Biology of *Pentalonia nigronervosa* (Hemiptera, Aphididae) on Banana Using Different Rearing Methods

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ABSTRACT The banana aphid, *Pentalonia nigronervosa* Coquerel, is present worldwide where banana (*Musa* spp.) is grown. It is the vector of *Banana bunchy top virus* (*Nanoviridae*, *Babuvirus*), the etiological agent of banana bunchy top disease, currently the most important constraint for banana producers in Hawaii. *P. nigronervosa* is not well studied, and effects of temperature on its growth and reproduction are unknown. We studied the longevity and fecundity of one clone of banana aphid on different types of plant materials to determine an effective method to study the insect in the laboratory. We found that insects performed better unconfined on plantlets, followed by leaf midrib cuttings. We also conducted complete life table studies with *P. nigronervosa* on banana leaf midrib cuttings at 20, 25, and 30°C, with a photoperiod of 12:12. Intrinsic rate of increase (r), net reproductive rate (R_0), doubling time (DT), nymphal mortality, and mean offspring per female all showed maximal rates at 25°C. Population growth was studied on whole banana plantlets as well, and growth rates were also highest at 25°C. We found r to be greater when aphids were reared on intact banana plantlets than on cuttings. Our results show the importance of comparing insect rearing methods for studies such as life tables.

KEY WORDS aphid, *Banana bunchy top virus*, growth rate, life table, vector

Pentalonia nigronervosa COQUEREL (Hemiptera: Aphididae), the banana aphid, was first described in the 19th century on the island of Reunion, then known as Isle de Bourbon, off Madagascar (Coquerel 1859). Coquerel found this aphid on banana and proposed a new genus for this insect based on its distinctive wing venation. *P. nigronervosa* is now widely distributed and is found in tropical and subtropical regions worldwide and in greenhouses in Europe and North America (Blackman and Eastop 1984). Besides banana, host plants of *P. nigronervosa* include other members of the family Musaceae, taro (*Colocasia esculenta* Schott), ginger (*Alpinia purpurata* Schum), cardamom (*Elettaria cardamomum* Maton), *Heliconia* spp., *Caladium* spp., *Alpinia* spp., and *Dieffenbachia* spp. (Blackman and Eastop 1984). Timberlake was the first to record the presence of *P. nigronervosa* in Hawaii in 1924 (Zimmerman 1948).

Few studies have been conducted on the biology and ecology of *P. nigronervosa*, and results reported are variable. Laboratory studies on the biology of *P. nigronervosa* on cardamom showed a life cycle of four instars that is completed in 10–15 d with adult longevity of 8–26 d and average offspring per female of 14 (Rajan 1981). Results obtained by rearing *P. nigronervosa* on banana leaf cuttings in the laboratory determined that the nymphal stage took 8–11 d, with adult longevity of 11–12 d and 22 average offspring per female (Padmalatha and Ranjit Singh 2002). In that work, aphids were not studied as individuals; instead, the number of young produced was divided by the number of adults present to obtain the mean rate of reproduction. Reproduction in both studies was viviparous and parthenogenetic. Indeed, the biology of banana aphid is almost exclusively anholocyclic. Sexual morphs have been reported only in India and Nepal (Blackman and Eastop 1984).

Reported differences in the biology of *P. nigronervosa* may be caused by variations of host plant, agroecological conditions, or species form used for experiments (Rajan 1981). Eastop (1966) described two different forms of *P. nigronervosa: P. nigronervosa* f. *typica* as found on host plants of the family Musaceae and *P. nigronervosa* f. *caladii* van der Goot as found on Araceae. The biology of *P. nigronervosa* in Hawaii may differ from populations in India because of differences in genotype, climate, or host plant cultivars, among other factors. Locally accurate information would be useful in contributing to aphid control efforts in Hawaii. Control of *P. nigronervosa* in Hawaii may help to control banana bunchy top disease (BBTD), currently the most important constraint to local banana growers. *P. nigronervosa* is the vector of *Banana bunchy top virus* (BBTV; *Nanoviridae*, *Babuvirus*), the etiological agent of BBTD (Magee 1927, Hu et al. 1996).

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Temperature regulates the developmental rate of insects and this is an essential component of the intrinsic rate of increase (r) when describing population growth (Birch 1948, Romoser and Stoffolano 1998). Studies indicate that the population growth of aphids tends to be highest at temperatures ~25°C and that r is negatively affected by higher and lower temperatures (McCornack et al. 2004). Ideal temperatures vary, with temperate species generally requiring lower maximal temperatures than species from warmer climates (Morgan et al. 2001). Results also show that reproductive rates and longevity may have different maximal temperatures for the same species. No information is currently available regarding the effects of temperature on *P. nigronervosa*'s biology.

We studied the effect of temperature and rearing methods on *P. nigronervosa* biology under laboratory conditions. Data on population growth, longevity, and fecundity of *P. nigronervosa* at different temperatures will be useful to develop prediction models for aphid populations under field conditions. The temperatures we chose, 20, 25, and 30°C, are representative of the range of banana growing regions in the Hawaiian Islands. We also show that rearing protocols can affect the outcome of aphid biology studies.

Materials and Methods

Insects and Plant Material. We established a *P. nigronervosa* colony in June 2004 with one apterous individual that was collected in Kahuku, Oahu. We maintained the colony on small potted banana plants, *Musa* AAA (Cavendish subgroup) 'Williams', in an air-conditioned greenhouse room, with temperatures of 26 ± 5°C. Plants were kept in box-type cages with glass tops, one glass side with a hole for access, and three sides covered with cloth mesh (Costa et al. 1993). The bottom of the cages had round holes that rested inside the rim of the plant pots. We replaced plants as needed because of size or when aphid numbers became high and honeydew production affected insect handling. Aphid-covered cuttings from an established colony were placed onto new plants to establish new colonies.

The banana plants (variety Williams) we used for all experiments were derived from tissue culture in our laboratory following modified methods of INIBAP, the International Network for the Improvement of Banana and Plantain (Carlier et al. 2002). Planting media was a mixture of soil-less potting mix (Sunshine Mix; Sun Gro Horticulture Distribution, Vancouver, Canada), vermiculite, and perlite at a ratio of 1:3:1, respectively. Slow release fertilizer (Osmocote 14:14:14 N:P:K; The Scott's Company, Marysville, OH) was added to the planting media at the time plants were placed into pots.

Comparison of Rearing Methods. We tested several plant tissues in search of an effective way to rear *P. nigronervosa* under laboratory conditions. We placed individual fourth-instar aphids into plastic petri dishes (60 by 15 mm) on six different types of banana leaf cuttings: (1) mature leaf >1 m in length, (2) young leaf <0.5 m in length, (3) leaf petiole, (4) leaf midrib, (5) symptomatic BBTV leaf, and (6) cigar leaf (newest unfurled leaf). BBTV leaves were not tested for presence of the virus; however, plants from which those were obtained had severe symptoms of the disease. In addition, we tested two reported alternate host plants: taro leaf and red ginger flower. Cuttings were ≈3 cm^2 and were placed on filter paper discs moistened with deionized water as required to prevent excessive desiccation of plant material. In the case of red ginger, individual flower bracts were used in the dishes. We replaced cuttings with fresh material every 3 d. We also placed aphids into modified Munger cell clip cages (University of Arizona Center for Insect Science Education Outreach 2001) attached to live banana plants The top portion of the cages was constructed using 25-mm-diameter aquarium uplift tubing cut into 1.5-cm lengths. Organza fabric was glued to the top of a cut piece of tubing, and a washer made of 3-mm-thick craft foam was glued to the bottom. The bottom of the cage was a 25-mm-diameter nylon washer that was covered with craft foam as above. Both the top and bottom of the cage were glued to a 9-cm-long hair clip, enabling the cages to be attached to a banana leaf. We placed the cages so that aphids had feeding access to the bottom surface of leaves as close as possible to the petiole, where insects are often observed in the field (J.R., unpublished data). In addition, we confined aphids on potted plantlets 15–20 cm in height covered with cloth mesh cages, mirroring field conditions. Because banana aphid is often found at the soil–plant interface, the goal of testing clip cages versus insects not confined on plants was to determine if confined insects, which are easier to work with, would develop as well as unconfined individuals on whole plants. We observed aphids daily until they reached adulthood, after which they were observed every 3 d. All new nymphs present were counted and removed in each evaluation. Adult longevity and fecundity were recorded. We chose to start with fourth-instar individuals to avoid missing early reproductive days. The experiment took place in a laboratory insect-rearing room with a temperature of 25 ± 2°C and a photoperiod of 12 h; light was supplied from both overhead fluorescent lighting and natural light from windows. We repeated the experiment three times, using 10 replicates per treatment in a completely randomized design. SAS PROC general linear model (GLM) was used to analyze the data, with Tukey pairwise comparisons of means for treatments, following significant GLM (SAS Institute 2004).

Life Tables at Three Different Temperatures. We placed individual adult aphids onto banana leaf midrib cuttings in petri dishes as described above. Trays with petri dishes/aphids were placed into controlled environment growth chambers at 20, 25, and 30°C with a 12-h photoperiod. We replaced leaf cuttings every 3–4 d. Plates were observed daily for the presence of offspring. When nymphs were first found, we removed the adults and left one offspring in each dish. We observed aphids individually on a daily basis until they reached adulthood to determine development time at

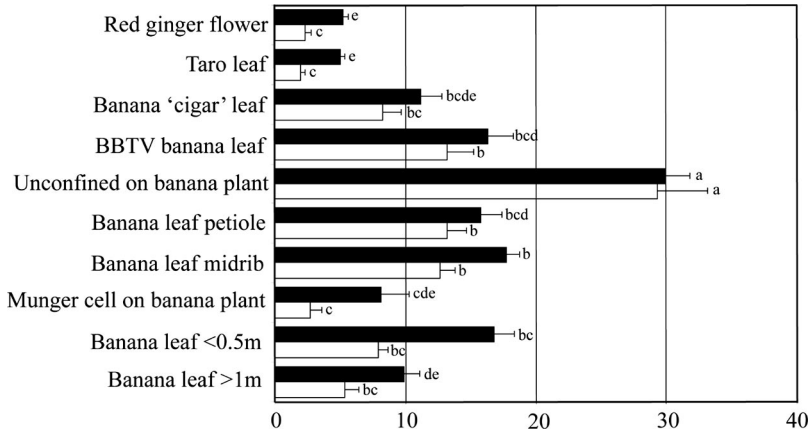

Fig. 1. Longevity in days (black bars) and mean number of offspring (white bars) ± SE of *P. nigronervosa* on different types of leaf cuttings in the laboratory. Bars followed by differing letters are significantly different ($P < 0.05$).

the different temperatures. After adulthood was reached, we recorded the number of offspring present daily. We constructed complete life tables according to Carey (1993) with the data collected. Intrinsic rate of increase (r), the number of offspring produced per unit time, was assessed according to Price (1984) using the equation

$$r = \log_e R_0 / T$$

Net reproductive rate, (R_o), the average number of female offspring born to a cohort of females; mean generation time (T), the mean age of reproduction (in days); and doubling time (DT), the time required in days for the population to double were assessed according to Carey (1993) using the following equations:

$$R_0 = \sum L_x m_x, \text{ where } L_x m_x \text{ is net maternity}$$

$$T = \ln(R_0) / r$$

$$DT = \ln 2 / r$$

We also calculated developmental data such as nymphal mortality (individuals not moving after contact with a brush and determined to be dead after inspection with a dissecting microscope), mean developmental time, mean longevity, and mean number of offspring per female. Analyses were performed using Minitab statistical software (Minitab 2000). We repeated the experiment three times, using 50 replicates per treatment in a completely randomized design. The trapezoidal rule (SimaPlot 2004) was used to estimate areas below the mx curves.

Population Growth on Plantlets. We placed individual fourth-instar aphids on potted banana plantlets at the five to six leaf stage that were kept in controlled environment growth chambers at three different temperatures: 20, 25, and 30°C. We kept plants in 8.9-cm square pots that were covered with cloth mesh cages. We used rubber bands around the cage and pot to prevent aphids from escaping. For each treatment, we placed 16 banana plantlets onto a tray that was placed onto a shelf in the growth chamber. Plants were watered as needed from below by pouring water into the tray. We randomly chose four plants from each treatment to count aphid numbers on a weekly basis for 1 mo, sampling without replacement. At this time, the plantlets were completely torn apart because we have observed that aphids often hide between the leaves and the pseudostem or at or below soil level. We repeated the experiment three times, using 16 replicates per treatment. We used the classic equation for exponential population growth:

$$N_t = e^{rt}$$

where N = number of individuals and t = time of measurement (Vandermeer and Goldberg 2003). This was used to estimate r for population growth on plantlets.

Results

Comparison of Rearing Methods. Because of limited available information on *P. nigronervosa*, we conducted a preliminary experiment to compare different rearing methods for this aphid. Analysis by GLM indicated significant differences in aphid longevity ($F_{9,288} = 24.01$; $P < 0.0001$) and fecundity ($F_{9,288} = 24.97$; $P < 0.0001$) between treatments used (Fig. 1). Longevity was highest when aphids were unconfined on potted banana plantlets, followed by banana leaf midrib, banana leaf <0.5 m in length, BBTV-positive leaf/banana leaf petiole, cigar leaf, Munger cells, leaf >1 m, and red ginger/taro leaf. Results for fecundity

Table 1. Effect of temperature on life table indices of *P. nigronervosa* reared on banana leaf midrib cuttings

Temperature (°C)	Intrinsic rate of increase (r)	Net reproductive rate (R_o)	Generation time (T)	Doubling time (DT)
20°C	0.087	8.998	25.253	7.967
25°C	0.155	17.502	18.467	4.472
30°C	0.053	2.118	14.160	13.078

Table 2. Effect of temperature on the development of *P. nigronervosa* on banana leaf midrib cuttings

Temperature (°C)	*n* original[a]	Nymphal mortality (%)	Mean developmental time (d ± SE)	Mean longevity (d ± SE)	Mean no. offspring/♀
20	150	37.0a[b]	14.5 ± 2.5a	24.7 ± 1.4a	9.3 ± 1.1a
25	150	17.0b	10.1 ± 0.1b	23.1 ± 1.0a	18.3 ± 1.3b
30	143	50.5a	9.4 ± 0.2b	11.2 ± 0.7b	2.4 ± 0.4c

[a] *n* adjusted to reflect mortality.
[b] Data in columns followed by differing letters are significantly different ($P < 0.05$, χ^2 test for mortality, ANOVA for other parameters).

were similar, with highest number of offspring on potted plantlets, followed by BBTV leaf/petiole/midrib, cigar leaf/leaf <0.5 m/leaf >1 m, and Munger cell/ginger/taro.

Aphid Development at Three Different Temperatures. We studied the biology of *P. nigronervosa* at 20, 25, and 30°C. Table 1 shows calculated life table parameters for the different treatments. Table 2 shows the effects of temperature on development parameters measured. Nymphal mortality, measured as a binomial response, showed significant differences between the three temperatures tested ($\chi^2 = 24.42$, df = 2, $P < 0.0001$). One-way analysis of variance (ANOVA) testing of mean development time ($F_{2,148} = 141.49$, $P < 0.0001$), mean longevity ($F_{2,148} = 45.25$, $P < 0.0001$), and mean fecundity ($F_{2,148} = 59.02$, $P < 0.0001$) also showed significant differences between treatments. Temperature affected both insect survival and fecundity (Fig. 2). Aphids survived shorter periods and had fewer offspring at 30°C and survived for >1 mo at 20 and 25°C. Fecundity was similarly affected; however, reproduction at 25°C was concentrated in a period of 4 wk, whereas at 20°C, it occurred over a period of 7 wk. Calculated areas below the fecundity (mx) curve in Fig. 2 using the trapezoidal rule showed that aphids performed better at 25°C

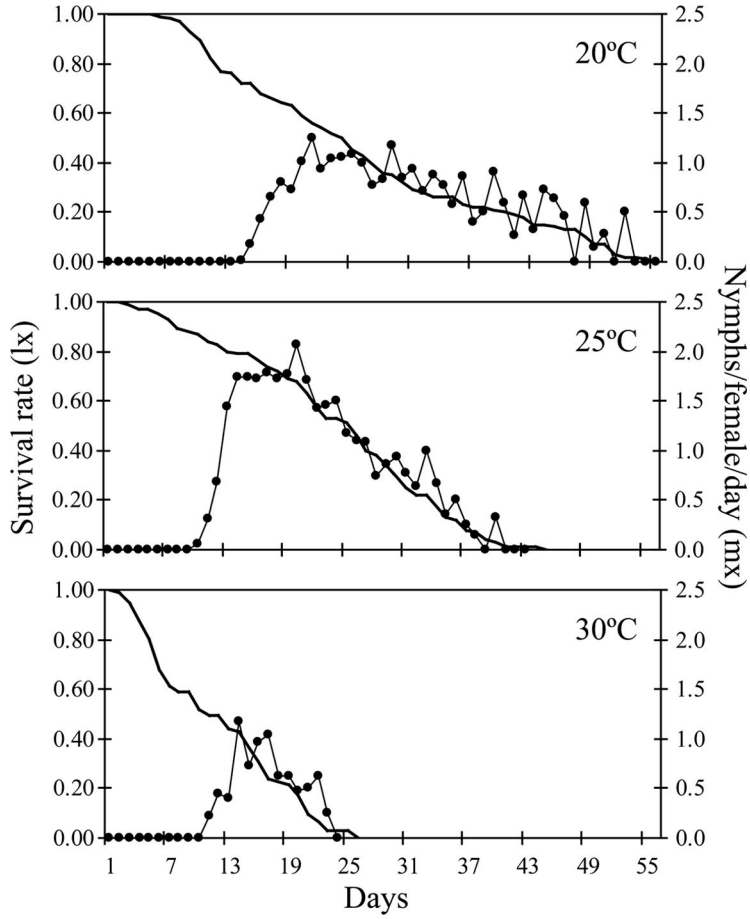

Fig. 2. Survival rate, l_x (line without markers), and fecundity, m_x (line with markers –●–), of *P. nigronervosa* at three different temperatures.

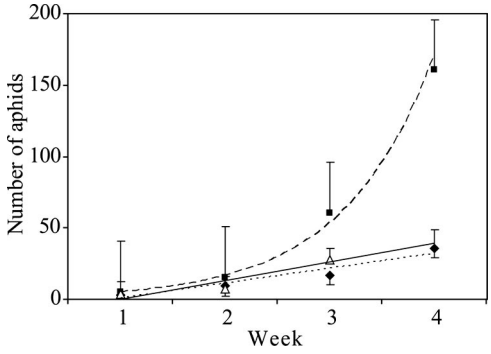

Fig. 3. Population growth of *P. nigronervosa* over 4 wk on banana plantlets at three different temperatures. ♦, 20°C; ■, 25°C; △, 30°C. Error bars are +SE for 25 and 30°C and –SE for 20°C. Lines are trendlines with a linear trend and fit of $r^2 = 0.927$ for 20°C (short dashes), exponential trend and fit of $r^2 = 0.996$ for 25°C (long dashes), and linear trend and fit of $r^2 = 0.944$ for 30°C (solid).

(mx area = 35.75) than 20 and 30°C (mx area = 25.60 and = 8.08, respectively).

Population Growth on Plantlets at Three Different Temperatures. Because our preliminary tests showed that *P. nigronervosa* performed better unconfined on banana rather than on cuttings, we also studied its performance at three temperatures on plantlets. Population growth of *P. nigronervosa* showed different rates and patterns over 4 wk of observations (Fig. 3). At 20°C, aphids reached a mean maximum of 35.9 individuals per plant, and population growth best fitted a linear curve ($y = 10.606x - 10.125$; $r^2 = 0.927$). At 25°C, aphids reached a mean maximum of 160.4 individuals per plant and population growth best fitted an exponential curve ($y = 1.596e^{1.168x}$; $r^2 = 0.996$), with a ≈20% increase in goodness-of-fit. Individuals per plant at 30°C reached a mean maximum of 40.0 and exhibited linear growth ($y = 12.881x - 12.594$; $r^2 = 0.944$).

Discussion

When comparing different methods of rearing *P. nigronervosa* in the laboratory, results showed that aphids reared free on banana plantlets had increased fecundity and longevity compared with the other treatments tested. However, aphids were found all over the plantlet, including below soil level on the pseudostem; they were also able to walk off the plantlet. Consequently, offspring were difficult to find, and plants often had to be destroyed to enumerate all aphids present. Combining practical aspects such as these with the data obtained suggest that midrib leaf cuttings may be the best alternative for rearing banana aphid in the laboratory compared with free on a plantlet for some experimental purposes. Aphids showed a range of performance on the different types of banana leaf cuttings and performed most poorly on the two alternative host plants tested—red ginger and taro.

Life table studies of *P. nigronervosa* revealed that temperature affects the development, longevity, and fecundity of this insect. Most of the life history parameters for *P. nigronervosa*, including r, R_0, DT, nymphal mortality, and mean offspring per female were maximal at 25°C compared with 20 or 30°C. Fecundity was also maximal at 25°C and considerably lower at 30°C compared with 20 or 25°C. Other aphids besides *P. nigronervosa* have been shown to develop optimally at 25°C; Dixon (1998) discussed how r for *Myzus persicae* and *Macrosiphum euphorbiae* increased with temperature until the maximal rate was reached at 25°C. Above this temperature, the decline in r was sharp. Another aphid, *Brachycaudus schwartzi*, also has a maximal r at 25°C (Satar and Yokomi 2002). In general, low temperatures slow down aphid development and decrease fecundity, but above an optimal temperature, these parameters also decrease (Dixon 1973). This is reflected in our findings. *P. nigronervosa* also showed maximal development and population growth rate at 25°C on plantlets. Although exponential population growth was observed on plantlets only at 25°C, we speculate that given adequate time, populations may reach exponential rates at 20 and 30°C as well. We only used one aphid clone for this study, but *P. nigronervosa* response to temperature in field populations probably vary within an undetermined range. It would be important to determine how other clones perform at different temperatures to better establish its impact on population growth under field conditions.

The experiments to observe aphid population growth on plantlets were carried out as controls mirroring field conditions for the life table experiments that used leaf midrib cuttings to rear *P. nigronervosa.* Extensive research such as the life table experiments would require a prohibitively large number of plants to be destructively sampled. We found that *P. nigronervosa* prefers areas of the plant where leaves are in close contact, requiring considerable plant damage to detect all aphids present. Because our results from comparing rearing methods indicated that aphids performed better on banana plantlets than on any type of leaf cuttings, we also calculated r from our population growth on plantlets experiment and compared it with the r estimated in our life table experiments with midrib leaf cuttings. Results indicate that r is underestimated for *P. nigronervosa* on leaf cuttings (Fig. 4). Studies concerning aphid population growth use different rearing methods; some use seedlings or plantlets (Daiber 1970, Morgan et al. 2001, Tsai and Wang 2001, Wang and Tsai 2001, McCornack et al. 2004), whereas others use cuttings or detached leaves (Wyatt and Brown 1977, Rajan 1981, Agarwala and Bhattacharya 1994, Padmalatha and Ranjit Singh 2002, Satar and Yokomi 2002). In addition, some plants possess inducible defenses that are produced after tissue damage occurs (Romoser and Stoffolano 1998); these chemicals may deter herbivores and affect the suitability of cut plant materials to support full growth potential of aphids in the laboratory. Our results show that it is important to conduct whole plant experiments because growth parameters may be underestimated using cuttings.

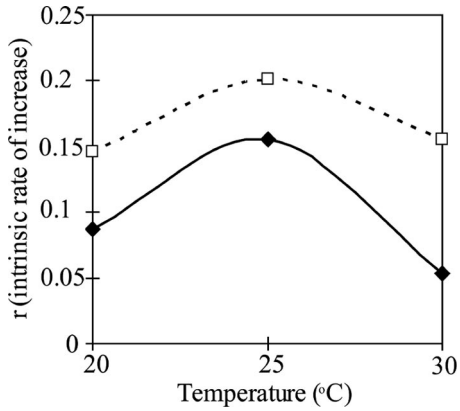

Fig. 4. Comparison between actual *r* obtained for *P. nigronervosa* in life table experiments (♦) and estimated *r* based on data obtained from population growth on plantlets experiment (□). Estimation made using an exponential growth equation for data points.

Overall, rates of population growth for *P. nigronervosa* are relatively slow compared with other aphids (r = 0.155 at 25°C). The r reported for many aphids is greater than what we found for *P. nigronervosa;* for example, maximal r was reported as 0.474 for *Aphis glycines* (McCornack et al. 2004), 0.286 for *B. schwartzi* (Satar and Yokomi 2002), and 0.308 for *Aphis spiraecola* (Tsai and Wang 2001). Results of these experiments may help predict at what temperatures banana aphid populations will build to greater numbers, assisting in the development of management practices aimed to control the banana aphid and BBTD. However, because we used one *P. nigronervosa* clone for this research, it will be important to determine the range of response to temperature in natural populations as well. Determining population thresholds that induce the production of alates may also be useful to reduce banana aphid and BBTD spread. In addition, future studies should include evaluations of biotic and abiotic factors affecting population growth of *P. nigronervosa* in the field.

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