A novel function of N-signaling in plants with special reference to *Trichoderma* interaction influencing plant growth, nitrogen use efficiency, and cross talk with plant hormones

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Abstract

Trichoderma spp. is considered as a plant growth promoter and biocontrol fungal agents. They colonize on the surface of root in most of the agriculture crops. They secrete different secondary metabolites and enzymes which promote different physiological processes as well as protect plants from various environmental stresses. This is part of their vital functions. They are widely exploited as a biocontrol agent and plant growth promoter in agricultural fields. Colonization of *Trichoderma* with roots can enhance nutrient acquisition from surrounding soil to root and can substantially increase nitrogen use efficiency (NUE) in crops and linked with activation of plant signaling cascade. Among *Trichoderma* species, only some *Trichoderma* species were well characterized which help in the uptake of nitrogen-containing compound (especially nitrate form) and induced nitric oxide (NO) in plants. Both nitrate and NO are known as a signaling agent, involved in plant growth and development and disease resistance. Activation of these signaling molecules may crosstalk with other signaling molecule (Ca^{2+}) and phytohormone (auxin, gibberellins, cytokinin and ethylene). This ability of *Trichoderma* is important to agriculture not only for increased plant growth but also to control plant diseases. Recently, *Trichoderma* strains have been shown to encompass the ability to regulate transcripts level of high-affinity nitrate transporters and probably it was positively regulated by NO. This review aims to focus the usage of *Trichoderma* strains on crops by their abilities to regulate transcript levels, probably through activation of plant N signaling transduction that improve plant health.

Keywords Nitrate · Nitrogen utilization efficiency · Plant growth · *Trichoderma*

Abbreviations

CEPs	C-terminal encoded peptides
SNP	Sodium nitroprusside
cPTIO	2-(4-Carboxyphenyl)-4,4,5,5-tetramethyl-imidazoline-1-oxyl-3-oxide potassium salt, 2-(4-Carboxyphenyl)-4,5-dihydro-4,4,5,5-tetramethyl-1H-imidazol-1-yloxy-3-oxide

MAPKs	Mitogen-activated protein kinases
PTMs	Post-transcriptional modifications
NUE	Nitrogen use efficiency

Introduction

In modern agriculture, chemical fertilizers are highly utilized that may be one issue for increasing pathogen incidence and increasing a range of pathogen infection in a single plant species. Indeed, application of chemical fertilizer adversely affects soil fertility which may further increase plant diseases and reduces crop productivity. There is a pressing requirement to minimize the chemical fertilizer to ensure a sustain study response for agricultural production with increasing food demand with rising world population. Several alternative approaches have been adopted by a farmer in agriculture which consists of an application of biocontrol agents. *Trichoderma* spp. is used

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as a biocontrol agent in disease management and crop production in the agricultural field worldwide. It has different properties like plant growth promotion activity, nutrient solubilization, antagonistic activity, antibiosis, mycoparasitism. Habitation of *Trichoderma* is rhizospheric soil and colonizes around on the surface of roots and produces some secondary metabolites with a biotechnological and pharmaceutical important application (Muller et al. 2013; Contreras-Cornejo et al. 2016). Production of these substances helps in communication between plants and their association with a microorganism; convey and exchange signal transduction. These signaling molecules affect plant system either positively or negatively. After perception of signal molecules to plant, maintained the homeostasis of a particular metabolism (Halverson and Stacey 1986). Convey of these signal molecules between the host plant and *Trichoderma* has been complicated and clear mechanisms are still unclear. Therefore, attention is needed to study the effects of these signal molecules involves in different plant physiological processes.

Recently, several pieces of evidence have suggested that *Trichoderma* secretes auxin-like metabolites and other proteinaceous compounds around the roots (Bae et al. 2011; Garnica-Vergara et al. 2015). Perception of these compounds by roots promotes plant hormonal mechanisms that help in agronomic traits development under normal or stress condition. Subsequently, colonization of *Trichoderma* with host plants protects host from a different soil-borne pathogenic microorganism. Its association also led to enhance the capability of nutrient and water uptake from the soil system (Contreras-Cornejo 2015; Singh et al. 2018).

N-signaling is important mechanism for the development of plant under normal or stress condition. Its regulation help in root development, flowering, abolish the effect of elevated temperature and disease resistance (Gupta et al. 2011; Singh et al. 2018). In recent year, it has been noticed that root development was highly affected in response to various forms of nitrogen (nitrate/ammonium) when applying exogenously to the plant (Sun et al. 2015). N supplement also affects plant immunity and help in disease management against fungal plant pathogen (Gupta et al. 2014). Similar to nitrate signaling, NO has also been correlated in disease management against the necrotrophic pathogen (Yoshioka et al. 2009). According to Baudouin et al. (2006), NO signal molecule was generated during plant with non-pathogenic microbe interaction. On the basis of highlighted evidences related to plant-microbe and interlinked N regulation in plant growth and development, in this present review, we illustrate the application of *Trichoderma* and emphasized that its association with plant root activates wide function such as biocontrol property, nitrogen utilization efficiency, cross talk with N-signaling and regulation of nitrogen in plant hormones signaling.

Interactions of *Trichoderma* with roots

Trichoderma species are versatile saprophytic, filamentous fungus strain residing in the rhizospheric region of all the plant species. It is symbiotically associated with plants colonizing on the entire root surface of mono and dicot plants with broad range beneficial effects viz., seed germination, nutrient uptake and plant growth (Shoresh et al. 2010; Brotman et al. 2012; Sarma et al. 2014; Singh et al. 2014, 2015, 2018). Subsequently, colonization of *Trichoderma* induces plant cells to deposit cell wall materials and phenolic compounds which restrict the penetration of hyphae of other fungal pathogens into intercellular cells of plants (Yedidia et al. 1999; Patel et al. 2017). *Trichoderma* association leads to secretion of secondary metabolites (like mycotoxin) and antibiotics around the rhizospheric region that prevent pathogen infection (Vinale et al. 2006, 2009; Navazio et al. 2007; Kumar et al. 2017). The plant provides a carbon source like hydrated polysaccharides around the rhizospheric region to encourage the growth of *Trichoderma* for root colonization and defense (Vargas et al. 2009). *Trichoderma asperellum* produces class I hydrophobin protein and Swollenin expansin-like protein on the outer surface of the root which supports root colonization possibly by enhancing attachment and protecting fungal hyphen tips from defense compounds secreted by plant roots (Viterbo and Chet 2006; Brotman et al. 2008). Similarly, *Trichoderma harzianum* T22 produces hydrophobin-like *HYTR1* that mimics the effects of fungus (Ruocco et al. 2007). Once hyphae enter inside the plant roots, they have admittance to plant nutrients, which facilitate the roots to proliferate; mainly, increase the size of primary/secondary roots and area of the root hair density (Harman et al. 2004; Peskan-Berghoefer et al. 2004). Even root branching was promoted after *Trichoderma* inoculation. It has been pre-assumed that during interactions, *Trichoderma* secretes several secondary metabolites which help in activation of plant Ca^{2+} signal transduction (Navazio et al. 2007; Vadassery et al. 2009; Singh et al. 2018). It also secretes some other secondary metabolites which are analogous to auxin; induce lateral root development in *Arabidopsis* (Vinale et al. 2008; Contreras-Cornejo et al. 2009). Like *Trichoderma*, another plant growth promoting microorganism that is *Piriformospora indica* which show mutualistic association with root, but reduced root growth in *Arabidopsis*; probably due to the lower production of auxin (Sirrenberg et al. 2007).

Trichoderma as a potent biocontrol agent

Nowadays, *Trichoderma* species are used as a biocontrol agent in the agricultural context point of view. The genus

of *Trichoderma* is filamentous fungal strains inhabited in the rhizospheric soil in agriculturally important crops. It is free-living fungal strains that are easily interacting with soil, root and foliar environments (Sherameti et al. 2005). These fungi are isolated from rhizospheric soil from forest/agricultural soils or both and can be cultured in lab condition for a long time (Harman 2000). They appear like a greenish and produce a characteristic smell due to the production of a 6-pentyl- α -pyrone volatile compound. Mode of mechanisms of their biocontrol activity against a broad range of soil pathogens is due to adopting antibiosis and myco-parasitic activity. They can produce a variety of antibiotic substances that help in capturing the pathogenic fungi via parasitic mechanism (Prakasam and Sharma 2012). They also compete for seed exudates which help in propagules germination of plant pathogen fungi as well others soil microorganism for nutrient availability and space in soil system (Shores and Harman 2008). A number of *Trichoderma* strains has been identified and

characterized, some of which are characterized as biocontrol agents (e.g., *Trichoderma harzianum*) for controlling plant-pathogens, while others are industrially important (e.g., *Trichoderma resei*).

A critical assessment of interaction of *Trichoderma* with plants has revealed that their association successfully prevents soil-borne disease for which no resistance have been previously demonstrated in plants. Their biocontrol potential has also been explored in several plant pathogens either arise by seeds or air. Likewise rhizobacteria, *Trichoderma* strains has been used effectively for plant growth. Interestingly, bio-formulation of *Trichoderma* with rhizobacteria was studied for plant growth and disease management (Jayaraj and Ramabadrana 1999). Several pieces of evidence have been demonstrated by a scientist in using a different strain of *Trichoderma* strains in different plant species against a broad range of plant pathogens as listed in Table 1.

Nature of biological control of *Trichoderma* spp. that obstruct with different plant pathogens and pests, is a

Table 1 Lists of plant pathogens controlled by *Trichoderma* spp. in various plant species

Trichoderma strains	Plant pathogens	Plant	References
<i>Trichoderma harzianum</i>	<i>Pythium aphanidermatum</i>	Tobacco	Devaki et al. (1992)
	<i>Pythium myriotylum</i>	Onion	Prakasam and Sharma (2012)
	<i>Alternaria porri</i>	Saffron	Gupta et al. (2011)
	<i>Phytophthora</i> sp.	Sapodilla	Bhale et al. (2013)
	<i>R. solani</i>		
<i>T. viride</i>	<i>Macrophomina</i>	Mungbean	Choudhary et al. (2011)
	<i>Phaseolina</i>	Groundnut	Biswas and Sen (2000)
	<i>Sclerotium rolfsii</i>	Saffron	Mir et al. (2011)
	<i>Meloidogyne incognita</i>	Soybean	John Rojan et al. (2010)
	<i>Fusarium oxysporum</i> f. sp. adzuki <i>Pythium</i>		
<i>T. lignorum</i>	<i>Polyporus sanguineus</i>	Bamboo	Kundu and Chatterjee (2003)
<i>Trichoderma</i> species	<i>Sclerotium rolfsii</i>	Mungbean	Bagwan (2011)
	<i>Aspergillus niger</i>	Chickpea	Dubey et al. (2011)
	<i>Aspergillus flavus</i>	Sugarcane	Dubey et al. (2007)
	<i>Rhizoctonia solan</i>	Chilli	Dubey et al. (2012, 2013)
	<i>Fusarium oxysporum</i> f. sp. ciceris	Mango	Gawade et al. (2012)
	<i>Fusarium wilt</i>		Joshi and Misra (2013)
	<i>Fusarium moniliformae</i>		Muthukumar et al. (2011)
	<i>Botryodiplodia theobromae</i>		Suhanna et al. (2013)
	<i>Colletotrichum falcatum</i>		Redda et al. (2018)
	<i>Pythium aphanidermatum</i>		
	<i>Fusarium oxysporum</i> f. sp. Cucumerinum		
<i>T. koningii</i>	<i>X. oryzae</i> pv. <i>oryzae</i>	Rice	Gomathinayagam et al. (2010)
	<i>Ustilago segetum</i>	Sapodilla	Bhale et al. (2013)
		Wheat	Mondal et al. (1995)
<i>T. asperellum</i>	<i>Erisiphe pisi</i>	Pea	Patel et al. (2017)
	<i>Corynespora cassiicola</i>	Lettuce	Singh et al. (2015)
	<i>Curvularia aerea</i>		Baiyee et al. (2019)
<i>T. asperelloides</i>	<i>Sclerotinia sclerotiorum</i>	Soybean	Sumida et al. (2018)

competition of space and nutrients, production of volatile and diffusible substance and production of several hydrolytic enzymes that degrade the outer wall of plant-pathogens (Howell 2003). These hydrolytic enzymes degrade pectinases and other enzymes that are required for pathogenic fungi to penetrate the leaf surface (Zimand et al. 1996). Several member of *Trichoderma* (*T. asperellum*, *T. asperelloides*, *T. koningii*, *T. lignorum*, *T. viride*, *T. harzianum*) are use as a biocontrol against air and soil-borne pathogens (*Pythium*, *Alternaria*, *Phytophthora*, *Macrophomina*, *Polyporus*, *Sclerotium*, *Sclerotinia*, *Erisiphe*, *Corynespora*, *Xanthomonas*, *Fusarium*, *Ustilago*, *Rhizoctonia*, *Colletotrichum*) in plants which prevent the damage caused by infection (Table 1). Root colonization of *T. harzianum* with several plants abolished pathogenicity of the fungal pathogen, providing sustain application as a bio fungicidal agent in place the chemical fungicides in the modern agricultural field (Prakasam and Sharma 2012). Another, commercial crops such as rice which are cultivated worldwide, suffering in the reduction of plant growth and yield production due to blight disease caused by *Xanthomonas oryzae* pv. *oryzae* and blight of rice incited by *Rhizoctonia solani*. A study highlighted that seed treated with *T. viride* and *T. koningii* were able to control the disease severity and increase the yield of the crop (Das and Hazarika 2000). Similarly, *T. koningii* treatment with wheat controlled the wheat pathogen *U. segetum* var. *tritici* (Mondal et al. 1995), *T. harzianum* controlled *R. solani*, *Pythium aphanidermatum*, *Pythium myriotylum*; *Alternaria porri*; *Phytophthora* sp.; *R. solani* in different plants listed in Table 1 (Devaki et al. 1992; Prakasam and Sharma 2012; Gupta et al. 2011; Bhalle et al. 2013). A use of *T. viride* with vegetable plants controlled broad range pathogens like *Macrophomina*, *Phaseolina*, *Sclerotium rolfsii*, *Meloidogyne incognita*, *Fusarium oxysporum* f. sp. *adzuki*, *Pythium* (Biswas and Sen 2000; Choudhary et al. 2011; Mir et al. 2011; John et al. 2010). Similar to *T. viride*, other class of different *Trichoderma* strains with a combination of either FYM (1:1) or along with chemicals were examined that show antagonistic property and controlled the incidence of pathogen infection and improved plant health as mentioned in Table 1.

Trichoderma use for plant growth and development

Plant growth promotion is one of the major traits of any agricultural important crops. Among plant growth promoting microbes, *Trichoderma* is one of the important fungal strains which enhanced plant growth and production (Shukla et al. 2012). Colonization of these fungi with roots of soybean has increased up to 123% in yield when inoculated *Trichoderma* strain T-22 (Harman 2000). Significantly increased 10–20% seed germination in case of pea seed treated with *T. asperellum* T42 (Singh et al. 2015). Association of these

fungi seems to increased height 127% in pea and 28% in soybean (Singh et al. 2015; Lindsey and Baker 1967). Similarly, use of *T. longipile* and *T. tomentosum* in plants increased 58–71% leaf area, 91–102% shoot dry weight and 100–158% root dry weight in cabbage (Rabeendran et al. 2000).

Furthermore, *Trichoderma* strains also increased agronomic root traits development like root hairs, lateral root, and total root biomass. In an experiment using tobacco seeds grown with and without *T. asperellum* T42 treated in lab condition, the fungus increased root hairs, the density of lateral root and total root biomass, and these effects sustain up to vegetative growth (Singh et al. 2018). Similarly, treatment of T22 with inbred maize line Mo17, fungal association increased root and shoot growth (Harman et al. 2004). When *Trichoderma* is inoculated in soil or seeds, it was observed that *Trichoderma* association induced metabolic pathways like carbohydrates metabolism and enhances photosynthetic machinery that provides carbon and energy source for plant growth (Harman et al. 2004; Shores and Harman 2008).

The role of *Trichoderma* in secondary metabolites secretion, it can solubilize soil nutrients present in the complex form into a simplex form which are easily availing to plants (Altomare et al. 1999). The nutrient status level was enhanced in the plant when cucumber seeds bio-primed with *Trichoderma* and grown in the nutrient supplement (Yedidia et al. 2003). Though, a symbiotic association of *Trichoderma* with roots could ensure a balanced nutrient supply by increasing roots branching and growth under conditions (Fig. 1). However, even under near-optimal conditions, *Trichoderma* inoculation in maize is considered to enhance yields (Harman and Shores 2007; Harman 2000; Harman et al. 2004).

Crosstalk between Trichoderma and N signaling

The association of *Trichoderma* with plant roots leads to increased nitrogen use efficiency (NUE) (Harman 2000; Harman et al. 2004; Rai et al. 2008; Sherameti et al. 2005; Singh et al. 2018). First evidence has highlighted the effect of *T. harzianum* T22 on NUE in maize crop, where plant morphology was changed under low soil nitrogen condition (Harman 2000). Generally, plant growth and yield attributes increase with the rise in N fertilizer, but at a threshold level, yield attributes are no longer increased with increased N fertilizer. However, *Trichoderma* inoculation has long time effect on NUE which lead to increase about 40–50% yield attributes (Harman and Donzelli 2001). Some negative effects of *Trichoderma* on yield production have been reported with a few genotypes (Harman 2006). Recently, it has been demonstrated that treatment of *Trichoderma asperellum* T42 with tobacco roots increased NUE and growth attributes in the presence of nitrate nutrient (Singh et al. 2018).

Fig. 1 Interaction of *Trichoderma* with plant roots. Induction of plant nitrate transporters helps nitrogen acquisition from soil system to plant roots. Nitrate reductase catalyzes nitrate to nitric oxide (NO) in stepwise reactions. This NO modulates several plant hormones genes and defense genes which involve in root differentiation and plant immunity. Plant immunity of the plant is at least in part due to the

colonization of the beneficial fungus *Trichoderma*, which induces NO production. Arrows indicate translocation of NO after production of NO. Additionally, *Trichoderma* colonization with roots released several molecules that may activate nitrogen sensing receptors on the surface of the roots thereby eliciting a signal response to nitrate transporters, which ultimately helps N uptake from soil to plants

Furthermore, our understanding about the mechanism of action of *Trichoderma* strains and their broad ability for NUE, N signaling, and plant growth is still under-covered (Brotman et al. 2012; Singh et al. 2014, 2018; Gupta et al. 2014). N signaling was activated during non-pathogenic plant-microbial interactions e.g., NO produced in contact with mycorrhizal in *Medicago* roots (Calcagno et al. 2012). Even, symbiotic association with plants elevated transcripts of nitrate reductase (Sherameti et al. 2005; Bae et al. 2009;

Shoresh et al. 2010). However, clear evidence of NO generation in the presence of *Trichoderma* strain with plant roots was demonstrated by Gupta et al. (2014), where the interaction of *T. asperelloides* with roots led to generate NO in *Arabidopsis*. This symbiotic association for increased NUE caused by *Trichoderma* has led to the extensive application in agricultural practices as a cost-effective approach to elevating endogenous N status. Nitrogen is an essential component of macronutrients which is not easily available to plants

due to leaching. Recently, most intensively studied nitrate transporters (NRTs) and nitrate reductase (NR) enzyme involved in NO_3^- or NH_4^+ acquisition and assimilation have been demonstrated in *Trichoderma asperellum* T42 inoculated tobacco plants (Singh et al. 2018), where, two high-affinity NRTs (*NRT2.1* and *NRT2.2*) and NR were shown to be up-regulated when plants fed with NO_3^- nutrient.

N signaling and plant response

Nitrate is a component of macronutrient which is not only used as N fertilizer, but is also known as a signaling agent that regulates N acquisition and metabolism (Crawford 1995; Stitt 1999; Forde 2002; Yamasaki 2005; Song et al. 2013; Sun et al. 2015; Fan et al. 2017). Nutrient deficient plants provided strong evidence to activate a set of morphological and physiological responses (Gruber et al. 2013), particularly root growth and proliferation in the nutrient-rich zone. Especially, root architectures enable the plant to balance for the non-uniform allocation of nutrient availability (Giehl et al. 2014). Therefore, root differentiation is considered to be an important agronomical trait for plant fitness. Studies on root distribution and proliferation in response to nutrient treatments (N, P, K) have been highlighted in different plant species (Hodge 2004). Recently, N nutrition ($\text{NO}_3^-/\text{NH}_4^+$) and their response as N signaling in plants for the development of root traits has been focused (Nacry et al. 2013; Sun et al. 2015), but the clear establishment of N signaling in response to NO_3^- nutrient has been lacking.

The effect of N richness and deprivation on root traits and crop development has been extensively investigated in plant system (Nacry et al. 2013; Singh et al. 2014, 2018; Krapp et al. 2014; Fan et al. 2017). Plant showed dual affinity in response to N uptake depending upon N availability. At high N concentration (> 10 mM), lateral root (LR) development is inhibited while the opposite results were demonstrated with a lower concentration (< 10 mM) (Gruber et al. 2013). Genomic studies revealed that several genes contributed in LR and root hair development in response to N supply (Krouk et al. 2010; Krapp et al. 2014; Vidal et al. 2015; Pii et al. 2016). These include: the nitrate transporters (NRT) family (*NRT1*, *NRT2*, *NRT3*), BTB and TAZ domain protein 1 (*BT1*) and *BT2*, transcription factors involved in N signaling, *SPL9*, *NAC4*, *TGA1/4*, the auxin-related modules *AFB3/miR393* and *ARF8/miR167*, the auxin biosynthetic enzyme *TAR2*, the CLE peptides and their receptor *CLV1* (Vidal and Gutierrez 2008; Marchive et al. 2013; Ma et al. 2014; Sun et al. 2015; Araus et al. 2016; Fan et al. 2017; Singh et al. 2018). Recently, root hairs, lateral root development, and total root biomass were increased after association of *T. asperellum* T42 with *Nicotiana tabacum* (Singh et al. 2018). Bio-primed tobacco seeds with *T. asperellum* T42 were grown in nitrate, and ammonium nutrient supplement

seems to increased status level of total nitrogen as compared to control. The genomic study revealed that nitrate transporters (*NRT2.1* and *NRT2.1*) were up-regulated in response to *Trichoderma* infection in tobacco. Further up-regulation of NR in the presence of *T. asperellum* T42 had confirmed that the association of fungus might help to increase the level of nitrogen in the plant. There is limited knowledge on interactions of these genes is available (Canales et al. 2014), such as interactions of *CHL1/NRT1.1*, *AFB3/miR393* and *NAC4* were demonstrated to engage in N signaling with the purpose of LR proliferation (Vidal et al. 2014). Indeed primary root (PR) and LR are regulated independently by N, but *nac4* and *npf6.3* mutation analysis showed that growth of LR was affected by these genes which were not the case with PR (Vidal et al. 2014). This means LR development depends on the dose of N concentrations. The findings highlighted from the above studies demonstrate that N-signaling positively crosstalk's with plant hormone signaling.

Moreover, a milestone study was highlighted by Ruffel et al. (2011) on the systemic transmission of N signaling, in which gene expression responds to local N signals whereas at a later stage genes were responded by systemic N signaling in root differentiation in *Arabidopsis*. Indeed, shoot played a key role in systemic N signaling in the root, and cytokinins are involved in N claim (Ruffel 2011). A novel NO_3^- transporter encoded a gene, i.e., *NRT2.1* has been demonstrated as both local and systemic regulator of N signaling in LR development (Li et al. 2014). However, the function of *NRT2.1* in the circulation of N signal from shoot to root in the presence of high NO_3^- concentration is unknown. Recently, regulation of NO_3^- in split-root was also identified. Where small C-terminal encoded peptides (CEPs) and their receptors as part of N signaling was shown to be involved in NO_3^- translocation from root to shoot (Tabata et al. 2014). Unfortunately, authors were unable to link the role of CEPs and their receptors in root morphology. Besides cytokinin and CEPs, some more molecules such as auxin and *miRNAs* are proposed to function as circulating signals involved in systemic N signaling in the root-shoot-root system (Li et al. 2014).

Till date, our knowledge is limited, and merely one gene (i.e., TCP-domain family protein 20; TCP20) showed both local and systemic regulation of N nutrient (Guan et al. 2014). CEPs are recognized as both local and systemic signal response that reduced LR growth (Bisseling and Scheres 2014). This dual effect of CEPs might be used as an engineering perspective for complete N sense. Additionally, several vital constituents of N signaling had been well documented in root tips (Castaings et al. 2009; Marchive et al. 2013). Overall, considering all information together, it is concluded that root tips are a central part of the plant for N perception. They sense and enable to convey a signal to the root-shoot-root via stele.

Plant growth and development are very complicated and regulated by different plant hormones like auxin, cytokinin (CK), gibberellic acid (GA), ethylene and ABA (Vanstraelen and Benkova 2012). Interestingly, the involvement of *Trichoderma* in shoot growth and lateral root development depend on auxin transport was also demonstrated in *A. thaliana* (Contreras-Cornejo et al. 2009). In that experiment, the interaction of *T. virens* was unable to promote root growth and development in auxin transport or signaling (AUX1, BIG, AXR1, EIR1) mutants plants. Similarly, effects of *T. atroviride* on root hair induction in the ET-related mutants *etr1* and *ein2* in *A. thaliana* was also elucidated. Analysis revealed that ET gene was involved in root induction in wild type *A. thaliana*. However, the effects of *T. atroviride* in mutated plants were unable to respond in the similar type of root formation.

Furthermore, a secondary metabolite analogue to auxin compound also promoted the activity of the mitogen-activate protein kinase 6, which is a negatively impact on the root hair formation (López-Bucio et al. 2013). Since N signaling correlated with other plant signaling network that helps in plant growth and development. An experiment conducted by Brotman et al. (2012) elucidated that colonization of *Trichoderma asperelloides* T203 with plant able to increase the content of several amino acids, which are the main form of transported nitrogen. Association of this fungus with plants have the ability to uptake, allocate and reuse nitrogen. This experiment stated that T203-inoculation in plants could be deciding factor to increase nitrogen utilization efficiency (NUE). Auxin is linked with N signaling and sturdily modulated the root architectures and seed germination (Ma et al. 2014; Tal et al. 2016). Although N controls the hormonal biosynthesis, regulation, and their transport locally as well as systemically which help in plant development (Ruffel et al. 2011), crosstalk between auxin and NO_3^- regulation has been known very earlier (Avery et al. 1937). Recently, Ma et al. (2014) found that regulation of TAR2, which is the main constituent of auxin biosynthesis, expressed in pericycle cells and vascular cells of the root, under low N condition. On the subject of auxin transport, NO_3^- provision helps in regulation of PINs transport in *Arabidopsis* (discussed in the review by Adamowski and Friml 2015). Likely, a NO_3^- transceptor (*CHL1/NRT1.1*) with the similar activity of an auxin transporter was transcriptionally regulated in the presence of low NO_3^- concentration (Krouk et al. 2010). This coupled model of auxin/ NO_3^- transceptor helps in understanding the regulation of NO_3^- dependent auxin transport and its homeostasis. But, the negative impact of this couple of auxin/ NO_3^- was also demonstrated on the mechanism of an auxin receptor AUXIN SIGNALING F-BOX3 (*AFB3*) and *miRNA 393* (Vidal et al. 2010). Induction of *AFB3* level led to increased expression of *NAC4* gene in the presence of NO_3^- concentration, which negatively reduced

with increased expression of *miRNA 393*, with reducing NO_3^- concentration. These results interlinked between the status of external inorganic N and internal N level of the plant which modulated auxin signaling and transport in plant development (Gutierrez 2012).

Similarly, the connection of plant hormone ethylene with N was highlighted by Tian et al. (2009) in *Arabidopsis*, where NO_3^- application increases ethylene biosynthesis through activation of 1-aminocyclopropane-1-carboxylate (ACC) synthase (ACS) and ACC oxidase (ACO) genes. NO_3^- provision also controlled the expression level of CK gene. Application of NO_3^- can activate isopentyl transferase3 (*IPT3*) transcript accumulation which is the main constituent of the NO_3^- dependent CK biosynthesis (Takei et al. 2004). A mutational analysis with *nptf6.3* mutant where the absence of transcript accumulation of *IPT3* indicated that *NPTF6.3* (*CHL1/NRT1.1*) NO_3^- transceptor activity is essential for *IPT3* dependent CK biosynthesis (Hu et al. 2009; Medici and Krouk 2014; Krouk 2016). Recently, Ondzighi-Assoume et al. (2016) demonstrated that ABA accumulated in a cell-specific manner as similar to transcript accumulation of *SCARECROW* gene in NO_3^- provision, especially the effect was raised with increasing NO_3^- concentration. This effect was may be due to the formation of ABA-glucose complex by the activity of a β -glucosidase1. Tal et al. (2016) interlinked ABA, GA and nitrate transporter (*NPF3*) in root endodermis of *Arabidopsis*. The effect of NO_3^- was also elaborated in seed germination (Matakiadis et al. 2009), where a Cytochrome P450 protein, similar to ABA 8'-hydrolyase like activity, controlled ABA degradation in NO_3^- provision and alleviated seed dormancy.

NO signaling and plant hormones

NO has gained engrossment in last two decades in several plant physiological processes such as photosynthesis, seed germination, stomatal closure, hypocotyl growth, root organogenesis, floral regulation, pathogen defense and ultimately senescence (Correa-Aragunde et al. 2004; Neill et al. 2008; Jasid et al. 2009; Sirova et al. 2011; Mur et al. 2013; Gupta et al. 2014; Sun et al. 2015; Singh et al. 2018). Increasing pieces of evidence corroborate that NO is suitably termed as “Plant Growth Regulator” similar to other plant growth regulators (Beligni and Lamattina 2001). This gas molecule endogenously synthesizes, and major sites for NO synthesis are in the chloroplast, mitochondria, peroxisomes, and cytoplasm (Roszer 2012). NR-mediated NO generation (the main enzyme for NO synthesis) are more dominated in vascular/higher plants (Jasid et al. 2006), but NOS-dependent NO synthesis was also highlighted in the higher plant (Corpas and Barroso 2017). NR uses NO_2^- as a substrate for NO synthesis in plants (Roszer 2012), whereas in an animal, L- arginine-dependent NO synthesis was catalyzed

by NOS. Several sources for NO synthesis depend on reductive/oxidative pathways in different part cells in the plant kingdom were noticed (Sami et al. 2018). Only few evidence had noticed where *Trichoderma* association elevated endogenous NO level. A short term NO generation was noticed in the interaction between *A. thaliana*, and *T. asperelloids* (Gupta et al. 2014). Recently, Singh et al. (2018) demonstrated that the interaction of *T. asperellum* T42 with the root of *Nicotiana tabaccum* induced NO generation. The specific mechanism of NO synthesis in the presence of *Trichoderma* in the plant is nevertheless unfamiliar.

NO affects plant growth in a dose-dependent manner. A lower concentration of NO donor (0–20 ppm) enhanced plant growth in plants like *Lycopersicon esculentum*, *Lactuca sativa*, and *Pisum sativum*, whereas, higher concentrations (40–80 ppm) retarded plant growth in tomato (Anderson and Mansfield 1979; Leshem and Haramaty 1996). Moreover, NO induces root growth in cucumber and rice (Pagnussat et al. 2002; Sun et al. 2015). A lower dose of NO donor (10^{-5} M; SNP), affected more prominently root/shoot length, fresh root mass and shoot fresh mass (Hayat et al. 2011), while higher concentration (1 M; SNP) inhibit total plant biomass as compared to control plants (Hayat et al. 2010). Treatment of 0.1 nM–0.1 μ M SNP induced root growth and elongation (Gouvea et al. 1997). These findings corroborated that NO donor plays a key role in adventitious and lateral root elongation in several plant species (Pagnussat et al. 2002) and analysis was further confirm by use of NO scavenger (methyl blue, cPTIO).

Correa-Aragunde et al. (2004) pointed out the interaction of auxin and NO that helped lateral root formation in tomato. Auxin regulates cell-division and differentiation, cell expansion, apical dominance, etc. A diffusion mechanism of shoot-derived auxin is different from polar auxin distribution occurring in roots. Auxin is transported from the lateral root cap to the basal meristem and back to the root tip (Overvoorde et al. 2010). Several transcriptomic pieces of evidence have shown that many proteins like TRANSPORT INHIBITOR RESPONSE 1 (TIR1) or AUXIN F-box PROTEINs (AFBs) with proteins of the Aux/IAA family are involved in auxin signaling in root differentiation (Overvoorde et al. 2010). TIR1 and AFB proteins help in ubiquitination of the movement of E3 ligase-dependent activity of SKP1-Cul1-F-box (SCF) complexes (Chapman and Estelle 2009). The IAA counter balanced the SCF complex interaction consequence which leads to degradation of Aux/IAA and promotes 26S proteasome activity to eliminate these proteins from the system (Maraschin Fdos et al. 2009). Similar to auxin response, NO treatment elevated cell differentiation minimizing cell-division (Fernandez-Marcos et al. 2011). Involvement of NO in apical root zone enables control of the auxin effect. A critical analysis had suggested that addition of NO reduced level of PIN-FORMED1 (PIN1)

protein in the meristem zone of chlorophyll a/b binding protein underexpressed 1/NO overproducer 1 (*cue1/nox1*) mutant plant. Phenotypically resemblance of the *pin1* mutant with surrounding cells of *cue1/nox1* double mutant and quiescent center suggested that NO and auxin signaling is involved in the development of size of the apical root differentiation (Fernandez-Marcos et al. 2011).

Furthermore, NO scavenger controlled cell cycle gene CYCD 3:1 in *Arabidopsis* plants that consequently regulates beginning of callus formation from somatic tissues. It was assumed that NO presence commanded the downstream of cytokinin involved in the cell cycle (Eber et al. 2013). Subsequently, up-regulation of mitogen-activated protein kinases (MAPKs) and cell cycle genes were also induced by NO during adventitious and lateral root formation, respectively (Correa-Aragunde et al. 2006; Fernandez-Marcos et al. 2011). NO addition further activated DELLA protein which is involved in primary root growth and hypocotyl elongation in *Arabidopsis* (Lozano-Juste and Leon 2011). Some other evidence has highlighted that NO application down-regulated GA20 oxidase and GA3 oxidase which are main enzymes for GA biosynthesis. These findings have been extensively correlated with crosstalk between NO, GA, and auxin signaling cascade in plants (Bethke et al. 2007; Lozano-Juste and Leon 2011).

NO has been intensively implicated in crosstalk with another phytohormone, i.e., ethylene. NO was quantified in a small amount with ethylene concentration in unripe fruit (Hayat et al. 2009). Use of NO as an exogenous was elevated ethylene biosynthesis in apple (Gniazdowska et al. 2007). It was mentioned that NO is treated as phytohormone in the presence of ACC oxidase and ACS synthase in the biosynthesis of ethylene precursor, the 1-aminocyclopropane 1-carboxylic acid. Further, feedback inhibition effect of ethylene biosynthesis was also observed, which blocks ethylene biosynthesis by binding of ACC-ACO-NO complex through S-nitrosylation (Manjunatha et al. 2010; Montilla-Bascon et al. 2017). Although knowledge of NO-mediated responses to environmental stresses has been elaborate, but not always, well documented, the precise pathways involved in NO signaling for each specific stress condition should be stressed. Some experimental evidence suggested that NO possibly operates through post-translational modification of proteins, mainly via S-nitrosylation, metal nitrosylation, carbonylation and tyrosine nitration (Kovacs and Lindermayr 2013).

Future prospective

The success of plant growth and development depend on the availability of nutrient and free from environmental stresses. Different species of *Trichoderma* are well known which function as a plant growth promoter and biocontrol agents.

The colonisation of *Trichoderma* with plant roots produces different kinds of secondary metabolites which have beneficial effects in activation of plant signaling mechanism like Ca^{2+} transduction and crosstalk with plant hormones. They also produce different kinds of enzymes which seem to be involved in biocontrol activity against both biotic and abiotic stresses. Their interaction may help in solubilization of different complex compounds into simplex form and nutrient uptake. Although mechanisms related to N signaling in response to *Trichoderma* interaction with plants have been studied, but variations in mechanism may also occur. For example, *T. asperelloides* interactions switch off the NO generation in response to pathogen infection, whereas the same organism elevated NO production when associated with *Arabidopsis* roots in the absence of pathogen stress. Similarly, biocontrol agent *Trichoderma asperellum* T42 induced NR dependent NO generation and nitrogen use efficiency after colonization with tobacco plant. Therefore, responses not only depend on the interaction of *Trichoderma*, but also on plant diversities. Interaction of *Trichoderma* leads to activation of N signaling since new targets of NO-dependent post-transcriptional modifications (PTMs), up and downstream elements of NO signaling cascades occur during plant development. Moreover, knowledge of gene activation and their products, associated with *Trichoderma* interaction are considered to major issues which require being further research intensively. This will provide a better opportunity for NO generation in plants and can increase NUE, thereby increasing nitrate availability and reducing nitrate pollution of waterways. Therefore, extensive research would lead to the identification of beneficial microbes capable of increasing uptake of N nutrient leading to an enhanced level of endogenous NO production for management of pathogens and increase in crop production in agricultural practices.

Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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