Review Article

Insect Vectors of Rice Yellow Mottle Virus

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Rice yellow mottle virus (RYMV) is the major viral constraint to rice production in Africa. RYMV was first identified in 1966 in Kenya and then later in most African countries where rice is grown. Several studies have been conducted so far on its evolution, pathogenicity, resistance genes, and especially its dissemination by insects. Many of these studies showed that, among RYMV vectors, insects especially leaf-feeders found in rice fields are the major source of virus transmission. Many studies have shown that the virus is vectored by several insect species in a process of a first ingestion of leaf material and subsequent transmission in following feedings. About forty insect species were identified as vectors of RYMV since 1970 up to now. They were essentially the beetles, grasshoppers, and the leafhoppers. For this review, we presented the chronology of their identification. Also, the biology, ecology, host range, distribution, and caused damage of these insects were briefly summarized.

1. Introduction

Plant viruses are necessarily endocellular parasites and depend on their host cells for their multiplication. Also, they must be able to move inside cells and had to be transmitted to another host for its survival. This periodic movement is essential to ensure the virus spread in nature [1].

Unlike animal virus, plant viruses are faced with two specific constraints to cross the vegetative wall: (i) their host (plant) cannot move like the animal so the virus needs the carrier to move from one plant to another; (ii) plant cells of plant are surrounded by a wall rigid hemicellulose, which is a barrier that virus is unable to cross in an autonomous way. This is why the plant viruses depend on biological carriers, called vectors, to transmit them from infected to healthy plants to guarantee their infectious power. Vectors are organisms that transmit a virus from an infected to a healthy host by a mechanism that is governed by specific features of virus, vector, and host [1, 2]. They can be found among fungi, nematodes, mites, and insects [1–3]. On rice, about fifteen diseases due to virus have been identified worldwide [4]. The increase of rice cultivation, introduction of improved yielding varieties, abusive use of pesticides, fertilizers, and irrigation

have favored the virus emergence and the spread of their effect. In Africa, *Rice Yellow Mottle Virus* (RYMV) is the main viral disease. Its transmission is mainly done by insects [5, 6]. The insects were putatively considered as vectors due to their presence in the rice fields but thereafter many studies have confirmed their involvement in the virus transmission and consequently in the spread of the disease in large scale.

In this review, we described RYMV and these insect vectors identified from 1970 to day. The objective was to report all identified insect vectors and give some information about their biology.

2. Rice Yellow Mottle Virus (RYMV)

2.1. Discovery and Geographical Distribution. RYM was identified for the first time on the rice cultivar “Sindano” by Bakker, in Otonglo near Lake Victoria in Kenya in 1966 [7, 8]. It is the main viral disease of rice in Africa [9]. Since its discovery, RYMV has been reported also in most countries in Africa [10] like Sierra Leone, Ivory Coast [11], Nigeria [12], Tanzania, Zanzibar, Liberia [13], Burkina Faso, Mali [14], Niger [15], Guinea [16], Rwanda [17], Democratic Republic

of Congo [18], and Central African Republic [19]. Thus far, RYMV is reported in 23 countries in Africa South of the Sahara [18–21] and in all rice ecosystems.

2.2. Symptoms

2.2.1. Visual Diagnostic Method. Visual assessment of symptoms proved to be efficient for identifying rice accessions which are highly susceptible to RYMV that is not possible for resistant accessions [22]. The initial symptom is yellowing of leaves which begin with an alternation of yellow and green spots, giving a mottled aspect to the leaf. Two weeks after infection, these spots develop and become parallel to the leaf veins. For some varieties, leaves become orange when plants get matured. The standard evaluation system (SES) on a scale of 1–9 is used (Figure 1) for visual diagnostic of symptoms [7, 8, 21]. Other symptoms such as the decrease of the spikelet number, the partial or total sterility of rice panicles, the significant reduction of the yield, and the death of the infected plant are also observed [8, 20, 22].

2.2.2. Serological Diagnostic Methods. RYMV symptoms can especially be difficult to identify for nontrained people. They can often be confused with nitrogen or iron deficiency [23]. Some infected rice varieties do not show RYMV symptoms, so visual assessment is combined with serological diagnostic. The serological detection methods were commonly used to detect the presence and viral titer of RYMV in the rice plant infected by the insects in the laboratory. They are precipitation method [24], electron microscopy [7], agar-gel diffusion test [25], nitrocellulose test [26], and enzyme linked immunosorbent assay (ELISA) procedure [9, 27, 28]. The precipitation method has been widely used previously [8, 11, 29], but this technique was efficiency limited and more or less weak on the sensitivity and needs a high quantity of antiserum. Since the ELISA development by Clark and Adams [27], it became the most applied method to test and detect plant viruses in their hosts. ELISA is economical and efficient for qualitative and quantitative measurements of virus in the extracts from infected plants or virus suspensions [11, 27, 30]. Many ELISA procedures and protocols are now available [5, 30, 31]. However, two general procedures are commonly used, that is, direct or indirect antibody sandwich (DAS) method [18, 27, 31] and the antigen coated plate (ACP) method [31, 32].

2.3. Pathogen. The pathogen is a member of sobemoviruses. Species within the *Sobemovirus* genus include also cocksfoot mottle virus (CfMV), Lucerne transient streak virus (LTSV), southern bean mosaic virus (SBMV), Sesbania mosaic virus (SeMV), and turnip rosette virus (TRoV). Actually 11 definitive species were registered in the *Sobemovirus* genus [33]. *Sobemovirus* genome is one of the smallest genomes of all known RNA virus genomes with a single-stranded positive-sense RNA molecule that typically comprises around 4 to 4.5 kb [34]. RYMV has an icosahedral particle with a diameter of 28 nm consisting of 180 subunits of capsids arranged in 60 triangulations of 3 subunits. After sequencing of the collected

FIGURE 1: Standard evaluation system (SES) for RYMV symptoms. 1 = no symptoms, 3 = leaves green but with spare dots or streaks and less than 5% of height reduction, 5 = leaves green or pale green with mottling and 6 to 25% of height reduction, flowering slightly delayed, 7 = leaves pale yellow or yellow and 26–75% of height reduction, flowering delayed, and 9 = leaves turning yellow or yellow orange, more than 75% of height reduction, no flowering or some dead plants (adapted from [21, 29]).

isolates, the genomic organization of RYMV is close to that of CfMV [35]. The 5' end has a covalently linked viral protein (VPg), while the 3' end is not polyadenylated [35, 36]. Its RNA genome is composed of 4450 nucleotides which were previously organized into four protein-coding ORFs (ORF1, ORF2a, ORF2b, and ORF3) but now in five ORFs with a new additional ORF (ORFx). ORFx was conserved in all sobemoviruses. ORFs 1, 2a, and 2b are translated from the genomic RNA while ORF3 is translated from a subgenomic RNA. ORF1 encodes protein P1 (12 to 24 kDa depending on species) which is essential in the suppression of silencing and virus movement, ORFs 2a and 2b encode the replicational polypeptides P2a and P2ab, and ORF3 encodes the coat protein. ORFx overlaps the 5' end of ORF2a in the +2 reading frame and also extends some distance upstream of ORF2a. ORFx lacks an AUG initiation codon and its expression is predicted to be also translated via leaky scanning and initiation at a near-cognate non-AUG codon, which in RYMV is a highly conserved CUG, by a proportion of the ribosomes that are scanning the region between the ORF1 and ORF2a initiation codons [36] (Figure 2). The viral particle is extremely stable and infectious [8]. However, the virus is inactivated after incubation at 65°C, during 10 min [37]. Under laboratory conditions (16–25°C), it remains infectious for 33 days but loses its pathogenicity after 51 days [21].

2.4. Transmission of the Disease. RYMV is spreading from rice to rice and rice to other weed host plants like gramineous crops. According to Bakker [8], the first rice plants infected in a field were always found at the boundary of irrigated rice fields following the entry of insects in the field. RYMV is transmitted from infected plants to healthy plants through injuries caused on the plants during transplanting and weeding, by also rats, birds [38], or domestic animals including

FIGURE 2: Map of the rice yellow mottle virus (RYMV) genome organization. The RNA genomic contained 4450 nucleotides organized into five protein-coding ORFs: ORF1, ORF2a, ORF2b, ORF3, and the newly identified ORFx. Each ORF codes for protein synthesis. Its 5' end is connected with the protein VPg and the 3' end has not been polyadenylated (from [36]).

cows and donkeys [39]. However, the insects are the main vectors of the disease [6].

3. Identification of the RYMV Insect Vectors

According to Nwilene [54], the regular presence of some insects in rice fields led to a belief that they were potential vectors when RYMV was discovered. Several studies were therefore conducted to identify these vectors and to know their implication in the transmission and propagation of RYMV. These insects spread RYMV mechanically during feeding. They share viral particles collected from infected plant to healthy plant on which they feed later [6, 8].

To this day, approximately forty insect species belonging to Coleoptera, Orthoptera, Homoptera, and Diptera orders were identified as vectors of RYMV [10, 49, 54]. In this review, these insects were classified into four feeding groups such as beetles, grasshoppers, leafhoppers, and flies (Table 1). These different groups are described as follows.

3.1. Beetles. About 15 beetle species were firstly identified as vectors right after RYMV discovery, with agar-gel diffusion and electron microscopy tests. They were essentially reported in East Africa where RYMV was identified for the first time. *Sesselia pusilla* Gerstaecker (Coleoptera: Chrysomelidae) was the first identified insect vector in Kenya by Bakker [7].

3.1.1. *Sesselia pusilla* Gerstaecker (Figure 3(a)). *S. pusilla* belongs to the Hispinae subfamily, characterized by the presence of spines on their thorax and body [42]. *S. pusilla* was able to retain the virus for 8 days and was often causing infection of seedlings on three or more consecutive days [8]. Electron microscopy method has been used to identify it [7]. Little information is available on description, distribution, ecology, and damages caused by this insect.

In Ahero Pilot Scheme, where *S. pusilla* was identified, Bakker [7] noted that its population was weak compared to the high incidence of the disease. This means that there were other insect vectors other than this vector. Therefore, he conducted additional investigations in 1971 and has identified three new beetles as vectors by agar-gel diffusion test. These were *Diadisa viridicyanea* Kraatz (Coleoptera: Chrysomelidae), *Trichispa sericea* Guerin Meneville (Coleoptera: Chrysomelidae), and

Chaetocnema pulla Chapuis (Coleoptera: Chrysomelidae) (Figure 2) [25].

3.1.2. *Diadisa viridicyanea* Kraatz (Figure 3(b)). Adults of *D. viridicyanea* are metallic blue-green, about 5 mm long, with five lateral spines on each side of the thorax and a series of alternately long and short lateral spines on the elytra. This hispine was recorded in West Africa (Ivory Coast, Burkina Faso, and Sierra Leone) [42] and in Central Africa (Congo) [27]. *D. viridicyanea* is found in upland rice at the vegetative stage as well as in lowland seedbed [55, 56].

3.1.3. *Trichispa sericea* Guerin Meneville (Figure 3(c)). Commonly named the rice hispid, adult of *T. sericea* (3–4 mm long) has dark grey beetle cover with upright spines. Only recorded in Africa and Madagascar [57], *T. sericea* was found in upland rice [56] but more in lowland irrigated rice [58]. It is a major pest of nursery seedlings especially on transplanted rice plants [54]. Adults and larvae feed on the leaf tissues of young rice, resulting, respectively, in irregular pale brown patches and narrow whitish streaks parallel to veins on the leaves [57]. The initial attacks are localized but spread rapidly. Severe attacks can lead to the plant death [58]. This hispine is not a highly mobile insect and can stay several hours feeding on the same plant. It is able to retain and transmit RYMV for one to two days according to the semipersistent transmission mode [8, 59]. *T. sericea* was confirmed as vector in Niger [15], Mali [60], Cameroon [51, 61], and Ivory Coast [6, 52, 59].

3.1.4. *Chaetocnema pulla* Chapuis (Figure 3(d)). *C. pulla* belongs to the Halticinae subfamily and is a small insect (approximately 2 mm long) with very developed metathoracic femurs adapted for jumping and is also characterized by a tooth on the dorsal side of the intermediate posterior tibiae [25, 56]. *C. pulla* is largely distributed in West Africa (Ivory Coast, Burkina Faso, Mali, etc.) and East Africa (Tanzania and Kenya) [42, 54, 58]. This insect is very abundant on the upland rice than lowland and irrigated ecologies. Damages caused during the feeding are minor [42, 54]. It is a polyphagous insect found also on maize (*Zea mays*) and millet. Unlike *T. sericea*, *C. pulla* is a highly mobile insect which has short feeding periods on the same plant, inducing a fast dissemination of the virus. It can acquire and retain the virus for about six days but is unable to transmit the virus for more than three days [8, 59]. *C. pulla* was confirmed as vector in Sierra Leone [60], Madagascar [48], Tanzania [28, 45, 46], Cameroon [51, 61], and Ivory Coast [6, 52, 59].

Three other *Chaetocnema* species were identified as RYMV vectors in 1974. They are *C. abyssinica* (Figure 3(e)), *C. kenyensis* (Figure 3(f)), and *C. pallidipes* (Figure 3(g)) [8]. Apart from *C. pulla*, little information exists on the biology of over 100 afroropical species of *Chaetocnema* [58]. Bakker [8] also identified other chrysomelids including *Cryptocephalus* sp., *Oulema dunbrodiensis* Jac. F. *nigripennnis* Hze., *Dactylispa bayoni* Gestro, *Diadisa paucispina* Weise, *Monolepta flaveola* Gerst., *M. haematuria*, and an insect close to *Apophyllia* genus. These beetles were abundant in the rice field like *Chaetocnema* spp. and *S. pusilla* and caused a fast

TABLE 1: Insect vectors of rice yellow mottle virus (RYMV) in Africa.

Insect vectors	Geographic distribution	References
Beetles		
Coleoptera: Chrysomelidae		
<i>Sesselia pusilla</i> , <i>Trichispa sericea</i> , <i>Dicladispa viridicyanea</i> , <i>D. paucispina</i> ,	East Africa	[7, 8, 25] [40]
<i>D. gestroi</i> , <i>Chaetocnema pulla</i> , <i>C. abyssinica</i> , <i>C. kenyensis</i> , <i>C. pallidipes</i> , <i>C. varicornis</i> ,	West Africa	[41–43] [20, 43, 44]
<i>Chaetocnema</i> sp. Nov, <i>Dactylispa lenta</i> , <i>D. bayoni</i> , <i>Cryptocephalus</i> sp.,	Tanzania	[28, 45–47] [22, 42]
<i>Oulema dunbrodiensis</i> , <i>Monolepta flaveola</i> , <i>M. haematuria</i> , <i>Aulacophora foveicollis</i>	Madagascar Africa	[41, 48]
Insect near to <i>Apophyllia</i> genus	East Africa	[47]
Coleoptera: Coccinellidae		
<i>Chnootriba similis</i> , <i>Xanthadalia effusa</i> , <i>Cheilomenes lunata</i>	Madagascar West Africa	[6, 42, 49]
Grasshoppers		
Orthoptera: Tettigoniidae		
<i>Conocephalus merumontanus</i>	East Africa	[8, 50]
<i>C. longipennis</i>	West Africa	[6, 42, 49]
Orthoptera: Acrididae		
<i>Oxya</i> spp., <i>Oxya hyla</i> , <i>Acrida bicolor</i>	Cosmopolitan	[42]
<i>Paracinema tricolor</i> , <i>Stenohippus aequus</i>	Africa, Europe	[42, 49, 51, 52]
Orthoptera: Tetrigidae		
<i>Paratettix</i> sp.	West Africa	[49]
Orthoptera: Pyrgomorphidae		
<i>Zonocerus variegatus</i>	Sub-Saharan Africa	[6, 42]
Orthoptera: Gryllidae		
<i>Euscyrtus</i> sp.	West Africa	[6, 42]
Leafhoppers		
Homoptera: Cicadellidae		
<i>Cofana spectra</i> , <i>C. unimaculata</i> , <i>Nephotettix modulatus</i>	West, East, and Central Africa	[6, 49]
Homoptera: Cercopidae		
<i>Locris rubra</i> , <i>L. maculata</i>	West Africa	[6, 49, 53]
Homoptera: Aphrophoridae		
<i>Poophilus costalis</i>	West Africa	[49]
Flies		
Diptera: Diopsidae		
<i>Diopsis thoracica</i>	West, East, and Central Africa	[42, 49, 51]

spread of the virus when rice varieties are highly susceptible to RYMV.

Seven (7) other beetle species were also identified as vectors mainly in West and Central Africa after RYMV spreading across Africa. The SES and ELISA protocols have been used in these studies [6, 28, 41, 49]. They were *Aulacophora foveicollis* Lucas (Coleoptera: Chrysomelidae), *Dicladispa gestroi* Chapman (Coleoptera: Chrysomelidae), *Chnootriba similis* Mulsant (Coleoptera: Coccinellidae), *Chaetocnema* sp. nov. (near *Chaetocnema varicornis* Jacoby), *Dactylispa lenta* Weise

(Coleoptera: Chrysomelidae), *Xanthadalia effusa* Erichson (Coleoptera: Coccinellidae), and *Cheilomenes lunata* Fabricius (Coleoptera: Coccinellidae).

3.1.5. *Aulacophora foveicollis* Lucas (Figure 3(h)). The red leaf beetle *A. foveicollis* is also named *A. africana* Weise [62]. *A. foveicollis* was reported as RYMV vector for the first time in Nigeria [47]. Entirely reddish-yellow and glabrous dorsally, the abdominal sternites are black, except apical segment

FIGURE 3: Some insect vectors of rice yellow mottle virus (RYMV). (a) *Sesselia pusilla*, (b) *Dicladispa viridicyanea*, (c) *Trichispa sericea*, (d) *Chaetocnema pulla*, (e) *Chaetocnema abyssinica*, (f) *Chaetocnema kenyensis*, (g) *Chaetocnema pallidipes*, (h) *Aulacophora foveicollis*, (i) *Dicladispa gestroi*, (j) *Chnootriba similis*, (k) *Dactylispa lenta*, (l) *Xanthadalia effusa*, (m) *Cheilomenes lunata*, (n) *Conocephalus longipennis*, (o) *Oxya hyla*, (p) *Zonocerus variegatus*, (q) *Paratettix* sp., (r) *Euscyrtus* sp., (s) *Acrida bicolor*, (t) *Paracinema tricolor*, (u) *Stenohippus aequus*, (v) *Cofana spectra*, (w) *Cofana unimaculata*, (x) *Locris rubra*, (y) *Locris maculata*, (z) *Nephotettix modulatus*, (aa) *Poophilus costalis*, and (ab) *Diopsis thoracica*. (a), (h), (i), (j), (k), (l), (n), (o), (p), (q), (r), (s), (t), (u), (v), (x), (y), (z), (aa), and (ab) from authors. (b), (c), (d), (e), (f), and (g) from [8]. (m) from Mike Plagens, Kenya Nature Guide mjplagens@arizonensis.org, http://www.ngkenya.com/inverts/cheilomenes_lunata.html. (w) from <http://naturalhistory.museumwales.ac.uk/sharpsshooters/browse/record.php?-recid=412>. NMW image number E003882.

which is yellow. Its elytra are fine, dense, confusedly punctured, shining, and not microsculptured. The body length is about 6–8 mm. Out of the rice [42], this cosmopolitan insect is found also on *Cucurbita maxima* (giant pumpkin), *Cucumis melo* (melon), and *Lagenaria siceraria* (bottle gourd) which were the preferred food plants of adults [63]. Adult feeding may lead to complete destruction of the seedlings and foliage riddled with holes or total defoliation of older plants. Floral parts such as anthers are also nibbled. *A. foveicollis* was reported as RYMV vector also in Niger [64] and recently confirmed in Benin [49]. It has been the first beetle reported as vector in West Africa.

After Bakker [25], another *Dicladispa* species named *D. gestroi* was identified as vector in Madagascar where RYMV was reported firstly in 1989 and is considered like one of the most important rice diseases on the island [43]. Subsequently, another beetle, *C. similis*, was discovered in Ivory Coast by Abo [41].

3.1.6. *Dicladispa gestroi* Chapman (Figure 3(i)). The entire life cycle of this hispine takes about one month [58] with four larva instars considering the head width [56]. *D. gestroi* is a pest of rice, known to come from Madagascar only [65]. This pest is found more in lowland (irrigated and rainfed) rice [58]. Out of rice, it is found on species of Gramineae and Cyperaceae like *Leersia hexandra*, *Pycnus mundtii*, *Ageratum conyzoides*, *Panicum* sp., *Eleocharis* sp., *Scirpus* sp., and *Echinochloa* sp. Adults feed on the leaf surfaces while larvae mine the leaves. Their damage results in a change of color from green to pale yellow of these leaves which resemble outbreak areas of rice leafhoppers [58, 65, 66].

3.1.7. *Chnootriba similis* Mulsant (Figure 3(j)). Also called *Epilachna similis*, adults of this beetle have 5–6 mm length and are orange-red with six black spots on each elytron [67]. But the spot arrangement on the elytra is variable according to individuals. Some spots are isolated or more or less coalesced [66]. *C. similis* is one of the major rice pests in West Africa (Benin, Burkina Faso, Cameroon, Chad, Ivory Coast, Ghana, Guinea, Guinea-Bissau, Liberia, Niger, Nigeria, Senegal, and Togo) and also in East Africa (Eritrea, Ethiopia, Kenya, and Tanzania) [42, 68]. This beetle is a very special insect being both phytophagous and predator and is more present in the upland than in the lowland irrigated ecology. In addition to rice, *C. similis* is found on maize, sorghum, millet, wheat, sugar cane, sesame, lettuce, potato, soya, and cotton [54, 67]. Many studies have also confirmed the vectorial capacity of this insect [6, 49, 52].

Three years after Abo's findings in Ivory Coast, Banwo et al. [45, 46] have identified two new beetle vectors, in Tanzania. These were *Chaetocnema* sp. nov. [28] and *D. lenta* [45].

3.1.8. *Chaetocnema* sp. nov. Little information exists on the afrotropical species of *Chaetocnema*. Other than rice, this *Chaetocnema* species feeds on other Gramineae, Cyperaceae, Marantaceae, and Zingiberaceae. Adults feed by scratching

the leaf surface leaving short, straight, and narrow transparent lines. Damages are more pronounced in this species than *C. pulla*. Both insects are found in lowland and upland rice [54, 58].

3.1.9. *Dactylispa lenta* Weise (Figure 3(k)). Like *Chaetocnema* sp. nov., only scant information exists on the biology and life cycle of this afrotropical species [45] which feeds on rice and also on other Gramineae. Larvae of this hispine mine in leaves, while adults eat the cuticula parallel to the leaf veins. *D. lenta* is found mostly in lowland rainfed rice [58].

Studies conducted to Cameroon by Sadou et al. [51] have permitted to identify for the first time a predator insect as RYMV vector. This was *X. effusa*.

3.1.10. *Xanthadalia effusa* Erichson (Figure 3(l)). *X. effusa* is a small predator (5–5.7 mm long). Its pronotum is yellow with a quadrate black band on anterior margin; elytra are yellow brown with black sutural line, two ovoid black spots in the middle of basal one-half pointed towards each other and a pair of irregularly round black spots diverging are also observed. This insect was found in rice field in West Africa [42, 49]. *X. effusa* was recently confirmed as RYMV vector by Koudamilo et al. [49].

In 2009, Nwile et al. [6] identified *C. lunata* as vector for the first time in West Africa. It is up to now that the last beetle and the second predator are known as vectors of RYMV.

3.1.11. *Cheilomenes lunata* Fabricius (Figure 3(m)). *C. lunata* is a small insect (6.5 mm long) with a black pronotum carrying three yellow spots. Its elytra are black with two pairs of yellow or orange spots globular along sutural margins and wide strips shaped C. They are shiny, smooth, and hairless. This ladybird was found in West Africa (Burkina Faso, Ivory Coast, Guinea, and Gambia) [42] and is a predator of aphid like *Aphis craccivora* Koch [55].

3.2. Grasshoppers. Ten (10) grasshoppers were tested and confirmed as vectors of RYMV [6, 8, 49] (Table 1).

3.2.1. *Conocephalus* spp. *Conocephalus merumontanus* Sjöstedt (Orthoptera: Tettigoniidae) was the first grasshopper identified as vector [8]. Usually called meadow grasshoppers, *Conocephalus* spp. are different from other grasshoppers with their long horn (longer than the whole body), a sickle-shaped ovipositor, and four segmented tarsi. Their body is bright green and their wings are brown. They were reported in both the forest and Guinea savanna climatic zones. *Conocephalus* genus also includes predatory species that parasitize some rice stemborers such as *Chilo suppressalis* Walker (Lepidoptera: Pyralidae) and *Scirpophaga incertulas* Walker (Lepidoptera: Pyralidae) [62, 69]. *C. merumontanus* is a common species of this group [8, 50].

Another *Conocephalus* species, *Conocephalus longipennis* Haan (Figure 3(n)), has been found as vector later in Ivory Coast [41]. *C. longipennis* is a minor pest of rice in West and East Africa [5, 54, 61]. It is more present in lowland ecologies on rice and a wide range of host plants like maize, barley,

wheat, millet, sorghum, and grasses. It is a predator of the rice bugs, eggs of the stem borers, and nymphs of other phytophagous insects [42, 70]. Its ability to transmit RYMV was confirmed later [6, 49, 52].

3.2.2. *Oxya* spp. After *C. merumontanus*, *Oxya* spp. have been the second grasshopper reported as vector, in Philippines [50]. Commonly called short-horned grasshopper, *Oxya* spp. were present on rice in Africa especially in upland, lowland, and irrigated rice ecosystems [42, 64]. Except on rice, *Oxya* spp. feed on nut grass (*Cyperus rotundus* L.), maize, and sugar cane (*Saccharum officinarum* L.) [42, 71]. *Oxya* spp. were later confirmed as vector in Madagascar [48].

In 2009, Nwilene et al. [6] have identified in Ivory Coast an *Oxya* species as vector, *Oxya hyla* Stål (Orthoptera: Acrididae) (Figure 3(o)). Known as short-horned grasshopper, *O. hyla* is found on rice plants in Africa and Asia. With filiform antennae, it is light green and has a distinctive black strip that extends laterally from each compound eye through the thorax to the base of the wings. The femur is brownish-yellow with black knee and the vertebral column is located in the bottom of the external lobe. The tibia has eight spines in the external row and nine in the internal row. The male is between 20 and 29 mm long and the female is between 30 and 37 mm [42, 72]. According to Heinrichs and Barrion [42], *Oxya*'s distribution is not well studied in West Africa, but it was reported in several countries including Burkina Faso, Ivory Coast, Mali, Nigeria, and Benin [73], in the upland and lowland ecosystems. Its damage is the same damage like the previous grasshoppers [42, 71].

In the same study, Nwilene et al. [6] found three new grasshoppers as vectors. They were *Paratettix* sp. (Orthoptera: Tettigidae), *Zonocerus variegatus* L. (Orthoptera: Pyrgomorphidae), and *Euscyrtus* sp. (Orthoptera: Gryllidae).

3.2.3. *Zonocerus variegatus* L. (Figure 3(p)). Commonly called stinking locust, *Z. variegatus* belongs to the short-horned group and is one of the most common rice grasshoppers in Africa, especially in West Africa. Characterized by a large size (female is between 35 and 52 mm long while male varies between 30 and 45 mm in length), *Z. variegatus* has striking color and can produce a repugnant protecting smell. Its head is vertical to the body with a black clypeus in the dorsal half with 6 yellow spots. Its ventral half is yellow. The femur has black spots in the apical part and the tibia III has six spines in the outer row and eight spines in the inner row [42, 72, 74]. *Z. variegatus* occurs between the Cancer and the Capricorn Tropic, predominantly in West Africa, East Africa, and Northern Sudan. It was met in the forest and savanna in the upland as well as in lowland with large host plants including gramineous, cassava, yam, cotton, cocoa, citrus, cola, and banana [74, 75]. Its damage on rice is sporadic and depends on the availability of other host plants near rice fields. Caused damage is similar to other grasshoppers and can lead to plant death [42].

3.2.4. *Paratettix* sp. (Figure 3(q)). Little information is available on distribution, ecology, and caused damage of *Paratettix*

sp. Two species of *Paratettix* (*P. scaber* and *P. dorsifer*) have been described in West Africa. *P. scaber* (13 mm long) is dull brown with a black shade between shoulders. Its femur III includes five oblique edges and tibia III has seven spines in the outer row. *P. dorsifer* (14.5 mm long) is black with a wide transverse white band between shoulders. Its femur III has 5–7 oblique edges with peg-like spines and tibia III contains eight spines in the outer row [42].

3.2.5. *Euscyrtus* sp. (Figure 3(r)). Little information is also available on distribution, ecology, and caused damage of this insect.

E. bivittatus Guérin-Meneville is the only *Euscyrtus* species which was described like rice feeding insect. It is a locust of 18 mm long with yellow-brown to dark brown color. A transverse ridge connects the eyes to the front. The antennae are yellow brown to dark brown with scape and pedicel. Legs are yellowish with, respectively, 10 to 11 and 12 long spines in the outer and inner rows of the tibia III [42].

Sadou et al. [51] have reported another grasshopper as vector, *Acrida* sp. (Orthoptera: Acridae) during their prospection in North of Cameroon.

3.2.6. *Acrida* sp. *Acrida* genus contains around 40 species, which are cosmopolitan. Four species would be present in West Africa. They are *A. bicolor* Thunberg, *A. sulphuripennis* Gerstäcker, *A. turrita* L., and *A. confusa* Dirsh [44]. *A. bicolor* (Figure 3(s)) may have four major pigment types: uniformly green or brown firstly and green or brown with several longitudinal and whitish stripes on the other part. The male is between 35 and 60 mm long and the female is between 70 and 100 mm. Its body is elongate and thin with conical head and antennae which are long and ensiform. The wings and elytra have a strong apex which exceeds abdominal tip. The posterior femora are long and slender [76]. *A. bicolor* can be easily confused with other species of the *Acrida* genus or with *Truxalis* species [77]. *Acrida* sp. is omnivorous and is a well-known pest of many agricultural crops including sorghum, wheat, rice, cotton, weed, sweet potato, sugar cane, and Chinese cabbage [72]. *A. bicolor* was found on rice in West Africa [42, 49]. It was confirmed as RYMV vector in Benin by Koudamilo et al. [49].

The last two grasshopper vectors of RYMV were identified for the first time in Benin. They were *Paracinema tricolor* Thunberg (Orthoptera: Acrididae) and *Stenohippus aequus* Uvarov (Orthoptera: Acrididae) [49].

3.2.7. *Paracinema tricolor* Thunberg (Figure 3(t)). With a slight conical head, *P. tricolor* is greenish and can become brownish with green lateral faces on the body and also has a brown dorsal face. Its pronotum has two lateral brown bands. The wings are hyaline or bluish. Their posterior tibiae expanded in the apical part are red bright. The antennae are filiform. Female and male are 32–40 mm and 24–29 mm long, respectively. *Paracinema* genus includes three species where two are typically from Sub-Saharan Africa: *P. tricolor* and *P. luculenta*. *P. tricolor* is a graminicole insect and has a strong

preference to resettle on grass stem with the head in upright position and also prefers wet habitat with tall grass [72].

3.2.8. *Stenohippus aequus* Uvarov (Figure 3(u)). *Stenohippus* genus includes nine species among them six are present in Africa [72, 78]. The antennae are filiform. Female and male are 16–27 mm and 13–20 mm long, respectively. *S. aequus* is variably brownish with lateral or dorsal bands which are bright or dark. Its hyaline wings are occasionally slightly smoked at the apex. The hind tibiae are yellow to greyish that makes a big difference with *Dnopherula* spp. which have the partially red tibiae. Its head is conical with lateral carinae of pronotum which are more or less marked [72]. Little information is available on distribution, ecology, and caused damage of this RYMV vector.

The first insects identified as RYMV vectors belonged to beetles (Coleoptera) and grasshoppers (Orthoptera). Agar-gel diffusion and electron microscopy tests were used to identify these vectors [8]. Any insect of Hemiptera or Diptera orders was unable to spread the virus [8, 40]. However, the homopterans are the main vectors of most plant viruses previously identified [2].

3.3. Leafhoppers. In addition to the above groups of vectors that are beetles or grasshoppers, leafhoppers are another important group containing RYMV vectors. Leafhoppers are biting and sucking insects of leaves, stems, and seeds. Their damage on plants is not automatically perceptible such as beetles and grasshoppers which are clearly opened.

The first studies carried out on the transmission of plant viruses by insects and the first insects identified as vectors were specifically aphids which are Homopterans [1, 55, 79, 80]. These leafhoppers are also important vectors of other rice viruses including rice hoja blanca virus (RHBV) transmitted by *Sogatodes orizicola* Muir (Homoptera: Delphacidae), rice tungro bacilliform virus (RTBV) and rice tungro spherical virus (RTSV) transmitted by *Nephotettix virescens* Distant (Homoptera: Cicadellidae), and the rice stripe virus (RSV) whose vector is *Laodelphax striatellus* Fallén (Homoptera: Delphacidae) [2, 4, 81]. It is also important to mention that these various viral diseases are endemics to Asia and America [42].

Generally leafhoppers transmit the viruses persistently, while RYMV was transmitted mechanically. Therefore, several studies have concluded that leafhoppers could not be potential vectors of RYMV like the beetles [8, 40, 41, 82]. Their high capacity for other viruses' transmission would have probably aroused the recent studies on the leafhoppers regarding RYMV transmission.

Up to now, six leafhoppers have been reported as vectors of RYMV (Table 1).

The first identification was done in Ivory Coast and concerned four insects. They were *Cofana spectra* Distant (Homoptera: Cicadellidae), *Cofana unimaculata* Signoret (Homoptera: Cicadellidae), *Locris rubra* Fabricius (Homoptera: Cercopidae), and *Locris maculata* Fabricius (Homoptera: Cercopidae) [6].

3.3.1. *Cofana spectra* Distant (Figure 3(v)) and *Cofana unimaculata* Signoret (Figure 3(w)). These white rice leafhoppers are the most important on rice fields in West Africa. *C. spectra* (7–9 mm long) is characterized by a large central black spot on the head vertex towards the posterior margin and has brown lines on the fore wings, which are absent with *C. unimaculata*. These vectors were found in Burkina Faso, Ivory Coast, Guinea, Guinea-Bissau, Mali, Nigeria, and Togo. *C. unimaculata* has also been found in Liberia. These insects are more abundant in lowland than the rainfed upland ecology. They infested at tillering and flowering stages [42]. Generally adults live on lower face of the leaves or at the tiller base. Adults and nymphs suck the leaves sap. These leaves turn to orange and fade, which delays the growth or causes plant death [42, 83]. They have been confirmed as RYMV vector in Benin. Several studies should be now conducted as they are known to be important vectors of RYMV [49].

3.3.2. *Locris rubra* Fabricius (Figure 3(x)) and *Locris maculata* Fabricius (Figure 3(y)). Few insect species of Cercopidae family are rice pests. These spittle bug species (10–11 mm long) are distinct from other insects through the boat-shaped form of their body and also their reddish coloration with characteristic strips. *L. rubra* has a transverse brown band in posterior pronotum and *L. maculata* has a black pronotum with humeral yellow gold band reduced to four spots. Endemic to Africa, *Locris* spp. are the only reported Cercopids and are abundant on rice in West Africa [42, 84]. *L. rubra* is found in Benin, Burkina Faso, Cameroon, Ivory Coast, Gambia, Guinea, Guinea-Bissau, Mali, Nigeria, Senegal, and Togo. *L. maculata* is found in Burkina Faso, Ivory Coast, Guinea, Guinea-Bissau, Liberia, Mali, Nigeria, and Togo [42]. Like *Cofana* spp., they are more abundant in the nonweeded fields and lowland ecology and suck the plant sap at the base of the stem. This spittlebugs damage on rice is not economically severe in West Africa. Except for rice, *L. rubra* feeds on other hosts like sorghum, maize, millet, rice, sugarcane, and numerous grass species [53].

The last two leafhoppers reported as vectors were identified for the first time in Benin. They were *Nephotettix modulatus* Melichar (Homoptera: Cicadellidae) and *Poophilus costalis* Walker (Homoptera: Aphrophoridae) [49].

3.3.3. *Nephotettix modulatus* Melichar (Figure 3(z)). Commonly named the green leafhopper, *N. modulatus* (3–5 mm long), also called *N. africanus* Emeljanov, has green color with black marks on the wings and has a head with yellow scutellum. It has a separated black band on the head vertex that can be reduced at the middle and is often confused with *N. nigropictus* Stål [40]. In West Africa, two species (*N. afer* Ghauri and *N. modulatus*) were found on rice. *Nephotettix* species were distributed in all rice ecologies with a preference for the lowland agrosystems. Apart from rice, *N. modulatus* can be found on grasses such as *Rottboellia cochinchinensis*, *Ischaemum rugosum*, and *Paspalum vaginatum* [42]. *N. modulatus* causes direct damage to rice plants and transmission of pathogen such as viruses [13].

3.3.4. *Poophilus costalis* Walker (Figure 3(aa)). Also called spittle bug, *P. costalis* is a small jumping insect of 9–11 mm long and is generally brownish. The nymphs always remain inside a foamy spittle mass. The anterior margin of the flat head is widely round with ovoid eyes. It has three black spots at mid-length with subquadrate plate below these spots. The scutellum is brownish, flat with a pointed yellow apex and a median longitudinal yellow band. Legs are also brown [42, 85]. *P. costalis* was recorded as rice pest in Japan, India [86], and also West Africa [42]. This froghopper feeds also on maize, sorghum, millet, sugarcane, and other grass species [87]. Mature plants become yellowing and wilting because of its damage which sometimes lead to seedling death [88]. *P. costalis* was also reported as vectors of Pierce's disease virus [89] and yellow leaf blotch of sorghum [90].

3.4. *Flies*. In this order, damage is generally caused by larval stages such as the stem borers on cereals and fruit flies [42]. *Diopsis thoracica* Westwood (Diptera: Diopsidae) was to date the only dipteran identified as RYMV vector [49, 82]. Commonly named stalked-eyed borer, *D. longicornis* Macquart and *D. macrophthalmalma* Dalman are the synonyms of *D. thoracica* (Figure 3(ab)). Adults of *D. thoracica* are the most abundant and most important of the various *Diopsis* species found in rice. They are characterized by eyes situated on the tips of long stalks, black thorax, and reddish-orange abdomen with high hairiness. Adults are about 9 mm long. Larvae are about 12–18 mm long whitish cream with yellow markings on the terminal segments and have very small head. *D. thoracica* was found in West, East, and Central Africa [42, 58]. In West Africa, This rice pest occurs in all rice ecosystems but it is most abundant in rainfed lowland and irrigated ecosystems. It is not known to attack crop plants other than cultivated rice [67]. *D. thoracica* is essentially known as an important rice stem borer in Africa. The emerged larvae move down the inside of the leaf sheath and feed above the meristem causing the “dead heart” at tillering stage and “whiteheads” at flowering stage symptoms on rice plant. In endemic areas, *D. thoracica* damage can reduce rice yield [91]. Like RYMV vector, it was later confirmed in Benin [49].

4. Conclusion

RYMV is the most important viral disease of rice and is also called the HIV/AIDS (human immunodeficiency virus infection/acquired immunodeficiency syndrome) of rice in some countries. Several insects of Coleoptera, Orthoptera, Homoptera, and Diptera orders were identified and confirmed vectors of the RYMV from rice to rice and from rice to other host plants. Approximately forty insect species have been now identified as vectors. The recent identification of homopterans and dipteran as vectors led to a conclusion that RYMV transmission is not only ensured by chewing insects.

5. Future Studies

It is therefore imperative to continue the work on the identification of insect vectors in order to discover new

species not yet identified. Future research should include studies to understand the mechanisms of virus transmission (semipersistent, persistent, and nonpersistent) used by each vector. This will be useful in the choice of effective control strategies for the management of these insect vectors.

Conflict of Interests

The authors certify that there is no conflict of interests concerning the publication of this paper.

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