mahdi et al. [58] who advocated gamma radiation as a viable procedure to improve the quality of broad bean from the nutritional point of view.

Research in the post decade has focused on the effect of gamma irradiation on various aspects of wheat quality such as milling characteristics, dough properties and baking quality. No apparent changes were observed in protein content of durum wheat grains irradiated at low or high dose levels [59]. In another study, wheat seeds were irradiated with gamma rays and the chemical composition of the seeds and the green mass was determined in terms of the total nitrogen, total protein, phosphorus, potassium, mineral residue and cellulose. The starch concentration decreased upon treatments, whereas proteins and total amino acids content increased in the irradiated wheat plants. The protein content was increased by 2–3 % in comparison with the non irradiated control at 15,000 R [28].

Gamma rays alter plant rhizosphere characteristics

Another important plant attribute of concern is the root induced chemical modifications of the rhizosphere which may be involved in the mobilization and exploitation of sparingly soluble source of nutrients especially P. Carboxylic acids like citric acids in root exudates are able to mobilize P. Significant amounts of soil P solubilisation due to carboxylic acids has been shown in cluster rooted plants and members of proteaceae etc. The production of root exudates is higher under stress. Changes in the rhizosphere can also be studied through use of isotopes and also the pattern of root release of exudates may change in relation to irradiation.

Gamma irradiation and post harvest storage and shelf life extension

Gamma irradiation has long been employed for decontamination and/or sterilization of dehydrated vegetables [60, 61], fruits [62–64] seasonings [65], and animal feed [66]. Gamma radiation was reported to be a good procedure to improve the quality of broad bean from the nutritional point of view [58].

Changes in physical and nutritional traits during storage

Irradiation causes the physicochemical changes and interferes with metabolic events thus resulting in an extended shelf life of the product and post-harvest preservation without compromising on their quality and safety [67]. A low dose (<1 kGy) controlling insects in grains and fruits, delays the ripening of some fruits/vegetables and improves their shelf life [68, 69]. Irradiation technology effective in reducing post-harvest losses, and controlling the stored product insects and the microorganisms. Due to the strong desire to reduce the use of chemicals applied to fruits and vegetables, the non-residual feature of ionizing radiation is an important advantage. Internationally, food irradiation has been considered a safe and effective technology by the World Health Organization (WHO), the Food and Agriculture Organization (FAO), and the International Atomic Energy Agency in Vienna [70]. For instance, gamma irradiation was employed to restrain potato sprouting, kill pests in grain, modify some ingredients, and bring about changes in the physical-chemistry and sensitization of food [71]. Gamma irradiation was shown to alter the physicochemical properties of nutrients and improved utilization of proteins and phosphorus from wheat bran at 0.5–5 Mrad [13].

Gamma irradiation and physiological and biochemical changes in horticultural produce

Basson et al. [72] found that for mango, irradiated with 1 kGy, the only compounds to undergo significant modifications are the sugars which account for nearly 99 % of the reactions. The other components which are slightly reactive are starch (0.2 %), protein (0.2 %), phenol (0.4 %), and ascorbic acid (0.2 %). Therefore, only carbohydrate degradation needs to be considered. Furthermore, carbohydrate reactivity tends to protect the other components from degradative changes. D'innocenzo and Lajolo [73] used irradiation treatment as an imposed stress to cause changes in firmness. Physiologically mature papaya fruits were irradiated (0.5 kGy) and allowed to ripen at 22 °C and 90 % RH. Irradiation caused a two-day delay on the onset of ripening time. The total soluble solids (°Brix) of both treated and control fruits, increased from 8 to 12 % and were not affected by irradiation.

A study was conducted on early and late season "Rio Red." Fruit was treated with 0, 0.07, 0.2, 0.4, and 0.7 kGy and then stored under 10 °C for 4 weeks followed by 1 week at 20 °C with 90–95 % relative humidity. It was demonstrated that irradiation doses of up to 0.7 kGy had no significant effect on the vitamin C content of early-season grapefruit. Late season fruit exposed to irradiation greater than or equal to 0.2 kGy caused a marked reduction in vitamin C content after 35 days of storage. Soluble solids (%) were not affected due to irradiation or storage of early-season fruit. On the other hand, late-season fruit had lower soluble solids (%) and acidity values than early-season fruit and the soluble solids/acid ratio after 35 days of storage were slightly higher than the initial ratios [74].

According to Assi et al. [75] mature green and pink tomato (*Lycopersicon esculentum* Mill.) fruit subjected to ionizing irradiation in the range of 0.7–2.2 kGy from gamma- or X-ray sources softened during post-irradiation storage (20 °C) but exhibited an apparently irreversible suppression in polygalacturonase activity, with levels remaining lower than 10 % of those of non-irradiated fruit. Polygalacturonase activity was less strongly affected in irradiated pink fruit than in mature-green fruit, but activity remained reduced relative to the controls. Pectin methylesterase and β-galactosidase activities were significantly enhanced in irradiated fruit of both ripening stages in the early period following irradiation, but reductions were noted after prolonged storage.

Wang et al. [76] measured and analyzed the enzyme activity in Golden Empress cantaloupe juice after ^{60}Co irradiation. Enzyme activity determination revealed that lipoxygenase was the easiest one to be inactivated by irradiation, followed by polyphenol oxidase and peroxidase. However, all three enzymes remained active even at 5 kGy. Fresh Tristar' strawberries were irradiated with electron beam irradiation at 0, 1, and 2 kGy. Fruit firmness decreased as irradiation dose increased. Water-soluble pectin increased and oxalate-soluble pectin decreased at 0 and 1 day after 1 and 2 kGy irradiation. Fruit firmness was correlated with oxalate soluble pectin content. Total pectin and non-extractable pectin were not affected by irradiation. The oxalate-soluble pectin content and firmness of irradiated strawberries increased slightly at the beginning of 2 °C storage and then decreased as storage time increased. No changes occurred in water-soluble pectin, non-extractable pectin, or total pectin during storage [63].

Susheela et al. [77] found no significant loss of sugar and ascorbic acid contents in three-quarter ripe and fully ripe pineapple fruit (*Ananas comosus*) irradiated at 0.15 kGy. Single-strength orange juice was exposed to 0, 0.89, 2.24, 4.23, and 8.71 kGy gamma radiation at 5 °C, and then stored at 23 °C for 6 days and 7 °C for 21 days. Both ascorbic acid (AA) and dehydroascorbic acid (DAA) concentrations decreased with increased radiation dose. Juice irradiated at all doses had lower AA and TAA content than non-irradiated juice. TAA loss following irradiation treatment was less than half that of AA. The conversion of AA to DHA was promoted by irradiation. Both the concentration and the percentage of DHA increased linearly with increased radiation dose. Irradiation did not alter the non- AA antioxidant activity [78]. Paull [79] reported that papaya fruits (*Curica papaya* L.) treated with 0.25 kGy of γ-irradiation frequently softened more uniformly than non-irradiated fruit. Fruit with less than 25 % of their surface colored yellow placed immediately into storage at 10 °C after irradiation developed skin scald. This was prevented by delaying storage by 12 h. Fruits that were irradiated when 30 % of the skin was yellowed softened at a slower rate than non-irradiated fruits. There was no difference in the softening rate between irradiated and non-irradiated fruits at the mature green stage. Fruit stored for 14 days at 10 °C before returning to 25 °C had a slightly slower rate of softening than fruit allowed ripening at 25 °C without storage. Premature flesh softening occurred occasionally in fruit that had between 8 and 18 % of the skin yellow and 70–90 % flesh coloring when irradiated.

Wang and Chao [80] investigated the irradiation effects on dehydration characteristics and quality of apples (Fuji apple). They found that the vitamin C content of apples, the dehydration rate, and the rehydration ratio were greatly affected by irradiation dose (1.5, 4.5, 5, and 6 kGy). It was shown that the greater the dose, the higher the dehydration rate, the less the vitamin C content, and the lower the rehydration ratio. Rubio et al. [81] studied the effects of irradiation (0.50, 0.75, and 1.00 kGy) on the vitamin C content of lettuce (*Lactuca sativa*), cabbage (*Brassica oleracea*), and celery (*Apium graveolens*). There was a marked difference in the natural total ascorbic acid content of the vegetables studied with cabbage showing the highest. Irradiation did not decrease these initial concentrations, and in the case of cabbage, it actually increased them. For lettuce, cabbage, and celery the initial ascorbic acid content was 2.357, 3.085, and 0.549 mg/100 g, respectively and after irradiation was 2.036, 5.018, and 0.616 mg/100 g, respectively irradiated with 1.00 kGy. According to Drake and Neven [82], irradiation can be applied to cherries, apricots, or peaches as a quarantine treatment at 0.3 kGy or less with little quality loss. Differences in stem condition and bruising were more evident for irradiated "Rainier" cherries than for methyl bromide (MeBr) treated "Rainier" cherries, but these differences were small. Use of irradiation resulted in some firmness loss, for "Bing" cherries when compared with MeBr, but irradiation treatment of cherries did not result in a loss of fruit and stem color, whereas the use of MeBr doses resulted in both fruit and stem color loss. Apricots ("Perfection" and "Rival") and peaches ("Regina") were tolerant to irradiation at 0.3 kGy with little quality loss. Loss of firmness, color changes, and increased internal breakdown were evident in both apricots and peaches at irradiation dose above 0.6 kGy. Drake et al. [83] found that titratable acidity (TA) of "Gala" apples was reduced at irradiation doses of 0.60 kGy and above. On the other hand no loss of TA due to the irradiation dose was evident, for "Fuji" or "Granny Smith" apples.

Vanamala et al. [84] exposed grapefruits (*Citrus paradise* c.v. Rio Red) to gamma irradiation at 0, 0.15, and 0.3 kGy and then stored at 10 °C for 36 days, followed by additional 20 days at 20 °C. Irradiation or storage did not result in considerable changes of the content of total soluble solids in grapefruits. However, there was a considerable decline in the acid content during storage. Fruits exposed to 0.3 kGy of irradiation had higher acidity compared to the control (0 Gy). Moreover, their results suggest that low-dose irradiation at 0.3 kGy enhanced or at least maintained the flavonoid content. Alonso et al. [85] found that X-ray irradiation doses of 0.195 and 0.395 kGy had minimal differences in juice yield between X-ray irradiated and cold-treated clementine mandarin fruits (*Citrus reticulate*), with no significant difference between the control and any irradiation treatment. Both acetaldehyde and ethanol contents of the irradiated fruit were higher along with both X-ray dosage and storage period (1.5 °C for 14 days). Fan and Sokorai [78] assessed the radiation sensitivity of fresh-cut vegetables using electrolyte leakage measurement. Fresh-cut vegetables were gamma irradiated at doses up to 3 kGy at 0.5 kGy intervals. Electrolyte leakage increased linearly with higher radiation dose for all vegetables. Red cabbage, broccoli, and endive had the highest radiation resistance while celery, carrot, and green onion were the most sensitive to radiation.

Sensory evaluation of gamma irradiated produce

The results of the sensory evaluation of carrot stored at room temperature for 3 days and 7 days indicated that irradiation with lower than 2.0 kGy had no significant effect on color, lightness, flavor, sweetness, odor, and taste. During storage, the overall acceptability of the control samples was not higher than the samples irradiated with doses below 2.0 kGy. The results of sensory evaluation of carrot stored at refrigerator temperature (4–7 °C) for 4 and 10 days indicated that color, lightness, odor, taste, sweetness, and flavor of samples irradiated with lower than 2.0 kGy (included 2.0 kGy) were not considerably different than those of the non-irradiated ones. The overall acceptability of samples irradiated with doses lower than 2.0 kGy was higher than that of the non-irradiated samples. Furthermore, color, taste, sweetness, and flavor of tomato stored at room temperature irradiated with doses higher than 1.0 kGy were significantly lower than control samples and in particular, taste and flavor. The overall acceptability of the non-irradiated samples was higher than that of the irradiated samples. Samples irradiated with doses above 2.0 kGy were not sensorially acceptable [86].

Landgraf et al. [87] examined the cubes of mango (*Mangifera indica*) cultivar Tommy Atkins were sensory accepted until day 4 when exposed to 1 kGy. This cultivar showed a better response to irradiation than the Haden cultivar. Pineapple (*Citrullus vulgaris*) and watermelon (*C. vulgaris*) in cubes exposed to 1 and 2.5 kGy irradiation were sensorially acceptable. Irradiation did not affect the watermelon sweetness or pineapple sourness. An increase in the ascorbic acid content with increasing dose from 0.03 to 0.18 kGy was observed in a study by Nandpuri et al. [88] while, according to Salems [89], a 18 % reduction of ascorbic acid was reported by 0.08 kGy irradiation. In a study on onion cultivars of Hungary, no significant differences in the vitamin C content of irradiated and non-irradiated samples were observed during a 10-month storage period and the vitamin C content of the irradiated samples seemed not to be influenced by the time of irradiation after harvest [90]. On the contrary, Guo et al. [60] reported a drastic reduction in the vitamin C content of onions immediately after irradiation at 0.1–0.5 kGy. However, the decrease in vitamin C during the remaining 8 months storage was much lower in irradiated than in control onions.

Regarding potatoes there have been many results reported in the literature on the effect of irradiation on sugar content of potatoes during storage [91, 92]. Pre-storage of potatoes for 4 weeks at 2–15.5 °C prior to irradiation to 0.1 kGy affected the sugar content during post irradiation storage. Pre-irradiation storage of tubers showed a marked temporary increase in sucrose, reaching a maximum after 3–7 days before decreasing to a level which was still higher than that of the non-irradiated tubers. Tubers stored at 2 °C exhibited an immediate decrease in sucrose after irradiation, followed within

3 days by a rise to values not significantly different from the controls [93]. A comparison of sugar changes in 0.1 kGy treated potatoes during storage at 14 °C and in non-irradiated potatoes at 4–5 °C for 6 months storage showed a 50 % lower content of reducing and total sugars as well as 15 % greater starch content in the irradiated tubers than in controls [94] cultivars revealed that sugar accumulation in non-irradiated tubers stored at 2–4 °C progressed at a more rapid rate than in irradiated tubers at 15 °C during a 6 month storage period [95]. Adesuyi and Mackenzie [96] reported that in yam tubers (*Dioscorea rotundata*) starch levels were almost identical in control and 0.15 kGy treated tubers after a storage period of 5 months under normal conditions (25–37 °C; RH 50–85 %). A decrease in starch level was recorded in tubers irradiated to 0.1 and 0.125 kGy but those exposed to 0.025, 0.05, and 0.075 kGy displayed higher starch content than 0.1 and 0.125 kGy treated samples.

Several workers have studied the stability of vitamin in potatoes irradiated for sprout inhibition purposes. Irradiation with 0.07–1.0 kGy, 2 weeks after harvest, had no effect on vitamin C [97]. In another study, no immediate change in vitamin C content was observed after exposure to 0.1–1.0 kGy whereas after one week the levels decreased in proportion to the increasing dose [98]. An immediate oxidation of vitamin C was observed following irradiation at 0.1 kGy but the difference in content between the irradiated and the non-irradiated tubers disappeared on prolonged storage [99]. Irradiated tubers stored at 15 °C recorded higher levels of ascorbic acid as compared to controls stored at 2–4 °C for identical periods [95, 100].

Studies with nine Indian potato cultivars displayed that irradiation at 0.1 kGy resulted in decreased levels of carotenoids in the tuber flesh, particularly at 15 °C where 50 % reduction in its content occurred after 6 months storage. A partial recovery of the carotenoids content occurred when such tubers were reconditioned at 34–35 °C for 6–12 days [101]. In the Indian potato cultivar, up-to-date, aspartic acid, asparagine, threonine, serine, alanine, isoleucine, leucine, lysine, and arginine displayed an increase in 24 h after irradiation at 0.1 kGy, while glutamic acid, proline, methionine, and phenylalanine decreased. The lysine content displayed a six-fold increase after 1 week storage, and at 1 month the concentration was still three times higher than the control values [102]. Exposure of potatoes to 0.07–0.1 kGy doses 2 weeks after harvesting or later did not appreciably affect the nitrogenous substances except during the initial storage period when some of the non-protein nitrogen increased at the expense of decomposition of protein nitrogen. With prolonged storage, protein nitrogen and non-protein nitrogen were found to be equal in irradiated and control tubers [97].

Although irradiation at 0.1 kGy had no effect on the total sulfur and thiosulfonate content of garlic bulbs during storage at 3 ± 1 °C and 80 ± 5 % RH for 10 months, the contents of both components exhibited a significant reduction in control and irradiated after 6–8 months storage compared to initial values [103]. Similarly, no appreciable changes were detected in either gas liquid chromatograms or visible and infra-red spectrographs of ether extracts of "red" garlic bulbs irradiated with 0.05 kGy and stored in a commercial warehouse (6–32 °C, RH 58–86 %) for 6 months [104]. A Canadian study revealed that the total weight loss due to sprouting and shrinkage of onion bulbs irradiated with 0.06 and 0.076 kGy was 5.7 % as against 23.2 % for the non-irradiated bulbs after 5 months storage at 12.8 °C [105]. In the cv "Valenciana Sint′etica 14" grown in Argentina, the weight loss at the end of a 270 day test storage in a commercial warehouse (6–32 °C, RH 50–90 %) was found to be 43.3 % in the control as against only 22.8 % in 0.03 kGy treated samples [106]. In a pilot-scale study conducted in India the weight losses due to dehydration after 4.5 months storage at ambient temperature under commercial conditions (23–32 °C, RH 60–80 %) was 15.2 % in irradiated (0.06 kGy) samples as against 27.7 % in non-irradiated bulbs [100]. In the garlic bulb cv "Red" the weight losses amounted to 55 and 24 % in the control and irradiated (0.03 kGy); respectively at the end of 300 days storage at 6–32 °C, RH 58–86 % [106].

Gamma irradiation and biomolecule dynamics

Gamma irradiation (Co-60 rays) in the range up to 30 kGy produced a decrease in wheat starch concentration [107]. Large gamma doses increase the quantity of reducing sugars but decrease the starch content [108]. In a separate study, seedlings produced from wheat grains irradiated at 800 Krad had a higher dry matter, protein and RNA content. Effect of gibberellin and gamma irradiation on wheat was studied by [109]. After exposing large doses of gamma rays, wheat seeds were sowed with solution of gibberellic acid. This research group suggested that gibberellin stimulates growth of irradiated plants more, than non irradiated control plant by means of increased cell expansion, cell division or both [109]. In photosynthetic organisms, carotenoids play a vital role in the photosynthetic reaction center [110]. Three centimeter apical leaf tips excised from 7 day old seedlings of wheat (*Triticum aestivum*) were irradiated by Patricia et al. [111]. Even a high dose of 1 Mrad of gamma irradiation produced no apparent affect on chlorophyll content [111]. Wheat, maize, chickpea, and mung bean seeds irradiated at 0.5, 1.0, 2.5 and 5.0 kGy were compared for their amino acid profiles. Their results showed that sulphur containing amino acids like cysteine and methionine were radiation labile, particularly in the legumes [54].

Gamma rays influence the plastid development and function, such as starch sugar inter-conversion. Gamma rays penetrate through the cells [59]. The effect of gamma rays on growth and cellular contents of soluble carbohydrates, protein and nucleic acids in sunflower were investigated by Mobashar and Yousif [112]. They found a significant increase in protein, carbohydrate and DNA but a significant reduction in RNA content in irradiated treatments [112]. Gamma treated plants showed significant increase in potassium, phosphorus, cellulose and total nitrogen [28]. Studies on the susceptibility of irradiated wheat starch revealed that irradiated plants constituents are more susceptible to enzyme actions, compared to their non- irradiated controls. Maltose was found to be the chief radiolytic breakdown product of starch at high dose of 1 Mrad [110]. Various gamma irradiation doses applied on the wheat plants showed a significant increase in micronutrients (Cu, Mn, Zn, and Fe) concentration upon gamma irradiation treatment, as compared to non irradiated control [113]. Initial reducing sugars were increased in irradiated wheat at dose level in the range 20–200 Krad. Both α and β-amylases retain their activities in irradiated wheat, but the sensitivities of starch to amylolysis is increased with radiation dose levels [110]. Potassium is one of the important plant nutrients and involved in regulating many physiological processes, potassium's impact on water relations, photosynthesis and enzyme activation can have direct consequences on crop productivity [114].

Ionizing radiation induced changes in chloroplast structure and function

Based on transmission electron microscope observations, chloroplasts were extremely sensitive to gamma radiation compared to other cell organelles, particularly thylakoids being heavily swollen [25]. These effects include changes in the plant cellular structure and metabolism e.g., dilation of thylakoid membranes, alteration in photosynthesis, modulation of the anti-oxidative system, and accumulation of phenolic compounds [10, 21, 25, 115]. High intensity gamma was shown to affect the quality of reducing sugar and starch content [108], so also the organic pigments i.e., carotenoids which occur naturally in chloroplasts of plants and absorb light energy for use in photosynthesis and are responsible for protecting chlorophyll from photo-damage and thereby are linked in metabolic functions.

Gamma irradiation and leaf pigments

The biological effect of gamma rays is based on the interaction with atoms or molecules in the cell, particularly water to produce free radicals, which can damage different important compounds of the plant cell. Plant types developed from seeds irradiated with cesium-137 gamma rays, at a dose rate of 4 Gray and dose intensity of 2 Gy/min, had higher vigour productivity and the photosynthetic pigments. Chl-*a*, Chl-*b* and carotenoids concentration in irradiated plants were high as compared to non irradiated control. High intensity gamma dose can also affect the quality of reducing sugar and starch contents [108]. Carotenoids are organic pigments that are naturally occurring in chromoplast of plants and some other photosynthetic organisms like algae, some types of fungi. Carotenoids absorb light energy for use in photosynthesis and they protect chlorophyll from photo-damage. Gamma rays affect pigments and thereby they are linked in metabolic functions. Gamma irradiation also affects rooting characteristics and thus the uptake of macronutrients (N, P, and K) and micronutrient (Fe, Mn, Zn, and Cu) [111].

Kiong et al. [11] reported that the reduction in chlorophyll *b* is due to a more selective destruction of chlorophyll *b* biosynthesis or degradation of chlorophyll *b* precursors. Furthermore, Kim et al. [21] have evaluated the chlorophyll content on irradiated red pepper plants; their results showed that plants exposed at 16 Gy may have some significant increase in their chlorophyll content that can be correlated with stimulated growth. Modulation in photosynthesis in irradiated plants might partly contribute to increased growth [21, 25]. Borzouei et al. [116] studied that, the chlorophyll content of gamma irradiated wheat displayed a gradual decrease at 200 Gy dose. In addition, it can be observed that the concentration of chlorophyll *a* was relatively higher than chlorophyll *b* in irradiated and non-irradiated plants. Singh and Datta [14] studied the response of different okra genotypes to gamma irradiation on chlorophyll and concluded that higher doses most effective to produce chlorophyll mutation.

Gamma irradiation and oxidative damage

Gamma radiation was reported to induce oxidative stress with overproduction of reactive oxygen species (ROS) such as superoxide radicals, hydroxyl radicals and hydrogen peroxide, which react rapidly with almost all structural and functional organic molecules, including proteins, lipids and nucleic acids causing disturbance of cellular metabolism [115, 117, 118]. To avoid oxidative damage, plants have evolved various protective mechanisms to counteract the effects of reactive oxygen species in cellular compartments

[11]. This defense was brought about by alteration in the pattern of gene expression. This led to modulation of certain metabolic and defensive pathways.

Azim et al. [119] studied the effect of gamma irradiation (0.0, 2.0 kGy) on moisture, protein, oil, fiber, carbohydrates and ash minerals content of groundnut seeds. No consistent pattern observed on protein, oil, fiber, carbohydrates and minerals content of groundnut seeds, however caused significant decrease (*P*# 0.05) in iodine value and significant increase in acid and peroxide values of two cultivars (Sodari and Madani), with exception of the acid value of Madani cultivar. While saponification value, refractive index and viscosity of groundnut oil for both cultivars were not affected significantly. Similar findings were obtained by Zeb and Ahmed [120] who reported that, the iodine value of sunflower and soybean oil decreased significantly with high gamma radiation (1, 5 and 20 kGys) while the acid values were increased. The decrease in iodine value may be attributed to the saturation of the double of unsaturated fatty acids bonds [121]. For saponification value, refractive index and relative viscosity, no change was observed between the irradiated and non-irradiated samples. This finding agreed with that reported by Zeb and Ahmed [120].

An increased radio sensitivity of starch to amylolysis [109] could cause a decline in starch concentration of irradiated to non-irradiated grains. Gamma radiation reduced the phytic acid and tannin content significantly while significantly increase in globulins, prolamins and glutelins in sorghum at 2 kGy treatment reported by Hassanein [122]. Singh and Datta [14] observed a decline in grain starch but grain protein, carotenoid and nucleic acid contents increased in irradiated grains when compared with non-irradiated sourced grains. The observed decrease in grain starch could be due to a poor rate of conversion of sucrose, the prominent transportable sugar into starch. These results find support from the findings of Mashev et al. [123] and Coksel et al. [124], who observed an increase in protein concentration even up to 0.15 kGy dose of gamma radiation, but contradict partly the findings of Maity et al. [125], who found a decrease in total nucleic acid at a radiation dose of 1 and 20 kGy, however even there, at lowest dose of 0.5 kGy, nucleic acid level.

Antioxidative characteristics and antinutritional factors

There is a hypothesis that the low dose irradiation will induce the growth stimulation by changing the hormonal signaling network in plant cells or by increasing the anti oxidative capacity of the cells to easily overcome daily stress factors such as fluctuations of light intensity and temperature in the growth condition [25]. Irradiation can influence the levels of antioxidants/phytochemicals and the capacity of a specific plant to produce them at different levels. It has been reported that under certain favorable conditions, the concentration of plant phytochemicals might be enhanced. These conditions include exposure to radiation sources, wounding, storage at low temperatures, and/or exposure to extreme temperatures [126]. Schindler et al. [127] reported that the gamma-irradiation treatment (2, 4, and 6 kGy) markedly reduced the concentration of the phenolic compounds like p-hydroxybenzaldehyde, p-coumaric acid, ferulic acid, rutin, naringenin in tomato. Treatment of soybean seeds with irradiation, alone or in combination with soaking has been shown to reduce the level of phytates compared with the non-irradiated control [128]. Duodu et al. [129] reported that cooking did not decrease phytic acid in sorghum porridge, but the combination of cooking and irradiation (1 kGy) resulted in a significant decrease (40 %).

The radiation sensitivity was not necessarily correlated with endogenous antioxidant capacity or phenolics content of the vegetables, which displayed large variation among the test samples. Song et al. [130] investigated carrot and kale juice during a three-day storage period (10 °C). They reported that the total phenolic contents of both vegetable juices were significantly higher in the irradiated (3 kGy) samples than in the nonirradiated control. The antioxidant capacity of the irradiated carrot juice was higher than that of the non-irradiated control. On the other hand, over the storage period, the antioxidant capacity decreased in spite of increase in the phenolic content of the kale juice.

Wang and Du [131] found that the vitamin C content, and the rehydration ratio of dried potato was greatly affected by the irradiation dose (2, 4, 5, 6, 8, or 10 kGy). They claimed that the greater the dose, the lower the vitamin C content and the rehydration ratio. The effects of cooking followed by irradiation (10 kGy) on vitamins B1 and C, and the antinutritional factors, phytic acid and nitrates, in a ready-to-eat meal of sorghum porridge and spinach-based relish were investigated by Duodu et al. [129]. Cooking reduced vitamin B1 and C contents of the spinach relish, and irradiation caused further losses. Cooking did not alter vitamin B1 content (0.28 mg g^{-1}) of the sorghum porridge but irradiation decreased it drastically (0.04 mg g^{-1}). Cooking did not decrease phytic acid in the sorghum porridge whereas irradiation caused a significant decrease. According to Mohacsi-Farkas et al. [132] a radiation dose of 1 kGy had no significant effect on total carotenoid and vitamin C content of sliced tomatoes (*Lycopersicon syn. L. esculentum*). However, this dose caused approximately 40 % decrease in α-tocopherol. Bandekar et al. [133] studied the effect of radiation processing on vitamin C, total carotenoids, texture, and organoleptic properties of carrot and cucumber. No significant difference in the vitamin C content and total carotenoids in the radiation processed (1 and 2 kGy) samples and control samples was reported. Variation in the content of vitamin C and carotenoids during storage was not statistically significant from the control samples. The trained test panel could not differentiate between the irradiated and the non-irradiated samples. In general, no substantial effect of irradiation on the sugar content of onions was observed [100, 134, 135]. Furthermore, gas chromatography of silylated extracts displayed no changes in the levels of glucose, fructose, or malic acid in four onion cultivars grown in Germany when irradiated with 10 MeV electrons at doses of 0.05 or 0.10 kGy and stored at 10 or 20 °C. The sucrose level was about 2.2 % of fresh weight at the beginning of the storage period and declined to 1.5 % in irradiated as well as non-irradiated bulbs [134, 136, 137]. The vitamin C content in three onion cultivars grown in Israel following irradiation to 0.07 kGy and 5 months storage at ambient temperature was essentially the same as in the nonirradiated controls [138].

Radiation protection strategies in plants

One of the protective mechanisms in the synthesis of osmolytes which is essential to plant growth was proline synthesis [139]. Al-Rumaih and Al-Rumaih [117] revealed that increase in proline content was observed in irradiated plants. There was a convincing evidence which showed that the osmolyte synthesis such as proline involved in protective mechanisms were altered with several environmental stresses, including gamma irradiation. Proline is a compatible osmolyte and it may interact with enzymes to preserve enzyme structure and activities. Indeed, proline has been shown in—vitro to reduce enzyme denaturations caused due to heat, NaCl stress, gamma stress, etc. [140, 141]. Proline contents of gamma irradiated seedlings showed a slight increase as the gamma doses increased. However, Falahti et al. [142] contradicted this statement by proposing that the radiation may have promoted the level of antioxidants and consequently there would be no need for extra amount of proline to cope with the same problem of oxidative reagents.

Sattar et al. [128] on the contrary, reported a loss of nutritive value of irradiated proteins. However, their investigations were carried out at sufficiently higher irradiation doses, i.e. up to 5 kGy. They found that sulphur containing amino acids was radiation tolerant and lysine content of irradiated legume seeds was higher.

Dissecting the radiation–plant relationship at molecular level

A previously developed high vigour breeding line "Vigour 18" was used to establish a large recombinant inbred family and framework map to identify a QTL on chromosome 6A that accounted for up to 8 % of the variation for coleoptile length, 14 % of seedling leaf width and was associated with increased plant height. The SSR marker NW 3106, nearest to the 6A QTL was also associated with greater leaf width in a breeding population. The Vigour 18 allele of the QTL on chromosome 6A promoted coleoptile length and leaf width during early plant growth but was also associated with increased plant height at maturity [143]. It would be interesting to record, if the above SSR marker can be used to deduce genetic pathway of leaf size and leaf area increase as observed in irradiated wheat plants in some earlier studies as well as in the present study. Din et al. [144] studied the effect of gamma irradiation on different wheat varieties at seed irradiation dose of 10, 20, 30 and 35 Krad. A higher dose of 30 and 35 Krad created some abnormalities in plant types for example, a tiller having two ears attached with each and/or prevalence of sterile ears etc. [144].

Conclusion

It can be safely concluded that gamma rays have immense potential for various agricultural applications as evidenced from their interaction at crop, plant, tissue and cellular level. Gamma radiation does interact with the biomolecules in the plant via reduced production, in vivo immobilization or degradation, thus may cause a reduction or an increase in the level of respective molecules and lead to apparent morphological and physiological changes to impact growth, vigor and yield of plants and even on stored agri-produce. There are still gaps in our knowledge, uncertainty and lack of information on the radiation dose–effect relationship for different crops and agri-applications. Behavior of radionuclide's, the source of gamma radiation in soils, uptake into plants, accumulation in economic harvest and transport in and across an ecological region and meteorological factors affecting the same. Variability of environments, crops, soil and agricultural practices make the assessment further complex and challenging. In order to develop a framework for the assessment of the impact of radiation on agriculture, it is, therefore, imperative to establish the relationship between exposure and the effect that may be induced in crop plant that may hit agriculture to an unperceived extent.

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