Competition between Colletotrichum species reduces anthracnose symptom development in Dioscorea alata yams: Potential for biopriming and breeding

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Competition between *Colletotrichum* species reduces anthracnose symptom development in *Dioscorea alata* yams: Potential for biopriming and breeding

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Abstract

Ecological interactions are a fairly overlooked component in agriculture, despite their known potential in productivity, pest and disease regulation. In this study, we assessed whether a potential low pathogenic congeneric competitor of *Colletotrichum gloeosporioides* could decrease disease onset in yams. We set up an experiment with artificial drop inoculation on detached leaves, with individual controls and treatments as either co-inoculation or inoculation with a harmless competitor 24h prior to inoculating the pathogen. Our results demonstrate that direct admixing translated into accrued competition and disease symptoms, while prior inoculation of the competitor tended to decrease symptom development. There was variation in how varieties responded to treatments and in strain competitive ability altering the protective effect, but nevertheless these results suggest that incorporating such interactions in breeding programmes or working towards increased use of commensals in agriculture might confer improved disease control for crops.

KEYWORDS
anthracnose, *Colletotrichum gloeosporioides*, *Colletotrichum truncatum*, pathogen competition, phyllosphere, water yam

1 | INTRODUCTION

The Green Revolution was foundational to modern agriculture and relied heavily on both genetics and elite cultivars improved for yield, and environmental control of field conditions (till, irrigation, fertilizers and weeds, pathogen and pest control via biocides). While the Green Revolution was a keystone in achieving food security in the face of an increasing global population, it also translated into a diverse array of issues pertaining to environmental degradation and deforestation (Carter et al., 2017), overuse of synthetic chemicals (Schreinemachers & Tipraqsa, 2012), carbon dioxide or greenhouse gas effects (Stavi & Lal, 2013) and negative impacts on both agrodiversity and biodiversity (Dudley & Alexander, 2017). Current trends in agricultural developments are thus focused on mitigating these negative impacts while trying to improve yield and maintain food security.

Avenues of research towards more sustainable agricultural systems are numerous and often revolve around the greatest weaknesses of the Green Revolution: targeting ecological interactions for improved productivity and increased resilience, even at landscape levels (Petit et al., 2020). Indeed, favourable prospects for the use of such interactions are documented throughout the literature (Gaba et al., 2015). They typically involve many levels, from soil-based interactions involving soil microbiota (e.g., Nkongolo & Narendrula-Kotha, 2020), tripartite soil–plant interactions (namely intercropping, e.g., Tilman, 2020) and biomass cycling and increased soil health and fertilization (Espie & Ridgway, 2020). They may also rely on crop diversity as a way to control disease spread

(Boudreau, 2013) and pest populations (Dively et al., 2020), including recourse to parasitoids, specific push–pull strategies aiming to trap pests out of crops (D'Annolfo et al., 2021), and even multiline varietal strategies to contain and slow down diseases within fields (Wuest, Peter, & Niklaus, 2021). As positive interactions within and between components of field diversity emerge as a way to complement or even substitute more conventional approaches, a thorough investigation of multiscale benefits is needed.

An important facet of these interactions deals with microbiota, as specialized microbial communities surrounding plant organs play an important role in crop health (e.g., Cui et al., 2021; Kumar et al., 2021). Crop diseases may result from community disruption if one pathogenic strain thrives, but conversely some communities or species combinations can prevent inoculation and disease onset (Arnold et al., 2003). Tracking beneficial species and the conditions required for these protective effects is an important component in the design of new approaches to disease control and management in agriculture (Vannier et al., 2019), and the potential for disease control is demonstrated (Cui et al., 2021). Community composition or even species complementation have not yet become part of the agriculture toolbox, but might well become an important path towards sustainability.

We thus investigated the potential impact of a congeneric on anthracnose disease development caused by members of the species complex *Colletotrichum gloeosporioides* in yams (*Dioscorea alata*). Anthracnose has become a major constraint on yam productivity in the Caribbean (Sweetmore et al., 1994) ever since epidemics seriously compromised harvest in the 1970s (McDonald et al., 1998). These pathogens are responsible for dramatic losses when they attack plants early and have a significant effect on control practice (Penet, Barthe, et al., 2016) and on varietal diversity in the Antilles, even pushing farmers to choose yam species that are less susceptible (Penet, Cornet, et al., 2016). Breeding programmes have tried to create more resistant varieties (Onyeka et al., 2006) thanks to the availability of a diversified gene pool from diverse landraces (Arnau et al., 2017). Because the species complex is understood as a worldwide set of often ubiquitous pathogens, it is also a threat to yams in many regions (Abang et al., 2006). Studies have shown that local dispersal often plays a significant role in local disease events (Dentika et al., 2022; Penet et al., 2014), in addition to an important genetic variability even at field level (Frézal et al., 2018), possibly due to inocula from local vegetation. Indeed, weeds have proven to be an important reservoir for *Colletotrichum* pathogens, and they contribute to the initiation of local disease (Dentika et al., 2021). Recent findings have emphasized subspecialization of *Colletotrichum* congenerics on weed communities at the local level, and the potential antagonism between species of the *C. gloeosporioides* complex and the *C. truncatum* complex (Dentika et al., 2021). We therefore investigated whether *C. truncatum* inoculation in yams would confer a protective effect against *C. gloeosporioides* species and anthracnose disease development. We thus set up an experiment with different inoculation treatments: simultaneous inoculation versus sequential inoculation (a strain from the *C. truncatum* complex inoculated 24 h prior to a strain from the *C. gloeosporioides* complex) in order to assess whether this translated into reduced development of disease symptoms.

2 | MATERIALS AND METHODS

2.1 | *Colletotrichum* strains

Prior to the experiment, *Colletotrichum* strains were collected *in natura* from diseased leaves of yam (*D. alata*; *N* = 10) (Dentika et al., 2021) and asymptomatic leaves of guava (*Psidium guava*; *N* = 10) from the fields (Dentika et al., 2022). Leaf pieces were surface disinfected with 70% ethanol and disinfectant mix (10% bleach + Tween 20), before three rinsing steps in distilled water (each step lasting about 30 s). Leaf pieces were then deposited on synthetic culture medium (S) and incubated for 2–3 days at room temperature. Once fungi had grown out of the leaf pieces, conidia of *Colletotrichum* fungi were selected under a microscope and monospore assays placed on potato dextrose agar (PDA) and incubated for 2–3 more days. After regrowth, hyphal tips were taken and transferred to new PDA Petri dishes and incubated for 7–10 days at 25°C under a regular 12 h light/dark cycle. *Colletotrichum* strains used in this study were thus sampled from fields and assigned to their corresponding species complex (using a morphospecies approach), based on spore morphology observed under light microscopy. Spore curvature was used as the main criterion for differentiating the two species (von Arx, 1957). Processing species assignation using barcoding methods, as adopted for current identification procedures for *Colletotrichum* species (see Cannon et al., 2012; Weir et al., 2012) is ongoing at the laboratory for our strain collection. Preliminary results demonstrated that local members of *C. gloeosporioides* complex in Guadeloupe segregate similarly among *C. alatae*, *C. siamense* and *C. fructicola* species (authors' unpublished results).

Two independently sampled strains of the species complex *C. gloeosporioides* were thus isolated from different hosts: A15 (guava) and 140 (yam), and one strain of the species complex *C. truncatum* was isolated from yam. Pathogenicity was not further assessed prior to the experiment beyond necrotic symptoms on yams at sampling, and difference in growth on Petri dishes was not initially compared. Strains were further multiplied on PDA and a conidial suspension of 10^7 spores/ml made with distilled water, which was then used for experimental inoculation. Each strain belonging to the *C. gloeosporioides* complex was used pure (no admixing) during the experiment, which allowed testing for specific strain effects.

2.2 | Inoculation experiment

We set up an artificial inoculation experiment on detached yam leaves in small greenhouse boxes in climatic rooms under controlled

WILEY | 3

TABLE 1 Analysis of variance model of disease scores at T9

Factor	Df	Sum of squares	Mean squares	F	Pr(>F)
Variety	1	31.9	31.93	27.448	2.4e−07***
Strain	1	19.9	19.90	17.109	4.2e−05***
Treatment	3	82.2	27.42	23.568	3.2e−14***
Variety×Strain	1	0.3	0.31	0.265	0.607
Variety×Treatment	3	27.1	9.03	7.761	4.6e−05***
Strain×Treatment	3	21.4	7.13	6.133	4.3e−04***
Variety×Strain×Treatment	3	2.8	0.95	0.813	0.487
Residuals	464	539.8	1.16		

$***p < 0.001.$

FIGURE 1 General effect of different treatments on anthracnose disease score in yam over time. Cg, inoculation of strain from *Colletotrichum gloeosporioides* complex; Ct, inoculation of strain from *C. truncatum* complex; Mix 0, inoculation of initial admixture; Mix 24, sequential inoculation (strain from *C. truncatum* complex inoculated 24 h prior to strain from *C. gloeosporioides* complex). The effect is averaged for the two *C. gloeosporioides* strains. $****p < 0.0001$, $*p < 0.05$. Dots represent experimental values occurring outside confidence interval.
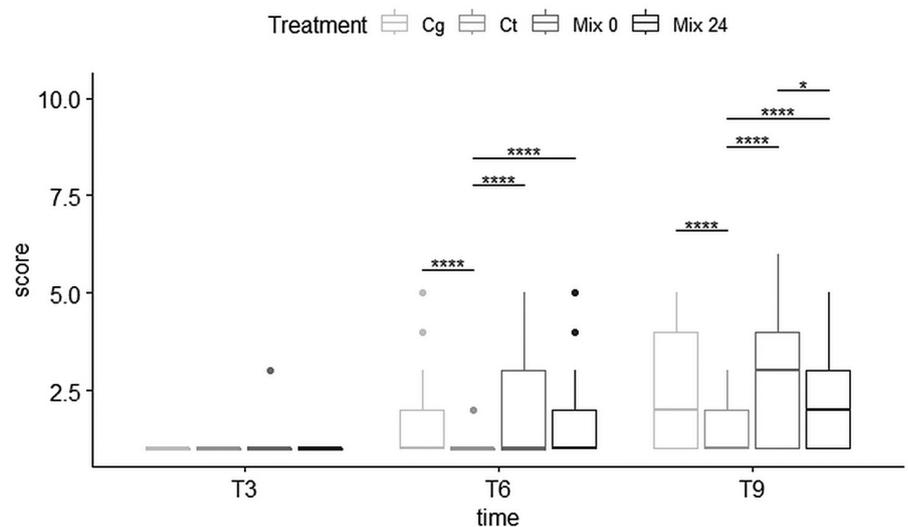
temperature and humidity conditions (at constant 25°C, saturated humidity levels and a 16-h photoperiod under Osram T8 L 36 W/865 Lumilux Daylight G13 neons). Leaves were sampled from healthy plants grown in an insect-proof collection greenhouse at INRAE, from resistant (Goana) and anthracnose-sensitive (Pyramide) varieties. Prior to inoculation, experimental leaves were surface disinfected in 2% sodium hypochlorite for 40 s and left to dry. Inoculations consisted of depositing three drops of 10 μl conidial suspension on a leaf. Three inoculation replicates were carried out on each experimental leaf at a minimal distance of 5 cm on the adaxial side of the leaf. Four inoculation treatments were used: inoculation with a strain from the *C. truncatum* complex only (Ct, nonpathogenic control), inoculation with a strain from the *C. gloeosporioides* complex only (Cg, pathogenic control), both strains from complexes of *C. gloeosporioides* and *C. truncatum* simultaneously (Mix 0), and both strains from complexes of *C. gloeosporioides* and *C. truncatum* with the latter inoculated 24 h prior to the first (Mix 24), each on a leaf, with a replication for each treatment (eight experimental leaves by variety, i.e., 16 experimental leaves by run for each of the 10 independent runs). Experimental leaves were then set naturally flat on large open Petri dishes (14 cm in diameter) on a grid plate with the stem immersed in water, and developing symptom severity was assessed every 3 days (T3, T6 and T9, after 3, 6 and 9 days, respectively). The scale used for symptom severity development was as follows: 0 = lack of any

symptom; 1 = light colour change; 2 = small individual necrotic infection (pin-sized) points; 3 = external mycelial growth or bigger infection points; 4 = light coalescence of necrotic points; 5 = full or nearly full necrotic coalescence; 6 = full necrosis expanding beyond initial inoculation area.

2.3 | Statistical analysis

We first conducted an analysis of variance (ANOVA) of disease score at T9 with variety, strain and treatment as dependent factors and full interactions. We then conducted a general one-way repeated measure ANOVA on symptom score with treatment as a random factor to evaluate effect of time on development of symptoms. We then assessed the effects of varieties (Goana, resistant variety; and Pyramide, susceptible variety) and the effects of strains from *C. gloeosporioides* complex (A15, strain from guava; and 140, strain from yam) by subsetting datasets and reconducting the repeated measure ANOVAs. Sample size was 480 total for each disease score (T3, T6 and T9): 2 varieties × 2 *C. gloeosporioides* complex strains × 4 treatments × 3 replicates over 10 independent runs. Results were consistent between runs (data not shown). Subset data thus had sample sizes of 240 each. QQ plots did not show departure from normal distribution, except scores for T3 (and T6 specifically for

strains from the *C. truncatum* complex) which were consistently lacking any symptoms (i.e., mostly zeros). However, because this was an initial scoring constraint, we proceeded with the analysis. Intra-individual comparisons were subjected to Bonferroni correction to avoid a surge of false positives. All analyses were run with R (R Core Team, 2021).

3 | RESULTS

All factors demonstrated significant effects on disease scores in the ANOVA (Table 1): the resistant variety had lower scores than the susceptible variety, strains differed in the symptoms they produced (the strain isolated from yam was more aggressive on yam compared to the strain isolated from guava). There were significant interactions between terms for variety × treatment and strain × treatment, and these were subject to further analyses. The only interactions that were not significant were variety × strain and the triple interaction variety × strain × treatment (Table 1).

Treatments resulted in greater disease scores over time and were mostly different from each other (Figure 1), with a few exceptions. This result was robust with data subsets and in subsequent analyses, except for the effect of the *Colletotrichum* admixture

(see below). In general, the Ct treatment had low disease scores, as the *C. truncatum* species complex is known as being not very pathogenic on yams, while the Cg treatment conformed to a pathogenic fungus producing disease on yams. The effect of the admixture treatment differed at different times. Overall, initial admixing resulted in an increasing disease score over time, with a greater variance in symptoms compared to Cg alone at T6 (although the difference was not significant), and a score at T9 greater than for Cg alone (Figure 1). This pattern was also significant for the different varieties (Figure 2a,b) with only a difference in mean score. It was also similar for the yam strain (Figure 3a), but not for the strain isolated from guava (Figure 3b), where initial admixing did not create a competitive effect resulting in more severe symptoms (on the contrary, it was sequential inoculation that produced symptom aggravation, see below). Overall, sequential inoculation (strain from *C. truncatum* complex inoculated 24h before strain from *C. gloeosporioides* complex) resulted in disease scores lower than Cg alone (Figure 1). This pattern held for the resistant variety (Goana, Figure 2a), though not for the susceptible variety (Pyramide, Figure 2b), where the disease score was greater at T6 and slightly lower at T9 compared to Cg alone. This pattern was similar when focusing on strains, with sequential inoculation demonstrating a silencing effect on disease with the strain originating from yam
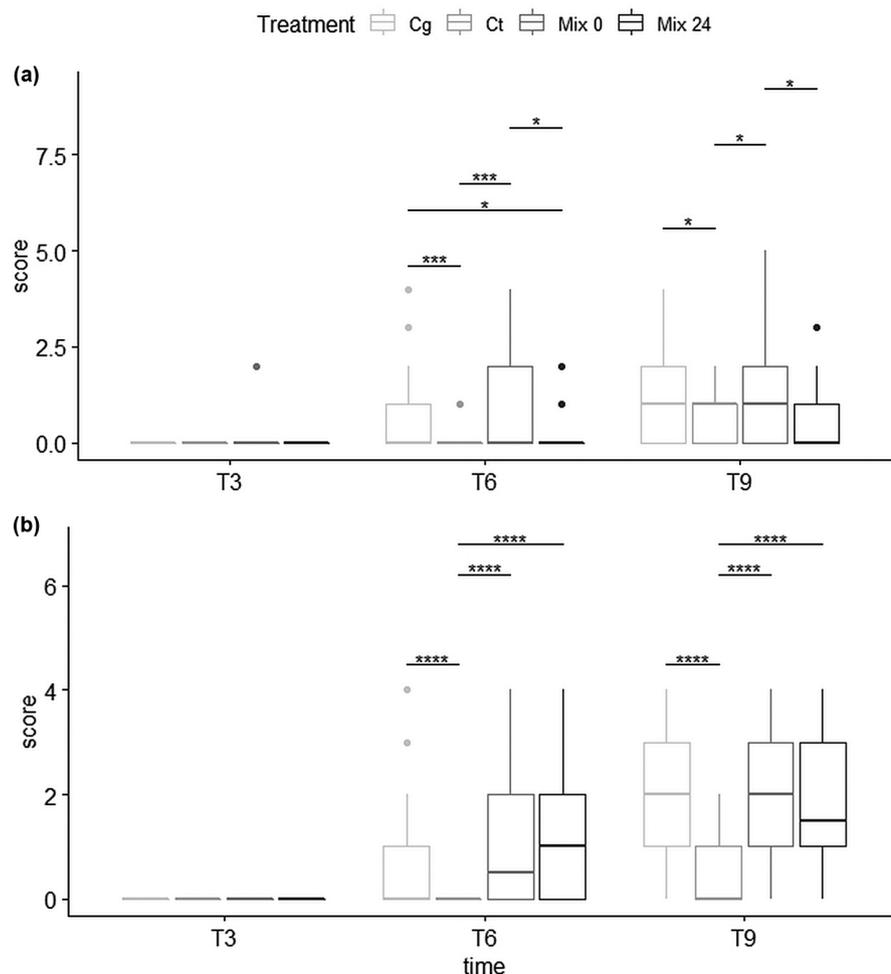

FIGURE 2 Varietal differences of treatments on anthracnose disease score over time in resistant yam variety Goana (a) and susceptible variety Pyramide (b). Cg, inoculation of strain from *Colletotrichum gloeosporioides* complex; Ct, inoculation of strain from *C. truncatum* complex; Mix 0, inoculation of initial admixture; Mix 24, sequential inoculation (strain from *C. truncatum* complex inoculated 24h prior to strain from *C. gloeosporioides* complex). The effect is averaged for the two *C. gloeosporioides* strains. ****$p<0.0001$, ***$p<0.001$, *$p<0.05$. Dots represent experimental values occurring outside confidence interval.

FIGURE 3 Strain differences of treatments on anthracnose disease score over time with yam strain (strain 140) (a) and guava strain (strain A 15) (b). Cg, inoculation of strain from *Colletotrichum gloeosporioides* complex; Ct, inoculation of strain from *C. truncatum* complex; Mix 0, inoculation of initial admixture; Mix 24, sequential inoculation (strain from *C. truncatum* complex inoculated 24 h prior to strain from *C. gloeosporioides* complex). Significance scales is as follows: ****$p < 0.0001$, ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$. Dots represent experimental values occurring outside confidence interval.
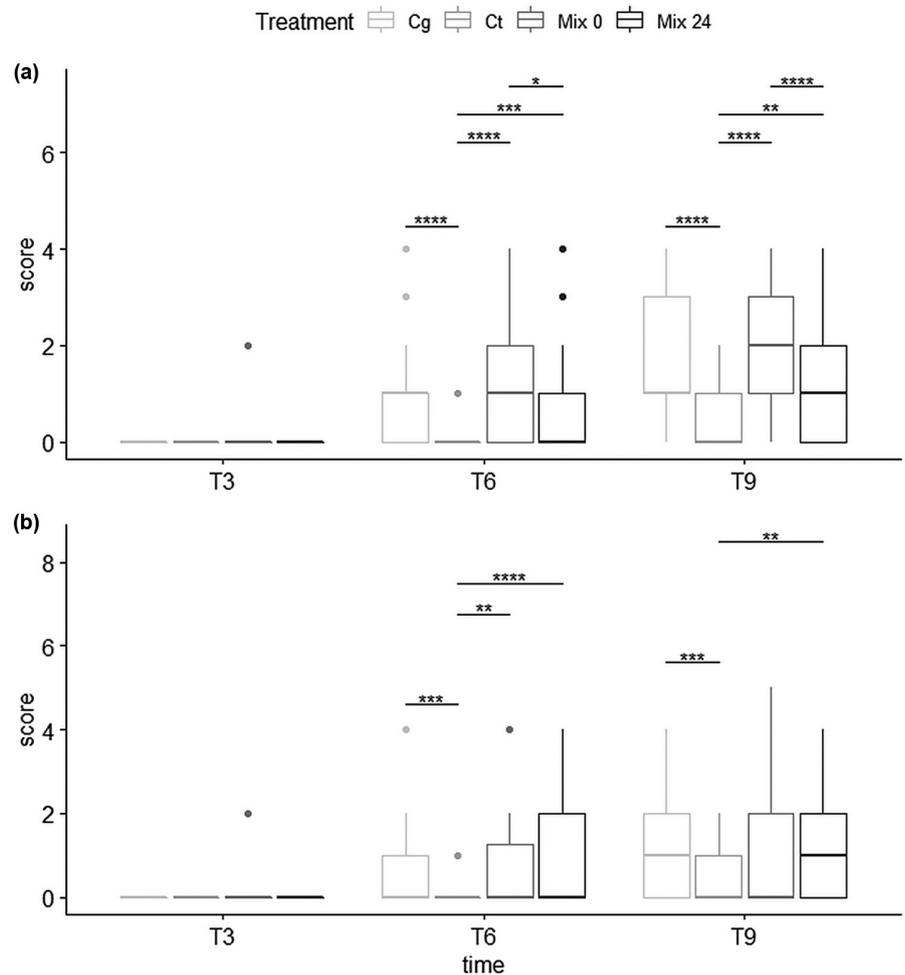
(Figure 3a), while demonstrating an exacerbating effect with the strain originating from guava (Figure 3b).

4 | DISCUSSION

We found that overall disease symptoms increased over time after inoculation, and initial admixing with a strain from the *C. truncatum* complex made disease symptoms worse than a strain from the *C. gloeosporioides* complex alone over time, while prior inoculation with a strain from the *C. truncatum* complex before a strain from the *C. gloeosporioides* complex resulted in alleviated symptoms. This effect was nevertheless dependent on both varietal resistance and the strain from *C. gloeosporioides*, with the exacerbating effect mostly found in the susceptible variety and for the yam strain, while for the guava strain sequential inoculation resulted in more disease symptoms at T6 and similar disease levels at T9. We will discuss these results in the light of current and potential disease control strategies.

Timing of infection may be crucial to disease development in the presence of interspecific competitors and competition increases symptom development (Dutt et al., 2021). Indeed, the difference between the two treatments, initial admixing versus sequential inoculation, demonstrates that competition can accelerate disease

appearance and symptom severity to a greater extent than if pathogens were infecting hosts in isolation from each other. While this effect has been known for some time (Tollenaere et al., 2016), few management strategies take it into account; for example, disease monitoring is often undergone separately for pathogen species. Our results demonstrated that varietal diversity can show disease mitigation by biopriming at the same level as general resistance, and breeding with such target criteria might prove efficient as a tool for controlling disease spread. Our results also illustrated that the process is subject to strain specificity, as it worked well in one case but did not seem to provide complete benefit in the second case. As a consequence, it is worthwhile remembering that many plant–pathogen interactions are occurring as arms races, sometimes even as diversifying strategies within species (e.g., Dutt et al., 2020), and the approach might translate into selecting for strains that have higher aggressiveness and competitive skills at the inoculation stage.

Prior inoculation with nonpathogenic or low-pathogenic competitors can reduce disease levels and delay symptom development from more aggressive pathogens. This has already been observed (Berg et al., 2014), although we are only beginning to tackle the gargantuan task of identifying commensal interaction sets that might prove efficient in crop disease control in diversified agricultural systems. Our results produced evidence that commensal

protection worked particularly well for the resistant variety yet was nearly insignificant for the susceptible variety, whose disease scores were either increased (T6) or were similar to actual pathogenic scores (T9). On the other hand, strain variation was fairly limited in our experiment, although symptoms were aggravated at T6 for the strain originating from guava, suggesting the protective effect might open the door to potential host jump and increased aggressiveness similar to the risk of co-inoculation events (see above, e.g. Brown et al., 2002).

In summary, interactions between conspecifics may promote competitive effects and translate into higher aggressiveness in the case of co-infection events, while it may hinder disease development when a nonpathogenic competitor is inoculated before the pathogen lands on the plant. Varietal effects are expected and are described in this study, furthering the idea that integrating multi-interaction phenotypes as a feature target in future breeding schemes might potentially provide increased efficiency for disease control in next-generation resistant varieties. On the other hand, strain variability also provided evidence that integrating competitors in cropping and breeding schemes may possibly result in the emergence of variants with increased aggressiveness—a long-standing issue in agriculture anyway.

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DATA AVAILABILITY STATEMENT

Data are available from the corresponding author on request.

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WILEY 7

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