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Journal

Bulletin of Entomological Research, 110(2)

ISSN

0007-4853

Authors

Doumtsop, Armand RPF
Hanna, Rachid
Tindo, Maurice
et al.

Publication Date

2020-04-01

DOI

10.1017/s0007485319000658

Bulletin of Entomological Research

cambridge.org/ber

Research Paper

Geographic distribution and abundance of the Afrotropical subterranean scale insect *Stictococcus vayssierei* (Hemiptera: Stictococcidae), a pest of root and tuber crops in the Congo basin

Armand R. P. F. Doumtsop[1,2,*], Rachid Hanna[1,†], Maurice Tindo[3], Willy K. Tata-Hangy[4], Apollin K. Fotso[1], Komi K. M. Fiaboe[1], Abraham Fomena[2], Adolph Kemga[1] and Benjamin B. Normark[5]

[1]International Institute of Tropical Agriculture (IITA), P.O. Box 2008, Messa-Yaounde, Cameroon; [2]Department of Animal Biology and Physiology, Faculty of Science, University of Yaounde I, P.O. Box 812, Yaounde, Cameroon; [3]Department of Animal Sciences, Faculty of Science, University of Douala, P.O. Box 24157, Douala, Cameroon; [4]IITA, 4163, Av. Haut Congo, C/Gombe, Kinshasa, Democratic Republic of Congo and [5]Department of Biology and Graduate Program in Organismic and Evolutionary Biology, 221 Morrill Science Center III, University of Massachusetts, 611 North Pleasant Street, Amherst, MA 01003, USA

*Present address: Department of Biological Sciences, Faculty of Science, University of Maroua, P.O. Box 814, Maroua, Cameroon.

†Present address: Institute of the Environment and Sustainability, Center for Tropical Research, Congo Basin Institute, Box 951496, University of California, Los Angeles (UCLA), Los Angeles, CA, USA.

Cite this article: Doumtsop ARPF, Hanna R, Tindo M, Tata-Hangy WK, Fotso AK, Fiaboe KKM, Fomena A, Kemga A, Normark BB (2019). Geographic distribution and abundance of the Afrotropical subterranean scale insect *Stictococcus vayssierei* (Hemiptera: Stictococcidae), a pest of root and tuber crops in the Congo basin. *Bulletin of Entomological Research* 1–9. https://doi.org/10.1017/S0007485319000658

Received: 20 November 2018
Revised: 6 July 2019
Accepted: 4 September 2019

Key words:
Anoplolepis tenella; ant; Central Africa; cocoyam; niche modeling; scale insect

Author for correspondence:
Armand R. P. F. Doumtsop,
E-mail: a.doumtsop@yahoo.fr

Abstract

Stictococcus vayssierei is a major pest of root and tuber crops in central Africa. However, data on its ecology are lacking. Here we provide an updated estimate of its distribution with the aim of facilitating the sustainable control of its populations. Surveys conducted in nine countries encompassing 13 ecological regions around the Congo basin showed that African root and tuber scale was present in Cameroon, Central African Republic, Congo, Democratic Republic of Congo, Equatorial Guinea, Gabon and Uganda. It was not found on the sites surveyed in Chad and Nigeria. The pest occurred in the forest and the forest-savannah mosaic as well as in the savannah where it was never recorded before. However, prevalence was higher in the forest (43.1%) where cassava was the most infested crop, compared to the savannah (9.2%) where aroids (cocoyam and taro) were the most infested crops. In the forest habitat, the pest was prevalent in all but two ecological regions: the Congolian swamp forests and the Southern Congolian forest-savanna mosaic. In the savannah habitat, it was restricted to the moist savannah highlands and absent from dry savannahs. The scale was not observed below 277 m asl. Where present, the scale was frequently (87.1% of the sites) attended by the ant *Anoplolepis tenella*. High densities (>1000 scales per plant) were recorded along the Cameroon–Gabon border. Good regulatory measures within and between countries are required to control the exchange of plant materials and limit its spread. The study provides information for niche modeling and risk mapping.

Introduction

Understanding a pest species' distribution and abundance is crucial for understanding its economic importance and management, and for predicting its future range and impact under climate change scenarios (Baskauf, 2003; Battisti and Larsson, 2015). This information can provide insights into the ecological requirements of the species, the success of an invasive population, the amount of effort required to eradicate or suppress that population, and the effectiveness of management and conservation strategies (Cerritos *et al*., 2012; Dicko *et al*., 2014; Macfadyen *et al*., 2018).

Stictococcus vayssierei was first reported as an agricultural pest in the early 1980s (Nonveiller, 1984). Its development displays neometabolan metamorphosis in males with five developmental stages and incomplete metamorphosis in females with three developmental stages (Richard, 1971; Williams *et al*., 2010). Males have rudimentary mouthparts and do not feed; consequently, they are tiny and short-lived, and adult males are rarely observed in the field. Females feed by sucking sap from underground shoots, stems, and roots of their host plants; they are much larger and longer-lived than males, are often abundant and conspicuous, and are responsible for all the damage to host plants. The host range of *S. vayssierei* includes more than 16 plant species belonging to 13 families. Cassava (*Manihot esculenta* Crantz), aroids (cocoyam *Xanthosoma sagittifolium* (L.) Schott and taro *Colocasia esculentus* (L.) Schott) and yams (*Dioscorea* spp. (L.)), collectively referred to as root and tuber crops (RTs), are the most infested plant species (Tindo *et al*., 2009), hence its common name the

African root and tuber scale (ARTS). RTs constitute a staple or subsidiary food for more than a quarter of the world's population. They are produced with very low inputs and they are also used as animal feed and as raw material for processing industries (Scott *et al.*, 2000; Janssens, 2001; Westby, 2002; Kenyon *et al.*, 2006; Graziosi and Wyckhuys, 2017). RTs are the second most cultivated agricultural products in tropical countries, after cereals (Lebot, 2009). Most of the world's production occurs in Africa (FAO, 2016) despite continue yield gap widening due to multiple interacting constraints (Fermont *et al.*, 2009; Tittonell and Giller, 2013). Together, cassava, aroids and yams represent 92% of total RT production in the Congo basin, with cassava comprising more than half (FAO, 2016).

The pest status of ARTS has been documented in many countries around Central Africa following outbreaks of its populations in the late 1980s, whose causes are still poorly understood. However, recent research has shown that conversion of forest into cropland promotes the dominance of the ant *Anoplolepis tenella* (Fotso *et al.*, 2015*a*), which is intimately associated with ARTS and contributes to the build-up of its populations (Dejean and Matile-Ferrero, 1996; Hanna *et al.*, 2004; Tata-Hangy *et al.*, 2006; Fotso *et al.*, 2015*b*; Toko *et al.*, 2019). Early bulking stages of the cassava are particularly susceptible to high levels of scale infestation (Ambe *et al.*, 1999; Tchuanyo *et al.*, 2000; Tata-Hangy *et al.*, 2006). Host plant residues in fallow are a scale reservoir and constitute the source for the infestation of newly established fields (Tindo *et al.*, 2009). Pest frequency on cassava plants increased from 12.5% in 1990 to 87.5% in 1994. The scale caused puny stems, extensive leaf fall, wilting, tip die-back and plant death. Plants that survived pest infestation yielded small and deformed storage roots, often covered with scales, and therefore unattractive to purchasers. At times, heavy infestation completely prevented bulking of the roots (Ngeve, 1995; Lutete *et al.*, 1997; Ambe *et al.*, 1999; Bani *et al.*, 2003). The pest can cause up to 27% depletion in cassava root yield (Ngeve, 2003). Details of the impacts on cassava, aroid and yam yields are still to be documented.

Scale insects of the family Stictococcidae are only known from Africa, where they are distributed between 12° North and 20° South latitude (Richard, 1971). *S. vayssierei* was first described by Richard (1971) from specimens collected from Cameroon in 1969 and from Central African Republic (CAR) in 1970. Previous data on its distribution are from an extensive survey in Cameroon (Tchuanyo *et al.*, 2000) and from more localized surveys in the Bas-Congo province in Democratic Republic of Congo (Lutete *et al.*, 1997; Lema *et al.*, 2000) and the western region of the Republic of Congo (Bani *et al.*, 2003). The presence of *S. vayssierei* in Uganda and Equatorial Guinea was documented by Williams *et al.* (2010) based on specimens collected by G. Goergen and one of us (RH). The pest lives in a close relationship (trophobiosis) with many ant species among which *A. tenella* is the most frequent and is a good indicator of the scale presence (Dejean and Matile-Ferrero, 1996). This ant is actively involved in the transport and dissemination of the scale (Fotso *et al.*, 2015*b*). While the scale is reported from the forest and forest-transition habitat, evidence of its presence in the savannah is not established. Further, there was no record of *A. tenella* in this area (Dejean and Matile-Ferrero, 1996) before the current study.

RTs are mostly propagated through cuttings or tubers. Fresh products are often sold or shared among farmers at a local or regional scale. This may lead to the rapid spread of plant feeding insects, especially pests. The purpose of this study was to update our understanding of ARTS distribution in the Congo basin and to identify some biophysical factors that can affect its distribution and abundance, to facilitate a sustainable and integrated management of the pest. The study was part of a regional food security project focusing on Cameroon and the Democratic Republic of Congo which together accounts for 75% of total cassava production in Central Africa (FAO, 2016), with additional effort made in neighboring countries.

Materials and methods

Study area

Nine countries around west and central Africa were surveyed at different times of year between 2002 and 2015 (table S1, supplementary material). Extensive surveys were carried out in Cameroon and Democratic Republic of Congo (DRC) which together account for 75% of total cassava production in Central Africa (FAO, 2016). More localized surveys were conducted in northern Gabon (Woleu-Ntem province), northern Republic of Congo (Sangha province), southwestern CAR (provinces of Mambere-Kadei and Sangha-Mbaere), and southeastern Nigeria (Cross River State). These surveys were supplemented by casual observation in Chad, Equatorial Guinea, and Uganda, as well as in some localities of the above countries. Some countries (Cameroon, DRC, and Gabon) were visited at least three times, but others (CAR, Chad, Congo, Equatorial Guinea, Nigeria, and Uganda) were visited only once. However, not always the same fields or villages were revisited. Surveyed localities were grouped into 13 ecological regions (Olson and Dinerstein, 1998; WWF, 2010) including forest and savannah vegetation types (table S2, supplementary material). The climate of the surveyed regions is all equatorial or tropical. The seasonal distribution of precipitation is bimodal in areas close to the equator but becomes unimodal further north or south (Godard and Tabeaud, 2009). Cassava is grown in the area mostly in a smallholder system, usually in mixed crop fields with groundnut, maize, cocoyam, taro, and other crops. The number of cropping seasons depends on the rainfall pattern; in areas with bimodal rainfall, there are two cropping seasons. However, farmers usually maintain the plants in the fields for up to 2 years for the continued use of both the cassava roots, eaten for subsistence, and the cassava stems, used as the source of vegetative planting material.

Surveys

Based on the accessibility and the intensity of cassava cultivation of different localities, villages were selected at 20–30 km intervals along transects following major road axes. With the farmer's consent, one cassava field (4–8 months old) was visited in each village. Surveys were conducted between January and May or November and December, corresponding to the period of high scale infestation in cassava fields (Ambe *et al.*, 1999; Tchuanyo *et al.*, 2000; Tata-Hangy *et al.*, 2006).

Sampling procedure

In each field, the global positioning system (GPS) coordinates were recorded. A destructive sampling protocol was applied with the farmer's consent and with financial compensation for the destroyed plants. The inspected plants were selected along the field's two major diagonals and uprooted to assess the

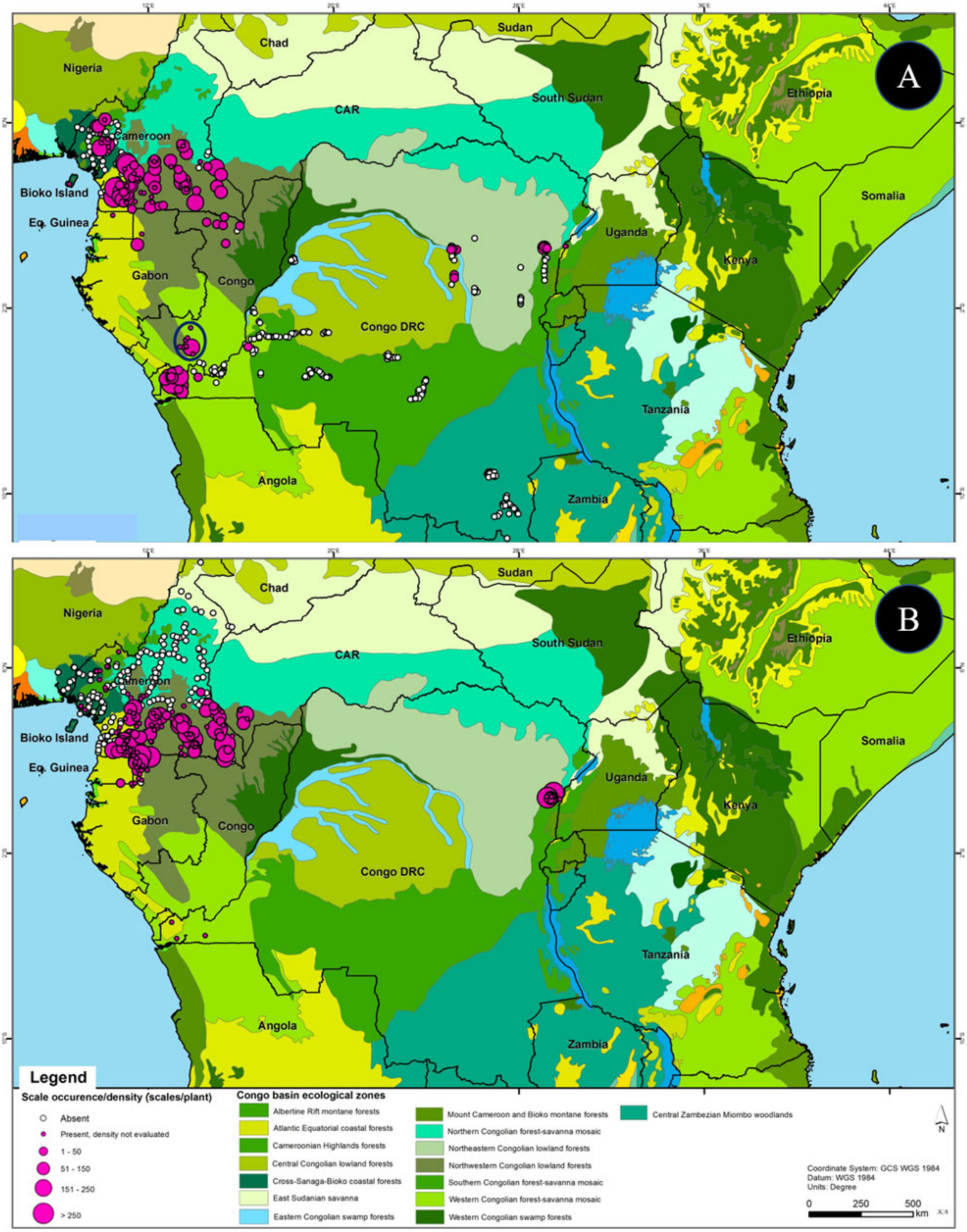

Fig. 1. Distribution and density of the ARTS, *S. vayssierei*, in the Congo basin between 2002 and 2008 (a) and 2009 and 2015 (b). Highlighted points in the blue circle are from GPS coordinates listed in Bani *et al*. (2003).

presence or absence of the scale; when the scale was present, the number of female scales was recorded. Ten cassava plants were sampled in each field. The distance between two consecutive plants depended on the field size and shape and was chosen to be representative of the field area. When aroids (cocoyam or taro) were present in the field, 5–10 aroid plants were also

Table 1. Incidence (%) and density (scales per infested plant) (mean ± SE) of *S. vayssierei* on different crops in cassava–aroid mixed crop fields in different vegetation types

Vegetation	*N* fields	Variable	Aroids	Cassava	*F*	df	*P*
Forest	35	Incidence	36 ± 6%	68 ± 5%	16.584	1	0.0001
		Density	43 ± 12	129 ± 24	7.717	1	0.0075
Savannah	6	Incidence	71 ± 14%	18 ± 6%	11.117	1	0.0076
		Density	77 ± 19	4 ± 2	6.184	1	0.0377
Forest + savannah	41	Incidence	41 ± 6%	61 ± 5%	6.474	1	0.0129
		Density	49 ± 11	113 ± 22	5.338	1	0.0240

sampled following the same protocol. Other known host plants of ARTS within the field or in the surrounding vegetation were also checked for the scale occurrence, up to a maximum of 30 plants sampled per field. However, for localized and casual surveys, sampling in some fields usually stopped after the scale presence was confirmed on few plants. The occurrence of *A. tenella* was evaluated by checking the presence of foraging workers in the field and under the uprooted plants (Dejean and Matile-Ferrero, 1996). When the scale was present, specimens were systematically collected for further taxonomic studies.

Data analysis

Occurrence data were pooled into two groups (2002–2008 and 2009–2015) over the survey period to assess the recurrence of the scale. Distribution maps based on the presence and absence data were designed with ArcMap (ArcGIS 10.3) using shape files of the ecological regions of central Africa (WWF, 2010). But further analyses focused on the spatial distribution of the species rather than the temporal distribution. ARTS' incidence (proportion of plants infested) and density (average number of scale insects per infested plants) were calculated from a subset of 99 fields where ARTS was present. The correlation between incidence and density was determined.

One-way analysis of variance was used to test the effect of crop species (cassava, cocoyam/taro) on scale incidence and density in 41 cassava–aroid mixed crop fields with positive ARTS occurrence. Means were separated using Tukey's HSD test. Regression analysis was used to evaluate the effect of altitude on scale density. Due to error in altitude given by GPS devices, elevation data used for analyses were gathered from the NASA SRTM3 worldwide database (90 m resolution) using the 'best available source' option of the GPS Visualizer program (www.gpsvisualizer.com). A χ^2 test was used to assess the effect of vegetation type and ecological region on ARTS prevalence (proportion of infested fields). The percentage that each variable contributed to the total prevalence was calculated as the number of positive samples per category/total number of positive samples for each variable (Ngo Kanga *et al.*, 2012). A two-tail Fisher's exact test was used to evaluate the effect of *A. tenella* occurrence on scale prevalence. Principal components analysis (PCA) was used to identify major variation patterns among the sampling sites. PCA was performed with four environmental variables (latitude, longitude, altitude, and vegetation type). Vegetation type was expressed as a binary numeric code (1, savanna; 2, forest), according to vegetation cover. Only significant factor loadings above 0.5 were considered. The PCA was run based on correlations using multivariate methods.

Results

Geographical distribution

Between 2002 and 2015, 720 waypoints corresponding to villages were visited and georeferenced during surveys in the Congo basin (fig. 1a, b). ARTS presence was recorded in 266 localities (36.9%) distributed in seven out of the nine surveyed countries from latitude S5.6863 to N6.6878 and longitude E8.6003 to E30.0383. The scale insect was not found in the surveyed sites in Chad and Nigeria. At a regional scale, pest's occurrence remained constant across all regions surveyed during both the first (2002–2008) and the second period (2009–2015) of observation. Specimens were collected from 14 host plant species across the surveyed area: Cassava (*M. esculenta* Crantz), cocoyam (*X. sagittifolium* (L.) Schott), taro (*C. esculentus* (L.) Schott), yams (*Dioscorea* spp.), groundnut (*Arachis hypogea* L.), plantain (*Musa* spp.), eggplant (*Solanum* sp.), *Amaranthus* sp., ginger (*Zingiber officinale* Roscoe), *Costus afer* Ker. Gawl., *Aframomum daniellii* K. Schum., *Palisota hirsuta* K. Schum., and two unidentified leguminous plant species.

Scale incidence and density

In ARTS-infested areas, incidence varied across surveyed localities from 13.3 to 100%, average 72.7 ± 2.5 (mean ± SE). Most surveyed localities (83.8%; $n = 99$) showed more than 40% infested plants. Mean density varied across localities from 1 to 1524 scales per plant, average 153.2 ± 20.1 (mean ± SE). Density significantly increased with incidence ($r = 0.371$, $n = 99$, $P = 0$) with less than 50% incidence at low density (1–50 scales per plant) and almost 90% incidence at high density (>250 scales plant).

Effect of crop plants on scale infestation

Across 41 surveyed cassava–aroid mixed crop fields where ARTS was found, the pest occurred on both cassava and aroids in 26 fields (63.4%), on cassava only in 13 fields (31.7%) and on aroid only in two fields (4.9%). Incidence and density were significantly higher on cassava compared to aroids. However, aroids were more infested than cassava in the savannah area while the opposite was observed in the forest area (table 1).

Effect of altitude on scale density

ARTS did not occur below 277 m asl. Although there was no significant effect of altitude on scale density, ARTS tends to occur predominantly between 300 and 800 m (fig. 2). Prevalence was very low (4.8%) below 300 m. Lowlands are usually associated

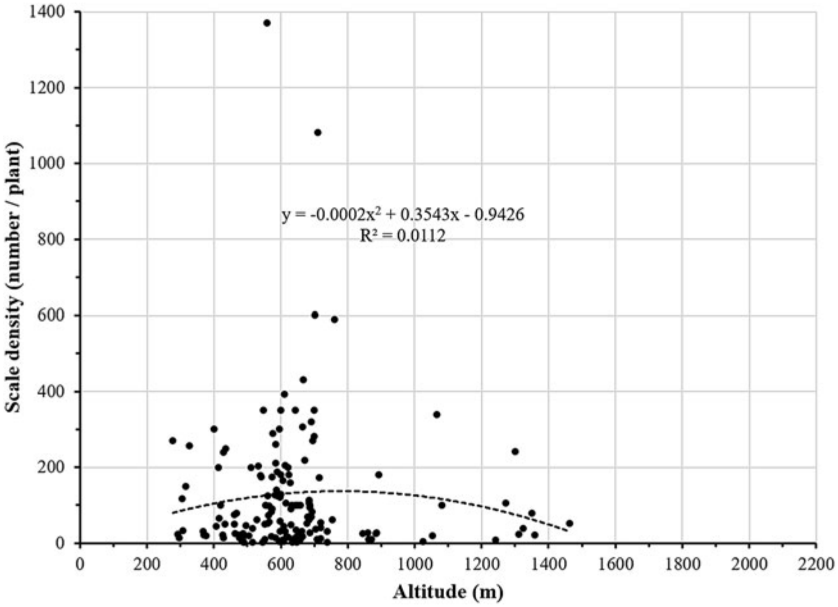

Fig. 2. Scale density vs. altitude in agroecosystems around the Congo basin.

with coastal regions. But, although ARTS was scarce in coastal areas, it occurred on Mount Cameroon above 500 m altitude.

Effect of vegetation types and ecoregions on scale prevalence

S. vayssierei was present both in the forest and the savannah, but its prevalence was strongly affected by vegetation type and ecological region (table 2). Specifically, ARTS occurred predominantly in the forest (41.1%) and less in the savanna (9.2%). In the savannah habitat, ARTS was restricted to the Cameroonian highland forest where 30.8% of the fields were infested. In the forest habitat, the pest was commonly found in the Western Congolian forest-savanna mosaic (36%), the Albertine Rift montane forest (51.1%), the Northwestern Congolian lowland forest (71.8%) and the Mount Cameroon and Bioko montane forest (100%).

Scale–ant interaction

The presence of *S. vayssierei* was strongly associated with the occurrence of the ant *A. tenella* ($\chi^2 = 569.6$, $n = 720$, $P < 0.0001$). The two trophobionts were both absent in 61.4% of the surveyed fields. In the remaining fields, ARTS usually (87.1% of the sites) co-occurred with *A. tenella* (fig. 3).

Distribution associated with interrelated variables

In the PCA of environmental variables, two factors accounted for 80.22% of variance in the data set (table 3). Factors were a combination of all four explanatory variables tested. Factor 1 (Prin 1) represented a gradient of increasing latitude (0.62) and altitude (0.51) from left to the right. Factor 2 (Prin 2) represented a gradient of increasing latitude (0.52) and vegetation type (−0.65) changing from forest to savannah from bottom to top. ARTS occurred at lower latitude in the mid- and high-altitude in the forest and at northernmost latitude in the mid-altitude savannah (fig. 4).

Discussion

Surveys showed that the ARTS occurs in seven countries of the Congo basin neighborhood, from the Bioko island (Equatorial Guinea) to western Uganda and from northwestern Cameroon to southwestern DRC. In addition to earlier reports of the presence of the scale in Cameroon, CAR, Congo, Equatorial Guinea, DRC, and Uganda, the results of this study provide solid evidence of the scale's presence in new areas such as Gabon, northern Congo, southwestern CAR, southwestern Cameroon at mid-altitude on Mount-Cameroon, western Cameroon highlands, and northeastern DRC. Scale insects belonging to the family Stictococcidae are only known from Africa, where they are distributed between the 12th and 20th parallels respectively north and south latitude (Richard, 1971). This distribution is similar to that of the African cassava belt (Williams *et al.*, 2010). The results of the current study will be useful for enhanced spatial analysis to predict the potential extend of occupancy at the edge of the current range and to highlight zones at risk of invasion in the future. Broadly, given the success of this species in exploiting cassava, we fear that it may expand its range westward, eastward, southward along the African cassava belt.

Overall densities were higher than those recorded in the 1990s (Tchuanyo *et al.*, 2000), with remarkably high densities observed in the area around the Cameroon–Gabon border. Factors that have led to the relatively rapid emergence of ARTS include land use pattern and association with ants. Indeed, forest conversion into cropland promotes the dominance of the ant *A. tenella* (Fotso *et al.*, 2015*a*) which is intimately associated with ARTS and contributes to the build-up of its populations (Dejean and Matile-Ferrero, 1996; Fotso *et al.*, 2015*b*; Toko *et al.*, 2019). High densities of sap-feeding insects usually show detrimental effects on crop yields (Nwanze, 1982; Schulthess *et al.*, 1991). However, moderate infestation has recently been shown to enhance crop yields, with positive implications for biological control (Thancharoen *et al.*, 2018). Studies of crop losses due to ARTS infestations have been very limited to date (Ngeve, 2003); particularly needed are empirical assessments of the impact of different infestation levels on crop yield, as well as socio-economic

Table 2. Distribution of the ARTS *S. vayssierei* in the Congo basin in different vegetation types and ecological regions

Categories	*N* fields	Prevalence (%)	Positive samples		χ^2	df	*P* value
			n	%			
Vegetation types					52.305	1	<0.0001
Forest	590	43.1	254	95.5			
Savannah	130	9.2	12	4.5			
Forest ecoregions					210.97	8	<0.0001
MCBMF	4	100.0	4	1.6			
NWCLF	259	71.8	186	73.2			
ARMF	47	51.1	24	9.4			
WCFSM	75	36.0	27	10.6			
NECLF	38	13.2	5	2.0			
CSBCF	60	11.7	7	2.8			
AECF	21	4.8	1	0.4			
CSF	20	0.0	0	0.0			
SCFSM	66	0.0	0	0.0			
Savanna ecoregions					30.847	3	<0.0001
CHF	39	30.8	12	100.0			
CZMW	44	0.0	0	0.0			
NCFSM	38	0.0	0	0.0			
ESS	9	0.0	0	0.0			

AECF, Atlantic Equatorial coastal forest; ARMF, Albertine Rift montane forest; CZMW, Central Zambezian Miombo woodland; CHF, Cameroonian highland forest; CSBCF, Cross-Sanaga Bioko coastal forest; CSF, Congolian swamp forest; ESS, East Sudanian savanna; MCBMF, Mount Cameroon and Bioko montane forest; NCFSM, Northern Congolian forest-savanna mosaic; NECLF, Northeastern Congolian lowland forest; NWCLF, Northwestern Congolian lowland forest; SCFSM, Southern Congolian forest-savanna mosaic; WCFSM, Western Congolian forest-savanna mosaic.

studies of its impacts. The latter studies could be of critical importance for the ecologically based management of its populations, with implications on the livelihood of smallholder farmers (Thancharoen *et al*., 2018).

Considerable effort has been devoted by the International Institute of Tropical Agriculture, in collaboration with national and international partners, to the development of management options based on host plant resistance, cultural, and biological controls (Nanga, 2005; Ngo Kanga *et al*., 2012; Hanna *et al*., 2015). Unfortunately, very few natural enemies have been identified associated with the scale and these do not contribute much to its mortality. Such enemies include entomopathogenic fungi (Nanga, 2005) and nematodes (Ngo Kanga *et al*., 2012), both with very low incidence. Further, tending by *A. tenella* probably provides considerable protection from natural enemies (Delabie, 2001). Experimental reduction of ant density resulted in consequent and significant reduction of the scale infestation and a 16% yield increase in cassava (Hanna *et al*., 2015).

The vegetation type significantly affected ARTS distribution. High prevalence in the forest habitat indicates that this is the most suitable and perhaps the original habitat for the scale, as earlier suggested (Richard, 1971). In addition, scale preference – relative incidence and density on a particular host – was shown to change from cassava to aroids depending on the forest or savannah area. Such response could indicate the existence of host biotypes or cryptic species (Xu *et al*., 2010). The ability to use different host plants is often associated with the presence of specific endosymbionts (Leonardo and Muiru, 2003; Hansen and Moran, 2014). Ongoing analysis of the cryptic diversity and endosymbiont profile of *S. vayssierei* in its geographic range will help clarify this issue.

The pest was previously unknown from the savannah habitat (Lutete *et al*., 1997; Lema *et al*., 2000; Tchuanyo *et al*., 2000). Our results show that it does occur in these habitats, possibly due to range expansion during the last decade from the human-modified forests to high-altitude moist savannahs (western highlands in Cameroon). Interestingly, the pest's most frequent ant trophobiont, *A. tenella*, was absent from this zone back in the 1990s (Dejean and Matile-Ferrero, 1996). There was strong association in the occurrence of the scale and the ant across the fields, as earlier reported (Dejean and Matile-Ferrero, 1996; Fotso *et al*., 2015*c*), indicating a likely similar geographic distribution of these trophobionts. However, a negative association between *A. tenella* and other ants such as *Myrmicaria opaciventris* (Fotso, 2011) could constitute a limiting factor to their distribution.

Ecological regions in each vegetation type also constrained ARTS distribution. Thus, the humid forest with a monomodal rainfall regime and dry savannahs (Guinean and Sudano-Sahelian) seemed to limit the spread of the pest. Given that ARTS' hostplants (e.g. cassava, yam) occur in these agroecological zones, we can hypothesize that the combination of abiotic parameters such as temperature variability, annual rainfall, and rainfall distribution

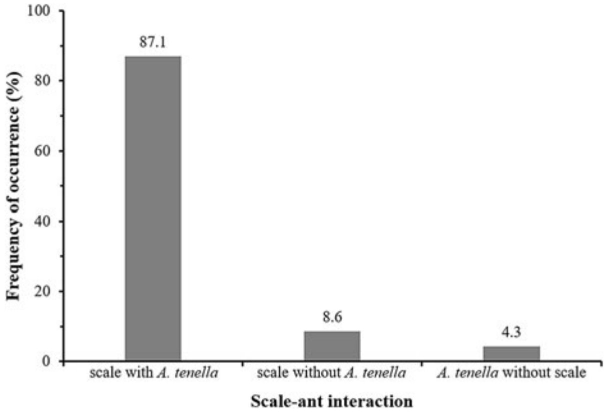

Fig. 3. Association between *S. vayssierei* and *A. tenella* in agroecosystems around the Congo basin.

Table 3. Eigen-vectors and eigen-values of principal components derived from environmental parameters used to characterize sampled localities in the Congo basin

	Factors	
Eigen-vectors	*Prin 1*	*Prin 2*
Latitude	−0.49582	**0.51881***
Longitude	**0.61906***	−0.30941
Altitude	**0.51271***	0.45647
Vegetation type	−0.32873	**−0.65325***
Eigen-values	1.9211	1.2877
Cumulative variance %	48.029	80.220

**p* < 0.0001 for bold values.

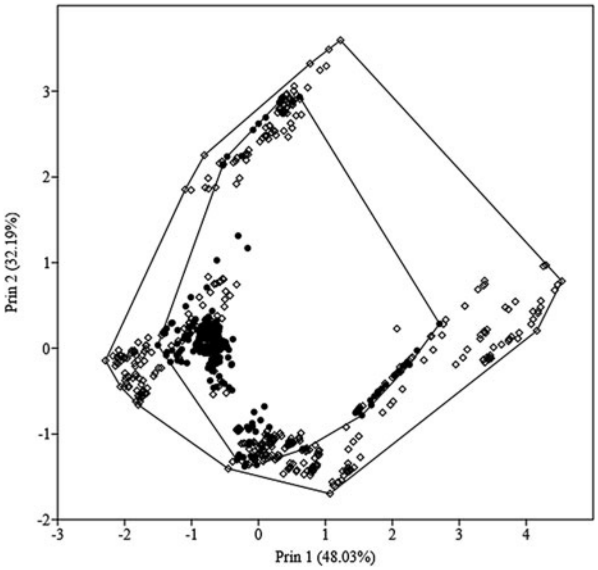

Fig. 4. Projection of sampled localities with ARTS absent (empty diamond) or present (black dot) on the planes defined by the two first factors of the PCA; along the *x* axis, longitude and altitude increased from left to right; along the *y* axis, latitude increased and vegetation type changed from forest to savannah from bottom to top.

over the year are the major factors controlling the distribution of ARTS. The scale occurs at low densities during the rainy season (Ambe *et al.*, 1999). Annual rainfall in Northwestern Congolian lowland forest, where the highest ARTS densities occurred, ranges from 1500 to 2000 mm. With 3000–10,000 mm annual rainfall recorded in the coastal regions, high precipitation and soil moisture could constitute limiting factors to the long-term establishment of the scale or its attendant ants. Ant attendance is apparently vital for ARTS survival (Hanna *et al.*, 2015; Fotso *et al.*, 2015*c*). However, ARTS' occurrence on Mount Cameroon at mid-altitude in the coastal region is a puzzling counterexample. In this case, other factors in relation to altitude are likely involved.

The surveyed area in southeastern Nigeria in the Cross-River state is a coastal area with altitudes below 200 m asl. Since low altitude and high precipitation apparently limit the scale's distribution, this is probably the reason why ARTS was not observed in this region. Yet specimens of the newly described species *S. subterreus* by Williams *et al.* (2010) were collected in that area at the vicinity (13 km) of Calabar between 1978 and 1981. *S. subterreus* is only the second known underground species in the family Stictococcidae, after ARTS (*S. vayssierei*). With poor regulatory measures in African countries, within-country as well as transboundary exchange of plant materials without control is common through trade and human migration. This contributes to rapid expansion and spread of herbivorous insects and especially pests. While additional surveys in Nigeria are needed to better investigate the distribution of both underground species of stictococcids, we can hypothesize a short-lived invasion of the Nigerian southeastern lowland back in late 1970s, with colonizing scales coming from yet-unidentified infested areas in Nigeria or Cameroon.

The continuous occurrence of the scale in the same regions from the first to the second period of observation as well as in regions of previously reported distribution indicates that its geographic range is not collapsing. It is likely that *S. vayssierei* is expanding its range and invading new habitats across Central Africa. Evidence for this includes the recent discovery of the pest in the savannah highlands and the apparent spread of its main trophobiont, *A. tenella*. Conditions favoring its spread include the mosaic of areas with high- and low-density populations, the extensive informal trade and movement of cassava and other root crops by humans, and the frequent conversion of forest to cropland. The broad ecological niche of *S. vayssierei*, including several host taxa, together with the recent discovery of a second subterranean *Stictococcus* species, hints that cryptic species diversity may be present and may further complicate the picture.

Conclusion

The ARTS *S. vayssierei* is known to occur in seven countries around the Congo basin. Although it mainly occurs in humid forest, it has recently been discovered in moist savannah highlands and may be expanding its range across the African cassava belt. Surveys in new areas will help clarify the geographic limits of this pest along with those of its most frequently associated ant, *A. tenella*. ARTS has also increased in density, with the Cameroon–Gabon border showing highest densities. Good regulatory measures within and between countries are required to control transboundary exchange of plant materials and limit the distribution of this challenging pest.

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S0007485319000658.

Acknowledgements. The authors are grateful to Jean Bruno Mikissa and Rufin Réo-Ndouba who facilitated surveys in Gabon and Central African Republic, respectively. Two anonymous referees provided valuable comments on the early versions of the manuscript. The work was supported by IITA core and CGIAR Consortium RTB funds, special project funds from the International Fund for Agricultural Development (IFAD), the US Agency for International Development, and a Borlaug-LEAP fellowship #016258-58 granted to A.R.P.F. Doumtsop.

References

Ambe JT, Ntonifor NN, Awah ET and Yaninek JS (1999) The effect of planting dates on the incidence and population dynamics of the cassava root scale, *Stictococcus vayssierei*, in Cameroon. *International Journal of Pest Management* **45**, 125–130.

Bani G, Mapangou Divassa S, Nzemba MD and Magem JM (2003) Présence au Congo-Brazzaville de *Stictococcus vayssierei* Richard, ravageur du manioc (*Manihot esculenta* Crantz) (Hem., Stictococcidae). *Bulletin de la Société Entomologique de France* **108**, 529–530.

Baskauf SJ (2003) Factors influencing population dynamics of the southwestern corn borer (Lepidoptera: Crambidae): a reassessment. *Environmental Entomology* **32**, 915–928.

Battisti A and Larsson S (2015) Climate change and insect pest distribution range. In Bjorkman C and Niemela P (eds), *Climate Change and Insect Pests*. CAB International, Wallingford, UK. pp. 1–15.

Cerritos R, Wegier A and Alavez V (2012) Toward the development of novel long-term pest control strategies based on insect ecological and evolutionary dynamics. In Soloneski S (ed.), Integrated Pest Management and Pest Control – Current and Future Tactics. InTech, Rijeka, Croatia. pp. 35–62. Available at http://www.intechopen.com/books.

Dejean A and Matile-Ferrero D (1996) How a ground-nesting ant species favors the proliferation of an endemic scale insect (Hymenoptera: Formicidae; Homoptera: Stictococcidae). *Sociobiology* **28**, 183–195.

Delabie JHC (2001) Trophobiosis between formicidae and hemiptera (Sternorrhyncha and Auchenorrhyncha): an overview. *Neotropical Entomology* **30**, 501–516.

Dicko AH, Lancelot R, Seck MT, Guerrini L, Sall B, Lo M, Vreysen MJB, Lefrançois T, Fonta WM, Peck SL and Bouyera J (2014) Using species distribution models to optimize vector control in the framework of the tsetse eradication campaign in Senegal. *Proceedings of the National Academy of Science of the USA* **111**, 10149–10154.

FAO (2016) FAOSTAT Statistics databases; annual production of root and tuber crops in Africa. Available at http://www.fao.org/faostat/en (Accessed May 2018).

Fermont AM, van Asten PJA, Tittonell P, van Wijk MT and Giller KE (2009) Closing the cassava yield gap: an analysis from smallholder farms in East Africa. *Field Crops Research* **112**, 24–36.

Fotso KA (2011) Towards the Development of Sustainable Control Options for the African Root and Tuber Scale on Cassava in Central Africa: Understanding the Biology and Ecology of the Tending Ant Anoplolepis Tenella (Hymenoptera: Formicidae). PhD dissertation, Basel.

Fotso KA, Hanna R, Tindo M, Nanga S and Nagel P (2015*a*) Ant diversity in dominant vegetation types of southern Cameroon. *Biotropica* **47**, 94–100.

Fotso AK, Hanna R, Tindo M and Nagel P (2015*b*) Transport and dispersal of *Stictococcus vayssierei* (Hemiptera, Stictococcidae) by *Anoplolepis tenella* (Hymenoptera, Formicidae). *Journal of Insect Behavior* **28**, 426–435.

Fotso AK, Hanna R, Tindo M, Doumtsop A and Nagel P (2015*c*) How plants and honeydew-producing hemipterans affect ant species richness and structure in a tropical forest zone. *Insectes Sociaux* **62**, 443–453.

Godard A and Tabeaud M (2009) *Les climats: mécanismes, variabilité, répartition*. Paris: Armand Colin.

Graziosi I and Wyckhuys KAG (2017) Integrated management of arthropod pests of cassava: the case of Southeast Asia. In Hershey C (ed.), Achieving Sustainable Cultivation of Cassava, vol **II**. Cambridge: Burleigh Dodds, pp. 1–26.

Hanna R, Tindo M, Wijnans L, Goergen G, Tata-Hangy KW, Lema K, Toko M, Ngeve JM, Dixon A and Gockowski J (2004) The African root and tuber scale problem in Central Africa: the nature of the problem and the search for control options. *Book of Abstracts of the 9th Triennial Symposium of the International Society for Tropical Root Crops – Africa Branch, 31 October–5 November 2004*. Mombasa, Kenya, p. 57.

Hanna R, Fotso KA, Nanga NS, Tindo M and Nagel P (2015) Boric acid for suppression of the ant *Anoplolepis tenella* and effects on an associated scale insect pest *Stictococcus vayssierei* in cassava fields in the Congo basin. *Crop Protection* **74**, 131–137.

Hansen AK and Moran NA (2014) The impact of microbial symbionts on host plant utilization by herbivorous insects. *Molecular Ecology* **23**, 1473–1496.

Janssens M (2001) Plantes à racines et plantes à tubercules: manioc. In Raemaekers RH (ed.), *Agriculture en Afrique tropicale*. Bruxelles: DGCI, pp. 194–218.

Kenyon L, Anandajayasekeram P and Ochieng C (2006) A synthesis/lesson-learning study of the research carried out on root and tuber crops commissioned through the DFID RNRRS research programmes between 1995 and 2005. Retrieved from http://r4d.dfid.gov.uk/PDF/Outputs/Root_Tuber_research_synthesis_P1.pdf.

Lebot V (2009) *Tropical Root and Tuber Crops: Cassava, Sweet Potato, Yams and Aroids*. Wallingford: CAB International.

Lema KM, Tata-Hangy K, Bidiaka M and Ndambi N (2000) Distribution, importance et dynamique des populations de la cochenille radicole du manioc (*Stictococcus vayssierei*, Homoptera: Stictococcidae) en Republique Democratique du Congo. *Annales de la Faculté des Sciences Agronomiques, Universite de Kinshasa* **1**, 40–49.

Leonardo TE and Muiru GT (2003) Facultative symbionts are associated with host plant specialization in pea aphid populations. *Proceedings of the Royal Society of London. Series B, Biological Sciences* **270**, 209–212.

Lutete D, Tata-Hangy K and Kasu T (1997) Présence au Zaïre de *Stictococcus vayssierei* (Homoptera, Stictococcidae), un ravageur du manioc (*Manihot esculenta*). *Journal of African Zoology* **111**, 3–7.

Macfadyen S, Mcdonald G and Hill MP (2018) From species distributions to climate change adaptation: knowledge gaps in managing invertebrate pests in broad-acre grain crops. *Agriculture, Ecosystems and Environment* **253**, 208–219.

Nanga NS (2005) Entomopathogenic Fungi Associated with Stictococcus vayssierei Richard (Homoptera, Sticticoccidae), a Pest of Cassava: Collection, Identification, and Pathogenicity. MSc thesis, University of Dschang. Dschang, Cameroon.

Ngeve JM (1995) Outbreak of a new tuberous root mealybug (*Stictococcus vayssierei*) [Homoptera: Stictococcidae] of cassava (*Manihot esculenta* Crantz) in Cameroon. *Proceedings of the 6th Symposium of the International Society for Tropical Root Crop-Africa Branch*. Lilongwe, Malawi, ISTRC-AB, p. 15.

Ngeve JM (2003) The cassava root mealybug (*Stictococcus vayssierei* Richard) (Homoptera: Stictococcidae): a threat to cassava production and utilization in Cameroon. *International Journal of Pest Management* **49**, 327–333.

Ngo Kanga F, Waeyenberge L, Hauser S and Moens M (2012) Distribution of entomopathogenic nematodes in Southern Cameroon. *Journal of Invertebrate Pathology* **109**, 41–51.

Nonveiller G (1984) *Catalogue des insectes du Cameroun d'interêt agricole*. Beograd: Institut pour la Protection des Plantes, Mémoires XV.

Nwanze KF (1982) Relationships between cassava root yields and crop infestations by the mealybug, *Phenacoccus manihoti*. *Tropical Pest Management* **28**, 27–32.

Olson DM and Dinerstein E (1998) The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. *Conservation Biology* **12**, 502–515.

Richard C (1971) Contribution à l'étude morphologique et biologique des Stictococcinae [Hom. Coccoidea]. *Annales de la Société Entomologique de France* **7**, 571–609.

Schulthess F, Baumgartner JU, Delucchi V and Gutierrez AP (1991) The influence of the cassava mealybug, *Phenacoccus manihoti* Mat.-Ferr. (Hom., Pseudococcidae) on yield formation of cassava, Manihot esculenta Crantz. *Journal of Applied Entomology* **111**, 155–165.

Scott GJ, Rosegrant MW and Ringler C (2000) Roots and tubers for the 21st century: trends, projections, and policy options. Food, Agriculture, and the

Environment Discussion Paper 31. Lima, International Food Policy Research Institute and International Potato Center.

Tata-Hangy K., Hanna R., Toko M., Lema K.M. and Solo M. (2006) Changes in population abundance of the African root and tuber scale *Stictococcus vayssierei* Richard (Homoptera; Stictococcidae) on cassava in the bas-fleuve district in the Democratic Republic of Congo. In Mahungu NM and Manyong VM (eds), *Advances in Root and Tuber Crops Technologies for Sustainable Food Security, Improved Nutrition, Wealth and Environmental Conservation in Africa. Proceedings of 9th ISTRC-AB Symposium*. ISTRC-AB, Mombassa, Kenya, pp. 574–582.

Tchuanyo M, Van Huis A and Van Lenteren JC (2000) Distribution, incidence and abundance of the cassava brown root scale insect, *Stictococcus vayssierei* in Cameroon. *Tropical Science* **40**, 20–24.

Thancharoen A, Lankaew S, Moonjuntha P, Wongphanuwat T, Sangtongpraow B and Ngoenklan R (2018) Effective biological control of an invasive mealybug pest enhances root yield in cassava. *Journal of Pest Science* **91**, 1199–1211.

Tindo M, Hanna R, Goergen G, Zapfack L, Tata-Hangy K and Attey A (2009) Host plants of *Stictococcus vayssierei* Richard (Stictococcidae) in non-crop vegetation in the Congo basin and implications for developing scale management options. *International Journal of Pest Management* **55**, 339–345.

Tittonell P and Giller KE (2013) When yield gaps are poverty traps: the paradigm of ecological intensification in African smallholder agriculture. *Field Crops Research* **143**, 76–90.

Toko M, Neuenschwander P, Yaninek JS, Ortega-Beltran A, Fanou A, Zinzou V, Wydra KD, Hanna R, Fotso A and Kpindou D (2019) Identifying and managing plant health risks for key African crops: cassava. In Neuenschwander P and Tamo M (eds), *Critical Issues in Plant Health: 50 Years of Research in African Agriculture*. Cambridge, UK: Burleigh Dodds Science Publishing, pp. 1–21.

Westby A (2002) Cassava utilization, storage and small-scale processing. In Hillocks RJ, Thresh JM and Bellotti AC (eds), *Cassava: Biology, Production and Utilization*. CAB International, Wallingford, UK. pp. 281–300.

Williams DJ, Matile-Ferrero D and Miller DR (2010) A study of some species of the genus *Stictococcus* cockerell (Hemiptera: Sternorrhyncha: Coccoidea: Stictococcidae), and a discussion on *Stictococcus vayssierei* Richard, a species injurious to cassava in Equatorial Africa with a description of a new species from Nigeria. *Zootaxa* **27**, 1–27.

WWF (2010) World Wildlife Fund – Global 200 (terrestrial) Ecoregions. Available at http://worldwildlife.org/publications/global-200 (updated in 2015).

Xu J, Lin KK and Liu SS (2010) Performance on different host plants of an alien and an indigenous *Bemisia tabaci* from China. *Journal of Applied Entomology* **135**, 771–779.