

Biocultural Drivers Responsible for the Occurrence of a Cassava Bacterial Pathogen in Small-Scale Farms of Colombian Caribbean

Darío Pérez^{1,2,3}, Anne Duputié⁴, Christian Vernière¹, Boris Szurek¹ and Sophie Caillon^{5*}

¹ PHIM Plant Health Institute, Univ. Montpellier, IRD, CIRAD, INRAE, Institut Agro, Montpellier, France, ² PALOC, IRD, Muséum National d'Histoire Naturelle, Paris, France, ³ GIMBBE, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia, ⁴ Univ. Lille, CNRS, UMR 8198 – Evo-Eco-Paleo, Lille, France, ⁵ CEFE, CNRS, Univ. Montpellier, EPHE, IRD, Montpellier, France

OPEN ACCESS

Edited by:

Thiago Gonçalves-Souza, Federal Rural University of Pernambuco, Brazil

Reviewed by:

Johnson Nyasani, Kenya Agricultural and Livestock Research Organization, Kenya Patrick Chiza Chikoti, Zambia Agriculture Research Institute (ZARI), Zambia

> *Correspondence: Sophie Caillon sophie.caillon@cefe.cnrs.fr

Specialty section:

This article was submitted to Conservation and Restoration Ecology, a section of the journal Frontiers in Ecology and Evolution

Received: 23 December 2021 Accepted: 04 April 2022 Published: 02 May 2022

Citation:

Pérez D, Duputié A, Vernière C, Szurek B and Caillon S (2022) Biocultural Drivers Responsible for the Occurrence of a Cassava Bacterial Pathogen in Small-Scale Farms of Colombian Caribbean. Front. Ecol. Evol. 10:841915. doi: 10.3389/fevo.2022.841915

Cassava (Manihot esculenta Crantz) is a primary crop for food security of millions of people worldwide. In Colombia, the Caribbean region contributes about half of the national cassava production, despite major socioeconomic constraints such as unequal land property, omnipresence of middlemen, low and unstable prices, armed conflict, climate change and phytosanitary issues. Among the latter is Cassava Bacterial Blight (CBB), a disease caused by the bacterial pathogen Xanthomonas phaseoli pv. manihotis (Xpm) that leads to irreversible damage to plants, impeding growth and productivity. In 2016, we analyzed the role of sociocultural and agricultural practices on CBB prevalence in small-scale fields of a village of the Colombian Caribbean region, where farmers live almost exclusively from the sale of their cassava production. Semi-structured interviews (48) were conducted with all farmers who cultivated cassava to document individual sociodemographic characteristics, cassava farming practices, and perceptions about CBB occurrence. Cassava Bacterial Blight was diagnosed in the field and the presence of Xpm was further confirmed upon laboratory analysis of collected diseased leaf samples. Our data show that (i) according to the risks perceived by farmers, CBB is the main disease affecting cassava crops in the village and it could indeed be detected in about half of the fields visited; (ii) CBB occurrence depends strongly on land property issues, likely because of an inadequate phytosanitary control during acquisition of cuttings when farmers are forced to rent the land; and (iii) there is a strong positive correlation between the use of commercial fertilizers and the occurrence of CBB in the village of Villa López.

Keywords: agricultural practices, cassava bacterial blight (CBB), fertilizer use, land property, Xanthomonas phaseoli pv. manihotis, circulation of propagative propagules, seed system

INTRODUCTION

Agriculture today is faced with a double challenge: coping with the impacts of climate change and reducing chemical inputs. It will become even more difficult to overcome these challenges, knowing that pest attacks are projected to decrease the yield of major grain crops by 10 to 25% per degree Celsius of warming (Deutsch et al., 2018). Root crops are particularly concerned by yield reduction

compared to cereals under drought conditions (Daryanto et al., 2017). Phytosanitary problems in a context of climate change could potentially deprive humanity of up to 82% of the attainable yield (Chakraborty and Newton, 2011). It is estimated that each year already, approximately 16% of global harvest is lost due to plant diseases (Strange and Scott, 2005). Economic losses caused by plant pathogens may affect food security, especially in food-deficit regions with fast-growing populations such as countries in Latin America, Sub-Saharan Africa, and the Indo-Gangetic Plain (Savary et al., 2019).

Cassava (Manihot esculenta Crantz) is extensively cultivated all over the tropics; its tuberous root is a major source of carbohydrates for hundreds of millions of people worldwide (Lebot, 2009). Because of its tolerance to heat and water stress, cassava is thought to be resilient to climate change (Jarvis et al., 2012; El-Sharkawy, 2014), and hence is considered a strategic food, especially in a context of human adaptation to climate change (Burns et al., 2010). In Colombia, cassava is one of the most cultivated food crops, with a production of approximately two million tons per year (FAOSTAT, 2019), ensuring the subsistence of farmer families that cultivate it. The Caribbean region contributes to about 50% of Colombian production (Departamento Nacional de Estadística [DANE], 2017), mainly through small-scale cultivation by local communities who not only use it as part of their traditional diets, but also as a source of income (Aguilera-Díaz, 2012).

Cassava is susceptible to several pests and diseases during its cycle that could significantly reduce its yields (Center for Agriculture and Bioscience International [CABI], 2021) bringing socioeconomic problems to small-scale farmers who depend on the crop for survival. Among the main diseases affecting cassava production is Cassava Bacterial Blight (CBB), which is caused by Xanthomonas phaseoli pv. manihotis (Xpm). Xpm is a systemic Gram-negative bacterium that penetrates host leaves through natural openings or wounds, and can move into distal leaves and stems upon colonization of the plant vascular system. The most severe symptoms include leaf wilting, vascular necrosis of the stem, and shoot dieback causing irreversible damage that impedes cassava's growth and productivity (Zárate-Chaves et al., 2021). Dispersal of the pathogen within and among fields is thought to occur mainly through agricultural practices. Cassava is propagated clonally through stem cuttings. The pathogen can be spread when contaminated tools are used to prepare stem cuttings at planting time, and to cut stems when the roots are harvested. Exchanges of infected stem cuttings can disperse the pathogen among fields (Lozano, 1986; Boher and Verdier, 1994; Zárate-Chaves et al., 2021). At a small-scale, within fields or between adjacent fields, the bacterium can be dispersed naturally via rain and wind (Lozano, 1986).

This bacterium was first reported in Brazil in 1912 (Lozano, 1986), and in Colombia in 1971 (Lozano and Sequeira, 1974). In Colombian Caribbean, a high genetic diversity of *Xpm* has been reported, in comparison with other regions where the disease is present. This higher diversity can be explained by the wide range of environmental conditions in which the crop is cultivated (Restrepo and Verdier, 1997; Restrepo et al., 2004). The frequencies and variation of *Xpm* haplotypes have changed

dramatically over time in different regions of Colombia, suggesting that populations may evolve rapidly (Restrepo et al., 2000, 2004) and possibly migrate within and between regions (Restrepo and Verdier, 1997).

The relative impact of farming practices and social drivers on CBB occurrence have not yet been clearly determined. Here, we investigate the role of local knowledge (i.e., perception of CBB), agronomic practices (i.e., fertilizer use, diversity of cultivated cassava varieties, circulation of plant propagative material) and socioeconomic factors (i.e., land tenure) on the occurrence of CBB, at the scale of a village in the Caribbean region of Colombia.

MATERIALS AND METHODS

Study Area

We chose to work in the Caribbean region of Colombia, because the cassava market is highly dynamic in this region and some localities, such as Chinú play a central role in cassava farmers meetings of cassava farmers during which propagative material may be exchanged. In addition, in this region Xpm is highly diverse (Trujillo et al., 2014), but to our knowledge, there have been no deliberate efforts to control CBB. The village of Villa López was selected because (i) its reasonably small size and concentrated habitat facilitate study; (ii) its main economic activity has relied on cassava production for at least three generations; and (iii) farmers expressed concern about the increasing incidence of CBB in their fields. Villa López is part of the municipality of San Juan de Betulia (Department of Sucre, Colombia), and is located at 9° 18' 14.7" N and 75° 13' 49.6" W, four kilometers away from the center of the municipality of San Juan de Betulia (Figure 1).

In 2016, when field study was conducted, almost all the families living in Villa López received income from the cassava value chain, as transporters, harvesters or merchants. Out of the 115 families, 48 families grew cassava as their main source of income. All farmers were men; these 48 farmers represent the totality of cassava growers living in this locality. The economy of other villages around Villa López also relies on cassava production (Agronet, 2020). A number of fields around Villa López are cultivated by farmers living in these villages such as Corozal, Las Cruces and Sabaneta, all 2-7 km away. Thirty-nine out of 48 men cultivating cassava were born in Villa López; the others were born in nearby municipalities and, in most cases, arrived after marrying women from this village.

Interviews

Of the 115 families living in Villa López between September and December 2016, we interviewed all the people who cultivated cassava during this period: 48 male farmers who cultivated 40 fields (**Table 1**). The number of fields does not correspond to the number of farmers because (1) two producers did not cultivate during that time because last season they did not have good results in selling their cassava production in the preceding season, (2) three farmers cultivate more than one field, and (3) twelve interviewed farmers (30 to 60 years old) shared the same collective field as they are part of a local association of



cassava producers named "Asoproagrovilo" (Cassava Producers' Association of Villa López).

Semi-structured interviews (77 questions) conducted at the farmer's home and then in the field (**Supplementary Materials 1, 2**) sought information about (1) sociodemographic characteristics of each farmer (i.e., gender, age, life history), (2) identification of cassava diseases, presence of CBB, the farmers' perception about its occurrence in the field, (3) cassava management practices [i.e., planting techniques, use of agrochemicals (fertilizers, insecticides and herbicides)], (4) the

TABLE 1 | Farmers interviewed and fields visited in Villa López.

Number of fields per farmer	Number of farmers interviewed	Number of fields visited	
0	3	0	
1	30	30	
2	1	2	
3	2	6	
1 field of the association	12	2	
Total	48	40	

diversity of cassava varieties planted and their characteristics based on local knowledge, (5) general information about each field (i.e., associated crops within the same field and in neighboring fields, farming calendar, crop rotation, associated land user rights and history), and (6) the origin of planting material (i.e., characteristics and circulation networks of cuttings). To analyze the origin of cassava stems for cuttings, we asked whether farmers (1) recycled stem cuttings from their own fields, or (2) if they received cuttings from other farmers (i.e., identity and localization of the donors; terms of the transaction: gift or purchase). In statistical analyses, the farmer association was considered as a single farmer, characterized by their collective way of managing their field.

Identification of Cassava Bacterial Blight

In each of the visited fields, the fields were surveyed for CBBlike symptoms: two apparently diseased leaves of up to five plants of each variety were sampled per field. Each sampled plant was documented and georeferenced. The isolation of strains of Xpm and PCR validation were performed as described by Trujillo et al. (2014). Leaf samples were sterilized with a 1% sodium hypochlorite solution and rinsed with sterile water. Subsequently, the tissue sample was macerated in a salt solution and drops of diluted macerate were plated onto LPGA medium (5g/L yeast extract, 5g/L peptone, 5g/L glucose, and 15g/L agar) and incubated at 28°C for 48 h. Bacterial colonies with typical *Xpm* morphology were selected and further validated through a PCR-based molecular diagnostic assay (Bernal-Galeano et al., 2018).

Statistical Analysis of Factors Explaining the Occurrence of Cassava Bacterial Blight

To identify factors that could explain the occurrence of CBB at the scale of individual fields, we assessed the impact of five qualitative explanatory variables on the occurrence of CBB (**Supplementary Data 1**): (1) land tenure (owned or rented), (2) cultivation time in the same field (3 consecutive years or fewer, versus 4 consecutive years or longer), (3) use of fertilizers (yes or no), (4) origin of the plant material (three modalities: acquired from other farmers, recycled from the same field, recycled from another field cultivated by the same farmer), (5) whether sampling occurred before or after harvest of the fields' cassava; and two quantitative variables: (6) the number of varieties of cassava cultivated in the field, (7) the number of other farmers who provided planting material for the focal field, (8) the proportion of external donors living in villages other than Villa López.

The date of collection was included, because CBB symptoms became increasingly visible over the plant's growth. Sampling took place in October (before harvest) and November (after harvest on plants left over because the farmers wanted to select these plants to provide vegetative propagules). Although the interviews asked about all agrochemicals used during the crop cycle, for the statistical analysis we only considered fertilizers because herbicides were used by few farmers and insecticides were used by almost all farmers. Thirty-eight fields had no missing data (the two missing ones were harvested before we sampled).

Prior to any analysis, we checked for multicollinearity using Pearson coefficient (Supplementary Figure 1). Two variables were removed from the analysis because they were strongly correlated with another variable: "cultivation time" (correlated to "land tenure", $r^2 = 0.63$) and "number of donors" (correlated with both "land tenure," $r^2 = 0.40$ and "cultivation time," $r^2 = 0.51$), resulting in six possible explanatory variables. We performed logistic generalized linear models, with CBB occurrence explained as a function of each possible combination of the six candidate explanatory variables $(2^6 = 64 \text{ models investigated})$. Models were ranked according to Akaike's information criterion modified for small samples (AICc, Burnham and Anderson, 2002). We measured the relative importance of each variable, by summing the Akaike weights of the models including this variable. Since each variable was present in exactly half of the models, variables with importance > 0.5 are the most relevant. Model comparison was implemented in the R package MuMIn (Bartoń, 2019).

For the two best models, Likelihood Ratio Tests (LRT) were performed comparing these models and those including all but one of each of the explanatory variables. Explanatory variables that combined high importance and significant LRT tests were considered as relevant.

RESULTS

Cassava, A Traditional Staple Crop in Villa López

Most Villa López farmers grew cassava in a single field averaging one hectare in size. Out of 40 visited fields, 28 were rented. Farmers usually rented their lands for six months or for a year through informal contracts. Farmers reported that they selected their field based on previous experience about soil characteristics, proximity to their home and cost of rental. Most fields were located within a 7 km radius of the center of the village. Landowners generally lived in the larger nearby municipalities, especially San Juan de Betulia and Corozal.

In 2016, cassava cultivation was the main source of income for the inhabitants of Villa López. Men were generally in charge of economic activities such as cassava selling or cattle breeding, while women were in charge of housekeeping. Growing cassava has been part of their daily life: 94% (45/48) of the consulted farmers had cultivated cassava for more than five years, and 92% (44/48) reported that their parents and grandparents had also cultivated cassava.

Cassava was grown in thirty-six fields out of the 40 visited, in association with either maize (*Zea mays*), yam (*Dioscorea* spp.), pumpkin (*Cucurbita maxima*), watermelon (*Citrullus lanatus*), sesame (*Sesamum orientale*) or beans (*Phaseolus vulgaris*). Normally, cassava was planted first, along with pumpkin or watermelon seeds if these are available, then maize, and finally yams. When the cassava was harvested, maize was usually sown again, accompanied by sesame. All these plants are part of their traditional food system and were available to be harvested throughout the year, favoring self-sustainability.

To supplement soil nutrition, 45% (18/40) of the visited fields used commercial NPK fertilizers. Prior to sowing cassava, the substrate of 14 fields (35%) was prepared by ploughing with a tractor and the technique locally named "aporque." It consists in accumulating soil at the base of the stem cutting, thus forming a small mound. In Villa López, both the use of mechanical plough and investment in external labor were limited, since profits from the sale of cassava production were small.

During the growth of the crop, the farmers mentioned that one of the most frequent problems was weed invasion. Most farmers weeded exclusively manually, since weed growth can be controlled by ground-covering associated crops, such as pumpkins or watermelons. About 20% of the fields were treated with herbicides.

During the growing season, most farmers applied insecticides (38 out of 40 fields), despite their high costs at the local market. Most of them (82% of fields) applied organophosphate insecticides, including Lorsban[®] and Roxion[®]. Questionnaires showed that these insecticides were applied mostly to prevent or control other pests and diseases during the cassava crop cycle. Usually, the doses applied were decided by trial and error, based on farmers' previous experience or on advice received

Biocultural Drivers Responsible for CBB

from those who sell the agrochemicals. As a preventive treatment against CBB, prior to planting, farmers soaked stem cuttings in copper oxychloride (17,5% of fields), and in organophosphate insecticides such as Lorsban[®] and Roxion[®] (32,5% of fields). Stem cuttings were not treated prior to planting in the other fields (50%). In two fields (5%) were used copper oxychloride and organophosphate insecticides at the same time.

Although most cassava plants were harvested at the end of October, the cultivation cycle can last from 6 to 12 months, depending on climatic variations, variety characteristics and market opportunities. During the harvest period, the intermediaries in charge of marketing at departmental and regional levels occasionally visited farmers to evaluate the yield and the qualities of the soil and the crop (plant health and size), so as to negotiate prices with farmers. Farmers reported that this informal market dynamic and the large number of levels of middlemen in the value chain contribute to lower prices and incomes.

Origins of the Cassava Cuttings

Farmers planted cassava during the March to June rainy season. They preferred to plant five days after the full moon, because they thought that this practice prevents plant rotting. Cassava was mainly propagated clonally through stem cuttings; we observed only a single volunteer plant issued from sexual reproduction in one field. Because cassava is generally harvested in October and planted in March, farmers had to store their own planting material for several months, or requested some from other farmers before planting. If farmers were able to use their own plant material, they might collect it either from the same previously cultivated field, or from a different field. In this case, they selected cassava cuttings considering the characteristics of the adult plants and the soil moisture.

According to farmers, the plant material that would be planted during the next cultivation cycle could be conserved either as stems under the shade of trees, or as living plants. If stored as stems, farmers reported that they needed to be watered daily for at least two weeks. Farmers said that the wound to the stem made during cutting was healed by the plant's natural latex. Just before planting, stems were cut with a machete into 30 cm long cuttings.

In 70% of the surveyed fields (28 out of 40), farmers kept a few living plants as planting stock. However, according to the interviews, this stored plant material was often left aside, either because farmers could not exploit the same field for the next cropping cycle, or because the plant material dried out due to delayed rainy seasons.

Even when farmers keep cassava planting material in their fields or under trees, they may still face a shortage of stems and need to request cuttings, just before the sowing period, from someone else living in or outside the village. Seventy-seven donors of cassava cuttings were identified in our surveys (**Figure 2**). A total of 304 actions of "seed" transfer were identified. The majority (74%) were undertaken by people from Villa López who exchanged seeds with their neighbors in the same village. Forty-five of the 48 local farmers were identified as having provided plant material to someone else (in 88% of cases not from the same family) in the preceding year (2015). The remaining



FIGURE 2 Cassava stem cuttings circulation among farmers from Villa López and from neighboring villages. A transaction is described as cuttings of a given variety provided by a farmer to a farmer from Villa López. The size of the arrow is proportional to the number of transactions and the direction of the arrows shows the provenance of cuttings planted in Villa López (from donors to receivers). Numbers: the number of incoming transactions/number of donors from each neighboring village. This figure only focuses on stem cuttings received in Villa López, since they may imply the transfer of *Xpm* in the village.

providers of plant material are settled in the surrounding villages, especially San Juan de Betulia (whose farmers provide 86% of the actions of seed transfer from outside the village).

Sociocultural Drivers of Cassava Bacterial Blight Occurrence in Villa López

Cassava Bacterial Blight (CBB) is known popularly by the common name "quema" (burning), because leaves look as though they are burnt when attacked by the pathogen (Figure 3). All consulted farmers declared to knowing the disease. They acknowledged that CBB occurs during rainy seasons, and that its characteristic symptom is a leaf blight starting from the apical part of the plant and progressing toward its base.

Perception of CBB occurrence as an importance risk in Villa López was relatively high, as 65% of the interviewees quoted CBB as a problem. However, out of the 26 fields that the farmers thought to be infected by CBB, only 16 actually had fields with infected plants, based on our field observations and further confirmed by molecular diagnostic-based analysis. Conversely, we found CBB in three fields where farmers initially thought that it was not present. To sum up, we observed that farmers made mistakes in reporting the presence of CBB in 32.5% of the fields when it was not present (ten instances), or the inverse (three instances).

Nineteen fields out of 40 were infected by CBB. Among all fields, 28 were rented (70%). Rented fields showed a higher prevalence of CBB than owned fields (respectively, 16/28 and



FIGURE 3 | Symptoms of Cassava Bacterial Blight in Villa López. (A) Angular leaf spot with water soaking on the leaf underside, (B) leaf blight symptom, and (C) wilting leaves on 7-month-old cassava.

TABLE 2 Sum of Akaike weights of the models for each variable.

Variable	Variable importance	Interpretation
Fertilizer use	0.77	Fertilizer use increases the probability of occurrence of CBB
Land tenure	0.73	Farmers who rent their field are more prone to CBB infection than those who own their field
External donors	0.44	Weak effect. Farmers requesting cuttings from farmers outside the village seem to have more CBB than those receiving cuttings from other farmers living within Villa López
Origin of planting material	0.30	Very weak effect
Cassava diversity	0.29	Very weak effect
Sampling date	0.23	Very weak effect

The last column indicates in which way the important variables affect the occurrence of CBB.

3/12 fields infected; odds-ratio = 4; **Figure 4**). Among all fields, commercial fertilizers were applied in 18 (45%). Fertilized fields showed a higher prevalence of CBB than unfertilized fields (respectively, 11/18 and 8/22 fields infected; odds-ratio = 2.75; **Figure 4**).

To try to find variables explaining for the occurrence of *Xpm* in fields, we evaluated 64 linear models, including or excluding each of the six explanatory variables. No model showed a strong superiority in explaining *Xpm* occurrence; however, over all models, fertilizer use and land tenure were the variables showing the greatest importance (**Table 2**).

LRT tests indeed confirmed that both these variables added explanatory power to the best model (P < 0.05 for both). The proportion of external donors and the origin of the planting material showed lower importance (i.e., these variables only contributed to models that sum an Akaike weight of < 50%). They were included in the second-best model, with LRT tests returning *P*-values just below 0.05 (0.047 and 0.048). These two variables may play a role in CBB occurrence, but our dataset seems too small to confirm this. The other most relevant models (*i.e.*, those within two AICc points of the best model) are listed in **Supplementary Figure 2** and **Supplementary Table 1** illustrates the Akaike weights of each of the 64 possible models and the variables included for each of them. Neither the diversity of cassava (measured by the number of planted varieties), nor the sampling date (before or after the harvest) significantly impacted CBB occurrence: these variables showed low importance and did not appear in the few most likely models.

Figure 5 shows the spatial distribution of infected fields as a function of land tenure. Indeed, 16 out of the 19 identified infected fields were rented parcels.

DISCUSSION

Farmers' Perception of Cassava Bacterial Blight

All farmers declared knowing CBB and name it *quema*, which means *burn* and is reminiscent of some leaf wilting symptoms observed at late stages. However, considering that cassava is subjected to various abiotic and biotic stresses, most of which occur in Latin America, the identification of CBB is not straightforward, since different stresses may lead to similar symptoms. In addition, CBB symptoms may vary according to the susceptibility of the host and the time of infection (Álvarez and Llano, 2002).

In 2016, the harvest in this village started in October, approximately at the same time when CBB symptoms appeared in the infected plants. We observed no significant effect of collection time (before or after harvest) on the occurrence of CBB. The symptoms were weak at all times (October through November), suggesting that the yield may not have been strongly impacted by CBB this particular year. According to Lozano (1986), CBB



can be responsible for the loss of up to 80% of the yield in wet years in tropical countries. However, the few years preceding our sampling were particularly dry years in the Caribbean region (IDEAM, 2020), and this may have led to a reduced impact of the disease. In addition, it should be noted that the most frequently cultivated varieties in Villa López, namely *venezolana* and *chirosa*, have a short cultivation cycle (six months), which gives little time for the bacteria to develop.

The Fields of Land Renters Are More Likely to Be Infected by *Xanthomonas phaseoli* pv. *manihotis*

National statistics about land use in the department of Sucre show that most rural areas are dedicated to extensive livestock production, progressively replacing food crops at the local scale (Departamento Nacional de Estadística [DANE], 2017). Because of competition with land for grazing, land for cultivation is scarce, and local farmers are constrained to work in small areas (about one hectare). Those who do not own land have to rent small fields, where they cultivate cassava for sale. In Villa López, cassava cultivated in fields owned by the farmer are less infected by CBB than in fields rented by the farmer (odds-ratio = 0.25).

When fields are rented over short periods, i.e., less than a year, farmers cannot conserve stem cuttings for the next cropping season. In consequence, they must optimize planting with the material available at the local cuttings market, either with farmers from Villa López or from neighboring villages; they do not have the option to control for the disease when choosing cuttings. Inadequate control and management of the propagative material before planting seems a key factor for CBB propagation (Mansfield et al., 2012). However, in the Villa López informal propagule network, control of propagule quality would be difficult to achieve without diagnostic tools, because plants may host the pathogen asymptomatically until the beginning of the rainy season (Wydra and Verdier, 2002). Thus, it is necessary to carry out control practices in each cassava cultivation stage to avoid spread of the pathogen. Crop rotation could be employed as a strategy to avoid the permanence of the pathogen in the crop's environment.

Fertilizer Use Increases the Probability of Occurrence of Cassava Bacterial Blight

Fertilizers used by Villa López farmers can supplement soil nutrition, but may also increase plant susceptibility to disease (Long et al., 2000; Veresogloua et al., 2013). Our data show



that the application of fertilizers significantly increased the probability of CBB occurrence (odds-ratio = 2.75; see Table 2). Fertilizers for instance increase the production of young cassava tissues, which are highly susceptible to CBB (Lozano, 1986). These young shoots can be quickly infected during the rainy season while natural infection is limited on mature tissues. In addition, for some plant-pathogen combinations, it has been shown that increased nitrogen supply can increase disease susceptibility (Dordas, 2008). Nitrogen fertilization has been shown to either increase or decrease susceptibility to various diseases in different agrosystems; the response notably depends on the form and amount of nitrogen applied (Mur et al., 2017; Sun et al., 2020). For example, nitrogen can impact some resistance genes in rice, resulting in higher susceptibility to fungal blast disease (Ballini et al., 2013). Effects of nitrogen fertilization have not been studied for CBB. However, the effect of nutrients may vary depending on the environment and on deficiencies or toxicities of some elements (Dordas, 2008).

Influence of Other Agricultural Practices on Cassava Bacterial Blight Occurrence

The cultivation of cassava remains a traditional activity for the inhabitants of Villa López. Methods for cassava production have been adapted to respond to the demands of commercialization in nearby rapidly growing cities such as Sincelejo and Cartagena. However, despite market pressures favoring an intensive agriculture, traditional family farming practices are still preserved, because cassava is also cultivated as a staple crop. Therefore, farmers cultivate following natural rain and drought cycles to optimize water use, they plant and harvest according to the moon cycles, and cultivate associated crops to provide household food needs. Intercropping may reduce CBB intensity in Villa López since it can act as a physical barrier and limit the dispersal of the bacterial pathogen within the field by rain and wind (Wydra and Verdier, 2002; Zinsou et al., 2004), but we were unable to test this here.

Another benefit of polycultures in cassava crops is the control of weeds owing to agroecological competition dynamics (Weerarathne et al., 2017). The establishment of polycultures probably plays a major role in controlling the proliferation of weeds in Villa López, and this, in addition to the increasing costs of agrochemicals, may explain the low use of herbicides in the village's fields. Spread of weeds decreases yields directly. By creating microclimates that favor the development of diseases and the proliferation of possible vectors, weeds can also increase the risk of dispersal of diseases and pests (Zandjanakou-Tachin et al., 2007; Uzokwe et al., 2016). For this reason, weed control is determinant in avoiding spread of bacterial blights (Sikirou and Wydra, 2008).

Furthermore, over the growing season, cassava can be impacted by a multitude of pests and/or diseases. The large majority of farmers used insecticides to control them, including as a preventive measure against CBB, even though the literature says there is no effective chemical treatment for it (Trujillo et al., 2014). Some reports indicate that copper-based treatments can be successful in managing bacterial diseases (Sundin et al., 2016). However, as farmers plant cassava at the beginning of the rainy season, the efficiency of such treatment is likely to be diminished due to leaching of cooper. Following strategies suggested by local institutions (Álvarez and Llano, 2002), about half of the farmers in Villa López applied copper oxychloride on stem cuttings before planting, to protect them from penetration of pathogens and rotting agents during growth. However, this superficial treatment of stem cuttings cannot kill bacteria located in the vascular tissues, and thus has little effect on limiting CBB occurrence.

CONCLUSION

Cassava has been the main livelihood and source of income for the inhabitants of Villa López for at least four generations. Although according to farmers' perceptions, CBB is the main disease affecting crops in the locality—especially because there is no effective control method—yields were not impacted during the year of our study because the rainy season came close to harvest and the disease appeared at a time when the root was already of marketable size.

Inadequate management and control of stem cuttings seems to be a determining factor for the spread of CBB, and this could be related to land tenure problems, since farmers must plant in rented locations and continually move to new fields, limiting crop rotation and the monitoring of phytosanitary problems of previous cycles. These circumstances promote the circulation of cuttings infected by the pathogen but showing no symptoms permitting its detection.

In addition, we observed a strong correlation between the application of commercial agrochemicals, essentially NPK fertilizers, and the occurrence of the disease in Villa López. Experimental studies are needed to confirm the impact of application of these products on the spread of CBB.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and

REFERENCES

- Agronet (2020). Estadística del Cultivo de la Yuca. Evaluaciones Agropecuarias Municipales. Available online at: https://www.agronet.gov.co/estadistica/ Paginas/home.aspx?cod=4 (accessed October 15, 2021).
- Aguilera-Díaz, M. (2012). La yuca en el Caribe colombiano: Del cultivo ancestral a agroindustrial. Documentos de Trabajo Sobre Economía Regional y Urbana. Bogotá: Banco de la República.
- Álvarez, E., and Llano, G. (2002). "Enfermedades del cultivo de la yuca y métodos de control," in La yuca en el Tercer Milenio: Sistemas Modernos de Producción, Procesamiento, Utilización y Comercialización, eds B. Ospina and H. Ceballos (Cali: CIAT), 131–147.

accession number(s) can be found in the article/**Supplementary** Material.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Universidad de los Andes. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

DP, AD, and SC conducted the field work. CV and BS conducted the lab work. AD and DP performed all the statistical analysis. All authors wrote the first draft of the manuscript, and contributed to subsequent versions and revisions.

FUNDING

This study was supported by the Agropolis Foundation (Grant No. 1 403-073) led by BS.

ACKNOWLEDGMENTS

We thank the farmers of Villa López who kindly hosted us for the development of this study, as well as the laboratories Manihot Biotec of the Universidad Nacional de Colombia and LIMMA of the Universidad de los Andes, for advises and allowing us to carry out part of the laboratory analyses in their facilities. DP was supported by MOPGA doctoral fellowship and by Ministerio de Ciencia, Tecnología e Innovación of Colombia (Convocatoria 885-2020). We also thank Doyle McKey for his final suggestions and support in revising and editing the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022. 841915/full#supplementary-material

Ballini, E., Nguyen, T. T., and Morel, J. B. (2013). Diversity and genetics of nitrogen-induced susceptibility to the blast fungus in rice and wheat. *Rice* 6:32.

- Bartoń, K. (2019). MuMIn: Multi-Model Inference. R package version 1.43.6. Available online at: https://cran.r-project.org/web/packages/MuMIn/index. html (accessed September 20, 2019).
- Bernal-Galeano, V., Ochoa, J. C., Trujillo, C., Rache, L., Bernal, A., and López, C. (2018). Development of a multiplex nested PCR method for detection of *Xanthomonas axonopodis* pv. *manihotis* in cassava. *Trop. Plant Pathol.* 43, 341–350. doi: 10.1007/s40858-018-0214-4
- Boher, B., and Verdier, V. (1994). Cassava bacterial blight in Africa: the state of knowledge and implications for designing control strategies. *African Crop Sci.* J. 2, 505–509.

- Burnham, K. P., and Anderson, D. R. (2002). Model Selection and Multimodel Inference, 2nd Edn. Berlin: Springer.
- Burns, A., Gleadow, R., Cliff, J., Zacarias, A., and Cavagnaro, T. (2010). Cassava: the drought, war and famine crop in a changing world. *Sustainability* 2, 3572–3607. doi: 10.3390/su2113572
- Center for Agriculture and Bioscience International [CABI] (2021). *Invasive* Species Compendium [dataset]. Available online at: https://www.cabi.org/isc/ datasheet/56952 (accessed 15 Dec, 2021).
- Chakraborty, S., and Newton, A. C. (2011). Climate change, plant diseases and food security: an overview. *Plant Pathol.* 60, 2–14. doi: 10.1111/j.1365-3059.2010. 02411.x
- Departamento Nacional de Estadística [DANE] (2017). *Tercer Censo Nacional Agropecuario*. Available online at: https://geoportal.dane.gov.co/geocna/index. html# (accessed May 16, 2019).
- Daryanto, S., Wang, L., and Jacinthe, P. A. (2017). Global synthesis of drought effects on cereal, legume, tuber and root crops production: a review. *Agric. Water Manage*. 179, 18–33. doi: 10.1016/j.agwat.2016.04.022
- Deutsch, C. A., Tewksbury, J. J., Tigchelaar, M., Battisti, D. S., Merrill, S. C., Huey, R. B., et al. (2018). Increase in crop losses to insect pests in a warming climate. *Science* 361, 916–919. doi: 10.1126/science.aat3466
- Dordas, C. (2008). Role of nutrients in controlling plant diseases in sustainable agriculture. a review. Agron. Sustain. Dev. 28, 33–46. doi: 10.1051/agro:2007051
- El-Sharkawy, M. A. (2014). Global warming: causes and impacts on agroecosystems productivity and food security with emphasis on cassava comparative advantage in the tropics/subtropics. *Photosynthetica* 52, 161–178. doi: 10.1007/s11099-014-0028-7
- FAOSTAT (2019). Food and agriculture data, Food and Agriculture Organization of the United Nations (FAO). Available online at: http://www.fao.org/faostat/en/ #data/QC/metadata (accessed 13 May, 2019).
- Jarvis, A., Ramirez-Villegas, J., Herrera-Campo, B. V., and Navarro-Racines, C. (2012). Is cassava the answer to African climate change adaptation? *Trop. Plant Biol.* 5, 9–29. doi: 10.1007/s12042-012-9096-7
- Lebot, V. (2009). Tropical Root and Tuber Crops: Cassava, Sweet Potatoes, Yams and Aroids. Wallingford: CABI.
- Long, D. H., Lee, F. N., and TeBeest, D. O. (2000). Effect of nitrogen fertilization on disease progress of rice blast on susceptible and resistant cultivars. *Plant Dis.* 84, 403–409. doi: 10.1094/PDIS.2000.84.4.403
- Lozano, J. C. (1986). Cassava bacterial blight: a manageable disease. *Plant Dis.* 70, 1089–1093. doi: 10.1094/PD-70-1089
- Lozano, J. C., and Sequeira, L. (1974). Bacterial blight of cassava in Colombia: II: epidemiology. *Phytopathology* 64, 83–88. doi: 10.1094/phyto-64-83
- Mansfield, J., Genin, S., Magori, S., Citovsky, V., Sriariyanum, M., Ronald, P., et al. (2012). Top 10 plant pathogenic bacteria in molecular plant pathology. *Mol. Plant Pathol.* 13, 614–629. doi: 10.1111/j.1364-3703.2012.00804.x
- Mur, L., Simpson, C., Kumari, A., Gupta, A. K., and Gupta, K. J. (2017). Moving nitrogen to the centre of plant defence against pathogens. Ann. Bot. 119, 703–709. doi: 10.1093/aob/mcw179
- Restrepo, S., Velez, C. M., Duque, M. C., and Verdier, V. (2004). Genetic structure and population dynamics of *Xanthomonas axonopodis* pv. *manihotis* in Colombia from 1995 to 1999. *Appl. Environ. Microbiol.* 70, 255–261. doi: 10.1128/AEM.70.1.255-261.2004
- Restrepo, S., Vélez, C. M., and Verdier, V. (2000). Measuring the genetic diversity of *Xanthomonas axonopodis* pv. *manihotis* within different fields in Colombia. *Phytopathology* 90, 683–690. doi: 10.1094/PHYTO.2000.90.7.683
- Restrepo, S., and Verdier, V. (1997). Geographical differentiation of the population of *Xanthomonas axonopodis* pv. *manihotis* in Colombia. *Appl. Environ. Microbiol.* 63, 4427–4434. doi: 10.1128/AEM.64.3.1166a-1166a. 1998
- Savary, S., Willocquet, L., Pethybridge, S. J., Esker, P., McRoberts, N., and Nelson, A. (2019). The global burden of pathogens and pests on major food crops. *Nat. Ecol. Evol.* 3, 430–439. doi: 10.1038/s41559-018-0793-y

- Sikirou, R., and Wydra, K. (2008). Effect of intercropping cowpea with maize or cassava on cowpea bacterial blight and yield. *J. Plant Dis. Prot.* 115, 145–151. doi: 10.1007/BF03356262
- Strange, R. N., and Scott, P. R. (2005). Plant disease: a threat to global food security. Annu. Rev. Phytopathol. 43, 83–116. doi: 10.1146/annurev.phyto.43. 113004.133839
- Sun, Y., Wang, M., Mur, L. A. J., Shen, Q., and Guo, S. (2020). Unravelling the roles of nitrogen nutrition in plant disease defences. *Int. J. Mol. Sci.* 21:572. doi: 10.3390/ijms21020572
- Sundin, G. W., Castiblanco, L. F., Yuan, X., Zeng, Q., and Yang, C. H. (2016). Bacterial disease management: challenges, experience, innovation and future prospects. *Mol. Plant Pathol.* 17, 1506–1518. doi: 10.1111/mpp.12436
- Trujillo, C. A., Ochoa, J. C., Mideros, M. F., Restrepo, S., López, C., and Bernal, A. (2014). A complex population structure of the cassava pathogen *Xanthomonas axonopodis* pv. *manihotis* in recent years in the Caribbean region of Colombia. *Microb. Ecol.* 68, 155–167. doi: 10.1007/s00248-014-0411-8
- Uzokwe, V., Mlay, D. P., Masunga, H. R., Kanju, E., Odeh, I. O. A., and Onyeka, J. (2016). Combating viral mosaic disease of cassava in the Lake Zone of Tanzania by intercropping with legumes. *Crop Prot.* 84, 69–80. doi: 10.1016/j.cropro. 2016.02.013
- Veresogloua, S. D., Bartoab, E. K., Menexescand, G. M., and Rillig, C. (2013). Fertilization affects severity of disease caused by fungal plant pathogens. *Plant Pathol.* 62, 961–969. doi: 10.1111/ppa.12014
- Weerarathne, L. V. Y., Marambe, B., and Chauhan, B. S. (2017). Does intercropping play a role in alleviating weeds in cassava as a non-chemical tool of weed management? – A review. *Crop Prot.* 95, 81–88. doi: 10.1016/j.cropro.2016.08. 028
- Wydra, K., and Verdier, V. (2002). Occurrence of cassava diseases in relation to environmental, agronomic and plant characteristics. *Agric. Ecosyst. Environ.* 93, 211–226. doi: 10.1016/S0167-8809(01)00349-8
- Zandjanakou-Tachin, M., Fanou, A., Le Gall, P., and Wydra, K. (2007). Detection, survival and transmission of *Xanthomonas axonopodis* pv. *manihotis* and *X. axonopodis* pv. *vignicola*, causal agents of cassava and cowpea bacterial blight, respectively, in/by Insect Vectors. *Phytopathology* 155, 159–169. doi: 10.1111/j. 1439-0434.2007.01210.x
- Zárate-Chaves, C. A., Gómez de la Cruz, D., Verdier, V., López, C. E., Bernal, A., and Szurek, B. (2021). Cassava diseases caused by *Xanthomonas phaseoli* pv. *manihotis* and *Xanthomonas cassavae*. *Mol. Plant Pathol.* 22, 1520–1537. doi: 10.1111/mpp.13094
- Zinsou, V., Wydra, K., Ahohuendo, B., and Hau, B. (2004). Effect of soil amendments, intercropping and planting time in combination on the severity of cassava bacterial blight and yield in two ecozones of West Africa. *Plant Pathol.* 53, 585–595. doi: 10.1111/j.0032-0862.2004.01056.x

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's Note: All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Copyright © 2022 Pérez, Duputié, Vernière, Szurek and Caillon. This is an openaccess article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.