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Research

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Arthropods in Relation to Plant Disease

The aphid *Pentalonia nigronervosa* (Hemiptera: Aphididae) takes advantage from the quality change in banana plant associated with *Banana bunchy top virus* infection

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Viral diseases can change plant metabolism, with potential impacts on the quality of the plant's food supply for insect pests, including virus vectors. The banana aphid, *Pentalonia nigronervosa* Coquerel, is the vector of the *Banana bunchy top virus* (BBTV), the causal agent of Banana bunchy top disease (BBTD), the most devastating viral disease of bananas in the world. The effect of BBTV on the life-history traits and population dynamics of *P. nigronervosa* remains poorly understood. We therefore studied the survival rate, longevity, daily fecundity per aphid, tibia length, population growth, and winged morph production of a *P. nigronervosa* clone grown on healthy or infected, dessert, or plantain banana plants. We found that daily fecundity was higher on infected banana than on healthy banana plants (plantain and dessert), and on plantain than on dessert banana plants (healthy and infected). Survival and longevity were lower on infected dessert bananas than on other types of bananas. In addition, virus infection resulted in a decrease in aphid hind tibia length on both plant genotypes. The survival and fecundity table revealed that the aphid net reproduction rate (R_o) was highest on plantains (especially infected plantain), and the intrinsic growth rate (r) was highest on infected plants. Finally, the increase of aphids and alate production was faster first on infected plantain, then on healthy plantain, and lower on dessert banana (infected and uninfected). Our results reinforce the idea of indirect and plant genotype-dependent manipulation of *P. nigronervosa* by the BBTV.

Key words: BBTV, *Musa* spp., banana aphids, life-history trait, population growth

Introduction

When a plant is infected by a virus, its defense capacities, the expressions of some proteins such as heat shock proteins and the production of phytohormones are modified (Whitham et al. 2006, Shi et al. 2021). The viral infection also changes the nutritional quality of the plant and its attractiveness for insects, including those vectors of viruses (Schoelz and Stewart 2018, Safari Murhububa et al. 2021). The banana aphid, *Pentalonia nigronervosa* Coquerel

(Hemiptera: Aphididae), is the vector of the *Banana bunchy top virus* (BBTV), the causal agent of banana bunchy top disease, which is currently the most serious viral infection of banana plants worldwide (Thomas and Iskra-Caruana 2000, Chandrassekar et al. 2011, Qazi 2016). The disease is characterized by dwarfed and narrow leaves, chlorosis of leaf margins, and dark-green discontinuous streaks on leaves, petioles, and pseudostem. The leaves of infected plants become progressively smaller and stand upright, giving the plant a bunchy appearance, which has potential deleterious effects on banana yield (Gatsinzi 1987). The BBTV is currently reported in Africa, Asia, and Australia, while the vector is present in all banana-growing regions, even where BBTV is not yet reported (CABI 2022a, 2022b). This virus belongs to the family *Nanoviridae* and the genus *Babuvirus*, with a capsid possessing multicomponent circular single-stranded DNA genomes encapsulated in small (18–20 nm) isometric particles (Burns et al. 1995, Timchenko and Bernadi 2007, Stainton et al. 2015, Mukwa et al. 2016, Guyot et al. 2022).

The BBTV is restricted to phloem tissues, and the cells surrounding the phloem contain an abnormal number of chloroplasts, giving rise to the macroscopic symptoms of dark-green streaks. After infection, the BBTV replicates and progressively accumulates in all parts of the plant, except in leaves formed before infection where the virus is present but does not replicate. The vector is unable to acquire the virus from these leaves (Hafner et al. 1995, Iskra-Caruana 2003). The BBTV is transmitted by the aphid in a persistent and nonpropagative way to a healthy banana plant after acquisition from an infected host plant (Iskra-Caruana 2003, Anhalt and Almeida 2008). As persistent virus, acquisition of BBTV requires prolonged feeding for at least a few hours on an infected plant. Virions must pass through the insect gut to survive in the hemolymph to pass to salivary tissues (hence "circulatory transmission"), without replicating in the banana aphid (hence "nonpropagative") (Wang and Ghabrial 2002, Ng and Falk 2006, Hogenhout et al. 2008, Bragard et al. 2013, Gray et al. 2014, Pinheiro et al. 2015).

The BBTV manipulates banana plants to produce a specific set of volatile organic compounds (VOC) attractive to *P. nigronervosa* (Safari Murhububa et al. 2021). This is consistent with the "Vector Manipulation Hypothesis—VMH" (Holmes and Bethel 1972, Poulin 1994, Ingwell et al. 2012), very relevant to aphids, predicting that a virus will promote its spread from plant to plant by influencing the selection behavior of the vector and by enhancing its reproductive performances, thereby promoting the epidemiology of the virus (Gildow 1980, Blua and Perring 1992, Eigenbrode et al. 2018). Most reports indicate that virus-infected plants are higher-quality hosts for the vectors compared with virus-free plants as they promote their fecundity, survival, and longevity (Eigenbrode et al. 2002, 2018, Colvin et al. 2006, Ingwell et al. 2012). This is the case in the study by Bosque-Pérez and Eigenbrode (2011) where 2 aphids, *Rhopalosiphum padi* transmitting *Barley yellow dwarf virus*-BYDV to wheat and *Myzus persicae* transmitting *Potato leafroll virus*-PLRV to potato, had improved life histories (growth rates and reproductive capacities) on infected plants.

The effect of a virus on the phenotypic traits of the vector may also vary according to genotypic or varietal characteristics of the host plant, for example its palatability for the vector, especially for persistent viruses. Chesnais et al. (2019) suggested that this is related to plant tolerance or host-plant genotype. In this study, the author observed that the aphid *My. persicae* prefers to settle, feed, and produce more offspring on the wild camelina genotype (*Camelina microcarpa*) infected but tolerant to *Turnip yellows virus* (TuYV), than on the cultivated genotype (*C. sativa*) and their F1 hybrid, thus leading to an increased number of viruliferous aphids. Because of the long feeding time required for the acquisition of persistent viruses, most of them improve the quality of the host plant for the vectors, and thus the life-history traits of the vectors (Mauck et al. 2012), as well as the growth rate, dispersal, and host-plant selection capacities of the vector. In contrast, in nonpersistent transmission viruses, infection often significantly reduces the quality of plants for aphid vectors, and in part due to significant changes in the carbohydrate/amino acid ratio in the phloem, which causes rapid dispersal of aphids from infected to healthy plants (Mauck et al. 2010, 2014).

In the present study, we investigated the effect of BBTV infection on life-history traits, population dynamics, and production of alates (winged individuals) of *P. nigronervosa* reared on infected and uninfected, dessert (Cavendish dessert banana [AAA genome]), and plantain banana plants (Pacific plantain [AAB genome]). The key question was whether BBTV could alter the quality of banana plants and make them more suitable hosts for *P. nigronervosa*, in terms of improved performance (fecundity, survival, longevity, and population growth). We hypothesize that the vector *P. nigronervosa* grows better and reproduces faster on infected banana plants than on healthy banana plants, and on plantain banana plants than on dessert banana plants.

Materials and Methods

Insects and Plants

Pentalonia nigronervosa reproduces exclusively asexually in tropical and subtropical regions (Foottit et al. 2010, Watanabe et al. 2013). However, this type of clonal reproduction does not exclude the existence of a strong phenotypic variation between clones but also within the same clone (Loxdale 2008, Foottit et al. 2010). As our objective was to compare the effect of the viral infection and the banana genotype on the growth potential of the aphid, we took the option of working on a single clone to control for any genotypic effect of the clone, as in the work of Robson et al. (2007) who used a single aphid clone for the analysis of the effects of rearing temperature. The starting colony of *P. nigronervosa* was therefore obtained from a parthenogenetic female taken from a healthy banana plant in the province of South Kivu (Democratic Republic of Congo), then raised continuously in plastic pots (red thermoformed pot MCI 17:2L) on a potting soil substrate. The aphids were kept in cages (200 × 100 × 100 cm) of small-mesh netting, on banana plants placed in growth chambers at 25 ± 2 °C, a relative humidity of 30 ± 5%, a relative humidity of 30 ± 5%, and a 12:12h (dark:light) photoperiod. All aphids used in this study were apterous.

The plant material consisted of dessert banana plants of the cultivar Cavendish (strict triploid *Musa acuminata*—AAA) and plantains of the cultivar Pacific (hybrids and triploids *Musa paradisiaca*—AAB), which were either symptomatic (with symptoms of BBTV) or asymptomatic (without symptoms of the disease). Four banana plant treatments were applied and used for both the life-history trait and for the aphid population development experiments: healthy dessert banana (HDB), healthy plantain banana (HPB), infected dessert banana (IDB), and infected plantain banana (IPB). Plants were identified and collected in subsistence farmer plantations in South Kivu in the Democratic Republic of the Congo (Dowiya et al. 2009), before being transported to Belgium (Earth and Life Institute, Univeristé catholique de Louvain, Louvain-la-Neuve). Plants were maintained and multiplied in the tropical greenhouse (greenhouse no. 13; G2) using the PIF (*Plants Issus de Fragments de tiges*, Plants from Stem Fragments) technique (Kwa 2003, 2009, Meutchieye 2009, Sadom et al. 2010, Mbunzu et al. 2019). Plants

were irrigated daily, until they reached 40–60 days of age (4–6 leaf stage), for their use in all tests. In this study, all plantlets obtained directly by the PIF technique from infected banana stem showed severe symptoms of BBTV. Indeed, banana plants suckers from an infected strain are known to be systemically infected and show severe symptoms of BBTV (Thomas and Iskra-Caruana 1999, van Regenmortel et al. 2000). This option was chosen because BBTV transmission by mechanical inoculation has never been successful (Thomas et al. 1994, Lepoivre 2003).

Before the rapid multiplication of banana plants, the plants were tested by PCR to determine the genotype (Supplementary Figure S1 in Safari Murhububa et al. 2021) and health status (Supplementary Figure S2 in Safari Murhububa et al. 2021) of each of them. Total DNA was extracted from 40 g of young symptomatic and asymptomatic banana leaves, using the CTAB extraction method applied to cotton leaves (Benbouza et al. 2006), and adapted to banana plants. Confirmation of the infected or uninfected state of banana plants was performed using the BBTV-specific primers DNA-R-2drc Forward and DNA-R-2rdc Reverse, designed to amplify 1068 bp products (Mukwa et al. 2016). Discrimination of banana strict Acuminata genome (AAA) and *Musa x paradisiaca* interspecific banana (AAB) was performed using the primer pair *Musa*-OLF/Musa-OLR designed to target the junction between the banana genome and eBSV (expected band at about 522 bp) (Chabannes et al. 2013).

Effect of BBTV on Aphid Life-History Traits

Non-viruliferous adult females of *P. nigronervosa* were placed on healthy and infected banana plants, dessert, and plantains (4 treatments), with one aphid per plant, to evaluate the effect of BBTV on their life-history traits (the survival rate, daily fecundity per aphid, longevity, maturation time of nymphs, and tibia length).

Each deposited adult female and the produced offspring were carefully removed from the plant 24 h later, using a fine brush, leaving only one nymph per plant (with 10 replicates per treatment, for a total of 40 plants used). Each remaining individual was then observed daily at the same time throughout its life. Thus, biological parameters such as daily fecundity and total fecundity per female aphid, aphid survival rate, average longevity (i.e., life span or age at death) (in days) of aphids, maturity time (age at first reproduction, development time) (in days) were determined. In addition, a survival and fecundity table was constructed, from which the net reproduction rate (R_o: corresponding to the total fecundity per surviving aphid in this work), intrinsic rate increase (r), regeneration time (T), and the doubling time (DT) were determined (Hance et al. 1994). In order to prevent aphids and/or nymphs from moving and hiding in other parts of the plant (e.g., spaces between the pseudostem sheaths), and to facilitate handling, aphids were placed at the base of the pseudostem, and a parafilm paper device, surrounded by sticky paper, was rolled up 20 cm from the neck of each banana plant; this approach was based on the fact that *P. nigronervosa* prefers to settle at the base of the banana plants, close to the ground, when aphid numbers are still low (Robson et al. 2006, Hooks et al. 2011). The whole set-up (banana plant–cage–aphids) was placed in an air-conditioned room, at a temperature of 25 ± 2 °C, a relative humidity of 40 ± 5%, and an artificial photoperiod of 12/12h.

Mortality tables were completed with data collected according to Carey (1993) (as used for *P. nigronervosa* in Robson et al. 2007). The intrinsic rate of increase (r) was estimated by iteration, according to Carey (1993), using the equation:

$$r = ln\,(R_o)\,/T$$

where R_o is the Net reproduction rate, which is the average number of female offspring born from a cohort of females. In practice, the R_o value integrates both fecundity and survival of females. It is therefore close to the definition of fitness: the expectation of the number of viable, reproductive offspring (Haldane 1932, Hance et al. 1994, Ismail et al. 2014); T is the mean generation time or average age of reproduction (in days) (here, the time required for a newborn female is replaced by the net reproduction rate [R_o], i.e., from her laying to the end of her reproduction period); DT is the doubling time, which is the time required in days for the population to double (Carey 1993).

The following formulae were used in these calculations:

$$R_o = \sum l_x m_x$$

where $l_x m_x$ is net maternity (offspring produced per original individual at each age).

$$T = ln(R_o)/r$$
$$DT = ln2/r$$

As the morphological parameters of aphids vary according to the experienced environmental conditions (Daly 1985, Williams and Dixon 2007), the length of the posterior tibia (mm) (representative for body size: Murdie 1969) was measured on adult aphids. Eighty adult aphids from 4 different types of banana plants (treatments), with 20 aphids (20 replicates) per treatment, were considered. The tibia size was measured using a stereomicroscope (LEICA MZ6) mounted on a camera.

Effect of BBTV on Aphid Population Growth

Individual non-viruliferous aphid nymphs (1 nymph per plant) of the fourth instar were placed on live banana plants (never exposed to aphids before, nor used in other experiments) of ≈50 cm height (4–6 leaves) of each genotype (plantain and dessert) and BBTV status (infected and healthy). For each of these 4 treatments, 30 banana plants (giving a total of 120 plants) were placed in an air-conditioned room, at a temperature of 25 ± 2 °C, a relative humidity of 40 ± 5%, and an artificial photoperiod of 12:12h. The plants were watered as needed from below by pouring water into the tray. Ten plants from each treatment were randomly selected for a weekly aphid count for 3 wk, sampling without discount (exhaustive sampling), in accordance with the method used by Robson et al. (2007), to quantify the population of aphids that developed on each of the 4 treatments.

Effect of BBTV on Winged Aphid Production

Twenty non-viruliferous apterous aphids, in the fourth instar, were placed on never-before-used live banana plants ≈50 cm tall (4–6 leaves), of each genotype (plantain and dessert) and BBTV status (infected and healthy). Four treatments—HDB, IDB, HPB, and IPB—were considered in this part of the work. For each treatment, 10 banana plants (giving a total of 40 plants) were placed in an air-conditioned room, at a temperature of 25 ± 2 °C, a relative humidity of 40 ± 5%, and an artificial photoperiod of 12:12h. The plants were watered as needed from below by pouring water into the tray. In contrast to apterous aphids, we found that *P. nigronervosa* alates were not found in inaccessible parts of the banana plant (spaces between the pseudostem sheaths); therefore, the number of alates produced was simply counted weekly for 10 wk, to quantify the development of winged aphids reared on the 4 types of banana plant.

Statistical Analyses

To analyze the differences in daily fecundity in aphids, we fitted a generalized mixed effect model (GLMM) with a Poisson family and a log-link function to the data, using the *glmmTMB* package in R (Magnusson et al. 2017). As fixed effect terms in the model, we used the treatment (4 levels) in interaction with the number of days after the start of analysis (quadratic covariate to account for increasing and decreasing fecundity slopes).

The identity of each individual aphid was used as a random effect term in the model to account for repeated measurements (nonindependence of data). The same type of model was used to analyze cumulated population growth, as well as winged aphid production, using the interaction between the week and the treatment terms as fixed effects. We fitted a Cox survival model to the data to analyze aphid longevity (survival probability) on each treatment. The differences in posterior tibia length and in the total number of aphids among each treatment were analyzed using generalized linear models fitted with a Gaussian and a Poisson family, respectively. Contrasts between levels of a significant variable ($P < 0.05$) were analyzed using the *emmeans* package (Lenth et al. 2018). Statistical analyses were all done on R v4.0 (R Core Team 2022).

Results

Effect of BBTV on Aphid Development

Daily fecundity per female varied with treatment ($\chi^2 = 21.3$, df = 3, $P < 0.001$; Fig. 1) and with time (days) ($\chi^2 = 654.6$, df = 1, $P < 0.001$; Fig. 1). Fecundity was higher for aphids reared on IPB than on the other banana types (HDB, IDB, and HPB) and lower for aphids reared on HDB than on the other banana types (IDB, HPB and IPB) (Fig. 1). The dynamics were broadly the same between treatments, except that a rapid drop of fecundity was found for IDB after the peak fecundity date. There was an interaction effect between day and treatment ($\chi^2 = 9.5$, df = 3, $P < 0.05$; Fig. 1), as for each of the 4 treatments, the daily fecundity per female was different depending on the time of larviposition. The 4 curves had different shapes regarding their amplitude (Fig. 1).

Aphid survival was lower on IDB than on all other treatments (HDB, HPB, and IPB) (Cox: coef = 2.03, $z = 3.61$, $P < 0.001$; Fig. 1), between which survival rates were similar (Cox: coef = 2.03, $z = 0.83$, $P = 0.40$; $z = 1.49$, $P = 0.13$; Fig. 1).

The longevity of aphids reared on dessert banana plant decreased with virus infection (Tukey contrasts, $z = 4.65$, $P < 0.001$) (Fig. 2B), while that of aphids reared on plantain plant did not change with virus infection (Tukey contrasts: $z = 1.29$, $P = 0.56$) (Fig. 2B). Aphid longevity also did not vary with plant genotype (Tukey contrasts: $z = -2.25$, $P = 0.10$; $z = 1.10$, $P = 0.68$) (Fig. 2A).

Furthermore, the time to maturity did not vary with viral infection (Tukey contrasts: $z = -0.281$, $P = 0.99$; $z = 0.44$, $P = 0.97$), or with genotype (Tukey contrasts, $z = -0.21$, $P = 0.99$; $z = -0.93$, $P = 0.78$) (Fig. 2B).

The infection status of banana plant made a difference regarding the length of the hind tibia (Tukey contrasts: $z = 5.83$, $P < 0.001$; $P = 5.36$, $P < 0.001$) (Fig. 2C), but not the plant genotype (Tukey contrasts: $z = -1.42$, $P = 0.48$; $z = -0.95$, $P = 0.77$) (Fig. 2C). For both genotypes, aphids reared on healthy banana plants (non-viruliferous aphids) had longer hind tibiae than aphids reared on infected banana plants (viruliferous aphids) (Fig. 2C).

Furthermore, the intrinsic growth rate (r), in contrast to the regeneration time (T) and slightly to the doubling time (DT), was higher in infected banana plants compared with healthy banana plants, while the net reproduction rate (R_o) was higher in IPB and lower in IDB (Table 1).

Effect of BBTV on Aphid Reproduction

The increase in the number of *P. nigronervosa* on banana plants varied according to the treatment ($\chi^2 = 434.84$, df = 3, $P < 0.001$; Fig. 3) and observation time (1 wk intervals) ($\chi^2 = 4{,}512.17$, df = 1, $P < 0.001$; Fig. 3). There was an interaction effect between time (in weeks) and treatment ($\chi^2 = 37.00$, df = 3, $P < 0.001$; Fig. 3), for all 4 treatments, the aphid population growth was different over the course of the experiments (at 1 wk intervals) (Fig. 3).

The aphid population increased more rapidly on plantain banana plant than on dessert banana plant, regardless of infection status

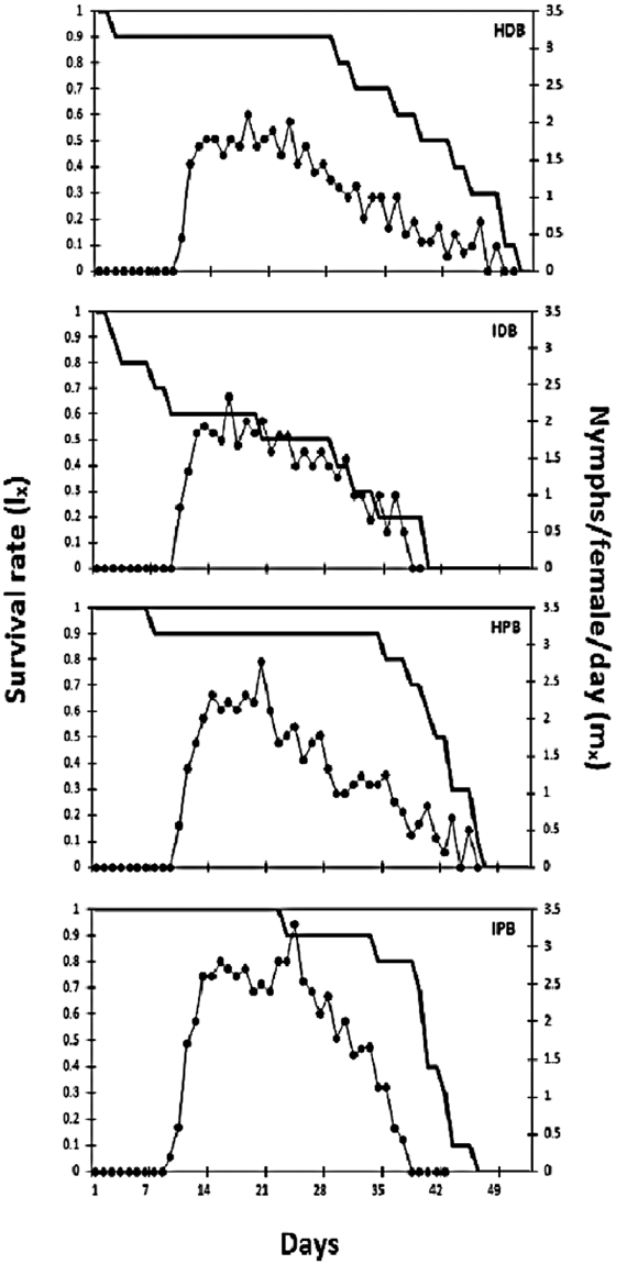

Fig. 1. Daily fecundity and survival rate of aphids on healthy and infected, dessert, and plantain banana plants ($n = 10$). Survival rate (l_x): line without markers, and fecundity (m_x): line with markers.

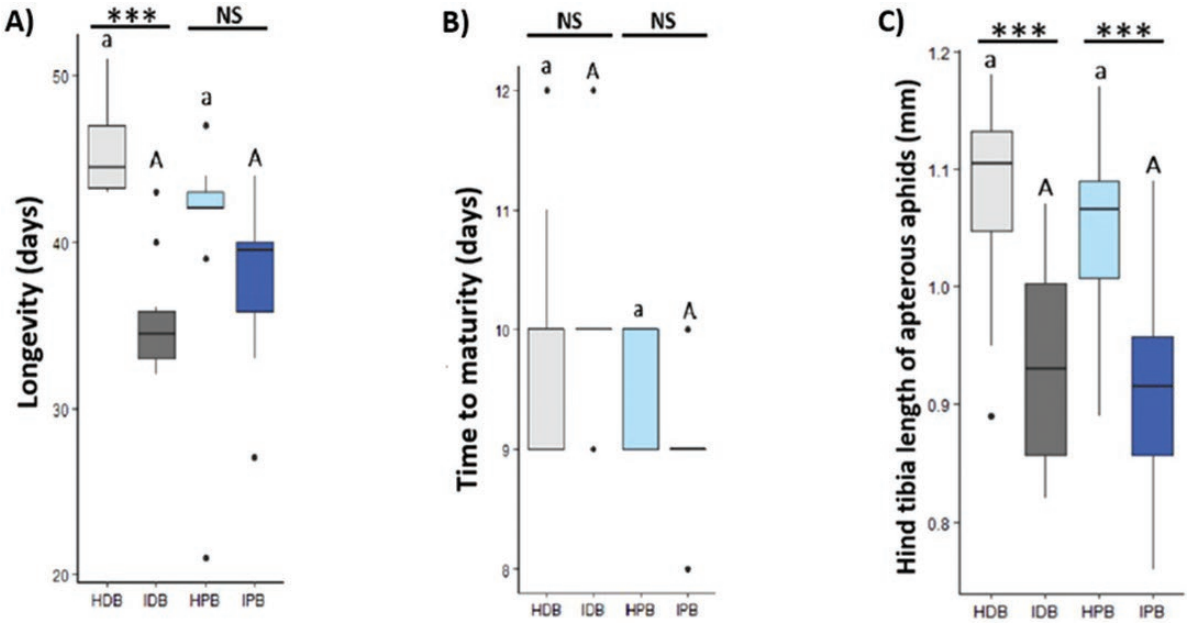

Fig. 2. Effect of BBTV on the development of *Pentalonia nigronervosa* reared on dessert and plantain banana plants. A) Longevity ($n = 10$); B) time to maturity ($n = 10$); and C) length of posterior tibia of adults ($n = 20$). Statistical results (GLM): NS indicate nonsignificant results ($P > 0.05$), stars indicate significant differences ($P < 0.05$) between infection status (for each genotype), and different letters indicate significant differences ($P < 0.05$) between genotypes (for each infection status).

Table 1. Effect of BBTV on survival and fecundity table indices of *Pentalonia nigronervosa* reared on dessert and plantain banana plants

	Net reproductive	Intrinsic rate	Generation	Doubling
Treatment	Rate (R_o)	Increase (r)	Time (T)	Time (DT)
HDB	34.8	0.0949	37.4	7.303
IDB	20.2	0.138	21.7	5.022
HPB	41.85	0.0972	38.4	7.131
IPB	52.7	0.125	31.7	5.545

(Fig. 3). Aphis populations increased more rapidly with virus infection only on plantain banana plants, while population growth curves were similar between virus infection on HDB and IDB. After 3 wk, aphid populations reached an average maximum of 89.64 ± 78, 94.17 ± 13.4, 155.9 ± 17.63, and 261.5 ± 24.57 individuals per plant for HDB, IDB, HPB, and IPB, respectively.

Effect of BBTV on Alate Production

The production of *P. nigronervosa* alates on banana plants varied by banana type ($\chi^2 = 1{,}198.04$, Df = 3, $P < 0.001$; Fig. 4) and over time (weeks) ($\chi^2 = 4113.05$, df = 1, $P < 0.001$; Fig. 4). Alate production occurred earlier on IPB, then on HPB, followed by HDB, and was slowest on IDB. Alates were thus produced more rapidly on plantain than on dessert banana, regardless of infection status. Their number increased more rapidly with virus infection only on plantain, while it decreased with virus infection on dessert banana. There was an interaction effect between time (in weeks) and treatment ($\chi^2 = 139.77$, df = 3, $P < 0.001$; Fig. 4), as for all 4 treatments, winged aphid production was different depending on the time of observation (each time at the interval of one week) and the curves had different shapes (Fig. 4).

Discussion

In our study, we evaluated the effect of BBTV on life-history traits, population dynamics, and alate production rate of *P. nigronervosa* reared on infected and healthy, plantain, and dessert banana plants. Daily fecundity per female varied with both virus infection and genotype, with stronger dynamics for infected plantain banana plant than for other banana types (healthy dessert banana, infected dessert banana, and healthy plantain banana plants), and lower for healthy dessert banana plant than for other banana types (infected dessert banana, healthy plantain banana, and infected plantain banana plants). Dessert banana plants are very susceptible to many diseases due to their narrow genetic base (Abadie et al. 2003, Ngatat et al. 2022). This is consistent with previous studies where aphids reared on infected plants produced higher numbers of nymphs than aphids reared on healthy plants (Colvin et al. 2006, Bosque-Pérez and Eigenbrode 2011, Eigenbrode et al. 2018). In addition, total aphid fecundity, in terms of net reproductive rate (Ro), differed by genotype and virus infection. Aphids reared on infected plantain banana plant had higher total fecundity, whereas on infected dessert banana plant had lower total fecundity. This is because aphid survival and longevity were lower on the infected dessert banana plant than on the other banana types (healthy dessert banana, healthy plantain banana, and infected plantain banana plants), where survival rates were similar.

Furthermore, the higher fecundity per aphid age, as well as the higher total fecundity per female (Ro), on plantain compared with dessert banana (irrespective of infection status) is thought to be due to the difference in internal resource composition between Cavendish (strict triploid—AAA) and Pacific plantain (triploid hybrid—AAB) genotypes, in particular to the ratio of carbohydrates to amino acids in the phloem (Simmonds 1962, Mauck et al. 2014). This is consistent with the recent study of Ngatat et al. (2022), who evaluated 44 *Musa* germplasm plants of different genetic compositions A and B for their performance against banana

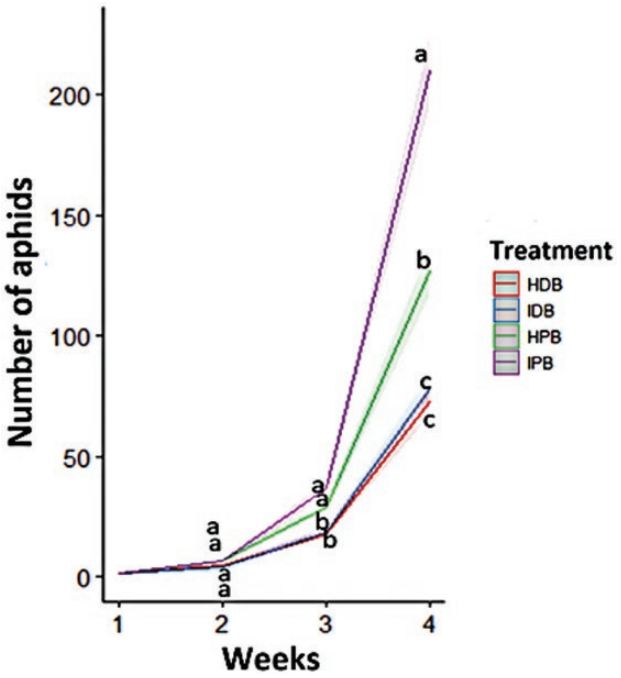

Fig. 3. Pullulation of *Pentalonia nigronervosa* on dessert and plantain banana plants, infected and uninfected ($n = 10$). Shaded areas around each predicted value represent 95% CI. Different letters indicate significant differences among treatments for a given week ($P < 0.05$).

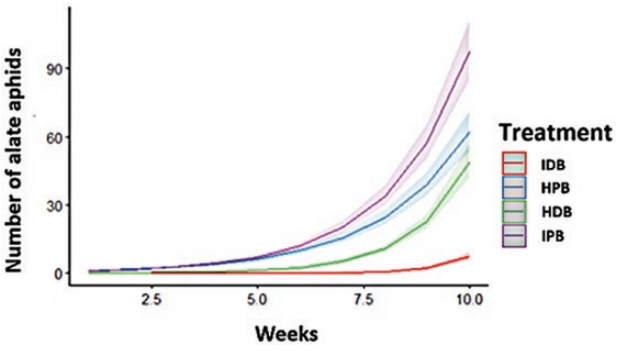

Fig. 4. Winged aphid production on infected and uninfected dessert banana and plantain ($n = 10$). Averages were observed on 10 replicates. HDB (green); HPB (blue); IDB (red); IPB (purple).

aphids. In general, dessert banana plants had the lowest aphid density per plant compared with plantain banana plants. However, the authors did not take into account the effect of virus on aphid performance.

The results of our study are consistent with those of Chakraborty et al. (2021) in which, on Cavendish dessert banana plants, aphids reared on infected banana plants had a shorter life span than aphids reared on uninfected banana plants. This highlights the negative effect of BBTV on the longevity and survival rate of *P. nigronervosa* on dessert banana plants, while the effect of BBTV appears to be neutral on the longevity of aphids reared on plantain banana plants. It is therefore conceivable that *P. nigronervosa* increases its daily fecundity to compensate for the decrease in longevity due to virus infection, particularly in susceptible genotypes such as Cavendish. Thus, there would be a trade-off between fecundity and longevity (and survival rate) in *P. nigronervosa* induced by viral infection, as also observed in females of the Mexican Bean Weevil *Zabrotes subfasciatus* Boheman (Chrysomelidae: Bruchinae) and induced by azadirachtin (Vilca Mallqui et al. 2014), as well as in Mediterranean *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) after heat stress (Zhi-Chuang et al. 2014).

In this work, virus infection had a positive effect on aphid population increase and alate production only on plantain, while it had no effect on population increase on dessert banana, and had a negative effect on alate production on the latter (dessert banana). This is because, as mentioned above for total fecundity per aphid (Ro), the high daily fecundity of dessert banana is counterbalanced by the very low longevity and survival rate of aphids on dessert banana plant. Thus, it appears that virus infection promotes aphid outbreaks on plantain, while this effect is neutral on dessert banana. Also in this work, the increase in aphids on plantain (infected and uninfected) was greater than that for aphids on dessert banana (infected and uninfected). This is again, as for fecundity and alate production, due to the phenotypic demarcation between the 2 genotypes. Indeed, it was observed that aphids seem to be attracted to, and multiply rapidly on genotypes resistant to the pathogens they transmit (Chesnais et *al.* 2019, Safari Murhububa et *al.* 2021). The increase in aphid population on banana plants and the production of viruliferous and non-viruliferous alates are consistent with each other simply because the appearance of the alates usually occurs when the aphid population density has increased significantly or when the quality of the banana host plant has decreased significantly (Braendle et al. 2006, Williams and Dixon 2007).

Pentalonia nigronervosa established and multiplied more rapidly on plantain plants, which are a wilder genotype (Simmonds 1962) and therefore less susceptible to BBTV, compared with Cavendish dessert bananas (severely damaged by BBTV), highly domesticated and known to be highly susceptible to BBTV (Su et al. 1992, Hooks et al. 2008, 2009, Ngatat et al. 2022). We therefore suggest that BBTV infection excessively deteriorates the dessert banana, to the extent that it is of poor quality for *P. nigronervosa* in terms of survival rate and longevity of the aphids that colonize it. As a result, the aphid population develops more slowly in this banana genotype. On the other hand, the more rapid multiplication of *P. nigronervosa* on plantain banana than on dessert banana plant, and the apparent BBTV tolerance of plantain banana plant, contributes to the survival of BBTV. Thus, plantain banana plant (more than dessert banana plant) would constitute a potential reservoir of BBTV and *P. nigronervosa* in agrosystems.

In this work, the virus infection reduced the length of the hind tibiae of aphids reared on both genotypes, while it increased their daily fecundity. Usually, tibia length and body size are positively correlated with fitness. However, our study shows that BBTV infection has a negative impact on aphid growth. Virus infection in banana plants thus leads to a trade-off between fecundity and body size in *P. nigronervosa*. Under specific conditions, such as pathogenic stress, such trade-off may appear. Indeed, during a viral infection, the aphid mobilizes its energy reserves (lipids, fats, and carbohydrates) toward reproduction. A number of studies have reported instances of trade-offs between fecundity and other traits in insects (Zhang et al. 2009, Khuhro et al. 2014). This is the case, for example, in the study of Ren et al. (2015), in which *My. persicae* aphids reared on tobacco plants infected with *potato virus* Y (PVY) were smaller, in terms of body and cornicle length, body and head width, and distance between compound eyes, with increased fecundity, than those reared on uninfected plants. Similarly, a study by Wosula et al. (2013) reported that

My. persicae reproduction increased when fed virus-infected sweet potato plants compared with healthy plants. Despite the negative effect of BBTV on aphid tibia length, the increased reproduction of *P. nigronervosa* increases the probability of virus acquisition and transmission.

The results of this work, as well as those of Safari Murhububa et al. (2021), tend to reinforce the "vector manipulation hypothesis" developed to explain the relationship between insect vectors and the plant viruses they transmit (Mayer et al. 2002, Ingwell et al. 2012, Roosien et al. 2013). This hypothesis, here applied to aphids, predicts that a virus will promote its spread from plant to plant by influencing the selection behavior of the host plant by the vector (Mayer et al. 2002, Ingwell et al. 2012) and by enhancing the reproductive performance of the vector to the point of early alate production (Johnson and Birks 1960, Gildow 1980, Blua and Perring 1992), thereby promoting the epidemiology of the virus. In fact, the pattern of plant-vector-virus interaction seems indeed to be favorable to the transmission mechanism of persistent viruses (such as BBTV) (Iskra-Caruana 2003, Eigenbrode et al. 2018), requiring sustained feeding in the phloem of an infected plant (Sylvester 1980, Montllor and Gildow 1986, Garret et al. 1996, Eigenbrode et al. 2018). Regardless of the mode of transmission, plants infected with plant viruses tend to release VOC that are more attractive to the vectors (Shi et al. 2021). The difference lies in the regulation of plant defense systems. In nonpersistent mode, virus infections significantly induce plant defense responses, which probably induces vectors to disperse and transmit viruses in a short period of time. In (semi-) persistent mode, virus infections reduce (or suppress) plant defense responses and manipulate plant traits to become feeding sites, leading to an increase in the vector population and facilitating virus transmission during vector epidemics (Shi et al. 2021).

The use of a single *P. nigronervosa* clone in this experiment limits generalizability. However, intraclonal phenotypic variability is widespread in aphids (Loxdale 2008) and could be due to several factors, including the presence of *Wolbachia* bacteria (Manzano-Marín 2020). This variability appeared well in our results and in other studies in which authors also used a single clone for their comparison (Robson et al. 2007, Safari Murhububa et al. 2021). In addition, the use of a single clone allowed the results to be contrasted enough to support our hypothesis so using a single clone, as classically done in aphid studies, does not appear to be a disadvantage, although future studies may need to look at inter-clonal and inter-populational variability in aphid response to different banana genotypes and virus infection.

Our study shows that BBTV infection in banana plants improves life-history trait values and population increase of *P. nigronervosa*, through improved reproductive capacity, despite the decrease in size of aphids reared on infected banana plants. However, as the plant host–vector–virus interaction involves a fourth partner, which are bacterial symbionts hosted in the vector body (Gray et al. 2014, Pinheiro et al. 2015), an assessment of the level of involvement of *P. nigronervosa*-associated endosymbionts in BBTV transmission is needed in future research.

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Consent for Publication

All coauthors consent for publication.

Author Contributions

Ignace MURHUBUBA SAFARI (Conceptualization-Equal, Data curation-Equal, Formal analysis-Equal, Investigation-Equal, Methodology-Equal, Resources-Equal, Validation-Equal, Visualization-Equal, Writing – original draft-Lead, Writing – review & editing-Equal), Kévin Tougeron (Formal analysis-Lead, Methodology-Equal, Supervision-Equal, Validation-Equal, Visualization-Equal, Writing – original draft-Lead, Writing – review & editing-Equal), Claude bragard (Conceptualization-Equal, Funding acquisition-Equal, Validation-Equal), Marie-Laure Fauconnier (Investigation-Equal, Methodology-Equal, Validation-Equal), David Bugeme (Supervision-Equal), Bisimwa Espoir Basengere (Supervision-Equal), Jean Walangululu Masamba (Project administration-Equal, Supervision-Equal), Thierry Hance (Conceptualization-Equal, Funding acquisition-Equal, Project administration-Equal, Resources-Equal, Supervision-Equal, Validation-Equal, Writing – review & editing-Equal)

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Supplementary Material

Supplementary material is available at *Journal of Economic Entomology* online.

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