Trichoderma

Subjects: Agriculture, Dairy & Animal Science

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Trichoderma spp. has the ability to inhibit fungal plant pathogens through several mechanisms like the production of hydrolytic enzymes, mycoparasitism, coiling, and antibiosis and is therefore recommended as a potential and native biocontrol agent for effective control of soil-transmitted diseases. Various species of *Trichoderma,* like *T. virens*, *T. asperellum, T. harzianum,* etc., have been explored for their biocontrol activity against phytopathogens. There are different *Trichoderma* species and strains with respect to plant pathogens. Efforts have been made to develop effective and efficient methods, such as microencapsulation use of different polymers, adjuvants, or carriers, to increase the shelf-life and efficacy of *Trichoderma* formulations.

biocontrol phytopathogen mycoparasitism soil-borne bio-pesticide

1. Introduction

Biological control of plant diseases has emerged as a promising area in phytopathology. These methods not only minimize reliance on synthetic pesticides but are also comparatively economical, feasible, robust, and sustainable [1][2]. Among the commercial biofungicides/fungal antagonists, *Trichoderma* has been broadly acknowledged as a source of potential biocontrol agent, particularly for lowering soil-borne phytopathogens such as *Fusarium oxysproum*, *Rhizoctonia solani* [3], *Macrophomina phaseolina* [4], *Sclerotinia rolfsii*, and others [5][6][7]. *Trichoderma* spp. are saprophytic, avirulent, and soil-inhabiting fungi, and they control pathogens with various biocontrol methods such as mycoparasitism [8], retard the pathogen growth by secreting cell-wall-destroying enzymes [9][10], nutrient uptake competition, and rhizospheric competence [2]. Because of its effectiveness against phytopathogens, its market demand is increasing yearly [11].

According to Harman (1991), [12] key points that are required for the production of any biological control system are (1) a potential biocontrol agent, (2) viable propagule with amplified shelf-life, (3) bioprotective delivery mechanisms that may offer the biocontrol agent an advantage to compete against existing microflora, and (4) steady field performance [13]. As mentioned above, the first and most principal step before mass production of a biocontrol agent is the identification of a robust propagule (hyphae, chlamydospores, and/or conidia) [14]. Once a reliable and efficient biocontrol agent is identified, large-scale production, design, and application ideas need to be performed cautiously for the product's stability during storage and later use. Both liquid and solid formulations are utilized in developing sufficient amounts of viable and active *Trichoderma* inoculums. Conidia and chlamydospores are the preferred propagules for formulations since they can withstand rigorous treatment procedures, whereas hyphae cannot be used because they are not dehydration-resistant [12][15]. Several reports (**Table 1**) related to the effectiveness of *Trichoderma* strains and their formulations have been published periodically [13]; however, reports

concerning advancements in mass production, persistent viability, and related field performance of *Trichoderma* species are fragmentary. Furthermore, the challenges related to the isolation and development methods for elevating the effectiveness and sustainable use of *Trichoderma* formulations in the field of health security and food also need to be addressed. In this research, researchers intend to fill this gap and unravel the recent developments regarding isolation, identification, preservation, substrates, consortium, quality control, mass production, delivery approaches, field performance, and registration and commercialization of *Trichoderma* formulations.

Table 1. Timeline of historical events in *Trichoderma* research.

Decades	Year	Landmarks in *Trichoderma* Research	References
1700s	1794	In this year, the name *Trichoderma* was introduced.	[16]
1800s	1865	The sexual stage of *Trichoderma viride* (*Hypocrea rufa*) was reported.	[17]
1900s	1932	First evidence that *Trichoderma lignorum* (*Hypocrea virens*) has mycoparasitic and biocontrol abilities.	[18]
	1934	The invention of the first anti-microbial compound (e.g., gliotoxin).	[19]
	1957	Discovery of the effect of light *on T. viride*; syn. *T. reesei*.	[20]
	1972	Demonstration of biocontrol activity of *T. harzianum* against *Sclerotium rolfsii* in field conditions.	[21]
	1979	RUT C30, a carbon catabolite mutant of *T. reesei*, was isolated using ultraviolet (UV) mutagenesis.	[22]
	1983	Cloning of the first *Trichoderma* species (e.g., *T. reesei*).	[23]
	1984	The first international workshop was held on *Trichoderma*.	-
	1985	Papavizas wrote the first review on biology, ecology, and potential for biocontrol by *Trichoderma*.	[15]
	1986	Report on the expression of growth promotion in the root.	[24]
	1987	Successful transformation of *T. reesei*.	[25]
	1989	First registration of commercial formulation (e.g., Binab T).	[26]
	1992	Evidence of cloning of lectin-coated fibers by *Trichoderma* species.	[27]
	1993	*prb1* gene cloning related to mycoparasitism and induced by cell wall.	[28]
	1997	Expression of enhanced plant immunity (ISR) by application of *Trichoderma* spp.	[29]
	1998	Identification of factors that induce genes for mycoparasitism.	[30]

Decades	Year	Landmarks in *Trichoderma* Research	References
2000s	1999	*Trichoderma* internal colonization of plant roots demonstrated.	[31]
	2002	Role of signaling pathways and G protein in mechanism of biocontrol and conidia formation.	[32]
	2003	Role of mitogen-activated protein kinase (MAPK), which negatively regulates conidiation in *T. virens*.	[33][34]
	2004	Identification of photoreceptors (*Brl1* and *Brl2*) in *T. atroviride*.	[35]
	2005	Function of *Trichoderma* MAPK (mitogen-activated protein kinase) in Induce systemic resistance (ISR).	[36]
	2006	Purification of the first true elicitor protein (*Sm1/EpII*) of *Hypocreaatro viridis* on glucose.	[37]
	2006	Cellulases and xylanases regulators identified in *T. reesei* (*XYR1*).	[38]
	2008	First genome sequenced of *Trichoderma* species (e.g., *T. reesei*).	[39]
	2009	Endophytic *Trichoderma* for stress tolerance in plants.	[40]
	2010	Discovery of VELVET protein (Vel1) as a key regulator in biocontrol agents (e.g., *T. virens*) and *Trichoderma* spp. peptide pheromone precursor genes have been identified.	[41]
	2011	Genome comparison of three species of *Trichoderma*.	[42]
	2012	Next-generation sequencing and high-throughput procedures were used for the sequencing of *Trichoderma* spp. (*T. asperellum*, *T. harzianum*, *T. citrinoviride*, *T. longibrachiatum*) genome.	[43]
	2022	Five new *Trichoderma* species were reported.	[44]
	2014–2022	144 *Trichoderma* strains were registered in 40 countries. [18][19]	[45]

oparasitic

eral other researchers have also obtained positive results with *Trichoderma* isolates as biocontrol agents of plant pathogens [46]. *Trichoderma* continues to hold a significant position among commercial biological control agents (BCAs) in a wide range of crop and disease management, either as a single ingredient or in combination with other ingredients [6][45][47][48]. Up till now, more than 80 species of *Trichoderma* have been reported [13], and among these, *T. harzianum*, *T. virens,* and *T. viride* are frequently deployed biocontrol agents. In India, commercialization of *Trichoderma* is limited to only two species, namely *T. viride* and *T. harzianum* [13]. However, there are ample reports on the effectiveness of *T. virens* and *T. asperellum,* but these are still unregistered under the Central Insecticide Board and Registration Committee (CIBRC) in India. This may be due to several hurdles, such as toxicity assessment, environmental effects of microbes and their formulation, and optimization of technology for mass-scale production [49]. Apart from these, some other constraints include multi-location trials for the purpose of proving its safety, followed by registration. In addition, some other challenges are inconsistent field presentation and low shelf-life of formulation, lack of patent protection, preliminary testing, high registration cost, alertness about the beneficial effect of *Trichoderma* formulations, and training and education shortfalls. Registration also requires

good and effective documentation and other confirmations. Moreover, the evaluation process itself (compilation and analysis of data) can be prolonged and costly. In the past, high registration fees were clearly seen as a delay or barrier to BCA market growth, especially for medium and small enterprises that are the chief manufacturers of biocontrol agents. Due to these reasons, there are now diverse products in the market that claim to be plant growth promoters or biofertilizers for managing plant diseases but are not yet registered. The biocontrol activity of *Trichoderma* spp. is represented in **Table 2**.

However, their safe use cannot be guaranteed without toxicological and efficacy data [50]. Combined with the competitive pesticide industry, BCA companies are finding it hard to generate enough revenue from product sales to justify the registration cost. Unluckily, this has led to some products being removed from the stores. For instance, *T. harzianum* T-39 (Trichodex) was launched in Europe and Israel in 1993 for the control of Botrytis fruit rot through biological methods but was detached from the market. It went bankrupt in 2005 due to low sales and the rising cost of registration. **Table 3** contains information on gene identification in *Trichoderma* species.

Table 2. Biocontrol activity of *Trichoderma* spp.

Name of *Trichoderma* Species	Name of Plant Pathogens	Crop Name	Inhibition/Efficacy (%)	Experiment Condition	References
T. harzianum	*Sclerotium rolfsii* and *Rhizoctonia solani*	Ryegrass	42–47	Greenhouse and field condition	[51]
T. harzianum	*Phytophthora cinnamon*	Pine	28.5–37.5	Greenhouse	[52]
T. hamatum and *T. harzianum*	*P. cinnamomi*	Avocado		Greenhouse	[53]
T. viride, *T. virens T. harzianum*, *T. pseudokoningii T. koningii*	*Aspergillus niger*, *Rhizoctonia solani* and *Geotrichum candidum*	*Sapodilla* (*Manilkara zapota* L.)	54–74	Laboratory	[54]
T. harzianum strain Ths97	*F. solani*	Olive trees	25–50	-	[55]
Trichoderma viride 1433 Mutant strains	*Pythium aphanidermatum*	Mustard	85	Lab and field	[56]
Trichoderma spp.	*Pythium aphanidermatum*	Chilli	88.00	Lab and field	[57]
Trichoderma harzianumRifai, *Trichoderma viride*	*Pythium aphanidermatum*	Tobacco	100	Lab and greenhouse	[58]

Name of *Trichoderma* Species	Name of Plant Pathogens	Crop Name	Inhibition/Efficacy (%)	Experiment Condition	References
Trichoderma virens Trichoderma harzianum, *Trichoderma viride*	*Phomopsis vexans*	Brinjal	38–49	Lab	[59]
Trichoderma harzianum T22	*Alternaria alternata*	Sunflower	75	Lab	[60]
T. atrobrunneum	*Armillaria mellea*	Strawberry	91	Field	[61]
Trichoderma harzianum	*Fusarium moniliforme*	Maize	73.33	Lab	[62]

S.No.	Identified Genes	*Trichoderma* Species	Function	References
1	*Tvsp1*	*T. virens*	This gene protects cotton seedlings against *Rhizoctonia solani*.	[64][65]
2	*Tag3*	*T. asperellum*	Responsible for glucanase production for cell wall degradation.	[66]
3	*TgaA* and *TgaB*	*T. virens*	Bicontrol efficacy for management of *R. solani* and *Sclerotium rolfsii*.	[67]
4	*ThPG1*	*T. harzianum*	This gene is required for beneficial interaction between *Trichoderma harzianum* and the host.	[68]
5	*ThPRT2*	*T. harzianum*	Mycoparasitism activity for *Botrytis cinerea*.	[69]
6	*tri5*	*T. brevicompactum IBT40841*	Production of antifungal activity and trichodermin against fungus causing infection in the human body (*Candida* spp. and *Aspergillus fumigatus*).	[70]
7	*erg1*	*T. harzianum* CECT 2413	Ergosterol biosynthetic pathway (EBP).	[71]
8	*TvGST*	*T. virens*	This gene provides enhanced tolerance against cadmium stress.	[72]
9	*TrCCD1*	*T. reesei*	This gene facilitates pigment production and hyphal growth.	[73]
10	*egl1*	*T. longibrachiatum*	Exhibits antagonistic activity against *Pythium ultimum.*	[74]
11	*qid74*	*T. harzianum*	Plant biofertilization and root architecture.	[75]

S.No.	Identified Genes	*Trichoderma* Species	Function	References
12	*Taabc2*	*T. atroviride*	ATP binding cassette transporter plays a major role in cell membranes.	[76]
13	*tac1*	*T. virens* IMI 304061	This gene shows mycoparasitism against *S. rolfsii* and *R. solani*.	[77]
14	*TrCCD1*	*T. reesei*	This gene promotes condia formation and elongation of fungal hyphae.	[73]
15	*gluc78 w*	*T. atroviride*	Cell wall disintegartion of *Pythium* and *Rhizoctonia* spp.	[78]
16	*SL41*	*T. harzinum*	Showed mycoparasitic action.	[79]
17	*Taabc2*	*T. atroviride*	This gene is important for biological control of necrotrophs (*B. cinerea* and *R. solani*).	[76]
18	Monooxygenase	*T. hamatum*	This gene shows antagonistic activity against *Sclerotinia sclerotiourum* and *S. cepivorum.*	[80]
19	*Xl1*	*Trichoderma strain Y*	This gene is helpful in hemicellulose breakdown.	[81]
20	*eg1*, β-1,4 glucanase	*T longibrachiatum*	This gene shows antagonistic activity against *Pythium ultimum* in cucumber.	[82]
21	*pacC*	*T. virens*	This gene acts as myctorphy.	[83]
22	*tvhydii1*	*T. reesei*	Important in mycoparasitism and plant-fungus interaction.	[84]
23	*hmgR*	*T. koningii*	These genes inhibit the pathogen *Rhizoctonia solani*.	[85]
24	*Tasx1*	*T. asperellum*	This gene plays a key role in morphological development, mycoparasitism, and antibiosis.	[86]
25	*gpr1*	*T. atroviride*	This gene is required for the stability of cell walls and hyphal growth.	[87]
26	*TvCyt2*	*T. virens*	*Trichoderma*–Arabidopsis interaction	[88]
27	*gluc31*	*T. harzianum*	Mycoparasitism ability and influence cell wall organization.	[89]
28	*ipa-1*	*T. virens*	Antibiosis of *R. solani*.	[90]
29	*TasXyn24.2*, *TasXyn29.4*	*T. asperellum*	Induced resistance and promoted growth in seedlings.	[91]

Phytopathogens

Trichoderma spp. have the ability to produce metabolites, modulate the plant defense responses, and act as a hyperparasite [93][94]. Moreover, *Trichoderma* strains are effective BCAs because of their high reproductive

S.No.	Identified Genes	*Trichoderma* Species	Function	References
30	*agl1*	*T. atroviride*	Biological control of plant pathogen.	[92]

zosphere, defense opulation densities [95]. *Trichoderma* BCAs can even have a beneficial impact on plants by promoting biofertilization, which increases plant development and enhances plant defense systems [96]. *Trichoderma* uses indirect and direct methods to control plant pathogens. The power of these mechanisms in the biocontrol method relies upon the type of *Trichoderma* strain, the antagonized pathogen, including its host, and the ecological situation [96]. The direct mechanism includes mycoparasitism and coiling, whereas the indirect mechanism includes challenges for nutrients and space, systemic acquired resistance, and antibiosis. Among them, mycoparasitism, competition, and antibiosis play a major role in *Trichoderma*-mediated biological control.

3.1. Mycoparasitism

Parasitism is one of the important mechanisms of fungal antagonist, where one fungus parasitizes (mycoparasite) another fungus (host), and this process is known as mycoparasitism. It has been observed that mycoparasitism involves four sequential steps: chemotaxis, recognition, attachment, and wrapping, as well as penetration of the pathogen cell wall and host digestion [97][98][99]. *Trichoderma* is widely used as a biofungicide against phytopathogens such as *B. cinerea* as well as the soil-borne pathogens *Rhizoctonia*, *Sclerotinia*, *Pythium,* and *Fusarium* spp. [14][100].

Trichoderma species employ several mechanisms to antagonize and mycoparasitize other pathogenic fungi, which includes competing for nutrients [101], releasing antibiotic metabolites, and activities like encircling the host and enlargement of the appressorium-like structure [51][102][103]. The degradation of host tissues containing pathogenic organisms occurs due to the enzymatic breakdown of cell walls facilitated by hydrolytic enzymes (such as chitinase, β-1,3-glucanase, and cellulase) that are synthesized by *Trichoderma* spp [104]. In *T. atroviride*, the *nag1* gene coding for N-acetylglucosaminidase has a significant effect on chitinase induction, followed by biocontrol [105]. In the parasite interaction between *Trichoderma* and *R. solani*, host-released dispersal factors are responsible for inducing ech42 (encoding endochitinase 42) gene transcription prior to physical touch [30][106]. Lectins present in the host cell wall cause the parasites to cover the hyphae of the host after direct contact [27][100][106].

3.2. Antibiosis

Antibiosis is a phenomenon where one organism is prevented/inhibited by another microorganism through secondary metabolites (SMs). *Trichoderma* spp. synthesizes SMs (pyrone, heterocyclic compounds, terpenoids, polyketides, etc.) [107] and also produces specific low molecular weight compounds/antibiotics for combatting plant pathogens [108]. Antibiosis has been reported to occur during contact among pathogen, plant, and *Trichoderma* spp., which triggers *Trichoderma* to produce antibiotics and SMs to reduce the growth of phytopathogens. More than 180 secondary metabolites have been extracted from *Trichoderma* spp., showing different classes of chemical compounds [109][110]. On the basis of their biosynthetic origin, these compounds can be classified as peptaiboles, polyketides, and terpenes [111]. Many species of *Trichoderma* genus are known to synthesize peptidols that are

non-proteinogenic amino acids (α-aminoisobutyric acid, a polypeptide antibiotic with a 500 to 2200 Da molecular weight). These compounds are acetylated at the N-terminus and contain an aminoalcohol at the C-terminus [112].

Different types of *Trichoderma* produce different antibiotics; for example, *T. viride* produces mucortoxins A and B, mucorin, trichophyton, and mucorin. Similarly, mucorin A and B were isolated from *T. mucorin*. *T. harzianum* produces tricholongins BI and BII, while longibrachins and trichokonins were extracted from *T. koningii*. Atroviridines A-C and neoatroviridines A-D have been obtained from *T. atroviride* culture. In addition, other antibiotics and fungicidal compounds have been isolated from *T. harzianum*, *T. koningii*, *T. aureoviride*, *T. virens*, *T. hamatum*, and *T. lignorum* [110].

Growth of soil pathogens such as *Phytophthora solani*, *P. middletonii*, *P. cinnamomi*, *Bipolaris sorokiniana,* and *Fusarium oxysporum* was adversely affected in the vicinity of Koninginin D [113]. Similarly, viridins obtained from *Trichoderma* spp. like *T. viride*, *T. koningii*, and *T. virens* inhibit the spore germination of *Colletotrichum lini*, *Botrytis allii*, *Penicillium expansum*, *Fusarium caeruleum*, *Stachybotry satra*, and *Aspergillus niger* [114]. Harzianic acids derived from *T. harzianum* show antimicrobial activity against *Sclerotinia sclerotiorum*, *R. solani,* and *Pythium irregulare* [115]. It has been found that *Trichoderma* spp. And *Gliocladium* suppressed the growth of various soil-borne plant pathogens (*Fusarium* spp., *Macrophomina*, *Sclerotium rolfsii*, and *Sclerotinia* spp.) [116][117]. Silva et al. (1998) studied the antibiosis mechanism of *Trichoderma* against *Colletotrichum* spp. [118].

3.3. Competition

Limitation and competition for nutrient sources can lead to the natural control of fungal pathogens [119]. *Trichoderma* is a cosmopolitan fungus and is found in all kinds of soils because of its outstanding competitive potential. It can fight with phytopathogens for nutritive sources, such as C, N, and Fe, and also acts as a biological antagonist towards soil-borne pathogens. It is also an aggressive competitor that grows rapidly and quickly colonizes its substrate and controls slow-growing pathogens [120]. *Trichoderma* is more competitive with other microorganisms due to certain abilities, such as a higher growth rate and enhanced aptitude to mobilize and utilize nutrients from soil/substrate [121][122]. Thus, competition for macro and micronutrients plays a key role in the interaction between *Trichoderma*-plant pathogen [123] because *Trichoderma* species compete with bacteria in the rhizosphere of crops for nutrients and sites of infection [124]. Compared to other rhizosphere bacteria, *Trichoderma* shows a better ability to produce and take up nourishment from soil; therefore, the management of certain disease-causing entities, such as *Botrytis cinerea,* using *Trichoderma* through food competition is possible [125]. It is observed that there are four major features of any organism that contribute to its saprophytic ability and inoculum potential: (i) fast germination of fungal propagule, rapid hyphal growth towards nutrients, (ii) production of suitable enzymes for carbon constituents of the host plant, (iii) secretion of growth inhibitor compounds (fungistatic and bacteriostatic), and (iv) tolerance to fungistatic substances produced by competing microorganisms. Antagonistic fungi can compete with the pathogens for food and space by colonizing the normal environment, i.e., plant tissue, rhizosphere, or phyllosphere [126]. It depends on the colonization level of the host plant and acclimatization to the environmental situations in which they are living [127]. In order to successfully compete with other fungal

phytopathogens for food and space, *Trichoderma* should exhibit efficient strategies for colonization of the plant and should be plentiful in an area where competition with other microorganisms occurs [126].

Trichoderma spp. produces iron chelating agents and siderophores, which make iron unobtainable for rhizospheric bacteria, which eventually leads to the extinction of the disease. Thus, *Trichoderma* acts as a competitor that helps control plant diseases [128]. Apart from this, due to its ability to colonize the rhizosphere and outcompete for nutrients, *T. harzianum* (T35 Strain) reduces the availability of nutrients and the amount of rhizospheric space available for the fungal wilt agent of watermelon (*Fusarium oxysproum* f.sp. *meloni*) to colonize [129]. Srinivasan et al. (1995) demonstrated the importance of competition between siderophore-producing *Trichoderma* strains and wood decay Basidiomycetes fungi [130].

Mokhtar et al. 2013 studied the interaction between *T. harzianum* and a few fungal species, such as *Alternaria alternata*, *Fusarium acuminatum,* and *A. infectoria*. The results revealed that lack of nutrients caused death of the pathogenic fungi [131]. It has also been found that *Trichoderma* can compete with plant pathogens, including *Colletotrichum* sp., *Botrytis* sp., and *Phytophthora* sp., for complex and simple substrates of carbon [132]. In order to successfully compete with other fungal phytopathogens for food and space, *Trichoderma* should exhibit efficient strategies for colonization of the plant and should be plentiful in an area where competition with other microorganisms occurs [126].

Trichoderma colonization of roots commonly improves nutrient absorption and utilization, crop yield, tolerance to abiotic stressors, and root growth and development [133]. *Trichoderma hamatum* or *Trichoderma koningii* can boost crop production up to 300% after addition in the field. In greenhouse experiments, a substantial increase in yield was reported after treating the seedlings with *Trichoderma* spores [95]. The ability of *Trichoderma* BCAs to produce metabolites that either prevent spore germination (fungistatic), kill cells (antibiosis), or alter the rhizosphere, for example, making the soil acidic, leads to biocontrol that is unsuitable for pathogen proliferation [96]. *Trichoderma* strains quickly proliferate when introduced to the soil because they are inherently resistant to a wide range of hazardous substances, including insecticides, fungicides, and herbicides like DDT [95].

3.4. Production of Antibiotics and Other Antifungal Compounds

It has been shown that the *Trichoderma* species produce a large number of secondary metabolites, about 370 of which are members of several chemical compound classes with potent antagonistic activities [126][134]. Peptaibols and polyketides are the most significant non-volatile and volatile organic compounds (VOCs) produced by the majority of *Trichoderma* strains [2]. The volatile antibiotic 6-phenyl-pyrone (6PAP), responsible for the distinctive coconut scent and the biological control of *F. oxysporum*, is produced by the *T. viride*, *T. harzianum*, and *T. koningii* species [135]. In addition, *T. harzianum* also produces harzianic acid, a tetramic acid that has strong antifungal action as well as the capacity to stimulate plant development and function as a chelator [136].

3.5. Induced Systemic Resistance

Trichoderma can trigger a host plant's defensive mechanism while preventing harmful pathogens from proliferating and growing, and it can also encourage crops to build self-defense mechanisms to gain local or systemic disease resistance [137]. Two methods are used to achieve *Trichoderma*-induced plant disease resistance: first, control the elicitors or elicitors that trigger the plant disease resistance response; and second, release oligosaccharides from the cell-wall-degrading enzymes produced by *Trichoderma* to cause plant resistance [138]. Saravanakumar et al. (2016) found that *Trichoderma* coated corn seeds dramatically increased the peroxidase (POD) and phenylalanine ammonia lyase (PAL) activity, and the plants were resistant to Curvularia leaf spot of corn [139].

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