Editorial Manager(tm) for Food Security: The Science, Sociology and Economics of Food Production and Access to Food Manuscript Draft

Manuscript Number: FOSE254R2

Title: Threats to cassava production: known and potential geographic distribution of four key biotic constraints

Article Type: Original refereed paper

Keywords: Cassava; whitefly; green mite; cassava mosaic disease; cassava brown streak disease; geographic distribution; ecological modeling

Corresponding Author: Beatriz Vanessa Herrera Campo

Corresponding Author's Institution: International Center for Tropical Agriculture

First Author: Beatriz Vanessa Herrera Campo

Order of Authors: Beatriz Vanessa Herrera Campo;Glenn Hyman;Anthony Bellotti

Abstract: Insect pests and plant diseases reduce cassava yields substantially, posing a threat to food security throughout the developing world. While agricultural scientists have recognized these threats, few assessments of the geographic distribution of cassava pests and diseases have been made at the global scale. The goal of this study is to make such an evaluation for four key biotic constraints to cassava production in developing countries: whiteflies, cassava green mites, cassava mosaic disease and cassava brown streak disease. Occurrence records were obtained from laboratory and biodiversity databases and from the scientific literature. These records were then used in ecological niche models to predict the potential distribution of cassava pests and diseases. The distribution maps were cross-validated by holding back 20 percent of the occurrence records. Potential distribution maps were developed by combining the results of the best ecological niche models. Hotspots for potential cassava pest and disease outbreaks include the Mato Grosso in Brazil, northern South America, the African rift valley, the southern tip of India and much of Southeast Asia, where all four biotic constraints show high potential suitability. Our work highlights how potential geographical shifts in infestation hotspots for several cassava biotic constraints will require intensified monitoring, evaluation and research to prevent yield losses and ensure food security.

Response to Reviewers:

Introduction

Cassava (*Manihot esculenta* Crantz, Family *Euphorbiaceae*) is one of the most important staple crops for farmers in the tropics due to its high calorie content, low production cost and ability to adapt to different soil types and climatic conditions (Cock, 1982; FAO and IFAD 2000; Mejía de Tafur, 2002). Recent estimates suggest that as many as 500 million to 1 billion people consume cassava, making it the third most important crop in the tropics after rice and maize (Dutt, 2005; Breu, 2005; FAO 2008). Tropical farmers produce 233 million tons of cassava on 18.6 million hectares. A total of 40 countries in Africa make up more than 50% of the production, while Asia and Latin America contribute 34% and 15% respectively.

Although socioeconomic factors, market conditions and abiotic constraints negatively affect cassava production, pests and diseases are well known to substantially reduce yields, resulting in multi-billion dollar crop losses (Fondong et al., 2000; Bellotti et al., 2002; Hillocks and Jennings, 2003; Legg et al., 2004; Coulibaly et al., 2004; Maruthi et al., 2004; Anderson and Morales, 2005; Renkow and Byerlee, 2010; Waddington et al., 2010). Biological control programs in Africa have been highly successful, preventing huge losses. Recently, cultivars with disease resistance have successfully reduced the damage from cassava mosaic disease (Abele et al., 2005). However, these attempts to prevent and control pests and diseases often lack objective evaluations of the state and magnitude of the problem across cassava-growing regions.

Agricultural experts are concerned about recurring or new pest and disease problems that have emerged over the last several years. The steady advance of cassava brown streak disease in Africa could be devastating if it spreads beyond its relatively limited distribution in southeastern Africa and the Great Lakes region. Recent discovery of increased incidence of whiteflies and mealybugs in Asia is another cause for concern, especially given the growing importance of cassava in this region. Green mites could be another problem for Asia. Cassava brown streak disease and mosaic disease could potentially devastate cassava production in Latin America, if they were to appear. The emergence of new whitefly biotypes or possibly even species is another concern for cassava production (Perring et al, 2001; De Barro et al., 2011).

Despite the (potential) severity of these constraints, no systematic and global effort exists to estimate the potential geographic distribution of cassava pests and disease problems across the tropics. This paper addresses the question of where environments are suitable for key cassava pest and disease problems. The known distribution of four important pests -- whiteflies, cassava green mites, cassava mosaic disease and cassava brown streak disease -- was documented.¹ Environmental ranges of the pests and diseases were determined by combining the known locations with a series of global, high-resolution environmental maps,

¹. The study excluded Cassava Mealybug due to the lack of information on the actual distribution of the pest. However, future research should include the mealybug due to its history of economic damage in Africa.

using a spatial overlay method implemented in a geographic information system (GIS). Ecological niche models were then used to estimate the potential distribution based on actual occurrence records for these pests and diseases. The paper delineates areas with high potential for these problems and suggests some implications for reducing damage and yield loss.

Key cassava pests and diseases

Important aspects of cassava pest and diseases suggest how they might be evaluated and how their negative consequences might be countered in prevention and control programs. The review below indicates criteria for determining modeling methodology and evaluating the potential geographic distribution of this species.

Whiteflies (Bemisia tabaci Gennadius, Family, Aleyrodidae)

The whitefly, *Bemisia tabaci* Gennadius, is a complex of morphologically indistinguishable cryptic species that show distinct geographical, biological and genetic differences (Brown et al., 1995; Ko et al., 2005; Liu et al., 2007; Xu et al., 2010; De Barro et al., 2011). The most invasive species type documented is the Middle East-Asia Minor 1(B), which, regarded as such, also impacted cassava in Africa, but probably has been recorded as *B. tabaci* (Anderson and Morales, 2005; Xu, et al., 2010; De Barro et al, 2011).

The recent studies described above indicate that *B. tabaci* may be a complex of species, instead of a complex species. But this hypothesis is still subject to ongoing debate. Our research is based on an analysis of collection records that do not distinguish between biotypes or species. Accordingly, this study regards *B. tabaci* as a complex species.

Whiteflies can move 7 km through downwind migratory flight and no more than 2 km in self-propelled flight between crops and crop fields (Hirano et al, 2003; Salas, 2003). Planting materials, stem cuttings and international trade of ornamentals are important elements in its expansion (CABI, 2007). *B. tabaci* species attack crops, weeds and ornamental plants in all growth stages, feeding upon the phloem of its host plants (Martin 1999; Ellsworth and Martinez-Carrillo, 2001). The pest causes damage from direct feeding and indirect damage through honeydew secretion, promotion of fungal growth and vectoring several plant viruses (Ko et al., 2005; Nunes et al., 2005; Anderson and Morales, 2005; Liu et al., 2007). More than 600 host plants suffer from *B. tabaci* attacks, causing yield losses as high as 100% in certain crops (Albergaria and Cividanes, 2002; Nunes et al., 2005; Anderson and Morales, 2005). *B. tabaci* causes substantial damage from the diseases that they transmit (Ko et al., 2005), most importantly, Cassava Mosaic Disease (CMD) and Cassava Brown Streak Disease (CBSD).

Found throughout equatorial and tropical zones and extending into temperate zones (CABI, 2007), *B. tabaci* (Gennadius) has been recorded in 42 countries in Africa, 30 in Asia, 30 in Europe, 28 in Central America and the Caribbean, 22 states and provinces of North America, 10 countries in South America and 19 countries of the Pacific region (Fig.1a; Anderson and Morales, 2005; EPPO,

2006a CABI, 2007). Although the geographical range of the invasive Middle East-Asia Minor (B) type is extensive, its recording is limited to 10 countries in Europe, 7 in Asia, 3 in Africa, 3 in North America, 15 in Central America and the Caribbean, 3 in South America and 11 in Oceania (Fig. 1b; EPPO, 2006b).

Fig 1. Reported distribution of Whitefly (*B. tabaci* and the Middle East-Asia Minor (B)²) and potential distribution of the species niche. **a**) Shows the reported distribution of *B. tabaci* Gennadius, **b**) reports the distribution of B. argentifolii and **c**) represents the potential niche of *B. tabaci*: values are classified in five categories of equal intervals between 50 and 100% from yellow to red-brown tones: brown-red tones show areas where the probability of presence is high due to suitable climatic conditions; the yellow tones show low probabilities of presence. Grey represents areas with suitability under 50% and White areas represent habitats with no suitability.

The latitudinal limit of *B. tabaci* is about 40° in the northern hemisphere and 30° in the southern hemisphere, limited by cold climates in the winter (CABI, 2007). However, the pest is often found in greenhouses in areas outside its natural range, which play an important role in the expansion of the pest (Cáceres, 2004). The range of *B. tabaci* includes areas with at least four months of dry season, where climates lead to savanna vegetation, in areas with less than 80 mm of monthly rainfall and average monthly temperatures higher than 21°C (Morales and Jones, 2004). Optimal temperatures are 20 to 30°C, but the insect can be found across a range from a minimum of 14°C to a maximum of 35°C. *B. tabaci* populations have been known to increase at the onset of the dry season (Nunes et al., 2005). Factors leading to increased mortality include extreme temperatures, low relative humidity, and intense and persistent rainfall (Nunes et al., 2005). In Latin America, *B. tabaci* is poorly adapted to climates above 1000 m elevation (Morales and Jones, 2004).

Cassava green mite *(Mononychellus tanajoa* Bondar, Family, Tetranichidae)

The Cassava Green Mite (CGM; *M. tanajoa*; Fam:Tetranichidae) has co-evolved exclusively with its host plant cassava. The mites feed on the terminal parts the plant, killing leaf cells and reducing photosynthesis (Gutierrez et al., 1988). The mites disperse over short distances by walking and by wind. They move over long distances, between countries and regions, through exchange of cassava stem cuttings and by attachment to people, vehicles and other physical mediums (Yaninek, 1989).

During the 1970s *M. tanajoa* was responsible for yield losses of 30 to 50% in Africa (IITA/CIAT, 1997; Doreste 1982). Losses up to 80% in dry regions of Africa were reported in the 1970s and 1980s (Doreste, 1982; Skovard, 1993). Reported yield losses due to CGM in commercial plantings in Colombia range from 21 to 53% depending on population levels, host plant resistance, and duration of attack. Under high mite populations, yields in experimental fields

² Reported as *B. argentifolii* or B biotype of *B. tabaci* (EPPO, 2006b)

were reduced by 15% in resistant cultivars compared with an average 67% loss in susceptible cultivars (Bellotti et al., 2002).

Native to South America, *M. tanajoa* appeared in Africa in the early 1970s, spreading to 27 countries throughout the cassava belt by 1985 (Yaninek, 1988; Fig. 2a). CGM is found in all cassava regions of Latin America and Africa, but is not yet a problem in East and Southeast Asia. However, a closely related species, *Mononychellus mcgregori*, was recently observed feeding on cassava in Vietnam (Bellotti, personal observation).

Fig 2. Reported and potential distribution of Cassava Greenmite. **a**) Represents the known distribution of the species and **b**) shows the potential distribution predicted.

Tropical regions with a distinct dry season and low elevations provide suitable habitats for CGM. Temperatures as low as 15° C limit its range. *M. tanajoa* generally thrives where average temperatures are from 24°C to 31°C, with values of relative humidity between 50 and 70% (Doreste, 1982). Intense and constant rainfall is a key factor in their mortality. Population growth rates of the green mite increase at the end of rainy season and the beginning of the dry season when foliage is abundant (Yaninek et al., 1989).

Cassava Mosaic Disease (*Cassava Mosaic Geminiviruses*, Family: Geminiviridae)

Cassava Mosaic Disease (CMD) is produced by different viruses related to the Geminiviridae family, *Begomovirus* genus (Fig. 3 a, b, c and d show the reported distribution of each one). While the disease can be propagated through exchange of stem cuttings, its rapid expansion is closely associated with high populations of whiteflies (*B. tabaci* B), the principal vector of the disease (Hillocks, 2000; Legg et al., 2002). CMD is not exclusive to domesticated cassava, but affects its wild relatives and other species (Alabi et al, 2008). Yellow spots on leaves, leaf distortion and stunted growth are the typical symptoms of CMD-infected cassava (Fig. 4; Legg and Thresh, 2000). Different strains of the virus are unique to geographical sub-regions. In some areas where these strains overlap, there is evidence for the development of new virus pseudo-recombinations (Pita et al., 2001; Okao-Okuja et al., 2004; Fondong, 2000).

Fig 3. Reported and potential distribution of Cassava Mosaic Disease (CMD). . Maps a, b, c and d: show known distribution of Cassava Mosaic Disease: **a**) shows the virus distribution in Africa and Asia. The latter three (b, c and d) represent the virus with major extension: **b**) Shows the distribution in the countries where African Cassava Mosaic Virus (ACMV) is reported, **c**) East African Cassava Mosaic Virus (EACMV), **d**) East African Cassava Mosaic Virus–Uganda strain (EACMV-UG). Colors in the known distribution maps represent viruses' distinction as follows: 1. ACMV, 2. ACMV and East African Cassava Mosaic Cameroon Virus (EACMCV), 3. ACMV and EACMV, 4. ACMV and EACMV-Ug, 5. ACMV, EACMV-UG and East African Cassava Mosaic Virus –2 Uganda strain (EACMV-UG2), 6. ACMV, EACMV and EACMCV, 7. ACMV, EACMV, EACMCV and EACMV-UG, 8.ACMV, EACMV and EACMV-UG, 9. ACMV, EACMV, EACMV-UG and EACMV-UG2, 10. EACMV-UG, 11. ACMV, EACMV, EACMV-UG and South African Cassava Mosaic Virus (SACMV), 12. ACMV, EACMV, SACMV, 13. EACMV, 14. EACMV-UG2, 15. EACMV-UG and EACMV-UG2, 16. EACMV and SACMV, 17. SACMV, 18. Sri Lankan Cassava Mosaic Virus (SLCMV), 19. Indian Cassava Mosaic Virus (ICMV), 20. SLCMV and ICMV. Map e) shows the potential distribution of CMD: values are classified in five categories of equal intervals between 50 and 100% from yellow to red-brown tones

Fig 4. Cassava plant showing symptoms caused by CMD.

Economic damage from CMD has been substantial. In 2002, the total losses in Africa were reported at 19.6 to 27.8% of annual production of 97 million tons (Zhang et al., 2005). Annual economic losses in East and Central Africa have been estimated at US\$ 1.9-2.7 billion dollars (Patil and Fauquet, 2009). Fauquet and Fargette (1990) estimate 50% yield loss on average in Africa in areas with CMD infection.

CMD has been reported in all countries of Africa and the Indian subcontinent where cassava is an important crop (Fig. 3a; Colvin, 2004; Patil et al., 2005; Sseruwagi, 2006; Otim and Thresh, 2006, Patil and Fauquet, 2009). The disease has not yet been reported in Latin America, the Caribbean, East Asia or Southeast Asia (Carabali, 2005; Patil and Fauquet, 2009). However, its vector, *B. tabaci* (B), has been found feeding on cassava in the Dominican Republic, Cuba and Colombia (Brown et al. 1995; Carabali et al., 2004).

The distribution of Geminiviruses is determined by their vectors, environmental conditions and modes of dispersion. High temperatures in the rainy season and increasing whitefly populations have been associated with incidence of African Cassava Mosaic Virus (ACMV; Legg and Ogwal, 1998). Maruthi et al. (2002) demonstrated co-adaption between *B. tabaci* and the geminivirus, indicating the complexity that influences its environmental range.

Cassava Brown Streak Disease (*Cassava Brown Streak Virus*, Family: Potyviridae)

Cassava Brown Streak Disease (CBSD) is caused by two viruses -- Cassava Brown Streak Virus that belongs to the family Potyviridae and genus *Ipomovirus* and the Ugandan Cassava Brown Streak Virus (UCBSV; Monger et al., 2001a, 2001b, 2010; Mbanzibwa et al., 2009, Winter et al., 2010; ICTV, 2010; Mbanzibwa et al., 2011). The disease also seems to be related to a mixed infection between the two viruses (Mbazimbwa et al., 2011). Although mostly related to cassava, the disease can use other host species in the *Nicotiana* genus, where it can reproduce and propagate. The virus causes a yellowing of the leaves, stem lesions and necrosis of the roots, rendering it unpalatable and unsuitable for the market (Fig. 5; Hillocks and Jennings, 2003).The disease is transmitted mechanically through propagation of stem cuttings (Lister, 1959) and there is some evidence that the disease can be transmitted by different species of whiteflies, such as *B. afer* (Legg and Raya, 1998; Hillocks and Jennings, 2003;

Maruthi et al., 2005), *B. tabaci* (Maruthi et al., 2005, Alicai et al., 2007; Ntawuruhunga and Legg, 2007) and *Aleurodicus dispersus* (Mware et al., 2010). Monger et al. (2001b) also suggest that mites could be related to transmission of CBSV.

Fig 5. Cassava plant showing symptoms caused by CBSD.

The disease is exclusive to cassava and has caused losses up to 80% in East Africa (FAO and IFAD 2005). At least 20 million people have been affected by this cassava disease, with annual losses of \$50 million (IITA 2007).

The disease has been found mostly along the coast of East Africa, in an area extending from Kenya south to the Zambezi River in Mozambique (Fig. 6a). Along the shores of Lake Malawi, the disease is present in Malawi and Tanzania, but not along the shoreline in Mozambique (Hillocks and Jennings, 2003). It has been suggested that Angola could be a probable area to find the disease, due to cultural and economic ties to Mozambique (Hillocks and Jennings, 2003). Recent research has reported the disease in Uganda, Bas-Congo (without confirmation), Mozambique, Zambia and Malawi (Alicai et al., 2007).

Fig 6. Reported and potential distribution of Cassava Brown Streak Disease (CBSD). **a**) Shows the reported distribution of CBSD in Africa, **b**) displays CBSD distributional area on the Africa continent as a whole and **c**) represents the potential predicted distribution of CBSD: values are classified in five categories of equal intervals between 50 and 100% from yellow to red-brown tones.

Although in some cases CBSD has been found up to 1700 m above sea level, the disease is normally found at elevations below 500 m (Legg and Hillocks, 2003). There has been some evidence of a relationship between elevation and damage severity, with losses greater at lower elevations (Hillocks, 2003). The most recent outbreaks have occurred in Uganda where the entire country has now been affected by the disease.

Materials and Methods

The known geographic distribution of a pest or disease can be used to predict the potential distribution. This principle is the foundation for a rapidly growing area of research on ecological niche modeling, using known locations of a pest to characterize the environmental profile and potential distribution (Peterson and Vieglais, 2001). The method can simplify an otherwise complex process of analysis of species invasions (Peterson, 2003). Recent research has focused on how to more closely link niche modeling to ecological theory and its potential application to the analysis of climate change impacts on agriculture (Guisan and Thuiller, 2005; Pearson and Dawson, 2003).

Records of the locations of whiteflies, CGM, CMD and CBSD were used with ecological niche models to identify habitats where these pests and diseases would find climatic conditions suitable for survival and growth. A database of the known distribution was developed from collection records of the entomology and

virology labs of the International Center for Tropical Agriculture (CIAT), from the online species distribution database of the Global Biodiversity Information Facility (GBIF), from an expert survey as a part of Harvest Choice project in collaboration with colleagues at the University of Minnesota and from known locations reported in the scientific literature. These known distributions of pests and diseases were characterized using 22 climatic variables, plus elevation and the presence of cassava cultivation. Ecological niche models were then used to predict the potential distribution of the pests and diseases. Finally an evaluation data set was used to examine how well these models predicted the distribution of the pests and diseases. We describe in detail below: the development of the presence database, the environmental characterization data set, the ecological niche models and the validation method.

Presence and absence data

Each data set of known occurrences of pests and diseases was divided randomly into a *training data set* equivalent to 80% of the records and a *validation data set* of the remaining 20% of the data records (Table 1). The study lacks records on the absence of pests and diseases – reports of locations where researchers searched for pests and diseases, but they were not found. This limitation was addressed using the concept of pseudo-absence data (Benito de Pando and Peñas de Giles, 2007; Wisz and Guisan 2009; Phillips et al., 2006; Phillips and Dudík, 2008). 10,000 pseudo-absence data points were generated randomly for use in the ecological niche models.

Species	Source	Presence records	Training (80%)	Validation (20%)
Whitefly	CIAT virology and entomology labs	251	200	51
Cassava Green mite	CIAT entomology lab/ Scientific literature (Delalibera et al, 2004)	215	172	43
Cassava Mosaid Disease	CIAT virology lab and scientific literature (Colvin, 2004; Legg & Raya, 1998; Okao -Okuja, 2004; Sseruwagi, 2005; Patil, 2005; Legg & Ogwal, 1998)	159	127	32
Cassava Brown Streak Disease	Scientific literature(Legg & Raya, 1998; Legg & Hillocks, 2003; Hillocks & Jennings, 2003; Alicai et al, 2007) and expert survey ¹	82	66	16

Table 1. Summary of presence record of species used in the study.

¹Information from an expert survey was acquired in collaboration with colleagues at the University of Minnesota through the Harvest Choice project (<u>http://www.harvestchoice.org</u>).

Environmental characterization data

The relevance of an environmental variable, the scale of the study and the practicality of developing a global data set drive the selection of variables for characterizing the known occurrence of cassava pests and diseases (Titeux, 2006). At the global scale, climate is considered the determining factor, while at local

scales topography, soil type and biotic interactions as well as management considerations play an important role (Pearson and Dawson 2003). This study was carried out at the global scale and relies primarily on climate interactions. Bioclimatic data, as developed by Busby (1991), made up the key variables used in this analysis. These data are developed from averages of monthly precipitation and temperature and minimum and maximum monthly temperatures and are available in the Worldclim dataset (www.worldclim.org; Hijmans et al., 2005). Additional variables included the Hargreaves evapotranspiration index, the aridity index, number of consecutive dry months (with rainfall less than 60 mm), altitude and harvested area of cassava (Trabucco et al., 2008; You and Wood, 2006). The variables represent annual and seasonal tendencies as well as limiting factors and extreme values.

Three different groups of variables were selected to test their applicability for characterizing environmental conditions of cassava pests and diseases: a subset of variables selected by the authors based on our knowledge of the pests and diseases (EXP), a reduced set of variables derived from principal components analysis (PCA) and a reduced set derived from analysis of spatial correlation (SCA, Table 2). The authors' selected set of variables was based on the ecology and biology of the species, as well as our knowledge of the scientific literature. Our selection of environmental characterization variables for whiteflies and green mites included data that describes both seasonal and annual variation in climate. The data set on the number of consecutive dry months was also considered important for describing these two pests. However, this global spatial analysis could not account for factors such as the age of the crop, host plant resistance and characteristics of natural enemies of pests – factors the scientific literature considers important.

Cod.	Variables(¹)	White		Whitefly		CGM		CMD			CBSD)
•	All	Р	S	Е	Р	S	Е	Р	S	E	Р	S	Е
Bio1	Annual mean temperature	х	Х		х	х		Х			х		
Bio2	Mean diurnal range (mean (period max-min))												
Bio3	Isothermality (bio2/bio7)							х	х				
Bio4	Temperature seasonality (coefficient of variation)			x			x						
Bio5	Max temperature of warmest period				x			x				x	
Bio6	Min temperature of coldest period												
Bio7	Temperature annual range (bio5-bio6)	x			x	x							
Bio8	Mean temperature of wettest quarter			х	x		х	х					
Bio9	Mean temperature of driest quarter	x		х	x		х	х			x		
Bio10	Mean temperature of warmest quarter			х	x		х	х	х		x		
Bio11	Mean temperature of coldest quarter	x		x	х		х	х			x		
Bio12	Annual precipitation				х	х		х	х				
Bio13	Precipitation of wettest period	x											
Bio14	Precipitation of driest period		х					х	х		x		
Bio15	Precipitation seasonality (coefficient of			x	х	х	x						

Table 2. List of variables and datasets used for training the models.

	variation)												
Bio16	Precipitation of wettest quarter	x		х			х						
Bio17	Precipitation of driest quarter	x		х			х				х	х	
Bio18	Precipitation of warmest quarter		х	х			х				x	x	
Bio19	Precipitation of coldest quarter			х			х						
Bio19	Number of dry consecutive months	x	х	х			х						
Alt	Altitude	x	х	х	x	х					х	х	
HI	Aridity index												
PET	Potential evapotranspiration index												
НАС	Cassava harvested area (MapSpam,	v					v	v	v	v	v	v	v
me	http://mapspam.info/)	л					л	л	л	л	л	л	л
EDBT	Potential distribution of <i>B. tabaci</i> ²									х			X

¹ Key for variable data sets; 1: all variables includes all the climatic variables, excludes HAC and EDBT, P: Principal Components Analysis (PCA), S: Spatial Correlation Analysis (SCA), E: variables selected by authors (EXP).

²The potential distribution of the vector (whitefly) of cassava mosaic disease is from the Environmental Distance model (ED), the model showing the greatest extent of habitat suitability. This map was only used in models of CMD and CBSD.

PCA and SCA analyses were conducted using the Spatial Analysis in Macroecology (SAM) program (Rangel et al., 2006). The elimination of variables based on the principal components analysis and autocorrelation was not consistent across the four pests/diseases. However, the mean diurnal range, minimum temperature in the coldest months, rainfall in the wettest months, the aridity index and the potential evapotranspiration index were excluded due to multicollinearity.

Ecological niche models

Ecological niche models (ENM) describe habitat suitability along environmental gradients, which are then projected onto geographic space. Model projection represents the potential distribution of a species according to one or several environmental dimensions (Phillips et al., 2006). Several approximations for predicting distributions or determining suitability of habitat have been used (Busby 1991; Elith et al., 2006; Drake et al., 2006; Phillips et al., 2006; Benito de Pando and Peñas de Giles, 2007; Ortega–Huerta and Peterson, 2008; Sutherst and Bourne, 2009). ENMs require presence records of species and a set of environmental variables, describing factors that determine environmental suitability of a species (Phillips et al., 2006).

Several models were used in order to compare and evaluate the potential distributions of whiteflies, CGM, CMD and CBSD. The Climate Space Model (CSM, version 0.4) is based on principal components analysis, employing the concept of "broken stick cut off" to select the number of components and their

threshold values for making the estimation (Sutton et al., 2007). The Environmental Distance model (ED; version 0.3) is based on the notion of dissimilarity metrics. Distances from reference values in variable space are calculated to estimate the probability of suitability based on where the pest or disease was collected. The Genetic Algorithm for Rule-set Production model (GARP, version 3.2) is based on the concept of assessing conditions under which a species can maintain their populations (Anderson et al., 2003). GARP models are non-deterministic and are the result of multiple iterations and rule sets developed by the analyst. The Maximum Entropy Species Distribution Model (Maxent, version 3.1.19) is based on machine learning and produces probability distributions as a function of the environmental variables included in the analysis (Phillips and Dudík, 2008). Finally, the Support Vector Machine (SVM, version 2.86) is a generalized linear classifier based on supervised learning methods. All of the models described above except for Maxent were applied using the Open modeller analysis environment (de Souza Muñoz et al., 2009; available for download from http://openmodeller.sourceforge.net/). Maxent Software can be downloaded from the Internet (Phillips et al., 2006; http://www.cs.princeton.edu/~schapire/maxent/

Evaluation and validation

Ecological niche models produce two kinds of errors. Validation for this study is based on identifying the specific combination of omission and commission errors found in each model evaluated (Ortega-Huerta and Peterson, 2008). A threshold value was established, from which the predicted distribution is classified into two categories: absence in the values of prediction below threshold and presence in values equal or up to the threshold value.

Errors of commission are given by:

$$1 - Specificity = \left\lceil d / (b + d) \right\rceil$$

where b is a false positive and d is a true negative, predicting the presence of the species where it actually does not occur. Errors of omission predict the absence of the species where it actually does occur, expressed by:

$$Sensitivity = \left[a / (a + c) \right]$$

where \mathbf{a} is a true positive and \mathbf{c} is false negative. The calculation of the statistics is realized by comparing the presence and absence (pseudo-absence) of the calibration data set and the results of each one of the models.

Another statistic for evaluating models and identifying thresholds is the evaluation of types of errors using the Kappa coefficient (K), a measure of model performance, defined by the precision of the prediction in relation to a random prediction. A high coefficient indicates that the prediction has low errors of omission and commission (Fielding and Bell, 1997). The statistic is calculated by:

$$Kappa = \frac{\left[(a+d) - \left(((a+c)(a+b) + (b+d)(c+d)) / N \right) \right]}{\left[N - \left(((a+c)(a+b) + (b+d)(c+d)) / N \right) \right]}$$

Where **a** is the number of occurrence records correctly predicted as present; **b** is the number of random records incorrectly predicted as present; **c** is the number of occurrences incorrectly predicted as absent; **d** is the number of random records predicted as absent and **N** is the total number of observations (N = a + b + c + d). This index permits the identification of suitability for each model and species through the relationship between the threshold and the maximum Kappa value.

To select the best models a fixed threshold of 75% in sensitivity with an error rate of 0.25 was used to evaluate accuracy (Peterson et al., 2008).

Consensus distribution maps

The final potential distribution maps were developed using the weighted overlay method. Each map was assigned weights according to the error rate and sensibility statistics described above, assigning greater influence to the best-performing models (see supplementary material, tables 1 and 2). Potential distribution areas were included only where the probability value was above a fixed threshold of 0.7. Individual map models were then overlaid and each pixel was summed to produce a final suitability score (Potential distribution maps).

Results

Model statistics

For *B. tabaci* acceptable Kappa coefficients were found with low threshold values, the model ED with expert dataset had a K value of 0.80 reached in a threshold value of 63%. As judged by the Kappa coefficient, the best models in the case of CGM were GARP according to the authors' variable selection, showing a K value of 0.85 and a probability threshold of 90%. The same model using spatial correlation selection of variables showed a K value of 0.86 and a threshold value of 70%. The environmental distance model with a variable data set drawn from principal components analysis showed a K value of 0.87 and a threshold of 75%.

In the case of CMD, the environmental distance model showed a high K coefficient of 0.92 and an acceptable threshold value of 65%. CBSD showed high K coefficient with low threshold values. Acceptable models were Maxent with a K coefficient of 0.96 and a threshold of 68% and the environmental distance model with a K coefficient of 0.91 and a threshold value of 57%.

The models that in general show high Kappa coefficients are Maxent, ED and SVM. Nevertheless, for some of these the threshold probability of maximum performance varies from very low to medium and therefore these are not reliable models (Table 3, Fig. 7)

	W	hitefly	C	GM	С	CBSD		CMD
Model ¹ and variable set ² combination	kappa	threshold	kappa	threshold	kappa	threshold	kappa	threshold
CSM ALL	0.79	3	0.828	3	0.858	4	0.864	15
CSM PCA	0.386	1	0.556	10	0.449	57	0.309	68
CSM SCA	0.312	5	0.464	47	0.382	20	0.362	62
CSM EXP	0.83	8	0.802	1				
ED ALL	0.796	60.1	0.849	62	0.919	57	0.924	65.1
ED PCA	0.532	80	0.87	75	0.445	71.1	0.493	80
ED SCA	0.312	5	0.868	64	0.36	68	0.483	79
ED EXP	0.802	63.1	0.85	67	0.539	90	0.357	90
GARP ALL	0.804	40	0.852	20	0.859	10	0.884	90
GARP PCA			0.83	20				
GARP SCA			0.868	70				
GARP EXP	0.806	30	0.858	90	0.828	70	0.632	30
MAX ALL	0.849	30.1	0.916	12	0.964	15	0.904	12.1
MAX PCA	0.662	30	0.892	17	0.786	29.1	0.755	24
MAX SCA	0.597	19.1	0.877	5	0.968	68	0.725	23
MAX EXP	0.842	23	0.92	22	0.825	26	0.5	0
SVM ALL	0.835	15.1	0.884	25	0.945	19	0.911	22.1
SVM PCA			0.857	11.1				
SVM SCA			0.896	18				
SVM EXP	0.823	25.1	0.878	15.1	0.754	41	0.73	56

Table 3. Performance of models and datasets evaluated with the Kappa coefficient

¹The ecological niche models used were Climate Space Model (CSM); Environmental Distance model (ED); Genetic Algorithm for Rule-set Production (GARP); Maximum Entropy Species Distribution Model (MAX); Support Vector Machine (SVM)

²The data variable sets used were All variables (ALL); Reduced variable set using Principal Components Analysis (PCA); Reduced variable set using Spatial Correlation Analysis (SCA); Reduced variable set according to author's selection (EXP).

Fig 7. Performance of models evaluated with the Kappa coefficient. The data set key refers to groups of variables: the entire set of variables (ALL), variable set reduced using principal components analysis (PCA), variable set reduced using spatial correlation (SCA) and variable selected by authors (EXP).



According to the sensitivity analysis the best models for predicting the distribution of CGM were GARP, ED and SVM. The best models for whiteflies were GARP, ED and CSM. In the case of the two viruses few models displayed acceptable levels of sensitivity (above 0.7). The models with the best performance were GARP and ED in the case of CBSD, and ED, GARP and SVM in the case of CMD. The distribution maps of each model are in the supplementary material.

Potential geographic distribution of cassava pests and diseases

Potential B. tabaci distribution extends across the tropical and subtropical zones up to the margins of the temperate zone (Fig. 1c). Given the tendency of related species, to have similar characteristics (Pearman et al., 2007), as can be expected of the Bemisia tabaci complex; the invasive Middle East-Asia Minor (B) represents a threat in all the regions where other whiteflies (B. tabaci) occur under natural conditions. The potential range of B. tabaci (B) could therefore be much wider than its known distribution. B. tabaci A (New World group, Xu et al., 2010; De Barro et al., 2011) is not found in Latin America associated with cassava (Brown et al, 1995; Bellotti, 2002). However, because the Middle East-Asia Minor (B) was found feeding in cassava in some areas of the Americas (Brown et al., 1995), it could colonize cassava using wild species or other cultivated host plants that serve as intermediaries, as was demonstrated in experimental conditions (Carabali et al., 2004; 2005). Synergies and interactions between whitefly populations species, such as occurred in China and Australia where the Middle East-Asia Minor (B) mated with indigenous whiteflies (Liu et al., 2007), could be a strategy for whiteflies to increase their populations in Latin America. The Middle East-Asia Minor (B) continues to be a threat in Africa, where high suitability was predicted for the entire cassava belt (Fig. 1c). The pest is limited by dryness northward into the Sahel region and by constant wetness in the heart of Central Africa. The potential natural distribution of whiteflies is more restrictive than the known distribution due to their presence in artificially controlled environments such as greenhouses and irrigated regions (Cáceres, 2004, CABI, 2007).

Cassava green mite (M. tanajoa) shows a wide potential distribution in Latin America, the center of origin for cassava, with which it has co-evolved over centuries (Fig. 2b). The potential distribution of green mite in Africa is found throughout the cassava belt where there was a large expansion of the pest in the 1980s, after its introduction from South America. The models accurately predict the presence of green mites in Africa, where our occurrence dataset lacks records. In South Asia and Southeast Asia, the models predict a wide potential distribution for green mites in areas where cassava production has increased recently. In Vietnam, Cambodia, Thailand, Laos, Malaysia, Indonesia, Myanmar and New Guinea suitability values greater than 50% are common. Although it is possible that the distribution of green mites in these zones is limited by high precipitation, these regions also have dry periods that are favorable to the development of the species. Several regions in Asia appear to be highly suitable for the establishment of the pest because potential distribution estimates are similar to values in Africa, where substantial economic damage from green mite invasions has already occurred.

The known distribution of CMD extends throughout the cassava belt of Africa, the southwest coast of India and the island nation of Sri Lanka, matching the predicted distribution quite well (Fig. 3 a and e). In Latin America – where CMD has not been reported – the prediction models show similarly high suitability values in Brazil, northern Venezuela, Colombia, Bolivia, southern Mexico, Guatemala, Honduras and Nicaragua. In Asia, high suitability values are found in Vietnam, Cambodia, Myanmar, Thailand, Indonesia and the Philippines – areas where the disease has not yet been reported.

Substantial areas in Latin America and Asia could suffer from the geographical dispersion of *B. tabaci* and CMD problems, as shown by combining the suitability maps of each of these (Fig. 8). The inability of *B. tabaci* to colonize cassava in Latin America has been suggested as a reason for the absence of cassava mosaic disease. Nevertheless, taking into account studies showing the possibility of adaptation of the Middle East-Asia Minor (B) to cassava, the possibilities of its establishment and growth in the region are very high and therefore the development of the disease is a potential threat (Carabali, 2004, Carabali et al., 2005). The evolution of the virulence of cassava mosaic disease is shown by its different combinations into variants, as well as the appearance of new virus types. The capacity for the disease to be transmitted by whiteflies increases the possibility of its geographic dispersion towards regions of high potential for its development.

Fig 8. Model coincidence between CMD and whitefly (*B. tabaci*) showing spatial conjunction of the potential distribution of the disease and its vector.

CBSD shows a relatively limited potential distribution, yet one that is much larger than the current known distribution along the coast of Tanzania and Mozambique and in some regions of Uganda (Fig. 6 a and c). The potential to spread to West Africa, Central Africa and the southwestern coast of Africa is indicated by Figure 6(c). In Latin America, areas of high potential distribution include Mexico, Central America (Guatemala, Honduras and Nicaragua), the northern coast of South America and some regions of eastern Brazil. The potential distribution is more limited in Asia. Nevertheless pockets of high suitability include southern India, Thailand and Vietnam.

Discussion and Conclusion

Geographic hotspots of cassava pests and diseases

The prediction models indicated high potential for the spread of whiteflies, CGM, CMD and CBSD in the African rift valley, the Mato Grosso in Brazil, northern South America and Southeast Asia, where different models and data sets were generally in agreement. Some areas of cassava production in countries of Central America, the Mato Grosso region in Brazil, coastal zones in the north of Venezuela and Colombia, the boundary region between Bolivia and Brazil and northern Argentina exhibit environmental conditions conducive to the development of whiteflies (*B. tabaci* complex) and high potential for transmission and reproduction of whitefly-borne viruses. Climatically suitable regions for the pests and diseases studied include India, Malaysia, and New Guinea, where cassava production plays an important role in agriculture.

Cassava brown streak disease will encounter favorable environmental conditions in the greater part of central Africa where vectors associated with this disease are present. Uncertainty about virus propagation could explain the absence of the disease in large parts of the Africa cassava belt (Maruthi et al., 2005; Hillocks and Jennings, 2003). Distinct possible vectors for the disease are considered: *Bemisia afer*, *B. tabaci* and *Aleurodicus dispersus*. If the vector is *B. tabaci*, a closer correspondence between the distribution of the virus and the vector would be expected, which is not the case.

Favorable environments for CBSD occur in northern Bolivia, southern and central Brazil, northern Venezuela and some countries of Central America and the Caribbean. Places where actual pest or disease occurrences do not match the predictions are due to reports from artificial environments such as greenhouses and irrigation zones.

Model performance

Our results showed that in general the GARP and ED models performed well at the global scale and for all four biotic constraints. SVM and CSM performed least well. Maxent appears to work well for geographically limited regions or local situations. The results show that higher numbers of occurrence records improve the reliability of the models.

Analysis with different variable sets showed the performance of PCA and SCA was lower (below 50%) than expert criteria (EXP). 70% of the models run with variables selected by the authors' criteria have good capacity of discrimination. The percentage of models with good performance diminishes utilizing the sensitivity statistic with a 75% threshold, but maintains the same trend.

Expert knowledge beyond the use of global climate variables constitutes fundamental criteria for model processing and interpretation. Species distribution responds to environmental, economic and social dynamics that are impossible to include in an ENM at global scale.

The use of these models should constitute a first approximation to the knowledge of the distribution of the pest and pathogens at global scale, owing to the emphasis on climatic variables. For this reason they serve as preliminary insights for more detailed studies that involve other types of information, such as host plant resistance, predator-prey interactions, crop management information and others.

Implications

Future research should take advantage of ecological niche modeling, as an easily accessible and useful tool. While it is easier to acquire data on the presence of pests and diseases, the information often lacks needed protocols for its organization and correct use. Problems related to data development include the lack of absence data and poor or no geo-referencing of field observations, all of which reduce the accuracy of analyses and limit the interpretation of the results.

More effort is needed on the study of host plants, virus and disease vectors and natural enemies across a range of scales. To determine strategies and policy for management, studies need to be initiated at regional, landscape and local scales, focusing on species dispersal and ecosystem interactions.

Research in the field of taxonomy and entomology of *B. tabaci* is urgent in order to clarify the distinctions and nominations of the species complex. The lack or inconsistency of information causes many difficulties and lowers accuracy in the geographic approximations to the distribution of the complex.

More attention needs to be paid to management considerations that affect the distribution of cassava pests and pathogens, such as effects of continuous cropping and unsafe movement of cassava germplasm (Calvert, 1994). The interactions between pests and diseases suggest that management plans need to be integrated across different pests and pathogens, host plants and natural enemies.

The research results reported in this paper can support economic impact studies oriented towards prioritizing agricultural research and development programs. These analyses can inform breeding programs designed to develop cultivars resistant to pest and diseases. They can help prioritize crop management interventions.

The cassava research and development community could implement more formal early warning systems that motivate more research and development, such as that described in this study, and that are oriented towards avoiding the dispersion of pests and pathogens in their potential environments. The dispersion of cassava pests and diseases disregards international borders, calling for international collaboration to reduce their negative impacts on food security.

Acknowledgements

We thank the staffs of the International Center for Tropical Agriculture's (CIAT) virology and entomology labs for providing data on their disease and pest collections. Clair Hershey and Kris Wyckhuys of CIAT and two anonymous reviewers provided valuable comments on the manuscript. We also thank Ramón Serna of the Universidad del Valle, Colombia, for excellent supervision of a related thesis. Jason Beddow of the University of Minnesota provided ongoing support in our effort to solicit expert opinion about the geographic distribution of pests and diseases. The research was made possible by financial support from the Harvest Choice project (http://harvestchoice.org).

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Beatriz Vanessa Herrera is a geographer from the Universidad del Valle. She is a young researcher at the International Center for Tropical Agriculture (CIAT) in the Climate Change and Decision Analysis group (DAPA). Whilst working at Ciat she conducted her thesis research on cassava pests. She completed her title in November 2010 with honours and has since been part of DAPAs research team. Other tasks concerned the distribution of invasive pests in South America and the potential distribution of fruit pests in Colombia. At the moment she is exploring ways to project the impact of climate change on agricultural pest pressure using ecological niche models. Her interest focuses on the different factors that are involved in the invasion process. Her motivation is to use the best available methods to yield results that help farmers all over the world to better prepare themselves for plagues.



Glenn Hyman is a geographer specializing in agriculture and geographic information science and technology. His regional interests include Central America, the Andes and the Amazon. He holds a Masters degree in geography from Appalachian State University and a doctorate in geography from the University of Tennessee. Glenn develops continental GIS databases of crops and population and conducts research as a member of the senior staff of the International Center for Tropical Agriculture (CIAT). Glenn participates in food security and poverty mapping initiatives (www.povertymap.net), phenotyping networks (www.africats.org) and agricultural GIS networks (www.csi-cgiar.org). He is an active member of the Association of American Geographers (AAG), the Conference of Latin Americanist Geographers (CLAG) and the Society of Latin American Remote Sensing Specialists (SELPER).



Anthony Bellotti is a Senior Scientist, Cassava Entomologist of the International Center for Tropical Agriculture (CIAT) with a PhD from Cornell University. He has been working for more than 35 years in the same position in the cassava program at CIAT. His large experience on numerous insect pests and mite complexes that damage cassava is focused on bio-ecological research, economic damage studies and control of cassava pests from varietal resistance, biological control and effects on natural practices to chemical control. His impressive record of publications included more than 250 scientific publications in refereed and non-refereed journals, chapters in books, symposium and workshop papers.

Threats to cassava production: known and potential geographic distribution of four key biotic constraints - Supplementary material

Beatriz Vanessa Herrera^{1,2}, Glenn Hyman¹ and Anthony Bellotti¹

- 1. International Center for Tropical Agriculture. AA 6713, Cali, Colombia.
- Corresponding author; b.v.herrera@cgiar.org; Tel. +57 (2) 4450000; Fax +57 (2) 4450000.

Supplementary maps

Figures 1 to 66 Show potential distribution of four cassava pest, according to each Ecological Niche Model and variable dataset used. Values are classified in five categories of equal intervals from yellow to red tones: brown-red tones show areas where the probability of presence is high due to suitable climatic conditions; the yellow tones show low probabilities of presence. White areas represent habitats with low or no suitability.

Maps 1 to 16. Potential distribution of Bemisia tabaci



Fig 1. Climate Space Model with all variable dataset.



Fig 2. Climate Space Model with Spatial Correlation variable dataset.



Fig 3. Climate Space Model with Experts criterion to variable dataset.



Fig 4. Climate Space Model with Principal Component Analysis variable dataset.



Fig 5. Environmental Distance model with all variable dataset.



Fig 6. Environmental Distance model with Spatial Correlation dataset



Fig 7. Environmental Distance model with expert criterion variable dataset.



Fig 8. Environmental distance model with Principal Component Analysis variable dataset



Fig 9. GARP model with all the variables dataset



Fig 10. GARP model with Expert criterion variable dataset.



Fig 11 Maxent model and all the variables



Fig 12. Maxent model with Spatial Correlation Analysis variable dataset.



Fig 13. Maxent model with Expert criterion analysis



Fig 14. Maxent model and Principal Component Analysis



Fig 15. Support Vector Machine model with all the variables



Fig 16. Support Vector Machine model with Expert criterion variable dataset



Maps 17 to 36. Potential distribution of Mononychellus tanajoa





Fig 18. Climate Spatial model with Spatial Correlation Analysis



Fig 19. Climate spatial model with Expert criterion dataset.



Fig 20. Climate Spatial Model and Principal Component Analysis.



120°W 40°W 120°E 80°W 0° 40°E 80°E 160°E Fig 21. Environmental Distance Model with all variables dataset



Fig 22. Environmental Distance Model with Spatial Correlation Analysis



Fig 23. Environmental Distance Model with Expert criterion



Fig 24. Environmental Distance Model with Principal Component Analysis





Fig 26. GARP with Spatial Correlation Analysis







Fig 28. GARP with Principal Component Analysis



Fig 29. Maxent model with all variables dataset.





Fig 31. Maxent model with Expert criterion



Fig 32. Maxent model with Principal Component Analysis



Fig 33 Support Vector Machine with all variables dataset.



Fig 34. Support Vector Machine with Spatial Correlation Analysis



Fig 35. Support Vector Machine with expert criterion dataset.



Fig 36. Support Vector Machine with Principal Components Analysis.

Maps 37 to 51. Potential distribution of Cassava Brown Streak Virus



Fig 37. Climate Space Model with all variables



Fig 38. Climate Space Model with Spatial Correlation Analysis



Fig 39. Climate Space Model with Principal Component Analysis.



Fig 40. Environmental Distance Model with all variables



Fig 41. Environmental Distance model, with Spatial Correlation Analysis



Fig 42. Environmental Distance Model with Expert criterion variables dataset



Fig 43. Environmental distance model with Principal Component Analysis



Fig 44. GARP with all variables dataset







Fig 46. Maxent model with all variables











Fig 49. Maxent model with Principal component Analysis.



Fig 50. Support Vector Machine with all variables



Maps 52 to 66. Potential distribution of Cassava Mosaic Virus



Fig 52. Climate Spatial Model with all variables





Fig 54. Climate Spatial Model with Principal Component Analysis



Fig 55. Environmental Distance Model with all variables



Fig 56. Environmental Distance Model with Spatial Correlation Analysis





Fig 58. Environmental Distance Model with Principal Component Analysis dataset





Fig 60. GARP with Expert criterion dataset.



Fig 61. Maxent Model with All variables dataset







Fig 63. Maxent model with Expert Criterion dataset.









Fig 66. Support Vector Machine with Expert Criterion dataset.

Table 1 and 2 show the best model performance of sensitivity statistic in a threshold value of 75% and the weight assigned in the final distribution maps for pest and diseases, respectively.

Specie		Whitefly		Green mite							
Model ⁽¹⁾	sensitivity	Error rate	Weight	sensitivity	Error rate	Weight					
GARP ALL	0.904	0.16	26.1	0.932	0.11	11.57					
GARP EXP	-	-	-	0.955	0.14	11.8					
GARP PCA	-	-	-	0.909	0.14	11.3					
GARP SCA	-	-	-	0.955	0.11	11.8					
ED ALL	0.942	0.05	27.23	0.773	0.04	9.6					
ED EXP	0.826	0.09	23.8	0.886	0.12	11					
ED PCA	-	-	-	0.955	0.111	11.8					
ED SCA	-	-	-	0.864	0.10	10.7					
SVM ALL	-	-	-	0.818	0.03	10.1					
CSM ALL	0.788	0.03	22.7	-	-	-					
Total			100			100					

Table 1. Statistical values for the Whitefly (*B. tabaci*) and the Green mite (*M. tanajoa*) models.

1. The ecological niche models with best performance were Climate Space Model (CSM); Environmental Distance model (ED); Genetic Algorithm for Rule-set Production (GARP); Support Vector Machine (SVM). ALL: includes all the climatic variables, PCA: Principal Components Analysis dataset, SCA: Spatial Correlation Analysis dataset and EXP: variables selected by authors.

and the Cassava Mosaic Disease (CMD) models.											
Virus		CBSD			CMD						
Model ⁽²⁾	sensitivity	Error rate	Weight	sensitivity	Error rate	Weight					
GARP ALL	0.879	0.13	53.7	0.722	0.04	30.9					
ED ALL	0.758	0.03	46.2	0.833	0.02	35.7					
SVM ALL	0.778	0.01	33.3	-	-	-					
Total			100			100					

 Table 2. Statistical values for the Cassava brown streak disease (CBSD)

 and the Cassava Mosaic Disease (CMD) models.

2. The ecological niche models with best performance were Environmental Distance model (ED); Genetic Algorithm for Rule-set Production (GARP) and Support Vector Machine (SVM) with ALL climatic variables.