Irradiation of Potatoes: Influence on Wound Periderm Formation and on Resistance to Soft Rot

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The susceptibility of the irradiated (10, 25, and 50 krd) potatoes to soft rot was assessed by a quantal response test. Though there was no apparent increase in susceptibility to soft rot at 10 krad, higher doses rendered the tubers more susceptible, concomitant with the doses employed. The irradiated tubers formed physically weaker periderm, and lower levels of resistance compounds were observed such as phenolics and phytoalexins as compared to unirradiated potatoes. The composition of free lipids of wound periderm and the aliphatic fraction of suberin was not, however, affected by the irradiation treatment. Tubers irradiated at a sprout inhibiting dose (10 krd) did not exhibit enhanced susceptibility to soft rot at temperatures below 20 °C.

Exposure of potatoes to γ-radiations (10 krad) not only imparts permanent dormancy to the tubers but also reduces the formation of chlorophyll and solanine and eliminates tuber moth infestation (Nair et al., 1973, 1981; Thomas et al., 1979). Despite these multiple advantages, this low-dose treatment does not arrest the soft rot pathogens during storage (Nair et al., 1973; Thomas et al., 1979). The doses required to inactivate the microorganisms are of much higher order (Lewis et al., 1972). It was nevertheless essential to ascertain whether the application of radiations could render the tubers more susceptible to soft rot. The increased tendency of the irradiated tubers to rotting is presumed to be due to the impaired wound periderm formation (Spark and Iritani, 1964; Spark, 1970). The present investigation compares wound periderm formation and soft rot development in γ-irradiated and unirradiated potatoes in order to correlate, if possible, these responses with the dose of irradiation.

MATERIALS AND METHODS

Irradiation Treatment. The mature and cured potatoes of cultivar Kufri Chandramukhi were washed in running tap water and air-dried for 24 h. The tubers were irradiated at 30 °C in a cobalt-60 γ cell 220 with air as the gas phase, with a dose rate of 3.5 krad/min determined by a Fricke dosimer (Fricke and Morse, 1927).

Inoculation of the Tubers. A strain of *Erwinia carotovora* var. *carotovora* was grown in nutrient broth (difco) for 24 h at 27 °C on a shaker. The cells were harvested and the tubers were infected by the quantal response method (De Boer, 1976). The inoculated tubers were stored at different temperatures, either in the open trays or in sealed polythene bags. At the stated intervals, the tubers were examined for initiation of the soft rot lesion at the site of injection.

Analysis of Wound Periderm. The tubers exposed to various doses of γ-irradiation were kept in open trays at different temperatures. After a period of 1 week, the tubers were cut into halves and infected with *E. carotovora* and the incubation was continued for 2 weeks. The wound periderm formed was isolated and lyophilized. Free phenolics were extracted by the method described by Huang and Agrios (1979) and estimated spectrophotometrically (Clifford and Wight, 1976). The individual components of phenolics were tentatively identified by a combination of paper chromatography (Hanson and Zucker, 1963) and high-performance liquid chromatography (HPLC) (Walter et al., 1979). Phytoalexins were extracted by employing the method of Henfling and Kuč (1979). Thin-layer and gas–liquid chromatographic techniques (Lyon and Bayliss, 1975a,b) were employed to identify and quantify the components.

Isolation of Suberin from Wound Periderm. The powdered wound periderm (10 g) was extracted with 300 mL of acetone for 1 h on a shaker at 30 °C. The supernatant was collected by filtration through Whatman No. 1 filter paper, and the residue was further extracted with 300 mL of a mixture of chloroform and methanol (2:1 v/v) for 2 h followed by filtration. This step was repeated twice, and all the extracts were pooled and evaporated under reduced pressure. The yellowish brown oily substance was designated as the free lipid fraction (Kolattukudy and Dean, 1974; Ghanekar and Nair, 1974). This was analyzed by TLC after washing with salt solution (Folch et al., 1957). The wound periderm residue was further extracted with chloroform in a Soxhlet apparatus to remove the leftover traces of lipids. The filtrate was discarded, and the residue was air-dried and designated as suberin (Kolattukudy and Dean, 1974).

Depolymerization of suberin was accomplished by trans esterification (Kolattukydy and Dean, 1974). The suberin samples were refluxed with 14% boron trifluoride in methanol (BDH), for a period of 24 h. This operation was carried out in a fume hood. For every gram of sample, 30 mL of solvent was used. About 50 mL of distilled water was added to terminate the reaction, and this was followed by filtration through Whatman No. 1 filter paper. The filtrate obtained was extracted 4 times with chloroform (50 mL). The chloroform extracts were pooled and evaporated to dryness under reduced pressure. The brown material recovered was the aliphatic fraction of suberin.

Thin-Layer Chromatography. TLC of the free lipid fraction was performed by using 0.25 mm thick Keiselgel G (E. Merck, West Germany) plates (20 × 20 cm) that were activated at 110 °C in a hot-air oven for 1 h. The samples were spotted followed by resolution in a mixture of petroleum ether (40–60 °C), diethyl ether, and acetic acid (85:15:1 v/v) for 45 min at 25 °C. The plates were developed either after exposing to I_2 vapors or spraying with concentrated H_2SO_4 followed by heating at 200 °C (5 min) in an oven (Ghanekar and Nair, 1974).

Qualitative TLC analysis of the aliphatic fraction of suberin (Kolattukudy and Agrawal, 1974) was performed as above, except that the activation of plates was carried out for 18 h. For the quantitative estimation of the components, preparative TLC was performed by using a 0.5-mm thickness of Keiselgel G. The samples were applied in a band form. Upon development and exposure to I_2 vapors, bands corresponding to various components were marked. Silica gel from these regions was scraped, followed by elution with a mixture of chloroform and methanol (2:1

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Table I. Soft Rot Incidence in γ-Irradiated Potatoes Stored in Open Trays at Different Temperatures[a]

	% incidence of soft rot at storage condition											
	2 °C, 90 days				10 °C, 60 days				15 °C, 30 days			
no. of cells inoculated	0 krd[b]	10 krd	25 krd	50 krd	0 krd	10 krd	25 krd	50 krd	0 krd	10 krd	25 krd	50 krd
1.0×10^7	6	4	8	20	4	6	12	14	8	10	18	18
2.5×10^6	0	0	0	0	0	0	0	0	0	0	0	0
6.25×10^5	0	0	0	0	0	0	0	0	0	0	0	0
1.56×10^5	0	0	0	0	0	0	0	0	0	0	0	0

[a] Each determination was with 50 tubers. Soft rot incidence is expressed as the percentage of the infected tubers. Relative humidities were observed to be 95–98, 85–90, and 78–83% at 2, 10, and 15 °C, respectively. [b] Radiation dose.

Table II. Soft Rot Incidence in γ-Irradiated Potatoes Stored in Open Trays at Different Temperatures[a]

	% incidence of soft rot at storage condition											
	20 °C, 21 days				25 °C, 12 days				32 °C, 8 days			
no. of cells inoculated	0 krd[b]	10 krd	25 krd	50 krd	0 krd	10 krd	25 krd	50 krd	0 krd	10 krd	25 krd	50 krd
1.0×10^7	14	10	26	42	34	36	100	98	78	84	100	100
2.5×10^6	0	0	0	0	0	0	12	54	0	0	24	90
6.25×10^5	0	0	0	0	0	0	0	0	0	0	6	40
1.56×10^5	0	0	0	0	0	0	0	0	0	0	0	8

[a] Experimental details are as in Table I. Relative humidities were observed to be 75–80, 60–65, and 58–63% at 2, 25, and 32 °C, respectively. [b] Radiation dose.

Table III. Soft Rot Incidence in γ-Irradiated Potatoes Stored in Polyethylene Bags at Different Temperatures[a]

	% incidence of soft rot at storage condition											
	2 °C, 90 days				10 °C, 60 days				15 °C, 30 days			
no. of cells inoculated	0 krd[b]	10 krd	25 krd	50 krd	0 krd	10 krd	25 krd	50 krd	0 krd	10 krd	25 krd	50 krd
6.25×10^5	6	8	18	26	100	100	100	100	100	100	100	100
1.56×10^5	0	0	0	0	50	52	66	74	40	56	76	88
4.00×10^4	0	0	0	0	0	0	0	0	0	0	0	0
1.00×10^4	0	0	0	0	0	0	0	0	0	0	0	0

[a] See the footnotes in Table I. [b] Radiation dose.

Table IV. Soft Rot Incidence in γ-Irradiated Potatoes Stored in Polyethylene Bags at Different Temperatures[a]

	% incidence of soft rot at storage condition											
no. of cells inoculated	20 °C, 21 days				25 °C, 12 days				32 °C, 8 days			
6.25×10^5	60	64	78	100	62	78	100	100	100	100	100	100
1.56×10^5	10	16	26	84	6	18	34	68	52	84	100	100
4.00×10^4	0	0	0	24	0	0	18	40	0	20	40	78
1.00×10^4	0	0	0	0	0	0	0	22	0	0	0	32

[a] See the footnotes in Tables I and II.

v/v). The eluants were evaporated under a stream of N_2, and the weight of the residues was determined.

RESULTS

Soft Rot Incidence in Irradiated Tubers. The incidence of soft rot in potatoes irradiated at various doses (0–50 krad) during storage in the open trays at different temperatures is shown in Tables I and II. The tubers were infected at various inoculum levels after the irradiation treatment and prior to storage. It was observed that the irradiated tubers, particularly those exposed to 25 and 50 krd, seemed to be more susceptible than the untreated tubers. This was observed in potatoes stored at temperatures above 20 °C. It is worth noting that at the sprout inhibiting dose of 10 krd, there was no increase in the susceptibility.

The extent of soft rot in the tubers kept in polythene bags was much higher as compared to those kept in open trays, as shown in Tables III and IV. This could be attributed to better oxygen availability in the open trays. It was observed that much lower inoculum levels were suf-

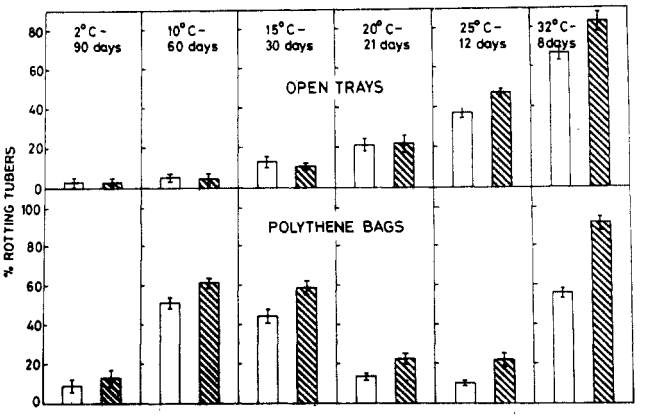

Figure 1. Soft rot susceptibility of unirradiated and irradiated (10 krd) potatoes under different conditions of storage. (□) Unirradiated; (▨) irradiated. Tubers stored in open trays were previously inoculated with 10^7 cells of *E. carotovora*. Those kept in polyethylene bags were inoculated with 1.5×10^5 cells except in the case of tubers kept at 2 °C where 6×10^5 cells were injected. Other experimental details are outlined in the text.

Table V. Composition of Wound Periderm of Irradiated Tubers[a]

temperature of storage, °C	radiation dose, krd	components of wound periderm: phenolics, μg	free lipids, mg	suberin, mg
2	0	275 ± 48	42.2 ± 2.5	594.0 ± 11.7
	10	241 ± 16	23.8 ± 1.0	458.5 ± 23.5
	25	139 ± 7	21.2 ± 1.7	430.0 ± 19.7
15	0	3489 ± 82	116.9 ± 3.3	810.0 ± 15.7
	10	3020 ± 118	86.6 ± 3.5	713.0 ± 18.7
	25	2448 ± 70	66.1 ± 2.5	697.0 ± 19.8
25	0	2707 ± 66	112.5 ± 2.5	789.5 ± 15.4
	10	2230 ± 49	87.6 ± 1.8	698.7 ± 20.9
	25	1901 ± 27	65.8 ± 1.8	633.1 ± 11.7

[a] Tubers were stored for 2 weeks at 15 or 25 °C and for 4 weeks at 2 °C. All values represent the amounts per gram dry weight of wound periderm.

Table VI. Composition of Phenolics in γ-Irradiated Potatoes Infected with *E. carotovora*[a]

phenolic components	% composition of phenolics in tubers exposed to: 0 krd	10 krd	25 krd	50 krd
total chlorgenic acid isomers	68.4	62.7	61.5	64.6
caffeic acid	9.1	7.2	9.1	6.8
ferulic acid	14.2	18.6	15.3	17.0
total unidentified compounds	9.6	11.4	14.0	11.6

[a] The potatoes were stored at 15 °C for 2 weeks after infecting them with *E. carotovora*. Phenolics were analyzed by HPLC. The experimental details are outlined in the text.

ficient to initiate the soft rot. The tubers treated with γ-rays showed higher susceptibility, particularly at higher storage temperatures (above 25 °C).

Figure 1 illustrates differences in susceptibilities of control and irradiated (10 krd) tubers. The tubers stored in the open trays at temperatures below 20 °C showed similar susceptibilities. However, the incidence of rotting seemed to increase in the irradiated tubers when the storage temperature was above 25 °C ($p < 0.01$). On the other hand, discernible enhancement in rotting due to irradiation could be observed when the tubers were kept in polyethylene bags. This effect was more significant at a higher temperature of 32 °C ($p < 0.001$).

Characteristics of Wound Periderm. *Physical Properties.* Unirradiated potatoes formed, in response to infection, dry and loosely bound (to cortex tissue) periderm. On the other hand, irradiated (10 krd) tubers formed moist, thin, and closely attached periderm. With the increasing doses of irradiation, the thickness decreased, the moisture content increased, and it was more tightly bound to the cortex tissue.

Chemical Composition. Table V shows levels of phenolics, free lipids, and suberin in the wound periderm formed in unirradiated and irradiated (10 and 25 krd) tubers, stored at different temperatures. The irradiated tubers showed lower levels of all these components as compared to the unirradiated ones, though the relative proportions of phenolics as determined by HPLC analysis were found to be unaltered by radiation even at a dose as high as 50 krd as shown in Table VI.

Qualitative analysis of free lipids by TLC indicated the presence of hydrocarbons, free fatty acids, triglycerides, fatty alcohols, diglycerides, and monoglycerides as shown in Figure 2. No qualitative difference could be detected in free lipid components present in wound periderms of unirradiated or irradiated potatoes.

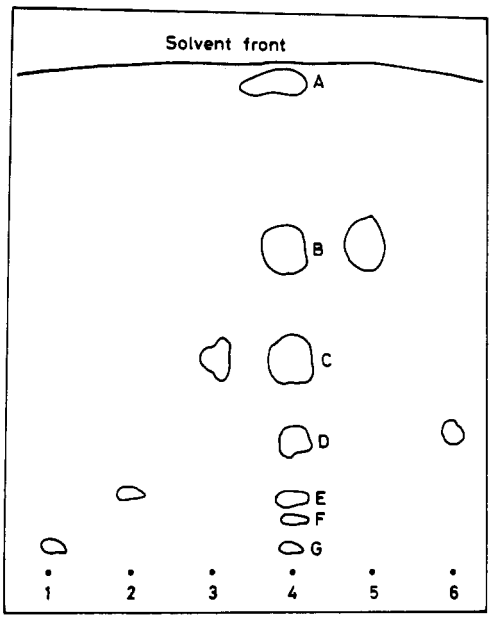

Figure 2. Separation of components of free lipids of wound periderm by thin-layer chromatography. 1, monoplamitin; 2, dipalmitin; 3, oleic acid; 4, free lipid fraction of wound periderm; 5, tripalmitin, 6, lauryl alcohol. A, hydrocarbon; B, triglycerides; C, free fatty acids; D, fatty alcohols; E, diglycerides; F, unidentified; G, monoglycerides. Experimental details are outlined in the text.

Table VII. Levels of Phytoalexins in Wound Periderm of Irradiated Tubers[a]

temperature of storage, °C	radiation dose, krd	phytoalexins, μg/g dry wt: rishitin	phytuberin
15	0	576.9 ± 64.4	144.2 ± 34.7
	10	280.6 ± 17.9	96.9 ± 20.3
25	0	441.0 ± 27.2	72.0 ± 15.6
	10	227.7 ± 18.2	35.7 ± 11.1

[a] Phytoalexins were extracted from wound periderm and analyzed by GLC as described in the text.

Table VII shows the levels of phytoalexins, namely, rishitin and phytuberin, in untreated and irradiated tubers. Levels of both these compounds were depleted in the irradiated tubers.

The aliphatic fraction of suberin, obtained on depolymerization, consisted of monocarboxylic fatty acids, dicarboxylic fatty acids, fatty alcohols, and ω-hydroxy and other unidentified hydroxy acids as shown in Figure 3. Gravimetric analysis by preparative TLC indicated that radiation treatment of tubers does not influence the composition of aliphatic portion of suberin as indicated in Table VIII. The hydroxy fatty acid components of the aliphatic fraction were isolated by TLC, and the presence of OH group was confirmed by infrared (IR) spectrophotometry by strong absorption at 2.85 μm. Figure 4 shows IR spectra of various components of the aliphatic fraction. The components D, E, and F were designated as hydroxy fatty acids and component C was designated as a fatty alcohol based on R_f values.

Chemical analysis of wound periderm thus showed that although the total content of various major groups of compounds were lower in the irradiated tubers, the relative proportions of their components remained unaltered.

DISCUSSION

In the present investigations, a quantal response test was employed to detect differences in the susceptibility of the tubers to soft rot infection. This technique involves in-

Table VIII. Quantitative[a] Analysis of the Aliphatic Fraction of Suberin

components	normal epiderm	% composition of components of aliphatic fraction of suberin formed in tubers stored at different temperatures								
		2 °C			15 °C			25 °C		
		0 krd	10 krd	25 krd	0 krd	10 krd	25 krd	0 krd	10 krd	25 krd
monocarboxylic fatty acids	8.2	10.2	10.3	9.2	10.4	10.3	10.8	11.7	12.2	12.2
dicarboxylic fatty acids	15.3	17.5	17.3	18.2	21.5	22.6	22.4	18.7	18.2	19.2
fatty alcohols	16.8	8.7	10.0	8.2	7.7	8.1	9.2	5.6	8.1	8.7
ω-hydroxy fatty acids	12.0	12.5	10.2	10.9	10.8	9.2	11.4	12.7	12.2	10.6
other hydroxy fatty acids	9.9	17.8	20.9	20.2	14.1	12.4	16.3	19.2	21.2	23.3
total unidentified	28.0	13.7	13.3	14.4	19.1	15.9	17.8	13.8	15.3	15.9

[a] Values represent the percentage of various components of the aliphatic fraction isolated from suberin depolymerized with BF_3-methanol. Total recovery of components from preparative TLC was between 80 and 90%.

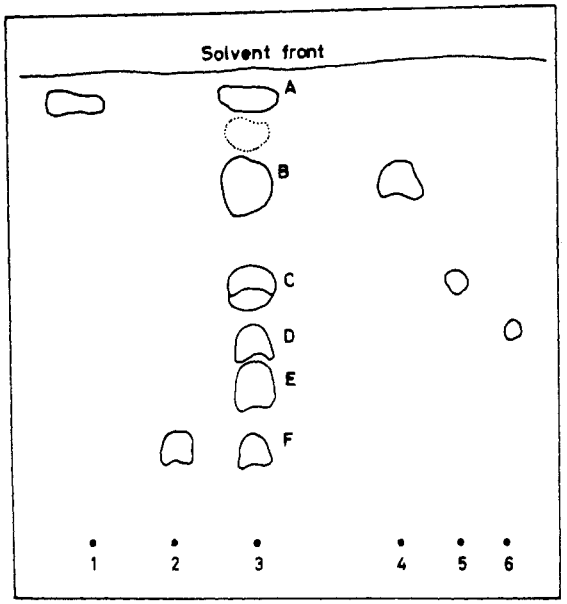

Figure 3. Separation of components of aliphatic fraction of suberin by thin-layer chromatography. 1, methyl oleate; 2, α-hydroxycaproic acid methyl ester; 3, aliphatic fraction of suberin isolated from wound periderm; 4, sebacic acid methyl ester; 5, lauryl alcohol; 6, 12-hydroxystearic acid methyl ester. A, monocarboxylic acid methyl esters; B, dicarboxylic acid methyl esters; C, fatty alcohols; D, hydroxy acid methyl esters; E, ω-hydroxyoleic acid; F, hydroxy acid methyl esters.

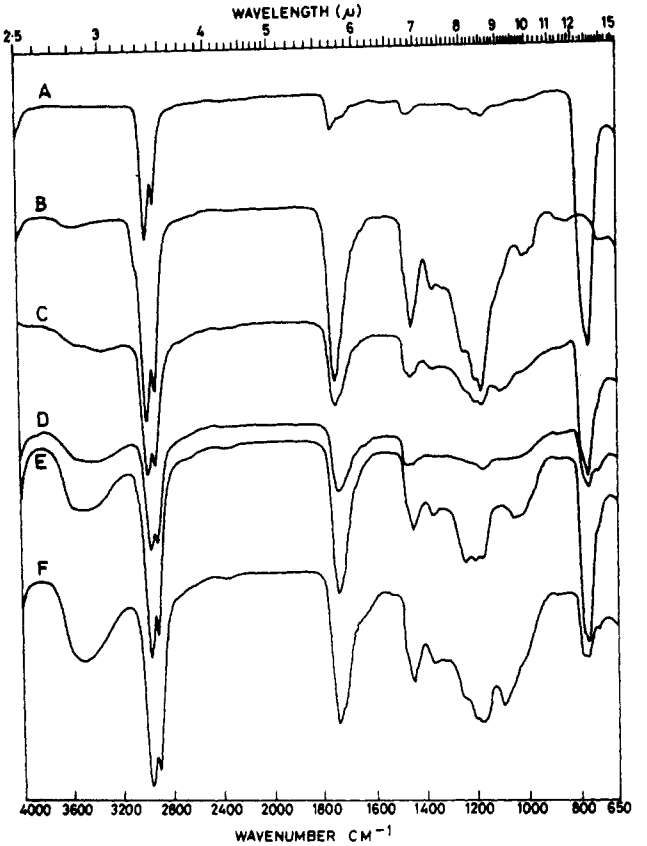

Figure 4. Infrared spectra of varius components of aliphatic fraction of suberin. A–F refer to the components isolated by TLC as shown in Figure 3. Components D–F show strong absorption at 2.85 μm, indicating the presence of hydroxy groups.

oculation of the tubers with different population densities of a pathogen so as to detect finer alterations in the susceptibility. This method has certain advantages over the assessment made earlier of losses due to soft rot (Nair et al., 1973; Thomas et al., 1979). The method of storing the tubers in jute bags and comparing the gross losses at the end of a certain period may not permit proper evaluation of the changes in susceptibility. Under such conditions, several other factors also could influence the extent of rotting. Thus, the lower incidence of soft rot reported in the irradiated tubers was attributable to the initial tuber moth infestation and the ability of γ-rays to eliminate this pest (Nair et al., 1973). On the other hand, the irradiated potatoes free of tuber moth had shown enhancement in the losses due to rotting (Nair et al., 1973). This had necessitated the precise assessment of susceptibility of the irradiated potatoes to soft rot.

The results presented above show that oxygen depletion resulted in a higher incidence of soft rot. This could be correlated with the reduced levels of the resistance factors like terpenoid phytoalexins and phenolics [see Ghanekar et al. (1983)]. The increased rotting observed in the tubers irradiated at 25 and 50 krd could be similarly attributed to the lower levels of resistance compounds. The recommended dose of irradiation for sprout inhibition (10 krd) did not seem to alter the susceptibility of the tubers to soft rot, when stored in the open trays below 20 °C. The irradiated tubers stored in polyethylene bags below 20 °C, however, had a higher soft rot incidence as compared to the untreated tubers. The difference in susceptibilities of irradiated and control tubers was significant only when the tubers were kept in polyethylene bags at higher temperature (32 °C). This could obviously be due to higher growth rate of *E. carotovora* at this temperature. The irradiation seems to render the tubers susceptible, but this susceptibility is only significant at doses higher than those used in potato irradiation and can only be expressed at temperatures higher than those used for potato storage.

Formation of new periderm cell layers and subsequent suberization have been recognized to be important for disease resistance in the tubers (Spark and Iritani, 1964; Spark, 1970; Kolattukudy, 1977). Radiation-induced soft rot has been attributed to the impaired periderm formation (Spark and Iritani, 1964; Spark, 1970). A dose as low as 2 krd has been found to be sufficient to impair periderm formation (Thomas, 1982). The reduced contents of free lipids, suberin, phenolics, and phytoalexins in suberized wound periderm, as observed in the present studies, could also contribute to the lowered resistance in irradiated tubers.

Analysis of aliphatic fraction of suberin component of potato wound periderm has been reported (Kolattukudy and Dean, 1974; Kolattukudy and Agrawal, 1974). The pattern of separation of this fraction by TLC observed in the present studies was similar to that reported by these workers. It has been shown that octadec-9-enedioic acid (a dicarboxylic acid) and ω-hydroxyoleic acid were the key components responsible for the ability of wound periderm to prevent moisture losses. In the present studies, though dicarboxylic acids were detected, their further characterization was not carried out. Similarly, ω-hydroxyoleic acid (compound E) in Figure 4 was tentatively identified based on its IR spectrum (absorption at 2.85 μm characteristic of OH group), its stronger affinity for I_2 vapors (due to unsaturation), and its relative position (R_f) on TLC plate between more polar α-hydroxycaproic acid and relatively less polar 12-hydroxystearic acid.

Registry No. Suberin, 8072-95-5; rishitin, 18178-54-6; phytuberin, 37209-50-0; chlorogenic acid, 327-97-9; caffeic acid, 331-39-5; ferulic acid, 1135-24-6.

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Dietary Fiber Content of Eleven Tropical Fruits and Vegetables

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Dietary fiber was determined in the following samples: yam, malanga, cassava, taro, avocado, date, coconut, calabaza, grapefruit albedo, and kiwi. Values were obtained for cellulose, hemicellulose, lignin, cutin, ash, neutral detergent residue (NDR), and enzymatic (soluble and insoluble) fractions. Ranges were (percent of fresh weight) as follows: for NDR, 0.53–8.6%; for cellulose, 0.20–3.8%; for hemicellulose, 0.07–4.2%; for lignin, 0.051–2.01%; for enzymatic insoluble, 0.91–6.9%; for enzymatic soluble, 0.64–4.7%. Cellulose and hemicellulose were most concentrated in coconut, and lignin was highest in dates. The enzymatic–soluble fraction was exceptionally high in the yam, *Dioscorea rotundata*, and in grapefruit albedo.

Because of the lack of detailed information on fiber in many foods, we undertook a study of dietary fiber components in the more common tropical fruits and vegetables. We were also interested in certain in vitro physiological properties of isolated fiber components which required water-soluble and -insoluble fractions prepared by an enzymatic procedure for further studies in vitro.

In an earlier study, values for fiber components in 15 samples from 8 fruits and vegetables were reported (Lund and Smoot, 1982). Since this study was completed, a more complete study of banana fiber (Kayisu et al., 1981) and the fiber composition of the yams *Dioscorea dumetorum* and *rotundata* have been published (Brillouet et al., 1981).

The modified forms of the Van Soest detergent and Hellendoorn enzymatic methods which we reported previously (Lund and Smoot, 1982) were employed in the current study. Several reports have recently appeared describing improvements in these methods for use with samples containing relatively large amounts of starch or pectin (Dovell and Harris, 1982; Selvendran and DuPont, 1980; Marlett and Lee, 1980; Collinge et al., 1980; Morrison, 1980; Jeltema and Zabik, 1980). Some of these procedures may eventually be incorporated into a standard method

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