Effects of Potato Tuber Age and Storage on Sesquiterpenoid Stress Metabolite Accumulation, Steroid Glycoalkaloid Accumulation, and Response to Abscisic and Arachidonic Acids

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ABSTRACT

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Incompatible races of *Phytophthora infestans* elicited a hypersensitive response in potato slices from tubers stored at 4 C. The response was characterized in part by the rapid accumulation of the fungitoxic sesquiterpenes, rishitin and lubimin. Compatible races grew and sporulated on slices from stored tubers and elicited little or no sesquiterpene accumulation. Potato slices from unstored tubers harvested in July, August, and September, however, accumulated low levels of rishitin and lubimin after inoculation with an incompatible race. Sesquiterpene accumulations in inoculated potato slices from tubers before cold storage were 10–20% of those from tubers after cold storage. Sesquiterpene accumulations were not different in slices from unstored tubers inoculated with a compatible or incompatible race, even though the disease reactions to these races were similar to those observed in slices from stored tubers. Storage at 4 C generally increased the accumulation of sesquiterpenes in slices treated with crude elicitor preparations from the fungus. Abscisic acid (ABA), which inhibits rishitin and lubimin accumulation and enables incompatible races to grow and sporulate on slices from tubers stored at 4 C, was ineffective in this regard in the unstored tubers. ABA increased sesquiterpene accumulations in the unstored tuber slices subsequently inoculated with an incompatible race and did not enable incompatible races to grow and sporulate. Storage of the tubers for at least 5 mo was required for ABA to reduce sesquiterpene accumulations and to induce compatibility to an incompatible race in potato slices. The pattern of accumulation of steroid glycoalkaloids did not appear to change dramatically in slices from tubers before or after cold storage. The results raise questions about the role of sesquiterpenoid phytoalexins as the sole determinants of resistance in the reaction of potato tubers to infection with *P. infestans*.

Additional key word: phytoalexins.

Terpenoid compounds have figured prominently in investigations of disease resistance mechanisms in the potato (15). Sesquiterpenoid stress metabolites (SSM) accumulate in tuber tissue during the hypersensitive response to incompatible races of the late blight fungus, *Phytophthora infestans* (Mont.) de Bary. At least five SSM are phytoalexins and have been implicated as disease resistance factors, although rigorous proof of their role in this regard is lacking. Wounding of potato tubers elicits the accumulation of fungitoxic steroid glycoalkaloids (SGA), whereas infection by either compatible or incompatible races of *P. infestans* suppresses SGA accumulation (19). The accumulation of SSM in the hypersensitive response and SGA in the wound response occurs by de novo synthesis via the acetate-mevalonate pathway (15).

Results of other studies have shown that tuber storage conditions can affect the accumulation of SSM in tissue slices (23). Zacharius et al (28) found that Kennebec tuber slices inoculated with an incompatible race of *P. infestans* contained higher levels of SSM if the tubers had been stored at 3.3 C than those stored at 10 C prior to challenge. Cheema and Haard (7) used toxic mercuric salts as elicitors and reported higher accumulations of SSM in slices from tubers stored for 1 mo at 4 C than in slices from tubers stored at 25 C. Fitzpatrick et al (9) reported that, in contrast to the SSM, SGA accumulations in potato slices did not change dramatically during storage of the tubers. Instead, they observed only somewhat reduced levels of total glycoalkaloids after prolonged storage and minor qualitative differences in the spectrum of glycoalkaloids accumulating in slices from potato cultivars.

Because potato tubers are used extensively in basic studies on disease resistance mechanisms, it is important to obtain additional information about factors that may affect the metabolic response of tubers to wounding and infection. In all of our previous studies, we used tubers stored at 4 C for at least 1 mo after harvest. The purpose of this investigation was to determine the accumulation of terpenoids in potato slices during tuber development and subsequent storage of the mature tubers at 4 C. The various agents used to elicit or suppress potato terpenoids were those used routinely in our studies of SSM and SGA metabolism and included compatible and incompatible races of *P. infestans*, elicitors from mycelium of *P. infestans*, and arachidonic and abscisic acids (4,13).

MATERIALS AND METHODS

General. Kennebec potatoes were used in all experiments and were grown at the experimental farm of the University of Kentucky from certified seed tubers (Fayette Seed Co., Lexington, KY 40506). Immature tubers were collected from plants growing in the field and were used immediately after collection for SSM and SGA experiments. Mature (fully expanded) tubers, harvested in August 1979 or September 1980, were used immediately for SSM and SGA assays or kept at ambient temperatures for 4–5 days after harvest and then stored in a cold room at 4 C. The stored tubers were removed from the cold room and kept at room temperature for 24 hr prior to being used in experiments. For a number of treatment dates, slices from "old tubers" (tubers from the previous season's crop and the same batch used for planting but stored at 4 C for at least 8 mo) were compared with "new tubers" (ie, current season's crop either unstored or stored at 4 C).

Assays. Tuber slices were inoculated with spore suspensions from compatible or incompatible races of *P. infestans* or treated with a crude elicitor preparation consisting of sonicated mycelium from the fungus (13). The predominant SSM, rishitin and lubimin, were extracted from the upper millimeter of the treated tuber slices and quantified by gas chromatography (11).

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SGA were extracted from aged tuber slices by a modification of previously published methods (19). Slices were prepared as for SSM analyses and incubated at 19 C until extraction. Ten-gram samples (fresh weight) per treatment were obtained from the upper 2 mm after 72 hr of aging. Each sample was homogenized in 100 ml of a mixture containing chloroform, acetic acid, and methanol (CAM, 50:5:45, v/v) for 2 min. The homogenate was held at room temperature overnight and then filtered through Whatman 54 filter paper with suction. The residue was washed with two 50-ml aliquots of CAM. The filtrates were combined and concentrated to near dryness by rotary evaporation under reduced pressure and brought to 20 ml with 2% aqueous acetic acid. The extracts were washed with an equal volume of chloroform, and the aqueous phase was collected and concentrated to approximately 10 ml by rotary evaporation. Insoluble material was removed by centrifugation at 10,000 *g* for 10 min. The pH of the supernatant was adjusted to >10 with concentrated NH_4OH and the mixture was heated for 30 min at 80 C in a water bath or oven. The extract was then placed at 4 C for at least 4 hr. The precipitated steroid glycoalkaloids were collected by centrifugation at 10,000 *g* for 10 min and the pellet was dried in a desiccator over P_2O_5.

Total glycoalkaloids were determined by a spectrophotometric assay (6). The dried extracts were suspended by sonication in 3 ml of 5% aqueous acetic acid. One-half milliliter of the sample was mixed with 1.5 ml of 85% H_3PO_4. One milliliter of freshly prepared paraformaldehyde reagent (0.2 g *p*-formaldehyde dissolved in 15 ml of distilled water and diluted to 100 ml with 85% H_3PO_4) was added, mixed in a vortex mixer, and then incubated at 60 C for 10 min. The absorbance of the samples at 600 nm was determined and values for glycoalkaloids were calculated by using a standard curve based on α-solanine (Sigma Chemical Co., St. Louis, MO 63178). Duplicate or triplicate determinations were made on each extract and two extracts were obtained per treatment.

Thin-layer chromatography was performed on silica-gel G (Uniplates, Analtech, Inc., Newark, DE 19711) with CAM as the developing solvent. Spots were visualized by spraying with a saturated solution of $SbCl_3$ in chloroform (Carr-Price reagent) and heating at 100 C for several minutes.

The methods used in the experiments with ABA (±-*cis*, *trans*-abscisic acid, Sigma) and with arachidonic acid (all *cis*-5,8,11,14-eicosatetraenoic acid, Sigma) were described in previous articles (4,13). Tuber slices were treated with 0.1 ml of 5% methanol or 0.1 ml of 5% methanol containing 100 μg ABA within 1 hr after cutting and 6 hr later were treated with 0.1 ml of an aqueous suspension of arachidonic acid (100 μg per slice). Rishitin and lubimin were extracted from the upper millimeter of tuber tissue 96 hr after the second treatment.

RESULTS

Effect of storage on SSM accumulation. SSM accumulations were low in slices from unstored tubers harvested in July, August, or September and inoculated with incompatible or compatible races (Fig. 1). After 1 mo of storage at 4 C, tubers responded to incompatible races by accumulating high amounts of SSM, but the compatible race elicited little or no accumulation. A similar effect of storage at 4 C on the SSM response was also observed in potato slices treated with a cell-free mycelial sonicate (Fig. 1). The disease reaction of slices from unstored tubers to these races did not appear different from that observed in slices from stored tubers. Regardless of harvest date or storage at 4 C, mycelial growth and sporulation were observed in slices inoculated with the compatible race 1.2.3.4 and a strong hypersensitive response was elicited by the incompatible races 0 and 4.

The accumulation of SSM in unstored tubers harvested in July, August, and September remained low throughout the period of time course studies (Fig. 2). In some experiments, accumulations were higher in the compatible than in the incompatible reactions of slices from unstored tubers. SSM accumulations in the inoculated slices from the old tubers stored for 9–11 mo showed the typical pattern, with high levels accumulating in the incompatible reaction and low levels accumulating in the compatible reaction (Fig. 2).

The effect of storage, ABA, and arachidonic acid on disease development and SSM accumulation. ABA at 100 μg per slice increased browning and SSM accumulations in unstored tubers harvested in July and September and inoculated with incompatible

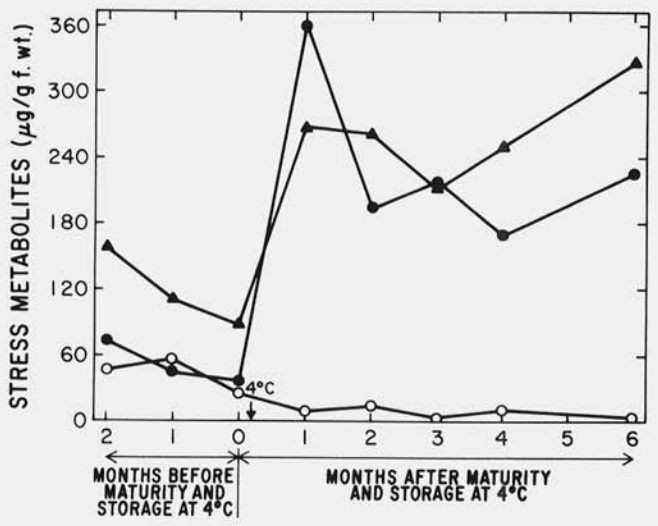

Fig. 1. The effect of cold storage on sesquiterpenoid stress metabolite accumulation (rishitin + lubimin) in Kennebec potato tubers. The reported values are the averaged data from the 1979 and 1980 growing seasons. Slices were prepared from unstored, fresh tubers sampled 0, 1, and 2 mo before maturity, or from tubers harvested at maturity and stored at 4 C beginning 1 wk after harvest. Slices were aged for 6–8 hr and then inoculated with 10^5 spores per slice of race 0 or race 4 of *Phytophthora infestans* (incompatible races, combined data), •——•; inoculated with 10^5 spores per slice of race 1.2.3.4 (compatible), O——O; or treated with a crude elicitor preparation consisting of sonicated mycelium of race 4, ▲——▲. The SSM were extracted 96 hr after inoculation or treatment.

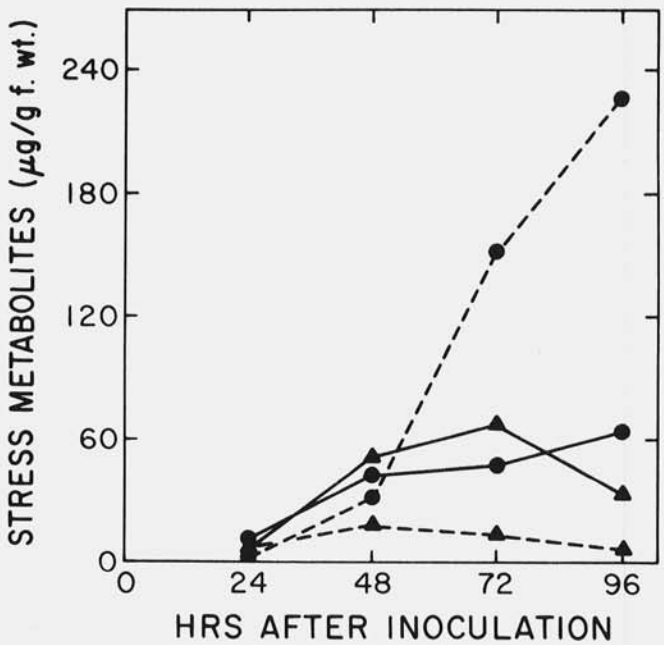

Fig. 2. Sesquiterpenoid stress metabolite (rishitin + lubimin) accumulation in slices from immature, mature, and stored Kennebec potato tubers as a function of time after inoculation with spores of *Phytophthora infestans*. Slices inoculated with 10^5 spores per slice of an incompatible race (0 or 4, averaged data), •; inoculated with 10^5 spores per slice of race 1.2.3.4 (compatible), ▲. Solid lines are the averaged data from experiments using freshly harvested immature and mature tubers. Broken lines are the averaged data using mature tubers stored at 4 C for 9–11 mo.

races of *P. infestans*. It did not induce compatibility to these races (Figs. 3 and 4). It was not until after 5 mo of storage of the tubers at 4 C that ABA inhibited SSM accumulation and induced compatibility. On several sampling dates old tubers, which had been in storage for at least 9 mo, were assayed with the new tubers. Treatment with ABA prior to inoculation with the incompatible race always reduced SSM accumulation in old tubers and induced compatibility.

In old tubers, 100 μg of ABA per slice inhibited the elicitor activity of 100 μg of arachidonic acid per slice by 91%. In new tubers sampled during the first 3 mo of storage, 100 μg of ABA per slice reduced the elicitor activity of 100 μg of arachidonic acid per slice by only 29%. In the newly stored tubers, only the elicitor activity of lower concentrations of arachidonic acid (25 μg per slice) was inhibited by ABA to the same degree as that observed in the old tubers.

Steroid glycoalkaloid accumulation. Although the variation among experiments was considerable, the pattern of SGA accumulation in new tubers did not appear to markedly change before or after cold storage. SGA accumulations were slightly higher in slices from new-unstored or stored tubers than slices from old-stored tubers (Table 1). Treatment with ABA had, at best, a slight inhibitory effect at 100 μg per slice and stimulatory effect at 1–5 μg per slice on SGA accumulation.

DISCUSSION

The results indicate that SSM accumulation in Kennebec potato slices changes dramatically after storage of the tubers at 4 C. SSM accumulations in unstored tubers, collected from plants in the field during July, August, and September, were not different in incompatible and compatible interactions. Accumulations in Kennebec tuber slices of the other major fungitoxic sesquiterpenes, phytuberin and solavetivone, also were low prior to storage at 4 C. This raises questions about the unique role of these compounds in the disease resistance of potato tubers and would imply that mechanisms other than SSM accumulation are important.

The increase in SSM accumulations after inoculation with incompatible races of *P. infestans* was evident after 1 mo of storage at 4 C, but the change in response of tuber slices treated with ABA and inoculated with an incompatible race occurred after 5 mo of cold storage. A possible explanation for the lack of suppression of SSM accumulation by ABA in inoculated slices from new-stored tubers is that these tubers are more responsive to elicitors produced by the fungus. In support of this are the findings that arachidonic acid generally elicited higher levels of SSM in new-stored tubers than in old tubers (3–5) and that the elicitor activities of low concentrations of arachidonic acid (<25 μg per slice) were markedly inhibited by ABA.

Although the concentrations of ABA used in these experiments greatly exceed endogenous levels in potato (3,20), ABA could be a useful chemical for studying the host-parasite interaction. ABA inhibits protein and nucleic acid synthesis in plant tissues (26), and its inhibition of the hypersensitive response could be similar to that observed with other metabolic inhibitors (8,18). However, in contrast to other inhibitors, ABA clearly induces compatibility. The fungus, *Cercospora rosicola*, produces ABA (2), and it would

TABLE 1. The effect of abscisic acid (ABA) on steroid glycoalkaloid accumulation in aged potato slices from new-unstored, new-stored, and old-stored Kennebec tubers[a]

Treatment	Steroid glycoalkaloids (μg/g fr. wt.)		
	New-unstored tubers	New-stored tubers	Old-stored tubers
5% methanol	188 + 33	239 ± 24	118 ± 10
1 μg ABA per slice	N.D.[b]	364 ± 44	164 ± 1
5 μg ABA per slice	381 ± 114	364 ± 47	166 ± 18
10 μg ABA per slice	N.D.	250 ± 11	177 ± 22
100 μg ABA per slice	155 ± 47	205 ± 29	84 ± 9
Unaged	N.D.	42 ± 4	41 ± 6

[a] Values are the mean and standard error of total SGA extracted after 72 hr of aging at 19 C. New-unstored tubers were tubers collected at 0, 1, and 2 mo before maturity from plants in the field and not stored at 4 C prior to assay. New-stored tubers were tubers stored at 4 C and sampled periodically during the first 3 mo of storage. Old-stored tubers were those that had been in cold storage for 8–12 months. Potato slices were washed with sterile, deionized water and then treated with 0.1 ml of 5% methanol or with 0.1 ml of 5% methanol containing the appropriate concentration of ABA within 1 hr after cutting. Unaged tissue was not treated with 5% methanol.

[b] N.D. = not determined.

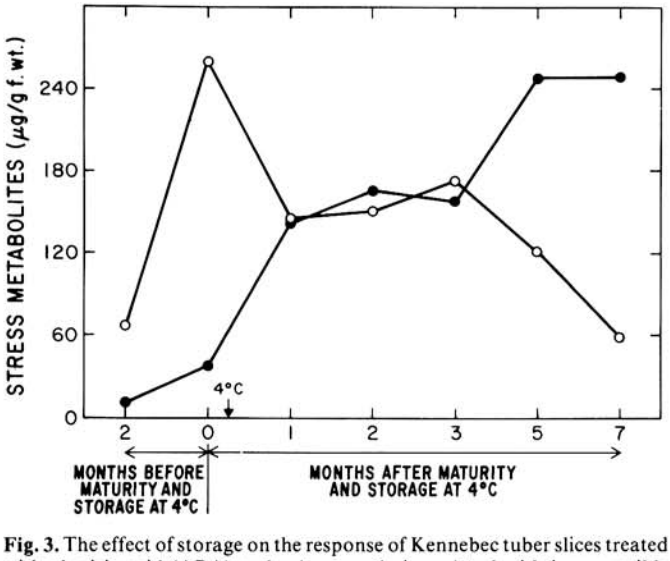

Fig. 3. The effect of storage on the response of Kennebec tuber slices treated with abscisic acid (ABA) and subsequently inoculated with incompatible race 4 of *Phytophthora infestans*. Slices were treated with 0.1 ml of 5% methanol (•——•) or 0.1 ml of 5% methanol containing 100 μg of ABA (O——O) and inoculated 6–10 hr later with 5×10^4 spores of race 4. In the September sampling, the potatoes were assayed prior to cold storage as indicated by the arrow. Mature new potatoes were harvested in September 1980.

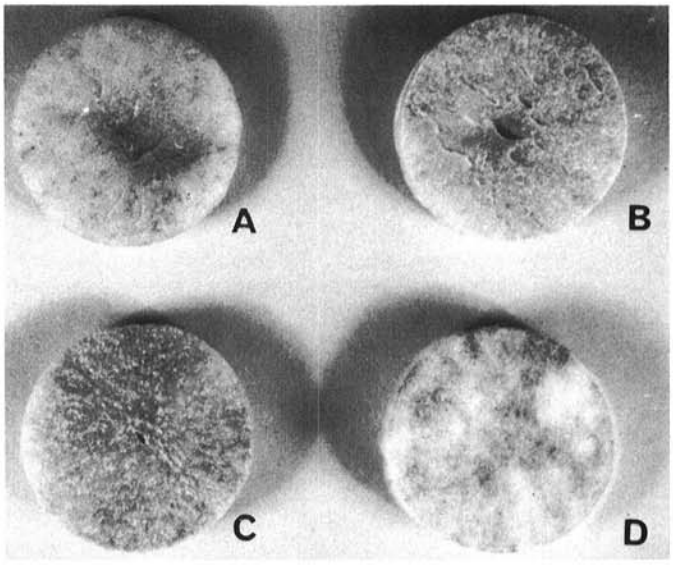

Fig. 4. The effect of abscisic acid on the resistance of Kennebec potato slices from new-unstored and old-stored tubers to race 4 of *Phytophthora infestans*. **A,** Slice from a new tuber treated with 0.1 ml of 5% methanol followed by 5×10^4 spores of race 4; **B,** slice from a new tuber treated with 0.1 ml of 5% methanol containing 100 μg ABA followed by race 4; **C,** slice from an old tuber treated with 5% methanol followed by race 4; **D,** slice from an old tuber treated with ABA followed by race 4.

be interesting if compatible races of *P. infestans* produce compounds that effect similar metabolic changes in potato.

The stimulation of SSM accumulation by ABA in inoculated slices from new-unstored tubers is perplexing. A possible explanation is that SSM metabolism may be regulated by a number of phytohormones, the levels of which change during development and storage of the tubers, and that the response of the tissue may be determined by the balance of interacting phytohormones rather than the absolute amount of any one (14). In other plants, the balance of hormones can determine the disease reactions of tissues to pathogens. For example, increasing the cytokinin-to-auxin ratio prevents the hypersensitive response and induces compatibility in tobacco callus to an incompatible race of *Phytophthora parasitica* var. *nicotiana* (10).

SGA accumulations in aged tuber slices did not change dramatically during storage of the tuber or in response to ABA. The results suggest that the processes during storage that influence SSM accumulations are independent of those that influence accumulations of SGA. One interpretation of these results is that ABA does not inhibit SSM accumulation in the acetate-mevalonate pathway at a point prior to the synthesis of farnesyl-pyrophosphate.

Tuber slices not washed in deionized water prior to aging had more than twice the SGA content than did washed slices (3). The patterns of stimulation and inhibition by ABA and washing were similar to their reported effects on suberization (20). The inhibitory effect of washing on SGA accumulation and suberization might be explained in part by an inhibition of protein synthesis that occurs in potato slices exposed to a hypotonic medium (17).

The capacity for CN-resistant respiration increases markedly in aged potato slices after cold storage of the tubers (16,24,25) and almost parallels the change in SSM response reported in this paper. Perhaps the CN-resistant pathway is involved in SSM metabolism as suggested by Alves et al (1). The nature of this involvement is obscure, although the capacity to respond to ethylene, which accompanies the development of CN-insensitivity (21,22), and the promoting effect of ethylene on SSM accumulation (1,12) might explain the results.

Potato tubers are a rich source for enzymes that could be involved in the release and metabolism of the fatty acid elicitors produced by *P. infestans* (4). Both lipolytic acyl hydrolase and lipoxygenase activities are initially low in freshly harvested tubers, but increase dramatically during the first month of storage (27). This fact, together with the observations in this paper, strongly suggest that the relationship of these enzymes to the elicitation of fungitoxic sesquiterpenes by incompatible races of *P. infestans* should be examined.

The data reported here indicate that the SSM response of potato tuber to *P. infestans* is affected markedly by the changes occurring in tuber physiology after storage. Although the results raise doubts about the role of fungitoxic sesquiterpenes as sole determinants of disease resistance in the interaction of potato tuber tissue and *P. infestans*, they also suggest intriguing avenues for further investigations. Emphasis should be placed on the identification of other disease resistance mechanisms in the potato, hormonal regulation of these resistance mechanisms, and the relationship, if any, of CN-resistant respiration to these mechanisms.

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