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Wound-induced suberization and periderm development in potato tubers as affected by temperature and gamma irradiation

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Summary

Histochemical evaluation of the wound-induced suberization and periderm formation, the processes of wound healing, in potato tubers (*Solanum tuberosum* L.) showed that both the processes occur most rapidly at 25 °C. Wound-healing is delayed at 10 or 15 °C while a temperature of 35 °C prevented periderm formation and retarded suberization. Gamma irradiation up to 100 Gy, the optimal dose for sprout inhibition, did not affect suberization, which suggests that the DNA-replicating mechanism is more radiation-sensitive than suberin biosynthesis. A dose of 20 to 30 Gy, which had no effect on sprouting inhibited wound periderm formation indicating that meristems in resting buds are apparently less sensitive to irradiation than nuclei of the potential periderm cells. It seems probable that a major cause for the bacterial soft rot occurring in tubers when stored under high tropical ambient temperatures or when irradiated for sprout inhibition is due to an impairment of the wound periderm formation.

Introduction

A major factor limiting the storage of potato tubers under tropical ambient conditions is bacterial soft rot. In a recent study with several Indian cultivars, losses of 30 to 70 % were caused by *Erwinia carotovora* soft rot during 2 to 4 months storage at 27 to 32 °C (Thomas et al., 1979). Apart from the infection through the lenticels (Pérembelon, 1973) wounds inflicted on the tubers during harvest, handling and transport can provide easy access for the entry of rot producing pathogens.

Losses due to diseases and desiccation can be minimized by proper wound healing as soon as potatoes are harvested and placed in storage. The wound healing process involves suberization – deposition of suberin, a lipid-phenolic polymer (Mader, 1958; Dean & Kolattukudy, 1977) on cell layers below the wound surface – followed by formation of wound periderm or cork. There are disagreements in the literature regarding the optimal temperature for wound-healing of potato tubers. According to Smith (1968) a temperature of 10 to 15 °C and high humidity (RH) hastens periderm formation whereas 24 °C and a RH above 80 % was found to be optimal by others (Priestly & Woffendon, 1923; Smith & Smart, 1955; Ali et al., 1975; Miller, 1980).

Gamma irradiation at sprout-inhibiting doses (100 Gy)* has been reported to suppress wound periderm formation in potatoes (Penner, 1970) though suberization was not affected (Thomas & Delincée, 1979). Irradiated potatoes generally show an increased tendency to microbial spoilage (El-Sayed, 1975; Thomas et al., 1979). The studies reported here were undertaken to gain more information on the influence of the high tropical ambient temperatures on wound healing of potato tubers and also to determine the minimum irradiation dose required for inhibition of wound-periderm development.

Materials and methods

Freshly harvested potatoes of cv. Kufri Chandramukhi were obtained from the local market. The tubers were irradiated in a Cobalt-60 Gamma Cell 220 in air to doses of 5, 10, 20, 30, 40, 50 and 100 Gy. The irradiated and non-irradiated control tubers were stored at 15 °C, 80–85 % RH for one week before they were cut into two equal halves along the longitudinal axis of the tuber.

The cut tuber halves were placed immediately in perforated polyethylene bags of 150 gauge (45 cm × 30 cm with 36 4-mm equidistant holes). The RH inside the bags was maintained at *ca.* 90 % by keeping petridishes containing distilled water in them. The rates of suberization and periderm formation in tuber halves kept inside the polyethylene bags were found to be similar to tuber halves kept inside a 14-litre glass desiccator through which humidified air was passed at a rate of 1 litre per hour.

The effect of temperature on suberization and periderm formation was studied by placing tuber halves in polyethylene bags at 10, 15, 20, 25, 28–30 and 35 °C.

Histochemical evaluation

For histological examination of suberization and periderm formation, tuber halves allowed to suberize for different periods were used. Preparation of tissue slices and staining were carried out according to the procedure of Nielsen (1973). Free hand sections, 0.5 mm to 1 mm thick were cut at right angles to the wound surface with a razor blade and transferred into FAA (50 ml 95 % ethyl alcohol + 5 ml glacial acetic acid + 10 ml formaldehyde 38–40 % + 35 ml water) and left for one hour before transfer to the staining solution.

Staining

For qualitative evaluation of suberization, tissue slices were stained using Sudan III and O-toluidine blue. 1 % (m/v) of Sudan III in ethyl alcohol was mixed with FAA in the ratio of 1:20 for staining the tissue slices. O-toluidine blue, was used as a 0.05 % solution in water (Borchert et al., 1974). The extent of suberization and the development of periderm were determined microscopically. A minimum of 5 tissue sections stained with each of the dyes were examined at each time for each of the different treatments. Suberized cell walls appear bright red after staining with Sudan III while non-suberized cells do not stain. O-toluidine blue stains suberized cell walls blue, and normal cell walls purple.

*The gray (Gy) is the SI unit of irradiation; 1 Gy = 100 rad = 0.1 krad.

Polyphenolics

Polyphenolic compounds present in the first 1-mm tissue layer below the wound surface (5 g fresh tissue pooled from 3 tuber halves of similar size) were extracted with 85 % aqueous ethyl alcohol and the quantity in the centrifuged supernatant was estimated using the Folin-Denis reagent (Swain & Hills, 1959).

The experiments were repeated at least three times and result presented are based on a typical experiment.

Results

Influence of temperature on suberization and periderm formation

The minimum time required for histochemical evidence of suberization and periderm formation at various temperatures is shown in Table 1. Both suberization and periderm development proceeded faster at 25 °C than at 10, 15, 20 or 35 °C. Deposition of

Table 1. Influence of storage temperature on rate of suberization and wound periderm formation.

	Time in days[1]					
	10 °C	15 °C	20 °C	25 °C	28–30 °C	35 °C
Days to initial indication of suberin deposition on outer cell layer[2]	7	2	2	1	1	2
Days to clear cut evidence of suberized cell layers (2–4 cell layers)[3]	16	9	4	3	4	7
Days to initial evidence of dividing cells[4]	16	6	3	2	3	–
Days to clear cut evidence of wound periderm[5]	–	11	4	3	4	–
Days to initial indication of suberization of wound periderm cells[6]	–	16	7	4	4	–
Minimum storage period required after slicing, to strip off the suberized cell layers from the wound surface[7]	–	7–8	4	3	3–4	–

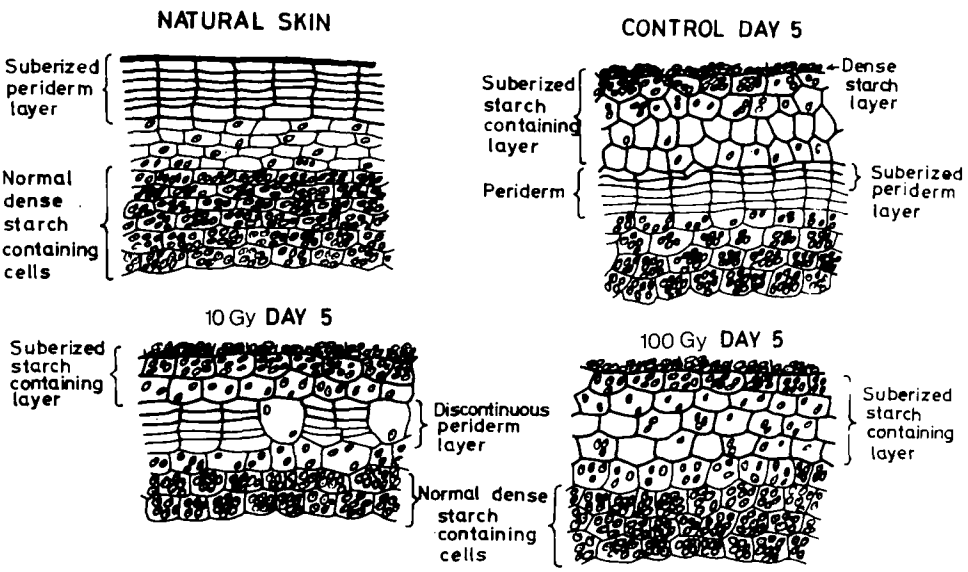
[1] *Zeit in Tagen – Durée en jours;* [2] *Zahl der Tage bis zu den ersten Anzeichen einer Suberinanlagerung in den äusseren Zellschichten – Durée avant indication initiale d'un dépôt de subérine sur la couche cellulaire externe;* [3] *Zahl der Tage bis zum deutlichen Nachweis suberinisierter Zellschichten (2–4 Zellschichten) – Durée avant évidence nette des couches cellulaires subérisées (2–4 couches de cellules);* [4] *Zahl der Tage bis zu den ersten Anzeichen sich teilender Zellen – Durée avant première observation de division des cellules;* [5] *Zahl der Tage bis zum deutlichen Nachweis von Wundperiderm – Durée avant évidence nette d'un périderme de cicatrisation;* [6] *Zahl der Tage bis zu den ersten Anzeichen der Suberinbildung in der Wundperidermzellen – Durée avant indication initiale d'une subérisation des cellules de périderme;* [7] *Kürzeste Lagerungsperiode nach dem Schneiden, die erforderlich ist, um die suberinisierten Zellschichten vom Wundperiderm abzustreifen – Durée de conservation minimale après coupure du tubercule, pour détacher la couche subérisée de la surface endommagée*

Tabelle 1. Einfluss der Lagerungstemperatur auf die Geschwindigkeit der Suberinisierung und Wundperidermbildung.

Tableau 1. Influence de la température de conservation sur la vitesse de subérisation et la formation de périderme de cicatrisation.

stainable material (suberin) on the outer parenchyma cells was observed after one day and periderm initiation after 2 days in tuber halves at 25 °C. At this temperature, 3–4 suberized cell layers below the wound surface and a continuous and well formed periderm comprising 4 to 6 layers of elongated cells beneath the suberized cells was evident 4 to 5 days after cutting (Fig. 1). On further storage deposition of suberin was also noticed on the cell walls of the newly formed periderm layer. In tuber halves kept at 20 and 28–30 °C, suberization and periderm development proceeded rather slowly whereas at 15 and 10 °C, both suberization and periderm formation was considerably delayed. After 15 days at 15 °C there was a well formed periderm consisting of 3–5 cell layers

Fig. 1. Histological changes during wound healing of gamma-irradiated and non-irradiated potato tubers stored at 25 °C.



Natural skin – *Natürliche Schale – Peau naturelle*
Suberized periderm layer – *Suberinisierte Peridermschicht – Couche de périderme subérisé*
Normal dense starch containing cells – *Normale, viel Stärke enthaltende Zellen – Cellules normales à forte teneur d'amidon*
Suberized starch containing cells – *Suberinisierte, Stärke enthaltende Zellen – Couche subérisée contenant de l'amidon*
Discontinuous periderm layer – *Unterbrochene Peridermschicht – Couche de périderme discontinue*
Control day – *Kontrolle Tag – Jour témoin*
Periderm – *Periderm – Périderme*
Dense starch layer – *Viel Stärke enthaltende Zellschicht – Couche à forte teneur en amidon*

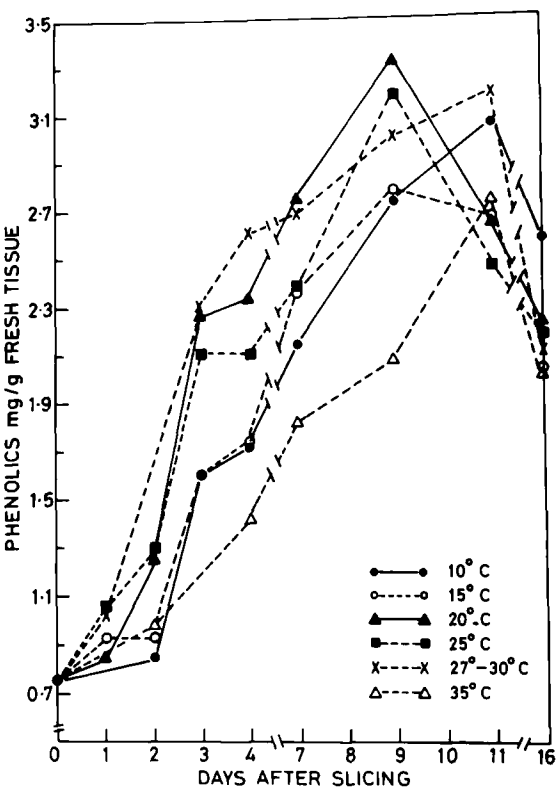
Abb. 1. Histologische Veränderungen während der Wundheilung bestrahlter und unbestrahlter Kartoffelknollen, Lagerung bei 25 °C.
Fig. 1. Changements histologiques pendant la cicatrisation de tubercules irradiés et non irradiés, conservés à 25 °C.

whereas at 10 °C it was a discontinuous layer consisting of only 2 to 3 cell layers. At 35 °C periderm formation was inhibited and suberization was retarded.

Effect of irradiation on suberization and periderm development

Histochemical observations showed that suberization progressed at a similar rate in tuber halves of control tubers and in tubers irradiated to doses ranging from 5 to 100 Gy of gamma rays and stored at 25 °C. However, the formation of the wound periderm was inhibited by doses as low as 20 to 30 Gy. In tubers subjected to 5 and 10 Gy, the wound periderm layer often showed discontinuity with the presence of occasional large paren-

Fig. 2. Pattern of polyphenol-formation in suberizing tissue layers of wounded potato tubers as affected by temperature.



Phenolics mg/g fresh tissue – *Phenole mg/g Frischgewicht – Teneur en phénols en mg/g de tissu frais*

Days after slicing – *Tage nach dem Schneiden – Jours après coupure*

Abb. 2. Einfluss der Temperatur auf die Polyphenolbildung in den suberinisierten Zellschichten verletzter Kartoffelknollen.

Fig. 2. Evolution de la teneur en polyphénols dans des couches se tubérisant après endommagement des tissus, en fonction de la température des tubercules.

chyma cells (Fig. 1). The newly formed wound periderm layer in control tubers could be easily stripped off the wound surface whereas in tubers irradiated to 20 Gy and above it could not be removed easily.

Polyphenol accumulation during wound-healing

The time-course of formation of polyphenolic compounds as a function of storage temperature in Fig. 2 shows that the rate of polyphenol formation was of a similar magnitude in tuber halves stored at 20, 25 and 28–30 °C as compared to a slower rate at 15 and 10 °C whereas at 35 °C it was considerably reduced. A comparative evaluation of polyphenolics in 14-day suberized tuber halves showed higher levels of polyphenolics in irradiated than in non-irradiated control tuber (Table 3).

Starch degradation as evidenced by disappearance of starch granules in parenchyma cells below the wound surface was visible under the microscope 24 h after slicing the tubers and this was not affected by the irradiation dose.

Discussion

Suberin is thought to play a key role in preventing weight loss (Kolattukudy & Dean, 1974; Soliday et al., 1979) and decay (Fox et al., 1971) of potato tubers while the cork layer acts as a barrier that is not usually penetrable by the pathogen (Agrios, 1969). The results of this study provide evidence for deposition of suberin within 24 h of slicing in

Table 2. Effect of gamma irradiation on suberization and periderm development in potato tuber halves at 25 °C, 90–95 % RH.

Treatment[1]	Number of cell layers stained[2]		Number of periderm cells observed[4]	
	Day[3]	Day 10	Day 4	Day 10
Control[5]	3–4	4–5	4–5, continuous cell layers[6]	4–6, continous cell layers
5 Gy	3–4	4–5	4–5, almost continuous cell layers with occasional break[7]	4–5, almost continuous cell layers with occasional break
10 Gy	3–4	4–5	3–4, discontinuous cell layers[8]	3–4, discontinuous cell layers
20 Gy	3–4	3–4	2–3, discontinuous cell layers	2–3, discontinuous cell layers
30 Gy	3–4	3–4	No periderm developed[9]	No periderm developed
50 Gy	3–4	3–4	No periderm developed	No periderm developed
100 Gy	3–4	3–4	No periderm developed	No periderm developed

[1] *Behandlung – Traitement;* [2] *Zahl der angefärbten Zellschichten – Nombre de couches cellulaires colorées;* [3] *Tag – Jour;* [4] *Zahl der beobachteten Peridermzellen – Nombre de cellules de périderme observées;* [5] *Kontrolle – Témoin;* [6] *Durchgehende Zellschichten – Couches cellulaires continues;* [7] *Fast durchgehende Zellschichten mit Brüchen an verschiedenen Stellen – Couches cellulaires continues dans l'ensemble, avec quelques ruptures;* [8] *Unterbrochene Zellschichten – Couches cellulaires discontinues;* [9] *Keine Peridermbildung – Périderme non développé*

Tabelle 2. Einfluss der Bestrahlung auf die Suberinisierung und Peridermentwicklung in Kartoffelknollenhälften bei 25 °C, 90–95 % rLf.

Tableau 2. Effet d'une irradiation gamma sur la subérisation et le développement d'un périderme sur des moitiés de tubercules à 25 °C, 90–95 % HR.

Table 3. Polyphenolics content of suberized cell layers below the wound surface as affected by gamma irradiation.*

Treatment[1]	Polyphenolics (mg/g fresh tissue)[2]	Increase over control value[3] (%)
Control[4]	2.85 ± 0.15	-
10 Gy	3.29 ± 0.03	15.4
30 Gy	3.19 ± 0.01	10.6
50 Gy	4.14 ± 0.10	45.2
100 Gy	3.38 ± 0.06	18.8

* The first 1 mm thick layer below the wound surface was used for the estimation of polyphenolics. Tuber halves were allowed to suberize at 25 °C. Values are mean of two independent estimations *- Für die Bestimmung der Polyphenole wurde die erste 1 mm dicke Zellschicht unter der Wundoberfläche verwendet. Die Suberinisierung der Knollenhälften erfolgte bei 25 °C. Die Werte sind Mittelwerte aus 2 unabhängigen Bestimmungen - La première couche d'1 mm d'épaisseur sous la surface endommagée a servi à l'estimation de la teneur en polyphénols. Les moitiés de tubercules ont pu subériser à 25 °C. Les valeurs sont une moyenne de 2 estimations indépendantes.*

[1] *Behandlung - Traitement;* [2] *Frischgewicht - Tissu frais;* [3] *Steigerung gegenüber der Kontrolle - Augmentation par rapport au témoin;* [4] *Kontrolle - Témoin*

Tabelle 3. Einfluss der Bestrahlung auf den Polyphenolgehalt der suberinisierten Zellschichten unter der Wundoberfläche.
Tableau 3. Teneur en polyphénols après irradiation gamma des couches cellulaires subérisées sous la surface d'endommagement.

tubers kept at 25 °C which agrees with similar observations by others (Artschwager, 1927; Borchert & Mcchesney, 1973; Ali et al, 1975). Our results also show that suberization and periderm development occur most rapidly at 25 °C. Though both these processes are not much affected up to 28–30 °C, a temperature of 35 °C prevented wound periderm development and retarded suberization. This confirms the earlier observations of Artschwager (1979).

Although quantitation of suberin deposited on cell layers below the wound surface has not been carried out, the histochemical evidence indicates that suberization is not affected by irradiation up to 100 Gy. This conclusion is supported by the data on the level of soluble phenols in the suberizing layers of irradiated tubers since phenolic materials are reported to constitute 50 to 75 % of the suberin polymer (Dean & Kolattukudy, 1977). Our results point to a generally increased accumulation of soluble phenols in irradiated tubers in response to cutting, which is contradictory to the observation of Ogawa et al. (1968), although it may be attributed to the different methods used for the estimation of soluble phenols.

It is interesting to note that the wound-induced periderm development is prevented by irradiation at doses as low as 20 to 30 Gy whereas the minimum dose required for sprout inhibition of tubers which were in a dormant state was 50 Gy. Both wound-induced periderm development and sprouting involve mitotic activity. Our results indicate that meristems in resting buds of potato tubers are apparently less sensitive to irradiation than nuclei of the potential periderm cells. The observation that suberized top cell layers can be easily stripped off the wound surface of the control tuber halves in comparison to

tubers irradiated to 20 Gy and above may provide a method for the identification of potatoes irradiated for sprout inhibition.

The results of the present study indicate that the high incidence of bacterial soft rot occurring in potatoes during storage at tropical ambient temperatures may be due to an impairment of the wound healing processes in addition to the possible enhanced virulence or pathogenicity of the rot organisms at such temperatures. Similarly the increased tendency of irradiated potatoes to microbial spoilage during storage may be attributed to the lack of wound periderm formation in addition to the suppression of natural immunity due to the reduced capacity of the tuber tissues to form phytoalexins in response to infection (El-Sayed, 1975, 1978).

Zusammenfassung

Einfluss von Temperatur und Bestrahlung auf die durch Verletzung induzierte Suberin- und Peridermentwicklung in Kartoffelknollen

Um die möglichen Gründe für den gesteigerten mikrobiellen Abbau von Kartoffein während der Lagerung unter tropischen Umweltbedingungen oder nach der Bestrahlung mit Röntgenstrahlen zur Keimhemmung aufzuklären, wurde der Einfluss von Temperatur und Bestrahlung auf die durch Verletzung induzierte Suberin- und Peridermentwicklung untersucht.

Es zeigte sich, dass sowohl die Suberinisierung als auch die Peridermentwicklung bei 25 °C schneller verlaufen, während sie bei 10–15 °C verlangsamt sind. Temperaturen über 35 °C verhindern die Peridermbildung und verzögern die Suberinisierung (Tabelle 1). Das Ausmass der Polyphenolbildung war im 1 mm unter der Verletzung bei 20, 25 und 28–30 °C ähnlich der bei 10 °C und 15 °C während es bei 35 °C verringert war (Abb. 2).

Histochemische Untersuchungen zeigten, dass die Suberinisierung in unbestrahlten Knollen und in Knollen, die bis zu 100 Gy erhalten hatten, der optimalen Dosis für die Keimhemmung, im gleichen Ausmass erfolgte (Tabelle 2). Aus diesen Ergebnissen wird geschlossen, dass der Verdopplungsmechanismus der DNS auf Bestrahlung empfindlicher reagiert als die Suberinsynthese. Der Gehalt an Polyphenolen in den suberinisierten Zellschichten war in bestrahlten Knollen vergleichsweise höher (Tabelle 3). 20–30 Gy an Röntgenstrahlen reichten aus, um die Wundperidermbildung zu unterbinden (Tabelle 2 und Abb. 1), während für die Keimhemmung eine Minimaldosis von 50 Gy benötigt wurde. Das bedeutet, dass die Meristeme in den ruhenden Knospen auf die Bestrahlung weniger empfindlich reagieren als die Kerne in den potentiellen Peridermzellen. Die suberinisierten Zellschichten können von der Wundoberfläche unbestrahlter Knollenhälften leicht abgeschoben werden, während das bei Knollen, die einer Bestrahlung von 20 Gy und mehr ausgesetzt waren, nicht möglich ist. Dieser Unterschied könnte als Methode zur Identifizierung bestrahlter Knollen verwendet werden.

Die Ergebnisse zeigen, dass die Schädigung der Wundperidermentwicklung ein Hauptgrund für die gesteigerte mikrobielle Fäule von Kartoffelknollen während der Lagerung bei tropischen Temperaturen oder nach Bestrahlung zur Keimhemmung ist.

Résumé

Influence de la température et de l'irradiation sur la subérisation d'une blessure occasionnée et sur le développement du périderme

L'influence de la température et de l'irradiation sur la subérisation d'une blessure occasionnée et sur le développement du périderme a été étudiée, dans le but d'expliquer les déchets de pourritures microbiennes sur des tubercules mis en conservation sous des conditions de climat tropical ou à la suite d'une exposition aux rayons gamma en vue de l'inhibition de la

germination.

Le développement du périderme et la subérisation se sont effectués rapidement à 25 °C mais les réactions ont été retardées à 10 ou 15 °C. Une température de 35 °C a empêché la formation de périderme et retardé la subérisation (tableau 1). Le taux de polyphénol dans la 1ère couche d'1 mm sous la blessure était sensiblement le même à 10, 15, 20, 25 et 28-30 °C mais il avait diminué à 35 °C (figure 2).

Les résultats de l'analyse hystochimique ont montré que la subérisation avait progressé à vitesse égale pour des tubercules non-irradiés et des tubercules irradiés à plus de 100 Gy, dose optimale correspondant à l'inhibition de la germination. Ces résultats suggèrent que le mécanisme de réplication de l'ADN est plus sensible à la radiation que la biosynthèse de la subérine. Le niveau de polyphénols dans les couches cellulaires en voie de subérisation était plus élevé dans les tubercules irradiés que dans les tubercules non irradiés (tableau 3). 20 à 30 Gy de rayons gamma ont suffi pour empêcher la formation du périderme de cicatrisation (tableau 2 et figure 1) tandis que la dose minimale nécessaire à l'inhibition de la germination était de 50 Gy. Les méristèmes de germes en dormance seraient donc moins sensibles à l'irradiation que les noyaux des cellules du périderme potentiel. Les couches cellulaires subérisées peuvent facilement se détacher de la surface endommagée lorsqu'il s'agit de tubercules non irradiés, tandis qu'elles sont difficilement séparables dans le cas de tubercules exposés à 20 Gy ou plus. Cette différence peut conduire à une méthode d'identification des tubercules irradiés.

La recrudescence des pourritures microbiennes sur tubercules mis en conservation à des températures tropicales ou exposés aux rayons gamma en vue d'inhibition de la germination, semble liée principalement au ralentissement du développement d'un périderme de cicatrisation.

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