Soft Rot Susceptibility of Potatoes with High Reducing Sugar Content

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ABSTRACT

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A highly significant correlation (r = 0.65) was obtained between reducing sugar (RS) content and soft rot severity in Norgold Russet potato tubers of various ages held at different storage temperatures. Tubers cool stored at 3–6 C had elevated levels of RS and developed more soft rot per tuber than did tubers warm stored at 21–26 C that had lower amounts of RS. Reconditioned tubers (warmed after cool storage) developed an intermediate amount of soft rot. Similarly, stem-end tuber parts with higher RS content developed more soft rot than did bud ends containing lower amounts of RS. When inoculated tubers were incubated in mineral oil or water, significantly more soft rot developed in water-immersed tubers irrespective of RS content. Oil immersion of tubers had no effect on soft rot development compared to that in nonimmersed tubers. Wound inoculation of tubers of Norgold and a relatively low-RS cultivar, Norchip, resulted in less soft rot in Norchip. However, lenticel infection was more severe in Norchip, which implies two types of soft rot susceptibility/resistance in potatoes. Soft rot severity as well as RS content during various points of a tuber "life cycle" are shown. The significance of RS in tubers is discussed in relation to soft rot development and in view of contrasting evidence reported from in vitro studies showing polygalacturonase transeliminase repression by glucose.

Erwinia carotovora var. *atroseptica* (van Hall) Dye is the main causal agent of potato soft rot in storage (22,26). Disease development is influenced by harvest and storage conditions (5,17,19,21), of which tuber wetness is the most important. Pathogenicity of the organism is mainly dependent on the activity of pectic enzymes (1,2,11,15). Pectate lyase is the principal enzyme that determines virulence in the pathogen (7), but other enzymes also are involved (11,12,33).

Results of various studies indicate the repression of pectic enzymes by sugars, especially glucose and sucrose, and the consequent retardation or inhibition of disease development in many host-pathogen systems (2,3,16,25). Interestingly, Hubbard et al (10) showed reversal of glucose repression of pectate lyase (PL) by adenosine 3′5′-cyclic monophosphate (cAMP) in *E. carotovora*. Furthermore, synthesis of PL was under the direct control of the cAMP regulatory mechanism. Most of these studies, however, were performed in virtro or in artificial host-pathogen systems.

Reducing sugars (RS) are important to the potato industry because processing of tubers with high RS content produces dark chips and fries which are undesirable (9,28). The primary RS present in potato tubers are glucose and fructose in approximately equal amounts (27,31). Content of RS in potato tubers varies in different cultivars, but storage factors, mainly temperature, may greatly alter sugar content. Cool storage usually causes accumulation of RS, resulting in higher RS levels (13,32); therefore, it is common practice to warm tubers for 3–4 wk prior to processing in order to lower RS levels. This process is referred to as "reconditioning."

Levels of RS differ between the stem end and bud end of the tuber (14,35), and between different potato cultivars (34). Iritani and Weller (13) reported that immature tubers have low RS levels that increase during cool storage. Furthermore, they noticed differences between potato cultivars Russet Burbank and Kennebec in the ability to accumulate and lose RS by temperature manipulation, Kennebec being the most responsive. None of these studies related RS levels to soft rot decay or susceptibility to decay. However, Kohn and Hendrix (18) reported significant correlation (r^2 = 72.3) between increasing sugar content of apples and increasing incidence of white rot caused by *Botryosphaeria dothidea*.

Because RS levels in tubers can be easily manipulated by harvest date (maturity) (13,23) and storage temperature, potatoes provide an interesting tool for studying the role of RS in disease development of a natural system. The objectives of this investigation were to detect differences in soft rot susceptibility of variously treated and conditioned tubers and to relate these differences to in vivo RS levels.

MATERIALS AND METHODS

Inoculum preparation. *Erwinia carotovora* var. *atroseptica* (Eca) was isolated on Stewart's medium (30) from a potato stem with blackleg. The isolate caused tuber decay and typical blackleg symptoms of potato in the greenhouse and conformed to the biochemical tests listed by Dye (6) and Graham (8). Eca inoculum was grown on Stewart's pectate or crystal violet pectate (4) plates. Distilled water suspensions of 48-hr-old cultures were prepared and

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adjusted to 10^6 cells per milliliter for inoculation.

Inoculation and incubation. Uniform "B" size (70–80 g) Norgold Russet tubers were washed, surface sterilized with 0.25% sodium hypochlorite for 15 min, rinsed in sterile water, and dried at room temperature prior to inoculation. One hundred fifty milliliters of inoculum suspension per replicate was placed in the inoculation container that had five 7-mm-long needles mounted in the bottom. Tubers were inoculated by immersing the stem end of each tuber into the inoculum and pressing it downward to force the needles into the tuber. Tubers were then wrapped in wet paper towels and incubated in a closed plastic box. Each plastic box contained 20 tubers that were periodically misted with 14 ml of distilled water to maintain wetness. Tubers prepared this way were incubated for 10 days in the dark at room temperature (21–26 C). Decay was rated by estimating the percent rotted area of a tuber cut lengthwise. We felt that this criterion was more consistently applicable than diameter of decayed area (5) since the decayed area was not always circular or semicircular. An average value from 10 tubers per replication was used for statistical analysis. Data in the range of 0–20% were transformed to $\sqrt{x}$ to obtain a normal distribution for statistical analyses.

Analysis of reducing sugars. Tuber juice for RS analysis was collected from 3 g of tuber tissue squeezed in a hand-held garlic press. RS determinations were conducted by using the Clinitest method as previously reported (24), which measures total reducing sugars present.

Correlation of reducing sugars and soft rot. The sprout inhibitor isopropyl-*N*-chlorophenyl carbonate (CIPC), storage temperatures, and tuber age were used to obtain seven tuber groups with varying levels of reducing sugars. Treatments consisted of: immature tubers from 8-wk-old plants; tubers cool stored at 3–6 C for 1 mo; tubers cool stored at 3–6 C for 9 mo; CIPC-treated tubers cool stored for 9 mo; tubers cool stored for 8 mo and then sprouted by warm storage at 21–26 C for 3 wk; mother tubers 3 wk after planting; and CIPC-treated seed tubers 3 wk after planting (no sprouting). Tuber lots consisted of 11–40 tubers each; a total of 214 tubers inoculated with Eca and incubated as described before. Soft rot decay was measured and RS was estimated by testing the remaining healthy tissue next to the bud end. Soft rot decay and RS levels were correlated for each treatment, and regression analysis was performed for the whole experiment to correlate RS and soft rot decay over a wide range of RS levels, the independent variable.

Three groups of Norgold Russet tubers stored: at room temperature (21–26 C), or in cool storage conditions (3–6 C), or cool stored, then reconditioned at room temperature for 1 wk, were needle-inoculated at the stem-end and bud-end portions and incubated for 5 days. Uninoculated tubers also were included in each treatment. Ten tubers per experimental unit and five replicates per treatment were tested. Soft rot was measured by cutting individual tubers in half lengthwise and then each half was again cut in half crosswise. The percentage of rotted area was estimated in each quarter tuber, and an average figure was obtained for each experimental unit. Five samples (7 mm thick) from each uninoculated tuber were obtained: two from the bud end, two from the stem end, and one from the pith (core tissue). These samples were each tested for RS content and 10 tubers per treatment were tested. LSD figures were obtained to compare storage treatments and student's *t* tests were performed to compare tuber parts (stem end vs bud end).

Anaerobic reconditioning. Two groups of Norgold Russet tubers were used to determine the effect of anaerobic reconditioning on both soft rot decay and RS content. A schematic diagram of the experimental procedures used can be seen in Table 1. Tubers stored for 3.5 mo in warm and cool conditions were surface sterilized in a 0.25% sodium hypochlorite solution for 12 hr, rinsed thoroughly, and air dried at room temperature for 1 hr. Each group of tubers was divided into three subgroups and subjected to the following treatments at room temperature: tubers immersed in sterile water, tubers immersed in sterile mineral oil, and tubers wrapped in wet paper towels. Before such treatments started, 50 tubers from each

TABLE 1. Schematic description of potato tuber incubation and the timetable used to test the effect of anaerobic reconditioning on reducing sugar (RS) content and soft rot development

Storage temp.(C)	Anaerobic recond.[a]	Tubers (no.)	Treatments, ratings, and tests			
			Day 0	Day 5	Day 7	Day 14
3–6 C	Water	20	Uninoc.		RS tested	
		50	Inoc.	Soft rot rated		
		50	Uninoc.		Inoculated and incubated in wet towels	Soft rot rated
	Oil[b]	20	Uninoc.		RS tested	
		50	Inoc.	Soft rot rated		
		50	Uninoc.		Inoculated and incubated in wet towels	Soft rot rated
	Air[c]	20	Uninoc.		RS tested	
		50	Inoc.	Soft rot rated		
		50	Uninoc.		Inoculated and incubated in wet towels	Soft rot rated
21–26 C	Water	20	Uninoc.		RS tested	
		50	Inoc.	Soft rot rated		
		50	Uninoc.		Inoculated and incubated in wet towels	Soft rot rated
	Oil	20	Uninoc.		RS tested	
		50	Inoc.	Soft rot rated		
		50	Uninoc.		Inoculated and incubated in wet towels	Soft rot rated
	Air	20	Uninoc.		RS tested	
		50	Inoc.	Soft rot rated		
		50	Uninoc.		Inoculated and incubated in wet towels	Soft rot rated

[a] All experiments were conducted at room temperature.
[b] Mineral oil.
[c] Tubers wrapped in wet paper towels.

group were inoculated with Eca and 70 were not. The inoculated group was rated for soft rot 5 days later. Of the 70 uninoculated tubers, 20 tubers were tested for RS content after 7 days, and the remaining 50 were inoculated with Eca at the same time and incubated at room temperature in wet paper towels for 7 additional days after which soft rot was evaluated.

Influence of cultivar. Norgold Russet, a cultivar with high levels of RS, and Norchip, a cultivar with low levels of RS, were tested for soft rot susceptibility by both lenticel and wound infection. For each cultivar tuber lots of 100 "B" size tubers that had been cool stored for 3.5 mo were washed, surface sterilized and wound inoculated with Eca at both ends as previously described. Uninoculated tubers also were included. Ten tubers of each cultivar were incubated in the same plastic box for 5 days and misted every 24 hr with 14 ml of distilled water. Five replications per cultivar were tested. Soft rot was measured in each quarter tuber and an average of percent rotted area was obtained for each tuber and then for each replicate. Another experiment was designed to detect differences in susceptibility to lenticel infection by Eca. Norgold Russet and Norchip tubers cool stored for 3 mo were used. Five replications of each treatment and 10 tubers per experimental unit were used. Tubers were surface sterilized, rinsed with distilled water, and sprayed with 14 ml per replication of a suspension containing 10^6 cells of Eca per milliliter. They were then individually wrapped with moist paper towels and incubated for 1 wk as previously described. Incubation boxes were misted with 14 ml of distilled water every 24 hr. Each replicate group of Norgolds was incubated with a replicate of Norchips. This helped to minimize differences in humidity affecting each cultivar. Uninoculated checks also were included. Soft rot was measured as a percentage of tubers rotted.

Reducing sugars and soft rot during the tuber life cycle. Norgold Russet tubers were assayed for soft rot susceptibility and RS content at representative stage of their "life cycle." These included: immature tubers obtained from 8-wk-old plants, tubers at harvest, 1 mo after harvest, after 2 mo in cool storage, after 4 mo in cool storage, after 8 mo in cool storage, after 8 mo in cool storage followed by warm storage for 2 wk after planting, and 8 wk after planting. Averages from at least 10 tubers for RS and 40 tubers for soft rot were obtained for each "life cycle" stage.

RESULTS

The results of the experiment in which CIPC and storage temperatures were used to manipulate RS revealed an overall highly significant correlation (r = 0.646) between soft rot severity and RS content of tubers (Fig. 1). Only tubers with low RS and the least susceptibility to soft rot (viz, immature and warm sprouted) did not correlate significantly.

Storage temperature had a significant effect on soft rot susceptibility and RS content (Fig. 2). Tubers inoculated after cool storage developed significantly more soft rot than did tubers inoculated after warm storage. Cool stored tubers reconditioned for 1 wk in warm storage had less soft rot than did cool-stored tubers, but more than in warm-stored tubers. Similarly, RS content was the highest in cool-stored tubers and lowest in the warm-stored

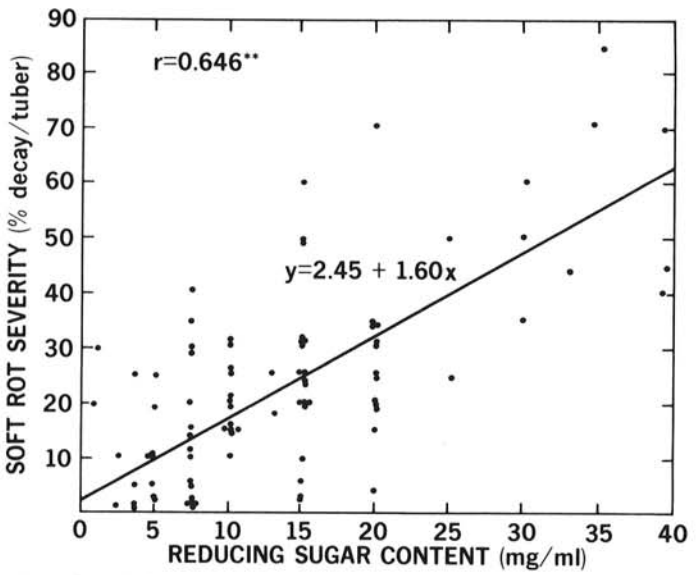

Fig. 1. Correlation (r = 0.646) between soft rot severity and reducing sugar (RS) content of Norgold Russet potato tubers variously conditioned by using isopropyl-*N*-chlorophenyl carbonate (CIPC) sprout inhibitor and manipualting storage temperatures. Soft rot and RS were measured 10 days after wound inoculation with *Erwinia carotovora* var. *atroseptica*.

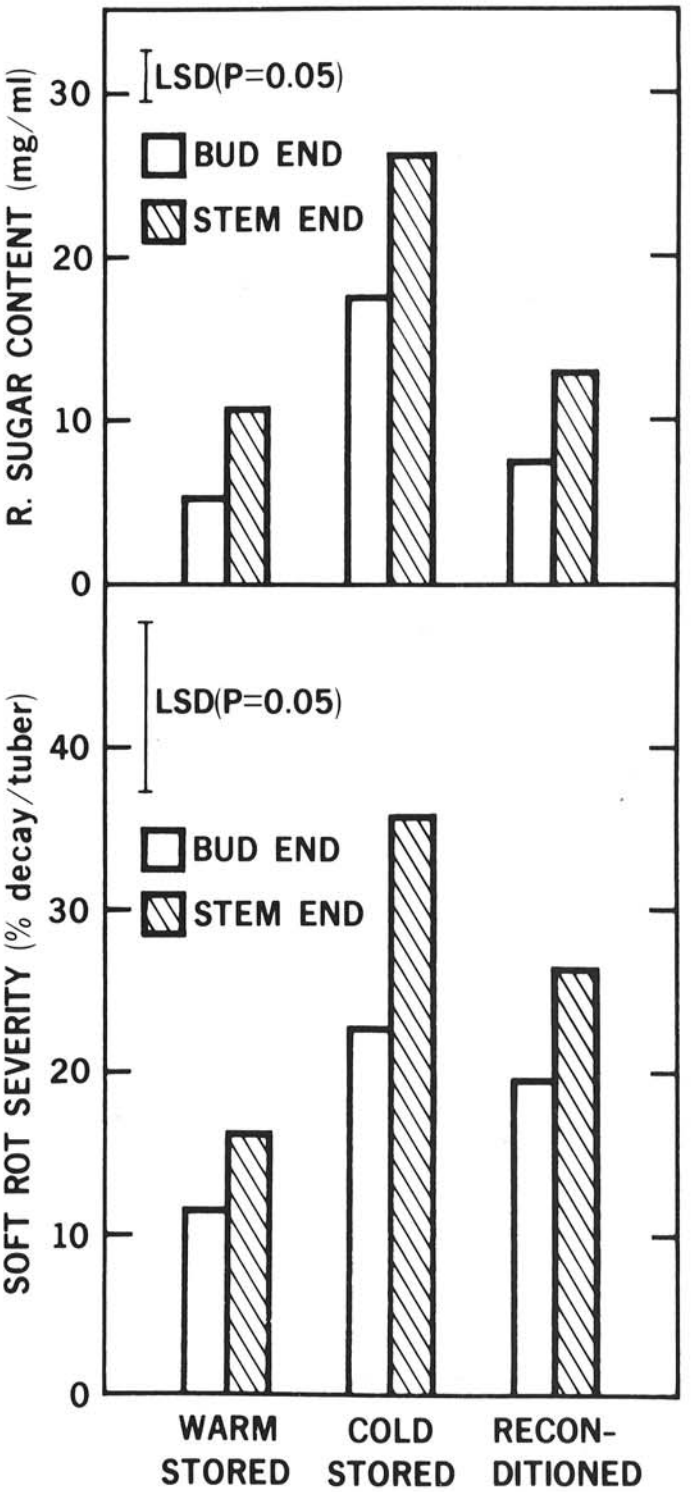

Fig. 2. Soft rot severity and reducing sugar content in the bud and stem ends of Norgold Russet potato tubers stored at cool (3–6 C) or warm (21–26 C) temperatures or reconditioned (3–6 C for 8 mo, then 21–26 C for 1 wk) 10 days after wound inoculation with *Erwinia carotovora* var. *atroseptica*.

tubers. Reconditioned tubers had significantly less RS than did cool-stored tubers, but more than warm-stored tubers.

There also were significant differences (Student's t test, $P=0.05$) in soft rot susceptibility between bud ends and stem ends of tubers (Fig. 2). The stem ends were consistently more susceptible to soft rot decay than bud ends, and the stem ends contained significantly higher RS levels than the bud ends.

Anaerobic incubation did not have an effect on RS content of Norgold Russet tubers (Table 2). Cool-stored tubers again contained a significantly higher level of RS than warm stored tubers, but within each temperature, RS levels were similar regardless of water, oil, or wet towel incubation. However, anaerobic incubation did have an effect on soft rot decay. Generally, incubation in oil, either before or after inoculation, resulted in the same amount of decay as nonimmersed controls (wet paper towel method) at both temperatures. Incubation in water generally resulted in significantly greater decay than that of the aerobic controls. Decay of warm-stored tubers equalled that of cool-stored tubers after water submersion, indicating that the soft rot susceptibility after submersion was independent of both temperature and RS content. Decay in uninoculated controls was minimal.

Wound-inoculated Norgold Russet and Norchip tubers that had been warm stored and consequently had low RS levels, did not show differences in susceptibility to soft rot. However, cool storage of these cultivars resulted in significantly more decay of Norgold in both the stem end and bud end after wound inoculation (Table 3). Levels of RS were higher in the cool-stored Norgold tubers than in cool-stored Norchips, but not significantly so. Norchip tubers were significantly ($P = 0.05$) more susceptible to soft rot by lenticel infection (no wounding) than were Norgold tubers. Cool-stored Norgold tubers showed an average of 4% infection compared to 21% in Norchips.

Figure 3 illustrates the changes in RS content and soft rot susceptibility of Norgold Russet tubers at representative points in the "life cycle" of a tuber. The data show that RS and soft rot susceptibility generally parallel each other, rising and falling as the other does, throughout the life of the tuber. Soft rot susceptibility and RS levels increase slowly during storage, drop off drastically when "seed" tubers are warmed prior to planting, and reach a maximum level in the seed piece approximately 8 wk after planting. Immature tubers contain low levels of RS and also show low susceptibility to soft rot decay.

TABLE 2. Soft rot severity[w] and reducing sugar (RS) content[x] of Norgold Russet potato tubers during incubation following aerobic (nonimmersed)[z] and anaerobic (immersed) reconditioning

Treatments[y]	21–26 C			3–6 C		
	Water	Oil	Air[z]	Water	Oil	Air[z]
Decay of tubers inoculated before incubation (%)	24.1 c	13.0 a	13.5 a	23.8 c	14.6 a	20.1 b
Decay of tubers inoculated after incubation (%)	21.9 a	9.0 b	8.2 b	17.5 a	17.5 a	17.9 a
Reducing sugar content after incubation (mg/ml)	6.5 a	5.8 a	5.3 a	13.0 b	12.9 b	13.9 b

[w] Average percent rotted area per half tuber. Values followed by the same letter in each row are not significantly different ($P = 0.05$) according to LSD test.
[x] RS content measured 7 days after the experiment began. Reported as milligrams per milliliter.
[y] See Table 1 for explanation of treatments.
[z] Tubers wrapped in wet paper towels.

DISCUSSION

Results of these studies of potato tubers show a positive correlation between soft rot severity and RS content over a wide range of conditions (viz, temperature, cultivar, tuber portion, and

TABLE 3. Reducing sugar content and soft rot development in cool stored (3–6 C) tubers of potato cultivars Norgold Russet and Norchip 5 days after wound inoculation with *Erwinia carotovora* var. *atroseptica* and storage at room temperature[x]

Measurement	Norgold Russet		Norchip	
	Bud end	Stem end	Bud end	Stem end
Soft rot[y] (%)	8.1 b	23.5 c	2.8 a	13.0 b
Reducing sugars[z]	13.5 a	21.4 b	9.3 a	19.3 b

[x] Data followed by the same letter in each row are not significantly different ($P = 0.05$) according to LSD test.
[y] Average percent soft rotted area per tuber.
[z] Milligrams per milliliter.

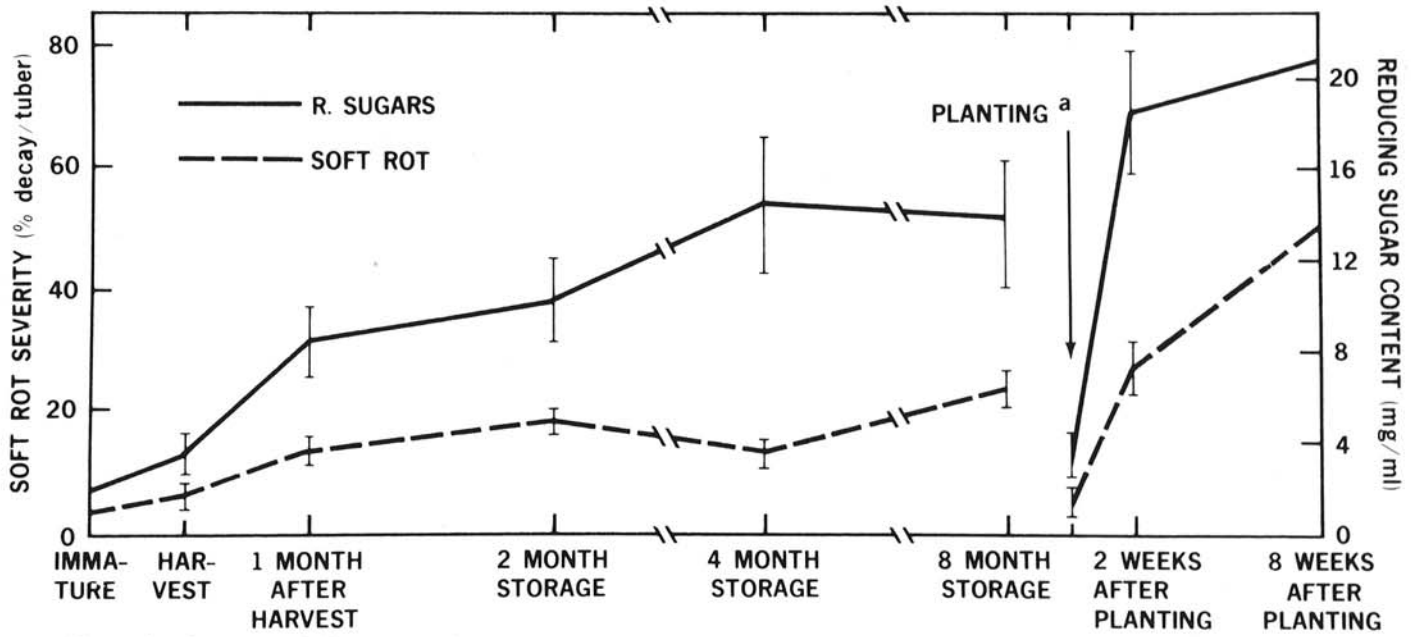

Fig. 3. Changes in soft rot susceptibility and reducing sugar (RS) content at various points in the "life cycle" of Norgold Russet potato tubers. Data are means and their standard deviation. [a]Seed was reconditioned (21–26 C for 2 wk) prior to planting to lower RS levels.

tuber age). However, this correlation did not exist for lenticel infection, or when tubers were submerged in water. Water-immersed tubers developed more soft rot without corresponding increases in RS. Oil-immersed tubers showed soft rot severity equal to that of tubers incubated in wet towels, which suggests that anaerobiosis per se did not influence the severity of soft rot caused by Eca. However, these results do not differ from reports of DeBoer and Kelman (5) who found increased soft rot susceptibility with lower O_2 concentrations but in environments with high relative humidity. Increased soft rot decay in water-immersed tubers may be due to a combination of lower O_2 concentrations (5) and greater changes in water potential, as suggested by Kelman et al (17). Both RS levels and tuber water potential may be involved in soft rot caused by Eca. These two factors, both physiologically complex, probably are interrelated, each influencing the other. It appears that the correlation between RS and soft rot severity is valid only under dry or moist aerobic conditions, but not when tubers are thoroughly wet and anaerobic. Water-free anaerobic conditions are not important in soft rot development. Wrapping the tubers in wet paper towels and incubating them in closed plastic boxes (wet towel method) may create anaerobic or semianaerobic conditions in the tubers. But because Eca is a facultative anaerobe, this should not influence the end results.

There are two mechanisms of tuber infection by Eca: lenticel infection and wound infection. If soft rot severity is equivalent to soft rot susceptibility, RS content appears to be directly involved in susceptibility to wound infection, but not to lenticel infection. Both mechanisms of infection may be important in testing cultivars for resistance to soft rot.

The evidence of a positive correlation between soft rot severity and RS content in tubers is opposed to the results of in vitro studies reported by Biehn et al (2) who demonstrated glucose repression of endo-polygalacturonate transeliminase. However, the possibility of a reversal mechanism of glucose repression in in vitro systems as proposed by Hubbard et al (10) and Mount et al (20), by an exogenous supply of 3′5′-cyclic adenosine monophosphate (cAMP), must be considered. It is not clear if cAMP exists in higher plants, but it is reported that *E. carotovora* contains a cAMP-generating mechanism (12) which, in a host-pathogen combination system, would account for this regulating phenomenon. This is feasible, especially if we analyze the reports by Shekar and Iritani (29), in which they find a highly significant positive correlation between inorganic phosphorus content of tubers and RS accumulation. It also is important to distinguish factors that affect susceptibility/resistance of the host and development of the pathogen and the interaction of both. In vivo systems usually involve more than one enzymatic reaction.

It can be postulated that by-products of bacterial growth, and/or host membrane leakage can set up exosmosis of sugars from within the cell to the intercellular spaces, which in turn serve as a readily usable food source for further bacterial growth and enzyme synthesis. This is supported by our unpublished data that show soft-rotted tissue to be void of RS. This may explain the more rapid soft rot development, but may not be the only factor affecting soft rot susceptibility in potato tubers.

The correlation between high RS and soft rot may explain why some high-sugar potato cultivars, such as Norchief, never became widely grown because of stand problems due to soft rot decay. It also may explain why no seed pieces are found at harvest in the Red River Valley. The highest RS levels and soft rot decay occur in the seed piece 8 wk after planting (Fig. 3). Interestingly, "blind" (unsprouted) seed pieces retain low RS and are often found at harvest.

Management of soft rot problems in storage and at planting may be possible by monitoring RS levels. Manipulations of storage temperature and warming seed to reduce RS levels prior to planting, may prevent excessive soft rot. Other considerations such as sprouting, cultivar, and the use of the stored potatoes also are important.

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