Factors Influencing the Susceptibility of Lemons to Infection by *Geotrichum candidum*

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ABSTRACT

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Lemons differed in susceptibility to infection by *Geotrichum candidum*, the causal agent of sour rot. Inoculation of wounds in the peel resulted either in a rapidly developing soft rot within 5–6 days or in a dry arrested lesion. Differences in susceptibility of fruit lots were expressed in the percentage active lesions after 5 days or in the number of spores required for 50% active lesions (ED_{50}). The expansion rate of active lesions was not correlated with fruit susceptibility to infection. Differences in susceptibility between the lemon cultivars Lisbon and Eureka were not significant. Susceptibility increased with physiological age, ie, with color change from light green to yellow and with duration of storage. Treatment with ethylene accelerated this increase. Water uptake or water loss resulting in a change of 2–10% in fruit weight and a change of 0.6–3.0 bars in peel water potential reduced or increased, respectively, the ED_{50} 3–30 times. The ED_{50} for lemons picked at 1400 hours was 2–10 times higher than that for fruit picked at 0800 hours. Lemons picked after rainfall were more susceptible than those picked during a dry, sunny period.

Additional key words: *Citrus limon*.

Sour rot of citrus fruits is a postharvest disease caused by the "citrus race" of *Geotrichum candidum* Link ex Pers. Members of this group are characterized by pathogenicity to citrus fruits and by other physiological characteristics (5). Healthy citrus fruits are infected by *G. candidum* only through wounds or by contact with decaying fruits. Inoculation of wounds in the peel of citrus fruits results in a variable and often low incidence of decay, whereas inoculation into the juice sacs generally produces a successful infection (5). The development of sour rot is dependent on high humidity and temperatures >10 C. Progress of the disease is most rapid at 25–30 C (21).

Although losses due to sour rot are relatively small worldwide, they may be large in some years, seasons, and areas (7,9,13). In California, the disease is more prevalent on lemons than on other citrus fruits, since lemons are stored for longer periods (up to 6 mo) and at higher temperatures (12–15 C). Susceptibility of citrus fruits to sour rot has been associated with ripeness and overripeness of the fruit and long storage periods (12), and with fruit picked after long, wet winters (9). The disease is prevalent on lemons shipped from the coastal areas of California June through August (7). Similarly, sour rot causes trouble in citrus fruits exported from Israel during the second half of the season when high temperatures prevail and fruit vitality is low (4).

Several reviewers have discussed factors that may influence susceptibility of fruits and vegetables to postharvest decay (8,10,13). However, few data relative to sour rot have been published.

We report here the results of our studies on the initiation of sour rot and on some of the factors that influence lemon susceptibility to wound infection by *G. candidum*. Portions of this investigation have been reported in abstract form (2).

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MATERIALS AND METHODS

Fruit. Lemons (*Citrus limon* (L.) Burm. 'Lisbon' or 'Eureka') were hand harvested or obtained from packinghouses in southern California before any postharvest treatment had been applied. The lemons were washed, dried, and stored in polyethylene bags at 10–13 C. Fruit color was recorded as dark green, light green (distinctly starting to change color), silver-green (yellow clearly showing, but still with large areas light green), silver-yellow (almost completely yellow with some green still showing), yellow, and deep yellow.

For treatment with high-oxygen or high-ethylene atmospheres, lemons in wire baskets were placed in 280-L stainless steel tanks. Air and industrial grade oxygen were mixed with the aid of pressure regulators, flow meters, and flow restrictors (tubes of various lengths, packed with Celite diatomaceous earth). Ethylene, under pressure regulated by a Mariotte bottle (19), was metered through a calibrated capillary tube into the airstream. The gas mixtures were humidified by bubbling through two consecutive bottles of water before being passed through a tank containing lemons. Oxygen, carbon dioxide, and nitrogen were measured gas chromatographically by using columns packed with Porapak T or Molecular Sieve 5A, 60–80 mesh (Applied Science Division, Milton Roy Co. Lab Group, State College, PA 16801) and a thermal conductivity detector. Ethylene was also measured gas chromatographically but by using an activated-alumina column and a flame ionization detector.

Where indicated, lemons were treated with 2,4-dichlorophenoxyacetic acid (2,4-D) dissolved in the fruit-coating formulation Sta-Fresh 200® (FMC Corp., Riverside, CA 92502). Two volumes of Sta-Fresh concentrate were diluted with one volume of water to give 9.4% (w/w) solids, and 2,4-D (acid form) was added to the diluted formulation to a final concentration of 400 mg/L.

Modification of fruit water status. Lemons were held at about 40% relative humidity (RH) and 25 C to reduce their water potential, and the weight loss of the fruit was measured. These lemons were held in a moist chamber for at least 20 hr before inoculation to dissipate water potential gradients within the fruit.

The water potential of lemons was increased by allowing the fruit to take up water through the attached stem. Mature lemons were picked with 15–20 cm of stem attached. The stems were cut under water to about 5 cm and each lemon was placed on a small beaker with the stem immersed in water. The beakers with the fruits were placed in a vacuum desiccator that was then evacuated to remove air from the stem. This procedure caused a subsequent 2–5% weight increase of the fruit within 2–3 days.

Disease production. *G. candidum* isolate GW20, isolated from a decayed lemon, was maintained on potato-dextrose agar supplemented with 1 g of yeast extract per liter. Inoculum was prepared by flooding 3- to 14-day-old slants with sterile potassium phosphate buffer pH 6 (0.05 or 0.1 M) or sterile potassium citrate buffer pH 4.5 (0.1 M) and gently rubbing the culture surface with a wire loop. The suspensions were filtered through sterile glass wool to remove hyphal fragments and the spore concentration was determined with a hemacytometer. The buffer did not significantly affect the infectivity of the inoculum. The same buffer and cultures of the same age were used when inoculations carried out at different times were compared.

Early in this investigation, lemons were inoculated with a pin (1 mm in diameter) that protruded 2.5 mm from a steel rod. The pin was dipped in the inoculum and pushed into the lemon peel. The resulting wound penetrated through the flavedo (exocarp) and into the albedo (mesocarp). The volume of inoculum deposited in the wound was determined by simulated inoculation with ^{14}C-labeled solutions. After inoculation, the peel surface was wiped with absorbent paper, and the wound with surrounding tissue was excised and combusted in a Biological Material Oxidizer (R. J. Harvey Instrument Corporation, Hillsdale, NJ 07642). The $^{14}CO_2$ was trapped in phenethylamine and the radioactivity was measured in a Beckman CPM-100 liquid scintillation spectrometer. The average deposit of inoculum was 1.92 μl per inoculation site (coeff. of variation 0.33). This value varied between fruits, presumably reflecting variation in the water-absorbing capacity of the peel. In later experiments, spore suspensions were injected into the peel with a 250-μl syringe equipped with a repeating dispenser (Hamilton Company, Reno, NV 89510) that delivered 5-μl volumes. The syringe was outfitted with a 1.07 mm o.d. (19-gauge) needle with a 45-degree tip that protruded 2.5 mm from a teflon sleeve. Fifty inoculations with this syringe gave an average deposit of ^{14}C-labeled spores equivalent to 4.55 μl per inoculation site (coefficient of variation 0.19). This value did not vary between fruits. The syringe was used for all inoculations, unless specified otherwise.

In most experiments, each lemon was inoculated at several sites equidistant on the equator or on both sides of the equator, but at least 25 mm from the stylar or stem end. No attempt was made to penetrate or avoid oil glands, unless indicated otherwise. The inoculated lemons were incubated on wire racks or in wire baskets at 25 C in the tanks described above. Air flowed through the tanks at 120–170 L/hr and was humidified by bubbling through water in two bottles in series. The water in the second bottle was heated to 30 C to insure water saturation of the air stream after it was cooled to 25 C. After entering the tank, the air was passed through a trap filled with glass wool to remove excess moisture.

Evaluation of disease. Susceptibility to infection was evaluated as the percentage of inoculation sites that developed into active lesions within 5 days. Few additional active lesions developed thereafter and individual decay lesions coalesced with further incubation. The probit of the percentage of active lesions was linearly related to the logarithm of the inoculum level (Fig. 1B). Therefore, fruit susceptibility was expressed also in terms of the number of spores required to produce decay at 50% of the inoculation sites (median infective dose, ED_{50}). When the line relating probit active lesions and log spore number was not sufficiently straight to permit calculation of the ED_{50} based on all inoculum levels, the ED_{50} was estimated visually, emphasizing the points closest to 50% decay. The ED_{50} was estimated by extrapolation when necessary. Statistical tests of differences were performed on the decay percentages. Lemons in each treatment were subdivided randomly into groups, each comprising about 20 inoculation sites. The number of active lesions per group was approximately normally distributed in agreement with the Central Limit Theorem.

The expansion rate of active lesions was determined by measuring lesion diameters daily. The incubation period, defined as the time interval between inoculation and establishment of an expanding lesion, was calculated by extrapolation of the lesion diameters to 3 mm (approximate diameter of the area occupied by the inoculum immediately after injection).

Measurement of water status. Water content of the peel was determined by drying samples at 90 C to a constant weight. The water potential of the peel (flavedo or albedo slices, 12 mm in diameter, 1–2 mm thick) was determined with a Richards and Ogata thermocouple psychrometer by the isopiestic technique (3). The correction for heat of respiration was omitted since it was minor. Xylem pressure potential of lemons that were picked with a short piece of stem attached was measured with a pressure chamber (1,14,23). The psychrometric technique measures the water potential of a small tissue sample, whereas the pressure chamber gives an integrated reading over the whole fruit.

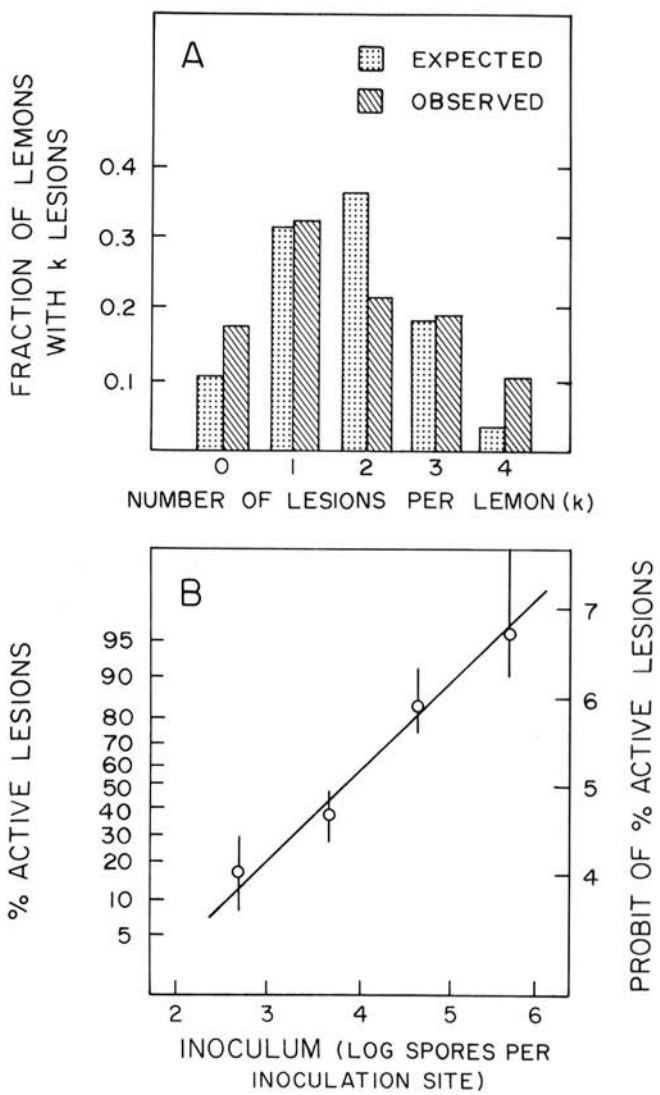

Fig. 1. Variability in susceptibility to infection by *Geotrichum candidum* in lemons that were harvested at one time from a single row of trees. **A,** The distribution of active lesions was significantly different ($P = 0.007$) from the binomial distribution expected if all lemons were equally susceptible. Each lemon was inoculated at four sites with 1,365 spores per site. **B,** Relationship between log number of spores and the percentage active lesions (probit scale). Each lemon was inoculated with four different spore concentrations, each at a different site per fruit. Error bars indicate 95% confidence intervals.

RESULTS

Infection and disease development. Two types of responses to inoculation of lemons with *G. candidum* were observed: In those of the first type, some infections developed into wet, macerated, nondiscolored lesions, whose diameter extended at a linear rate (active lesions); a brown area sometimes developed around the inoculation site, but after a few days this usually developed into an active lesion with a brown center; and incubation periods generally varied between 20 and 85 hr. In those of the second type, the remaining infections, even after long periods, remained restricted to a flask-shaped pocket (2–3 mm in diameter) of grey-brown, dry-appearing peel tissue around the wound. Mycelium of *G. candidum* could be seen in these "arrested infections" and the fungus was isolated from over 80% of 29-day-old infections. Nevertheless, few of the infections that remained arrested for 5–6 days became active thereafter, even though the lemons became more susceptible to new inoculation as they aged. Incubation of inoculated light-green lemons for 5 days in air containing about 100 μl of ethylene per liter to accelerate aging did not significantly increase the incidence of active lesions. Incubation of the lemons with arrested infections for 24 more days until they were deep yellow did not result in activation of the arrested infections, but did increase the susceptibility of these fruits to infection at new inoculation sites. The new inoculations resulted in 95% active lesions, whereas the first inoculations (24 days earlier) resulted in only 28–56% infection.

TABLE 1. Relationship between color and susceptibility of lemons to infection and colonization by *Geotrichum candidum*

Fruit color	ED_{50}[a]	Lesion expansion[b] (mm/day)
Yellow	3.8 (3.5–4.3)	14.3 ± 1.4 (70)
Silver-green	4.4 (4.1–4.6)	14.8 ± 1.7 (54)
Light green	5.3 (5.0–5.8)	14.5 ± 1.9 (26)

[a] Logarithm of the number of spores per inoculation site required to produce active lesions at 50% of the inoculation sites. Ranges given in parentheses are the 95% confidence intervals.

[b] Mean, standard deviation, and (in parentheses) number of lesions measured.

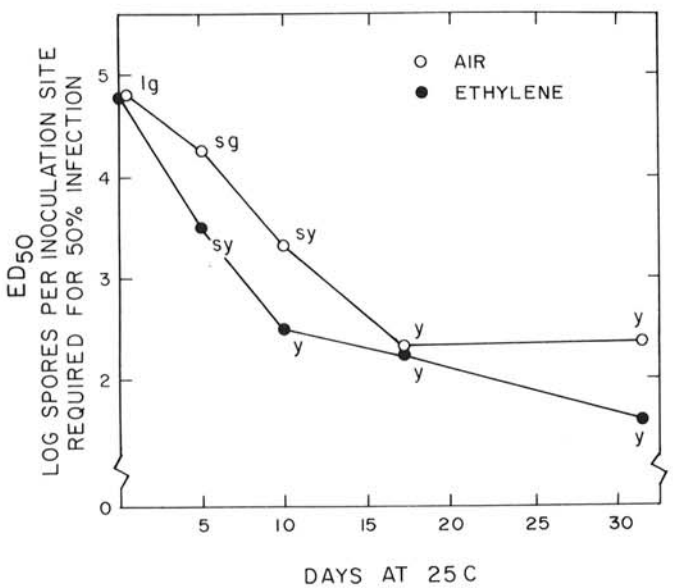

Fig. 2. Effect of storage in air or in air with added ethylene (20–50 μl/L, fluctuating) on color development and susceptibility of lemons to infection by *Geotrichum candidum*. The air treatment contained 1–2 μl/L ethylene due to the presence of some decay caused by *Penicillium*. The color of the fruit at each inspection is indicated: lg = light green; sg = silver-green; sy = silver-yellow; and y = yellow.

Deliberate inoculations through oil glands resulted in 25–50% more decay than when an attempt was made to avoid injuring oil glands. Inoculation at random sites on the fruit surface resulted in an incidence of decay similar to that obtained by inoculation through oil glands. The stylar and stem halves of the fruit did not differ in susceptibility to infection.

Sections through the margins of active lesions revealed that maceration in the albedo was usually 1–3 mm ahead of maceration in the flavedo. The fruit epidermis over the lesion retained its coherence because the cells were held together by the cuticle. The mycelium of *G. candidum* eventually erupted through the epidermis and cuticle in older sour rot lesions.

Variation in fruit susceptibility. Lemons of uniform color, harvested at one time from a single row of trees, often varied significantly in susceptibility to sour rot. Figure 1A shows the frequency distribution of the number of active lesions on each fruit that had been inoculated at four sites with the same number of spores. In five of eight tests, the observed distribution deviated significantly ($P = 0.05$) from the binomial distribution expected if all lemons were equally susceptible: there were more lemons with either low or high numbers of lesions than expected.

The plot of percent infection (probit scale) versus logarithm of the number of spores in the inoculum should have a slope of 2.0 at the ED_{50} if spores act independently and the hosts are uniformly susceptible (17). In most of our experiments, the slope was significantly less than 2.0 for lemons of one harvest from a single row of trees (Fig. 1B), providing additional evidence that individual lemons differed in susceptibility to infection by *G. candidum*. Similar variability was obtained when all inoculations were carried out either through oil glands or between oil glands rather than at random. Lemons of commercial lots, even when selected for uniform color, usually were less uniform in susceptibility than lemons of one harvest from a single grove.

Several potential sources of heterogeneity in susceptibility were investigated. There were no significant differences in susceptibility between lemons from different trees in one grove, between lemons grown on the outside or on the inside of the tree canopy, or between lemons from tree positions higher than 1.5 m and those from lower positions. The ED_{50} for lemons from the south side of a tree was only slightly larger (not significant at $P = 0.05$) than that of north exposed fruit. Large lemons were sometimes more susceptible than smaller fruit of the same color, but this result was not obtained consistently.

Cultivars. Eureka and Lisbon are the lemon cultivars most extensively planted in California. Fruits of two intravarietal selections of Eureka (Allen and UCLA) and of Lisbon (Monroe and Limoneira) were harvested on three dates from a seaside grove and an inland valley grove. No consistent differences were found in susceptibility of the fruit from the cultivars and selections over the three sampling dates. The fruit from different sampling dates showed greater variation in susceptibility than the fruit from different cultivars and selections.

Effect of physiological age on susceptibility. Lemons are harvested in California when they attain a marketable size and may then range from green to yellow. They continue to undergo changes in color, texture, and other characteristics during subsequent storage. In this investigation, physiological age was assumed to be correlated with color and postharvest age.

Yellow lemons were more susceptible to infection by *G. candidum* than greener fruit harvested from the same grove at the same time (Table 1). The incubation period was shorter in yellow fruits (median of 37 hr in yellow fruit and 54 hr in light-green fruit), but the rate of lesion expansion was not significantly different in yellow and green fruits (Table 1). The rate of lesion expansion differed somewhat among fruits from different groves, but was not correlated with fruit color or with susceptibility to infection.

Susceptibility increased with storage time at 25 C; the addition of ethylene (20–50 μl/L) to the atmosphere hastened both color change and the increase in susceptibility (Fig. 2). The influence of ethylene was considerably greater in some fruit lots than in the experiment shown in Fig. 2. Susceptibility increased most rapidly during color change from light green to yellow and more slowly

thereafter. Fruit degreening was more rapid in an atmosphere containing 40–60% oxygen, but this environment slightly inhibited the increase in fruit susceptibility. Treatment of light-green lemons with 2,4-D (400 mg/L) somewhat retarded the rate of color change during storage at 13 C, but this treatment did not significantly delay the increase in susceptibility to infection.

Effect of weather and harvest time on susceptibility. During February through April 1979, lemons were harvested 12 times from the same eight trees in a grove that received water only from rainfall during that period. Fifty lemons were picked on each harvest date. Most lemons on the trees were yellow on the first sampling date and the few light-green fruits were removed and discarded. Lemons were picked at 0800 and 1400 hours on most dates and placed in polyethylene bags. The fruits were inoculated later the same day, usually with 10^5, 10^6, 10^7, and 10^8 spores per milliliter, each spore concentration at a different site on each fruit. Figure 3 shows the susceptibility of the lemons of each harvest and also presents weather data collected less than 1 km from the grove. Fruits harvested at 1400 hours were 2–10 times more resistant than fruits picked at 0800 hours. Differences in susceptibility between lemons picked in the morning and in the afternoon were smaller on overcast than on sunny days. A significant drop in resistance was observed between 28 February and 2 March and between 14 and 21 March, both periods of substantial rainfall. Resistance to sour rot tended to increase during dry, sunny periods.

The effect of fruit water status on susceptibility. The xylem pressure potential of lemons picked at 1400 hours on sunny sampling dates was about 2 bars lower than that of the more susceptible fruit picked at 0800 hours on the same day. The average water potential of the peel at 0800 and 1400 hours differed by only 0.7–1.5 bars. The standard deviation of the pressure potential and water potential measurements was typically 1.0–1.5 bars.

The relationship between the water status of the peel and sour rot susceptibility was studied further in three lots of lemons from a coastal area (Santa Barbara County, CA) and three lots of lemons from an inland area (Riverside County, CA). Sixty lemons from each lot were inoculated at four sites each by means of the inoculation pin. After 3–5 days, five of the most susceptible fruits (three to four active lesions) and five of the most resistant fruits (zero to one active lesions) were selected from each lot and the water potential and water content of the peel were measured. The experiment was repeated with fruit from the same lots after storage at 12 C for 3 wk. Since none of the interaction terms in the analysis of variance was significant ($P = 0.05$), only the main effects are shown in Table 2. The peel water content differed between susceptible and resistant fruits, but the water potential did not. The comparison between coastal and inland fruit was based on only three replications and was therefore less sensitive than the other

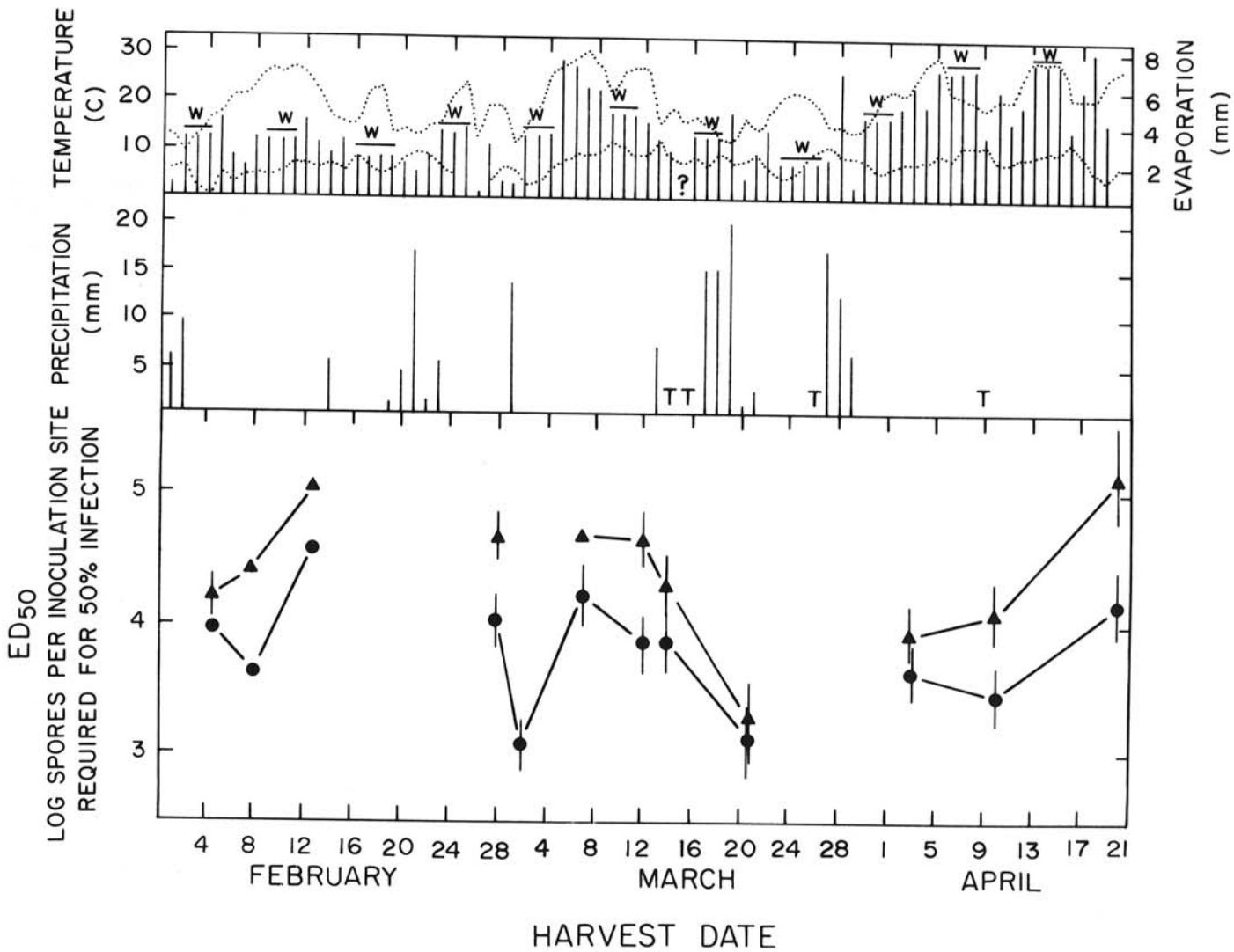

Fig. 3. Influence of harvest date and hour, and weather conditions on the susceptibility of lemons to infection by *Geotrichum candidum*. Lemons were harvested from the same trees throughout the experiment. Each lemon was inoculated on the day of harvest with three or four different spore concentrations, each at one site per fruit. Error bars represent 95% fiducial limits, and are omitted where the probit line was not sufficiently straight to base the ED_{50} on all points. (●) Fruit picked at 0800 hours; (▲) fruit picked at 1400 hours; T = trace of precipitation; w = weekend, the total evaporation during the weekend was averaged over the 3 or 4 days; ? = no data available; dotted lines indicate maximum and minimum temperatures; and vertical lines represent evaporation and precipitation.

comparisons. Water potential, water content, and percent decay (46 versus 59% of all inoculations) were all lower in inland fruit, although only the first difference was significant. In most of our other tests, we also found that coastal fruit tended to be more susceptible to infection by *G. candidum* than similar appearing inland fruit. The water potential and water content of the lemons decreased during storage at 12 C for 3 wk, whereas the percentage active lesions increased from 45 to 59% during the same period. This indicates that for these fruits physiological age was a more important determinant of susceptibility than was water status.

Lemons held at 25 C and 40% RH for 2–4 days lost 5–15% of their initial weight, whereas lemons with an attached stem immersed in water increased in weight by 2–5%. A weight change of 1% corresponded to a change in peel water potential ranging between 0.29 and 0.35 bars and to a change in peel water content ranging 0.07–0.25% in three tests. Susceptibility to infection increased with water uptake by the fruit and decreased with water loss (Fig. 4), even when injury to oil glands was avoided by inoculating carefully with a thin needle. This indicates that the difference was not due to a difference in likelihood of rupture of the oil glands. Water loss resulted in a significant ($P = 0.0001$), but small, decrease in the rate of lesion expansion in one of two tests and also resulted in a longer incubation period. For example, the median incubation periods after 1.4, 7.6, and 10.5% water loss were 40, 56, and 61 hr, respectively.

Injection of 1–2 ml of water into the albedo (spongy mesophyll) increased the susceptibility of the flooded area to infection by *G. candidum* when inoculated 1 hr later, even though the peel was not visibly water-soaked at the time of inoculation and appeared normal several days after the flooding treatment. Virtually every inoculation site, even on light-green lemons, that was continuously covered with a few drops of water for the first 24–48 hr after inoculation developed an active lesion. Lemons submerged in water for about 20 hr at room temperature became somewhat more susceptible to infection although they gained little weight. Lemons submerged for longer periods developed physiological breakdown of the peel (soft, water-soaked areas) similar to that resulting from storage at low oxygen levels (*unpublished*). Areas of the peel so afflicted were extremely susceptible to infection by *G. candidum*.

TABLE 2. The relationship of the peel water status of lemons and susceptibility to infection by *Geotrichum candidum*, production area, and storage

Comparison	Water potential[a] (bars)	Water content[a] (% of fresh weight)
Susceptibility[b]		
Susceptible	−10.62	82.52**
Resistant	−10.91	79.84**
Production area		
Coastal	− 9.73*	82.05
Inland	−11:81*	80.31
Storage[c]		
Before	−10.28**	82.19**
After	−11.26**	80.17**

[a]Each value is based on 60 determinations. ** = Difference significant, $P = 0.01$; * = difference significant, $P = 0.05$. None of the interactions was significant, $P = 0.05$.

[b]Three or 4 days after inoculation with 1.8×10^4 spores per inoculation site at four sites per fruit, five of the most susceptible (three or four active lesions) and five of the most resistant (no or one active lesion) lemons were selected for water status determination.

[c]12 C for 3 wk.

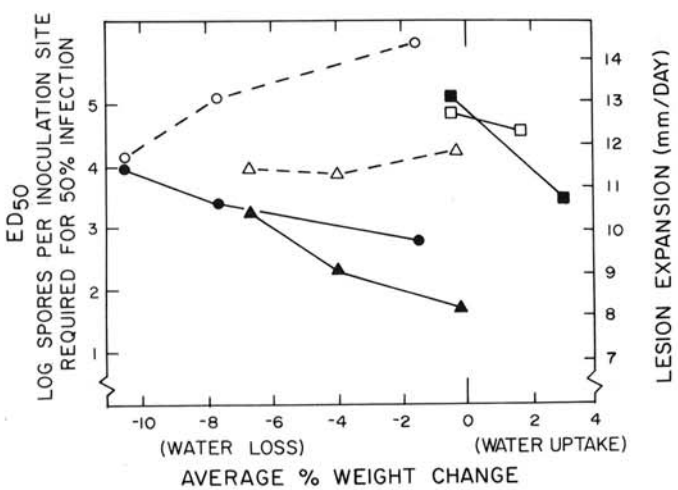

Fig. 4. Influence of water loss or gain by lemons on subsequent susceptibility to infection and the rate of colonization by *Geotrichum candidum*. Solid symbols, ED_{50}; open symbols, rate of lesion expansion. Different shapes of symbols indicate separate experiments.

DISCUSSION

Wound inoculation of lemons with spores of *G. candidum* produced either an actively developing soft rot or a small dry quiescent lesion. Distinct differences in susceptibility were measured by the percentage of inoculation sites that developed into active lesions. There was significant variability in susceptibility among individual fruits, even within a fruit lot of uniform color harvested from a single row of trees. Differences in incubation period and lesion expansion rate between resistant and susceptible fruit were minor.

Differences in susceptibility between fruit from different lemon cultivars and selections were less than day-to-day variation in fruit from a single grove. Expected differences in susceptibility of fruit with north or south exposures on the tree (1) or with vertical height on the tree (26) were not detected by our techniques.

Important factors influencing the susceptibility of lemons to sour rot were physiological age as measured by color change and storage time, and water status of the fruit. The relative importance of physiological age cannot be assessed at this time because aging of citrus fruit is a complex phenomenon (18) and we do not know which components of aging are associated with sour rot susceptibility. There was no consistent relation between susceptibility and color change. Color change was accelerated by degreening in a high-oxygen atmosphere and retarded by 2,4-D plus low temperature storage, but these treatments did not alter susceptibility significantly. Furthermore, fruit age was not inevitably correlated with susceptibility since yellow lemons held on the tree from February to April 1979 did not show an overall increase in susceptibility with time, although the onset of senescence was evident from the progressive ease of abscission.

The following evidence indicates that fruit water status influences the susceptibility of lemons to sour rot: lemons were more susceptible when harvested after rainfall and were more resistant during dry, sunny periods; lemons picked at 0800 hours were more susceptible than those harvested at 1400 hours; and lemons became more susceptible after taking up water and less susceptible after losing water. Diurnal fluctuations in peel water potential of Valencia oranges in the range of 2–5 bars have been measured by the thermocouple psychrometer (11,15) and by the pressure chamber (1). We usually obtained smaller fluctuations in our measurements on lemons. Differences in xylem pressure potential between 0800 and 1400 hours were more pronounced than differences in water potential, perhaps because the xylem potential changes by mass flow, whereas changes in tissue water potential require slower, diffusive movement. Psychrometer and pressure chamber readings on the same fruits sometimes differed by several bars. Nevertheless, the agreement between the two techniques was comparable to that reported by Kaufmann (14) for measurements of orange leaf water status. We found similar variability in psychrometer readings of tissue samples from the same lemon. This variability makes it difficult to assess the relative importance of water potential as a determinant of fruit susceptibility to sour rot. Nonetheless, the differences in susceptibility (three- to 10-fold) and water potential (0.7–2.0 bars)

between lemons picked at 0800 and at 1400 hours agree well with the differences in susceptibility (three- to 30-fold) and water potential (1.5–3.0 bars) that result from a 5–10% weight change due to water uptake or loss by the fruit. Fluctuations in water potential may explain the reported differences in overall decay of oranges harvested at different times of the day or in successive weeks (13).

Variations in peel water content may indicate differences in water potential, but may also reflect structural differences, eg, smaller cells or thicker cell walls in the tissues of lemons grown under different environmental conditions (26) or in fruits of different physiological age (20). This may explain why resistant and susceptible lemons from the same fruit lot differed in water content, but not in water potential (Table 2).

Lemons submerged in water at 20 C for 20 hr became slightly more susceptible to infection by *G. candidum* although there was no measurable increase in fruit weight. This increase in susceptibility could be due to the movement of a small amount of water into the subepidermal tissues (24) or to a reduction in oxygen level of the peel tissue. The growth of *G. candidum* is stimulated by a low-oxygen environment (27). A reduction in oxygen level may be partially responsible for the increased susceptibility of inoculation sites that were covered with water for 12 hr.

A low water potential may either predispose a plant to disease (22) or it may increase plant resistance to potential pathogens (6). A positive correlation between host water potential and disease susceptibility has been reported often for soft rot diseases (28). The susceptibility of potato tubers to infection by *Erwinia carotovora* decreased about 80-fold when the water potential of the tuber decreased from −6.7 to −8.0 bars (16). Detached susceptible leaves of Chinese cabbage became resistant to formation of elongated lesions caused by *E. carotovora* when the leaves were held at 30% RH for 2 hr (25). This treatment reduced the water potential of the leaf tissue from −6.5 to −9.1 bars. Growth and movement of the bacteria were markedly inhibited in the drier leaves.

We have identified physiological age and water status of lemons as significant factors influencing susceptibility to wound infection by *G. candidum*. The degree to which susceptibility is dependent on these factors alone cannot be assessed at present because we do not know which components of physiological age account for susceptibility differences and because small differences in water potential cannot be measured with sufficient accuracy. Environmental factors such as temperature regime and fertilization influence the structure, composition, and physiology of the lemon peel and could also influence its susceptibility to infection by *G. candidum*.

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