Indian Journal of Plant Sciences ISSN: 2319–3824
Online, International Journal, Available at http://www.cibtech.org/jps.htm
2023 Vol.12, pp.18-40/Basuchaudhuri
Review Article (Open Access)

EFFECTS OF 1-NAPTHALENEACETIC ACID ON ROOT GROWTH OF MAJOR CEREALS AND GENES ASSOCIATED IN ROOT DEVELOPMENT

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ABSTRACT
In recent years the growth and development of different forms of roots in plant system is gaining importance. Aboveground growth of plants, drought tolerance and nutrient dynamics are all related to root architecture. It is suggested that the senescence of plant is to some extent manipulated by better root architecture and efficient nutrition dynamics. Plant hormones influence the RSA. In the review it was elaborately discussed about the effects of 1-Naptheleneacetic acid on crown root, lateral root, adventitious root root hairs and the genes associated with them. Results indicated that mutant OsAUX1 inhibited the effects of IAA and 2,4-D but the influx of NAA is not affected, which the rooting of the mutant in rice. Reducing the expression of OsPIN1using RNA interference inhibited adventitious root development, that is rescued by application of exogenous NAA, suggesting a role for OsPIN1 in regulation of adventitious root development via auxin pathway. In wheat, expression ofTaPIN2 was induced by TaSRL1 but repressed byTaTIFY9 in the presence of TaSRL1. A low NAA concentration (0.01micro mole) marginally inhibited primary root elongation but increased the total number of LRs after 48h in maize seedlings .For NAA which is polar auxin transporter of the plant promoted the primary, seminal and lateral roots The application of exogenous NAA greatly increase cellulose fibre formation in plants.

INTRODUCTION

The root system is important for plants to efficiently obtain nutrients and water. In contrast to the primary root system of plants, roots of monocot cereals consist almost entirely of a complex fibrous system and a mass of adventitious roots (ARs). AR formation is the process of root initiation from the stem base post-embryonic stage, which is tightly regulated to prevent the loss of valuable plant resources for non-essential root formation. A lack of stable and credible morphological data makes it difficult to study physiological and molecular mechanisms governing AR growth. However, comprehensive understanding of AR development should have important implications for manipulating root architecture, which contributes to both improving crop yield and optimizing agricultural land use.

Several plant hormones control AR formation, in which auxin plays a pivotal role. Indole-3-acetic acid (IAA) is the predominant form of active auxin in plant, and it induces both AR and lateral root (LR) formation. It significantly effects in promoting development of pointed ends for the root system, resulting in more, straighter and thicker roots at early stage of growth and then declined gradually. RSA (root system architecture) is considered of the primary, lateral, adventitious and accessory roots. Each RSA is determined by parameters such as length, diameter, number and angle of these root components.

Generally, the exposure of roots to temperatures higher than the optimal causes a decrease in the primary root length, number of lateral roots and their angle of emergence. Moreover, the increase in temperature causes the initiation of

second and third order lateral roots that are characterized by a larger diameter. The negative effect of increasing temperatures usually reduces the surface between root and soil, therefore decreasing nutrient and water uptake (Nagel *et al.*, 2009). Seminal and crown roots retarded their emergence and elongation when wheat seedlings are grown at high temperature (Huang *et al.,* 1991a). In maize adult plants, the increase in temperature slows down lateral root growth to promote the development of long axile roots to reach the water of the deeper soil layers (Hund *et al.*, 2008). Another strategy used by roots to cope with changing

environmental conditions that affect water and nutrient availability is increasing the number of root hairs and their length. This increase enhances root surface area that in turn will improve soil exploration, and therefore, water and nutrient uptake (Pregitzer *et al.*, 2000). Moreover, since genes that participate in early sensing and adaptation to high temperature are switched off in barley root-hairless mutant plants, it has been suggested a role of root hairs as sensors of environmental soil condition (Kwasniewski *et al.*, 2016).
Undisturbed soil cores, to a depth of 100 cm, from a field experiment were used to investigate and quantify the interaction between soil structure viz. macroporosity and wheat rooting patterns for the first time. Soil macroporosity was not significantly affected by wheat genotype but decreased significantly with depth, probably due to soil pressure. The number of roots observed with depth followed a similar trend to the macroporosity. A positive relationship between root number density and soil macroporosity suggests that macropores in the subsoil, most probably biopores, have great impact on rooting behaviour of wheat (Figure1). Strategies which create biopores such as those encourage earthworm populations and zero tillage, are likely to be beneficial for improving the utilization of water and nutrients from deeper parts of the soil profile.

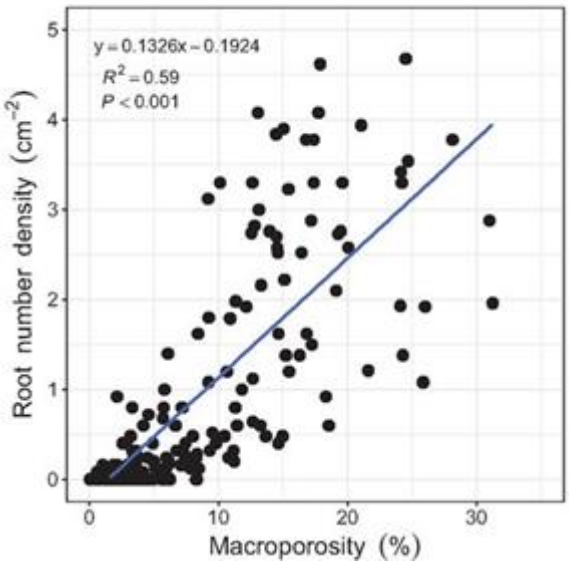

Figure 1 Relationship between wheat root number density and macroporosity at the depth of 0–100 cm. Root number density number of roots cm^{-2}. After Zhou *et al,* 2021.

RICE

NAA, a synthetic auxin, when applied in spray influences the life cycle of rice via metabolic processes to manifest beneficially through translocating assimilates from source to sink, and hence the yield. It may be coined that application of NAA has the following effects (i) Efficient root activities which improve nutrient uptake for better growth of rice plant; (ii) Improves growth parameters effectively; (iii) Most of the yield attributing factors are enhanced; (iv) Significant increase in grain yield; (v) Delayed senescence to improve mobilization of assimilates from source to sink (Basuchaudhuri,2016)
Using the minirhizotron micro-video camera technique, it was developed a description of the seasonal pattern of paddy rice root growth under the culture practiced in Arkansas. Root growth, measured as root length, is rapid and linear during vegetative development of the rice plant. Maximum root length is observed by panicle initiation or booting and is maintained at nearly a constant level until heading. Following heading, root length declines until milk stage where it may remain at a reduced level or may increase by physiological maturity (Beyrouty *et al*.,1997).

Study on the effect of Napthaleneacetic Acid (NAA) and three irrigation frequencies on root growth and yield of BRRIDhan28, with control Ho; tap water-control, H1; 50 ppm NAA, H2; 100 ppm NAA and H3; 150 ppm NAA for growth regulator and irrigation frequencies were W1 always flooded condition, W2 flooded 10 days interval and W3 flooded 20 days interval. Root length, root volume and root weight (dry & fresh) significantly increased using 100 ppm NAA under flooded condition. The highest root length, root volume, root weight (fresh and dry), dry plant weight and yield were obtained from 100 ppm NAA. It was also observed that the combined application of NAA and flooded irrigation were more effective than others It revealed that the combined application of100 ppm NAA+ flooded irrigation was found to be superior to other treatments for yield, root length and other growth parameters (Table 1).

Table 1. Root length (A) and volume (B) in field grown BRRIdhan28 at different growth stages. Modified from Sarker *et al,* 2008.

A. Root length (cm)

NAA (ppm)	21DAT	41DAT	61DAT	81DAT
0	10.3	20.6	21.8	26.0
50	11.2	22.1	23.6	28.0
100	11.7	23.7	25.5	30.6
150	10.6	21.2	22.2	28.3

B. Root volume (cc)

NAA(ppm)	21DAT	41DAT	61DAT	81DAT
0	3.3	11.4	28.9	36.3
50	3.6	13.9	29.3	40.3
100	3.8	17.8	29.3	45.0
150	3.2	13.6	29.3	41.6

Studies indicated that NAA, CSN, and DA-6 can increase the vigour, length, and surface area of rice seedling roots under drip irrigation. These changes could promote Fe uptake at the seedling stage and reduce chlorosis.

IBA and NAA mixture soaked seeds, can increase the rice adventitious root number, weight and length, which can increase the tillers and increase yield. It also can improve rice seed germination rate and vital indices, is an efficient rooting agent.

Use of IBA and NAA mixture soak seeds, can intensify plant cells activity, break seed dormancy, improve germination rate and time, strengthen seedling, more and deeper roots, enhance the seedlings resistance to the bad environment.

Rice plants are most sensitive to high temperature at reproductive stage which significantly enhances the pollen sterility. Reproductive stage demands optimum level of phytohormones like auxin and other energy producing compounds. Pot experiment was conducted to examine the application of different concentrations of NAA (0, 10, 20, 30, 50 μmol L^{-1}) on rice crop grown under natural and heat stressed environment at flowering stage. NAA was applied immediately after flowering and then subjected to heat stress later on for few hours. It was found that heat stress at flowering stage significantly reduced the rice crop yield and quality but exogenous application of Naphthaleneacetic acid (NAA) improved the crop tolerance to heat stress which leads toward better crop productivity.

The model assumption that nutrient movement to roots is primarily by mass flow and diffusion was verified in a field study on a silt loam soil for paddy rice. In the 0- to 5-cm soil depth, mass flow accounted for 9, 14, and 32% of NH_4^+, P, and K movement to roots, respectively, while diffusion accounted for 91, 86, and 68% of the movement of NH_4^+, P, and K, respectively. Contact exchange supplied negligible quantities of these nutrients. Mass flow has a greater influence on K uptake on submerged soils than is typically found on upland conditions.

The monocot cereal rice (*Oryza sativa* L.) develops an embryonic and post-embryonic root system displaying complex root structures with several types, including primary, lateral, and adventitious roots

(Hochholdinger *et al*., 2004). It is known that the plant hormones, auxin and cytokinin, play important roles in regulating root development. The genes that affect auxin or cytokinin biosynthesis, homeostasis, transport, or signal transduction also affect root development (Aloni *et al*., 2006; Dello Ioio *et al*., 2007; De Smet and Jurgens, 2007; McSteen, 2010). In rice, the auxin-regulated genes, CRL1 and WOX11, are crucial regulators of root development (Inukai *et al*., 2005; Zhao *et al*., 2009). Besides, ABA and sugars also regulate root growth and development.

After NAA had been added in the test tubes at concentrations of 10 nM,100 nM, 1 µM, and 10 µM, the shoot and root growth parameters were analyzed which showed a concentration dependent decrease in growth (Figures 2&3).

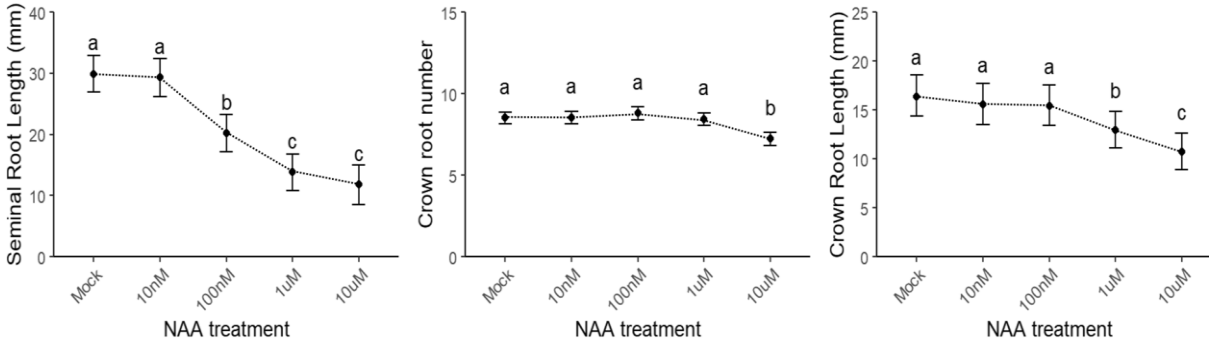

Figure 2. Screening by means of a concentration range of 1-naphthaleneacetic acid (NAA). The root parameters are lengths (in mm) of the seminal and crown roots and the number of emerged crown roots.

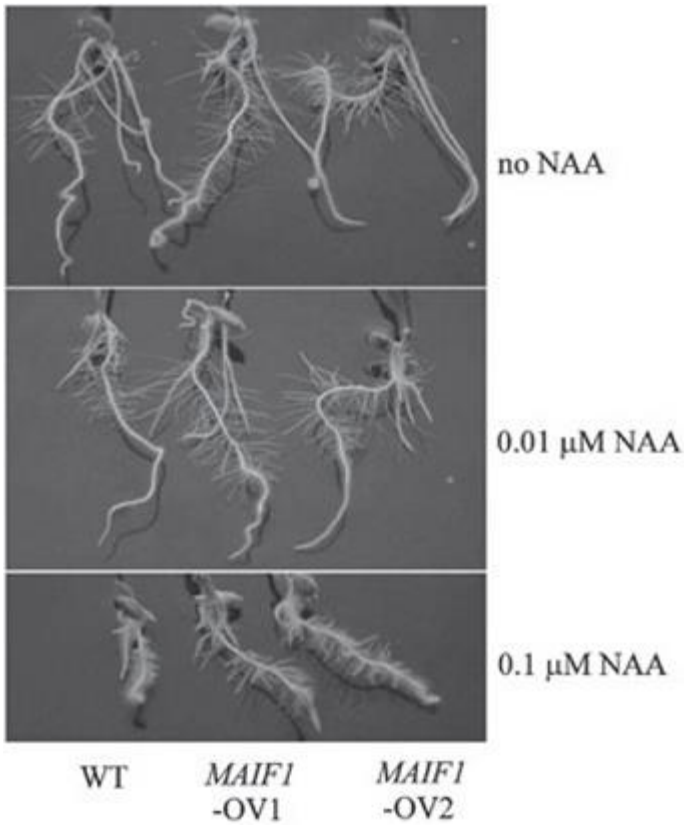

Figure 3. Phenotypes of Overexpressing MAIF1 Rice Plants. After Vlaminck *et al,* 2020.

The PRs of the three osaux1 lines were all 30% longer than those of the wild-type (WT) (Dongjin, DJ) grown under hydroponic culture conditions for 7 days, while PRs of OsAUX1 over-expression lines were 30% shorter than those of the WT. PRs of osaux1 mutants were insensitive to IAA and the synthetic auxin and herbicide 2,4-dichlorophenyloxy acetic acid (2,4-D), but over-expression lines were hyper-sensitive to them. Interestingly, PRs of the three osaux1 mutants as well as the OsAUX1 over expressing lines were sensitive to 1-naphthaleneacetic acid (NAA), which diffuses into cells and thus rescues osaux1 mutants.
A phenotypic analysis revealed that the mean lengths of the RHs of osaux1 were one-third those of WT. Interestingly, the shorter RHs in osaux1 mutants were not rescued by IAA and 2,4-D treatments but were not rescued by NAA treatment.
These results indicate that mutation of OsAUX1 disturbs IAA and 2,4-D transport, which depend on auxin transporters, but does not influence NAA influx, which is AUX1/LAX-independent.
Interestingly, the repression of root growth and development caused by Cd stress was retarded by simultaneous NAA application as indicated by PR length and LR density. Further, RH growth in the osaux1-1 mutant under Cd+NAA treatment was significantly increased compared to Cd treatment alone (Figure 4). Root growth responses to Cd+IAA treatment show similar trends to Cd+NAA treatment. These results imply that the sensitivity to Cd stress may be dependent on local changes in auxin concentrations caused by reduced auxin transport in osaux1-1.

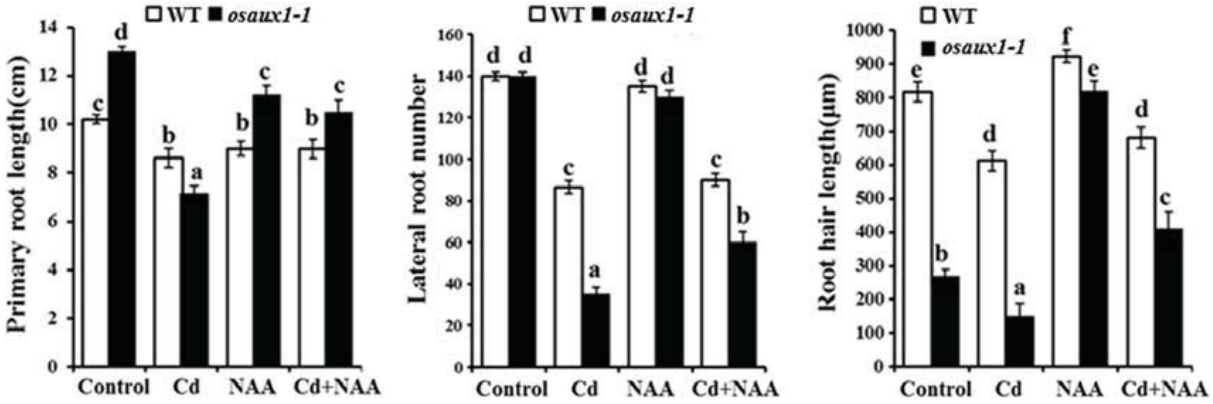

Figure 4. Quantification of root phenotypes. PR lengths, LR numbers and RH lengths were measured in WT and the osaux1-1 mutant grown under control conditions and treated with 50 lM $CdCl_2$, 10 nM NAA or10 nM NAA plus 50 lM $CdCl_2$ for 7 days. After Yu *et al,* 2015.

It was reported that ethylene promotes abscisic acid (ABA) biosynthesis and cortical cell radial expansion. Rice mutants of ABA biosynthetic genes had attenuated cortical cell radial expansion in compacted soil, leading to better penetration. Soil compaction-induced ethylene also up-regulates the auxin biosynthesis gene OsYUC8. Mutants lacking OsYUC8 are better able to penetrate compacted soil. The auxin influx transporter OsAUX1 is also required to mobilize auxin from the root tip to the elongation zone during a root compaction response. Moreover, osaux1 mutants penetrate compacted soil better than the wild-type roots and do not exhibit cortical cell radial expansion. It was concluded that ethylene uses auxin and ABA as downstream signals to modify rice root cell elongation and radial expansion, causing root tips to swell and reducing their ability to penetrate compacted soil (Figure 5).
Physiological studies have provided additional evidence of auxin playing an important role in crown root development, and the growth of functional genomics has meant that growing numbers of auxin-related genes have been found to be involved in this developmental process. Plants over expressing the auxin biosynthesis gene OsYUCCA1 have a higher auxin content, which leads to more crown roots (Yamamoto *et al.* 2007). Two crown rootless mutants, crown rootless 4 (crl4) and Osgnom1, were found to be allelic

lines with mutations in a membrane associated guanine-nucleotide exchange factor of the ADP-ribosylation factor G protein (GNOM). GNOM1 regulates the traffic of PIN-FORMED 1 (PIN1) auxin efflux carrier

Figure 5. Soil compaction triggers higher auxin response in rice primary root epidermal cells to restrict epidermal cell expansion. After Huang *et al,* 2022.

proteins, and consequently mediates polar auxin transport, suggesting that appropriate polarized auxin transport mediated by CRL4/OsGNOM1 is required for crown root initiation (Kitomi *et al.*, 2008; Liu *et al.*, 2009). Consistent with this, reducing the expression of OsPIN1 using RNA interference inhibited adventitious root development, a phenotype that could be rescued by the exogenous application of α-naphthylacetic acid (α-NAA), suggesting a role for OsPIN1 in regulation of adventitious root development via auxin pathway (Xu *et al.*, 2005). Over expressing OsRPK1, which encodes a leucine-rich repeat receptor-like kinase (LRRRLK), resulted in undeveloped adventitious roots and LRs, and a reduced RAM caused by lower expression of most OsPIN genes, suggesting that OsRPK1 also functions in an auxin-related pathway (Zou *et al.* 2014). Moreover, the gain-of-function mutant Osiaa23, which accumulates an auxin response protein, had defects in the initiation of its crown roots and LRs, and maintenance of the quiescent centre (QC) in the root tip (Ni *et al.*, 2011). Recently NARROW LEAF 1 (NAL1), was also found to mediate rice crown root development, as the loss-of-function mutant nal1 produced fewer adventitious roots. NAL1 encodes a putative trypsin-like serine/cysteine protease that affects the expression levels of many genes associated with leaf development and auxin transport; consequently,
exogenous auxin treatment rescued the nal1phenotype (Cho *et al.*, 2014). Another auxin signalling gene, OsCAND1, named after its *Arabidopsis* homolog CULLIN-ASSOCIATED AND NEDDYLATION-DISSOCIATED 1(CAND1), is also required for the emergence of crown roots (Wang *et al.*, 2011). In addition, CHROMATIN REMODELING 4 (CHR4; Zhao *et al.*, 2012), also named CROWN ROOTLESS 6 (CRL6; Wang *et al.*, 2016), encodes a member of the large chromodomain, helicase/ATPase, and DNA-binding domain protein family, and is known to affect both auxin signalling and crown root development in rice. OsCHR4/CRL6 is most highly expressed in the basal region of the stem where crown roots are initiated. The defective crown root formation in crl6 can be rescued by auxin treatment, and furthermore, the expression of the OsIAA genes was down-regulated in crl6, providing evidence that OsCHR4/CRL6 plays a role in crown root development through the auxin-signalling pathway (Wang *et al.*, 2016).
A recent study further indicates that the inositol polyphosphate kinase OsIPK2 interacts with OsIAA11 to protect it from degradation and thereby inhibits lateral root formation (Chen *et al.*, 2017). Another IAA family gene, OsIAA23, is specifically expressed in the quiescent centre cells of the root tip during the development of primary, lateral, and crown roots, and the gain-of-function mutant Osiaa23 exhibited a pleiotropic phenotype, producing no crown root, no LRs, and no root cap (Ni *et al.*, 2011).
Using a forward genetic approach, OsCYCLOPHILIN 2 (OsCYP2) was cloned and functionally identified, and the loss-of-function mutant Oscyp2 was found to exhibit defects in LR formation (Kang *et al.*, 2013).

Map-based cloning revealed that lrt2 is allelic to Oscyp2 (Zheng *et al.,* 2013). OsCYP2 is a cyclophilin-type peptidylprolyl cis/trans isomerase that efficiently catalyses the cis/trans isomerization of OsIAA11 and directly regulates its stability; therefore, the OsCYP2 mutation reduces the interaction between OsTIR1 and OsIAA11, causing the accumulation of OsIAA11 and inhibiting auxin signalling mediated LR development (Jing *et al.,* 2015).

A study demonstrated that OsZFP, a C2HC-type zinc finger protein, can interact with OsCYP2 in the nucleus to regulate LR development (Cui *et al.,* 2017).

Furthermore, the inhibition of LR initiation was also reported in the auxin influx transporter mutant, Osaux1 (Zhao *et al.,* 2015a). These indicate that auxin is a very important regulator of LR development in rice. Root hairs are long tubular outgrowths that form on the surface of specialized epidermal cells. They are required for the uptake of nutrients and water, particularly in upland conditions. Root hair development can be divided into three phases cell specification, initiation, and elongation (Cavell and Grierson ,2000). The outgrowth of root hairs are strictly regulated by genetic and environmental factors. The first root-hairless mutant reported in rice was rh2 (Suzuki *et al.,* 2003). An exogenous application of NAA could induce very short root hairs in rh2, suggesting that the absence of root hairs in this mutant may be due to a shortage of endogenous auxin; however, the gene has not yet been identified. OsWOX3A was reported to control root hair formation through the regulation of auxin transport genes (Yoo *et al.,* 2013), further suggesting that auxin is required for root hair elongation. Root hairs are initiated normally in the Oscellulose synthase-like d1 (Oscsld1) mutant; however, this gene, which is expressed only in root hair cells, is required for their elongation (Kim *et al.,* 2007; You *et al.,*2011). OsRHL1, a bHLH transcription factor expressed specifically in root hair cells, also regulates root hair elongation in rice; the loss-of-function mutants Osroothairless 1–1 (Osrhl1–1) and Osrhl1–2 produced very short root hairs without affecting root length or the number of LRs and adventitious roots, suggesting that OsRHL1 functions, in root hair elongation (Ding *et al.,* 2009).

OsFORMIN HOMOLOGY 1 (OsFH1) was also found to regulate rice root hair elongation; the loss of function mutant osfh1 exhibited root hair defects when grown submerged in solution but produced normal root hairs in contact with the air. This root hair phenotype could not be rescued by an external supply of hormones or carbohydrates (Huang *et al.,* 2013a). It is well known that root hair growth requires extensive cell wall modification, and recent research revealed that OsEXPA17, encoding an expansin involved in cell wall remodelling, plays a crucial role in root hair elongation. OsEXPA17 is exclusively expressed in root hair cells, and its null mutant forms short root hairs (Yu *et al.,* 2011). Another rice gene, OsSEC14-NODULIN DOMAIN-CONTAINING PROTEIN1 (OsSNDP1), encoding a phosphatidylinositol transfer protein (PITP), promotes root hair elongation via phospholipid signalling and metabolism, suggesting that the mediation of these processes by PITP is required for root hair elongation in rice (Huang *et al.,* 2013b).

The response of plant root development to nutrient deficiencies is critical for crop production.

To directly test the role for auxin under compacted soil conditions, when examined root elongation of wild-type (cv. Nipponbare) and ethylene-response mutants oseil1 and osein2 in compacted soil with and without co -treatment with 1 naphthaleneacetic acid (NAA, a synthetic auxin). Consistent with auxin acting downstream of ethylene signalling, exogenous NAA application restored root elongation inhibition in oseil1 and osein2 mutants under compacted soil conditions. External NAA application to oseil1 and osein2 mutant roots in compacted soil did not induce radial swelling of cortical cells (<20%) as compared to ABA treatment (more than twofold). Hence, ethylene inhibits root elongation via auxin during soil compaction stress.

WHEAT

In plants, there are two biosynthetic pathways for the production of the plant hormone indole-3-acetic acid (IAA), namely the Trp-dependent and the Trp-independent pathways. Shao *et al.* (10.1104/pp.17.00094) had performed a genome-wide analysis to identify a key gene in wheat that functions in the tryptophan-

dependent pathway of IAA biosynthesis, namely *Tryptophan Aminotransferase of Arabidopsis1/Tryptophan Aminotransferase-Related* (*TAA1/TAR*).

TAR converts Trp to indole-3-pyruvic acid, an intermediate that is then converted by other enzymes to form IAA. Unlike other IAA biosynthesis genes, the over expression of *TAA1/TAR* genes does not result in growth defects. By sequence mining together with gene cloning, researchers identified 15 *TaTAR* genes in wheat. *TaTAR2.1* had the most abundant transcripts among the *TaTAR2* genes and was expressed mainly in roots and up regulated by low nitrogen (N) availability. Knockdown of *TaTAR2.1* caused vegetative and reproductive deficiencies and impaired lateral root growth under both high- and low-N conditions. Over expressing *TaTAR2.1-3A* in wheat enhanced lateral root branching, plant height, spike number, grain yield, and aerial N accumulation under different N supply levels. In addition, over expressing *TaTAR2.1-3A* in *Arabidopsis* elevated the accumulation of IAA in the primary root tip, lateral root tip, lateral root primodia, cotyledon and hypocotyl. Over expression of *TaTAR2.1-3A* also led to an increase in primary root length, lateral root number, and shoot fresh weight under high- and low-N conditions. These results suggest that *TaTAR2.1* is critical for wheat growth and also shows potential for genetic engineering with the goal of improving the grain yield of wheat.

The role of root structure and architecture in water supply and plant viability cannot be underestimated and it is especially important if plants are subjected to stress at the juvenile stage (Bramley *et al.*,2009).Since roots grow underground, they are the first to perceive changes in external conditions such as water and nutrient content in soil, pH, temperature, etc., and adjust their genetic program for post-embryonic development to withstand the resulting stress (Bengough *et al*.,2011). These changes are integrated into the development program and various structural modulations and realignments of the root system architecture (RSA). The genetic control of the processes, it is noted that the RSA of different species showed different levels of plasticity and reacts differently to adverse conditions (Bao *et al.*,2014). The degree of interaction of the root with the environment is determined by different levels of response molecular, cellular, histological, and organ based (Lovelli *et al.*,2012; Khan *et al.*,2016). In the process of acclimation, the structure of the root system can be reconfigured by activating or declining the water potential, metabolism level, and enzymatic activity (Woodrow *et al.*, 2017). These changes can be both adaptively expedient and an expression of stress-related pathologies.

Yang *et al. (*2016) showed that the growth of root cells depended primarily on their osmotic potential and turgor. A slight loss of water in the root could increase tensile strength, while a significant loss of water can lead to a decrease in the root's ability to elongate. Roots use various morphophysiological developmental strategies, e.g., they can change the growth rate, diameter, and density of tissue, adapting to various stressors (Nie *et al.*,2013; Suseela *et al.*,2017; Carrillo *et al.*,2014) and the changes in the root diameter within the root system of a specific species can vary (Wu and Guo, 2014). However, a too small root diameter restricts root penetration through soil and does not contribute to the development of internal structures that transport water and nutrients (Clark *et al.*,2008; Jaramillo *et al.*,2013). There is evidence that these signs also affect the ability of the root to stretch (Yang *et al.*, 2016). As shown by Genet *et al. (*2005), negative correlations of the root diameter with tensile strength and positive correlations with its tensile resistance. Qian Wu *et al. (*2016) state that the basal diameter of the root determines its potential length. As a rule, the longest roots are those that maintain (and sometimes increase) their diameters during elongation. Root elongation is the result of both cell enlargement and mitotic activity of apical meristem cells, which are constantly formed due to their division. Attempting to link root elongation to cellular processes, Shimazaki *et al. (*2005) concluded that an insufficient water supply in apical meristem zone could lead to significant reduction in root growth. Moreover, the negative effect of salt stress was observed not only on water content in root cells, but also on their chromosomal apparatus of sensitive wheat forms (Terletskya *et al.*,2019). The results of induced water deficit did not show such a destructive effect on the wheat species, but in meristematic cells of primary roots of *T. monococcum* and *T. aestivum* were observed the development of strong plasmolysis under osmotic stress conditions. In *T. aestivum*, strong plasmolysis was

also observed in root hair cells, whose purpose in RSA is to significantly enlarge the root surface area, increasing absorption of water and soil solutions into the root (Gahoonia *et al.*,2001; Tanaka *et al.*,2014).
Understanding root system morphology in bread wheat is critical for identifying root traits to breed cultivars with improved resource uptake and better adaptation to adverse environments. Variability in root morphological traits at early vegetative stages was examined among 184 bread wheat genotypes originating from 37 countries grown in a semi-hydroponic phenotyping system. At the onset of tillering (Z2.1, 35 days after transplanting), plants had up to 42 cm in shoot height and 158 cm in root depth. Phenotypic variation existed for both shoot and root traits, with a maximal 4.3-fold difference in total root length and 5-fold difference in root dry mass among the 184 genotypes. Of the 41measured traits, 24 root traits and four shoot traits had larger coefficients of variation (CV $\geq$ 0.25). Strong positive correlations were identified for some key root traits (i.e., root mass, root length, and these parameters at different depths) and shoot traits (i.e., shoot mass and tiller number) (P $\leq$ 0.05). The selected 25 global traits (at whole-plant level) contributed to one of the five principal components (eigen values> 1) capturing 83.0% of the total variability across genotypes. Agglomerative hierarchical clustering analysis separated the 184 genotypes into four (at a rescaled distance of 15) or seven (at a rescaled distance of 10) major groups based on the same set of root traits.
Strong relationships between performance traits (dry mass) with several functional traits such as specific root length, root length intensity and root tissue density suggest their linkage to plant growth and fitness strategies (Table 2& Figure 6).

Table 2. Descriptive statistics of 25 important traits (22 root traits, and four shoot traits) in 184 wheat genotypes grown in a semihydroponic phenotyping platform.

Trait	Minimum	Maximum	Mean	CV	Signif.
Seminal root length zone1	27.7	120	85.3	0.17	-
Seminal root length zone2	6.8	37.7	24.1	0.23	-
Maximal root depth	44.3	158	109	0.17	-
Seminal & primary root no.	5.67	48.3	11.1	0.29	0.258
Total root length	670	3538	1902	0.29	-
Root diameter	0.26	0.48	0.31	0.07	0.052
Specific root length	60.5	172.7	122.3	0.15	-
Root length intensity	8.12	31.1	17.8	0.26	-
Root tissue density	75.4	175	117	0.15	0.334
Root length s1	260	1245	687	0.31	-
Root diameter s1	0.26	0.40	0.30	0.07	0.939
Root length s2	93.9	1313	652	0.33	-
Root diameter s2	0.23	0.43	0.28	0.09	0.001
Root length s3	59.3	1266	563	0.40	-
Root diameter s3	0.29	0.69	0.35	0.12	-
Root length in sub-root layer	153	2455	1215	0.34	-
Root diameter in subroot layer	0.27	0.56	0.31	0.10	-
Root length ratio	0.30	3.81	0.65	0.49	-
Root mass	50.7	305	159	0.33	-
Shoot mass	47.5	450	230	0.36	-
Total dry mass	98.2	975	390	0.43	-
Root mass ratio	0.45	1.12	0.74	0.20	-
Shoot height	8.87	42.7	21.9	0.27	-
Leaf number	3.67	35.0	8.50	0.37	-
Tiller number	1.00	5.33	2.40	0.35	-

Fourteen of 25 Traits with CVs (coefficients of variation) ≥0.25 appear in red and bold type. Probability (P) values were based on a GLM multivariate analysis of 184 genotypes

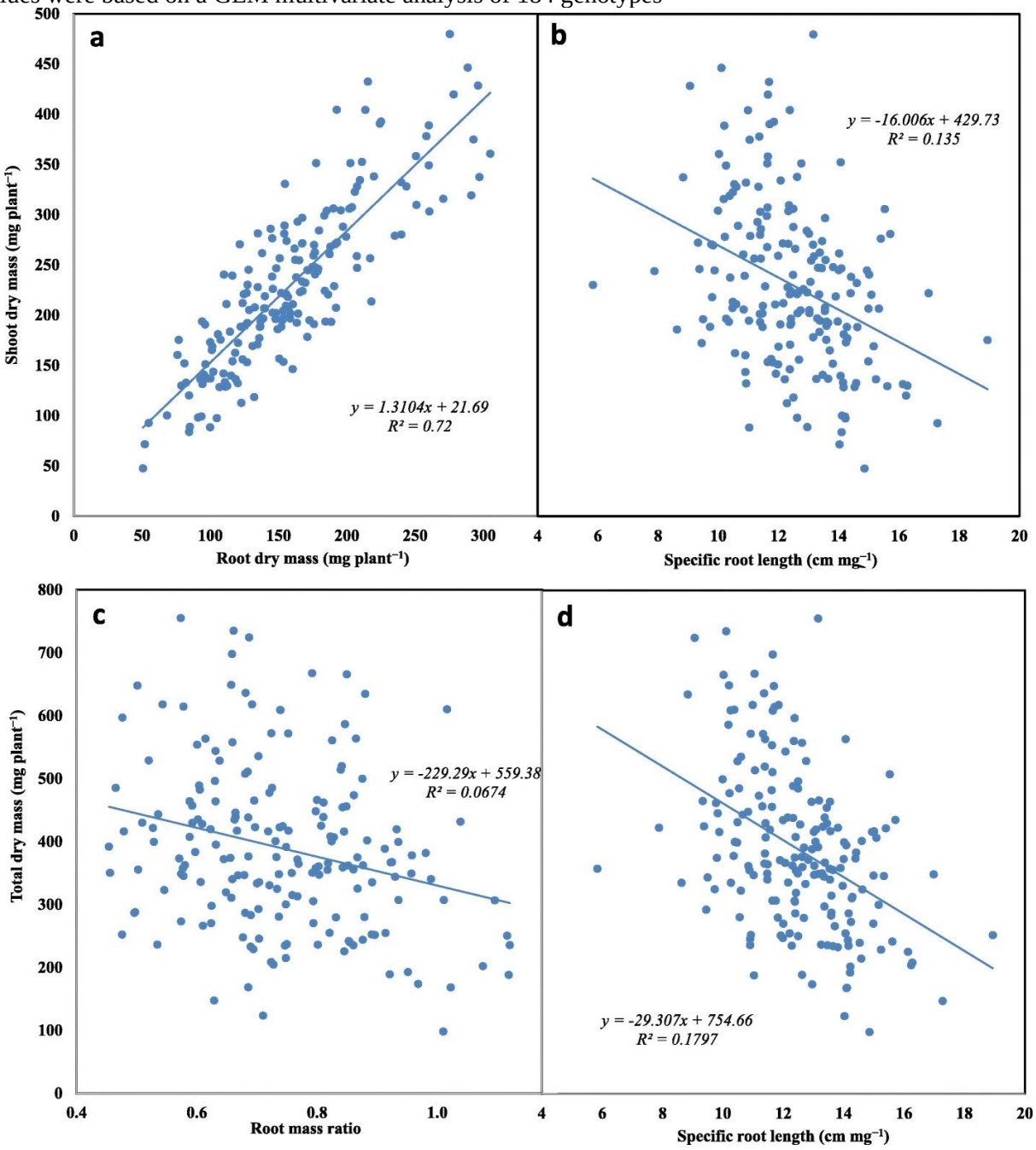

Figure 6. Some correlations related to root parameters. After Chen *et al,* 2020.

Alam *et al*., (2002) noticed that NAA at 20 mg l^{-1} enhanced the straw yield and GY of wheat cultivars 'Sarsabz', 'Soghat' and 'S-232'. NAA has been used to enhance the growth and yield of cereals by promoting and improved root system, resulting in more, straighter and thicker roots (Bakhsh *et al.*, 2011b; Yan *et al.*, 2014; Basuchaudhuri, 2016). PGRs also significantly increased root growth (RDW) and promoted new roots in rice sprayed with 10 or 100 mg l^{-1} NAA at the tillering stage (Raoofi *et al.*, 2014;

Basuchaudhuri, 2016). Their results indicated that the application of NAA at different growth stages of wheat were more effective for RFW, RDW, RL and TDM of wheat genotypes than the control (Table 3).

Table 3. Combine effect of time of application of NAA and wheat genotypes on root fresh weight, dry weight and root length at different growth stages of wheat.

Combine effect of time of application of NAA and genotypes	RFW (mg cc^{-1} soil) at 10 cm depth of upper soil		RDW (mg cc^{-1} soil) at 10 cm depth of upper soil		RL (m cc^{-1} soil) at 10 cm depth of upper soil	
NAA at 20,35&50 DAS	Y1	Y2	Y1	Y2	Y1	Y2
Kanchan	0.98wx	0.95x	0.18z	0.17z	1.14y	1.13y
Protiva	2.15de	2.17de	0.85ijk	0.88ij	1.49n-q	1.50n-q
Sourav	1.59nop	1.57nop	0.65mno	0.63m-p	1.37u-w	1.34u-w
Gourav	2.20d	2.17de	1.13d	1.06e	1.77ef	1.75ef
BAW 944	1.84i	1.80ij	0.88ij	0.86ijk	1.55h-m	1.53h-m
BAW 953	2.00fgh	1.98ghi	0.85ijk	0.88ij	1.67g	1.70g
BAW 994	1.63mno	1.60mno	0.63nop	0.58pqr	1.501-o	1.4901-o
Akbar	1.76ijk	1.75i-l	0.50stu	0.48tuv	1.61hi	1.58h-k
Agrahani	1.98fgh	1.98fgh	0.63nop	0.61opq	1.56h-l	1.54h-l
Sonalika	1.96gh	1.94hij	0.63nop	0.60opq	1.40s-v	1.41s-v
NAA at 20 and 35 DAS x Kanchan						
	1.70ilm	1.65mn	0.60opq	0.63opq	1.50m-p	1.48n-r
Protiva	2.30c	2.25cde	1.05e	1.03ef	1.42r-u	1.43r-u
Sourav	2.50b	2.45bc	1.40b	1.53b	1.79e	1.80e
Gourav	2.65a	2.58ab	1.67a	1.70a	2.51a	2.54a
BAW 944	1.28st	1.25stu	0.53rst	0.50stu	1.55i-m	1.53k-n
BAW 953	1.15uv	1.11uvw	0.38wx	0.35x	1.63h	1.61h
BAW 994	1.48pqr	1.46pqr	0.95gh	0.90hi	1.80e	1.79e
Akbar	1.53opq	1.50opq	0.63nop	0.68mn	1.59h-k	1.58h-k
Agrahani	2.45bc	2.45bc	1.43b	1.51b	1.70g	1.68g
Sonalika	1.08vw	1.10uvw	0.53rst	0.50stu	1.90d	1.93d
Kanchan	1.30s	1.28st	0.50stu	0.48tuv	1.58h-k	1.57h-k
Protiva	1.20tu	1.18uvw	0.35x	0.33x	1.312w	1.32w
NAA at 20 and 50 DAS x Sourav						
	2.48bc	2.50b	1.30c	1.35c	1.70fg	1.72fg
Gourav	1.65mn	1.68lmn	0.50stu	0.49stu	1.47n-r	1.48n-r
BAW 944	1.30s	1.28st	0.70m	0.68m	1.58h-k	1.59h-k
BAW 953	1.43r	1.45qr	0.38wx	0.39wx	1.23x	1.202x
BAW 994	1.48pqr	1.50opq	0.56qrs	0.55qrs	1.59h-k	1.60h-j
Akbar	1.03wx	1.08vw	0.29y	0.28y	1.42r-u	1.41s-v
Agrahani	1.60mno	1.59nop	0.61nop	0.63nop	1.76ef	1.78ef
Sonalika	0.95x	0.98l-x	0.18z	0.18z	1.58h-k	1.56h-k
NAA at 35						

and 50 DAS x Kanchan						
	1.93h	1.94h	0.781	0.801	1.59h-k	1.58h-k
Protiva	2.05fg	2.00fgh	0.86ijk	0.85ijk	1.50m-p	1.53k-n
Sourav	2.08ef	2.05fg	1.03ef	1.00ef	1.05l-o	1.02l-o
Gourav	1.98fgh	2.0fgh	0.81kl	0.80kl	1.42p-t	1.41p-t
BAW 944	1.52opq	1.55pqr	0.44vw	0.43vw	1.55h-m	1.53k-n
BAW 953	1.08vw	1.03wx	1.68a	1.70a	2.02b	2.10b
BAW 994	1.70 ilm	1.68lmn	0.90hi	0.88ij	1.535j-m	1.55j-m
Akbar	1.80ij	1.78ijk	0.50s-u	0.53rst	1.57h-k	1.58h-k
Agrahani	1.83i	1.80ij	0.83j-l	0.84j-l	2.02c	2.05bc
Sonalika	1.75i-l	1.76ijk	0.60opq	0.63nop	1.35vw	1.36vw
No NAA x Kanchan	1.55pqr	1.55pqr	0.35x	0.38wx	1.53k-n	1.56h-k
Protiva	1.76ijk	1.75i-l	0.50stu	0.53rt	1.44p-t	1.41s-v
Sourav	1.08vw	1.18uvw	0.23yz	0.22yz	1.56h-l	1.55j-m
Gourav	1.55pqr	1.57pqr	0.63nop	0.62nop	1.36t-v	1.38t-v
BAW 944	0.98l-x	0.95x	0.38wx	0.35x	1.42p-t	1.44p-t
BAW 953	2.00fgh	1.98fgh	0.98fg	0.95gh	1.69e	1.68e
BAW 994	1.45q-r	1.56pqr	0.68mn	0.70lm	1.90d	1.89d
Akbar	1.65lmn	1.70klm	0.59pqr	0.58pqr	1.50o-s	1.49o-s
Agrahani	1.08vw	1.05wxy	0.23yz	0.24yz	1.44p-t	1.43p-t
Sonalika	1.40r	1.43qrs	0.46uv	0.45uv	1.42r-u	1.41s-v
F-test	**	**	**	**	**	**
CV (%)	3.55	3.15	4.35	3.75	1.48	1.50

NAA, 1-naphthaleneacetic acid; DAS, days after emergence; Y1, first year (2009-10); Y2, second year (2010-11); RFWT, root fresh weight; RDWT, root dry weight; RL, root length; mg, milligram; m, meter; cc, cubic centimetre

Genetic variation in seminal root angle exists in wheat. It has been suggested that narrow root angles contribute to adaptation to summer–dominant rainfall zones and wide angles are important in the Mediterranean climates of southern Australia. This hypothesis was tested by measuring root angles in wheat and examining its relationship with yield and root distribution. Root angles of 52 genotypes, defined as the angle subtending the first pair of seminal roots of 14-day old seedlings, were measured in a root box (Table 4) (McDonald *et al.*,2010).

Table 4. Mean grain yield (tha^{-1}) of wheat varieties, classified by seminal root angles.

Root angle	All sites (N = 233)	WA (N = 65)	SA (N = 113)	VIC (N=31)	NSW (N=22)	QLD (N=2)
Narrow (69)	2.43 ± 0.08	2.54 ± 0.13	2.33 ± 0.12	2.24 ±0.18	2.86 ± 0.27	3.04 ±0.19
Intermediate (84)	2.40 ±0.08	2.54 ±0.13	2.31 ± 0.12	2.14 ± 0.18	2.73 ± 0.26	3.05 ±0.15
Wide (100)	2.30 ± 0.07	2.44 ± 0.13	2.22 ± 0.11	2.03 ± 0.17	2.65 ± 0.25	3.03 ± 0.22

The root is the main organ for water and nutrient uptake and sensing environmental stimuli in the soil. The optimization of root system architecture contributes to stress tolerance and yield improvement. ERF (ETHYLENE RESPONSIVE FACTOR) is one of the plant-specific transcription factor families associated with various developmental processes and stress tolerance. When cloned a novel ERF transcription factor gene *TaSRL1* (*SHORT ROOT LENGTH 1*) of wheat

(*Triticum aestivum*) which is mainly expressed in root. Ectopic expression of *TaSRL1* in rice resulted in short root length and plant height. TaSRL1 regulated expression of genes related to auxin synthesis, transport, and signalling.

Further studies revealed that TaSRL1 induced expression of the auxin transport gene *TaPIN2* by directly binding to its promoter, while the interaction of TaSRL1 and TaTIFY9 repressed *TaPIN2* expression. Sequence polymorphisms and association analysis showed that *TaSRL1-4A* was associated with root depth and angle, plant height, and 1000-grain weight of wheat. The haplotype *Hap*-4A-2 with shallow roots, short plant height, and high 1000-grain weight has been positively selected in the Chinese wheat breeding process. It was demonstrated that TaSRL1 functions as a direct regulator of *TaPIN2* in the auxin-dependent pathway and integrates auxin and jasmonate signalling by interacting with TaTIFY9 to repress root growth. The molecular marker of *TaSRL1-4A* is valuable for the improvement of the root system, plant architecture, and yield in the wheat breeding process.

The expression of *TaSRL1* was repressed by 1 nM NAA, but it was induced by 0.1 μM NAA, indicating that TaSRL1 may act as a negative regulator in the auxin-dependent regulatory pathway of root growth.

A further study revealed that TaSRL1 regulates expression of genes involved in auxin biosynthesis, transport, and signalling (Mao *et al.*, 2020), and binds to the promoter of the auxin transporter gene *TaPIN2*.The PIN proteins, which are auxin efflux carriers, are polar localized and determine auxin distribution (Barbosa *et al.*, 2018; Sauer and Kleine-Vehn, 2019). OsPIN2 participates in root elongation growth and the lateral root formation pathway by regulating auxin distribution in rice (Inahashi *et al.*, 2018). These results demonstrated that TaSRL1 represses root growth through an auxin-dependent pathway. Furthermore, TaSRL1 interacts with a JAZ protein, TaTIFY9. During root elongation, JAZ proteins act as transcriptional repressors of JA-responsive genes by interacting with their partners (Chini *et al.*, 2007; Thines *et al.*, 2007; Toda *et al.*, 2013). It was revealed that expression of *TaPIN2* was induced by TaSRL1, while it was repressed by TaTIFY9 in the presence of TaSRL1 (Figure 7), implying that TaSRL1 directly induces *TaPIN2* expression, and TaTIFY9 interferes with its function through their interaction. Thus, TaSRL1 is an integrator of auxin and JA pathways during root growth. Informations are available for the crosstalk of auxin and JAs during root development. Based on the above, a working model was developed for the interactions of TaSRL1 with auxin, *TaPIN2*, and TaTIFY9 in regulating root growth (Figure 7).

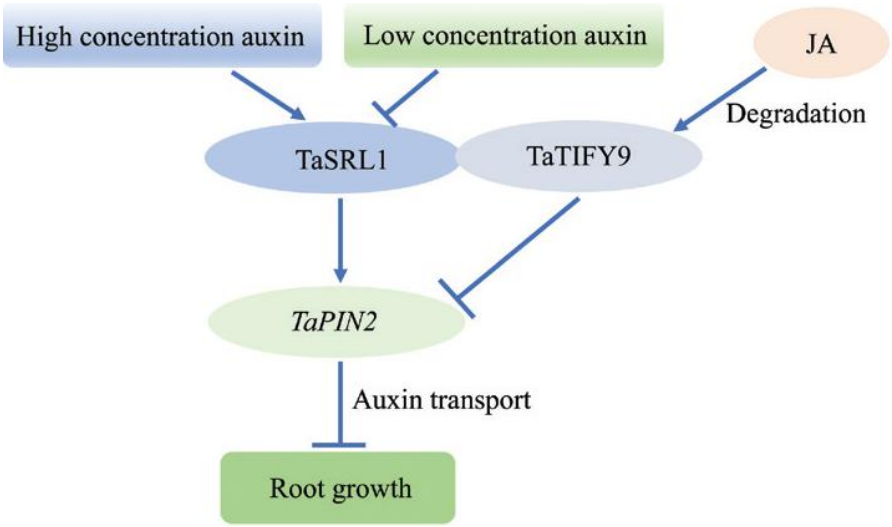

Figure 7.A proposed model for the regulation of root growth by TaSRL1in auxin and JA signalling pathways. The expression level of *TaSRL1* is enhanced by a high concentration of auxin and repressed by a low concentration. TaSRL1 directly induces expression of the auxin transport gene *TaPIN2* regulating the auxin concentration in root tips and inhibits root growth. After Zhuang *et al*, 2021.

MAIZE

The maize primary root is a cylindrical structure formed by consecutive zones (a) the root apex contains the apical meristem, where cell divisions occur; (b) the elongation zone in which cells stop dividing and start to elongate; and (c) the maturation zone, where cells reach their definitive lengths, cell differentiation begins, and lateral roots initiate. In the root, three main tissue systems can be distinguished the epidermis, the cortex, and the vascular cylinder. The first layer of the vascular cylinder is the pericycle. Cell cycle activation in pericycle cells is clearly connected with lateral root initiation. Root grows basically by the elongation of its cells and branches through proliferation of pericycle founder cells. Auxin is the main hormone in regulating these both processes. Exogenous auxin inhibits root growth, increases transversal expansion, and enhances lateral root formation. As auxin also enhances ethylene production, it is difficult to know whether certain auxin effects are mediated by ethylene or not. The emerging model is that auxin and ethylene regulate root elongation depending on concentration and that both regulators interact to regulate root growth. The role of auxin in regulating lateral root formation is clearly established. However, ethylene does not seem to have such a direct role in this process (Alarcon *et al.*, 2014).

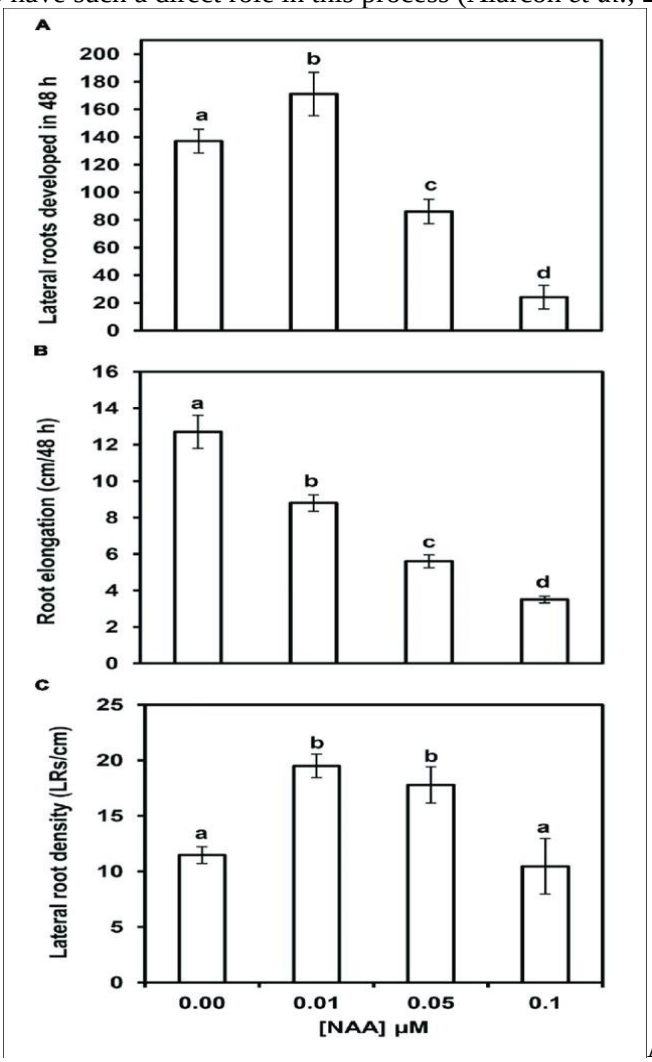

Figure 8. Effects of different NAA concentrations on (A) Lateral root development (B) Root elongation (C) Lateral root density in maize. After Alarcon *et al*, 2019.

Maize primary root elongation was inhibited by NAA treatment in a concentration-dependent manner, with a consequent reduction of the area where LRs can develop. A low NAA concentration (0.01 µM)

marginally inhibited primary root elongation but increased the total number of LRs after 48 h of treatment (Figures 8A, B). However, higher NAA concentrations elicited a large reduction in the absolute number of LRs (Figure 8A), as well as a strong concomitant reduction in primary root elongation. Therefore, the inhibition of LR formation could be due, at least in part, to the reduction in primary root elongation. Concentrations of NAA in the 0.05–0.1 µM range resulted in stronger inhibition of root elongation (up to 75%), and 0.5 µM NAA completely inhibited primary root elongation.

The application of 0.01 µM NAA stimulated the formation of LRs in the primary root of maize. This stimulation was observed as a wide extension of the parent root, mainly affecting the more distal root segments (Figure 9); in the youngest root segments grown after NAA treatment, significant LRD stimulation (treated 24.3 ± 3.0 LRs/cm vs. control 15.9 ± 2.5 LRs/cm) was observed. Promotion of LR formation also occurred in new segments formed after beginning of treatment. In contrast, more proximal root zones were apparently insensitive to auxin treatment (Figure 9).

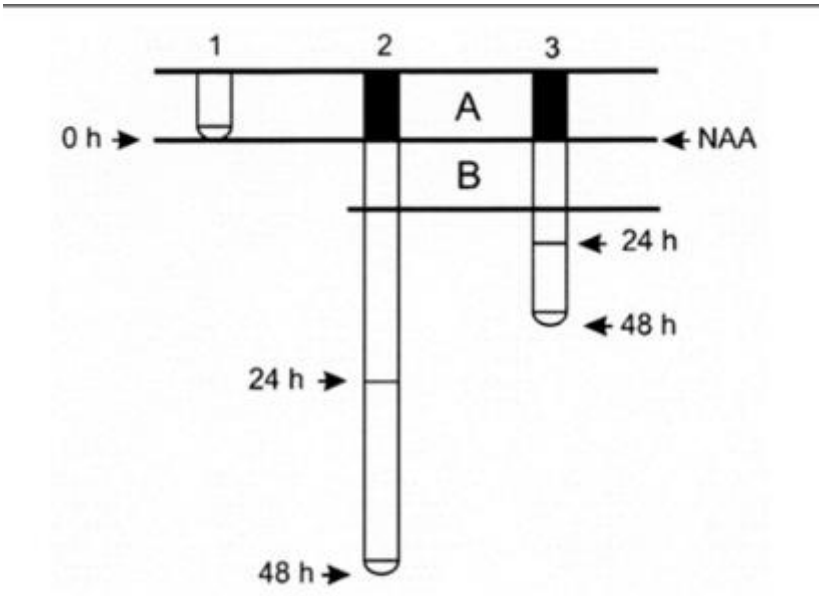

Figure 9. Formation of two 2-cm long consecutive zones in the maize primary root after NAA application. At time 0, treatment was performed by applying NAA to the growth medium (1). Zone A (filled) is elongated before auxin application, hence cell elongation occurred without auxin influence. In contrast, zone B (unfilled) elongated in the presence of auxin. Subsequently, the root grows, and lateral roots develop in both zones under the influence of exogenous auxin. Note that after 48 h, root elongation was greater in control (2) than in auxin-treated roots (3). After Alarcon *et al,* 2019.

Lateral root initiation in maize begins with transversal divisions of pericycle cells associated with phloem poles, when two adjacent cells opposite the phloem undergo two almost simultaneous oblique asymmetrical divisions and later more transversal and periclinal divisions (Casero *et al.,* 1995). In maize, periclinal divisions related to LR initiation occur 21–24 mm behind the tip (Casero *et al.,* 1995). In most species, initiating LR primordia are located in the maturation zone (Lloret and Casero,2002); consequently, the pericycle cells involved in this process are usually considered to be differentiated at the moment of LR initiation (Alarcón *et al.*, 2016) (Figure 10).

The LR distribution pattern along the primary root of maize is shown in Figure 10 . The number of LRs plus LR primordia per cm was determined in 2-cm long control and 0.01 µM NAA-treated root segments. The distribution of the LRs in control roots showed a characteristic pattern with several different zones. In the basal-most parent root segment, the density was relatively low (15–17 LRs/cm). In the segment

between 2 and 4 cm from the base, the LRD then increased until the zone of highest density (30–35 LRs/cm), and then decreased sharply to 15 LRs/cm in the segment located 6–8 cm from the root base. From this point toward the apex, the LRD declined slowly and then stabilized at a value close to 12 LRs/cm. LR primordia were not detected in the zone adjacent to the root apex.

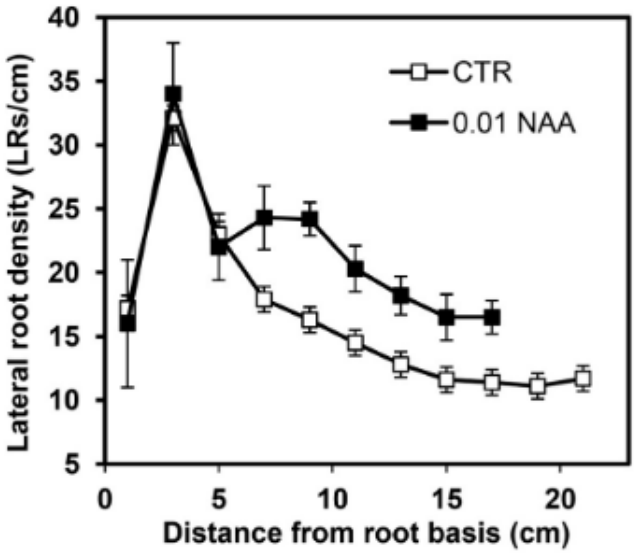

Figure 10. Effect of 0.01 µM NAA treatment on lateral root density (LRD) in the maize primary root. LRD was measured in 2-cm-long root segments from the base to the root tip. Auxin was applied when the roots were 8 cm long and LR formation was followed during a subsequent 48 h period. Note the inhibitory effect of NAA on root elongation and the stimulating effect on LRD in the youngest root zones analyzed. Values represent mean ± SD (*n* = 10). after Alarcon *et al,* 2019.

The LR density per unit of root length (LRD), and the mean phloem pericycle cell length. The total number of phloem pericycle cells (PPCs) per unit of root length was then calculated. Considering that each LR primordium is initiated from four founder cells (FCs), the percentage of PPCs (%PPC) that behave as FCs in a specific root zone was estimated by dividing the number of pericycle cells by four times the LRD. This index was utilized to describe LR initiation. Root zones elongated in the presence of a synthetic auxin (1-naphthaleneacetic acid, NAA) at low concentrations (0.01 µM) showed reduced cell length and increased LRD. However, a high concentration of NAA (0.1 µM) strongly reduced both cell length and LRD. In contrast, both low and high levels of NAA stimulated LRD in zones elongated before auxin application. Analysis of the percentage of FCs in the phloem pericycle in zones elongated in the presence or absence of NAA showed that low concentrations of NAA increased the %PFC, indicating that LR initiation is promoted at new sites; however, high concentrations of NAA elicited a considerable reduction in this variable in zones developed in the presence of auxin. As these zones are composed of short pericycle cells, it was proposed that short pericycle cells are incapable to participate in LR primordium initiation and that auxin modulated initiation of LRs is linked to pericycle cell length.

NAA enhances radial expansion by nearly 200 %, whereas ACC only increases it by about 40 %, so that NAA seems to be more effective than ACC as a root swelling promoter (Alarco´n *et al*., 2012).

There are essentially three lines of experimental evidence concerning the transport of auxin in regulating the LR formation process. First, elimination of the plant's aerial organs (the source of auxin) reduces the LR frequency, and then application of exogenous auxin to the aerial part of the mutilated plant reverses this effect (Hinchee and Rost, 1986). Second, mutants with defects in the auxin transport system (tir3) present fewer LRs (Ruegger *et al.*, 1997). And third, NPA, an inhibitor of auxin transport, suppresses the formation of LRs in tomato (Muday and Haworth,1994) and *Arabidopsis* (Reed *et al.*, 1998; Casimiro *et al.*, 1999,

2001). Together, these three lines of evidence clearly reflect a fundamental role for auxin transport in the formation of LRs.

For NAA, which is independent of the polar auxin transporters of the plant, in addition to the developed growth of the primary, seminal root, the growth of lateral roots was also promoted. Auxin transport inhibitor (NPA) retarded the growth of roots (Figure 11). When seedlings from the ZmPIN1a sense and antisense lines, the pyramiding lines of ZmPIN1a antisense, ZmPIN1b antisense and the WT line were exposed to IAA, NAA and NPA solution at the shoot apex, the ZmPIN1a sense plants in these treatments showed a robust root system with a modified architecture as described above, and the application of IAA promoted the elongation of the primary and seminal roots of WT and antisense lines just as in the phenotype caused by ZmPIN1a over expression. The application of exogenous IAA and NAA had different biological effects on maize root development. IAA was restricted by a complex auxin transport system composed of different transporters, while the synthetic hormone NAA was verified to greatly increase cellulose fibre formation in plants without selection of cell types. An increase in IAA transport to roots through over expression of auxin transporter (ZmPIN1a) or alteration of the homeostasis of the auxin sink and pool (application of IAA to WT plants) leads to a developed root system with longer seminal roots and denser lateral root (Figure11).

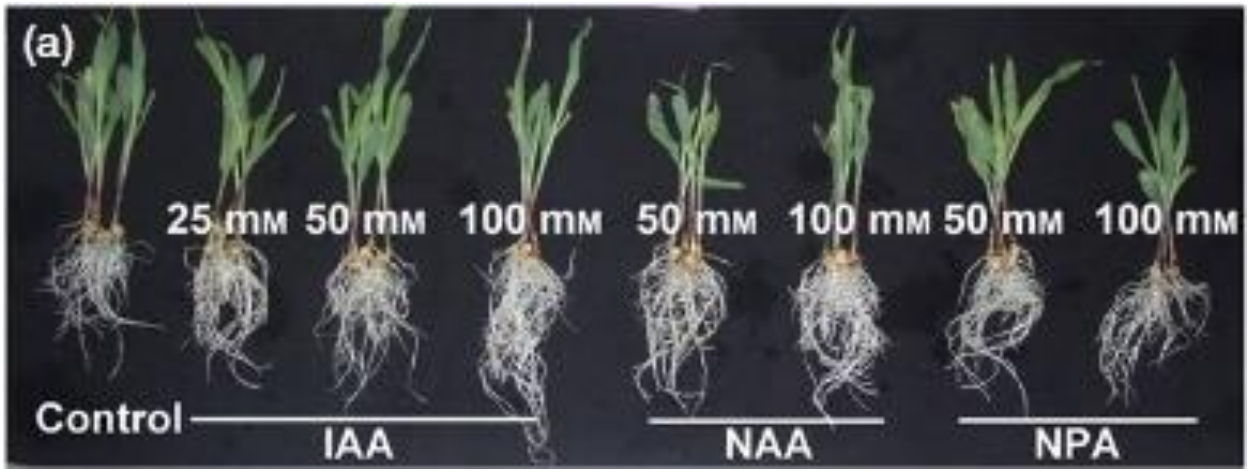

Figure 11. Morphological changes of WT plants after treatment with IAA, NAA, NPA and control treatment.

A genomewide transcriptome analysis showed that altering ZmPIN1a expression led to wide-ranging gene expression changes (GEO GSE57291). Comparative expression analysis of genes revealed IAA28-ARFs, which mediated cell specification, ARF6/8, which regulated cell elongation, and ARF3/4, which controlled lateral root growth (Guilfoyle and Hagen, 2007; Lavenus *et al.*, 2013; Overvoorde *et al.*, 2010), all of which showed significant changes in the sense line. The down-regulated genes of AUX/IAA32 (orthologue of AtIAA1/2/3/4/5/6/19), AUX/IAA7 (orthologue of AtIAA15), ZmIAA4 (orthologue of AtIAA18/26/28), ZmARF26 (orthologue of AtARF3/4) and ZmARF27 (orthologue of AtARF7/19) and the dramatically up-regulated gene of ZmARF16 (orthologue of AtARF6/8), all implied that auxin signalling is pivotal in modifying root growth and dwarfing plant height. However, their interaction, regulation of root growth, lateral root initiation and elongation must still be elucidated. The dramatically induced expression of AVP1 (positive regulator of root growth (Schilling *et al.*, 2017)) and reduced expression of AXR4 (negative regulator of root development (Hobbie and Estelle, 1995)) may contribute to the root morphology alteration under non stress as well as various abiotic stress conditions, as in *Arabidopsis* (Figure 12).

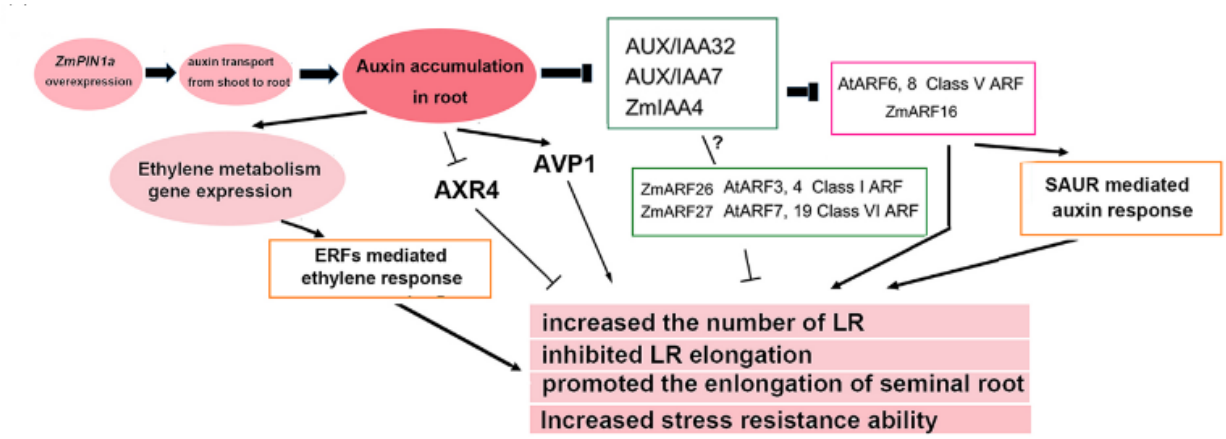

Figure12.Model summarizing the main results regarding *ZmPIN1a* over expression on root morphology changes in maize. After Li *et al,* 2018

CONCLUSION

Some important research works had been done on growth and development in cereals showing influences of NAA either as priming or exogenous application.

Genetic studies also suggested that a sizeable number of genes had been identified for enhancement and repression of the effects of NAA on root growth. Similarly mutants are being evolved for testing. However, in considering the importance of present situation of the goal of climate smart crops it is necessary to boost up researches to find out academic as well as applications in the field for increasing productivity.

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