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ORIGINAL ARTICLE

Endophyte *Chaetomium globosum* improves the growth of maize plants and induces their resistance to late wilt disease

Ibrahim E. Elshahawy[1] · **Abd El-Nasser A. Khattab**[2]

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Abstract

Late wilt is a soil-borne disease caused by *Cephalosporium maydis* that severely limits maize production. In this study, endophytic *Chaetomium* isolates were screened for their abilities to control *C. maydis* on agar plates. In a dual culture test, *Chaetomium* spp. isolate Ch-1 inhibited 91.0% mycelial growth of *C. maydis*. The pathogen's mycelial growth and conidial germination were also inhibited by its crude extracts. This isolate was identified as *C. globosum* (Chg-1) based on sequencing of the internal transcribed spacer regions of the rRNA gene. There are three Chg-1 application methods viz. grain treatment GT, soil application SA either individually or in combination GT + SA and two maize cultivars viz. landraces and fine seed 1005 were applied in pots and field plot experiments in controlling late wilt disease. In pots, Chg-1 treatments significantly reduced late wilt disease incidence and increased plant growth of the two maize cultivars, with a high efficacy for GT + SA compared to the positive control. Despite minor differences, treatments GT and SA provided adequate protection against late wilt. After 90 days of cultivation, the endophyte Chg-1 was re-isolated from the internodes of treated maize plants without causing any symptoms. This endophytic fungus reduced late wilt incidence in pots not only directly by antagonizing the pathogen, but also indirectly by inducing resistance mechanisms in maize plants. The induction of antioxidant enzymes (including peroxidase and polyphenoloxidase), chitinase, chlorophyll content, total phenols, and flavonoids was responsible for the indirect effects of Chg-1 against the pathogen. In the field, the endophyte not only reduced late wilt symptoms but also increased ear yield on both maize cultivars when compared to the untreated control. A combination of soil application and grain treatment with Chg-1 (GT + SA) outperformed any of these treatments individually in terms of reducing late wilt incidence and increasing grain yield in maize.

Keywords Late wilt · *Cephalosporium maydis* · *Chaetomium globosum* · Endophyte · Maize plants

Introduction

Maize (*Zea mays* L.) is a crop that is grown all over the world. Various diseases are common during maize growth, resulting in yield loss and quality decline. The most common and dangerous of these is late wilt or black bundle disease. This vascular wilt disease of *Zea mays* (corn, maize) is caused by the soil-borne and seed-borne fungus *Cephalosporium maydis* Samra, Sabet, and Hingorani (Samra et al. 1963). It has been reported in Egypt (Samra et al. 1962). In Egypt, a highly significant positive correlation was found between late wilt incidence and grain yield losses (El-Assiuty et al. 1999; Elshahawy and El-Sayed 2018; Elshahawy and Abd El-Wahed 2022). The fungus reproduces asexually, and the disease causes relatively rapid wilting of maize plants, usually before tasseling and until just before maturity (Zeller et al. 2002). The first symptoms of wilting appear about 60 days after sowing, and it lasts until just before maturity (Degani 2021). It progressed steadily from the lower to the upper leaves, first turning the leaf tissues between the veins a pale green color, then rolling the entire leaf inward lengthwise (Sabet et al. 1970). Yellowish or reddish-brown streaks appeared on the stalk's basal internodes as the leaf wilting progressed, drying up and shrinking. When the stalk was split, a brown discoloration ran along the internodes. Fewer ears develop, and those that do

✉ Ibrahim E. Elshahawy
ibrahim_nrc@yahoo.com

[1] Plant Pathology Department, Agricultural and Biology Research Institute, National Research Centre, Cairo 12622, Egypt

[2] Genetics and Cytology Department, Biotechnology Research Institute, National Research Centre, Cairo 12622, Egypt

develop poorly and may become infected with the pathogen (Drori et al. 2012). The number of seeds is inversely proportional to the severity of the disease. *C. maydis*, a fungus, was isolated from maize plants as well as soil. The fungus was generally a soil-borne pathogen, but it could be isolated from dead plant seeds in some cases, implying that it could also be seed-borne (Drori et al. 2012). Currently, the primary control option for this disease is synthetic fungicides with acceptable antifungal activity against *C. maydis* (Degani et al. 2018). Pesticide residues are frequently produced by chemical-based control measures, which disrupt the balance of soil microbes and have negative effects on both the environment and human health (Satapute et al. 2019). The use of beneficial microorganisms for plant disease control not only improves agricultural yield and quality, but also reduces the use of chemical pesticides and ensures food and environmental safety; thus, the use of beneficial microorganisms is an environmentally friendly technology for sustainable agricultural development (Bonanomi et al. 2018). As a result, new alternative disease control methods based on sustainable agriculture principles are required (Elshahawy et al. 2018a; Degani 2022; Mohamed and Elshahawy 2022).

Endophytic fungi are microorganisms that live within the tissues of host plants without causing any visible symptoms of infection (Petrini et al. 1992). Endophytes have been shown in various studies to stimulate plant growth, increase disease resistance, improve plant resistance to environmental stresses, and recycle nutrients (Latz et al. 2018; Madbouly et al 2020). *Chaetomium*, a strictly saprophytic fungus in the *Ascomycota* family *Chaetomiaceae*, is one of the most diverse saprophytic ascomycete genera, with over 350 species worldwide (Zhang et al. 2012). *Chaetomium globosum* (Kunze ex Fr.) has been isolated from soil and organic compost, as well as living plant tissues as an endophyte (Soytong et al. 2001). It has been recovered as an endophyte from a variety of gymnosperms, dicots, and monocots, including *Ginkgo biloba* (Li et al. 2014), *Vitis vinifera* (Longoni et al. 2012), and *Oryza sativa* (Naik et al. 2009). Some *Chaetomium* species have been shown to be antagonists to a variety of plant pathogens (Charoenporn et al. 2010; Sibounnavong et al. 2012). Among these, *C. globosum* has been identified as a promising endophytic biocontrol agent (Abou Alhamed and Shebany 2012; Zhao et al. 2017). Hung et al. (2015a) demonstrated the in vitro and in vivo effects of *C. globosum*, *C. lucknowense*, *C. cupreum*, and their crude extracts as biological control agents against the citrus root rot pathogen *Phytophthora nicotianae*. Pan et al. (2016) discovered that the endophytic *C. globosum* has potent antifungal activity against the phytopathogen *Botrytis cinerea*. Fierro-Cruz et al. (2017) discovered that the endophyte *C. globosum* significantly inhibited the growth of *Fusarium oxysporum*. According to Huang et al. (2020), endophytic *Chaetomium* strains had good suppressive effects on cucumber *Rhizoctonia* root rot. Arunkumar et al. (2022) reported that, among 40 fungal isolates tested in vitro, *C. globosum* Cg-6 exhibited maximum inhibition potential against *R. solani*, the causal agent of black scurf disease in potatoes. However, research on the use of maize endophytic fungi for late wilt disease control is still limited. The objectives of this study were to characterize the fungal endophytic community of *Chaetomium globosum* isolates associated with *Zea mays* plants and to test their ability to protect maize plants from infection with *Cephalosporium maydis*, the pathogen that causes late wilt disease.

Materials and methods

Maize cultivars

The current study used the susceptible cultivar Landraces from the Crops Department, Agricultural and Biology Institute, National Research Centre, and the moderately resistant cultivar Fine seed 1005 from Fine Seeds International Company, Giza, Egypt. Maize grains were thoroughly cleansed (to remove any remaining pesticide coatings) by rinsing them in water and immersing them in a large amount of sterilized distilled water for 16 h while constantly stirring. Maize grains were surface sterilized by immersing them in a 2% NaOCl solution for 2 min, followed by a 2 min soak in 70% ethanol. After that, the seeds were rinsed four times with sterilized water.

Late wilt pathogen

In this study, Cm3, a virulent isolate of *Cephalosporium maydis*, was chosen and used. This isolate was previously isolated from wilting maize plants collected during the 2018 growing season in a maize field in Gharbia Governorate, Egypt (Elshahawy and El-Sayed 2018). The isolate was grown in complete darkness on PDYA at 28 ± 2 °C. A 1000 ml Erlenmeyer flask containing 200 g of wet autoclaved sterile sorghum grain was filled with 10 colony agar disks (5 mm diameter each) taken from the margins of a 7 days old colony to make inocula. Cultures were grown in an incubator at 28 ± 2 °C in the dark for 4 weeks. The inoculum was then harvested and homogenized.

In vitro trails

Isolation of fungal endophytes from maize plants

The Naik et al. (2009) procedure was used to isolate endophytic fungi from healthy maize plants. During the 2020 growing season, scattered healthy maize plant samples (cv. Fine seed 2005) were collected from field-grown plants in

Gharbia Governorate, Egypt, at 90 days of age (tasseling stage). The affected fields in this region had high late wilt incidences and symptoms, affecting approximately 30% of the hybrid varieties. Endophytic fungi were isolated from maize plant samples within 24 h of collection. Each maize plant's first and second internodes above ground were cleaned under running water and cut into 1 cm segments. Washing with 70% ethanol for 2 min, a sodium hypochlorite solution (2% available chlorine) for 5 min, and 70% ethanol for 30 s, followed by two rinses in sterile distilled water, was used to sterilize the surface. Internode segments were placed on 9 cm Petri plates containing potato dextrose agar (PDA) medium supplemented with streptomycin (250 mg/L) to slow bacterial growth. To test the efficacy of the surface sterilization procedure and to confirm endophytic isolations only from internal plant tissues, sterilized filter paper segments were pressed on the surface of PDA medium. The absence of fungi growth on the medium demonstrated that the surface sterilization procedure was effective at removing surface fungi (Schulz et al. 1993). Petri plates were incubated in an incubator at 28 ± 2 °C for 10 days. Fungi derived from plant tissues were transferred to new PDA medium. The final pure cultures were transferred to PDA slants in test tubes after several rounds of purification. Based on morphological characteristics such as terminal hair type and lateral hairs covering ascomata, as well as structural characteristics of the perithecia, asci, and ascospores, three endophytic isolates were identified as *Chaetomium* (Seth 1973). Endophytic *Chaetomium* isolates were labeled with the letters Ch-1, Ch-2, and Ch-3.

Screening for antifungal activity of fungal endophytes against C. maydis

Using the dual culture technique described by Huu Phong et al. (2016) the obtained endophytic fungi, *Chaetomium* spp. (Ch-1, Ch-2, and Ch-3) were tested for their ability to inhibit *C. maydis*. PDAY, a potato dextrose agar medium with 0.2% yeast extract, was chosen for dual culture because it promotes the growth of *C. maydis*. A mycelial disk (5 mm in diameter) of *C. maydis* was placed singly (as controls) or oppositely to the mycelia disk of each of the above-mentioned endophytic fungi in Petri dishes (9 cm in diameter) containing PDAY. The experiment was conducted in a completely randomized design (CRD) with four replications, with the incubation temperature set at 28 ± 2 °C. Data on the pathogen's average growth area (cm^2) in dual culture plates and the control were collected after 10 days of incubation. *C. maydis* mycelial growth inhibition was calculated as follows: Inhibition (%) = [(Growth area of the pathogen in the control plate—Growth area of the pathogen in the dual culture plate) × 100]/Growth area of the pathogen in the control plate.

Molecular identification of the fungal endophyte

The most antagonistic isolate in the antagonistic test bioassay using dual culture technique, *Chaetomium* spp. isolate Ch-1, was grown for 10 days on potato dextrose broth (PDB) medium at 28 ± 2 °C. Following the incubation period, the fungal mycelium was harvested and dried on absorbent paper. Fresh mycelium (100 mg) from a Ch-1 isolate was powdered using liquid nitrogen. The DNA was extracted according to the manufacturer's instructions using the i-genomic BYF DNA extraction Mini Kit (iNtRON Biotechnology Inc., South Korea). For rDNA ITS region amplification, the forward primer ITS1 (5′TCCGTAGGT GAACCTGCGG-3′) and reverse primer ITS4 (5′ TCCTCC GCTTATTGATATGC-3′) were designed and used (White et al. 1990; Morsy and Elshahawy 2016). All primers were supplied by the Operon Technologies Company in the Netherlands. The final 50 µl reaction mixture contained1 × PCR buffer (NEB, England), 1 nmol of dNTPs,1 pmol of 2 mM $MgSO_4$, 0.25 pmol of forward and reverse primers, 1 unit Taq DNA polymerase (NEB, England), and 10 µl template DNA (White et al. 1990). The PCR program started with a 2 min denaturation at 94 °C, then 35 cycles of denaturation at 95 °C for 30 s, annealing at 56 °C for 30 s, elongation at 72 °C for 60 s, and final extension at 72 °C for 10 min. The amplified products were separated on 1% agarose gels in 1X TBE (Tris–borate–EDTA) buffer at a constant 100 V for about 2 h. The sizes of the bands were determined by comparing them to a 100 bp ladder (iNtRON Biotechnology Inc., South Korea), and the separated bands were stained with 0.5 g/ml^{-1}ethidium bromide and photographed with the Gel Documentation System with UV Transilluminator. The PCR product was purified using the GeneJETTM PCR Purification Kit (Thermo K0701). The purified PCR product was sequenced using a forward primer on an ABI 3730xl DNA sequencer (GATC Company, Germany). The fungal isolate's DNA sequence was compared to sequences in the NCBI GenBank database using the Basic Local Alignment Search Tool (BLAST) (http://www.ncbi.nlm.nih.gov). The sequence was compared to reference taxa found in public databases. The parameter model was used to calculate the evolutionary distance, and the phylogenetic tree was constructed using the neighbor-joining method (Saitou and Nei 1987).

Antifungal activity of the endophyte crude extract

Because it has a high antagonistic property against *C. maydis*, the endophytic fungus Chg-1 was chosen. Autoclaved PDB medium was used in a 250 ml conical flask. Four flasks of PDB medium were inoculated with Chg-1 and incubated for 4 weeks at 28 ± 2 °C before collecting fresh fungal biomass, which was then dried to obtain dried fungal biomass. The Huu Phong et al. (2016) procedure was used to extract

and evaluate the crude extraction of dried fungal biomass. The dried biomass was first ground and extracted with hexane (1:1 v/v), then shaken for 72 h at room temperature. The filtrate was then collected, and the marc was separated by filtration through filter paper (Whatman No. 4), before being subjected to a rotary vacuum evaporator to yield hexane crude extract. Using the same procedure as described above, the marc from the hexane extraction was extracted with ethyl acetate (EtOAc) and then with methanol (MeOH), yielding EtOAc and MeOH crude extracts, respectively. Bioactivity against *C. maydis* mycelial growth and conidial germination was determined using crude extracts. The crude extract (30 mg) was dissolved in 800 µl of dimethyl sulfoxide at a concentration of 2%. Partitions of this solution were added to molten PDAY (after autoclaving at 121 °C for 20 min) to achieve the desired concentrations of 0 (control), 125, 250, 500, and 1000 µg/ml for the mycelial growth assay. After pouring crude extract-adjusted media into three plates, *C. maydis* was inoculated at the center of the plate, and radial growth and percent growth inhibition were measured until the control plate reached full growth. For the spore germination assay, *C. maydis* conidia were suspended in 2% PDBY containing the desired concentrations of each crude extract. As a control, spores suspended in 2% PDBY without crude extract were used. Following careful mixing, 0.2 ml of each treatment was pipetted onto sterile glass microscope slides, and the suspension was kept within a rectangle drawn with liquid paraffin wax on the slides. In moist Petri dishes, the prepared slides were incubated for 18 h at 28 ± 2 °C. Following that, direct counts were performed using microscopy to determine the rate of germination. All experiments were conducted in triplicate. In a completely randomized design CRD, the experiment was set up as a two-factor factorial design with three replications. The three crude extracts listed above represented Factor A. The following concentrations 0, 125, 250, 500, and 1000 µg/ml were used and represented Factor B. To calculate inhibition (%) in radial growth and/or spore germination, we used the following formula: $I = C - T/C \times 100$, Where C represents *C. maydis*'s radial diameter or conidial germination in the control and T represents *C. maydis*'s radial diameter or conidial germination in the crude extract treatment.

Manufacture and application of Chg-1

The isolate of Chg-1 was used to create the following liquid and solid formulations:

Grain treatment (GT)

In pots and field trials, the effects of Chg-1 were studied using a grain treatment. Chg-1 was grown in 90 mm Petri dishes on PDA medium at 28 ± 2 °C in the dark. When the fungal spores had reached maturity, they were harvested by filling the dishes with sterile water containing 0.05% Tween 80 and scraping the plate with a sterile razor blade. Autoclaved cheesecloth was used to filter the spores. For grain treatment, a hemacytometer (Thomas Scientific, Philadelphia, PA, USA) was used to measure spore concentration, which was set at 10^7 spores ml^{-1}. Surface-sterilized maize grains were immersed in spore suspensions (10^7 spores ml^{-1}, approximately 100 grains 500 ml^{-1}) overnight. Grain for the control treatment was treated with an equal volume of sterile water under the same conditions.

Soil application (SA)

The effects of Chg-1 in pots and field trials were studied using a soil application. Chg-1 mass multiplications were carried out on a wheat bran-cottonseed preparation [Glucose (20 g); KH_2PO_4 (3 g); and $MgSO_4$7H2O (1.5 g); dissolved in 1 L deionized water, which was then blended with 250 g wheat bran and 250 g cottonseed shell] according to standard procedure (Zhai et al. 2018). This preparation was sterilized before being used as a medium for endophyte Chg-1 culture in a dark environment. The number of Chg-1 spores was determined to be 2×10^9/g after 4 weeks of culture using the hemocytometry method, and the preparation was then used as a soil treatment. One week before sowing, Chg-1 preparation was applied to *C. maydis* infested soil in pot trials (at a rate of 1% *w/w*). According to Elshahawy et al. (2018b), a powder preparation of Chg-1 was added to the soil in field trials 1 week before sowing (at a rate of 300 g powder preparation/m length of the row).

Greenhouse trails

Preparation of pots

A pot study was carried out in an open greenhouse at the Plant Pathology Department, National Research Centre, Giza, Egypt, during the summer of 2021. The minimum and maximum temperatures during the experiment were 20–30 °C and 32–40 °C, respectively. The experiment was carried out in 30 cm diameter plastic pots filled with 5 kg autoclaved clay sandy loam soil with a pH of 7.32, 137.2 ppm available nitrogen (N), 23.6 ppm available phosphors (P), and 312.5 ppm available potassium (K). The pots were sterilized before filling by soaking them in a 7% formaldehyde solution for 10 min and then aerating them for 10 days. Except for the negative control treatment pots, inocula of *C. maydis* prepared on sorghum grains was thoroughly mixed in the soil of all pots (30 g fungal inoculum per kg soil). The pots were watered and left for a week to allow the inoculum to establish. Five grains of each cultivar were sown in each pot (experimental unit) on 14/8/2021,

and plants were thinned to two plants per pot 7 days after germination. Before sowing, 11 g of phosphate rock (P_2O_5) was added per pot, and 5.5 g of ammonium nitrate was added per pot. Ammonium nitrate fertilizer was applied at rates of 5.5 g pot^{-1} at 20, 30, and 40 days after sowing, and plants were irrigated as needed.

Experimental design

A two-factor factorial experiment in Randomized Complete Block Design (RCBD) with six replications was used. Two maize cultivars and five Chg-1 treatments in the factorial treatment combination were used. The cultivars used were Landraces, a susceptible cultivar, and Fine seed 1005, a relatively resistant cultivar. The Chg-1 treatments were: grain treatment (GT), soil application (SA), grain treatment and soil application integration (GT + SA), negative control (non-treated grains sowing in non-infested and non-treated soil) (NC), and positive control (non-treated grains sowing in infested soil) (PC). There are two distinct experiments. The first experiment was carried out 25 days after planting in order to assess the effects of Chg-1 treatment on maize plant physiological traits and growth promotion. The second experiment was conducted 90 days after planting to assess the effects of Chg-1 treatment on late wilt disease incidence.

Experiment I: effects on physiological traits and growth promotion of maize plant

The following five treatments, each with six replications for each cultivar, were set up to investigate the effect of Chg-1 application on physiological traits and growth promotion of landraces and fine seed 1005 cultivars:

NC, Negative control.
PC, Positive control [*Cephalosporium maydis*].
GT, Grain treatment with Chg-1 + *C. maydis.*
SA, Soil application withChg-1 + *C. maydis.*
GT + *SA*, Grain treatment + soil application with Chg-1 + *C. maydis.*

Several physiological tests were conducted on fresh maize plant leaves 25 days after sowing. Pre-existing procedures were used to determine chlorophyll content, total phenols content, total flavonoids content, peroxidase activity, polyphenoloxidase activity, and chitinase activity. Total chlorophyll was calculated using Königer and Winter's method (Königer and Winter 1993). The pigment content was expressed in mg g^{-1} fresh weight of leaves. According to Chandra et al. (2014), total phenols and flavonoids were also determined and expressed as mg g^{-1}dry weight of leaves. Maize leaf samples (g) were homogenized with 0.2 M Tris–HCl buffer (pH 7.8) at 0 °C containing 14 m-M-mercaptoethanol at a rate of 1/3 w/v to extract the enzymes. Peroxidase activity was measured using guaiacol as the hydrogen donor and expressed as an increase in absorbance at 470 nm/g fresh weight/minute, as described by Bashan et al. (1985). Polyphenoloxidase activity was measured by measuring the rate of quinine formation after oxidizing 3,4-dihydroxyphenylalanine (DOPA), and this activity was expressed as the increase in absorbance at 475 nm/g fresh weight/minute, as described by Bashan et al. (1985). As described by Monreal and Reese (1969), chitinase activity was measured using colloidal chitin as a substrate and dinitrosalicylic acid (DNS) as a reagent to measure reducing sugars. At 540 nm, chitinase activity was measured as mM N-acetylglucose amine equivalent released/gram fresh weight/60 min. The maize plants were harvested after 25 days by mulching them from their pots. Vegetative growth of maize plants viz, plant height (cm $plant^{-1}$) and fresh weight (g $plant^{-1}$) were measured. The harvested plants were dried at 70 °C until they reached a constant weight, and the dry weight per plant was recorded.

Experiment II: Effects on late wilt and internodes colonization by Chg-1

The five treatments as mentioned above, with six replications of each treatment for each cultivar, were set up to investigate the effect of Chg-1 application on the incidence of late wilt disease in landraces and fine seed 1005 cultivars. At the end of the experiment (90 days after planting), the percentage of infected plants with late wilt infection was calculated as follows: Late wilt infection (%) = [number of dead plants during the growing season due to late wilt infection/total number of maize plants] × 100. Maize plants were uprooted 90 days after planting, transported to the laboratory, and processed within 24 h to determine internode colonization with Chg-1. Each plant's first and second internodes above ground were cleaned with running water and cut into 1 cm segments. Surface sterilization of internode segments and endophyte isolation were carried out, as previously stated. The growth of the Chg-1 isolate from internodes tissues was confirmed by comparing the initially inoculated fungal isolate with the mother plates, as described by Muvea et al. (2014). Endophyte colonization was calculated by dividing the total number of internode segments yielding a given fungus by the total number of segments incubated (Muvea et al. 2014).

Field trails

The effect of Chg-1 application on the incidence of maize late wilt as well as ear yield of maize plant was studied in the field at Gharbia Governorate, Egypt, during the 2021

growing season. For more than 10 years, this field (clay soil) site was distinguished by a contiguous maize-growing region in which maize suffered from severe late wilt disease and was naturally infested with a high *C. maydis* inoculum (Elshahawy and El-Sayed 2018). Landraces and fine seed 1005 maize grains were used in this study. A two-factor factorial experiment in Randomized Complete Block Design (RCBD) with four replications (plots) was used. In the factorial treatment combination, two maize cultivars and four Chg-1 treatments were used. Grain treatment (GT), soil application (SA), grain treatment and soil application integration (GT + SA), and non-treated control(NC) were the Chg-1 treatments. The following four treatments, each with four replications (plots) for each cultivar, were used to investigate the effect of Chg-1 application on late wilt disease incidence and maize yield of landraces and fine seed 1005 cultivars:

NC, Non-treated control.
GT, Grain treatment with Chg-1.
SA, Soil application with Chg-1.
GT + *SA*, Grain treatment + soil application with Chg-1.

Each replicate plot had five 6 m-long, 0.7 m-wide ridges. One hundred maize plants of each cultivar were used in each replicate plot. Grains were planted in holes (twenty per ridge, three grains per hole) and thinned to one plant per hole. Irrigation, fertilizer levels, and agronomic practices were carried out in accordance with Agricultural Extension recommendations. During plowing, superphosphate fertilizer (15% P_2O_5) was applied at a rate of 450 kg/ ha, and potassium sulfate (48%K_2SO_4) was applied at a rate of 125 kg/ ha. Following planting, 300 N unit/ha of ammonium nitrate fertilizer (33.5% N) was applied in two treatments: the first before the first irrigation and the second before the second irrigation. Three weeks after planting, the first irrigation occurred. Irrigation was then scheduled every 12 days until it was completed 3 weeks before harvest. Weeds were removed by hand as soon as they appeared. The disease incidence of late wilt was monitored on a regular basis beginning 60 days after sowing based on wilt symptoms. At the end of the experiment (110 days after planting), the percentage of infected plants with late wilt infection was calculated as follows: Late wilt infection (%) = [number of dead plants due to late wilt infection during the growing season/total number of maize plants] × 100. During the harvest period, quantitative maize yield was measured as the weight (kg) of harvested ears per plot.

Statistical analysis

Data were checked for normality and variance homogeneity prior to statistical analysis. Percentage data were transformed using an arcsine square root transformation to improve variance homogeneity; however, untransformed data were presented. All data were subjected to analysis of variance (ANOVA) to see if there was a significant difference in the mean of measured variables in response to Chg-1 applications and maize cultivars. Duncan's multiple range test was estimated using CoStat6303Win.exe software to compare the means at $P = 0.05$.

Results

Laboratory experiments

Isolation, bioactivity, and identification of endophytic fungi

Three endophytic fungi were isolated from healthy cv. Fine seed 2005 maize plants' internodes. These endophytic fungi were identified as *Chaetomium* spp. based on morphological characteristics. Using a dual culture antagonistic test, endophytic fungi were bioassayed against *C. maydis*. At 10 days, the tested antagonists inhibited the growth of *C. maydis*in dual culture plates by 58.3–91% when compared to the control, as shown in Table 1. *Chaetomium* spp. isolates Ch-2 and Ch-3 exhibit moderate inhibitory activity against *C. maydis* (Online Resource 1). They inhibited *C. maydis*mycelium growth by 61.5 and 58.3%, respectively. *C. maydis* mycelial growth was inhibited by *Chaetomium* spp. (isolate Ch-1) by 91.0%. Furthermore, it was observed to grow rapidly over the *C. maydis* colony and degrade the pathogen's mycelia after 10 days, resulting in a color change from white to light yellow–brown and partial or complete colony death (Online Resource 1). In a dual culture antagonistic test, isolate Ch-1 outperformed isolates Ch-2 and Ch-3 significantly. As a result, this endophytic isolate was selected, identified via rDNA sequencing of the ITS region, and assigned a GenBank accession number. Total DNA from this isolate was

Table 1 Growth area (cm^2) and inhibition of *C. maydis* in dual culture with the *Chaetomium* spp. endophytes isolates as well as in control

Endophyte isolate	Average growth area and inhibition	
	Growth area (cm^2)	Inhibition (%)
Chaetomium spp. isolate Ch-1	05.7 ± 0.05 d	91.0
Chaetomium spp. isolate Ch-2	24.5 ± 0.04 c	61.5
Chaetomium spp. isolate Ch-3	26.5 ± 0.03 b	58.3
Control	63.6 ± 0.00 a	–

Values are mean of four replicates for each *Chaetomium* spp. isolate as well as the control. Growth area (cm^2) of *C. maydis* was calculated using a planimeter. Means ± standard errors within a column followed by the same letter are not significantly different according to Duncan's multiple range test at $P = 0.05$

extracted and analyzed using agarose gel electrophoresis (Fig. 1). The 18S rRNA gene was amplified in a thermal cycler using ITS1 and ITS4 as forward and reverse primers. When compared to the DNA marker, the PCR product was 500 Pb in size. On the purified PCR products, sequencing was performed. The obtained sequencing data were compared to the global recorded database in the National Centre for Biotechnology Information (NCBI) using the BLAST program. The phylogenetic trees revealed that this isolate was very similar to the type isolate of the *Chaetomium globosum* genera, which was deposited in the NCBI Culture Collection Centre and uploaded to GenBank as accession number MN689080.1 (Fig. 2).

Antifungal activity of Chg-1 crude extract

Three crude extracts from Chg-1 were tested at different concentrations to see if they could inhibit *C. maydis* mycelial growth and conidial germination. As shown in Table 2, when compared to the control (0 µg/ ml), all crude extracts at concentrations ranging from 125 to 1000 µg/ml significantly reduced *C. maydis* mycelial growth. The inhibitory efficiency of crude extracts on *C. maydis* mycelial growth increased with increasing concentrations (Table 2). When compared to hexane and methanol crude extracts, ethyl acetate crude extract inhibited *C. maydis* mycelial growth more effectively. In the presence of higher (1000 µg/ml) ethyl acetate extract, the tested pathogen did not grow at all. Hexane and methanol extracts were more effective at this tested concentration of 1000 µg/ml, reducing *C. maydis* mycelial growth by 83.3 and 84.4%, respectively (Table 2). After 18 h of experimentation, data on spore germination were collected. When compared to the control (0 µg/ml), all crude extracts of Chg-1 significantly inhibited conidial germination of *C. maydis*. The inhibitory efficiency of crude extracts on *C. maydis* spore germination gradually increased as concentrations increased (Table 2). At a concentration of 1000 µg/ml, the most effective extract was ethyl acetate extract, which reduced spore germination by 94.7%. At 1000 µg/ml concentration, hexane and methanol extracts reduced spore germination by 90.3 and 91.7%, respectively.

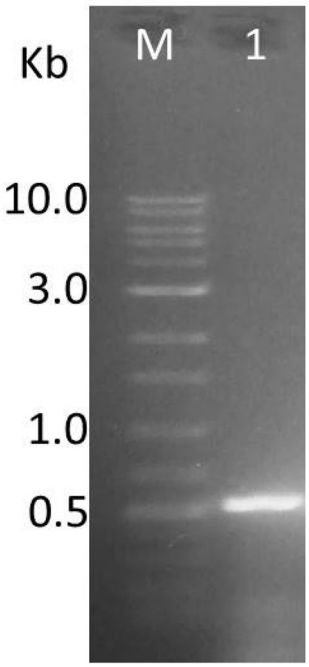


Fig. 1 Agarose gel electrophoresis for PCR products of 18S rRNA analysis of *Chaetomium* isolate Ch-1: M-DNA ladder (100 bp) and 1-*Chaetomium* isolate Ch-1

Greenhouse trails

Effect of Chg-1 application on plant growth promotion

In comparison to the controls, all Chg-1 treatments increased plant height, fresh weight, and dry weight of the two maize cultivars significantly ($P = 0.05$) (Fig. 3). On plant height and fresh weight, there were significant interactions between maize cultivars and Chg-1 treatments, but not on dry weight (Online Resource 2). Plant height in the negative control of landraces and fine seed 1005 cultivars was 48.3 and 45.0 cm, respectively, which was significantly reduced by 13.5 and 15.6% in the positive control due to *C. maydis* inoculation. Treatments with Chg-1 increased plant height significantly more than positive controls in both cultivars (Fig. 4). The application of Chg-1 as GT + SA (Fig. 3) had the greatest effect on plant height against *C. maydis* stress, increasing plant height by 52.9 and 55.7%, respectively, in landraces and fine seed 1005 cultivars. Individual treatment of GT or SA was closely followed. In soil inoculation with *C. maydis*, plant fresh weight of landraces and fine seed 1005 was reduced by 26.4 and 21.3%, respectively. When compared to the positive control, the use of various Chg-1 treatments significantly reduced fungal stress and increased fresh weight of the two maize plant cultivars (Fig. 3). The use of Chg-1 as GT + SA had the greatest effect on fresh weight against *C. maydis* stress, with 62.5 and 56.0 g plant^{-1} in landraces and fine seed, respectively (Fig. 3). The dry weights of the negative controls were 7.3 and 6.7 g, respectively, while the dry weights of the positive controls were 2.2 and 2.8 g for the two maize plant cultivars (69.9 and 58.2% reduction). The use of Chg-1 improved dry weight to varying degrees depending on the method of application. With 14.3 and 13.5 g plant^{-1} in landraces and fine seed1005, respectively, the application of Chg-1 as GT + SA had the greatest effect on dry weight against *C. maydis* stress (Fig. 3).

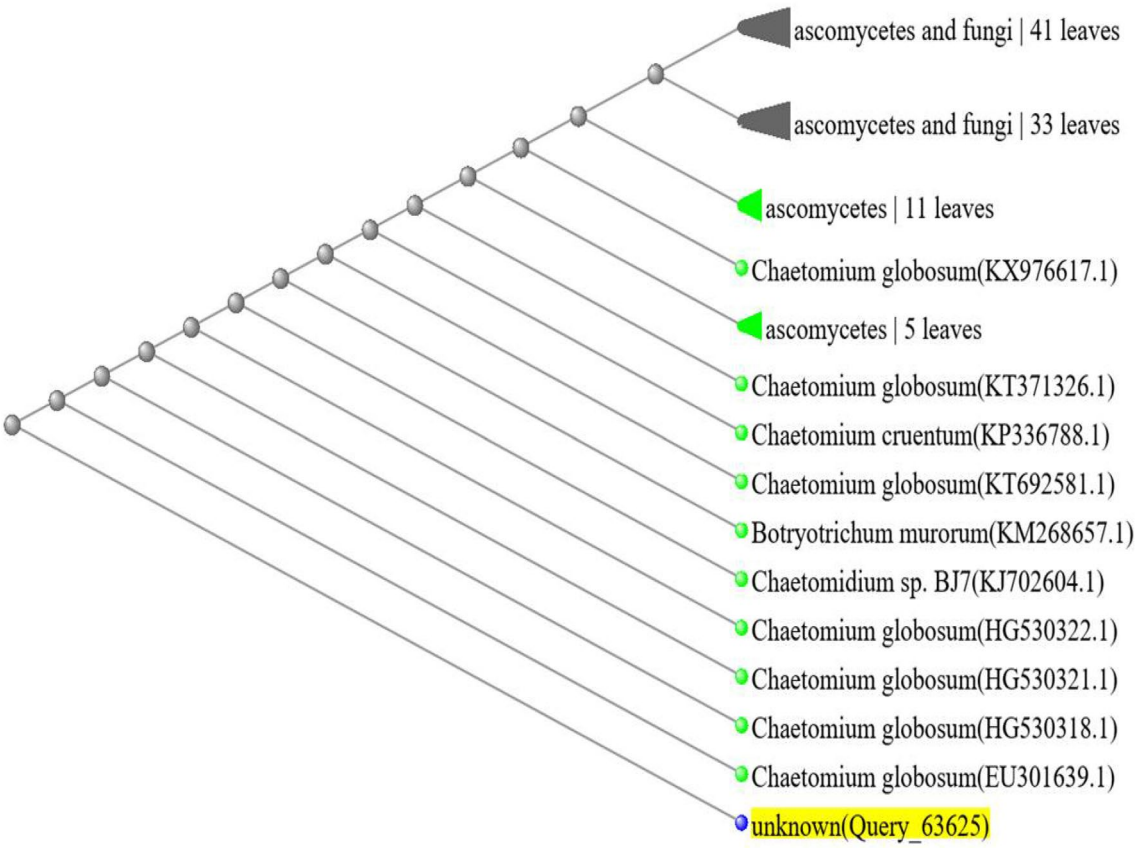


Fig. 2 Phylogenetic tree constructed from the 18 SrRNA sequence of *Chaetomium globosum* (isolate Chg-1) and their related strains in Gene Bank

Table 2 Effect of the crude extracts of the endophyte Chg-1 on mycelial growth and spore germination of *C. maydis* under in vitro conditions

Treatment	Crude extract concentration (µg/ml)				
	0.0	125	250	500	1000
Mycelial growth (cm)					
Hexane	9.0 ± 0.00 a	7.4 ± 0.05 c	5.5 ± 0.07 f	3.5 ± 0.07 h	1.5 ± 0.08 j
Ethyl acetate	9.0 ± 0.00 a	6.9 ± 0.03 d	4.6 ± 0.21 g	2.3 ± 0.02 i	0.0 ± 0.00 k
Methanol	9.0 ± 0.00 a	7.8 ± 0.05 b	6.1 ± 0.09 e	3.3 ± 0.14 h	1.4 ± 0.07 j
Spore germination (%)					
Hexane	86.4 ± 0.81 a	61.2 ± 0.58 c	44.2 ± 0.37 e	19.2 ± 0.37 h	8.4 ± 0.24 j
Ethyl acetate	86.4 ± 0.81 a	55.0 ± 0.45 d	37.6 ± 0.51 g	15.8 ± 0.37 i	4.6 ± 0.24 k
Methanol	84.0 ± 0.81 a	63.0 ± 0.71 b	42.0 ± 0.55 f	17.8 ± 0.37h	7.0 ± 0.32 j

Values are means of three replications ± standard errors; values in the columns and the rows of three crude extracts followed by the same letters are not significantly different by Duncan's multiple range test at $P = 0.05$. Spore germination assay was after 18 h incubation with each concentration of crude extracts

Effect of Chg-1 application on plant physiology

In general, no statistically significant difference in chlorophyll content was found between the Chg-1 treatments. Significant interactions did exist, however, between the Chg-1 treatments and the maize cultivars (Online Resource 2). When compared to the negative controls of landraces and fine seed 1005, *C. maydis* inoculation reduced chlorophyll content in the positive control by 30.3 and 29.3%, respectively (Table 3). The use of Chg-1 increased chlorophyll content in the two cultivars by 40.4–48.7% when compared to the positive controls (Table 3). Total phenols and total flavonoids content differed insignificantly between Chg-1 treatments. There were significant interactions between the

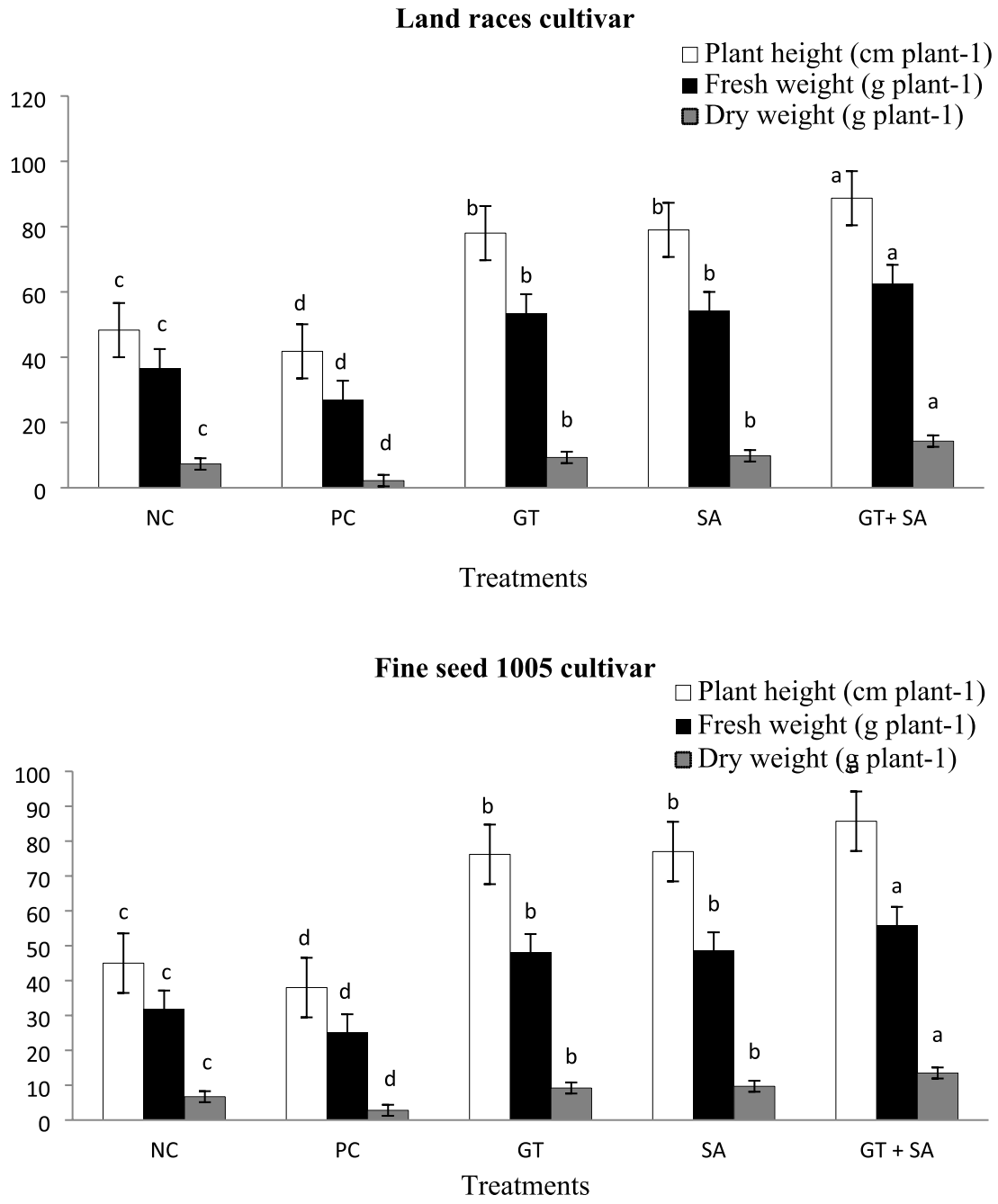
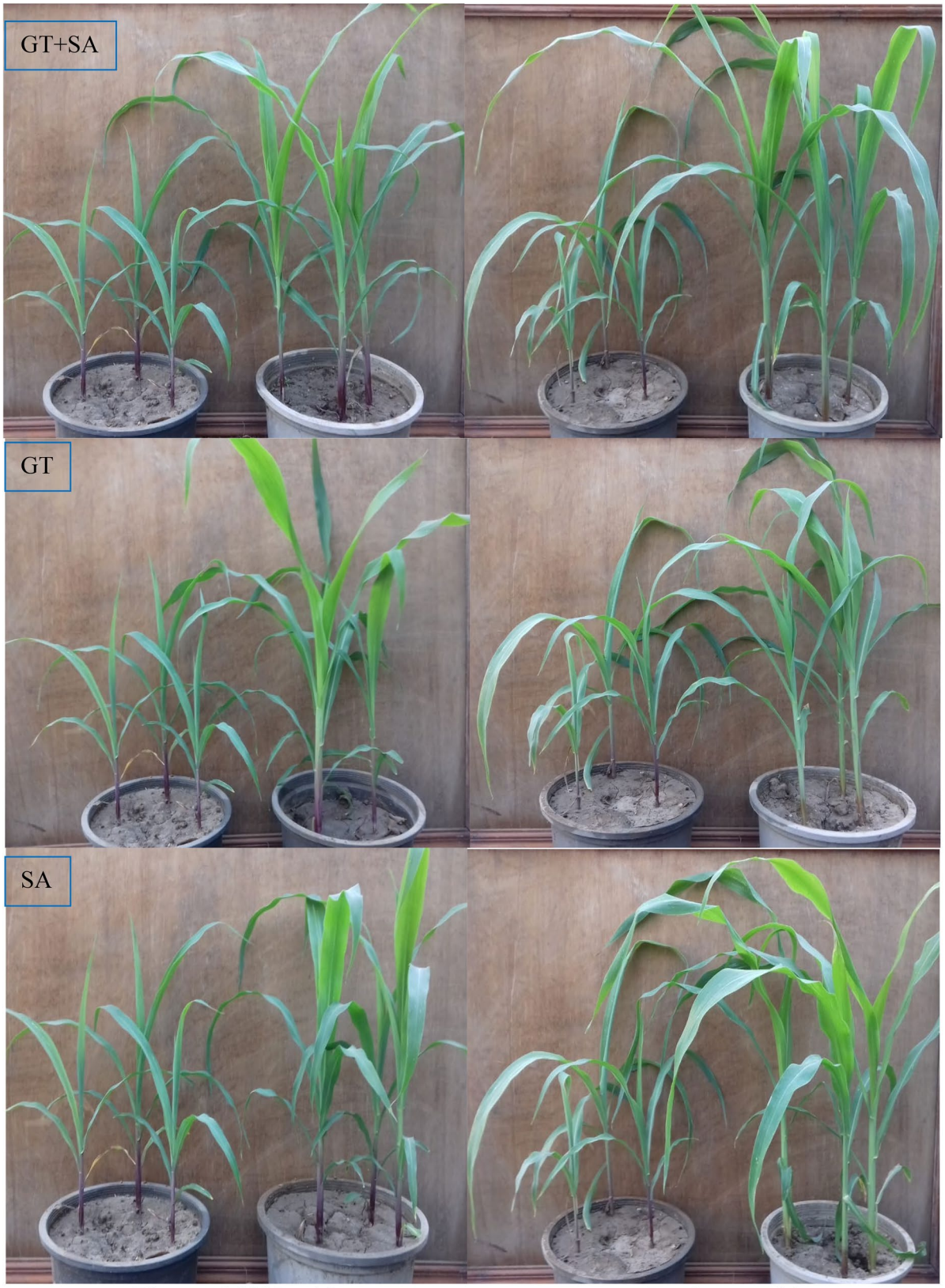


Fig. 3 Effect of application with the endophyte Chg-1 on plant growth promotion of maize plants, 25 days after sowing, grown under greenhouse conditions. Negative control (NC), positive control (PC), grain treatment (GT), soil application (SA), grain treatment plus soil application (GT + SA). Values are mean of six replications for each treatment as well as the positive and negative controls. Bars with the same letters within each variable indicate that the means ± standard errors are not significantly different at $P = 0.05$, according to Duncan's multiple range tests

Chg-1 treatments and the maize cultivars, except for the flavonoids content. The positive control treatment contained more phenols (11.9 and 12.6 mg g^{-1} DW) than the negative controls (10.8 and 11.0 mg g^{-1} DW) of both landraces and fine seed 1005 cultivars (Table 3). In various Chg-1 treatments, the phenol content of both cultivars was found to be in the range of 14.6–16.6 mg g^{-1} DW and was generally higher than that of the positive controls (Table 3). In the negative control treatment, the flavonoids contents of the landraces and fine seed 1005 cultivars were 0.057 and 0.059 mg g^{-1} DW, respectively, and increased to 0.068 and 0.072 mg g^{-1} DW in the positive control treatment. In various Chg-1 and


GT+SA
GT
SA
Fine seed 1005 cultivar
Landraces cultivar

◂**Fig. 4** Effect of *C. maydis* inoculation and various treatments with the endophyte Chg-1 on plant height of maize plants, 25 days after sowing under greenhouse conditions. Left (positive control, soil infested with *C. maydis*) and right (various treatments with the endophyte Chg-1). GT, grain treatment + *C. maydis*, SA, soil application + *C. maydis*, GT + SA, grain treatment plus soil application + *C. maydis*

C. maydis treatments, the flavonoids contents of both landraces and fine seed 1005 cultivars were generally comparable to those of the corresponding negative control treatments (Table 3). In comparison to the positive and negative controls, all Chg-1 treatments significantly ($P = 0.05$) increased the activities of the two maize cultivars' peroxidase, polyphenoloxidase, and chitinase enzymes (Fig. 5). Interactions between maize cultivars and treatments, on the other hand, were insignificant(Online Resource 2). Enzyme activities in both landraces and fine seed 1005 cultivars followed a similar pattern in various Chg-1treatments. In the Landraces cultivar, the use of Chg-1 treatments in conjunction with *C. maydis* resulted in a significant increase in enzymatic activities (by 40.9% for peroxidase, 18.0% for polyphenoloxidase, and 16.3% for chitinase) over the positive control (Fig. 5).

Effects on late wilt incidence and internodes colonization by Chg-1

There was no disease detected in the negative control for either cultivar. The positive control, on the other hand, had a 100% disease incidence (Fig. 6). The use of various Chg-1 treatments, namely GT, SA, and GT + SA, had a significant effect on the incidence of late wilt disease. In GT and SA treatments, the disease incidence of both landraces and fine seed 1005 cultivars was 50.0%. The use of Chg-1 as GT + SA was found to be the most effective treatment against *C. maydis* stress, with disease incidences of 25.0 and 16.7% in both the landraces and fine seed 1005 cultivars, respectively (Fig. 6). The method of application influenced the frequency of Chg-1 re-isolation from maize internodes tissue (Fig. 6). When Chg-1 was applied to grains (GT) and grains combined with soil application (GT + SA), the highest frequency of re-isolation was observed, being 54.2, 62.5% and 58.3, 62.5%, for the landraces and fine seed 1005 cultivars, respectively. There was no endophytic fungus found in either the negative or positive controls.

Field trails

Effect of Chg-1 application on late wilt incidence

All Chg-1 treatments significantly ($P = 0.05$) reduced the incidence of late wilt in the two maize cultivars when compared to non-treated controls (Online Resource 3). There were significant interactions ($P = 0.05$) between maize cultivars and Chg-1 treatments. In the absence of Chg-1, non-treated maize plants (non-treated controls) exhibited a late wilt rate of 45.25 and 32.0% for the landraces and fine seed 1005 cultivars, respectively (Fig. 7). When Chg-1 was applied, the incidence of late wilt was reduced by 70.2–89.8% in both cultivars when compared to non-treated controls. GT + SA was found to be the most effective of the three treatments using Chg-1, reducing late wilt by 86.2 and 89.8% in landraces and fine seed 1005 cultivars, respectively (Fig. 8).

Effect of Chg-1 application on ear yield

In comparison to the controls, all Chg-1 treatments significantly ($P = 0.05$) increased average ear yield of the two maize cultivars (Online Resource 3). On ear yield, there were no significant interactions between maize cultivars and Chg-1 treatments ($P = 0.05$). Various Chg-1 treatments increased the ear fresh biomass of the two maize cultivars by 52.4–66.7% compared to the non-treated control treatment (Fig. 7). The use of Chg-1 as GT + SA had the greatest effect on ear fresh biomass, accounting for 66.7% in the Landraces cultivar and 60.1% in the Fine seed 1005 cultivar (Fig. 7).

Discussion

In this study, morphological tools were used to identify endophytic fungi isolated from the internodes of healthy maize plants as *Chaetomium* spp. The pathogen responsible for maize late wilt disease, *C. maydis*, was found to be antagonized by all three *Chaetomium* spp. isolates (Table 1, Online Resource 1). *Chaetomium* spp. (isolate Ch-1) showed the highest percentage of inhibition against *C. maydis* (91.0%). Several previous studies discovered variations in the biological activities of fungal isolates from the same species (Park et al. 2003). Using molecular biological tools, the most effective endophytic isolate (isolate Ch-1) was identified as *Chaetomium globosum* (Chg-MN689080.1) and used to control maize late wilt in vitro, greenhouse, and field.

C. maydis mycelia degradation observed in a dual culture test with Chg-1 in vitro is typical of mycoparasitism. Mycoparasitism is characterized by the use of various lytic enzymes to degrade the host's cell wall, resulting in the death of the target organism (Sun et al. 2006). *Chaetomium* species have been found to produce lytic enzymes as well as a variety of other secondary metabolites, which may contribute to their antagonistic activity (Zhang et al. 2012). In culture substrates and under mycoparasitism conditions, *Chaetomium* spp. frequently secretes degrading enzymes such as chitinase and β-1,3-glucanase (Sun et al. 2006; Liu et al. 2008). Shanthiyaa et al. (2013) discovered that *C. globosum* isolate Cg-6 had higher exo- and endo-glucanase

Table 3 Phenols, flavonoids, and total chlorophyll in maize leaves resulted from the application of Chg-1, 25 days after maize planting in pots

Treatment	Chlorophyll (mg g^{-1} FW)	Phenols (mg g^{-1} DW)	Flavonoids (mg g^{-1} DW)
Landraces cultivar			
Negative control	3.37 ± 0.07 b	10.8 ± 0.03 c	0.057 ± 0.00 c
Positive control	2.35 ± 0.03 c	11.9 ± 0.08 b	0.068 ± 4.94 b
Grain soaking	3.95 ± 0.01 a	14.7 ± 0.04 a	0.186 ± 2.11 a
Soil amendment	3.94 ± 0.01 a	14.6 ± 0.02 a	0.187 ± 6.15 a
Grain soaking + soil amendment	3.96 ± 0.01 a	14.7 ± 0.04 a	0.186 ± 3.07 a
Fine seed 1005 *cultivar*			
Negative control	3.45 ± 0.05 b	11.0 ± 0.11 c	0.059 ± 0.00 c
Positive control	2.44 ± 0.01 c	12.6 ± 0.18 b	0.072 ± 8.43 b
Grain soaking	4.63 ± 0.16 a	16.5 ± 0.11 a	0.188 ± 7.18 a
Soil amendment	4.76 ± 0.14 a	16.6 ± 0.11 a	0.187 ± 6.15 a
Grain soaking + soil amendment	4.63 ± 0.12 a	16.5 ± 0.08 a	0.188 ± 4.01 a

Values are mean of six replications for each treatment as well as the positive and negative controls. Chlorophyll contents were expressed in mg g^{-1} fresh weight of leaves. Total phenols and flavonoids were expressed as mg g^{-1} dry weight of leaves. Means ± standard errors within a column followed by the same letter are not significantly different according to Duncan's multiple range test at $P = 0.05$

enzyme activity. Because the *C. maydis* cell wall is primarily composed of glucan and chitin constituents, Chg-1 is thought to have greater biocontrol activity. Similarly, Hung et al. (2015a, b b) discovered that all of the *Chaetomium* species tested positive for parasitizing hyphae as well as growing over and degrading *Phytophthora palmivora* colonies. *C. globosum* can parasitize and lyse the hyphae of *P. cinnamomi* and *P. nicotianae*, according to Heller and Theiler-Hedtrich (1994). According to Gao et al. (2005), during the mycoparasitic process with *Rhizoctonia solani*, the endophytic *Chaetomium spirale* ND35 produced β-1,3-glucanases and chitinases. Other studies, however, have suggested that the mechanism of action of *C. globosum* against *Colletotrichum gloeosporioides*, *Fusarium* spp., *Pyricularia oryzae*, *R. solani,* and *Curvularia lunata* is antibiosis (Soytong et al. 2001; Charoenporn et al. 2010; Sibounnavong et al. 2011). Antibiosis is a type of antagonism caused by secondary metabolite production that is toxic to other microorganisms (Alabouvette et al. 2006). *Chaetomium globosum* was thought to be capable of producing a diverse array of antifungal active substances (Zhang et al. 2012). The majority of these compounds were extracted using organic solvents, and different solvents, including methanol, ethanol, dichloromethane, ethyl acetate, acetone, and chloroform, were used to extract compounds from *C. globosum* (Jiang et al. 2017). Our results show that crude extracts of Chg-1 in hexane, EtOAc, and MeOH significantly inhibited *C. maydis* mycelial growth and conidial germination. The antagonistic substances (crude extracts) test results suggested that Chg-1 has an antibiosis mechanism against *C. maydis*. Many studies have shown that antagonistic substances and hydrocarbons derived from *C. globosum*, such as phenols, terpenoids, and sulfur compounds, can inhibit mycelial growth and conidia production in *C. gloeosporioides*, *B. sorokiniana*, *Fusarium oxysporum* f. sp. *lycopersici*, *Pythium ultimum*, *R. solani*, *Sclerotinia sclerotiorum*, *Sclerotium rolfsii*, *F. oxysporum* and *Macrophomina phaseolina* (Sibounnavong et al. 2012; Huu Phong et al. 2016; Kumar et al. 2020). Furthermore, *C. globosum* has been shown to produce antifungal compounds such as chaetomium (Di Pietroet al. 1992), chaetoviridins A and B (Zhang et al. 2021), chaetoglobosins A and C (Jiang et al. 2017) and chaetglotone (Ji et al. 2021). The interactions found in this study between Chg-1 and *C. maydis* showed characteristics typical of both of these mechanisms.

In pot trials, the endophytic fungus Chg-1produced significant results on maize plants. In both maize cultivars, all Chg-1 treatments, GT, SA, and GT + SA, significantly reduced late wilt disease. This showed that Chg-1 inhibited *C. maydis* pathogenicity. These findings are consistent with those of Zhang et al. (2021) who discovered that *C. globosum* strain CEF-082 could control *Verticillium dahliae*-caused cotton wilt. Chg-1 colonized the internodes of both maize cultivars successfully in our study. The GT and GT + SA treatments have no discernible difference. Plants from SA treatment, on the other hand, had the lowest rate of colonization. *C. globosum* strain TAMU 520 was found to systemically colonize cotton plants via seed treatment, according to Zhou et al. (2016). Another *C. globosum* strain, CEF-082, was discovered in a study by Zhang et al. (2021) to systemically colonize cotton plants via root irrigation. In our pot trails where the soil was inoculated with the *C. maydis* pathogen, we found a high percentage of dead plants. As shown in Fig. 6, GT + SA of Chg-1 was more effective in controlling maize late wilt than individual treatments. Furthermore, 25 days after planting, Chg-1-treated maize plants were typically taller

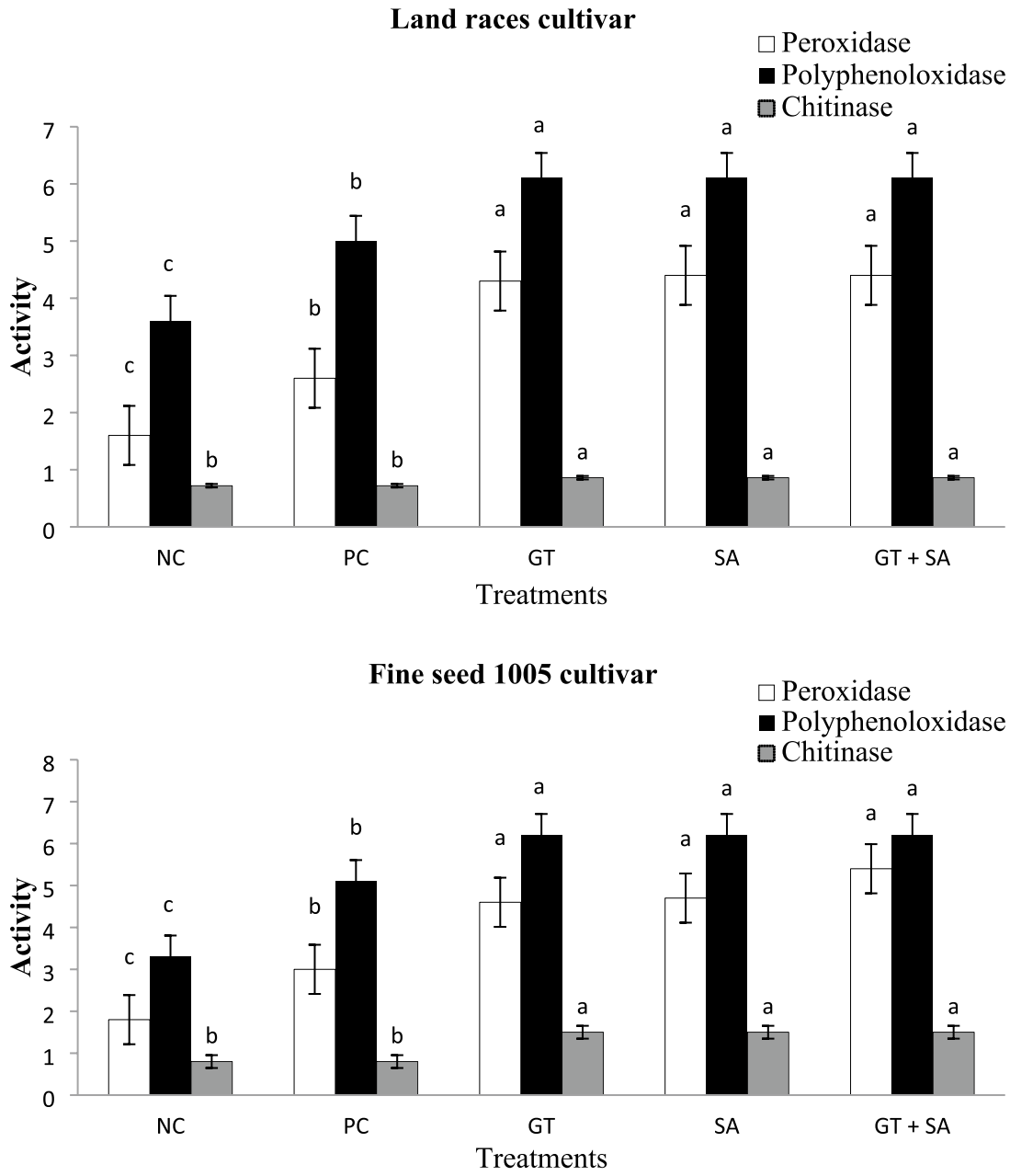


Fig. 5 Peroxidase, polyphenoloxidase, and chitinase activities in maize leaves resulted from the application of the endophyte Chg-1, 25 days after sowing, grown under greenhouse conditions. Negative control (NC), positive control (PC), grain treatment (GT), soil application (SA), grain treatment plus soil application (GT + SA). Values are mean of six replications for each treatment as well as the positive and negative controls. Bars with the same letters within each variable indicate that the means ± standard errors are not significantly different at $P = 0.05$, according to Duncan's multiple range tests. Peroxidase activity was expressed as the increase in absorbance at 470 nm/g fresh weight/minute. Polyphenoloxidase activity was expressed as the increase in absorbance at 475 nm/g fresh weight/minute. Chitinase activity was expressed as mM *N*-acetylglucosamine equivalent released/gram fresh weight/60 min at 540 nm

than non-treated maize plants. Furthermore, Chg-1-treated plants yielded plants with higher fresh and dry weight in both maize cultivars. These findings are consistent with those of other studies. *Chaetomium* spp. has the ability to control root rot diseases and increase plant growth in black pepper, citrus, cotton, potato, strawberry, and *Salvia miltiorrhiza* (Shanthiyaa et al. 2013; Zhou et al. 2016; Zhai et al. 2018).

According to previous research, *C. globosum* has a multimechanism of action for controlling plant pathogens, which includes mycoparasitism via the production of chitinase, *β*-1–3-glucanase, *β*-1–4-glucanase,

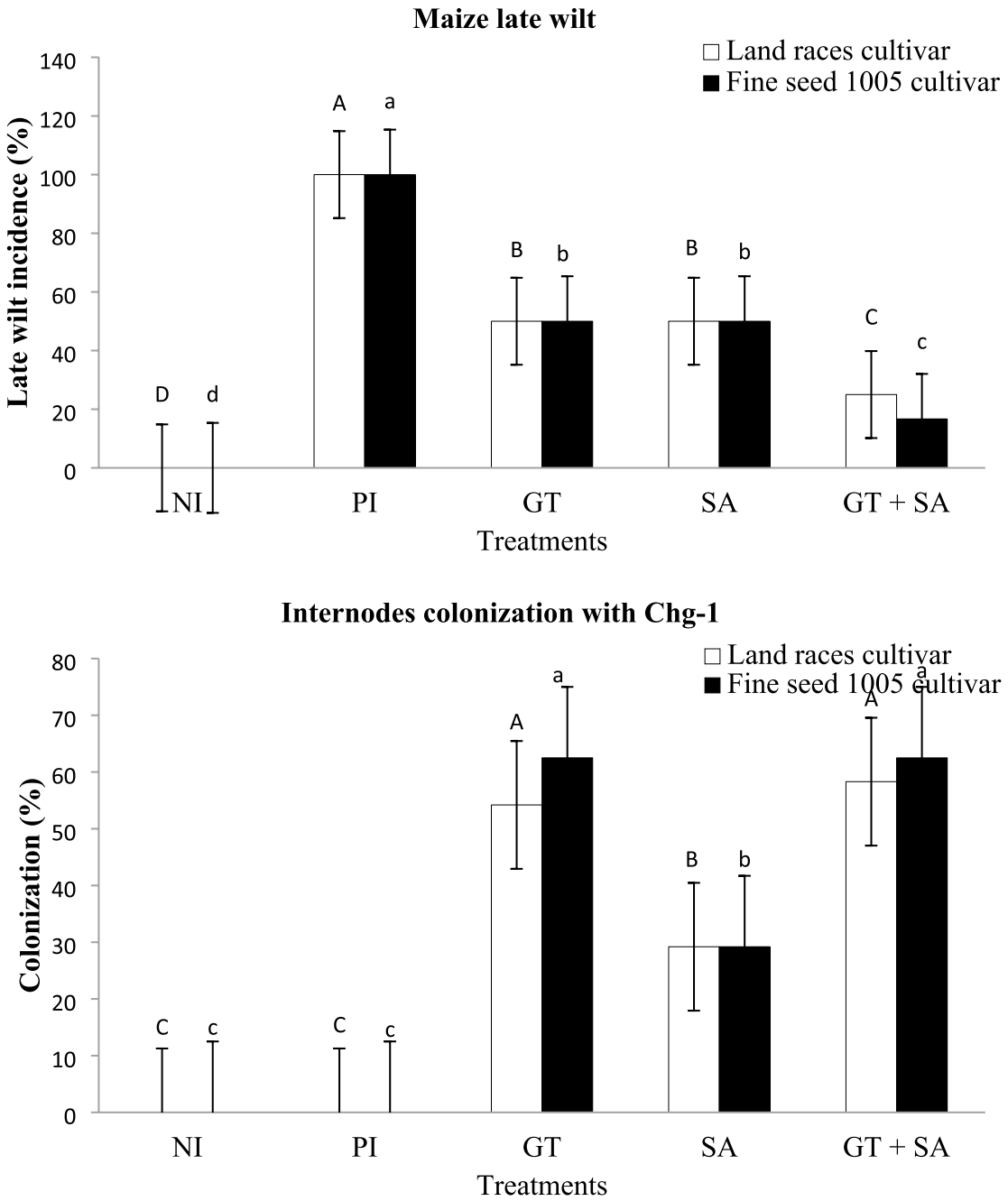


Fig. 6 Effect of the endophyte Chg-1 application on the incidence of late wilt disease and internodes colonization with Chg-1, 90 days after sowing of maize plants in greenhouse trails. Negative control (NC), positive control (PC), grain treatment (GT), soil application (SA), grain treatment plus soil application (GT + SA). Values are mean of six replications for each treatment as well as the positive and negative controls. Bars with the same letters within each variable indicate that the means ± standard errors are not significantly different at $P = 0.05$, according to Duncan's multiple range tests. Percentages data of late wilt disease incidence (dead plants due to late wilt infection) were transformed into arcsine square root transformed data for analyses of variance; however, untransformed data are present

antibiotic, competition, induced resistance and inactivation of pathogen-produced enzyme during infection (Pieterse et al. 2014; El-Naggar et al. 2016). Pathogen inoculation reduced chlorophyll content in the current study, possibly due to xylem vessel choking caused by fungal toxin release (Sabet et al. 1972). The leaf's photosynthetic pigment, on the other hand, improved as a result of Chg-1 application could be attributed to a reduction in fungal toxin released by pathogens. The positive control treatment increased the phenolic and flavonoid content of the leaves, possibly in

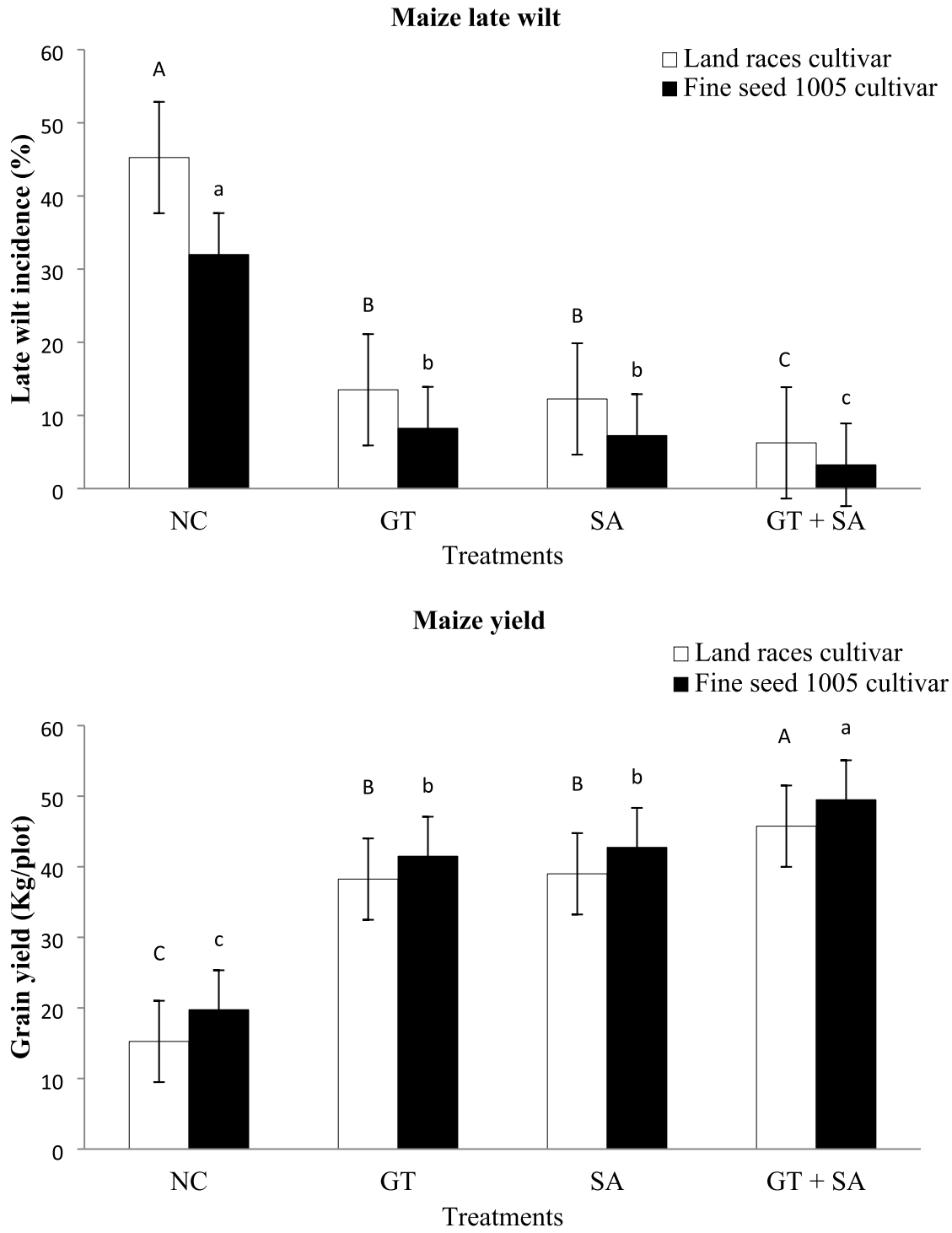


Fig. 7 Effect of the endophyte Chg-1 application on the incidence of late wilt disease and on ear yield (kg ear/plot) of maize plants grown under field conditions, 110 days after sowing. Non-treated control (NC), grain treatment (GT), soil application (SA), grain treatment plus soil application (GT + SA). Values are mean of four replications for each treatment as well as the control. Bars with the same letters indicate that the means ± standard errors are not significantly different at $P = 0.05$, according to Duncan's multiple range tests

response to pathogenic pressure, which disrupted nitrogen availability. Doley and Jite (2013) discovered an increase in total phenolics in groundnut plants infected with *M. phaseolina*. The accumulation of phenolic compounds at the challenged site may aid in the localized accumulation of reactive oxygen species (ROS), triggering a general

Fig. 8 Integration effect of grain treatment and soil application (GT + SA) with the endophyte Chg-1 on late wilt disease of maize plants grown under field conditions. Left (non-treated control) and right (GT + SA) treatment

plant defense response (Volpin et al. 1994). As a result, increasing the activities of enzymes was insufficient to deal with the increased ROS concentration, whereas ROS may facilitate pathogen penetration by increasing the activities of cell wall degrading enzymes, thereby weakening the host defense system. In various treatments of combined application of Chg-1 and *C. maydis*, the phenolic and flavonoid contents of both maize cultivars were generally comparable to those of corresponding negative control treatments. Phenolics are secondary metabolites that help plants defend themselves against a variety of pathogens (Taheri and Tarighi 2011). Furthermore, phenolics act as radical scavengers, reducing the toxic effects of reactive oxygen species (ROS) (Shoaib et al. 2018). According to this discovery, *C. globosum* reduced the severity of *Bipolaris sorokiniana* in wheat by activating phenolics accumulation (Biswas et al. 2003). Chg-1 treatments significantly increase the specific activity of defense-related enzymes such as peroxidase, polyphenoloxidase, and chitinase in maize leaves 25 days after planting. Daroodi et al. (2021) recently reported that the indirect effects of *Acrophialophora jodhpurensis* (*Chaetomium jodhpurense* Lodha) on the pathogen *R. solani* in vivo were due to activation of tomato defense responses, such as induction of antioxidant

enzymes. Increased peroxidase and polyphenoloxidase activity may lead to increased oxidative stress as a result of increased H_2O_2 production (Vance et al. 1980). H_2O_2 and other free radicals are toxic to a variety of microbial pathogens (Wu et al. 1995). The oxidative potential of H_2O_2 during plant-pathogen interactions also contributes to the formation of lignin via peroxidase-mediated cross-linking of proline-rich structural proteins and phytoalexin biosynthesis during oxidative burst, as well as the conversion of O-dihydroxyphenols to toxic o-quinones via polyphenoloxidase (Mayer and Harel 1997). Pre-inoculation of cotton plants with the endophytic fungus *Fusarium solani*, according to Wei et al. (2019), reduced disease progression by increasing lignin accumulation. Chitinase enzymes, on the other hand, help plants defend themselves against fungi by hydrolyzing their cell walls. Because chitin is a major structural component of many pathogenic fungi's cell walls, their numbers increase significantly, and they play an important role in the defense reaction against fungal pathogens by degrading cell walls.

In field trials, GT + SA of Chg-1 was the best treatment under natural conditions, reducing late wilt incidence and improving ear yield in both maize cultivars (Fig. 7). The endophyte Chg-1 may reduce the occurrence of late wilt, resulting in an increase in yield. This finding is consistent with the findings of Charoenporn et al. (2010), who found that a registered bio-fungicide formulated from *C. globosum* N0802 could reduce disease incidence and increase yield of tomato wilt. Shanthiyaa et al. (2013) discovered that using *C. globosum* increased tuber yield by reducing late blight infection in field trials. This study's findings are also supported by the work of numerous reports. *C. globosum* has successfully controlled sugar beet damping off (*P. ultimum*), grape anthracnose disease (*C. gloeosporioides*), tomato wilt (*F. oxysporum*), corn leaf spot (*Setosphaeria turcica*), Pomelo root rot (*P. palmivora*), citrus root rot (*P. nicotianae*), and cucumber root rot (*R. solani*) (Zhang et al. 2013; Hung et al. 2015a, b b; Huang et al. 2020). However, Khan et al. (2012) discovered that this endophyte's phytohormone production capacity was confirmed in another study. They also claimed that *C. globosum* can be used to improve plant growth and yield of pepper (*Capsicum annuum* L.) in the field by secreting plant hormones such as gibberellins (GAs) and indole acetic acid (IAA). These hormones are thought to increase soil nutrient uptake, transduce signals between plant organs and integrate them to produce adequate defense responses to biotic or abiotic stresses (Vessey, 2003; Ghanashyam and Jain 2009). Recently, Tian et al. (2022) found that the infection and colonization events of *C. globosum* strain ND35 increased cucumber growth through complex regulation of plant hormones biosynthesis and metabolism. Although *Chaetomium* spp. have been shown to inhibit a variety of pathogens, this was the first report to show that the endophytes *C. globosum* (Chg-1) could control *C. maydis*, the causative agent of maize late wilt.

Conclusion

In this study, we isolated and identified *C. globosum* (Chg-1) as an endophyte isolate obtained from the internodes of healthy maze plants from a field with late wilt symptoms. The high antagonism of this isolate against *C. maydisin vitro*, as demonstrated in this study, supported the conclusion that Chg-1 could control maize late wilt. We also clearly demonstrated that the tested Chg-1 and their crude extracts strongly inhibited the growth of *C. maydis* in vitro and caused a significant reduction in the rate of late wilt in *C. maydis*-infected plants grown in greenhouse conditions. In field trials, the application of Chg-1 not only controlled late wilt disease but also resulted in the highest ear yield of maize. Thus, our findings shed light on the use of this endophyte in the control of *C. maydis* late wilt of maize plants.

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Authors' contributions I. E. Elshahawy and A. A. Khattab participated in the planning and designing of the experiments. A. A. Khattab provided the molecular identification of the endophyte. I. E. Elshahawy participated in writing and revising of the paper scientifically and checking analysis. All authors read and approved the final manuscript.

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Data availability All data and materials are available.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Human and animals rights This article does not contain any studies with human participants or animals performed by any of the authors.

Informed consent Informed consent was obtained from all individual participants included in the study.

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