



The banana aphid *Pentalonia nigronervosa*: ecology, virus transmission, and management in banana production systems

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With 6 figures and 1 table

Abstract: The banana aphid, *Pentalonia nigronervosa* (Hemiptera: Aphididae), is the primary vector of banana bunchy top virus (BBTV), one of the most destructive pathogens of banana worldwide. BBTV infection causes severe stunting, leaf deformation, and substantial yield losses, which may reach 100% under severe epidemics. Despite its economic importance, *P. nigronervosa* remains understudied as a virus vector. This review synthesizes current understanding of *P. nigronervosa* biology, distribution, virus transmission, and control. The aphid is associated with tropical and subtropical environments and spreads locally through winged morphs, whereas long-distance dispersal is driven by the movement of infested planting material. BBTV is transmitted in a persistent, circulative, and non-propagative manner, influenced by aphid morphs, viral load, and host plant genotype. Recent genomic studies have clarified its phylogenetic placement in the tribe Macrosiphini and uncovered stable associations with endosymbionts *Buchnera aphidicola* and *Wolbachia*, which affect aphid fitness and defense against pathogens. Current management strategies rely on chemical, biological, and botanical controls, although RNA interference and the development of tolerant or less susceptible host cultivars are promising alternatives. We also highlight major knowledge gaps in vector-virus-host interactions and emphasize the need for integrated, sustainable management strategies to mitigate BBTV's impact on banana production.

Keywords: banana bunchy top virus; sustainable aphid control; BBTV transmission; aphid endosymbionts; pest surveillance; food security; vector competence; invasive pest

1 Introduction

Among vector-borne plant viruses that threaten global food security, banana bunchy top virus (BBTV) is one of the most destructive pathogens affecting *Musa* crops, including bananas and plantains. The virus is transmitted primarily by banana aphids, *Pentalonia nigronervosa* Coquerel (Hemiptera: Aphididae) (Fig. 1a). BBTV infection disrupts the development of newly emerging leaves and produces the characteristic bunchy top symptoms, including narrow

leaves with wavy and chlorotic margins (Fig. 1b) (Umer et al. 2019). Infected plants seldom produce marketable fruit and may die within a few years (Jekayinoluwa et al. 2020), while yield losses may reach 100% during severe outbreaks (Mahuku & Kumar 2023).

Although BBTV is best known as a pathogen of *Musa* spp., it has also been reported from taro, *Colocasia esculenta*, in India (Vikrant et al. 2024), supporting earlier indications that its host range extends beyond banana (Ram & Summanwar 1984; Pinili et al. 2013). Such alternative hosts

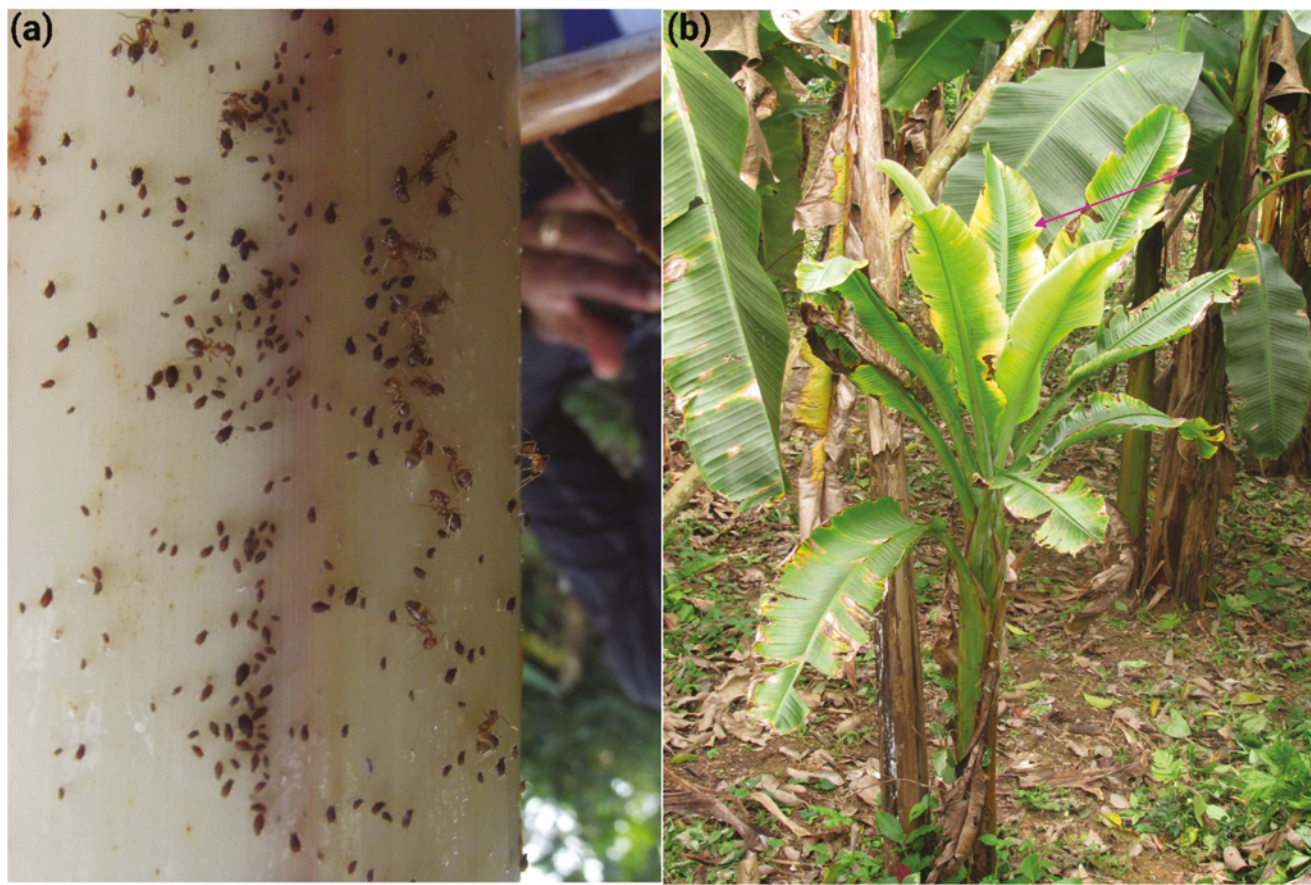


Fig. 1. (a) Banana aphid (*P. nigranervosa*) and (b) Banana plant exhibiting banana bunchy top virus symptoms of BBTB infection.

may be epidemiologically important if they function as reservoirs that facilitate virus persistence. In addition to BBTB, *P. nigranervosa* has been implicated in the transmission of other economically important viruses, including abaca bunchy top virus, banana bract mosaic virus, and cardamom bushy dwarf virus, extending its agricultural importance beyond banana production alone (Selvarajan et al. 2010; Señeris et al. 2022; Vikrant et al. 2025).

The banana aphid-BBTB pathosystem has a long and well-documented history of study. Because *P. nigranervosa* has limited flight capacity, the spread of BBTB over long distances is associated mainly with the transport of infected vegetative planting material, including suckers, rhizomes, and tissue-cultured plants (Adil & Quraishi 2023).

In the absence of curative treatments, virus-free planting material and strict exclusion measures remain the foundation of BBTB management, while aphid control helps reduce secondary spread within and between fields. Continued expansion of BBTB highlights the need for a clearer understanding of banana aphid biology, invasion ecology, and management (Ocimati et al. 2021; Shimwela et al. 2022). Although reviews have focused on BBTB spread in Africa or

on host resistance, comprehensive syntheses centered specifically on the vector remain limited (Elayabalan et al. 2015; Bouwmeester et al. 2023). This review consolidates current knowledge of *P. nigranervosa* biology, monitoring, virus transmission, genomics, symbionts, agricultural impacts, and management, and identifies future major research priorities.

2 Global distribution of *Pentalonia nigranervosa* and BBTB

Pentalonia nigranervosa was first described from Réunion Island by Coquerel in 1859. BBTB was first reported from Fiji in 1889, and the role of *P. nigranervosa* as a vector was established by Magee (1927). Although the aphid was originally described from the southwestern Indian Ocean region, current evidence suggests that it most likely originated in Southeast Asia (Stainton et al. 2015; CABI 2022). However, both *P. nigranervosa* and BBTB are now widely distributed across tropical and subtropical regions, particularly in areas with banana cultivation (Fig. 2a, b). The expansion of both the vector and the virus is consistent with repeated introduc-

tions followed by local establishment in banana-producing areas. Further, their current range reflects a combination of historical spread and continued human-mediated dispersal through infected vegetative planting material (Waterhouse 1987; Tripathi et al. 2021).

In Africa, BBTv was first documented in Egypt in 1901 and subsequently reported from the Democratic Republic of Congo, Gabon, Benin, Nigeria, South Africa, and Togo (Wardlaw 1972; Foure & Manser 1982; Blomme et al. 2013; Lokossou et al. 2012; Adegbola et al. 2013; Jooste et al. 2016; Kolombia et al. 2021). Early records of the banana aphid (*P. nigronervosa*) in the region include its original description from banana on Réunion Island in 1859 (Coquerel 1859) and subsequent documentation from Egypt by the early twentieth century (Hall 1926). Phylogenetic evidence further supports a history of long-distance dispersal of BBTv. For example, isolates from the Democratic Republic of Congo cluster within the South Pacific clade, indicating movement of infected plant material rather than dispersal by the aphid alone (Mukwa et al. 2016).

3 Biology and life history of *P. nigronervosa*

3.1 Description and life cycle

Pentalonia nigronervosa is a reddish-brown to black aphid with conspicuous cornicles (siphunculi) that release alarm pheromones, primarily (E)- β -farnesene, in response to predation or disturbance (Footitt et al. 2010; Chaudhary 2013). Wingless (apterous) and winged (alate) morphs occur, with alate forms commonly arising after several (7 to 10) generations of apterous reproduction, although environmental stress can also induce wing development (Mau et al. 1994; Nelson et al. 2004; Young & Wright 2005). As in many aphids, reproduction in *P. nigronervosa* is viviparous and development includes four nymphal instars (Fig. 3), with developmental rate affected by host plant and heat unit accumulation (Adjalla et al. 2026).

On banana, nymphal development may be completed in 9.4 days at 30 °C but may require up to 14.5 days at 20 °C (Robson et al. 2007). On red banana, development ranges from 9 to 12 days, whereas on taro (*Colocasia esculenta*) it ranges from 12.5 to 14.5 days (Amsavalli et al. 2022). Comparable developmental periods have been recorded on the banana cv. Putri and other monocot hosts, including torch ginger (*Etlingera elatior*), Javanese turmeric (*Curcuma xanthorrhiza*), and cardamom (*Amomum compactum*) (Basak et al. 2015; Efendi et al. 2022). Adult longevity is usually 10 to 14 days (Rajan 1981; Viswanathan & Regupathy 1992), although survival may extend to one month under favourable conditions (Völkl et al. 1990; Yasmin et al. 1999).

Temperature is a major determinant of development, survival, fecundity, and vector performance in *P. nigroner-*

vosa. Robson et al. (2014) showed that higher temperatures (30 °C) accelerate development but also increase nymphal mortality and reduce fecundity, whereas 25 °C appears to be more favourable for survival and reproduction. Temperature also affects BBTv transmission efficiency (Anhalt & Almeida 2008; Chakraborty et al. 2021). Flight activity is similarly temperature dependent, with no flight reported below 14 °C (Jones et al. 2010).

3.2 Population dynamics and dispersal

Population dynamics of *P. nigronervosa* are influenced by both biotic and abiotic factors, although the direction and magnitude of these effects vary among regions. Rainfall patterns influence banana aphid population dynamics, with high rainfall generally reducing populations (Young & Wright 2005). In Burundi, aphid populations peak during dry seasons, when temperatures generally range from 24 to 32 °C (Niyongere et al. 2013). In contrast, studies from India and Egypt have recorded peak abundance during cooler and wetter months rather than during summer (Menon & Christudas 1967; Abdel-Moniem 2003; Basak et al. 2015). These differences most likely reflect local climatic conditions, cropping systems, and broader agroecological contexts.

Altitude also affects banana aphid abundance and risk of BBTv transmission. Higher infestation levels are generally reported in lowland production zones, where temperatures are more suitable for aphid development, as documented in the Democratic Republic of Congo and Burundi (Walangululu et al. 2010; Niyongere et al. 2011). Agronomic practices can further modify aphid populations. De-leafing and de-suckering have both been shown to alter aphid density (Niyongere et al. 2013; Young & Wright 2005). Plantation size may also influence local build-up, with one study suggesting that smaller or more fragmented fields favoured higher local populations (Hooks et al. 2011). Seasonal increases in aphid abundance near plantation borders have also been documented in Hawaii and Egypt (Abdel-Moniem 2003; Menon & Christudas 1967; Young & Wright 2005). The number of aphid generations completed per year varies markedly by region, ranging from about four in Guangdong, China, to as many as 30 generations in Hawaii (Yang 1989).

The banana aphid is a relatively weak flier, and within-field spread of BBTv generally occurs over short distances within about 20 m from infected plants (Allen 1978). Local dispersal is mediated mainly by alate aphids, which facilitate movement within and between banana fields (Stainton et al. 2015). By contrast, long-distance dissemination of BBTv occurs primarily through the transport of infected vegetative planting material, particularly suckers, often via informal or poorly regulated trade networks (Nelson et al. 2004; Young & Wright 2005). Transboundary agricultural corridors such as the Nigeria-Benin border, the Bugarama/Rusizi Valley, and the Togo-Benin corridor may therefore represent zones of elevated phytosanitary risk.

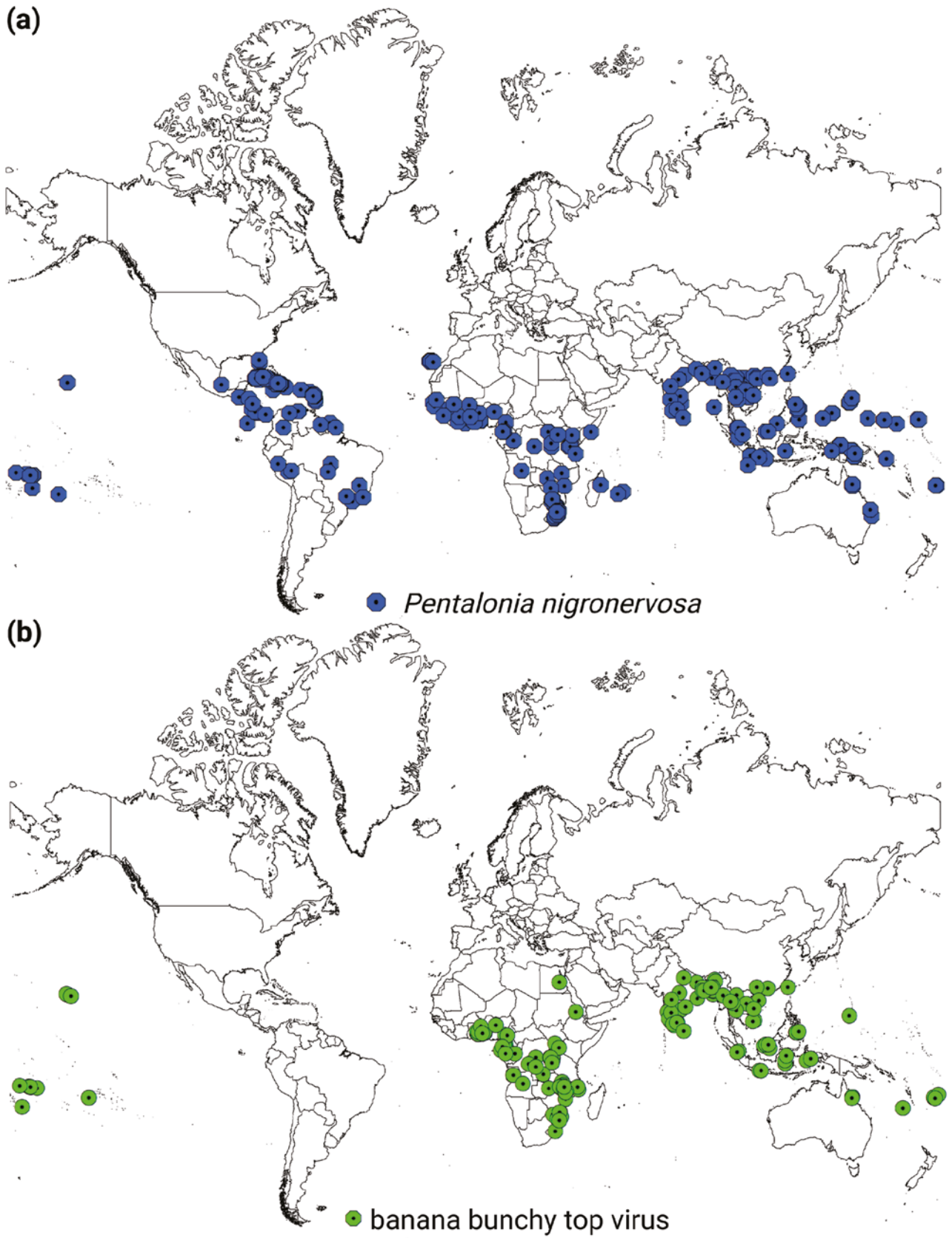


Fig. 2. Global distribution of *Pentalonia nigronervosa* and banana bunchy top virus as of 2025. (a) *Pentalonia nigronervosa*, and (b) banana bunchy top virus.

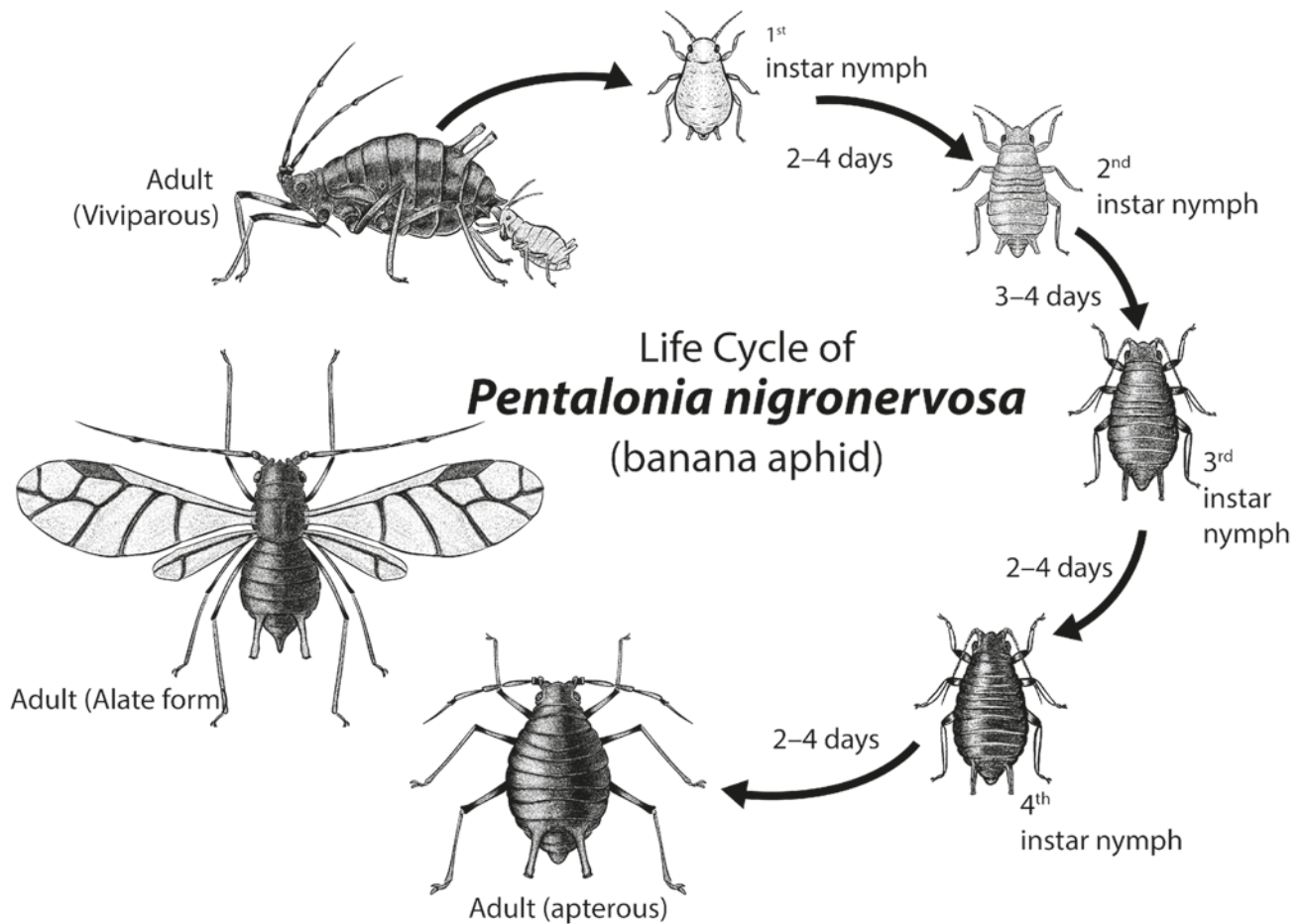


Fig. 3. Life cycle of the banana aphid (*Pentalonia nigronervosa*). Adapted from Rajan (1981).

4 Ecology of *Pentalonia nigronervosa* and interactions with host plants

The ecology of *P. nigronervosa* is shaped not only by climatic conditions but also by host plant identity and plant-mediated effects on aphid performance. Although banana is its principal host, the species has been reported from several monocotyledonous plants, including *Alpinia purpurata*, *Colocasia esculenta*, *Xanthosoma sagittifolium*, *Canna indica*, and *Zingiber officinale* (Footitt et al. 2010; Gunawan et al. 2017). However, studies combining morphological and molecular evidence indicate that *P. nigronervosa* is primarily associated with *Musaceae*, particularly *Musa* spp., and that some records from alternative hosts may reflect misidentification with the closely related *Pentalonia caladii* (Footitt et al. 2010; Footitt & Maw 2019).

On banana, heavy infestations can reduce plant vigour directly, while honeydew excretion by dense colonies promotes the development of sooty mould, thereby lowering fruit quality and marketability (CABI 2015). Host suitability, plant architecture, and ant-mediated protection together play important roles in determining colonisation success in banana systems. Aphid persistence on host plants is also influenced by biotic interactions, especially mutualisms with honeydew-attending ants. Ant attendance can protect colonies from natural enemies and may therefore enhance aphid survival and local persistence (Biale et al. 2017; University of Hawaii CTAHR 2006). These interacting factors influence not only aphid establishment and persistence but also the broader epidemiology of BBTv by affecting the abundance and distribution of vector populations within and among fields (Robson et al. 2006; Adjalla et al. 2025a).

5 Role of *Pentalonia nigronervosa* in BBTV transmission

Banana aphids acquire BBTV while feeding from the phloem of infected leaves and transmit the virus to healthy plants in a persistent, circulative, non-propagative manner (Fig. 4) (Magee 1927; Thomas & Iskra-Caruana 2000; Anhalt & Almeida 2008). Reported transmission parameters vary among studies. Minimum acquisition access periods range from 4 to 17 h, whereas inoculation access periods range from 15 min to 2 h (Magee 1927; Hu et al. 1996; Thomas & Iskra-Caruana 2000). After acquisition, virions move through the aphid from the anterior midgut to the principal salivary glands. Virus retention may last for 13–20 days (Hu et al. 1996), and a latent period of several hours to approximately 20 h is generally required before aphids become infective (Magee 1940; Anhalt & Almeida 2008).

There is no evidence of transovarial transmission or viral replication within the vector, confirming the non-propagative nature of BBTV in *P. nigronervosa* (Hafner et al. 1995; Watanabe & Bressan 2013). All life stages can transmit the virus, although efficiency may differ between nymphs and adults (Magee 1940; Wu & Su 1990). At the level of individual aphids, transmission efficiency has been reported to range

from 46% to 67% (Magee 1927; Wu & Su 1990; Hu et al. 1996). Temperature also exerts a strong influence on transmission dynamics. Transmission is generally highest at 25–30°C, lower at 20°C, and greatly reduced or absent at 10–16°C (Magee 1940; Wu & Su 1990; Anhalt & Almeida 2008).

Transmission efficiency is also affected by host-related factors. In the field, both alate and apterous morphs tend to preferentially colonise BBTV-infected plants, which emit elevated levels of volatile organic compounds that enhance vector attraction (Murhububa et al. 2021). This may be further mediated by aphid-associated endosymbionts, which can modify plant volatile profiles and influence vector–virus interactions (Shi et al. 2021). Host plant genotype also affects aphid behaviour and may therefore influence disease spread. For example, *P. nigronervosa* is generally more abundant on AAB plantains than on some other banana genomic groups (Ngatat et al. 2017, 2022). Conversely, certain accessions, such as *Musa balbisiana*, remain symptomless and BBTV-free even under high inoculum pressure, possibly because of reduced aphid preference, restricted virus replication, or barriers to virus acquisition and inoculation. These responses contrast with those observed in highly susceptible genotypes such as *M. acuminata* subsp. *errans* and cv. ‘Lakatan’ (Damasco et al. 2006; Dela Cueva et al. 2023).

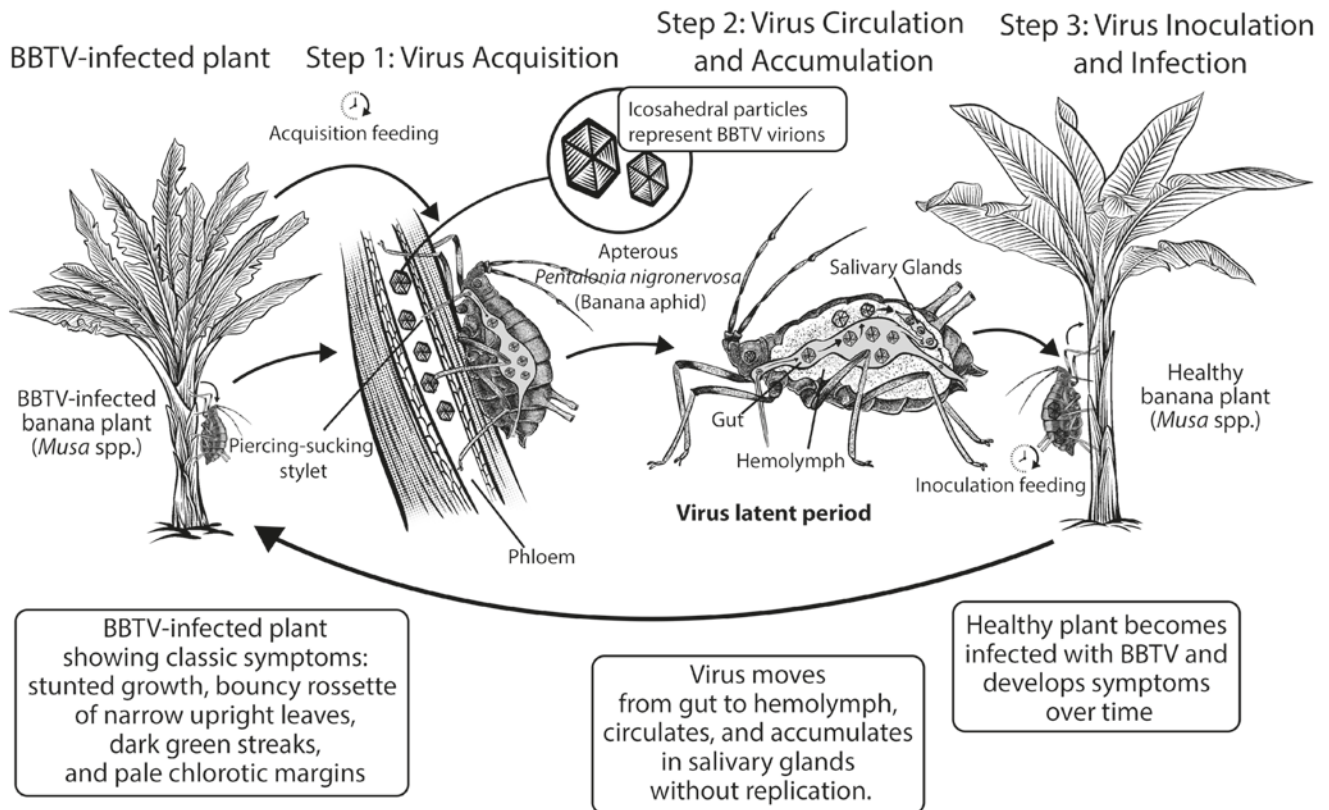


Fig. 4. Circulative, non-propagative transmission of Banana bunchy top virus (BBTV) by the banana aphid.

Abiotic stress may further modify transmission by altering host plant physiology and aphid feeding behaviour. Changes in phloem composition, nutritional quality, and secondary metabolite production can affect both virus acquisition and inoculation efficiency. In aphid-virus systems more broadly, water stress can alter feeding behaviour and enhance or suppress transmission, depending on the nature of the host response (Nachappa et al. 2016; van Munster 2020).

6 Genomics of *Pentalonia nigronervosa* and endosymbionts

The first genome sequence of *P. nigronervosa*, and of the genus *Pentalonia*, was published in 2020, providing an important foundation for studies of aphid evolution, genomics, and vector biology (Mathers et al. 2020). The assembly was generated from a clonal lineage collected from a banana plantation in Nairobi, Kenya. Comparative analyses placed *P. nigronervosa* in a basal position within the tribe Macrosiphini, highlighting its distinct evolutionary position relative to other sequenced aphids (Julca et al. 2019; Mathers et al. 2020). Genome-based analyses also revealed the presence of two bacterial endosymbionts in *P. nigronervosa*. The obligate mutualist *Buchnera aphidicola* provides essential amino acids that are lacking in the aphid's phloem-based diet, whereas *Wolbachia* occurs as a facultative symbiont that is unusually prevalent in this lineage (De Clerck et al. 2014; Mathers et al. 2020). Because *Wolbachia* is uncommon in most aphid species, its consistent occurrence in geographically distinct populations of *P. nigronervosa* suggests a stable and potentially adaptive association (Higashi et al. 2024).

Earlier hypotheses proposed that *Wolbachia* might complement the nutritional functions of *Buchnera*. However, genomic and transcriptomic evidence has not supported a metabolic co-obligate role for *Wolbachia* in *P. nigronervosa* (De Clerck et al. 2015; Manzano-Marín 2020). More recent studies instead suggest that *Wolbachia* may confer context-dependent benefits, including increased survival, enhanced fecundity, and protection against the specialist fungal pathogen *Pandora neoaphidis* (Higashi et al. 2024). These effects appear to be specific rather than general, as comparable protection has not been demonstrated against generalist pathogens or parasitoids (Higashi et al. 2024). The persistence of *Wolbachia* in *P. nigronervosa* may reflect a combination of selective advantages, such as improved performance under stress, reproductive manipulation, or the clonal expansion of infected lineages. It is also possible that the symbiont contributes to tolerance of oxidative or phenolic stress associated with host plant defences. Although these hypotheses remain to be tested more directly, they highlight the potential importance of microbial associates in shaping the ecology and evolutionary success of this aphid.

7 Monitoring strategies for *Pentalonia nigronervosa* and BBTv

Timely detection of *P. nigronervosa* is essential for effective BBTv management and for limiting associated crop losses (Dahal et al. 2000; Daniells et al. 2001; Thangavelu et al. 2000). In practice, visual scouting remains the most widely used approach, but disease management depends primarily on use of clean planting material, rouging of infected plants, and quarantine measures, whereas aphid control mainly reduces secondary spread. Symptoms associated with BBTv, including chlorosis, bunchy top growth, and dark green streaking on petioles, are useful indicators of infection but do not necessarily reflect current aphid abundance, because infection may have occurred earlier through viruliferous aphids or infected planting material.

Visual scouting nevertheless remains important for identifying active infestations. Its main limitations are that it is labour-intensive and may fail to detect low-density or incipient populations because *P. nigronervosa* is small and typically colonises concealed microhabitats. Aphids commonly aggregate in leaf axils, tightly packed leaf sheaths, and pseudostem bases, where they are partly shielded from observation. To complement direct inspection, suction samplers and yellow sticky traps have been used to monitor aerial dispersal and seasonal population trends (Gavarrá & Eastop 1976; Viswanathan & Regupathy 1991). However, these methods may underestimate banana aphid abundance because the species is relatively sedentary and spends much of its life in protected parts of the host plant (Smith et al. 1998).

Molecular diagnostics have substantially improved detection sensitivity for BBTv. Recent surveillance studies further highlight the continued occurrence and genetic diversity of banana-associated viruses in African production systems (Masangwa et al. 2026). Quantitative PCR using TaqMan® probes enables early detection of the virus in both host plants and aphid vectors, including infections that remain asymptomatic at the time of sampling (Jebakumar et al. 2018). SYBR Green-based qPCR can also be used to estimate viral load, and higher titres have been associated with increased transmission efficiency (Jebakumar et al. 2018). In addition, immunofluorescence microscopy has confirmed the circulative route of BBTv within the aphid by localising virions in the anterior midgut and principal salivary glands (Watanabe et al. 2013).

ELISA-based approaches, including triple antibody sandwich ELISA, complement PCR-based assays and may provide more accessible diagnostic options for BBTv surveillance, particularly in resource-limited settings (Kolombia et al. 2021). These methods indicate that effective monitoring of the BBTv pathosystem requires a combination of field-based inspection and sensitive laboratory diagnostics, with the most appropriate approach depending on surveillance objectives, resource availability, and the stage of epidemic development.

8 Potential invasion risks and impacts of *P. nigranervosa* and BBTV

Banana bunchy top virus is among the most destructive pathogens affecting banana production worldwide. In India, annual economic losses have been estimated to exceed USD 50 million across major banana-producing states (Selvarajan et al. 2011; Rao & Reddy 2020). Historical records further illustrate the severity of its impact. In Australia, the introduction of BBTV led to the abandonment of more than 5,000 ha of banana plantations (Magee 1927). In Pakistan, epidemics during 1991–1992 reduced cultivated area by 55% and yield by 90% within a single year, while in Fiji the disease caused an 80% collapse in banana production between 1892 and 1895 (Thomas 2008). Together, these examples demonstrate the capacity of BBTV to rapidly destabilise banana production systems where efficient vector populations reside.

Global occurrence records of *P. nigranervosa* and BBTV were analysed to assess their global invasion risk. Niche-space analysis indicated a moderate overlap between *P. nigranervosa* and BBTV (Jaccard index = 0.418; 41.8%), suggesting partial divergence in their ecological niches and currently occupied geographic ranges (Fig. S1). Although the virus depends on its vector for transmission, this incomplete overlap indicates that additional environmental constraints may influence the spatial congruence of the vector and the disease it transmits. Model performance was acceptable for both *P. nigranervosa* (AUC = 0.9, TSS = 0.6, CBI = 0.9; Table S1) and BBTV (AUC = 0.8, TSS = 0.5, CBI = 0.8; Table S2). Jackknife analyses (Fig. S2 and S3) identified mean diurnal temperature range (bio2) as the most influential predictor for both the vector and the virus. For *P. nigranervosa*, the main contributing variables were mean diurnal range (41.7%), precipitation of the driest month (20.1%), precipitation of the wettest month (18.6%), and isothermality (12.5%) (Table S3). For BBTV, habitat suitability was driven chiefly by mean diurnal range (80.5%), followed by precipitation of the wettest month (8.4%), isothermality (4.9%), and annual mean temperature (3.5%) (Table S3). These results highlight the importance of thermal variability in shaping both aphid distribution and virus suitability.

Response curves (Fig. S4 and S5) further indicated that habitat suitability for both *P. nigranervosa* and BBTV is greatest under warm, humid, and moderately stable climatic conditions. Suitability increased with annual mean temperature to an optimum of approximately 25–28 °C for the aphid (Fig. S4a), with a comparable though slightly broader optimum for the virus, before declining at higher temperatures. Both organisms showed highest suitability under low to moderate diurnal temperature range, with a marked decline at higher temperature variability (Fig. S4b and S5b). Isothermality likewise showed a unimodal relationship, with peak suitability at intermediate values (Fig. S4c and S5c).

Precipitation also played a major role in determining suitability. For both the vector and the virus, suitability increased

with precipitation during the wettest month, indicating a strong dependence on humid conditions (Fig. S4d and S5d). By contrast, precipitation during the driest month showed an optimum at low to moderate values, with suitability declining under both extremely dry and excessively wet conditions, particularly for BBTV (Fig. S4e and S5e). Precipitation seasonality also followed a unimodal pattern, with reduced suitability under highly seasonal regimes (Fig. S4f and S5f). These climatic patterns are consistent with experimental evidence showing that temperatures between 25 and 30 °C favour banana aphid development and enhance BBTV transmission, whereas cooler conditions substantially reduce infectivity (Magee 1940; Wu & Su 1990; Anhalt & Almeida 2008). Adequate moisture may further support host vigour and sustained aphid colonisation, thereby facilitating movement between plants and increasing opportunities for virus spread. Conversely, marked temperature variability and extreme moisture conditions may disrupt aphid feeding and movement, ultimately reducing transmission efficiency. BBTV epidemiology therefore appears to be strongly conditioned by climatic regimes that favour both vector persistence and virus suitability.

Model projections further suggested suitable habitats for both *P. nigranervosa* and BBTV extend beyond their currently known distributions, with high-risk regions identified in Central and South America, West and East Africa, and Southeast Asia (Figs. 5 and 6). Although records in Europe are largely restricted to glasshouse infestations (Blackman & Eastop 1984), some parts of southern and western Europe may also be climatically suitable. However, suitability for both the vector and the virus is projected to decline under future climate scenarios (SSP585, 2090s). Given the strong effects of abiotic factors on transmission efficiency (Anhalt & Almeida 2008; Chakraborty et al. 2021), these projections likely identify regions where overlap between vector suitability and virus suitability may generate the greatest epidemiological risk.

9 Management of *P. nigranervosa*

9.1 Chemical control

Synthetic insecticides are key for banana aphid management, particularly in production systems affected by BBTV. Neonicotinoids such as imidacloprid and thiamethoxam, together with organophosphates such as diazinon, are widely used because of their rapid activity and relative affordability (Jose 1981; Kakati & Nath 2019). However, efficacy may vary with application method and leaf age. For example, Robson et al. (2007), found that foliar imidacloprid effectively controlled *P. nigranervosa* on sprayed banana leaves, particularly older leaves, but did not move systemically within the plant; consequently, leaves emerging after application were not fully protected. Regional recommendations reflect this continued reliance, with imidacloprid and diazinon commonly used in Hawaii and thiamethoxam- and pyrethrin-based products applied in some African and Caribbean banana systems under

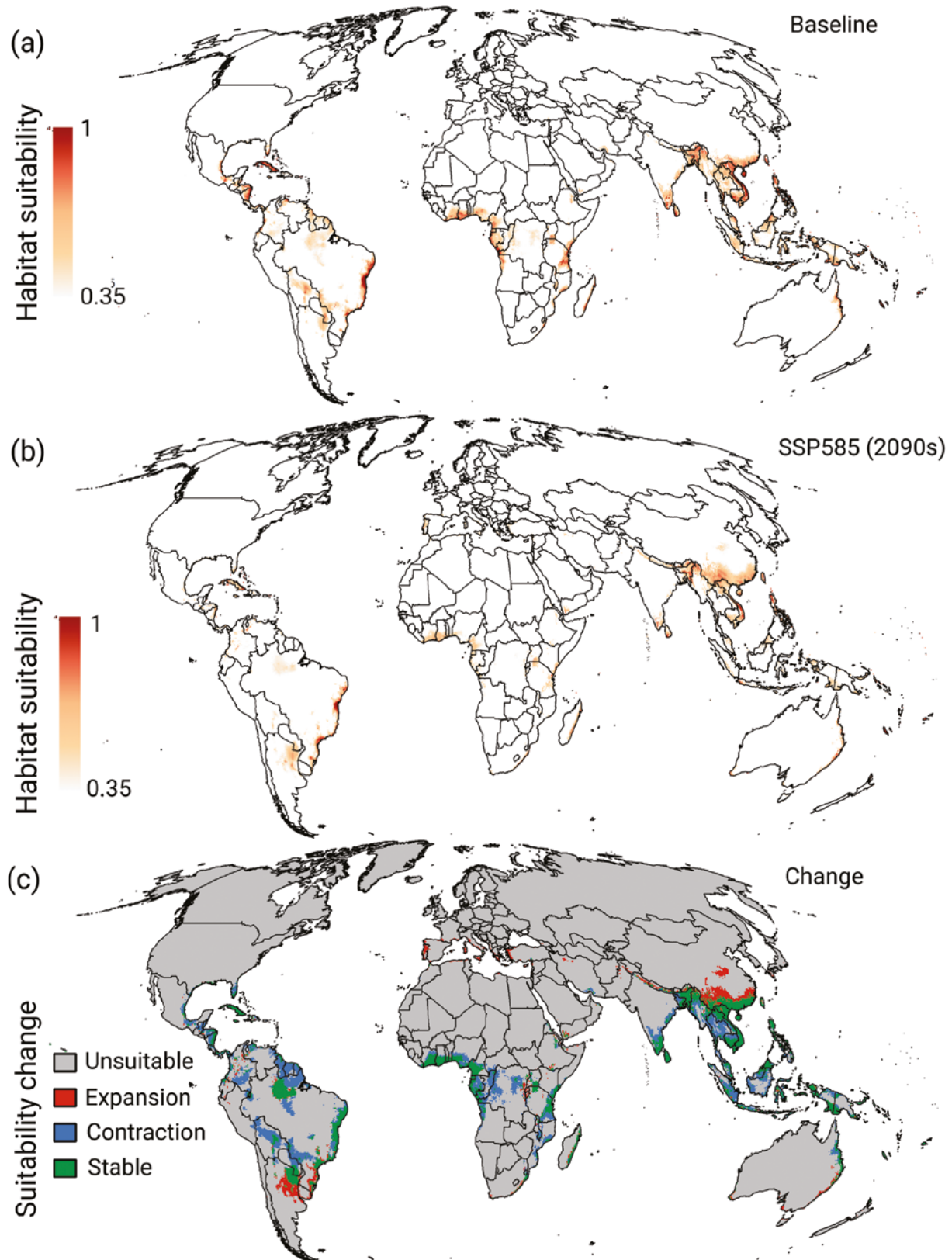


Fig. 5. Global habitat suitability predicted for *Pentalonia nigronervosa*. (a) Baseline projection for 1970–2000; (b) future projection based on the mean of six General Circulation Models (BCC-CSM2-MR, CNRM-CM6, EC-Earth3-Veg, IPSL-CM6A-LR, MIROC6, and MRI-ESM2-0) under SSP5-8.5 for 2081–2100; and (c) projected change in habitat suitability for *P. nigronervosa*.

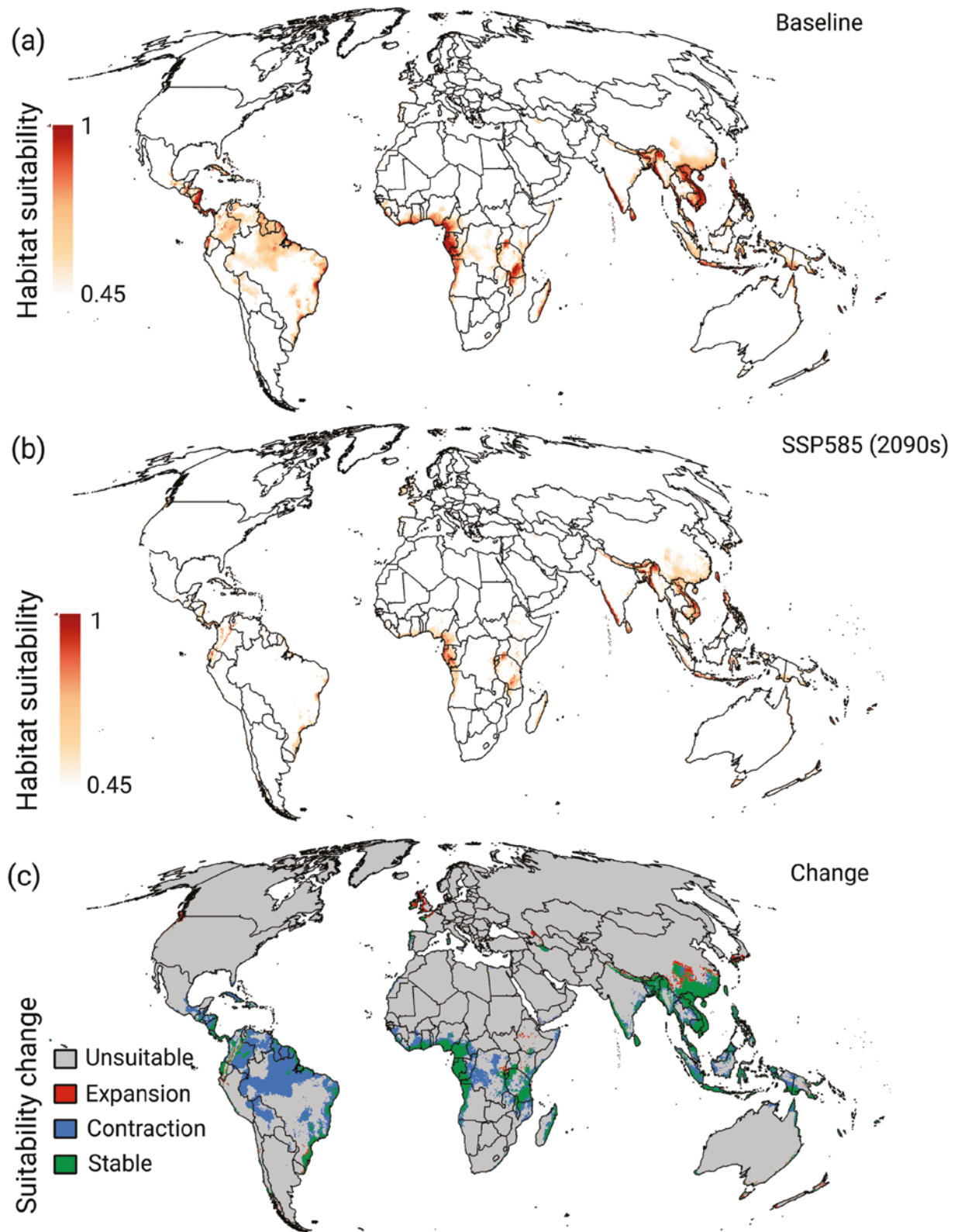


Fig. 6. Predicted global habitat suitability for banana bunchy top virus (BBTV). (a) Baseline suitability for 1970–2000, (b) future suitability projected from the mean of six General Circulation Models (BCC-CSM2-MR, CNRM-CM6, EC-Earth3-Veg, IPSL-CM6A-LR, MIROC6, and MRI-ESM2-0) under the SSP5-8.5 scenario for 2081–2100, and (c) predicted change in habitat suitability for banana bunchy top virus.

export-oriented guidelines (Constantinides & McHugh 2003; Comité de Liaison Europe–Afrique–Caraïbes–Pacifique [COLEACP] 2011).

Contact insecticides, including insecticidal soaps and horticultural oils, are also used for rapid suppression, although their limited residual activity necessitates repeated application. Pyrethrins, derived from *Tanacetum cinerariifolium* (Asteraceae), provide rapid knockdown but generally do not ensure prolonged control (Baltzegar et al. 2021). Newer chemistries may also be effective, although responses differ among active ingredients. Under field conditions, Baloch et al. (2023) reported that spinetoram reduced banana aphid populations by 70–91%, whereas spinosad and chlorantraniliprole produced lower and more variable reductions.

Despite their utility, broad-spectrum insecticides raise concerns regarding resistance selection, environmental contamination, and non-target effects. These concerns are especially relevant in export-oriented banana systems, where pesticide choice is increasingly constrained by maximum residue limits imposed by major importing markets, including the European Union, the United States, and Japan (European Commission 2005; Ministry of Health, Labour and Welfare [MHLW] 2020; U.S. Environmental Protection Agency [US EPA] 2025). Consequently, lower-residue and more selective products are becoming increasingly important components of integrated management programmes. Botanical insecticides may contribute to such programmes. Neem-based formulations containing azadirachtin, derived from *Azadirachta indica* (Meliaceae), have shown suppressive and growth-disrupting effects against aphids (US EPA 2001; Baloch et al. 2023). Recent experimental studies also demonstrate that botanical and soap-based treatments can effectively suppress *P. nigronevosa* populations (Ogwal et al. 2025). Products based on pongamia oil from *Pongamia pinnata* (Fabaceae) have shown pesticidal potential (Ngegba et al. 2022). Tobacco-derived preparations from *Nicotiana tabacum* (Solanaceae) also exhibit aphicidal activity, although concerns regarding toxicity and regulatory compliance limit broader use (Ngegba et al. 2022). Field experience in Hawaii and sub-Saharan Africa further indicates that azadirachtin-based products and horticultural oils can provide moderate suppression when incorporated into integrated programmes, although frequent reapplication is often necessary because of their short residual persistence (Constantinides & McHugh 2003; Nyalugwe 2018).

9.2 Biological control

A range of natural enemies has been associated with *P. nigronevosa* (Table 1), although robust evidence of field-level efficacy remains limited. Several parasitoids, including *Lipolexis bengalensis*, *Lysiphlebus fabarum*, *Aphidius colemani*, and *Trioxys angelicae*, have been reported from banana aphid populations or evaluated as biological control agents. Quantitative efficacy data specific to *P. nigronevosa*, however, remain scarce for most species. In South Sumatra, *Lipolexis bengalensis* parasitised up to 98% of banana aphids

in parasitism assays, whereas for *Lysiphlebus fabarum*, *Aphidius colemani*, and *Trioxys angelicae*, the literature mainly reports laboratory suitability, occurrence, or establishment rather than robust field efficacy estimates (Völkl et al. 1990; Muratori et al. 2009; Tricahyati et al. 2022). Their impact may also be reduced by ant-aphid mutualisms, because dominant ant species frequently defend aphid colonies against parasitoid attack (Carver et al. 1993; Stechmann et al. 1996; Tricahyati et al. 2022).

Predatory arthropods may also contribute to banana aphid suppression (Biale et al. 2017; Tricahyati et al. 2022). Reported predators include coccinellids, syrphids, earwigs, and spiders. Most studies, however, describe predator occurrence and abundance rather than quantitative control (Abdel-Moniem 2003; Adjalla et al. 2025b). In controlled assays, predation ranged from 3.66 to 23.67 aphids per predator within 2 h, corresponding to 12.2–78.9% predation (Tricahyati et al. 2022). The highest rates were recorded for *Scymnus* sp. and *Forficula auricularia*, each consuming 23.67 aphids, whereas syrphids showed intermediate predation and spiders lower rates. Entomopathogenic fungi such as *Beauveria bassiana*, *Metarhizium anisopliae*, and *Lecanicillium/Akanthomyces* spp. have demonstrated substantial potential for banana aphid management under laboratory and semi-field conditions (Table 1). In Cameroon, selected isolates of *B. bassiana* and *M. anisopliae* caused high mortality of *P. nigronevosa* (Enoh et al. 2024). Similarly, Ashif et al. (2025) reported mortality of up to 96.38%, 94.0%, and 77.40% following treatment with *L. fusisporum*, *B. bassiana*, and *M. anisopliae*, respectively. More recently, Viswakethu et al. (2026) showed that *A. lecanii* and its metabolites adversely affected banana aphid survival and behaviour, further supporting the potential of entomopathogenic fungi as components of integrated banana aphid management. Because of their specificity and potential to reduce reliance on conventional insecticides, entomopathogenic fungi warrant further development for banana aphid control.

9.3 RNAi-based approaches

RNA interference represents a promising emerging strategy for the management of *P. nigronevosa* through targeted gene silencing. One important target is *acetylcholinesterase* (*AChE*), an enzyme essential for terminating neural signalling (Trang & Khandhar 2025). Silencing of *AChE* disrupts neurotransmission and can induce mortality, developmental arrest, and reduced growth in banana aphids. Under controlled conditions, RNAi-based targeting of *AChE* has reduced aphid populations by up to 75% (Jekayinoluwa et al. 2020, 2021). Despite this promise, large-scale implementation remains constrained by several factors, including limitations in dsRNA delivery, production cost, regulatory approval, and operational scalability. RNAi should therefore be viewed as a highly promising but still emerging component of banana aphid management rather than as a near-term replacement for existing control measures.

Table 1. A list of biological control agents of *P. nigronervosa*. References are: (1) Biale et al. 2017, (2) Tricahyati et al. 2022, (3) Völkl et al. 1990, (4) Muratori et al. 2009, (5) Kakati et al. 2018, (6) Amsavalli et al. 2022, (7) Padmalatha et al. 2004, (8) Baloch et al. 2023.

Control agent type.	Order and Family	Species and Reference Number(s)
Insect parasitoid	Hymenoptera, Aphidiidae	<i>Trioxys angelicae</i> (1)
Insect parasitoid	Hymenoptera, Braconidae	<i>Aphidius colemani</i> (1)
Insect parasitoid	Hymenoptera, Braconidae	<i>Lipolexis bengalensis</i> (2)
Insect parasitoid	Hymenoptera, Braconidae	<i>Lysiphlebus fabarum</i> (3)
Insect parasitoid	Hymenoptera, Braconidae	<i>Lysiphlebus testaceipes</i> (3)
Insect parasitoid	Diptera, Cecidomyiidae	<i>Endaphis fugitive</i> (4)
Insect predator	Coleoptera, Coccinellidae	<i>Chilocorus bipustulatus</i> (1)
Insect predator	Coleoptera, Coccinellidae	<i>Coccinella transversalis</i> (2)
Insect predator	Coleoptera, Coccinellidae	<i>Menochilus sexmaculatus</i> (2)
Insect predator	Coleoptera, Coccinellidae	<i>Micraspis discolor</i> (2)
Insect predator	Coleoptera, Coccinellidae	<i>Micraspis hirashimai</i> (2)
Insect predator	Coleoptera, Coccinellidae	<i>Nephus fenestratus</i> (1)
Insect predator	Coleoptera, Coccinellidae	<i>Rhyzobius lophanthae</i> (1)
Insect predator	Coleoptera, Coccinellidae	<i>Scymnus apetzi</i> (1)
Insect predator	Coleoptera, Coccinellidae	<i>Scymnus flavicollis</i> (1)
Insect predator	Coleoptera, Coccinellidae	<i>Scymnus frontalis</i> (1)
Insect predator	Coleoptera, Coccinellidae	<i>Scymnus interruptus</i> (1)
Insect predator	Coleoptera, Coccinellidae	<i>Scymnus nubilus</i> (1)
Insect predator	Coleoptera, Coccinellidae	<i>Scymnus subvillosus</i> (1)
Insect predator	Coleoptera, Coccinellidae	<i>Verania lineata</i> (2)
Insect predator	Dermaptera, Forficulidae	<i>Forficula auricularia</i> (2)
Insect predator	Diptera, Cecidomyiidae	<i>Aphidoletes aphidimyza</i> (1)
Insect predator	Diptera, Syrphidae	<i>Epistrophe balteatus</i> (1)
Insect predator	Diptera, Syrphidae	<i>Ischiodon aegyptius</i> (1)
Insect predator	Diptera, Syrphidae	<i>Paragus compeditus</i> (1)
Arachnid predator	Araneae, Oxyopidae	<i>Oxyopes salticus</i> (2)
Arachnid predator	Araneae, Salticidae	<i>Hasarius adansoni</i> (2)
Arachnid predator	Araneae, Salticidae	<i>Menemerus bivittatus</i> (2)
Arachnid predator	Araneae, Salticidae	<i>Plexippus paykulli</i> (2)
Entomopathogen	Hypocreales, Clavicipitaceae	<i>Metarhizium anisopliae</i> (5,6)
Entomopathogen	Hypocreales, Cordycipitaceae	<i>Beauveria bassiana</i> (5,6)
Entomopathogen	Hypocreales, Cordycipitaceae	<i>Lecanicillium lecanii</i> (5,6)
Entomopathogen	Hypocreales, Hypocreaceae	<i>Acremonium</i> sp. (7)
Entomopathogen	Pseudonocardiales, Pseudonocardiaceae	<i>Saccharopolyspora spinosa</i> (8)

9.4 Cultural and integrated strategies

Preventive measures remain the foundation of management for both *P. nigronervosa* and banana bunchy top disease. These include the use of virus-free planting material, prompt roguing and complete removal of infected mats, and the maintenance of buffer zones intended to reduce aphid pressure and limit virus spread (Jekayinoluwa et al. 2020; Omondi et al. 2020, 2023). Because *P. nigronervosa* is attracted to BBTV-infected plants through virus-associated volatile cues, rapid removal of infected plants is particularly important for reducing both local inoculum and vector attraction (Murhububa et al. 2021).

Roguing is most effective when it is implemented consistently and when control efforts are coordinated at community and landscape scales rather than at the level of individual farms alone (Abiola et al. 2020; Omondi et al. 2023). In smallholder systems, additional low-input measures such as soap-based sprays and horticultural oils may provide supplementary aphid suppression. These methods are best regarded as complementary rather than stand-alone cultural tactics, but they may still contribute meaningfully to integrated management in resource-limited production systems (Ogwal et al. 2025).

10 Knowledge gaps and future research directions

Although *P. nigronevosa* is widely distributed, BBTv prevalence remains highly uneven across regions that appear suitable for both the host and the vector. This disparity suggests geographic variation in vector competence, host susceptibility, local agroecological conditions, or other epidemiological drivers that remain insufficiently understood (CABI 2022; Kumar 2017). The distribution models presented here provide a preliminary indication of where overlap between aphid and virus is most and least likely, but comparative studies are still needed to identify the ecological and genetic mechanisms underlying these regional differences.

More broadly, research on aphid-virus-host interactions in other systems has shown that plant viruses can alter vector behaviour in ways that enhance transmission, as demonstrated for potato leafroll virus and barley yellow dwarf virus (Ingwell et al. 2012; Rajabaskar et al. 2014). Recent evidence suggests that BBTv may similarly modify the feeding behaviour and host preference of *P. nigronevosa*, with potentially important consequences for disease spread and vector ecology (Murhububa et al. 2024). These findings highlight the need for management strategies that target the full vector-virus-host pathosystem rather than focusing on a single component in isolation. For example, predictive frameworks that integrate degree-day accumulation for aphid development with agent-based simulations of aphid movement and human-mediated spread could improve forecasting for both *P. nigronevosa* and BBTv. Such approaches may be especially useful for anticipating seasonal outbreaks and identifying regions at elevated risk of invasion or disease escalation.

Advances in RNA sequencing and RNA interference also offer promising opportunities for future research. These tools may facilitate the identification of key functional genes involved in survival, feeding, reproduction, and virus transmission, thereby supporting the development of novel control strategies. For example, transgenic bananas expressing dsRNA targeting acetylcholinesterase have already produced substantial reductions in aphid populations (Jekayinoluwa et al. 2020, 2021). Comparable advances in other crop systems, including the identification of resistance loci through QTL mapping in maize and wild soybean, suggest that similar approaches could eventually support the breeding or engineering of banana cultivars with improved resistance to aphid infestation or BBTv transmission (Wang et al. 2023; Zhang et al. 2017). Future work should therefore prioritise a more integrated understanding of vector biology, host resistance, microbial symbionts, and environmental drivers of transmission. In particular, the roles of endosymbionts in vector competence, the behavioural effects of BBTv infection on aphid host selection, and the development of scalable low-input management options remain important areas for further study. Progress in these areas will be essential for designing more durable and sustainable strategies for the long-term management of banana bunchy top disease.

11 Conclusion

Pentalonia nigronervosa occupies a pivotal role in the BBTv pathosystem as both a direct pest of banana and the principal vector of the virus. Considerable progress has been made in understanding its biology, geographic distribution, and vectoring capacity, yet important questions remain regarding its interactions with host plants, microbial associates, and viral pathogens. Advances in genomics and diagnostics have improved species delimitation and strengthened epidemiological surveillance, but current management continues to rely heavily on clean planting material, sanitary measures, and complementary aphid suppression.

Emerging approaches, including RNA interference, remote sensing, and predictive ecological modelling, offer promising opportunities for more sustainable management, although their large-scale implementation will require further validation, infrastructural support, and enabling policy frameworks. At the same time, the potential role of facultative symbionts such as *Wolbachia* in vector competence and ecological adaptation remains insufficiently understood and warrants closer investigation. As climate change and shifting agroecological conditions continue to reshape banana production systems, effective management of BBTv will require flexible, interdisciplinary strategies that integrate ecology, molecular biology, epidemiology, and farm-level practice. A deeper understanding of *P. nigronevosa* will therefore be essential for safeguarding banana production in vulnerable regions worldwide.

Acknowledgements: We are grateful to Bonaventure Aman Omondi, Liesl Oeller, and George Town for their helpful comments on an earlier version of this manuscript.

Authorship contribution statement: Author Contributions: Conceptualization: OFA; Methodology: OFA; Statistical analyses: OFA; Investigation: SN; Supervision: DWC; Writing – original draft preparation: OFA, CKT, FLS, BOB, FOB and FKA; Writing – review and editing: OFA, SN and DWC. All authors have read and agreed to the published version of the manuscript.

Declaration of competing interest: The authors declare no conflict of interest

References

- Abdel-Moniem, A., (2003). Incidence of *Pentalonia nigronervosa* coquerel (Homoptera: Aphididae) and associated predators on banana plants in Egypt. *Archives of Phytopathology and Plant Protection* 36, 119–128. <https://doi.org/10.1080/0323540031000149131>
- Abiola, A., Zandjanakou-Tachin, M., Aoudji, K. N. A., Avocevou-Ayisso, C., & Kumar, P. L. (2020). Adoption of roguing to contain banana bunchy top disease in south-east Bénin: Role

- of farmers' knowledge and perception. *International Journal of Fruit Science*, 20(4), 720–736. <https://doi.org/10.1080/1553836.2.2019.1673277>
- Adegbola, R., Ayodeji, O., Awosusi, O., Atiri, G., & Kumar, P. L. (2013). First report of banana bunchy top virus in banana and plantain (*Musa* spp.) in Nigeria. *Plant Disease*, 97(2), 290. <https://doi.org/10.1094/PDIS-08-12-0745-PDN>
- Adil, S., & Quraishi, A. (2023). An aphid transmitted banana bunchy top disease of banana and its detection: A Review. *NewBioWorld*, 5(1), 10–19. <https://doi.org/10.52228/NBW-JAAB.2023-5-1-3>
- Adjalla, C. C., Madodé, Y. E., & Omondi, B. A. (2025a). The banana bunchy top disease enhances vector survival: effect of the banana bunchy top disease on host suitability of the banana aphid *Pentalonia nigronervosa*. *International Journal of Tropical Insect Science*, 45(4), 1579–1595. <https://doi.org/10.1007/s42690-025-01539-y>
- Adjalla, C., Omondi, B. A., Ogwal, G., Ocimati, W., Wasswa, P., & Blomme, G. (2025b). Aphid control using natural enemies: Lessons for fine-tuning banana-aphid management. *Biological Control*, 210, 105905. <https://doi.org/10.1016/j.biocontrol.2025.105905>
- Adjalla, C. C., Ogwal, G., Omondi, B. A., Ocimati, W., Wasswa, P., Safari, N. K., ... Blomme, G. (2026). Banana aphid *Pentalonia nigronervosa* coquerel (Hemiptera: Aphididae) rearing: optimizing low-cost approaches for banana research purposes. *International Journal of Tropical Insect Science*, 46(1), 1–11. <https://doi.org/10.1007/s42690-025-01707-0>
- Allen, R. N. (1978). Epidemiological factors influencing the success of roguing for the control of bunchy top disease of bananas in New South Wales. *Australian Journal of Agricultural Research*, 29(3), 535–544. <https://doi.org/10.1071/AR9780535>
- Amsavalli, V., Shinde, B., Narangalkar, A., Sawardekar, S., & Joshi, M. (2022). Biology of black aphid, *Pentalonia nigronervosa* (Coquerel) (Hemiptera: Aphididae) on host red banana and taro under laboratory condition. [IJARESM]. *International Journal of All Research Education and Scientific Methods*, 10, 211–217.
- Anhalt, M., & Almeida, R. (2008). Effect of temperature, vector life stage, and plant access period on transmission of Banana bunchy top virus to banana. *Phytopathology*, 98(6), 743–748. <https://doi.org/10.1094/PHYTO-98-6-0743>
- Ashif, K., Padmanaban, B., & Jerald, I. J. A. (2025). Screening of Fungal Entomopathogens against Banana Aphid *Pentalonia nigronervosa* Coq. *Indian Journal of Entomology*, 904–906. <https://doi.org/10.55446/IJE.2024.1766>
- Baloch, S. A., Lanjar, A. G., Syed, T. S., Khanzada, M. A., Nahiyo, S. A., Baloch, M. U., & Rustamani, F. A. (2023). Efficacy of different insecticides and botanicals against Banana aphids (*Pentalonia nigronervosa*) under field conditions. [PAB]. *Pure and Applied Biology*, 12(2), 1302–1314. <https://doi.org/10.19045/bspab.2023.120134>
- Baltzegar, J., Vella, M., Gunning, C., Vasquez, G., Astete, H., Stell, F., ... Gould, F. (2021). Rapid evolution of knockdown resistance haplotypes in response to pyrethroid selection in *Aedes aegypti*. *Evolutionary Applications*, 14(8), 2098–2113. <https://doi.org/10.1111/eva.13269>
- Basak, G., Banerjee, A., & Bandyopadhyay, B. (2015). Studies on some bio-ecological aspects and varietal preference of banana aphid, *Pentalonia nigronervosa* Coquerel (Hemiptera: Aphididae). *Journal Crop and Weed* 11, 181–186.
- Biale, H., Mendel, Z., & Srooker, V. (2017). Insects associated with the banana aphid *Pentalonia nigronervosa* Coquerel (Hemiptera: Aphididae) in banana plantations with special emphasis on the ant community. *Phytoparasitica* 45, 361–372.
- Blackman, R. L., & Eastop, V. F. (1984). *Aphids on the World's Crops. An identification and information guide*. United Kingdom: Wiley.
- Blomme, G., Ploetz, R., Jones, D., De Langhe, E., Price, N., Gold, C., ... Pillay, M. (2013). A historical overview of the appearance and spread of *Musa* pests and pathogens on the African continent: Highlighting the importance of clean *Musa* planting materials and quarantine measures. *The Annals of Applied Biology*, 162(1), 4–26. <https://doi.org/10.1111/aab.12002>
- Bouwmeester, H., Blomme, G., Omondi, A. B., & Ocimati, W. (2023). Banana bunchy top disease in africa-predicting continent-wide disease risks by combining survey data and expert knowledge. *Plant Pathology*, 72(8), 1476–1490. <https://doi.org/10.1111/ppa.13764>
- CABI. (2015). Banana aphid: *Pentalonia nigronervosa*. <https://doi.org/10.1079/pwkb.20157800215>
- CABI. (2022). *Pentalonia nigronervosa* (banana aphid). CABI Compendium. <https://doi.org/10.1079/cabicompium.39598>
- Carver, M., Hart, P., & Wellings, P. (1993). Aphids (Hemiptera: Aphididae) and associated biota from the Kingdom of Tonga, with respect to biological control. *The Pan-Pacific Entomologist*, 69, 250–260.
- Chakraborty, S., Barman, M., Samanta, S., Roy, M., Tarafdar, J. (2021). Effect of banana bunchy top virus on the heat shock protein genes of *Pentalonia nigronervosa* during temperature susceptibility and its effect on virus transmission. *Agronomy* 11, 1866.
- Chaudhary, R. (2013). *Functional Characterization of Aphid Salivary Proteins and Their Role in Modulating Plant Defense*. (PhD Doctoral Thesis). UC Riverside, California, USA.
- COLEACP. (2011). Guide to good crop protection practices for banana. PIP/COLEACP, 54. Retrieved from https://resources.colead.link/en/system/files/file_fields/2016/02/19/gbpb-banane-oct2011-uk.pdf
- Constantinides, L. N., & J. J. McHugh, Jr. (2003). Pest management strategic plan for banana production in Hawaii, pp. 1071. In Pearl City Urban Garden Center, Workshop Summary. (<http://www.ctahr.hawaii.edu/bbtd/downloads/HIBananaPMSP.pdf>)
- Coquerel, C. (1859). Note sur quelques insectes de Madagascar et de Bourbon. *Annales de la Société Entomologique de France* (3ième série), 7, 239–260.
- Dahal, O., Tenkouano, H., & Thottappilly, V. (2000). Relationship between natural occurrence of banana streak badnavirus and symptom expression, relative concentration of viral antigen, and yield characteristics of some micropropagated *Musa* spp. *Plant Pathology*, 49(1), 68–79. <https://doi.org/10.1046/j.1365-3059.2000.00420.x>
- Damasco, O., Estrella, J., Caymo, L., Dizon, T., Rabara, R., Cruz, F. d., Jr., & Mendoza, E. (2006). Banana bunchy top virus (BBTV) resistance in cultivar “lakatan” developed via gamma irradiation of shoot tips. *Philippine Journal of Crop Science*, 31, 21–34.
- Daniells, J., Geering, A. D., Bryde, N., & Thomas, J. (2001). The effect of Banana streak virus on the growth and yield of dessert bananas in tropical Australia. *The Annals of Applied Biology*, 139(1), 51–60. <https://doi.org/10.1111/j.1744-7348.2001.tb00130.x>
- De Clerck, C., Fujiwara, A., Joncour, P., Léonard, S., Félix, M.-L., Francis, F., ... Massart, S. (2015). A metagenomic approach from aphid's hemolymph sheds light on the potential roles of co-existing endosymbionts. *Microbiome*, 3(1), 63. <https://doi.org/10.1186/s40168-015-0130-5>
- De Clerck, C., Tsuchida, T., Massart, S., Lepoivre, P., Francis, F., & Jijakli, M. H. (2014). Combination of Genomic and Proteomic

- Approaches to Characterize the Symbiotic Population of the Banana Aphid (Hemiptera: Aphididae). *Environmental Entomology*, 43(1), 29–36. <https://doi.org/10.1603/EN13107>
- Dela Cueva, F. M., Perez, N. A. M., Benjamin, A. F. A., Yanos, L. A., Gueco, L. S., & Thomas, J. E. (2023). Resistance of *Musa balbisiana* accessions of the Philippines to banana bunchy top virus. *Plant Disease*, 107(7), 1973–1978. <https://doi.org/10.1094/PDIS-10-22-2427-SC>
- Efendi, R. A., Suparman, S., & Hamidson, H. (2022). Biology of *Pentalonia nigronervosa* Coquerel on Various Zingiberaceous Crops. *BIOVALENTIA. Biological Research Journal*, 8, 118–129.
- Elayabalan, S., Subramaniam, S., Selvarajan, R., (2015). Banana bunchy top disease (BBTD) symptom expression in banana and strategies for transgenic resistance: A review. *Emirates Journal of Food & Agriculture* (EJFA) 27. <https://doi.org/10.9755/ejfa.v27i1.19197>
- Enoh, A. C., Akoachere, J.-F., Fossi, T. B., Membang, G., Ngatat, S., Fotso Kuate, A., ... Fiaboe, K. K. M. (2024). Potential of Cameroonian isolates of *Beauveria bassiana* and *Metarhizium anisopliae* for the biocontrol of the banana aphid, *Pentalonia nigronervosa*, vector of banana bunchy top virus. *PLoS One*, 19(11), e0310746. <https://doi.org/10.1371/journal.pone.0310746>
- European Commission, E. (2005). Regulation (EC) No 396/2005 of the European Parliament and of the Council of 23 February 2005 on maximum residue levels of pesticides in or on food and feed of plant and animal origin. *Official Journal of the European Union*. <https://eur-lex.europa.eu/eli/reg/2005/396/oj/eng>
- Footitt, R., & Maw, H. E. L. (2019). Geographic distribution, host preferences and molecular diversity within the genus *Pentalonia* (Hemiptera: Aphididae). *Zootaxa*, 4701(4), 383–391. <https://doi.org/10.11646/zootaxa.4701.4.4>
- Footitt, R., Maw, H., Pike, K., & Miller, R. (2010). The identity of *Pentalonia nigronervosa* Coquerel and *P. caladii* van der Goot (Hemiptera: Aphididae) based on molecular and morphometric analysis. *Zootaxa*, 2358, 25–38.
- Foure, E., & Manser, P. D. (1982). Note sur l'Apparition au Gabon d'une Grave Maladie Virale des Bananiers et Plantains: Le Bunchy Top. *Fruits*, 37, 409–414.
- Gavarrá, M., & Eastop, V. (1976). Notes on the estimation of alate aphid populations using Moericke yellow trays. *Philippine Entomologist*, 3(3 and 4), 246–249. <https://doi.org/10.59852/TPE-A97V3I3and4>
- Gunawan, S., Arsi, P., & Cameron, R. (2017). Alternative hosts of banana aphid *Pentalonia nigronervosa* Coq. (Hemiptera: Aphididae), the vector transmitting banana bunchy top virus. *Journal of Advanced Agricultural Technologies*, 4(4), 354–359. <https://doi.org/10.18178/joaat.4.4.354-359>
- Hafner, G. J., Harding, R. M., & Dale, J. L. (1995). Movement and transmission of banana bunchy top virus DNA component one in bananas. *The Journal of General Virology*, 76(9), 2279–2285. <https://doi.org/10.1099/0022-1317-76-9-2279>
- Hall, W.J. 1926. Ministry of Agriculture, Egypt: Technical and Scientific Service Bulletin 68:44
- Higashi, C. H. V., Patel, V., Kamalaker, B., Inaganti, R., Bressan, A., Russell, J. A., & Oliver, K. M. (2024). Another tool in the toolbox: Aphid-specific protect against fungal pathogens. *Environmental Microbiology*, 26(11), e70005. <https://doi.org/10.1111/1462-2920.70005>
- Hooks, C. R., Wang, K.-H., Pradhan, N. C., Manandhar, R., Wright, M. G., & Vorsino, A. (2011). Population distribution and density of *Pentalonia nigronervosa* (Hemiptera: Aphididae) within banana mats: influence of plant age and height on sampling and management. *Journal of Economic Entomology*, 104(3), 947–955. <https://doi.org/10.1603/EC10323>
- Hu, J. S., Wang, M., Sether, D., Xie, W., & Leonhardt, K. W. (1996). Use of polymerase chain reaction (PCR) to study transmission of banana bunchy top virus by the banana aphid (*Pentalonia nigronervosa*). *The Annals of Applied Biology*, 128(1), 55–64. <https://doi.org/10.1111/j.1744-7348.1996.tb07089.x>
- Ingwell, L. L., Eigenbrode, S. D., & Bosque-Pérez, N. A. (2012). Plant viruses alter insect behavior to enhance their spread. *Scientific Reports*, 2(1), 578. <https://doi.org/10.1038/srep00578>
- Jebakumar, R. M., Balasubramanian, V., & Selvarajan, R. (2018). Virus titre determines the efficiency of *Pentalonia nigronervosa* (Aphididae: Hemiptera) to transmit banana bunchy top virus. *Virusdisease*, 29(4), 499–505. <https://doi.org/10.1007/s13337-018-0493-x>
- Jekayinoluwa, T., Tripathi, J. N., Dugdale, B., Obiero, G., Muge, E., Dale, J., & Tripathi, L. (2021). Transgenic Expression of dsRNA Targeting the *Pentalonia nigronervosa* acetylcholinesterase Gene in Banana and Plantain Reduces Aphid Populations. *Plants*, 10(4), 613. <https://doi.org/10.3390/plants10040613>
- Jekayinoluwa, T., Tripathi, L., Tripathi, J. N., Ntui, V. O., Obiero, G., Muge, E., & Dale, J. (2020). RNAi technology for management of banana bunchy top disease. *Food and Energy Security*, 9(4), e247. <https://doi.org/10.1002/fes3.247>
- Jones, R. A. C., Salam, M. U., Maling, T. J., Diggle, A. J., & Thackray, D. J. (2010). Principles of Predicting Plant Virus Disease Epidemics. *Annual Review of Phytopathology*, 48(1), 179–203. <https://doi.org/10.1146/annurev-phyto-073009-114444>
- Jose, P. (1981). Field evaluation of different insecticides for control of the banana aphid (*Pentalonia nigronervosa* Coq.). *Agricultural Research Journal of Kerala*, 18, 109–110.
- Jooste, A. E. C., Wessels, N., & van der Merwe, M. (2016). First Report of Banana bunchy top virus in Banana (*Musa* spp.) from South Africa. *Plant Disease*, 100(6), 1251. <https://doi.org/10.1094/PDIS-12-15-1422-PDN>
- Julca, I., Marcet-Houben, M., Cruz, F., Vargas-Chavez, C., Johnston, J. S., Gómez-Garrido, J., ... Gabaldón, T. (2019). Phylogenomics Identifies an Ancestral Burst of Gene Duplications Predating the Diversification of Aphidomorpha. *Molecular Biology and Evolution*, 37(3), 730–756. <https://doi.org/10.1093/molbev/msz261>
- Kakati, N., Dutta, P., Das, P., & Nath, P. (2018). Compatibility of Entomopathogenic fungi with commonly used insecticides for Management of Banana Aphid transmitting Banana bunchy top virus (BBTV) in Assam Banana production system. *International Journal of Current Microbiology and Applied Sciences*, 7(11), 2507–2513. <https://doi.org/10.20546/ijemas.2018.711.285>
- Kakati, N., & Nath, P. (2019). First Report on Development of Sustainable Management Strategy against *Pentalonia nigronervosa* Coq. Vector of Banana Bunchy Top Virus Disease, Its Seasonal Variation and Effect on Yield of Banana in Jorhat District of Assam – A North Eastern State of India. *Journal of Entomology and Zoology Studies*, 7(2), 158–167. <https://doi.org/10.22271/j.ento.2019.v7.i2.2.07>
- Kolombia, Y. A., Oviasuyi, T., Dzola, A. K., Ale Gonh-Goh, A., Atsu, T., Oresanya, A., ... Kumar, P. L. (2021). First report of banana bunchy top virus in banana (*Musa* spp.) and its eradication in Togo. *Plant Disease*, 105(10), 3312. <https://doi.org/10.1094/PDIS-03-21-0473-PDN>

- Kumar, L. (2017). *Banana bunchy top virus (bunchy top of banana)*. CABI Compendium; <https://doi.org/10.1079/cabicompendium.8161>
- Lokossou, B., Gnanvossou, D., Ayodeji, O., Akplogan, F., Safiore, A., Migan, D., ... Kumar, P. (2012). Occurrence of Banana bunchy top virus in banana and plantain (*Musa* sp.) in Benin. *New Disease Reports*, 25(1), 13. <https://doi.org/10.5197/j.2044-0588.2012.025.013>
- Magee, C. J. P. (1940). Transmission Studies on the Banana Bunchy-top Virus. *Journal of the Australian Institute of Agricultural Science*, 6(2), 109–110 pp. <https://www.cabidigitallibrary.org/doi/full/10.5555/19410500254>
- Magee, C. J. P. (1927). Investigation on the bunchy top disease of the banana. (Australia). *Bulletin of the Council for Scientific and Industrial Research*, 30, 1–64.
- Mahuku, G., & Kumar, P. (2023). Banana Bunchy Top Virus (BBTV) Delimiting Survey in Tanzania: Phase 1 Survey Summary Report (Ibadan: IITA;), 13.
- Manzano-Marín, A. (2020). No evidence for Wolbachia as a nutritional co-obligate endosymbiont in the aphid *Pentalonia nigronervosa*. *Microbiome*, 8, 72.
- Mathers, T. C., Mugford, S. T., Hogenhout, S. A., & Tripathi, L. (2020). Genome sequence of the banana aphid, *Pentalonia nigronervosa* Coquerel (Hemiptera: Aphididae) and its symbionts. *G3 (Bethesda, Md.)*, 10(12), 4315–4321. <https://doi.org/10.1534/g3.120.401358>
- Masangwa, J. I. G., Pareta, N. F., Moses, P., Hřibová, E., Doležel, J., Fandika, I., & Massart, S. (2026). Surveillance and molecular characterization of banana viruses associated with *Musa* germplasm in Malawi. *PLoS One*, 21(1), e0306671. <https://doi.org/10.1371/journal.pone.0306671>
- Mau, R., Kessing, J. M., Tenbrink, V., & Hara, A. (1994). *Pentalonia nigronervosa* (Coquerel). Crop Knowledge Master. *UH-CTAHR Integrated Pest Management Program*, 12, 11–12.
- Menon, M., & Christudas, S. (1967). Studies on the population of the aphid *Pentalonia nigronervosa* Coq. on banana plants in Kerala. *Agricultural Research Journal of Kerala*, 5, 84–86.
- Ministry of Health, Labour and Welfare. (2020). *Imported foods monitoring and guidance plan for FY 2020*. Retrieved from <https://www.mhlw.go.jp/content/000623550.pdf>
- Mukwa, L. F. T., Gillis, A., Vanhese, V., Romay, G., Galzi, S., Laboureaux, N., & Bragard, C. (2016). Low genetic diversity of Banana bunchy top virus, with a sub-regional pattern of variation, in Democratic Republic of Congo. *Virus Genes*, 52, 900–905.
- Muratori, F. B., Gagne, R. J., & Messing, R. H. (2009). Ecological traits of a new aphid parasitoid, *Endaphis fugitiva* (Diptera: Cecidomyiidae), and its potential for biological control of the banana aphid, *Pentalonia nigronervosa* (Hemiptera: Aphididae). *Biological Control*, 50(2), 185–193. <https://doi.org/10.1016/j.biocontrol.2009.04.007>
- Murhububa, I. S., Bragard, C., Tougeron, K., & Hance, T. (2024). Preference of *Pentalonia nigronervosa* for infected banana plants tends to reverse after Banana bunchy top virus acquisition. *Scientific Reports*, 14, 2993.
- Murhububa, I. S., Tougeron, K., Bragard, C., Fauconnier, M.-L., Bisimwa Basengere, E., Walangululu Masamba, J., & Hance, T. (2021). Banana Tree Infected with Banana Bunchy Top Virus Attracts *Pentalonia nigronervosa* Aphids Through Increased Volatile Organic Compounds Emission. *Journal of Chemical Ecology*, 47(8-9), 755–767. <https://doi.org/10.1007/s10886-021-01298-3>
- Nachappa, P., Culkin, C. T., Saya, P. M., Han, J., & Nalam, V. J. (2016). Water Stress Modulates Soybean Aphid Performance. Feeding Behavior, and Virus Transmission in Soybean. *Frontiers in Plant Science, Volume 7–201*. <https://doi.org/10.3389/fpls.2016.00552>
- Nelson, S. C., Messing, R., Hamasaki, R., Gaskill, D., & Nishijima, W. (2004). Banana bunchy top: Detailed signs and symptoms. *Knowledge (Beverly Hills, Calif.)*, 1–22.
- Ngatat, S., Hanna, R., Kumar, P. L., Gray, S. M., Cilia, M., Ghogomu, R. T., & Fontem, D. A. (2017). Relative susceptibility of *Musa* genotypes to banana bunchy top disease in Cameroon and implication for disease management. *Crop Protection (Guildford, Surrey)*, 101, 116–122. <https://doi.org/10.1016/j.cropro.2017.07.018>
- Ngatat, S., Hanna, R., Lienou, J., Ghogomu, R. T., Nguidang, S. P. K., Enoh, A. C., ... Kumar, L. P. (2022). *Musa* Germplasm A and B Genomic Composition Differentially Affects Their Susceptibility to Banana Bunchy Top Virus and Its Aphid Vector, *Pentalonia nigronervosa*. *Plants*, 11, 2026. <https://doi.org/10.3390/plants11091206>
- Ngegba, P. M., Cui, G., Khalid, M. Z., & Zhong, G. (2022). Use of Botanical Pesticides in Agriculture as an Alternative to Synthetic Pesticides. *Agriculture*, 12(5), 600. Retrieved from <https://www.mdpi.com/2077-0472/12/5/600>
- Niyongere, C., Losenge, T., Ateka, E., Ntukamazina, N., Ndayiragije, P., Simbare, A., ... Blomme, G. (2013). Understanding banana bunchy top disease epidemiology in Burundi for an enhanced and integrated management approach. *Plant Pathology*, 62, 562–570. <https://doi.org/10.1111/j.1365-3059.2012.02676.x>
- Niyongere, C., Losenge, T., Ateka, E. A., Nkezabazizi, D., Blomme, G., & Lepoint, P. (2011). Occurrence and distribution of banana bunchy top disease in the Great Lakes region of Africa. *Tree and Forestry Science and Biotechnology*, 6, 102–107.
- Nyalugwe, N. (2018). *Banana bunchy top-Malawi*. PlantwisePlus Knowledge Bank. <https://doi.org/10.1079/pwkb.20207800166>
- Ocimati, W., Tazuba, A. F., Tushemereirwe, W. K., Tugume, J., Omondi, B. A., Acema, D., ... Blomme, G. (2021). First report of banana bunchy top disease caused by Banana bunchy top virus in Uganda. *New Disease Reports*, 44(2), e12052. <https://doi.org/10.1002/ndr2.12052>
- Ogwal, G., Wasswa, P., Ocimati, W., Omondi, B. A., Tazuba, A. F., Otim, M. H., & Blomme, G. (2025). Screening for the efficacy of botanicals and soaps in controlling the Banana Aphid *Pentalonia nigronervosa* (Hemiptera: Aphididae) under laboratory and greenhouse conditions. *Insects*, 17(1), 23. <https://doi.org/10.3390/insects17010023>
- Omondi, B. A., Soko, M. M., Chabi, M. C., Nduwimana, I., Adjalla, C. C., Athindehou, F., ... Staver, C. (2023). Tools for the management of the banana bunchy top disease in small holder systems. *Acta Horticulturae*, 1367, 233–242. <https://doi.org/10.17660/ActaHortic.2023.1367.27>
- Omondi, B. A., Soko, M. M., Nduwimana, I., Delano, R. T., Niyongere, C., Simbare, A., ... Staver, C. (2020). The effectiveness of consistent roguing in managing banana bunchy top disease in smallholder production in Africa. *Plant Pathology*, 69(9), 1754–1766. <https://doi.org/10.1111/ppa.13253>
- Padmalatha, C., Singh, A., Dhasarathan, P., & Jeyapaul, C. (2004). An entomopathogenic fungus *Acremonium* on banana aphid, *Pentalonia nigronervosa* Coq. *Indian Journal of Microbiology*, 44, 139–140.
- Pinili, M. S., Nagashima, I., Dizon, T. O. T., & Natsuaki, K. (2013). Cross-Transmission and New Alternate Hosts of Banana bunchy top virus. *Tropical Agriculture and Development*, 57(1), 1–7. <https://doi.org/10.11248/jsta.57.1>

- Rajabaskar, D., Bosque-Pérez, N. A., & Eigenbrode, S. D. (2014). Preference by a virus vector for infected plants is reversed after virus acquisition. *Virus Research*, 186, 32–37. <https://doi.org/10.1016/j.virusres.2013.11.005>
- Rajan, P. (1981). Biology of *Pentalonia nigronervosa* f. caladii van der Goot, vector of 'katte' disease of cardamom. *Journal of Plantation Crops*, 9, 34–41.
- Ram, R., & Summanwar, A. S. (1984). *Colocasia esculenta* (L) Schott. a reservoir of bunchy top disease of banana. *Current Science*, 53(3), 145–146
- Rao, G., & Reddy, M. G. (2020). Overview of yield losses due to plant viruses. *Applied plant virology* (pp. 531–562). Elsevier.
- Robson, J. D., Wright, M. G., & Almeida, R. P. (2006). Within-plant distribution and binomial sampling of *Pentalonia nigronervosa* (Hemiptera: Aphididae) on banana. *Journal of Economic Entomology*, 99(6), 2185–2190. <https://doi.org/10.1093/jee/99.6.2185>
- Robson, J. D., Wright, M. G., & Almeida, R. P. (2007). Effect of imidacloprid foliar treatment and banana leaf age on *Pentalonia nigronervosa* (Hemiptera, Aphididae) survival. *New Zealand Journal of Crop and Horticultural Science*, 35, 415–422.
- Robson, J. D., Wright, M. G., & Almeida, R. P. P. (2014). Biology of *Pentalonia nigronervosa* (Hemiptera, Aphididae) on Banana Using Different Rearing Methods. *Environmental Entomology*, 36, 46–52.
- Selvarajan, R., Balasubramanian, V., Sheeba, M. M., Raj Mohan, R., & Mustafa, M. M. (2011). *Virus-indexing technology for production of quality banana planting material: a boon to the tissue-culture industry and banana growers in India*, 897 ed. *International Society for Horticultural Science (ISHS)*(pp. 463–469). Belgium: Leuven.
- Selvarajan, R., Mary Sheeba, M., Balasubramanian, V., Rajmohan, R., Dhevi, N. L., & Sasireka, T. (2010). Molecular characterization of geographically different banana bunchy top virus isolates in India. *Indian Journal of Virology : an Official Organ of Indian Virological Society*, 21(2), 110–116. <https://doi.org/10.1007/s13337-010-0020-1>
- Señeris, G. T., Vedasto, E. P., & Ragaas, M. L. (2022). Prevalence of Insect Pests, Beneficial Organisms and Diseases of Abaca (*Musa textilis* Nee) in Two Municipalities of Aklan, Philippines. *Universal Journal of Agricultural Research*, 10, 275–287.
- Shi, X. B., Yan, S., Zhang, C., Zheng, L. M., Zhang, Z. H., Sun, S. E., ... Zhou, X. G. (2021). Aphid endosymbiont facilitates virus transmission by modulating the volatile profile of host plants. *BMC Plant Biology*, 21(1), 67. <https://doi.org/10.1186/s12870-021-02838-5>
- Shimwela, M. M., Mahuku, G., Mbanzibwa, D. R., Mkamilo, G., Mark, D., Mosha, H. I., ... Kumar, P. L. (2022). First Report of Banana Bunchy Top Virus in Banana and Plantain (*Musa* spp.) in Tanzania. *Plant Disease*, 106(4), 1312. <https://doi.org/10.1094/PDIS-07-21-1387-PDN>
- Smith, M., Holt, J., Kenyon, L., & Foot, C. (1998). Quantitative epidemiology of banana bunchy top virus disease and its control. *Plant Pathology*, 47(2), 177–187. <https://doi.org/10.1046/j.1365-3059.1998.00230.x>
- Stainton, D., Martin, D. P., Muhire, B. M., Lolohea, S., Halafihi, M. I., Lepoint, P., & Varsani, A. (2015). The global distribution of Banana bunchy top virus reveals little evidence for frequent recent, human-mediated long distance dispersal events. *Virus evolution*, 1, vev009.
- Stechmann, D. H., Völkl, W., & Starý, P. (1996). Ant-attendance as a critical factor in the biological control of the banana aphid *Pentalonia nigronervosa* Coq.(Hom. Aphididae) in Oceania. *Journal of Applied Entomology*, 120, 119–123.
- Thangavelu, R., Selvarajan, R., & Singh, H. (2000). Status of banana streak virus and banana bract mosaic virus diseases in India, Banana: improvement, production and utilization. Proceedings of the conference on challenges for banana production and utilization in 21st century. AIPUB, NRCB, Trichy, pp. 364–376.
- Thomas, J. E. (2008). Banana Bunchy Top Virus. In B. W. J. Mahy & M. H. V. Van Regenmortel (Eds.), *Encyclopedia of Virology* (3rd ed., pp. 272–279). Oxford: Academic Press. <https://doi.org/10.1016/B978-012374410-4.00636-1>
- Thomas, J. E., & Iskra-Caruana, M. L. (2000). Banana bunchy top virus. In D. R. Jones (Ed.), *Handbook of Diseases of Banana*. Abacá and Enset (pp. 362). Oxfordshire, UK: CABI.
- Trang, A., & Khandhar, P. B. (2025). *Physiology, Acetylcholinesterase*. Treasure Island, FL: StatPearls Publishing.
- Tricahyati, T., Suparman, S., & Irsan, C. (2022). Natural enemies of *Pentalonia nigronervosa*, vector of banana bunchy top virus. *Biodiversitas (Surakarta)*, 23(7). <https://doi.org/10.13057/biodiv/d230745>
- Tripathi, L., Ntui, V. O., Tripathi, J. N., & Kumar, P. L. (2021). Application of CRISPR/Cas for diagnosis and management of viral diseases of banana. *Frontiers in Microbiology*, 11, 609784. <https://doi.org/10.3389/fmicb.2020.609784>
- Umer, M., Liu, J., You, H., Xu, C., Dong, K., Luo, N., ... Wang, G. (2019). Genomic, morphological and biological traits of the viruses infecting major fruit trees. *Viruses*, 11, 515. <https://doi.org/10.3390/v11060515>
- University of Hawai'i at Mānoa, College of Tropical Agriculture and Human Resources (CTAHR). (2006). *Colonies of Pentalonia nigronervosa* the banana aphid. Retrieved April 9, 2026, from https://www.ctahr.hawaii.edu/bbtd/aphid_colonies.asp
- U.S. Environmental Protection Agency. (2025). *Neem oil pesticide product label* U.S. EPA. Retrieved April 9, 2026, from https://www3.epa.gov/pesticides/chem_search/ppls/093771-00001-20250408.pdf
- U.S. Environmental Protection Agency. (2001). *Azadirachtin; clarified hydrophobic extract of neem oil (G-127): Fact sheet*. U.S. EPA. https://www3.epa.gov/pesticides/chem_search/reg_actions/registration/fs_G-127_01-Oct-01.pdf
- van Munster, M. (2020). Impact of Abiotic Stresses on Plant Virus Transmission by Aphids. *Viruses*, 12(2), 216. <https://doi.org/10.3390/v12020216>
- Vikrant, Chowdhury, S., & Majumder, S. (2025). First report and molecular characterisation of banana bunchy top virus infecting *Musa × Paradisiaca* Cv. Chiniya from West Bengal, India. *Vegetos*, 1–8.
- Vikrant, Singh, J., and Majumder, S. (2024). First report of banana bunchy top virus infecting *Colocasia esculenta* (L.) Schott, from India. *Journal of Plant Pathology*, 106, 757–757. <https://doi.org/10.1007/s42161-023-01577-w>
- Viswakethu, V., Ramasamy, V., Balakrishnan, P., & Narayanasamy, B. (2026). Biological control of banana aphid *Pentalonia nigronervosa* by *Akanthomyces lecanii*, role of volatile-mediated interactions. *Journal of Invertebrate Pathology*, 108673.10.1016/j.jip.2026.108673
- Viswanathan, S., & Regupathy, A. (1991). Studies on banana aphid *Pentalonia nigronervosa* f. typica Coq field population and in yellow sticky trap catches. *South Indian Horticulture*, 39, 124–129.
- Viswanathan, S., Regupathy, A. (1992). Bioecology of banana aphid *Pentalonia nigronervosa* f. typical. In Goel, S. C. (Ed.), *Proceedings*

- of the *Proceedings of the National Symposium on Growth, Development Control Technology of Insect Pests, 1992, India.*
- Völkl, W., Stechmann, D., & Stary, P. (1990). Suitability of five species of Aphididae (Hymenoptera) for the biological control of the banana aphid *Pentalonia nigronervosa* Coq. (Homoptera, Aphididae) in the South Pacific. *International Journal of Pest Management*, 36, 249–257.
- Walangululu, M. J., Matara, M. R., Bahati, L., Niyongere, C., Lepoivre, P., & Blomme, G. (2010). Assessing the spread and seasonal influence of fruit peel disease and banana bunchy top disease in South Kivu, Eastern DR-Congo. *Tree and Forestry Science and Biotechnology*, 4, 98–104.
- Wang, T., Wang, K., Wang, C., Zhao, Y., Tao, Z., Li, J., ... Li, P. (2023). Combining quantitative trait locus mapping with multiomics profiling reveals genetic control of corn leaf aphid (*Rhopalosiphum maidis*) resistance in maize. *Journal of Experimental Botany*, 74(12), 3749–3764. <https://doi.org/10.1093/jxb/erad113>
- Wardlaw, C. (1972). Banana diseases including plantains and abaca. (No. Ed. 2, pp. ix+878)
- Watanabe, S., Greenwell, A. M., & Bressan, A. (2013). Localization, concentration, and transmission efficiency of Banana bunchy top virus in four asexual lineages of *Pentalonia* aphids. *Viruses*, 5(2), 758–776. <https://doi.org/10.3390/v5020758>
- Waterhouse, D. F. (1987). *Pentalonia nigronervosa* Coquerel. In W. K. R. Norris (Ed.), *Biological Control: Pacific Prospects*. D. F. (pp. 42–49). Melbourne: Inkata Press.
- Wu, R.-Y., & Su, H.-J. (1990). Transmission of banana bunchy top virus by aphids to banana plantlets from tissue culture. *Botanical Bulletin of Academia Sinica*, 31(1), 7–10.
- Yang, L., (1989). Bionomics of *Pentalonia nigronervosa* Cog. *Insect Knowledge*, 26, 145–146.
- Yasmin, T., Ehsan, U., Khalid, S., & Malik, S. (1999). Some studies on biology of *Pentalonia nigronervosa* Conquarrel, the vector of banana bunchy top virus. *Pakistan Journal of Biological Sciences*, 2, 1398–1400. <https://doi.org/10.3923/pjbs.1999.1398.1400>
- Young, C. L., & Wright, M. G. (2005). Seasonal and spatial distribution of banana aphid, *Pentalonia nigronervosa* (Hemiptera: Aphididae), in banana plantations on Oahu. *Proceedings of the Hawaiian Entomological Society*, 37, 73–80.
- Zhang, S., Zhang, Z., Bales, C., Gu, C., DiFonzo, C., Li, M., ... Wang, D., (2017). Mapping novel aphid resistance QTL from wild soybean, *Glycine soja* 85–32. *Theoretical and Applied Genetics*, 130, 1941–1952.

Manuscript received: August 22, 2025

Revisions requested: March 7, 2026

Final revised version received: June 6, 2026

Manuscript accepted: July 3, 2026

The pdf version (Adobe JavaScript must be enabled) of this paper includes an electronic supplement:
Supplementary methods, Table S1–S3, Fig. S1–S5.