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THE THERMAL ENVIRONMENT OF IMMATURE CARIBBEAN FRUIT FLIES,
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ABSTRACT

Because many plants regulate their internal temperatures, there is no *a priori* reason to believe air temperature accurately reflects the temperatures faced by tephritid larvae inhabiting fruit interiors. Larvae also move across and burrow into soil to pupate, and immature flies at this point are also likely to encounter temperatures that might be less than or exceed air temperature. Using thermocouples and a computerized data logger we measured a range of temperatures in the 4 major hosts of *Anastrepha suspensa* (Loew), the Caribbean fruit fly: (Surinam cherry, *Eugenia uniflora* L., Cattley guava, *Psidium cattleianum* Sabine, guava, *Psidium guajava* L., and loquat, *Eriobotrya japonica* (Thunb.)), and in grapefruit, *Citrus paradisi* Macf., an economically important secondary host. Generally, temperatures were higher in the southwestern portions of tree canopies relative to those in the northeastern interiors. Fruit on the ground was warmer than in the tree, but there was no significant pattern of maximum fruit core temperatures being warmer than subcutaneous pulp. Soil temperatures were also higher than fruit-in-tree temperatures, and decreased and displayed less variance with increasing depth. Fruit in trees seldom reached temperatures ± 0.05 of air temperatures, but fruit on the ground could be more than 0.25 the adjacent air temperature. There were positive relationships between the ratio of mean and minimum fruit temperature/adjacent air temperature and fruit diameter. Information on the temperatures confronted by immature fruit flies can be used to model population dynamics, and to design temperature sensitive strains through conditional gene expression for mass-rearing and release.

Key Words: larvae, pupae, heat, cold, conditional gene expression

RESUMEN

Debido a que muchas plantas regulan su temperatura interna no hay una razón *a priori* para creer que la temperatura ambiental refleja es precisamente la temperatura enfrentada por las moscas tefritidos que habitan el interior de las frutas. Las larvas a su vez cruzan y escavan en el suelo para empupar, y las moscas inmaduras en este punto también son mas propicias para encontrar temperaturas que pueden ser menos o más alta que la temperatura ambiental. Usando un termoelectrico y una grabadora de datos computerizados, nosotros medimos el rango de temperaturas en 4 de los hospederos mas importantes de *Anastrepha suspensa* (Loew): (*Eugenia uniflora* L., *Psidium cattleianum* Sabine, *Psidium guajava* L., y *Eriobotrya japonica* (Thunb.)), y en toronja, *Citrus paradisi* Macf. que es un hospedero secundario de importancia económica. En general las temperaturas más altas fueron en las áreas suroeste de las copas de los árboles en relación con las de la parte interior de los árboles en el noreste. Las frutas en el suelo estaban más calidas que las frutas en el árbol, pero no hubo un patrón significativo en la temperatura máxima del interior de la fruta siendo mas caliente que la pulpa subcutánea. Las temperaturas del suelo también fueron más altas que las temperaturas del fruto en el árbol, y disminuyeron y mostraron menos variación con el aumento de la profundidad. Las frutas en el árbol raramente alcanzaron temperaturas de ± 0.05 de temperatura ambiental, pero la temperatura de la fruta en el suelo pudo ser más alta de 0.25 que la temperatura ambiental adyacente. Hubo una relación positiva entre la razón del promedio y la temperatura mínima de la fruta/la temperatura ambiental adyacente y el diámetro de la fruta. Información sobre las temperaturas enfrentadas por los estados inmaduros de las moscas de la fruta puede ser usada para hacer un modelo de la dinámica de la población, y para diseñar razas sensibles a la temperatura por medio de la expresión genética condicional para la cría y liberación masiva.

Plants are relatively sessile and exposed to their parts, such as shapes that minimize surface whatever light falls upon them. Characteristics of areas to volumes and high moisture contents,

might evolve for a number of reasons, but can also result in internal temperatures quite different from the surrounding air. This includes fruit, particularly larger species such as apples, which in full sunlight, can be 14°C warmer than an ambient temperature of 27°C (Thorpe 1974). Nor are plants necessarily passive in terms of heat and cold, but rely on several non-behavioral mechanisms to regulate their temperatures. These commonly include (1) emission of infra-red radiation, (2) heat conduction and convection, and (3) evaporative cooling (e.g., Jones 1992; Nobel 1999; Roth-Neblesick 2001). The thermal consequences of various adaptations can be substantial. For example, the alpine cushion plant, *Silene acaulis* ssp. *excapa* [All.] J. Braun, and its relatives exploit, among other things, a small, prostrate growth form to avoid heat-loss into the atmosphere and reach temperatures 15-25°C above ambient (Neuner et al. 2000). Flowers of the sacred lotus, *Nelumbo nucifera* (L.) Druce, can maintain temperatures up to 10°C below effective ambient through evaporative cooling (Seymour & Shultze-Motel 1998), as can the leaves of the perennial *Phragmites communis* (Cav.) Trin. (Percy et al. 1972). Fig fruit, *Ficus* spp., in sunlight have temperatures no more than 2-3°C above ambient, but reach temperatures 3-8°C above ambient when an experimentally applied oil coating prevents their evaporative cooling through transpiration (Patiño et al. 1994).

Organisms that inhabit the interior tissues of plants, such as the eggs and larvae of frugivorous tephritid fruit flies, are also relatively limited in their ability to move to different environments to regulate their body temperatures. To a substantial degree they must tolerate the temperature they encounter within the confines of the fruit they infest. However, given the capacity of some plants to maintain temperatures different from the ambient and the variety of lighting that exists within most tree canopies (Aluja & Birke 1993; Aluja et al. 2000; Sivinski et al. 2004), the range of thermal environments encountered by fruit fly larvae may be considerable and is largely undescribed.

The difficulty in simply estimating the temperature faced by immature fruit flies through extrapolation from air temperature is further complicated by the pupation behavior of the larvae that typically exit fallen fruit to pupate in the soil at depths of near-surface to more than 5 cm (e.g., Hodgson et al. 1998). Soil temperatures are known to vary with depth (e.g., Hillel 1982), season and microhabitat (Thomas 1993, 1995).

A better description of tephritid thermal environments would yield several benefits. Temperature is a critical component in modeling population dynamics (e.g., Meats 1981). In addition, proposed new autocidal techniques for tephritid control and eradication rely on temperature sensitivity in offspring (Handler 2002, 2004). Mass-reared and released males would carry

genes that, when expressed in immature offspring, result in death after a certain temperature is reached. Such a scheme would avoid the sterilizing radiation believed to diminish male sexual success and which may compromise the Sterile Insect Technique (=SIT) (Lux et al. 2003). The success of the Conditional Gene Expression Technique (=CGE) could be optimized by predicting the minimum and maximum temperatures eggs and larvae are likely to encounter in different locations within the canopies of different hosts fruiting at different times of the year.

The model tephritid we considered was the Caribbean fruit fly, *Anastrepha suspensa* (Loew). Originally from the Greater Antilles, it was accidentally introduced into southern Florida during the mid-1960s and subsequently spread over ~2/3 of the state's peninsular region (Baranowski et al. 1993). Larvae develop in over 90 species of fruit (Norrbom & Kim 1988), but a smaller number of roughly sequentially-fruiting hosts are characteristically the most highly infested. These include: Surinam cherry, *Eugenia uniflora* L. (typically late spring-early summer), Cattley guava, *Psidium cattleianum* Sabine (typically mid-late summer), guava, *Psidium guajava* L. (typically late summer-early autumn), and loquat, *Eriobotrya japonica* (Thunb.) (typically late winter-early spring) (Sivinski et al. 1999). In addition, a number of citrus species are attacked, including grapefruit, *Citrus paradisi* Macf. (Simpson 1993). The temporal distribution and size differences among these fruit suggest that larvae confront considerable within-year variance in temperature (Sivinski et al. 2004).

The present study documented the temperatures near the surfaces and at the cores of the primary hosts (+ grapefruit) in and under tree canopies as they occurred in several geographical locations within the range of the fly. In addition, the temperatures of mature and fallen fruit were measured in the field, as were soil temperatures at several likely pupation depths. Particular attention was given to the minimum and maximum temperatures since these may be important in the distribution/abundance of the fly and its parasitoids (Eitam et al. 2004) and in the design of CGE systems. Finally the relationship of fruit temperatures to air temperature was determined so that the temperature of larval habitats might be estimated by making relatively simple air temperature measurements.

MATERIALS AND METHODS

Sampling Procedure

Four sets of fruit and 4 sets of soil temperatures were obtained from each host tree, this number determined by the capacity of the measuring and data logging device. Ripe intact fruit on the tree were chosen from what would typi-

cally be those portions of the canopy most and least exposed to sunlight, one on the southwestern exterior and one in the northeastern interior, respectively. Intact, fallen fruit were placed on the soil under the southwest portion of the canopy along an imaginary line extending down from the canopy margin in order to maximize exposure to sunlight. Intact, fallen fruit under the northeast portion of the canopy were placed <0.5 the distance between the canopy margin and the trunk in order to minimize exposure to sunlight.

Thermocouple devices to measure temperature were placed in 2 locations in each piece of fruit, 1 directly under the skin/rind and another as close as possible to the center. For fruit in trees, thermocouple wires were supported by 1 or more twists of wire attached to branches. In some cases, relatively large seeds prevented absolute-center measurements, but regardless, the range of locations potentially occupied by larvae within the fruit pulp was taken into account. A drop of cyanoacrylate gel glue was used to hold thermocouples in the fruit, and cover the wound. Soil temperature measurements were taken within 10 cm of the fruit at 5 depths: on the surface directly under the fruit, at 5 mm, 15 mm, 25 mm, and 50 mm. Air temperature was obtained from within 2 cm above each piece of fruit examined. Tabular data describing actual temperatures in various microhabitats consist of first 24 h of data alone when fruit condition presumably most closely resembled the undisturbed state.

To compare the temperature of larval fruit-microhabitats to local air temperatures, ratios of fruit temperature over air temperature were calculated as follows. Minimum, maximum, and average fruit temperatures from a particular microhabitat (subcutaneous or core, tree canopy or ground, southwest canopy, or northeast canopy) were divided by the minimum, maximum, or average air temperatures recorded directly above the fruit for the same period of time. Because fruit size might influence the thermal dynamics of fruit, these ratios are presented graphically in relation to the log of fruit diameter. In order to balance the needs of maximizing the data set while at the same time minimizing deterioration of the fruit, only the first 3 days of data were considered for comparisons with air temperature regardless of how long the thermocouples were in place.

Temperature Measuring Device

Temperatures were measured by 32 Type T thermocouples 18.29 m in length which were inserted into fruit and soil at the depths described above. The thermocouple consist of shielded thermocouple wire with factory manufactured measuring junctions 1 mm in diameter and covered in Omega Bond (OB-101), a high thermally conductive epoxy to prevent corrosion due to fruit acids.

All the thermocouples measuring air temperature were shielded from the effect of thermal radiation by a small sheet of highly reflective aluminum foil.

The thermocouples were connected to a Campbell Scientific CR-10 Datalogger through a Campbell Scientific AM 416 Relay Multiplexer. A thermocouple reference thermistor was wired to the CR-10 datalogger to provide temperature compensation and power was provided by a 12-V car battery. A fifth-order polynomial, resident in the datalogger, converts the EMF to temperature in Celsius. Although calibrated by the manufacturer with an accuracy of $\pm 0.5^{\circ}\text{C}$, the 32 thermocouples connected to the Multiplexer and datalogger were left to acclimate in the lab and their readings compared the reference thermistor and the internal datalogger temperature. All the readings were within the accuracy provided by the manufacturer.

The datalogger and multiplexer were housed in UV protected-plastic box (45 cm \times 30 cm) to protect them from the elements. Temperature data were obtained every min, and averaged and stored every 30 min.

Fruit Tree Locations

Trees were chosen on the basis of being as isolated as possible so that sunlight on the canopy was unimpeded by neighboring plants. The additional necessity of being secure enough to leave unattended computer equipment resulted in the use of different numbers of trees of the various species. In several cases, as noted in the individual descriptions of the sites, different fruit were later sampled on the same tree to obtain a second data set. All sites were within the perennially-occurring range of *A. suspensa* (Baranowski et al. 1993).

Citrus paradisi. (Two trees, 2 sets of temperature measurements/tree for a total of 4 sets of measurements, dates started: 30-Oct-03, 6-Nov-03, 20-Nov-03, 2-Dec-03): Near Dundee, Florida, Polk County, Florida (28°17'1"N, 81°6'22"W; soil in the area is described as Candler-Tavares-Apopka: excessively drained, moderately drained and well drained, sandy soils underlain by loamy or clayey material; USDA 1990a).

Eriobotrya japonica. (Two trees, 2 sets of temperature measurements on one tree and 1 set on the other for a total of 3 sets of measurements, dates started: 2-Mar-04, 11-Mar-04, 26-Mar-04): Ft. Pierce, Florida, St. Lucie County, (27°44'6"N, 80°32'5"W; soil is described as Waveland-Lawnwood: poorly drained soil, sandy throughout with dark subsoil weakly cemented; USDA 1980).

Eugenia uniflora. (Two trees with 2 sets of temperature measurements on each tree for a total of 4 sets of measurements, dates started: 9-Apr-04, 16-Apr-04, 21-Apr-04, 5-May-04): LaBelle, Florida, Hendry County (26°44'6"N, 80°32'5"W; soil is described as Holopaw-Basinger association: poorly drained or very poorly drained, sandy,

loamy and organic soils that have a loamy subsoil; USDA 1990b).

Psidium cattleianum. (Three trees, 1 set of temperature measurements/tree for a total of 3 sets of measurements, starting dates: 17-July-03, 2-Aug-03, 22-Aug-03): LaBelle, Florida, Hendry County (soil described as Oldsmar-Wabasso association: poorly drained, sandy soils that have a sandy and loamy subsoil with organic staining in the sandy layers; USDA 1990b) and Clewiston, Florida, Hendry County (26°45'12"N, 80°56'1"W; soil is described as Margate association: poorly drained, sandy soils that are underlain by limestone; USDA 1980).

Psidium guajava. (One tree, 1 set of temperature measurements, starting date: 29-Aug-03): LaBelle, Florida, Hendry County (see *P. cattleianum* above).

Statistical Analyses

Mean, minimum, and maximum temperatures were initially and individually compared on the basis of species, location (within the canopy and on the ground), and the interaction of these 2 variables with SAS (proc GLM) (SAS Inst., Inc., Raleigh, NC). Where applicable, means were compared through analysis of variance followed by the Waller separation of means test (proc ANOVA). Paired comparisons of temperatures fruit in and under particular portions of tree canopies were made by the nonparametric Wilcoxon paired-sample test (Zar 1974). Regressions of fruit diameter to minimum, maximum and mean temperatures were performed with SAS (proc GLM) (SAS Inst., Inc., Raleigh, NC).

RESULTS

As suspected, our "thermal snapshots" demonstrated that immature *A. suspensa* within fruit and in the soil confront a range of temperatures over both a seasonal and spatial scale (Tables 1 and 2). The following are some noteworthy points about this thermal diversity.

Effect of Location In and Under the Canopy on Temperature Maxima and Minima

The maximum fruit temperatures were significantly higher in and under the southwest portion of the canopies. Fruit in the southwest portions of the canopies reached significantly higher temperatures than those in the northeast (Table 3) as did fallen fruit along the southwest margins of the canopy. However, there were no significant differences in the mean and minimum temperatures of fruit in or under the southwestern and northeastern portions of the canopies. This was probably due to maxima occurring during daylight hours with more light striking fruit on the margins of the southwest

canopy, while minima occurring during the night when location was relatively unimportant.

Tree species consistently and significantly influenced mean, minimum, and maximum fruit temperatures, but any interspecific differences in fruit and canopy morphology co-occurred with seasonal variation in temperature. However, because there were no significant interactions between tree species and the sites of the fruit within their canopies it is reasonable to assume that tree morphologies were homogeneous relative to seasonal temperature differences.

Within Fruit Differences in Temperature

There was relatively little difference in mean, minimum, or maximum temperatures measured under the surface of fruit and at their cores and no significant pattern in those temperature differences that did occur (Tables 1, 2 and 3). Concentrating on the southwest portion of the trees where temperatures were consistently more extreme, neither fruit still in the tree or on the ground had warmer subcutaneous than core temperatures.

Effect of Remaining on the Tree and Falling on the Ground on Maximum and Minimum Temperatures

In the southwest portion of the canopy, maximum core fruit temperatures were higher in fallen fruit on the ground than, in some case as much as 15°C hotter (Tables 1; $T = 0$, $P < 0.001$). This was also the case in the northeast ($T = 16.5$, $P = 0.05$), although the mean temperature differences between fruit cores in the tree and on the ground was much less in the northeast (6.8°C [southwest] vs. 2.8°C [northeast]; $T = 12$, $P < 0.01$). There are at least 2 reasons for the warmer temperature of the fallen fruit: (1) less effective evaporative cooling after leaving the parent plant, and (2) the higher temperature of the ground surface relative to the air. The later is particularly plausible given the relative insignificance of a ground-effect in the more shaded areas in and under the canopy.

Relationship of Fruit to Air Temperature

As might be expected from the above, the relationship of fruit temperature to the air temperature immediately above the fruit differed in regards to fruit on the tree and on the ground (Figs. 1 and 2). The temperatures of tree-fruits were seldom ± 0.05 of the air temperature. However, ground fruit were sometimes ± 0.25 of the air temperature. There were no relationships between fruit size and the maximum temperatures fruits reach relative to air temperature. However, there was a consistent pattern of fruit size being positively correlated to minimum and mean temperatures and this pattern held regardless of location

TABLE 1. THE MEAN (SD), MINIMUM, AND MAXIMUM TEMPERATURES OF VARIOUS *ANASTREPHA SUSPENSIS* HOST FRUITS (SUBCUTANEOUS TEMPERATURES AND AS NEAR THE CORE AS SEEDS ALLOWED) IN THE TREE CANOPIES AND ON THE GROUND UNDER CANOPIES. FRUIT WERE MEASURED IN AND UNDER THOSE PORTIONS OF THE CANOPY MOST AND LEAST EXPOSED TO SUNLIGHT: THE SOUTHWESTERN MARGIN OF THE CANOPY AND THE NORTHEASTERN INTERIOR OF THE CANOPY. TEMPERATURES WERE RECORDED FOR THE FIRST 24 H AFTER THERMOCOUPLE INSERTION, WHEN THE FRUIT WAS LEAST DECAYED.

Fruit	SW ts	SW tc	NE ts	NE tc	SW gs	SW gc	NE gs	NE gc
Cattley	28.4 ± 4.4	28.5 ± 4.8	27.7 ± 3.1	27.7 ± 3.2	31.0 ± 7.6	31.0 ± 7.7	28.8 ± 4.6	28.9 ± 4.5
Guava 1	(23.7-39.2)	(23.4-40.5)	(23.8-33.5)	(23.9-33.8)	(24.4-48.0)	(24.2-48.1)	(23.7-41.1)	(23.7-41.1)
Cattley	28.5 ± 3.7	24.3 ± 3.6	28.6 ± 3.9	28.0 ± 3.3	31.5 ± 8.1	31.1 ± 6.7	29.1 ± 4.6	28.8 ± 3.9
Guava 2	(24.2-36.4)	(23.7-35.5)	(23.6-36.5)	(23.7-34.8)	(24.6-48.6)	(25.2-44.5)	(24.0-40.7)	(24.4-37.8)
Cattley	27.5 ± 4.7	27.8 ± 5.3	27.0 ± 4.3	27.1 ± 4.4	29.3 ± 6.1	29.0 ± 5.9	29.1 ± 5.7	29.1 ± 5.3
Guava 3	(22.2-37.6)	(22.0-39.8)	(22.1-35.8)	(22.2-37.2)	(23.4-47.5)	(23.0-45.9)	(23.0-41.5)	(23.4-40.0)
Guava	26.4 ± 3.5	26.6 ± 3.6	26.0 ± 2.9	26.0 ± 2.8	27.8 ± 4.7	27.6 ± 4.5	26.3 ± 2.6	26.2 ± 2.2
	(22.6-33.8)	(22.6-34.5)	(22.6-31.5)	(22.6-31.3)	(23.0-38.1)	(22.9-37.4)	(23.3-31.0)	(23.5-30.3)
Surinam	19.9 ± 5.8	20.0 ± 5.9	18.8 ± 4.6	18.9 ± 4.7	22.1 ± 9.1	22.6 ± 9.1	18.6 ± 3.9	18.7 ± 3.7
Cherry 1	(12.9-28.6)	(12.9-28.7)	(12.8-25.2)	(12.9-25.2)	(13.0-40.4)	(13.7-40.8)	(13.4-24.5)	(13.8-24.5)
Surinam	24.9 ± 3.3	25.0 ± 3.4	24.5 ± 2.8	24.5 ± 2.7	27.5 ± 7.4	27.8 ± 7.7	24.5 ± 2.4	24.4 ± 2.3
Cherry 2	(21.3-32.0)	(21.3-32.4)	(21.3-29.9)	(21.4-29.8)	(20.8-46.0)	(20.9-47.6)	(21.6-29.0)	(21.6-28.9)
Surinam	—	22.2 ± 5.7	20.0 ± 5.4	22.0 ± 5.3	24.8 ± 9.5	24.5 ± 8.7	21.9 ± 4.4	21.9 ± 4.4
Cherry 3		(14.1-30.6)	(14.0-29.9)	(14.0-29.5)	(14.6-49.1)	(15.0-46.0)	(15.3-29.5)	(15.5-30.8)
Surinam	22.2 ± 7.1	22.1 ± 7.0	21.4 ± 6.0	21.4 ± 5.9	23.7 ± 10.6	22.8 ± 9.1	21.3 ± 5.8	21.3 ± 6.2
Cherry 4	(12.9-33.3)	(12.9-33.2)	(13.1-29.2)	(13.1-29.2)	(13.0-45.4)	(12.7-39.1)	(13.7-31.9)	(13.1-32.4)
Loquat 1	23.4 ± 5.3	23.3 ± 5.1	22.6 ± 4.2	22.6 ± 4.5	23.8 ± 7.8	23.8 ± 7.8	22.4 ± 5.4	22.5 ± 5.7
	(17.8-36.7)	(17.8-35.5)	(17.6-30.2)	(17.4-31.2)	(16.8-45.8)	(16.8-44.8)	(16.6-32.5)	(16.4-33.6)
Loquat 2	16.7 ± 8.1	16.9 ± 8.3	16.2 ± 7.5	17.1 ± 9.3	18.2 ± 10.2	18.6 ± 10.8	16.4 ± 8.9	16.6 ± 9.1
	(7.6-29.5)	(7.6-29.8)	(7.4-28.1)	(7.2-34.4)	(8.6-42.6)	(8.5-43.4)	(7.2-34.8)	(7.3-34.9)
Loquat 3	22.5 ± 3.5	22.6 ± 3.8	21.6 ± 2.2	21.5 ± 2.2	24.8 ± 7.5	24.4 ± 6.7	21.4 ± 2.6	21.7 ± 3.3
	(17.1-28.8)	(16.8-29.6)	(17.2-25.3)	(17.3-25.6)	(17.5-41.6)	(17.7-39.4)	(18.2-41.3)	(17.7-36.6)
Grapefruit	23.9 ± 6.7	24.2 ± 7.5	21.8 ± 3.7	21.9 ± 3.7	24.2 ± 6.4	25.5 ± 7.8	22.0 ± 3.4	22.0 ± 3.4
1	(16.8-37.7)	(17.0-37.9)	(17.6-28.7)	(17.8-28.7)	(17.4-37.1)	(17.5-40.5)	(18.1-28.4)	(18.1-28.2)
Grapefruit	23.1 ± 2.7	22.8 ± 1.7	22.5 ± 1.3	22.5 ± 1.3	23.7 ± 3.0	23.7 ± 2.2	22.7 ± 1.3	22.9 ± 1.2
2	(21.3-33.3)	(21.4-27.5)	(21.2-26.3)	(21.3-26.1)	(21.7-33.8)	(22.0-30.6)	(21.6-26.7)	(21.8-26.3)
Grapefruit	20.5 ± 8.1	20.3 ± 7.9	16.3 ± 3.5	16.3 ± 3.4	20.0 ± 10.2	20.2 ± 8.8	16.7 ± 3.3	16.6 ± 3.3
3	(11.4-34.9)	(11.4-33.8)	(12.1-25.0)	(12.1-23.2)	(9.8-37.9)	(10.9-36.6)	(12.7-26.7)	(12.7-28.0)
Grapefruit	18.3 ± 8.1	18.1 ± 7.5	15.3 ± 4.0	15.4 ± 4.0	18.5 ± 9.5	19.8 ± 9.5	15.4 ± 4.0	15.5 ± 3.4
4	(9.1-32.0)	(9.4-29.3)	(10.1-21.8)	(10.2-21.9)	(7.9-35.9)	(9.3-36.5)	(10.3-21.9)	(11.0-21.0)

(tree NE mean int. = 1.0 b = 0.002; tree NE minimum int. = 0.99 b = 0.006; tree SW mean int. = 0.99 b = 0.005; tree SW minimum int. = 1.0 b = 0.001; ground NE mean int. = 0.99 b = 0.002; ground NE minimum int. = 1.007 b = 0.005; ground SW mean int. = 1.01 b = 0.007; ground SW minimum int. = 1.009 b = 0.009). There was considerable variance in many of relative temperature relationships (see r^2 values in Figs. 1 and 2), due presumably to a complex set of factors that differed under individual circumstances (Tables 1 and 2; Figs. 1 and 2). All other things being equal, larger fruits should retain greater amounts of heat derived from sunlight. However, it should be noted that while fruit size and temperatures were sometimes correlated, the different sized fruit also had a variety of morphologies, and that it is possible that it was these morphological differences that were related to temperature. If so, the

size relationship was coincidental, and particular attention might be focused on the thermodynamics of grapefruit, the largest fruit measured.

Relationship of Soil Depth to Temperature

As in fruit, maximum soil temperatures were higher under the southwestern margin of the canopy than under the northeastern interior (Table 2; surface temperature: $T = 0$, $P < 0.001$). Maximum temperatures declined with depth on the southwestern canopy margin, but there was no relationship in northeast soils (Table 3).

DISCUSSION

In general, fruit temperatures were higher in the southwestern portions of tree canopies relative to those in the northeastern interiors. Fruit

TABLE 2. THE MEAN (SD), MAXIMUM, AND MINIMUM TEMPERATURES OF VARIOUS *ANASTREPHA SUSPENS*A HOST FRUITS (SUBCUTANEOUS TEMPERATURES AND AS NEAR THE CORE AS SEEDS ALLOWED) ON THE GROUND BENEATH THE CANOPIES. TEMPERATURES AT GROUND LEVEL BENEATH FALLEN FRUIT AND AT DEPTHS OF 5, 25, AND 50 MM WOULD BE ENCOUNTERED AS LARVAE LEFT FALLEN FRUIT AND BURROWED INTO THE SOIL TO PUPATE. FRUIT WERE MEASURED IN THOSE POSITIONS UNDER THE CANOPIES MOST AND LEAST EXPOSED TO SUNLIGHT: BELOW THE SOUTHWESTERN MARGIN OF THE CANOPY AND BELOW THE NORTHEASTERN INTERIOR OF THE CANOPY. TEMPERATURES WERE RECORDED FOR THE FIRST 24 H FOLLOWING THERMOCOUPLE INSERTION, WHEN THE FRUIT WAS LEAST DECAYED.

Fruit	SW s	SW 5	SW 25	SW 50	NE s	NE 5	NE 25	NE 50
Cattley Guava 1	30.9 ± 6.3 (25.3-45.5)	30.7 ± 4.5 (26.4-42.4)	30.4 ± 3.4 (26.7-38.5)	30.2 ± 2.6 (27.2-35.8)	28.7 ± 3.1 (25.5-37.7)	29.0 ± 3.4 (25.5-38.9)	28.6 ± 2.3 (26.0-33.8)	28.6 ± 2.0 (26.2-32.8)
Cattley Guava 2	31.0 ± 5.9 (25.6-44.7)	30.2 ± 4.2 (26.2-39.2)	30.1 ± 3.2 (26.6-36.6)	29.9 ± 2.7 (26.9-35.8)	28.5 ± 2.3 (25.8-33.7)	28.5 ± 2.4 (25.7-34.7)	28.4 ± 2.0 (25.9-33.3)	28.3 ± 1.7 (26.2-31.6)
Cattley Guava 3	30.2 ± 6.0 (24.6-48.2)	29.2 ± 2.7 (26.2-35.8)	29.3 ± 2.3 (26.6-34.8)	29.3 ± 1.7 (27.1-32.5)	29.8 ± 4.1 (25.0-37.7)	29.8 ± 4.0 (25.1-36.8)	29.5 ± 2.8 (25.9-34.4)	29.4 ± 2.3 (26.3-33.2)
Guava	28.3 ± 4.9 (23.6-41.7)	27.8 ± 3.9 (23.7-37.4)	27.7 ± 3.2 (24.1-34.7)	27.6 ± 2.7 (24.5-33.4)	26.0 ± 1.2 (24.5-28.5)	26.0 ± 1.3 (24.3-28.5)	26.0 ± 1.1 (24.6-28.2)	26.1 ± 0.8 (24.8-27.6)
Surinam Cherry 1	22.6 ± 7.2 (15.3-37.9)	22.8 ± 4.5 (17.8-31.7)	23.0 ± 4.2 (18.5-31.3)	23.2 ± 4.0 (18.6-31.2)	18.1 ± 2.3 (14.9-21.2)	18.1 ± 1.8 (15.4-20.6)	17.9 ± 1.2 (15.9-19.6)	17.8 ± 1.1 (16.1-19.3)
Surinam Cherry 2	26.7 ± 6.3 (20.6-42.7)	28.2 ± 5.9 (22.7-43.3)	27.7 ± 4.7 (23.2-39.5)	27.5 ± 3.1 (24.3-34.3)	24.4 ± 2.1 (21.9-28.3)	24.3 ± 1.9 (22.0-28.1)	24.0 ± 1.4 (22.2-26.5)	23.7 ± 1.2 (22.2-25.9)
Surinam Cherry 3	24.4 ± 6.0 (17.3-39.7)	24.8 ± 4.7 (19.2-35.8)	24.7 ± 3.6 (20.3-32.3)	24.8 ± 3.5 (20.4-32.0)	21.0 ± 2.1 (17.5-24.1)	21.1 ± 2.1 (17.8-24.1)	20.8 ± 1.5 (18.2-22.9)	20.6 ± 1.2 (18.6-22.3)
Surinam Cherry 4	23.9 ± 10.7 (13.4-46.1)	24.2 ± 4.6 (19.2-33.7)	24.0 ± 3.1 (20.3-30.2)	24.0 ± 2.8 (20.7-29.3)	21.0 ± 4.4 (14.9-27.2)	21.4 ± 4.1 (14.1-28.3)	20.9 ± 3.1 (16.6-27.8)	21.4 ± 1.6 (19.0-26.0)
Loquat 1	23.6 ± 6.2 (18.0-40.9)	22.5 ± 3.0 (19.3-30.3)	22.3 ± 2.4 (19.7-28.3)	22.1 ± 1.8 (20.0-26.2)	22.4 ± 5.4 (16.7-33.1)	22.0 ± 3.5 (18.1-28.4)	22.0 ± 2.9 (18.8-28.1)	21.6 ± 1.7 (19.6-25.0)
Loquat 2	19.1 ± 10.2 (9.7-45.6)	19.9 ± 6.2 (13.7-34.9)	19.9 ± 4.5 (15.1-30.0)	20.0 ± 2.8 (16.6-26.0)	17.3 ± 8.3 (8.8-33.9)	17.8 ± 6.3 (11.0-29.4)	18.8 ± 5.0 (13.2-28.8)	19.3 ± 3.1 (15.5-24.7)
Loquat 3	25.6 ± 8.0 (18.1-45.0)	25.2 ± 6.7 (18.4-41.3)	24.8 ± 5.8 (18.4-36.6)	24.7 ± 4.5 (19.6-33.9)	21.6 ± 3.4 (17.9-33.0)	21.4 ± 2.7 (18.3-29.5)	21.0 ± 1.6 (18.8-24.0)	21.1 ± 1.6 (18.9-23.6)
Grapefruit 1	25.8 ± 4.9 (20.4-35.5)	26.0 ± 4.9 (20.1-36.1)	25.0 ± 4.4 (20.5-34.7)	25.9 ± 3.4 (21.8-32.6)	21.8 ± 2.1 (19.2-25.5)	21.6 ± 1.9 (19.3-25.3)	21.6 ± 1.4 (19.8-24.1)	21.6 ± 1.1 (20.2-23.5)
Grapefruit 2	24.4 ± 2.3 (22.7-30.3)	24.2 ± 1.9 (22.4-31.9)	24.0 ± 1.7 (22.8-29.8)	24.4 ± 1.5 (23.1-28.7)	22.5 ± 1.2 (21.2-26.4)	23.0 ± 0.7 (22.3-25.0)	23.1 ± 0.7 (22.4-25.0)	23.3 ± 0.5 (22.7-24.7)
Grapefruit 3	21.9 ± 7.8 (13.4-36.6)	21.9 ± 7.3 (13.3-35.1)	22.3 ± 7.0 (14.1-35.0)	20.2 ± 6.2 (14.7-30.1)	16.7 ± 2.7 (14.0-30.5)	16.9 ± 1.9 (14.4-23.8)	17.1 ± 2.0 (15.1-27.9)	18.1 ± 1.7 (16.7-28.3)
Grapefruit 4	20.8 ± 7.7 (12.1-35.1)	20.6 ± 7.5 (11.5-34.9)	20.9 ± 6.5 (12.1-34.9)	19.1 ± 6.2 (13.1-31.1)	15.5 ± 2.1 (12.1-19.7)	15.3 ± 1.8 (12.8-17.8)	15.5 ± 1.5 (13.3-17.7)	16.2 ± 1.0 (14.7-17.5)

on the ground were warmer than those in the tree, but there was no significant pattern of maximum fruit core temperatures being warmer than subcutaneous pulp. Soil temperatures were also higher than fruit-in-tree temperatures, and decreased and displayed less variance with increasing depth. Fruit in trees seldom reached temperatures ± 0.05 of adjacent air temperatures, but fruit on the ground could be more than 0.25 the adjacent air temperature. There were significant relationships between the ratio of minimum and mean fruit temperatures/adjacent air temperature and fruit diameter. Typically, air temperature in various portions of the canopy are unlikely to grossly underestimate the minimum temperatures faced by the local immature tephritids, but maximum temperatures encountered by larvae in

fallen fruit can be substantially higher than suggested by air temperatures. Thus, air temperature could generally be a useful tool in estimating many fruit fly thermal environments.

Fruit Temperature Relative to Ambient and the Function of Cooling

Moist spherical objects in sunlight, sheltered from winds that increase heat flux, will retain solar energy and reach temperatures well above ambient (Thorpe 1974). However, certain fruit, e.g., *Ficus* spp. evaporatively cool by transpiring water through stomata on their surface (Patiño et al. 1994). Fruit in the canopy examined in the present study, even the more exposed southwest portion, tended to show little deviation from sur-

TABLE 3. RESULTS OF ANOVA WITH MEANS COMPARED BY WALLER TEST. THOSE MEANS SHARING A LETTER ARE NOT SIGNIFICANTLY DIFFERENT. SW REFERS TO SOUTHWESTERN PORTION OF THE OUTER MARGIN OF THE CANOPY. NE REFERS TO THE NORTHEASTERN PORTION OF THE INNER MARGIN OF THE CANOPY.

Canopy site	Mean	Minimum	Maximum
SW fruit surface	a 23.3 (0.98)	a 17.2 (1.5)	a 33.8 (0.91)
SW fruit core	a 22.8 (0.94)	a 17.0 (1.4)	a 33.2 (1.0)
NE fruit surface	a 22.0 (1.1)	a 17.1 (1.4)	b 29.1 (1.1)
NE fruit core	a 22.2 (1.0)	a 17.1 (1.4)	b 29.5 (1.2)
Ground Site	Mean	Minimum	Maximum
SW fruit surface	a 24.7 (1.1)	a 17.0 (1.5)	a 42.5 (1.3)
SW fruit core	a 24.8 (1.0)	a 17.4 (1.4)	a 41.8 (1.3)
NE fruit surface	a 22.0 (1.2)	a 17.5 (1.4)	b 32.1 (1.7)
NE fruit core	a 22.5 (1.5)	a 17.6 (1.4)	b 31.6 (1.5)
SW soil depth	Mean	Minimum	Maximum
surface	a 25.3 (0.93)	a 18.7 (1.3)	a 41.0 (1.3)
5 mm	a 25.2 (0.88)	a 20.0 (1.2)	b 36.3(1.0)
25 mm	a 25.0 (0.85)	a 20.7 (1.9)	bc 33.8 (0.87)
50 mm	a 25.9 (0.92)	a 21.2 (1.1)	c 31.5 (0.79)
NE soil depth	Mean	Minimum	Maximum
surface	a 22.4 (1.2)	a 18.7 (1.4)	a 29.9 (1.3)
5 mm	a 22.4 (1.1)	a 19.1 (1.3)	a 27.9 (1.5)
25 mm	a 22.3 (1.1)	a 19.8 (1.2)	a 27.5 (1.4)
50 mm	a 22.5 (1.1)	a 20.5 (1.0)	a 25.7 (1.2)

rounding maximum air temperature. This suggests the possibility of adaptive cooling. Patiño et al. (1994) argued that cooling in *Ficus* spp. was required to protect mutualist pollinators, since figs prevented from transpiration reached temperatures fatal to the agaonid wasps harbored inside the fruit. It is difficult to propose such a hypothesis in the present case since most of the insects located inside the fruit are frugivores, or parasitoids of frugivores that would disperse and be unlikely to protect the subsequent fruit of any particular individual fruit tree (see discussion of larval behavior below). Perhaps such high temperatures damage seeds as well, and fruits are sometimes designed and located to cool and protect plant genetic material.

Temperature and Population Dynamics

The distributions of *Anastrepha* spp. and other tephritids are believed to be influenced by abiotic environmental factors (e.g., Messenger & Flitters 1954; Meats 1981; Drew & Hooper 1983; Sivinski et al. 2000), and temperature is also a principal factor in the distribution of *Anastrepha* spp. parasitoids. For example, the relative abundance of 2 introduced braconid parasitoids of *A. suspensa* in Florida is related to temperature and the effects

of temperature on host fruit diversity and availability (Eitam et al. 2004).

On a smaller spatial scale, Aluja & Birke (1993) found fewer *Anastrepha obliqua* (MacQuart) ovipositing in exposed as opposed to shaded host trees. While females might avoid the warmer and drier microenvironment of the exposed trees for their own wellbeing, they could also be seeking more suitable larval habitats in the shade. As to the distribution of subtropical and tropical fruit fly and parasitoid larvae within tree canopies, several studies have yielded somewhat mixed results with the emergence of relatively weak patterns (Sivinski et al. 1997, 1999, 2004). Perhaps the multitudinous combinations of microhabitat-abiotic effects, local natural enemies and competitors make it difficult to generalize about the role of any particular variable. Thomas (1993) found similarly weak correlations between temperature and moisture extremes and the survival of *A. ludens* pupae in the field, and argued that the effects of weather variables were probably masked by predation.

As previously noted, the present work suggests that larval-environment temperatures vary with microhabitat, but are relatively similar to the air temperatures in the same vicinities. However, there are significant relationships between

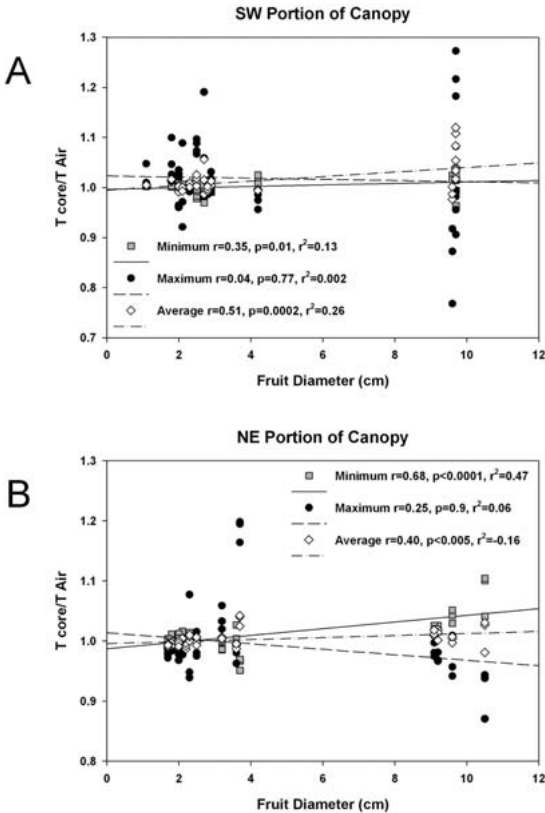


Fig. 1. (A) The ratio of fruit temperature to air temperature in the south west portions of the canopies for each of the first 3 d of monitoring in relation to the diameter of the fruit. The minimum, maximum, and mean ratios of fruit on the southwest margins of the canopies are considered. Because there were no significant differences between subcutaneous and core temperatures, only core temperatures are considered. (B) As above in the north east portions of the canopies.

minimum and mean temperatures relative to air temperature and fruit size.

Temperature and Larval Behavior

Heating through “forced air” or in water baths has long been used to disinfest fruit destined for export (e.g., Hawkins 1932). In general, but with some variance depending on species, temperatures in excess of 45°C will quickly kill fruit fly eggs and larvae (e.g., Armstrong 1992). At 43°C, the exposure time required for 95% of 3rd instar *A. suspensa* larvae to perish depends on both the medium in which the insects were reared and that in which they are heated (Hall 1996). The adult “L(ethal)T(ime)₉₅” of larvae reared in grapefruit and exposed in grapefruit juice, the most natural of the tested regimens, was 24 min. Using temperature probes inserted into olive (*Olea euro-*

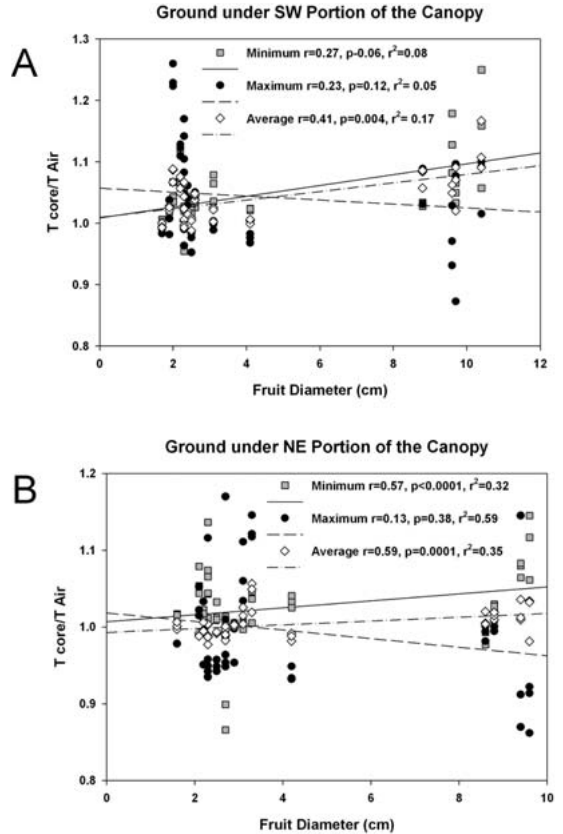


Fig. 2. (A) The ratio of fruit temperature / air temperature for fruit on the ground at the south west margin of the canopies for each of the first 3 d of monitoring in relation to the diameter of the fruit. The minimum, maximum, and mean ratios of fallen fruit on the southwest margins of the canopies are considered. Because there were no significant differences between subcutaneous and core temperatures, only core temperatures are considered. (B) As above, but under the north east-interior portions of the canopies.

paea L.) drupes, Pucci et al. (1981) correlated mortality in immature olive fruit flies *Bactrocera oleae* (Gmelin) to temperature. Eighty-five percent of eggs and first-instar larvae and 95% of mature larvae died when daily maximum temperatures reach just 36°C for a period of a week. Given that fruit in the present study, particularly fallen fruit on the southwest margin of tree canopies, often reached temperatures in excess of 43°C and sometimes temperatures that approached 50°C, it would seem that larvae could frequently find themselves in danger of overheating.

Once on the soil surface, a fruit-exiting larva could still face lethal temperatures. Even 5 mm below the surface temperatures sometimes reached 43°C, and it was only at depths of 25 mm that no temperatures >40°C were recorded. At a

site inhabited by fruit flies in northern Mexico, Thomas (1993) measured temperatures as high as 38°C at depths of 30-40 mm, and noted that exposed soils were 6-7° warmer at than those under shade. In addition to harmful temperatures just beneath the surface, ant predators and pupal parasitoids tend to be more efficient at lesser pupation depths (Hogdson et al. 1998; Baeza et al. 2002; Guillén et al. 2002). Not surprisingly, in one Mexican field survey of *Anastrepha* spp. pupations depths no pupae were found on the surface, 56% were uncovered at depths up to 20 mm and most of the rest at depths of 20-50 mm. Only one occurred deeper than 50 mm (Hogdson et al. 1998).

Perception of soil surface temperature appears to influence the speed with which *Anastrepha* larvae begin to burrow. Under warm condition in Mexico larvae quickly burrow directly beneath, or close to, the fruit they developed within (Aluja et al. 2006). However, under cooler conditions, Thomas (1995) describes *A. ludens* wandering on the surface to find suitable pupations sites.

Temperature and Conditional-effect-lethal Strains

Sterilization through irradiation often harms the performance of released insects and, as a consequence, SIT sometimes fails to reach its theoretical potential (e.g., Proshold 1993; Barry et al. 2003b). Autocidal strains that result in offspring death or sterility and also avoid radiation may be more effective (Alphey 2002). Such strains, based on the conditional regulation of genes that encode lethal products, might be most easily produced through genetic transformation (Robinson & Franz 2000; Handler 2002; Handler & Atkinson 2006). A variety of mutant and normal genes affecting cell viability can be used, including mutant lethal genes affecting vital processes, normal genes involved in programmed cell death (White et al. 1994), and genes for toxin subunit molecules (Kalb et al. 1993). A critical component to the use of these genes is the ability to regulate their expression in terms of developmental stage, tissue, and sex-specificity for the desired phenotype so that breeding populations can be maintained. This can be achieved by conditional regulation where lethal gene expression is determined by manipulation of temperature, chemical treatment, or by interbreeding 2 independent strains. Model systems have already been tested in *Drosophila* spp. with temperature-sensitive lethal alleles and by creating female lethals and steriles by tetracycline-dependent transcriptional repression (Heinrich & Scott 2000; Horn & Wimmer 2003).

Among the temperature regulated lethal systems developed in *Drosophila* is the inclusion of a cold-sensitive allele that kills both heterozygous and homozygous individuals when the temperature falls below 18°C (Fryxell & Miller 1995). Thus the offspring of homozygous individuals reared

and released at higher temperatures would die as temperatures fell. In the *A. suspensa* habitats examined minimum temperatures were frequently well above 18°C (e.g., *Psidium* spp.) and this particular scheme, if transferable to *A. suspensa*, would require an upward temperature adjustment to have an immediate effect. However, the proportion of individuals carrying such a gene could be increased by repeated releases during warm seasons of the year and the population would then crash with the onset of winter. Alternatively, conditional systems under consideration/development would release fruit flies reared at relatively low temperatures whose offspring would perish after encountering warmer temperatures in the field (Handler & Atkinson 2006).

In summary, immature Caribbean fruit flies faced a variety of temperatures, but with the exception of fallen fruit exposed to strong sun light, these temperatures are similar to ambient air temperatures. While fruit size was correlated to the mean and minimum temperatures reached, it did so to a relatively minor extent. If other host fruit of other tephritid species have similar thermal properties, then air temperature should be a useful tool to estimate the thermal environments of immature fruit flies outside of Florida. It should be kept in mind that not all subtropical pest tephritids face temperatures identical to those recorded in the present study. For example, *A. ludens* in northern Mexico sometimes encounter and survive below freezing temperatures (Thomas 1993).

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