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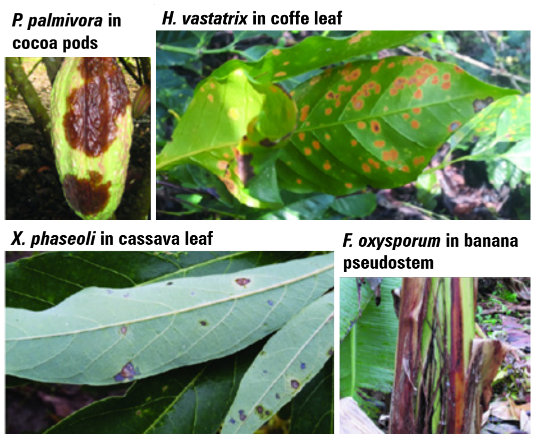
Current status of plant pathogens of agricultural importance for Colombia. A review

Estado actual de fitopatógenos de importancia agrícola para Colombia. Una revisión



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Plant disease in Colombia.

Photos: R.E. Mora-Moreno, J.E. Vargas Acosta, L. Rodríguez-Polanco, and J.S. Márquez

ABSTRACT

Plant disease still plays a major role in limiting agricultural production worldwide. Pathogens and pests reduce crop yield and can cause large reductions in crop quality. Colombia is no exception as it contends with many devastating pathogens that present a major threat to the country's agricultural sector. This review is important because it highlights four of the more damaging pathogens that affect the economics of important crops in Colombia - *Xanthomonas phaseoli* pv. *manihotis* (*Xpm*), *Fusarium oxysporum* f. sp. *cubense* (*Foc*), *Phytophthora palmivora*, and *Hemileia vastatrix*. This paper was based on an extensive literature search for plant diseases in Colombia in databases such as PubMed and Google Scholar. Moreover, this search was complemented with research on crop production in the country in databases made available by the Food and Agriculture Organization of the United Nations (FAO). The four pathogens reviewed in this paper were chosen not only because of their current devastating effects on Colombia's agricultural production but also because of their potential to cause further damage in the near future. Understanding the current situation of these crop pathogens in Colombia is imperative for state directives aimed at developing informed and efficient control strategies.

Additional keywords: *Xanthomonas phaseoli* pv. *manihotis*; *Fusarium oxysporum*; *Phytophthora palmivora*; *Hemileia vastatrix*; climate change; plant-pathogen interaction.

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RESUMEN

Las enfermedades de las plantas constituyen todavía un gran factor limitante para la producción agrícola a nivel global. Los patógenos y plagas vegetales disminuyen el rendimiento agrícola y pueden causar grandes reducciones en la calidad de los cultivos cosechados. Colombia no es una excepción, ya que lucha contra muchos fitopatógenos devastadores que representan una gran amenaza para el sector agrícola del país. Este artículo de revisión es importante ya que destaca cuatro de los fitopatógenos más devastadores que afectan económicamente cultivos de gran importancia en Colombia - *Xanthomonas phaseoli* pv. *manihotis* (*Xpm*), *Fusarium oxysporum* f. sp. *cubense* (*Foc*), *Phytophthora palmivora*, y *Hemileia vastatrix*. Este trabajo fue desarrollado a través de una búsqueda extensiva de literatura acerca de enfermedades vegetales en Colombia en bases de datos como por ejemplo PubMed y Google Scholar. Además, esta búsqueda fue complementada con un rastreo acerca de la producción agrícola del país en bases de datos que se encuentran disponibles por la Organización de las Naciones Unidas para la Alimentación y la Agricultura (FAO). Los cuatro patógenos descritos en este trabajo fueron elegidos no solamente por sus actuales efectos devastadores en la producción agrícola colombiana pero también por su potencial para causar aún más daño en un futuro cercano. El entendimiento de la situación actual de estos fitopatógenos en Colombia es esencial para que se implementen políticas públicas que promuevan el desarrollo de nuevas estrategias de control eficientes e informadas.

Palabras clave adicionales: *Xanthomonas phaseoli* pv. *manihotis*; *Fusarium oxysporum*; *Phytophthora palmivora*; *Hemileia vastatrix*; cambio climático; interacción planta-patógeno.

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INTRODUCTION

The diverse climates and topographies of Colombia allow for the cultivation of a wide variety of crops, including maize, coffee, rice, plantain, sugarcane, cassava, fruit trees, potato, African oil palm, common bean, cocoa, cotton, sorghum, banana, vegetables, and flowers (Hudson, 2010; Lau *et al*., 2013). In 2013, these agricultural activities generated 5.2% of Colombia's gross domestic product (GDP), with agricultural products accounting for approximately 11% of total exports. The importance of agriculture to the Colombian economy is best exemplified by employment in the agricultural sector, which accounted for 17.5% of the jobs in Colombia in 2013 (OECD, 2015).

Despite this clear importance, the weight of agriculture in the Colombian economy is falling, from 16.5% of the GDP in 1990 to 5.2% in 2013 (OECD, 2015). While this can mean improved economic activities in other sectors, there is cause for concern when looking at the export-to-import ratio. In 1990, there was a trade surplus of USD$2.4 billion for Colombian agriculture; however, by 2013, this value decreased to USD$0.5 billion. Furthermore, crop production has decreased from 62% of Colombia's total agricultural production in 1990, to 59% in 2013 - corresponding to decreases in Colombian agricultural land usage from 45 to 43 million ha over the same period (OECD, 2015). The cause of this relative decrease in the importance of Colombian agriculture to the economy is complex and multi-faceted. One solution for current challenges faced by the Colombian agricultural sector would be to increase the production potential of current agricultural lands.

Plant pests and diseases are major threats to reaching food security worldwide (Oerke, 2006; Donatelli *et al*., 2017). Food security was described by the United Nations world food summit as "when all people, at all times, have physical and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life" (FAO, 2006; Chakraborty and Newton, 2011). Hence, the development and implementation of efficient and sustainable crop protection strategies against pests and pathogens is crucial. The development of these strategies is more urgent because of climate change, which will have a direct impact on the incidence of pests and diseases in crops (Ávila and Romero, 2017; Raza *et al*., 2019).

To be able to effectively deploy strategies to fight plant pests and diseases in the field, a profound understanding of the pathogen´s biology and interaction with plant hosts is essential. Hence, several studies have been conducted that aimed to increase understanding of the mechanisms involved in a diverse range of plant diseases (Dean *et al*., 2012; Mansfield *et al*., 2012; Kamoun *et al*., 2015). However, most studies focused on pathogens of economic importance to the developed world. Whereas, pathogens that affect crops in tropical areas, mainly in developing countries, are repeatedly neglected. This situation is made more problematic by the fact that crops in the tropics have double the losses of crops in temperate zones (Drenth and Guest, 2016). Thus, more studies focused on plant diseases in tropical regions are of paramount importance.

This paper was based on an extensive literature search for plant diseases in Colombia in databases such as PubMed and Google Scholar in 2020. Several search words were used, including “plant disease”, “Colombia”, and “crop yields”, among others. After the pathogens were selected, individual searches were performed for each pathogen and crop in the same databases. For the pathogens, all articles mentioning these diseases in Colombia were read and considered for this review. This paper describes pathogens that are likely to cause immense damage to four crops of high economic importance in Colombia in the near future. These pathogens are: *Xanthomonas phaseoli* pv. *manihotis* affecting cassava, *Fusarium oxysporum* f. sp. *cubense* (*Foc*) affecting banana, *Phytophthora palmivora* affecting cacao, and *Hemileia vastatrix* affecting coffee. *Xpm* was reviewed because it causes large losses in cassava production, reaching 57% losses in susceptible cassava cultivars (Fanou *et al*., 2018). This is highly problematic because Colombia is the fourth biggest producer of this crop in the Americas (1.0 million tons) (FAO, 2019). *Foc* was mentioned because of the arrival to Colombia of a new race (Tropical Race 4) that has had catastrophic effects on banana production in other parts of the world. This pathogen could have a huge impact on Colombia in terms of banana and plantain production, which accounts for 20.6% of Colombian agriculture production (Lau *et al*., 2013). *P. palmivora* was chosen because of the social importance that cocoa production has for populations that previously produced illegal cocaine. While there is little information on the effects of this pathogen on cocoa production, it was shown that *P. palmivora* consistently caused cocoa losses of more than 70 kg ha^{-1} $year^{-1}$ (valued at approximately USD$82.6) (Ramírez, 2016). Finally, *H. vastatrix* was chosen because of its large impact on coffee production, the most valuable agricultural product in Colombia (coffee), accounting for 17.3% of the countries agricultural value (Lau *et al*., 2013; FAO, 2018).

The reason each pathogen was selected is detailed, along with a summary of current knowledge on their biology. Moreover, each pathogen has a proposed new method of control that could and should be used in the field in Colombia. This review compiles a range of relevant information for those seeking to control tropical pathogens efficiently and intelligently in the field. The hope is it will motivate new studies on these devastating pathogens, not only in Colombia but also in all countries with similar tropical climates.

XANTHOMONAS PHASEOLI* PV. *MANIHOTIS

The genus *Xanthomonas* includes a large number of gram-negative phytopathogenic bacteria that are able to infect a huge number of hosts (Hayward, 1993; Ryan *et al*., 2011; Marin *et al*., 2019), including economically important crops such as rice (Zhang and Wang, 2013), citrus (Bansal *et al*., 2017), tomato (Abrahamian *et al*., 2019), and banana (Ocimati *et al*., 2019). The genus *Xanthomonas* comprises 27 species, with each individual species being divided into pathovars that can exhibit host and/or tissue specificities (Ryan *et al*., 2011). This review focused on *Xanthomonas phaseoli* pv. *manihotis* (*Xpm*) because of its devastating effects on cassava in Colombia.

Cassava (*Manihot esculenta* Crantz) is an important crop in tropical regions, where it represents the staple food for more than 600 million people (López and Bernal, 2012; Lin *et al*., 2019). Because of its inherent drought tolerance, cassava’s importance as a staple crop is predicted only to increase with climate change, better adapting to the changing climatic conditions (Jarvis *et al*., 2012). Cassava is an important crop for Colombian agriculture, ranked fourth for cassava producing countries in the Americas at 1.0 million tons in 2019 - only surpassed by Brazil (17.4 million tons), Paraguay (3.3 million tons) and Perú (1.2 million tons) (FAO, 2019). Additionally, cassava accounted for 9.3% of Colombian agricultural production and 4% of the agricultural value in 2013 (Lau *et al*., 2013). Despite this, the importance of cassava production in Colombia is decreasing, representing only 6.2% of the Colombian agricultural production in 2018 (FAO, 2018). This is reflected in yields that were reduced to an average production yield of 12.4 t h^{-1} $year^{-1}$, as compared to yields as high as 37 t ha^{-1} $year^{-1}$ (Howeler *et al*., 2013; DANE, 2016). Several aspects have contributed to this reduced production yield, one being the prevalence of diseases in cassava, such as *Xpm* (Howeler *et al*., 2013).

The bacterial agent *Xpm* is responsible for the disease called cassava bacterial blight (CBB), which is a major cassava disease along with the cassava mosaic disease and cassava brown streak disease (Lin *et al*., 2019). The first reported case of CBB was in Brazil in 1912 (Fanou *et al*., 2018), and it now affects cassava production in all production zones worldwide (Fanou *et al*., 2018; Lin *et al*., 2019). In Colombia, CBB disease is highly prevalent within endemic zones, being found in the Colombian regions: eastern planes, northern coast, and Cauca (Trujillo *et al*., 2014; Cadavid, 2006; Álvarez, 2006). Crop losses from CBB vary considerably but can be significantly damaging (Verdier *et al*., 2004), with reported yield losses of 57% in susceptible cassava cultivars (Fanou *et al*., 2018). In addition to yield losses, CBB has reduced the nutritional value of cassava tubers and leaves (Obigbesan and Matuluko, 1976).

The symptoms of CBB disease are diverse and include angular leaf lesions, blight, wilt, stem exudates, and stem canker (Fig. 1; Mansfield *et al*., 2012). The disease cycle of CBB is thought to begin in the rainy seasons with the development of *Xpm* as an endophyte in leaves (Boher and Verdier, 1994). After this phase, *Xpm* enters the plant via stomata or wounds, reaching the vascular tissue of the plant where it can move systematically. Ultimately, *Xpm* blocks plant veins, causing the disease symptoms described above (Boher and Verdier, 1994; López and Bernal, 2012). Disease spreads when *Xpm* is dispersed from plant to plant via splashing raindrops and between fields by

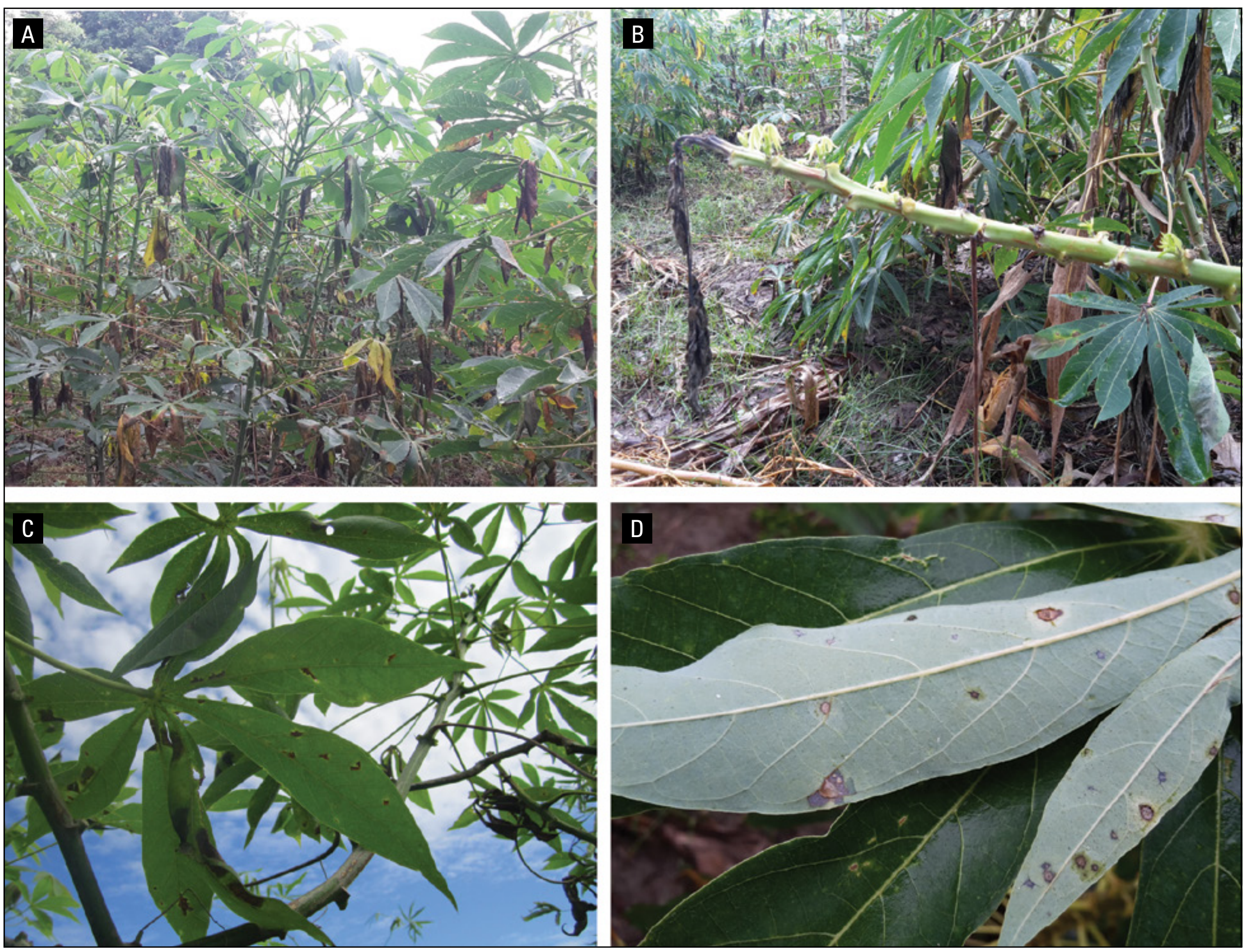

Figure 1. Symptoms of *Xanthomonas axonopodis* pv. *Manihotis* (*Xam*) infection in cassava plants grown in Colombia. A, extensive leaf necrosis; B, stem rot and wilt; C and D, angular leaf lesions. Source: R.E. Mora-Moreno, Universidad Nacional de Colombia, Bogota.

infected propagative material (Lozano and Sequeira, 1974; Lozano, 1986; López and Bernal, 2012).

Several procedures have been used to try to control CBB in the field. Better cultural practises (crop rotations, use of clean planting material, choice of planting times, and pruning above-ground plant material) and improved sanitary control of plant material transport, coupled with planting more resistant cassava varieties, were shown to decrease or even eradicate CBB in some Colombian regions (Lozano, 1986). Additionally, biological control strategies have been suggested, with foliar applications of *Pseudomonas* spp., which reduces CBB disease symptoms in cassava plants (Lozano, 1986; Hernandez *et al*., 1986; Marin *et al*., 2019). However, foliar applications have only been tried in a small number of studies for cassava (Marin *et al*., 2019), possibly because of environmental concerns. Despite these practises being used for decades, this disease is still reducing cassava production worldwide. Cultural and sanitary practises are crucial but are insufficient alone, and biological control options are still in the developmental stages. Thus, the use and generation of more resistant cassava cultivars is the best option to face the challenges posed by *Xpm* for the immediate future (López and Bernal, 2012).

The use of resistant cultivars is widely regarded as the most viable approach to reducing *Xpm* infections (Restrepo *et al*., 2000; Álvarez, 2006; López and Bernal, 2012). Resistance to *Xpm* originated from crosses with the wild relative of cassava, *M. glaziovii* (Fanou *et al*., 2018), and has been quantitative in nature. The resistance levels acquired have been associated with general plant defence mechanisms that limit colonisation of the xylem, such as lignification, callose deposition, suberization, accumulation of phenolic compounds, and vessel occlusion (Kpemoua *et al*., 1996; Jorge *et al*., 2000). In recent years, several QTLs have been found to be connected to *Xam* resistance in cassava, with specific genes linked to CBB resistance (Soto *et al*., 2017; Fanou *et al*., 2018; Herrera *et al*., 2018; Díaz *et al*., 2018). These discoveries open potential new possibilities by incorporating these QTLs and genes into varieties with desired genetic backgrounds. Additionally, the use of several QTLs simultaneously – known as gene pyramiding – may achieve more effective and durable resistance (Fanou *et al*., 2018).

Despite the prospects of resistance gene transfer, the management of *Xpm* under field conditions remains incredibly challenging for two main reasons: pathogen genetic variability and the sporadic nature of *Xpm* infections. Genetic variability has been repeatedly reported across *Xpm* field isolates, yet it remains difficult to connect this variability to variations in disease severity in the field (Restrepo *et al*., 2000; Restrepo *et al*., 2004; Wydra *et al*., 2004; Lin *et al*., 2019). This lack of understanding linking the genetic variability of *Xpm* to its pathogenicity makes finding durable genetic resistances to control CBB a very ambitious goal (Lin *et al*., 2019). The other hurdle for managing *Xpm* is the lack of understanding of conditions that favour *Xpm* infections. It is clear that some environmental conditions trigger highly severe CBB, but these conditions are still poorly understood (Lin *et al*., 2019), making the cultural practices mentioned above difficult to apply efficiently. An increased understanding of *Xpm* biology is imperative for developing durable controls under field conditions.

Many gram-negative pathogenic bacteria release effector molecules aimed at subverting host immunity and enhancing pathogen colonization – via a type III secretion system (Büttner and He, 2009). Correspondingly, *Xpm* has been shown to successfully deploy these effectors in large numbers (Bart *et al*., 2012; Arrieta-Ortiz *et al*., 2013; Medina *et al*., 2017). Thus, further research on the conserved and virulence determinant effector molecules in *Xpm* could play an important role in the search for durable resistance to this pathogen (Chavarriaga-Aguirre, 2016; Medina *et al*., 2017). In addition to studies on effector biology, it is critical to deploy strategies to monitor *Xpm* field populations. A study by Bernal-Galeano *et al*. (2018) describes a promising strategy using multiplex nested PCRs to detect *Xpm* under field conditions regardless of the strain virulence. Additionally, another recent study developed a detection method for *Xpm* based on a variable number of tandem repeat analyses (MLVAs), obtaining reproducible results (Rache *et al*., 2019). The deployment of these new methods could greatly increase the amount of available information for *Xpm* population dynamics, allowing the application of improved disease management strategies in the near future.

In summary, cassava is an important food crop for Colombia and other tropical countries, and this importance is predicted to increase in coming years

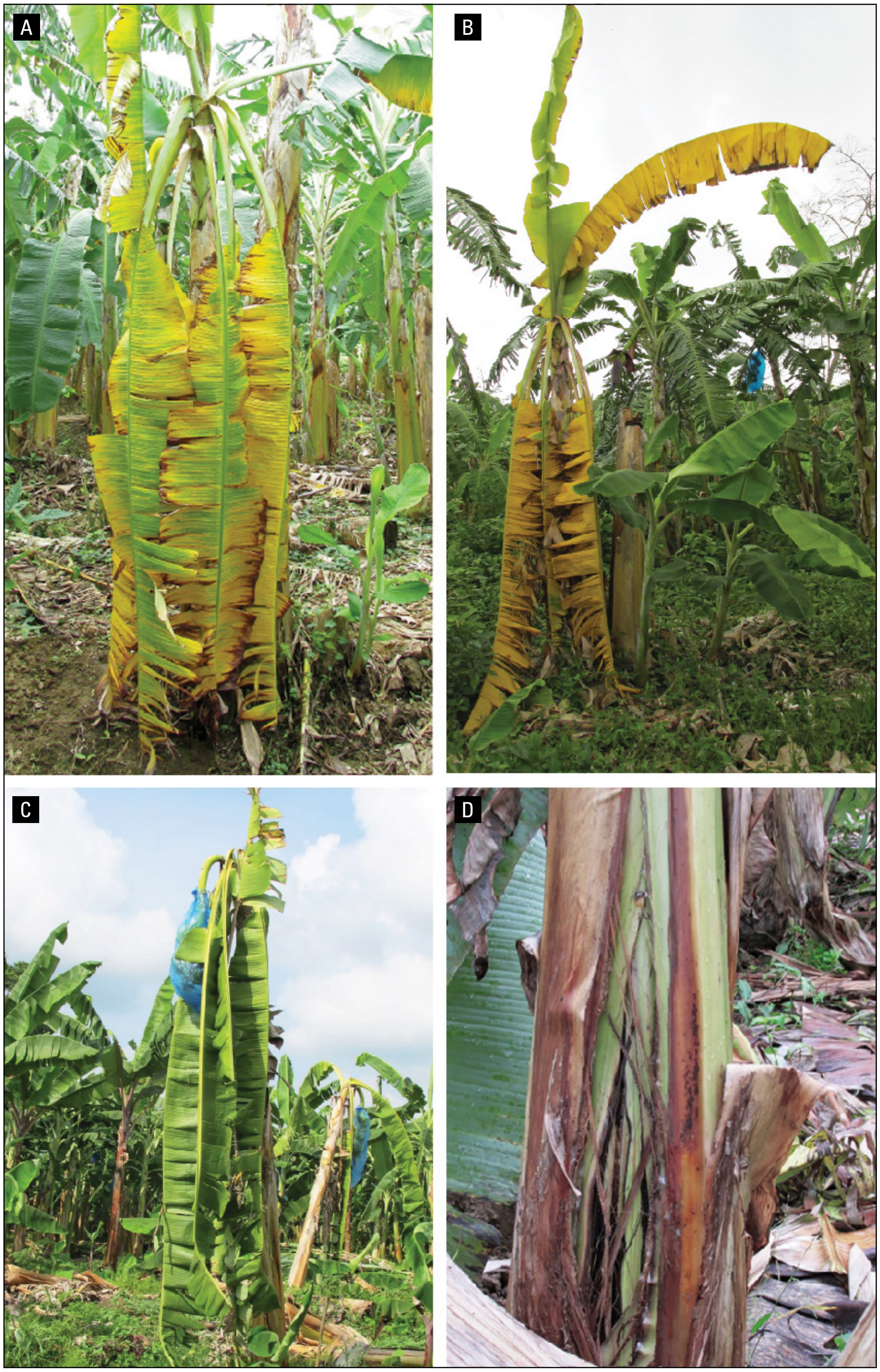

Figure 2. Symptoms of *Fusarium oxysporum* f. sp. *cubense* (*Foc*) race 1 and race 2 infections in banana plants grown in Colombia. A, B and C, yellowing and wilting of leaves; D, vascular discolouration of the pseudostem, shown with a longitudinal cut. Source: J.E. Vargas Acosta, Banana Research Center (CENIBANANO).

because of climate change (Jarvis *et al*., 2012). However, the production of cassava is greatly reduced by crop losses associated with *Xpm* infections. This is in part due to our limited knowledge on *Xpm* biology, despite some valuable efforts from the scientific community (Lin *et al*., 2019). Thus, it is critical that more *Xpm* research is conducted to control the damage that this devastating pathogen produces in cassava fields in Colombia and worldwide.

FUSARIUM OXYSPORUM

The genus *Fusarium* comprises several fungal species, distributed worldwide, that are mostly known for being plant pathogenic and for producing mycotoxins that contaminate human and animal food (Di Pietro *et al*., 2003).

In the *Fusarium* genus, the most common species is *F. oxysporum* (Lombard *et al.*, 2019). Diverse *F. oxysporum* strains can infect a wide variety of host plants, including most cultivated crops - with the exception of grasses and trees. This article focused on *Fusarium oxysporum* f. sp. *cubense* (*Foc*) (also known as *Fusarium odoratissimum*) (Maryani *et al*., 2019) because of the immense threat that this pathogen poses to banana and plantain (*Musa* spp.) production in Colombia and worldwide (Dita *et al*., 2018).

Bananas and plantains are grown in over 135 countries, producing a reported total of 148 million tons in 2016, making banana the most produced fruit on earth (Dusunceli, 2017; Bubici *et al*., 2019). Bananas are a staple food for over 400 million people worldwide, and this number is predicted to increase because climate change will increase the productive area of bananas in subtropical and tropical highlands (Bubici *et al*., 2019). Since 2005, banana cultivation has been of high economic importance in Colombia, ranked as the 10th largest producer and the 3rd largest exporter worldwide (Hudson, 2010). Banana and plantain production accounted for 20.6% of Colombian agriculture production, generating 14.2% of its value in 2013 (Lau *et al*., 2013). This importance can still be observed in data from 2018, where bananas represented 10.4% of the agricultural production in Colombia (FAO, 2018).

The fungal agent *Foc* is responsible for the devastating banana and plantain disease commonly known as Panama disease (Ordonez *et al*., 2015; Ploetz, 2015a). *Foc* has been divided into four different pathogenic races according to their host range, including Race 1 (Foc 1), Race 2 (Foc 2), Race 3 (Foc 3) and Race 4 (Foc 4) (Qin *et al*., 2017). In the early 20th century, this disease devastated banana plantations worldwide, which relied almost completely on the banana cultivar Gros Michele. However, this cultivar was susceptible to *Foc* (Race 1), causing billions of dollars of economic damage and critical social problems. By the second half of the 20th century, almost all banana production shifted to the Cavendish cultivar, which is resistant to *Foc* (Ploetz, 2005). Because of the spread of the Cavendish variety, *Foc* stopped posing a serious immediate threat to banana production (Dita *et al*., 2018). However, in the 1990s, a new race of *Foc*, capable of infecting Cavendish bananas, was identified and named tropical Race 4 (TR4). For some decades, TR4 could only be found in east Asia and northern Australia, but recently it has spread throughout Asia and has been identified in Africa (Mozambique) and South America (Colombia) (Dita *et al*., 2018; Graham, 2019; García-Bastidas *et al*., 2020). The strain *Foc* TR4 is capable of infecting 80% of the banana and plantain cultivars currently in use (Ploetz, 2006). Therefore, it is expected that the spread of *Foc* TR4 will have devastating consequences for banana production and dependent populations – particularly in countries that produce and export bananas, such as Colombia (Ploetz, 2015b; García-Bastidas *et al*., 2020).

The lifecycle of *Foc* is extremely versatile, with many characteristics that make control in the field extremely challenging. Firstly, *Foc* is a soil-born fungus that can persist in soil for more than twenty years in the form of chlamydospores, even in the absence of its primary host (Dita *et al*., 2018). Moreover, this pathogen has been shown to grow as hyphae in organic residues and to survive as an endophyte in various non-host plants (Hennessy *et al*., 2005; Pegg *et al*., 2019). Therefore, significant reductions in *Foc* levels will be difficult in extensive banana plantations with conventional cultural practices (such as crop rotations and use of cover crops) (Zhang *et al*., 2013; Pattison *et al*., 2014; Wang *et al*., 2015; Thangavelu *et al*., 2020).

Infection of new material occurs once *Foc* chlamydospores perceive the presence of host plants with exudates or by contact with root tissues. They then germinate and start the infection process by entering secondary or tertiary feeder roots (Dita *et al*., 2018). After entering the root system, *Foc* quickly spreads within the host plant, with its growth resulting in extensive blockage of the plant´s xylem vessels, exhibiting the characteristic phenotypes of yellowing and wilted leaves (Fig. 2; Pegg *et al*., 2019; Thangavelu *et al*., 2020). This growth inside the plant vascular system also poses an additional hurdle when trying to control *Foc* using chemical and biological methods. After infection, *Foc* spreads between plants via root proximity or water dispersal, and, because of global communication and commerce, it can travel between different fields, countries, and even continents (Dita *et al*., 2018; Pegg *et al*., 2019). Thus, it is of paramount importance that countries and regions with low incidences of *Foc* TR4 implement strict exclusion and containment measures to contain this pathogen.

Analysis of the *Foc* lifecycle shows why the control of this pathogen is extremely difficult; nonetheless, several strategies are being tested (Dita *et al*., 2018; Pegg *et al*., 2019; Thangavelu *et al*., 2020). Besides the cultural practices mentioned above, combinations of chemical and biological control measures have been tested to keep *Foc* infection at bay. Chemical control measures, such as fungicides, inhibit *Foc* infections under laboratory and greenhouse conditions (Nel *et al*., 2007); however, it remains unclear if these chemicals will function under field conditions. Furthermore, the application of chemicals in the environment raises many ecological concerns that need to be addressed before any field trials.

Environmentally friendly strategies using biological control measures to control *Foc* have received attention lately (Bubici *et al*., 2019); however, effective biological control measures are far in the future. The strength of biological controls relies on incorporating several biological control measures with appropriate cultural practises in an integrated disease management framework (Bubici *et al*., 2019). However, whilst these frameworks provide exciting prospects for controlling plant diseases such as *Foc* in the field, they are difficult to implement rigorously by many producers in developing countries such as Colombia. Therefore, the development of banana varieties resistant to *Foc* TR4 infections is the most promising strategy for disease control. However, despite the various trials currently taking place, it has been difficult to generate commercially accepted banana varieties with significant resistances to *Foc* TR4 (Dita *et al*., 2018; Zhang *et al*., 2018; Sun *et al*., 2019; Chen *et al*., 2019). Controlling *Foc* TR4 in the field is full of complicated obstacles, yet it is crucial that more research is conducted on the control of this pathogen because it will devastate the economy of Colombia and other banana producing countries across the globe if allowed to spread.

PHYTOPHTHORA PALMIVORA

The genus *Phytophthora* belongs to the family of oomycetes and comprises a great number of plant pathogenic species that seriously impede agricultural production worldwide (Erwin and Ribeiro, 1996; Ho, 2018). *P. palmivora* is particularly damaging in tropical and sub-tropical regions, causing root, bud, and fruit rotting diseases in several tropical crops such as cocoa, oil palm, rubber, papaya, cassava, coconut, mango, and citrus (Evangelisti *et al*., 2017). In Colombia, *P. palmivora* generates devastating effects on the production of oil palm (Torres *et al*., 2016; Maizatul-Suriza *et al*., 2019). However, this article focused on the effects of this pathogen on cocoa production because production of this crop is crucial for the social development of Colombia, where the effects of *P. palmivora* on cocoa production are largely unknown. A study developed over three years (2010-12) on a production farm in the Antioquia region showed that this pathogen consistently caused cocoa losses of more than 70 kg ha^{-1} $year^{-1}$ (valued at approximately USD$82.6) (Ramírez, 2016). Despite having an area of over 666,000 ha, Colombian cocoa growers could not meet the domestic demand of 52,000 t in 2010 (generating a production deficit of 22.95%) because of low production yields (Rodríguez and Vera, 2015). Cocoa production in Colombia increased in 2018, with 52,743 t of cocoa beans, accounting for 0.1% of agricultural production (FAO, 2018). Nevertheless, low cocoa production yields in Colombia remains. However, regardless of the low yields, cocoa production is seen as a priority in Colombia because it is a good replacement for illegal cocaine production (The Bogota Post, 2017; Zaragovia, 2018).

P. palmivora can infect several cocoa plant tissues including stems, flowers, and leaves (Marelli *et al*., 2019), but the principal symptom is water-soaked lesions on the pod that are related to the pathogen infection process (Fig. 3). Under optimal conditions, coffee coloured necrotic lesions will appear 3-5 d post infection, and, after 10-14 d, the entire pod, including the cocoa beans, is infected. Infected pods remain in the tree and are a source of inoculum for approximately 3 years (Rodríguez and Vera, 2015).

Current methods for controlling *P. palmivora* include cultural, biological, and chemical control, along with the deployment of resistant cocoa varieties (Rodríguez and Vera, 2015). Cultural, biological and chemical control strategies are important but are normally insufficient and incur economic and environmental costs. Thus, deployment of resistant cocoa varieties is possibly the best strategy to control *Phytophthora* infections in the field (Surujdeo-Maharaj *et al*., 2001). However, the search for effective resistances in cocoa has been a slow process because of the *P. palmivora* complex hemibiotrophic lifecycle, as well as the lack of in-depth molecular knowledge on the interaction between *P. palmivora* and cocoa plants (Rodríguez and Vera, 2015).

P. palmivora, like many other *Phytophthtora* species, has an hemibiotrophic lifecycle. Its predominant asexual lifecycle begins with the adhesion of motile zoospores to the host tissue, followed by encystment and germ tube formation (Judelson and Blanco, 2005; Evangelisti *et al*., 2017). Using entry structures called appressoria, *Phytophthtora* enters host tissues and generates an apoplastic hyphal network. Simultaneously, structures called haustoria are formed close to the plant cell, allowing for the acquisition of nutrients by *Phytopththora* and for the delivery of pathogen effectors into the host cells (Petre and Kamoun, 2014). All this occurs during the biotrophic stage of infection, which is then followed by host tissue necrosis and the production of sporangia in the necrotrophic stage of infection (Hardham, 2007).

This infection process occurs in the context of an evolutionary battle between plants and their pathogens, where plants try do deploy resistance mechanisms, and pathogens try to avoid them – achieving virulence by secreting effector molecules into the host cell (Jones and Dangl, 2006). Hence, the identification and characterisation of core effectors, which are deployed by *P. palmivora* in Colombia to surpass the immunity of cocoa plant varieties, could be extremely useful in deploying effector-aided resistant breeding that is less time consuming and more durable than conventional breeding strategies (Evangelisti *et al*., 2017). These effector studies could be aided by a recent study that redefined the genomic structure of *P. palmivora*, allowing for the identification of several new effectors from this pathogen (Morales-Cruz *et al*., 2020).

In conclusion, cocoa is a crop that could greatly change Colombian agriculture and society in coming decades if good production yields are achieved. Thus, it is extremely important that further studies are conducted on *P. palmivora's* impact on Colombian cocoa production. Furthermore, it is crucial that innovative and environmentally friendly strategies are developed to efficiently control *P. palmivora* infections in Colombia.

HEMILEIA VASTATRIX

Hemileia consists of a genus of biotrophic rust fungi, where the most studied species is *H. vastatrix* because

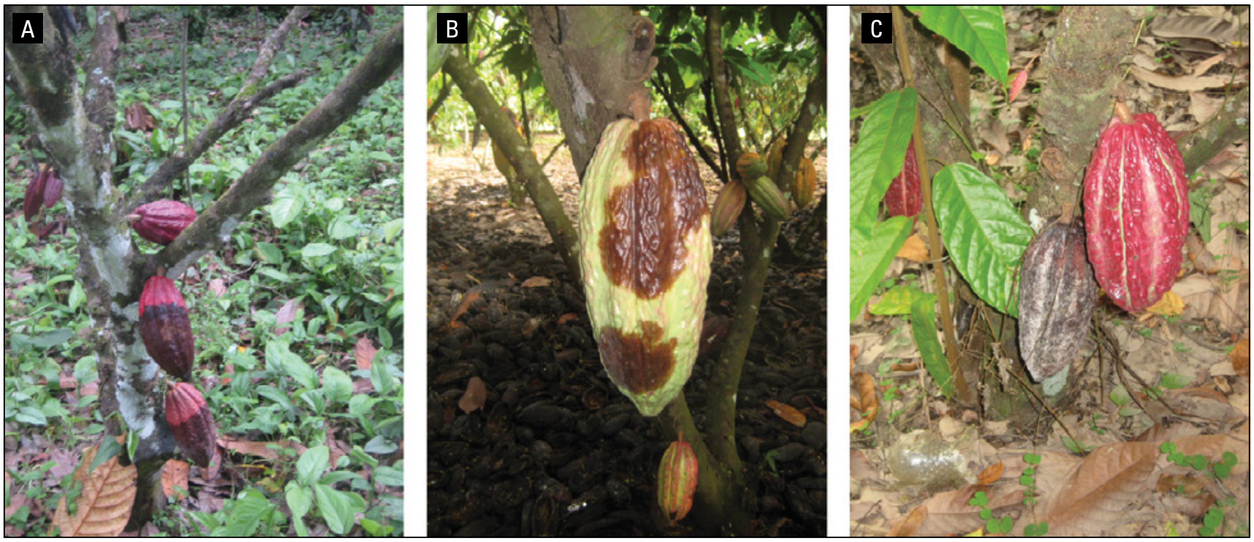

Figure 3. Symptoms of *Phytophthora palmivora* infection in cocoa plants grown in Colombia. Characteristic coffee-colored necrotic lesions caused by *P. palmivora* infection can be observed in cocoa pods grown in Colombia. Source: L. Rodríguez-Polanco, Colombian Corporation for Agricultural Research (AGROSAVIA).

of its capacity to infect and cause economic losses on coffee plantations worldwide (Kushalappa and Eskes, 1989; McCook and Vandermeer, 2015). *H. vastatrix* causes the coffee leaf rust disease, first reported in Sri Lanka and Southern India in 1869. Today, coffee leaf rust is considered the major threat to coffee production worldwide (McCook and Vandermeer, 2015; Talhinhas *et al*., 2017).

Coffee has great economic and social value and is produced in more than 70 countries - many of which suffer from poverty with over 10% of their population living in extreme poverty (defined as earning less than USD$1.25 a day) (Ponte, 2002; FAO, 2015). In 2019, Colombia was the third largest coffee producer worldwide with a production of 885,120 t, behind only Brazil (3009402 t) and Vietnam (1,683,971 t) (FAO, 2019). In the Colombian agricultural sector, coffee production was shown to be the most valuable agricultural product, accounting for 17.3% of the agricultural value despite accounting for only, approximately, 1% of agricultural production in Colombia by weight (Lau *et al*., 2013; FAO, 2018). However, this importance could be dramatically increased if higher yields of production were achieved. Colombian production yields of coffee were 8,464 hg/ha in 2014; whilst productions for Brazil and Vietnam were 14,215 and 24,991 hg/ha, respectively (FAO, 2015).

The low yields in coffee production in Colombia are probably caused by a vast number of factors, including some that have a complicated social nature. Nevertheless, coffee production yields could be greatly increased by better management of coffee diseases, such as coffee leaf rust (Avelino *et al*., 2015). Whilst symptoms of *H. vastatrix* infection can be minimal, under the right conditions, these symptoms can become more acute – posing a serious threat to coffee production. In extreme cases, this can lead to a loss of fruits before harvest. When this occurs, it is considered an epidemic – such as occurred in Colombia in 1987-88 and 2008-11. These epidemics are associated with specific climatic factors, such as increased rainfalls and abnormal temperatures, and cause severe

Figure 4. Symptoms of *Hemileia vastatrix* infection in coffee plants grown in Colombia. A, defoliation; B, distinctive yellow-orange powdery lesions on the abaxial leaf surfaces; C, extensive damage caused by *H. vastatrix* on a coffee plantation in Colombia. Source: J.S. Márquez.

losses in coffee production yields. For example, between 2008-11, coffee production was reduced by an average of 31% from production in 2007 (Avelino *et al*., 2015). Thus, it is extremely important to understand and predict these epidemics so effects can be mitigated, especially since there are likely to be increases in these climatic conditions as the result of climate change.

There is a clear need to understand *H. vastatrix* infections to predict and prevent coffee leaf rust outbreaks. However, knowledge on infection mechanisms underpinning the disease caused by this biotrophic rust fungal species remains elusive. The infection process in susceptible plants has been reported to start with the differentiation of an appressoria over the stomata and a consequent penetration of leaves by an infection hypha. These infection hyphae subsequently form haustorial mother cells that break plant cell walls, leading to the formation of the haustorium. After intense intracellular hyphal growth, infection culminates in the production of distinctive yellow-orange powdery lesions on the abaxial leaf surface (Fig. 4; Ramiro *et al*., 2009). While the infection cycle of *H. vastatrix* is relatively well described, the molecular mechanisms underlying this infection process remain poorly understood. Like many other plant pathogenic fungi, *H. vastatrix* surpasses plant immunity by delivering effector proteins into the host cells. Genome sequencing efforts have identified hundreds of candidate effector proteins encoded in the genome of *H. vastatrix*; however, the functional roles of these effectors have not been well-described (Ramiro *et al*., 2009; Porto *et al*., 2019). Effectors from plant pathogens can be recognized by plant resistant proteins, which enhance the plant defense response – following a gene-to-gene model (Van Der Biezen and Jones, 1998; Cristancho *et al*., 2014). Thus, increased knowledge on the effector repertoire of *H. vastatrix*, and resistant proteins encoded by resistant coffee plants could be of extreme importance to resistance breeding efforts for coffee plants. Despite many efforts and the generation of multiple new cultivars using current techniques, resistance is always evaded by rapidly evolving pathogen strains; this increased repertoire of effector and resistance proteins could play a role in outpacing adaption of the pathogen and maintaining a high level of overall resistance (Zambolim, 2016).

Current measures used in Colombia to counteract *H. vastatrix* infections involve huge efforts planting cultivars with increased resistance, implementation of early detection strategies in the field, and preventive deployment of fungicides (Avelino *et al*., 2015). Nonetheless, without increased insights on the molecular mechanisms underlying this plant-pathogen interaction, a durable solution to protect coffee production in Colombia and worldwide remains elusive.

CONCLUSION

The production of food crops in Colombia is constantly threatened by a vast range of plant pests and diseases. This review looked at four plant diseases that are likely to greatly hamper Colombian agricultural production in the coming decades. Besides the economic issues regarding crop losses associated with these pathogens, these pathogens will also have huge social impacts because they affect crops that provide basic income for a vast number of small-scale producers. Hence, solutions to impede the devastating effects of these pathogens are of paramount importance.

For each of the pathogens analyzed in this review, different strategies to fight their effects should be considered. However, there is a common need to gain a deeper understanding of the molecular basis of their infection processes. This increased knowledge could translate into the deployment of more durable plant resistance in the field. Moreover, excessive use of agrochemicals that present several environmental issues could be avoided. Therefore, governments and governmental institutions in developing countries, such as Colombia, should note the critical importance of investing in research on plant pathology. While durable resistance is pursued, immediate measures should be put in place to combat crop diseases. These measures vary but should always include efforts to educate agricultural producers, along with a national-level implementation of integrated strategies that control the incidence and dispersal of pests, without compromising the economic and ecological viability of agricultural production.

We are still far from understanding the plant-pathogen interactions for the diseases mentioned above, and perhaps even farther away from making the social changes needed for this knowledge to be applied in the field, yet we hope that this review will raise awareness of the urgency to integrate biological, economic, and social sciences to face the challenge of food security in both Colombia and the rest of the world.

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