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Carbohydrate metabolism in ripening banana and its alteration on gamma irradiation in relation to delay in ripening

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Abstract

Ripening, of climacteric class of fruits like banana, is accompanied with an upsurge in respiration, indicating a change in metabolism from hexose monophosphate shunt pathway to glycolytic pathway. The key enzyme in glycolytic pathway, namely, phosphofructokinase, is activated and this activation paralleled with the increase in respiration rate. The enhancement in the activity of enzymes of glycolytic and Kreb's cycle help the fruit to assimilate energy as ATP produced from the breakdown and oxidation of storage starch. The demand for energy supply is great for the different ripening processes.

Gamma irradiation of the fruit at the preclimacteric stage delayed the onset of climacteric to about 7 to 8 days, thereby extending the ripening to 15–20 days. This delay was brought about by the alterations in the metabolism of carbohydrate. There is a predominance of HMP pathway in irradiated banana. This along with the activation of phosphatases like FDPase and F-6-Pase restricted the entrance of sugar phosphate esters to Kreb's cycle for oxidation. The functioning of Kreb's cycle is also affected by the inhibition of succinic dehydrogenase. But activation of glyoxylate shunt pathway helped to maintain the levels of Kreb's cycle intermediates like citrate and malate, although energy production is reduced. Finally the activation of gluconeogenic pathway helps in channelling the metabolities back to sugars. All these metabolic changes cause a considerable depletion in the production of ATP.

Key words : Banana, *Musa Cavendishii*, Carbohydrate metabolism in ripening, Gamma irradiation, delay in ripening, regulation of carbohydrate metabolism, glyoxylate pathway, gluconeogenesis.

1. Introduction

The biochemical mechanisms involved in the ripening of fruits are not well understood, although a huge amount of work is reported on this subject[1]. There are a number of excellent reviews dealing with this subject, which will provide an up-to-date knowledge on the recent developments in different aspects of fruit ripening[2–4]. Ripeness is a stage when the fruit is best for eating. Ripening is a sequential phase in the life of the fruit and there are diversified views about the mechanism of the process. The two major

concepts developed to explain the mechanism of ripening are: (i) It results from a progressive increase in cell permeability, leading to increased contact between enzymes and substrates already present in the tissue[5-7]. (ii) It is a differentiation process under genetic control and involves the programmed synthesis of specific enzymes[8-10]. During the ripening phase there is an enhancement of a variety of metabolic activities[11]. Based on their metabolic activity, Biale[12] has classified fruits into two major groups, climacteric and non-climacteric. Banana belongs to climacteric class of fruits, which exhibits a typical respiratory pattern during the ripening after harvest. The exact reason for this marked increase in the respiration rate during the climacteric is not yet well understood, although several mechanisms have been proposed to explain this phenomenon[13]. Detailed information on the physiology and biochemistry of ripening of banana is available from the monograph by Loescke[14], Simmonds[15], Tai[17] and Hulme[1]. Hence the present review is devoted to elaborate a more specific aspect, *viz.*, the metabolism of carbohydrate in ripening banana and also on the recent studies on the effect of gamma irradiation on this metabolic process.

2. Carbohydrate metabolism in ripening banana

2.1. *Overall changes during ripening*

There are a number of biochemical processes associated with the upsurge in respiration. The noticeable changes taking place are : (*a*) change of colour from green to yellow or red, due to breakdown of chlorophyll, (*b*) breakdown of starch, hemicellulose and pectic substances resulting in softness of the tissue, (*c*) production of ethylene concomitant with increase in respiration rate, (*d*) conversion of unpolymerized tannis to polymerized ones which removes the astringency, (*e*) production of volatiles imparting characteristic flavour of the fruit. Out of these processes the breakdown of starch and its further metabolism is an important event in the ripening process, because it provides the input of energy needed for the synthesis of various compounds characteristic for each fruit, like volatiles, pigments, organic acids, etc.

2.2. *Metabolism of starch*

Banana is a starchy fruit and carbohydrates play an important role in structural appearance and textural behaviour of the fruit. As the fruit ripens the most striking change is the decrease in the concentration of starch due to its hydrolysis and accumulation of sugars and other metabolic products. The degradation of starch takes place by two mechanisms. It can be performed by amylases or phosphorylase. Amylases α- and β-hydrolyse starch to maltose units by acting at α 1,4-linkages while phosphorylases reversibly transfer a glucose residue from starch molecule to phosphate conserving most of the glycosidic bond energy. The biochemical mechanism of activation of amylase or phosphorylase in ripening fruit is not clear at present. But there is evidence that in mangoes the increase in activity is rendered by the degradation of natural inhibitor during ripening[14].

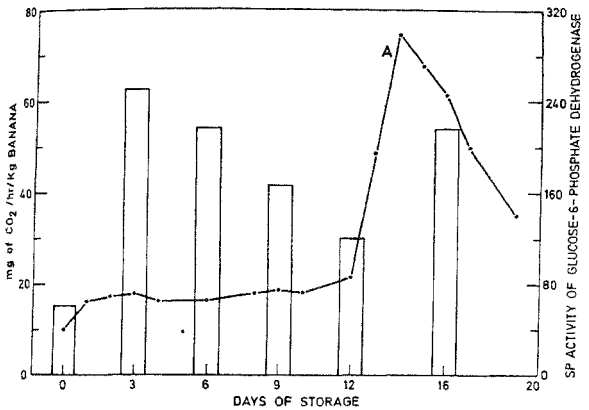

FIG. 1. Changes in glucose-6-phosphate dehydrogenase activity at different stages of ripening of bananas. (A = respiration).

2.3. *Pathways for carbohydrate metabolism*

Starch is the source of energy in the ripening fruit. The major pathways involved in its metabolism are glycolytic pathway (E M P pathway), which provides large amount of energy, and hexose monophosphate shunt pathway responsible for providing a number of intermediates for biosynthetic pathways. Tager and Biale[15] have demonstrated that during climacteric a shift occurred from HMP pathway to EMP pathway. In the unripe banana HMP pathway will be predominant over the EMP pathway. Surendaranthan and Nair[16] have verified this by determining the activity of glucose-6-phosphate dehydrogenase, the first enzyme of HMP pathway. There was a close relationship between the fall in G-6-P dehydrogenase activity and the increase in respiratory climacteric in ripening bananas (Fig. 1). As the ripening progressed G-6-P dehydrogenase activity declined. The level of this activity dropped to a minimum at 9–12 days at the initiation of climacteric upsurge in respiration. This observation supported the suggestion of Tager and Biale[15] that there is a shift from the pentose phosphate pathway to glycolytic pathway in ripening bananas.

For the enhanced functioning of glycolytic pathway a necessary prerequirement is the activation of key regulatory enzyme phosphofructokinase (PFK). Studies by Barker and Solomas[17] demonstrated the increase in fructose 1,6, diphosphate (FDP) concentration paralleling the respiratory climacteric raise. Later studies by Salminen and Young[18] on bananas after induction of ripening with ethylene showed that the increase

Table I

Concentration of various glycolytic cycle intermediates at different stages of ripening of banana

Intermediate	*n* moles/gm dry weight				
	0 day	6th day	12th day	15th day	19th day
1. Glucose-6-phosphate	340	354	411	614	200
2. Fructose-6-phosphate	243	235	201	427	91
3. Fructose, 1,6-diphosphate	9	10	84	162	50
4. Triose phosphate	83	85	112	302	200
5. Phosphoenolpyruvate	154	163	230	507	253
6. Pyruvate	141	152	293	429	307

in the level of PFK corresponded well with the upsurge in respiration and FDP content. A determination of the concentration of glycolytic intermediates at different stages of ripening will illustrate this fact more clearly (Table I). At preclimacteric stage *i.e.* up to 6th day, the concentration of all intermediates did not change from the initial value and the concentration of FDP was the least among the other intermediates. As the fruit reached climacteric the FDP concentration also increased to 18-fold when the respiration rate was also maximum. A cross-over plot determines the control sites in a pathway; such a plot on the above data from the first day of harvest to the 12th day of climacteric-exhibited regulatory site is at PFK level (Fig. 2). A recent study by Nair and Darak[19] gave evidence for the activation of PFK in the ripening bananas. The increase in the level of FDP in the ripening bananas at climacteric stage is attributed to the activation of PFK rather than *de novo* synthesis of the enzyme. This activation may be due to a conformational change in the subunit structure or due to changes in the amount and availability of enzymic effectors, thus altering the kinetic properties. Tager and Biale[15] found that both fructose 1,6, diphosphate aldolase and pyruvic acid decarboxylase showed very low activity in preclimacteric bananas but enhanced activities were observed during climacteric. The major regulatory steps in carbohydrate metabolism were identified at phosphoenol pyruvate/pyruvate level and F-6-P/FDP level.

2.4. *Organic acid metabolism*

The increased respiration rate observed during the climacteric is a result of increased oxidation of carbohydrates, obtained from the breakdown of starch through the Kreb's cycle. The organic acids are important source of energy and also contribute to the

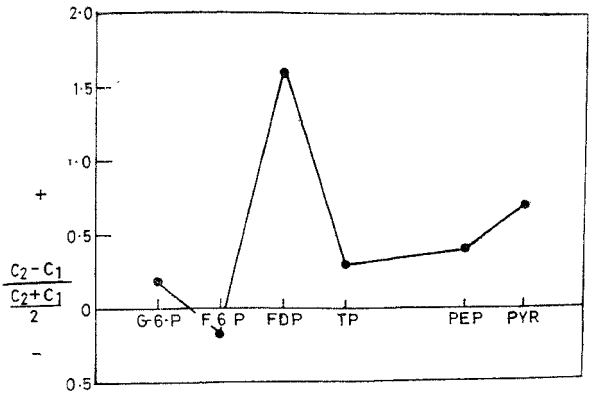

FIG. 2. Cross over plot for glycolytic intermediates from 0 to 12th day. C_1 concentration of intermediate on 0 day and C_2 are the same on 12th day.

flavour of the fruit. The changes in the organic acids of banana show a decreasing trend during maturation of the fruit[20] and then a sharp increase as the ripening is initiated[21]. Almost all the TCA cycle intermediates are present in banana fruit. Some organic acids like isocitrate are present in traces while others like melate and citrate accumulate in large amounts. An increase in pyruvic, α-ketoglutaric and oxaloacetic acids in ripening bananas was reported by Barker and Solomas[17]. Wyman and Palmer[22] while determining the organic acid content of the fruit failed to identify isocitrate and fumarate in banana. Steward *et al*[23] could identify about 22 organic acids in banana along with prominent keto acids like α-ketoglutarate, glyoxylate, oxaloacetate, succinic-semialdehyde.

Organic acids have an important place in general metabolism. The main pathway for the metabolism of organic acids are the respiratory oxidation, and carboxylation and decarboxylation reactions. But specific reactions may be involved for individual acids of the fruit. Numerous reports are available on the enzymes of respiratory pathways of banana. Tager[24] and Hultin[25] could successfully isolate active mitochondria from ripening banana which were efficient in the oxidation of TCA cycle intermediates. Succinic oxidase was found to have increased during climacteric raise in respiration[22]. Kreb's cycle enzymes have also showed marked changes during the climacteric. The climacteric is accompanied by the enhanced activation of malic enzyme and pyruvic carboxylase. This increase occurred both in the peel and pulp. More activity was in the peel tissue. After the climacteric the activities of these enzymes

Table II

Utilization of glucose-6-^{14}C and glucose-1-^{14}C by unirradiated and irradiated banana

Sample	CO_2 liberated				$^{14}CO_2$ (G–6–^{14}C) / $^{14}CO_2$ (G–1–^{14}C)	Incorporation into fructose —cpm/50 μl extract	
	Cpm		Sp. activity				
	G–6–^{14}C	C–1–^{14}C	C–6–^{14}C	C–1–^{14}C		G–6–^{14}C	G–1–^{14}C
Unirradiated	5596 ± 56	9200 ± 73	2087 ± 42	2921 ± 37	0·71 ± 0·026	1161 ± 87	1713 ± 35
Irradiated	1260 ± 39	5707 ± 49	311 ± 27	824 ± 27	0·31 ± 0·011	2006 ± 41	1027 ± 18

Values given are mean ± S.E. Experimental details are described in Surendranathan and Nair[18].

decrease in a parallel manner[8]. These studies explained the observed change in respiratory quotient during the ripening. Although several studies have been carried out on the metabolic pathways in ripening banana fruit, more is to be known about the intracellular distribution, function and regulation of multiple enzyme systems and their interdependence on highly coordinated cellular metabolism. Such an attempt is made in the latter part of this review, to illustrate our recent studies on the alterations in carbohydrate metabolism in ripening banana. We aim with the following studies to give a plausible explanation for the radiation-induced delay in ripening in banana.

3. Delay of ripening of bananas by ionizing radiation

3.1. *Irradiation technology*

We do not wish to go into the details of the technological, wholesomeness and economical aspects of gamma irradiation process for the preservation of bananas and other climacteric fruits. A number of extensive reviews are available covering these aspects[27–32]. Some salient points which emerged from the studies on irradiation preservation of banana are: (*a*) The shelf-life of the fruit increases to about 15 days when the fruits are stored at 20° C[33]. (*b*) In the case of banana, irradiation has proved effective only when fruits are irradiated at preclimacteric stage[33]. (*c*) The physiological state of the fruit including variety, maturity are most important criteria for selecting the dose for gamma irradiation[33]. If the maturity of the fruits is higher, the total delay obtained is reduced. (*d*) Doses higher than threshold dose for each variety caused damage to the fruit which is manifested as browning of the skin on storage and cracking of the fruit[34]. (*e*) Irradiation does not affect the nutritionally important constituents and when ripened the fruits retain the original flavour, texture, and colour[31]. While these technological aspects are thoroughly investigated, till recently due attention has not been paid towards the understanding of biochemical mechanisms involved in the delay of ripening of bananas.

3.2. *Effect of gamma irradiation on carbohydrate metabolism*

Gamma irradiation of bananas at preclimacteric stage delay the ripening process, thereby extending the onset of climacteric for seven to eight days[33]. Since ripening process required energy in the form of ATP derived from the complete oxidation of carbohydrate, a comparitive study on the changes in carbohydrate metabolism was initiated with an idea that it may give an insight into the mechanism of delay in ripening. These studies were restricted to changes at preclimacteric level, *i.e.*, only up to 7–8 days after harvest. After this period strict comparison cannot be made with unirradiated sample because climacteric induced changes are also discernible in these fruits.

In bananas, during ripening there is change from hexose monophosphate pathway to glycolytic pathway. Therefore, the studies were initiated by assessing the status of glycolytic and HMP pathways by determining the utilization of 1-^{14}C-glucose and 6-

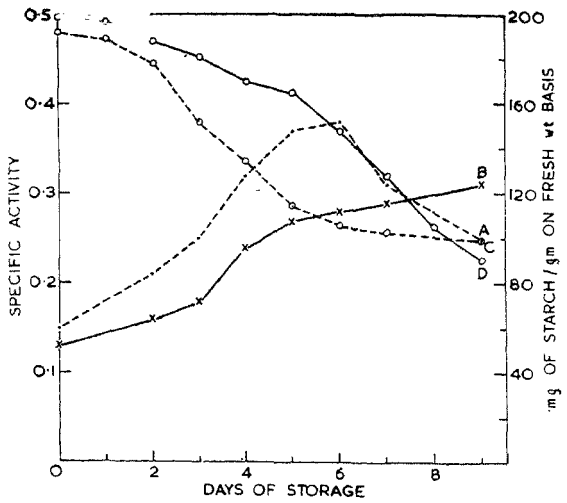

FIG. 3. Effect of gamma irradiation in starch phosphorylase activity ; curve *A* (– – –) irradiate curve *B* (X —— X) unirradiated, and starch content of bananas ; curve *C* (O – – – O) irradiat curve *D* (O —— O) unirradiated.

^{14}C-glucose in irradiated and unirradiated bananas[16]. The ratio of specific activity CO_2 was halved in irradiated banana suggesting a shift from glycolytic pathway to pe tose phosphate pathway[85] (Table II). In unirradiated banana, the radioactivity fructose obtained from both the specifically labelled glucose molecules did not sh any difference indicating that glucose utilization is mainly through glycolytic pathwa But in irradiated banana label from 6-^{14}C-glucose was twice more than 1-^{14}C-glucos thus substantiating the activation of pentose phosphate pathway.

A comparative study on the individual enzymes in carbohydrate metabolism unirradiated and irradiated banana was made to confirm these observations. In banana irradiation has caused an immediate increase in starch phosphorylase activity whi reached a maximum in four to five days after irradiation (Fig. 3). There was a conc mitant decrease in starch content with the increase in phosphorylase activity. Unirr diated bananas showed this increase in activity only after the 7th day of harves Glucose-1-phosphate has to be converted to glucose-6-phosphate by phosphoglu mutase before it can enter either EMP or HMP pathway. Studies in banana ha shown that an appreciable increase in the specific activity of this enzyme was resulte

Table III

Effect of gamma irradiation on glucose-6-phosphate dehydrogenase and phosphoglucomutase

Sample	μ moles of NADPH formed/min/mg protein					
	G–6–P–dehydrogenase			Phosphoglucomutase		
	0 day	3rd day	6th day	0 day	3rd day	6th day
Unirradiated	24	300	250	150	1480	1600
Irradiated	40	370	320	300	1960	1890

The values given are mean of four independent determinations. The activity of G–6–P dehydrogenase and phosphoglucomutase were estimated as described in ref. (16).

even immediately after irradiation (Table III). The activation of glucose-6-phosphate dehydrogenase on irradiation adds support to the shift in EMP pathway to HMP pathway. The enzyme activity was almost doubled in irradiated sample within a few minutes after irradiation. This activation will help in channelling G–6–P to pentose phosphate pathway.

The accelerated functioning of pentose phosphate pathway will also help in the production of fructose-phosphate esters. We will now discuss how further metabolism of these esters was affected by gamma irradiation. Unirradiated banana showed two FDPase activity, one of which had maximum activity at acidic pH (6.6) and the other at alkaline pH (8.8). These activities were very low and did not alter much till 7 days of ripening. Gamma irradiation caused an appreciable and very consistent increase in these two activities within three days after irradiation (Fig. 4). The purification and regulatory properties of both the enzymes were studied by Surendranathan and Nair[35]. Similarly there was a two-fold activation of fructose-6-phosphatase activity also[18]. The combined effect of these changes, resulted in an increased accumulation of fructose in irradiated bananas initially (Fig. 5).

3.3. *Stimulation of glyoxylate shunt pathway*

These alterations can cause only a partial curb in the energy production because Kreb's cycle is the major source for production of energy. One of the important enzymes in the energy harnessing process is succinic dehydrogenase. Although there are suggestions that this enzyme is highly susceptible to gamma irradiation[37] no clear cut demonstration of this susceptibility is available in literature. Gamma irradiation resulted in a marked decrease in succinic dehydrogenase activity in banana[38]. Maximum inhibi-

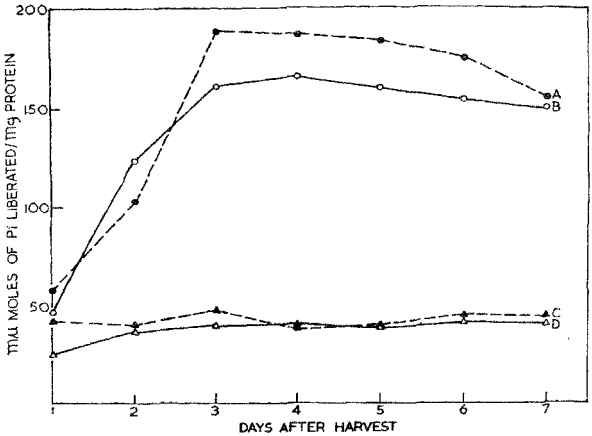

FIG. 4. Activation of fructose, 1,6-diphosphatase in bananas by gamma irradiation. Curve (A acidic enzyme irradiated, (B) alkaline enzyme irradiated, curve (C) acidic enzyme control, (D) alkaline enzyme control.

tion (about 50%) was observed on the 3rd day of irradiation. Up to the 6th day there was no increase in the activity of the enzyme in irradiated sample (Fig. 6).

Even though gamma-irradiation of banana inhibited succinic dehydrogenase, the incorporation of 2-^{14}C acetate into citrate, malate and succinate, showed that the impairment of succinic dehydrogenase did not cause any hindrance in the replenishment of these intermediates (Table IV). This clearly suggested that even with an impaired succinic dehydrogenase activity TCA cycle operation was not affected. An alternative to circumvent this block in metabolism is the operation of glyoxylate shunt pathway. On stimulation of glyoxylate bypass the possibility of an increased rate of formation of glyoxylate and succinate by the action of isocitrate lyase is possible. Studies on the incorporation of 2-^{14}C-acetate into three major keto acids showed an increase in the incorporation into glyoxylate and decrease in α-ketoglutarate, thus suggesting the enhanced operation of this pathway (Table IV). Confirmative evidence for the stimulation of glyoxylate shunt pathway was obtained by demonstrating the activation of enzymes isocitrate lyase and malate synthetase. Irradiation caused immediate activation of these enzymes in banana (Fig. 7). Maximum activation was observed on the 3rd and 5th days of storage. Moreover the isocitrate lyase was purified from gamma irradiated banana pulp tissue on the 3rd day after irradiation[39]. The purified enzyme showed multiple forms and did not require Mg^{2+} ions for activity unlike

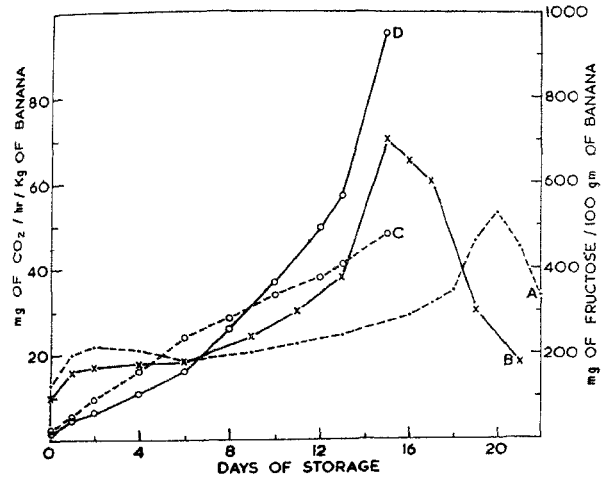

FIG. 5. Increase in fructose content and shift in climacteric respiration by gamma irradiation of bananas. Curves (A) and (B) : respiration of irradiated and unirradiated banana respectively. Curves (C) and (D) : fructose contents of irradiated and unirradiated bananas respectively.

other isocitrate lyases. The enzyme also showed regulatory properties. It is regulated by Kreb's cycle intermediate as well as by other intermediates in gluconeogenic pathway (Table V). In this case the inhibitory activity decreased as the compound is near to glucose. Since oxaloacetate is the first intermediate linking the gluconeogenic pathway its influence on glyoxylate pathway through the inhibition of the first enzyme has great significance in the regulation of enzyme activity. Similarly the inhibition of this enzyme by the other intermediates of gluconeogenic pathway, *viz.*, PEP and FDP may be of physiological significance in irradiated banana.

3.4. *Gluconeogenesis*

The stimulation of glyoxylate shunt pathway and the activation of FDPase, an enzyme in gluconeogenic pathway favoured gluconeogenesis in gamma irradiated banana. The studies on the incorporation of acetate-2-^{14}C into sucrose, glucose and fructose showed that the incorporation was increased to about 2 fold after irradiation of preclimacteric banana (Table IV). Similarly as shown earlier there was significant reduction in the incorporation of 2-^{14}C-acetate into oxaloacetate, whereas incorporation into citrate and

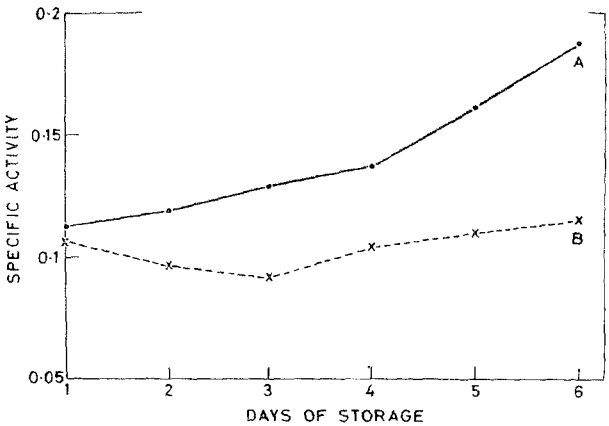

FIG. 6. Changes in succinic dehydrogenase activity in gamma irradiated banana. Curve (A) unirradiated, Curve (B) irradiated.

malate has increased. This observation suggested faster turn over of oxaloacetate which was reflected in the levels of oxaloacetate in irradiated banana. On the 3rd day when glyoxylate shunt pathway was stimulated the concentration of oxaloacetate was 3 nmoles/g fresh weight in banana pulp tissue. The low levels of this prime inhibition for isocitrate lyase might have helped in the stimulation of glyoxylate shunt pathway.

Oxaloacetate can be metabolized either by condensation with acetyl CoA (citrate synthetase) or transformation into malate or aspartate. But in a predominantly gluconeogenic tissue oxaloacetate is converted to PEP which enhances sugar synthesis. The unique enzymes of gluconeogenesis are: (1) pyruvic carboxylase, (2) PEP carboxykinase and (3) fructose, 1,6; diphosphatase. Out of these the key enzyme is PEP carboxykinase. In irradiated banana, level of this enzyme is increased to about 5-fold, when there is appreciable gluconeogenesis ascertained by the incorporation of ^{14}C-acetate into sugars. The decarboxylation of oxaloacetate to PEP by PEP CK is an energy requiring process. But in the absence of ADP, PEPC will act on PEP to yield oxaloacetate functioning only in the carboxylation direction. If PEPC activity is also increased as a result of irradiation there will be a disturbance in gluconeogenic process because some of the PEP may be converted back to oxaloacetate. To test this possibility the changes in the levels of PEPC were also determined. There was almost no change in PEPC activity as a result of irradition. On the other hand activation of PEPCK was instantaneous and maximum level was attained on the 4th day after which the activity declined.

Table IV

Incorporation of 2-^{14}C acetate into organic acids, keto acids and sugars of banana

	Days of storage			
	1st day		3rd day	
	Unirradiated cpm/50 µl	Irradiated cpm/50 µl	Unirradiated cpm/50 µl	Irradiated cpm/50 µl
Organic acids				
Citric acid	7084 ± 154	8975 ± 116	8219 ± 95	9114 ± 67
Malic acid	9734 ± 108	9832 ± 128	9955 ± 244	10908 ± 299
Succinic acid	5627 ± 188	5906 ± 201	7182 ± 66	8674 ± 466
Keto acids				
Glyoxylate	872 ± 52	1324 ± 91	2062 ± 138	3795 ± 191
Oxaloacetate	860 ± 8	1080 ± 48	1074 ± 67	852 ± 61
α-ketoglutarate	2255 ± 41	2169 ± 104	2685 ± 250	750 ± 136
Sugars				
Sucrose	492 ± 41	925 ± 33	325 ± 9	1043 ± 39
Glucose	206 ± 8	265 ± 4	304 ± 35	466 ± 31
Fructose	213 ± .13	314 ± 30	300 ± 35	522 ± 39

Values given are mean ± S.E.

Another important enzyme in the gluconeogenic pathway is pyruvate carboxylase, the first enzyme unique to gluconeogenesis from 3 carbon precursors. This enzyme is known to be controlled by the level of acetyl CoA[23]. This enzyme activity maintained a constant level throughout the storage period after harvest. But irradiation accelerated the activity which reached maximum on the 3rd day and thereafter continued at the same level. This indicates that there is an imbalance in the functioning of TCA cycle, *i.e.*, the capacity of TCA cycle to oxidise acetyl CoA is reduced. The reduction in the oxidation of acetyl CoA, due to inhibition of succinic dehydrogenase, may in turn activate pyruvic carboxylase, which can utilize 3 carbon substrate for gluconeogenesis.

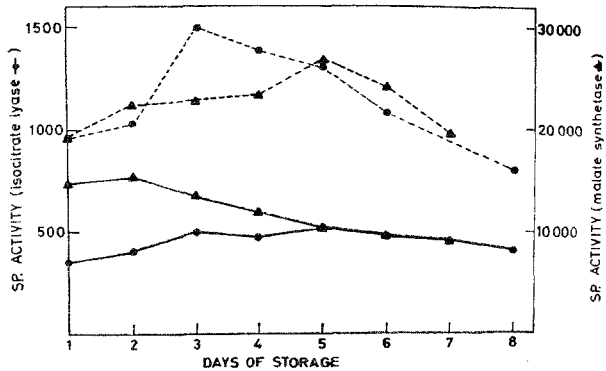

FIG. 7. Increase in isocitrate lyase and malate synthetase activities. Isocitrate lyase (●——●) unirradiated, (●- - -●) irradiated. Malate synthetase (▲——▲) unirradiated, (▲- - -▲) irradiated.

The rapid decarboxylation of oxaloacetate catalysed by PEPCK is dependent on ATP-ADP ratio. ATP required for gluconeogenesis is generated at least in part by the residual functioning of TCA cycle, with an impaired succinic dehydrogenase. Thus part of the ATP produced is consumed for decarboxylation of oxaloacetate causing further depletion in the energy level.

3.5. *The overall pathway*

The stimulation of shunt pathway also contributes towards the channelization of the metabolites into gluconeogenesis and curb the energy production. Oxaloacetate concentration plays a key role in this process. The amount of oxaloacetate in unirradiated banana, 3 days after harvest was about 6 *n* moles per gram tissue, but in irradiated tissue at this stage it was reduced to half. Reduction in the level of oxaloacetate as a result of decarboxylation by PEPCK, may in turn help in the activation of isocitratelyase and glyoxylate cycle. The enhanced activity of glyoxylate shunt pathway and activation of pyruvate carboxylase help in the replenishment of oxaloacetate. Another important enzyme in gluconeogenic pathway which is also activated by gamma irradiation is FDPase. This caused a reduction in the levels of FDP—thus channelling metabolites towards the synthesis of sugars. The overall alteration in the metabolism of carbohydrate due to gamma irradiation resulting in the accumulation of free sugar mainly fructose with concomitant reduction in energy production is depicted in Fig. 8. The two enzymes unique to gluconeogenesis are Asp- α-KG and Ala- α-KG transaminases. The studies on the status of these enzymes at different days of storage after irradiation of preclimacteric banana showed that both these activities are enhanced. But alanine

Table V

Effect of Kreb's cycle and gluconeogenic intermediates on isocitrate lyase activity

Intermediate added	Concentration in μmoles	Type of inhibition	Activity	Per cent inhibition
None	..		145	..
Oxaloacetate	0·05	Competitive	90	38
	1·00		23	84
	3·00		8	95
Malate	5·00	Non-competitive	135	7
	10·00		68	53
Succinate	5·00		145	..
	10·00		143	..
Tartarate	5·00		97	33
	10·00		60	66
Phosphoenolpyruvate	2·5	Non-competitive	54	63
	5·0		47	68
Fructose 1,6-bis phosphate	5·0	Competitive	115	20
	10·0		80	45
Aspartate	5·0		73	50
	10·0		61	58
Glycine	5·0		70	52
	10·0		58	60

transaminase showed much more activity. The products of these enzymes, oxaloacetate and pyruvate will help to enhance the gluconeogenic flux from proteins. There is strong possibility that the intermediates of TCA cycle formed as a result of increased breakdown of starch can also be recycled through gluconeogenic pathway instead of complete oxidation.

4. Conclusion

From the foregoing discussion it is evident that the events following gamma irradiation of preclimacteric banana, altered the metabolic pathways in such a way that energy production is reduced accompanied by the accumulation of free sugars. However, this delay does not affect the production and supply of vital intermediates of the metabolic

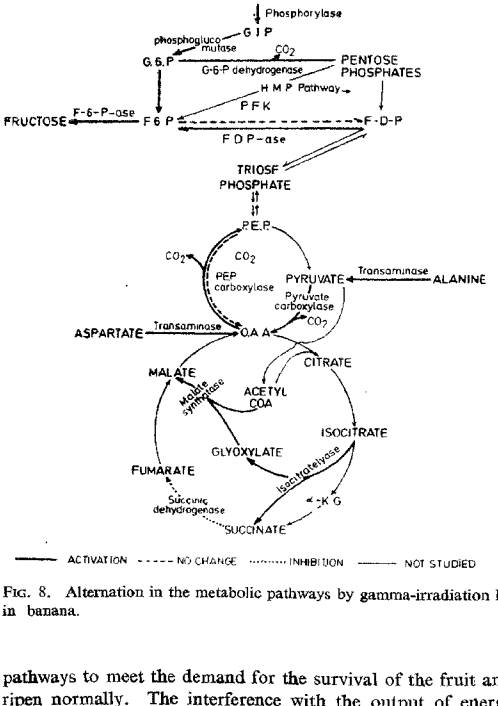

FIG. 8. Alternation in the metabolic pathways by gamma-irradiation leading to the synthesis of sugars in banana.

pathways to meet the demand for the survival of the fruit and eventually allow them to ripen normally. The interference with the output of energy from the metabolism of carbohydrates by regulating certain key enzymes of glycolytic, Kreb's cycle and gluconeogenic pathways is one of the main reasons responsible for the gamma irradiation-induced delay in ripening of banana.

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