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Review

Mealybug vectors: A review of their transmission of plant viruses and their management strategies

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Abstract: Mealybugs cause mechanical damage and diseases to plants. Through their feeding activities, they reduce the yield, quality and productivity of crops. This review discusses mealybug vectors of plant viruses, the economic losses they cause, mealybug species and their hosts. Among the numerous mealybug species, *Planococcus* species are the most effective vector of plant viruses, transmitting many Ampeloviruses. Diverse methods for the control and regulation of mealybugs are also discussed. Physical, cultural and biological control methods are labor-intensive but environmentally friendly compared to chemical methods. However, chlorpyrifos are one the active ingredients of insecticides effective against several mealybug species. Using plant products such as neem oil as a biocontrol method has been effective, similar to other insecticides. Notwithstanding, the biological method of controlling mealybugs is effectively slow but safe and highly recommended. The Anagyrus species have the highest success rate amongst other natural parasites of mealybugs. Also, farm sanitation and pruning as cultural methods help reduce mealybug populations.

Keywords: Mealybugs; *Planococcus*; *Pseudococcus longispinus*; *Dysmicoccus brevipes*; Closteroviridae; Ampeloviruses

1. Introduction

The world's population is growing so fast that at the end of 2021 it was 7.9 billion people [1]. This is a rapid growth rate compared to ten years ago (6.194 billion) [2]. With this growth rate, it is estimated that the world population will be around 9,782,061,758 in 2051 [3].

This exponential growth trend has an adverse impact on food security. To meet the dietary requirements for this population growth, food production needs to be scaled up. Among the various food sources, plants are the largest food source for humans. A total of 50–90% of the human diet is of plant origin [4]. However, these contributions of plant products to the human diet are likely to diminish due to several factors. The decrease in agricultural land use size, plant diseases and other biotic factors threaten plant productivity. Among these factors, plant pathogenic diseases are the major problem, where 16% of annual plant yield losses are due to plant pathogenic diseases [5].

Plant pathogens contributes a troubling decline in global food security and crop production [6]. Plant pathogens are transmitted through a variety of vectors. Insects and nematodes [7] play a role in pathogen transmission. Insects, the most popular and effective of all the vectors, pose a concern for plants, animals and human health [8].

Two orders of insects (Hemipterans and Thysanopteras) have the most devastating effect on crop yield [9]. Among the various orders of insects, Hemipteran [10], Coleopteras [11], Thysanoptera (generally thrips) [12–15], Lepidoptera [16] and Diptera [17,18] are known vectors of plant viruses, fungi and bacteria. Close to one-fourth of all plant viruses require insect vectors for effective transmission [9]. Coleopterans are effective transmitters of Bromoviruses, Carmoviruses, Comoviruses, Machlomoviruses, Sobemoviruses and Tymoviruses [19]. Hemipterans (aphids, whiteflies and leafhoppers), transmit most plant viruses and bacteria. They are infamous for the transmission of more than one pathogen. Furthermore, their brisk reproductive cycles and diverse plant hosts give them an advantage in plant virus transmission [20,21]. Although thrips, aphids and whiteflies account for over 50% of plant virus transmission [22,23], the role of mealybugs in plant viruses transmission is noteworthy. Of the Homoptera insect order, mealybugs are one of the major vectors of plant viruses [24]. With various biotic problems of plants, viral diseases are one of the biggest constraints to plant health [25]. Transmission of plant viruses is dependent on the mealybug life stage, temperature and suitable host. However, information about the viruses transmitted by mealybugs is not comprehensive as that of aphids, whiteflies and thrips. This article provides a comprehensive review of the different types of plant viruses transmitted by different species of mealybugs, and various management strategies to reduce and control the devastating effects of mealybugs.

2. Morphology of mealybugs

Mealybugs (*Pseudococcidae*) are destructive insect pests of crop plants. Mealybugs are either monophagous [26] or polyphagous. Mealybugs perfectly homogenize with their host plant, thanks to the wax produced by the host plant, which covers them and offers them camouflage. It is estimated that 149 mealybug species feed on plants with their piercing and sucking feeding behavior. The *Planococcus* species are the most common and destructive [27], causing severe mechanical damages to crop plants. Despite having a diverse feeding host, woody and herbaceousplants are most preferred. They pierce and suck the plant sap, which causes sooty mold from releasing sap materials, reduces the plant chlorophyll content and thus affect photosynthesis [28–30]. During feeding, viral particles (especially those retained in the stylet and foregut) are released through their stylet [31]. The stylets are withdrawn into the body after and when not feeding [32].

Mealybugs are approximately 5mm long [33], with adult females 3-5mm and males average 3mm long [34,35]. Adult females retain some nymph-like features attributable to incomplete metamorphosis and are wingless. Similarly, male adults also undergo incomplete metamorphosis, but they are much smaller than the females and possess wings that aid them in moving to female mealybugs for mating [26,33,36].

2.1. Life cycle of mealybugs

The lifecycles of mealybugs differ according to their sex and species [37]. Male and female mealybugs have the same life cycle from the egg stage to the 2nd instar stage. In males, the prepupa stage is the next stage after the 2nd instar stage, then follows the Pupa, and finally to the adult male stage. However, unlike the male, the female mealybug has a 3rd instar stage that ends at the adult stage [38], as observed in Figure 1a and b below.

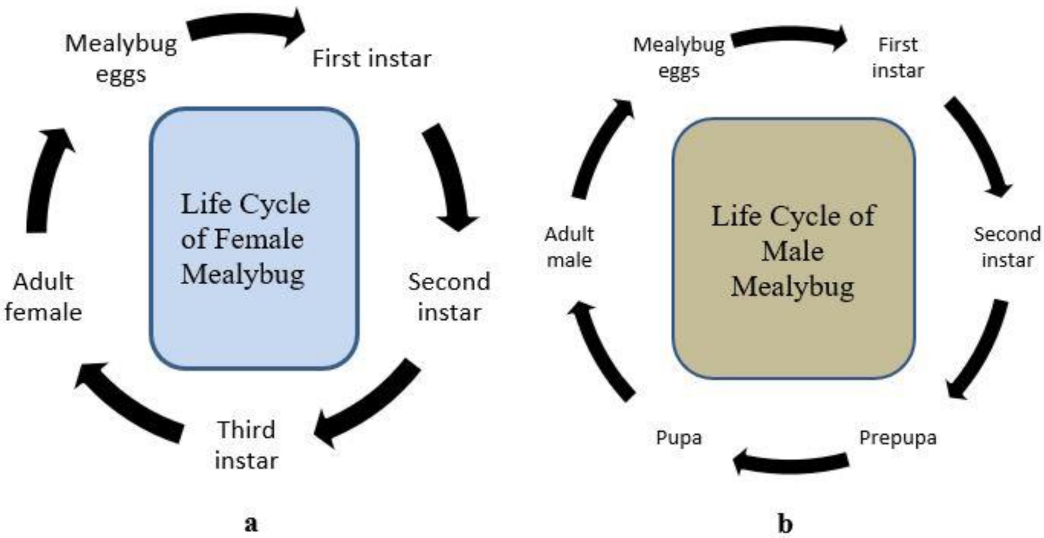

Figure 1. Illustration of female and male mealybug lifecycles (adapted and altered from [37,38]).

As observed from Figure 1a and b, male and female mealybugs have similar life cycles. However, certain mealybug species may require additional stages. The male pineapple mealybug (*Dysmicoccus brevipes* Cockerell), longtailed mealybug (*Pseudococcus longispinus*) were confirmed to have a third Instar stage between the second instar and prepupa stage [37,39]. Also, the female pineapple mealybug had a crawler stage instead of the first instar stage. Daane et al. (2008) also reported a similar life cycle of *Planococcusficus* to that of *Dysmicoccus brevipes.*

2.2. Hosts of mealybugs

Different species of mealybugs are found on plants in greenhouses, nurseries, plants and landscapes. Over the world, approximately 246 of several plant families serve as hosts for almost 5000 species of mealybugs [41]. Poaceae are the most popular host plants (585 species) for mealybugs, with Cyperaceae having the least number of host plants (75 species), and [42–44] emphasized that mealybugs feed on nearly 149 plant species, through the sucking of plant sap which causes leaves to distort and fall.. Destruction and pathogen transmission by mealybugs have been reported on guava, citrus, pomegranate, grapes, sugarcane, banana, black pepper, pineapple plantain, stone fruit, berries, yam, cassava, cashew, papaya, pawpaw and cocoa [31,42,45–50].

Weeds such as *Amaranthus vividus, Bidens Pilosa, Sonchus oleraceus, Chenopodus ambrosoides, Commelina sp., Cucumis anguria, Momordica charantia, Cyperus rotundus, Chamaesyce hirta, Croton sonderianus, Jatropha urens, Mimosa pudica, Piptadenia moniliformis, Serra macranthera, Herissanthia crispa, Sida cordifolia, Sida galheirensis, Sida rhombifolia, Sidastrum micranthum, Sidastrum sp., Digitaria horizontalis, Talinum paniculatum, Watheria douradinha, Malva sylvestris* L., *Redroot pigweed, Amaranthus retriflexus* L., *Crimson clover, Trifolium incarnatum* L., Toadflax, *Linaria sp.* and *Chorizococcus rostellum* also serve as host plants for mealybugs [51,52]. Various degrees of mealybug infestation have been reported in Kenya [53], Nigeria [54], Ghana [48,50,55,56], Indonesia [57], New Zealand [58], India [57,59–61] and Israel [26]. In Turkey, 25 weed species from 14 plant families were found to host 5 mealybug species [51].

2.3. Some reported economic losses due to mealybugs

Several studies have confirmed the economic losses caused by the destructive effects of mealybugs and the virus diseases they transmit. According to Asare Bediako et al. [50], the mealybug wilt of pineapple (MWP) causes approximately US $248/ha in losses to pineapple fruit yield in Ghana, while causing 30–50 % of fruit yield loss in Hawai in the United States, depending on the age of the plant. Three cassava mealybugs (*Phenacoccus manihoti*, *Planococcus herreni* and *Planococcus* spp.) have been reported to cause cassava yield reduction in Sub-Saharan Africa. *Phenacoccus manihoti* is estimated to cause an 80% reduction in cassava yield [62]. Similarly, the Hibiscus mealybug (*Maconellicoccus hirsutus*) is indicated to cause a US $75 million loss annually in the United States of America [26]. Prabhakar et al.[30] reported various economic losses in several countries due to cotton mealybug (*Phenacoccus solenopsis),*Papaya mealybug (*Paracoccus marginatus*) and several mealybugs on cotton plant yields. Previous studies show that green coloration occurs in situations where both the male and female mealybug are found (especially between *Dysmicoccus brevipes and Dysmicoccus neobrevipes*) but are absent in a situation where only one parent was found (either male or the female) [63]. This green colouration affects the quality and market value of the produce. It is worth noting that the direct effect of viruses transmitted by mealy bugs is difficult to estimate since other factors in combination with the virus diseases cause economic damages to the crops. In a review by Franco et al. [64], *Planoccocus citri* and other species of mealybug cause economic losses in citrus orchards in the Mediteranean regions.

Table 1. A summary of selected plant virus mealybug vectors, their common names and host plant information.

Species of Mealybugs	Common Names	Host Plants	References
Pseudococcus longispinus	Longtailed mealybug	Citrus, grapes, nursery stock, indoor ornamentals, citrus, taro, avocado, guava, eggplant.	[34,35,65]
Pseudococcus maritimus	Grape mealybug	Grapes, Pears, Pomegranate other fruit trees, apricots	[34,35,66]
Planococcus citri (cryptus)	Citrus mealybug	Citrus, landscape shrubs	[34,35,51]
Planococcus ficus	Vine mealybug	Grapes, fruits, ornamental plants	[34,35,40,67]
Rastrococcus iceryoides and *R. invadens*	Mango Mealybug	Mango and Citrus	[35,68]
Dysmicoccus brevipes	Pineapple mealybug	Pineapple, avocado, banana, celery, citrus, clover, cocoa, coconut, coffee, custard apple, figs, ginger, guava, maize, mango, oil palm, orchids, groundnut, peppers, plantain, potato and sugarcane.	[26,35,69,70]
Planococcus kenyae	Kenya mealybug	Coffee, yam, pigeon pea, passion fruit, sugarcane and sweet potato	[27,71]
S*accharicoccus sacchari*	Sugarcane mealybug	sorghum, rice and some grasses, sugarcane	[26,72]
Ferrisia virgata	Striped mealybug	Common on most crops	[26,34]
Ferrisia gilli	Gill's mealybug	Pistachios	[73]
Heliococcus bohemicus	Bohemian mealybug	Grapevine	[74]
Phenacoccus aceris	Apple mealybug	Grapevine, apple	[74]
Planococcus solani Ferris *Phenococcus solenopsis* Tinsley	Solanum mealybug	Solanaceous crops	[34,35]
Maconellicoccus hirsutus	Pink hibiscus mealybug	Hibiscus	[35,75]
Paracoccus marginatus	Papaya mealybug	Papaya, Solanaceous crops, cotton, pomegranate, pea, sweet potato.	[30,53,76]
Nipaecoccus viridis	Spherical mealybug	Cotton	[77]
Planococcus kraunhiae	Japanese mealybug	Broad bean	[26,78]
Planococcus minor	Passionvine mealybug	Vine	[79]
Planococcus njalensis	Cocoa mealybug	Cocoa	[54]
Pseudococcus viburni	Tuber mealybug	Donkey lettuce, Whitestem filaree, Tubular flower, Spanish needle, Hairy fleabane, grapes, persimmon	[80–82]

3. Mealybug vectors of plant viruses

Compared to aphids and whiteflies, mealybugs are transmitters of a few genera of plant viruses. Due to their less mobile nature, they are less effective in transmitting plant viruses than aphids, leafhoppers and other insect vectors. In addition, the sex and age of mealybugs affect virus transmission rates. For example, old female mealybugs are less efficient in transmitting plant viruses [83]. Also, the life stages of the nymph affect their transmission rate of viruses (adults are more effective than nymphs) [19].

Mealybugs transmit viruses of the genus Ampelovirus [31,63], and some Closteroviruses [84], of the Closteroviridae family. Mealybugs also transmit badnavirus [47,85] of the Caulimoviridae family. Closteroviridae generally consists of four genera- Closterovirus, Ampelovirus and Crinivirus, Velarivirus [86,87]. Some studies have also confirmed the transmission of vitiviruses by some mealybug species [83]. These viruses trigger leaf discoloration, deformation, mottling and leaf yellowing.

3.1. Ampeloviruses transmitted by mealybugs

Based on the organization of the positive-strand RNA genomes, Ampeloviruses can be subdivided into different groups [87]. Ampeloviruses have a non-enveloped capsid, 1400–2200 nm long virion, 13.0–18.5 kb segmented genome [86] and filamentous shape. The genome of Ampelo-like air potato virus 1 (AiPoV1) is estimated to be around 13,398 nucleotides [88]. Mealybugs are the main vectors of Ampeloviruses. In a semi-persistent manner, mealybugs transmit Ampelovirus and other viruses in the Ampelovirus genus in a semi-persistent mode (GLRaV 3) [31,89]. In semi-persistent (foregut-borne) virus transmission, viruses are spread from the stylet of the insect up to the foregut. The virus does not spread beyond the foregut of the insect vector. Within 20 minute-period, the mealybug picks up the virus and infects the host [90]. The virus does not reproduce and multiply in the vector, and retention of the virus in the host spans from hours to days [9]. Studies indicate that semi-persistent viruses influence the feeding behavior of their host [91]. The injuries caused by their stylets during feeding, triggers plant defense response [62]. During feeding, the saliva of some mealybug species, especially *Maconellicoccus hirsutus*, causes harmful effects to plants [92]. Ampeloviruses cause vascular diseases with obscure symptoms. However, studies show that Ampelovirus, when combined with other viruses, causes mixed infection in plants [88]. Most Ampeloviruses are transmitted by *Dysmicoccus brevipes* (*Pseudococcus brevipes*), *Dysmicoccus neobrevipes* [63] and *Pseudococcus longispinus*.

From Table 1, *Planoccocus* mealybug species are more active in transmitting plant Ampeloviruses. *Planococcus ficus* is a regular transmitter of five strains of Grapevine leafroll associated viruses [93]. These can cause mixed infections since the mealybugs are vectors of numerous viruses [88] as observed in Table 2. According to a study by Sether et al. [94], Pineapple mealybug-associated wilt viruses, when associated with pineapple's Mealybug wilt virus, resulted in 100% yield loss. Also, mealybugs acquire and transmit viruses with or without association with other viruses. For example, mealybugs (*Dysmicoccus brevipes* and *Dysmicoccus neobrevipes*) were found to transmit Pineapple Mealybug-associated virus-3 (PmaV-3) without the transmission of PmaV-1 [94], although they are vectors of these two viruses [95]. It is worth noting that some other insect species do actively transmit Ampeloviruses. For example, *Parthenolecanium corni* (Coccidae) was reported to transmit GLRaV-3 [96].

Table 2. A summary of some ampeloviruses and their mealybug vectors.

Virus species	Mealybug vectors	Hosts	References
Air potato ampelovirus (AiPoV 1)	*Planococcus* spp.	Air potato	[88]
Blackberry Vein banding associated virus	*Planococcus* spp.	Blackberry	[97,98]
Grapevine leafroll-associated virus 1	*Planococcus ficus, Pseudococcus longispinus, Phenacoccus aceris, Heliococcus bohemicus*	Grapevine	[19,74,99]
Grapevine Leafroll - associated virus 3	*Planococcus ficus, Pseudococcus. longispinus, Ferrisia gilli, Phenacoccus aceris, Pseudococcus calceolariae, Heliococcus bohemicus,Pseudococcus maritimus*	Grapevine	[19,74,96,99–102]
Grapevine leafroll-associated virus 4	*Planococcus ficus, Pseudococcus longispinus, Phenacoccus aceris*	Grapevine	[19,101,103]
Grapevine leafroll associated virus 13	*Planococcus ficus, Pseudococcus longispinus*	Grapevine	[19,95]
Pineapple mealybug associated viruses 1 and 3	*Dysmicoccus brevipes,Dysmicoccus neobrevipes*	Pineapple	[19,104]
Pineapple mealybug associated virus 2	*Dysmicoccus brevipes, Dysmicoccus neobrevipes*	Pineapple	[19,50,63,98]
Pistachio ampelovirus	*Planococcus ficus*	Pistachio	[105,106]
Fig leaf mottle associated viruses 1 and 2	*Ceroplastes* spp.	Fig	[107,108]
Manihot esculenta virus 1	*Phenacoccus manihoti, Phenacoccus herreni*	Cassava	[62]

3.2. Closteroviruses transmitted by mealybugs

The genus Closterovirus belongs to the family Closteroviridae. Closteroviruses have two huge gene modules: one for genome replication, and the other for genome packaging and transport within the cells. The genome of Closterovirus is linear, positive RNA, with a maximum size of 19.3 kb [109].

In comparison to Ampeloviruses, fewer Closteroviruses are transmitted by mealybug vector species. For example, the Little cherry virus 2 belonging to the closterovirus genera is transmitted by *Phenacoccus aceris* [83,110].

3.3. Badnavirus transmitted by mealybugs

The genus Badnavirus belongs to the Caulimoviridae family. Viruses found in Caulimoviridae have semicircular double-stranded DNA. They have a genome length range of 7.2–9.2 kbp. Eight divisions (Badnavirus, Caulimovirus, Cavemovirus, Petuvirus ,Rosadnavirus, Solendovirus, Soymovirus and Tungrovirus) are members of the Caulimoviridae family based on host range, insect vector and the basis of genome organization [111]. Badnaviruses affect monocots and dicots. Most Badnaviruses are horizontally transmitted through mealybugs and aphids [111,112]**.** Fewer or no symptom is associated with Badnavirus infections [113]. The effectiveness of their transmission is dependent on the species of mealybugs. Badnavirus often have more than one species of the same vector as transmitters (Table 3). For example, 14 established vectors of Cocoa Swollen Shoot Virus [114], of which *Planoccoides njalensis*, *Planococcus citri*, *Ferrissia virgata* are potent transmitters of the Cocoa Swollen Shoot Virus [115]. Mealybugs usually feed on the flowers and pods. Like Ampelovirus, Badnaviruses are transmitted by mealybugs in a semi-persistent manner [115].

Table 3. A summary of badnaviruses transmitted by mealybug vectors.

Virus Species	Mealybug vectors	Hosts	Reference
Cocoa Swollen Shoot Virus	*Planoccoides njalensis, Planococcus citri, Ferrissia virgata*	Cacao	[114,115]
Banana Streak Virus	*Planoccocus citri Risso,Saccharicoccus sacchari,Dysmicoccus brevipes,Ferrisia virgata*	Banana	[69,83]
Citrus Yellow Mosaic Badnavirus	*Planococcus citri*	Citrus	[33]
Sugarcane bacilliform virus	*Saccharicoccus sacchari*	Sugarcane	(Sastry, 2013)
Piper yellow mottle virus	*Ferrisia virgata,Planococcus citri,Pseudococcus elisae,*	Black pepper	[19,83]
Sugarcane mild mosaic virus	*Saccharicoccus sacchari*	Sugarcane	[19]
Taro bacilliform badnavirus	*Pseudococcus solomonensis*	Taro	[83]
Schefflera ringspot virus	*Planococcus citri*	Schefflera	[83]
Dioscorea bacilliform RT virus	*Planococcus spp*	Yam	[116]

3.4. Vitiviruses transmitted by mealybugs

Vitiviruses belong to the family Flexiviridae and they are flexuous, filamentous, 12–13 in diameter [117] and 725–825 nm in length [118]. They are monopartite, positive sense and single-stranded**.** Vitiviruses were initially considered Trichoviruses, but the differences in their genome organizations provided a basis for their differentiation [119]. Their virions contain RNA genome in a tail-like structure facilitating their transmission to plants by their insect vector [117].

Table 4. A summary of vitiviruses and mealybug vectors.

Plant virus	Mealybug vector	Hosts	References
Grapevine virus A (Kober Stem Grooving)	*Pseudococcus spp,Planococcus ficus*	Grapevine	[31,82,83]
Grapevine virus B (Corky bark disease)	*Planococcus ficus*	Grapevine	[31,82,83]
Grapevine Virus D	*Phenacoccus spp*	Grapevine	[83]
Grapevine Virus E	*Heliococcus spp*	Grapevine	[31,83]

Vitiviruses are transmitted by mealybugs and other insect genera (*Pseudococcus, Planococcus, Phenacoccus, Heliococcus, Neopulvinaria, Parthenolecanium, Cavariella* and *Ovatus*)(Table 4) in a semipersistent manner [83].

4. Management strategies for mealybugs

Recent technological advances have influenced the methods and dynamics of controlling and managing mealybugs. Feeding behaviors determine the control strategy. The common management strategies are physical, chemical, cultural and biological. Environmental conditions such as temperature, humidity and others are considered when designing pest management strategies.

Table 5. A summary of mealybug species and physical control.

Mealybug Species	Physical Method	Key findings	Reference
Dysmicoccus brevipes, Dysmicoccus neobrevipes	Ant barriers	Red ants were controlled causing the decrease in pink pineapple mealybug transportation	[120]
Planoccocus njalensis	Crop barriers, Barrier cropping	Farms with barrier crops had low mealybug infestation cases in comparison to those with none	[115,121]
Drosica mangiferae	Crop rotation	Adequate control of mango mealybug	[122]
Planococcus ficus	51–53 °C hot water treatment of grape cuttings	Eradication of more than half of *Planococcus ficus* population	[123]
Planococcus ficus	Ultralow oxygen treatment	Complete eradication of all life stages of *Planococcus ficus*	[82]
Dysmicoccus brevipes, Dysmicoccus neobrevipes	50 °C-30 minutes hot water treatment of pineapple propagules	Most of the mealybug population were destroyed	[124]
Planococcus citri Rossi, *Pseudococcus odematti* Miller and Williams	Hot water immersion of propagules	90–95% of the mealybug population were eliminated	[123]

4.1. Physical methods

The physical (mechanical) pest control method involves using hurdle to reduce the contact between the pest and the crop. Physical control eliminates the pest or triggers behavioral or feeding changes in the pest [125].

Most physical methods share some similarities in their pest-elimination strategies. Despite their effectiveness, they are time-consuming and labor-intensive. Hand-picking of mealybugs, and cutting off tree parts heavily infested by mealybugs control mealybugs [34,35,115]. Growing barrier crops and destroying wild mealybug host plants have reduced contact between the mealybug vector and the host plant. Ameyaw et al.[115] reported on using citrus and oil palm in cocoa farms as barrier crops since they are not appropriate hosts for the mealybug vectors of Cocoa Swollen shoot virus. These crops break the mealybug vectors cycle since they are unsuitable hosts.

Results from studies performed by Franco et al.(2004) on pheromone traps to control *Planococcus citri* and *Pseudococcus cryptus* male mealybugs indicated that male mealybugs of the *Planococcus citri* population was significantly reduced. Also, trapping and eliminating mealybugs have proven to be a population regulator of mealybugs. Sticky plate traps help regulate some mealybugs species, especially *Planococcus citri* [26]. Similarly, the pheromone of some mealybug species can be manipulated to attract predators or natural enemies to them (as in the case of *Anagyrus pseudococci* in the control of *Planococcus ficus*) [26]. Also,the use of biological barriers,heat treatment amongst others are suitable in the control of mealybug species as seen in Table 5.

4.2. Cultural Methods

Like other pest control methods, cultural methods are diverse. They are environmentally friendly but labor-intensive. The cultural method involves a combination of practices that reduces the population and interrupt the infection cycle of pests. They include crop rotation, sanitation practices [34,35] and humidity control on the farm (Table 6).

Table 6. A summary of mealybug species and cultural controls.

Mealybug species	Cultural method	Key findings	References
Planococcus ficus	resistant rootstocks (IAC 572,10-17A, RS-3)	Resistant rootstocks were more resistant to *Planococcus ficus* infested as compared to other rootstocks	[82,123,126]
Planococcus ficus	Low soil nitrogen content	Grape plants on low nitrogen level soil had low mealybug presence in comparison to other grape plants on soils with high nitrogen content	[82]
Formicoccus njalensis, Planococcus citri	Breeding resistant varieties	Mealybug infestation was less in comparison to non-resistant varieties	[121]
Sachharicoccus sacchari	Resistant varieties (Giza 96/74, Ph 8013)	Self-peeling varieties were less infected by the S*accharicoccus* mealybug as compared to other varieties	[127,128]
Planococcus njalensis	Roguing and pruning	Cocoa crops with pruned diseased parts had less mealybug infestation as compared to those not pruned	[121]
Saccharicoccus sacchari	Flood irrigation, burning of dry leaves in the field	Number of mealybug infestation per plant was reduced	[128]
Saccharicoccus sacchari	Low nitrogen fertilizer application, roguing, farm sanitation	Mealybug population was lower in farms where these practices were enforced	[128]
Saccharicoccus sacchari	Drip irrigation	Increased drip irrigation method significantly reduced S*accharicoccus sacchari* population	[128]

Some crops have a genetic combination that helps them rejuvenate and regenerate after heavy mealybug feeding. AR23 (cassava genotype), an improved variety of cassava, was found to develop new leaves and rejuvenate into a healthy plant after severe damage was caused by the cassava mealybug [62]. Inter-Upper Amazon Hybrids of cocoa also have resistivity against heavy mealybug infestation [90]. However, there is innate resistance in some plants against some species of mealybugs. For example, different citrus varieties are reported to show varying levels of susceptibility to the citrus mealybug [79]. This underlines mealybug species preferences for special kinds of plants over others.

In addition, regular pruning of trees in and around the farm is encouraged. Mealybugs develop and multiply rapidly in a warm and humid environment [83]. Pruning trees deprives mealybugs of the necessary moist conditions. Thus, it exposes them to harsh weather conditions, such as sunlight that will slow or stop their rapid growth and gradual extinction.

Sanitation practices on the farm should be considered. The destruction of old and new heavily infested plant propagules should be practiced. In addition, farm equipment should be sanitized to reduce the transport of mealybug eggs within the farm. The destruction of cocoa trees affected by the Cocoa swollen Shoot Virus reduced the spread of the plant virus to healthy cocoa plants [90].

Also, fertilizers and irrigation within the farm should be regulated. Studies have demonstrated a relationship between wet soils coupled with high nitrogen content and mealybug growth [92]. There is a significant multiplication of mealybugs in the farm if the soil has high water content with significantly higher nitrogen levels. Daane et al. [40] confirmed the increase in the *Planococcus ficus* population due to increased nitrogen fertilizer use. Soils with high moisture content and adequate nitrogen levels help regenerate new plant parts. The mealybug then has new and succulent plant parts to feed on, and reproduction is encouraged. Adversely, Rae et al. [72] observed an increase in the *Saccharicoccus sacchari* at 320mg/L of nitrogen, but their population declined at a relatively higher nitrogen concentration.

4.3. Biological control

Biological pest control methods use natural enemies to eliminate or reduce the population of pests. Biological control methods, although labor-intensive, are environmentally friendly. Recently, biological pest control methods have been gaining popularity. Several natural parasitoids of mealybugs have been enacted, but only a few have proven very effective. Aphelinidae and Platygasterida species have yielded appreciable results [26]. Natural enemies of mealybugs are numerous e.g. parasitic wasps, ladybird beetles, hoverflies, lacewings [35], etc. This wasp lays its eggs on the maturing mealybugs, killing these mealybugs and feeding on them. *Gyranusoidea*, *Coccophagus, Leptomastix, Allotropa, Pseudaphycus* and *Acerophagus* are reported to be parasitic wasps of mealybugs [26,129]. In Africa and South America, *Apoanagyrus lopezi and Epidicarno lopezi* are reported to be effective in regulating the Cassava mealybug (*Phenaccocus manihoti*) [35,62]. *Gyranusoidea tebygi* and *Anagyrus mangicola* are natural enemies of the mango mealybugs, *Rastrococcus invadens and Rastrococcus iceryoides* [34,35]. In addition, the population of citrus mealybug is reported to be reduced by natural parasites, such as *Leptomastidea abnormis* (Girault), *Leptomastix dactylopii* Howard, *Chrysoplatycerus splendens* Howard and *Anagyrus pseudococci* (Girault). However, parasitic fungus, such as *Entomophthora fumosa and* other natural parasites (brown lacewing, *Sympherobius barberi* (Banks) and green lacewing, *Chrysopa lateralis* Guérin, trash bugs, syrphid fly larvae and scale-eating caterpillars, *Laetitia coccidivor, Cryptolaemus montrouzieri* Mulsant, *Decadiomus bahamicus* (Casey) *Scymnus flavifrons* Melsheimer, *Chilocorus stigma* (Say) and *Olla abdominalis* var. *plagiata* (Say), are reportedly effective against some species of mealybug [130].

The mode of action by which these parasitoids and predators suppress and eliminate different species of mealybugs differs. For example, *Epidicarnosis lopezi*, a parasitoid of cassava mealybugs, lays eggs on the mealybug and their larvae feed on them [26]. Similarly, the mealybug predator *Cryptolaemus montrouzieri*, reported by Anjana and Joy [37], can feed on a maximum of 5000 mealybug eggs in various life stages. Additionally, *Anagyrus kamali* controls the pink mealybug population by piercing the adult mealybug and laying eggs in them. The eggs hatch and the contents of the mealybug are used to nourish itself until it attains adulthood [37].

Consideration should be given to other insects (especially ants) that may antagonize the success of this biological control based on their relationship with mealybugs. The population of ants must be under control since they can mitigate the effectiveness of this method. Some ants have a mutualistic relationship with mealybugs [26,37,40], since they benefit from the honeydews made by mealybugs. Ants have an antagonistic relationship with the natural enemies of mealybugs. Also, ants play a role in the transportation and dispersion of several mealybug species [90], as several studies have demonstrated the transport and dispersal of mealybugs by ants [26,131].

The citrus mealybug (Planococcus citri) is reported to be effectively controlled by a range of parasites such as *Eptomastidea abnormis* (Girault), *Leptomastix dactylopii* Howard,*Chrysoplatycerus splendens* Howard and *Anagyrus pseudococci* (Girault) (Table 7).

Table 7. A summary of mealybug species and biological control agents.

Mealybug species	Natural Predators	Key findings	References
Planococcus citri	*Leptomastix dactylopii*	L*eptomastix* was superior to other natural enemies	[26,132]
Phenacoccus manihoti	*Apoanagyrus lopezi*, *Epidinocarsis lopezi*,*Apoanagyrus diversicornis*	Apoanagyrus species had maximum control of the cassava mealybug species in relation to other natural enemies	[133–135]
Rastrococcus invadens	*Gyranusoide tebygi*, *Anagyrus mangicola*	Effective control of *Rastrococcus invadens*	[35]
Planococcus ficus	*Anagyrus pseudococci*, *Nephus angustus, Nephus quadrivattus, Nephus ninaevatus, Nephus sp., Hyperaspis felixi, Sycmnus nubilis Mulsant, Cynodia lunata, Rhizobiellus sp., Hippodamia sp., Chrysopa sp.*	The Anagyrus species was more effective in controlling *Planoccocus ficus* mealybug	[26,136]
Phenacoccus solenopsis	*Oenopia* (Synharmonia) *conglobata*(L.), *Cheilomenes propingua* (Mulsant) *Chrysoperla carnea* (Stephens), *Chrysoperla mutata* (Mc Lachlan) (Neuroptera: Chrysopidae), *Sympherobius elegans* (Stephens); *Sympherobius fallax* (Navas), (Neuroptera: Hemerobiidae)	These parasitoids had higher parasitizing activity as compared to other predators	[137,138]
Dysmicoccus brevipes	*Heterorhabditis amazonensis* (NEPET 11 and IBCD.n40)	These two isolates reduced over 80% of t*he Dysmicoccus brevipes* population	[139]

Continued on the next page

Mealybug species	Natural Predators	Key findings	References
Dysmicoccus brevipes	*Metarhizium anisopliae, Beauveria bassiana and Lecanicillium lecanii*	These fungi had maximum control of pink pineapple mealybug and other mealybugs	[140]
Planococcoides njalensis	*Acerophagus notativentis, Acerophagus pallidus, Aenasius abengoroui, Aenasius martini, Anagyrus aurantifrons, Anagyrus beneficiens, Arhopoides sp., Blepyrus saccharicola, Leptomastix bifasciatus, Leptomastix dactylopii, Platynapsis higginsi, Pseudaphycus sp., Scymnus sp., Tetracnemoidea sydneyensis, Tropidophryne melvillei*	These predators have higher success in the control of *Planococcoides njalensis*	[141]
Maconellicoccus hirsutus	*Anagyrus kamali*	*Anagyrus kamali* fed on more than 78 % of *Maconellicoccus hirsutus* reducing their population	[142,143]

The use of chemicals during biocontrol methods should be regulated. In addition, non-selective insecticides tend to kill or neutralize several beneficial insect pollinators.

4.4. Chemical control

In recent times, chemical control methods have generated public outcry due to the accumulation of chemical residues in plant and food products [144,145] and their negative effects on the environment [146,147]. Cocco et al. [82] reported on the harmful levels of imidacloprid and chlorpyrifos (active ingredients in the control of several mealybug species) in waterbodies in Spain.Similarly, Babar et al. [148] emphasized on the need to regulate the use of profenofos, carbosulfan and methidathion during the control of *Drosicha mangiferae* on citrus farms in Pakistan. Mansour et al. [149] proposed in their review paper that the use of spirotetramat in combination with other treatments will effectively help reduce the population of *Planococcus ficus* and *Planococcus citri*. Chemicals used in pest control include acaricides, insecticides, rodenticides, fungicides, larvicides.

The use of insecticides in the control of mealybugs is not recommended because their outer covering, made up of wax, protect them against the insecticides [26]. With time, they develop resistance to these chemical insecticides. *Phenacoccus solenopsis* is reported to show a minimal reaction to insecticides that are lethal to other mealybug species [150]. Also, mealybugs hide underneath leaves and their large group makes it difficult for the chemicals to have maximum contact [150]. Their rapid reproduction cycle is also reported to contribute to their resistivity to insecticides [151]. Insecticides containing dinotefuran, imidacloprid, or pyrethroids [26,152], which are active ingredients that are effective against crawling mealybugs but have serious irritations on other beneficial insect pollinators. Daane et al. [40] confirmed the reduction in the population of *Planococcus ficus* when insecticides with chlorpyrifos active ingredients were applied.

Alcohol is effective in the control of mealybug. A previous study confirmed the association between alcohol application and mealybug mortality. A spray with a 70% concentration of isopropyl alcohol killed 70-80% of most mealybug species when applied against them [92].

Biopesticides where plant extracts are used to combat mealybugs infestation are also effective against mealybugs. Extracts from plants, such as neem, have proven effective against plant pathogens and pests [153–156]. According to Abul Monjur Khan et al. [157], 2% of neem oil effectively reduced 30% of the papaya mealybug when applied. Azadirachtin, a compound in neem trees, slows insect metamorphosis and reproduction. the Azadirachtin compound leads to a reduced growth rate and death of insects [158]. Neem Kernel water extracts are deadly to young cassava mealybugs [34,35]. 1–2% concentration of insecticidal soaps and vegetable oil as biopesticides have successfully controlled mealybugs [34,35]. Additives, such as oil, dissolve and break up the thick covering of the mealybug [26].

Insecticides that disrupt the nervous system of insects, like the organophosphates class of insecticides (chlorpyrifos, acephate, dichlorvos and diazinon), are recommended to control mealybugs (Table 8). When applied in the right amount, this class of insecticides has been proven to eliminate most species of mealybugs [26].

Table 8. A summary of some chemical controls on mealybug species.

Mealybug species	Chemical Control	Key Findings	References
Dysmicoccus brevipes (Cockerell)/Pineapple mealybug	50% Fenithrothion,50% Fenthion,40.8% Chlorpyrifos	After 21 days, the mixture of these chemicals resulted in higher mealybug mortality after the second dose than the other tested chemicals	[159]
Dysmicoccus brevipes	Omethoate,48mg of AI Phorate per plant	More than half of the *Dysmicoccus brevipes* population were eliminated	[160]
Phenacoccus solenopsis	Acephate, Chlorpyrifos	*Planococcus solenopsis* mealybug was reduced by 69% after Acephate and Chlorpyrifos as compared to other chemical treatments	[161]
Phenacoccus solenopsis	Brufozen	After 3 days, Brufozen decreased the mealybug population by 95%	[161]
Phenacoccus manihoti	Diazinon,Phosphamidon, Methidathion	Diazinon, Phosphamidon and Methidathion were 12.7,10.8 and 7.3% effective in controlling the cassava mealybug as compared to the control	[162]
Pseudococcuscoccus njalensis	(CR409) Bisdimethylamino-fluoro-phosphine oxide	CR409 was superior in the control of the cocoa mealybug	[163]
Planococcus citri	0.075% Zethiol,0.075% Nogos 100 EC, Bisdimethylamino-fluoro-phosphine oxide (CR409)	0.075% Zethiol and 0.075% Nogos 100EC completely eliminated *Pseudococcus citri*.CR409 had complete control over *Planococcus citri*	[164]
Maconellicoccus hirsutus	Spirotetramat, bifenthrin, flypyradifurone, fenpropathrin	In the nymph stage, the fecundity of mealybug was highly affected after day 6	[165]
Planococcus ficus	Chlorpyrifos, Mevinphos	Chlorpyrifos, mevinphos had superior control as compared to other methods	[126]

5. Conclusions

This paper reviewed the economic losses caused by mealybugs, mealybug-transmitted plant viruses, their mode of transmission, host plants of mealybugs and the control methods of mealybugs. The paper also highlighted someeconomic losses of mealybugs. In times of evolving plant viruses, the role of mealybugs cannot be underestimated.

Mealybugs are active in transmitting plant viruses' genera belonging to the Closteroviridae family. Of these genera, Ampeloviruses and Badnaviruses are actively transmitted by mealybug species.

Due to various environmental pollution problems, chemicals should be reduced or replaced by other safe control methods. Therefore, the biological control method of environmentally friendly mealybugs should be encouraged. For example, the *Anagyrus* species are effective against several mealybug species as biological control methods. Additionally, the use of plant products with insecticidal properties (neem seeds, leaves) to control mealybugs should be well researched.

Breeding of more mealybug-resistant varieties of plants should be encouraged. Genes that allow crop plants to withstand the aggressive feeding of mealybugs must be well studied. The acquisition and use of more tolerant varieties will help small-scale farmers who cannot afford expensive control methods.

Using one control method at a time makes the mealybug species build up resistance in a shorter time. In effect, further studies should be conducted on using Integrated Pest Management (IPM) strategies in the management of mealybug species. IPM strategies are critical in controlling and managing mealybugs in the long term.

Use of AI declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

Conflict of interest

The authors declare they have no conflict of interest.

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