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Review: Consequences of the plant root system grown under phosphorus constraint conditions

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Abstract
Phosphorus is an essential macronutrient contributing to the plant's development. Phosphorus is mainly found in the bound form in the soil which restricts the plant's uptake and utilization. The availability or un-availability of phosphorus (P) imposes a great impact on the morphological, physiological and biochemical attributes of the plant. The root plays the pivotal role in determining the P availability or scarcity in the soil which can be deciphered by the altered root structure, shape, root hair formation patterns, nodulation as well as subsequent transport of P to other plant parts. This review focuses on the alterations in the root morphology, physiological responses as well as various factors related to root development under the phosphorus deficit and sufficient conditions.

Keywords: Phosphorus deficit, root hair, root structure

Introduction

Phosphorus is considered among one of the most essential macro-nutrients required for plant's growth and development. It plays an important role in the energy generating processes of plant like photosynthesis and respiration and is often found as a component of energy-rich compounds like phospho-enol pyruvate (PEP), adenosine triphosphate (ATP), uridine triphosphate (UTP), guanosine triphosphate (GTP) and cytidine triphosphate (CTP) etc. It is also an essential component of the nucleic acids as well as involved in the process of protein synthesis and reproduction. It plays role in various signaling processes of the plant, synthesizing membrane proteins and maintaining its stability. Under low phosphorus conditions, plants show reduction in its growth which may be conferred from the reduced rate of the energy generating processes resulting in 30% to 40% reduction in crop yield. In the agricultural fields, the phosphorus use efficiency (PUE) ranges from 15% to 20% indicating that even on applying phosphate fertilizers, majority of it undergoes leaching resulting in eutrophication (Correll, 1998; Smith 2003) [5]. Many adaptive mechanisms opted by plants to combat the phosphorus stress and maintain phosphorus homeostasis is governed by the chemical and biological changes in its rooting system (Hinsinger 2001) [8]. The spatial arrangement of the roots in the soil plays a key role in P uptake (Lynch, 1995). Alterations in root biomass, root length, cluster-root formation and releasing organic substances are among the many processes that a plant performs to cope up with the altered phosphorus conditions in the soil.

Alterations in root morphology and architecture in response to low Phosphorus conditions

In model plant *Arabidopsis thaliana,* a reduction in growth of primary root has been reported under low phosphorus conditions (Williamson *et al*., 2001; Linkohr *et al*., 2002; Lo´pez-Bucio *et al*., 2002, 2003; Jain *et al*., 2007; Pe´rez-Torres *et al*., 2008; Tyburski *et al*., 2010, 2012) [33, 14, 16, 17, 10, 23, 30, 31]. Inhibition of root growth is determined by genetic regulation rather than controlled by metabolic processes which was demonstrated by the 73 ecotypes of Arabidopsis among half of the tested ecotypes exhibited stunted primary root growth and a quarter of the population was not at all affected by Phosphorus availability (Chevalier *et al*., 2003) [4]. Studies in Arabidopsis have also shown profuse lateral root growth rather than primary root growth under P deficient conditions (Williamson *et al*., 2001; Linkohr *et al*., 2002; Reymond *et al*., 2006) [33, 14, 24]. Rice (*Oryza sativa)* shows evident alterations in their primary root system (Wissuwa, 2003; Shimizu *et al*., 2004; Yi *et al*., 2005) [34, 27, 36] whereas in case of maize, at 55% of field water capacity and low phosphorus conditions (11mg P/KG) maximum root length is achieved along with maximum root surface area (Chen *et al*., 2022) [37]. Furthermore, in maize, the main axis exhibited dense root hairs along with the first-order laterals of nodes which conferred to the improved plant performance under phosphorus starvation conditions (Bayuelo-Jime´nez *et al*., 2011) [1]. Among 25 genotypes of chickpea analysed by Kaur *et al*.,2021, ICC67, ICC867 and ICC2580 were reported to be negatively affected showing a reduced root area whereas ICCV92337, ICCV2, IG72070 and ICCV95423 showed no alteration in root area due to lateral root formation. A change in the basal root angle leading to a shallow yet broadly distributed rooting system has been reported in common bean (Bonser *et al*., 1996) [2] and sugarcane (Yi *et al*., 2022) [37]. Increased proliferation of root hair is among one of the early plant responses to limited phosphorus availability (Ma *et al*., 2001, 2003; Jain *et al*., 2007) [19, 20, 10]. Cluster roots are specialized root structures consisting of secondary roots which are densely clustered. Clustered roots actively participate in releasing carboxylates and protons which are effective for P uptake from the soil (Shane *et al*., 2003; Shen *et al*., 2003; Lambers *et al*., 2011; Cheng *et al*., 2011) [25, 26, 12, 3]. White lupins grown hydroponically without phosphorus source exhibited cluster root formation as an early sign of response to Phosphorus deficiency (Neumann *et al*., 2000) [22]. Later, it was demonstrated that in white lupins, the cluster root formation was controlled by the internal shoot Phosphorus concentration rather than in roots (Li *et al*. 2008 and Zhou *et al*. 2008) [13, 38]. In a study on lentils, root morphology analysis of a similar variety grown under P sufficient and P deficient conditions revealed differential root branching patterns as illustrated by Figure 1 and Figure 2. the In case of leguminous plants, phosphorus is needed for fixation of nitrogen in root nodules. Under phosphorus stress conditions, biosynthesis of carotenoids, metabolic processes involving those of glycerol-phospholipid and sugar were adversely affected nitrogen fixation (Yao *et al*., 2022) [35]. An increase in nodule formation were reported in plants grown under phosphorus deficit conditions (Míguez-Montero *et al*., 2020) [21]. In soybean, the purple acid phosphatase GmPAP12 plays an essential role in root nodule formation and its growth under limited supply of phosphorus (Wang *et al*., 2020) [32].

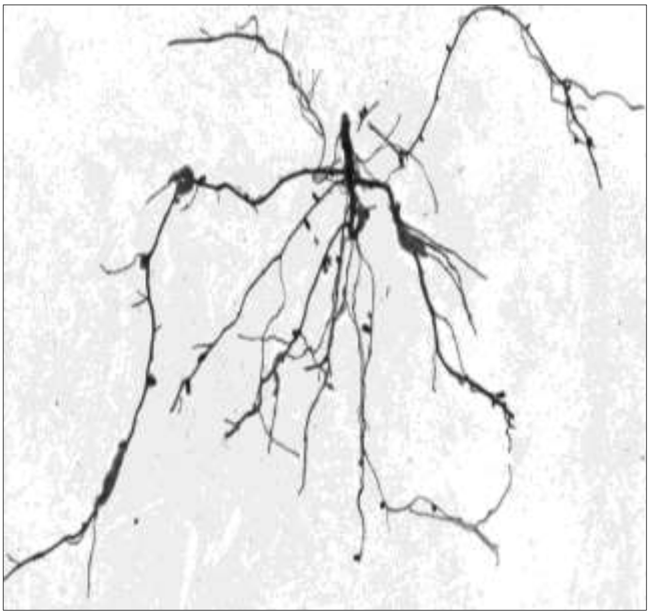

Fig 1: BCl 10210 grown under high soil P.

Fig 2: BCl 10210 grown under low soil P.

Several studies have reported that signal mediated by sugar concentrations under P starvation conditions in white lupins mediate the expression of genes induced by Phosphorus deficiency (Liu *et al*., 2005; Tesfaye *et al*., 2007; Zhou *et al*., 2008) [15, 29, 38]. LaPT1 and LaPEPC3 gene expression are controlled by two sugar-signalling mediated regulating system Zhou *et al*. (2008) [38]. Transport inhibitor response 1 (tir1)- and auxin response factor 19 (ARF19)-dependent auxin signals are known to play a crucial role in development of lateral root under low Phosphorus conditions (Pe´rez-Torres *et al*., 2008) [23]. Under low phosphorus availability, cluster root formation was found to be affected in relation to hampered auxin transport (Gilbert *et al*., 2000) [7]. In plants, cytokinin concentration is reduced upon low phosphorus condition in the soil, hence, exhibits a directly proportional relation (Horgan and Wareing, 1980; Kuiper *et al*., 1988) [9, 11]. Also, a decrease in the cytokinin receptor CYTOKININ Response 1 (CRE1) expression (Franco-Zorrilla *et al*., 2002) [6] [6] supressing lateral root formation. Ethylene too negatively regulates lateral root formation in Phosphorus deficit conditions.

Conclusion

The review illustrates the importance of phosphorus in the optimal plant growth and development with major focus on plant root growth under varying P conditions. Further studies in this field is needed to develop a vivid learning and understanding the root responses under differential soil nutrient conditions specific to certain crops.

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