Tolerance to and Alleviation of Abiotic Stresses in Plants Mediated by *Trichoderma* spp.

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Contents

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1 Introduction

Climate change, as an ongoing scenario, is already markedly interfering with agricultural productivity and food security in the world, with a gloomy scenario in the near future (Zari 2014; Daryanto et al. 2016; Naumann et al. 2018). According to a FAO report (FAO 2007), less than 5% of the entire land area of the planet has not yet been altered by human activity. Food production issues associated with abiotic stresses in plants will remain in evidence in the near future, partially driven by (i) the consequences of COVID-19's huge impact in global economy, (ii) the necessity of reducing carbon footprint on Earth (Stern 2016), and (iii) the loss of biodiversity that will affect ecosystems and economy in an interdependent manner (Dasgupta 2008; Trisos et al. 2020; Rousseau and Deschacht 2020).

Throughout evolution, plants have accumulated mechanisms of response to various environmental factors that cause stress, allowing their adaptation to a variety of environments (Devi et al. 2017). These responses involve individually or jointly regulated signaling pathways, involving molecules such as ions, metabolites, cofactors, phytohormones, reactive oxygen species (ROS), and mitogen-activated phosphorylation cascades (MAP kinases activities) for induction of adaptive responses (Lata et al. 2018). In addition, plants make symbiotic/mutualistic interactions with rhizospheric and phyllospheric microorganisms that often result in an integrated relationship in which the roles of endophytes help induce abiotic stress tolerance for the holobiont (Lewis 1985; Marasco et al. 2012; Hardoim et al. 2015). To cope with harmful effects of abiotic stresses, microorganisms can directly synthesize anti-stress protective compounds (e.g., amino acids, glycine betaines, polyamines, amides, etc.) or act indirectly, through interfering with plant gene expression and synthesis of enzymes, hormones, and signaling proteins/molecules that activate the plant's stress-response system soon after exposure (Schulz et al. 2002; Chakraborty et al. 2015). In addition, microbes can promote growth, which aids in the prevention of losses in plant vitality (Harman and Uphoff 2019).

The fungal genus *Trichoderma* stands out in the context of microbial-induced beneficial effects to plants, as it is the basis for a variety of commercially available biopesticides, biofungicides, biofertilizers, and soil conditioners (Harman et al. 2004; Vinale et al. 2008; López-Bucio et al. 2015). This is possible because this genus has several species with multiple abilities, such as antagonism to a diversity of plant pathogens, enhancement of plant defense mechanisms, and improvement of plant growth and development (Loguercio et al. 2009a; El_Komy et al. 2015; Jalali et al. 2017; Ghorbanpour et al. 2018; Lombardi et al. 2018). Another interesting characteristic that has been described for *Trichoderma* species is related to their contribution to the relief of abiotic stresses in plants (e.g., Xiang et al. 2012; Calvo et al. 2014). Species of this fungus display a genetic arsenal that allow the production of an array of metabolites with antifungal and antibiotic activity, as well as with bioactivities of potential pharmaceutical use (Duran et al. 2010). Some of these metabolites can also help plant hosts to cope with harmful effects of abiotic stresses (Meena et al. 2017). In this context, the multifunctional properties of *Trichoderma*

are highly advantageous for the development of environmentally sustainable strategies for agriculture (Harman 2011a, b; Glare et al. 2012; Berg et al. 2013; Chakraborty et al. 2015; Chojnacka 2015; Kumar and Verma 2018; Lata et al. 2018).

In this chapter, we adopted a systematic/integrative evaluation of the literature to describe the use of *Trichoderma* spp. in the alleviation of the negative effects of abiotic stresses in plants. The methods were based on qualitative and quantitative assessments of the scientific literature according to the methods described below. The main topics analyzed were (i) temporal and geographic aspects of the selected studies, (ii) species of *Trichoderma* and the plants/crops involved, (iii) types of abiotic stresses, (iv) mechanisms that *Trichoderma* use to minimize the negative effects of abiotic stresses in plants, and (v) plant genes possibly involved in interactive mechanisms with *Trichoderma* that ameliorate the stresses. Application potentialities and future research directions on this issue were also addressed.

2   Overview of the Methods and Procedures

The elaboration of the questions and the research protocol (Table 1) for the systematic part of the review research in this chapter were based on five components of the method described by Kitchenham (2004): (i) *population*, plant species that suffer the effects of abiotic stress; (ii) *intervention*, *Trichoderma* species/isolates applications; (iii) *comparison*, stress-bearing plants with vs without effects from interactions with *Trichoderma* species; (iv) *hypothesis*, *Trichoderma* spp., on average, which reduce the negative effects caused by abiotic stresses on plants; and (v) *type of study*, scientific articles containing primary studies. Quantitative and qualitative data collection during the research was based, therefore, on the question of what is the magnitude of the *Trichoderma* species' potential to ameliorate the negative effects caused by abiotic stresses on plants. The overall sequence of systematic steps of this chapter is described briefly as follows: the literature research was carried out using two keywords, "*Trichoderma*" and "abiotic stress," with the aid of the "Publish or Perish" version 6.2 program (P&P) (Harzing 2007) for the publications until February 2018; the Google Scholar was chosen as the main database used through the P&P program because it provides access to studies from virtually all databases and publishers available on the web. For the period of 2018–2020, the same two keywords were searched directly in the Web of Science, Scopus, and PubMed databases; this procedure aimed to provide a more representative sampling of the literature, with emphasis on the more recent research covered in the three mostly accessed databases. The initial search by P&P was performed using the two keywords above located anywhere in the full text of the publications. Since the P&P's criterion for ranking the retrievable studies is their number of citations, which we considered as an important parameter for quality and representativeness of our sampling (Harzing 2007), the research was limited to the first 1000 studies in English retrievable by P&P. The first approach to all these retrieved studies was based on the detailed reading of the corresponding titles and abstracts to retain only

Table 1 Research protocol for the systematic review of web-based scientific literature

General information		
Description	The genus *Trichoderma* is widely known to have isolates that are used as biocontrol agents of plant diseases and promoters of plant growth. In addition, other studies suggest that isolates of this genus may also provide plant tolerance to a variety of abiotic stresses. This study aims to describe the current situation of knowledge about *Trichoderma* species/isolates that showed this improvement effect in plants submitted to different types of abiotic stress	
Objectives	Check which *Trichoderma* species can increase the plant's tolerance to stressful abiotic factors	
	Use data collection to investigate information on plant/crop amplitude researched on stress relief	
	To analyze the types of abiotic stresses, the species of the genus *Trichoderma* can decrease in plants	
	Evaluate the methodologies used in the studies regarding the mechanisms of action that are observed in the *plant-Trichoderma* interaction to reduce the effects caused in the plant due to the abiotic stress suffered	
	Gather information on the alteration of the expression of plant genes involved in the mechanisms of action against the negative effects of abiotic stress in the presence of species of the genus *Trichoderma*	
Aspects of research		
Question	What is the magnitude of the potential of *Trichoderma* fungal species to control or decrease the negative effects caused by abiotic stresses on plants?	
Population	Plant species that suffer from abiotic stress and interact with *Trichoderma* spp.	
Intervention	Decreased effects of abiotic stress on plant interaction with *Trichoderma* species	
Comparison	Measurable effects of plants with stress and no interaction with *Trichoderma* vs plants with stress and interaction with *Trichoderma* species/isolates	
Hypothesis	*Trichoderma* spp. decreases the negative effects caused by abiotic stresses on plants	
Expected result	The systematic analysis of the related literature will allow to verify the hypothesis formulated in relation to the mitigation of stresses caused by abiotic factors in plants as a result of its interaction with *Trichoderma* spp.	
Type of studies	Primary studies in the form of scientific articles	
Identification of studies		
Keywords	"*Trichoderma*," "abiotic stress"	
Search string	"*Trichoderma*" **and** "abiotic stress"	
Font selection criteria for search	Peer-reviewed editors/journals and editorial boards	
	Available on the Internet	
List of search sources	PubMed	
	Scopus	
	Web of Science	
	Google academic (Publish or Perish)	

Table 1 (continued)

Online search strategy	*Google Scholar*-based "Publish or Perish" v. 6.2 (Harzing 2007) until 2018 (Research in 07/Feb2018)
	Research in *PubMed*, *Scopus* and *web of science* databases for 2018–2020 (research in 08/Sep/2020)

| **Selection and evaluation of studies**	
Inclusion and exclusion criteria for studies	*Inclusion*:
	Written in English
	Primary studies/articles (including special editions)
	Articles focused on abiotic stress
	Exclusion:
	Not aligned with the object of study
	Simple or expanded abstract, review, chapter/book, dissertation, and thesis
	Article that has no plant experiments
	Article focusing on biocontrol and/or other biotic stressors (e.g., phytopathogens)
	Failure or inconsistency between methodology and results/conclusions
Strategy for the initial selection of studies	Detailed reading of:
	Title
	Summary
	Keywords
Strategy for the final selection of studies	Detailed reading of the full text of the article
	Presence of all inclusion criteria
	Absence of all exclusion criteria
Evaluation of the quality of the study	*Research* online:
	"Publish or Perish" quality criteria (based on the number of citations per year)
	Selected studies:
	Inclusion and exclusion criteria
	Subjective judgment of agreement between hypotheses, experimental procedures, results, and conclusions

(continued)

those specifically dealing with the central theme of this research. From this procedure, 134 papers were selected (Fig. 1), including 71 primary studies, 30 reviews, 28 book chapters, 3 theses/dissertations, and 2 open letters. To confirm the quality and consistency of these studies, the criterion of displaying a recognized peer review system and editorial board was observed. Based on this experience, for the studies retrieved directly from the three databases indicated above for the years 2018–2020, the focus was directly on the "title" and "abstract" sections to select studies specifically related to our investigation. With this procedure, 46 primary studies were initially retrieved, and, after the analysis of the abstract contents, 19 papers were retained and added to the local database under assessment (Fig. 1).

Table 1 (continued)

Data synthesis and presentation of results	
Data extraction strategy	*Items to collect/evaluate:*
	Objective (Abstract)
	Conclusions (abstract)
	Keywords;
	Country where the study was done
	Trichoderma species involved in stress mitigation
	Trichoderma isolates
	Type of stress
	Plant/crop used for the experiments
	Genes involved in the interaction plant-*Trichoderma*
	Variables/effects measures: increase of biomass (plant size, fresh and dry weight); higher gene expression (plant or fungus); physiological parameters etc.
	Mean and standard deviation or error of measures of effect
	New ideas raised in the evaluated study (*Discussion Section*)
Data summarization strategy	Tables, graphic, images, description in text
Publishing strategy	Scientific journal with scope of agricultural sciences, plant biology, applied microbiology, and biotechnology

In the next step, we applied a series of inclusion/exclusion criteria established in the protocol, so that those studies presented in the form of proceedings' abstracts, theses, dissertations, reviews, book chapters, and open letters were removed; only the 71 research articles containing primary studies remained. For the three databases direct search, two papers were removed, leaving us with 17 studies for the next steps (Fig. 1). With all these initially selected studies, the reading of the full text was performed for data extraction and qualitative/quantitative assessments. During this process, three articles from the P&P search and five from the three databases direct searches were further removed based on lack of key information required for our research analyses (i.e., they did not meet inclusion criteria), leaving us with a final number of 68 + 12 articles (Fig. 1), in a total of 80 primary studies articles that composed the literature database used for the systematic part of this chapter (Table 2). Further validation and integration of the systematized knowledge collected were achieved by assessing related publications, through regular (classical) database search, according to specific aspects of interest suggested by the up-to-date literature obtained in the systematic review.
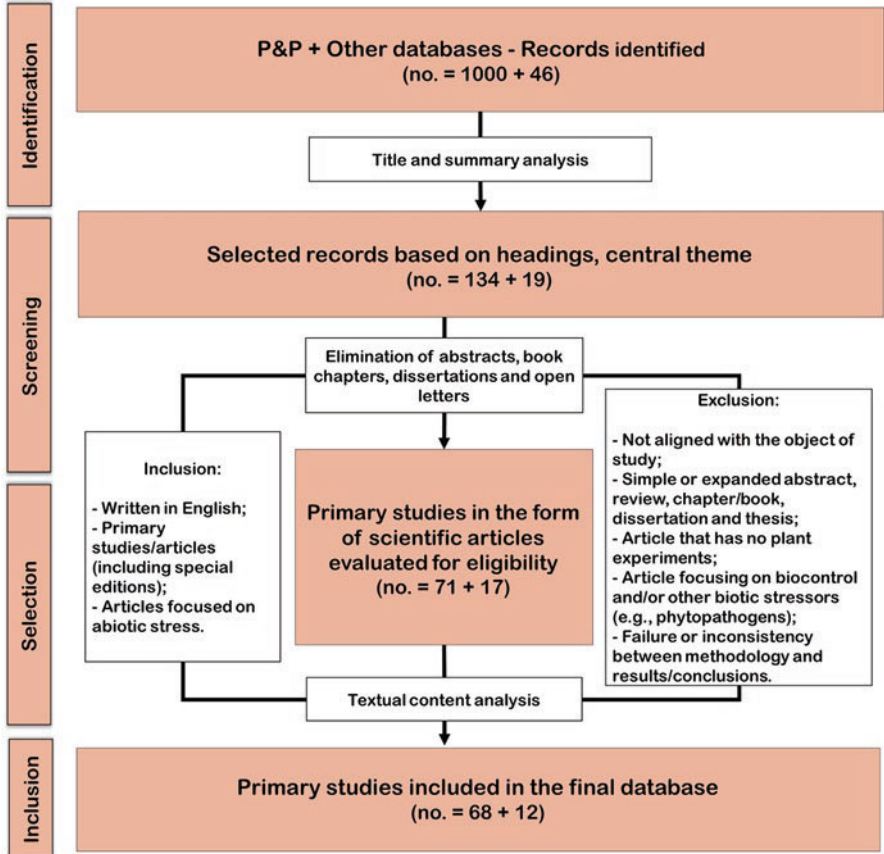
Fig. 1 Flow diagram of the search strategy, selection of studies, and data management procedure on the role of the genus *Trichoderma* in generating plant tolerance to a variety of abiotic stresses

3 When, Where, and How *Trichoderma* Has Been Tested for Abiotic Stress Alleviation?

3.1 Language and Timing of the Science on Trichoderma-*Plant-Abiotic Stress Interactions*

Considering the most recurring words in the titles of the 1046 initial studies retrieved and in the 80 finally selected papers, and after taking the searching keywords "*Trichoderma*" and "abiotic stress" away from the analyses, the words "plant(s)," "*harzianum*," and "growth" (Fig. 2) were highlighted. After selection of the studies according to the established criteria (see review methods), the words related to the

Table 2 Final database of articles included in the systematic review

Authors	Scientific journal	DOI access
Abd El-Baki and Mostafa 2014	*Acta Biologica Hungarica*	https://doi.org/10.1556/ABiol.65.2014.4.9
Ahmad et al. 2015	*Frontiers in Plant Science*	https://doi.org/10.3389/fpls.2015.00868
Azarmi et al. 2011	*African Journal of Biotechnology*	https://doi.org/10.5897/AJB10.1600
Babu et al. 2014	*Journal of Environmental Management*	https://doi.org/10.1016/j.jenvman.2013.10.009
Badar et al. 2015	*Journal of Pharmacognosy and Phytochemistry*	https://www.phytojournal.com/archives/2015/vol3issue6/PartB/3-6-38.1-841.pdf/3-6-38.1.pdf
Bae et al. 2009	*Journal of Experimental Botany*	https://doi.org/10.1093/jxb/erp165
Bakhshandeh et al. 2020	*Plant Growth Regulation*	https://doi.org/10.1007/s10725-019-00556-5
Becquer et al. 2018	*Cuban Journal of Agricultural Science*	http://scielo.sld.cu/pdf/cjas/v51n4/2079-3480-cjas-51-04-489.pdf
Brotman et al. 2013	*PLoS Pathogens*	https://doi.org/10.1371/journal.ppat.1003221
Buysens et al. 2016	*Applied Soil Ecology*	https://doi.org/10.1016/j.apsoil.2016.04.011
Caporale et al. 2014	*Journal of Plant Physiology*	https://doi.org/10.1016/j.jplph.2014.05.011
Chepsergon et al., 2016	*British Microbiology Research Journal*	https://doi.org/10.9734/BMRJ/2016/26015
Chepsergon et al. 2018	*Plant Pathology & Quarantine*	https://doi.org/10.5943/ppq/8/1/5
Contreras-Cornejo et al. 2014	*Molecular Plant-Microbe Interactions*	https://doi.org/10.1094/MPMI-09-13-0265-R
Contreras-Cornejo et al. 2015	*Journal of Plant Growth Regulation*	https://doi.org/10.1007/s00344-014-9471-8
Dana et al. 2006	*Plant Physiology*	https://doi.org/10.1104/pp.106.086140
Devi et al. 2017	*Indian Journal of Experimental Biology*	http://nopr.niscair.res.in/bitstream/123456789/41180/1/IJEB%2055%284%29%20235-241.pdf
Dixit et al. 2011	*PLOS ONE*	https://doi.org/10.1371/journal.pone.0016360
Donoso et al. 2008	*Applied and Environmental Microbiology*	https://doi.org/10.1128/AEM.02013-07
Elkelish et al. 2020	*Environmental and Experimental Botany*	https://doi.org/10.1016/j.envexpbot.2019.103946
Fu et al. 2017	*PLOS ONE*	https://doi.org/10.1371/journal.pone.0179617
Ghorbanpour et al. 2018	*Scientia Horticulturae*	https://doi.org/10.1016/j.scienta.2017.11.028
Govarthanan et al. 2018	*Ecotoxicology and Environmental Safety*	https://doi.org/10.1016/j.ecoenv.2018.01.020

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Guler et al. 2016	*Acta Physiologiae Plantarum*	https://doi.org/10.1007/s11738-016-2153-3
Gusain et al. 2014	*African Journal of Agricultural Research*	https://doi.org/10.5897/AJAR2014.8575
Hanci et al. 2014	*Tarım Bilimleri Araştırma Dergisi*	http://ijans.org/index.php/ijans/article/view/287/280
Hashem et al. 2014	*Journal of Plant Interactions*	https://doi.org/10.1080/17429145.2014.983568
Hermosa et al. 2011	*Journal of Plant Physiology*	https://doi.org/10.1016/j.jplph.2011.01.027
Jalali et al. 2017	*Fungal Ecology*	https://doi.org/10.1016/j.funeco.2017.06.007
Khomari and Davari 2017	*Journal of Plant Physiology and Breeding*	https://breeding.tabrizu.ac.ir/article_6350_6427f52ffa3652b6761f0e890a3c2ef1.pdf
Khomari et al. 2017	*New Zealand Journal of Crop and Horticultural Science*	https://doi.org/10.1080/01140671.2017.1352520
Khoshmanzar et al. 2020	*International Journal of Environmental Science and Technology*	https://doi.org/10.1007/s13762-019-02405-4
Kumar et al. 2016	*Journal of Basic Microbiology*	https://doi.org/10.1002/jobm.201600369
Ma et al. 2020	*Pakistan Journal of Botany*	https://doi.org/10.30848/PJB2020-3(25)
Mastouri et al. 2010	*Phytopathology*	https://doi.org/10.1094/PHYTO-03-10-0091
Mastouri et al. 2012	*Molecular Plant-Microbe Interactions*	https://doi.org/10.1094/MPMI-09-11-0240
Mishra et al. 2016	*World Journal of Microbiology and Biotechnology*	https://doi.org/10.1007/s11274-016-2086-4
Mona et al. 2017	*Journal of Integrative Agriculture*	https://doi.org/10.1016/S2095-3119(17)61695-2
Montero-Barrientos et al. 2010	*Journal of Plant Physiology*	https://doi.org/10.1016/j.jplph.2009.11.012
Nongmaithem and Bhattacharya 2017	*International Journal of Current Microbiology and Applied Sciences*	https://doi.org/10.20546/ijcmas.2017.606.116
Nzioki and Mutisya 2016	*International Journal of Agriculture and Environmental Research*	http://ijaer.in/uploads/ijaer_02__55.pdf
Pandey et al. 2016	*Planta*	https://doi.org/10.1007/s00425-016-2482-x
Pehlivan et al. 2017	*Acta Physiologiae Plantarum*	https://doi.org/10.1007/s11738-017-2375-z

Table 2 (continued)

Authors	Scientific journal	DOI access
Poosapati et al. 2014	SpringerPlus	https://doi.org/10.1186/2193-1801-3-641
Poveda et al. 2019	Frontiers in Plant Science	https://doi.org/10.3389/fpls.2019.01478
Poveda 2020	Agronomy	https://doi.org/10.3390/agronomy10010118
Qi and Zhao 2012	Journal of Basic Microbiology	https://doi.org/10.1002/jobm.201200031
Rawat et al. 2011	Plant and Soil	https://doi.org/10.1007/s11104-011-0858-z
Rawat et al. 2012	Journal of Plant Pathology	https://doi.org/10.4454/JPP.FA.2012.026
Rawat et al. 2013	Archives of Phytopathology and Plant Protection	https://doi.org/10.1080/03235408.2013.769316
Rawat et al. 2016	Molecular Soil Biology	https://doi.org/10.5376/msb.2016.07.0004
Roatti et al. 2013	Phytopathology	https://doi.org/10.1094/PHYTO-02-13-0040-R
Rouphael et al. 2017	Frontiers in Plant Science	https://doi.org/10.3389/fpls.2017.00131
Rubio et al. 2017	Frontiers in Plant Science	https://doi.org/10.3389/fpls.2017.00294
Sánchez-Montesinos et al. 2019	International Journal of Environmental Research and Public Health	https://doi.org/10.3390/ijerph16112053
Sharma and Singh 2014	Journal of Applied and Natural Science	https://doi.org/10.31018/jans.v6i2.479
Shukla et al. 2012	Plant Physiology and Biochemistry	https://doi.org/10.1016/j.plaphy.2012.02.001
Shukla et al. 2014	Annals of Applied Biology	https://doi.org/10.1111/aab.12160
Singh and Dwivedi 2018	Journal of Pharmacognosy and Phytochemistry	http://www.phytojournal.com/archives/2018/vol7issue2/PartAJ/7-2-300-161.pdf
Singh et al. 2018	International Journal of Current Microbiology and Applied Sciences	https://doi.org/10.20546/ijcmas.2018.705.174
Singh et al. 2019	Plant Physiology and Biochemistry	https://doi.org/10.1016/j.plaphy.2019.09.015
Singh et al. 2020b	Scientific Reports	https://doi.org/10.1038/s41598-020-61,140-w
Soliman et al. 2020	Phyton	https://doi.org/10.32604/phyton.2020.08795
Song et al. 2014	Applied Soil Ecology	https://doi.org/10.1016/j.apsoil.2014.09.007
Su et al. 2017	Chemosphere	https://doi.org/10.1016/j.chemosphere.2017.02.048
Tripathi et al. 2013	Ecotoxicology and Environmental Safety	https://doi.org/10.1016/j.ecoenv.2012.10.017

Tripathi et al. 2017	*Environmental Pollution*	https://doi.org/10.1016/j.envpol.2016.12.073
Vargas et al. 2017	*Environmental and Experimental Botany*	https://doi.org/10.1016/j.envexpbot.2017.01.009
Vieira et al. 2017	*Plant Physiology and Biochemistry*	https://doi.org/10.1016/j.plaphy.2017.10.012
Vithya et al. 2018	*Journal of Plantation Crops*	https://doi.org/10.25081/jpc.2018.v46.i1.3535
Yasmeen and Siddiqui 2017	*Acta Botanica Croatica*	https://doi.org/10.1515/botcro-2016-0054
Zaidi et al. 2017	*Field Crops Research*	https://doi.org/10.1016/j.fcr.2017.05.003
Zhang et al. 2015	*Plant Physiology and Biochemistry*	https://doi.org/10.1016/j.plaphy.2015.05.007
Zhang et al. 2016a	*Canadian Journal of Plant Science*	https://doi.org/10.1139/cjps-2014-0265
Zhang et al. 2016b	*Frontiers in Plant Science*	https://doi.org/10.3389/fpls.2016.01405
Zhang et al. 2018	*Ecotoxicology and Environmental Safety*	https://doi.org/10.1016/j.ecoenv.2018.03.047
Zhang et al. 2019a	*BMC Plant Biology*	https://doi.org/10.1186/s12870-018-1618-5
Zhang et al. 2019b	*International Journal of Molecular Sciences*	https://doi.org/10.3390/ijms20153729
Zhao and Zhang 2015	*Journal of Integrative Agriculture*	https://doi.org/10.1016/S2095-3119(14)60966-7
Zhao et al. 2014	*Journal of Basic Microbiology*	https://doi.org/10.1002/jobm.201400148

main types of stresses investigated became highlighted. Other frequent title words found for the 1046 studies were "tolerance," "resistance," "induced," "response," "stresses," "gene," and "expression," thus referring to the interaction between *Trichoderma* and plants (Fig. 2a). When observing the wording of the 80 finally selected primary studies, the following groups of terms acquired more relevance: (i) "growth," as the main response variable for plant studies of this nature; (ii) "*harzianum*" and "*asperellum*," related to the most common *Trichoderma* species used in the studies; (iii) "rice" and "maize", indicating the most tested plant species; (iv) "drought," "salt," and "salinity," as well as "cadmium" and "arsenic' (representing metal-polluting elements), which refer to the most studied stresses; and (v) "seed(ling)" as the main part of the plant for inoculation/assessments (Fig. 2b). The word "gene" is relatively recurrent in both word clouds. These results, at a first glance, point to the trend that the research specifically dealing with abiotic stresses is focusing on those two *Trichoderma* species, three crops, and three types of stress, with a preferable form of inoculation.

From a temporal standpoint, research on *Trichoderma*, beyond their use as biocontrol agents against phytopathogens, began to grow exponentially from 2006 onward (Fig. 2), likely due to, at least in part, an increased consciousness of the negative consequences of global warming and climate changes for sustainable agriculture. It is worth to highlight the years of 2014, followed by 2017, in which more studies were published. The number of articles on *Trichoderma* in general began to increase in the 2000s, roughly coinciding with the raise in the number of commercially available bioproducts (Waghunde et al. 2016). Since 2014, there are already more than 250 registered bioproducts in the world that are based on *Trichoderma* species, either individually or in combinations (Woo et al. 2014), which correspond to around 60% of the world's biofungicide market. *Trichoderma harzianum* comprises ~83% of these products (Topolovec-Pintarić 2019) and also corresponds to one of the most recurrent words in the recovered studies (Fig. 2b). Bioproducts represent a small share of the plant-protection market, mainly due to their slow activity and dependence on environmental factors, which has been seen as a constraint to their effectiveness in the field (Singh et al. 2018); further issues related to difficulties and costs of registration add to this context (Topolovec-Pintarić 2019). However, the reported increase in their utilization likely reflects the current demand for healthier foods, free from chemical residues (Gomiero 2018). The use of *Trichoderma* as biofertilizers to improve plant growth has facilitated registration, thereby increasing its availability in the market (Topolovec-Pintarić 2019). It is noteworthy that the potential of offering bioproducts at lower costs for smallholders to deal with their production necessities can assist with food security globally (Harman 2011b).
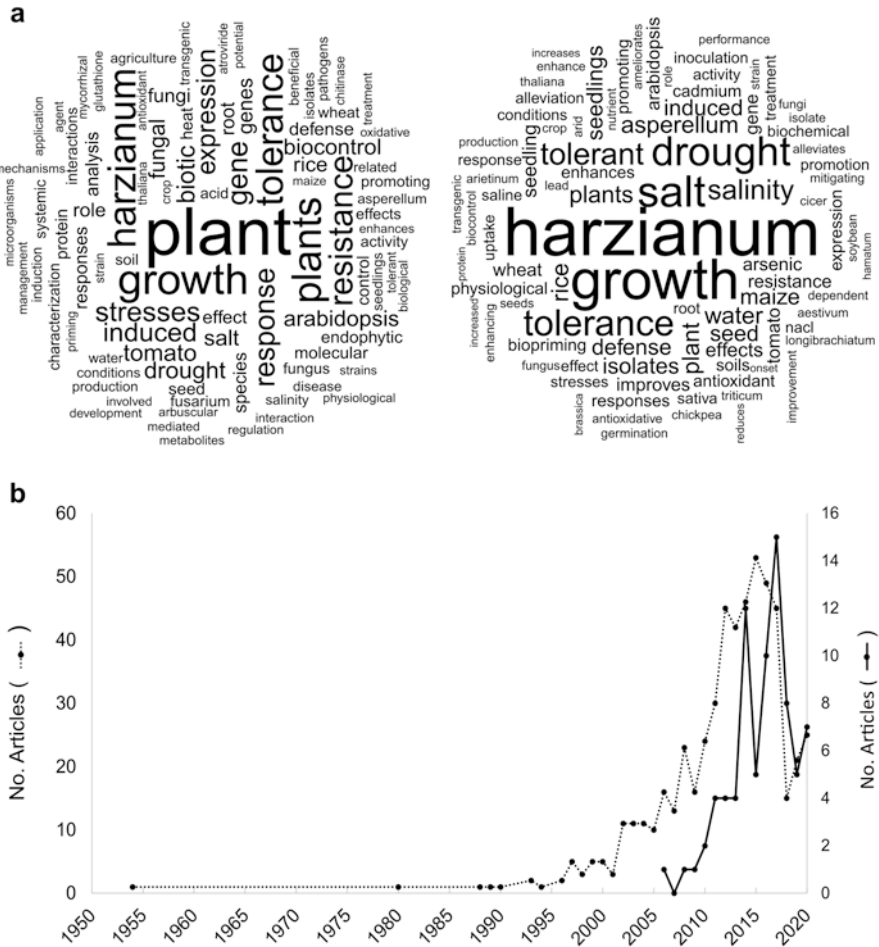
Fig. 2 Temporal distribution of scientific publications involving "*Trichoderma*" and "abiotic stress." The word clouds were assembled with the most repeated words in the titles of the 1046 of the total search (**a**) and with the 80 articles systematically selected (**b**) (the size of the words indicating the frequency of appearance). The time curves represent the number of publications selected; the dotted-line curve (Y-axis on the left) corresponds to the 1046 initial studies retrieved and the solid-line curve (Y-axis on the right) to the final database of 80 articles

3.2 Geographic Distribution of Studies with **Trichoderma** and Abiotic Stresses in Plants

To assess whether there was any geographical tendency for studies of this nature, the articles systematically retrieved were distributed as indicated on the map (Fig. 3), and the type of experiment performed was also registered. The 80 selected studies were performed in 19 countries, where 67.5% were from Asia, followed by

countries from Europe and the Americas (15 and 11.25% respectively), and from Africa (6.25%). The significant number of studies in Asia was due to India's outstanding contribution (30% of total articles), followed by China (16.25%). This is consistent with the fact that India contributes to ~90% of Asian market of *Trichoderma*-based products (Woo et al. 2014; Singh et al. 2018). From the selected publications, 74.1% of the studies were performed in greenhouses and growth chamber (90% and 10%, respectively), 17.3% in fully controlled environments (in vitro), and 8.6% under field conditions (Fig. 3).

India and China have their economies composed by agriculture as an important component (Foley et al. 2011), combined with a very strong and consistent industrial development allied to high population counts. These circumstances tend to be associated with issues such as environmental degradation and pollution (Ballescá 2016; Chopra 2016), especially by heavy metals (Sodango et al. 2018). Furthermore, human population growth, urbanization, and climate changes are further challenges to be faced, in order to cope with food production in an environmentally sustainable way (Foley et al. 2011; Du et al. 2018). All these issues must be dealt properly to assure global food security (Godfray et al. 2010; He et al. 2013). It has been proposed that investments in agronomic research and development toward sustainable strategies and products (e.g., *Trichoderma*-based bioproducts) can not only help solving those challenges but also stimulate agricultural productivity on a long-term scale (Heisey and Fuglie 2018).
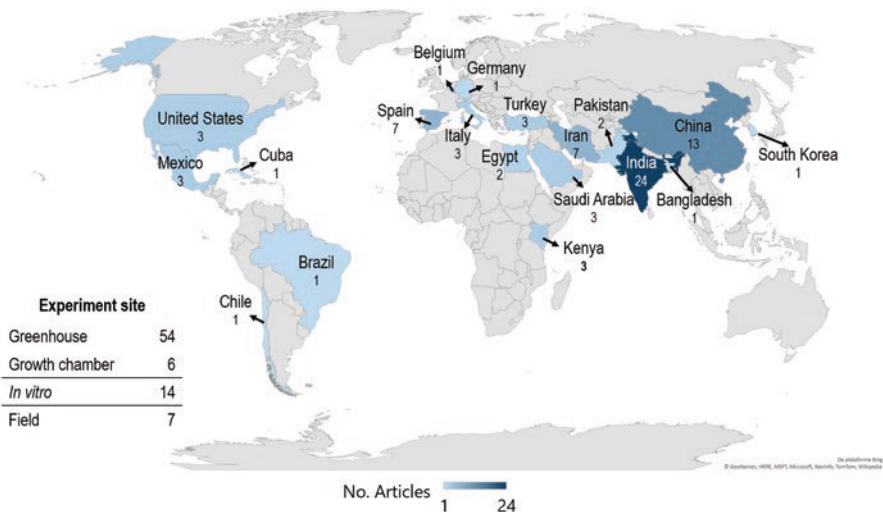
Fig. 3 Geographic distribution and types of experiments for the systematically selected primary studies of our search

3.3   Trichoderma *Species, Their Origin, Targeted Plants, and Inoculation Methods*

A total of 175 *Trichoderma* isolates were associated with abiotic stresses in the selected studies, with 78.9% distributed in 16 species and the remaining not identified to the species level (Fig. 4a). As indicated by the word clouds (Fig. 2b), *T. harzianum* and *T. asperellum* were the most abundant species, with 75 and 21 isolates, respectively, within the 138 isolates that were identified up to the species level. The other species all together occurred in a frequency of 30.4%: *T. longibrachiatum* with eight; *T. atroviride* with six; *T. afroharzianum* and *T. britannicum* with five isolates each; *T. virens* with four; *T. parareesei* with three; *T. asperelloides*, *T. hamatum*, and *T. reesei* with two isolates each; and *T. aggressivum*, *T. koningiopsis*, *T. simmonsii*, *T. saturnisporum*, and *T. viride* with one representative each (Fig. 4a). The data obtained on the sources of these isolates indicated that most came from collections of the study-affiliated or collaborating institutions (38.3%) or from rhizospheric soil (28.6%, Fig. 4a). Considering only isolates from collections' material, 55.2% were *T. harzianum*. When collection isolates were not taken into account, 72.2% of the isolates were from soil. Isolates from contaminated environments (mining tailings and contaminated soil) were specifically tested against stresses caused by heavy metals. Only in four studies, *Trichoderma* species (*T. harzianum*, *T. asperellum*, and *T. atroviride*) were used as formulated bioproducts, which were then tested for their effects on plant responses to abiotic stresses (Fig. 4a). In general, data suggest that the observed roles of *Trichoderma* in abiotic stress relief come from research primarily aimed at complementing the current knowledge on activities, applications, and bioproducts' development of particular isolates, most of them already known as biocontrol agents (e.g., Woo et al. 2014; Waghunde et al. 2016; Anam et al. 2019). Since only a small proportion of different *Trichoderma* species/isolates have been studied as mitigators of abiotic stresses (Fig. 4), there is still much exploration to be done, given the large diversity found in this genus worldwide (De Souza et al. 2006; Loguercio et al. 2009a; Kubicek et al. 2011; Feitosa et al. 2019).

The most frequent plant species found in the selected studies were maize (*Zea mays*, 12.8%), rice (*Oryza sativa*, 11.6%), tomato (*Solanum lycopersicum*, 10.5%), *Arabidopsis thaliana* (9.3%), and wheat (*Triticum aestivum*, 8.1%) (Fig. 4b; also see Fig. 2). Among the methods used to inoculate *Trichoderma*, seed biopriming alone (i.e., soaking seeds with suspensions of fungal spores to allow seed germination before planting) was the most used (Fig. 4b). *Trichoderma* spore suspensions directly applied into the soil (liquid or powder) or on the roots (by spraying) corresponded to 44.2% of the studies. Other inoculation methods, including mycelium discs for volatile compounds experiments and in vitro techniques, as well as inoculation of flowers and leaf tissues comprised the remaining 17.5% (Fig. 4b). These three predominant inoculation methods correspond to those usually planned for and used in large-scale crop applications, mainly for the most studied plant species (Fig. 4b), which combine ease of product manipulation and delivery with lower costs (Parnell et al. 2016; Rocha et al. 2019).
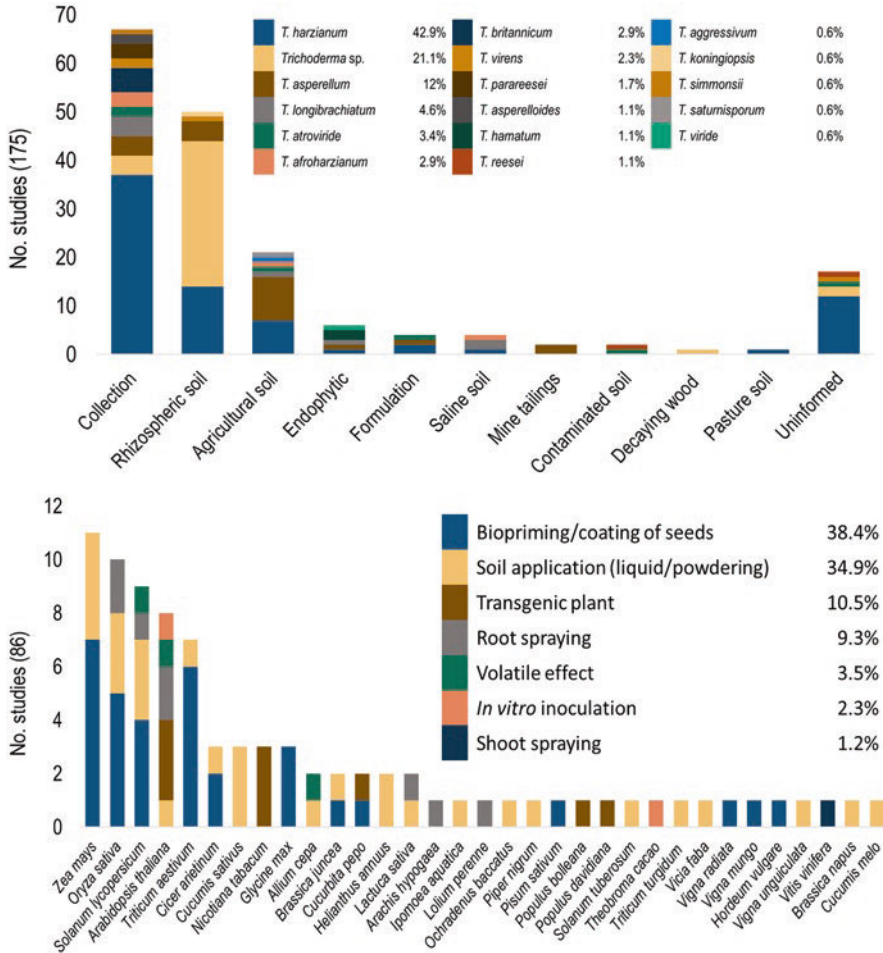
Fig. 4 Distribution of *Trichoderma* species and sources, inoculation methods, and host plants. (**a**) The sources of *Trichoderma* isolates for the reported studies are shown in the X-axis; the taxonomic definition found for the experimental isolates within the 80 articles is appearing in the center of the graph. All isolates in which their species were not defined are collectively represented by "*Trichoderma* spp." (**b**) Plant species used in the experiments as targets for the applied stresses and inoculated with the *Trichoderma* isolates; distribution of the modes of inoculation appear in the center of the graph. The total number of studies considered (86) exceeded the 80 systematically selected articles, as in some of them, there was more than a single type of study/experiment being reported

Trichoderma is one of the most abundant and widespread fungal genus in the world and has characteristics that justify the amount and depth of studies on them (e.g., reviews by Harman et al. 2004; Vinale et al. 2008; Schuster and Schmoll 2010; López-Bucio et al. 2015). *Trichoderma* spp. can adapt to a diversity of environments, not only due to their ability to sporulate in response to a complex and

intertwined variety of environmental factors (Loguercio et al. 2009b; Steyaert et al. 2010a, b, c) but also due to a phylogenetic and genome-printed high opportunism (Druzhinina et al. 2011) that allow the occupation of a broad array of niches and environmental gradients (Mukherjee et al. 2013; Egidi et al. 2019; Jiao and Lu 2020). The production of a variety of hydrolytic enzymes (e.g., reviewed by Schuster and Schmoll 2010; Mukherjee et al. 2013; Waghunde et al. 2016), a great ability to control cell-wall synthesis and repair in themselves and in their hosts (Gruber and Seidl-Seiboth 2012; Kappel et al. 2020), and some tolerance of certain isolates to higher temperatures (>32 °C) during growth (Chang et al. 1997) certainly contribute to this wide niche occupancy (including a great variety of plant hosts). Some species have an endophytic lifestyle, colonizing plants by penetrating root cells and remaining throughout the plant life cycle (Harman et al. 2004, 2019; Contreras-Cornejo et al. 2018). *Trichoderma harzianum* is the most used species in bioproducts and in experiments to control plant pathogens and the one most commonly found in soil environments (Vinale et al. 2008; Mukherjee et al. 2013; Woo et al. 2014; Waghunde et al. 2016), which explains why it is the species most frequently found in this review (Fig. 4a). Since *T. harzianum* is a species complex, with multiple cryptic species, i.e., a complex group of morphologically indistinguishable species (Chaverri et al. 2015), this is likely another reason for its higher frequency in the systematically retrieved studies dealing with abiotic stress relief in plants. *Trichoderma* spp. are predominantly saprophytic fungi in soil, litter, organic matter, and rhizospheric ecosystem of all climatic zones, and their diverse metabolic capacity allows them to colonize soils of different habitats (Vinale et al. 2008; Druzhinina et al. 2011; Mukherjee et al. 2013). It is such a strong competitive nature of these fungal species that provide rapid rhizospheric establishment, root colonization (including interaction with arbuscular mycorrhizal fungi; Mehta and Sirari 2019), pathogenic microflora control, and plant-growth promotion (Hidangmayum et al. 2018). These characteristics, therefore, allow to explain their frequent interaction with the surface of plant roots, so that strategies of isolation (or inoculation) of these isolates tend to be often related to forest or agricultural soils and seed coating/biopriming (Topolovec-Pintarić 2019; Rocha et al. 2019) (Fig. 4).

The experimental plants used for the interactive experiments with *Trichoderma* tend to be mainly crop species that are mostly recognized as displaying short life cycles, small sizes, easy propagation, and considerable economic importance, being well-established model plants for a great variety of research in plant biology and agricultural sciences (Fig. 4b). Moreover, the high frequency of inoculation methods involving seeds and/or soil (~3/4) suggests a natural overlap between basic/applied research and technological development of methods/products for agricultural applications. The biopriming of seeds with *Trichoderma* spp. has been used to improve seedling vigor, which can be triggered by the release and/or production of enzymes and phytohormones involved in seed viability and germination rates and speed (Kumar et al. 2014; Babychan and Simon 2017), as well as in resistance against pathogens (Mastouri et al. 2010; Singh et al. 2019, 2020). With *Trichoderma* inoculation in roots/soil, additional features occur such as alteration of soil microflora and increase of nutrients availability, due to degradation of many complex

substrates. Currently, the use of changing microbial communities of cultivated soils and improvement of the performance and vigor have been widely used in agricultural production (Harman and Uphoff 2019).

4   Types of Abiotic Stresses in Plants Alleviated by *Trichoderma*

From the 80 final articles selected, 105 abiotic stresses were identified, which were classified into 13 groups (Fig. 5). The highest proportion of the studied stresses were saline stress (36.2%), agreeing with the word clouds (Fig. 2); within this fraction, 92.7% corresponded to the effects of the salts as a single factor, with the remaining three studies (7.3%) assessing this factor in combination with high temperature and osmotic and alkaline stresses (one study each) (Fig. 5). Drought stress was the second most represented (27.6%), with water deficit being analyzed in combination with heat stress in one study (Fig. 5). Stresses caused by heavy metals comprised 21% of the studies retrieved. These 22 studies included 7 chemical elements and were distributed as follows: arsenic (six), cadmium (five), lead (four), copper (three), zinc (two), and chromium and nickel (one each) (Fig. 5). Taken together, these three types of abiotic stress comprised 83.8% of the experiments involving *Trichoderma* isolates and plants.
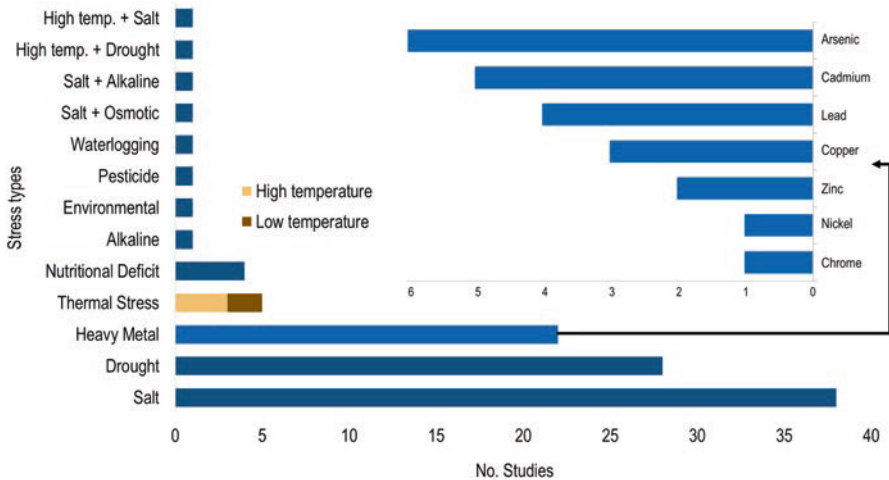
Fig. 5 Types of abiotic stresses in plants alleviated by *Trichoderma*. Twelve different types of abiotic stresses (single or in combination) were found in the selected studies (left-side graph). The number of studies reporting stresses caused by heavy metals were discriminated by each metal (right-side graph). Thermal stress was further divided (proportionally) into high and low temperatures

Under the circumstances of climate change, salinity and drought can be viewed as the most relevant types of abiotic stress that can affect crop production (Munns and Gilliham 2015); moreover, they are interconnected not only due to their direct relationship with water availability (Nuccio et al. 2018) but also through their effects in the osmotic balance and regulation in plant cells (Mastouri et al. 2010; Ikram et al. 2019; Poveda 2020). From this standpoint, our analysis indicated that ~2/3 of the current science on *Trichoderma*-mediated abiotic stress relief deals with the physiological and/or biochemical responses of plants toward osmoregulation and water use efficiency (Munns and Gilliham 2015; Ikram et al. 2019; Khoshmanzar et al. 2020), which are major issues expected to affect plant survival, growth, and productivity in a climate change context (Daryanto et al. 2016; Naumann et al. 2018; Khoshmanzar et al. 2020).

By disrupting osmotic equilibrium, saline stress alters membrane stability, increases the toxicity of ions within the plant cells, and affects photosynthetic rates (Khomari and Davari 2017; Meena et al. 2017; Mona et al. 2017; Ikram et al. 2019). Due to the lower availability of water created by a higher osmotic pressure (an effect similar to that caused by drought), the plants tend to respond physiologically to these stresses as if they were in a process of acclimation (Farooq et al. 2009; Filippou et al. 2013). The stress induces changes in membrane function, which tends to disrupt the ionic phase, so that cell toxicity results from accumulation of ions, which causes oxidative stress and biochemical imbalances (Begum et al. 2019); depending on their intensity, duration, and speed, these changes can lead to either acclimation or apoptosis (Filippou et al. 2013; Yang and Guo 2018). Furthermore, plants under drought conditions suffer from water supply limitations both by the root system and from the transpiration losses (Tardieu et al. 2018), although a decrease in transpiration rates is a major plant response to this stress (Farooq et al. 2009). The consequent decrease in water potential interferes with the photosynthetic process, by affecting the stomatal opening/conductance, much as a result of responsive-hormones synthesis, as well as of changes in the chlorophyll and carotenoid contents (Mona et al. 2017; Begum et al. 2019). In terms of cellular processes, these water-deficit stresses affect cell division, cell-wall dynamics, primary and secondary metabolism, regulation of hormones and synthesis, and accumulation of reactive oxygen species (ROS) (Bray 2007; Takahashi et al. 2018; Tardieu et al. 2018; Zhang et al. 2019a, b). Reduction in size of leaves and seeds, root growth suppression, and flowering/fruiting delays are additional stressing effects at morphological and physiological levels (Mastouri et al. 2012; Osakabe et al. 2014). Since all of these effects ultimately lead to decrease in plant growth and productivity, *Trichoderma* treatments appear as a relevant option (Mona et al. 2017; Ikram et al. 2019; Zhang et al. 2019a; Poveda 2020) for the development of salt- and drought-tolerance to cope with those additional types of stresses (Farooq et al. 2009; Filippou et al. 2013).

The next most recurrent stress in the studies was caused by heavy metals (Fig. 5). *Trichoderma* spp. applications have shown to be promising alternatives for amelioration of this stress, either alone or combined with salinity. Interestingly, such

conditions allow improved phytoremediation activities for plants in metal-polluted soils (Anam et al. 2019; Li et al. 2019). In general, the presence of these metals in soil can affect plants in a variety of forms, such as reducing seed germination, chlorophyll contents, photosynthesis, and ATP synthesis; altering water balance, nutrient absorption by roots, mitochondrial and chloroplast activities, cell signaling, and enzymatic activities; and increasing membrane lipid peroxidation, levels of ROS, etc. (Ghori et al. 2019; Arif et al. 2019). Usually, all these disturbances can lead to a net effect of decreasing and/or halting plant growth and to necrosis of parts or the whole plant (Groppa et al. 2007). Soil, water, air, and trophic chain pollution is mainly caused by anthropic actions of industrial (power and heat, metallurgy, steelmaking, leather, paper, textile, electroplating, electronics, petrochemistry, waste and landfills, etc.), agricultural (chemical fertilizers and pesticides, sewage irrigation), mining (coal, crude oil, iron, and other metals), and urban life (He et al. 2013; Hu et al. 2014; Etesami 2018). For instance, due to the large and strong industrial, urban, and rural development of the last decades in densely populated regions, India and China have shown one of the highest levels of soils, water, and air contamination by heavy metals in the world (Hu et al. 2014; Paul 2017; Mukherjee et al. 2020), especially in rural areas, which have been generating much concern about food security and human health (He et al. 2013; Huang et al. 2018; Yang et al. 2018). Hence, these circumstances also help explaining the highest proportion of studies found for these two countries (Fig. 3).

5 Parameters Evaluated in the Studies of *Trichoderma*-Plant-Abiotic Stresses

The most assessed variables in studies with plant-*Trichoderma*-abiotic stress interactions can be classified as indirect or direct responses: in the former group, the final phenotypic effects (i.e., plants growth and development) are evaluated, whereas in the latter, biochemical/cellular pathways and compounds related to physiological and photosynthetic processes are gauged (Table 3). To act on recovery and/or amelioration of the adverse effects that the abiotic stresses cause in plants, *Trichoderma* spp. interfere in the physiology, biochemistry, and morphology of the host through the diverse genetic and metabolic arsenal available in this fungal genus. The quantification of relief effects of abiotic stresses in plants by *Trichoderma* has been studied by an array of response variables, which, in some cases, can link to possible mechanisms of action. These parameters are related to physiological, morphological, physical, and (bio)chemical aspects, which could be classified into four main categories by conceptual affinity (Table 3; Fig. 6).

Table 3 Parameters used to study mechanisms possibly involved in the alleviation of abiotic stresses in plants by *Trichoderma*[a]

Response variables	No. articles	Δ ("trat" – "ctrl")[b] Min (%)	Max (%)	References[c]
1. Growth/development (173)[d]				
Grain yield	5	−12.6	1160.0	Becquer et al. 2018; Tripathi et al. 2017
Number leaves	6	−39.0	77.7	Azarmi et al. 2011
Leaf area	7	−96.8	993.0	Azarmi et al. 2011; Singh and Dwivedi 2018
Shoot fresh wght	15	−75.2	744.1	Azarmi et al. 2011
Root fresh wght	17	−73.8	374.4	Azarmi et al. 2011; Abd El-Baki et al. 2014
Germination	18	−8.3	516.3	Montero-Barrientos et al. 2010; Nzioki and Mutisya 2016
Root dry weight	24	−74.7	4457.7	Mastouri et al. 2012; Abd El-Baki et al. 2014
Shoot dry weight	25	−87.7	416.7	Azarmi et al. 2011; Hashem et al. 2014
Shoot length	27	−28.6	199.6	Abd El-Baki et al. 2014; Shukla et al. 2014
Root length	29	−20.7	290.9	Mishra et al. 2016; Vieira et al. 2017
2. Physiology/photosynthesis (93)				
Transpiration	3	−17.8	82.2	Vieira et al. 2017
Intercell CO_2*	3	3.8	*−24.8*	Vieira et al. 2017
Chl fluoridation	7	−46.9	132.9	Azarmi et al. 2011; Rawat et al. 2012
Net photosynth.	7	−15.9	412.5	Vieira et al. 2017
Stomat. conduct.	8	−59.6	243.6	Azarmi et al. 2011; Shukla et al. 2012
Relate H_2O content	13	−1.1	170.0	Vieira et al. 2017; Shukla et al. 2014
Photosynthetic pigments				
Chlorophyll α	12	−48.0	123.5	Singh and Dwivedi 2018; Badar et al. 2015
Chlorophyll b	12	−23.5	428.0	Singh and Dwivedi 2018; Hashem et al. 2014
Total chlorophyll	18	−25.0	525.0	Jalali et al. 2017
Total carotenoid	10	−39.4	122.9	Singh and Dwivedi 2018; Elkelish et al. 2020
3. Stress-related activities (117)				
Transloc. factor	2	−23.8	300.0	Vargas et al. 2017
Lipid peroxid.*	3	*−6.9*	*−58.1*	Dixit et al. 2011; Nongmaithem and Bhattacharya 2017
Electrolytic leak*	5	*2.4*	*−58.5*	Poveda 2020
Membrane stability index	11	−57.4	101.6	Tripathi et al. 2013; Hashem et al. 2014
Malondialdehyde (mda)*	20	*−99.9*	*−137.3*	Abd El-Baki and Mostafa 2014; Kumar et al. 2016

(continued)

Table 3 (continued)

Response variables	No. articles	Δ ("trat" – "ctrl")[b]		References[c]
		Min (%)	Max (%)	
Antioxidant enzyme activity				
GPX	7	−10.3	148.7	Singh et al. 2019; Dixit et al. 2011
GR	9	−15.5	200.0	Pehlivan et at. 2017; Tripathi et al. 2017
APX	10	10.0	764.7	Guler et al. 2016; Singh et al. 2019
POD	10	−44.8	136.8	Fu et al. 2017; Devi et al. 2017
CAT	19	−30.2	563.2	Fu et al. 2017; Chepsergon et al. 2016
SOD	21	−40.3	359.9	Singh et al. 2019; Chepsergon et al. 2016
4. Compounds' levels/content (102)				
Flavonoids	2	409.8	502.8	Mona et al. 2017; Elkelish et al. 2020
Superox. dismutase (O^{2-})*	2	*−25.7*	*−63.5*	Fu et al. 2017
Siderophores	2	0	151.7	Zhao et al. 2014
Amino acids	3	–	–	–
Soluble sugar	5	9.8	47.6	Fu et al. 2017
Phytohormones	8	−78.1	1154.5	Singh et al. 2019
Heavy metal conc.*	9	*75.0*	*−84.2*	Song et al. 2014; Vargas et al. 2017
Protein	10	−48.5	68.5	Abd El-Baki and Mostafa, 2014
Ions	10	−67.6	2335.3	Azarmi et al. 2011
Total phenol	11	−4.4	192.2	Kumar et al. 2016; Rawat et al. 2013
H Perox (H_2O_2)*	16	108.5	*−77.9*	Shukla et al. 2014; Pehlivan et at. 2017
Proline	24	−81.7	350.0	Abd El-Baki and Mostafa 2014; Rawat et al. 2012

[a]The four categories were defined according to a conceptual affinity among their response variables
[b]Differences (in %; control = 100%) between the values obtained for each variable, considering the treatments with application of *Trichoderma* ("trat") in relation to the treatments with only the abiotic stress(es)("ctrl"). The "Min" and the "Max" columns correspond to the lowest and highest D values (differences between "trat" and "ctrl") found for a given parameter in the set of articles containing it (see "No. articles" column). "*" indicates those variables that describe damaging stress effects to the plants; *italicized* "min" and "max" values in the table are those in which *negative* D values indicate *positive/favorable* effects of *Trichoderma* to the plant host in the amelioration of the stress
[c]The references in this column belong to the final selected database of articles used in the systematic review treated in this chapter (see Table 2)
[d]The numbers within parentheses for each of the four main categories indicate the total number of *experiments* (i.e., *variables per article*) and correspond to the sum of values for the "No. articles" column within each category; this column, therefore, indicates the amount of articles systematically selected to compose our final database, in which a given response variable (indicated on the left) was found. Hence, a single article can be counted more than once, in case it has reported various response variables at the same time
[**note**: the underlined citations refer to studies also related to molecular analyses discussed for Fig. 6, Sect. 6]
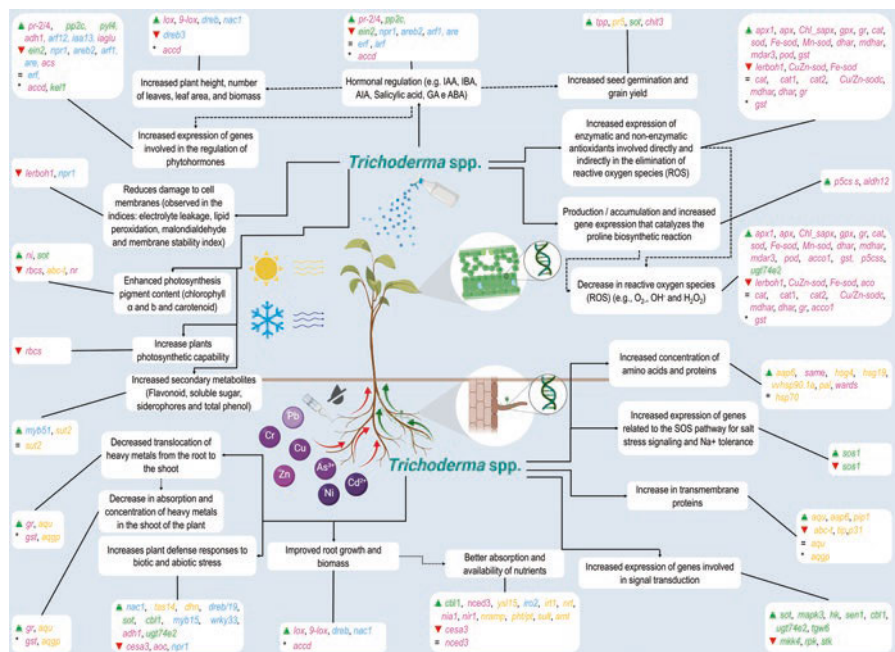
Fig. 6 Possible mechanisms involved in the interaction between *Trichoderma* and plants in response to abiotic stresses. The information retrieved on genetic products in this figure refers to 13 articles in which studies of gene expression were found. Different colors represent four main groups of activities/functions identified for the plant genes involved in stress mitigation: blue, transcription factors; pink, metabolic pathways; green, signal transduction; orange, structural proteins and protective compounds. The symbols located on the left inside the balloons represent gene expression modulation in relation to treatment *Trichoderma*-plant-stress vs plant-stress only: ▲ green, upregulation of gene expression; ▼red, downregulation in gene expression; '=' expression level without significant difference; '∗' transgenic plants expressing *Trichoderma* genes

5.1 Influence of **Trichoderma** *on Plant Growth and Development*

Out of the 485 experiments found in the 80 systematically selected articles whose data was collected (Table 3), the most frequent group of variables were growth and development parameters (35.7%), mainly root and shoot biomasses (fresh and dry length and weight), which are measures of plant vitality as evidence of their recovery from stresses. Taking the results of *Trichoderma* application into account, the overall positive effects on plant growth and development could be observed, with increases in relation to control treatments varying from 77.7% improvement in the number of leaves to 4457.7% raise in root dry weight (Table 3).

Another relevant group of parameters evaluated in addressing *Trichoderma* effects on plant stresses was more specifically related to plant physiology, mostly focusing on photosynthesis and represented 19.2% of the variables evaluated in this

study (group # 2, Table 3). Photosynthetic efficiency reflects growth, development, and biomass production, and it was assessed in the studies on saline and drought stresses (56% and 25.8%, respectively).

All *Trichoderma* species are mycoparasites, having thus developed a diversified and unusual biosynthetic machinery, including metabolites acting both on antagonism and survival (Druzhinina et al. 2011; Kubicek et al. 2011). As a consequence of such a metabolic variety, members of the *Trichoderma* genus can reduce the concentration of toxic substances in the soil, solubilize phosphates and micronutrients, synthesize siderophores, increase nitrogen fixation, and produce plant hormones (Mukherjee et al. 2013; Hidangmayum et al. 2018; Lombardi et al. 2018). Rhizospheric and endophytic *Trichoderma* have been reported to help host plants to adapt to abiotic stress conditions and promote their growth also through biosynthetic pathways of plant hormones (Yan et al. 2019), as well as through a variety of secondary metabolites synthesized, which aid in the solubilization of mineral compounds that increase availability of nutrients and so nutritional uptake and root growth (Rajput et al. 2019).

5.2 Alleviation of Oxidative Stresses by Trichoderma

The other two categories of variables addressed in experiments with *Trichoderma* were represented in our dataset as follows: 24.1% for variables related to enzyme activities and cellular functions directly affected by the stresses and 21% for levels and rates of compounds synthesized as responses to the stresses (Table 3). Within the group of variables gauging activities directly related to stress responses (group # 3, Table 3), almost the totality of the retrieved studies deals with either antioxidant activities (65%) or membrane/lipid effects (33.3%). Within the antioxidant enzyme activities related to oxidative stress response/regulation, superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR) and peroxidase (GPX) were the most prominent found (Table 3). In terms of membrane-related studies, the most prevalent specific activities were lipid peroxidation (with special interest in the use of malondialdehyde), which made up 51.2% of the analyses in this subgroup (Table 3). The composition and stability of the plasma membrane, which was used to test stress damage levels to plant cells, made up 28.2% of the studies, and the remaining four assessments dealt with electrolytic leak and translocation factors (two studies each).

The parameters relating to the content of certain substances synthesized by plants (Table 3, group # 4) were grouped as such because they are indicators of, or relate to stress states, or yet belong in metabolisms or processes that assist in physiological recovery from the action of abiotic stresses. As a result from the higher concentration of studies in saline/drought stresses (Fig. 5), the highest frequency of studies in this category # 4 (Table 3) were related to proline levels (22.5%), which corresponded 62.5% of the studies with saline stress and 20.8% of the studies on drought tolerance (Fig. 5). Among the compounds identified in the systematically retrieved

studies, there was a focus on secondary metabolites related to stress responses, such as ROS (17.6%), phenolics (10.7%), and phytohormones (7.8%). Ions and heavy metal contents also appeared well represented (9.8 and 8.8%, respectively), as some of the research was focused on this type of abiotic stress (Fig. 5).

As much as biotic factors (e.g., fungal diseases, herbivory, etc.), stressing factors of abiotic nature also cause the overproduction of reactive oxygen species (ROS) in plants, which lead to metabolic toxicity, damage to the membranes, inhibition of photosynthetic apparatus and steps, and changes in hormonal levels, among others (Selvakumar et al. 2012). The major ROS species formed (superoxide, O_2-, hydroxyl, $OH-$, and hydrogen peroxide, H_2O_2) react chemically with virtually all metabolites of the plants, including proteins, lipids, and nucleic acids (Nath et al. 2013; Harman et al. 2019). As in low concentrations, ROS act as signaling molecules, with specific signatures of their steady-state levels, depending on the type of cell of the plant (Choudhury et al. 2017). The regulation of ROS levels is very precise in plant cells, being related to a fine-tuned balance between their perception and detoxification, and the redox state of the cell, with a particular relevance for chloroplasts in this metabolism (Farooq et al. 2009; Meyer et al. 2020). In this context, antioxidant compounds and enzymes act coordinately on the fine modulation of these mechanisms (Mittler 2002). *Trichoderma* spp. have shown to also depend on ROS signaling for a variety of their own cellular processes and responses to environmental cues (Cruz-Magalhães et al. 2019), thereby having a clear modulatory interference in plants, when interacting with them.

The majority of the studies on abiotic stresses involving plants and *Trichoderma* have shown to focus on drought/salinity (Fig. 5). Knowledge generated in this aspect indicates that major protection of plant cells against these stresses occurs by the promotion of osmolites' synthesis or accumulation, which increases both the water absorption and retention capacity of the cells and the activities of enzymatic and non-enzymatic antioxidants (Hameed et al. 2014; Waghunde et al. 2016; Pachauri et al. 2019). A recurrent mechanism of action found in the studies with *Trichoderma* spp. was the production and accumulation of proline, an amino acid that acts as cellular osmoprotector (Harman et al. 2019), mostly in three ways: (i) by protecting intracellular macromolecules against reactive oxygen species (ROS) attack, (ii) by serving as a source of carbon and nitrogen for the cell as a result of its oxidative metabolism, and (iii), as discussed above, by acting as a modulator of the osmotic balance of the cell (Christgen and Becker 2019). Some underlying mechanisms of exogenous phytohormones production by *Trichoderma*, such as similar forms of abscisic acid (ABA), can also protect the plant from oxidative damage (Bano et al. 2012; Khan et al. 2015), as well as modulate other stress-response metabolisms. Members of the *Trichoderma* genus are outstanding producers of secondary metabolites with functions already known (Table 3, Fig. 6), although many of such compounds are still unknown. There are more than 2000 natural products, such as peptaibols, non-ribosomal peptides, polypeptide, terpenes, and steroids produced by *Trichoderma* ssp., which play important roles in their interaction with plants (Mukherjee et al. 2012). As mentioned above, *Trichoderma* species throughout evolution have developed the ability to produce a large amount of extracellular

enzymes and secondary metabolites (Mukherjee et al. 2012; Kubicek et al. 2019), as well as very effective systems of resistance and repair of cellular and molecular damages (Duran et al. 2010; Ghorbanpour et al. 2018), a capability that can extend the protection to their hosts (Harman et al. 2019).

6 Plant Genes Influenced by *Trichoderma* in Response to Abiotic Stresses

6.1 Outline of the Studies

The analytical review of this chapter allowed us to provide a glance on the current status of research on genes and their products that can be related to the beneficial fungus-host interaction in response to abiotic stresses. Out of the systematically assembled database, about 26.3% of its articles were identified as comprising studies of this nature, dealing with in vivo biochemical and molecular methods; all the data we found on gene expression patterns related to *Trichoderma*-plant-stress interaction were related to plant genes (Table 3; Fig. 6), and all of them were previously known to be involved in plant stress responses and in the transport of macro and micronutrients. The largest amounts of these studies were on drought (33.3%) and saline stresses (28.6%); of the remainder, 9.5% by heavy metals evaluated stress by high temperature, low temperature, nutritional deficit, and waterlogging with 4.8% each, and 9.5% gauged combined stresses (drought + high temperature and salinity + osmotic stress). The species of *Trichoderma* used in these molecular genetics' studies were *T. harzianum* (seven), *T. parareesei* (six) *T. britannicum* (three), *T. asperelloides*, and *T. longibrachiatum* (two each); *T. afroharzianum*, *T. asperellum*, *T. hamatum*, *T. virens*, and *T. reesei* (one each); and a study in which there was no identification at the species level. The plant species investigated in these studies were *Arabidopsis thaliana*, *Brassica napus*, *Solanum lycopersicum*, *Nicotiana tabacum*, *Cicer arietinum*, *Oryza sativa*, *Populus bolleana*, *Triticum aestivum*, *Theobroma cacao*, *Zea mays*, and *Vitis vinifera*. The studies on stress-responsive genetic expression reported the majority of the genes (77.2%) as being upregulated as the result of stress, both in the above- and belowground parts of the plants (Fig. 6). It is important to mention that 23.8% of these studies were performed with transgenic plants, in which overexpression of *Trichoderma*-derived transgenes (supposedly induced in the fungus as a response to some abiotic stress) were investigated on their effects in modulating plant gene expression in response to the abiotic stresses (e.g., Meena and Swapnil 2019; Mota et al. 2019).

The studies selected concerning the molecular aspects of the stress alleviation mechanisms of plants by *Trichoderma* were sufficiently consistent with the physiological characteristics of the assessed plants under abiotic stress conditions (Table 3). Essentially, there were four major groups of activities identified for the plant genes involved in stress mitigation: (i) transcription factors (TFs) directly

involved in stress-response gene expression modulation, (ii) genes responsive to metabolism and oxidative stresses, (iii) signal-transduction pathways, and (iv) synthesis of structural/protective proteins and compounds (Table 4; Fig. 6).

6.2   Transcription Factors

With regard to the genes encoding TFs, studies related to their expression altered in response to the *Trichoderma*-plant-stress interaction showed a tendency of them to refer mostly to hormonal and pathogen-related signaling pathways and dehydration-responsive genes; they were *nac1/nac6* (Ghorbanpour et al. 2018; Singh et al. 2019); *dreb* (dehydration-responsive element binding proteins, Brotman et al. 2013; Pandey et al. 2016; Rubio et al. 2017; Singh et al. 2020b); *zfp* and *p13* (zinc-finger domain factors related to transcriptional repression, Bae et al. 2009); *erf* (ethylene-responsive factor, Roatti et al. 2013; Elkelish et al. 2020; Poveda 2020); *npr1, are*, *areb2*, *arf* (TFs related to salicylic acid, ABA, and auxin signaling pathways, Rubio et al. 2017; Singh et al. 2019; Elkelish et al. 2020); *iaa13*, *myb15*, *myb51*, *wrky33* (TFs related to secondary metabolites synthesis, auxin, jasmonate/salicylate signaling pathways, Brotman et al. 2013); *iro2* (iron-regulated transcription factor, Singh et al. 2019). Interestingly, recent full-genome comparisons have shown the class of transcription factors genes as one of the most abundant in the core genome of *Trichoderma* (Kubicek et al. 2019).

6.3   Plant Genes Responsive to Oxidative Stresses

Another relevant biological function identified for the studied plant genes was associated with pathways of direct response to stresses and to metabolic changes resulting from the stress effects (Fig. 6). The genes within this category included *p5cs* (encoding pyrrolin-5-carboxylate synthetase enzyme, which catalyzes a rate-limiting step reaction of proline synthesis, Ghorbanpour et al. 2018); methyltransferase and alcohol dehydrogenase (Brotman et al. 2013; Ma et al. 2020; Elkelish et al. 2020); *chit3* and *pr-2* (acid endochitinase and pathogenesis-related type 2 protein, i.e., beta-1,3-glucanase) (Roatti et al. 2013); *acc deaminase* and *oxidase* (Zhang et al. 2016a; Zhang et al. 2019a; Elkelish et al. 2020; Poveda 2020;); small subunit of Rubisco complex (catalyzes the limiting step of CO_2 fixation), cellulose synthase, lipoxygenase (oxylipin synthesis), phosphatase involved in the last step of trehalose synthesis, invertase involved sucrose hydrolysis, and nitrate/ferredoxin-nitrite reductase (Bae et al. 2009; Roatti et al. 2013; Singh et al. 2019); and genes/enzymes involved in ROS metabolism, such as *nadph* oxidase 1, dehydroascorbate reductases, *gst* (glutathione transferase), and all those genes encoding the antioxidant enzymes indicated in Table 3 (Montero-Barrientos et al. 2010; Dixit et al.

Table 4 Identification of plant genes from the systematically retrieved studies

Different colors represent the categories indicated in Fig. 6. Blue, transcription factors; pink, metabolic pathways; green, signal transduction; orange, structural proteins and protective compounds

Abbreviation	Gene function
are	ABA-responsive element binding protein 2
arf	Auxin response factor like
dreb	Dehydration responsive element bindings protein
erf	Ethylene-Responsive transcription factor
iaa13	Auxin-responsive protein IAA13-like
iro2	Protein iron-related transcription factor 2
nac	NAC domain-containing protein
npr1	Regulatory protein NPR1
myb	MyB-Domain Protein
wrky33	Member of the 'WRKY' family of transcription factors
zfp, p13	Protein with 'zinc finger' domain
accd	1-AminoCyclopropane-1-Carboxylate deaminase
acco/aco	1-aminocyclopropane-1-carboxylate oxidase 1
acs	1-aminocyclopropane-1-carboxylic acid synthase
adh	Alcohol Dehydrogenase
aldh	Delta-1-pirrolina-5-carboxilato desidrogenase
aoc	Cyclam se of allene oxide
apx	Ascorbate peroxidase enzyme
cat	Catalase enzyme
cesa3	Putative protein with cellulose synthase activity
chit3	Acid Endochitinase 3
dhar	Enzyme Desidroascorbate Reductase
gpx	Enzyme Glutathione Peroxidase
gr	Enzyme Glutathione Reductase
gst	Glutathione Transferase enzyme
iaglu	Indole-3-acetate beta-glucosyltransferase
lerboh1	NADPH oxidase 1
lox	Lipoxygenase enzyme
mdhar	Enzyme Monodesidroascorbato Reductase
nced3	9-cis-epoxycarotenoid dioxygenase
ni	Putative alkaline/neutral lnvertase
nia1	Nitrate reductase [NADH] 1-like
nir1	Ferredoxin-nitrite reductase
nr	Nitrate reductase
p5cs s	Delta 1-Pyrrolin-5-Carboxylato Synthetase
pal	Phenylalanine ammonia-lyase activity
pod	Peroxidase
pr-2	Pathogenesis Related prot. no.2 (beta-1, 3-glucanase)
rbcs	Small subunit of rubisco complex
same	S-adenosyl-L-methionine-Dependent Methyltransferase
sod	Enzyme Superoxide Dismutase
tpp	Trehalose-6-phosphate phosphatase
wards	Alanine aminotransferase
cbl1	Calcineurin B-Like protein 1

(continued)

ein2	Protein insensitive to ethylene 2
hk	Enzyme Histidine kinase
kel1	Protein with 5 repeated Kelch-like domains
mapk3	MAP kinase 3
mkk4	MAP kinase kinase 4
pp2c	Phosphatase protein 2C
pyl4	Receptor for abscisic acid (ABA)
rpk	Putative receptor protein kinase
sen1	Protein associated withsenescence
sos1	Salt overly sensitive 1
sot	Sorbitol transporter
stk	Serine/threonine protein kinase
sult	Sulfotransferase gene 1
ugt74e2	UDP-glycosyltransferase 74E2
aap6	Amino Acid Permease 6
abc-t	Transmembrane protein that binds to ATP
amt	Ammonium transporter
aqgp	Transmembrane protein 'Aquaglyceroporin' (family of aquaporins)
aqu	Transmembrane protein 'Aquaporin'
dhn	Protein 'Dehydrin'
hsg4	Heat-Shock Gene 4
hsg19	Heat-Shock Gene 19
hsp70	Heat-Shock Protein 70
irt1	Iron regulated metal transporter
nramp	Nramp metal transporter Mn uptake
nrt	Nitrate transporter gene
osm-1	Osmotic stress
pip1	Aquaporin PIP1
pht/pt	Phosphate transporter
pr-4	Pathogenesis Related prot. no. 4 (thaumatin-like PR-protein)
pr-5	Pathogenesis Related prot. no 5
sut2	Sucrose transporter protein involve in flowering and grain development
tas14	Dehydratorine (Group 2 LEA Proteins)
tip, p31	Intrinsic protein of the tonoplasto
vvhsp90.1a	Heat-Shock Protein 90
ysl15	Iron (III)-deoxymugineic acid transporter

Different colors represent the categories indicated in Figure 6. blue: transcription factors; pink: metabolic pathways; green: signal transduction; orange: structural proteins and protective compounds.

2011; Mastouri et al. 2012; Brotman et al. 2013; Rubio et al. 2017; Tripathi et al. 2017; Zhang et al. 2019a, b; Elkelish et al. 2020; Singh et al. 2020).

6.4   Signal Transduction Pathways

The third group of genes identified as having their expression altered as a function of abiotic stress effects was related to signaling proteins involved in stress-response physiology of plants (Table 4; Fig. 6). This group comprises the following

genes/proteins: *sos1* (signal protein of the *salt overly sensitive* pathway, Montero-Barrientos et al. 2010; Rubio et al. 2017; Zhang et al. 2019a); *hk*, *rpk*, *mapk*3, and 4, *stk* (histidine, receptor protein, MAP, and serine/threonine kinases), *sen1* (senescence associated), *pp2c* (phosphatase protein 2C, possibly related to ABA pathway), and *sot* (sorbitol transporter) (Bae et al. 2009); *ein2* (ethylene-insensitive protein, central to this hormone signaling pathway, Rubio et al. 2017); *pyl4* (abscisic acid receptor – required for ABA-mediated responses, Poveda 2020); *cbl1* (*calcineurin B-like 1* protein, sensor of calcium levels, interacting/regulating a family of kinases located in endomembranes) and *ugt*74e2 (UDP-glycosyltransferase 74E2, related to signaling of drought stress and auxin homeostase, Brotman et al. 2013); *kel1* (encodes a protein with 5 repeated Kelch-like domains, characteristic of gene families involved in cell morphology and protein-protein interactions, Hermosa et al. 2011); and *tgw6* (Trafficking protein particle complex subunit, Zhang et al. 2019a).

6.5 Genes Involved in Transport and Protection Against Abiotic Stresses

Finally, the last group of stress-responsive plant genes are those encoding proteins with either a directly protective activity to ameliorate the effects of the stressing agent or a transporting activity for molecules and substances used for this protection (Table 4; Fig. 6). In the former subgroup, we found *tas14* (dehydratorine of group 2 late embryogenesis abundant proteins, Ghorbanpour et al. 2018) and *dhn* (dehydrin, cellular protection against dehydration, also a LEA protein, Pandey et al. 2016; Singh et al. 2020b); *hsp70*, *-4*, *-19 -90* (heat shock chaperones, Monteiro-Barrientos et al. 2010; Roatti et al. 2013); and *osm1* (osmotic stress-sensitive mutant, belonging in the superfamily of SNARE proteins involved in vesicle/membrane fusion, Roatti et al. 2013). In the second subgroup of genes/proteins with transporting activity, there were *Aqgp*, *aqu*, *tip*, *p31*, *pip1* (aquaporin-type transmembrane proteins, Bae et al. 2009; Pandey et al. 2016; Vieira et al. 2017; Elkelish et al. 2020; Singh et al. 2020b); *abc* and *pr-5* (ATP-binding transporters) and pathogenesis-related type 5, i.e., osmotin-like membrane located protein (Bae et al. 2009); *aap6* (amino acid permease 6, transmembrane transporters, Brotman et al. 2013); and *Ysl15*, *irt1*, *nrt*, *nramp*, *sut2*, *pht/pt*, *amt* (macro and micronutrient transporters, Singh et al. 2019).

The assessment of expression modulation of genes investigated in the *Trichoderma*-plant-abiotic stress interaction suggest an interplay of a variety of cellular and physiological mechanisms, many with a cross talk among signaling and metabolic pathways responsive to both biotic and abiotic stresses (Choudhury et al. 2017; Mendoza-Mendoza et al. 2018; Meyer et al. 2020). Plants have to deal simultaneously with multiple environmental stress-related cues, thus displaying a complex integration of stimuli and defense signals. Prioritizing certain physiological

responses is a fine-tuned regulation resulting from plant-microbe interactions, whose understanding will be advantageous for crop improvements (Schenk et al. 2012). Further studies supported by the multi-omics, high-throughput, and comparative genomics approaches can unravel structural and functional aspects of these complex regulatory networks with unprecedent detail (Zeilinger et al. 2016; Meena et al. 2017; Kubicek et al. 2019; Arif et al. 2019), thereby providing additional opportunities for biotechnological development of *Trichoderma*-based bioproducts directed toward mitigation of plant stresses caused by abiotic factors (Waghunde et al. 2017; Szczałba et al. 2019; Topolovec-Pintarić 2019).

7   Conclusions and Perspectives

Environmental degradation imperils quality of life on Earth, and bioeconomy is a recent view that may properly handle the threatening circumstances. Bioeconomy has been developed on the basis of three visions – bio-ecology, bio-resources, and bio-technology (Bugge et al. 2016). In this regard, a vast array of studies on *Trichoderma* spp. have been widely reported in the literature, mostly due to their efficiency as biological control agents of plant pathogens, direct plant growth promotion, and the synthesis of a diverse of compounds with industrial applications (Vinale et al. 2008; Schuster and Schmoll 2010; Mukherjee et al. 2013). Nevertheless, from the beginning of this century, researchers have been pointing out that this fungal genus is even more multifaceted and so with an increasing potential for a wider diversity of applications akin to the bioeconomy view.

In this chapter, we systematically reviewed and discussed the use of *Trichoderma* to mitigate the negative effects of abiotic stresses on plants and discussed the consequences and potential applications of these findings, including areas of knowledge with strengths and gaps in this theme. An up-to-date sampling of articles containing primary studies reported in journals relevant to the areas of biological control, mycology, bioprospection, biotechnology development, and bioproducts were gathered, with their data being collected and assessed in details in this chapter. With specific tools, it was possible to prioritize the retrieval of more highly cited publications, which helped us to work with an amount of representative research of quality in this field (Figs. 1 and 2). Our survey was able to retrieve interesting information on the current status of research with *Trichoderma*, their interaction with plants, and the mitigation of abiotic stresses (Figs. 3, 4, 5 and 6).

Trichoderma of various species are commonly used as biocontrol agents and/or growth promoters, making up about 3/5 of the biofungicide market in the world (Topolovec-Pintarić 2019); since a multifunctional characteristic can add value to bioproducts, *Trichoderma* isolates with additional phenotypes of abiotic stress-relief for plants (Zhang et al. 2016a; Anam et al. 2019; Szczałba et al. 2019; Poveda 2020) can provide a very advantageous benefits/costs relationship for environmentally sustainable food production strategies (Harman 2011a). In a region with various environmental degradation issues to solve (Chopra 2016), India is an example

of a country taking robust steps in this direction, with a significant contribution not only on *Trichoderma* spp. science but also on their bioproducts' market (Woo et al. 2014). Despite having more than 300 species already described in this genus (Kubicek et al. 2019), and also a great fraction of functional isolates not yet characterized up to species level, more than 3/4 of the studies involving *Trichoderma*-plant-abiotic stress interactions have appeared to be restricted to 16 main species, with a highlight for *T. harzianum* and *T. asperellum*. The two main sources of isolates for these studies (~1/3 each) are institutional collections and rhizospheric soils. Therefore, there is yet plenty of opportunity for bioprospection and basic studies, not only to unravel novel *Trichoderma* isolates/species bearing abiotic stress-relief effects on plants but also to further understand the underpinning mechanisms of this desirable phenotype.

A tendency was found for the studies to focus on model plants with agronomic/economic relevance, most with short reproductive cycles. Moreover, the competitive ability of *Trichoderma* species that allows rapid rhizospheric establishment and roots colonization likely explains the preference for experimental inoculations based on soil application and seed coating and biopriming; the ease of later field applications for bioproducts developed in this manner adds to this circumstance. With regard to the abiotic stresses studied in the context of plant-*Trichoderma* interactions, the focus has been essentially on those caused by excess of salt, drought, and heavy metals, which can be considered as coherent with the major environmental issues affecting the security and sustainability of food production worldwide. As a consequence, the parameters assessed are all directly and indirectly related to shoot and root weight and length, as well as major physiological processes, such as photosynthesis, general cellular redox state and oxidative-stress control/response, and protective compounds synthesis. Not unexpectedly, the molecular and genetic mechanisms studied in this regard have been strictly related with those response variables and could be conceptually classified as transcription factors, metabolic/oxidative stress and signaling pathways, and direct stress-protective molecules. Metanalytical approaches are currently underway to advance the dissection of current information on the *Trichoderma* effects in the improvement of plant growth and development under abiotic stresses. Taking all this information together, and assessing knowledge-integration studies and reviews, it became evident the astonishing complexity of regulatory mechanisms and networks already unveiled in the *Trichoderma*-plant interaction, as well as the universe yet to be researched in this field.

We reviewed here the state-of-the-art of knowledge on the use of *Trichoderma* spp. in aiding plants to cope with a variety of stresses caused by climatic and edaphic abiotic factors; despite some trends and gaps observed in the pertinent investigated literature, the great potential of this fungal genus for developing alternative applications of biotechnological interest (agriculture, industry, environment, and health) is clear. Augmentation of salinity and pollution by an array of xenobiotics (Rosegrant et al. 2009; Munns and Gilliham 2015), as well as global warming effects such as high temperatures, alterations in rainfall cycles, and longer droughts (Godfray et al. 2010; Foley et al. 2011), are relevant examples of these

environmental impacts. More than 4/5 of global ecosystems functioning and processes that underpin support services for people are already affected by climate change (Ogar et al. 2020), with a significant role for abiotic factors. The current issues on food production and security will require robust and coordinated actions on scientific and political arenas to bring forth environmentally sustainable solutions for the global economy, hugely impacted by the COVID-19's pandemic. Those solutions depend upon consistent reductions in both our carbon footprint on the planet (Stern 2016) and in the biodiversity losses, which interdependently affect ecosystems and economy (Dasgupta 2008; Trisos et al. 2020). The large spectrum of compounds and bioproducts that can be extracted from and formulated on the basis of species/isolates of the *Trichoderma* genus can certainly contribute to broaden the strategies and options for agricultural production with environmental sustainability and safety. Considering current unresolved issues related to the bioproduct registration system and the scope of its applicability, e.g. (Berg et al. 2013; Chojnacka 2015), it may be considered advantageous for a biotechnological product to bear multiple simultaneous functions, a possibility that is clearly present in *Trichoderma* (Vinale et al. 2008; Schuster and Schmoll 2010; Mukherjee et al. 2013; Hidangmayum et al. 2018). The various biological activities of *Trichoderma* with beneficial effects for their host plants have a high potential for adding economical and sustainability values to existing and yet to be developed bioproducts and derivatives.

References[1]

Anam GB, Reddy MS, Ahn YH (2019) Characterization of *Trichoderma asperellum* RM-28 for its sodic/saline-alkali tolerance and plant growth promoting activities to alleviate toxicity of red mud. Sci Total Environ 662:462–469. https://doi.org/10.1016/j.scitotenv.2019.01.279

Arif N, Sharma NC, Yadav V et al (2019) Understanding heavy metal stress in a rice crop: toxicity, tolerance mechanisms, and amelioration strategies. J Plant Biol 62(4):239–253. https://doi.org/10.1007/s12374-019-0112-4

Babychan M, Simon S (2017) Efficacy of *Trichoderma* spp. against *Fusarium oxysporum* f. sp. *lycopersici*. (FOL) infecting pre-and post-seedling of tomato. J Pharmacogn Phytochem 6(4):616–619

Ballescá AB (2016) China's economic development and its effects on air pollution: accountability, policies and health risks. Universitat Autònoma de Barcelona

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[1] Please, note that the references included in the systematic review are listed in Table 2 only, regardless if they are cited in the text or not.

Bano A, Ullah F, Nosheen A (2012) Role of abscisic acid and drought stress on the activities of antioxidant enzymes in wheat. Plant Soil Environ 58(4):181–185. https://doi.org/10.17221/210/2011-pse

Begum N, Ahanger MA, Su Y et al (2019) Improved drought tolerance by AMF inoculation in maize (*Zea mays*) involves physiological and biochemical implications. Plan Theory 8(12):579. https://doi.org/10.3390/plants8120579

Berg G, Zachow C, Müller H et al (2013) Next-generation bio-products sowing the seeds of success for sustainable agriculture. Agronomy 3:648–656. https://doi.org/10.3390/agronomy3040648

Bray EA (2007) Plant response to water-deficit stress. In: Encyclopedia of life sciences. John Wiley & Sons, Ltd, Chichester. https://doi.org/10.1038/npg.els.0001298

Bugge M, Hansen T, Klitkou A (2016) What is the bioeconomy? A review of the literature. Sustainability 8(7):691. https://doi.org/10.3390/su8070691

Calvo P, Nelson L, Kloepper JW (2014) Agricultural uses of plant biostimulants. Plant Soil 383(1):3–41. https://doi.org/10.1007/s11104-014-2131-8

Chakraborty U, Chakraborty B, Dey P, Chakraborty A (2015) Role of microorganisms in alleviation of abiotic stresses for sustainable agriculture. In: Chakraborty U, Chakraborty B (eds) Abiotic stresses in crop plants. CABI, Wallingford/Boston. https://doi.org/10.1079/9781780643731.0232

Chang P-FL, Xu Y, Narasimhan ML et al (1997) Induction of pathogen resistance and pathogenesis-related genes in tobacco by a heat-stable *Trichoderma* mycelial extract and plant signal messengers. Physiol Plant 100(2):341–352. https://doi.org/10.1111/j.1399-3054.1997.tb04792.x

Chaverri P, Branco-Rocha F, Jaklitsch W et al (2015) Systematics of the *Trichoderma harzianum* species complex and the re-identification of commercial biocontrol strains. Mycologia 107(3):558–590. https://doi.org/10.3852/14-147

Chojnacka K (2015) Innovative bio-products for agriculture. Open Chem 13(1):932–937. https://doi.org/10.1515/chem-2015-0111

Chopra R (2016) Environmental degradation in India: Causes and consequences. Int J Appl Environ Sci 11(6):1593–1601

Choudhury FK, Rivero RM, Blumwald E, Mittler R (2017) Reactive oxygen species, abiotic stress and stress combination. Plant J 90(5):856–867. https://doi.org/10.1111/tpj.13299

Christgen SL, Becker DF (2019) Role of proline in pathogen and host interactions. Antioxid Redox Signal 30(4):683–709. https://doi.org/10.1089/ars.2017.7335

Contreras-Cornejo HA, Macías-Rodríguez L, del-Val E, Larsen J (2018) The root endophytic fungus *Trichoderma atroviride* induces foliar herbivory resistance in maize plants. Appl Soil Ecol 124:45–53. https://doi.org/10.1016/j.apsoil.2017.10.004

Cruz-Magalhães V, Nieto-Jacobo MF, van Zijll de Jong E et al (2019) The NADPH oxidases Nox1 and Nox2 differentially regulate volatile organic compounds, fungistatic activity, plant growth promotion and nutrient assimilation in *Trichoderma atroviride*. Front Microbiol 9:3271. https://doi.org/10.3389/fmicb.2018.03271

Daryanto S, Wang L, Jacinthe PA (2016) Global synthesis of drought effects on maize and wheat production. PLoS One 11(5):e0156362. https://doi.org/10.1371/journal.pone.0156362

Dasgupta P (2008) Creative accounting. Nature 456:44. https://doi.org/10.1038/twas08.44a

De Souza JT, Pomella AWV, Bowers JH et al (2006) Genetic and biological diversity of *Trichoderma stromaticum*, a mycoparasite of the cacao witches'-broom pathogen. Phytopathology 96(1):61–67. https://doi.org/10.1094/PHYTO-96-0061

Druzhinina IS, Seidl-Seiboth V, Herrera-Estrella A et al (2011) *Trichoderma*: the genomics of opportunistic success. Nat Rev Microbiol 9(10):749–759. https://doi.org/10.1038/nrmicro2637

Du JB, Han TF, Gai JY et al (2018) Maize-soybean strip intercropping: achieved a balance between high productivity and sustainability. J Integr Agric 17(4):747–754. https://doi.org/10.1016/S2095-3119(17)61789-1

Duran R, Cary JW, Calvo AM (2010) Role of the osmotic stress regulatory pathway in morphogenesis and secondary metabolism in filamentous fungi. Toxins 2(4):367–381. https://doi.org/10.3390/toxins2040367

Egidi E, Delgado-Baquerizo M, Plett JM et al (2019) A few Ascomycota taxa dominate soil fungal communities worldwide. Nat Commun 10(1):1–9. https://doi.org/10.1038/s41467-019-10373-z

El_Komy MH, Saleh AA, Eranthodi A, Molan YY (2015) The plant pathology journal characterization of novel *Trichoderma asperellum* isolates to select effective biocontrol agents against tomato *Fusarium* Wilt. Plant Pathol J 31(1):50–60. https://doi.org/10.5423/PPJ.OA.09.2014.0087

Etesami H (2018) Bacterial mediated alleviation of heavy metal stress and decreased accumulation of metals in plant tissues: mechanisms and future prospects. Ecotoxicol Environ Saf 147:175–191. https://doi.org/10.1016/j.ecoenv.2017.08.032

FAO (2007) Mapping biophysical factors that influence agricultural production and rural vulnerability. http://www.fao.org/tempref/docrep/fao/010/a1075e/a1075e00.pdf. Accessed 12 Nov 2019

Farooq M, Wahid A, Kobayashi N et al (2009) Plant drought stress: effects, mechanisms and management. In: Sustainable agriculture. Springer Netherlands, pp 153–188. https://doi.org/10.1007/978-90-481-2666-8_12

Feitosa YB, Cruz-Magalhães V, Argolo-Filho RC et al (2019) Characterization of genetic diversity on tropical *Trichoderma* germplasm by sequencing of rRNA internal transcribed spacers. BMC Res Notes 12(1):1–6. https://doi.org/10.1186/s13104-019-4694-1

Filippou P, Tanou G, Molassiotis A, Fotopoulos V (2013) Plant acclimation to environmental stress using priming agents. In: Plant acclimation to environmental stress. Springer, New York, pp 1–27. https://doi.org/10.1007/978-1-4614-5001-6_1

Foley JA, Ramankutty N, Brauman KA et al (2011) Solutions for a cultivated planet. Nature 478:337–342. https://doi.org/10.1038/nature10452

Ghori NH, Ghori T, Hayat MQ et al (2019) Heavy metal stress and responses in plants. Int J Environ Sci Technol 16(3):1807–1828. https://doi.org/10.1007/s13762-019-02215-8

Glare T, Caradus J, Gelernter W et al (2012) Have biopesticides come of age? Trends Biotechnol 30(5):250–258. https://doi.org/10.1016/J.TIBTECH.2012.01.003

Godfray HCJ, Beddington JR, Crute IR et al (2010) Food security: the challenge of feeding 9 billion people. Science 327(5967):812–818. https://doi.org/10.1126/science.1185383

Gomiero T (2018) Food quality assessment in organic vs. conventional agricultural produce: findings and issues. Appl Soil Ecol 123:714–728. https://doi.org/10.1016/j.apsoil.2017.10.014

Groppa MD, Tomaro ML, Benavides MP (2007) Polyamines and heavy metal stress: the antioxidant behavior of spermine in cadmium- and copper-treated wheat leaves. Biometals 20(2):185–195. https://doi.org/10.1007/s10534-006-9026-y

Gruber SG, Seidl-Seiboth V (2012) Self versus non-self: fungal cell wall degradation in *Trichoderma*. Microbiology 158(1):26–34. https://doi.org/10.1099/mic.0.052613-0

Hameed A, Dilfuza E, Abd-Allah EF et al (2014) Salinity stress and arbuscular mycorrhizal symbiosis in plants. In: Miransari M (ed) Use of microbes for the alleviation of soil stresses, vol 1. Springer, New York, pp 139–159. https://doi.org/10.1007/978-1-4614-9466-9_7

Hardoim PR, van Overbeek LS, Berg G et al (2015) The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. Microbiol Mol Biol Rev 79(3):293–320. https://doi.org/10.1128/mmbr.00050-14

Harman G (2011a) *Trichoderma*-not just for biocontrol anymore. Phytoparasitica 39(2):103–108. https://doi.org/10.1007/s12600-011-0151-y

Harman GE (2011b) Multifunctional fungal plant symbionts: new tools to enhance plant growth and productivity. New Phytol 189(3):647–649. https://doi.org/10.1111/j.1469-8137.2010.03614.x

Harman GE, Uphoff N (2019) Symbiotic root-endophytic soil microbes improve crop productivity and provide environmental benefits. Scientifica. https://doi.org/10.1155/2019/9106395

Harman GE, Howell CR, Viterbo A et al (2004) *Trichoderma* species — opportunistic, avirulent plant symbionts. Nat Rev Microbiol 2(1):43–56. https://doi.org/10.1038/nrmicro797

Harman GE, Doni F, Khadka RB, Uphoff N (2019) Endophytic strains of *Trichoderma* increase plants' photosynthetic capability. J Appl Microbiol 130(2):529–546. https://doi.org/10.1111/jam.14368

Harzing AW (2007) Publish or Perish. Computer Program. https://harzing.com/resources/publish-or-perish

He B, Yun ZJ, Shi JB, Bin JG (2013) Research progress of heavy metal pollution in China: sources, analytical methods, status, and toxicity. Chin Sci Bull 58(2):134–140. https://doi.org/10.1007/s11434-012-5541-0

Heisey PW, Fuglie KO (2018) Agricultural research investment and policy reform in high-income countries. ERR-249, U.S. Department of Agriculture, Economic Research Service. doi:https://doi.org/10.22004/AG.ECON.276235

Hidangmayum A, Dwivedi P, Padmanabh Dwivedi C (2018) Plant responses to *Trichoderma* spp. and their tolerance to abiotic stresses: a review. J Pharmacogn Phytochem 7:758–766

Hu H, Jin Q, Kavan P (2014) A study of heavy metal pollution in China: current status, pollution-control policies and countermeasures. Sustainability 6(9):5820–5838. https://doi.org/10.3390/su6095820

Huang Y, Chen Q, Deng M et al (2018) Heavy metal pollution and health risk assessment of agricultural soils in a typical peri-urban area in Southeast China. J Environ Manag 207:159–168. https://doi.org/10.1016/j.jenvman.2017.10.072

Ikram M, Ali N, Jan G et al (2019) *Trichoderma reesei* improved the nutrition status of wheat crop under salt stress. J Plant Interact 14(1):590–602. https://doi.org/10.1080/17429145.2019.1684582

Jiao S, Lu Y (2020) Abundant fungi adapt to broader environmental gradients than rare fungi in agricultural fields. Glob Chang Biol 26(8):4506–4520. https://doi.org/10.1111/gcb.15130

Kappel L, Münsterkötter M, Sipos G et al (2020) Chitin and chitosan remodeling defines vegetative development and *Trichoderma* biocontrol. PLoS Pathog 16(2):e1008320. https://doi.org/10.1371/journal.ppat.1008320

Khan AL, Hussain J, Al-Harrasi A et al (2015) Endophytic fungi: resource for gibberellins and crop abiotic stress resistance. Crit Rev Biotechnol 35(1):62–74. https://doi.org/10.3109/07388551.2013.800018

Kitchenham B (2004) Procedures for performing systematic reviews. [Online] Available at: https://pdfs.semanticscholar.org/d36f/e9d7839596d58fa008121db57dc7cadda338.pdf

Kubicek CP, Herrera-Estrella A, Seidl-Seiboth V et al (2011) Comparative genome sequence analysis underscores mycoparasitism as the ancestral life style of *Trichoderma*. Genome Biol 12(4):1–15. https://doi.org/10.1186/gb-2011-12-4-r40

Kubicek CP, Steindorff AS, Chenthamara K et al (2019) Evolution and comparative genomics of the most common *Trichoderma* species. BMC Genomics 20(1):1–24. https://doi.org/10.1186/s12864-019-5680-7

Kumar A, Verma JP (2018) Does plant—microbe interaction confer stress tolerance in plants: a review? Microbiol Res 207:41–52. https://doi.org/10.1016/j.micres.2017.11.004

Kumar S, Thakur M, Rani A (2014) *Trichoderma*: mass production, formulation, quality control, delivery and its scope in commercialization in India for the management of plant diseases. Afr J Agric Res 9(53):3838–3852. https://doi.org/10.5897/AJAR2014

Lata R, Chowdhury S, Gond SK, White JF (2018) Induction of abiotic stress tolerance in plants by endophytic microbes. Lett Appl Microbiol 66(4):268–276. https://doi.org/10.1111/lam.12855

Lewis D (1985) Symbiosis and mutualism: crisp concepts and soggy semantics. In: Boucher DH (ed) The biology of mutualism. Croom-Helm, London, pp 29–39

Li X, Zhang X, Wang X et al (2019) Bioaugmentation-assisted phytoremediation of lead and salinity co-contaminated soil by *Suaeda salsa* and *Trichoderma asperellum*. Chemosphere 224:716–725. https://doi.org/10.1016/j.chemosphere.2019.02.184

Loguercio LL, de Carvalho AC, Niella GR et al (2009a) Selection of *Trichoderma stromaticum* isolates for efficient biological control of witches' broom disease in cacao. Biol Control 51(1):130–139. https://doi.org/10.1016/J.BIOCONTROL.2009.06.005

Loguercio LL, Santos LS, Niella GR et al (2009b) Canopy-microclimate effects on the antagonism between *Trichoderma stromaticum* and *Moniliophthora perniciosa* in shaded cacao. Plant Pathol 58(6):1104–1115. https://doi.org/10.1111/j.1365-3059.2009.02152.x

Lombardi N, Vitale S, Turrà D et al (2018) Root exudates of stressed plants stimulate and attract *Trichoderma* soil fungi. Mol Plant-Microbe Interact 31(10):982–994. https://doi.org/10.1094/MPMI-12-17-0310-R

López-Bucio J, Pelagio-Flores R, Herrera-Estrella A (2015) *Trichoderma* as biostimulant: exploiting the multilevel properties of a plant beneficial fungus. Sci Hortic 196:109–123. https://doi.org/10.1016/j.scienta.2015.08.043

Marasco R, Rolli E, Ettoumi B et al (2012) A drought resistance-promoting microbiome is selected by root system under desert farming. PLoS One 7(10):e48479. https://doi.org/10.1371/journal.pone.0048479

Mastouri F, Björkman T, Harman GE (2010) Seed treatment with *Trichoderma harzianum* alleviates biotic, abiotic, and physiological stresses in germinating seeds and seedlings. Phytopathology 100(11):1213–1221. https://doi.org/10.1094/PHYTO-03-10-0091

Meena M, Swapnil P (2019) Regulation of *wrky* genes in plant defence with beneficial fungus *Trichoderma* : current perspectives and future prospects. Arch Phytopathol Plant Prot 52(1–2):1–17. https://doi.org/10.1080/03235408.2019.1606490

Meena KK, Sorty AM, Bitla UM et al (2017) Abiotic stress responses and microbe-mediated mitigation in plants: the omics strategies. Front Plant Sci 8:172. https://doi.org/10.3389/fpls.2017.00172

Mehta CM, Sirari K (2019) A review on mycorrhiza-mycoparasite interactions in the rhizosphere. Plant Arch 19(2):508–511

Mendoza-Mendoza A, Zaid R, Lawry R et al (2018) Molecular dialogues between *Trichoderma* and roots: role of the fungal secretome. Fungal Biol Rev 32(2):62–85. https://doi.org/10.1016/j.fbr.2017.12.001

Meyer AJ, Dreyer A, Ugalde JM et al (2020) Shifting paradigms and novel players in Cys-based redox regulation and ROS signaling in plants - and where to go next. Biol Chem 402(3):399–423. https://doi.org/10.1515/hsz-2020-0291

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7(9):405–410. https://doi.org/10.1016/S1360-1385(02)02312-9

Mota TM, Oshiquiri LH, Lopes ÉCV et al (2019) Hsp genes are differentially expressed during *Trichoderma asperellum* self-recognition, mycoparasitism and thermal stress. Microbiol Res 227:126296. https://doi.org/10.1016/j.micres.2019.126296

Mukherjee PK, Horwitz BA, Kenerley CM (2012) Secondary metabolism in *Trichoderma* - a genomic perspective. Microbiology 158(1):35–45. https://doi.org/10.1099/mic.0.053629-0

Mukherjee PK, Horwitz BA, Singh US et al (2013) *Trichoderma* in agriculture, industry and medicine: an overview. In: Mukherjee PK, Horwitz BA, Singh US et al (eds) *Trichoderma*: biology and applications. CABI, Wallingford, pp 1–9

Mukherjee I, Singh UK, Singh RP et al (2020) Characterization of heavy metal pollution in an anthropogenically and geologically influenced semi-arid region of East India and assessment of ecological and human health risks. Sci Total Environ 705:135801. https://doi.org/10.1016/j.scitotenv.2019.135801

Munns R, Gilliham M (2015) Salinity tolerance of crops - what is the cost? New Phytol 208(3):668–673. https://doi.org/10.1111/nph.13519

Nath K, Jajoo A, Poudyal RS et al (2013) Towards a critical understanding of the photosystem II repair mechanism and its regulation during stress conditions. FEBS Lett 587(21):3372–3381. https://doi.org/10.1016/j.febslet.2013.09.015

Naumann G, Alfieri L, Wyser K et al (2018) Global changes in drought conditions under different levels of warming. Geophys Res Lett 45(7):3285–3296. https://doi.org/10.1002/2017GL076521

Nuccio ML, Paul M, Bate NJ et al (2018) Where are the drought tolerant crops? An assessment of more than two decades of plant biotechnology effort in crop improvement. Plant Sci 273:110–119. https://doi.org/10.1016/j.plantsci.2018.01.020

Ogar E, Pecl G, Mustonen T (2020) Science must embrace traditional and indigenous knowledge to solve our biodiversity crisis. One Earth 3(2):162–165. https://doi.org/10.1016/j.oneear.2020.07.006

Osakabe Y, Osakabe K, Shinozaki K, Tran LSP (2014) Response of plants to water stress. Front Plant Sci 5:86. https://doi.org/10.3389/fpls.2014.00086

Pachauri S, Sherkhane PD, Mukherjee PK (2019) Secondary metabolism in *Trichoderma*: chemo- and geno-diversity. In: Satyanarayana T, Das S, Johri B (eds) Microbial diversity in ecosystem sustainability and biotechnological applications. Springer, Singapore, pp 441–456. https://doi.org/10.1007/978-981-13-8487-5_17

Parnell JJ, Berka R, Young HA et al (2016) From the lab to the farm: an industrial perspective of plant beneficial microorganisms. Front Plant Sci 7:1110. https://doi.org/10.3389/fpls.2016.01110

Paul D (2017) Research on heavy metal pollution of river ganga: a review. Ann Agrar Sci 15(2):278–286. https://doi.org/10.1016/j.aasci.2017.04.001

Rajput RS, Ram RM, Vaishnav A, Singh HB (2019) Microbe-based novel biostimulants for sustainable crop production. In: Microbial diversity in ecosystem sustainability and biotechnological applications. Springer, Singapore, pp 109–144

Rocha I, Ma Y, Souza-Alonso P et al (2019) Seed coating: a tool for delivering beneficial microbes to agricultural crops. Front Plant Sci 10:1357. https://doi.org/10.3389/fpls.2019.01357

Rosegrant MW, Ringler C, Zhu T (2009) Water for agriculture: maintaining food security under growing scarcity. Annu Rev Environ Resour 34:205–222. https://doi.org/10.1146/annurev.environ.030308.090351

Rousseau S, Deschacht N (2020) Public awareness of nature and the environment during the COVID-19 crisis. Environ Resour Econ 76(4):1149–1159. https://doi.org/10.1007/s10640-020-00445-w

Schenk PM, Carvalhais LC, Kazan K (2012) Unraveling plant-microbe interactions: can multi-species transcriptomics help? Trends Biotechnol 30(3):177–184. https://doi.org/10.1016/j.tibtech.2011.11.002

Schulz B, Boyle C, Draeger S et al (2002) Endophytic fungi: a source of novel biologically active secondary metabolites. Mycol Res 106(9):996–1004. https://doi.org/10.1017/S0953756202006342

Schuster A, Schmoll M (2010) Biology and biotechnology of *Trichoderma*. Appl Microbiol Biotechnol 87(3):787–799. https://doi.org/10.1007/s00253-010-2632-1

Selvakumar G, Panneerselvam P, Ganeshamurthy AN (2012) Bacterial mediated alleviation of abiotic stress in crops. In: Maheshwari D (ed) Bacteria in agrobiology: stress management. Springer-Verlag, Berlin/Heidelberg, pp 205–224. https://doi.org/10.1007/978-3-642-23465-1_10

Singh P, Singh J, Ray S et al (2020) Seed biopriming with antagonistic microbes and ascorbic acid induce resistance in tomato against *Fusarium* wilt. Microbiol Res 237:126482. https://doi.org/10.1016/j.micres.2020.126482

Sodango TH, Li X, Sha J, Bao Z (2018) Review of the spatial distribution, source and extent of heavy metal pollution of soil in China: impacts and mitigation approaches. J Heal Pollut 8(17):53–70. https://doi.org/10.5696/2156-9614-8.17.53

Stern N (2016) Economics: current climate models are grossly misleading. Nature 530(7591):407–409. https://doi.org/10.1038/530407a

Steyaert JM, Weld RJ, Loguercio LL, Stewart A (2010a) Rhythmic conidiation in the blue-light fungus *Trichoderma pleuroticola*. Fungal Biol 114(2–3):219–223. https://doi.org/10.1016/J.FUNBIO.2010.01.001

Steyaert JM, Weld RJ, Mendoza-Mendoza A, Stewart A (2010b) Reproduction without sex: conidiation in the filamentous fungus *Trichoderma*. Microbiology 156(10):2887–2900. https://doi.org/10.1099/mic.0.041715-0

Steyaert JM, Weld RJ, Stewart A (2010c) Ambient pH intrinsically influences *Trichoderma* conidiation and colony morphology. Fungal Biol 114(2–3):198–208. https://doi.org/10.1016/J.FUNBIO.2009.12.004

Szczałba M, Kopta T, Gąstoł M, Sękara A (2019) Comprehensive insight into arbuscular mycorrhizal fungi, *Trichoderma* spp. and plant multilevel interactions with emphasis on biostimulation of horticultural crops. J Appl Microbiol 127(3):630–647. https://doi.org/10.1111/jam.14247

Takahashi F, Kuromori T, Sato H, Shinozaki K (2018) Regulatory gene networks in drought stress responses and resistance in plants. In: Iwaya-Inoue M, Sakurai M, Uemura M (eds) Advances in experimental medicine and biology. Springer, New York, pp 189–214. https://doi.org/10.1007/978-981-13-1244-1_11

Tardieu F, Simonneau T, Muller B (2018) The physiological basis of drought tolerance in crop plants: a scenario-dependent probabilistic approach. Annu Rev Plant Biol 69:733–759. https://doi.org/10.1146/annurev-arplant-042817-040218

Topolovec-Pintarić S (2019) *Trichoderma*: invisible partner for visible impact on agriculture. In: *Trichoderma* - the most widely used fungicide. IntechOpen. https://doi.org/10.5772/intechopen.83363

Trisos CH, Merow C, Pigot AL (2020) The projected timing of abrupt ecological disruption from climate change. Nature 580(7804):496–501. https://doi.org/10.1038/s41586-020-2189-9

Vinale F, Sivasithamparam K, Ghisalberti EL et al (2008) *Trichoderma*-plant-pathogen interactions. Soil Biol Biochem 40(1):1–10. https://doi.org/10.1016/j.soilbio.2007.07.002

Waghunde RR, Shelake RM, Sabalpara AN (2016) *Trichoderma*: a significant fungus for agriculture and environment. Afr J Agric Res 11(22):1952–1965. https://doi.org/10.5897/AJAR2015.10584

Woo SL, Ruocco M, Vinale F et al (2014) *Trichoderma*-based products and their widespread use in agriculture. Open Mycol J 8(1):71–126. https://doi.org/10.2174/1874437001408010071

Xiang W, Zhao L, Xu X et al (2012) Mutual information flow between beneficial microorganisms and the roots of host plants determined the bio-functions of biofertilizers. Am J Plant Sci 3(8):1115–1120. https://doi.org/10.4236/ajps.2012.38134

Yan L, Zhu J, Zhao X et al (2019) Beneficial effects of endophytic fungi colonization on plants. Appl Microbiol Biotechnol 103(8):3327–3340. https://doi.org/10.1007/s00253-019-09713-2

Yang Y, Guo Y (2018) Elucidating the molecular mechanisms mediating plant salt-stress responses. New Phytol 217(2):523–539. https://doi.org/10.1111/nph.14920

Yang Q, Li Z, Lu X et al (2018) A review of soil heavy metal pollution from industrial and agricultural regions in China: pollution and risk assessment. Sci Total Environ 642:690–700. https://doi.org/10.1016/j.scitotenv.2018.06.068

Zari M (2014) Ecosystem services analysis in response to biodiversity loss caused by the built environment. SAPIENS 7:1–14

Zeilinger S, Gruber S, Bansal R, Mukherjee PK (2016) Secondary metabolism in *Trichoderma* - chemistry meets genomics. Fungal Biol Rev 30(2):74–90. https://doi.org/10.1016/j.fbr.2016.05.001