Dengue fever is a mosquito-borne-disease of growing public health importance in Africa. The continuous increase of number and frequency of outbreaks of dengue fever, especially in urban area in Africa underline the need to review the current data available on vectors involved in dengue virus transmission in Africa. Here, we summarized the available data on vectors involved in the transmission of dengue virus in the sylvatic and urban environments, vertical transmission, vector competence studies, and vector control strategies used in Africa. The virus was isolated mainly from *Aedes furcifer*, *Ae. luteocephalus*, and *Ae. taylori* in the sylvatic environment and from *Ae. aegypti* and *Ae. albopictus* in the urban areas. Prospective and urgently needed studies on vectors biology, behavior, and alternative control strategies are suggested.

1. Introduction

Dengue virus (DENV), the causative agent of Dengue fever, transmitted by several *Aedes* spp., is one of the most important arboviral diseases in the world. Indeed, this disease caused by four genetically related but antigenically distinct viruses (DENVs 1–4; genus *Flavivirus*, family *Flaviviridae*), is endemic in more than 128 countries with around 390 million people infected each year [1, 2]. With 16% of these infections, Africa is one of the most affected regions [3]. Evidence of dengue circulation has been detected in local populations or travelers returning from more than 30 African countries (Figure 1).

In Africa, DENV-2 was the most frequently reported serotype before 2000s and was responsible of several epidemics in East Africa (Somalia, Djibouti, Kenya, and Tanzania) and sylvatic emergence with sporadic human cases in West Africa (Senegal, Burkina and Côte d’Ivoire) [4, 5, 6, 7, 8]. In West Africa, DENV-2 epidemics were only detected in Nigeria and Burkina Faso before 2000 [9,10]. The DENV-3 emerged only in Mozambique in 1985 and Somalia in 1993 [8,11], while DENV-1 outbreaks were observed in Sudan in 1984, Comoros in 1993, Nigeria in 1960s and Senegal in 1979 [6,9,12]. In recent decades, the number and frequency of dengue epidemics have increased dramatically in Africa [13, 14, 15]. DENV-2 and 3 are the main serotypes involved in the...
epidemics on the African continent, although the circulation of the other two serotypes have been documented [16]. In East Africa, DENV-2 has remained very active in countries that were affected during the last century, but has emerged also in several other countries, including Ethiopia in 2013, Tanzania in 2014 and Mozambique in 2014–2015 [17, 18,19,20]. Sylvatic amplification and urban epidemics of DENV-2 have occurred in several West African countries (Mali in 2008, Senegal in 2015–2018, Mauritania in 2014–2020, and Burkina Faso in 2013, 2016 and 2017), as well as in Central African countries (Gabon in 2007 and Angola in 2013 and 2018) [13,21,22,23,24]. Outbreaks of DENV-3 have been reported in Tanzania, Zanzibar, Comoros, Benin, Cape Verde, Gabon and Senegal in 2009–2018 [25,26,27,28]. Epidemics of DENV-1 were detected in Angola, Kenya, Senegal and Somalia in 2011–2018 [17,29,30,31].

Because dengue is becoming a major threat to public health in Africa, it is essential to better understand some poorly characterized aspects of the mosquito vectors involved in the epidemiology and transmission of this disease. Since there is no specific treatment or available vaccine for dengue, a better understanding of these factors will be a key driver for designing effective and sustainable vector control methods and strategies.

The goal of this review is to compile the available data on the dengue virus vectors in Africa based mainly on virus isolation from field collected mosquitoes and vector competence studies.

2. Mosquito species associated to dengue virus in the field

Several mosquito species have been associated with DENV in field collected mosquitoes from both urban and sylvatic environments (Table 1).

2.1. Vectors in the urban environment

In Africa, DENV is transmitted in the urban environment, between humans and the mosquito species Ae. aegypti and Ae. albopictus during epidemics. In urban environments, Aedes vectors were found breeding indoors and outdoors in human associated water storage containers (clay jars, drums, jerrycans, cement tanks, etc), discarded containers, used tires, flower pots, miscellaneous, etc. [32, 33, 34, 35]. These Aedes are mainly anthropophilic, but were also found to have fed on other animals [36, 37, 38]. Ae. aegypti is considered as mainly endophilic, endophagic, and daytime feeder, but it was collected feeding and resting outdoors within used tires, bricks and scrap metals indicating that it can also transmit viruses outdoors [39]. Alternatively, Ae. albopictus is considered as being a more opportunistic and outdoor feeder [37, 38]. Climatically suitable areas for Ae. aegypti related to dengue incidence was predicted to increase in the future [40]. These authors found that temperature and precipitation (by providing breeding sites and stimulates egg hatching) are important climatic factors that will influence Ae. aegypti development and distribution.

The DENV was associated with Ae. aegypti in an urban cycle, in Senegal, Nigeria, Burkina Faso, Cabo Verde, Tanzania, Kenya and Sudan during outbreak investigations and/or routine entomological studies (Figure 2). Despite its presence in several African countries, Gabon is actually the only country where DENV is associated with Ae. albopictus in continental Africa.

In Nigeria, Ae. aegypti and Ae. albopictus have been collected during entomological studies but only Ae. aegypti was found infected with all DENV serotypes in the field [41, 42]. A pool of Ae. aegypti collected in August 1969 in Ibadan was found positive for DENV-2. Viral RNAs of the four DENV serotypes were detected in Ae. aegypti collected in different localities of Nigeria in 2001–2002. Three pools of Ae. albopictus were found infected in 2 neighborhoods of Dakar (2 pools in Plateau and 1 pool in Parcelles Assainies), during the first urban epidemic of DENV-3 in Senegal [27]. The Stegomyia indexes in Dakar were above the epidemic risk threshold (between 6.6-195.2 for the Breteau index and 15-63.2 for the container index). Ae. albopictus was also the only potential vector present in high abundance in all the following urban epidemics and sporadic cases of dengue in 2015 (DENV-2; Mbour), 2017 (DENV-3; Louga) and 2018 (DENV-1 and 2 in Fatick; DENV-1 and 3 in Touba; DENV-1 in St Louis) that occurred in Senegal [28, 31, 43]. In Burkina Faso, DENV was isolated from Ae. aegypti in 1982 (1 pool) and 1986 (1

Figure 1. Map showing African countries where dengue circulation has been detected in local populations or travelers.
pool) during DENV-2 epidemics in the urban area of Bobo-Dioulasso [44]. During the first dengue epidemic that occurred in Cabo Verde in 2009, DENV-3 was isolated from a pool of Ae. aegypti collected at Praia, the capital city of the country. Two other serotypes (3 strains of DENV-2 and 5 strains of DENV-4) were later detected from the same country by RT-PCR from Ae. aegypti mosquitoes collected in 2014 and 2015, in

Table 1. Mosquito species found naturally infected with dengue virus in Africa.

| Environment   | Countries     | Species                                      | Years                  | Serotypes | References |
|---------------|---------------|----------------------------------------------|------------------------|-----------|------------|
| Urban         | Senegal       | Ae. (Stegomyia) aegypti                      | 2009                   | 3         | [27]       |
|               | Burkina Faso  | Ae. (Stegomyia) aegypti                      | 1982, 1986             | 2         | [59]       |
|               | Nigeria       | Ae. (Stegomyia) aegypti                      | 1969                   | 2         | [41, 42, 57] |
|               | Côte d'Ivoire | Ae. (Stegomyia) aegypti                      | 2017                   | 3         | [46]       |
|               | Tanzania      | Ae. (Stegomyia) aegypti                      | 2014                   | 2         | [19]       |
|               | Kenya         | Ae. (Stegomyia) aegypti                      | 2014                   | 2         | [47]       |
|               | Sudan         | Ae. (Stegomyia) aegypti                      | 2016–17                | ??        | [48]       |
|               | Cabo Verde    | Ae. (Stegomyia) aegypti                      | 2009, 2014–15          | 2, 3, 4   | [45]       |
|               | Seychelles    | Ae. (Stegomyia) albopictus                   | 1976–77                | 2         | [51]       |
|               | Gabon         | Ae. (Stegomyia) albopictus                   | 2007, 2010             | 2         | [23, 50]   |
| Rural/Sylvatic| Senegal       | Ae. (Stegomyia) aegypti, Ae. (Diceromyia) furcifer, Ae. (Diceromyia) taylori, Ae. (Stegomyia) luteocephalus, Ae. (Aedimorphus) dalinei, Ae. (Aedimorphus) vittatus, Ma. (Mansonoides) africana | 1974, 1981–82, 1989, 1999–2000 | 2 | [4, 53, 84] |
|               | Burkina Faso  | Ae. (Stegomyia) luteocephalus, Ae. (Stegomyia) africana, Ae. (Aedimorphus) cumminsii | 1980, 1983, 1986 | 2 | [44, 59]   |
|               | Côte d'Ivoire | Ae. (Stegomyia) aegypti, Ae. (Diceromyia) furcifer, Ae. (Diceromyia) taylori, Ae. (Stegomyia) luteocephalus, Ae. (Stegomyia) africana, Ae. (Stegomyia) ophii | 1980, 1985–87 | 2 | [4, 59]    |
|               | Nigeria       | Ae. (Stegomyia) luteocephalus, Ae. (Stegomyia) africana, Ma. (Mansonoides) africana | 1969, 1977 | 1, 2, 3 | [66, 61]   |
|               | Guinea Conakry| Ae. (Stegomyia) luteocephalus, Ae. (Stegomyia) africana | 1981 | 2 | [4]        |

Figure 2. Map showing African countries where dengue virus was detected from mosquitoes in the urban (A) and sylvatic/Rural cycle (B), and vector competence studies (C) were done.
Palmarejo (7 strains) and Fonton (1 strain), 2 neighborhoods of Praia city [45]. DENV-3 was detected by RT-PCR from 3 Ae. aegypti pools (2 from host-seeking females and 1 from emerging adults collected as larvae) collected at Abidjan, the economic capital city of Côte d’Ivoire, during the 2017 outbreak [46]. The Breteau (213 and 297), House (69 and 82%) and containers (35 and 41%) indexes were high in the 2 localities investigated during this outbreak.

The first association of DENV with Ae. aegypti in Tanzania was detected by an entomological investigation during the 2014 dengue outbreak [19]. DENV-2 was detected in 8.2% of 330 Aedes mosquito pools tested by RT-PCR. Only 2 out of the 27 positives Ae. aegypti pools were collected as adults. The Aedes indexes (Breteau index: 20.8–30.6 and container index: 65.2–80.2%) were very high, suggesting high risks of infection in all the districts investigated within Dar es Salaam. DENV-2 was isolated from a pool of 2 males Ae. aegypti collected during an outbreak in Mombasa in 2013–2014, suggesting that this species was the vector of this urban epidemic in eastern Kenya [47]. The Aedes indexes were all high in the study area (Breteau index: 123.1–358.6 and container index: 23.3–44.1%). During a routine entomological investigation in Kassala States in eastern Sudan, DENV RNA was detected in one out of 329 Ae. aegypti adults tested by RT-PCR. This species was the only vector identified during this study. The house and Breteau indexes were 32.8 % and 35.96, respectively [48]. The serotype was not identified during this outbreak but all dengue serotypes have been previously detected in Sudan. DENV-1 and DENV-2 were the most commonly found in this country [48, 49].

While both Ae. aegypti and Ae. albopictus were collected during a DENV-2 outbreak in Gabon in 2007 [23], the virus was only detected in Ae. albopictus (3 pools) in the suburbs of the capital city, Libreville, suggesting Ae. albopictus was the primary vector during this epidemic. Importantly, this was the first detection of DENV in Ae. albopictus in continental Africa and Ae. albopictus was more abundant than Ae. aegypti in this suburban environment. Aedes albopictus was also the vector of a second DENV-2 outbreak in Franceville, in Gabon in 2010 when the virus was detected in 18 out of 46 pools of this species tested [50]. One female was found coinfected with dengue and chikungunya viruses during this outbreak. Prior to the Gabon outbreaks, DENV-2 was isolated from 8 pools of Ae. albopictus collected during a dengue outbreak in the Seychelles in 1976–1977 [51]. Although multiple other dengue fever outbreaks have occurred in several other African countries, data on which mosquito species were involved is lacking because no entomological investigation was carried out during these outbreaks [4, 13, 52].

2.2. Vectors in the sylvatic and rural environments

Detection of DENV from several mosquito species (Ae. furcifer, Ae. taylori, Ae. luteocephalus, Ae. vittatus, Ae. africanus, Ae. opok, Ae. cumminsii, Ae. dalsieli, and Ae. aegypti) in sylvatic and rural areas follows a seasonal pattern. Dengue virus has mainly been detected between August and November in forest galleries and villages [53]. Some of these species (Ae. furcifer, Ae. taylori, Ae. luteocephalus, Ae. africanus and Ae. opok) are known to be crepuscular feeders [54]. Moreover, depending on the species considered, several of them (Ae. furcifer, Ae. taylori, Ae. luteocephalus, Ae. africanus, and Ae. opok) seem to feed almost exclusively on human and or non-human primates. Although they are found readily feeding on men, Ae. vittatus, Ae. cumminsii, Ae. dalsieli, sylvatic Ae. aegypti, and Ma. africana are considered as mainly zoophilic [55]. Some species like Ae. luteocephalus and Ae. taylori feed mainly in the forest-canopy, while others could be found feeding in almost all land-cover classes found in the sylvatic environment, including villages (outdoors and indoors) and agricultural areas where feeding on humans is possible [56]. Aedes furcifer females infected with DENV were collected within villages investigated in southeastern Senegal from 2009 to 2020, suggesting that they are involved in DENV-2 transmission to humans in this area [53]. The main breeding places are tree holes and fruit husks for most sylvatic vectors (Ae. furcifer, Ae. taylori, Ae. luteocephalus, Ae. africanus, and Ae. opok), rock pools and puddles for Ae. vittatus [32], ground pools and puddles for Ae. dalsieli and Ae. cumminsii, and grissy ponds for Ma. africana.

The sylvatic cycle of DENV has been described in five West African countries and mainly for DENV-2 (Table 1 and Figure 2) [53]. The first isolations of DENV-2 from naturally infected mosquitoes in Africa date to 1969 when one strain was isolated most likely from Ae. (Stegomyia) luteocephalus in Jos in Nigeria [57]. Later, DENV-2 was isolated from mosquitoes collected in wooded areas in Senegal [53, 58], Côte d’Ivoire [59], Guinea [4] and Burkina Faso [44]. The virus was isolated mainly from Ae. luteocephalus, Ae. furcifer and Ae. taylori in Senegal and Côte d’Ivoire, and Ae. luteocephalus in Burkina Faso. Several other species were sporadically found associated with DENV in the sylvatic environment in Senegal (Ae. aegypti, Ae. vittatus, Ae. dalsieli, Ma. africana), Burkina Faso (Ae. africanus, Ae. cumminsii) and Côte d’Ivoire (Ae. africanus, Ae. opok, Ae. cumminsii). DENV-2 was isolated from 4 pools of mosquitoes (3 Ae. africanus and 1 Ae. luteocephalus) collected in November 1981 in Guinea [4].

DENV-1 was isolated from two pools of Ae. africanus collected in the Mamu River Forest reserve in eastern Nigeria in 1997 [60]. DENV-3 viral RNA was also detected in 30 pools of Ma. africana collected in the rural locality of Ikarama, state of Bayelsa in Nigeria in 2015 [61]. The real importance of Ae. africanus and Ma. africana in the transmission of dengue in the rural human dwelling area need further studies.

3. Vertical transmission studies

In Africa, DENV is likely maintained in nature during unfavorable periods, by vertical transmission as suggested by detection of the virus from male mosquitoes, adults collected as immatures during field studies and progeny of infected females. Indeed, DENV was detected from male mosquitoes belonging to several species including Ae. aegypti in Nigeria [41] and Kenya [47], Ae. furcifer-taylori in Côte d’Ivoire in 1980 [59], Ae. taylori [62] and Ae. furcifer in a forest gallery in Kedougou [53] and unidentified Aedes species in Nigeria [41]. Most of the DENV-2 positive pools of Ae. aegypti (25 out of 27), detected by RT-PCR during the 2014 dengue outbreak in Dar es Salaam, the capital city of Tanzania were collected as immatures [19]. More recently, DENV-3 was detected by RT-PCR from a pool of emerging adults collected as larvae during the 2017 outbreak in Côte d’Ivoire [46]. Dengue virus was detected from one pool of F1 progeny of a population of Ae. aegypti from Nigeria (Lagos), infected with the New Guinea c DENV-2 strain, indicating vertical transmission [63].

4. Vector competence studies

The vector competence of field populations of mosquitoes associated with DENV in Africa is poorly characterized (Table 2) in few countries (Figure 2). Except for DENV-2 [64,65,66], few studies have been performed with DENV-1, 3 and 4 [67,68,69]. Vector competence studies were done mainly with sylvatic and domestic Ae. aegypti populations from Senegal, Cabo Verde, Kenya, Gabon, Cameroon, Ghana, Nigeria, Republic of Congo and Burkina Faso. Populations of Ae. aegypti from Nigeria (Lagos) and Burkina Faso (Kari) infected with a DENV-2 (New Guinea c strain) by intrathoracic inoculation were able to transmit the virus to suckling mice [63]. The first study by Diallo et al. [70] showed a low susceptibility of two populations of Ae. aegypti from Senegal to an epidemic and sylvatic DENV-2 strains. In this study, the infection and dissemination rates ranged between 0-25% and 67–100%, respectively. The low susceptibility of six populations of Ae. aegypti from Senegal, from different bioclimatic zones, to DENV-2 (a sylvatic and an epidemic strain) was confirmed later by Diallo et al. [64]. After 14 days post exposure, they found that these populations of Ae. aegypti had low infection rates (0–26%) and dissemination rates ranging between 10 and 100%. The authors did not find geographic variations of the vector competence of Ae. aegypti for DENV-2.
| Species | Mosquito tested in | Country and localities | Titer of the blood meals | Virus serotype (strains; Origin) | Origin | Inf (%) | Diss (%) | Trans (%) | DPE (days) | References |
|---------|-------------------|------------------------|--------------------------|-------------------------------|--------|---------|---------|----------|------------|------------|
| Aedes (Stegomyia) aegypti | Senegal | Kedougou, Koung Koung, Ndougoubene, Ngoye, Dakar and Barkdji | $10^{7.5}$ and $10^{7}$ TCID$_{50}$/mL | DENV-2 (ArD 140875; Kedougou) | Sylvatic | 0–26 | 0–75 | 14 | [64] |
| | | | $10^{6}$ TCID$_{50}$/mL | DENV-2 (ArA 6894; Bobo-Dioulasso) | Epidemic | 0–1.85 | 50–100 | 14 |
| | | Koung Koung, Kedougou | $6.2–8.8 \log_{10}$ TCID$_{50}$/mL | DENV-2 (NGC; New Guinea and 1349; Burkina Faso) | Epidemic | 0–25 | 67–100 | 14 | [70] |
| | | | $6.2–8.8 \log_{10}$ TCID$_{50}$/mL | DENV-2 (PM33974; Guinea and DakAr2022; Burkina Faso) | Sylvatic | 0–3 | 0–100 | 14 |
| | | Dakar, St-Louis, Kedougou | $4.9 \times 10^{5}$–$4.7 \times 10^{7}$ PFU/mL | DENV-1 (SH 29177; Bandia) | Epidemic | 71.4–92.5 | 50–93.8 | 2.9–5.9 | 7,15 | [67] |
| | | | $3.5 \times 10^{5}$–$2.4 \times 10^{7}$ PFU/mL | DENV-3 (S-162 Tvp-3622; Somalia) | Epidemic | 62.5–100 | 50–88.2 | 3.3–7.5 |
| | | | $1.2 \times 10^{5}$–$2.6 \times 10^{7}$ PFU/mL | DENV-4 (SH 38549; Dakar) | Epidemic | 71.4–93.8 | 56.7–93.8 | 2.9–20 |
| | | Saint-Louis, Digale, Dakar, Ngoye, Tambacounda, Goudiry, Niemenike, Ngari, PK10, Deux rivières, Fongolimb | $10^{7.5}$–8.5 pfu/mL | DENV-2 (JAM1409; Jamaica) | Epidemic | up to 90 | 14 | [65] |
| | | Kedougou, Fatick, Bigona, Richard-Toll, Goudiry, PK10, Mont Rolland, Rufisque | $6.02 \log_{10}$ PFU/mL | DENV-2 (75505; Kedougou) | Sylvatic | 50–91 | 29–93 | 14 | [71] |
| | | Dakar, Kedougou | $5.1 \times 10^{4}$ and $5.1 \times 10^{3}$ MID$_{50}$/mL | DENV3 (HB7; Hawaii) | Epidemic | 2.4–15.2 | 0–8.3 | xx | 7, 15, 20 | [72] |
| | | Dakar, Kedougou | $5.1 \times 10^{4}$ and $5.1 \times 10^{3}$ MID$_{50}$/mL | DENV1_btb28328; (Badan) | Epidemic | up to 50 | up to 50 | xx |
| South Africa | Palm Beach, Durban, Richard Bay, Ndurum, Skukuza | | $6.1–8.4 \log_{10}$ MID$_{50}$/mL | DENV-1 (Canim, Durban) | Epidemic | NA | 6–68 | 50–100 | 13–20 | [80] |
| | | | | DENV-2 (BC 5007; Taipei) | Epidemic | NA | 11–64 | 33–100 | 14–20 |
| Cape Verde | Santiago (seven counties) | | $2 \times 10^{5}$–$5 \times 10^{6}$ FFU/mL | DENV-1 (42735; BR PE) | Epidemic | 0–27 | 0–100 | 0 | 7,14,21 | [68] |
| | | | $1.4 \times 10^{5}$–$2 \times 10^{6}$ PFU/mL | DENV-2 (3808; BR-PE) | Epidemic | 50–80 | 20–93.3 | 5.0–65.0 | 7, 14, 21 |
| | | | $1.0 \times 10^{5}$–$2 \times 10^{6}$ PFU/mL | DENV-3 (85469; BR-PE) | Epidemic | 10–80 | 50–87.5 | 0.0–75.0 | 7,14,21 |
| | | | $1.0 \times 10^{6}$–$2 \times 10^{6}$ PFU/mL | DENV-4 (1385; Brazil) | Epidemic | 0–9 | 0 | 0 | 7,14,21 |
| | | | $10^{7}$ PFU/mL | DENV-2 (D25S32; Bangkok) | Epidemic | 41.6 | 8.3 | 14 | [72] |
| | | | | DENV-3 (Prata; Cabo Verde) | Epidemic | 27.3–80 | 0–20 | 7,10,14 |

(continued on next page)
| Species                  | Mosquito tested          | Titer of the blood meals | Virus serotype (strains; Origin) | Origin | Inf (%) | Diss (%) | Trans (%) | DPE (days) | References |
|-------------------------|--------------------------|--------------------------|----------------------------------|--------|---------|---------|-----------|------------|------------|
| **Country**             | **localities**           |                          |                                  |        |         |         |           |            |            |
| Madagascar              | Mahaleja, Joffreville    | $10^{8.8}$ MID$_{50}$/mL | DENV-2 (D2S32; Bangkok)          | Epidemic | 25.0–40.0 | xx      | x         | 14         | [79]       |
| Cameroon                | 19 localities including Douala, Marme and Yaoundé | $10^{8.1}$ MID$_{50}$/mL | DENV-2 (D2S32; Bangkok)          | Epidemic | 17.2–59.7 |        |           |            |            |
| Yaoundé, Douala, Tibati and Bénoué National Park | $10^7$ FFU/mL | DENV-2 (D2S32; Bangkok) | Epidemic | 70.8–100 | 58.8–100 | 0–50 | 14,21 | [75]       |
| Kenya                   | Kilifi, Nairobi          | $10^{5.06}$ FFU/ml      | DENV-2 (008/01/2012; Mandra)     | Epidemic | 6.8–21   | 7.02–42.9 |        | 7,14,21   | [66]       |
| Gabon                   | Franceville              | $10^8.3$ MID$_{50}$/mL  | DENV-2 (D2S32; Bangkok)          | Epidemic | 52.0, 69.6 | 14     |           |            |            |
| Nigeria                 | Lagos                    | $0.001$ PFU/mL           | DENV-2 (NGC; New Guinea)         | Epidemic | 37–56    |        |           |            |            |
| Burkina Faso            | Kari                     | $0.001$ PFU/mL           | DENV-2 (NGC; New Guinea)         | Epidemic | 0        |        |           |            | [63]       |
| Ghana                   | Hohe, Accra, Larabanga, Jirapa | $1 \times 10^6$ FFU/mL | DENV-1 (/NIID100/2014; Saitama) | Epidemic | 15.4–75.9 | 0–90.9 | 0         | 7,14       | [69]       |
|                           |                          | $1 \times 10^6$ FFU/mL | DENV-2 (P299/2017; Ghana)        | Epidemic | 0–30.2   | 0–12.5 |        | 14,21      | [75]       |
| Republic of Congo       | Brazzaville              | $10^7$ fflu/mL           | DENV-2 (D2S32; Bangkok)          | Epidemic | 77.3–95.8 | 88.2–95.6 | 36.4    | 14,21      | [75]       |
| *Aedes (Stegomyia) albopictus* | Madagascar, Anamakia, Antisiranana, Joffreville | $10^{8.2}$ MID$_{50}$/mL | DENV-2 (D2S32; Bangkok)          | Epidemic | 33.3–93.0 | xx      | xx       | 14         | [79]       |
| Gabon                   | Libreville               | $10^9$ MID$_{50}$/mL     | DENV-2 (D2S32; Bangkok)          | Epidemic | 13, 21.4 | 14     |           |            | [77]       |
| Cameroon                | 12 localities including Yaoundé and Douala | $10^{8.3}$ MID$_{50}$/mL | DENV-2 (D2S32; Bangkok)          | Epidemic | 13.3–47.5 | 14     |           |            | [74]       |
| Yaoundé, Douala, Tibati |                          |                          |                                  |        |         |         |           |            |            |
| Republic of Congo       | Brazzaville              | $10^7$ fflu/mL           | DENV-2 (D2S32; Bangkok)          | Epidemic | 14,21    |        |           |            | [75]       |
| La Reunion Island       | 10 localities including La Marine, Sainte Marie, Saint Pierre | $10^{8.2}$ MID$_{50}$/mL | DENV-2 (D2S32; Bangkok)          | Epidemic | 18–52    |        |           | 14         | [78]       |
| *Ae. (Diceromyia) furcifer* | Senegal                    | $6.5–9.2$ TCID$_{50}$/mL | DENV-2 (NGC; New Guinea and 1349; Burkina Faso) | Epidemic | 58–94    | 22–75 | 14     |            | [70]       |
| Senegal                 | Kedougou                 | $7.0–8.0$ TCID$_{50}$/mL | DENV-2 (PM33974; Guinea and DakAr2022; Burkina Faso) | Epidemic | 58–94    | 22–75 | 14     |            | [70]       |
|                           |                          | Sylvant                  | 26–97                            | 0–48    |           |        |           |            |            |
| Kedougou                |                          | $1.6 \times 10^6$       | DENV-4 (Haïti73; Haïti)          | Epidemic | 88.5     | 84.6   | 0       | 14         | [67]       |
|                           |                          | $3.1 \times 10^6$       | DENV-3 (Carec 01–11828; Barbados) | Epidemic | 86.6     | 77.8   | 0       |            |            |
| South Africa            | Mica                     | $6.8–7.1$ Log$_{10}$ MID$_{50}$/mL | DENV-1 (Canim; Durban)        | Epidemic | 0–3      | 0      | 15,17   |            | [80]       |
|                           | Mica, N’damu             | $8.2–8.4$ Log$_{10}$ MID$_{50}$/mL | DENV-2 (BC 5067; Taipei)       | Epidemic | 9, 17    | 50     | 15–18   |            |            |
| *Ae. (Stegomyia) lutescens* | Senegal                    | $5.5–8.2$ TCID$_{50}$/mL | DENV-2 (NGC; New Guinea and 1349; Burkina Faso) | Epidemic | 0–89    | 50     |           |            | [70]       |

(continued on next page)
| Species                        | Mosquito tested | Titer of the blood meals | Virus serotype (strains; Origin) | Origin | Inf (%) | Diss (%) | Trans (%) | DPE (days) | References |
|-------------------------------|-----------------|--------------------------|----------------------------------|--------|---------|---------|----------|-----------|------------|
| Sylvatic                      | 58              | –                        | DENV-2 (PM3974; Guinea and Dakar2022) | Syl    | 58-79   | 13-27   |          |           |            |
| Epidemic                      | 77.3            | 72.7                     | DENV-3 (S-162 TvP-3022; Somalia) | Epid   | 69      | 0       | 4.5      | 7.15      | [67]       |
| Sylvatic                      | 5.5             | 9.2 TCID50/mL             | DENV-1 (Cassim; Durban)          | Epid   | 3.5     | 6.5     | 6.7      | 7.15      | [67]       |
| Epidemic                      | 54, 60          | 29                       | DENV-2 (BC 5007; Taipei)         | Epid   | 7.1     | 5.6     | 35%      | 21-14     | [67]       |
| Epidemic                      | 33              | 0                        | DENV-2 (NGC; New Guinea)         | Epid   | 5.8     | 6.5     | 41%      | 70        | [70]       |
| Sylvatic                      | 6.5-8.8 TCID50/mL|                        | DENV-1 (Cassim; Durban)          | Epid   | 0       | 6        | 60-100   |           |            |

TCID50/mL: 50% tissue culture infectious doses; MID50/mL: 50% of mosquito infectious dose for Ae. aegypti; PFU/ml: Plaque formed unit; ffu/ml: Foci-Formed unit; Inf: infection rate; Diss: Dissemination rate; Trans: transmission rate; DPE: days post exposure when mosquitoes were tested.

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These infection rates varied geographically and were higher in the east coast of the island, while the disseminated infection rates of the 12 populations from Cameroon that ranged between 13.3 and 47.5% and were comparable [74]. Populations of Ae. albopictus collected from Cameroon (3 populations) and the Republic of Congo (1 population from Brazzaville) in 2017–2018, orally infected with a DENV-2 strain from Bangkok, were all able to transmit the virus [75]. Three populations from Madagascar showed susceptibility to the virus ranging between 33.3 and 93% [79].

The first vector competence study on sylvatic DENV vectors from Senegal showed high susceptibility of Ae. furcifer (infection rates: 26–97%; dissemination rates: 0–75%) and Ae. luteocephalus (infection rates: 0–89%; dissemination rates: 13–50%) to infection by the sylvatic and epidemic DENV-2 strains [70]. Ae. vittatus also showed low infection (0–19%) but high dissemination rates (60–100%) to DENV-2 during this study. Following the first DENV-3 outbreak in Senegal in 2009, another study tested the vector competence of Ae. furcifer (for DENV-3 and 4), Ae. taylori (for DENV-1, 3 and 4) and Ae. luteocephalus (for DENV-4) populations from Senegal [67]. The infection and dissemination rates of Ae. furcifer varied, between 86.6 to 88.5% and 77.8–84.6%, respectively. Like Ae. furcifer, the infection and dissemination rates of the other sylvatic vectors were high for all serotypes tested. Only Ae. luteocephalus (for DENV-4: 4.5%) and Ae. taylori (for ENV-3; 6.7%) transmitted the virus among sylvatic species tested. Populations Ae. furcifer and Ae. striatulae from South Africa were susceptible to DENV-1 and 2 with head squash infection rates varying between 0 and 17% for Ae. furcifer and 33–60% for Ae. striatulae [80]. The transmission rates were 0–50% for Ae. furcifer and 0–29% for Ae. striatulae.

Thus, vector competence data indicate great variability in the susceptibility of mosquito vectors to DENVs. This variability has been observed between populations of different geographic origins, and for the same population with different viral strains. The influence of the temperature on Ae. aegypti vector competence to DENVs was also showed [66].

5. Vector control

Very little data is available on vector control efforts during outbreaks in Africa. Vector control during dengue outbreaks in Africa relay on several interventions including insecticides spraying, sources reduction and larviciding [81]. Insecticide spraying in and around houses of dengue positive cases has been widely used during dengue outbreaks in Senegal, Cabo Verde and Côte d’Ivoire. Massive space spraying of insecticides outdoors in the neighborhood or entire city of positive cases has been the most widely used control method used in Senegal, Mauritania, Cabo Verde and Côte d’Ivoire. The susceptibility status of the targeted vector populations to the used insecticides were generally not studied [81]. Insecticides susceptibility tests should be always done before insecticide spraying operations [82]. To the best of our knowledge, larviciding using abate and larvivorous fishes to control dengue vectors were only used in Cabo Verde. Domiciliary visits with social sensitization associated with the removal of breeding sites were implemented during the 2018 dengue outbreak in Fatick and Touba, Senegal. The effectiveness of these interventions has never been evaluated.

6. Knowledge gaps and prospects for the future

Nationwide distribution, vector competence and insecticides susceptibilities status of Ae. aegypti and other dengue vectors remain largely unknown for most African countries. These questions deserve urgent attention of the medical entomology community while urban dengue epidemics number and frequency are increasing in Africa. It is also essential to study the bio-ecology of mosquito populations, in particular Aedes populations in urban areas in Africa. Most of the data currently available has been obtained in the framework of epidemic investigations [27, 46]. However, these investigations are punctual and usually take place at times when the dynamics and diversity of the vectors do not necessarily reflect the situation that caused the epidemic. A simplified dichotomous morphological key of dengue vectors is needed for the rapid identification of these species in the field. This key will allow scientists involved in dengue studies and mosquito control personal to more rapidly characterize mosquito populations, assess the epidemic risk, and respond efficiently to dengue outbreaks.

It would also be very useful to investigate the spatial distribution of vectors and the environmental and socio-economic risk factors associated with epidemic dynamics in order to propose targeted, efficient and sustainable control strategies [83]. The control strategies usually implemented during epidemics have never been monitored and evaluated. New innovative control strategies need to be developed and evaluated. These strategies should ideally use a package of low-cost technologies developed in Africa. These technologies must be produced and maintained at local and national levels. Strategies must be easy to understand, culturally acceptable and not labor intensive to implement by local communities. Finally, the efficacy and efficiency of these strategies must be regularly monitored and evaluated by public health authorities.

There is very little data available on other Aedes species present in urban areas in Africa that could play an important role in dengue transmission. With the progressive urbanization and gradual destruction of the forests, which are the natural habitats of the sylvatic vectors, it is essential to examine the evolution of these sylvatic Aedes to understand how they will adapt to the urban environment. Until now, DENV-2 is the main serotype detected in the forest environment in Africa [53]. The possibility of DENV-1, 3, and 4 to invade the forest environment and establish sylvatic cycles is unknown and should be investigated. Adaptation of sylvatic Aedes into a more urban environment and DENV-1,3 and 4 to the sylvatic environment could complicate the epidemiology of dengue fever in Africa and result in more frequent outbreaks. Finally, it is essential to study the vector competence of the Ae. aegypti, Ae. albopictus and all Aedes species populations in all African cities where they are abundantly present for all dengue serotypes from Africa, Asia and the Americas.

7. Concluding remarks

The objective of this paper was to review available data on dengue vectors in Africa. Evidences incriminated Ae. aegypti as a dengue vector in the urban setting in several countries in Africa (Senegal, Nigeria, Burkina Faso, Cabo Verde, Tanzania, and Kenya), while Ae. albopictus was only incriminated in Gabon. The sylvatic cycle of DENV, involving mainly arboreal mosquitoes and non-human primates, was described for DENV-2 in Nigeria, Senegal, Côte d’Ivoire and Burkina Faso. Several Aedes species (Ae. furcifer, Ae. taylori, Ae. luteocephalus, Ae. vittatus, Ae. africanus, Ae. apok, Ae. cumminsii, Ae. dalzieli, and Ae. aegypti) were associated with DENV in the sylvatic environment. Detection of the virus from male mosquitoes and adults collected as immatures during field studies in some countries suggested that DENV is probably maintained in nature by vertical transmission.

Vector competence studies done with sylvatic and domestic Ae. aegypti populations (from Senegal, Cabo Verde, Kenya, Gabon and Cameroon) showed great variability in the susceptibility of these populations. This variability was geographic origin, viral serotypes, and temperature dependent. Several populations of Ae. albopictus from Gabon, La Réunion Island, and Cameroon infected with a DENV-2 virus showed variables susceptibilities. Vector competence studies on sylvatic DENV vectors from Senegal, showed high susceptibility of Ae. furcifer and Ae. luteocephalus to infection. Ae. vittatus also showed low infection but high dissemination rates to DENV-2. The infection and dissemination rates of Ae. taylori were also high for all serotypes tested.

Data on distribution, vector competence and insecticide susceptibilities status of Ae. aegypti and other dengue vectors are lacking for most African countries. These questions need to be investigated. Specifically, studies on the bio-ecology of Aedes species in urban areas are needed. A
simplified dichotomous key of dengue vectors will be helpful for that purpose. The other questions that need to be investigated include environmentally and socio-economic risk factors associated with dengue vectors dynamics, control strategies and adaptation of vectors and viral serotypes to new environments.

Declarations

Author contribution statement

Diawlo Diallo, Babacar Diouf, Alionaye Ghoue, El hadji NDIaye, Ndeye Marie Sene, Ibbieba Diama and Mawlooth Diallo: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

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Additional information

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