

Strategies to Cope with Late Wilt of Maize

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Zea mays L. (maize, corn) is one of the world's leading crops for food, feed, and fuel and as a raw material for different industrial products. Control of maize late wilt disease (LWD) has been at the forefront of research efforts since the discovery of the disease in the 1960s. The disease has become a major economic restraint in highly affected areas such as Egypt and Israel and is of constant concern in other countries. LWD causes dehydration and collapsing at a late stage of maize cultivation, starting from the male flowering phase. The disease causal agent, *Magnaportheopsis maydis*, is a seed- and soil-borne phytoparasitic fungus, penetrating the roots at sprouting, colonizing the vascular system without aboveground symptoms, and spreading upwards in the xylem, eventually blocking the water supply to the plant's upperparts. Nowadays, the disease's control relies mostly on identifying and developing resistant maize cultivars. Still, host resistance can be limited because *M. maydis* undergoes pathogenic variations, and virulent strains can eventually overcome the host immunity. This alarming situation is driving researchers to continue to seek other control methods. The current entry will summarize the various strategies tested over the years to minimize the disease damage. These options include agricultural (crop rotation, cover crop, no-till, flooding the land before sowing, and balanced soil fertility), physical (solar heating), allelochemical, biological, and chemical interventions. Some of these methods have shown promising success, while others have contributed to our understanding of the disease development and the environmental and host-related factors that have shaped its outcome. The most updated global knowledge about LWD control will be presented, and knowledge gaps and future aims will be discussed.

Keywords: corn ; late wilt disease (LWD)

1. Introduction

Zea mays L. (maize, corn) is one of the world's leading crops for food, feed, and fuel and as a raw material for different industrial products ^[1]. Worldwide annual maize production is expanding at a rate of 1.6%. It was forecast that this rate will not meet the global demand in 2050 ^[2]. Among many diseases threatening this cultivar ^{[3][4]}, late wilt disease (LWD) has been reported so far in 10 countries and is considered a major concern in highly infected countries such as Egypt ^[5], Israel ^[6], India ^[7], Spain, and Portugal ^[8]. Economic losses due to LWD were up to 40% in Egypt ^[9], 50-100% in Israel ^{[10][11]}, and 51% in India ^[12]. Incidences of the disease can reach 100% in Egypt and Israel, and 70% in India. Although the disease has not been reported in the United States, *M. maydis* is regarded as a potentially high-risk phytopathogen ^{[13][14]}. LWD harms yield production by erupting at the flowering growth phase, resulting in severe dehydration and plant death.

Since the discovery of LWD in Egypt in the early 1960s ^[15], worldwide scientific efforts have led to much progress in understanding the disease mode and the pathogen causing it, *Magnaportheopsis maydis* ^[13]. Moreover, specific research tools for the study of LWD were developed and applied in the lab, in growth room experiments under controlled conditions, and in field trials. A significant part of these efforts was dedicated to creating diverse control methods to restrict the disease's burst and spread and minimize its effect on commercial maize manufacture. Previously the techniques developed over the years to study LWD and monitor its causal agent were reviewed ^[16]. A follow-up review summarized the accumulated scientific knowledge and future perspectives. These aspects include the geographic disease distribution, the pathogenesis (including the environmental factors affecting it), the symptoms' evolvement, and their outcome effect on commercial production ^[17]. All the updated information regarding the pathogen itself, *M. maydis*, was also summarized.

The current entry focuses on the vast efforts dedicated in the past 60 years to late wilt disease control. The inspected control methods produced different degrees of success and include agricultural options (flood following and balanced soil fertility) ^{[18][19]}, biofriendly approaches ^[20], physical (solar heating) ^[21], allelochemical ^[22], and chemical pesticide ^{[6][23][24]} practices. Recently, the tillage system's impact, the cover crop, and the crop rotation have been shown to serve as bioprotective factors against *M. maydis* ^{[25][26]}.

2. Late Wilt Disease

The late wilt causal agent, *M. maydis*, is a seed-borne and soil-borne vascular wilt fungal pathogen that penetrates the host roots and colonizes the xylem tissue [27][28]. The taxonomic tree of this fungus is: phylum: Ascomycota, subphylum: Pezizomycotina, class: Sordariomycetes, subclass: Sordariomycetidae, family: Magnaporthaceae, genus: Magnaporthiopsis, species: Magnaporthiopsis maydis. Former scientific names are *Cephalosporium maydis* (Samra, Sabet, & Hing, 1963) [29] and *Harpophora maydis* (Samra, Sabet, & Hing, 1963; Gams, 2000) [30].

maydis spread as sclerotia, spores, or hyphae on the plants' residues [28]. The pathogen can persist in the stubble and maize debris; no-till systems may help maintain it [13]. *M. maydis* can survive in the ground for lengthy periods or by thriving inside diverse host plants, such as lupine (*Lupinus termis* L.) [31], cotton (*Gossypium hirsutum* L.) [32][33], watermelon (*Citrullus lanatus*), and green foxtail (*Setaria viridis*) [32][34].

LWD has been reported so far in 10 countries: Egypt (1961) [35], India (1970) [36], Hungary (1998) [37], Spain and Portugal (2011) [38], Israel (2013) [11], and possibly Nepal (2015) [39]. There are also unconfirmed reports (summarized by Johal et al., 2004 [13]) that LWD was discovered in Italy, Romania, and Kenya (Figure 1).

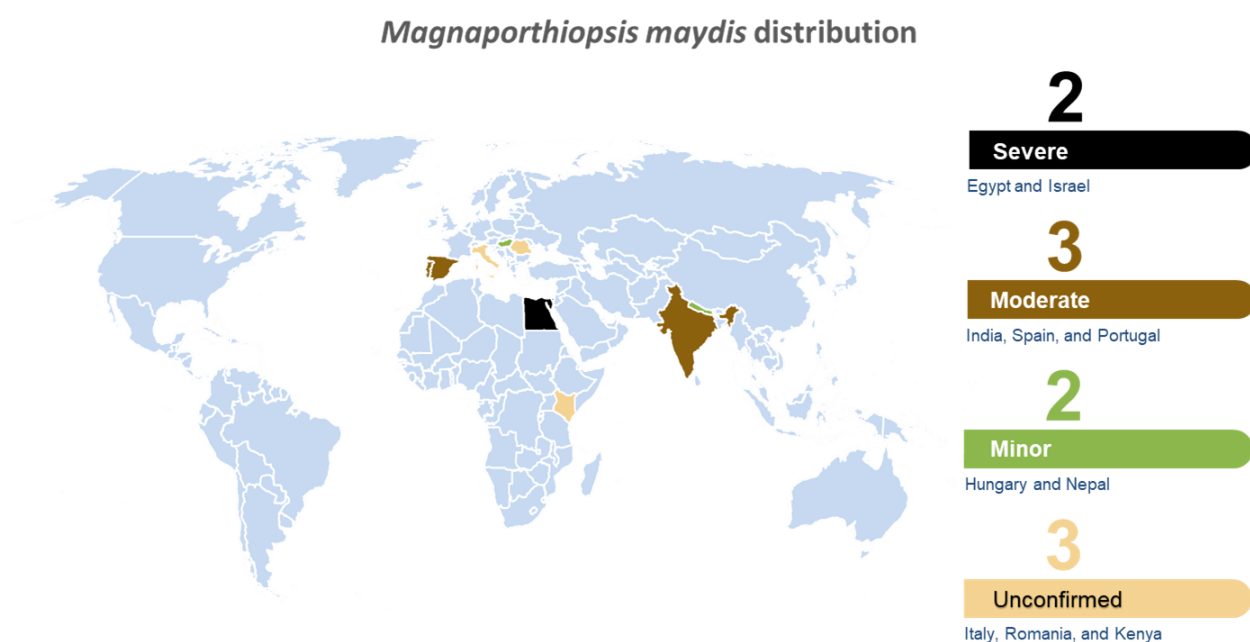


Figure 1. World distribution map for *Magnaporthiopsis maydis*. Disease severity is appraised according to the literature reports and is based on three categories: severe (4, Egypt and Israel); moderate (3, India, Spain, and Portugal); minor (2, Hungary and Nepal); and not certain/unconfirmed reports (1, Italy, Romania, and Kenya) [17].

The disease mode in LWD-sensitive maize cultivars is well detailed in the scientific literature (Figure 2). *M. maydis* infects maize seedlings during the first three weeks by sowing through their roots or mesocotyl (the seed-coleoptile connecting tissue). As the plants grow, they are less infected and become LWD-resistant about 50 days after sowing [28]. After root penetration, *M. maydis* colonizes xylem tissue (identified 21 days after sowing) and is rapidly transferred to the upper parts of the plant. *M. maydis* may occasionally cause seed rot or pre-emergence damping-off under high inoculum pressure [40].

The second critical infection phase starts when tassels first emerge (ca. day 55–65, R1 silking, silks visible outside the husks). At this stage, the fungus hyphae and conidia appear throughout the stalk [28], pathogen DNA levels reach their highest point in the stems [11], and the first aboveground symptoms are revealed. Later, when *M. maydis* colonizes the entire stalk, a vascular tissue occlusion by hyphae and gum-like secreted materials occurs, resulting in water supply suffocation, rapid dehydration, and death [13][28]. Although the disease appears as patches scattered in the field in many cases [16], LWD may result in total field infection and yield loss in heavily infected areas planted with susceptible maize cultivars [10][24]. A parallel asymptomatic infection mode, with some delay, occurs in resistant cultivars. This process can result in infected seeds that enhance the pathogen spread [10][11].

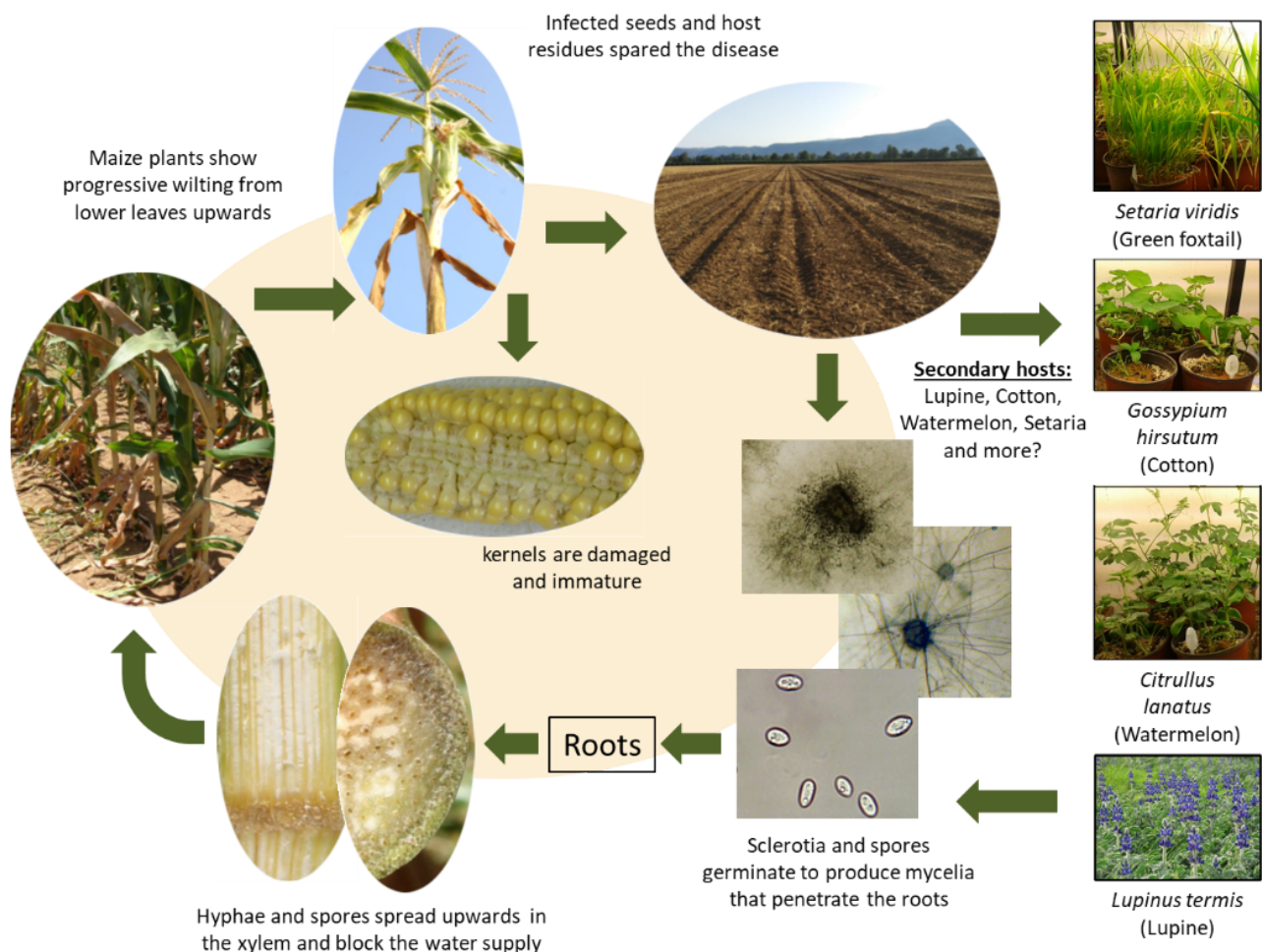


Figure 2. Disease cycle of maize late wilt caused by *Magnaporthiopsis maydis* ^[17] .

3. Control Strategies

3.1. Host Resistance

The use of resistant genotypes is considered the best, most practical, eco-friendly, and cost-effective method of controlling the disease ^{[41][42]} (Figure 3). This method is preferred even though resistant hybrids to LWD are often low-yielding or have other undesirable agronomic characteristics ^[43].

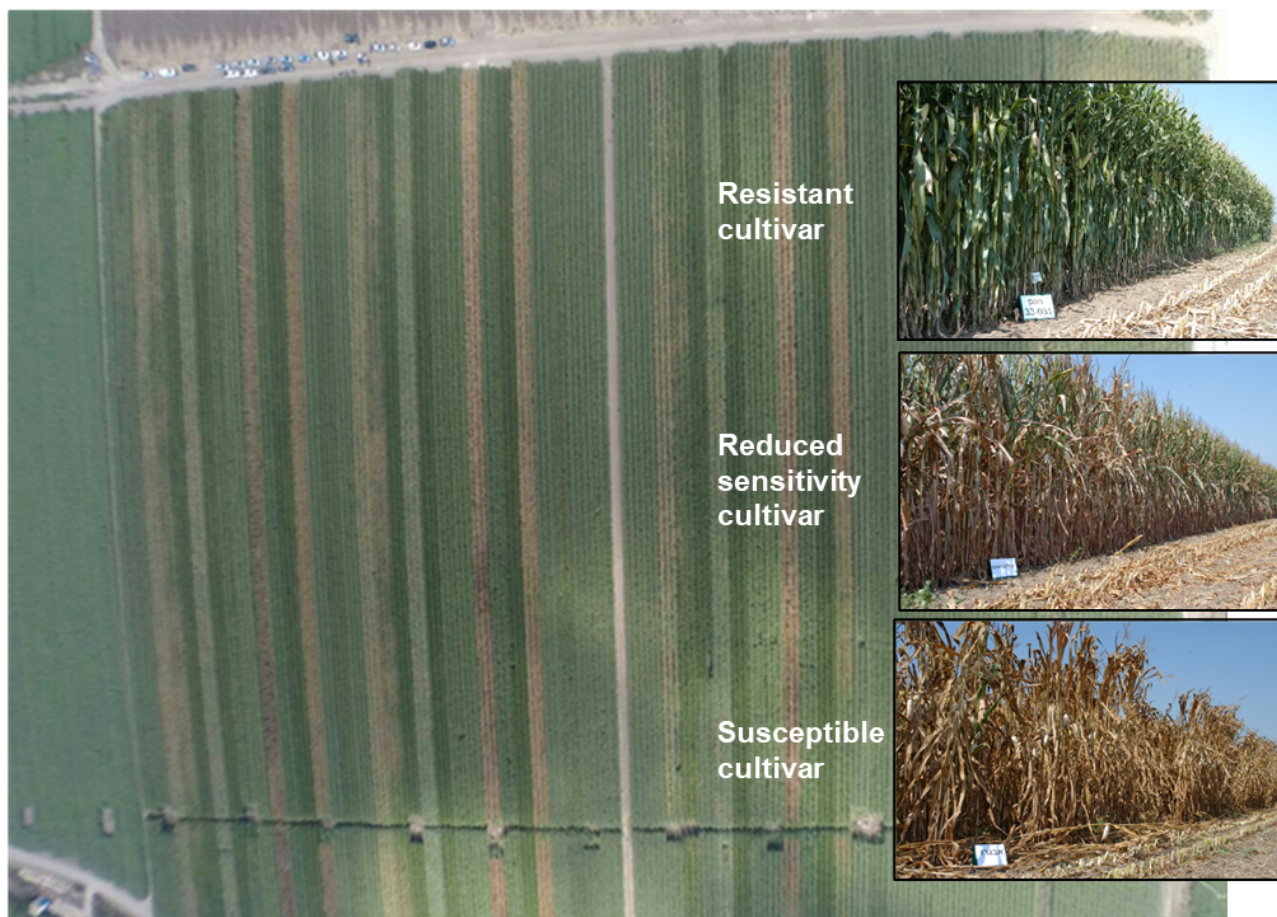


Figure 3. Cultivars' resistance test for late wilt disease (adapted from [44]). A semi-commercial examination of fodder corn genotypes was conducted in the southern coastal plain of Israel (Yavne field) in 2014. The experiment included 14 maize cultivars in 3 repetitions, with each plot containing 6 rows measuring about 200 m in length. The experimental area photo was taken close to harvesting (day 99 from sowing) by David Katsav. The brown lines are late wilt diseased cultivars with severe dehydration, while the green lines are healthy cultivars. The photos on the right: resistance cultivar—Pan 33-031 (Eden Seeds, Hatzav, Israel); reduced sensitivity cultivar—Colossus from HSR Seeds (CTS, Hod Hasharon, Israel); susceptible cultivar—Avgaro (Hazera Seeds Ltd., Berurim MP Shikmim, Israel).

Significant efforts were directed towards using specific genetic markers for LWD to identify resistant germplasm and subsequently develop genetically resistant maize inbred lines [45]. Despite these meaningful efforts, the reasons for LWD susceptibility differences among maize cultivars remain obscure. It was gradually revealed that the infection process' outcome results from chemical and histological differences between cultivars [46]. Alongside these efforts, the development of new methods for tracking the pathogen [7][47][48], estimating its distribution and damage [8][14][49], and controlling it in various ways [22][25][41][50][51] remain major goals.

3.2. Chemical Control

3.2.1. From In Vitro Evaluation to a Field Assay of Selected Fungicides

It is important to locate LWD antagonists' fungicides while evaluating their phytotoxicity and efficiency against *M. maydis* and other associated fungi (the stalk-rot complex) involved in LWD [52]. Together with this effort, developing rapid and efficient screening approaches to assess the potential of these fungicides is needed [10][53]. Preliminary tests on growth media plates aimed at screening many chemical preparations rapidly and indicating their efficiency can be conducted with minimal investment and can save time and effort. After eliminating inadequate potential fungicides, selected compounds will be verified in seeds, detached roots, and sprouts' assays. Only in the final phase will a limited number of high-potential selected pesticides be tested in a field experiment throughout the growth season (Figure 4).

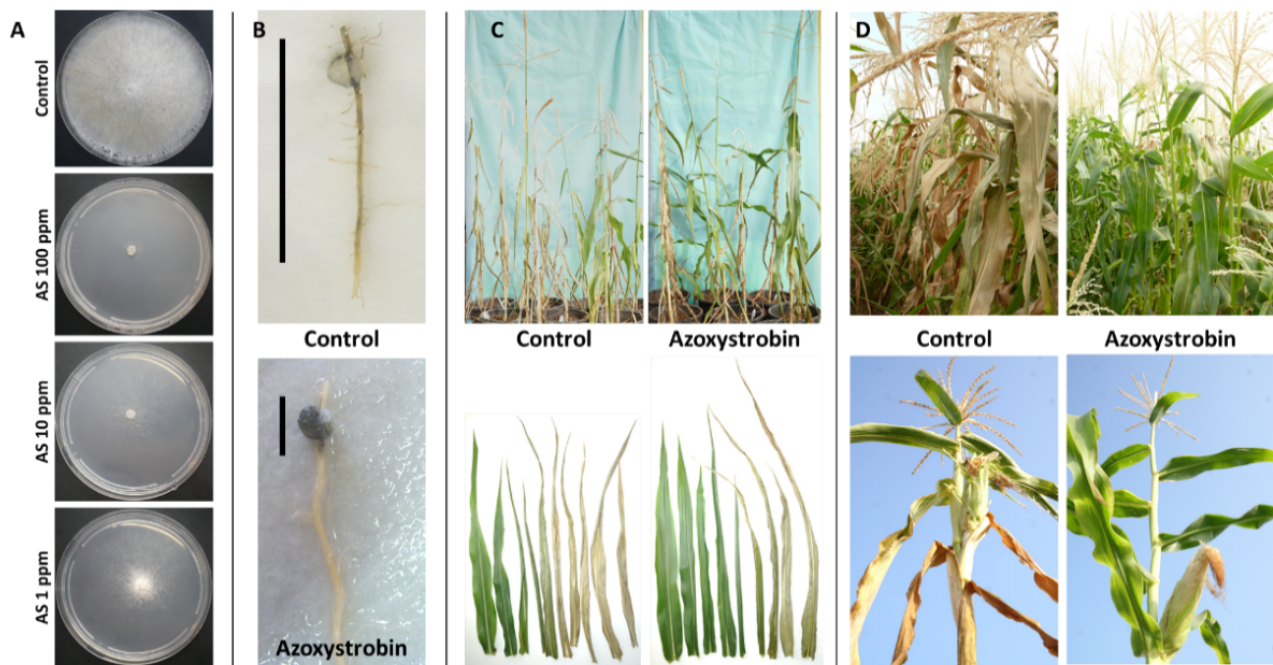


Figure 4. From in vitro evaluation to a field assay of Azoxystrobin. **(A)** Agar plate assay to evaluate the inhibition of *Magnaporthiopsis maydis* mycelial growth by Azoxystrobin (AS, CAS no. 131860-33-8, Amistar, Makhteshim Agan, Airport City, Israel) (adapted from [6]). Photos were taken five days after incubation at 28 °C in the dark. The fungicide was evaluated at a rate of 1, 10, and 100 mg/L active ingredients. Control—potato dextrose agar (PDA) plate without fungicide. **(B)** Detached root pathogenicity assay (adapted from [6]). The main (longest) inner feeder root was cut from a potted 3-week-old Jubilee cv. maize sprout. The detached root was inoculated by placing an *M. maydis* culture disk (6 mm diameter) taken from the margins of a 4–6-day-old colony, two cm away from its cut end. The inoculated roots were incubated in a moist atmosphere, in Petri dishes, at 28 °C in the dark for six days. The pathogen infection thread (a dark filament) within the root is marked in the photos by a black line near each root. Control—root inoculated with *M. maydis* without fungicides. **(C)** Effect of Azoxystrobin seed coating (0.002 cm³/seed) on plant development in a greenhouse (adapted from [54]). A photograph of all the plants' aboveground parts (upper panel) and leaves (lower panel) in the treatment and the non-protected control groups 72 days after sowing (DAS), 13 days after fertilization (DAF). **(D)** Late wilt disease symptoms in a field experiment 71 DAS, 16 DAF (adapted from [55]). Upper panel—wilt symptoms of a non-protected plot (control) compared to an Azoxystrobin-treated plot. Lower panel—representative plants. The fungicide was applied in seed coating (0.002 cm³/seed, Azoxystrobin + Difenconazole, "Ortiva-Top", Syngenta, Basel, Switzerland, supplier Adama Makhteshim, Airport City, Israel) and at three intervals, 18, 31, and 45 DAS, 2.25 L/hectare. Disease symptoms include drying-out that progresses upwards in the plant, stem and leaf yellowing, and dehydration.

3.2.2. Seed Coating

Since the initial infection occurs during the seedling development period [28], the LWD can be managed efficiently with a fungicide seed treatment. Indeed, such attempts have been made in the past. In India, Begum et al. (1989, 1996) showed that seed treatments with captan, carboxin, carbendazim, and thiram significantly reduced late wilt severity and increased yield in the field [56][57]. Yield increased by 25.9% for carbendazim and 34.1% for captan (at 1 g/kg seed).

In contrast, seed treatments failed to prevent late wilt in Egyptian trials [23][58]. According to Johal et al. (2014) [13], such differences can result from variances in the virulence, chemical sensitivity of *M. maydis* isolates, or the consequences of the stalk-rot disease complex in Egyptian soils [52]. Nonetheless, non-chemical seed treatments were tested successfully in Egypt [50][59].

In Israel, in relatively resistant maize with only minor LWD symptoms, the Azoxystrobin seed coating (0.0025 mg active ingredient/seed) prevented fungal development and increased plant and cob weight [10]. Yet, this treatment could not defend a susceptible maize cultivar in heavily infested soil at the disease's wilting burst (60 DAS) and later on. In follow-up work [54], the Azoxystrobin + Difenconazole seed coating (AS + DC, "Ortiva-Top", manufactured by Syngenta, Basel, Switzerland, supplied by Adama Makhteshim, Airport City, Israel) was applied. This treatment was efficient in the initial growth stages (up to 50 DAS). At the later growth stages, the AS-DC seed coating provided an additional layer of protection when combined with the injection of fungicides into the irrigation system, as elaborated in the following section (3.2.3).

3.2.3. Soil Treatments

Systemic fungicides and their fungi-toxic products translocate to maize leaves within two days and can last in maize roots for 90 days [23], so *M. maydis* may be repressed by these chemicals within the root, as well as in the soil. Thus, soil treatments with systemic fungicides, such as Benomyl (Benlate, methyl 1-(Butylcarbamoyl)-1H-1,3-benzimidazol-2-yl methylcarbamate, CAS no. 17804-35-2), were the preferred method of dealing with the disease.

The application method can be game-changing in this regard, as was proven in Egypt [23] and Israel. Abd-el-Rahim and colleagues (1982) found that the systemic fungicide Benylate applied at four 15-day intervals (2.5 kg/acre) after sowing resulted in the best LWD control [13]. In Israel, the application of fungicides into a dripline assigned for each row at 15-day time intervals from sowing inhibited wilt symptom development and recovered cob yield by 100%. More recently, an efficient and more economically applicable solution to LWD was suggested that could be applied on a large scale to shield-susceptible corn varieties in commercial fields [54]. This application is based on antifungal mixtures having a different mode of action to prevent resistance development. The method involved seed coating and injection of Azoxystrobin and Difenconazole mixture (AS+DC) into the irrigation system at three 15-day intervals from sowing. Economic efficacy was reached using one dripline for two adjacent rows (a row spacing of 50 cm instead of 96 cm).

Nowadays, drip irrigation is considered one of the most effective chemical methods to restrict maize LWD but it is the most expensive of the present alternatives [54]. Moreover, growing resistance to these antifungals and the resulting control failure have become a significant problem [60]. Since fungicide treatment limitation exerts increasing pressure in many countries due to environmental and potential health risks, searching for alternatives to cope with LWD is a continuous effort.

3.3. Biological Control

3.3.1. Strengthening Beneficial Microorganism Communities in the Soil and Their Secreted Metabolites

Biopesticides are environmentally friendly and occupy an increasingly central place in worldwide scientific research. Many studies were directed towards LWD biological control [20][61][62][63][64]. These methods include operating and strengthening beneficial microorganism communities in the soil (for example, by compost addition [61]) or direct intervention using antagonistic bacteria and fungi or their secreted metabolites. Plant-growth-promoting rhizobacteria and seed treatments with biocontrol formulations (*B. subtilis*, *Bacillus pumilus*, *P. fluorescens*, *Epicoccum nigrum*) were suggested for maize LWD control and tested in the field with encouraging results [51]. Another example is the use of a filtrate of mixed strains of the cyanobacteria *Anabaena oryzae*, *Nostocmuscorum*, and *N. calcicola* [61]. An alternative approach was to use marine algae and cyanobacteria *A. oryzae* extracts exhibiting antifungal activities to target the LWD pathogen [62].

3.3.2. *Trichoderma* spp. Maize Late Wilt Biocontrol

Late wilt disease can also be biologically controlled using *Trichoderma* spp. This genus' species can form endophytic mutualistic relationships with various plant species [65]. Other *Trichoderma* species have been identified to possess biocontrol potential against plants' fungal pathogens [66]. For instance, *Trichoderma cutaneum* reduced the incidence of LWD of maize under greenhouse conditions [63]. Likewise, *Trichoderma harzianum* treatment was efficient against *M. maydis* in the field [67]. The application of *Trichoderma viride* alone, or even better with chitosan NPs combined with the mycorrhizae *Glomus mosseae*, controlled late wilt and enhanced the plants' growth indices [68]. To maximize the impact of *Trichoderma*-based treatments, Elshahawy and El-Sayed (2018) [20] showed that extracts of the microalgae, *Chlorella vulgaris*, with each of the *Trichoderma* species, *T. virens* and *T. koningii*, led to effective LWD control.

The potential for using *Trichoderma*-based treatment against Israeli *M. maydis* strains has only recently been tested [69]. *Trichoderma longibrachiatum* (T7407) and *Trichoderma asperelloides* (T203) isolates have solid antagonistic activity against the Israeli *M. maydis* strain. These eco-friendly agents were tested in a series of experiments in the laboratory (Figure 5) until their final examination in pots under field conditions throughout an entire growing season (Figure 6).

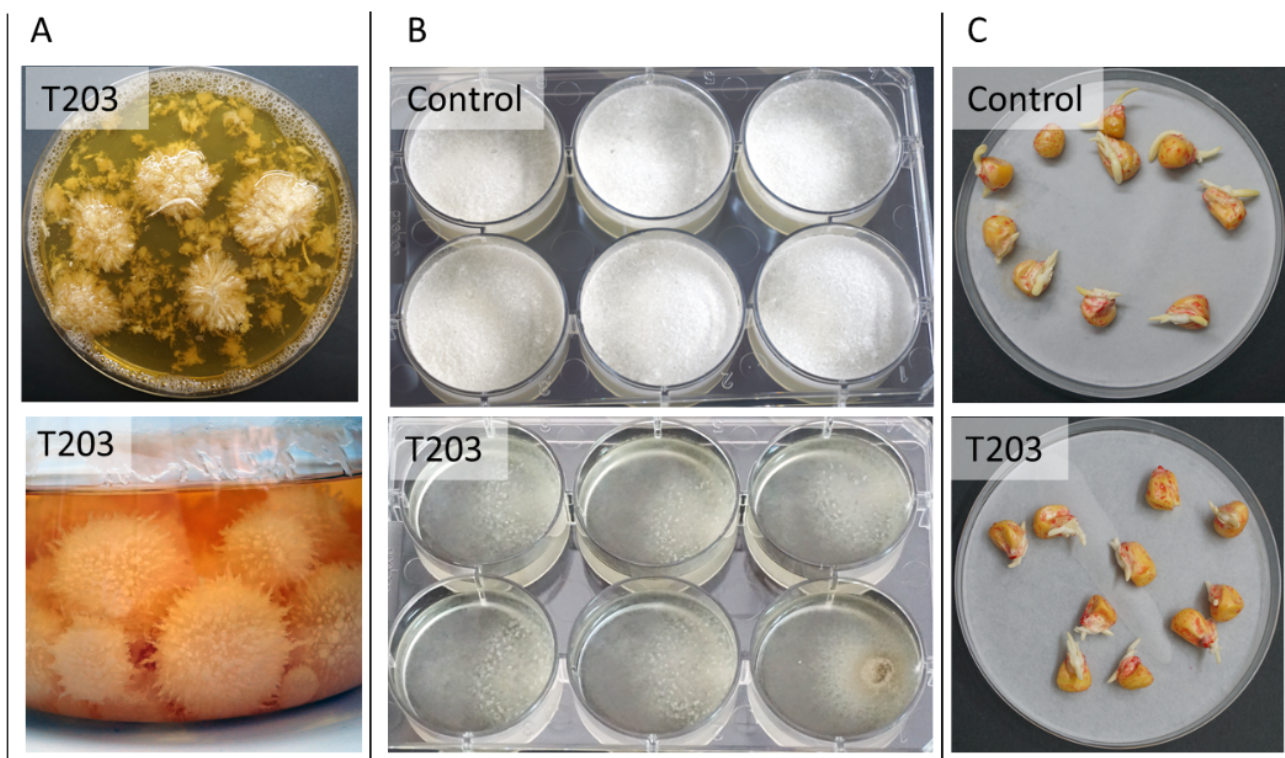


Figure 5. In vitro estimation of *Trichoderma asperelloides* (T203)-secreted metabolites-based biological control against *Magnaporthiopsis maydis* (adapted from [69]). (A) T203-submerged cultures grown with shaking (150 rpm) for isolating secreted metabolites. (B) Static shallow media cultures of *M. maydis* on potato dextrose broth (PDB) medium containing T203-secreted metabolites filtrate. Control is PDB medium *M. maydis* cultures maintained under the same conditions. (C) Effect of growth media of T203 isolate on corn seed germination. The seeds were germinated in Petri dishes soaked in 4 mL of PDB (control) or PDB + secretion products (growth medium filtrate six days after T203 growth). All images are displayed after 5–6 days incubation at 28 ± 1 °C in the dark.

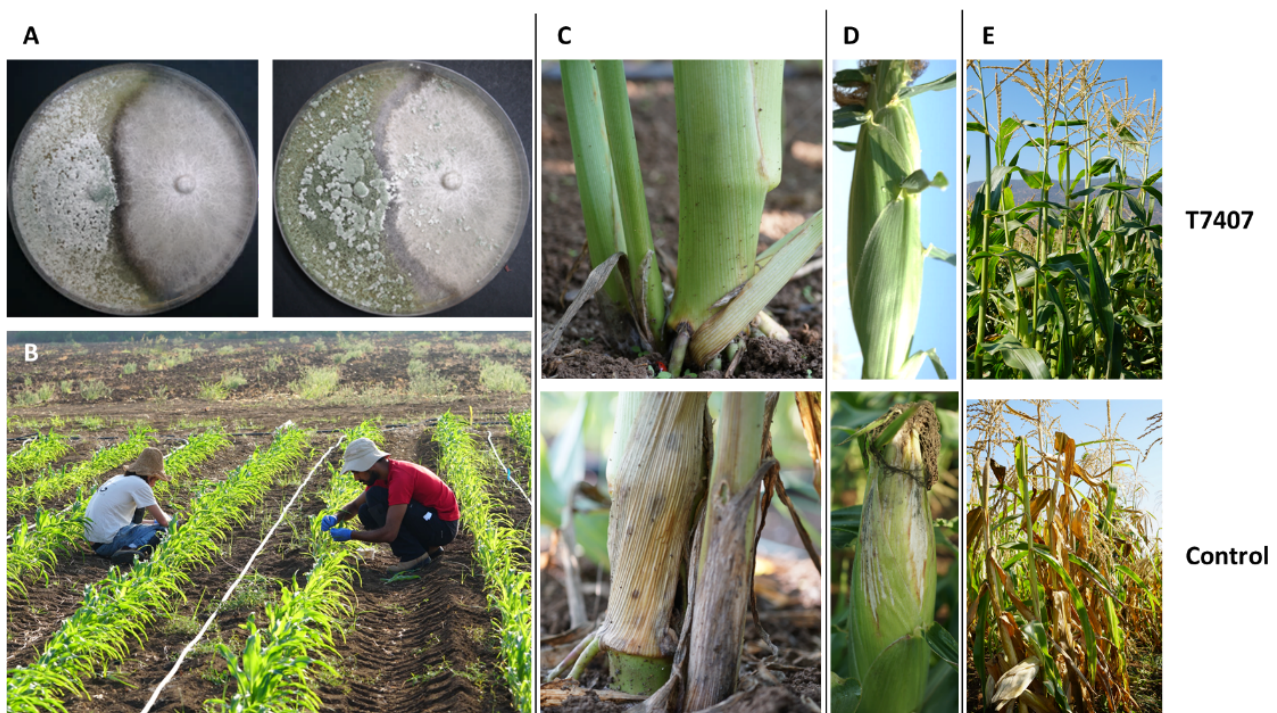


Figure 6. *Trichoderma longibrachiatum* (T7407) biological control against *Magnaporthiopsis maydis* in the lab and the field (adapted from [69][70]). (A) Plate mycoparasitism assay to identify interactions between *Magnaporthiopsis maydis* and T7407 in a potato dextrose agar (PDA)-rich medium. The two fungi were placed opposite each other, T7407 on the left and *M. maydis* on the right. Photos were taken after 3 and 10 days of growth. (B) Field inoculation of 20-day-old seedlings by an *M. maydis*-infected toothpick. The toothpicks were used for stabbing each plant at the near-surface portion of the stem. (C) The lower stem (first aboveground internode) disease symptoms. (D) The cobs' spathes disease symptoms. (E) The experiment's plots. Representative images of the field plants were taken 82 days after sowing. Controls are unprotected diseased plants.

In solid and submerged media culture growth assays, these species secrete soluble metabolites that inhibit or kill the maize pathogen [69]. Such a metabolite was recently isolated and identified as pyrone 6-pentyl-2H-pyran-2-one (6-pentyl- α -pyrone or 6-PP) [71]. This potent *M. maydis* antifungal compound is secreted by *Trichoderma asperellum* (P1), an endophyte separated from maize seeds of a cultivar susceptible to LWD [72]. The 6-PP metabolite was previously identified as one of the key bioactive compounds of several *Trichoderma* species [73].

3.3.3. Manipulating the Plant Microbiome

The soil pathogen, *M. maydis*, interacts with the maize endophytes, which may provide the plant's first defense line. Recently, such endophytes were isolated from six sweet and fodder maize hybrids with deferent sensitivity to LWD [72]. These include ten fungal species belonged to *Chaetomium*, *Trichoderma*, *Penicillium*, *Rhizopus*, *Alternaria*, and *Fusarium* genera, and one bacterial species, *B. subtilis*.

In cotton plants, interactions between *M. maydis* and *Fusarium oxysporum* (the cotton wilt agent) led to an interesting result—reduced symptoms of the cotton wilt disease [33]. Similar antagonistic relationships in cotton plants were found between *M. maydis* and *Macrophomina phaseolina*, the charcoal rot disease agent [32].

3.4. Agrotechnical Measures

3.4.1. Various Cultural Methods

Agrotechnical applications were also reported in varying degrees of maturity in field experiments. These methods, which had a beneficial impact on LWD suppression, include excessive irrigation (pot experiments conducted in an open-air enclosure) [74] and applying plant extracts (*Lycium europaeum* [22], aloe vera (*Barbados Aloe*) fleshy leaves, onion bulbs, garlic cloves, jimsonweed, and peppermint leaves). In addition, soil solarization to increase temperatures above 35 °C with transparent polyethylene film [21], balanced soil fertility [19][76], and avoiding drought stress[74][77] can reduce LWD severity and yield losses. *Magnaportheiopsis maydis* survival is restricted to the top 20 cm of soil [78], and survival depends mainly on infected crop residues. Thus, sanitation measures such as deep tillage and annual plowing may significantly impact LWD (Dr. J. Leslie, personal communication) [14]. Finally, it was shown that organic compounds [59] and non-traditional methods such as adding nanosilica and zinc oxide nanoparticles [51] have promising potential to reduce late wilt in the field.

3.4.2. Beneficial Mycorrhizal Communities

Preserving soil mycorrhizal fungi between growth periods has been essential in crop protection (summarized by [64]). Preserving the integrity and continuity of the soil mycorrhizal networks may provide the plant with higher resistance to soil diseases [79], including late wilt disease [25]. In Portugal, Patanita et al. (2020) [25] showed that *M. maydis* presence reduction and grain production were significantly improved when both minimum tillage and cover crop were applied. It was also found that arbuscular root colonization was higher following these practices.

In Israel, agricultural practice based on conserving soil microflora integrity (by avoiding tillage) and influencing its nature (by cultivating specific crops in a dual-season growth) was applied [26]. When maize was seeded on wheat soil, a significant improvement in growth parameters and LWD repression was measured. This achievement was not affected drastically by tillage. Indeed, crop plants acquired a mycorrhizal community closely related to that of the former host plant and different from that found when the soil was disturbed by tillage or not cropped before the growth [80].

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