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A Plant Root Warmer for Studying Phytophagous Insect Development and Fecundity at Temperatures Below Host Plant Tolerance

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ABSTRACT A simple root-warming device maintains the plants' roots at a higher temperature than that at which the rest of the plant is held. This permits the host plant to retain turgor, not wilt, and therefore remain suitable for and attractive to phytophagous insects. The technique was demonstrated in a development and fecundity test using the cotton aphid, *Aphis gossypii* Glover, reared on cotton seedlings, *Gossypium hirsutum* L., at foliar temperatures of 10.0 and 12.5°C. Root temperatures were held at 20°C. The device was also tested at a foliar temperature of 7.5°C in an additional fecundity test. In a control test, no differences were found in development rate, fecundity, or survivorship for aphids reared on plants with foliage at 15°C and roots at 15 or 20°C.

KEY WORDS Insecta, *Aphis gossypii*, *Gossypium hirsutum*, survival

DEVELOPMENT AND FECUNDITY studies of phytophagous insects often are conducted by maintaining the insects on host plants, particularly if artificial diets are unavailable. Usually, development is linear in response to temperature in the middle range of temperatures selected to conduct such studies. Development studies are easiest to conduct in this middle range, where the insects' higher survival rates allow results to be obtained from relatively large numbers of insects. The upper limit of the linear response is reached as the optimal temperature for development is approached (Wagner et al. 1984). At temperatures below the low end of the linear response to temperature, the development rate decreases more and more gradually as the zero development rate is approached. Development studies in this region are difficult because development takes so long that fewer individual insects survive to adulthood. Similar difficulties beset studies of fecundity; the adults do well in the middle range, but survival is short above the optimal temperature, and often the insects have long survival times at temperatures below the linear response range.

Development and fecundity studies may be confounded further by the response of the host plant to temperature. Fortunately, at the mid-range temperatures of most development studies, temperature is such a strong parameter that it masks the variability from minor nutritional changes that occur in the host plant. This may not be true at the

extremes of the temperature range. Changes in nutritional value or other physical changes in the host plant may change the observed development rate or fecundity of the phytophagous insect being studied.

Recently, we have studied the development and fecundity of the cotton aphid, *Aphis gossypii* Glover, using cotton seedlings, *Gossypium hirsutum* L. We found that the lower thermal minimum for these cotton seedlings was below 15 but above 12.5°C. This minimum falls within the range of 12.8–15.5°C used as lower development thresholds for most degree-day (DD) calculations used in cotton production (Fry 1983, El-Zik & Sevacherian 1985). At temperatures below the minimum, the cotton plant loses turgor and becomes limp (i.e., wilts). Insects caged on wilted cotton plants quit feeding and leave. However, the response to temperature by the cotton aphid is still linear at 15°C on cotton (unpublished data) and citrus (Komazaki 1982). The lower threshold for development often is calculated by determining the x intercept from the regression of development rate against temperature within the linear response range. We elected to determine the lower limit of linear response and to acquire empirical data suitable for a nonlinear response model. There are few options available to study development and fecundity of the cotton aphid at temperatures below the lower thermal minimum of cotton plants. The insects could be reared at lower temperatures on excised leaves maintained with nutritive solutions (Lykouris 1985) or on artificial diets if available. We investigated a third alternative, a method that maintains the plant foliage at temperatures below 15°C but retains plant turgor.

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¹ Retired.

Fig. 1 and 2. (1) Components of the root warmer: container, wire support, wooden dowels, foil heater, variable transformer, two cotton plants with aphid cages, and insulation strips. (2) Root warmer with 12 plants, assembled for use.

It is known that plants (particularly those of tropical origin) lose turgor because of reduced water absorption when roots fall below physiological minima (Kramer 1949, McWilliams et al. 1982). The loss of water absorption has been attributed to reduced permeability of root membranes; i.e., a reduction in the hydraulic conductivity of the roots (McWilliams et al. 1982). Slow closure of stomata on the leaves is a shorter-term problem than the one posed by impaired roots (McWilliams et al. 1982).

Studies with energy conservation in greenhouses, conducted to promote good plant growth with the least expenditure of energy (Maher 1978, White 1982), have focused on a concept known as root zone warming (Cooper 1973, Moustafa & Morgan 1981). This allows good root growth but permits ambient air temperatures (and therefore foliar temperatures) to be lower than the root temperatures; most important, plant turgor is maintained. Two ways in which higher root temperatures have been achieved are by recirculating warm nutritive solution (Moustafa & Morgan 1981) or by warming the bench on which the plants are held (van Weel 1984).

For our studies on development and fecundity of the cotton aphid on cotton seedlings, we used the concept of root zone warming by constructing a root warmer that maintains the roots at 20°C but permits the rest of the plant (foliage) to be held at lower temperatures. The device is simple, has alternate methods of construction depending on available resources and applications, can be used in incubators, and can be modified for different plant sizes.

Materials and Methods

Cotton. Cotton seedlings, *G. hirsutum* cv. Stoneville 825, were grown at 25°C in 5-cm² pots under greenhouse conditions and natural photoperiod. They were used at 3 wk of age; only the first true

leaf was retained. Plants on test were used about 2 wk before replacement by younger plants.

Aphids. A colony of the cotton aphid, *A. gossypii*, was maintained at 25°C in cotton seedlings in an incubator with an 18:6 (L:D) photoperiod. Under these conditions, most adult aphids produced were apterous parthenogenetic viviparous females with few alate adults. Apterous aphids selected for tests were caged on the cotton seedlings with small plastic clip cages constructed from plastic vials with snap-cap lids. The bottoms of the vials were removed and the tube was fastened to a velvet-covered balsawood base with a hair-clip hinge. A circular portion of the top of the snap-cap lids was replaced with a fine-mesh nylon screen. The cages were fastened to plant support stakes with paper binder clips (Fig. 1 and 2).

Construction Details of Root Warmers. Styrofoam shipping containers were used for the bodies of the root warmers. Two sizes of shipping containers were used; they measured 27.5 by 22 cm, 27 cm high (small root warmer) or 33.8 by 26.5 cm, 17.5 cm high (large root warmer). Root warmers of these dimensions held 6 or 12 square pots with 5-cm sides.

Refrigeration defrost heaters (foil type) were used to warm the roots. A 10-watt heater was used for the small root warmer and a 15-watt heater was used for the large root warmer (Gemline aluminum foil heaters, 10 watt at 36.8 by 14 cm and 15 watt at 26.7 by 26.7 cm; Gem Products, Garden Grove, Calif.). Each heater was adjusted by a variable transformer (Superior Electric Co., Bristol, Conn.). The heaters were placed in the bottoms of the root warmers and folded upward slightly along the sides.

A wire support, constructed of hardware cloth with 0.63-cm mesh, was set in each root warmer 7.5 cm below the top edge of the root warmer. The basket was supported by two wooden dowels (0.63 cm diameter) passing through the length of the box including the walls. The potted cotton plant seedlings with insect cages in place were set in the

containers on the wire support. Then, strips (6.3 cm wide) of fiberglass insulation (R 5.6, paper-faced) were placed over and between the plant pots (paper facing up) as a removable cover to keep the temperature constant in the root warmer. The insulation strips between the plants were creased to fit better. A two-probe temperature device (Fluke 52 K/J; John Fluke Mfg. Co., Everett, Wash.) or a calibrated recording potentiometer (Speedomax H Recorder; Leeds & Northrup, North Wales, Pa.) were used with T-type thermocouples to monitor soil and air temperatures. Dial thermometers were used for manual backup. Mean temperature, SEM, and range were determined, and temperature excursions from opening incubator doors or watering soil were monitored. The transformers were adjusted until the soil temperatures were held at 20°C; at incubator temperatures of 12.5 or 10°C, this registered between 70 and 90 volts on the variable transformers. Fig. 1 shows the components of a 12-plant root warmer with the foil heater, the wire support, the two dowels, and the variable transformer. Two plants with aphid cages also are shown. An assembled root warmer is shown in Fig. 2.

Tests. As a control, a comparative test of cotton aphid development, fecundity, and survival was made on plants held at 15°C with their roots maintained at either 15 or 20°C. Assembled root warmers and plants were placed in incubators in an 18:6 (L:D) photoperiod at $15 \pm 0.5^\circ\text{C}$. The transformers were kept in or out of the incubators depending on convenience and were adjusted to maintain root temperatures of 15.0 or $20.0 \pm 0.5^\circ\text{C}$. Three or four adjustments were required within 24 h to hold the roots at the selected temperature. Although the incubators were set for 15°C, root warmers were needed to hold the control roots precisely at 15°C because evaporative cooling reduced their temperature about 1°C without them. Then, cotton aphids were caged on the plants. Plants with caged aphids were removed briefly each day for examination of the cotton aphids. In two tests that followed, foliar temperatures were varied and the plant roots were maintained at 20°C. Development and fecundity were studied at foliar temperatures of 10.0 and $12.5 \pm 0.5^\circ\text{C}$; likewise, fecundity and survival were studied at $7.5 \pm 0.5^\circ\text{C}$.

Voucher specimens have been deposited in the museum collection of the Department of Entomology, University of Arizona, Tucson.

Results and Discussion

The control test was designed to determine whether plants with roots at a higher temperature than the foliage would differ enough from plants with roots and foliage at the same temperature that aphid development on them also would differ. Development times of aphids in the control test did not differ significantly ($F = 0.51$; $df = 1, 456$; $P = 0.48$; ANOVA). For plants with foliage at 15°C, aphids on plants with roots at 15°C had a mean

development time of 14.35 d (SEM = 0.082, $n = 231$) compared with 14.44 d (SEM = 0.95, $n = 227$) for aphids on plants with roots maintained at 20°C. Likewise, the fecundity of the aphids in the control test did not differ. For aphids on plants with roots at 15°C and for those on plants with roots at 20°C (foliage at 15°C for both groups), the fecundity rate was 0.46 progeny per aphid per day (12 adults per group; 211 and 209 total progeny for 15 and 20°C, respectively). Survivorship was also identical.

We had chosen 20°C for root temperatures somewhat arbitrarily but observed immediately that it maintained turgor at a 10°C foliar temperature. Earlier, we had determined that plant turgor was a very important parameter for keeping aphids feeding on plant leaves. Also, in the course of adjusting the root temperatures to 20°C, we observed that cotton seedlings at 10°C foliar temperature could tolerate root temperatures of 15–17°C without noticeable loss of turgor. However, at a foliar temperature of 7.5°C, a rapid loss of turgor occurred within 12 h if the roots were held at 15°C; turgor was maintained at a root temperature of 20°C. Further study showed that the turgor of foliage at 7.5°C was not maintained by root temperatures of 18–19°C. Obviously, the minimal differential between foliar plant temperatures and root temperatures required to support turgor increased as the foliar plant temperature decreased; i.e., temperatures of roots must increase as air temperatures decrease.

The use of the root warmers has permitted us to study development and fecundity in *A. gossypii* at temperatures below 15°C. The results showed that this aphid could develop at 12.5°C and even at 10°C, although 24.6 d were required, and the aphid could still produce nymphs at a rate of 0.24/d (Table 1). Adult survival has been as long as 87 and 60 d at 12.5 and 10°C, respectively. At 7.5°C, fecundity was 0.068 ± 0.011 SEM nymphs/d. All three of these fecundity rates were greater than those predicted by the linear regression of fecundity rates for temperatures of 15–27.5°C (unpublished data). The linear regression predicted zero fecundity at 14.25°C. The empirical determination of these nonlinear development and fecundity values for lower temperatures represent data useful for development modeling. An early study on development rates and fecundity of *A. gossypii* on cotton reported data for temperatures as low as 13°C; however, the data below 17°C were highly variable (Isely 1946). Our major data on development, fecundity, and survival of the cotton aphid will be reported elsewhere.

Four (of six) root warmers have been in use for more than 2 yr and have worked well. Our first two root warmers (functional prototypes) were constructed from styrofoam coolers, but the wall thicknesses were less than those of the shipping containers. The thicker walls of the shipping containers retained heat better and were more efficient. Also, we initially used light bulbs (40 watt) as heaters

Table 1. Development and fecundity of the cotton aphid at temperatures below the physiological minimum for the cotton host plant

Temp °C	Development ^a		Fecundity ^b	
	Days		Nymphs/d	
	n	$\bar{x} \pm \text{SEM}$	n	$\bar{x} \pm \text{SEM}$
12.5	90	21.11 $\pm$ 0.19	26	0.41 $\pm$ 0.03
10.0	97	24.62 $\pm$ 0.25	54	0.20 $\pm$ 0.05

^a Mean development significantly different at $P < 0.01$; t test.

^b Mean fecundity significantly different at $P < 0.05$; t test.

and lined the outside of the root warmers with aluminum foil to prevent light from interfering with the photoperiod used in the studies. This was a difficult procedure; the foil heaters have worked much better. We also tried to adjust the foil heaters with dimmer switches used for room lighting. However, the dimmer switches did not adjust the heat output adequately; the variable transformers were much better. We considered using thermostats to turn the heaters on or off in response to soil temperature. However, we already possessed the variable transformers and we did not pursue this method of temperature control. Thermostats probably would have worked well and would have been no more expensive than variable transformers.

The actual regulation of the soil temperature by the root warmers was within 0.08°C SEM with a range of $\leq 0.5^\circ\text{C}$ under steady-state conditions. Watering the plants changed the temperature for 30–60 min depending on the differential between the water and soil temperature. Also, removal of the plants from the incubator for more than 15 min usually caused enough change in soil temperature to require about 30 min to regain a temperature of 20°C. Opening of the incubator door had little effect on the soil temperature because of the presence of the insulation barrier despite an almost immediate change in the air temperature in the incubator. The plants themselves appeared to do well—turgor was maintained, leaf color was normal, new leaves formed, and stems did not elongate.

We suggest that root zone warming should be useful in most insect development studies that use semitropical plants as hosts.

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