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Management factors used for studies on potato scab control were evaluated for their effect on tuber russeting and related biochemical and anatomical parameters during 1971 and 1972.

Russet Burbank potatoes were irrigated in 1971 to maintain high available soil moisture (between 90% and field capacity) for 0, 3, 6 and 9 weeks, beginning one week after plant emergence. Soil moisture was maintained between 60% and field capacity during the time it was not held above 90%. In 1972, plots for four soil-moisture treatments were irrigated to maintain minimum levels of 90%, 75%, 60% and 45%, respectively, throughout the season beginning one week after emergence.

Subplot treatments in 1971 were soil compaction, pentachloronitrobenzene (PCNB) at 28 kg/ha, Super-X (mixture of PCNB and 5-ethoxy-3 trichloromethyl 1, 2, 4 thiadiazole) at 28 kg/ha, sulfur at 896 kg/ha, and N-serve [2 chloro, 6 (dichloromethyl) pyridine] at 1.7

kg/ha, and an untreated check. In 1972, subplots were PCNB at 28, 22 and 17 kg/ha; sulfur at 896, 672 and 448 kg/ha, and an untreated check.

Reduction of tuber russeting (net) resulted from increased length of high-moisture period in 1971, and increased available soil-moisture percentage in 1972. Soil compaction at the high-moisture level reduced net in 1971. PCNB, Super-X and N-serve did not change net significantly, but sulfur increased net. In 1972, PCNB reduced net, and sulfur with low soil moisture reduced net.

Net was found to consist of collapsed, lignified, unsuberized cork cells above columnar layers of slightly flattened, suberized cork cells. Together these form the periderm of Russet Burbank tubers. Periderm areas with net had more layers of suberized cork cells below the net than did areas without net. The number of cork-cell layers increased with visual estimates of the amount of net.

Histological stains showed that lignin content was highest in net tissue, lower in suberized cork, and absent beneath the cork. Suberin was present in cork cells below the net and absent in other tissue. Pectins were evident beneath the cork, but were found only in small amounts in cork tissue. Histochemical stain tests for cellulose were negative in walls of suberized cork, presumably due to a suberin covering. Histochemical evidence

thus indicates that lignin is responsible for intercellular adhesion in net tissue.

Thin-layer chromatography of tuber periderm extracts showed a predominance of chlorogenic acid, caffeic acid and coumarin. Other unidentified phenols were found in smaller amounts. The concentration of phenolic acids was reduced by high soil-moisture treatments and PCNB.

It is suggested that reduced tuber net was due to reduced lignin in net cells. Reduced net from high soil-moisture treatments and from compaction was probably due to inhibition of lignin synthesis in the net as a result of low soil oxygen. Water extraction of phenolic precursors from periderm may be a contributing factor. Reduction of net by PCNB is apparently due to inhibition of lignin synthesis.

On the basis of these results, soil moisture, sulfur and PCNB may generally be used in pathogen control programs without seriously reducing net if excesses are avoided.

PHYSIOLOGICAL AND AGRONOMIC RESPONSE OF POTATO PERIDERM RUSSETING TO MEASURES FOR CONTROL OF COMMON SCAB

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PHYSIOLOGICAL AND AGRONOMIC RESPONSE OF POTATO PERIDERM RUSSETING TO MEASURES FOR CONTROL OF COMMON SCAB

INTRODUCTION

A. The current significance of russet periderm

The Russet Burbank potato is the predominant variety by far in the Pacific Northwest and in certain other areas of the U. S. It is a standard of quality with which new introductions are compared in those areas. "Russet" and "net" are synonymous terms applied to the brown, netted appearance of the surface of some potato varieties (figure 1).

The russet "skin" or periderm is a prime identifying characteristic of this variety for the fresh-market consumer in the same respect that red color is for Red Delicious apples. Like color in apples, the russet periderm has not been shown to directly influence true quality. The long russet type of potato commands a premium price on the market due to the reputation of the Russet Burbank as an excellent quality potato. Development of Norgold Russet and other introductions are attempts to improve upon certain other characteristics while retaining a distinct russeted periderm. Production of the genotype, however, does not invariably result in the desirable phenotype, and

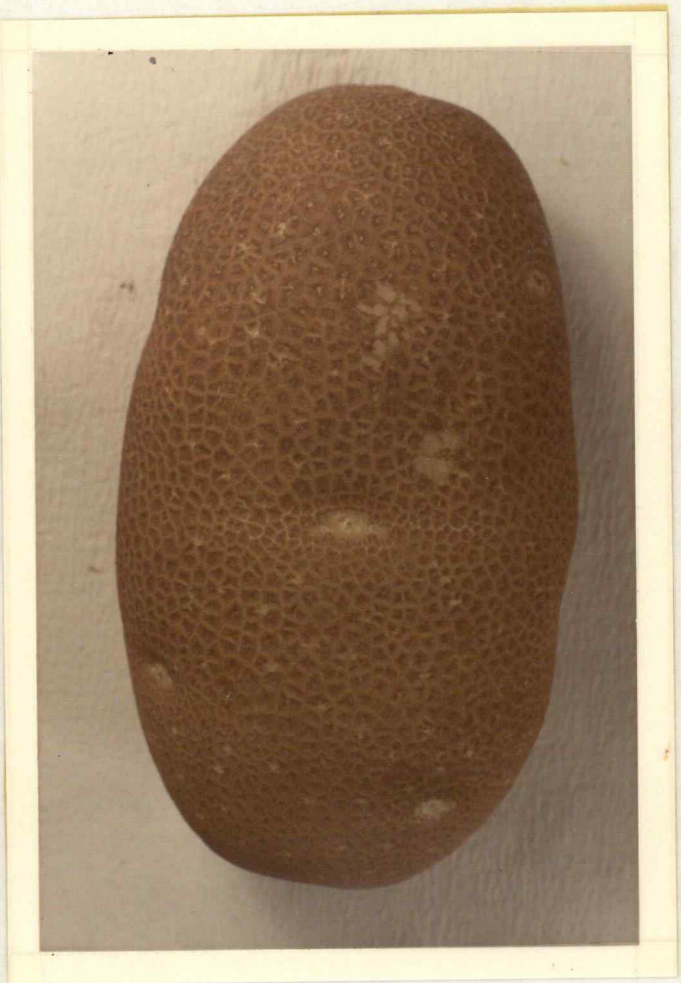

Figure 1.

Net on Russet Burbank Tuber

each year considerable evidence of "poor net" is observed. Although this character is not a specific factor in U. S. grade standards, poor net on russet potatoes is discriminated against by marketing standards (Idaho, 1972) as well as potato buyers, and a lower market price results.

Inadequate russeting is often associated with "skinning" or "feathering", a condition due to loosening of tuber periderm and normally considered to be evidence of immaturity. This poor retention of russet periderm has resulted in great losses in market value to the industry according to Owens et al. (1970).

Since net is a virtual trademark of the potato industry where the Russet Burbank variety predominates, an important market quality feature is to be considered.

B. Future significance of russet periderm

Quality features that are peculiar to fresh market value are likely to be of significance for the foreseeable future, although fresh potato consumption in the United States is in a period of distinct decline (USDA, 1972b). Since 1960, total U. S. per capita consumption of potatoes has increased from 49 kg to 54 kg (+.5 kg/yr increase). Per capita consumption of fresh potatoes has dropped linearly from 80% of the total in 1960 to 45% in 1971, giving way to processed potatoes. This national trend will likely continue for some time before fresh potato useage becomes

more stable.

The future of the Russet Burbank potato, however, is not well represented by the national averages cited. During the above period, fresh shipments of potatoes from the major production area for Russet Burbank potatoes, have increased (USDA, 1972a, Dalling, 1972). Fresh potato packing facilities expansion has occurred during that period, new packing plants have appeared, and average fresh potato prices have shown a steady demand.[1] It appears, therefore, that the market for Russet Burbank potatoes has not reflected the trends for the nationwide potato industry. It may be reasoned that this is an indication that areas producing Russet Burbank potatoes have a uniquely strong marketing position. It therefore appears that variety and cultural practice improvement programs for Russet Burbank growing areas should continue to focus on that phenotype.

C. Investigation background and objectives

Prior University of Idaho studies conducted for control of potato scab on Russet Burbank potatoes resulted in an observation that the chemical treatments used appeared to influence the amount of russeted periderm.

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[1]Moore, E. Executive Manager, Idaho Grower-Shippers Association. Personal Communication, November 30, 1972.

Since the use of controlled high soil moisture and fungicides for control of potato scab were not previously developed or widely used in Russet Burbank producing areas, their effects upon net had not been described. The purpose of this study was to characterize and explain the anatomical and physiological nature of the influence of these management factors upon russeted periderm.

The objectives of this study were threefold:

1. To identify the anatomical and biochemical nature of net on Russet Burbank tubers.
2. To identify relationships between scab control management practices and the biology of net.
3. To determine the degree to which those management practices influence the amount of net.

REVIEW OF LITERATURE

A. Periderm development

Russet Burbank periderm consists of cork (phellem) 7-11 cells thick, below which is a cork cambium (phellogen). Underneath this is a phelloderm, formed by phellogen activity but resembling cortical parenchyma cells (Reed, 1910; Artschwager, 1924; Yamaguchi, Timm and Spurr, 1963; Reeve et al. 1969a). The epidermis, according to Reed[2] and Artschwager[3], is sloughed away while the tubers are small, and the protective function is assumed by the periderm. Tuber growth stretches the young cork cells tangentially, and they become successively flattened in the surface layers. According to Emilsson and Heiken (1956), very small tubers of some varieties have the same number of cork cells as fully grown tubers, whereas in others, the cell layers nearly double in number during growth. Russet Burbank was not included in their report.

Lignification of the primary cellulose walls normally occurs when cells have attained their final size, and suberin then forms over the lignified lamella (Esau, 1965; Jaffe, 1965).

The "net" in Russet Burbank, as described by Yama-

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[2] Op. cit.
[3] Op. cit.

guchi, Timm and Spurr, is composed of patches of cork tissue which are separated by superficial periderm cracks due to stretching.

B. Developmental factors important in periderm formation

Lignin concentration in plant cells increases toward the middle lamella; according to Wood (1967), this is the most heavily lignified zone in some cells. Lignin deposition usually begins in the middle lamella and then spreads into the primary and secondary walls (Esau, 1965). According to Mallette et al. (1960), it is deposited in the interstices between microfibrils and micellar strands of cellulose and other material to form a three-dimensional plastic which serves as a cementing substance for the woven pattern of the other cell wall components. It is not known whether lignin is chemically bound to cellulose or only linked by hydrogen bonds. Meyer, Anderson and Bohning (1960) state that lignified walls are freely permeable to water and solutes.

Lignin is an amorphous yellow or brown substance of indeterminate molecular weight, consisting of phenylpropane units, with a C:H:O ratio of about 63:6:31, depending upon origin and separation method. It contains a large proportion of aromatic rings and methoxyl groups. While the exact chemical constitution of lignin is not known,

the proportion of main alcohol constituents varies somewhat among plant taxons. Oxidation yields syringaldehyde and vanillin, and small quantities of nonaromatic substances such as formic, acetic and oxalic acids have been isolated (Mallette, 1960).

Higuchi (1957), Robinson (1967) and Freudenberg (1965) show the synthesis of lignin or lignans to be a pathway wherein p-coumaric acid and caffeic acid are precursors to p-hydroxycinnamyl alcohol, sinapyl alcohol, and coniferyl alcohol, which conjugate to form the highly polymerized lignin material. Gamburg (1967) has shown with 14 labelled aromatics in cell culture that the phenolics caffeic, p-coumaric, and shikimic acid were readily absorbed in lignin biosynthesis by potato cells, and the labelled carbon was traced through to lignin aldehydes and lignin in the potato cells.

Higuchi (1957) suggested that lignin biosynthesis results primarily from the action of phenolase and peroxidase enzyme systems resulting in oxidation and subsequent conjugation of coniferyl alcohol in the absence of a reducing system.

Phenolic acid lignin precursors as a group, and particularly caffeic acid and the polyphenol chlorogenic acid, are concentrated primarily in the periderm tissue of potatoes (Johnson and Schaal, 1952; Sanford and Grimble, 1944;

Kuc et al., 1956; Jaffe, 1956; Sanford, 1926; Taylor, 1966; Hughes and Swain, 1960; Livingston, 1966; Reeve et al., 1969).

Johnson and Schaal (1952) noted that potato varieties differ in amount of chlorogenic acid in the tuber surface layers, but do not relate this to other periderm characteristics except scab resistance. They suggest that chlorogenic acid or its quinone may be directly or indirectly involved in the formation of suberized periderm.

Suberins are highly polymerized products of fatty acids (Esau, 1953). Rodriguez-Miguens and Ribas-Marques (1972) reported obtaining a mixture of straight-chain monocarboxylic acid from potato cork. After extraction of interfering substances, potato cork contained 20% suberin. The suberin was depolymerized to yield 35.5% cis-18-hydroxy-9-octadecanoic acid, 17.5% cis-9-octadecen-1, 18-dioic acid, 1.5% 24-hydroxy tetracosanoic acid, and a mixture of n-monocarboxylic acids.

Deposition of suberin is apparently a result of esterification of these acids one with another, and occurs normally sometime after the tuber is in the 10 mm diameter stage (Cooper, Stokes and Rieman, 1954). Time of suberization during tuber ontogeny differed among genotypes, however. After a tuber surface is cut, suberization begins within a day and deposition is complete within ten days

(Nielsen, 1968; Priestly and Woffenden, 1923). Rate and completion of deposition is dependent upon temperature and possibly other environmental factors (Artschwager, 1927; Reeve, 1969).

C. Soil factors important in periderm formation

Fertilizers have been frequently linked to net. Phosphorus additions are reported by Metzger (1938), Harrington (1937) and Iritani and Painter (1963) to improve net, particularly under high nitrogen conditions. Excess nitrogen applications have been reported to result in poor net, by Kunkel and Dow (1961), Iritani and Painter (1963), Painter (1959), Metzger (1938) and Harrington (1935). Potassium was found to reduce net by Holstad (1967), Harrington (1935), Metzger (1938), Murphy and Goven (1965), Iritani and Painter (1963), and Johnson (1966). McLean, Sparks and Binkley (1944) reported that use of copper and iron together or in combination with other minor elements resulted in thicker periderms in Red McClure, a nonrusseted potato, and that thin periderms were associated with zinc where zinc reduced yield.

Jaffe (1965) found that potato tubers produced in cultures deficient in calcium or boron produced more lignin than controls with a complete nutrient medium, although no association with periderm character was made.

Blodgett and Snyder (1946) reported that saline soil conditions produced poor russeting, and Schoeneman (1954) stated that acidity decreased russeting.

Yamaguchi, Timm and Spurr (1963) reported that temperatures of 60 F and below reduced russeting, and Ruf (1963) reported that high temperatures (90 F) as well as low temperatures (45 F) reduced russeting. Both of these were pot culture studies. Holstad (1967) reported high soil temperatures and dry soil reduced russeting in outdoor bed culture.

Mylius (1913) observed that tubers grown in excessive soil moisture prevents cork maturation, and Owens et al. (1970) suggested that a loss of net and slow maturation of periderm was associated with heavy irrigation and late-season irrigation. Kuster (1925) suggested that moisture may suppress cork suberization in some species entirely and induce development of callus tissue instead of cork.

Johansen (1965) noted that coarse textured soil produces a particularly good net on the Norgold variety. Nielsen (1968) reported that potatoes from sand soils had thicker periderm than tubers from heavier soils, and that potatoes grown on humus soil had significantly thinner periderm, as judged by the number of layers of suberized cork cells.

D. Plant disease factors and net formation

Hooker (1954) suggested that mild superficial russeting of Cobbler commonly obtained on Iowa peat is probably a response to a mild type of scab infection, since he observed a reduction in mild russeting of this smooth skinned variety along with scab control as a result of the use of sulfur and pentachloronitrobenzene at 4480 and 560 kg/ha respectively.

Since scab is primarily a disease of periderm hyperplasia, it follows that factors which influence scab development may also influence periderm development per se, and vice versa. Cooper, Stokes and Rieman (1954) examined 17 potato varieties and found that scab-susceptible varieties retained defunct outer periderm cells, while the outer periderm tissue of resistant varieties consisted of living, nucleated cells. Russet Burbank was not among varieties examined. They concluded the scab organism enters senescent cells prior to their collapse and continues to penetrate deeper cells as they become senescent. Their conclusion that scab is a disease of senescent cells suggests that scab resistance and russeted periderm would tend to be somewhat mutually exclusive. Studies by Emilsson and Heiken (1956) on eleven European varieties confirmed that there is a definite correlation between scab resistance and periderm structure. They

noted, however, that the relation does not always hold because of the quantitative nature of scab resistance. They concluded that while tuber periderm structure may influence pathogenicity by the scab organism, it does not appear to be the primary factor in the host-parasite relationship.

METHODS AND MATERIALS

A. Site

Experimental treatments were applied to field-grown potato plants during 1971 and 1972. The site for experimental treatments was a 12 ha field bordered by a lava flow, 24 km north of Blackfoot, Idaho (figure 2). The soil was a slightly rolling Pancheri silt loam, a xerollic calciorthid. This field was abandoned for potato production due to extreme scab infection in potatoes the third year after breaking the land out of sagebrush in 1956.

B. Nonexperimental husbandry treatments

The following nonexperimental husbandry treatments were applied both years to the entire study area:

1. Cultivation: The field was uniformly plowed 30 cm deep, disked and harrowed before any experimental work.

2. Planting: Certified uncut potato seed was spaced 23 cm apart in rows which were 91.5 cm apart. The entire area, including buffers, was planted to reduce the effects of unplanted borders on evapotranspiration variations. The potatoes were hilled to a 15 cm amplitude after planting.

3. Fertilization: 202 kg/ha of nitrogen as ammonium sulfate and 168 kg/ha of P_2O_5 as triple superphosphate were applied uniformly over the entire study area. The

Figure 2.

Aerial View of 1971 Field Plots

fertilizer was banded 5 cm to the side of the seedpiece with a planter-mounted applicator.

4. Pest Control: Granular disulfoton (Di-Syston[4]) was placed in the fertilizer band at 3.4 kg/ha active ingredient with a planter-mounted applicator for insect control. EPTC (Eptam[5]) at 3.4 kg/ha active ingredient plus trifluralin (Treflan[6]) at 0.55 kg/ha active ingredient were pre-plant incorporated for weed control with a rototiller. In 1971, dalapon (Dowpon[7]) at 3 kg/ha plus linuron (Lorox[8]) at 1.7 kg/ha were applied to emerged weeds just prior to potato emergence for supplementary weed control.

Two midseason foliar sprays of maneb (Manzate D[9]) were applied in July and August by a commercial flying service for control of early blight (Alternaria solani).

DNBP (Dow General[10]) at 2.8 kg/ha was applied as a potato vine dessicant by a commercial flying service three weeks prior to harvest to facilitate harvest.

5. Irrigation: A short preharvest soil conditioning irrigation was applied a week prior to harvest to

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[4]Chemagro Corporation, Kansas City, Missouri.
[5]Stauffer Chemical Company, New York, New York.
[6]Elanco Products Company, Indianapolis, Indiana.
[7]The Dow Chemical Company, Midland, Michigan.
[8]E. I. duPont de Nemours and Company, Wilmington, Delaware.
[9]The Dow Chemical Company, Midland, Michigan.
[10]E. I. duPont de Nemours and Company, Wilmington, Delaware.

eliminate clods and facilitate collection of clean, sound tuber samples.

C. 1971 Experimental treatments

1. Experimental design

The experimental treatments were arranged in a five-replicate randomized block with split-split plots. Main irrigation plots (18 x 22 m) were divided into two subplots (9 x 22 m) to allow for imposition of a soil compaction treatment. Each subplot was further divided into five four-row plots (3.66 x 9 m) to provide for five chemical fungicide treatments.

2. Experimental procedure

a. Irrigation treatments

Irrigation treatments used for russeted periderm studies were primarily designed to investigate the findings of Sanford (1926) who reported that high moisture reduced scab infection in the greenhouse, and Lapwood (1970) and Barnes (1971) who reported scab control with high soil moisture during a three-week period after tuber initiation. Since tuber initiation of the Russet Burbank potato in Idaho continues well into midseason, irrigation during several time periods was used as a treatment variable.

The irrigation treatments consisted of comparing the conventional recommended irrigation practice (irrigating

to prevent soil moisture from dropping below 60% available) with a higher soil moisture level for three overlapping time intervals. The 1971 treatments were as follows:

Treatment 1: Soil moisture was maintained between 60% and field capacity. This treatment was continued throughout the irrigation season. It may be considered to be the check treatment.

Treatment 2: Soil moisture was maintained between 90% and field capacity for a three-week period beginning one week after potato plant emergence[11]. For the remaining time, soil moisture was held between 60% and field capacity, identical to Treatment 1.

Treatment 3: Soil moisture was maintained between 90% and field capacity for a six-week period beginning one week after potato plant emergence. For the remaining time, soil moisture was maintained as in Treatment 1.

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[11]Potato plant emergence was defined as the date when 50% of the potato plants had emerged from the soil, and was assumed to occur about one week prior to initiation of the earliest tubers. Emergence was observed June 8, 1971, 21 days after planting.

Treatment 4: Soil moisture was maintained between 90% and field capacity for a nine-week period beginning one week after potato plant emergence. For the remaining time, soil moisture was maintained as in Treatment 1.

The plots were individually irrigated to bring the soil-moisture level in the upper 23 cm to field capacity each time evapotranspiration reduced the soil moisture in the individual treatments to the above predetermined percentages of available soil moisture.

Four solid-set sprinkler irrigation systems were designed to apply the irrigation treatments. These were interlaid just prior to potato plant emergence on the test site to provide four independent, randomized irrigation treatments in each of five replicates. Plots were separated from one another by 26-meter buffer strips to insure against overlapping of irrigation treatments by the circular sprinkler pattern and by wind disturbance. A manifold with four valves was constructed to deliver water independently to the four irrigation systems from a single mainline riser. Each valve controlled one irrigation treatment, providing the same flow rate to that treatment in all replicates (figure 3). Sprinkler head placement was designed to provide the same pattern for all plots

Figure 3.

Irrigation System With Manifold For Irrigating Individual Treatments Separately

with the best uniformity attainable with impact agricultural sprinklers.

Beginning June 14, 1971, the soil moisture had dropped to 70% available soil moisture at the 23 and 53 cm depths as determined by tensiometers, so all plots were irrigated to field capacity on June 15. From this date forward, the four irrigation treatments were maintained as previously described.

Occasional stolon inspection in border rows revealed the first observed tuber initiation, i.e. the stolon tip expanded to twice the diameter of the stolon (Lapwood, 1970), on June 20, 1971, 12 days after emergence.

Soil moisture was monitored by daily tensiometer (Irrometer[12]) readings in each main plot in replicate three and four. These plots were assumed to represent analogous plots in all replicates. Tensiometers placed in the field were calibrated by oven-dry determinations of soil moisture. Field spotchecks by the calcium carbide method, also calibrated with oven-dry moisture determinations, were used on soil samples from other places in the plots to confirm the reliability and representative validity of the tensiometers.

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[12]Irrometer Company, Riverside, California.

Physical limitations on irrigation timing, such as delays due to excessive wind, availability of adequate water flow, and temporary system failures, generally precluded irrigation at the exact time of day a precise soil moisture percentage was reached. For this reason, plots were frequently irrigated slightly ahead of schedule or slightly behind schedule. To plan for a scheduled irrigation, the rate of soil moisture depletion was projected from day to day to predict the time that the allowable soil moisture depletion[13] would be attained. The depletion rate was projected on the basis of a composite of average measured consumptive use (evapotranspiration) curves by potatoes at Aberdeen for three years (McMaster, 1966, 1967, 1969). Scheduled irrigation quantities were determined on the basis of an application rate vs nozzle pressure curve. This procedure resulted in continual maintenance of acceptable tolerances for the desired minimum soil-moisture levels.

On August 20, all treatments were irrigated to field capacity together for the last irrigation of the growing season so that the soil moisture in all plots would be uniform for subsequent operations. This irrigation provided adequate soil moisture for growth until the vines

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[13]Allowable depletion is the difference between field capacity and the percentage of available soil moisture desired at the time of replenishment to field capacity.

were killed.

b. Compaction

One-half of each main irrigation treatment was compacted to evaluate the effect of equipment compaction under moist soil conditions. This treatment was not related directly to scab control, but was included to simulate the effect of compaction on plant development.

The compaction treatment was imposed after planting and hilling by rolling the hill with a tractor-drawn two-row, weighted press wheel device (figure 4). This weighed 636 kg and produced a calculated pressure of approximately 0.7 kg/cm^2.

c. Chemical treatments

The purpose of including chemicals in the scab control study was to apply the findings of previous workers to Idaho conditions and to evaluate their performance under conditions of high soil moisture.

Chemicals used were (1) PCNB[14], reported by Fink (1956), Houghland and Cash (1957), and Menzies (1957) to be effective for scab control when used at rates as low as 28 kg/ha, (2) Super-X[15], (3) Sulfur, reported by Hooker

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[14]Pentachloronitrobenzene. Olin Mathieson Chemical Corporation, Agricultural Division, Fresno, California.

[15]Mixture of .24 kg/L PCNB and .06 kg/L 5-ethoxy-3 trichloromethyl 1, 2, thiadiazole. Olin Mathieson Chemical Corporation, Agricultural Division, Fresno, California.

Figure 4.

Compaction Device

and Potter (1968) and Davis (1970) to be effective at 1120 and 672 kg/ha, respectively and (4) N-serve[16], reported by Potter, Norris and Lyons (1971) and Watson (1969) to be effective at the rate of 1.7 kg/ha. The chemical rates of active ingredient per hectare chosen for this study were:

1.	PCNB (Terraclor)	28 kg/ha
2.	Super-X	28 kg/ha PCNB
3.	Sulfur	896 kg/ha
4.	N-serve	1.7 kg/ha

Before planting, the plots were staked and the PCNB and Super-X treatments were sprayed on the soil surface. The entire study area was then uniformly tilled 15 cm deep with a 4-meter-wide power rotary tiller (Menzies, 1957) on the herbicide spray tractor, incorporating treatments 1 and 2, together with the herbicide (figure 5).

The plots were then restaked and marked in 91.5 cm rows with a marking tractor, and furrows were cut 15 cm deep in the planting rows for the sulfur treatment. The sulfur treatment was applied by sprinkling flowers of sulfur into the furrow bottom, and the sulfur was covered to prevent wind disturbance before planting.

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[16] 2-chloro-6 (dichloromethyl) pyridine. The Dow Chemical Company, Midland, Michigan.

Figure 5.

Fungicide Incorporation

The experiment site was planted May 10, 11, and 12, 1971. The N-serve treatments were banded in the planter operation. This was done by stopping the blanket fertilizer application when the planter came to an N-serve plot, and applying the same fertilizer mix, but treated with N-serve to provide a rate of 1.7 kg/ha (figure 6).

3. Evaluation

a. Visual analysis

Tubers from 5.5 m of row from the two center rows of each plot were harvested on October 6 and 7, 1971, for tuber evaluations. These samples were stored in a humidified storage at 7.2 C, graded, weighed and rebagged for evaluation.

The tubers were separated into four classes according to the percentage of surface covered with net (figure 7), as follows:

Class 1	$<25\%$
Class 2	26-50%
Class 3	51-75%
Class 4	$>75\%$

Data for individual samples were reduced by calculating an index, $I=C^2\%$, where I=index, C=numerical class, and %=percentage by weight of tubers in that class.

Figure 6.

N-Serve Application with Planting
N.....N-Serve Belt
ST....Seed Chain Tube
F.....Blanket Fertilizer Bin

Figure 7.

Tuber Sample Illustrating Net Classes

Specific gravity was determined on 10-lb samples of U. S. No. 1 tubers from each plot.

b. Chemical analysis

For phenolic acid analysis, ten tubers between 170 and 340 g were randomly drawn from the check, PCNB, and sulfur treatment samples from each noncompacted subplot. Because of the similarity between PCNB and Super-X, and because the compaction treatment was considered to be of secondary importance, the Super-X and compaction treatments were omitted from the phenolic analyses to reduce the number of samples to an economically manageable level. The periderm was removed from one-half of the tuber from stem-end to bud-end with a vegetable peeler to a depth of 1-2 mm. The tissue was immediately immersed in liquid nitrogen, lyophilized for 12 hr and ground in a Wiley mill with a 40 mesh screen.

Phenolic acids and coumarins were extracted from 0.5 g samples for 12 hr in a Soxhlet apparatus with 150 ml of 83% isopropanol-water azeotrope. At the end of the extraction, a 0.5 ml sample was removed from each extract, diluted in 2.5 ml of 83% isopropanol, and the U. V. absorbance spectrum was determined on a Perkin-Elmer model 124 spectrophotometer.

The remaining bulk of each extract was concentrated by flash evaporation to a 15 ml volume. Ten-microliter

samples from the check and PCNB treatments were compared with commercial chlorogenic, caffeic, ferulic, ortho, meta, and paracoumaric acids, scopoletin, esculetin, umbelliferone and coumarin by thin-layer chromatography. The samples were spotted on 300 micron layers of Avicel PH-105 microcrystalline cellulose[17], steamed, dried, and developed in a solvent of isopropanol-formic acid-water, 5:4:95 v/v/v/ (Winkler, 1967). The plates were inspected and the samples compared with standards for identification of unknown compounds under ultraviolet light. The plates were then sprayed with 2N sodium hydroxide, inspected once again, then sprayed with diazotized nitroanaline and inspected once more for comparison of samples and standards by Rf values and colors.

Seventy-lambda samples of the check and PCNB treatments were spotted in rows of 10-lambda spots on Avicel, and developed as previously described. The two major spots fluorescing with U. V. light and coinciding with commercial chlorogenic and caffeic acid were eluted with 3 ml of 83% isopropanol and centrifugated at 12,500 rpm for 20 min at 20 C. Ultraviolet absorption of the supernatant was then determined for chlorogenic acid at 330 nm and for caffeic acid at 320 nm.

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[17]FMC Corporation, American Viscose Division, Newark, Delaware.

c. Histochemical and anatomical analysis

A single tuber from each of the four net categories was randomly selected from each of four replicates for anatomical study. Periderm development was evaluated by counting suberized cells as described by Nielsen (1968). This procedure was modified for efficient collection of data from many samples. Two 5 x 15 mm tissue blocks of periderm and cortex, about 5 mm thick, were cut from the top center of each tuber and fixed in FAA. Sections from these samples were hand cut to approximately 250 microns with a razor blade for periderm evaluations. The sections were stained in FAA with 0.5% Sudan III for 15 to 30 min, rinsed in water for 15 min, and transferred to a glass cover slip where the excess water was blotted off with paper. The section was then covered with melted agar to prevent drying of the tissue. A frame was cut from a plastic embedding dish holder and glued to a glass slide to form a device upon which the agar mount could be inverted in a manner analagous to the hanging-drop slide technique. It was found that this procedure provided a very clear view of the section for microscopic examination when used under a 4x or 16x epiplanatic lens with vertical illumination. The agar drop maintained the section in good condition under a microscope for at least an hour, and could be preserved for many days if stored in a moist chamber or

covered with paraffin.

The procedure outlined provided a means by which a section could be removed from a tuber and data gathered within 30 min if the FAA step were omitted, or in 15 min if material had been previously fixed in FAA. The described procedure was employed for histochemical studies using safranin and phloroglucin for lignins, analine blue for cellulose, and ruthenium red for pectins.

D. 1972 Experimental treatments

1. Experimental design

The 1972 plots were offset into the 1971 buffer area to avoid confounding effects of prior plot treatments. The main design was changed in 1972 to a 4 x 4 split-plot latin square, next to the site of 1971 replicates 1 to 4. A fifth block was added in the area of the 1971 replicate 5, to be used as a randomized block in the event of loss of a block from the latin square. The sprinkler equipment was redesigned to fit the latin square.

The plots were planted May 11, 1972, with uncut seed, parallel with the latin square columns, and hilled slightly. Planting continued between latin square rows to maintain a uniform crop surface over the study site and reduce the border effect. The areas between latin square columns was planted for the same purpose, but Gaines winter wheat

was used to save cost.

The irrigation system was installed prior to emergence, which occurred on June 7.

2. Experimental procedure

a. Irrigation treatments

The irrigation treatments were different from those used in the prior year's study. Whereas the 1971 soil-moisture treatments consisted of variable lengths of the high-moisture period, the 1972 treatments were selected percentages of available soil moisture and were maintained throughout the irrigation season.

The plots were irrigated to bring the soil-moisture level in the upper 23 cm to field capacity each time the soil moisture depleted to the selected percentages of available soil moisture. The treatments were as follows:

Treatment 1: Soil moisture was maintained between 90% and field capacity.

Treatment 2: Soil moisture was maintained between 75% and field capacity.

Treatment 3: Soil moisture was maintained between 60% and field capacity.

Treatment 4: Soil moisture was maintained between 45% and field capacity.

Treatment 3 may be considered a check treatment for practical purposes. The entire area was uniformly irrigated to field capacity on June 15, to start the treatments. Soil moisture monitoring and moisture replenishment procedures were done as in 1971, but to accommodate the 1972 treatments. These treatments were continued throughout the irrigation season.

b. Chemical treatments

Subplot treatments were also different; the 1972 treatments consisted of selected rates of effective scab control chemicals used in the 1971 study. These were:

1.	Check	
2.	PCNB	17 kg/ha
3.	PCNB	22 kg/ha
4.	PCNB	28 kg/ha
5.	Sulfur	448 kg/ha
6.	Sulfur	672 kg/ha
7.	Sulfur	896 kg/ha

The PCNB was applied and thoroughly incorporated with the herbicide application prior to planting, as in 1971. The two center rows of the sulfur plots were marked, furrowed out and the sulfur was spread across the full width of the furrow (figure 8). Soil was spread over the sulfur to prevent wind disturbance until the potato seed was

Figure 8.

Sulfur Application in 1972 Plots Showing Distribution Across Full Width of Furrow

planted in the treated furrow.

3. Evaluation

a. Visual analysis

Tubers were harvested on August 24 from the untreated check, PCNB and sulfur treatments.

Periderm russeting differences were less pronounced than in the 1971 data; therefore periderm russeting was evaluated by separating tubers into two classes:

Class 1: <80% of the surface covered with net.

Class 2: 80% or less of the surface covered with net.

b. Chemical analysis

Periderm samples were taken from the 28 kg/ha PCNB rate, the 896 kg/ha sulfur rate, and the untreated check, for quantitative phenol analysis. Periderm was removed from tubers as was done for the 1971 samples, but was placed immediately in 85% isopropanol and extracted on the Soxhlet. One-half ml of the extract was diluted 1:10 with 83% isopropanol, and ultraviolet absorbance was measured at 330 nm.

An additional 0.5 ml from each sample was diluted 1:7 with pH 11 $NaCO_3$ - $NaHCO_3$ buffer, and fluorescence was compared with chlorogenic acid and caffeic acid standards on a Turner model 110 fluorimeter. A 7-60 narrow-pass

Wratten filter was used on the primary (excitation) side, and a No. 2A sharp-cut filter together with a No. 48 narrow-pass filter were placed on the secondary (emission) side (Winkler, 1967). Spectral transmission data for these filters was supplied by the manufacturer, and is shown graphically in figure 9.

c. Anatomical analysis

Periderm sections from representative tubers were taken from the same treatments for cork layer determinations. Sections were stained with Sudan III as previously described, and the number of layers of stained cork cells was counted at 10 sites for each treatment sample.

E. Statistical treatment of data

Where numerical data were gathered, statistical analysis appropriate for the particular design used was conducted. Unless otherwise specified, the probability level accepted for significance was .95. Where percentage data were analyzed, arcsin conversions were substituted for the data. Data presented in graphs indicate the use of Duncan's new multiple range test at the .95 probability level by the notation DMR. Significant differences are denoted by conventional use of small letters, wherein data associated with the same letter are not significantly different from one another. Where single comparisons are

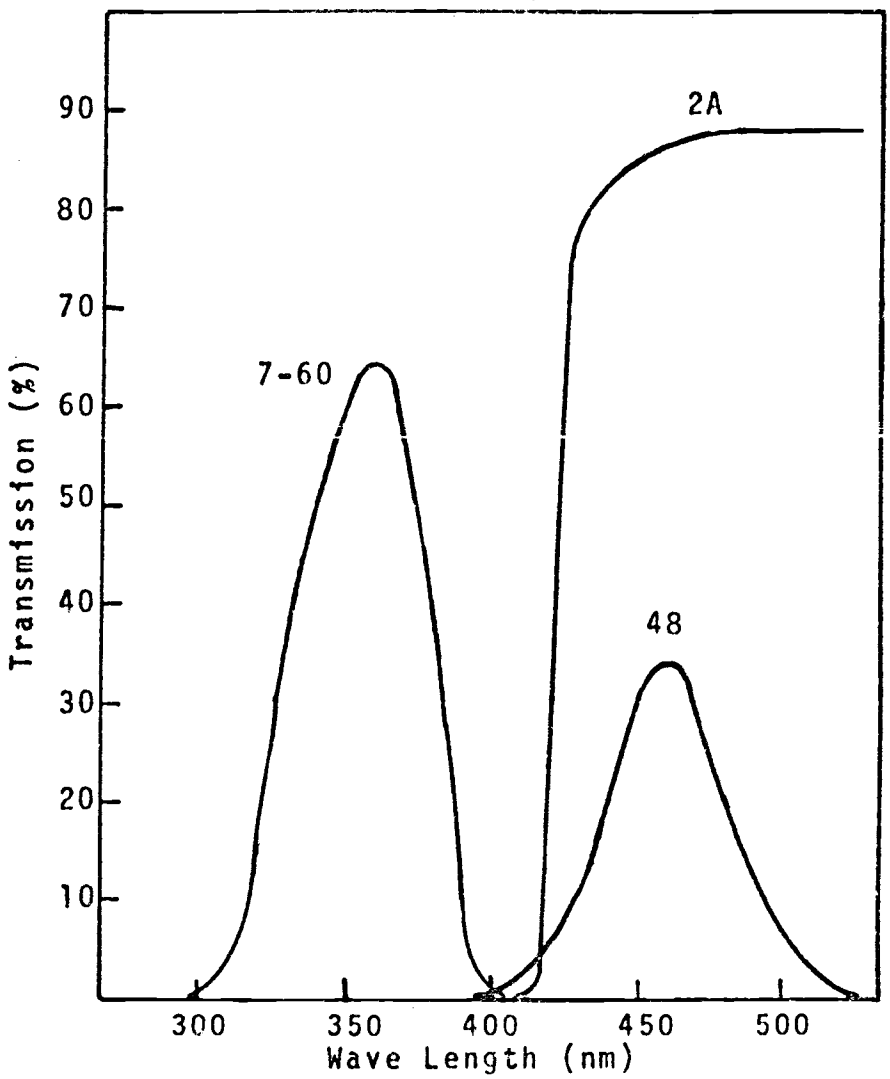

Figure 9. Spectral transmittance of filters used in comparing fluorescence of buffered extracts of periderm samples.

made, only probability (P) values are given. Actual mean values, together with the statistical analyses, are summarized in the appendix.

RESULTS

A. 1971 Experimental treatments

1. Visual evaluations

a. Net classification

Tubers produced in the 1971 field plots exhibited distinct variation in periderm character. The range of net indices is depicted in figures 10, 11, 12, and 13. Figures 10 and 13 show indices near the extremes, and the index for the tubers in figure 12 is near the grand mean (10.3) for the experiment.

Reduced net was manifested on individual tubers by a somewhat random occurrence of areas without net, or on tubers with very little net, by a random occurrence of areas with net.

A pronounced effect of length of period of high soil moisture can be seen in figure 14. Duncan's multiple-range test shows homogeneous subsets. The nine-week high-moisture treatment produced tubers with distinctly less net than did the zero or three-week treatments. This suggests that the longer soil moisture was held at a minimum of 90% available soil moisture, the greater was the reduction of periderm net.

Soil compaction resulted in an average reduction in net; figure 15 shows this effect to be very slight, but

Figure 10. Net Index 4.8

Figure 11. Net Index 7.6

Figure 12. Net Index 10.7

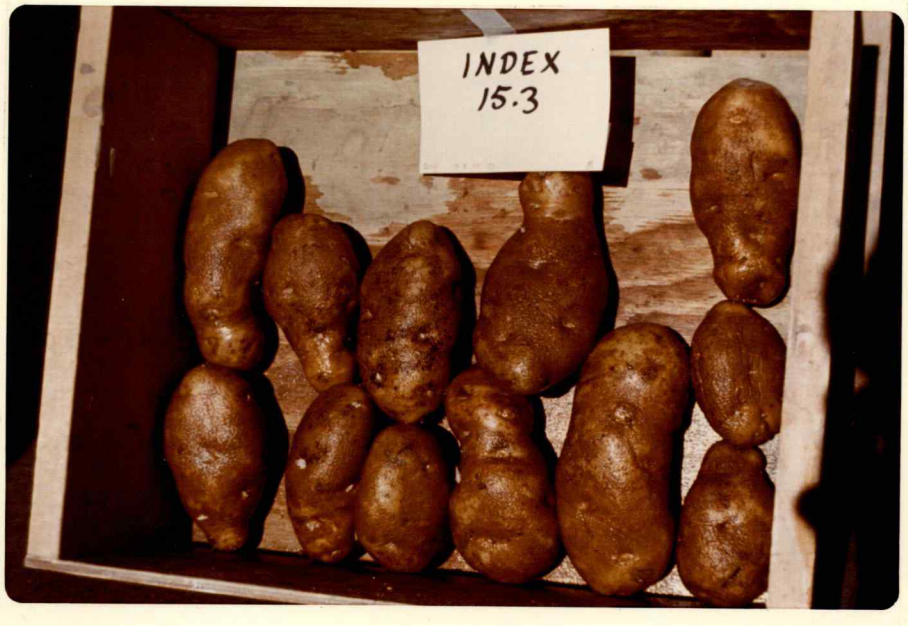

Figure 13. Net Index 15.3

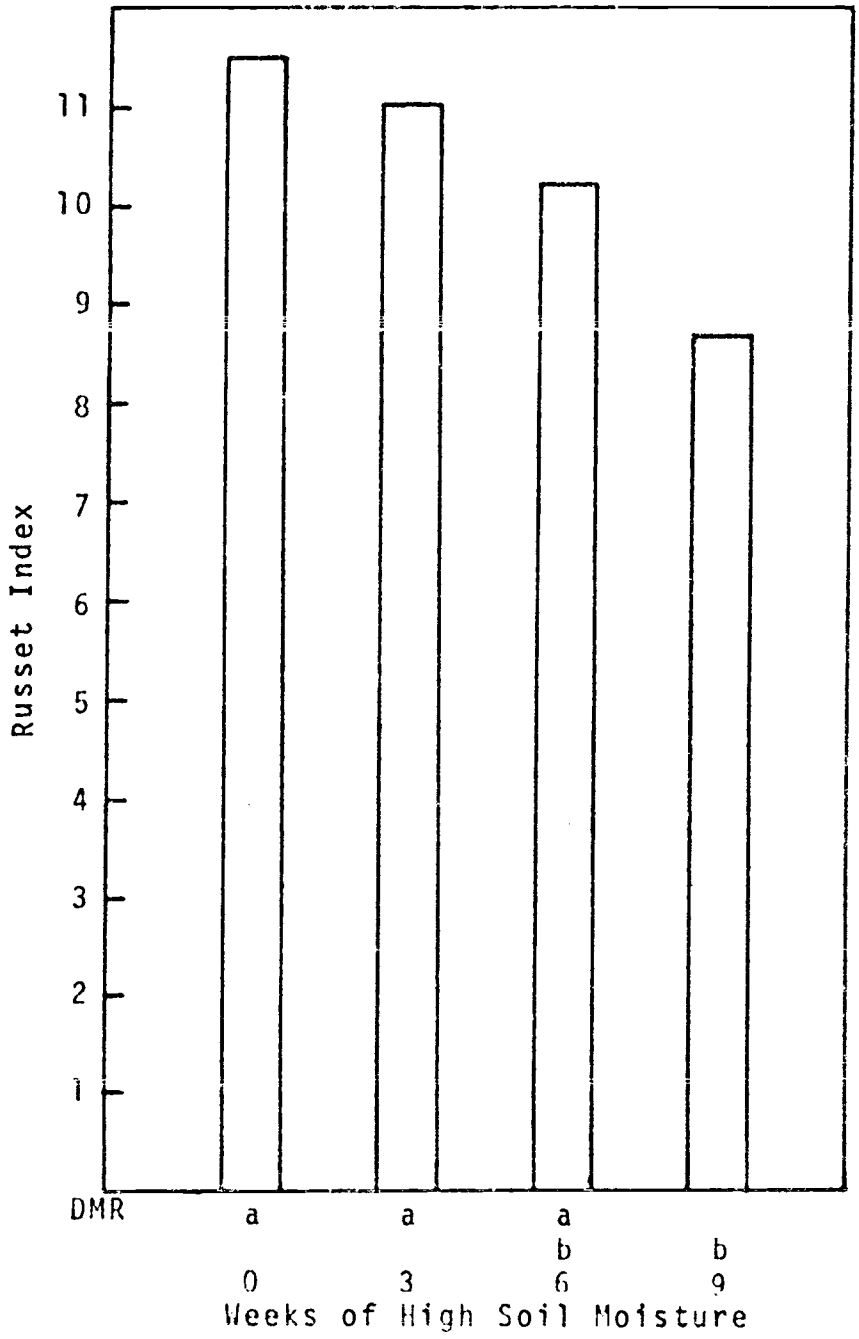

Figure 14. The Influence of High Soil Moisture on Russet Index.

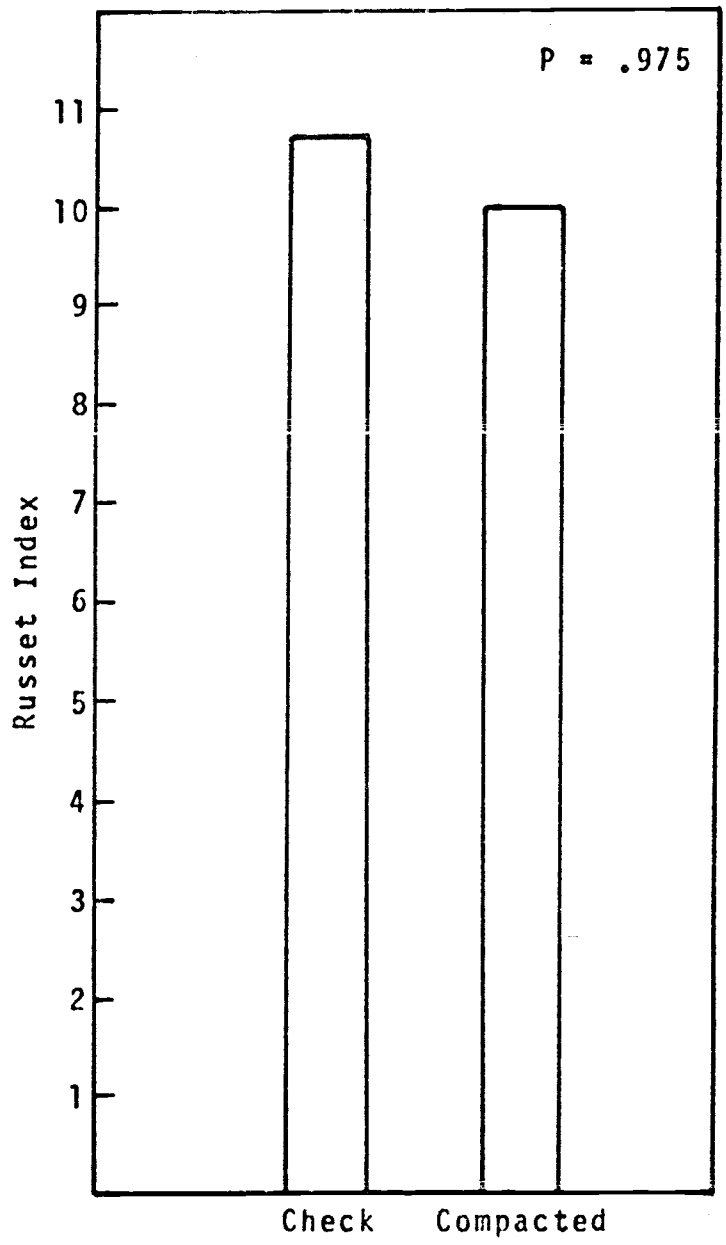

Figure 15. Influence of Soil Compaction on Russet Index.

real. When compaction was considered with individual soil-moisture treatments, an interaction effect became evident (figure 16). Net on tubers from check plots that were allowed to deplete to 60% soil moisture showed no difference due to compaction; but a constant difference between index values from compacted and noncompacted plots was observed in each of the high moisture treatments.

Differences in the response of russeting to chemical applications can be seen in figure 17. The chemical applications did not result in net indices significantly higher or lower than that for the untreated check, but differences among values for chemicals did exist. Indices for PCNB and N-serve were lower than those for Super-X and sulfur, with the check being a common member of both statistical subsets.

b. Yield and quality

The nine-week high soil-moisture treatment resulted in a 20% yield reduction ($P \sim .94$), but other irrigation treatments did not result in significant yield differences (Appendix, table 4). Compaction reduced yield by 6% (Appendix, table 4). The sulfur application was the only chemical treatment that influenced total yield, resulting in a 13% reduction (Appendix, table 4). The sulfur treatment also reduced specific gravity of tubers from compacted plots (Appendix, table 3).

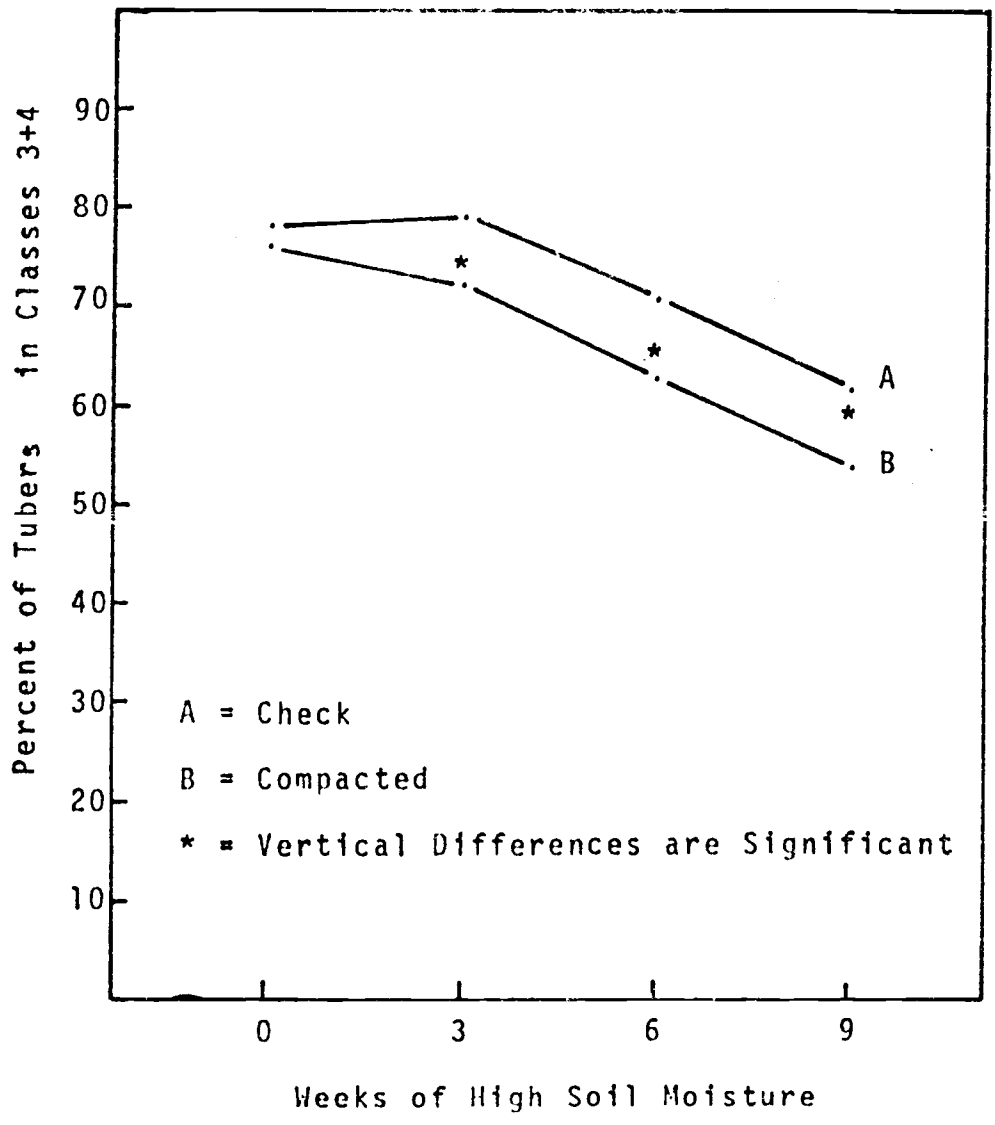

Figure 16. The Influence of Compaction and Soil Moisture on Russeting.

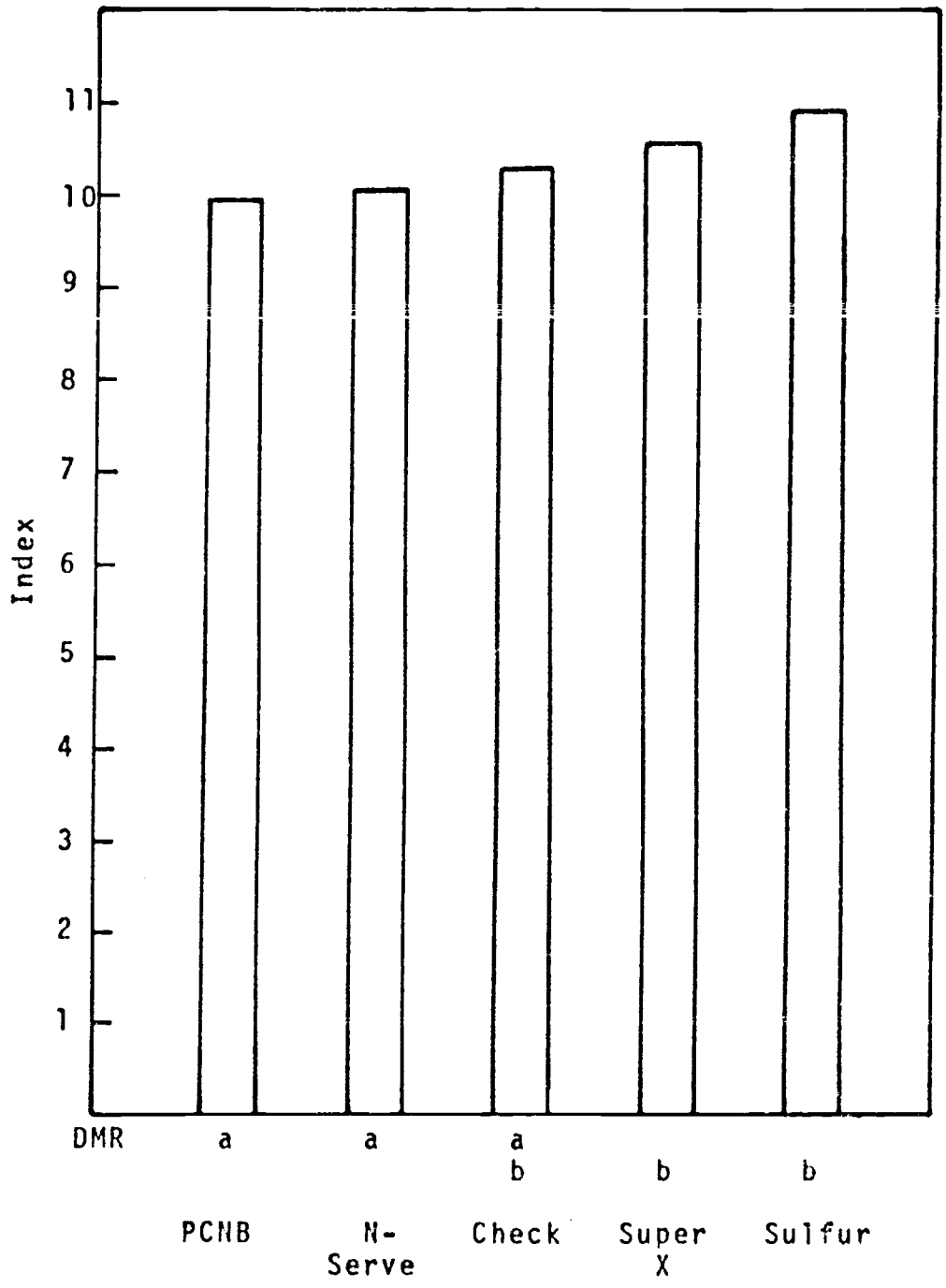

Figure 17. The Influence of Chemical Treatments on Russet Index.

2. Chemical evaluations: 1971 tubers

a. Thin-layer chromatography

The two major fluorescing spots resulting from thin-layer chromatographic separation coincided with Rf values for chlorogenic acid and caffeic acid standards (figure 18 and table 1). Fluorescence intensity under U. V. and color changes after spraying the plates with the base and diazotized nitroanaline solutions were used to confirm the identity of the two spots (table 1). A third major spot coincided with the coumarin standard in color reaction and Rf.

b. Spectrophotometry

Ultraviolet absorbance curves for periderm extracts in 83% isopropanol showed a major peak at 330 nm, and a secondary peak at 290 (figure 19). The absorbance for the chlorogenic acid standard was maximum at 330 nm, and for caffeic acid the absorption peak was 320 nm (figure 20). Absorbance for both of these phenolic acids was linear with concentration (figure 21).

Ultraviolet absorbance of the eluted chromatographed spots from the untreated check and PCNB treatment are shown in figure 22. The untreated samples absorbed more U. V. at 330 and 320 nm than did the samples from PCNB treatments ($P>.94$).

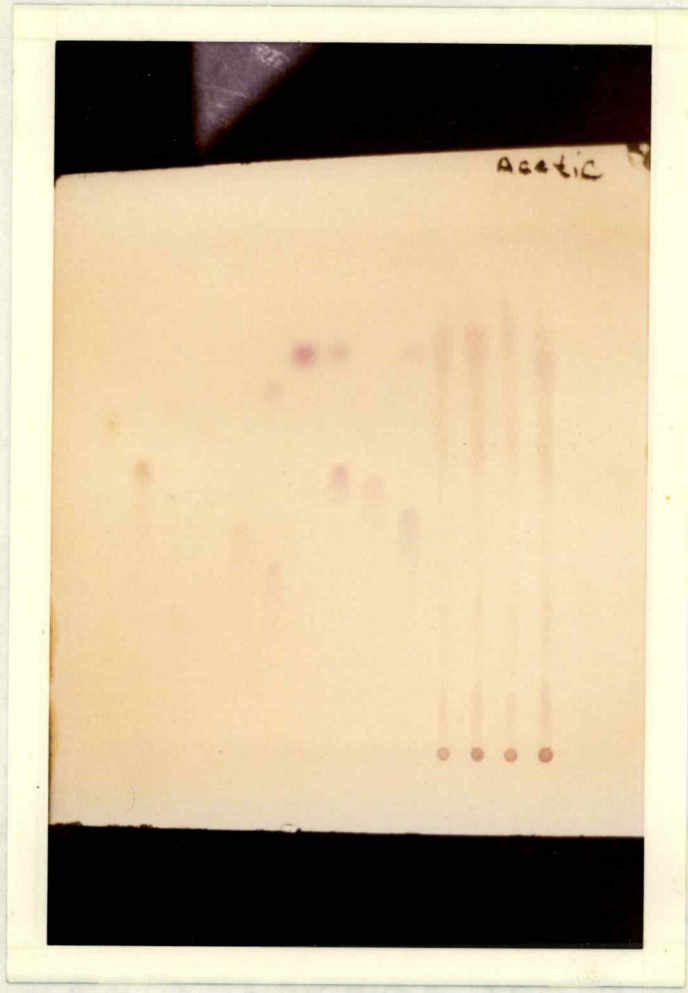

Figure 18.

Thin-Layer Chromatogram with Periderm Samples and Standards, after Spraying with Diazotized Nitroanaline

Table 1: Identifying Characteristics of Chromatographed Periderm Extracts.

Rf	Fluorescence	Color with NaOH	Color with Diazotized Nitroanaline	Matching Standard
11	Light blue	deep blue	purple	unknown
28	blue	blue	brown	caffeic acid
33	blue	blue-pink	disappears	unknown
57	blue	yellow-green	brown	chlorogenic acid
73	blue	deep blue	gray-brown	unknown
77	blue	light blue-brown	gray-purple	unknown
89	none	blue	purple	coumarin

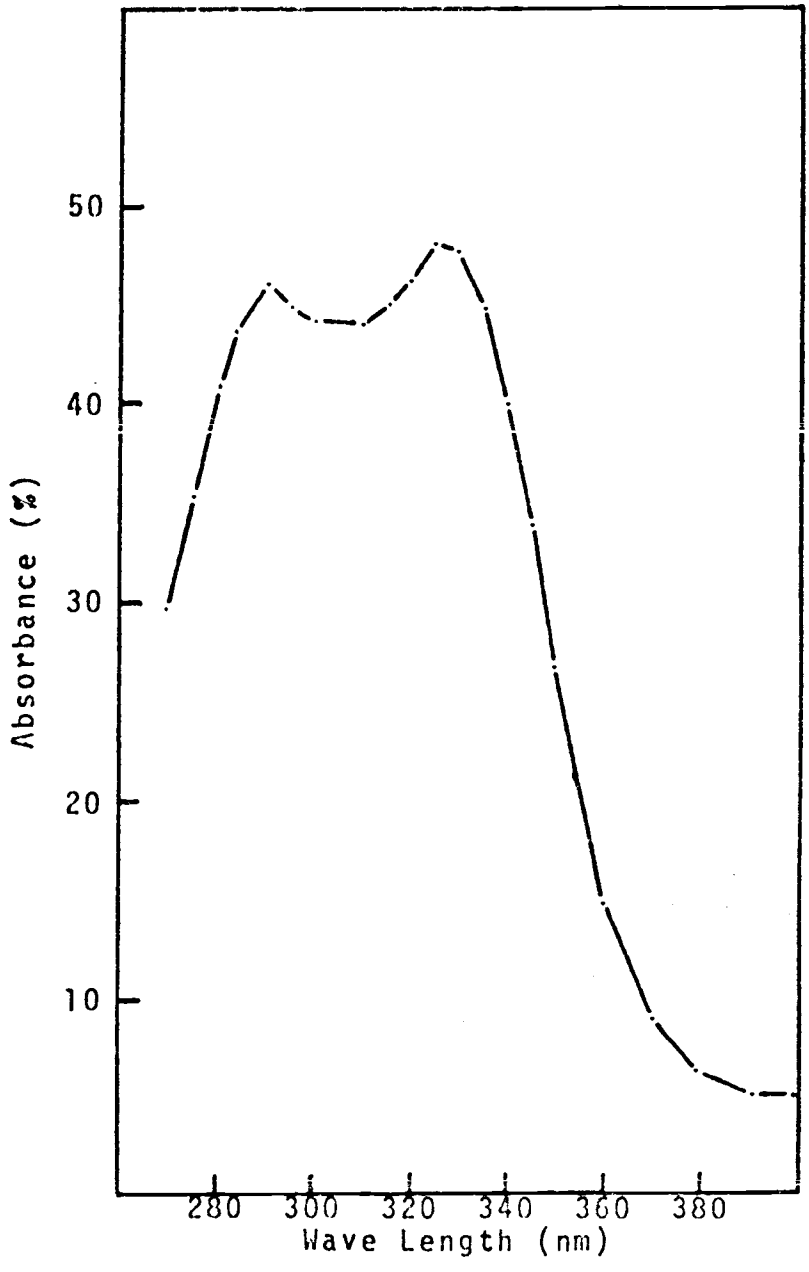

Figure 19. Spectral Absorbance of 83% Isopropanol Extracts of 1971 Periderm.

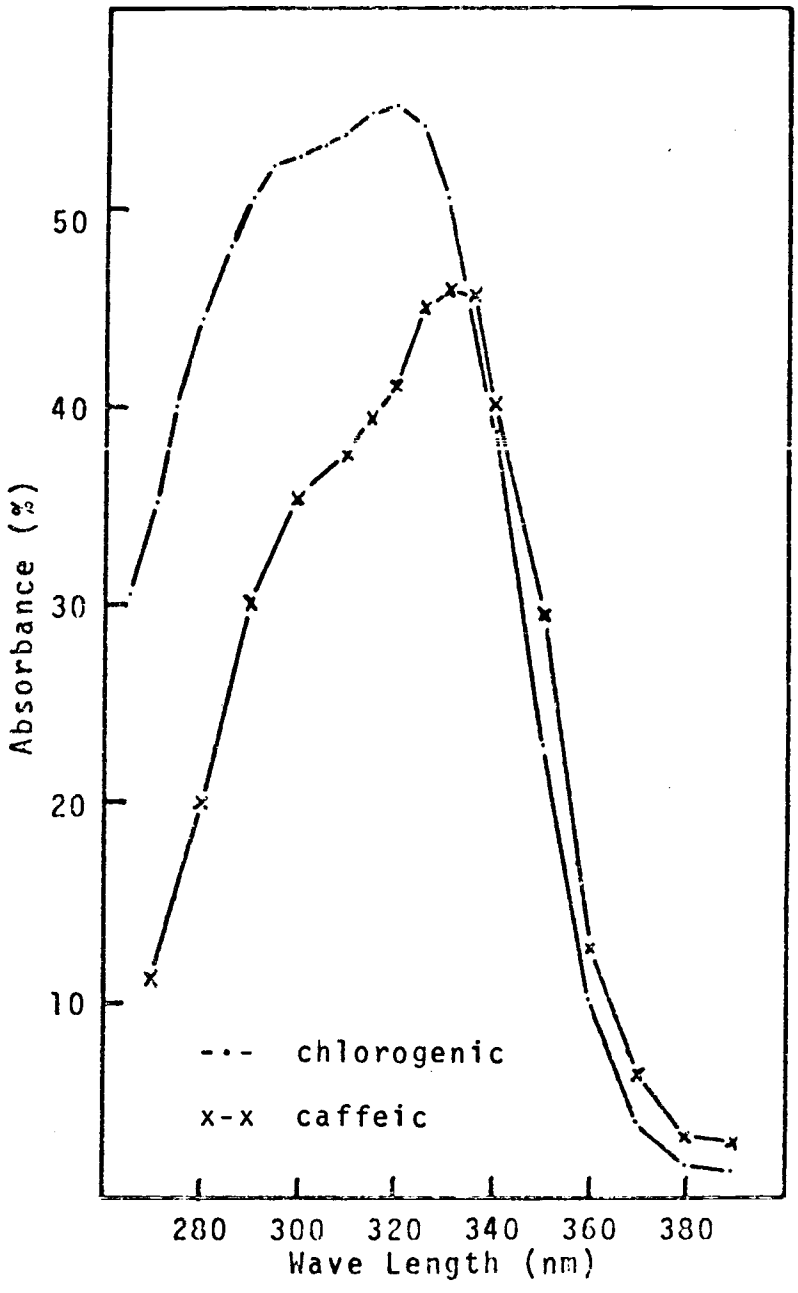

Figure 20. Spectral Absorbance of Caffeic and Chlorogenic Acid in 83% Isopropanol.

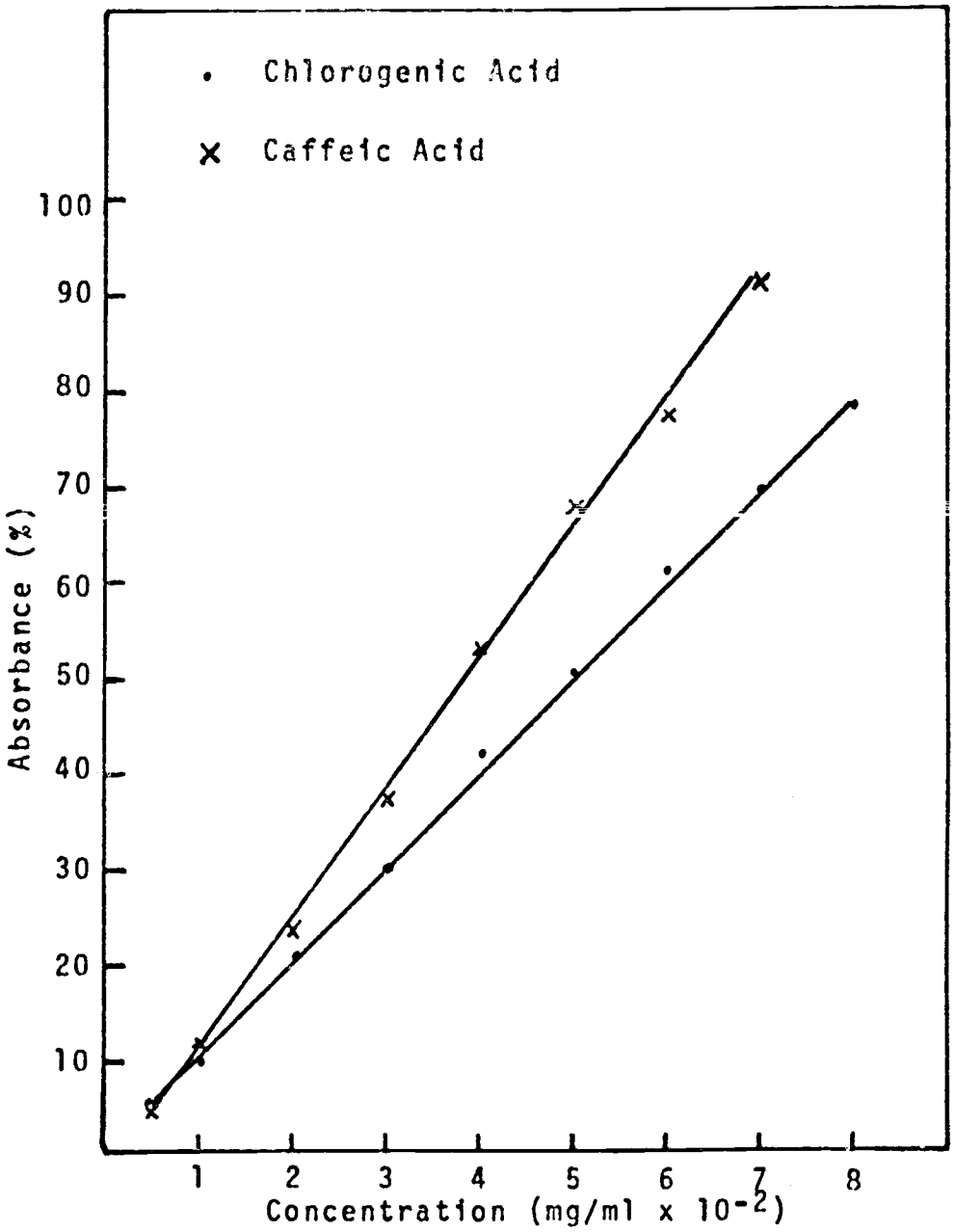

Figure 21. UV Absorbance of Two Major Periderm Phenolic Acids in 83% Isopropanol.

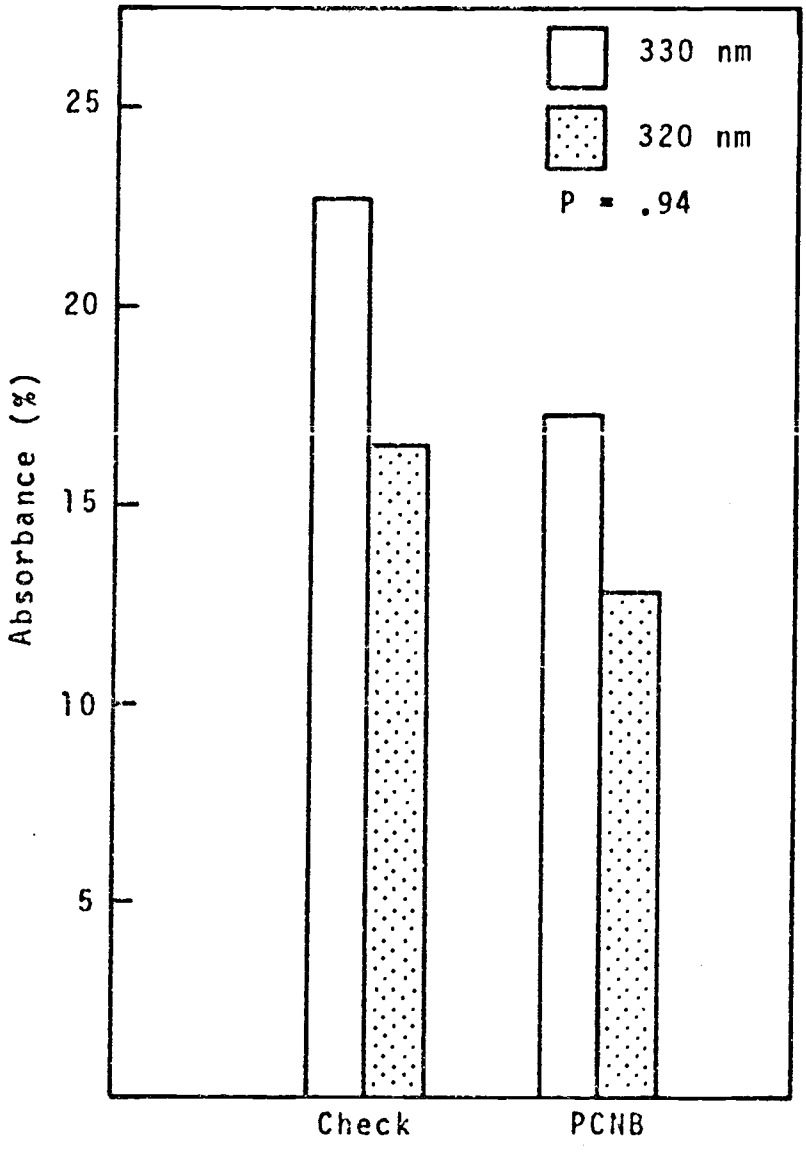

Figure 22. The Influence of PCNB on UV Absorbance by Eluted Chromatographed Fluorescent Spots of Periderm Extract.

3. Histochemical and anatomical evaluations

a. Anatomical character of net

Superficial observations showed net to exist generally in polygonal patches, separated by rifts. The patches were connected to one another by strands of tissue which gave the appearance of stretched cell material (figure 23). The patches appeared darker around the edges than in the center, which appeared as a depression in the patch.

Net was observed in radial and transverse sections to consist of collapsed surface cells above whole cork cells (figure 24). These cells were isodiametric, periclinally flattened, highly vacuolated, and arranged in bricklike columnar fashion. This columnar cork was normally 5-12 cells deep. The edge of each patch was considerably thicker than the center, and the tissue composition was less dense at the edge (figure 24). Tuber areas without net had whole cork cells at the periderm surface with very little evidence of surface cell degeneration (figure 25).

b. Histochemical analysis of periderm

Cork cell walls of periderm sections treated for two hours in phloroglucin for lignin detection were lightly stained (figures 26, 27). Untreated sections show very slight yellow coloration in net tissue

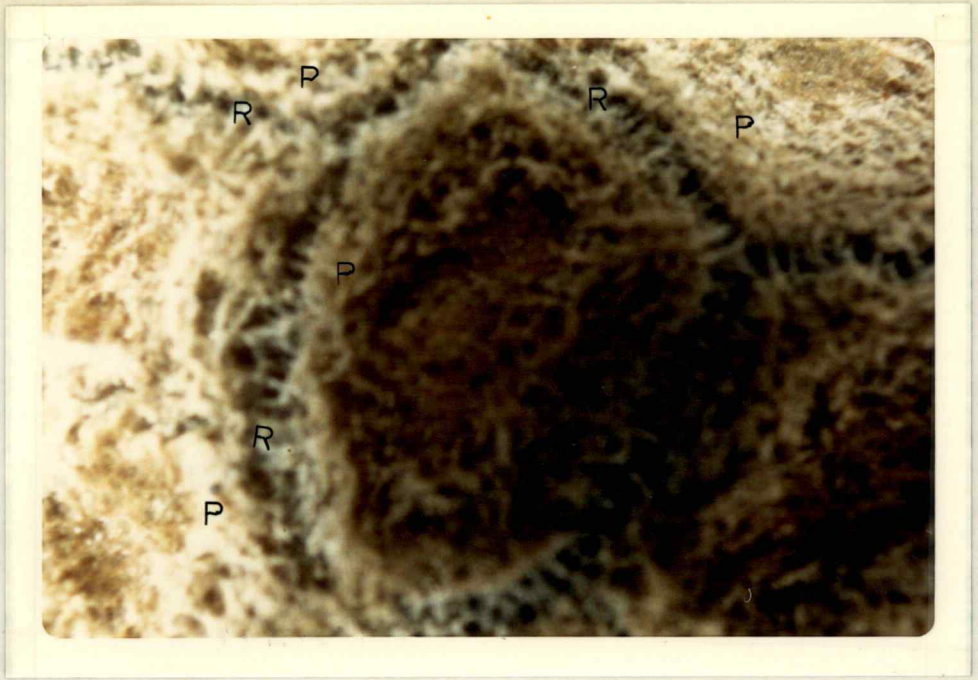

Figure 23 - Superficial View of Net Patch
P - Net patch R - Rift

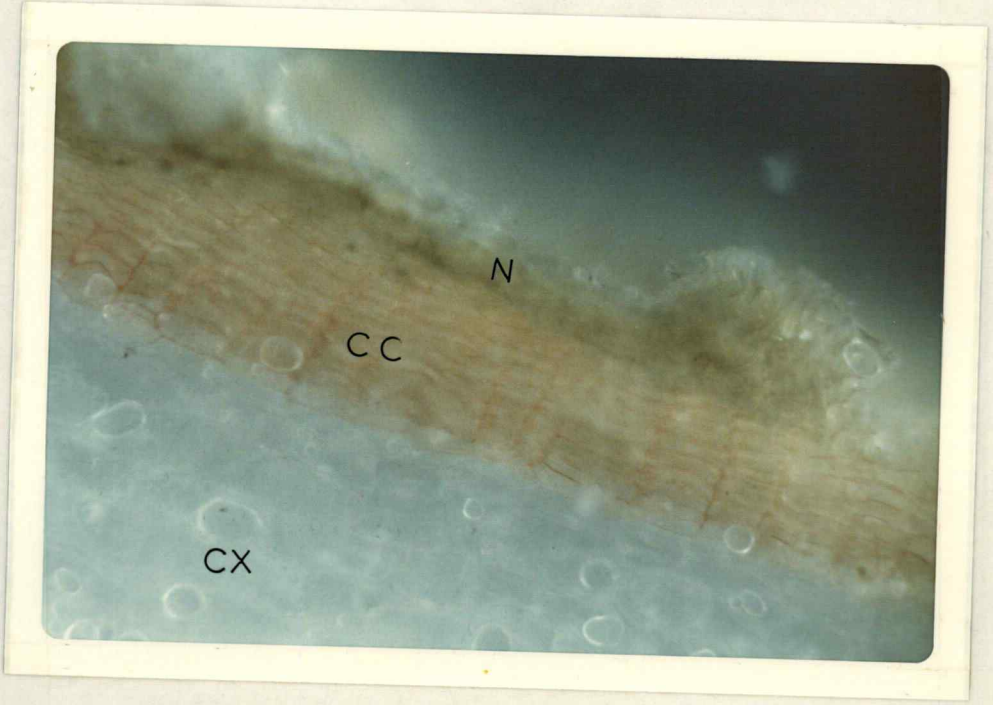

Figure 24 - Cross Section of Net Patch
N-Net CC-columnar cork CX-cortex

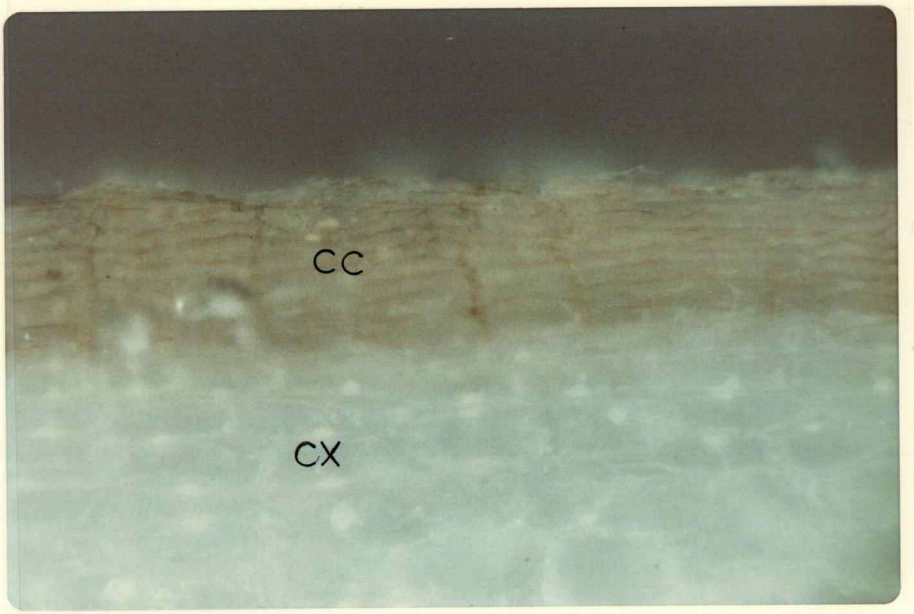

Figure 25 - Cross Section of Periderm Without Net
CC-columnar cork CX-cortex

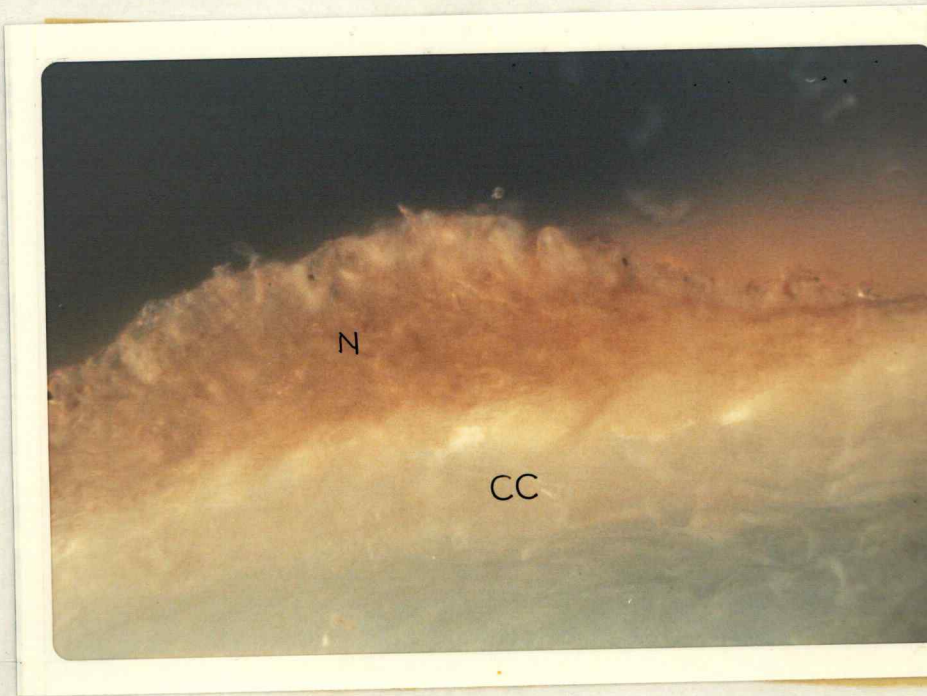

Figure 26 - Cross Section of Cork
Stained with Phloroglucin
N - net CC-columnar cork

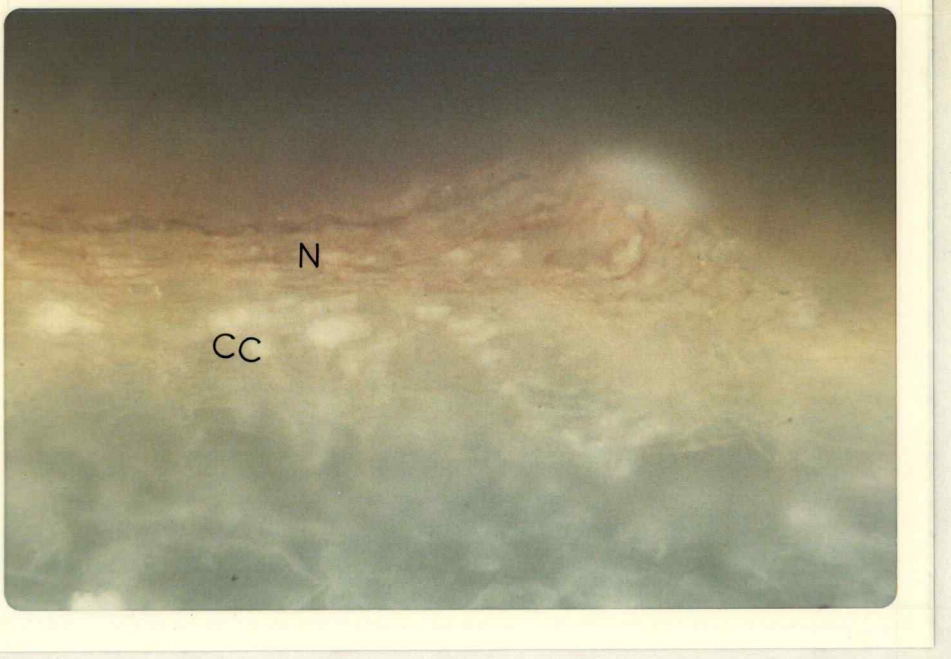

Figure 27 - Cross Section of Cork Showing Stained Cell Walls of Phelloid Cells (Net)

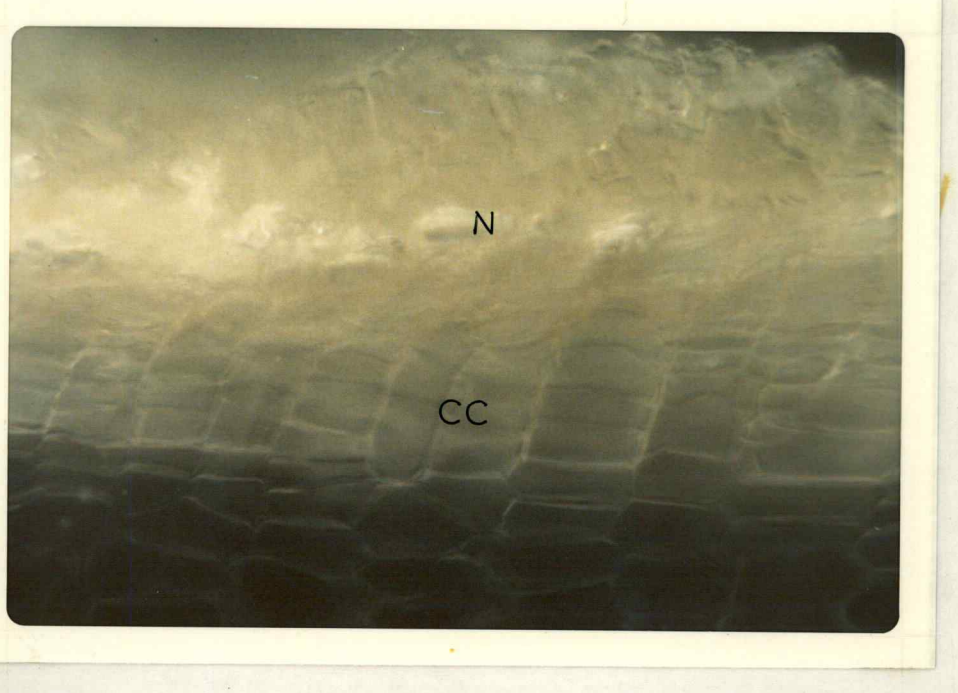

Figure 28 - Unstained Periderm
N-net CC-columnar cork

(figure 28). The middle lamellae of the collapsed surface cells forming the net were stained (figure 26), and the degenerated condition of these cells gave the net tissue the appearance of a generalized tint from the phloroglucin stain. Stain was much less evident in the lamellae of all columnar cork cells, but appeared to be heaviest in the outer half of these layers. No phloroglucin stain was seen in tissue below the cork.

Analine blue used for cellulose detection thoroughly stained the cell walls of the phellogen, phelloderm and cortex, but did not stain the columnar cork (figure 27). There was some blue staining, however, in some of the collapsed cells of the net.

Sudan III, for suberin, stained the walls and lamellae of the columnar cork cells providing distinct cell outlines (figures 24, 25, and 29). Stain was not found below the cork. Only slight staining by Sudan III was seen in the degenerated net cells.

Ruthenium red, a pectin stain, stained the middle lamellae of all cortical, phelloderm, and phellogen cells, the lower cork cells, and stained occasional discrete areas in the collapsed cork (figure 30). It was frequently seen to stain in a 3-4 cell band in the middle of the columnar cork, with virtually no staining in the outer cells of columnar cork.

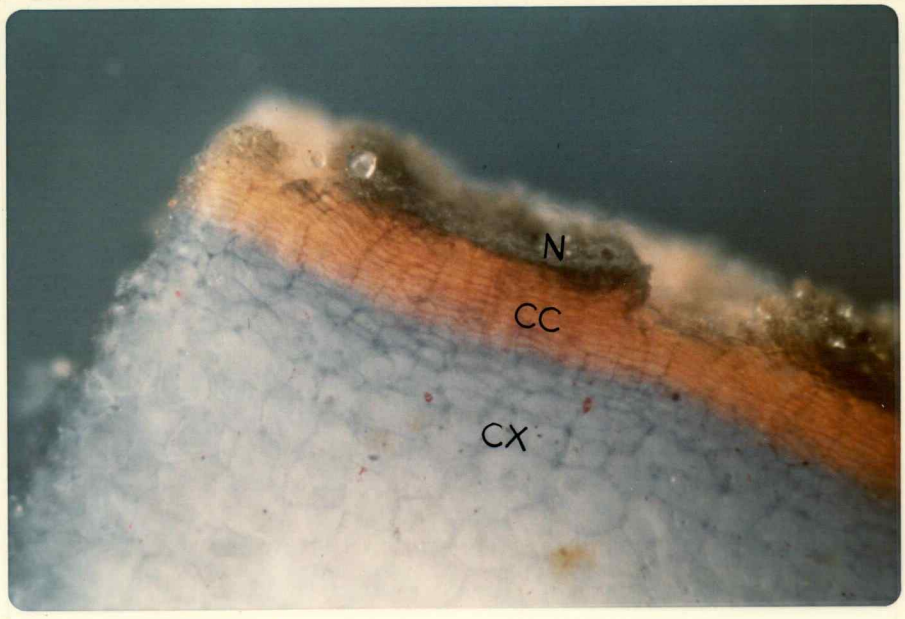

Figure 29 - Periderm Section Stained with Sudan III (orange) and Analine Blue
N-net CC-columnar cork CX-cortex

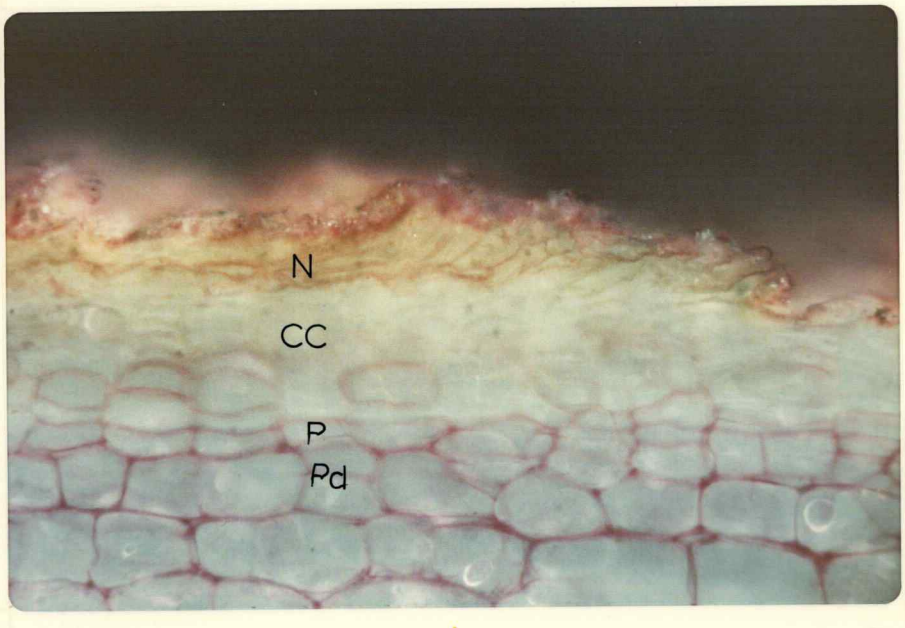

Figure 30 - Cross Section of Periderm Stained with Ruthenium Red (1:5000) for 15 min.
N-net CC-columnar cork P-phellogen Pd-phelloderm

c. Cork thickness

Cell counting was first done by counting ten randomly chosen data points, each consisting of a single column of whole cork cells.

The number of cells per column appeared to be too variable for consistent data, until it was noted that much of the variation was due to the random selection of the columns on a section. If a data column was beneath a stretch crack, fewer cells were counted than if it were beneath a net patch. By choosing a column beneath a net patch (figure 31) where cells could be reliably counted, variation within individual mounted sections was much reduced.

A significant relationship was found between the visual classes used in net indexing and the number of cells per column (figure 32). This relationship held true whether the counts were made in an area of the tuber with russeting or in a "smooth" area. In the greater-than-75% coverage class, the mean cell number below a net patch was 7.5, whereas in the less-than-25% class, it was 5.3. Differences between the two middle classes were not found to be statistically significant. The columnar cork beneath net was on the average one cell thicker than in a smooth area without net.

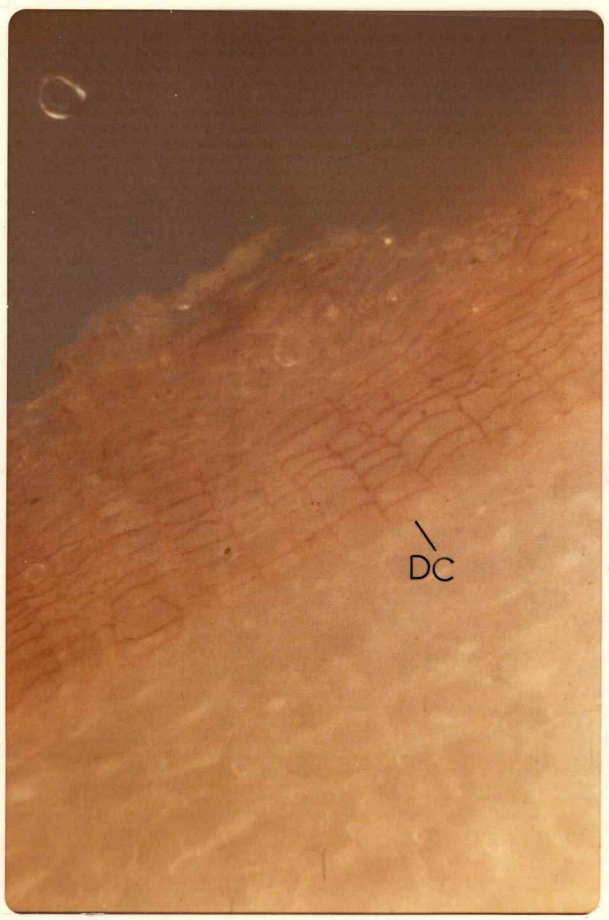

Figure 31.

Cross Section of Periderm
Showing Selection of Data Column
DC = data column

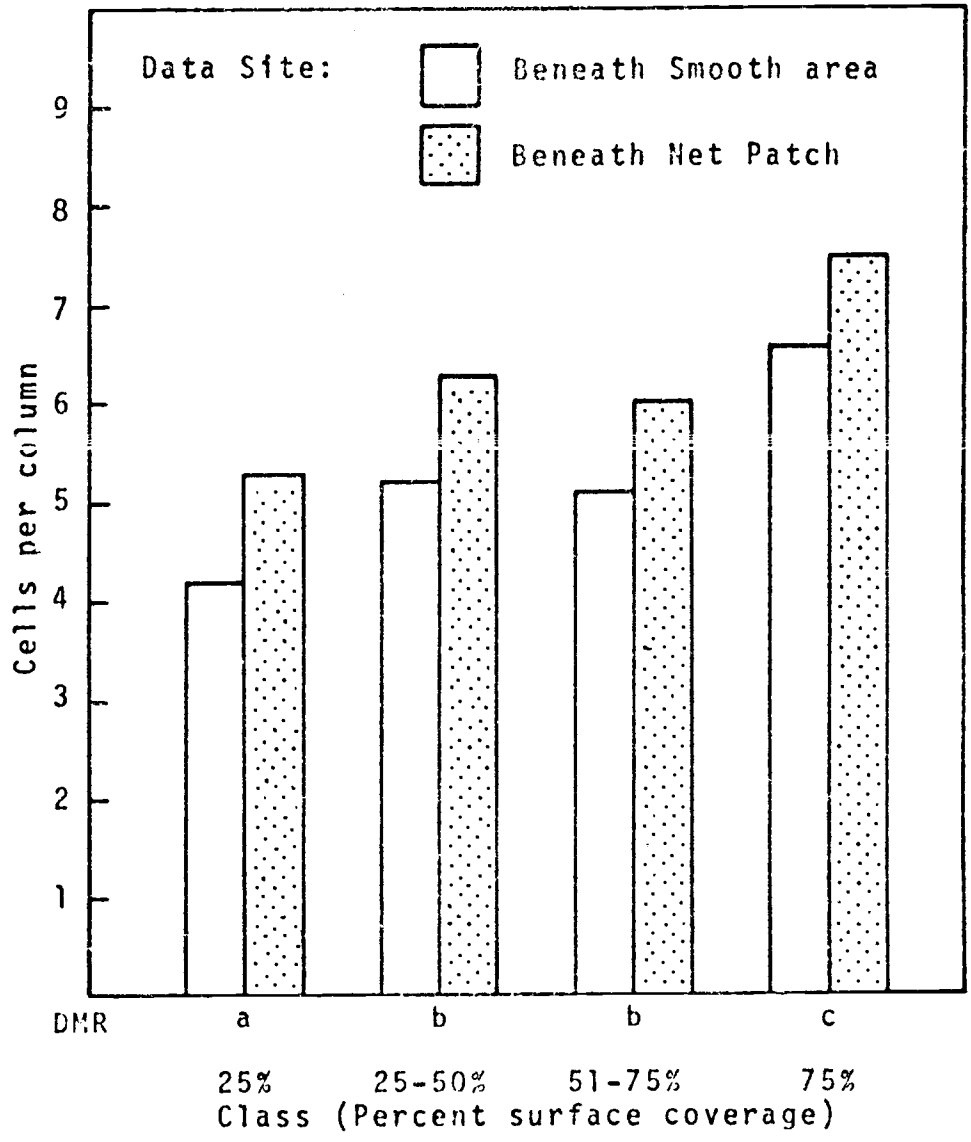

Figure 32. The Relationship of Cork Cell Layers to Russeted Periderm Classes.

B. 1972 Experimental treatments

1. Visual evaluations

a. Net classification

On inspection, gross differences in net due to treatment could be seen. It was observed that russeting decreased with increasing soil-moisture levels, and that PCNB-treated samples were noticeably less russeted than untreated samples. Sulfur treatments were also considered to be less russeted, but the difference due to sulfur was not as pronounced. Several observers viewed the tuber samples, and all considered that there was no difference due to rate of either sulfur or PCNB.

When tubers were systematically classed, distinct differences were evident among irrigation treatments and chemical treatments (figure 33). The regression coefficient for the relationship between minimum available soil moisture and percent tubers with 80% surface russeting was -0.38. Adjacent soil-moisture levels, however, did not result in differences in net when differences were compared in a multiple-range test.

PCNB had a depressing effect on tuber russeting at all soil-moisture levels, and sulfur depressed tuber russeting at the lower soil-moisture levels (figure 34).

b. Plant growth and yield observations

Plant growth appeared to be satisfactory in all

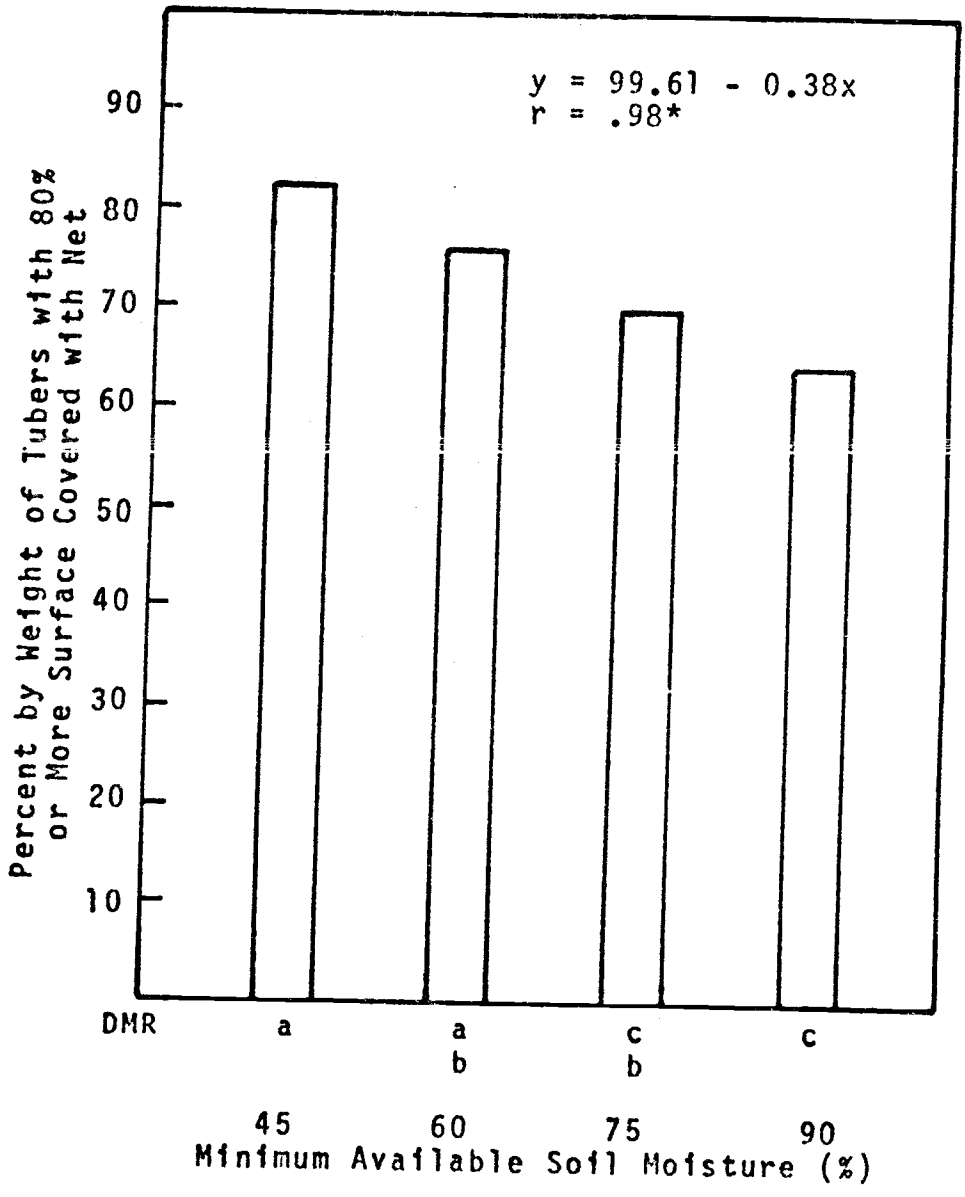

Figure 33. The Effect of Available Soil Moisture on Russeting.

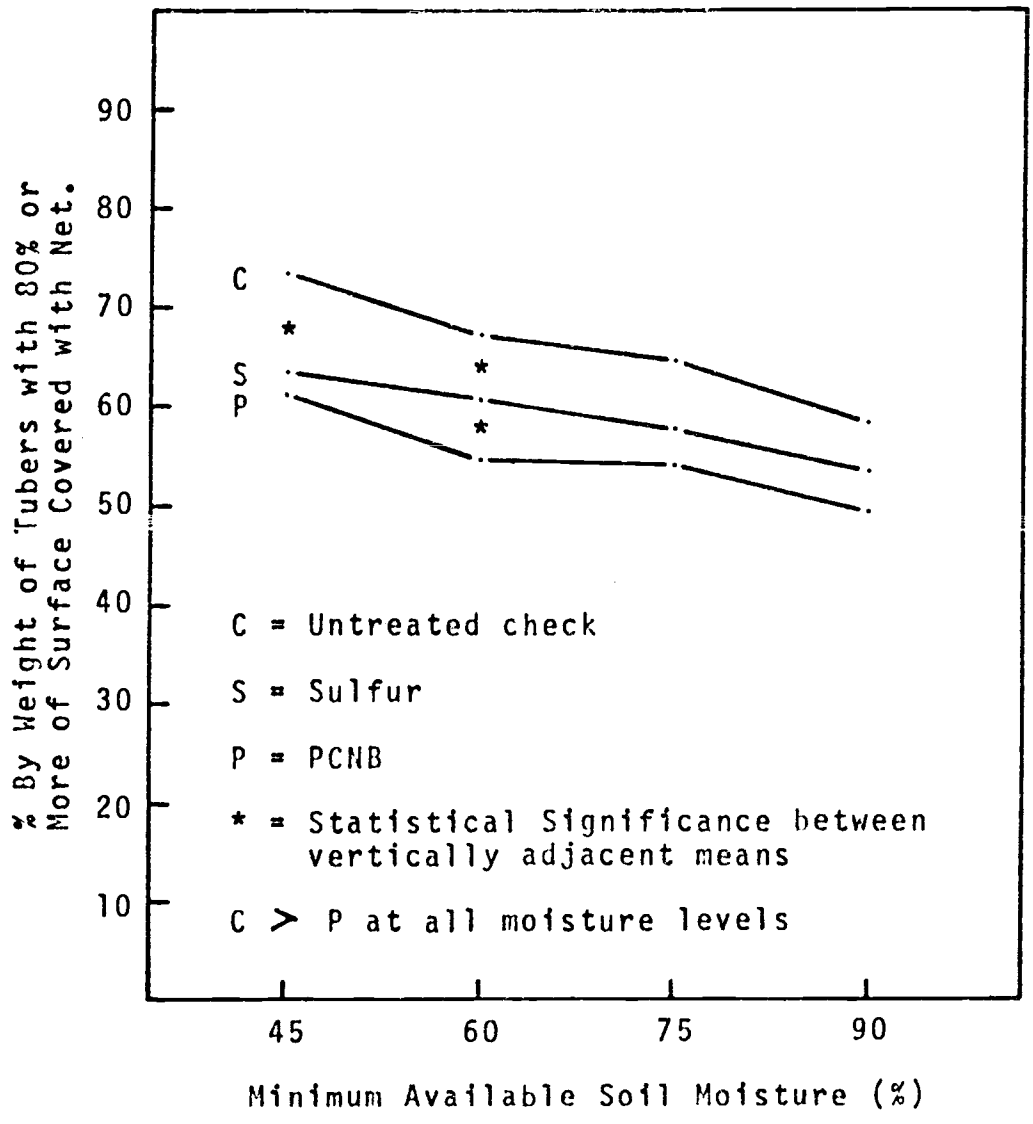

Figure 34. The Effect of Chemicals and Soil Moisture on Russeting.

except the 45% soil-moisture treatments, where growth was slightly retarded. In the 90% soil-moisture treatment, vine growth was apparently the most vigorous. Tuber lenticels from the 90% soil-moisture treatment were apparently more enlarged than those from the lower soil-moisture treatments.

The yield of tubers harvested from the 45% soil-moisture treatment was significantly less than yields from the higher soil-moisture treatments. Yields from chemical treatments did not differ.

2. Chemical evaluations

a. Spectrophotometry

The U. V. absorption curve for periderm extracts was nearly identical to that for the 1971 samples (figure 35). The absorbance maximum was at 325 nm; both the major peak and the minor peak were at wave lengths only 5 nm shorter than the peaks for the 1971 samples.

U. V. absorbance values for alcohol extracts of periderm samples (figure 36) showed a difference between the two high and the two low levels of soil moisture but no difference was found in other comparisons. No difference was found among chemical treatments.

b. Fluorometry

Fluorometric tests showed fluorescence to be linear with chlorogenic acid concentration in basic buffer

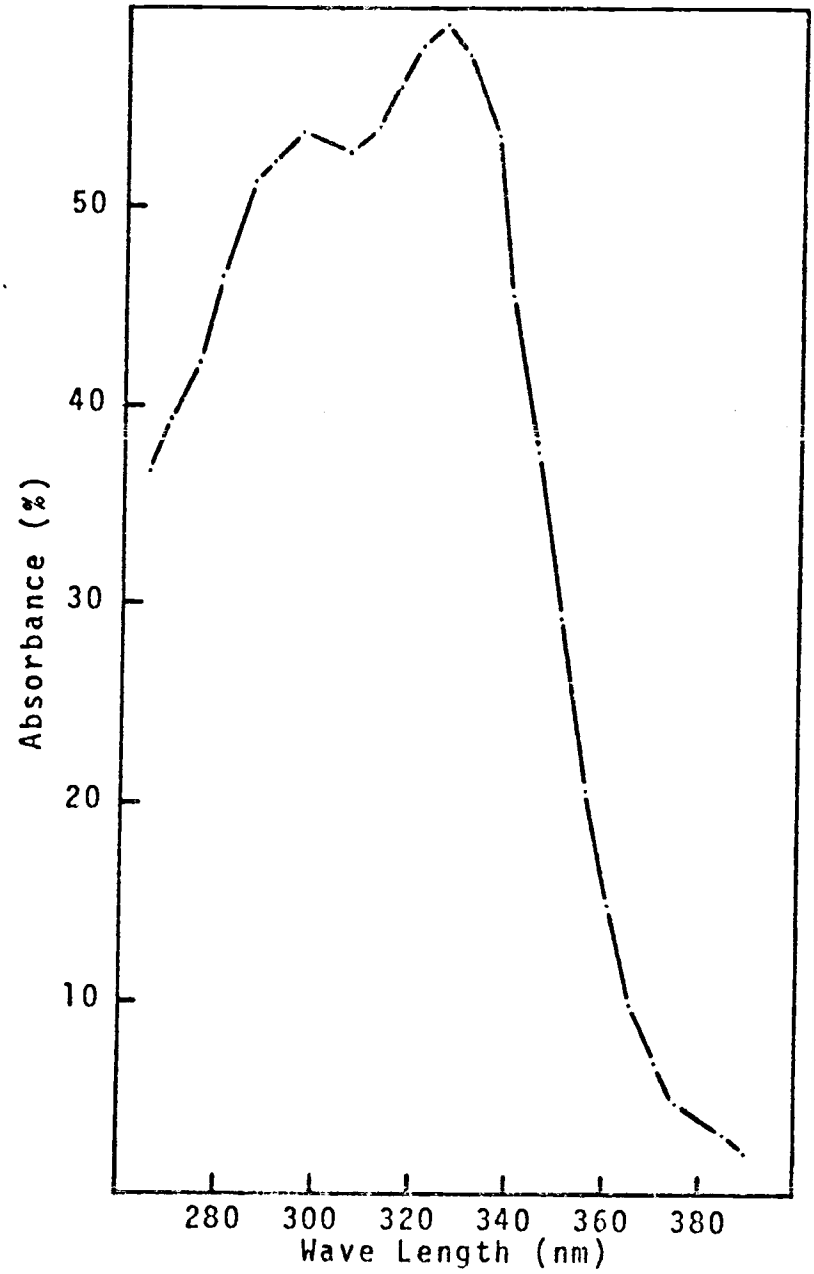

Figure 35. Spectral Absorbance for 83% Isopropanol Extracts of 1972 Periderm Tissue.

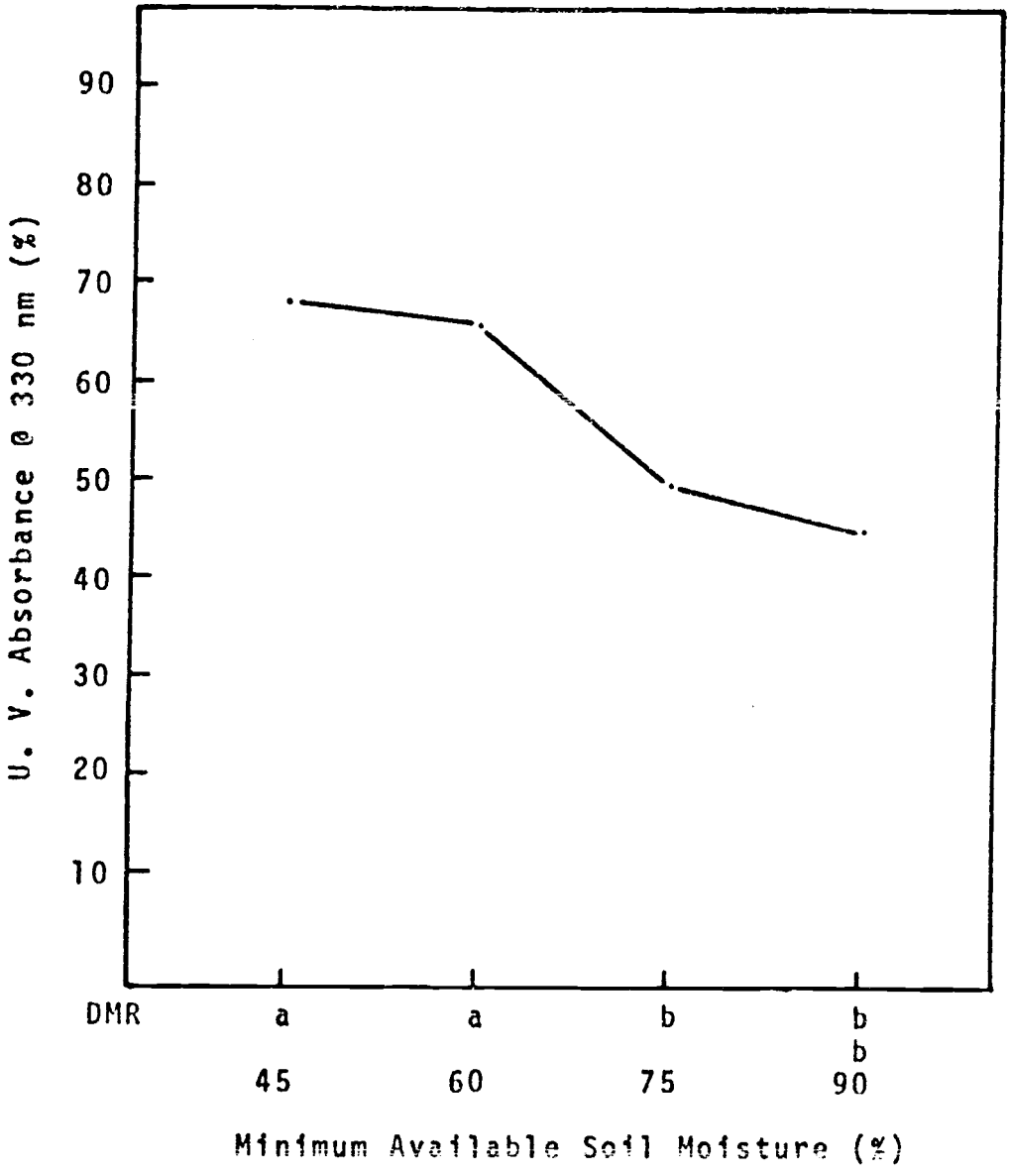

Figure 36. The Effect of Soil Moisture on U. V. Absorbance by Periderm Extracts.

(figure 37), so fluorometry values were assumed valid for chlorogenic acid analysis. Values for the untreated check, sulfur and PCNB differed, with the check and PCNB at the high and low positions respectively (figure 38). There were no differences due to irrigation treatments or chemical-irrigation interaction.

3. Anatomical evaluations

Differences in number of cork cell layers in the columnar cork of periderm samples were evident when soil-moisture levels were compared (figure 39). The 45% level produced tubers with the most cells per column (9.5). Data from the three remaining soil-moisture treatments fell into two statistically homogeneous subsets, but there was a clear trend toward fewer cells per column with increasing soil moisture. The mean value for cells per column from the checks was higher than that from the chemical treatments, and the mean value for PCNB treatments was lower (figure 40), but the probability of differences being due to chemical treatments was only slightly above 90%.

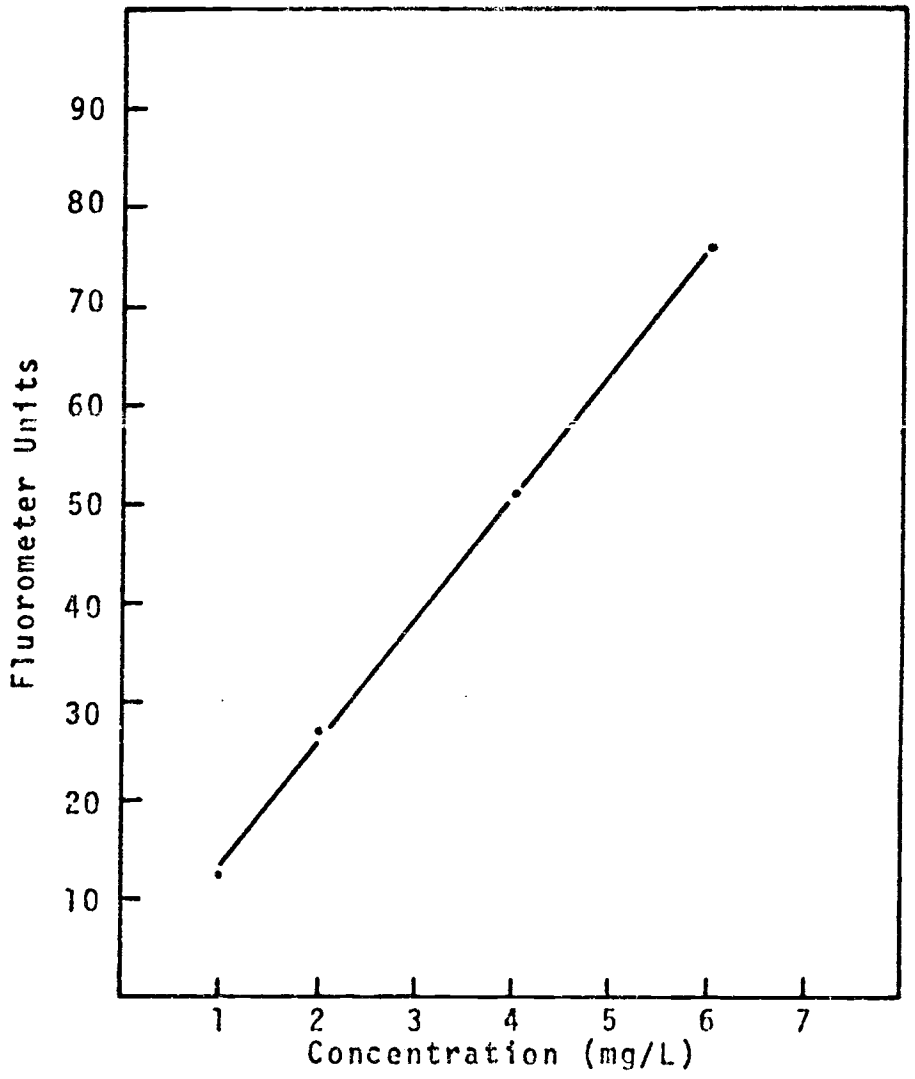

Figure 37. Fluorescence of Chlorogenic Acid in pH 11.0 Carbonate-Bicarbonate Buffer. Fluorometer Range 1X.

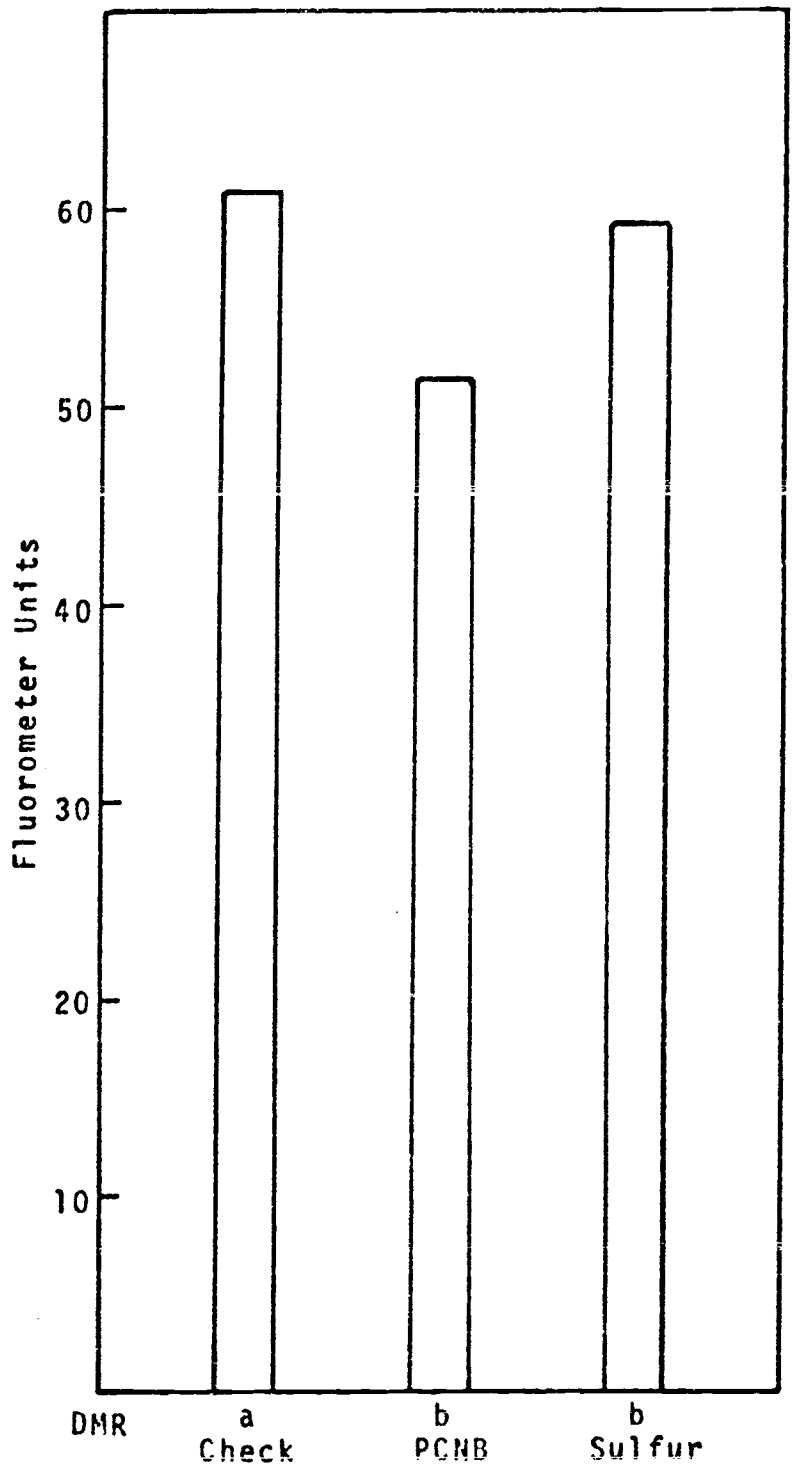

Figure 38. The Influence of Chemical Treatments on Periderm Extract Fluorescence.

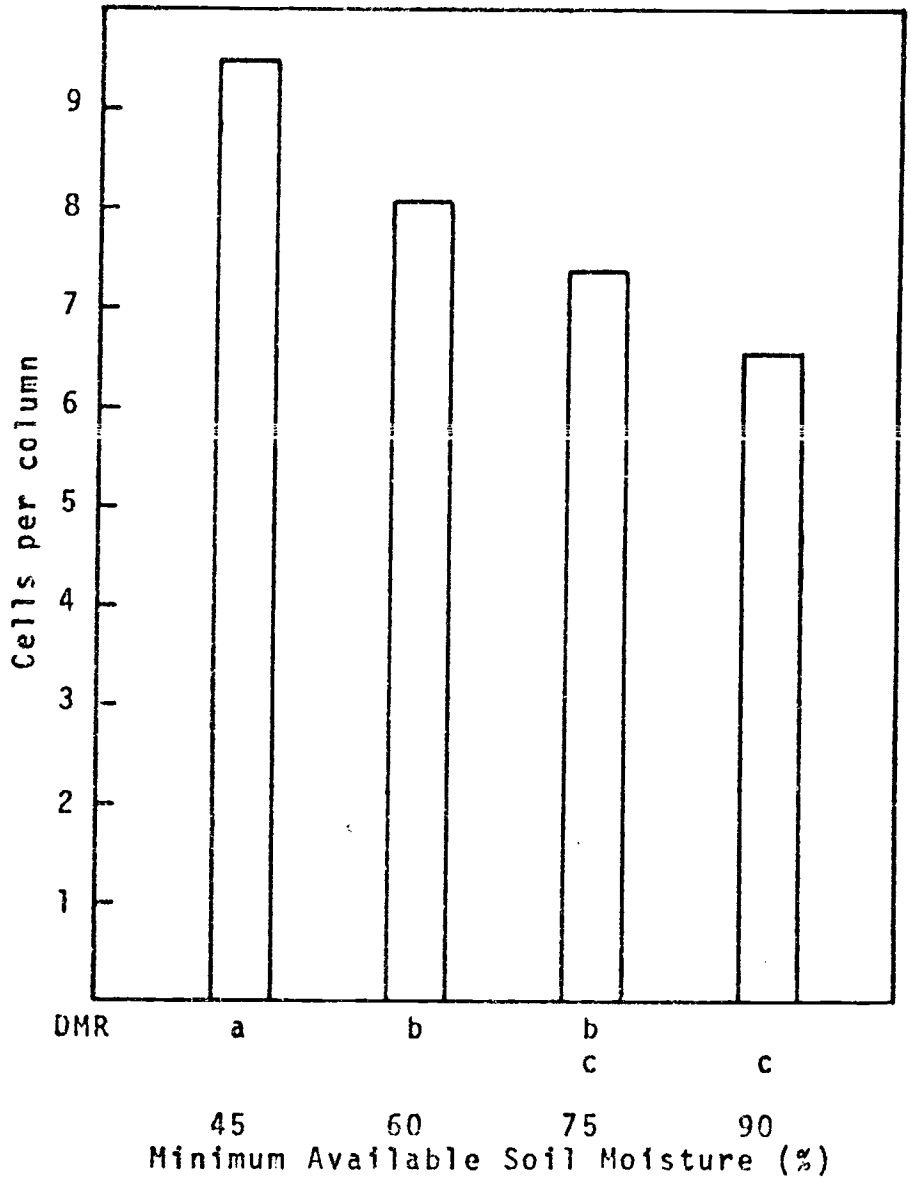

Figure 39. The Effect of Soil Moisture on Cells Per Column in Columnar Cork

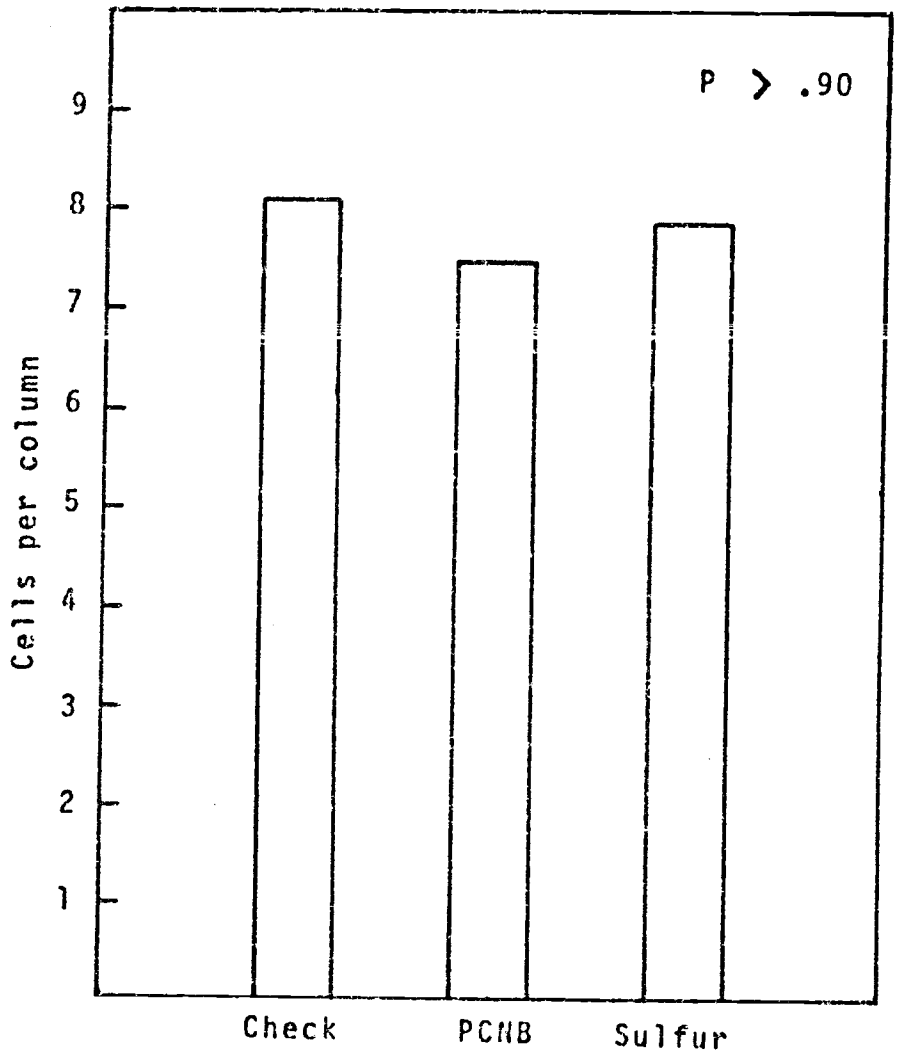

Figure 40. The Effect of Chemical Treatments on Cells Per Column in Columnar Cork.

DISCUSSION

A. Introduction: The character of Russet Burbank cork

1. Histochemistry

Comparisons of tuber periderm tissue by histochemical methods revealed distinct differences in composition between the net tissue and the underlying columnar cork. Treatment of periderm with Sudan III showed that the walls of cork beneath the net were uniformly suberized. The net itself, however, had no suberin and was therefore considered phelloid tissue or nonsuberized cork. (Esau, 1965).

Absence of suberin in net may have been due to hydrolysis of previously-occurring suberin. This is suggested by the absence of suberin in cell walls of columnar cork on the sides of a net patch, bordering a stretch crack. It is also possible that the outer net phelloids had never been suberized; this would be likely if this tissue originated from primary epidermis, which does not normally suberize (Esau, 1965).

Lignin, indicated by phloroglucin stain, was found to be present in all cork tissue. Potato periderm lignin produced a yellow-orange color reaction to phloroglucin; a much less intense color than that which results from coniferous wood lignin. This suggests a lower lignin

concentration and/or a different lignin composition than is found in wood lignin. The lignin concentration was much more pronounced in the phelloid cells of the net than in the columnar cork cells. It appears likely that lignin is the main material which could be responsible for intercellular adherence of phelloid cells.

Analine blue stain for cellulose did not color the columnar cork, indicating that suberization and/or lignification effectively penetrated the cellulose wall to sheath all cellulose microfibrils. Since analine stain was seen in some, but not all phelloid cells, it is likely that suberin was largely responsible for preventing stain from contacting cellulose walls of the columnar cork, and lignin had somewhat less effect.

Ruthenium red, a stain for pectic materials, showed that pectic materials were evident primarily in nonsuberized and nonlignified cells below the cork. Much of the cork tissue did not stain with ruthenium red, suggesting partial disappearance of pectins by hydrolysis and loss of sugar components and/or partial shielding by suberin and lignin. This indicates that pectins probably do not constitute a main intercellular adhesive in the net, and probably serve a minor role in the suberized columnar cork.

2. Anatomy

Net tissue was generally too disorganized due to cell collapse to identify individual cells. The rifts which occurred in this tissue apparently released tension on cell walls, resulting in curling back of the tissue bordering the rifts. The phelloid cell wall material in the center of a net patch was more compact. Apparently as the tuber expands, the degenerated net cells are stretched and drawn down toward the suberized layers, with rifts developing to form net patches.

The sharp delineation of the boundary between the net and underlying cork, as well as the difference in chemical makeup suggests that the nonsuberized net may have arisen from an epidermal phellogen; however, the ontogeny of net is not clearly established. The developmental anatomy of cork tissue of russeted tubers should be further investigated.

The number of suberized cell layers in columnar cork proved to be a reliable criterion for quantitative evaluation of the effect of cultural and chemical treatments on cork tissue. There was usually good agreement between the subjective means of comparing treatments by visual estimates of net, a gross morphological character, and the more objective method of counting suberized periderm layers, even though net and suberized cork are anatomi-

cally different tissues. Visual net evaluation on individual tubers was more rapid, but required judging and weighing large quantities of potatoes to obtain precise differentiation between net classes.

3. Phenolics

Phenolic acids were investigated in this study because of their part as intermediate products in lignin biosynthesis, as discussed in the literature review. Comparative measurement and detection of phenolic acids by U. V. absorbance or fluorescence and chromatography is a reasonably straightforward process, and was found to be possible with minimum sample preparation and purification.

Thin-layer chromatography of periderm extracts yielded several spots which fluoresced under U. V. The two major fluorescing spots exhibited Rf values, fluorescence color, reaction color and U. V. absorption maximum values characteristic of chlorogenic and caffeic acid. The predominance of these two phenolics found in potato periderm in this study is in agreement with the findings of Jolliot and Come (1972) and Metlitskii and Ozereskovskaya (1968). The U. V. absorption maximum of diluted extracts was identical to that of chlorogenic acid. The relationship between the results from thin-layer chromatography and those from spectrophotometry indicates that U. V. absorbance of extract dilutions should bear a reliable

relationship to the concentration of these phenolics in potato periderm. Coumarin was detected in chromatographed periderm extract as a major spot on the chromatogram, but was not studied further. It has been previously reported to be present in potato tubers (Austin and Clarke, 1966).

B. Experimental treatments

1. Soil moisture

A distinct inhibitory effect of high soil moisture upon net was found. This effect was evident as a result of not only increased levels of soil moisture, but also as a result of the increased time during which soil moisture percentage was held at a high level. These results are in contradiction with the conclusion by Holstad (1967) that dry soil reduced russeting.

Each time-increment added to the period during which soil moisture was maintained at the 90% level resulted in a decrease in net, but these incremental decreases did not become significantly different from the continuous 60% moisture treatment until the time period of 90% moisture covered nine weeks. On the basis of this study, 90% moisture period of as much as six weeks would therefore not be expected to cause a significant reduction of net below that resulting from the currently recommended 60% moisture level.

The 1972 study and the 1971 study had two treatments in common, i.e. the season-long 90% soil-moisture level and the 60% soil-moisture level. In both years, the 90% level resulted in tubers with significantly less net than did the 60% level.

The 1972 data shows that maintaining the percent of soil moisture above 45% resulted in less net. Although a distinct regression was found, it should be pointed out that any given 15% difference in soil-moisture level did not result in significant differences in net, whereas a 30% difference in soil-moisture level did.

The random occurrence of areas without net on individual tubers suggests that the environmental factors responsible for reduced net may act directly on periderm sites to produce a localized effect rather than moving via root uptake to produce translocated effects on tuber metabolism. A general change in tuber physiology would likely result in more uniform anatomical changes. The possibility of a change in the physiological sensitivity of a plant to microenvironmental variations should not be overlooked, however.

Even though the soil-applied treatments were incorporated thoroughly from a mechanical application standpoint, great variation in sulfur concentration over the tuber surface was visually discernible during the process

of harvest. It is probable that PCNB and soil-moisture concentration, as well as soil composition per se, over the exposed tuber surface also varied. This would likely produce local effects rather than general effects.

Penetration of treatment factors into the net tissue should be possible, since this tissue can allow free passage of water. High soil moisture may accentuate movement of solutes through phelloid cells. Solutes may also pass into columnar cork also, prior to suberization.

The number of suberized cell layers, which can be considered a measure of periderm thickness (Nagdy and Boyd, 1965) followed the same relationship to soil-moisture level and length of high-moisture period as did net. This is in agreement with the observation by Nielsen[18] that tubers grown in wet soils in Denmark are known to normally have very thin periderms.

The presence of excess water in soil pores may reduce the air capacity by two-thirds or more and may reduce airflow by a factor of 10,000 (Baver, 1948; Leytey, 1967). The effect of high soil moisture on tuber russeting may therefore be due to partial oxygen exclusion from the soil environment by frequent water saturation and possibly to saturation of periderm tissue. Potatoes are known to be sensitive to soil aeration. Low tuber yield from nine weeks of 90% soil moisture was consequently

another indication that aeration was inhibited by high soil moisture.

Soil temperature differences may have exerted some influence on net. Occasional temperature measurements in 1971 showed that the 90% soil moisture plots were, on the average, 1 C cooler at the 15 cm depth than the 60% plots. Cooler soil temperature under potato canopies, resulting from frequent irrigation, has been previously established. Sanders and Nylund (1972) reported maximum soil temperature differences up to 1.7 C at the 15 cm depth between nonirrigated potato plots and plots that received daily irrigations. If the greenhouse studies by Ruf (1963) and Yamaguchi, Timm and Spurr (1963) are applicable to the field, it would appear that such temperature reductions from irrigation should be insufficient to account for significant reduction in net. It is possible, however, that slight temperature reductions have an additive effect, so that when taken together with other irrigation effects, net reduction could be intensified.

2. Compaction

The case for implicating oxygen exclusion is supported by the reduction of net as well as yield by soil compaction, since compaction is known to reduce soil oxygen. Baver (1948) reported that soil air capacity is

frequently reduced eight-fold by compaction alone, and that the presence of a thin compacted layer in the upper soil profile may reduce air movement to an exceedingly low rate.

Association of reduced lignins with factors known to diminish the soil oxygen supply complements the results of Higuchi's (1967b) investigation of lignin biosynthesis. He found that certain oxidation inhibitors (sodium azide and salicylaldoxime) reduced oxygen consumption by coniferyl alcohol. He therefore postulated the necessity of an oxygen supply for its conjugation in lignin formation.

Freudenberg (1965) has shown that lignin is formed from coniferyl alcohol under the influence of phenol oxidase and oxygen. Higuchi's further studies of lignin synthesis with peroxidase and H_2O_2 support Freudenberg's proposal, and thus provide a basis for the theory that reduced net in high soil moisture or a compacted moist soil is due to low oxygen.

Partial oxygen exclusion may be responsible for inhibition at other steps in lignin synthesis. According to Zucker and Levy (1959), chlorogenic acid synthesis by potato disks is inhibited by anaerobic conditions. This may be a reflection of inhibition of synthesis of the chlorogenic acid precursors, caffeic and quinic acid. Such a mechanism would also mean reduction of lignin

precursors, since caffeic acid is involved, and the same inhibiting factors could likewise inhibit formation of other phenolic acids, such as p-coumaric acid, which are precursors in lignin development.

The interaction of soil compaction with weeks of high soil moisture during 1971 suggests that the influence on net that was exerted by compaction occurred during the first three-week period of high moisture, since additional weeks of high moisture resulted in no further change. Since length of high-moisture period was not included in the 1972 study due to physical and economic limitations, this study has not established whether percent soil moisture and length of high-moisture period may interact in influencing net.

The reduced number of cells per column in the columnar cork associated with high soil moisture may also have been a result of lower soil oxygen. This possibility is supported by the findings of Lipton (1967) who reported pronounced reduction in wound periderm cell formation when atmospheric oxygen was held at 5% or less.

It is possible that maintenance of high soil moisture by frequent irrigation reduced net by lignin inhibition via more than one mechanism. The phenolic acids utilized in lignification of phelloid cells are sparingly soluble in cold water, and their solubility increases

with increased water temperature (The Merck Index, 1968). When the soil moisture content varies due to frequent irrigation or is maintained near the saturation point, continual free passage of water within the permeable peripheral tissue over an extended period of time may result in significant extraction of soluble materials from cellulose wall areas, thus diminishing the supply of components important in lignin synthesis.

Since the moisture and compaction treatments in this study were managed so that they affected primarily the surface 23 cm, the proposal that reduced soil oxygen was responsible for reduced net does not conflict with the generally good plant growth and yield. Presumably aeration in the root zone below 23 cm was adequate for plant requirements except for the nine-week 90% soil-moisture treatment in 1971.

3. Chemicals

PCNB treatments did not result in a statistically significant effect on net indices in 1971, although the mean net index was below the index for the check. In 1972, however, PCNB treatment resulted in a significant reduction in net.

The PCNB treatments reduced U. V. absorbance by periderm extracts when this parameter was measured at the absorption maxima for chlorogenic and caffeic acids.

These results support the findings of Mondy (1966) who reported that PCNB soil treatments reduced the phenolic content of tubers. She also reported higher polyphenol oxidase activity, and suggested that this indicated probable conversion of phenols to quinones which would not show up in her colorimetric analysis procedure.

Columnar cork thickness was not considered to be changed significantly by PCNB, although the mean value for cells per column was lower than that for the check.

Sulfur did not significantly influence net in 1971, although the mean net index was higher than that for the check. In 1972, some interaction was found. Sulfur plots yielded tubers with less net than was observed on tubers from the check plots, when compared at 45% and 60% soil moisture, but when this comparison was made at the higher soil-moisture levels, no difference was found.

The difference between the results from 1971 and those from 1972 may be due in part to the method by which sulfur was applied. In 1971, the sulfur was laid in a narrow concentrated band in the bottom of a v-shaped furrow, whereas in 1972, the sulfur was spread across the full width of the furrow. The 1971 sulfur treatment apparently resulted in phytotoxicity, evidenced by the low yield from the sulfur treatments. This may have hastened maturity processes leading to earlier lignifica-

tion resulting in more net. The 1972 treatment did not result in phytotoxicity. The reduced russeting due to sulfur was found only in the lower moisture treatments; the effect was slight enough that the depressing effect of soil moisture on net may have masked that of sulfur, particularly at high soil-moisture levels.

The inhibitory effect of sulfur on net was not accompanied with a reduction of phenolics as in the case of PCNB and soil moisture or by a decrease in the number of cells per cork column as in the case of soil moisture, or by a change in plant vigor or productivity as in the case of the 1971 sulfur treatments. This suggests that a different mode of action may have been involved.

4. Additional factors

Conclusions based on results reported herein do not exclude the possibility that factors not considered might modify the responses observed. For example, since ample fertilizer rates provided major nutrients slightly in excess of plant growth requirements, addition of these elements would likely not modify the reductions in net which were observed. It is possible, however, that high soil moisture or chemicals might interact with such conditions as phosphorus deficiency or soil salinity to accentuate a reduction in tuber russeting. Although no individual factor may entirely control russeting, it is apparent

from the literature and from this study that several factors may have significant effects. These may work together to produce interacting or additive effects.

CONCLUSIONS

The russeting phenomenon in Russet Burbank potato tubers is the result of a process of lignification, death and collapse of outer cork phelloid cells which adhere to the underlying suberized columnar cork. It is proposed that reduced net is due to inadequate or delayed lignification and consequent sloughing of phelloid cells. This lack of intercellular adhesion results in a whiter appearance of Russet Burbank tubers without net, as is characteristic of White Rose and similar nonrusseted cultivars.

Reduced net was associated with lower phenolic acid content in the periderm and with fewer layers of suberized cork cells, when the cause was high soil moisture, soil compaction, or PCNB treatment. It is postulated that a lower phenolic acid concentration constituted a reduced precursor supply for lignin synthesis, resulting in inadequate lignification for intercellular adhesion, and a consequent reduction in tuber russeting. When sulfur treatments were the cause of reduced net, these associations were not found. Extrapolation of these relationships beyond the factors studied in this investigation should therefore be done only with great care.

Evidence from this study suggests that normal tuber

russeting may be reduced as a result of more than one factor. Evidence favors the hypothesis that high soil moisture and compaction reduce the oxygen supply to the tuber periderm tissue, resulting in inhibition of the biosynthetic pathway to lignin formation. Localized water extraction of phenolic acid precursors may also contribute to reduced lignin.

PCNB apparently interferes with lignin precursor synthesis or metabolism, possibly by increasing polyphenol oxidase activity.

The variable effects of sulfur on net were not accompanied by the same anatomical and biochemical changes as were effects from other treatments, and are probably not explained by the same hypothesis. It is suggested that the 1971 increase in net was due to a phytotoxic induction of advanced plant maturity caused by sulfur application technique. The 1972 reduction in net was not associated with any dependent or independent variables; it is possible that an unseen effect on plant maturity via nutrition or pathogen control may have been responsible.

Although the use of high soil moisture, PCNB and sulfur for potato scab control were found to reduce net, practical use of these treatments is not likely to be detrimental to the market value of potatoes thereby produced.

The results of this study indicate that maintenance of above-normal soil moisture levels for scab control is not likely to reduce net to a significant degree if the soil moisture is allowed to deplete to 75% before irrigation. If it is not allowed to drop below 90% during the irrigation season, significant loss of net, and occasionally yield, will likely occur. If the period during which 90% soil moisture is maintained is limited to no more than the first six weeks, however, loss of net will probably not be significant.

SUMMARY

Management factors used for studies on potato scab control were evaluated for their effect on tuber russeting and related biochemical and anatomical parameters during 1971 and 1972.

Russet Burbank potatoes were irrigated in 1971 to maintain high available soil moisture (between 90% and field capacity) for 0, 3, 6 and 9 weeks, beginning one week after plant emergence. Soil moisture was maintained between 60% and field capacity during the time it was not held above 90%. In 1972, plots for four soil-moisture treatments were irrigated to maintain minimum levels of 90%, 75%, 60% and 45%, respectively, throughout the season beginning one week after emergence.

Subplot treatments in 1971 were soil compaction, pentachloronitrobenzene (PCNB) at 28 kg/ha, Super-X (mixture of PCNB and 5-ethoxy-3 trichloromethyl 1, 2, 4 thiadiazole) at 28 kg/ha, sulfur at 896 kg/ha, and N-serve [2 chloro, 6 (dichloromethyl) pyridine] at 1.7 kg/ha, and an untreated check. In 1972, subplots were PCNB at 28, 22, and 17 kg/ha; sulfur at 896, 672 and 448 kg/ha, and an untreated check.

Reduction of tuber russeting (net) resulted from increased length of high-moisture period in 1971, and

increased available soil-moisture percentage in 1972. Soil compaction at the high moisture level reduced net in 1971. PCNB, Super-X, and N-serve did not change net significantly, but sulfur increased net. In 1972, PCNB reduced net, and sulfur with low soil moisture reduced net.

Net was found to consist of collapsed, lignified, unsuberized cork cells above columnar layers of slightly flattened suberized cork cells. Together these form the periderm of Russet Burbank tubers. Periderm areas with net had more layers of suberized cork cells below the net than did areas without net. The number of cork-cell layers increased with visual estimates of the amount of net.

Histological stains showed that lignin content was highest in net tissue, lower in suberized cork, and absent beneath the cork. Suberin was present in cork cells below the net and absent in other tissue. Pectins were evident beneath the cork, but were found only in small amounts in cork tissue. Histochemical stain tests for cellulose were negative in walls of suberized cork, presumably due to a suberin covering. Histochemical evidence thus indicates that lignin is responsible for intercellular adhesion in net tissue.

Thin-layer chromatography of tuber periderm extracts showed a predominance of chlorogenic acid, caffeic acid,

and coumarin. Other unidentified phenols were found in smaller amounts. The concentration of phenolic acids was reduced by high soil-moisture treatments and PCNB.

It is suggested that reduced tuber net was due to reduced lignin in net cells. Reduced net from high soil-moisture treatments and from compaction was probably due to inhibition of lignin synthesis in the net as a result of low soil oxygen. Water extraction of phenolic precursors from periderm may be a contributing factor. Reduction of net by PCNB is apparently due to inhibition of lignin synthesis.

On the basis of these results, soil moisture, sulfur, and PCNB may generally be used in pathogen control programs without seriously reducing net if excesses are avoided.

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APPENDIX

Table 1

THE INFLUENCE OF HIGH SOIL MOISTURE, COMPACTION, AND CHEMICALS ON RUSSET INDEX

Weeks of high soil moisture	Mean russet index	Multiple-range test subset @P=.95
0	11.52	a
3	11.03	a
6	10.21	a b
9	8.68	b
Compaction		
compacted	10.01	a
check	10.71	b
Chemicals		
PCNB	9.95	a
N-serve	10.08	a
Check	10.30	a b
Super-X	10.56	a b
Sulfur	10.90	b

Analysis of variance

Source of variation	Degrees of freedom	Mean square
Replicates (R)	4	62.807*
Moisture (M)	3	77.423*
Error a	12	16.559
Compaction (S)	1	24.318*
MxS	3	3.420
Error b	16	1.593
Chemical (C)	4	5.824**
MxC	12	2.028
SxC	4	1.352
MxSxC	12	1.726
Error c	128	1.677
Total	199	

Table 2

THE INFLUENCE OF HIGH SOIL MOISTURE, COMPACTION AND CHEMICALS ON TUBERS IN CLASSES 3+4

Weeks of 90% moisture	Mean arcsin % of tubers in classes 3+4	Multiple range test subset @P=.95
0	77.363	a
3	75.559	a
6	66.521	a b
9	57.467	b
Compaction		
compacted	66.306	a
check	72.148	b
Chemicals		
PCNB	66.996	a
N-serve	68.686	a b
Check	68.728	a b
Super-X	69.280	a b
Sulfur	72.264	b
Interaction		
Weeks of 90% x Compaction*		
9 x S_1	53.576	a
9 x S_0	61.358	b
6 x S_1	62.523	b
6 x S_0	70.518	c
3 x S_1	72.088	c
0 x S_1	77.069	d
0 x S_0	77.658	d
3 x S_0	79.059	d

*S_1=compaction
S_0=check

Table 2 (Continued)

Analysis of variance

Source of variation	Degrees of freedom	Mean square
Replicates (R)	4	2598.577**
Moisture (M)	3	4198.717**
Error a	12	436.324
Compaction (S)	1	1706.255**
MxS	3	155.621**
Error b	16	20.988
Chemicals (C)	4	145.776[1]
MxC	12	82.042[1]
SxC	4	72.725
MxSxC	12	51.144
Error d	128	57.057
Total	199	

[1] $P > .80$

Table 3

THE INFLUENCE OF HIGH SOIL MOISTURE, COMPACTION AND CHEMICALS UPON SPECIFIC GRAVITY

Chemical	Mean Specific Gravity	Multiple range test subset @P=.95
Sulfur	1.07397	a
PCNB	1.07535	b
Check	1.07607	b c
Super-X	1.07612	b c
N-serve	1.07722	c

Interaction Chemical	Compaction*		
Sulfur	S_1	1.07310	a
Sulfur	S_0	1.07484	b
PCNB	S_0	1.07530	b c
PCNB	S_1	1.07540	b c
Super-X	S_0	1.07544	b c
Check	S_1	1.07587	b c
Check	S_0	1.07626	b c
N-serve	S_0	1.07642	b c
Super-X	S_1	1.07680	c d
N-serve	S_1	1.07800	d

*S_1 = compacted
S_0 = check

Analysis of variance

Source of variation	Degrees of freedom	Mean square
Replicates (R)	4	3505.655
Moisture (M)	3	5642.245
Error a	12	2768.112
Compaction (S)	1	167.445
MxS	3	148.618
Error b	16	632.660
Chemicals (C)	4	5701.445**
MxC	12	633.732
SxC	4	1835.832*
MxSxC	12	431.689
Error c	128	544.708
Total	199	

Table 4

THE INFLUENCE OF HIGH SOIL MOISTURE AND CHEMICALS ON TOTAL YIELD OF TUBERS

Weeks of 90% moisture	Mean total yield, cwt/A	Multiple range test subset @P=.95
0	272.9	a
3	261.0	a
6	278.2	a
9	215.8	a
Compaction		
compacted	264.6	a
check	249.4	b
Chemicals		
untreated	265.3	a
N-serve	274.7	a
Sulfur	229.8	b
Super-X	259.2	a
PCNB	255.9	a

Analysis of variance

Source of variation	Degrees of freedom	Mean square
Replicates (R)	4	25752.37
Moisture (M)	3	40227.393[1]
Error a	12	12335.67
Compaction (S)	1	11621.981*
MxS	3	1906.996
Error b	16	1696.2493
Chemicals (C)	4	11261.373*
MxC	12	1295.0094
SxC	4	1058.8265
MxSxC	12	1978.9122
Error c	128	1937.4335
Total	199	

[1] $P > .90$

Table 5

THE RELATIONSHIP OF CORK CELL LAYERS
TO RUSSETED PERIDERM CLASSES

Class (% netted surface)	Mean no. of cork cell layers	Multiple range test subset @P=.99
< 25	4.75	a
25-50	5.73	b
51-75	5.60	b
> 75	7.05	c
Data site		
Beneath net Patch (N)	6.29	
Beneath Smooth area (S)	5.28	
Interaction		
Class x Site		
< 25 x N	5.28	b
< 25 x S	4.22	a
25-50 x N	6.28	c
25-50 x S	5.2	b
51-75 x N	6.1	c
51-75 x S	5.1	b
> 75 x N	7.52	e
> 75 x S	6.58	d

Analysis of variance

(10 data sites per observation)

Source of variation	Degrees of freedom	Mean square
Main treatments (MT)	15	
Replicates (R)	3	28.28*
Classes (C)	3	722.11**
Error a	9	5.72
Site (S)	1	830.28**
SxC	3	999.5**
Error b	12	-52.87
Total	31	

Table 6

THE INFLUENCE OF SOIL MOISTURE LEVEL AND CHEMICAL TREATMENTS ON UV ABSORBANCE BY PERIDERM EXTRACT

% Minimum available soil moisture	UV Absorbance Values	Multiple range test subset @P=.95
45	67.9	a
60	65.8	a
75	49.6	b
90	44.4	b

Analysis of variance

Source of variation	Degrees of freedom	Mean square
Main Plots	15	
Rows (R)	3	48.39
Columns (C)	3	25.83
Moisture (M)	3	1636.22**
Error a	6	45.94
Chemicals (c)	2	43.90
CxM	6	29.20
Error b	24	40.48
Total	47	

Table 7

THE EFFECTS OF SOIL MOISTURE LEVEL AND CHEMICAL TREATMENTS ON CELLS PER COLUMN IN COLUMNAR CORK

Treatment chemical	Mean no. of cork cell layers	Multiple range test subset @P=.95
Check	8.1	a
PCNB	7.6	a
Sulfur	7.9	a
Minimum available soil moisture		**P = .99**
45	9.50	a
60	8.08	a b
75	7.38	b
90	6.57	c

Analysis of variance

Source of variation	Degrees of freedom	Mean square
Main plots	15	
Rows (R)	3	0.26
Columns (C)	3	2.65**
Moisture (M)	3	18.54**
Error a	6	0.21
Chemicals (c)	2	0.96
cxM	6	0.05
Error b	24	0.23
Total	47	

P .90

Table 8

THE INFLUENCE OF SOIL MOISTURE LEVEL
AND CHEMICAL TREATMENT ON TOTAL YIELD

Soil moisture level	Mean yield, cwt/A	Multiple range test subset @P=.95
45	181.9	a
60	232.3	b
75	242.9	b
90	246.3	b

Analysis of variance

Source of variation	Degrees of freedom	Mean square
Main plots (MP)	15	
Rows (R)	3	15482.75
Columns (C)	3	3532.78
Moisture (M)	3	25028.87*
Error a	6	4071.7
Chemicals (c)	6	447.5
Mxc	18	906.2
Error b	72	1036.6
Total	111	

Table 9

THE INFLUENCE OF PCNB ON UV ABSORBANCE BY ELUTED CHROMATOGRAPHED FLUORESCENT SPOTS OF PERIDERM EXTRACT

Treatment	Mean UV absorbance 330 nm	320 nm
check	22.38	16.5
PCNB	17.25	12.75

Paired comparison analysis

$d = 41$

$(d)^2 = 1681$

$(d^2) = 315$

$S^2 = 39.375$

$t = 2.31$

P @ 7d.f. $= .94$

Table 10

THE EFFECT OF SOIL MOISTURE LEVEL AND CHEMICAL TREATMENTS ON TUBER RUSSETING

% minimum soil moisture	Arcsin % tubers with 80% net	Multiple range test subset @P=.95
45	66.19	a
60	60.80	a b
75	58.84	b c
90	53.63	c
Chemical treatment		
check	65.97	a
PCNB	54.67	b
Sulfur	58.39	b

Analysis of variance

Source of variation	Degrees of freedom	Mean square
Main plots	15	
Rows (R)	3	52.9*
Columns (C)	3	8.9
Moisture (M)	3	322.97**
Error a	6	9.089
Chemicals (c)	2	520.7*
cxM	6	8.9
Error b	24	14.573
Total	47	