Pedosphere **28**(1): 16–34, 2018
doi:10.1016/S1002-0160(18)60002-5
ISSN 1002-0160/CN 32-1315/P

Published by Elsevier B.V. and Science Press

PEDOSPHERE

www.elsevier.com/locate/pedosphere

Perspectives of Using L-Tryptophan for Improving Productivity of Agricultural Crops: A Review

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(Received June 3, 2017; revised January 26, 2018)

ABSTRACT

Plant growth regulators are biologically active signaling molecules that regulate a number of plant physiological processes. Auxin (indole-3-acetic acid) is an important plant growth regulator and is synthesized within plant tissues through L-tryptophan (L-TRP)-dependent and -independent pathways. It has been found that plants respond to exogenously applied L-TRP due to insufficient endogenous auxin biosynthesis. The exogenous application of L-TRP is highly significant for normal plant growth and development. L-tryptophan is applied through foliar spray, seed priming, and soil application. Soil-applied L-TRP is either directly taken up by plants or metabolized to auxin by soil microbiota and then absorbed by plant roots. Similarly, foliar spray and seed priming with L-TRP stimulates auxin synthesis within plants and improves the growth and productivity of agricultural crops. Furthermore, L-TRP contains approximately 14% nitrogen (N) in its composition, which is released upon its metabolism within a plant or in the rhizosphere and plays a role in enhancing crop productivity. This review deals with assessing crop responses under the exogenous application of L-TRP in normal and stressed environments, mode of action of L-TRP, advantages of using L-TRP over other auxin precursors, and role of the simultaneous use of L-TRP and auxin-producing microbes in improving the productivity of agricultural crops. To the best of our knowledge, this is the first review reporting the importance of the use of L-TRP in agriculture.

Key Words: auxin biosynthesis, auxin precursors, auxin-producing microbes, crop productivity, indole-3-acetic acid, plant growth-promoting rhizobacteria, plant response to abiotic stresses

Citation: Mustafa A, Imran M, Ashraf M and Mahmood K. 2018. Perspectives of using L-tryptophan for improving productivity of agricultural crops: A review. *Pedosphere*. **28**(1): 16–34.

INTRODUCTION

Plant growth regulators are biologically active small signaling molecules, organic in nature, effective at very low concentration, and critical in controlling plant physiological processes (Frankenberger and Arshad, 1995; Ahmad *et al*., 2007; Mustafa *et al*., 2016). These plant growth regulators control plant growth and development throughout ontogeny. In normal conditions, these hormones are synthesized by the plants themselves. However, when growth and environmental conditions are not favorable, plants are not able to produce a sufficient enough level of these hormones to maintain optimum plant growth and yield (Arshad *et al*., 1995; Sarwar and Kremer, 1995; Zahir *et al*., 1999, 2005). The exogenous application of these hormones and/or their precursors improves the plant growth and yield by altering the level of endogenous hormones (Zahir *et al*., 2005; Mustafa *et al*., 2016). Auxin is an important plant growth regulator and is active in the plant as indole-3-acetic acid (IAA) (Akhtar *et al*., 2007; Hussain *et al*., 2011; Mano and Nemoto, 2012). Free IAA comprises only up to 25% of the total amount of IAA; the major forms of IAA conjugates are low-molecular-weight ester or amide forms, but there is increasing evidence of the occurrence of peptides and proteins modified by IAA (Ludwig-Müller, 2011). It regulates coleoptile bending (Anjum *et al*., 2011; Mustafa *et al*., 2016), cell division (Muneer *et al*., 2009; Abbas *et al*., 2013; Mustafa *et al*., 2016), cell elongation (Abdoli *et al*., 2013; Mustafa *et al*., 2016), cell differentiation (Sudadi and Suryono, 2015), the formation of adventitious roots (Zahir *et al*., 2000a; Ahmad *et al*., 2008b; Etesami *et al*., 2009b; Ahemad and Kibret, 2014; Mustafa *et al*., 2016), apical dominance (Abdoli *et al*., 2013; Mustafa *et al*., 2016), and cellular responses by controlling membranes and cytoskeletal functions (Reed, 2001). Auxin can be synthesized through many pathways, depending on the presence and absence of L-tryptophan (L-TRP) (Pollmann *et al*., 2009; Mano and Nemoto, 2012). Due to its high importance for plants and involvement in many physi-

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ological processes, a disruption in the synthesis of auxin in plant tissues results in the impairment of plant growth and subsequent yield losses.

L-tryptophan is known as β-3-indolylalanine. It is an essential amino acid not only for plants but also for animals, humans, and some bacteria (Frankenberger and Arshad, 1991). It was discovered by English chemist Frederick Gowland Hopkins in 1901. It is one of the nine amino acids essential to humans. L-tryptophan is a unique amino acid bearing an indole ring (Palego *et al.*, 2016). It is a biologically active precursor of auxin (Abbas *et al.*, 2013; Ahn, 2014; Hassan and Bano, 2015; Mustafa *et al.*, 2016), and its exogenous application increases the auxin level in plant tissues (Ahemad and Kibret, 2014). L-tryptophan is applied to plants through various ways, including soil application (Chen *et al.*, 1997; Muneer *et al.*, 2009), foliar spray (Yassen *et al.*, 2010; El-Awadi *et al.*, 2011), and seed priming (Parvez *et al.*, 2000; Abbas *et al.*, 2013). The exogenously applied L-TRP is actively metabolized into auxin (Frankenberger *et al.*, 1990; Mustafa *et al.*, 2016). On its application to plants, the amount of auxin released from L-TRP varies intra- and interspecifically (Abbas *et al.*, 2013). A positive response of L-TRP application in improving crop growth and productivity has been documented by different studies (Chen *et al.*, 1997; Muneer *et al.*, 2009; Yassen *et al.*, 2010; El-Awadi *et al.*, 2011; Abbas *et al.*, 2013; Hassan and Bano, 2015; Mustafa *et al.*, 2016). It has been reported that the stimulatory effect of L-TRP is further enhanced by the combined application of L-TRP and auxin-producing microbes (Ahmad *et al.*, 1999; Asghar *et al.*, 2002; Zahir *et al.*, 2010a; Anjum *et al.*, 2011; Rahmatzadeh *et al.*, 2012).

In this review, we summarize the effect of L-TRP application alone and in the presence of auxin-producing microbes to highlight the importance of L-TRP use in improving the performance of different agricultural crops.

MECHANISMS OF ACTION OF L-TRP

Biosynthesis of auxin from L-TRP

It has been reported that the exogenous application of L-TRP increases auxin production not only within the rhizosphere, but also in the plant body (Ahmad *et al.*, 1999; Abbas *et al.*, 2013). There are four L-TRP-dependent auxin biosynthesis pathways in plants: the indole-3-pyruvic acid (IPA) pathway, indole-3-acetamide (IAM) pathway, tryptamine (TAM) pathway, and indole-3-acetaldoxime (IAOx) pathway (Fig. 1) (Mano and Nemoto, 2012; Ljung, 2013). In the IPA pathway, L-TRP is converted into IPA by tryptophan aminotransferase (Tao *et al.*, 2008) with the release of ammonia; it is then converted into IAOx, which is catalyzed to IAA (Zhao, 2010; Won *et al.*, 2011). In the IAM pathway, IAA is synthesized from L-TRP after deamination of IAM (Zhao, 2010; Novák *et al.*, 2012; Spaepen and Vanderleyden, 2015). In the TAM pathway, tryptophan decarboxylase

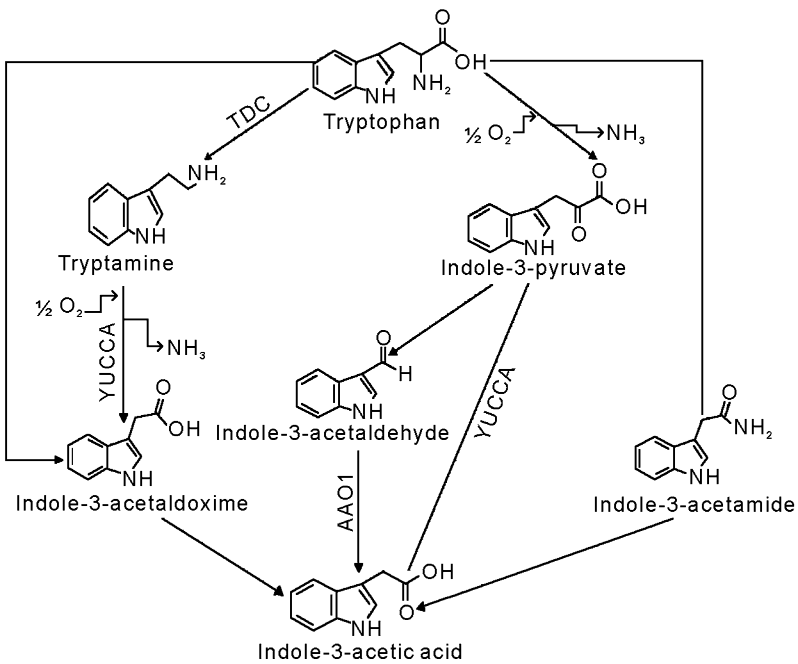

Fig. 1 L-tryptophan-dependent auxin biosynthesis in plant tissues. TDC = tryptophan decarboxylase; AAO1 = *Arabidopsis* aldehyde oxidase 1; YUCCA = YUC family of flavin-containing monooxygenase.