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Response of Tropical Horticultural Commodities to Insect Disinfestation Treatments

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Postharvest treatments are required to disinfest fresh fruits, vegetables, and flowers of economically important quarantined insects. The damage caused by such insects includes small surface blemishes, destruction of the edible flesh, fruit drop, and spoilage from decay organisms entering the fruit at the site of insect activity (Hagen et al., 1981). These insect pests are of quarantine importance because they are absent from the importing country or region, or the importing country has a "zero tolerance" for all live insects regardless of their economic importance (Armstrong and Couey, 1989). Monitoring insect populations and having regulatory personnel inspect commodities are required to ensure that quarantine treatment protocol and regulations are carried out properly, including proper handling to preclude reinfestation after treatment. Failure to apply disinfestation protocols correctly can result in expensive quarantine and eradication procedures, product losses due to infestation, and costly new quarantine treatments due to introduction of a new pest (Armstrong, 1992). Recent outbreaks of Mediterranean fruit flies in California attest to these failures.

Expansion of world trade in fresh horticultural products has compounded problems associated with regulating quarantine treatments.

The expansion of international passenger traffic and short transit times has meant repeated violations of quarantine barriers. The greatest risk may be associated with contraband fruit smuggled by airline passengers rather than commercial fruit shipments. For example, a 1-week inspection "blitz" during May 1990 of all passenger baggage coming through Los Angeles International Airport from selected Central and South American countries resulted in 677 interceptions of contraband fruit. The total weight seized was almost 1 t and contained 61 fruit fly larvae. This contrasts with the average interception rate of 434 contraband fruit per week with random baggage inspections of all international arrivals.

The reproduction rate, short life cycle, and adaptability of pest insects, as well as their destructive potential, underscore the need for quarantine treatments and regulatory and physical barriers (Carey and Dowell, 1989; Mitchell and Saul, 1990). The reproduction rates for many insects of quarantine importance are rapid, especially under optimum conditions, including moderate to high temperatures and the absence of low winter temperatures (Fletcher, 1987). The time required for life cycle completion differs with environmental factors and species. Development times are similar for all fruit fly species: egg, 1–

2 days; larvae, 7–9 days; pupae, 10–11 days at 25C (Fletcher, 1987). Oriental fruit flies (*Dacus dorsalis* Hendel) can have three to 18 generations per year (Saeki et al., 1980; Vargas et al., 1984), depending on temperature (O'Loughlin et al., 1984). This time can be modified by moisture content, ripeness of fruit and degree of larvae crowding (Couey et al., 1985; Ibrahim and Rahman, 1982; Vargas et al., 1983). Most adults have long life spans (50–93 days) and high fecundity (800 to 1600 eggs/female) (Vargas et al., 1984).

Insect host status clearly depends on stage of host development, i.e., stage of fruit ripeness, and cultivar (Greany, 1989). Green fruit normally are not hosts. Fruit flies apparently do not infest mature-green 'Brazilian', 'Valery', and 'William's' bananas (*Musa* spp., AAA group) and 'Sharwil' avocados (*Persea americana* Mill.) (Armstrong, 1983; Armstrong et al., 1983), although these fruits are fruit fly hosts when ripe. At commercial maturity, 'Eureka' and 'Lisbon' lemons [*Citrus limon* (L.) Burm.f.] are not hosts for the Mediterranean fruit fly (*Ceratitis capitata* Weideman) (Spitler et al., 1984); and papaya (*Carica papaya* L.) with <25% skin yellowing are not preferred fruit fly hosts (Seo et al., 1982). Pineapples [*Ananas comosus* (L.) Merr.] having at least 50% 'Smooth Cayenne' parentage are not fruit fly hosts (Armstrong and Vargas, 1982; Armstrong et al., 1979; Seo et al., 1973).

Increased restrictions on the use of postharvest fungicides means that safe postharvest disease control treatments need to be developed. Heat treatments have been the method of choice (Couey, 1989). Until 1984, ethylene dibromide was the fumigant of choice, with methyl bromide used for some commodities. Ethylene dibromide was banned in 1984, and methyl bromide's use is seriously threatened. This review will focus on the physiological response of horticultural products to alternative physical insect disinfection treatments.

QUARANTINE TREATMENTS AND PLANT RESPONSES

Irradiation

There is some uncertainty regarding the irradiation dose required to satisfy insect quarantine requirements. Dose levels of 200 to 300 Gy have been proposed for fruit fly sterilization (Balock et al., 1966; Seo et al., 1973), 74 to 101 Gy for Australian fruit flies (Heather et al., 1991), and 50 Gy for codling moth (*Cydia pomonella* Linne) (Toba and Burditt, 1992). Horticultural responses of few fruit have been studied at these dose levels. Limited data is available on disinfection of flowers using gamma irradiation (Goodwin and Wellham, 1990; Wit, 1986). This lack of information is due in part to the apparent greater sensitivity of the tissue (unpublished data) and the possible wide spectrum of insects involved.

Gamma irradiation was initially studied in the 1960s and recommended for extending the shelf life of fresh fruit, including papaya (Akamine and Moy, 1983). A semicommercial irradiator also operated in Hawaii during the late 1960s (Dollar et al., 1971). However, the availability of less expensive alternative technologies, such as fumigation, made irradiation uneconomical (Maxie et al., 1971). Irradiation has potential, however, as an insect quarantine procedure (Sommer and Mitchell, 1986), and irradiation ≤1.0 kGy was approved for use in the United States (U.S. Food and Drug Administration, 1986). There are consumer concerns regarding the use of irradiation on food products (Schultz et al., 1989); however, a commercial irradiator (Vindicator, Mulberry, Fla.) is operating in Florida.

Fruit responses to irradiation can vary widely. Papaya can tolerate up to 1 kGy γ -radiation before surface scald occurs, surface color development is not disrupted by up to 2 kGy, flavor and aroma 4 kGy, and tissue breakdown 5 kGy (Akamine and Moy, 1983; Akamine and Wong, 1966). A 0.75-kGy dose was considered optimum for retaining fruit firmness in papaya, with only slight control of storage decay (Akamine and Wong, 1966). Papaya respiratory activity immediately after irradiation is initially elevated, but returns to the level of non-treated controls within 24 h (Akamine and Goo, 1971). A delay in climacteric peak and, hence, ripening occurred only in fruit with <25% surface color at time of treatment (Akamine and Goo, 1977a, 1977b).

Irradiated papaya ripen more uniformly as a cohort than nonirradiated fruit. Fruit placed immediately into storage at 10C after

irradiation and having <25% yellow developed skin scald. Delaying storage by 6 to 12 h after treatment prevents skin scald (unpublished data). Irradiation slightly retarded softening in papaya fruit during fruit ripening. Premature softening of papaya flesh occasionally occurs in fruit that had 15% to 35% yellowing when irradiated. Preharvest conditions that predispose fruit to more rapid fruit softening following irradiation are known but not understood.

Heat

Heat treatments offer a viable alternative to other quarantine treatment technologies. Heat treatments also can provide disease control (Couey, 1989), are easy to apply, and leave no residues. The disadvantages are the potential for fruit damage, individual commodity variability in response, and higher application cost compared to fumigation. Some heat treatments can improve fruit quality (Klein and Lurie, 1991; Lurie and Klein, 1992). Insect responses to heat treatment and thermal death relationships are better understood than commodity responses (Jang, 1986, 1991; Moss and Jang, 1991; Yokoyama et al., 1991). Mortality due to heat depends on O₂ availability, pH, previous temperatures, general energy status of the insects, and insect age and stage (Jang, 1991; Moss and Jang, 1991).

Hot-water immersion treatments have been developed to disinfest Mediterranean fruit fly, melon fly (*Dacus cucurbitae* Coq.), and oriental fruit fly from bananas (Armstrong, 1982) and papayas (Couey and Hayes, 1986; Hayes et al., 1984) in Hawaii; Caribbean fruit fly (*Anastrepha suspensa*) in guava (*Psidium guajava* L.) (Gould and Sharp, 1992); and Caribbean fruit fly, Mexican fruit fly (*Anastrepha ludens* Loew.), and West Indian fruit fly (*Anastrepha obliqua* Macquart) from Florida, Mexican, Haitian, or Peruvian mangos (*Mangifera indica* L.) (Animal and Plant Health Inspection Service, 1987; Sharp, 1986, 1989; Sharp and Picho-Martinez, 1990; Sharp and Spalding, 1984; Sharp et al., 1989b). Possible heat treatments are being considered for codling moth (Yokoyama et al., 1991), oriental fruit moth (*Grapholitha molesta* Busck) (Yokoyama and Miller, 1987), and Caribbean fruit fly in stone fruit (Sharp, 1990), carambola (*Averrhoa carambola* L.) (Hallman and Sharp, 1990), and flowers (Hansen et al., 1992). A 20-min, 49C water-bath dip (Akamine and Arisumi, 1953) has been used widely for effective control of some postharvest diseases of papaya. Similar heat treatments have been tested to control disease in other fruit with varying success (Couey, 1989).

Vapor heat was first used in the United States to kill Mediterranean and Mexican fruit flies (Baker, 1952; Hawkins, 1932). Easy-to-use and inexpensive chemical fumigants [ethylene dibromide (EDB) and methyl bromide] for quarantine meant interest in vapor heat faded with their introduction. Research was conducted to develop vapor heat treatments for bell pepper (*Capsicum annum* L.), chinese peas (*Pisum sativum* L.), cucumber (*Cucumis sativus* L.), eggplant (*Solanum melongena* L.), green beans (*Phaseolus vulgaris* L.), lima beans (*Phaseolus lunatus* L.), litchi (*Litchi chinensis* Sonn.), mango, papaya, tomato (*Lycopersicon esculentum* Mill.), and yellow wax beans (*Phaseolus vulgaris* L.) (Balock and Kozuma, 1954; Balock and Starr, 1946; Jones, 1940b; Seo et al., 1974). Commercial vapor heat facilities for many tropical commodities, especially papaya, were built in the United States after 1984, when EDB fumigation was banned. Commercial facilities operate in Okinawa, Philippines, and Thailand.

A high-temperature, forced-air quarantine treatment to kill Mediterranean fruit fly, melon fly, and oriental fruit fly on papaya has been developed (Armstrong et al., 1989; Hansen et al., 1989). This treatment is similar to the vapor heat treatment without the saturated vapor, and is equally as effective.

Heat effects on plant cells. The effect of heat stress on plant cell physiology has been reviewed recently (Alexandrov, 1977; Berry and Bjorkman, 1980; Blum, 1987; Lange et al., 1981; Levitt, 1980; Paull, 1990b). Heat damage is similar in most cells, and in extreme cases, leads to the death of cells, tissues, organs, or the whole plant.

Transferring plants from an ambient to an elevated temperature produces stress. The severity of stress is determined by the temperature differential and duration of exposure. Other factors, such as rapidity of the change in temperature and the previous growing conditions, are also important (Levitt, 1980; Paull, 1990b). The effect of exposure

time, although recognized by many (Alexandrov, 1977; Blum, 1987; Levitt, 1980; Paull, 1990b), has not been fully investigated and its implications are unclear. A short exposure to near-lethal temperature, such as in insect disinfestation, is a "crisis" situation that relates to survival and the capacity to recover, while longer exposures to less extreme temperatures are more difficult to quantify. Excessive exposure leads to death of plant tissue, and high temperatures can only be tolerated for short periods (Paull, 1990b).

Cellular membranes have been stressed with heat (Alexandrov, 1977). Levitt (1980), in his work on chilling, suggested the use of the term "phase transition." The meaning of this term is unclear, although Levitt (1980) claims cell death occurs at the point of lipid "liquefaction." Much of the chilling-related work on lipids has been on bulk cellular extracts, and its relevance in vivo has been questioned (Blum, 1987). The loss of cellular membrane integrity with increasing temperature is gradual, with repair and reversibility possible up to the point where a lethal cell temperature is reached.

The role of the membrane in cell death induced by heat has been reviewed (Blum, 1987; Lange et al., 1981) and many hypotheses have been proposed to explain heat injury (Crisan, 1973; Levitt, 1980). Most involve protein denaturation or protein synthesis disruption. Denaturation at lethal temperatures is regarded as nonreversible, while lower temperatures can lead to a reversible inactivation. Heat effects on proteins and enzymes also were reviewed (Alexandrov, 1977; Bernstam, 1978; Brandts, 1967). Lower than lethal temperatures can lead to disruption of transcription and translation steps in protein synthesis (Bernstam, 1978) and possibly protein secretion. Single amino acid substitutions in a protein can significantly alter its thermal stability (Matthews et al., 1980).

Heat shock response. Bacteria, plants, and animals exposed to high temperatures (38–42°C) for a brief period acquire transient thermotolerance in the heat shock (HS) response (Burdon, 1988; Chen et al., 1982; Cooper et al., 1984; Kanabus et al., 1984; Key et al., 1981, 1985; Lindquist and Craig, 1988; Yarwood, 1961). As thermotolerance develops, a unique group of proteins is synthesized. These proteins are produced within 30 min after exposure to temperatures between 34 to 42°C (Kanabus et al., 1984) and are called heat-shock proteins (HSP). Thermotolerance and associated HSP have been reported for field-grown cotton (*Gossypium hirsutum* L.) (Burke et al., 1985) and soybean [*Glycine max* (L.) Merr.] leaves (Kimpel and Key, 1985), sorghum [*Sorghum bicolor* (L.) Moench] (Ougham and Stoddart, 1986), and papaya fruit (Paull and Chen, 1990). This phenomenon confers a temporary, acquired heat resistance to sublethal temperatures (Altschuler and Mascarenhas, 1982). There appears to be a fundamental but unclear role for these HSP in cellular function during high-temperature stress (Johnson and Kucay, 1988; Yost and Lindquist, 1988). Tolerance acquired by sudden HS differs from tolerance acquired by sustained growth at a moderately high temperature. Apparently, there is a different mechanism of tolerance induced by the two treatments (Wu and Wallner, 1984). This is supported by HSP being produced at higher temperatures when the temperature is raised slowly (3°C/h) vs. more rapidly (Altschuler and Mascarenhas, 1982), thus emphasizing the importance of the HS profile.

Physiological and biochemical evidence exists for HS response in ripening fruit (Klein and Lurie, 1990; Paull and Chen, 1990). Exposing ripening papaya fruit to either 42°C for 4 h or to 38 to 42°C for 1 h followed by 3 h at 22°C results in thermotolerance to the otherwise injurious heat treatment of 49°C for 70 min (Paull and Chen, 1990). Polypeptides with molecular weights similar to those of HSP are translated on extracted polysomal RNA following the 42°C treatment. The levels of all these polypeptides peaked 2 h after heat treatment and declined within 24 h. The amount of these polypeptides in the nonheated control varied with season of fruit harvest.

Fruit ripening and heat treatments. The lethal temperature for tissue is 45°C for tomatoes, 63°C for grapes (*Vitis vinifera* L.), and 49 to 52°C for apples [*Malus domestica* (L.) Borkh.] (Huber, 1935). Even below such nonpermissive temperatures, growth and metabolism can be adversely affected by heat. For example, avocado fruit stored at 30 and 34°C ripened abnormally and showed considerable surface pitting, and poor flavor. Ethylene treatment increases the threshold temperature for injury in this fruit (Lee and Young, 1984). Tomato fruit held

for more than 6 h at >41°C show delayed ripening (Hall, 1964a, 1964b) and increased electrolyte leakage (Inaba and Crandall, 1988). Treatment at 49°C for 20 min is near the limit for heat tolerance in papaya (Akamine, 1960; Hayes et al., 1984; Paull, 1990b). Papaya ripen poorly above 30°C (An and Paull, 1990). Couey (1989) grouped fruit as heat-tolerant or heat-sensitive to hot-water treatment. The heat-tolerant fruit were bananas, papaya, mangos, pears [*Prunus communis* (L.) Batsch], and litchis, while the heat-sensitive fruit were peaches [*Prunus persica* (L.) Batsch], raspberries (*Rubus idaeus* L.), bell peppers, and muskmelons (*Cucumis melo* L.). Thermotolerance can vary with cultivar, fruit size, maturity, and postharvest handling (Claypool and Vines, 1956; Jones, 1942; Paull, 1990b; Paull and Chen, 1990; Sinclair and Lindgren, 1955; Sharp et al., 1989a).

Exposing pears (Maxie et al., 1974), tomatoes (Biggs et al., 1988; Ogura et al., 1976; Picton and Grierson, 1988; Yoshida et al., 1984), and papaya (An and Paull, 1990) to temperatures >30°C for ≥48 h disrupted ripening. This disruption is characterized by a failure to develop normal pigmentation, abnormal softening, and a marked decline in ethylene production (Biggs et al., 1988; Maxie et al., 1974; Paull and Chen, 1990; Picton and Grierson, 1988; Yoshida et al., 1984). Soluble solids concentration is not affected by heat treatment, while titratable acidity declines in apples (Klein and Lurie, 1990; Liu, 1978; Porritt and Lidster, 1978); both are unaffected in grapefruit (*Citrus paradisi* Macf.) (Miller and McDonald, 1992).

High temperatures affect respiration rate and ethylene synthesis (Akamine, 1966; An and Paull, 1990; Inaba and Chachin, 1988; Jones, 1940a; Maxie et al., 1974; Ogura et al., 1976; Paull and Chen, 1990). Temperatures >25°C reduce the extent of the respiratory climacteric in avocado (Biale and Young, 1971), and respiratory rise between the initial preclimacteric level and the climacteric peak was 250% at 25°C and only 30% at 30°C. Twelve or more days at ≈33°C suppress tomato respiration, ethylene synthesis, and fruit softening, and this action is not completely reversed after returning the tomato fruit to ambient temperatures (Cheng et al., 1988; Inaba and Chachin, 1988; Ogura et al., 1976; Yoshida et al., 1984). Ripening inhibition above 30°C has been ascribed to disrupted protein action during ethylene synthesis (Maxie et al., 1974; Ogura et al., 1975), disrupted polygalacturonase generation or activation (Chan et al., 1981), and suppressed ripening-related mRNA synthesis (Paull and Chen, 1990; Picton and Grierson, 1988).

Ethylene synthesis is reversibly inhibited at higher temperatures (Biale, 1960; Chan, 1991; Field, 1984; Paull and Chen, 1990). Temperatures >35°C cause endogenous ACC to accumulate in apple tissue (Yu et al., 1980), with accompanying reduced ethylene production. The conversion of ACC to C₂H₄ apparently is highly inhibited by heat. A rapid loss (75%) of ACC oxidase occurs in papaya and other fruit exposed for short periods to temperatures >40°C (Chan, 1986a, 1986b, 1991; Dunlap et al., 1990; Klein and Lurie, 1990; Paull and Chen, 1990). The heat inactivation in papaya and cucumber is biphasic (Chan, 1986a, 1986b). ACC oxidase activity fully recovers within 3 days in papaya (Paull and Chen, 1990), apples (Klein and Lurie, 1990), and muskmelon (Dunlap et al., 1990) after removing heat. Fruit exposed to high temperature for long periods quickly recover ethylene synthesis ability (Biggs et al., 1988; Dunlap et al., 1990; Ogura et al., 1976). The loss of ACC oxidase activity due to heat treatment in cucumber fruit can be modified by conditioning for 24 h at 32.5°C (Chan and Linse, 1989a, 1989b). Recovery of ethylene production may require protein synthesis (Biggs et al., 1988), which suggests low-level production of ethylene-related mRNA (Picton and Grierson, 1988), or reactivation of pre-existing proteins.

Heating leaves to 44°C leads to loss of chloroplast activity, especially photosystem II electron transport (Berry et al., 1975). Chlorophyll fluorescence has been used to monitor heat stress (Smillie and Gibbons, 1981). Delayed light emission, an associated characteristic, declines in papaya skin with first-order kinetics when fruit are heated between 42 to 48°C (Chan and Forbus, 1988). Heat inactivation is biphasic at higher temperatures (49 to 51°C). Color changes associated with ripening in tomato are inhibited at storage temperatures >30°C (Cheng et al., 1988; Goodwin and Jamikorn, 1952). Above 30°C, bananas (Burg, 1962) and papaya (An and Paull, 1990) fail to ripen normally and develop soft and watery pulp.

Electrolyte leakage from tomato disks is induced by increasing temperatures, although the fruit did not exhibit any visible heat injury (Inaba and Crandall, 1988). Critical exposure times for leakage were 34 min at 55C, 105 min at 50C, and 166 min at 45C. Fifty percent higher electrolyte leakage occurred in apple disks held at 38C (Lurie and Klein, 1990) than at ambient temperatures. After transferring disks to 20C, leakage declined within 2 days to control levels. Another factor crucial to interpreting leakage data is the increased leakage rate as fruit ripen (Chan, 1991).

Exposing ripening pear fruit to 40C led to protein synthesis disruption via a loss of polysomes (Romani and French, 1977). This response is readily reversible and established a close correlation between the protein synthesizing machinery and ripening progression. Apples held at 38C for 4 days have reduced S³⁵-methionine incorporation into what may have been HSP (Lurie and Klein, 1990). Papaya fruit protein synthesis changes following exposure to 38C for 2 h; there was no accumulation in the control held at 22C for 10 h. Translated polysomal RNA confirm that new polypeptides are synthesized following heat shock induction (Paull and Chen, 1990). Thermotolerance decreases with continued exposure of papaya fruit to 42C, suggesting that 42C is the limit for induction of tolerance. Continued exposure to 42C, though still allowing HS-polypeptide synthesis, also caused damage. These results agree with those for tomato fruit treated for long periods at 35C (Picton and Grierson, 1988). The synthesis of ripening-specific mRNAs and new enzymes is induced during ripening of tomatoes (Christoffersen et al., 1982; Grierson, 1986; Spiers et al., 1984; Tucker and Grierson, 1982). The elevated temperature treatments may lead to softening inhibition, reduced expression of softening, or both, and other ripening-related mRNAs (Picton and Grierson, 1988).

Thermal injury (46C for 65 to 90 min) in papaya results in uneven ripening and hard lumps in the flesh and is correlated with a 90% decrease in normal polygalacturonase levels with a partial recovery to 25% of normal after 6 days at 24C (Chan et al., 1981). A similar reduction occurred in tomatoes held for several days at 33C (Ogura et al., 1975). The injury is more severe in riper papaya fruit (one-fourth to one-half ripe). Responses similar to those observed in our laboratory (Paull and Chen, 1990), i.e., heated fruit showing delayed ripening and leaving a 1- to 1.5-cm-thick area of hard tissue at the center, had already been noted by Chan et al. (1981). The conclusion from this work is that when polygalacturonase activity or other wall-degrading enzymes are increasing in a particular area of the flesh (Paull and Chen, 1983), and transcription is disrupted by heat or protein denaturation, tissue can lose its capacity to soften. This disruption could occur as ribosomes release mRNAs, which has been documented in pears heated to 40C (Romani and French, 1977). The failure to soften could also be attributable to suppression of mRNA for wall-softening enzymes, as found in tomatoes (Picton and Grierson, 1988). The loss of polygalacturonase mRNA in heated tomatoes is not overcome by exogenous ethylene (Picton and Grierson, 1988). Polygalacturonase activity, however, does return after a 6-day lag when the fruit is returned to 25C (Ogura et al., 1975; Yoshida et al., 1984). A similar reversibility in fruit softening occurred in apples held at 38C for 4 days (Lurie and Klein, 1990) or 12 h at 46C (Klein and Lurie, 1992). Polygalacturonases show little loss of activity when heated to 45C in vitro (Chan and Tam, 1982; Tucker et al., 1980); hence, heat denaturation is unlikely to be the cause of reduced polygalacturonase activity.

Between 35 to 60C, considerable (87%) purified glucanase activity is lost from tomato fruit (Hinton and Pressey, 1980), also 50% glucanase activity can be lost by exposure to 50C for 5 min (Pressey, 1983). The role of these enzymes in fruit softening is unclear. Pectinesterase activity is suppressed in tomatoes held at 33C (Ogura et al., 1975), and the activity several days after returning fruit to room temperature is only one-third of normal ripening fruit.

Modifying heat response. Many procedures have been empirically developed to reduce the injury caused by heat treatment. Disruption of papaya fruit softening by heat treatment is reduced or prevented by a 4-h pretreatment at 42C or a 1-h pretreatment at temperatures higher than 35C followed by 3 h at 22C (Paull and Chen, 1990). The 8-h approach time to 44C for the papaya vapor heat treatment (Seo et al., 1974) is designed to reduce subsequent injury when the fruit is exposed

to 44C for an additional 8.75 h. The approach time would be expected to provide the conditions necessary to develop HSPs and associated thermotolerance. The same would likely occur in deciduous fruits (Claypool and Vines, 1956). The quick rise to 49C using vapor heat always damaged Valencia oranges [*Citrus sinensis* (L.) Osbeck] and grapefruit (Sinclair and Lindgren, 1955), but they are tolerant when heated for 8 h at 43C before the 49C treatment. Cucumber can be preconditioned by a 24-h treatment at 32.5C to tolerate subsequent exposure to hot water at 46C for 50 min (Chan and Linse, 1989b). Although 32.5C is lower than the temperature normally used to induce HSPs, the 24-h duration could probably induce HSPs.

The extent of protection against softening disruption depends on season, stage of fruit ripeness at exposure, and pretreatment time and temperature. The seasonal variation could be due to field-induced thermotolerance. Understanding the conditions necessary to induce thermotolerance is essential to optimize heat treatments used for insect disinfestation and disease control.

Cold

Cold treatments for insect disinfestation theoretically are easy to apply and leave no residue. Cold treatments have been suggested for fruit disinfestation based on the success of refrigeration against Mediterranean fruit fly (Back and Pemberton, 1916). Cold quarantine treatments are used to kill Caribbean fruit fly, Mediterranean fruit fly, and Queensland fruit fly (*Dacus tryoni* Frogg.) on a wide range of fruits (Animal and Plant Health Inspection Service, 1985; Benschoter, 1984, 1988; Gould and Sharp, 1990; Hill et al., 1988; Rippon and Smith, 1979). Eggs and larval stages of fruit flies are killed below 10C, with at least 10 days required below 2.8C (Burditt and Balock, 1985). The length of these treatments and the commercial difficulties of imposing these treatments during shipment limit the use of cold treatments. Most tropical fruit are damaged by extended storage below 10C (Chen and Paull, 1985; Couey, 1982; Paull, 1990a). For example, mature-green papaya can only withstand 7 days at 1C (Chen and Paull, 1985). Only temperate fruit and those tropical fruit that can tolerate temperatures <2C, such as litchi, which can be shipped at 0 to 1.1C (Chen and Paull, 1985) and carambola (Paull, 1990a; Miller et al., 1991), are candidates for cold treatment.

The postharvest storage life of tropical and subtropical crops gradually increases with decreasing storage temperature only within specific limits. The postharvest storage life of tropical, subtropical, and temperate crops reaches a maximum at ≈10 to 12C, 4 to 7C, and 0C, respectively. Higher temperatures allow continued senescence and ripening with an expected Q₁₀ of 2 to 4. Below the 10 to 12C or 4 to 7C thresholds, storage life decreases due to chilling injury (CI), and ripening and senescence are severely restricted (Paull, 1990a). This pattern explains why most storage recommendations for tropical commodities are just in the range where CI occurs. For example, papaya can be stored for ≈25 days at 10C and still have up to 1 week of life at 20C without developing chilling injury (Chen and Paull, 1985). Commercially, papaya is shipped at 7 to 10C. These storage temperature × duration relationships are in direct contrast to the increasing storage life found for temperate commodities stored at decreasing temperatures to near 0C (Hardenburg et al., 1986).

The response of plant tissue to CI has frequently been separated into primary and secondary responses. This separation is based on a series of events involving multiple events cascading from the primary event after a certain level of CI. Two distinct possibilities are suggested as the primary event: lipid changes or protein changes. Changes in either lipids or proteins as the primary event in CI are thought to occur instantaneously when the tissue is subjected to chilling temperatures. The lipid hypothesis has received the most attention since it was originally proposed in 1965 (Bishop, 1986; Graham and Patterson, 1982; Lyons, 1973). It gained more support, at least for green tissue, after Murata et al. (1992) demonstrated the ability to genetically engineer altered chilling sensitivity.

CI symptoms generally develop after transfer from chilling to nonchilling temperatures. Symptom development is slow, and the symptoms are similar to those that occur for other stresses and injury. CI symptoms have been described by many authors and are summa-

ized by Morris (1982). Surface lesions are most common and take the form of pitting (eggplant) (McColloch, 1966), scald (papaya, citrus) (Chen and Paull, 1985; Wardlaw, 1937), and large sunken areas (peppers) (Miller and Risse, 1986). Internal brown discoloration of pulp [pineapple, taro [*Colocasia esculenta* (L.) Schott]] (Paull and Rohrbach, 1985; Rhee and Iwata, 1982), vascular strands (avocado) (Chaplin and Scott, 1980), and seeds (eggplant, tomato) (Autio and Bramlage, 1986; McColloch, 1966) also is common. Water soaking of tissue coupled with wilting and desiccation [ung choi (*Ipomoea aquatica* Forsk.)] (Hirata et al., 1987) are common symptoms in leaves. The above visual symptoms frequently occur with dysfunction of several developmental processes. The most commonly reported is a failure of fruit to ripen (banana, mango, papaya) (Chen and Paull, 1985; Hatton et al., 1965; Wardlaw and McGuire, 1931) and accelerated senescence (ung choi) (Hirata et al., 1987). These symptoms often lead to reduced postharvest life and increased susceptibility to decay (Chen and Paull, 1985; Sommer and Mitchell, 1987). The sequence of events leading to visible symptoms after primary sensing of chilling temperatures clearly vary with tissue. Physiological CI symptoms in papaya include increased ethylene production and electrolyte leakage (Chan et al., 1985), and alternaria rot (Sommer and Mitchell, 1987); they occur before the appearance of visible symptoms. At 10C, increased ethylene production occurs after 7 days, electrolyte leakage after 14 days, and visible symptoms after 24 days. The relationship between physiological CI symptoms, ethylene production and electrolyte leakage, and visible CI symptoms in papaya is unknown. Information on the time-temperature response to incipient CI for tropical and subtropical fruit and vegetables is limited (Paull, 1990a), although such information is essential for developing optimum postharvest handling and disinfestation procedures.

Fruit ripeness stage and leaf tissue age at the time of low-temperature storage significantly influence sensitivity to visible CI symptom development. The preclimacteric stage is generally more sensitive than the postclimacteric stage for avocado, papaya, 'Honey Dew' melons (*Cucumis melo* L.), tomatoes, and mango. The extreme sensitivity of bananas to chilling does not allow a difference to be determined. However, banana fruit in less mature apical hands are less susceptible to CI than the more mature distally borne fruit (Marriott, 1980; Marriott et al., 1979). Avocado (Kosiyachinda and Young, 1976) and papaya (An and Paull, 1990) increase in CI sensitivity up to the climacteric, then sensitivity declines. Conditioning some commodities before cold treatment and intermittent warming can give some increased chilling tolerance (Wang, 1982, 1989). Prestorage heat treatments (38C, 3 days) can also increase chilling tolerance of some fruit (Lurie and Klein, 1992).

Controlled atmospheres

Controlled atmospheres (CA) (reduced O₂, elevated CO₂, added CO, or all three) have been evaluated as possible insect control treatments in several studies (Aharoni et al., 1981; Benschoter, 1987; Davis and Jay, 1977; Delate et al., 1990; Gaunce et al., 1981; Klaustermeyer et al., 1977; Lidster et al., 1984; Morgan and Gaunce, 1975; Soderstrom, 1977; Soderstrom and Brandl, 1990; Soderstrom et al., 1990; Yahia et al., 1992). This method is safe only when O₂ and CO₂ concentrations are used, as it does not employ toxic, flammable compounds and leaves no residue. Most fresh, tropical horticultural crops will not tolerate high CO₂ concentrations and <2% O₂ for the long periods effective in insect control in dry cereals and legumes (Bailey and Banks, 1975; Fleurat-Lessard, 1990). CA combinations may be effective in controlling certain insects, possibly in conjunction with other quarantine treatments (Klag, 1985). Little information is available on the effects of CA on tephritid fruit fly growth, development, and mortality. To my knowledge, there are no approved quarantine treatments using CA to disinfest fruit flies from tropical or temperate fruit.

Holding strawberries (*Fragaria × ananassa* Duch.) at 2.5C for 48 h in high CO₂ killed all western flower thrips (*Frankliniella occidentalis* Pergrande) and reduced fruit decay (Aharoni et al., 1981), but some flavor was lost and juice pH was higher (Ke et al., 1991a). Caribbean fruit fly eggs and larvae are susceptible to 40% and 100% CO₂ for 48

h at 10C and 22 to 23C, respectively (Benschoter et al., 1981). Aphids (*Myzus persicae* Sulzer) and cabbage loopers (*Trichoplusia ni* Hubner) on lettuce (*Lactuca sativa* L.) are not significantly affected by 70% CO₂ and 5% O₂ for 7 days at 2.5C (Klaustermeyer et al., 1977). San Jose scale [*Quadraspidiotus perniciosus* (Comstock)] on apples is controlled by 90% CO₂ and 1% O₂ for 2 days at 12C without quality loss (Morgan and Gaunce, 1975). Codling moth larvae in apples are not completely controlled after 132 days at CA levels normally used for this fruit (Glass et al., 1961). The survivors could have been diapausing larvae, as control of nondiapausing larvae is obtained with 13 weeks storage in normal CA (Toba and Moffitt, 1991). Apple maggots (*Rhagoletis pomonella* Walsh) do not survive beyond 7 days at 0C in 100% N (Kositrakun, 1989). Storing sweetpotato [*Ipomoea batatas* (L.) Lam.] roots at 25C, 2% to 4% O₂, and 60% CO₂ may control adult sweetpotato weevils (*Cylas formicarius* Fab.) (Delate et al., 1990). This method, however, cannot be applied during curing, but only during postcuring to avoid quality loss (Delate and Brecht, 1989). Dried fruit, such as raisins, can be stored in insecticidal atmospheres of <0.5% O₂ and 14% CO₂ at 27C (Soderstrom and Brandl, 1984, 1990). Most fresh fruit, including tropical products, cannot withstand insecticidal CA treatments (40% CO₂, 0.25% to 0.5% O₂, or both) without quality loss, especially if coupled with low temperature. Bananas are a possible exception, as they are harvested when mature green and can withstand modified-atmosphere storage (Scott et al., 1971). Valencia orange is a subtropical fruit that can withstand low O₂ but not high CO₂ (Ke and Kader, 1990).

Apples and pears stored in N gas at 0C for 25 days accumulated CO₂, had higher pyruvate decarboxylase and alcohol dehydrogenase activities, and increased acetaldehyde and ethanol levels (Ke et al., 1991b; Kositrakun, 1989). ACC oxidase decreased and aminocyclopropane carboxylic acid concentration increased in the same system. Blueberries (*Vaccinium* spp.), red raspberries, and blackberries (*Rubus ulmifolius* L.) could be kept under the same conditions for 9, 7, and 5 days, respectively. Longer periods lead to off-flavor that does dissipate (Kositrakun, 1989). Nectarines (*Prunus persica* L.) are probably unable to withstand the low-O₂ (0.5%) conditions needed to control insects; 6 days at 5C caused abnormal ripening, suppressed ethylene production, elevated ethanol and acetaldehyde levels, and increased internal browning (Smilanick and Fouse, 1989). Papaya can only be stored in low O₂ (0.4%) for 3 days at 20C before developing an off-flavor (Yahia et al., 1992), while mango tolerates up to 5 days (Yahia and Vazquez-Morena, 1993).

Reduced pressure

Limited information exists that shows this technology may be effective against some pests. Exposing lettuce to 2.66 kPa for 52 h killed all green peach aphids (*Myzus persicae* Sulzer) without apparently injuring lettuce (Aharoni et al., 1986).

Washing

Washing is only effective for surface insects, such as scales, and can only be used on those commodities able to withstand washing. It is used widely in conjunction with insecticidal soaps to disinfest flowers and ornamental cut-leaf materials (Hata et al., 1992).

SUMMARY

Heat treatments either alone or in combination with other treatments offer the best current alternative for insect disinfestation for tropical and subtropical commodities. The physiological changes that occur during short-term stress are poorly understood. Work is underway to understand these processes and develop approaches to reduce the impact of this stress. However, this work cannot be successfully implemented without understanding how preharvest factors influence a commodity's sensitivity to heat. In addition, the interaction of heat stress and susceptibility to disease is not understood. The optimum method would include heat treatment that achieves insect disinfestation and minimal fungicidal doses to control disease.

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