

Puncture Resistance in 'Sharwil' Avocado to Oriental Fruit Fly and Mediterranean Fruit Fly (Diptera: Tephritidae) Oviposition

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ABSTRACT The physiological basis for host antibiosis or nonpreference to a quarantine pest is often not understood. Studies are needed on the mechanisms that impart resistance to better understand how resistance might fail. Experiments were conducted to examine the infestability of 'Sharwil' avocados by oriental fruit fly, *Bactrocera dorsalis* (Hendel), and Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), after harvest and to quantify the effect of avocado skin hardness on resistance to infestation by oriental fruit fly. Infestation rate increased with decreasing fruit firmness, but fruit were generally poor hosts. Fruit with a patch of skin removed produced more flies than intact fruit, suggesting that skin puncture resistance was an important deterrent to oviposition. This study showed that fruit can be infested within 1 d after harvest, suggesting that fruit should be transferred to fruit fly-proof containers as they are harvested to minimize the risk of attack. Although risk of infestation is negatively correlated with fruit firmness, even some hard fruit may become infested. Therefore, fruit firmness cannot be used alone as an indicator to ensure fruit fly-free 'Sharwil' avocados. Measuring fruit firmness may be a useful component of a multiple component systems approach as an additional safeguard to reduce risk of infestation.

KEY WORDS quarantine pest, host status, nonhost, poor host, medfly

Avocados, *Persea americana* Miller, grown in Hawaii cannot be exported to the United States mainland without quarantine treatment for *Bactrocera cucurbitae* (Cocquillet) (melon fly), *Bactrocera dorsalis* (Hendel) (oriental fruit fly), and *Ceratitis capitata* (Wiedemann) (Mediterranean fruit fly). The most widely grown cultivar of avocado is 'Sharwil', a Mexican-Guatemala hybrid that has been grown in Hawaii since 1955. Avocado growers would like to export 'Sharwil' fruit to United States mainland markets. Methyl bromide and cold quarantine treatments are approved for export of 'Sharwil' avocado to the United States mainland but are not used because of degradation in fruit quality and reduced shelf life.

Avocado is generally considered to be a poor host for tephritid fruit flies (Hennessey et al. 1995, Jang 1996, Aluja et al. 2004). Armstrong et al. (1983) and Armstrong (1991) reported that 'Sharwil' avocados in Hawaii attached to the tree were not naturally infested by the melon fly, oriental fruit fly, and Mediterranean fruit fly at harvest maturity, suggesting that 'Sharwil' avocados might be exported as a nonhost under certain conditions. Avocados are typically harvested at the hard, mature green stage and ripened at room temperature until they soften before consumption. 'Sharwil' avocado, like other avocado cultivars, becomes an increasingly favorable host for fruit flies as

it ripens and softens after harvest (Oi and Mau 1989, Armstrong 1991). Armstrong (1991) suggested that fruit could be exported safely as a nonhost using a systems approach where fruit are harvested with stems attached and brought to the packinghouse within 12 h, culled to remove damaged fruit, and packed in fruit fly-proof cartons. A systems approach for export of Hawaii 'Sharwil' avocados to the U.S. mainland based on nonhost status was approved by USDA-APHIS, but the rule was rescinded in 1992 when live oriental fruit fly larvae were found in mature green fruit attached to the tree.

Liquido et al. (1995) subsequently showed that "firm ripe" and "fully ripe" fruit can occur on the tree late in the season (2.2% ripe fruit) and are much more likely to be infested by oriental fruit fly than hard, mature green fruit. In their study, fruit firmness in the field was determined subjectively as hard, firm, or soft. Fruit were held in the hand, and hard fruit were mature green with no soft spots; firm ripe fruit were relatively hard, ripening fruit with a softer portion; and soft fruit were fully ripe. Penetrometer measurements of fruit firmness in the laboratory were also taken, but no attempt was made to correlate firmness or puncture resistance measurements of individual fruit with fruit infestation levels (Liquido et al. 1995).

The physiological basis for host antibiosis or nonpreference to a quarantine pest is often not understood (Greany 1989). Studies are needed on the mech-

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anisms that impart resistance to better understand how resistance might fail. Previous studies suggested that the skin is a barrier to oviposition and may be a source of resistance in mature green avocado fruit (Armstrong 1991, Oi and Mau 1989, Liquido et al. 1995). Experiments were conducted to quantify the relationship between infestability of 'Sharwil' avocados by oriental fruit fly and Mediterranean fruit fly and the firmness of the fruit.

Materials and Methods

Experiments were conducted to test the infestability by oriental fruit fly and Mediterranean fruit fly of 'Sharwil' avocados and the effect of fruit hardness on resistance to infestation by oriental fruit fly, the primary field pest. All tests used laboratory flies obtained from colonies maintained at USDA-ARS laboratory in Honolulu, HI, that were reared on standard diets for each species (Vargas 1989). 'Sharwil' avocados with stems attached were collected from the Sinclair Farm (elevation, 530 m; 19°11.75'N, 155°51.98'W) near Milolii in the Kau District on Hawaii Island.

In the first experiment, fruit collections were made during the early (January), middle (April), and late (May) part of the harvest season. On each collection date, harvest mature fruit with stems attached were brought back to the laboratory (USDA-ARS, Hilo, HI) and held at 21°C. Mean fruit weights for early, middle, and late season fruit were 310.9 ± 4.5, 231.0 ± 2.4, and 214.7 ± 2.4 (SE) g, respectively. On each day for 7 d, four fruit were placed in a 25 by 25 by 25-cm cage with 25 gravid females for 24 h; four replicate cages were set up for oriental fruit fly and Mediterranean fruit fly on each day. The 24-h exposure period was used to maximize the chance of oviposition and infestation. After 24 h, fruit were removed from cages and placed in a 3.8-liter plastic bucket with a screened lid and held at 20–25°C. Approximately 300 g of sand was added to the bucket as a pupation medium. After 2 wk, fruit and sand were inspected for larvae and pupae. Pupae were transferred to 120-ml plastic cups for adult emergence. Ripe papayas, which are a preferred host, were exposed similarly during all tests as controls to demonstrate oviposition competence.

In the second experiment, fruit were collected toward the end of the harvest season during April–May. Three fruit collections were made at 2-wk intervals and either used for tests immediately or ripened at 21°C during 6 d to varying degrees of softness. Intact fruit or fruit with a patch of skin (average size, 3.5 cm²) shaved away to expose the flesh were exposed individually to 25 gravid oriental fruit fly adult females in a 25 by 25 by 25-cm screen cage for 4 h. A 4-h exposure period was used rather than 24 h so that infestability could be more accurately linked to different degrees of fruit firmness. A total of 64 fruit from each collection date were exposed to fruit flies, either intact (32 fruit) or with a shaved patch (32 fruit). Mean fruit weight was 247.6 ± 3.2 g ($n = 192$). Ripe papayas were exposed similarly during all tests as controls to demonstrate oviposition competence. Penetrometer read-

ings of the avocado skin were taken after fruit were exposed to flies to quantify fruit firmness. The penetrometer was a Chatillon LTCM-100 Motorized Force Tester (Ametek, Largo, FL), and we used a conical tip that measured 6.5 mm in diameter at the base and was 6.0 mm from base to tip. Force measurements (Newtons [N]) were taken by puncturing the skin to the depth of the cone (6 mm), and four measurements were taken around the equator of the fruit at equidistant points and averaged. After penetrometer readings were taken, individual fruit were placed in separate 2-liter plastic containers with screen lids and held for 2 wk for any fruit fly emergence. Approximately 2 d after the exposure period to fruit flies, fruit were examined and the number of oviposition sites was recorded. Oviposition sites are easily visible as small holes in the fruit skin or flesh at any time after oviposition. For fruit with a shaved patch, oviposition sites were counted on the flesh, flesh/skin border, and skin. At the time oviposition sites were scored, 300 g of sand was added to the holding containers as a pupation medium. After 2 wk, fruit and sand were inspected for larvae and pupae. Pupae were transferred to 120-ml plastic cups for adult emergence.

In the first experiment, a two-way analysis of variance (ANOVA) was done on the number of pupae developing from fruit for Mediterranean fruit fly and oriental fruit fly to determine the effect of harvest season (early, middle, late) and days after harvest (0–6 d). Linear regression analysis was done on the time after harvest and the number of pupae emerging from fruit after pooling data from early, middle, and late harvests. Because larvae complete development in the fruit and leave the fruit to pupate, pupae were considered the best measurement of successful development in the fruit. In the second experiment, all fruit from the three collections were pooled for analysis; linear regression was done on fruit firmness measurements and number of oviposition sites, and number of emerging pupae. Data were log transformed after examining residuals to meet assumptions of equal variance and normality.

Results

In the first experiment, few 'Sharwil' avocados fruit were infested by Mediterranean fruit fly or oriental fruit fly. ANOVA on the number of pupae developing in fruit was not significant for the effect of season (early, middle, or late harvest), day after harvest (0–6 d), or the season by day interaction for Mediterranean fruit fly or oriental fruit fly. However, the trend was that the number of pupae developing from avocados increased as the days after harvest increased (Fig. 1). The regression line describing the predicted number of pupae per fruit over time was $y = -0.07 + 0.24 (d)$ ($P = 0.06$; $R^2 = 0.01$) for Mediterranean fruit fly, and $y = -0.60 + 0.58 (d)$ ($P = 0.002$; $R^2 = 0.03$) for oriental fruit fly. When fruit were exposed to flies on the day of harvest (day 0), none were infested by Mediterranean fruit fly ($n = 48$ fruit), and only 2 of 48 fruit were infested by oriental fruit fly, producing a total of 10

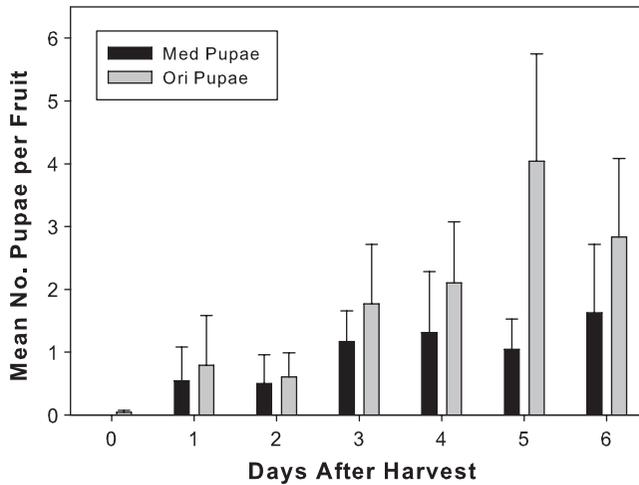


Fig. 1. Production of Mediterranean fruit fly and oriental fruit fly pupae from ‘Sharwil’ avocados in laboratory cage infestation tests (experiment 1). Fruit defenses diminish through time after harvest. The regression lines describing the predicted number of pupae per fruit over time was $y = -0.07 + 0.24 (d)$ ($P = 0.06$; $R^2 = 0.01$) for Mediterranean fruit fly, and $y = -0.60 + 0.58 (d)$ ($P = 0.002$; $R^2 = 0.03$) for oriental fruit fly.

pupae (Fig. 1). On day 5 after harvest, 5 of 48 fruit were infested by Mediterranean fruit fly and produced a total of 50 pupae, whereas 7 of 48 fruit were infested by oriental fruit fly and produced 221 pupae. This is a relatively low level of infestation compared with a preferred host such as papaya. For ripe papaya controls, all fruit were infested ($n = 42$ fruit) and produced an average of 0.99 Mediterranean fruit fly pupae/g and 0.79 oriental fruit fly pupae/g; by comparison, 10 and 15% of avocado fruit were infested on day 5 after harvest by Mediterranean fruit fly and oriental fruit fly, and infested fruit produced 0.048 and 0.11 pupae/g, respectively. Thus, ‘Sharwil’ avocado with skin intact was a poor host for both fruit fly species, even after it had ripened. The rate of pupal development to adult was $49.9 \pm 6.7\%$ for Mediterranean fruit fly and $46.9 \pm 4.6\%$ for oriental fruit fly; the difference between the two species was not significant ($t = -0.39$, $df = 52$, $P = 0.69$).

In the second experiment, fruit softened over time, but not all fruit softened at the same rate. The range of values in firmness measurements at 2 and 6 d after harvest were 45.1–77.9 and 8.4–70.9 N, respectively (Fig. 2); the coefficient of variation in firmness was more than five time higher at 6 d after harvest (63.4) than at 2 d after harvest (12.4). The regression line describing the relationship between firmness and time after harvest was $\text{firmness (N)} = 83.70 - 7.97 (d)$ ($R^2 = 0.42$). ANOVA for the effect of time after harvest on firmness was significant ($F_{1,95} = 62.4$, $P < 0.001$). Mean firmness measurements on days 2 and 3 of 63.9 and 61.5 N, respectively, were not significantly different, but mean firmness on day 5 of 50.5 N was significantly lower than day 1 and 2 firmness, and mean firmness on day 6 of 32.0 N was significantly lower than all earlier days (Tukey’s, $P < 0.05$).

Fruit with readings in the range of 60–80 N felt hard when held in the hand, 40- to 60-N fruit were firm, and

<10-N fruit were soft. Once fruit had softened to $\approx 15\text{--}25$ N, the fruit skin could be depressed by firmly applying pressure with the thumb.

As firmness decreased, more oriental fruit fly larvae developed in fruit; however, peeled fruit and intact fruit showed dramatic differences in infestation levels. For intact fruit, the slope of the regression line describing the number of oviposition sites in fruit of varying firmness did not differ significantly from zero ($F_{1,95} = 2.3$, $P = 0.14$). However, the number of pupae developing from fruit was significantly affected by the firmness of the fruit ($F_{1,95} = 6.1$, $P = 0.02$); as firmness decreased, fruit produced more pupae {number of pupae = $14.13 - 0.18 (\text{firmness [N]})$ } (Fig. 3). A mean of $50.6 \pm 8.3\%$ of pupae emerged as adults. Oviposition sites were detected in only 10 of 96 fruit used in the

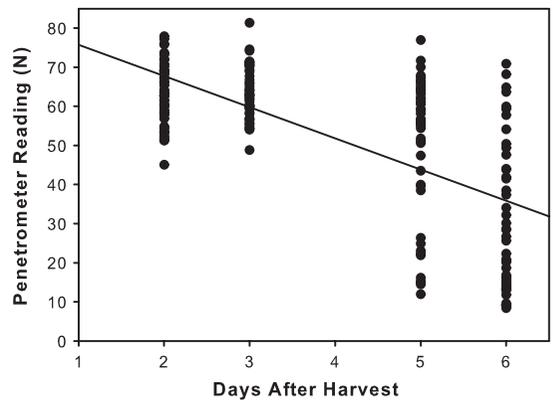


Fig. 2. Firmness (N) of ‘Sharwil’ avocado fruit at four different times after harvest (experiment 2). Fruit soften after harvest, but not all fruit soften at the same rate. The regression equation describing fruit firmness over time was $y = 83.70 - 7.97 (d)$ ($R^2 = 0.42$; $P < 0.001$).

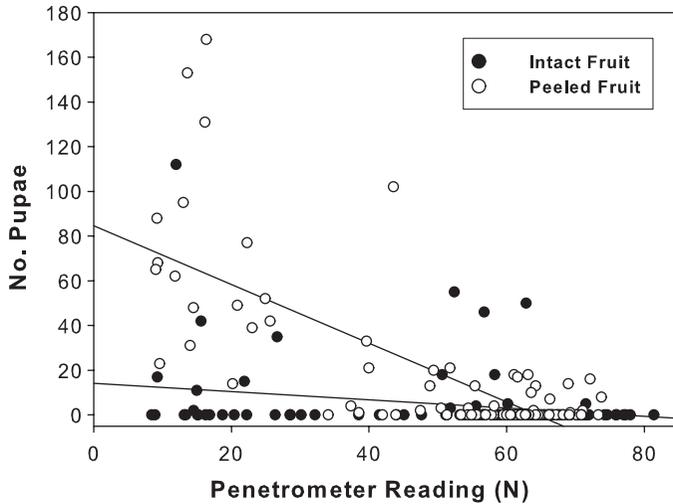


Fig. 3. Number of oriental fruit fly oviposition sites in 'Sharwil' avocado fruit of varying degrees of firmness, with a patch of skin removed (peeled fruit) or with skin left intact (intact fruit) (experiment 2). Higher penetrometer measurements (N) indicate firmer fruit. The regression equation for the number of oviposition sites for intact fruit was $y = 0.37 - 0.004$ (firmness [N]) ($R^2 = 0.02$; $P = 0.13$), and the equation for peeled fruit was $y = 33.12 - 0.45$ (firmness [N]) ($R^2 = 0.47$; $P < 0.001$).

test, and 18 fruit produced pupae. Of the 18 fruit-producing pupae, 11 showed no obvious oviposition scars, highlighting the difficulty in culling infested fruit by using visual inspection.

For fruit with a patch of skin shaved off to expose the flesh (peeled fruit), the number of oviposition sites was affected by fruit firmness ($F_{1,95} = 84.5$, $P < 0.001$); the number of oviposition sites increased with decreasing firmness [number of oviposition sites = $84.55 - 1.31$ (firmness [N])] (Fig. 4). The number of pupae developing from fruit was also affected by fruit firmness ($F_{1,95} =$

112.8, $P < 0.001$); the number of pupae increased with decreasing firmness [number of pupae = $14.13 - 0.18$ (firmness [N])]. Most ovipositions were in the flesh (55.0%) or in the damaged skin around the perimeter of the shaved patch (44.5%); only 0.4% of the ovipositions were located in the intact skin of peeled fruit. Oviposition sites were detected in 89 of 96 fruit used in the test, but only 42 fruit produced pupae. The rate of pupal development to adult was $56.9 \pm 8.0\%$ for intact fruit and $51.2 \pm 5.0\%$ for peeled fruit, which was not significantly different ($t = -0.60$, $df = 55$, $P = 0.55$).

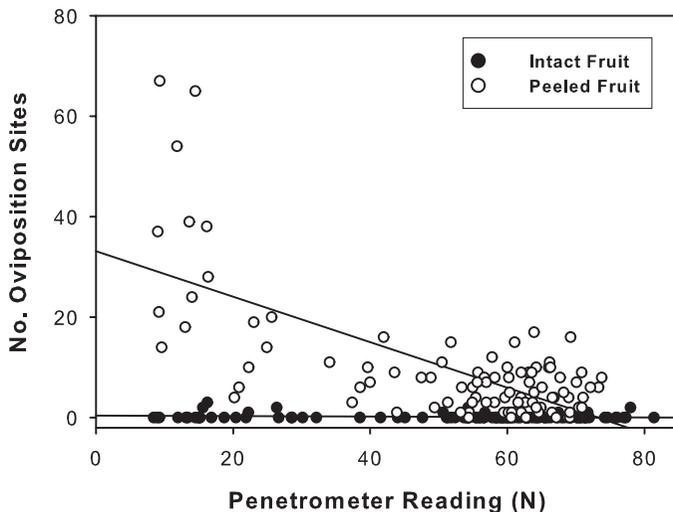


Fig. 4. Number of oriental fruit flies developing to the pupal stage in 'Sharwil' avocado fruit of varying degrees of firmness, with a patch of skin removed (peeled) or with skin left intact (experiment 2). Higher penetrometer measurements (N) indicate firmer fruit. The regression equation for the number pupae emerging for intact fruit was $y = 14.13 - 0.18$ (firmness [N]) ($R^2 = 0.06$; $P = 0.02$), and the equation for peeled fruit was $y = 84.55 - 1.31$ (firmness [N]) ($R^2 = 0.54$; $P < 0.001$).

Discussion

The tendency was for infestation rate to increase with increasing fruit softness, but fruit were generally poor hosts for oriental fruit fly and Mediterranean fruit fly. Fruit with a patch of skin removed had more oriental fruit fly oviposition sites and produced more flies than intact fruit, suggesting that skin puncture resistance was an important deterrent to oviposition. However, fully firm fruit with intact skin occasionally produced pupae that developed to adults indicating that puncture resistance is not complete. Fruit flies will oviposit multiple times in the same holes when populations are high (Back and Pemberton 1915). Multiple ovipositions in the same holes may have helped defeat the puncture resistance in our cage tests using artificially high fly densities. It is known that softening starts in small areas as the fruit begins to ripen, but it is not known whether fruit flies can locate these softer areas and select them as oviposition sites. Behavioral studies of oviposition behavior on firm fruit combined with targeted penetrometer readings might shed light on this question.

Armstrong (1991) reported that 'Sharwil' avocados with stems attached were not susceptible to fruit fly infestation for up to 12 h after harvest in the laboratory, but then they became good hosts. Inspection of >114,000 harvest mature fruit over two seasons indicated no fruit fly infestations, suggesting 'Sharwil' avocado might be a nonhost under these conditions. Oi and Mau (1989) showed that 'Sharwil' avocados became infested at low levels when Mediterranean fruit flies and oriental fruit flies were caged with fruit still attached to the tree, casting doubt on the nonhost status. Our data indicate harvest mature fruit can become infested by oriental fruit fly within 4–24 h after harvest if not protected from attack.

Liquido et al. (1995) studied natural infestation rates in the field for 2 yr. In the first year, oriental fruit flies were found in 15 of 3,248 harvest-ripe 'Sharwil' avocados collected off the tree, but in the second year, 0 of 5,004 fruit were infested. Of the 15 infested fruit, 5 fruit had no visible indications of infestation, emphasizing the low sensitivity of detection of infestation as determined by visual external inspection in mature green avocados (Liquido et al. 1995). Our results show that increasing infestation is positively correlated with decreasing fruit firmness; however, even relatively hard, mature green fruit are susceptible to infestation by oriental fruit fly, albeit rarely. Also, a substantial fraction of infested fruit in our study showed no signs of oviposition activity. This suggests that fruit must be transferred to fruit fly proof containers as they are harvested to minimize the risk of attack and that fruit firmness cannot be used alone as an indicator to ensure fruit fly-free avocados.

Other potential sources of resistance in avocados exist such as skin thickness, callous formation, and idioblast oil cells. Willard and Mason (1929) showed that different varieties of avocado varied in fruit skin thickness, but skin thickness was not correlated with the ability of Mediterranean fruit fly to oviposit in the

fruit. Callus tissue formation around fruit fly eggs deposited into the pulp has been reported (Armstrong et al. 1983, Liquido et al. 1995, Aluja et al. 2004), but the frequency of its occurrence has never been quantified, and the mechanism causing mortality has not been determined. Callous formation occurs while fruit are still on the tree (Aluja et al. 2004). The possibility that stressed trees (e.g., drought stress) might be less able to produce calluses than healthy trees has been postulated (Aluja et al. 2004) but not tested. The production of callous tissue in fruit of different maturity levels (pre- and postharvest) and its effect on egg hatch and larval survival deserve further study. Idioblast oil cells in avocado fruit contain persin and avocadofurans with antifeedant and toxic effects (Rodriguez-Saona et al. 1998, Rodriguez-Saona and Trumble 2000). A generalist herbivore, *Spodoptera exigua*, that does not normally feed on avocado avoided diet treated with idioblast oil cells and showed higher mortality and reduced larval growth compared with controls when fed diet containing idioblast oil cells. It is unlikely that idioblast oils cells could explain the increased infestability of avocados during ripening, however, because their biochemical content remains constant during fruit development and ripening, and the specialized cell wall of idioblast cells is immune to the effects of the hydrolytic enzymes cellulase and polygalacturonidase that cause softening (Platt and Thomson 1992).

There remains strong interest in Hawaii in exporting 'Sharwil' avocados to the U.S. mainland. Our results and results reported in Liquido et al. (1995) suggest that oriental fruit fly will rarely occur in avocado fruit exported from Hawaii. The question is whether the previous multicomponent systems approach can be modified to reduce the risk to an acceptable level and what additional mitigation components could be used to accomplish this (Follett and Neven 2006). Recently, a new proposal was submitted to export 'Sharwil' avocados using a systems approach based on poor host status, limited distribution (28 northern states during the winter months of November through March), and low prevalence. The limited distribution and low prevalence components are additions to the previous protocol to further reduce the risk of oriental fruit fly introduction. This approach is similar to that used to import Mexican Hass avocados from 1997 to 2001 (Peterson and Orden 2006). Measuring fruit firmness may be a useful component of a multiple component systems approach as an additional safeguard to reduce infestation and the risk of introducing oriental fruit fly. Alternatively, a cold treatment has been approved for Hawaii 'Sharwil' avocado that provides quarantine security against tephritid fruit flies. This treatment is not currently used because of perceived quality problems (chilling injury; Nishijima et al. 1995), the potential interruption of the treatment during transit (Jang et al. 2001), and the availability of Canadian markets that do not require any quarantine treatment or measures for tephritid fruit flies. A heat shock pretreatment for inducing cold tolerance in 'Sharwil' avocado fruit before quarantine cold treat-

ment has been developed (Sanxter et al. 1994), thus minimizing chilling injury. Because of the complexities in developing, validating, and operating any systems approach, use of the cold treatment might be the simplest option for Hawaii avocado growers.

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