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Evaluating the potential of soil management to reduce the effect of *Fusarium oxysporum* f. sp. *cubense* in banana (*Musa* AAA)

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Abstract *Fusarium oxysporum* f. sp. *cubense* (Foc) causes Fusarium wilt in banana (Musa *AAA*). Foc Race 1 devastated the subgroup Gros Michel during the first half of the twentieth century. The Gros Michel was largely replaced by the resistant subgroup Cavendish in the 1950s. However, in the 1980s, Foc Tropical Race 4 started to spread affecting Cavendish bananas. No proper control measures have been found to deal with the disease. This paper re-takes an important research line from the 1950s to evaluate the potential of soil management for Fusarium wilt management. The role of soil properties on Fusarium wilt in bananas was studied in two greenhouse experiments. It was evaluated whether the influence of two main soil properties (pH and N) on Fusarium wilt is similar for Race 1 and Tropical Race 4. Two soil pH levels (lower than 5.2 and higher than 6.0) respectively ensured through acidification and liming; and three levels of N (ammonium nitrate, 33.5% N) weekly doses (low:0 N g, medium: 0.08 N g and high: 0.25 N g per plant) were achieved. The first experiment in Costa Rica confirmed the earlier results about the influence of soil pH and nitrogen on Fusarium wilt (Race 1) on Gros Michel bananas. The second experiment in The Netherlands evaluated the influence of pH and N on interactions between Foc (both Race 1 and Tropical Race 4) and Cavendish bananas. Results in both experiments showed that soil pH affected crop development and the disease. Besides, the interaction of the lower pH x the higher N accelerated the infection and reduced plant development. As such, the results showed that soil management has the potential to reduce the impacts of Fusarium wilt while dealing with Race 1 and Tropical Race 4 although it requires confirmation and further evaluation under field conditions.

Keywords Crop disease · Crop protection · Nitrogen · Plant nutrition · Panama disease · Soil fertility

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Introduction

Fusarium wilt (also known as 'Panama disease') is a soil-borne disease caused by the fungus *Fusarium oxysporum* f. sp. *cubense* (Foc). The disease has strongly affected global banana production (Dita et al. 2018; Ordoñez et al. 2015; Pocasangre et al. 2017). Desert bananas and cooking bananas (including plantain) are an important staple in developing countries, where they represent a major part of the subsistence economy for millions of people (Aurore et al. 2009). In addition,

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desert bananas, dominated by the subgroup Cavendish (*Musa* AAA), are an important and valuable agricultural commodity for many exporting countries (Butler 2013; Ploetz 2015). The first major outbreak of Fusarium wilt (caused by the so-called Race 1 strain of Foc) decimated the large-scale production of the susceptible banana subgroup Gros Michel (*Musa* AAA). A gradual shift to resistant Cavendish (*Musa* AAA) cultivars controlled the epidemic in Latin America and the Caribbean during the last century (Harper 1950; Perez-Vicente 2004; Ploetz 1990; Stover 1961). This shift to Cavendish cultivars saved the banana industry. However, another Foc strain, commonly called Tropical Race 4 (TR4; Foc vegetative compatibility group VCG 01213), currently affects or threats Cavendish plantations worldwide.

Foc TR4 may lead to a new, more widespread, wave of Fusarium wilt, as many banana cultivars are susceptible to this strain (Molina et al. 2008; Ordoñez et al. 2016). Foc TR4 has been reported in various countries, such as Malaysia, China, Indonesia, and the Philippines in South East Asia (Molina et al. 2008), Jordan (García-Bastidas et al. 2014) and Pakistan (Ordoñez et al. 2016), where it already destroyed thousands of hectares. Recently, Foc TR4 has also been reported in Latin America (García-Bastidas et al. 2020). The potential effect of further dissemination could cause chaos, damage the economies of many banana-producing countries, and affect food security (Dita et al. 2013). There are no effective control measures (such as fungicides or cultural practices) for the disease. A transgenic TR4 resistant Cavendish cultivar (Dale et al. 2017) and somaclonal variation in resistance in Cavendish cultivars (Hwang and Ko 2004) are being promoted, but these options require more validation and studies before large-scale implementation. Given the fact that it takes several years to develop and distribute resistant banana cultivars, and the ineffectiveness of fungicides or other crop protection agents, it is appropriate to consider alternative strategies to reduce disease incidence in the short term (Geense et al. 2015).

Soil properties are known to influence the predisposition of crops to diseases (Doran and Zeiss 2000; Ghorbani et al. 2008; Huber et al. 2012) and they can be managed through e.g., fertilization, liming, tillage, and drainage. Therefore, soil management can potentially reduce the impact of crop diseases (Amir and Alabouvette 1993; Höper et al. 1995). Nevertheless, soil management receives little attention as a strategy for crop disease management. Although Rishbeth (1955) and Stover (1961) already discussed the potential of soil management in the case of Foc Race 1 in bananas, the research into soil management to control Fusarium wilt became less relevant with the discovery and introduction of Cavendish bananas. Problems with Race 1 in the small-scale production of susceptible varieties and the recent spread of Foc TR4 renewed the interest into soil management for Fusarium wilt management. Recently, several authors discussed the potential role of soil properties (e.g., pH, drainage, and nutrients) in relation to Fusarium wilt in bananas, mainly focusing on Fusarium wilt by Foc Race 1 (Domínguez et al. 2008; Geense et al. 2015; Haddad et al. 2018; Orr and Nelson 2018; Segura et al. 2018, 2019). The current threat of Fusarium wilt by Foc TR4 makes it necessary to corroborate the previous results obtained with Foc Race 1. However, despite the need for more insight in Foc TR4, it is practically impossible to carry out field experiments with Foc TR4 in most places around the world for phytosanitary reasons. As a result, many studies use Foc Race 1 and susceptible varieties under the assumption that these results are also valid for Foc TR4 (e.g., Bowen et al. 2019).

Literature confirms the effects of soil pH on crop disease incidence. A low soil pH has been linked with a higher predisposition to diseases in crops (Huber et al. 2012; Rengel 2000): Fusarium wilt in flax (Höper et al. 1995) and bananas (Domínguez et al. 2001), root rot (*Aphanomyces* spp.) in pea (Persson and Olsson 2000), common scab (*Streptomyces scabiei*) in potatoes (Goto 1985; Lacey and Wilson 2001; Lambert et al. 2005), and phytophtora root rot (*Phytophthora cinnamomi*) in avocado (Fernandez-Falcon et al. 1984). However, there are also examples that a high soil pH is associated with a higher crop disease incidence: black root (*Thielaviopsis basicola*), causing black root rot in tobacco (Harrison and Shew 2001; Oyarzun et al. 1998) and take-all (*Gaeumannomyces graminis* Sacc.) in wheat (Duffy et al. 1997). Despite these reports, where a relation between soil pH and the incidence of crop diseases was found, there are also other studies that did not confirm this relationship (Janvier et al. 2007).

It is generally accepted that soil N influences crop diseases (Huber et al. 2012; Janvier et al. 2007; Rengel 2000). However, the results are inconsistent and varied according to e.g., the applied N form, the pathogen, the crop or its growth stage (Dordas 2008; Harrison and Shew 2001; Huber and Watson 1974). Both positive and negative relationships between N concentrations and crop disease incidence have been reported. For instance, a lower N concentration was related with increased incidence of early blight (*Alternaria solani*) in potatoes (Miller and Rosen 2005), Xanthomonas wilt (*Xanthomonas campestris* pv. *musacearum*) in bananas (Atim et al. 2013), grey mould (*Botrytis cinerea*) in tomatoes (Hoffland et al. 1999), and bacterial speck (*Pseudomonas syringae*) and powdery mildew (*Oidium lycopersicum*) in tomatoes (Hoffland et al. 2000). N concentrations are especially important for disease incidence in wheat and other cereals. The incidence of take-all caused by *Gaeumannomyces graminis* (Brennan 1992), Septoria tritici blotch (*Mycosphaerella graminicola*), brown rust (*Puccinia recondite*), powdery mildew (*Blumeria graminis*) and foot rot (*Fusarium* spp.) increased with higher N concentrations (Leitch and Jenkins 1995; Olesen et al. 2003; Rodgers-Gray and Shaw 2000; Tiedemann 1995; Walters et al. 1984).

This paper aims to re-take an important research line from the 1950s to evaluate the potential of soil management to control Fusarium wilt in bananas. Based on the importance of soil pH and N in crop production and the reported impact of these soil properties on crop response to diseases their role on the expression of Fusarium wilt in bananas was studied. In addition, this study evaluates whether the influence of those soil properties on the occurrence of Fusarium wilt is similar for Foc Race 1 and Foc TR4.

Materials and methods

Two separate greenhouse experiments with a similar experimental setup were carried out. The first experiment, performed in Costa Rica, aimed to evaluate previous results about soil properties and the disease reported in the literature with the model between the subgroup Gros Michel and Foc Race 1 (present in Costa Rican soils). The second experiment, performed in The Netherland under strict biosecurity rules, aimed to study the effect of soil properties on the subgroup Cavendish and Foc TR4 to evaluate whether this new strain of the fungus provides similar results.

In the first greenhouse experiment (in Costa Rica), the development of Fusarium wilt by Foc Race 1 was studied. The aim was corroborating previous results reported in the literature about the incidence of Fusarium wilt in the model between Gros Michel banana and Foc Race 1. It was performed in the facilities of the CORBANA's Research Center (132 m.a.s.l., 10°15′54" N, 83°46′26" W, minimum temperature of 17 °C and maximum temperature of 35 °C). Two types of inoculation were tested in this experiment: a control without any inoculation and inoculation with Foc Race 1 (collected from Costa Rican soils and cultivated by CORBANA's Laboratory of Biological Control). Plant inoculation was performed following protocols previously reported (García-Bastidas et al. 2014; Ordoñez et al. 2016), using root dipping for 30 min in a solution of 1.10^{-6} Foc conidia per mL. After inoculation, plants were transferred to 2 L pots filled with a medium-texture and fertile (2.5% organic matter, 11.3 g kg soil^{-1} Ca, 7.05 g kg soil^{-1} Mg, 0.16 g kg soil^{-1} K and 0.01 g kg soil^{-1} P) soil. This soil type is commonly used for growing bananas in Costa Rica and was therefore also used to test the plant response against the disease according to soil management. Treatments of the evaluated soil properties (pH-N) consisted in two soil pH levels (lower than 5.2 and higher than 6.0) and three N doses (low, medium, and high). The natural soil pH was approximately 6.1 and it was considered the higher level of soil pH (pH_{high}). For the low pH level (pH_{low}), the pH was decreased to 5.1 through the application of a hydrochloric acid solution (10% HCl). N doses were achieved through weekly differentiated N doses of ammonium nitrate (AN, 33.5% N): N_{low} with no N addition relying on natural N in the soil; 2) N_{med} with 0.08 N g plant^{-1} week^{-1} supplied through 0.24 g of AN plant^{-1} week^{-1}; and 3) N_{high} with 0.25 N g plant^{-1} week^{-1} supplied through 0.75 g of AN plant week^{-1}. These N doses were respectively achieved through applications of 300 mL of solutions of AN in water with concentrations of respectively 0.00 g L^{-1} N, 0.14 g L^{-1} N and 0.43 g L^{-1} N, two times week^{-1}. Because the soil in this experiment originated from a banana plantation, also the pots not receiving any additional AN had a basic level of available N. Each treatment was replicated three times resulting in a total of 36 hardened tissue culture plants (approximately 3 months-old). Although the greenhouse in this experiment gave some protection, the plants were exposed to the climatic conditions of a banana growing region.

The second experiment (in The Netherlands) aim was to explore the impact of soil properties on the response of Cavendish bananas to both Fusarium wilt by Foc Race 1 and Foc TR4. The experiment was performed under controlled greenhouse conditions (28 °C, 80% relative humidity and 16 h of light) at the facilities of Plant Research International of Wageningen University and Research (WUR). It was possible to include Foc TR4 in this experiment due to the controlled and strict biosecurity conditions offered by the greenhouse facilities and because there is no risk of spreading the disease to banana plantations. Three types of inoculation were tested in this experiment: a control without any inoculation, inoculation with Foc Race 1 (Foc CNPMF 008–01-R1 collected from Brazil and stored at WUR collection), and inoculation with Foc TR4 (Foc II-5 TR4 reference isolate collected from Indonesia and stored at WUR collection). The experimental setup in regarding of plant inoculation and the treatment of the selected soil properties (pH-N) was similar than in the first experiment.

Plants from this experiment were transferred to 2 L pots filled with a light-textured soil with intermediate fertility (2.6% organic matter, 0.04% N, 0.09 g kg soil^{-1} Ca, 0.06 g kg soil^{-1} Mg, 0.03 g kg soil^{-1} K and 0.0013 g kg soil^{-1} P). The same level of soil pH (lower than 5.2 and higher than 6.0) and the same three N doses (0, 0.08 and 0.25 g N plant week^{-1}) were tested with four replications per each inoculation (control, Foc Race 1, and Foc TR4) resulting in an experimental design in which 72 approximately 3 months old plants were evaluated. The natural soil pH level was approximately 5.1 considered the lower soil pH (pH_{Low}). For the higher pH level (pH_{high}), it was increased applying liming (with $CaCO_3$). Inputs of Ca in this treatment were compensate with CaCl in the pH_{low}. N doses per plant were achieved following the same experimental setup with the same N source (AN) as in the first experiment. Also, this soil had a basic level of available N.

The disease expression was measured in terms of its (negative) effect on the total biomass and leaf area per plant at the harvesting moment, 54 days after inoculation (d.a.i.) in the first experiment and at 33 d.a.i. in the second experiment. Because the inoculated plants were exposed to the fungus, the presence of symptoms can be attributed to Foc. This was further confirmed as the non-inoculated plants did not show symptoms. Therefore, a non-intrusive way to measure the disease according to the management of the soil properties was used to follow the development of the wilting. A disease index (DI) was calculated in each treatment of each experiment. The DI was obtained adapting the McKinney's formula (McKinney 1923) that was also used by Haddad et al. (2018) and Rocha et al. (2020) in the same way. However, in this case, it was based on the number of sick plants and the wilted leaves: $DI(\%) = 100.\sum(f/n)\cdot(v/x)$, where; f = number of sick plants; n = total of plants; v = number of leaves with symptoms; and x = total number of leaves (with symptoms and healthy). The presence of the typical symptoms of the wilting of the leaves in previously inoculated plants is reported as a valid element to corroborate the presence of the disease in bananas (Dita et al. 2010; García-Bastidas et al. 2014 and 2020; Ordoñez et al. 2016). In addition, the dissection of wilted plants was performed to corroborate the presence of the typical internal symptoms of the disease. The data results of the experiments were independently analyzed through a factorial analysis of variance, considering in each case three factors (inoculation, soil pH and N dose) and their interactions. Differences between factors were evaluated for significance through a Tukey's range test.

Results

Experiment 1

Plant biomass and leaf area in non-inoculated plants were different ($P \leq 0.050$) between pH_{high} and pH_{low} for all the N doses (Table 1). For both variables, pH_{high} plants had a better performance. The differences were more evident in the case of leaf biomass. Plants grown in pH_{high} produced around 6 times biomass than those grown in pH_{low}. The difference followed the same behavior for the leaf area but with a less dramatic difference. In this case plants from pH_{high} produced around 4 times the leaf area produced in plants grown in pH_{low}. Although, N soil concentrations appeared in most of the cases to be enough to fulfill the plant requirements, the lower value of the biomass was found in N_{high} of the pH_{low} group. The natural effect of the soil pH, the N, and their interactions in the development of the banana plant was evidenced with those results.

A higher biomass and leaf area per plant were found in plants from the control treatment for both pH_{low} and pH_{high} ($P \leq 0.0001$) in comparison with those which were inoculated. However, both variables were lower at pH_{low} ($P \leq 0.0001$) for both the control and the inoculated plants (Fig. 1). Even inside the inoculated group of plants the lower biomass was found in those growing in pH_{low}. A highly significant interaction of pH x

Table 1 Tukey's analysis of the comparison of biomass and leaf area at 54 days after planting from non-inoculated (control) Gros Michel banana plants (Musa AAA) grown in two soil pH levels (lower than 5.2 and higher than 6.0) and three N (with ammonium nitrate, 33.5%N) doses (N_{low} with no N, N_{med} 0.08 N g plant week^{-1}, and N_{high} 0.25 N g plant week^{-1}) in a greenhouse experiment (standard deviation between parentheses)

Variable	Soil pH	N dose			
		Low	Med	High	Average
Biomass (g plant^{-1})	Low	4.2	6.0	2.8	4.4
	High	24.6	29.7	29.0	27.8
		(15)	(17)	(19)	(12)
	Average	14.4	17.9	15.9	16.1
(pH_{low} – pH_{high})		−20.4*	−23.7*	−26.2*	−23.4*
Leaf area (cm^2 plant^{-1})	Low	57.1	95.4	62.8	71.7
	High	210.4	247.8	316.0	258.0
		(108)	(108)	(179)	(132)
	Average	133.8	171.6	189.4	164.9
(pH_{low} – pH_{high})		−153.3*	−152.4*	−126.6*	−186.3*

** $P \leq 0.010$; *$P \leq 0.050$

inoculation was observed ($P \leq 0.0001$). A higher plant development and growth were found in pH_{high}. A high correlation ($r = 0.95$) between those variables (biomass and leaf area per plant) was found in these plants. The single effect of the N doses did not induce a significant difference on the evaluated variables. However, the soil pH x N interaction was almost significant ($P = 0.068$).

There were differences ($P \leq 0.0001$) in each N dose for both variables when changes of obtained values were compared between the inoculated and the control groups. At the same time, the more extended gaps in this comparison (control-inoculation) were observed for N_{med} and N_{high}. The differences in N_{low} kept the pH x inoculation significance, but this N dose had a minor difference between inoculated and control plants (Table 2).

The DI of Fusarium wilt was higher in plants from the pH_{low} ($P \leq 0.050$). For both pH_{low} and pH_{high}, first symptoms were detected after the third week since planting. The pH x N interaction was found significant ($P \leq 0.050$) to the DI. Besides, a higher DI was calculated in the higher N doses for both soil pH levels. This interaction (pH x N) was linear and more accentuated in pH_{low} (Fig. 2). No symptoms were identified in non-inoculated plants. However, some plant from pH_{low} showed a chlorotic (not wilted) appearance attributed to the extreme lower pH in this treatment (Fig. 3).

Experiment 2

Biomass and leaf area in plants from the control (not inoculated) group are presented in Table 3. Although there were higher values in biomass and the leaf area for plants grown in pH_{high}, only the biomass ($P \leq 0.050$) was found different according to soil pH. Although N_{low} presented a lower biomass on average, no significant differences were found for N doses. Inoculated and non-inoculated plants grown at pH_{high} had significantly ($P \leq 0.001$) higher biomass and leaf area than those plants grown at pH_{low} (Fig. 4). Soil pH and the inoculation interacted on the plant biomass and leaf area ($P \leq 0.0001$). Inoculated plants at pH_{low} had less biomass and leaf area than those of the control. At pH_{high}, Foc Race 1 inoculated plants equaled the biomass and surpassed the leaf area of the control. The lower soil pH resulted in a significant reduction of biomass and leaf area in inoculated plants. Comparing inoculation against non-inoculation, the biomass in the control exceeded the average of the inoculated groups (both Foc Race 1 and Foc TR4). Inoculated plants with Foc TR4 had consistently lower biomass and leaf area in both soil pH levels. Although the biomass and the foliar area were higher in the plants from pH_{high}, this effect was hidden through Foc TR4 ($P = 0.703$) inoculation due to the stronger pathogenic effect of this fungus. At the end of the experiment, inoculated plants from pH_{low} manifested more symptoms than those from pH_{high} for

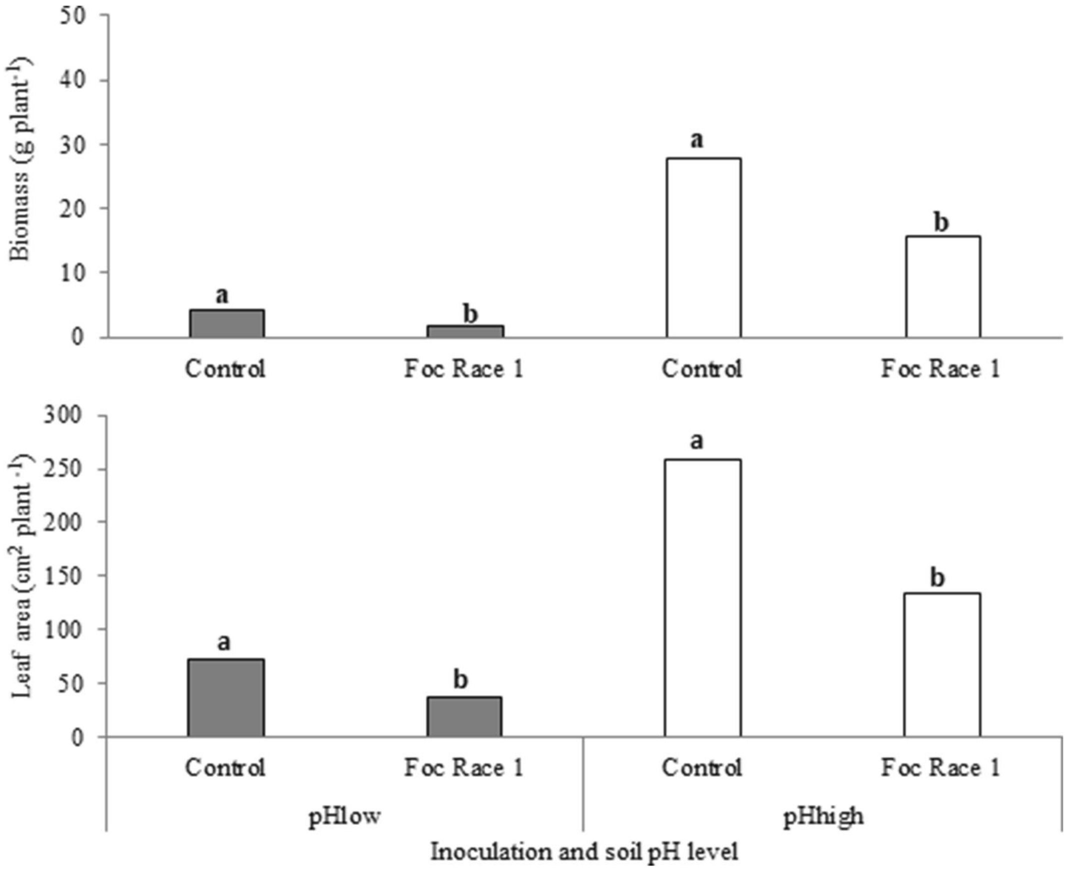

Fig. 1 Biomass and leaf area from non-inoculated (control) and inoculated Gros Michel banana plants (*Musa* AAA) with *Fusarium oxysporum* f. sp. *cubense* Race 1 grown in two soil pH levels (lower than 5.2 and higher than 6.0) at 54 days after inoculation in a greenhouse experiment in Costa Rica. Small letters indicate differences between the treatments in each pH level. Segura et al.

Table 2 Tukey's analysis of the comparison of biomass and leaf area at 54 days after inoculation between the inoculation with *Fusarium oxysporum f. sp. cubense* Race 1 against the control from Gros Michel banana plants (*Musa* AAA) grown in two soil pH levels (lower than 5.2 and higher than 6.0) and three N (with ammonium nitrate, 33.5%N) doses (N_{low} with no N, N_{med} 0.08 N g plant week^{-1}, and N_{high} 0.25 N g plant week^{-1}) in a greenhouse experiment in Costa Rica

Variable	Soil pH	N-dose			
		N_{low}	N_{med}	N_{high}	Average
Change in biomass (g plant $^{-1}$)	Low	−1.3**	−6**	−0.7**	−2.7**
	High	−5.4**	−11.2**	−20**	−12.2**
	Average	−3.4	−8.6	−10.4	−7.5
Change in leaf area (cm^2 plant $^{-1}$)	Low	−4.5**	−95.4**	−2.3**	−34.1**
	High	−55.4**	−96.8**	−222**	−87.8**
	Average	−29.9	−96.1	−112.2	−60.9

** $P \leq 0.010$; * $P \leq 0.050$

both Foc Race 1 and Foc TR4 inoculation. All (100%) inoculated plants for both Foc strains showed symptoms of the disease. A higher aggressive level of the symptoms was shown in pH_{low} with Foc TR4 inoculation. No Fusarium wilt incidence was detected in the control group.

A significant pH x N interaction ($P \leq 0.050$) was found in most of the plant growth variables. Plants from the control group were compared against those from inoculated groups (Table 4). Differences between the variables of inoculated plants were lower than those from the control. The N dose determined the magnitude of the differences. A higher significance level ($P \leq 0.010$) was found in pH_{low} for both Foc strains. Although infected plants showed lower values than the control in both pH levels, with N_{high} those differences were significant and more contrasting for the Foc Race 1 inoculated group. Differences according to N dose in Foc

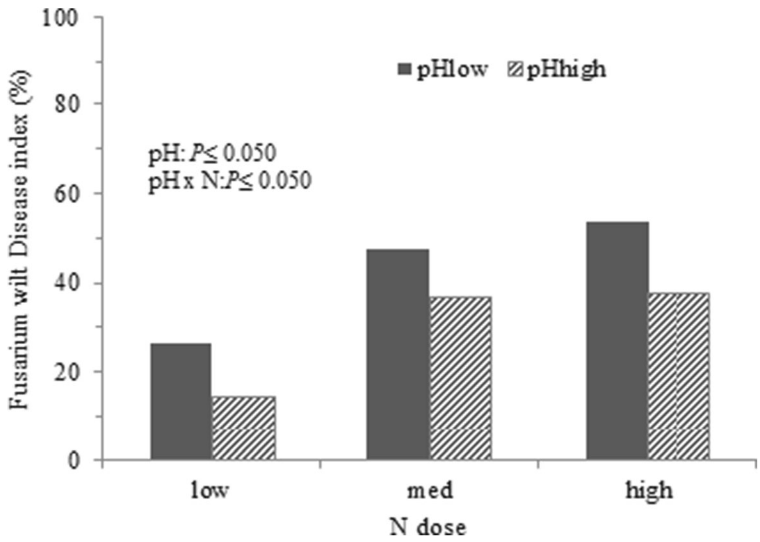

Fig. 2 Disease Index of Fusarium wilt *by Fusarium oxysporum* f. sp. *cubense* Race 1 at 54 days after inoculation from Gros Michel banana plants (*Musa* AAA) grown in two soil pH levels (lower than 5.2 and higher than 6.0) and three N (with ammonium nitrate, 33.5%N) doses (N_{low} with no N, N_{med} 0.08 N g plant week^{-1}, and N_{high} 0.25 N g plant week^{-1}) in greenhouse experiment in Costa Rica. Segura et al.

Race 1 infected plants against the control were not significant in pH_{high}. Foc TR4 showed stronger ($P \leq 0.005$) differences in pH_{low} and N_{high} in almost all the variables, except for biomass. The effect of the Foc TR4 inoculation was significant in most of the cases, but less contrasting in the case of pH_{high}. Furthermore, the effect of the N doses was significant at least in one of the measured variables in both soil pH levels in Foc TR4 inoculation. Both Foc strains (Race 1 and TR4) induced symptoms in the tested banana cultivar, the Cavendish. Symptoms appeared during the first and second weeks after the inoculation and they were stronger at pH_{low} and with Foc TR4 inoculation. Symptoms from Foc race 1 inoculation were fewer and more attenuated at the end of the experiment. However, even at the end of the experiment, plants showed symptoms for both Foc strains (Fig. 5).

The DI (Fig. 6) showed a significant effect of a pH x N interaction ($P \leq 0.010$). The wilting was more aggressive in Foc TR4 infected plants for both soil pH levels and all the N doses. DI in TR4 infected plants from pH_{low} reached almost 100% and around 80% in Foc Race 1. In pH_{high} the DI in the plants was higher for TR4 inoculation respect to the Race 1 inoculation, but it was lower than in pH_{low} from both inoculations.

Discussion

Although the literature shows the opportunities for the use of soil management in crop disease control, its actual implementation requires insight into the relationships between individual soil properties and crop diseases. However, reality is complex and, in general, a combination of multiple soil properties determines crop development and disease expression. Therefore, the relationship between a soil property and a crop disease is found to be context-specific, and the response to individual soil properties, hard to establish. In addition, it is well known that crop status differs according to the multitude of soil properties. As a result, the relatively simple conceptual plant disease triangle (Huber and Haneklaus 2007) representing host, pathogen and environment interaction is actually comprised of highly complex interrelationships involving a plethora of different factors that are extremely difficult to unravel and translate in straightforward soil management recommendations. This is probably also the underlying explanation for the inconsistencies in reported results in the literature.

The complex puzzle that represents implementing soil management is constrained by the limitations of this practice. Soil properties differ in the way they can be managed. Soil texture, for instance, is reported as a property that can influence crop diseases, but it is a given and, except in some very specific cases, cannot be changed through soil management. However, it can be considered while planning new plantations. Other soil properties, for example, nutrient concentrations and soil organic matter, can be managed through mineral and organic fertilizers.

Some soil properties, such as soil pH and nutrient concentration, appear as attractive options to develop strategies for crop diseases control, as: i) they can be managed through e.g., fertilization and liming, and ii)

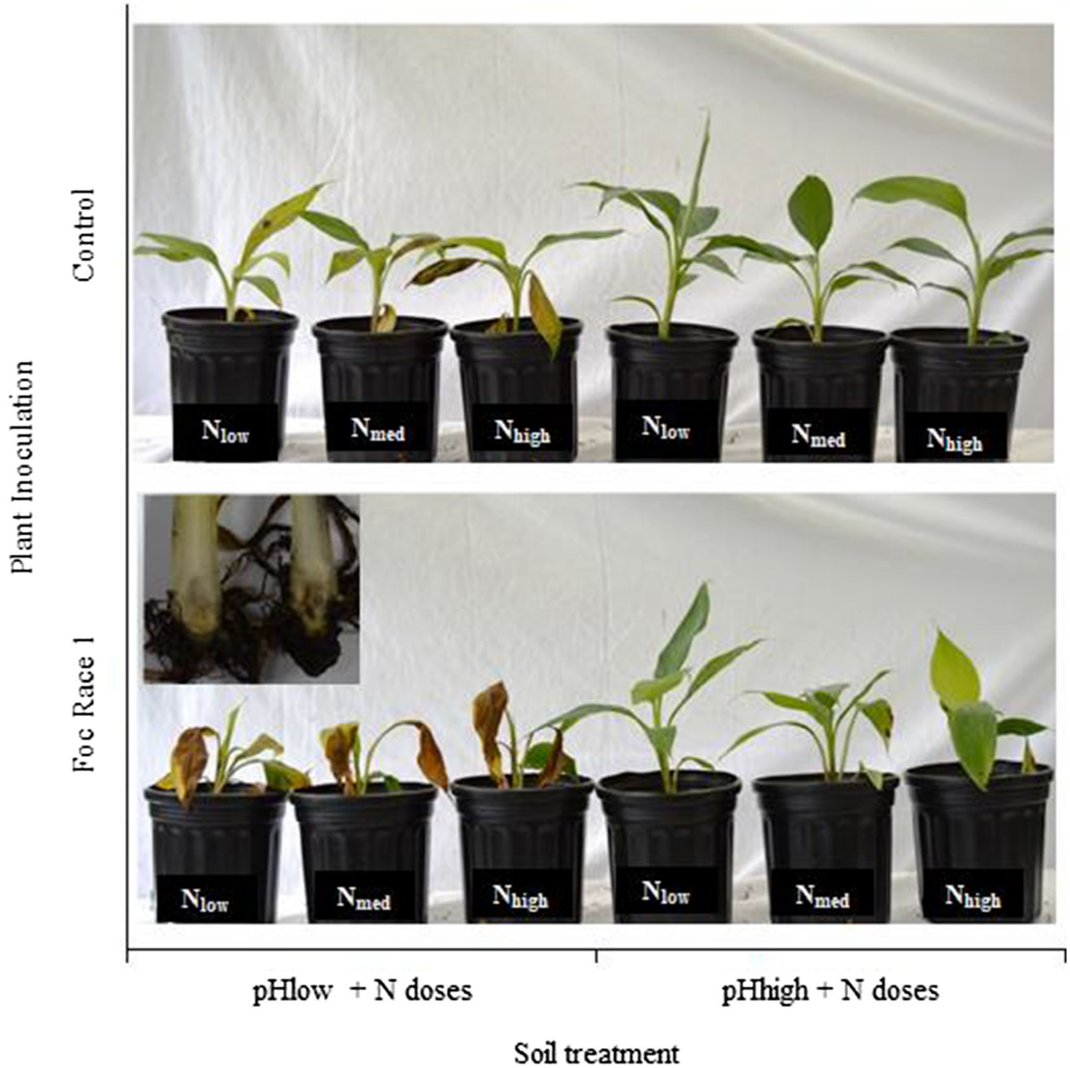

Fig. 3 External and internal Fusarium wilt symptoms by *Fusarium oxysporum* f. sp. *cubense* Race 1 at 54 days after inoculation from Gros Michel banana plants (*Musa* AAA) grown in two soil pH levels (lower than 5.2 and higher than 6.0) and three N (with ammonium nitrate, 33.5% N) doses (N_{low} with no N, N_{med} 0.08 N g plant week^{-1}, and N_{high} 0.25 N g plant week^{-1}) in a greenhouse experiment in Costa Rica. Segura et al.

they play a role in crop diseases. However, for the development of management strategies, quantitative insight into the relation between soil properties and crop diseases is needed. This insight would allow farmers to take the economic decisions to invest in soil management. However, if the relationship is context-specific, the general validity of a relationship is limited, and it almost needs to be derived for each individual case.

Banana is an important crop with a very aggressive disease as Fusarium wilt, but with no effective conventional control options. Besides, there are not indications of soil suppressiveness against this pathogen (Deltour et al. 2017). The experiments demonstrated the role of soil pH and N and their interactions with disease incidence and severity. Soil pH is an important soil quality indicator in banana soils and higher crop productions generally coincide with a higher soil pH (Segura et al. 2015). Acidification due to heavy fertilization is indicated as a serious problem in crop management and liming is common practice (Stoorvogel and Segura 2018). In intensive production systems, banana plants are highly fertilized with up to 400 kg N ha year^{-1}. Following the literature on Fusarium wilt, the intensively managed system may be highly susceptible to this

Table 3 Tukey's analysis of the comparison of biomass and leaf area at 33 days after planting from non-inoculated (Control) Cavendish banana plants (Musa AAA) grown in two soil pH levels (lower than 5.2 and higher than 6.0) and three N (with ammonium nitrate, 33.5%N) doses (N_{low} with no N, N_{med} 0.08 N g plant week^{-1}, and N_{high} 0.25 N g plant week^{-1}) in a greenhouse experiment in the Netherlands (standard deviation between parentheses)

Variable	Soil pH	N doses			
		Low	Med	High	Average
Biomass (g plant^{-1})	Low	223	291	292	269
		(107)	(102)	(73)	(104)
	High	312	364	335	337
		(40)	(50)	(41)	(44)
	Average	268	328	313	303
($pH_{low} - pH_{high}$)		−189	−73	−43	−68*
Leaf area (cm^2 plant^{-1})	Low	1423	1259	1574	1419
		(962)	(412)	(287)	(554)
	High	1524	1878	1460	1621
		(321)	(118)	(449)	(296)
	Average	1473	1569	1517	1520
($pH_{low} - pH_{high}$)		−101	−619	114	−202

** $P \leq 0.010$; *$P \leq 0.050$

disease due to the acidification and N fertilization. General recommendations based on current literature would include liming and possibly a reduction in N fertilization.

The difference in the duration of the experiments was due to the rapid development of the plants in the second experiment under the optimal and controlled conditions relative to the more natural conditions in the first experiment. However, for both experiments, the effect of soil pH and the interaction of soil pH and N on the disease expressed as the biomass, the leaf area and the DI evaluated how the predisposition of Gros Michel banana to Foc Race 1 (and TR4) can be modulated. The effect of those soil properties was also reported in field experiences (Rishbeth 1955; Stover 1961). This effect of those soil properties could have played a role in the devastation of Gros Michel by Foc Race 1 in Latin America during the last century. The decimation of the former main banana subgroup (the Gros Michel) appears expectable with the incipient knowledge about the fungus and its dissemination (Dita et al. 2018) and the recently reported interactions of Foc with e.g., soil nematodes (Rocha et al. 2020) and the banana weevil (Guillén et al. 2021). Due the lack of awareness about the importance of tested soil properties in the expression of the disease, the standard management of the crop with the common application of high rates of N (and the consequent drop of pH) could increase the severity of the disease. In the case of this research, the effect of the N doses in dropping soil pH was almost absent due the implemented procedure of N application in a solution.

The potential of soil management in Fusarium wilt incidence was clear when the Cavendish cultivar showed symptoms caused by Foc Race 1 in the second experiment. Although those cultivars are widely accepted as resistant to Foc Race 1(Harper 1950; Perez-Vicente 2004; Ploetz 1990), the extreme stress in pH_{low} induced a higher predisposition to the disease. It is reported that Cavendish can be affected by Foc Race 1 in young stages under stress conditions, such as extreme soil temperatures and high inoculum level (Brake et al. 1995; Smith et al. 2008). Besides, a lower pH can be considered as an extreme condition with potential to accelerate the disease incidence in young Cavendish plants, as was found in the second experiment.

The differences in biomass and leaf area between pH levels in the control plants for both experiments can be attributed to the effect of soil pH on the plant nutritional intake. At the same time, this condition could more highly predispose the plant to Fusarium wilt because of the lack of nutrients. Besides, the additional effect of the lower pH is a higher solubilization of aluminum (Al). A higher Al concentration is reported to negatively affect banana production (Segura et al. 2015). Nutrients may be required to grow and to activate the plant responses against the fungus. Under the extreme soil condition of pH_{low}, even a Foc Race 1- resistant plant as the Cavendish, can be affected by the diseases. In pH_{high}, the plant can take up more nutrients and water from the soil (Neumann and Römheld 2012) which increased the biomass production.

The experiments showed that previous reports on Fusarium wilt and Gros Michel banana can be replicated. It was shown that soil properties can modulate disease incidence by Foc TR4 in Cavendish. Besides, it seems like the response of Gros Michel to the disease according to soil pH differences is more contrasting than the Cavendish cultivar. The experiments showed a slightly higher predisposition of Gros Michel to Foc Race 1 than Cavendish to Foc TR4 to the management of this soil property. This could suggest that the impact of Foc TR4 on Cavendish would be less severe than the

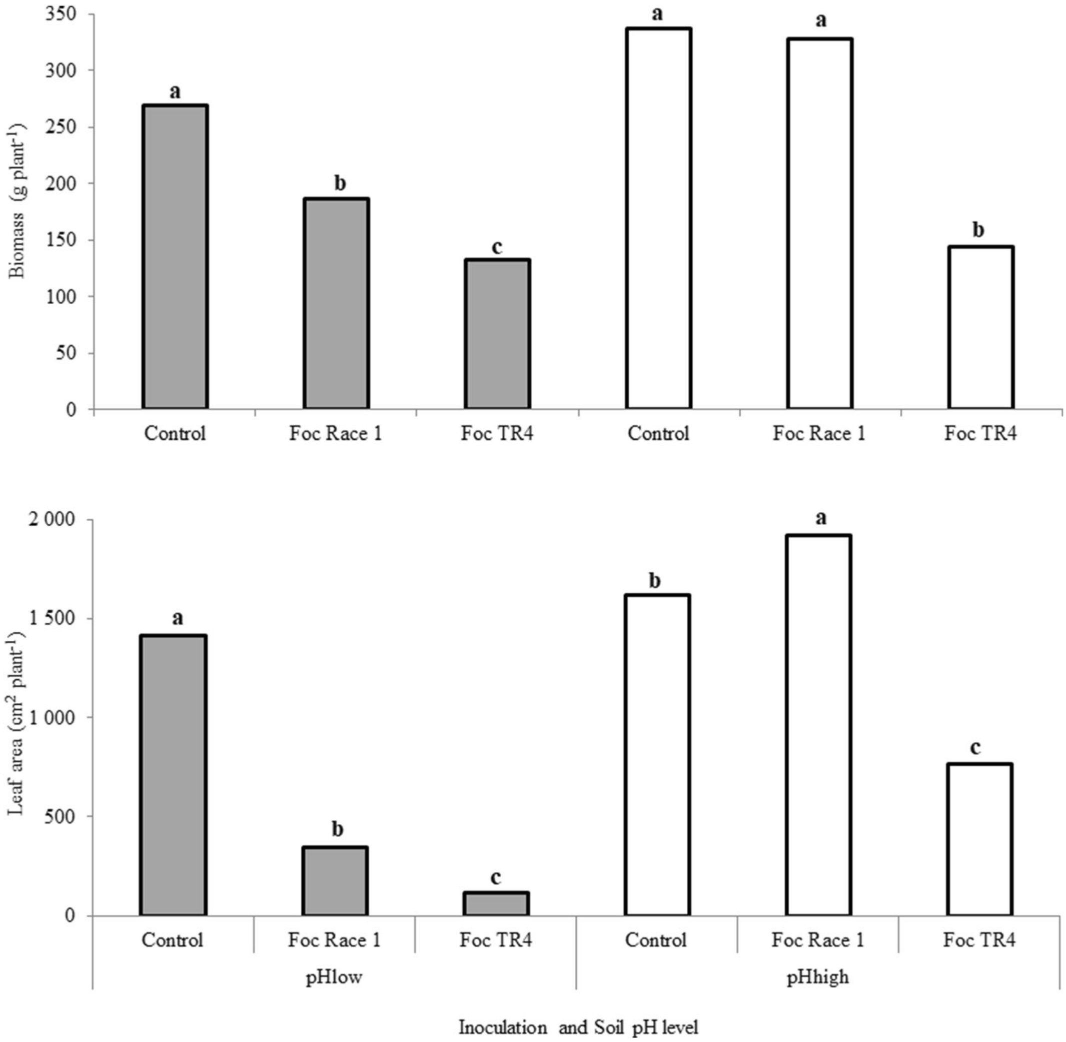

Fig. 4 Biomass and leaf area at 33 days after inoculation from non inoculated (Control) and inoculated Cavendish banana plants (*Musa* AAA) with *Fusarium oxysporum* f. sp. *cubense* (Race 1 and TR4) grown in two soil pH levels (lower than 5.2 and higher than 6.0) in a greenhouse experiment in the Netherlands. Small letters indicate differences between the treatments in each pH level. Segura et al.

impact of Foc race 1 on Gros Michel. However, this comparison is difficult, as conditions differ between greenhouse and the field, and because crop management has been intensified over the years.

Both experiments showed the potential of soil management as a component for an integrated control of Fusarium wilt in bananas. The effect of managing soil properties on Foc Race 1 in the Gros Michel subgroup was confirmed. In addition, soil management appears to have similar effects on Foc TR4. The results indicate the importance of the selected soil properties (pH and N) and their role in the predisposition of banana to the disease. The concept of soil management strategy in crop disease management requires more detailed studies, but the results support investing in this alternative approach to crop disease management in present and future crop production. This is particularly applicable for Fusarium wilt in banana, where this kind of studies is highly needed due to the direct threat of Foc TR4.

Conclusions

Crop production is constantly threatened by diseases. There are an important number of diseases for each crop and new diseases are also common in crop production.

Table 4 Tukey's analysis of the comparison of biomass and leaf area at 33 days after inoculation between *Fusarium oxysporum f. sp. cubense*, (Race 1 and TR4) inoculation against not inoculation (Control) in Cavendish banana plants (*Musa* AAA) grown in two soil pH levels (lower than 5.2 and higher than 6.0) and three N (with ammonium nitrate, 33.5%N) doses (N_{low} with no N, N_{med} 0.08 N g plant week^{-1}, and N_{high} 0.25 N g plant week^{-1}) in a greenhouse experiment in the Netherlands

Variable	Soil	Foc Race 1 - Control				Foc TR4 - Control			
	pH	N_{low}	N_{med}	N_{high}	Average	N_{low}	N_{med}	N_{high}	Average
Change in biomass (g plant $^{-1}$)	Low	−34	−10	−32	−82*	−121	−124	−164	−136*
	High	33	−31	−29	9	−161	−187*	−232*	−193*
	Average	−1	21	−31	24	−141	−156	−198	−165
Change in leaf area (cm^2 plant $^{-1}$)	Low	−1008*	−923*	−1293**	−1075**	−1345**	−1142**	−1426**	−1304**
	High	414	72	415	300	−797	−755	−1018*	−857**
	Average	−297	−426	−439	−388	−1071	−949	−1222	−1081

** $P \leq 0.01$; * $P \leq 0.050$

The role of soil properties in crop disease expression differs according to the disease and the soil property. The case of pH and N in Fusarium wilt in banana illustrates the opportunity for soil management to deal with this disease. The relationship of these soil properties in the incidence of the disease by Foc Race 1 in Gros Michel subgroup was confirmed. Besides, it was demonstrated that Cavendish and TR4, the current major threat in banana production, followed similar trends than those found for Gros Michel and Foc Race 1. Since the Cavendish is largely resistant to Foc Race 1, the induced expression of symptoms shows the potential of soil properties in the plant predisposition to the disease. Based on these results and given the current impact of Foc TR4 in banana production, continuing the studies in this discipline appears to be attractive and necessary. Although practices of soil management as liming to increase soil pH and balanced use of N sources (e.g.

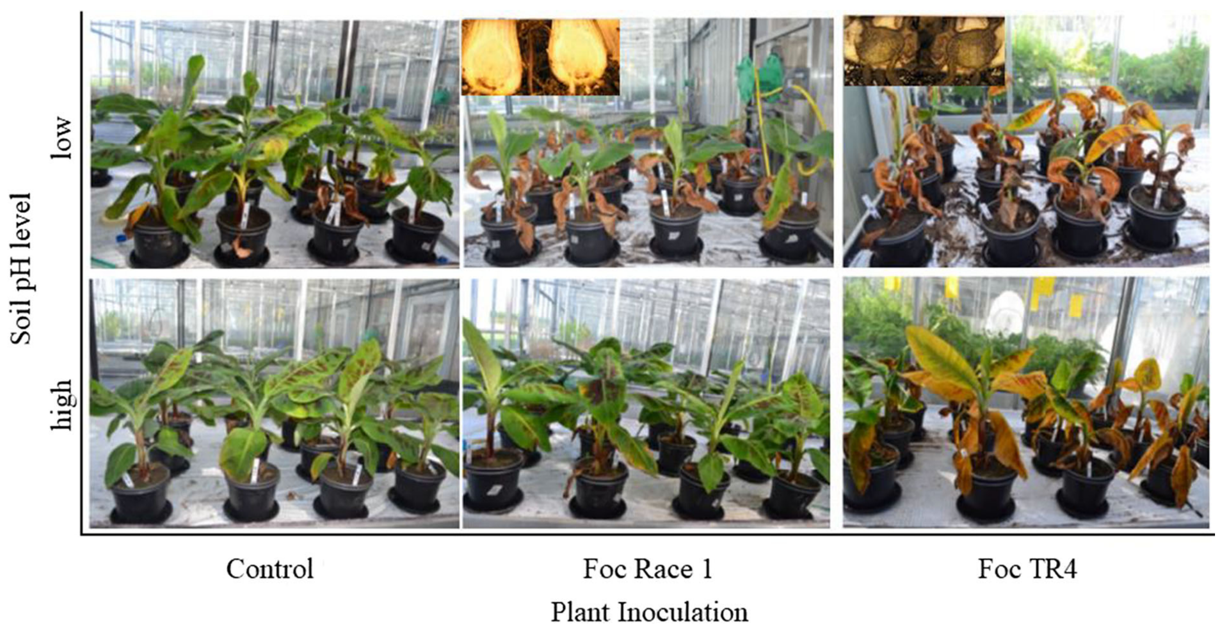

Fig. 5 External and internal Fusarium wilt symptoms by *Fusarium oxysporum* f. sp. *cubense* (Race 1 and TR4) at 33 days after inoculation from Cavendish banana plants (*Musa* AAA) grown in two soil pH levels (lower than 5.2 and higher than 6.0) in a greenhouse experiment in the Netherlands. Segura et al.

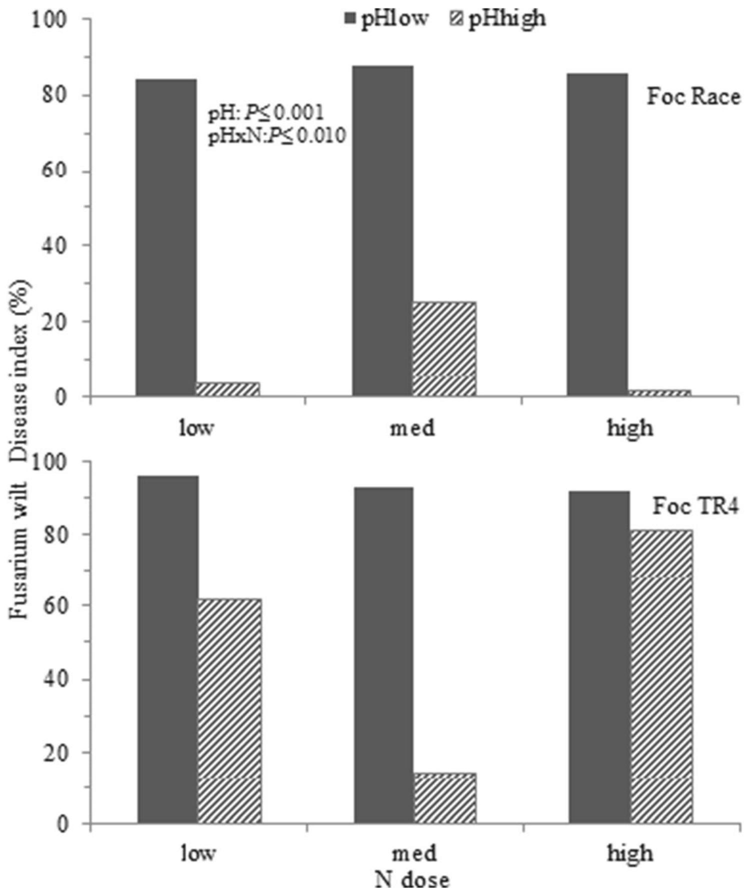

Fig. 6 Disease index of Fusarium wilt by *Fusarium oxysporum* f. sp. *cubense* (Race 1 and TR4) at 33 days after inoculation from Cavendish banana plants (*Musa* AAA) grown in two soil pH levels (lower than 5.2 and higher than 6.0) and three N (with ammonium nitrate, 33.5% N) doses (N_{low} with no N, N_{med} 0.08 N g plant week^{-1}, and N_{high} 0.25 N g plant week^{-1}) in a greenhouse experiment in the Netherlands. Segura et al.

ammonium nitrate as in this case) can be considered as preventing measures to reduce Fusarium wilt in the banana crop, the results need to be confirmed in experiments under field and/or farm conditions.

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Author's contribution All the authors took part in conceptualization of the research and editing the manuscript and consent its publication. RS, JJS and JAS performed the greenhouse experiment in Costa Rica. RS, MS, FG, JJS and GK performed the greenhouse experiment in the Netherlands. RS, JJS and JAS wrote the manuscript which was edited by all authors to obtain the final version.

Declarations

Ethical statement The manuscript is not submitted to another journal. The submitted manuscript is original and it is not published elsewhere in any form or language (partially or in full), and it does not concern an expansion of previous work. The study is not split up into several parts to increase the quantity of submissions and submitted to various journals or to one journal over time. Results are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation. Data was collected from greenhouse experiments and managed with statistical software with total honestly and transparence. No data, text, or theories by others are presented as if they were the author's own. All collected data, and the performed analysis are available. Proper acknowledgements to other works are given. This piece of work respects third parties' rights such as copyright and/or moral rights.

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