Title

Phenotypic plasticity of root traits for improving deficit irrigation and growth performance in maize

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Abstract

Root system architecture (RSAch) is central to drought management in plants. In this study, the mechanism of paclobutrazol (PBZ)-mediated improvement in tolerance to water deficit using five maize varieties was investigated. Comprehensive pot experiments were conducted during 2017, 2018 and 2019 and maize plants were subjected to 60% of evapotranspiration demand both in early deficit (EDI) and terminal deficit (TDI) irrigation regimes. Findings revealed that application of PBZ decreased plant height; while traits like stem diameter, root biomass, root length and root surface area under EDI and TDI improved significantly. Structural equation modelling of root traits revealed PBZ induced increase in root surface area (RSA) and length of seminal roots in EDI. For TDI, PBZ induced changes in RSA, length of seminal and brace roots and several reproductive attributes of the plant. Altogether, these findings propose improvement of root traits as an effective strategy to increase Water Use Efficiency of maize varieties with minimal impact on agronomic traits.

Key words: maize, root system architecture, deficit irrigation, cob yield, water budgeting, economic attributes, phenotypic plasticity, root plasticity

1.0 Introduction

Maize is mainly a rain fed crop in Indian subcontinent. Annual monsoon has been disturbed consistently in recent years and has become a great concern not only for India, but also other countries in South Asia, where ~1.9 billion people live [1-2]. Maize cultivation is synchronized with monsoon, and few days' late monsoon arrival causes' negative impact on growth of young maize plants[1-4]. Irregular rain patterns and climate change impact maize cultivation pan India[3-4]. Soil water shortage in months of June-September often causes drought conditions or soil water deficit, resulting in poor plant growth and establishment of young maize plants (early water deficit) and successful transition of vegetative stage to reproductive stage[5-6]. Water deficit poses alarming threat to crop loss worldwide, reduces average 50% yield [7-12]. Impact of water deficit is proven more critical during flowering time (terminal water deficit) and results in approximately 40-60% yield loss[7-12].

Maize responses to water deficit or drought are multiple and inter linked with reduced leaf surface area, leaf water potential, relative water content and transpiration rate[13-14]. Sunken stomata, lowered stomatal density and shorter stem and delayed in onset of tassel and ear formation occur under drought[13]. Root adaptations include shallower root system or deep root system depending on soil water availability, reduction or increase in lateral roots on all the three different root types' viz. crown roots (CRs), brace roots (BRs) and seminal roots (SRs). In general, plastic responses of roots under drought or water deficit have been noted in plants[15-21]. Physiological perturbations induced under drought include reduced photosynthesis, photochemical efficiency and net assimilation rate (NAR)[22-23]. Root traits and their prospective role in water deficit management in crop plants are least explored in maize. Root traits such as root biomass, root length, root density, root surface area and root depth contribute towards water stress avoidance and regulate plant growth performance under drought[15-21]. A proliferated root system is helpful in extracting water from considerable depths, while a shallower system accounts for less damage to roots under drought[15-21].

Climate change and its impact on soil water availability and rain patterns across world have posed a serious challenge to crop management and world food security[24-28]. In Indian sub-continent, rain water is a main source of maize irrigation (85% of total maize cultivation); maize cultivators are facing a severe challenge of drought posed by erratic monsoon arrival or rain period[29-31]. India ranked seventh (17,300,000 tonnes) in maize production, with tally topped by USA (333,010,910 tonnes) at the world level in 2016-2017. Productivity of maize /ha is dismal low in India (2.54 million MT, 2016-17) compared to world average (5.82 MMT, 2016-17) and US (10.96 MMT, 2016-17). Primary reasons for this low productivity in India include dependence on rain fall (monsoon- south west and north east monsoon), salinity and other abiotic and biotic stresses[29-31]. Our extensive state-wise data analyses of maize production in India for the past 10-15 years have revealed interesting findings. Maize is cultivated throughout the year in different parts of the country mainly for grain, cobs and fodder. Nearly 15% of area under maize cultivation is irrigated, leaving 85% rain fed (mainly monsoon) source of irrigation[32-34]. In general, it is obvious to have low maize productivity in Indian states having irregular or shorter spell of monsoon rains. Our data analysis of past years (1999- 2018) showed a positive correlation between number of drought affected districts (DADs) and maize productivity at the National level (Supplementary Table 1 and 2, Supplementary Fig. 1 a-b). Deep analysis of data further revealed that, it was irregular monsoon episodes at state levels which brought reduction in maize productivity. For instance, reduction in monsoon rains (2013-14, 2014-15 and 2015-16) in Andhra Pradesh, with increase in number of DADs showed a linear relationship with reduction in maize productivity and yield, though area under cultivation increased over consecutive years in the state (Supplementary Fig. 2 a-b). Similar observations were noted for Karnataka (Supplementary Fig. 2 a-b), Madhya Pradesh (Supplementary Fig. 3 a-b**),** Uttar Pradesh (Supplementary Fig. 3 c-d) and Union territory of Jammu and Kashmir (Supplementary Fig. 4 a-b) though at different years and DADs. Summing these observations, drought conditions imposed by irregular monsoon patterns and lack of proper irrigation facilities are factors responsible for low maize productivity in India compared to world level. Improving maize productivity offers a new paradigm to increase farmers' income compared to other crops cultivated in India[35]. It has been speculated that, India would require 45 MMT of maize by year 2022 and to achieve this target, innovative ideas of improving maize productivity in rain fed areas require more attention[35].

Deficit irrigation both in terms of early deficit irrigation (EDI) and terminal deficit irrigation (TDI) offers an alternate method of conventional irrigation, where in a substantial amount of irrigation water could be saved by reducing evapotranspiration demand of plants with minimal effects on yield performance[36-38]. Our earlier studies showed positive impact of PBZ on WUE of tomato and mulberry plants *via* increasing root surface area and bringing physiological changes in both upper and lower parts of tomato and mulberry plant body under drought and salinity stress[22-23]. Understanding root growth kinetics (RSA, root length and root numbers) in maize and its impact on shoot growth kinetics and overall plant growth performance under drought or deficit irrigation needs to be explored using structural equation modeling (SEM). Predictive modeling will help to explore the role of different root traits and their potential role in making maize plants more efficient in WUE, water productivity (WP) with minimal effect on yield performance (cob yield) and farmers income. All these questions have been explored in the current study, where in early deficit irrigation (EDI) mimicked late arrival of monsoon, thereby affecting crucial stages of seed germination and seedling establishment and terminal deficit irrigation (TDI) embarking shorter monsoon spell affecting successful transition of vegetative to reproductive stage and crop yield. Studies were conducted on five hybrid maize varieties (DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621) over a period of three years in polyhouse conditions and results showed least explored contributory roles of maize root traits in making few varieties best adapted for deficit irrigation (EDI and TDI) with minimal impact on crop yield.

2.0 Results

2.1 Deficit irrigation and paclobutrazol alters plant growth kinetics

Early deficit irrigation (EDI) reduced shoot extension rate (ShVd) in all the five varieties both at 25 and 35 DAS, with significant reduction in DDKL, DKC-9144 (at 35 DAS only) and PG-2320, while increased significantly for Bio-9621at $p < 0.05$. EDI with paclobutrazol (PBZ) improved ShVd in all maize varieties, with maximum increase occurred in PG-2475 and PG-2320 at DAS 25 over EDI ($p > 0.05$). Only PBZ reduced ShVd significantly in PG-2320 at 25 and 35 DAS ($p < 0.05$) and in other varieties insignificantly, while ShVd increased in Bio-9621 at 25 DAS at $p <0.05$ over control (Fig. 1 a).

Under terminal deficit irrigation (TDI) DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 showed significant reductions in shoot extension rate (ShVdt) at 74 DAS (DDKL, DKC-9144 and PG-2475) and 84 DAS (PG-2320 and Bio-9621) at $p < 0.05$ (Fig. 1 b). PBZ with TDI significantly improved ShVdt 84 DAS (DDKL), 74 DAS (DKC-9144, PG-2475, PG-2320 and Bio-9621), compared to TDI alone at $p < 0.05$. Overall reduction in ShVdt was noted for PBZ in control conditions at all time points in DDKL, DKC-9144 and PG-2475 (except at 94 DAS), while increased Shvdt noted for PG-2320 and Bio-9621 (Fig. 1 b). Besides measuring the shoot growth kinetics, shoot mophpometerics revealed impact of EDI and TDI on shoot height, stem thickness, leaf number and leaf surface area (only for TDI) with or without PBZ (for details Supplementary Results, Supplementary Fig. S5 panel A and B).

Root growth extension rate (RoVd) for seminal root growth (SRRoVd), brace root growth (BRRoVd) and crown root growth (CRRoVd) were measured for EDI (Fig. 1 c-d). CRRoVd under EDI alone increased significantly in DKC-9144, PG-2475 and DDKL over control at $p < 0.05$. PBZ in EDI showed significant increases in DKC-9144 CRRoVd over control alone at $p < 0.05$ (Fig. 1 c-d). PBZ alone maximally increased CRRoVd in PG-2475 at $p < 0.05$ and reduced it in Bio-9621 compared to control at $p > 0.05$ (Fig. 1 c-d). For BRRoVd, at 35 DAS EDI alone, no significant change in RoVd in all varieties noted at $p > 0.05$. PBZ in EDI caused small increases in BRRoVd across all the varieties compared to control and EDI plants (Fig. 1 c-d). No significant changes in BRRoVd noted for PBZ alone under control conditions. For SRRoVd, both at 25 and 35 DAS, EDI alone, increased in DKC-9144 compared to control at $p < 0.05$ (Fig. 1 c-d). While PBZ with EDI at 25 and 35 DAS increased SRRoVd in DDKL compared to control at $p < 0.05$(Fig. 1 c-d).

Root morphometeric observations under EDI and TDI alone with or without PBZ showed altered root number, root length and root surface areas, with DKC-9144 and DDKL emerging as best adapted varieties (for details Supplementary Results, Supplementary Fig. S6 panel A and B). Harvested root system of maize plants under EDI and TDI showed visible differences in the maize root system. Such that EDI and TDI alone showed visible reduction in root growth compared to control, while PBZ under EDI and TDI improved root growth over EDI and TDI alone (Fig. 2). Visible differences in the growth of pot grown plants were also noted (Supplementary Fig. S4A). Besides, root and shoot growth kinetics, laterals root number (LRNs) were counted only at 35 DAS, (lateral roots on all root types viz. CR, BR and SR), improved LRNs were observed in all the maize varieties under EDI compared to control. PBZ under EDI was seen to reduce LRNs in all the varieties, while alone PBZ showed more inhibitory impact on LRNs across all the varieties over respective controls (Table 1).

2.2 Reproductive traits under deficit irrigation improved by paclobutrazol

TDI with or without PBZ impacted tassel (male inflorescence) developmental attributes (Fig. 3 a-i). TDI alone reduced tassel diameter (diaT) in DDKL and DKC-9144 insignificantly at $p > 0.05$, while increased diaT in PG-2475 at $p < 0.05$ (Fig. 3 a). PBZ with TDI increased diaT in DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 compared to TDI insignificantly. PBZ alone increased diaT significantly in PG-2475 at $p < 0.05$, while small non significant reduction in DKC-9144 compared to control (Fig. 3 a). Tassel length (LeT) under TDI significantly increased in DDKL and decreased in DKC-9144 over control at $p < 0.05$ (Fig. 3 b). PBZ with TDI increased LeT in DDKL and reduced in PG-2475 at p <

0.05. PBZ in control reduced LeT in all varieties insignificantly (Fig. 3 b). TDI reduced dry biomass of tassel (DBT) significantly in DDKL and PG-2320, while increased DBT in PG-2475 and Bio-9621 compared to control at $p < 0.05$ (Fig. 3 c). PBZ with TDI increased DBT in DDKL, DKC-9144 and PG-2320, while reduced DBT in PG-2475 and Bio-9621 over TDI at $p > 0.05$. Compared to control, PBZ alone increased DBT in DDKL and Bio-9621, while significant reduction in PG-2475 and PG-2320 respectively at $p < 0.05$ (Fig. 3 c).

TDI reduced number of male flowers/plant and number of anthers/flower in DKC-9144 and PG-2475 at $p < 0.05$ over control (Fig. 3 d-e). PBZ plus TDI increased both number of male flowers/plant and number of anthers/flower significantly in DKC-9144 compared to TDI at $p < 0.05$. PBZ under control improved number of male flowers/plant and number of anthers/flower in all varieties compared to control in a non significant manner at $p > 0.05$ and significantly in DDKL and PG-2320 ($p < 0.05$) (Fig. 3 d-e).

TDI impacted spikelet number, with maximum increase in DDKL, PG-2475 and Bio-9621 over control at $p < 0.05$ (Fig. 3 f). PBZ with TDI reduced spikelet number in all the varieties except DKC-9144 and Bio-9621 over TDI alone (Fig. 3 f). PBZ alone improved spikelet number in all varieties except PG-2320 compared to control at $p > 0.05$ (Fig. 3 f). Spikelet length under TDI reduced significantly in DDKL and DKC-9144, while increased in PG-2475 over control at $p < 0.05$ (Fig. 3 g). PBZ under TDI increased spikelet length in all varieties, with significant increase in PG-2475, PG-2320 and Bio-9621 over TDI alone at $p < 0.05$. PBZ in control conditions increased spikelet length significantly in PG-2475 and PG-2320 at $p < 0.05$ (Fig. 3 g).

Silk length under TDI maximally reduced in DDKL; while increased in DKC-9144 over control at $p < 0.05$ (Fig. 3 h). PBZ under TDI reduced silk length in PG-2475 compared to TDI at $p < 0.05$. PBZ in control conditions improved silk length significantly in DKC-9144 and PG-2320 over control (Fig. 3 h). Cob dry weight (CDW) in TDI alone reduced in all maize varieties significantly over control at $p < 0.05$. PBZ under TDI increased CDW significantly in DKC-9144, PG-2475, PG-2320 and Bio-9621 compared to TDI at $p < 0.05$ (Fig. 3 i). Under control, PBZ increased CDW in all varieties, with maximum increase in DDKL compared to control at $p < 0.05$ (Fig. 3 i).

Reproductive effort (RE%) tassel formation increased significantly in DKC-9144, PG-2475, PG-2320 and Bio-9621 under TDI over control at $p < 0.05$. Further, RE% tassel formation significantly increased in DDKL and DKC-9144, while decreased in PG-2475 and Bio-9621 for PBZ plus TDI compared to TDI at $p < 0.05$ (Table 1). PBZ under control enhanced RE% tassel significantly in Bio-9621; while decreased in PG-2320 over control (p

< 0.05). RE% ear formation under TDI, reduced in a non significant manner in PG-2475 and increased in PG-2320 to control. For PBZ under TDI, RE% ear formation maximally increased in PG-2475 compared to TDI alone at $p < 0.05$. For PBZ under control, RE% ear formation increased in PG-2475 ($p < 0.05$); while no significant decrease noted in other varieties at $p < 0.05$ (Table 1).

2.3 Deficit irrigation and paclobutrazol alters plant dry biomass, water use efficiencies and root hydraulics

For root dry weight (RDW), TDI alone significantly decreased brace root dry weight (BRDW) in DDKL, DKC-9144 and PG-2320, crown root dry weight (CRDW) in all maize varieties except Bio-9621, where it increased significantly at $p < 0.05$. Lateral root dry biomass (LRDB) a unique trait analyzed drought and deficit irrigation induced response in maize plants. TDI alone significantly reduced LRDB in DDKL and DKC-9144 and increased LRDB in PG-2475 and PG-2320 over control at $p < 0.05$. PBZ plus TDI significantly improved LRDB in DDKL and reduced in PG-2320 compared to TDI alone at $p < 0.05$. PBZ alone increased LRDB in DDKL and DKC-9144 over control at $p < 0.05$ (Fig. 4 a-d). Seminal root dry weight (SRDW) reduced significantly in DDKL, DKC-9144 and PG-2320 Bio-9621 over control at $p < 0.05$ (Fig. 4 a-d). PBZ under TDI significantly improved BRDW, CRDW and SRDW in all varieties, compared to TDI at $p < 0.05$. PBZ alone improved dry weights of all root types compared to control (Fig. 4 a-d).

Reduced shoot dry weight (ShDW) in all varieties noted under TDI, with most significant reduction in DDKL, DKC-9144 and Bio-9621 compared to control ($p < 0.05$). PBZ under TDI improved ShDW in DKC-9144 and Bio-9621; while reduction in PG-2475 over TDI at $p < 0.05$. PBZ under control increased ShDW in PG-2475 significantly over control at $p < 0.05$ (Fig. 4 f-g). Similar pattern of total root dry biomas (TotRDB) was noted across all the varieties. Under TDI alone, root/shoot ratio (RSR) significantly decreased in PG-2320 compared to control ($p > 0.05$). PBZ with TDI maximally increased RSR in PG-2475 and Bio-9621 ($p < 0.05$). PBZ under control conditions increased RSR significantly in DKC-9144 and Bio-9621 over control ($p < 0.05$) (Fig. 4 h).

Evapotranspiration demand (EVTD) varied across all the varieties at 54 DAS at the onset of TDI and PBZ. EVTD declined under TDI among all the maize varieties (Supplementary Fig. S7 a). Enhanced EVTD in PBZ plus TDI in all the varieties could be attributed to improved plant growth compared to TDI (Supplementary Fig. S7 a). Water use efficiency (WUE) was measured for plant dry weight (PDW) (shoot + root) and CDW. TDI alone increased WUE-PDW significantly in DDKL, DKC-9144, PG-2475 and Bio-9621 compared to control at $p < 0.05$. PBZ under TDI improved WUE-PDW in DKC-9144, PG-2475 and PG-2320 compared to TDI significantly at $p < 0.05$ (Supplementary Fig. S7 b-c). PBZ alone under control increased WUE-PDW in all varieties in a non significant manner ($p > 0.05$).

WUE-CDW under TDI alone significantly increased in DDKL, DKC-9144, and Bio-9621 over control ($p < 0.05$) (Supplementary Fig. 7 b-c). PBZ under TDI enhanced WUE-CDW in DDKL, PG-2475 and Bio-9621; while reduction of WUE-CDW noted in PG-2320 compared to control ($p < 0.05$). PBZ alone increased WUE-CDW significantly in DDKL and Bio-9621 compared to control ($p < 0.05$) (Supplementary Fig. 7 b-c). Impact of EDI and TDI was observed on hydraulics conductance (HC) of all root types. PBZ under EDI and TDI was able to improve HCs of all root types compared to EDI and TDI (for details Supplementary results).

2.4 Modulation of root plasticity and physiological markers improve deficit irrigation potential

For root plasticity indices, maximum scope of plastic response (SPR) (5), relative trait range (RTR) (0.16) and response coefficient (RC) (1.2) for CRs noted for DKC-9144 under PBZ+TDI compared to TDI alone (Table 2). For BRs, maximum SPR (3 in DKC-9144), RTR (0.115 in PG-2475) and RC (1.12 in DKC-9144) were measured in PBZ plus TDI compared to TDI alone. For SRs, maximum SPR (8 in PG-2475), RTR (0.318 in Bio-9621) and RC (1.46 in Bio-9621) were noted in PBZ plus TDI over TDI alone (Table 2).

For drought indices under TDI alone, maximum RDI noted for PG-2475 over control. PBZ under TDI reduced RDI significantly in DDKL and DKC-9144 compared to TDI alone at $p < 0.05$. Most TDI susceptible variety noted was PG-2475 with SSI, while PBZ under TDI reduced SSI maximally in DKC-9144 compared to TDI alone at $p < 0.05$. Maximum TOL under TDI recorded for DDKL, while PBZ improved TOL in all the varieties. MP under TDI were maximum in DDKL followed by DKC-9144; while PBZ improved MP maximally and in DDKL and DKC-9144 respectively over TDI alone at $p < 0.05$. GMP maximum under TDI was observed in DDKL and DKC-9144; while PBZ under TDI improved GMP in DDKL and DKC-9144 over TDI alone significantly ($p < 0.05$) (Table 3). Maximum STI was noted for DDKL and DKC-9144 in TDI alone; while PBZ under TDI improved STI in DDKL and DKC-9144 at $p < 0.05$. Maximum YSI under TDI noted for DDKL and DKC-9144 ($p < 0.05$), furthermore, PBZ improved YSI in all varieties compared to TDI alone in a non significant manner ($p > 0.05$). Significantly maximum YI observed for DDKL and DKC-

9144 under TDI; while PBZ under TDI improved YI in DDKL and DKC-9144 ($p < 0.05$). For TDI alone, maximum HM was noted for DDKL and DKC-9144, while PBZ improved HM significantly in DDKL and DKC-9144 compared to TDI alone at $p < 0.05$ (Table 3). EDI with or without PBZ affected seed germination indices and emergence timings of different root types in all the maize varieties (Supplementary results 2.2).

Ascorbic acid (ASA) and glutathione (GSH) are key regulators of abiotic stress management in plants. Commencement of TDI from 54 DAS, showed progressive increases in ASA and GSH under TDI compared to control, furthermore PBZ improved ASA and GSH levels significantly in DDKL and DKC-9144 over TDI alone ($p < 0.05$). Levels of glycine (Gly) and proline (PL) enhanced in TDI, while PBZ application further improved these markers significantly in DDKL and DKC-9144 ($p < 0.05$). Membrane damage in terms of enhanced MDA levels noted for all varieties under TDI (for details Supplementary Fig. 8). PBZ under TDI reduced MDA production in all the varieties tested, most significantly in DDKL and DKC-9144 compared to TDI alone. Activities of antioxidant enzymes such as SOD, CAT, APOX, GPOX and GR and of root health indicator, urease enzyme were altered in TDI conditions, while PBZ modulated activities of these enzymes to improve deficit irrigation tolerance (for details Supplementary Fig. 8). Leaf relative water (LRWC) content declined in TDI conditions in all varieties, whereas PBZ under TDI improved LRWC maximally in DKC-9144 and DDKL ($p < 0.05$) (for details Supplementary Fig. 9)

2.5 Deficit irrigation and paclobutrazol impacts photosynthetic performance and molecular regulation of root traits

Chlorophyll *a* and *b* contents under TDI declined in all varieties, whereas PBZ under TDI improved these pigments compared to TDI alone (for details Supplementary Fig. 9). In TDI, leaf area index (LAI) reduced in all maize varieties, with significant reductions occurred in DKC-9144 and PG-2320 compared to control at $p < 0.05$. PBZ under TDI non-significantly increased LAI in all maize varieties compared to TDI ($p > 0.05$) (Table 1). PBZ alone increased LAI of all maize varieties compared to control. Net assimilation r-ate (NAR) under TDI increased in all maize varieties, with maximum increase in DDKL over control ($p < 0.05$). PBZ under TDI improved NAR in all the varieties in a non significant manner. Alone PBZ reduced NAR in all varieties though insignificantly compared to control ($p > 0.05$) (Table 1).

Among five varieties, two varieties selected (on the basis of WUE-CDW and cob yield) DKC-9144 (best performing) and PG-2475 (median performing) were examined for changes in photosynthetic parameters using Licor[22-23]. Net photosynthetic rate (P_N) was affected under EDI in both varieties compared to control plants. P_N reduced in DKC-9144 and PG-2475 over control at 25 and 35 DAS. PBZ under EDI reduced P_N at 25 DAS; while at 35 DAS P_N improved in DKC-9144 and PG-2475 over EDI plants at $p < 0.05$ (Fig. 5 a) in a non significant manner.

Intercellular CO_2 (Ci) decreased significantly at 25 DAS ($p < 0.05$), while non significant reductions occurred at 35 DAS in DKC-9144 and PG-2475 respectively compared to control at $p > 0.05$ (Fig. 5 b). PBZ under EDI significantly increased Ci at 25 DAS in DKC-9144 at $p < 0.05$; while at 35 DAS not significantly improved Ci values both in DKC-9144 and PG-2475 over EDI alone. Stomatal conductance (gs) increased in a non significant manner under EDI alone and with PBZ at 25 DAS in DKC-9144 and PG-2475 over control (Fig. 5 c). While at 35 DAS, EDI significantly reduced gs in DKC-9144 and PG-2475 over control at $p < 0.05$. Small enhancements in gs noted at 35 DAS for PBZ with EDI over EDI alone in DKC-9144 and PG-2475. No significant reduction in leaf transpiration rate (E) occurred in DKC-9144 and PG-2475 at 25 DAS under EDI alone or with. While significant reduction in E value occurred under EDI at 35 DAS in DKC-9144 and PG-2475 compared to control at $p < 0.05$. PBZ under EDI at 35 DAS improved E value in a non significant manner in DKC-9144 and PG-2475 over EDI alone (Fig. 5 d). EDI alone increased total soluble sugars (sugar content) in DKC-9144 and PG-2475 over control (Fig. 5 panel A). Improved photosynthetic parameters in DKC-9144 and PG-2475 in EDI plus PBZ could be linked with further improvement in sugar content compared to EDI (Fig. 5 e).

Expression of key genes regulating architecture of seminal and lateral root initiation was measured at different stages of EDI in DKC-9144 and PG-2475 (Fig. 5 f-j). At 15 DAS, several folds higher expression of *ZmRTCS*, *ZmARF34* and *ZmRTCL* noted in DKC-9144 compared to PG-2475; while 2-fold higher expression of *ZmMel* was observed in PG-2475 compared to DKC-9144 at 15 DAS (Fig. 5 f). At 25 DAS, EDI alone improved of *ZmMel* (2.22-fold), *ZmRTCS* (1.12-fold) and *ZmARF34* (1.34-fold) expressions, while reduced expression of *ZmRTCL* (15-fold) in DKC-9144 compared to control (Fig. 5 h). However, in PG-2475 reduced expressions of *ZmMel* (3.21-fold), *ZmARF34* (2.46-fold) and *ZmRTCL* (35-fold); while elevated profile of *ZmRTCS* (2.46-fold) noted compared to control. PBZ under EDI reduced expressions of *ZmMel* (1.20-fold) and *ZmARF34* (3.98-fold) and *ZmRTCL* (3.28-fold); while increased expression of *ZmRTCS* (4.38-fold) over EDI alone in DKC-9144. For PG-2475, PBZ with EDI improved expressions of *ZmMel* (4.15-fold), *ZmRTCS* (9.57-fold), *ZmARF34* (1.99-fold) and *ZmRTCL* (1.85-fold) compared to EDI alone (Fig. 5 h). At

35 DAS, EDI alone up-regulated expressions of *ZmMel* (3-fold) *ZmARF34* (1.22-fold) only and down-regulated *ZmRTCS* (44-fold) and *ZmRTCL* (29-fold) in DKC-9144; while in PG-2475 elevated expressions of *ZmMel* (1.76-fold), *ZmRTCS* (1.47-fold), *ZmARF34* (1.77-fold) and *ZmRTCL* (2.6-fold) compared to EDI alone (Fig. 5 i). PBZ under EDI at 35 DAS up-regulated *ZmRTCS* (13-fold) and *ZmRTCL* (16-fold) and down-regulated *ZmMel* (1.28-fold) and *ZmARF34* (1.88-fold) in DKC-9144 compared to EDI (Fig. 5 i). Under same conditions, PG-2475 showed elevated expressions of *ZmMel* (1.76-fold), *ZmRTCS* (1.47), *ZmARF34* (1.77-fold) and *ZmRTCL* (2.6-fold) over control (Fig. 5 j). PBZ under EDI at 35 DAS showed down-regulation of *ZmMel* (0.6-fold) and *ZmARF34* (0.37-fold) and up-regulation of *ZmRTCS* (3.82-fold) and *ZmRTCL* (1.25-fold) compared to EDI alone (Fig. 5 j).

2.6 Structural equation modeling reveals root traits required to improve water use efficiencies and growth performances

For EDI and TDI conditions with or without PBZ, contributions of root types and their traits scored differently as a root factor responsible for WUE, shoot height (SH) and stem thickness (ST) for DKC-9144 and PG-2475 (Fig. 6 a-f).

SEM analyses under control conditions showed significant positive impact of CR on SH than WUE but had negative impact on ST; while for PG-2475; it had very less impact on explaining the variations for WUE, SH and ST (Fig. 6 a-b). Contribution of BR was positive on SH than WUE but negative on ST in DKC-9144 when compared to its impact for PG-2475, these traits showed less negative contribution on WUE and ST with 0.16 impacts on SH. The effect of SR was negative on WUE and SH with little positive (0.04) on ST in DKC-9144, while for PG-2475 its effect was positive on WUE (0.08) and ST (0.12) but negative on SH (-0.19) (Fig. 6 a-b).

Under EDI alone in DKC-9144, the effect of CR is more positive on SH (1.01) than WUE (0.13) but negative on ST (-0.16), while for PG-2475, its effect was positive on WUE (0.01) and negative on SH (-0.22) but no effect on ST (Fig. 6 c-d). BR showed positive effect on SH (1.70) and negative on WUE (-0.8) and ST (-0.16) in DKC-9144, while for PG-2475, the effect of BR was negative on SH (-0.33) but showed no effect on WUE and ST respectively. The effect of SR was positive on ST (0.18) and WUE (0.01) but negative on SH (-1.16), while for PG-2475, its effect was negative on SH (-0.7) and no effect on WUE and ST (Fig. 6 c-d).

Under EDI+PBZ conditions effect of CR on WUE, SH and ST were 0.01, -0.08 and -0.07 in DKC-9144 but for PG-2475, effects were -0.03, 0.07 and 0.13, respectively (Fig. 6 e-f). BR contributed 0.04, -0.01 and 0.16 on WUE, SH and ST in DKC-9144, while for PG-2475, these were 0.11, -0.09 and -0.03, respectively. The effect of SR on WUE, SH, and ST were 0.12, -0.08 and 0.09 in DKC-9144, while for PG-2475, the effects were -0.10, -0.14 and -0.09, respectively (Fig. 6 e-f).

For TDI, under different conditions (i.e. CN, TDI and TDI+PBZ), contributions of root types and their traits for WUE, SH and ST on DKC-9144 and PG-2475 varieties were shown in (Fig. 6 g-l). Under control conditions, effect of BR was more positively significant on SH (2.06) than WUE (1.83) and negative on ST in DKC-9144, while for PG-2475, effect on WUE was 0.08, on SH is 0.02 and on ST is -0.06. Effect of CR was more positive on SH (2.36), WUE (2.12) and ST (0.29) in DKC-9144, but for PG-2475, effect on WUE was -0.03, SH 0.05 and ST 0.12. The SR contribution was negative on SH (-0.53) and WUE (0.49) but positive on ST (0.04) in DKC-9144, while for PG-2475, negative on WUE (-0.09), SH (-0.05) and ST (-0.07) (Fig. 6 g-h).

Under TDI alone, in DKC-9144, effect of BR was negative on WUE (-0.05) and ST (-0.44), while positive on SH (3.69); for PG-2475, effect of BR on WUE was 0.11, on SH 1.95 and on ST negative -0.47 (Fig. 6 i-j). The effect of CR on WUE was -0.11, SH 2.19 and ST -0.14 in DKC-9144, while for PG-2475, effect of BR on WUE was -0.17, SH 1.77 and ST 0.09. The SR showed negative effects on WUE (-0.43) and ST (-0.48), and positive on SH is 2.92 in DKC-9144, while the effect of SR on WUE was -0.28, SH 1.23 and ST -0.70 (Fig. 6 i-j).

Under TDI+PBZ conditions, for DKC-9144, the effect of BR on WUE was 0.08, SH -0.01 and ST 0.06, while for PG-2475, effect of BR on WUE was 0.06, SH 0.08 and ST 0.67 (Fig. 6 k-l). Effect of CR on WUE was -0.03, SH 0.05 and ST 0.12 in DKC-9144, while for PG-2475, effect of BR on WUE was -0.04, SH 0.67 and ST -0.27. For DKC-9144, effect of SR on WUE was -0.01, SH -0.05 and ST -0.07, while the effect of SR on WUE was 0.08, SH -0.27 and on ST -1.11 (Fig. 6 k-l).

2.7 Water economics and its applications in raising farmers' income under deficit irrigation and paclobutrazol

Amount of water required/plant (evapotranspiration demand, EVTD) in control irrigation varied, with maximum amount ~ 4.54 liter/plant each for DKC-9144 and PG-2475 and minimum 3.27 liter/plant for Bio-9621 (Fig. 7 a). TDI maximally reduced EVTD to 2.11 liter/plant in Bio-9621 across all the varieties. In general, PBZ plus TDI enhanced EVTD in all the varieties compared to TDI. Approximate water savings under TDI at 1000 plants and at hectare (ha) area of arable land showed maximum water savings 3106, 2819 and 2791 liter/ha for PG-2475, PG-2320 and DKC-9144 without yield consideration (Fig. 7 b-c). PBZ with TDI improved water savings /plant maximally by 2.32 liter/plant for PG-2320, while maximum water savings 429 liter/ha for DDKL compared to TDI alone (Fig. 7 a).

Cob yield parameter drew a comparison among varieties, with significant reductions in cob yield kg/ha noted for DDKL, DKC-9144, PG-2475 and PG-2320 under TDI compared to control (Fig. 7 d). Water productivity (WP, Kg/ET for cob yield without drawing cob yield comparison among varieties) enhanced significantly in DDKL, DKC-9144, PG-2320 and Bio-9621 under TDI alone at $p < 0.05$. PBZ with TDI improved WP, with significant increase in PG-2320, PG-2475 and DKC-9144 compared to TDI at $p < 0.05$ (Fig. 7 e). PBZ improved WP in all varieties except PG-2320 in a non significant manner at $p > 0.05$ (Fig. 7 e).PBZ improved cob yield kg/ha in all the varieties, with maximum increase noted for PG-2475 and DKC-9144 compared to TDI alone ($p < 0.05$). Overall maximum % increase in cob yield kg/ha under TDI and PBZ was approximated for DKC-9144 compared to TDI (Fig. 7 f).

TDI impacted cob yield/kg ha, which in turn when approximated affected farmer's income. Maximum income minimum support price (MSP)/ha under control irrigation was for DDKL (18990 INR or 246 $ USD) and DKC-9144 (16583 INR or 215 $ USD), while minimum MSP for PG-2475 (6978 INR or 90 $ USD) and median values noted for PG-2320 (11947 INR or $ 155 USD) and Bio-9621 (8101 INR or 105 $ USD) approximated (Fig. 7 f). TDI alone reduced MSPs/ha by 26%, 32%, 41%, 20% and 13% in DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 compared to control irrigated MSPs. PBZ with TDI improved MSPs/ha over TDI alone 15%, 34%, 51%, 13.5% and 17% in DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621. PBZ under control improved MSPs 23%, 13%, 21%, 7% and 24% in DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 compared to control (Fig. 7 f). It was speculated that water saved during TDI and TDI plus PBZ if used to irrigate more maize plants in extra arable land under TDI conditions with or without PBZ could improve MSPs in DDKL (22% and 42%), DKC-9144 (14% and 53%), PG-2475 (49% PBZ plus TDI only), PG-2320 (34% and 83%) and Bio-9621 (44% and 69%) both in terms of INR and $ USD compared to their respective control MSPs/ha (Fig. 7 f).

3.0 Discussion

Extensive data analyses of monsoon patterns in India for past 18 years indicated a strong correlation between drought induced by irregular monsoon arrival and rain spell with national maize productivity[32-34] (Supplementary Figs. 1-5). Published researches show morphological adaptations in maize seedlings under drought with reduced shoot and root growth kinetics, leaf area, elongation rate and final leaf length[39]. Our study showed altered shoot and root growth kinetics and shoot and root morphometerics in all maize varieties tested under deficit irrigation (EDI and TDI) and PBZ (Figs. 1 and 2, Supplementary Figs. 1-2). Inter varietal impact of EDI and TDI was least for DKC-9144 and more specifically when applied with PBZ (Fig. 1). Flowering and early seed development phases are sensitive to drought and proven detrimental for maize yield[40]. Water deficient conditions lower water potential in both vegetative and reproductive sinks resulting in poor seed formation and flower development. A week-long water deficit could impact floral development and grain number in maize variety DH4866[41]. Compared to control irrigation anthesis-silking interval was 2.53-fold higher, while reduction in ear length, pollen viability and grain number per plant occurred in water deficit conditions[41]. Chilling stress could negatively impact tassel branches and spikelet pair's initiation in maize inbred F53 at end of vegetative phase and start of floral transition stage[42]. Decreased silk growth rate and silk emergence has been noted in maize under water deficit conditions [43]. Yield reduction under drought or water deficit is an outcome of a selective strategy of young reproductive organs abortion to enable older fertilized ovaries to mature and complete the process of ear formation[19]. Both silk emergence and male anthesis are water turgor dependent processes followed by ear biomass accumulation[18]. Current study showed negative impact of TDI on developmental attributes of tassel and silk length and ear formation in all the maize varieties with minimum impact noted for DKC-9144 and DDKL. PBZ with TDI reduced negative impact of TDI on all reproductive developmental attributes compared to TDI alone (Fig. 3). Inter varietal reproductive effort (RE %) for tassel and cob formation was maximum for DKC-9144 in response to PBZ and TDI (Table 1).

Hydraulic conductance plays important role in drought management in plants. Strong relationship between root hydraulics of whole roots (Lp-WR) and drought resistance recorded in maize[44]. A positive correlation between Lpr-WR and leaf water potential and transpiration rate also noted, under water deficit Lpr-WR decreased with associated decrease in leaf photosynthetic parameters and respiration[44]. Correlation between root hydraulics and stomatal opening and closure offers instant water crisis management, while leaf area development has emerged as a long-term strategy for maximizing WUE in plants[45]. Simulation studies conducted in plants indicate that circadian oscillations of root hydraulic conductance could play key roles in acclimation to water stress *via* increasing root water uptake, leading to improved plant growth and photosynthesis [46]. Present study also showed a correlation between hydraulics of whole roots and TDI (Supplementary Fig. 8). Hydraulics improved under PBZ and TDI application more specifically in DKC-9144 and DDKL among all varieties (Supplementary Fig. 8, unpublished results). Deep rooting is a strategy for drought avoidance in plants. A comprehensive study conducted on maize inbred lines (CML444, Ac7729, TZSRW, Ac7643) under drought revealed that rooting depth was greater for CML444 and Ac7729/TZSRW (P2) compared to SC-Malawi and Ac7643 (P1) [47]. Increased number of lateral roots in the upper part of the soil was positively correlated with increased transpiration, shoot dry weight and stomatal conductance. Further CML444 had thicker (0.14 mm) and longer (0.32 m) CRs compared to SC-Malawi, thereby suggested that a combination of high WUE and water acquisition with a deep root system could improve drought tolerance in CML444 [47]. Reduced LRs number and branching has been associated with improved deep rooting and reduction in lateral root respiration per unit of axial root length, which in turns improves leaf relative water content, stomatal conductance and ~ 50% increase in shoot biomass[20]. Findings strongly advocates reduced lateral root branching density for improving drought tolerance in maize plants[20]. Under water stress a positive correlation between SRs length and drought tolerance index has been noted in maize seedlings[48]. Another study conducted on 22 maize cultivars subjected to water stress at flowering and grain filling stages showed a strong correlation between root traits and drought management. A positive association of drought tolerance indices was noted for CRL and CRN, root circumference and roots dry weight under water stress conditions. While a negative correlation was noted for brace root whorls, and a positive one for CRs number, BRs branches and CRs branching in all the maize cultivars[49]. Parallel to these observations, our study showed a positive correlation between SPR, RTR and RC with crown and brace roots (Table 2). Inter varietal drought indices showed better performances for DKC-9144 and DDKL under TDI alone and more so when TDI was accompanied by PBZ (Table 3).

Drought induced physiological perturbations impacts water use efficiency (WUE), chlorophyll florescence and photosynthesis in maize hybrid lines[39]. Current study showed reduction in shoot growth and root growth kinetics, reduction in leaf surface area (LSA) and leaf area index (LAI) and NAR in all maize varieties (Table 1). Increased RSR in maize seedlings has been recorded under drought [50]; similar observations were noted for TDI in all the varieties except PG-2475. PBZ under TDI increased RSR except for DKC-9144 (Fig. 4).

Maize cultivars (Rung Nong 35 and Dong Dan 80) subjected to drought (35% of field capacity) compared to control irrigation (80% of field capacity) showed reduction in growth and yield in Rung Nong 35 compared to Dong Dan 80[51]. Higher LRWC, PL and carbohydrate and antioxidant activity (SOD, POD, CAT and GR) was noted in Dong Dan 80 with lowered membrane damage resulted in better growth of the Dong Dan 80 under drought compared to Rung Nong 35 [51]. Observations made for EDI and TDI also showed increased LRWC, PL and Gly accumulation, higher antioxidant activities (ASA, GSH, SOD, POD, GR and CAT) in DKC-9144 variety (best performing under deficit irrigation) compared to Bio-9621 and PG-2475. PBZ under TDI also improved these morphological and physiological attributes with DKC-9144 emerging as best adapted variety for deficit irrigation (Figs. 1 and 3). Severe water deficit could reduce yield, root biomass, root length and increase in root diameter with least impact on roots surface area in maize plants[52]. Our study also showed impact of TDI on yield, root biomass and root surface area in all the varieties, with DKC-9144 showing better attributes under study (Figs. 1 and 3). Among five varieties, DKC-9144 and PG-2475 were selected as best performing varieties under EDI and TDI in terms of WUE, cob yield and over all plant growth performances.

Improved photosynthetic performance of DKC-9144 and PG-2475 subjected to EDI and PBZ showed positive impact of PBZ on regulation of photosynthesis and emerged as best adapted and moderate variety under EDI and TDI (Fig. 5 a-e). Root architecture specifically initiation of CRs is regulated by *ZmRTCS* and *ZmRTCL* and their binding patterns *ZmARF34* and *ZmMel* in maize[53]. Improved root system of DKC-9144 over PG-2475 could be attributed to regulation of maize root architecture at the molecular level by *ZmMel*, *ZmRTCS*, *ZmRTCL* and *ZmARF34* (Fig. 5 f-j). Structural equation modeling (SEM) offers a reliable tool in identification and characterization of a variable and its contribution towards a desired trait [54-55]. SEM on maize root traits has never been performed to-date. Extensive SEM analysis explored the contribution of root traits for WUE, SH and ST showed differences among DKC-9144 and PG-2475. RSA of SRs emerged as an important root trait for improving WUE, SH and ST in DKC-9144 over PG-2475 in EDI and TDI (Fig. 6 a-l). From SEM, we envisaged that root surface area (RSA) was an important measure for roots in order to accommodate the variability while CR plays an important root type to explain the variability for WUE and SH. SR was significantly important root type for ST to DKC-9144. Also, under control conditions for PG-2475, SR is important root for ST (Fig. 6 a-l).

Drought impacts maize yield and farmer economics world over [56-57]. Impact analysis of drought and its frequency of occurrence in relation to north east monsoon were studied over a period 1961 to 2017. Results showed that irregular monsoon patterns could induce drought conditions in the area, with increase in frequency of drought episodes by 15% and 25% in the period 1998-2017 compared to 1961-1980. These drought episodes declined maize production by more than 14% particularly in month of September and consequently reducing farmer's income[58]. Deviation of monsoon from normal pattern in Indian state of Manipur also showed decline in maize productivity[3]. Delayed arrival of monsoon has been a causative factor for maize seeds germination and establishment in water deficit soils in India (Reuters, 2019). Our data analysis spread over five states of India (Andhra Pradesh, Madhya Pradesh, Gujarat, Uttar Pradesh) purported that irregular monsoon patterns in these states coincided with declaration of drought affected districts (DADs) and annual maize productivity and yield in kg/ha in these states (Supplementary Figs. 1-5). Water budgeting showed a substantial amount of water savings under TDI alone and TDI plus PBZ across all the maize varieties. Further, inter varietal analysis in terms of WUE-PDW and WUE-CDW showed that DKC-9144 followed by DDKL were most adapted varieties under TDI alone or in combination PBZ (Fig. 7). Extrapolation of the observations on water savings at hectare area of arable land showed that TDI particularly with PBZ could improve the net income generated by the maize growers/ha considering the utilization of saved water for irrigation of more area under maize cultivation (Fig. 7).

4.0 Methods

4.1 Plant material and growth conditions

Zea mays L. (maize or corn) seeds of five maize varieties i.e. DDKL, DKC-9144-9144, PG-2475, PG-2320 and Bio-9621 were procured from Agricultural Research Station Jammu, India. Seeds were tested for their germination indices. These varieties are well adapted in the climatic conditions of North India with average yield grown in irrigated and rain fed areas as follows: DDKL (5500 kg/ha), DKC-9144-9144 (6386 kg/ha), PG-2475 (3600 kg/ha), PG-2320 (3500 kg/ha) and Bio-9621 (2600 kg/ha) as per yield reports[59]. Randomized factorial design, with each variety subjected to control irrigation regime (CN, 100% evapotranspiration demand (EVTD), deficit irrigation (DI) with 60% EVTD met and paclobutrazol (PBZ) application at 60 ppm in a soil drench method. Experiments over a consecutive period of three years (2017, 2018 and 2019) were conducted in the Polyhouse at Botanic Garden (32.7194° N, 74.8681° E) University of Jammu, Jammu, India (Supplementary Fig. 1).

Early deficit irrigation (EDI): To mimic late monsoon arrival, seeds were sown at least 10 days later than their usual biological clock (1^{st} week of June, 2017, 2018 and 2019) and subjected to EDI with or without PBZ commencing from 15 days after sowing (DAS) until 35 DAS. Over a three year period, a total of 300 young maize seedlings were grown till establishment of young plants i.e. 35 DAS. In brief, for each variety 60 young maize seedlings were sown in control conditions until 15 DAS, with 20 plants/year in pot conditions. Each variety was subjected to four different treatments CN (100% EVTD), EDI (60% EVTD), EDI plus PBZ (EDI+PBZ) and CN plus PBZ (CN+PBZ).

Terminal deficit irrigation (TDI): To mimic shorter rain spell 54 DAS, plants were segregated into four groups viz. control, TDI, TDI plus PBZ and Control plus PBZ for each maize variety. Experiment was performed on consecutive three years period (2017, 2018 and 2019) in a Polyhouse (30 m^2) in the Botanical garden of University of Jammu, in the months of June –September as a kharif crop. Over a three year period a total of 300 maize plants were grown till harvest. In brief, for each variety 60 plants were sown and fully grown until harvest over a three year period, with 20 plants/year. Each variety was subjected to four different treatments CN (100% EVTD), EDI (60% EVTD), EDI plus PBZ (EDI+PBZ) and CN plus PBZ (CN+PBZ). EVTD was measured with Pen Men and Monneth equation[22] using variables of the local environment on biweekly basis.

4.2 Plant growth kinetics x

Impact of deficit irrigation (EDI and TDI) with or without PBZ on growth patterns is a key factor in evaluating potential of the five maize varieties. For EDI, growth kinetics were measured for shoot growth rates (ShVd) at 25 and 35 DAS, while root growth patterns were measured for brace roots (BRs), crown roots (CRs) and seminal roots (SRs) at 25 and 35 DAS using 15 DAS values as a reference line. For TDI, only shoot growth kinetics (ShVdt) was measured on every ten days basis commencing from TDI (at 54 DAS) until harvest (104 DAS) with or without PBZ as described[60].

Besides measuring growth kinetics, shoot morphometerics viz. stem height (cm), stem thickness (cm), leaf number (LN), shoot dry weight (ShDW) and root morphometerics viz.

root number (RN), root length (cm), root surface areas (cm^2) were measured for EDI and TDI. While root dry weights (RDW) was measured only for TDI.

4.3 Reproductive traits

Impact of TDI on successful transition of vegetative stage to reproductive stage i.e. 54 DAS to 75 DAS (stage specific for formation of reproductive organs), developmental attributes of male reproductive organs: tassel, male inflorescence included tassel diameter (diaT), length (LeT), dry biomass (DBT), number of male flowers/plant, number of anthers/inflorescence, number of spikelets/flower, spikelet length/flower; for female reproductive organs: silk length and ear number were measured. Cob dry weight (CDW) was measured at the time of harvest. Reproductive effort (RE %) was calculated for tassel and ear formation using standard procedures[61].

4.4 Root plasticity, drought indices and physiological stress markers

Root plasticity indices assess a root response towards a given stressor. Scope of plastic response (SPR), relative trait range (RTR) and response coefficient (RC) for crown roots (CRs), brace roots (BRs) and seminal roots (SRs) were measured in TDI with or without PBZ [62-63]. Drought response indices namely relative drought index (RDI), stress susceptibility index (SSI), tolerance (TOL), mean productivity (MP), geometric mean productivity (GMP), stress tolerance index (STI), yield stability index (YSI), harmonic mean of yield (HM) and yield index (YI)) were determined for TDI to identify best adapted variety (s) as described [64]. Physiological stress indices and antioxidant activities were measured as described elsewhere[23].

4.5 Photosynthetic performance and molecular regulation of root traits

Photosynthetic pigments (chlorophyll *a* and *b*), carotenoids (CAR), leaf area index (LAI), net assimilation rate (NAR) were measured for TDI with or without PBZ [22-23].
Among five varieties, two varieties i.e. DKC-9144-9144 and PG-2475 were selected on the basis of role of root system architecture (RSAch) on growth performance and water use efficiency (WUE) in terms of cob yield and plant height. Selected varieties were subjected to EDI conditions with or without PBZ and photosynthetic parameters (net photosynthesis, P_N), intercellular CO2 (Ci), stomatal conductance (gs) and leaf transpiration rate (E) were measured using LI-6400 XT infrared gas analyzer (Li-Cor, Lincoln, NE, USA)[22-23], starting form 15 DAS, and two time points 25 and 35 DAS.

For quantitative real time polymerase chain reaction (qPCR), total RNA was extracted from root tissues of DKC-9144-9144 and PG-2475 at three time points (15, 25 and 35 DAS) with or without PBZ using Nucleospin RNA plant kit[65] (Macherey-Nagel, Germany). cDNA synthesis and qPCR was performed as described previously[64] on Roche Light Cycler 96 (Roche Diagnostics, Mannheim, Germany). *Zea mays elongation factor* (*ZmEF α1*) was used as a house keeping gene. Three independent biological replicates (n=3) with each biological replicate with three technical replications were performed. Transcript levels of *ZmMel* (*metallothionein-like protein*), *ZmRTCS* (*gene regulating rootless crown and seminal roots*), *ZmRTCL* (*The RTCS-LIKE gene*), *ZmARF34* (*Zea mays Auxin response factor 34*) were performed using primers published elsewhere[53] (Supplementary Table 3). Students t-test was used to evaluate differential gene expression ($P \leq 0.05$; n = 4).

4.6 Structural equation modeling for water use efficiencies and growth performances

We performed structural equation modeling (SEM) to test how changes in RSA, RL and RN affected BR, CR and SR which further affected WUE, SH and ST. SEM is an advanced and robust multivariate statistical method that allows for hypothesis testing of complex path-relation networks[54-55]. AMOS, statistical software was used for the analysis of a moment structures. AMOS provided the overall Chi-square (χ^2) value, together with its degree of freedom and probability value. The AMOS output gave various indices viz. Comparative fit index (CFI ≥ 0.95), Tucker-Lewis Index (TLI ≥ 0.95) and root mean square error of approximation (RMSEA ≤ 0.05) as defined by various researchers, and these indices were in acceptable range hence model fit was strengthened. SEM models considered in our study satisfied above mentioned indices. Further, we have shown the results of significant relationships in Figure 6 of root types and their traits for WUE, SH and ST under different conditions.

4.7 Water budgeting and economic attributes

Amount of irrigation water saved using TDI with or without PBZ and its impact on yield, and farmer's income attributes were measured. WUE/plant height and WUE/cob yield, water productivity (WP, Kg/ET for cob yield), net water savings/plant, approximate water savings/1000 plants and approximate water savings/ha were measured for each variety. % reduction in cob yield and net income generation considering the irrigation water buyers cost, yield loss under TDI, yield gain with or without PBZ, extra yield with usage of water saved from TDI alone or with PBZ. Other associated cost (fertilizers, pesticides, harvesting, transportation and procurement costs) of maize cultivation were approximated to calculate the income attributes of maize crop growers in Indian rupees and in $ USD using minimum support price (MSP of maize fixed by the Govt. of India, 2018-2019).

4.8 Statistical analyses

The experiments were arranged in a randomized factorial design with seven replications in each consecutive year (2017, 2018 and 2019). The data obtained were analyzed by ANOVA and all means were separated at the $p < 0.05$ level using the Duncan test. All calculations and data analyses were performed using the IBM SPSS 20.0 for Windows software package; the values were expressed by means and standard error (SE).

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Author contributions

S.P. conceived and designed the experiments; M.U., H.R.H., S.S., M.S. and M.K. performed the experiments. S.P., D.V., S.B.S. and S.B. performed data analysis, prepared figures and wrote the article.

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Figure legends

Figure graphical Abstract

Life cycle of maize plants (*Zea mays* L.) is sensitive towards soil water availability, in particular establishment of young maize plants (from 0 days after sowing (DAS) to 35 DAS, early deficit irrigation, EDI) and 50 DAS to 65 DAS, a phase showing transition of vegetative to reproductive stage. Maize being a rain fed crop is mainly dependent upon rainwater, thus late arrival of monsoon or shorter spell of monsoon period in Indian sub continent poses water deficit or drought like conditions, consequently affecting the establishment of young plants and successful transition of vegetative to reproductive phase. In current study, early deficit irrigation (EDI) supplied 60% of the evapotranspiration demand (EVTD) commenced with or without paclobutrazol (PBZ) on 15 DAS to 35 DAS (for a period of 20 days) young maize plants mimicked the late arrival of monsoon by a period of 10-15 days. While, terminal deficit irrigation (TDI) supplied 60% of EVTD with or without PBZ at 54 DAS to 104 DAS (for a period of 50 days) plants mimicked shorter spell of monsoon, thereby reducing the soil water availability, affecting successful transition of vegetative to reproductive phase and formation of reproductive structures. Structural equation modeling (SEM) showed improved root traits and their contribution in enhancing water use efficiency resulting in better adaptation of maize under EDI and TDI, more specifically when applied with paclobutrazol. Happy maize plants in terms of improved water use efficiency (WUE) under TDI resulted in more cob yield specifically with paclobutrazol application, leading to enhanced farmers income and economic prosperity.

Figure 1. Deficit irrigation and paclobutrazol alter growth kinetics in maize.

(a) Early deficit irrigation (EDI) imposed on young maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 15 days after sowing (DAS) until 35 DAS for a period of 20 days mimicked late arrival of rainwater spell of monsoon, altered shoot growth kinetics (a), showed EDI impact with or without paclobutrazol (PBZ) on shoot growth patterns (ShVd, cm/10 days interval), such that ShVd 25 days calculated used 15 DAS shoot growth value as base line, while ShVd 35 days calculated used 25 DAS shoot growth value as a base line.

(b) Terminal deficit irrigation (TDI) imposed on maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 54 days after sowing (DAS) until 104 DAS for a period of 50 days mimicked shorter rainwater spell of monsoon, altered shoot growth kinetics measured at a gap of ten days each at 54-64, 64-74, 74-84, and 84-94 , showed impact of TDI with or without paclobutrazol (PBZ) on shoot growth patterns (ShVdt, cm/10 days interval) of maize plants, such that ShVdt 64 days calculated used 54 DAS shoot growth value as base line, ShVdt 74 days calculated used 64 DAS shoot growth value as base line and similar for 84 and 94 DAS ShVdt.

(c-d) Early deficit irrigation (EDI) imposed on young maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 15 days after sowing (DAS) until 35 DAS for a period of 20 days mimicked late arrival of rainwater spell of monsoon, showed impact of EDI with or without paclobutrazol (PBZ) on root growth extension patterns (Vd, cm/10 days interval) of on brace root (BR) and crown root (CR), seminal roots (SR) extension pattern kinetics, such that Vd 35 days of BR, CR was calculated with 25 DAS BR and CR growth value as base line, (d) For SR, Vd was calculated both at 25 DAS and 35 DAS, such that Vd 25 days of SRs calculated used 15 DAS SRs growth value as base line, while SRVd 35 days of SR calculated used 25 DAS SR growth value as a base line. Data presented are means ± standard errors (n = 15, biological replicates). Asterisk symbol (*) indicate significant differences from control in all combinations (Tukey's test, $P \leq 0.05$).

Abbreviations: control irrigation, CN, control+paclobutrazol CN+PBZ, early deficit irrigation, EDI, early deficit irrigation+paclobutrazol, EDI+PBZ, terminal deficit irrigation, TDI, terminal deficit irrigation+paclobutrazol, TDI+PBZ.

Figure 2. Root system of maize plants

(a) Harvested root system of young maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621at 35 days after sowing (DAS) subjected to early deficit irrigation (EDI, 60% of evapotranspiration demand, EVTD) with or without paclobutrazol (PBZ) at 15 DAS until 35 DAS for a period of 20 days mimicked late arrival of rainwater spell of monsoon, and (b) harvested root system of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621subjected to terminal deficit irrigation (TDI, 60% of evapotranspiration demand, EVTD) with or without paclobutrazol (PBZ) at 54 DAS until 104 DAS for a period of 50 days mimicked shorter rainwater spell of monsoon. Scale bars represent 100 mm.

Figure 3. Deficit irrigation and paclobutrazol impacts reproductive attributes of maize plants.

Terminal deficit irrigation (TDI) with or without paclobutrazol (PBZ) imposed on maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 54 days after sowing (DAS) until 104 DAS for a period of 50 DAS, altered reproductive attributes. (a), tassel diameter (diaT, cm), (b) oftassel length (LeT, cm), (c) dry biomass of tassel (DBT), (d) number of male flowers / plant, (e) average number of anthers /flower (anthers/flower), (f) number of spikelets/flower, (g) average spikelet length (cm), (h) silk length (cm) and agronomic trait viz. average cob dry weight (g)/plant at 104 DAS. Data presented are means ± standard errors (n = 15, biological replicates). Asterisk symbol (*) indicate significant differences from control in all combinations (Tukey's test, $P \leq 0.05$), while symbol of # indicate significant difference from TDI irrigation in all combinations (Tukey's test, $P \leq 0.05$).

Abbreviations: control irrigation, CN, control+paclobutrazol CN+PBZ, terminal deficit irrigation, TDI, terminal deficit irrigation+paclobutrazol, TDI+PBZ.

Figure 4. Dry biomass changes in maize in deficit irrigation and paclobutrazol (PBZ) applications.

Terminal deficit irrigation (TDI) with or without paclobutrazol imposed on maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 54 days after sowing (DAS) until 104 DAS for a period of 50 DAS, showed impact on, (a) average brace root dry biomass (BRDB, g), (b) the average crown root dry biomass (CRDB, g), (c) average lateral root dry biomass (LRDB, g), (d) average seminal root dry biomass (SRDB, g),

(e) the shoot dry biomass, (f) total root dry biomass and (g) the root/shoot ratio. Data presented are means ± standard errors (*n* = 15, biological replicates). Asterisk symbol (*) indicate significant differences from control in all combinations, while # indicate significant difference from TDI only (Tukey's test, $P \leq 0.05$).

Abbreviations: control irrigation, CN, control+paclobutrazol CN+PBZ, terminal deficit irrigation, TDI, terminal deficit irrigation+paclobutrazol, TDI+PBZ

Figure 5. Deficit irrigation and paclobutrazol (PBZ) impacts photosynthetic efficiencies and molecular regulation of root growth in maize.

Early deficit irrigation (EDI) with or without paclobutrazol (PBZ) imposed on the young maize plants of DKC-9144 and PG-2475 at 15 days after sowing (DAS) until 35 DAS for a period of 20 DAS altered (a) net photosynthesis (P_N, µmol CO2 m^{-2} S^{-1}), (b) intercellular CO2 (Ci, µmol CO2 mol^{-1} air), (c) stomatal conductance (g^s, mol H_2O m^{-1} S^{-1}) (d) transpiration rate (E, mm H_2O m^{-2} S^{-1}) (e) sugar content (mg/g dry weight), (f) relative expression of *ZmMel* (*metallothionein-like protein*), *ZmRTCS* (*gene regulating rootless crown and seminal roots*), *ZmRTCL* (*The RTCS-LIKE gene*), *ZmARF34* (*Zea mays Auxin response factor 34*) of DKC-9144 relative to PG-2475 (base expression) at 15 DAS before the commencement of EDI and PBZ application, (g-h) relative expression of *ZmMEL, ZmRTCS*, *ZmRTC* and, *ZmARF34* of DKC-9144 at 25 DAS after the commencement of EDI and PBZ in DKC-9144 relative to control (h) and of PG-2475 relative to control, (i-j) relative expression of *ZmMEL*, *ZmRTCS*, *ZmRTC* and, *ZmARF34* of DKC-9144 at 35 DAS after the commencement of EDI and paclobutrazol application in DKC-9144 (i) and of PG-2475 (j). Data presented are means ± standard errors (*n* = 15, biological replicates) for Figs a-e. Letters (a & b) indicate significant differences from control and early deficit irrigation respectively (Tukey's test, $P \leq 0.05$), Color code indicates differences across the row and column (for Fig. e). Data presented are means ± standard errors (*n* = 3, biological replicates) for Figs. f-j.

Figure 6. Structural equation modeling (SEM) of maize root traits and their contribution in growth performance under early deficit irrigation (EDI).

Structural equation modeling (SEM) of maize root traits subjected to early deficit irrigation (EDI) and terminal deficit irrigation (TDI) showed contribution of selected root factors towards improving water use efficiency (WUE-cob dry weight), shoot height (SH) and stem thickness (ST).

(a-b) Under control irrigation regime (CN), SEM model showed contribution of different root types such as crown roots (CRs), brace roots (BRs) and seminal roots (SRs) and their different traits such root number (RN), root length (RL) and root surface area (RSA) towards WUE, SH and ST in DKC-9144 (a) and PG-2475 (b).

(c-d) Under EDI (60% of evapotranspiration demand), SEM model showed contribution of different root types such as CRs, BRs and SRs and their different traits such RN, RL and RSA towards WUE, SH and ST in DKC-9144 (c) and PG-2475 (d).

(e-f) Under application of paclobutrazol (PBZ, 60 ppm) in EDI (EDI, 60% of evapotranspiration demand), SEM model showed contribution of different root types such as CRs, BRs and SRs and their different traits such RN, RL and RSA towards WUE, SH and ST in DKC-9144 (e) and PG-2475 (f).

(g-h) Under control irrigation regime (CN), SEM model showed contribution of different root types such as crown roots (CRs), brace roots (BRs) and seminal roots (SRs) and their different traits such root number (RN), root length (RL) and root surface area (RSA) towards WUE, SH and ST in DKC-9144 (a) and PG-2475 (b).

(i-j) Under TDI (60% of evapotranspiration demand), SEM model showed contribution of different root types such as CRs, BRs and SRs and their different traits such RN, RL and RSA towards WUE, SH and ST in DKC-9144 (c) and PG-2475 (d).

(k-l) Under application of paclobutrazol (PBZ, 60 ppm) in TDI (TDI, 60% of evapotranspiration demand), SEM model showed contribution of different root types such as CRs, BRs and SRs and their different traits such RN, RL and RSA towards WUE, SH and ST in DKC-9144 (e) and PG-2475 (f).

Blue, black and red colored lines represents BRs, CRs and SRs, contributions of these root traits i.e. RN, RL and RSA for WUE, SH and ST are given in scores placed over respective colored lines merging into WUE, SH and ST.

Figure 7. Impact analysis of terminal deficit irrigation (TDI) and paclobutrazol (PBZ) on water budgeting and economic attributes of maize cultivation.

Maize plants grew under TDI with or without PBZ commenced at 54 days after sowing (DAS) until harvest at 104 DAS for DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621. Values represent mean ± S.E. of 15 individual plants (n = 15) grown over a period of three years (2017, 2018 and 2019) for each treatmentt type i.e. control irrigation (CN, 100% evapotranspiration demand, EVTD), terminal deficit irrigation (TDI, 60% of EVTD) and TDI plus PBZ (60 ppm) and CN plus PBZ.

(a) Water savings in liter/plant

(b) Approximate water savings in liter/1000 plants

(c) Approximate water savings in liter/hectare

(d) % reduction in cob yield/plants

(e) Approximate income generated in minimum support price in Indian rupees fixed at 1700 MSP in terms of yield kg/ha in TDIwith or without PBZ and amount of water saved used with TDI (TDI sav) and with TDI plus PBZ (TDI + PBZ sav). Extra amount of water saved TDI sav and TDI+PBZ sav projected to use for extra cultivation of maize crop in extra arable land and additional yield produced and MSP/ha.

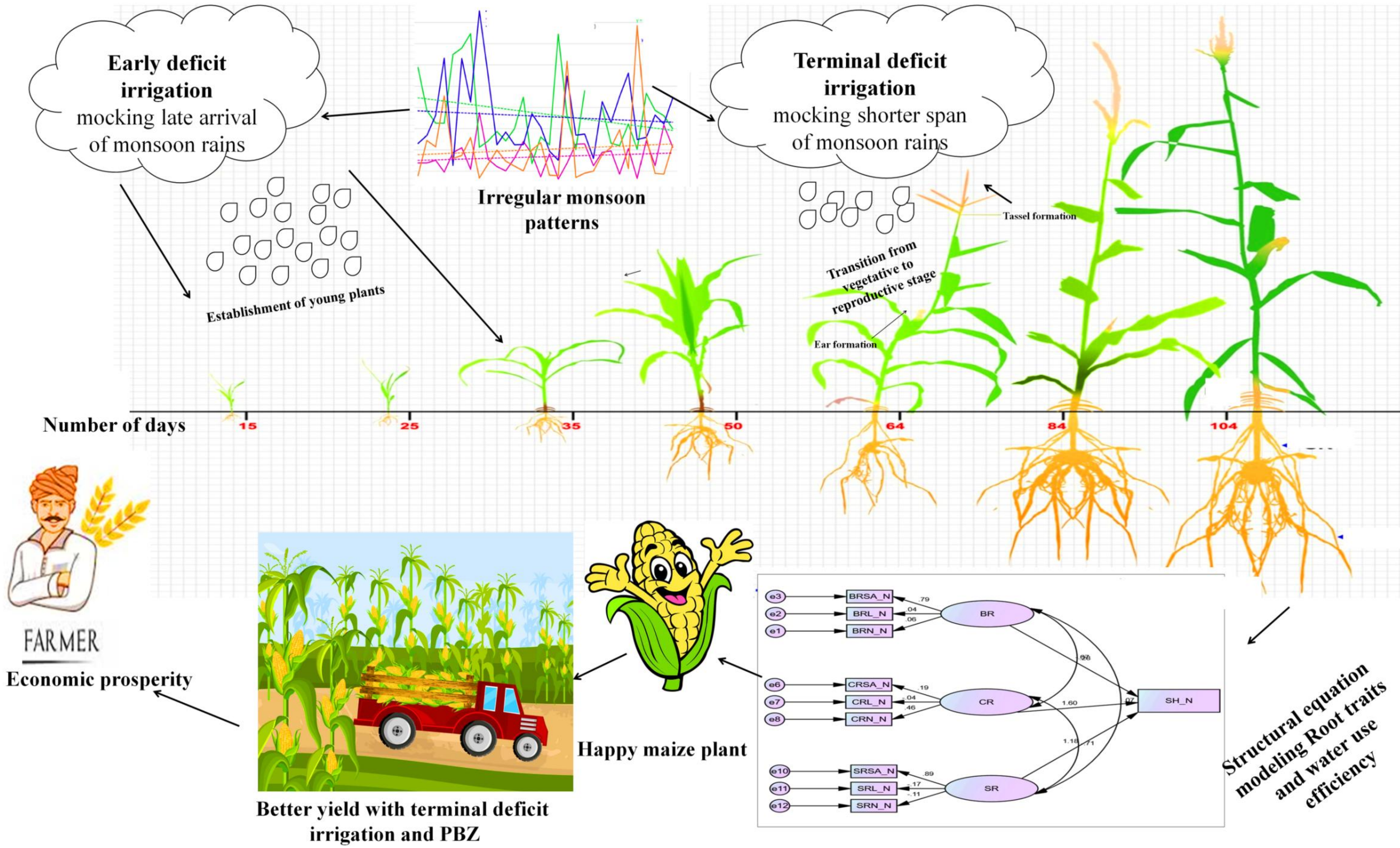

Figure graphical Abstract.

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Life cycle of maize plants (*Zea mays* L.) is sensitive towards soil water availability, in particular establishment of young maize plants (from 0 days after sowing (DAS) to 35 DAS, early deficit irrigation, EDI) and 50 DAS to 65 DAS, a phase showing transition of vegetative to reproductive stage. Maize being a rain fed crop is mainly dependent upon rainwater, thus late arrival of monsoon or shorter spell of monsoon period in Indian sub continent poses water deficit or drought like conditions, consequently affecting the establishment of young plants and successful transition of vegetative to reproductive phase. In current study, early deficit irrigation (EDI) supplied 60% of the evapotranspiration demand (EVTD) commenced with or without paclobutrazol (PBZ) on 15 DAS to 35 DAS (for a period of 20 days) young maize plants mimicked the late arrival of monsoon by a period of 10-15 days. While, terminal deficit irrigation (TDI) supplied 60% of EVTD with or without PBZ at 54 DAS to 104 DAS (for a period of 50 days) plants mimicked shorter spell of monsoon, thereby reducing the soil water availability, affecting successful transition of vegetative to reproductive phase and formation of reproductive structures. Structural equation modeling (SEM) showed improved root traits and their contribution in enhancing water use efficiency resulting in better adaptation of maize under EDI and TDI, more specifically when applied with paclobutrazol. Happy maize plants in terms of improved water use efficiency (WUE) under TDI resulted in more cob yield specifically with paclobutrazol application, leading to enhanced farmers income and economic prosperity.

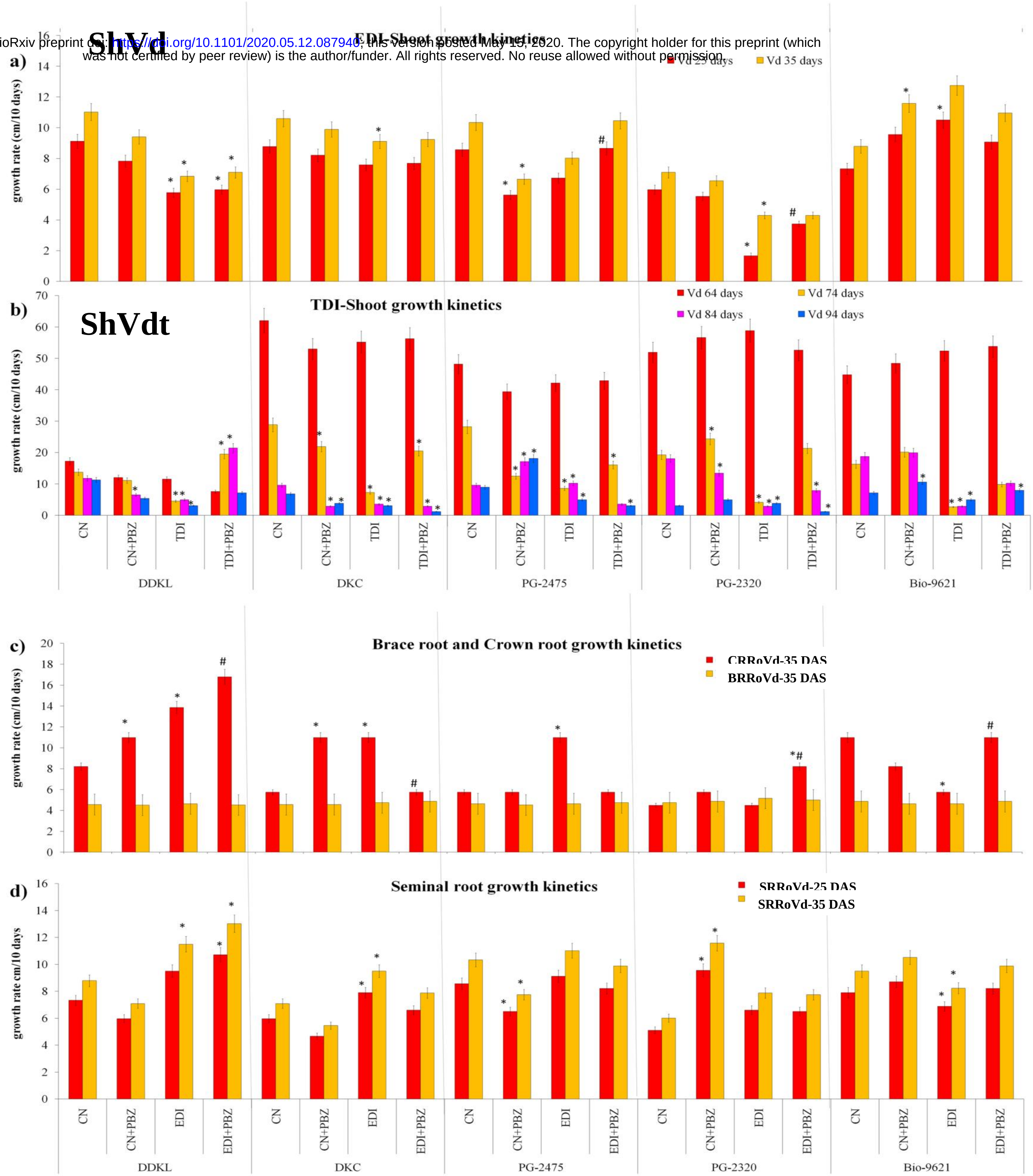
a)
ShVd
EDI-Shoot growth kinetics
Vd 25 days
Vd 35 days
growth rate (cm/10 days)
b)
ShVdt
TDI-Shoot growth kinetics
Vd 64 days
Vd 74 days
Vd 84 days
Vd 94 days
growth rate (cm/10 days)
CN
CN+PBZ
TDI
TDI+PBZ
DDKL
DKC
PG-2475
PG-2320
Bio-9621
c)
Brace root and Crown root growth kinetics
CRRoVd-35 DAS
BRRoVd-35 DAS
growth rate (cm/10 days)
d)
Seminal root growth kinetics
SRRoVd-25 DAS
SRRoVd-35 DAS
growth rate cm/10 days
CN
CN+PBZ
EDI
EDI+PBZ
DDKL
DKC
PG-2475
PG-2320
Bio-9621

Figure 1

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(b) Terminal deficit irrigation (TDI) imposed on maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 54 days after sowing (DAS) until 104 DAS for a period of 50 days mimicked shorter rainwater spell of monsoon, altered shoot growth kinetics measured at a gap of ten days each at 54-64, 64-74, 74-84, and 84-94 , showed impact of TDI with or without paclobutrazol (PBZ) on shoot growth patterns (ShVdt, cm/10 days interval) of maize plants, such that ShVdt 64 days calculated used 54 DAS shoot growth value as base line, ShVdt 74 days calculated used 64 DAS shoot growth value as base line and similar for 84 and 94 DAS ShVdt.

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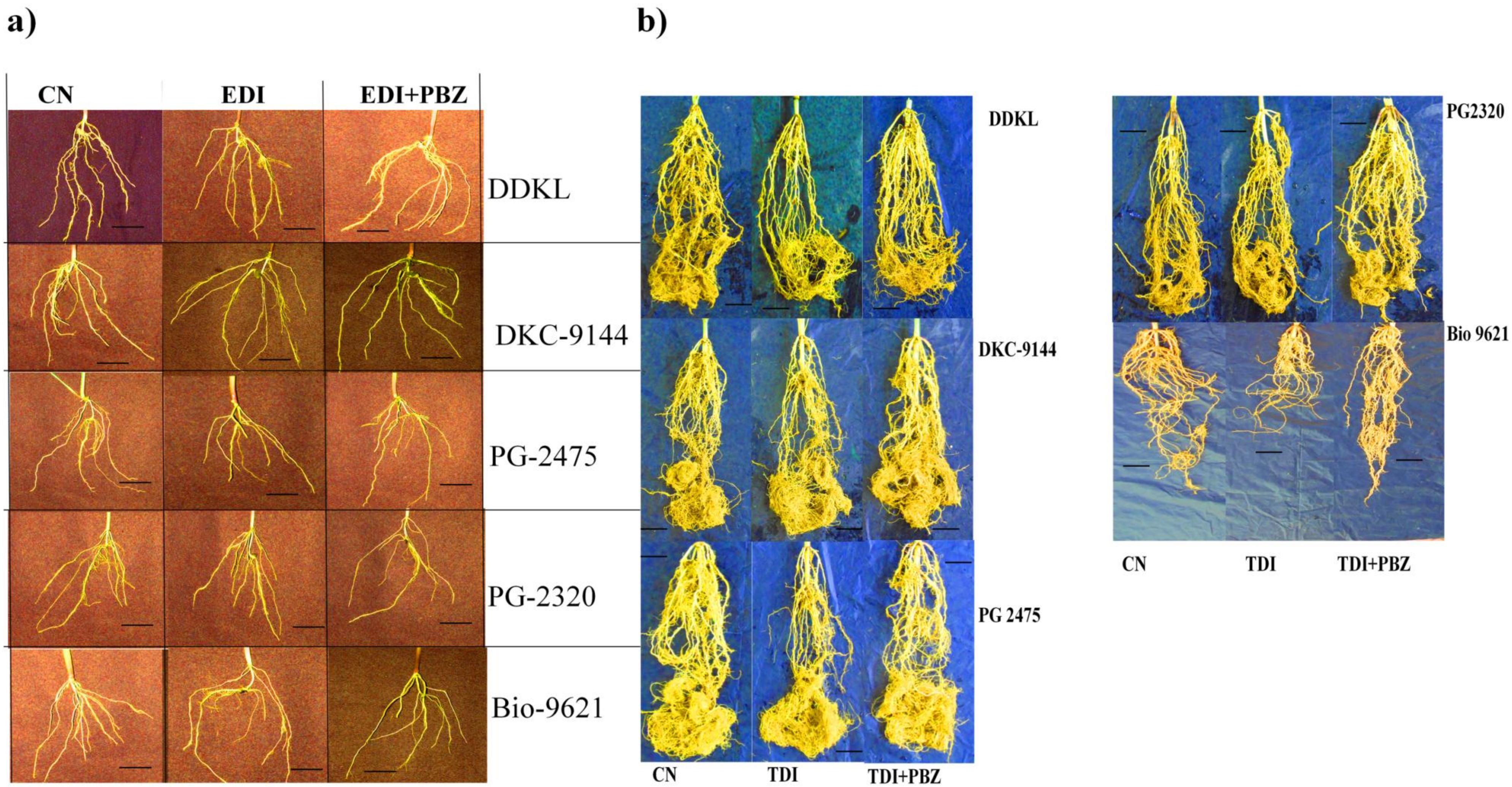
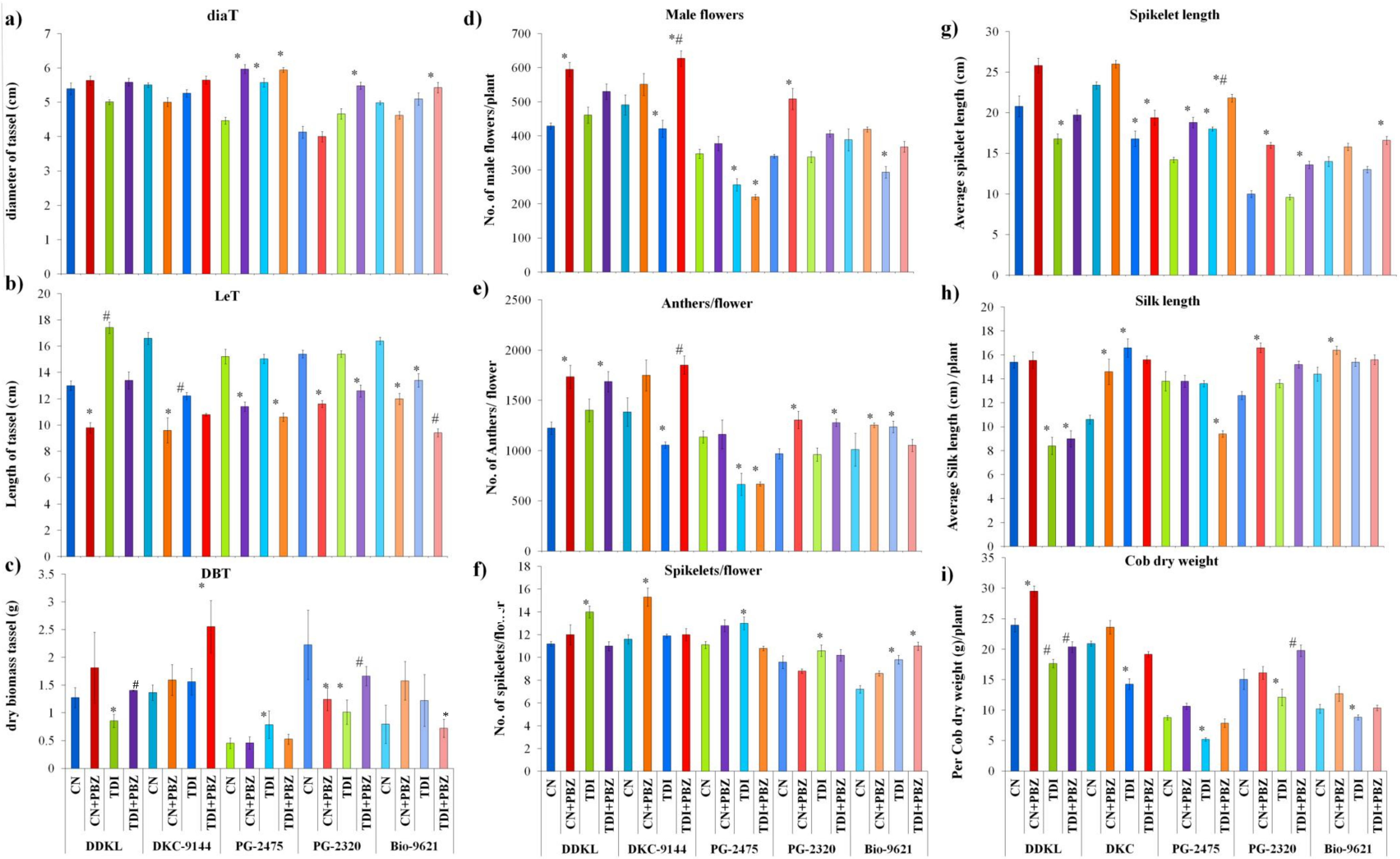


Figure 2. Root system of maize plants

(a) Harvested root system of young maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 35 days after sowing (DAS) subjected to early deficit irrigation (EDI, 60% of evapotranspiration demand, EVTD) with or without paclobutrazol (PBZ) at 15 DAS until 35 DAS for a period of 20 days mimicked late arrival of rainwater spell of monsoon, and (b) harvested root system of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 104 DAS subjected to terminal deficit irrigation (TDI, 60% of evapotranspiration demand, EVTD) with or without paclobutrazol (PBZ) at 54 DAS until 104 DAS for a period of 50 days mimicked shorter rainwater spell of monsoon. Scale bars represent 100 mm.



a)
diaT
diameter of tassel (cm)
b)
LeT
Length of tassel (cm)
c)
DBT
dry biomass tassel (g)
d)
Male flowers
No. of male flowers/plant
e)
Anthers/flower
No. of Anthers/ flower
f)
Spikelets/flower
No. of spikelets/flo..er
g)
Spikelet length
Average spikelet length (cm)
h)
Silk length
Average Silk length (cm)/plant
i)
Cob dry weight
Per Cob dry weight (g)/plant
CN
CN+PBZ
TDI
TDI+PBZ
DDKL
DKC-9144
DKC
PG-2475
PG-2320
Bio-9621

Figure 3

Figure 3. Deficit irrigation and paclobutrazol impacts reproductive attributes of maize plants.

Terminal deficit irrigation (TDI) with or without paclobutrazol (PBZ) imposed on maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 54 days after sowing (DAS) until 104 DAS for a period of 50 DAS, altered reproductive attributes. (a), tassel diameter (diaT, cm), (b) oftassel length (LeT, cm), (c) dry biomass of tassel (DBT), (d) number of male flowers / plant, (e) average number of anthers /flower (anthers/flower), (f) number of spikelets/flower, (g) average spikelet length (cm), (h) silk length (cm) and agronomic trait viz. average cob dry weight (g)/plant at 104 DAS. Data presented are means ± standard errors (n = 15, biological replicates). Asterisk symbol (*) indicate significant differences from control in all combinations (Tukey's test, $P \leq 0.05$), while symbol of # indicate significant difference from TDI irrigation in all combinations (Tukey's test, $P \leq 0.05$).

Abbreviations: control irrigation, CN, control+paclobutrazol CN+PBZ, terminal deficit irrigation, TDI, terminal deficit irrigation+paclobutrazol, TDI+PBZ.

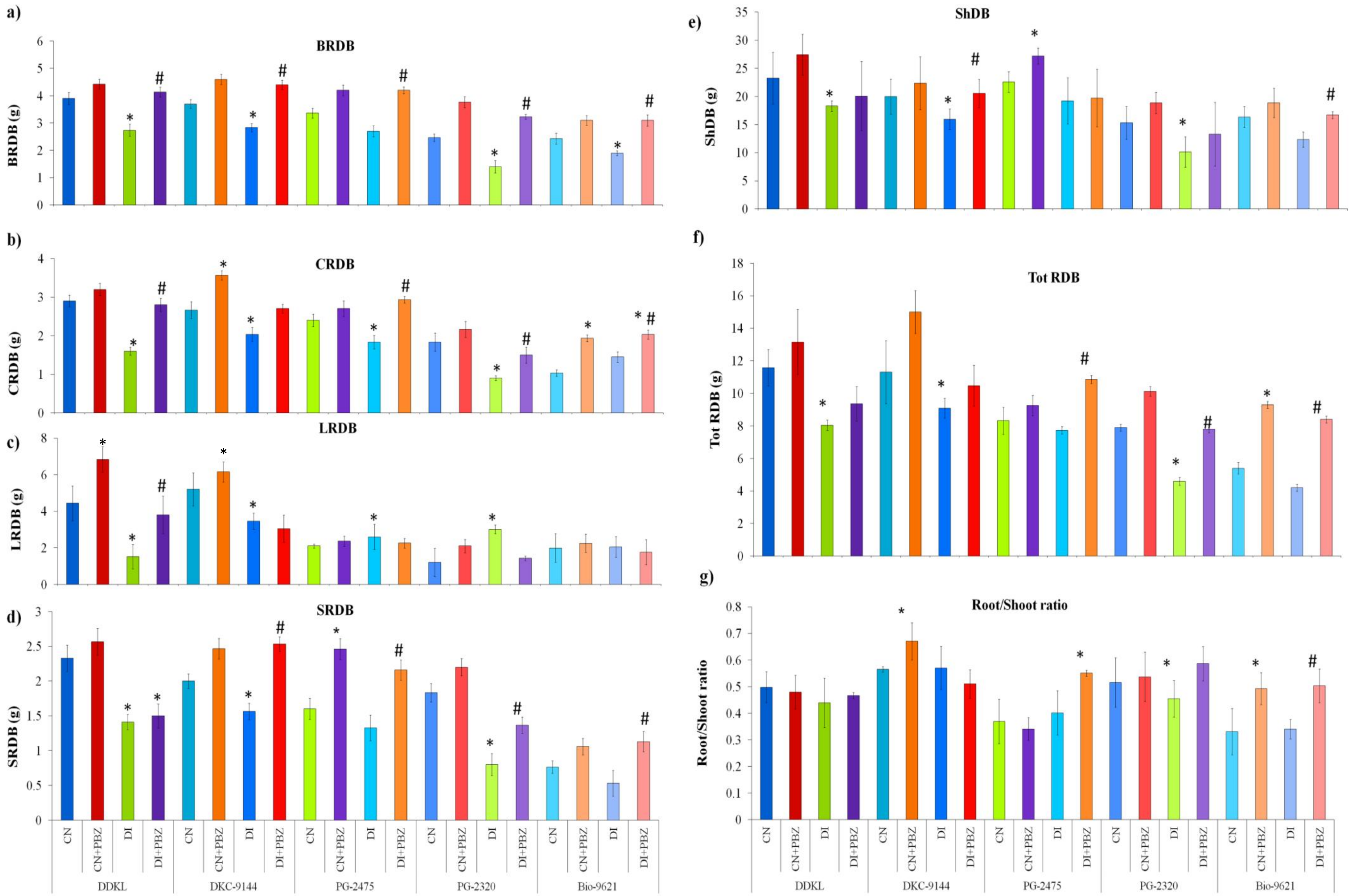

a)
BRDB
BRDB (g)
b)
CRDB
CRDB (g)
c)
LRDB
LRDB (g)
d)
SRDB
SRDB (g)
e)
ShDB
ShDB (g)
f)
Tot RDB
Tot RDB (g)
g)
Root/Shoot ratio
Root/Shoot ratio
CN
CN+PBZ
DI
DI+PBZ
DDKL
DKC-9144
PG-2475
PG-2320
Bio-9621

Figure 4

Figure 4. Dry biomass changes in maize in deficit irrigation and paclobutrazol (PBZ) applications.

Terminal deficit irrigation (TDI) with or without paclobutrazol imposed on maize plants of DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 at 54 days after sowing (DAS) until 104 DAS for a period of 50 DAS, showed impact on, (a) average brace root dry biomass (BRDB, g), (b) the average crown root dry biomass (CRDB, g), (c) average lateral root dry biomass (LRDB, g), (d) average seminal root dry biomass (SRDB, g), (e) the shoot dry biomass, (f) total root dry biomass and (g) the root/shoot ratio. Data presented are means ± standard errors (n = 15, biological replicates). Asterisk symbol (*) indicate significant differences from control in all combinations, while # indicate significant difference from TDI only (Tukey's test, $P \leq 0.05$).

Abbreviations: control irrigation, CN, control+paclobutrazol CN+PBZ, terminal deficit irrigation, TDI, terminal deficit irrigation+paclobutrazol, TDI+PBZ

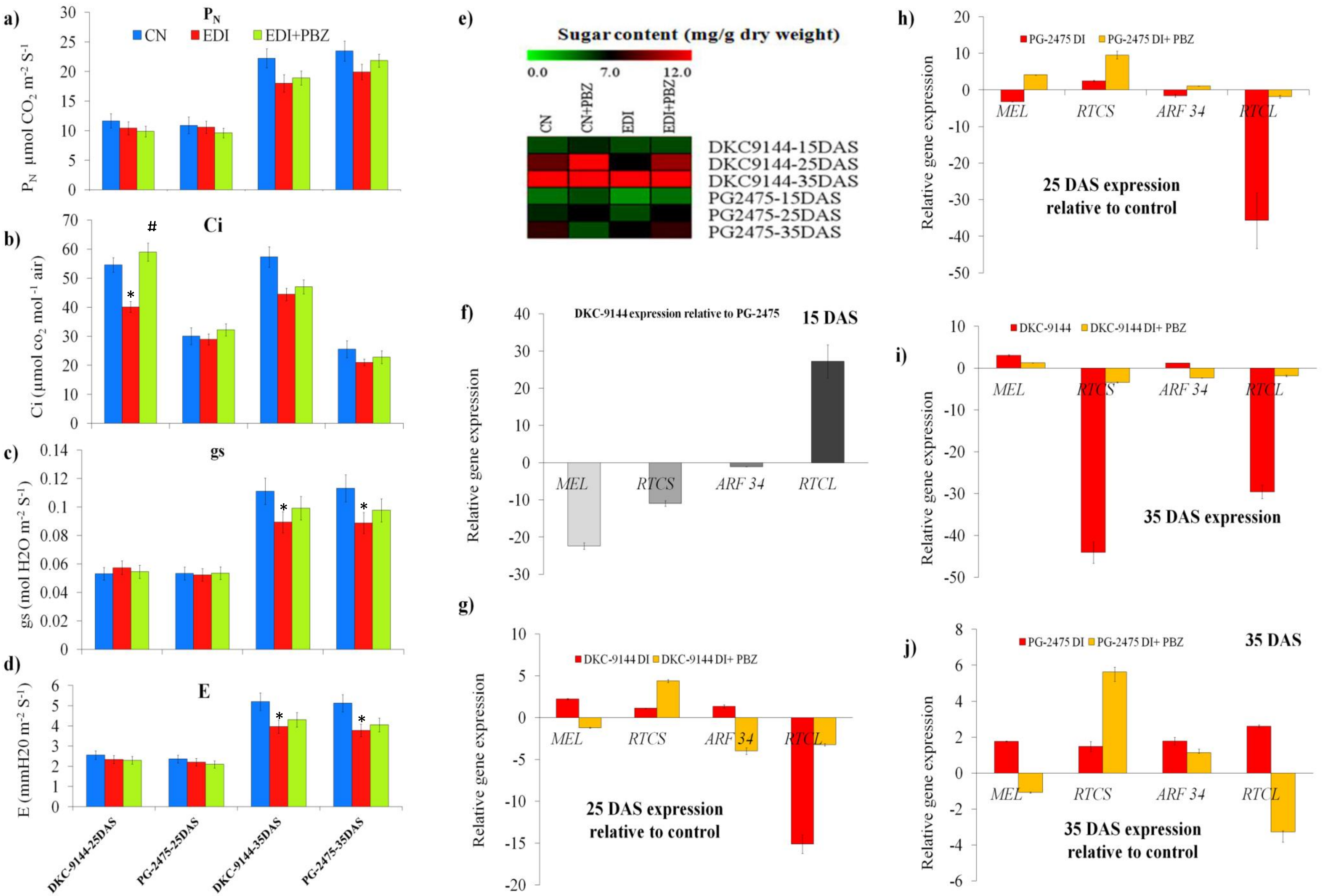

a)
P_N
CN
EDI
EDI+PBZ
P_N µmol CO_2 m^{-2} S^{-1}
b)
Ci
Ci (µmol co2 mol-1 air)
c)
gs
gs (mol H2O m-2 S-1)
d)
E
E (mmH20 m-2 S-1)
DKC-9144-25DAS
PG-2475-25DAS
DKC-9144-35DAS
PG-2475-35DAS
e)
Sugar content (mg/g dry weight)
0.0
7.0
12.0
CN
CN+PBZ
EDI
EDI+PBZ
DKC9144-15DAS
DKC9144-25DAS
DKC9144-35DAS
PG2475-15DAS
PG2475-25DAS
PG2475-35DAS
f)
DKC-9144 expression relative to PG-2475
15 DAS
Relative gene expression
MEL
RTCS
ARF 34
RTCL
g)
DKC-9144 DI
DKC-9144 DI+ PBZ
25 DAS expression relative to control
h)
PG-2475 DI
PG-2475 DI+ PBZ
25 DAS expression relative to control
i)
DKC-9144
DKC-9144 DI+ PBZ
35 DAS expression
j)
PG-2475 DI
PG-2475 DI+ PBZ
35 DAS
35 DAS expression relative to control

Figure 5

Figure 5. Deficit irrigation and paclobutrazol (PBZ) impacts photosynthetic efficiencies and molecular regulation of root growth in maize.

Early deficit irrigation (EDI) with or without paclobutrazol (PBZ) imposed on the young maize plants of DKC-9144 and PG-2475 at 15 days after sowing (DAS) until 35 DAS for a period of 20 DAS altered (a) net photosynthesis (P_N, µmol CO2 m^{-2} S^{-1}), (b) intercellular CO2 (Ci, µmol CO2 mol^{-1} air), (c) stomatal conductance (g^s, mol H_2O m^{-1} S^{-1}) (d) transpiration rate (E, mm H_2O m^{-2} S^{-1}) (e) sugar content (mg/g dry weight), (f) relative expression of *ZmMel* (*metallothionein-like protein*), *ZmRTCS* (*gene regulating rootless crown and seminal roots*), *ZmRTCL* (*The RTCS-LIKE gene*), *ZmARF34* (*Zea mays Auxin response factor 34*) of DKC-9144 relative to PG-2475 (base expression) at 15 DAS before the commencement of EDI and PBZ application, (g-h) relative expression of *ZmMEL, ZmRTCS, ZmRTC* and, *ZmARF34* of DKC-9144 at 25 DAS after the commencement of EDI and PBZ in DKC-9144 relative to control (h) and of PG-2475 relative to control, (i-j) relative expression of *ZmMEL, ZmRTCS, ZmRTC* and, *ZmARF34* of DKC-9144 at 35 DAS after the commencement of EDI and paclobutrazol application in DKC-9144 (i) and of PG-2475 (j). Data presented are means ± standard errors (n = 15, biological replicates) for Figs a-e. Letters (a & b) indicate significant differences from control and early deficit irrigation respectively (Tukey's test, $P \leq 0.05$), Color code indicates differences across the row and column (for Fig. e). Data presented are means ± standard errors (n = 3, biological replicates) for Figs. f-j.

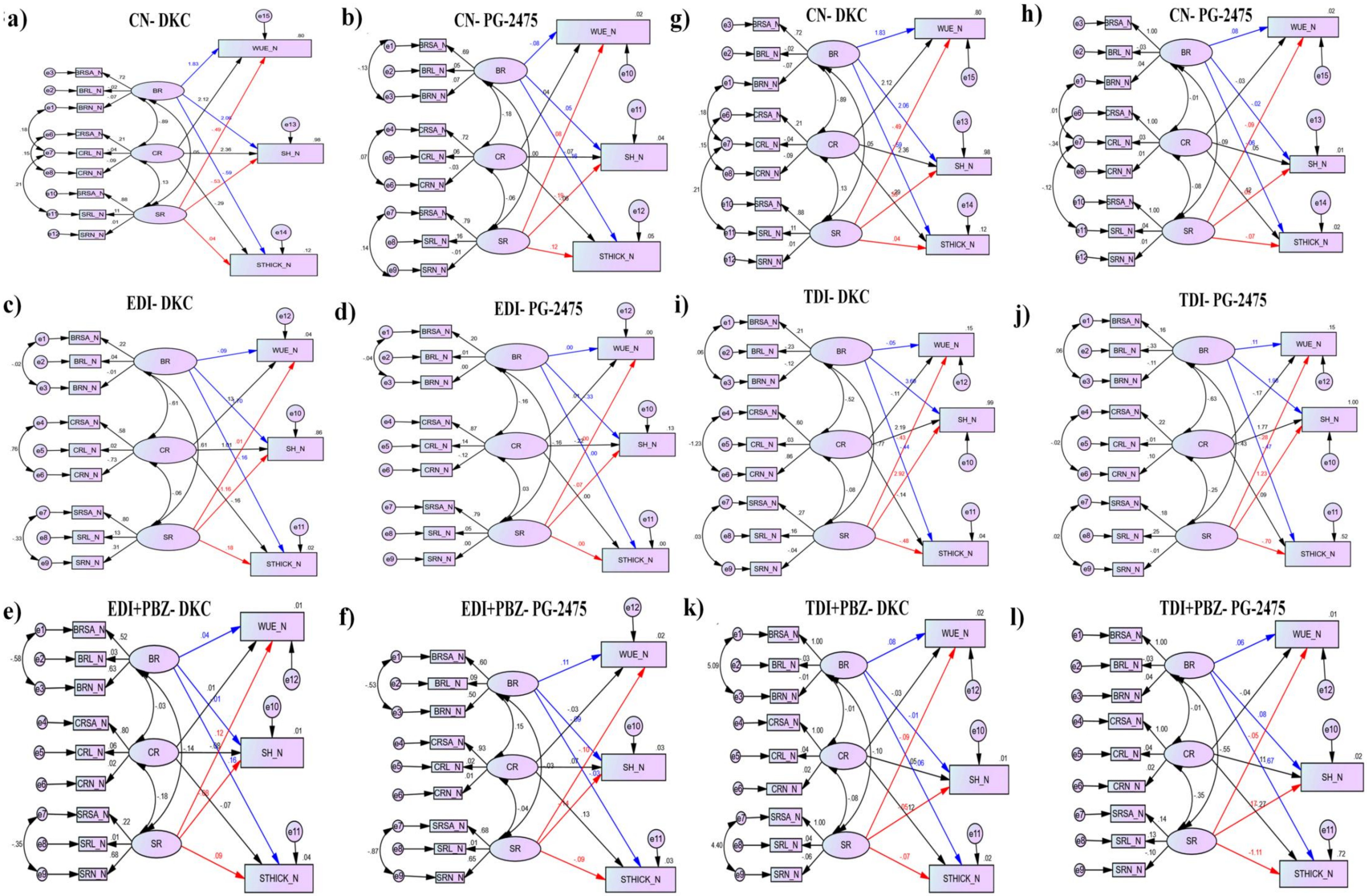

a) CN- DKC
b) CN- PG-2475
g) CN- DKC
h) CN- PG-2475
c) EDI- DKC
d) EDI- PG-2475
i) TDI- DKC
j) TDI- PG-2475
e) EDI+PBZ- DKC
f) EDI+PBZ- PG-2475
k) TDI+PBZ- DKC
l) TDI+PBZ- PG-2475

Figure 6

Figure 6. Structural equation modeling of maize root traits and their contribution in water use efficiency.

Structural equation modeling (SEM) carried on the root traits of maize plants subjected to early deficit irrigation (EDI) and terminal deficit irrigation (TDI) showed contribution of selected root factors towards improving water use efficiency (WUE-cob dry weight), shoot height (SH) and stem thickness (ST).

(a-b) Under control irrigation regime (CN), SEM model showed contribution of different root types such as crown roots (CRs), brace roots (BRs) and seminal roots (SRs) and their different traits such root number (RN), root length (RL) and root surface area (RSA) towards WUE, SH and ST in DKC-9144 (a) and PG-2475 (b).

(c-d) Under EDI (60% of evapotranspiration demand), SEM model showed contribution of different root types such as CRs, BRs and SRs and their different traits such RN, RL and RSA towards WUE, SH and ST in DKC-9144 (c) and PG-2475 (d).

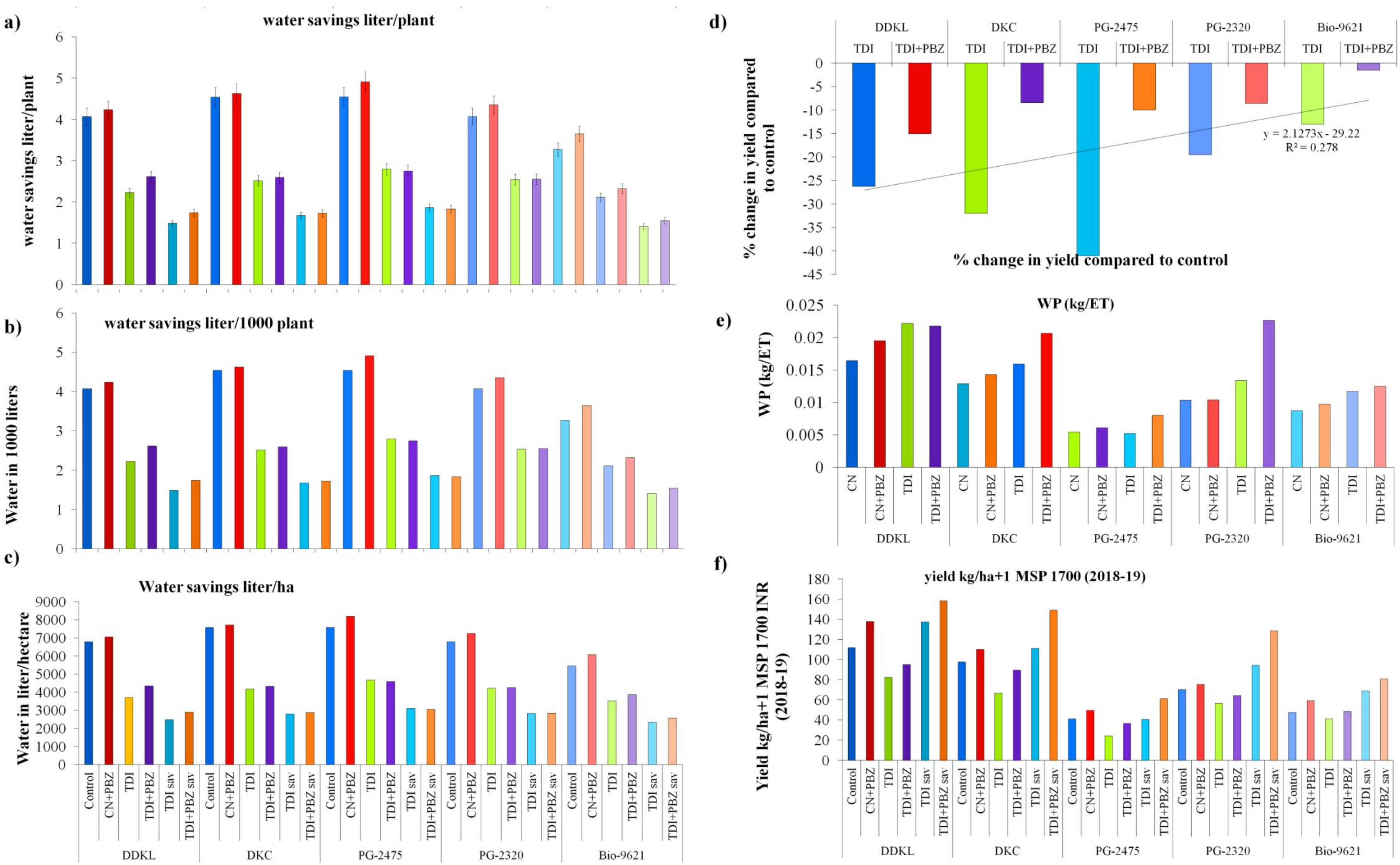
(e-f) Under application of paclobutrazol (PBZ, 60 ppm) in EDI (EDI, 60% of evapotranspiration demand), SEM model showed contribution of different root types such as CRs, BRs and SRs and their different traits such RN, RL and RSA towards WUE, SH and ST in DKC-9144 (e) and PG-2475 (f).

(g-h) Under control irrigation regime (CN), SEM model showed contribution of different root types such as crown roots (CRs), brace roots (BRs) and seminal roots (SRs) and their different traits such root number (RN), root length (RL) and root surface area (RSA) towards WUE, SH and ST in DKC-9144 (a) and PG-2475 (b).

(i-j) Under TDI (60% of evapotranspiration demand), SEM model showed contribution of different root types such as CRs, BRs and SRs and their different traits such RN, RL and RSA towards WUE, SH and ST in DKC-9144 (c) and PG-2475 (d).

(k-l) Under application of paclobutrazol (PBZ, 60 ppm) in TDI (TDI, 60% of evapotranspiration demand), SEM model showed contribution of different root types such as CRs, BRs and SRs and their different traits such RN, RL and RSA towards WUE, SH and ST in DKC-9144 (e) and PG-2475 (f).

Blue, black and red colored lines represents BRs, CRs and SRs, contributions of these root traits i.e. RN, RL and RSA for WUE, SH and ST are given in scores placed over respective colored lines merging into WUE, SH and ST.



a)
water savings liter/plant
water savings liter/plant
b)
water savings liter/1000 plant
Water in 1000 liters
c)
Water savings liter/ha
Water in liter/hectare
Control
CN+PBZ
TDI
TDI+PBZ
TDI sav
TDI+PBZ sav
DDKL
DKC
PG-2475
PG-2320
Bio-9621
d)
% change in yield compared to control
y = 2.1273x - 29.22
R² = 0.278
% change in yield compared to control
e)
WP (kg/ET)
WP (kg/ET)
CN
CN+PBZ
TDI
TDI+PBZ
f)
yield kg/ha+1 MSP 1700 (2018-19)
Yield kg/ha+1 MSP 1700 INR (2018-19)

Figure 7

Figure 7. Impact analysis of terminal deficit irrigation (TDI) and paclobutrazol (PBZ) on water budgeting and economic attributes of maize cultivation.

Maize plants grew under TDI with or without PBZ commenced at 54 days after sowing (DAS) until harvest at 104 DAS for DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621. Values represent mean ± S.E. of 15 individual plants (n = 15) grown over a period of three years (2017, 2018 and 2019) for each treatmentt type i.e. control irrigation (CN, 100% evapotranspiration demand, EVTD), terminal deficit irrigation (TDI, 60% of EVTD) and TDI plus PBZ (60 ppm) and CN plus PBZ.

(a) Water savings in liter/plant

(b) Approximate water savings in liter/1000 plants

(c) Approximate water savings in liter/hectare

(d) % reduction in cob yield/plants

(e) Approximate income generated in minimum support price in Indian rupees fixed at 1700 MSP in terms of yield kg/ha in TDIwith or without PBZ and amount of water saved used with TDI (TDI sav) and with TDI plus PBZ (TDI + PBZ sav). Extra amount of water saved TDI sav and TDI+PBZ sav projected to use for extra cultivation of maize crop in extra arable land and additional yield produced and MSP/ha.

Table 1. Effect of terminal deficit irrigation with or without paclobutrazol on lateral roots number (LRN), reproductive effort (RE%) for tassel formation (RE tassel %) and RE ear formation (RE ear %), leaf area index (LAI) and net assimilation rate (NAR g m^{-2} leaf $area^{-1}$ °C d^{-1}) rate of DDKL, DKC-9144, PG2475, PG2320 and Bio-9621 maize varieties subjected to control irrigation (100% evapotranspiration demand, EVTD), terminal deficit irrigation (TDI, 60% EVTD) with or without paclobutrazol (60 ppm). Values indicate mean ± S.E, where number of biological replicates (n = 15). Different letters (a, b, & c) in a column indicate significant differences from each other.

		LRN	RE tassel %	RE ear%	LAI	NAR (g m^{-2} leaf $area^{-1}$ °C d^{-1})
DDKL	CN	345±14	1	1	368±18	0.338±0.034
	CN+PBZ	381±12	1.182	1.036	418±23b	0.326±0.017
	TDI	727±18a	0.883	1.011	329±17	0.397±0.016a
	TDI+PBZ	352±16	1.441a	1.005	340±13	0.394±0.013
DKC-9144	CN	723±29	1	1	400±26	0.334±0.019
	CN+PBZ	455±8	0.991	0.978	461±8b	0.298±0.004
	TDI	1136±49a	1.444a	0.951	339±17a	0.361±0.008a
	TDI+PBZ	456±34	1.336	0.947	366±11	0.386±0.014
PG-2475	CN	427±24	1	1	393±24	0.344±0.020
	CN+PBZ	245±19a	0.849	1.015	443±8b	0.307±0.004
	TDI	479±21	2.077a	0.772a	364±8	0.362±0.007
	TDI+PBZ	435±27	0.546b	1.421b	380±16	0.351±0.013
PG-2320	CN	218±14	1	1	350±12	0.375±0.011
	CN+PBZ	130±8a	0.489a	0.934	387±9	0.345±0.007
	TDI	759±29b	0.663	1.164	298±13a	0.430±0.017a
	TDI+PBZ	1187±47c	1.073	1.068	328±9	0.395±0.009
Bio-9621	CN	518±27	1	1	241±12	0.515±0.025
	CN+PBZ	279±29a	1.345	1.228a	275±11	0.460±0.017
	TDI	568±25	1.892a	1.065	238±12	0.523±0.007
	TDI+PBZ	457±21	0.378b	1.136	249±15	0.535±0.024

Table 2. Effect of terminal deficit irrigation with or without paclobutrazol on the root plasticity indices (scope of plastic response, SPR), relative trait range (RTR) and response coefficient (RC) of crown roots, brace roots and seminal roots of DDKL, DKC-9144, PG2475, PG2320 and Bio-9621.

TDI/TDI+PBZ	**Scope of Plastic Response**	**Relative Trait Range**	**Response Coefficient**
Crown Root			
DDKL	0	0	1
DKC	**5**	**0.16**	**1.2**
PG2475	4	0.12	0.9
PG2320	2	0.08	1.08
BIO9621	2	0.09	1.1
TDI/TDI+PBZ	**Scope of Plastic Response**	**Relative Trait Range**	**Response Coefficient**
Brace Root			
DDKL	2	0.083	1.09
DKC	**3**	**0.107**	**1.12**
PG2475	3	0.115	1.13
PG2320	1	0.037	1.03
BIO9621	3	0.111	1.12
TDI/TDI+PBZ	**Scope of Plastic Response**	**Relative Trait Range**	**Response Coefficient**
Seminal Root			
DDKL	1	0.043	1.045
DKC	**1**	**0.045**	**1.047**
PG2475	8	0.266	1.36
PG2320	3	0.107	1.12
BIO9621	7	0.318	1.46

Table 3. Behavior of drought related indices viz. stress susceptibility index (SSI), tolerance (TOL), mean productivity (MP), geometric mean productivity (GMP), Stress tolerance index (STI), yield stability index (YSI), yield index (YI) and harmonic mean (HM) of five maize varieties i.e. DDKL, DKC-9144, PG-2475, PG-2320 and Bio-9621 subjected to control irrigation (100% evapotranspiration demand, EVTD), terminal deficit irrigation (TDI, 60% EVTD) with or without paclobutrazol (PBZ, 60 ppm). Values indicate mean ± S.E, where number of biological replicates (*n* = 15). Values without asterisk indicate ratio of cob yield under TDI over control, while asterisk symbol (*) indicate ratio of paclobutrazol plus TDI over TDI. Letter *a* row wise indicate significant difference between values of TDI vs PBZ plus TDI.

	SSI	SSI*	TOL	TOL*	MP	MP*	GMP	GMP*	STI	STI*	YSI	YSI*	YI	YI*	HM	HM*
DDKL	1.007	0.362a	5.289	2.51a	20.09	18.70	19.91	18.66	1.67	2.49a	0.76	1.14a	1.134	1.841a	19.74	18.61
DKC-9144	1.073	0.407a	5.03	2.47a	17.78	16.50	17.60	16.45	1.311	1.93a	0.75	1.161a	0.993	1.521a	17.42	16.41
PG-2475	1.540	1.854	3	4	6.93	7.43	6.76	7.15	0.193	0.36	0.64	1.736a	0.353	0.658a	6.60	6.89
PG-2320	0.872	1.589a	3.06	7.65a	13.66	15.95	13.57	15.49	0.779	1.71a	0.79	1.630a	0.788	1.054a	13.48	15.03
Bio-9621	-0.428	1.947a	1.372	6.83a	9.52	12.25a	9.50	11.77a	0.381	0.99a	0.86	1.773a	0.574	1.202a	9.47	11.30a