

Alternaria Fruit Rot of Ripening Chile Peppers

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We thank Julie Baca, Deena Baca, and Kevin Blackstone for their excellent technical assistance. This research was supported by the New Mexico Agricultural Experiment Station.

Accepted for publication 30 November 1992.

ABSTRACT

Wall, M.M., and Biles, C.L. 1993. *Alternaria* fruit rot of ripening chile peppers. *Phytopathology* 83:324-328.

New Mexican-type chile peppers are susceptible to a fruit rot caused by *Alternaria alternata*. Experiments were conducted to determine the relationship between the rate of decay from *A. alternata* and chile pepper maturity. Flowers were tagged at anthesis, and peppers were harvested on a weekly basis, wounded, and inoculated with a conidial suspension of *A. alternata*. *Alternaria* disease severity increased as peppers matured and ripened, with the largest lesions occurring on fruits harvested 61 days after flowering. This harvest date corresponded to the period when peppers were turning red, total sugar content peaked (13.0 mg/ml), and reducing sugar content increased fourfold. The seasonal data were con-

firmed by the differential reaction of peppers from four maturity stages to *A. alternata* decay. Ten days after inoculation, green peppers had small lesions averaging 6.7 mm in diameter. Peppers that were 10% red, 50% red, or 100% red had mean lesion diameters of 17.5, 23.2, and 22.3 mm, respectively. When *A. alternata* was cultured on fruit extracts from chile peppers at different maturity stages, mycelial dry weights were greatest on extracts from 100% red and 50% red fruit, in which the total and reducing sugar contents were highest. *A. alternata* showed little preferential growth among media amended with cell walls extracted from chile peppers at the four maturity stages.

The New Mexican-type chile pepper (*Capsicum annuum* L.) is a versatile crop in which the fruit are harvested at either the mature green or red stages of maturity. Mature green chile peppers are consumed fresh or processed. When allowed to fully ripen on the plant, the peppers turn red and dehydrate. Red chile peppers are processed into chile powder or paprika, depending on the pungency of the peppers. Chile peppers are susceptible to several distinct fruit rots. One of these fruit rots is caused by the fungus *Alternaria alternata* (Fries) Keissler (21). The disease was first reported in New Mexico in the 1950s as an internal mold of red chile peppers, most noticeable after frost (15). Symptoms of *Alternaria* rot begin as water-soaked, gray lesions on either the side or blossom-end of the fruit (22). As the lesions progress, they darken and become covered with spores. Internal necrosis and mycelial growth occurs on the seeds, placenta, and pericarp, but is not noticed until the pepper is cut (13).

Infection can occur through the flowers, or following insect injury, mechanical damage, chilling injury, sunburn, or blossom-end rot (1,4,13,17). The black mold indicative of *Alternaria* fruit rot appears most often on mature red peppers either before or after harvest. Red chile peppers harvested during wet periods and improperly stored before processing quickly develop *Alternaria* rots (21). Green chile peppers packaged, stored, and shipped for the fresh market can also develop *Alternaria* infections (16).

Investigations of the environmental and physiological criteria for *A. alternata* fruit rot development have been limited to tomatoes. In tomatoes, *Alternaria* fruit rot increases in proportion to the magnitude and duration of exposure to chilling temperatures (0–10 C) (17). In general, *A. alternata* is unable to incite active fruit rots on healthy, mature green tomatoes. Inoculation of ripe fruits frequently results in large, sunken lesions, whereas inoculations of green fruit results in quiescent lesions that fail to enlarge after the fruit ripens (17). When both mature normal and nonripening mutant fruits were wounded and inoculated with *A. alternata*, lesion development was higher in normal tomatoes (1).

The relationship between fruit maturity and sugar content with *A. alternata* disease has not been reported for any pepper types. Our objectives were to determine the relative susceptibility of chile peppers to *Alternaria* infections as fruit develop and mature,

and to determine the changes in fruit sugar content (total and reducing) with respect to maturity and disease severity. We also investigated differences in pathogen growth on fruit extracts and isolated cell walls from peppers at four maturity stages, and on media of varying sugar contents.

MATERIALS AND METHODS

Plant material. New Mexican-type chile peppers (cv. New Mexico 6-4) were planted on 1 May 1991 in a field plot south of Las Cruces, NM. The plots were cultivated and maintained according to local practices (3). Flowers were tagged at anthesis (24 July 1991), and peppers were harvested weekly beginning 13 August 1991. In addition, peppers at different maturity stages were harvested from individual plants on 13 and 23 September and 17 October. The four maturity stages were distinguished according to fruit color and were 100% green, 10–20% red, 50–60% red, and 100% red peppers.

Inoculation methods. Chile peppers were inoculated with *A. alternata* the same day that they were harvested from the field. The pathogen was previously isolated from chile peppers grown in Las Cruces, NM. The fungus (isolate NM #9) was grown on potato-dextrose agar (PDA) for 6 days at 24 C under diurnal (12 h), cool-white fluorescent light. Aerial mycelium was scraped and the cultures were uncovered, inverted, and placed in diurnal light at ambient room temperature for 24 h to induce sporulation (2). Conidia were dislodged with sterile distilled H₂O containing 0.1% Tween 20 and quantified with a hemacytometer to a concentration of 100,000 spores per milliliter.

Freshly harvested peppers were washed, air-dried, and wounded in two places on each pod. The wound diameter was 3 mm and was made by rotating a small scalpel 2 mm deep into the fruit. The peppers were inoculated with a 50- μ l spore suspension in the wounds, and sterile distilled H₂O was used as a control. All peppers were placed in humidity chambers (92% RH) at 24 C in the dark; lesion diameters were measured after 5 and 10 days.

The peppers were harvested and inoculated weekly, beginning mid-August. Each week, 16 peppers were inoculated with *A. alternata*, and four peppers were inoculated with sterile distilled H₂O. In a separate experiment, peppers from four maturity stages were harvested on the same day, and 10 fruit per maturity group were inoculated with *A. alternata* or sterile H₂O. The experiment was conducted a total of three times on different days.

Fruit sugar assays. A minimum of 20 peppers were frozen at -20 C immediately following each harvest for later evaluations of total and reducing sugar contents. Total sugars were measured with the phenol/ H_2SO_4 method (4) and reducing sugars with the dinitrosalicylic acid (DNS) method of Miller (19). In brief, acetone powders were produced from three peppers harvested at each date throughout the season. Ten grams of frozen peppers was homogenized in room temperature acetone (100%) for 2 min. The slurry was filtered through Whatman #1 paper and washed at least three times with 100% acetone. The powders were allowed to dry at room temperature and stored at -20 C . Total sugars were extracted from the acetone powders with 3 ml of 0.05 M acetate buffer (pH 5) per sample. The extracts were centrifuged for 5 min at 15,000 rpm and passed through a $0.22\text{-}\mu\text{m}$ syringe filter. Fifty microliters of the extract was diluted $10\times$ and used in both total and reducing sugar assays. All extractions and assays were conducted three times.

Pathogen culture on different sugars. *A. alternata* (isolate NM #9) was cultured on media of varying sugar contents to investigate the carbohydrate requirements for pathogen growth. A basic salts medium containing L-asparagine (2 g), MnSO_4 (3 mg), KH_2PO_4 (1 g), MgSO_4 (0.5 g), FeSO_4 (0.01 mg), and ZnSO_4 (8.7 mg) in 1 L of distilled deionized H_2O was prepared and amended with either 1 or 10 g of one of the following sugars: D-glucose, D-fructose, D-galactose, D-xylose, L-rhamnose, and carboxymethyl cellulose (CMC). In total, there were 12 sugar treatments, and the basic salts medium served as a control.

Each experimental unit contained 100 ml of media in 250-ml flasks. Each flask was inoculated with 1 ml of a conidial suspension, with a concentration of 10,000 spores per milliliter. The cultures were kept at room temperature (24 C) on a continuous rotary shaker at 120 rpm. After 6 days, each culture was vacuum filtered with Whatman #1 filter paper, and the mycelia were dried in an oven (40 C) for dry weight determination. There were four replications of each treatment, and the experiment was conducted twice.

Pathogen culture on water-soluble fruit extracts. *A. alternata* mycelial growth was compared on water soluble extracts from chile peppers from each of the four maturity groups. Equal proportions of frozen chile and H_2O (500 g/500 ml) were homogenized in a blender for 3 min. The slurry was filtered sequentially through four layers of cheesecloth, Miracloth, and glass filters. The final solution was refiltered through glass filters two times and Whatman #1 filter paper once. The extracts were transferred to 250-ml flasks (100 ml per flask) and autoclaved for 20 min. Each flask was inoculated with 1 ml of a conidial suspension (10,000 spores per milliliter) and maintained at room temperature (24 C) on a continuous rotary shaker (120 rpm). After 6 days of growth, dry weights were determined as stated previously. Total and reducing sugars were measured in the fruit extracts before inoculation and after 6 days of pathogen growth using the methods previously discussed. There were four replications of each treatment, and the experiment was conducted twice.

Pathogen culture on fruit cell walls. Cell walls were extracted from chile peppers from each of the four maturity groups, and *A. alternata* was grown on both solid and liquid media amended with the cell walls. Cell walls were prepared according to a modified technique of Gross (8). Frozen peppers (50 g) were homogenized in 80% ethanol for 2 min, filtered, and rinsed with ethanol through Miracloth using a Buchner funnel. The residue was rinsed in 20 mM HEPES and transferred to a 250-ml beaker. The residue was covered with a phenol/acetic acid/double-distilled H_2O (2:1:1) solution and stirred at room temperature (24 C) for 20 min. The suspension was refiltered through Miracloth and rinsed with 20 mM HEPES. The residue was transferred to a 250-ml beaker, suspended in a chloroform/methanol (1:1) solution and stirred for 5 min. The suspension was filtered through Miracloth and rinsed with 100% acetone three times. The cell walls were dried for 24 h at 50 C .

Cell walls (1 mg/ml) from the different maturity groups were added to water agar, and the solid media was inoculated with mycelial plugs (4 mm) in the center of the petri dishes. Water

agar was used as a control. Cultures were maintained at room temperature (24 C) for 6 days, and fungal growth was measured as the mycelial diameter after 6 days.

Liquid cultures were prepared with the basic salts medium (described above) and amended with isolated cell walls (1 mg/ml) from the four maturity groups. The basic salts medium served as a control. Flasks were inoculated with 1 ml of a conidial suspension (10,000 spores per milliliter), maintained and weighed as previously explained. There were five replications of each treatment, and each experiment was conducted twice.

Experimental design and analysis. All data were analyzed using the Statistical Analysis System (SAS Institute, Cary, NC). Analyses of variance (ANOVA), means, and standard errors of the means were computed for all experiments. Correlation and regression coefficients were computed for the lesion diameter and fruit sugar content data.

Data from weekly fruit inoculations over the season were analyzed as a pooled ANOVA for measurements over time, based on a randomized complete block design (7). A completely randomized block (CRD) design was used for the three experiments which measured lesion diameter in relation to maturity group (green to red). Assumptions for homogeneity of variance were met, and a combined analysis of variance was performed for these three experiments. Data from fruit sugar assays and pathogen growth on media amended with sugars, cell walls, or fruit extracts also were analyzed according to a CRD design.

RESULTS

New Mexican chile peppers inoculated with *A. alternata* were most susceptible at 61 days after flowering, when peppers were at the turning stage of color development (Fig. 1). At that harvest date, pepper lesion diameters averaged 12.7 and 23.4 mm when measured 5 or 10 days after inoculation, respectively. Green peppers harvested earlier in the season (20–55 days after flowering) had relatively small lesions ranging from about 4 to 6 mm in diameter. The lesion expansion of these green pods was just slightly greater than the 3 mm wound of the control pods.

When peppers were harvested on the same day at different stages of maturity and inoculated with *A. alternata*, disease severity was greatest on peppers from the 50% red or 100% red maturity

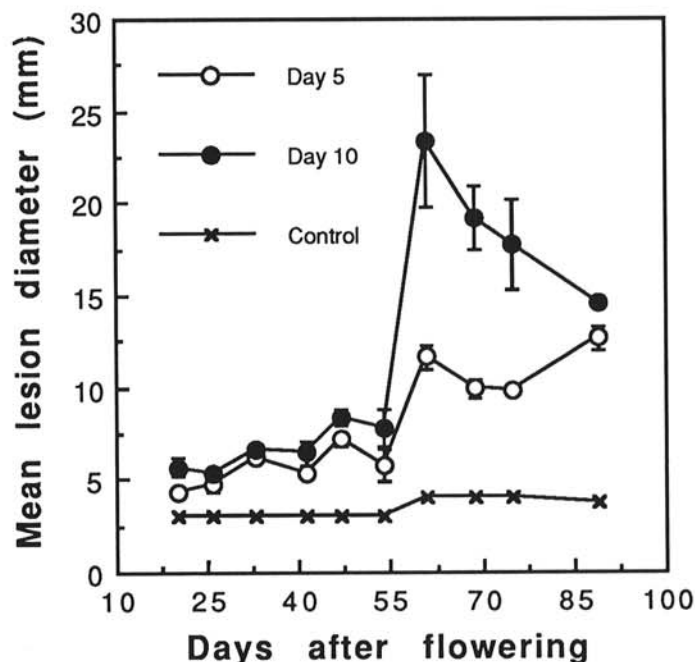


Fig. 1. Lesion diameters on developing chile peppers inoculated with *Alternaria alternata* throughout the season. Lesion diameters were measured 5 and 10 days after inoculation. Peppers were 10% red 54 days after flowering and 50% red 61 days after flowering. Vertical bars represent SE of the means.

groups. Green peppers had small lesions averaging 5.5 and 6.7 mm after 5 or 10 days of incubation, respectively (Fig. 2). Peppers beginning to change color (10% red) had mean lesion diameters of 17.5 mm after 10 days. Peppers that were 50% red or 100% red had mean lesion diameters of 23.2 and 22.3 mm, respectively, at the 10-day measurement. Peppers from the control treatment had 4.0-mm wounds only.

Susceptibility to *Alternaria* fruit rot correlated positively with an increase in fruit sugar content. Although both total and reducing sugars increased in ripening peppers (Fig. 3), the increase

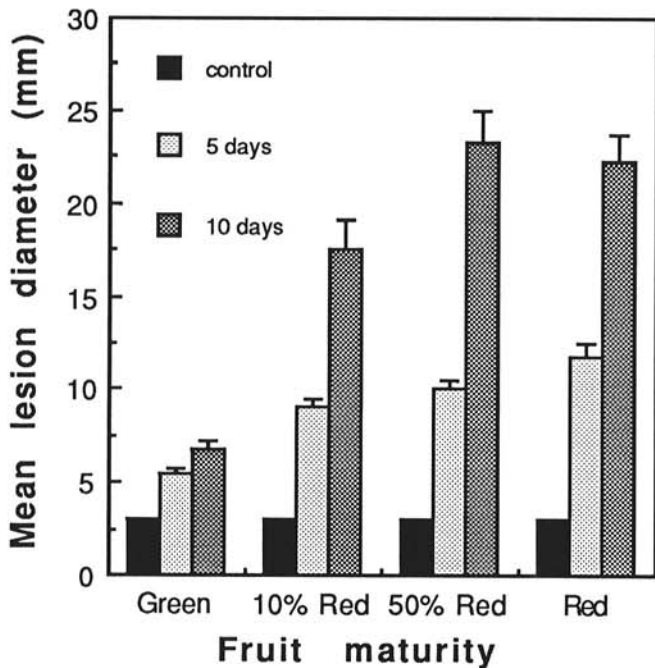


Fig. 2. Lesion size on chile peppers harvested on the same day from different maturity groups and inoculated with *Alternaria alternata*. Vertical bars represent SE of the means.

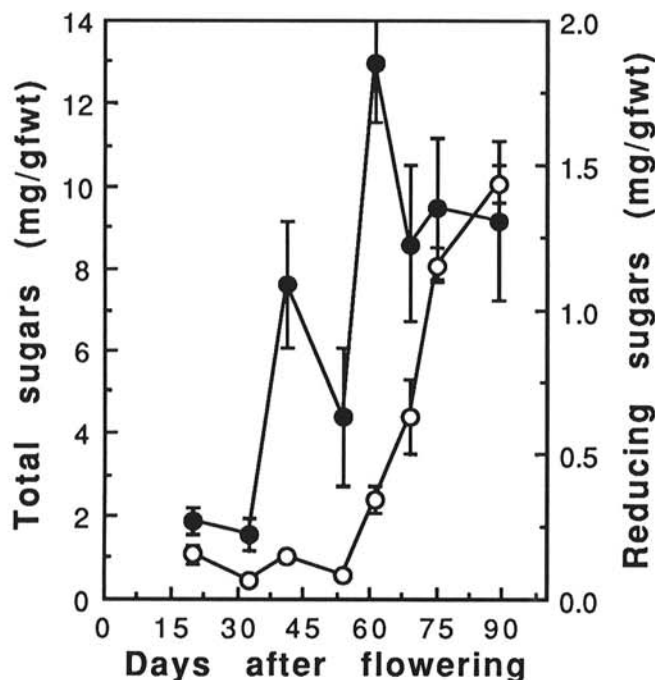


Fig. 3. Total and reducing sugar contents in developing chile peppers harvested throughout the season. Closed circles and open circles represent total sugar and reducing sugar data, respectively. Peppers were 10% red 54 days after flowering and 50% red 61 days after flowering. Vertical bars represent SE of the means.

in total sugars preceded the rise in reducing sugars. Fruit rot severity was more closely associated with an increase in total sugars ($r = 0.89$, $R^2 = 0.79$) than with reducing sugars ($r = 0.53$, $R^2 = 0.28$). Total sugars were greatest (13 mg/ml) in peppers harvested 61 days after flowering (Fig. 3). Reducing sugars significantly increased beginning 61 days after flowering, coincident with the largest lesion diameters in inoculated fruit (Fig. 1).

A. alternata cultures had the greatest mycelial growth on media amended with 10 g of xylose, fructose, glucose, or galactose (Fig. 4). The more complex sugars, rhamnose, and carboxymethyl cellulose, were not readily metabolized by the fungus. When *A. alternata* was cultured on fruit extracts from chile peppers at different maturity stages, mycelial dry weights were greatest on extracts from 100% red and 50% red pods (Table 1), in which the initial

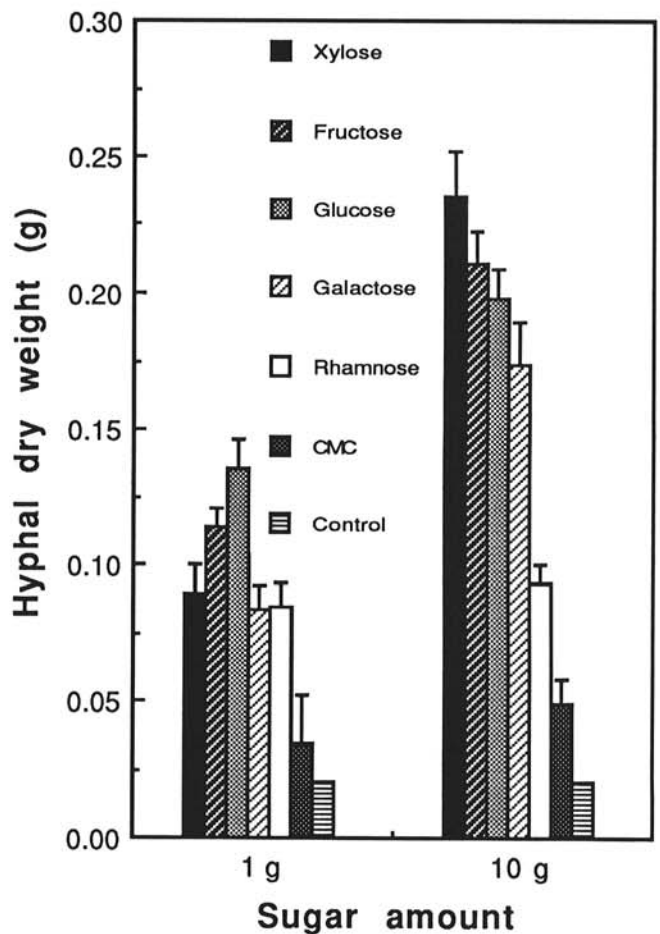


Fig. 4. Hyphal dry weights of *Alternaria alternata* cultured on media amended with different sugars. Vertical bars represent SE of the means.

TABLE 1. Growth of *Alternaria alternata* on fruit extracts of chile peppers from four maturity groups and the corresponding sugar contents of the extracts

Maturity	Mycelial dry wt. (g) ^w	Total sugars ^x		Reducing sugars ^y		pH
		Initial	Final (mg/ml)	Initial	Final (mg/ml)	
Red	0.166 a ^z	0.471 a	0.024 b	0.261 a	0.023 ab	7.83
50% Red	0.147 b	0.468 a	0.041 a	0.235 b	0.032 a	7.79
10% Red	0.115 c	0.345 b	0.033 ab	0.062 d	0.016 b	8.04
Green	0.086 d	0.201 c	0.027 ab	0.084 c	0.024 ab	7.97

^wTreatments were inoculated with 1 ml of a conidial suspension (10,000 spores/ml) and mycelial dry weights were determined after 6 days of growth.

^x Measured before inoculation and after 6 days growth using the phenol/H₂SO₄ method.

^y Measured before inoculation and after 6 days of growth using the dinitrosalicylic acid method.

^z Mean separation within columns according to Fisher's LSD ($P = 0.05$).

total and reducing sugar contents were highest. Mycelial dry weights were highly correlated with the initial total sugar content ($r = 0.97$, $R^2 = 0.94$) and reducing sugar content ($r = 0.90$, $R^2 = 0.81$) of the extracts. The fungus appeared to metabolize most of the available sugars from each extract, as indicated by the final measurements.

A. alternata showed little preferential growth among media amended with cell walls extracted from peppers at the four maturity stages (Table 2). Significant differences in hyphal growth were detected between red and green groups when cell walls were added to water agar, but no differences were observed among the liquid media treatments.

DISCUSSION

New Mexican-type chile peppers became most susceptible to *A. alternata* infection as they matured and ripened. Disease severity increased significantly on fruits inoculated 61 days after flowering. This harvest date corresponded with the period when peppers were about 50% red and fruit sugar content increased. The seasonal data were confirmed by the differential reaction of peppers from four maturity stages to *A. alternata* infection. Lesion diameters were greatest on 50% red and 100% red peppers, with only slight lesion expansion on green fruit.

In previous studies with chile peppers (24), a large rise in ethylene was found to occur during the period when fruit were turning red (61 days after flowering), with a peak at 69 days after flowering. Also, ethylene production of red fruit was found to be twice that of mature green fruit. However, the exact role of ethylene in the disease process has not been determined. Ethylene most likely stimulates the physiological changes that predispose the fruit to pathogen infection. One such change is the accumulation of sugar in ripening peppers.

At later stages of maturity (61 days after flowering), total and reducing sugars increased in the fruits, and *A. alternata* lesions expanded. In culture, *A. alternata* growth was greatest when glucose, fructose, xylose, or galactose were the carbohydrate sources, and diminished on media with rhamnose or carboxymethyl cellulose. Although we did not investigate the enzymatic potential of *A. alternata*, others have reported the production of β -glucosidase, β -glucanase, and pectin methyl galacturonase by *Alternaria* species (12,18). Glucose and galactose stimulated pectin methyl galacturonase production, whereas starch inhibited this enzyme (18). In studies with ripening tomatoes, glucose and fructose dissolved in dew on fruit surfaces stimulated *Alternaria* conidial germination (20). Conidia of *Colletotrichum piperatum* germinated profusely on leachates from red *Capsicum* fruit in which high levels of sucrose were present (11).

Small differences were measured in pathogen growth on extracted cell walls from the four maturity groups, with growth slightly stimulated on cell walls from red peppers. Gross and Moline (9) reported stimulated growth of *Botrytis cinerea* and *Mucor mucedo* on unfractionated, red-ripe, tomato cell walls, as compared to growth on mature-green cell walls. Any differences in pathogen growth on cell walls from ripening peppers may be related to changes in neutral sugar composition (10). However, based on our results, the pathogen responds primarily to changes

in fruit sugar content in ripening peppers and very little to changes in cell walls.

Results from pathogen growth in culture were consistent with those from inoculation of whole fruit. Hyphal growth was greatest when *A. alternata* was cultured on fruit extracts from 100% red and 50% red pods, in which the sugar contents were high. The fungus metabolized most of the available sugars from each extract, regardless of fruit maturity. Therefore, pathogen growth on the 100% green and 10% red extracts was probably limited by the lower initial sugar content of these extracts. These results suggest that sugars stimulate infection and colonization by the pathogen; however, penetration must precede disease development.

A. alternata is generally considered a weak pathogen that gains entry into the fruit via wounds or natural openings, and remains quiescent until the fruit ripens (17). Our studies support this premise on peppers and provide an example of the classic decay pattern for wound pathogens. Other wound-related pathogens include species of *Colletotrichum*, *Cladosporium*, *Penicillium*, and *Monilinia* (6,22). Latent infections of *Colletotrichum* species on peppers, tomatoes, banana, and mango increase with ripening. On lemons, *Alternaria citri* causes a stem end rot upon ripening, and on apples *Penicillium expansum* increases with maturity and bruise injury (6).

There are three possible explanations for this increased susceptibility of a host coincident with ripening (23). The immature or unripe fruits may contain compounds that are toxic or inhibitory to the pathogen; the ripe fruits may have an increase in available nutrients for pathogen growth; or the cell walls of the ripe fruit may be more susceptible to enzymatic attack by the pathogen. These theories are not necessarily exclusive of each other. Our data provide evidence that sugar accumulation in ripened chile peppers has an important role in the increased susceptibility of the fruit to *A. alternata*.

The susceptibility of red chile peppers to *Alternaria* fruit rot has practical implications for New Mexico's processing industry. As the trend toward mechanical harvesting becomes widely adopted, the incidence of *Alternaria* rot will probably increase. Mechanically harvested fruit typically incur more injury, are exposed to more debris and inoculum during harvest, and require an advanced, uniform stage of maturity. Under these conditions, red peppers destined for processing will require careful quality inspections, because several *Alternaria* strains are known toxin producers (14). Future investigations on the presence of toxic metabolites in chile, the role of ethylene on *Alternaria* development, and methods for disease control are needed.

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TABLE 2. Growth of *Alternaria alternata* on media amended with cell walls extracted from chile peppers at four stages of maturity

Maturity	Solid media ^x	Liquid media ^y
	Mycelial diameter (mm)	Mycelial dry weight (g)
Red	51.54 a ^z	0.143 a
50% Red	50.44 a	0.148 a
10% Red	49.17 ab	0.150 a
Green	45.94 b	0.126 a
Control	37.90 c	0.021 b

^x Water agar amended with 1 mg/ml isolated cell walls.

^y Basic salts medium amended with 1 mg/ml isolated cell walls.

^z Mean separation within columns according to Fisher's LSD ($P = 0.05$).

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