Engineering abiotic stress response in plants for biomass production

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Abbreviations: ABA, Abscisic Acid; ACC, 1-Aminocyclopropane-1-Carboxylic Acid; ACDS, 1-Aminocyclopropane-1-Carboxylate Deaminase; BR, Brassinosteroid; BES1, BRII-EMS-Suppressor-1; BIN2, Brassinosteroid Insensitive-2; BRII, Brassinosteroid Receptor Kinase 1; CesA, Cellulose Synthase; CCR, C-C motif Chemokine Receptors; CK, Cytokinin; CKX, Cytokinin Oxidase; ERF11, Ethylene-Responsive Transcription Factor-11; EXPA4, Expansin-A4; EXPB2, Putative Expansin-B2; GA, Gibberellins; GSK3, Glycogen Synthase Kinase-3; HDA, Homolog of dnaA; HDC1, Histone Deacetylase Complex-1; IAA, Indole Acetic Acid; IPT, IsoPentenyl Transferase; NAC, NAM ATAF1,2 and CUC2; NCED, 9-Cis-Epoxycurotenoid Dioxygenase; PGPB, Plant Growth Promoting Bacteria; PIKK, Phosphatidylinositol-3-Kinase-related Kinase; pSARK, Senescence Associated Receptor Protein Kinase Promoter; ROS, Reactive Oxygen Species; RXT3, Regulator of Transcription-3; SAM, Shoot Apical Meristem; SPL8, Squamosa Promoter-binding-Like protein-8; SUSY, Sucrose Synthase; TORC1/2, Target Of Rapamycin Complex-1; XTH3, Xyloglucan endoTransglucosylase/Hydrolase-3; YUCCA, Flavin-containing Monoxygenase

Keywords: Abiotic stress, biomass, secondary cell wall, phytohormone, plant-microbe interaction

ABSTRACT

One of the major challenges in today’s agriculture is to achieve enhanced plant growth and biomass even under adverse environmental conditions. Recent advancements in genetics and molecular biology have enabled identification of a complex signaling network contributing towards plant growth and development on the one hand and abiotic stress response on the other. As an outcome of these studies, three major approaches have been identified having potential to improve biomass production in plants under abiotic stress conditions. These approaches deal with having changes in (i) plant-microbe interactions, (ii) cell wall biosynthesis, and (iii) phytohormone levels. In addition, and at the same time, employing functional genomics and genetics-based approaches, a very large number of genes have been identified which play a key role in abiotic stress tolerance. Our review is an attempt to unveil the crosstalk between the transcriptional circuitries for biomass production and abiotic stress response that has just started emerging. This knowledge may serve as a valuable resource to eventually custom design the crop plants for higher biomass production in a more sustainable manner, in marginal lands under variable climatic conditions.

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Introduction
Despite considerable success in crop improvement programs, farmers still lose almost 20-70% of their potential crop yield because of biotic and abiotic stresses (1). Abiotic stresses are one of the key challenges for plant growth and agricultural productivity in arable lands, with estimated annual loss of billions of dollars (2, 3). This challenge is expected to grow enormously with the proposed expansion of agricultural activities in less fertile and marginal areas, which is now becoming crucial in satisfying the growing food demands (4). Since about 86% of the freshwater is utilized for the production of agricultural biomass, an additional pressure is likely to come on the fresh water resources with the ongoing shifts from the era of ‘fossil energy’ to the era of ‘energy from biomass’ (5). To keep pace with this alarming situation, novel approaches are vital to enhance plant biomass production under adverse environmental conditions (6).

The acclimation of plants to abiotic stress is a complex and coordinated response involving hundreds of genes and their interactions with various environmental factors throughout the developmental period of the plant (7, 8, 9). Accordingly, a thorough understanding of the molecular responses in plants is essential for targeting any improvement in plant biomass or yield. In addition, identifying suitable phenotypes that respond to multiple abiotic stresses appearing either simultaneously or sequentially, under field conditions is indeed a tedious task, but it is the need of our time (10). However, to minimize the “yield gap” caused by these abiotic stresses, it is vital to understand the gene regulatory networks operating in plants. We hope that the recent advances in molecular biology including tissue or developmental stage-specific gene expression, stringently regulated and induced gene expression, site-specific integration of the transgene, and gene pyramiding will assist us in enhancing the photosynthetic efficiency in plants contributing eventually to produce higher biomass when grown under marginal lands (11).

The development of human civilization is inextricably linked to the plant biomass, where the wood and the fiber is being used for numerous purposes, including energy production, textiles, paper-making as well as bioenergy resources in the form of biofuels. As of today, there is a tremendous increase in the demand for plant biomass production due to the expanding human population, inadequate food availability and need for bioenergy (12). However, with the ongoing debate on ‘food vs fuel’, we need to reassess the options and the resources available to us. Even if we plan to use biofuels to satisfy the 20% of the growing demand for oil products, there will be nothing left to eat. Keeping this fact in mind, it is imperative to design our future food crops which will have the potential to give high yield and biomass even under marginal lands.

Biomass accumulation in plants occurs either by an increase in cell number or by cell expansion (13, 14). Dissecting out the regulatory network involved in cell wall biosynthesis, provides an attractive strategy to improve plant architecture and biomass (15,16). In recent years, considerable attention has also been given to plant cell wall polymers, which form a major component of plant biomass. The composition and amount of these polymers in cell wall change with plant development and in response to stress conditions (17). Further, there is a need to delineate the genes responsible for the biosynthesis of different cell wall components, along with the assembly and the regulation of cell wall dynamics and heterogeneity (17). In addition to the above strategy, manipulating endogenous plant hormone content provides still another possibility for improving abiotic stress tolerance as well as biomass of plants. The third crucial area to be explored for plant biomass enhancement and sustainable agriculture is ‘plant-microbe interaction’. Plant roots and microorganisms interact and compete for nutrients, making a complex system within the rhizosphere (18). However, a complete understanding is needed about the effect of these microbes in improving abiotic stress tolerance and in inducing higher biomass production in plants (19).

One of the goals of our review is to understand the crucial strategies being developed to engineer abiotic stress response and to enhance biomass production in plants. Here, the focus is on the above three major strategies which can be utilized to mitigate abiotic stress response,
besides enhancing biomass production. In this review, we present several examples where plant-microbe partnerships have been utilized to cope with the abiotic stress response leading to higher biomass production. Further, we discuss recent advances in molecular studies that reveal key transcriptional switches regulating secondary wall biosynthesis under abiotic stress. We also highlight the key facets of the plant growth regulators having a direct role in the regulation of plant growth under various abiotic stresses. The knowledge of these master switches will simultaneously improve our understanding to develop new strategies to genetically modify the composition and quantity of lignocellulosic biomass besides increasing abiotic stress tolerance.

(A) Exploiting plant-microbe interactions

Several studies have demonstrated that plant-microbe interactions influence abiotic stress tolerance along with growth and biomass. Plants form highly complex and diverse associations with co-evolved microbial communities (20). Microbial communities show plant specificity in terms of their morphology and secondary metabolism (21). Diverse mechanisms have been proposed for varied associations of plant growth promoting bacteria (PGPB) and fungal endophytes, after their colonization in the rhizosphere/endosphere of plants (22). The plant-microbe interactions significantly affect carbon sequestration, nutrient cycling, plant growth and productivity (23, 24) besides ameliorating plant responses against abiotic stresses (22). Many studies have shown that diverse bacterial species, belonging to different genera, contribute towards tolerance against various abiotic stresses to the host plants resulting in enhanced biomass (25).

There is now good evidence from recent agricultural practices that the use of Plant Growth Promoting Bacteria (PFPB) are a strong, viable and vital option to overcome productivity constraints besides mitigating environmental stresses in crops, e.g., soybean, barley, maize and rice (26). On the one hand, the microbes induce local or systemic inducible response mechanisms in plants to overcome abiotic stress, while, on the other hand, they contribute towards sustaining the biomass and growth through - uptake, mobilization and synthesis of nutrients. Hormones such as auxins, cytokinins and gibberellins along with other organic compounds that stimulate cell growth and division under various environmental stresses have also been implicated in such complex interactions (27). Schematic diagram depicting the complex interaction of PGPB in increasing plant growth and biomass under stress is shown in Figure 1. Various PGPBs possess not only the ability to induce ROS-scavenging enzymes, but also to increase the photosynthetic efficiency, of plants, under abiotic stress, thus leading to enhanced plant growth (28). Seed priming with these PGPB strains significantly improves biomass and nutrient uptake under stress conditions (29). Recently, the multifaceted action of microorganisms has been shown by Khan et al. (30), where enhanced expression of antioxidant enzyme machinery through Bacillus pumilus inoculation led to improved growth under high salt and boron stress in rice. Furthermore, PGPBs help plants through phytoremediation of excessive salts, leading to improved biomass production under salt stress (31). Bacteria, such as Pseudomonas spp., Burkholderia caryophylli, Achromobacter piechaudii, were shown to reduce endogenous ethylene levels in plants by producing 1-aminocyclopropane-1-carboxylic acid (ACC)-deaminase, thus resulting in increased root growth, and improved tolerance of salt and water stress (31). In addition, synthesis of Indole Acetic Acid (IAA) or enhancing ACC deaminase (ACCD) activity in the rhizosphere by Trichoderma atroviride or Pseudomonas putida in tomato results in improved growth and stress tolerance (32). Similarly, knocking down the expression of ACCD gene from T. asperellum showed reduced root elongation in canola seedlings, suggesting its role in root growth promotion (33). Burkholderia phytofirmans strain PsJN improves leaf area, chlorophyll content, photosynthetic rate and water-use efficiency, ultimately resulting in the enhanced shoot and root biomass under various abiotic stress in a wide spectrum of host plants including potato, tomato and grapevine (34).

Considerable progress has been made in unraveling the morphological, physiological and molecular mechanisms of growth promoting bacteria mediated abiotic stress tolerance in plants (35). However, delineating the signaling
molecules released by PGPB that enhance plant growth and defense responses still remains a challenge. Similarly, extensive research on enhancing the effectiveness and consistency of microbial inoculants in multiple-stress amelioration under field conditions will help us in the screening of suitable bio-inoculants to improve crop productivity under different environmental vagaries (36). Certainly, novel bacterial strains must be tested in the future to get better insight into the plant-microbe interaction in order to achieve this target. However, encompassing different omics approaches to study microbe mediated stress mitigation strategies will further strengthen our knowledge on the mechanisms of plant-microbe interactions with the naturally associated or artificially inoculated microorganisms. Primary targets for optimizing beneficial plant-microbe interactions include quorum sensing, bacterial motility, biofilm formation and their signaling pathways. Current evidence supports the plant-microbe interaction in mitigating abiotic stress response during varied edaphic and climatic conditions. At present, a range of bacterial formulations are already available commercially for their use as ‘bioprotection agents’ or ‘biofertilizers’ to improve biomass and yield under biotic stresses. Utilizing these microorganisms will further enhance tolerance against various abiotic stresses, thus establishing novel and promising techniques for sustainable agriculture.

(B) Regulation of cell wall biosynthesis

Around 430 million years ago, vascular plants appeared on land and co-evolved with the ability to develop secondary cell wall. Plant cell wall functions as an ‘exoskeleton’ by providing mechanical and structural support to the entire cell as well as acting as a physical barrier against abiotic and biotic stresses (17, 37). The principle components of a secondary cell wall are cellulose, hemicelluloses and lignin; interestingly, they are quite unique to each cell type and vary in their amount and composition along with development and in response to various biotic and abiotic stresses (17, 37). Thus, we can conclude that plants have inherently evolved intricate mechanisms to regulate biosynthetic pathways for cell wall components and have assembled them for the proper functioning of the cell. For example, plants show higher production of lignin biosynthesis enzymes during abiotic stresses (37). Similarly, severe dwarfing and altered wood anatomy were observed by silencing 4-coumarate-coenzyme A ligase, which reduces the lignin content in tracheal elements (38). At present, there is fair interest in unraveling the molecular processes regulating secondary wall development in plants as it is the most abundant plant biomass in the form of fiber and timber (39).

Immense progress has been made for the identification and functional validation of cell wall polysaccharide biosynthetic genes (including those for cellulose, glucomannan, xyloglucan, xylan, and pectin), as well as sugar nucleotide donors of these pathways (17). In plants, cellulose microfibrils, composed of β-1,4-glucan chains mainly contribute towards the above-ground biomass and their biosynthesis and accumulation play a vital role in providing defense against climatic vagaries (40). Cellulose synthase (CesA) gene superfamily regulates the synthesis of cellulose in plants (40). brassinosteroid signaling activates BES1 transcription factor, which binds to the E-box (CANNTG) in the promoter of CesA causing its upregulation and thus resulting in enhanced cellulose accumulation in Arabidopsis (41). Similarly, CESAl kinase activity was shown to be enhanced by the degradation of its inhibitor BRASSINOSTEROID INSENSITIVE2 (BIN2) (42). In addition, introgression of BR receptor containing chromosome segment (7DL) from Agropyron elongatum results in enhanced drought tolerance in wheat (43). However, increase in UDP-Glc (a substrate for synthesis of various sugars, necessary for different wall polymers) levels by overexpressing sucrose synthase (SuSY) and UDP-glucose pyrophosphorylase (UGPase) encoding genes leads to enhanced drought tolerance and cellulose accumulation (44). Similarly, heavy metal stress in rice and wheat causes enhanced lignin accumulation in cell wall, which improves defense response against biotic and abiotic stresses (45).

Transgenic Arabidopsis plants overexpressing CaXTH3, encoding a xyloglucan biosynthesis gene (xyloglucan endotransglycosylase/hydrolases), have
abnormal leaf morphology and severely wrinkled leaf shape and enhanced tolerance against water stress (46). β-expansin encoding gene \textit{EXPB2} showed higher expression under water stress and seemed to be involved in improvement of root system architecture under water deficit in soybean (47). Similarly, silencing of \textit{NAC2} or its downstream gene \textit{EXPA4} has been shown to result in reduced drought tolerance during the petal development in rose (48). In contrast, overexpression of \textit{RhEXPA4} conferred improved phenotype with shorter stems, curly leaves, compact inflorescences and enhanced drought tolerance in \textit{Arabidopsis} (48). However, higher transcript abundance of cinnamoyl-CoA reductase (\textit{CCR}) in maize inhibited cell wall extensibility and root growth under water deficiency (49). Similarly, expansin acts as a key component in heat stress tolerance as its higher expression in \textit{Agrostis} leads to increased cell wall elasticity, which maintains cellular functions (50). \textit{Arabidopsis MYB41} and rice R2R3-type \textit{MYB} transcription factor \textit{MPS} (MULTIPASS) are induced under salinity, which then enhances expression of cell wall-biosynthesis genes, during vegetative and reproductive stages, while suppressing the transcript of expansin and endoglucanase genes (51). Similarly, overexpression of \textit{TOR}, a Ser/Thr kinase of the phosphatidylinositol-3-kinase-related kinase (\textit{PIKK}) family leads to enhanced cellular biomass and stress tolerance (52). However, \textit{AtTOR} RNAi lines show high sensitivity towards osmotic stress (52).

Integrating the knowledge of key regulatory genes with their cell-specific promoters and transcriptional regulation of secondary cell wall biosynthesis through the cascade of activators, repressors and feedback regulators is expected to enable the development of designer plants with enhanced biomass under stress conditions (16,17). Schematic diagram depicting the transcriptional regulatory network modulating secondary cell wall formation in plants is shown as Figure 2. These studies also provide deep insight into the complex transcriptional machinery to genetically modify cell wall composition for tolerance against abiotic stresses.

(C) Manipulation of phytohormone levels

Of the various factors regulating plant biomass production under abiotic stresses, manipulation of plant hormone content is the most efficient approach (53). Of these hormones, auxins, cytokinins (\textit{CKs}), gibberellins (\textit{GAs}), brassinosteroids (\textit{BRs}) and abscisic acid are markedly involved in the regulation of plant growth and biomass production during stress conditions (53). Figure 3 depicts the crosstalk between various phytohormones leading to enhanced stress tolerance resulting in higher biomass production in plants. Dissecting the molecular mechanism of these hormone biosynthesis and regulation provide an insight into the complexity of various processes such as time, rate and extent of cell division and cell expansion to manipulate the regulation of meristematic division and plant growth under stress conditions (54). While cytokinins (\textit{CKs}) have an important role in delaying natural senescence in many plants (55), the concentration of the bioactive \textit{CKs} decreases during exposure to water and salt stresses (56).

Plants exhibiting negative regulation of cytokinin activity, such as plants overexpressing \textit{CKX} (\textit{CYTOKININ OXIDASE}) or mutation in the cytokinin receptors, show smaller SAM (shoot apical meristem) and decreased leaf area (57). Similarly, it is known that knocking down \textit{CKX2} expression in rice results in the maintenance of photosynthetic rate, panicle branching and reduction in yield gap under salinity stress condition (58). Most of the studies on transgenic plants with \textit{pSARK} promoter regulated isopentenyltransferase (\textit{IPT}) gene expression have reported delayed leaf senescence, higher photosynthetic activity and enhanced biomass and/or yield-related parameters under drought stress in tobacco (59), rice (60), broad bean (61), creeping bent grass (62), peanut (63) and under salt stress in cotton (64).

Under heavy metal and salt stress, IAA increases shoot as well as root growth in plants (27). Transgenic poplars overexpressing an abiotic stress responsive \textit{YUCCA6} gene, which is involved in tryptophan-dependent IAA biosynthesis pathway using stress-inducible \textit{SWPA2} promoter, exhibit rapid shoot elongation and reduced main root development with enhanced root hair formation (65). Earlier studies
demonstrated that down-regulation of SPL8 (Squamosa Promoter-binding-Like protein-8) transcription factor significantly increased branching by promoting axillary bud development and enhanced forage biomass yield, besides enhancing salt and drought tolerance in alfalfa (66); these transgenic plants showed reduced GA accumulation, while spl8 mutants showed significantly higher GA transcript abundance. Furthermore, GA2-ox6, which is the prime GA deactivation enzyme, is significantly up-regulated by SPL8 (66). These results suggest that SPL8 regulates GA signaling, and GA2-ox is a possible key node of this signaling network (67). Under saline conditions, GA application improved stomatal conductance, water use efficiency, growth and yield in tomato plants, thus supporting the above hypothesis (68).

The Arabidopsis homolog of RXT3 (REGULATOR of TRANSCRIPTION 3), named HISTONE DEACETYLASE COMPLEX1 (HDC1) shows direct interaction with histone deacetylases HDA6 and HDA19 (69). The hda6, hda19 and hdc1-1 mutant showed hypersensitivity towards NaCl and ABA during seedling stage (69). However, HDC1 overexpression reduces NaCl and ABA sensitivity and increases biomass (70). Transgenic tomato plants overexpressing abscisic acid (ABA) responsive complex (ABRC1) form barley HVA22 gene, maintained growth and yield besides tolerating cold, drought and salt stress (71). Furthermore, AtERF11 was shown to negatively modulate the ABA-mediated regulation of ethylene biosynthesis; further, its overexpression conferred ABA hypersensitivity during post-germination growth under stress conditions (72). ABA3/LOS5 encodes a Mo-cofactor sulfuran (MCSU) that catalyzes abscisic aldehyde to ABA conversion and its constitutive expression in rice leads to significantly higher yield during drought stress under field conditions (73). Similarly, overexpression of MoCo sulfuran gene in soybean resulted in enhanced biomass and yield along with improved drought tolerance attributed to increased ABA accumulation, reduced water loss and induced antioxidant enzymatic machinery (74). Furthermore, 9-cis-epoxy carotenoid dioxygenase (NCED) has been shown to catalyze the conversion of neoxanthin to xanthoxin. In addition, T-DNA insertional nced3 mutants displayed impaired drought tolerance and limited ABA accumulation under water stress, while tobacco plants constitutively expressing NCED1 enhanced ABA accumulation in leaves, which leads to improved drought and salt stress tolerance (75). Similarly, in tomato constitutive overexpression of NCED1 displayed enhanced ABA accumulation, reduction in assimilation rates, leaf chlorosis and higher biomass because of counteracting positive effects of ABA on leaf expansion and increased water status (76).

Similarly, brassinosteroid (BR) pre-treated seeds demonstrated significantly higher accumulation of dry mass and antioxidant enzyme activity in alfalfa under salt stress (77) and ameliorated growth and survival of Robinia pseudoacacia during water stress (78). In addition, BR application causes enhanced seedling growth in sorghum under osmotic stress (79). Knockout T-DNA insertion mutant of Osgsk1 (a rice GSK3/SHAGGY-like protein kinase gene, ortholog of AtBIN2/AtSK21, a negative regulator of BR-signaling), depicted enhanced tolerance towards abiotic stress, while OsGSK1 overexpression resulted in stunted growth in Arabidopsis (80). In addition, hormones target various members of protein families playing a significant role in growth either individually or in co-regulated manner, thereby indicating the synergistic action of metabolic pathways (81). Biotechnological manipulation of these key proteins could allow not only the adaptation under adverse environmental conditions, but also determine the flux in phytohormone biosynthesis for securing, in the long run, improved food production.

**Future Outlook**

With the apparent changes in the global environment, agricultural production systems are liable to change. Thus, there may be a need to produce cost-effective biomass to replace the existing fossil fuel in the near future. At the same time, to ensure availability of enough food for 9 billion people is indeed a daunting task. One possible solution to this challenge could be to make use of marginal lands with low input crops capable of providing high-biomass yield. Attempts are already being made to modify the
plant architecture in such a way that will lead to ‘transgressive overyielding’ of plant biomass. Further, there are numerous options to explore plant-microbe interactions for enhanced biomass production in marginal and arable lands. It is noteworthy that the most of these interactions are currently unexplored, making it important to closely observe the soil, the rhizosphere and the endophyte populations. Engineered plants and their beneficial symbionts will pave the way for future strategies to modify them for higher biomass production to meet the demands of growing population in a changing climate scenario. Similarly, understanding how cellular differentiation occurs during cell wall development will provide deep insight into designing cell wall architecture to enhance biomass under environmental stresses. More importantly, identifying the key transcription factors directly regulating secondary cell wall biosynthesis genes will not only provide valuable clues to understand the evolution of secondary wall biosynthesis in vascular plants but also uncover the complexity of the dynamic changes during cell wall development and abiotic stress response. Similarly, the phytohormones have been found to be involved directly in plant responses to different stresses. However, identification and maintenance of optimal dose/response ratio of hormones still remains a tedious task, since the hormonal balance should be moderate in order to maintain homeostasis to provide abiotic stress tolerance and retain growth and biomass. Much work has been done in the past decades on the molecular pathways modulating hormone biosynthesis and signaling and dissecting out their role in response to varied climatic conditions. Our review will thus be fruitful in suggesting ways to genetically manipulate hormone biosynthesis pathways for abiotic stress tolerance and for enhanced crop productivity. In the future, it will be highly desirable to study the response of plants towards a combination of stresses mimicking the field conditions, as none of the stress ever comes alone!

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References
1. Berry, P., Ramirez-Villegas, J., and Branseley, H. (2013) Regional impacts of climate change on agriculture and the role of adaptation. In: Plant genetic resource and climate change (pp 78-97). CABI, USA
2. Pareek, A., Sopory, S. K., Bohnert, H. J., and Govindjee (2009) Abiotic stress adaptation in plants: Physiological, molecular and genomic foundation. Springer Netherlands
3. Pereira, A. (2016) Plant abiotic stress challenges from the changing environment. Front. Plant Sci. 7, 1123.
4. Koh, L. P., Koellner, T., and Ghazoul, J. (2013) Transformative optimisation of agricultural land use to meet future food demands. PeerJ, 1, e188
5. Gerbens-Leenes, P. W., Hoekstra, A. Y., and Van der Meer, T. H. (2009) The water footprint of energy from biomass: A quantitative assessment and consequences of an increasing share of bioenergy in energy supply. Ecol. Econom. 68, 1052-1060
6. Farrar, K., Bryant, D., and Cope-Selby, N. (2014) Understanding and engineering beneficial plant-microbe interactions: plant growth promotion in energy crops. Plant Biotech. J. 12, 1193-1206
7. Kumari, S., nee Sabharwal, V. P., Kushwaha, H. R., Sopory, S. K., Singla-Pareek, S. L., and Pareek, A. (2009) Transcriptome map for seedling stage specific salinity stress response indicates a specific set of genes as candidate for saline tolerance in Oryza sativa L. Funct. Intger. Genom. 9, 109-123
8. Sharan, A., Soni, P., Nongpiur, R. C., Singla-Pareek, S. L., and Pareek, A. (2017) Mapping the ‘Two-component system’ network in rice. Sci. Rep. 7, 9287
9. Lakra, N., Kaur, C., Anwar, K., Singla-Pareek, S. L., and Pareek, A. (2017) Proteomics of
contrasting rice genotypes: Identification of potential targets for raising crops for saline environment. *Plant Cell Environ.* doi: 10.1111/pce.12946

10. Joshi, R., Prashat, R., Sharma, P. C., Singla-Pareek, S. L., and Pareek, A. (2016). Physiological characterization of gamma-ray induced mutant population of rice to facilitate biomass and yield improvement under salinity stress. *Ind. J. Plant Physiol.* **21**, 545-555

11. Nongpiur, R. C., Singla-Pareek, S. L., and Pareek, A. (2016) Genomics approaches for improving salinity stress tolerance in crop plants. *Curr. Genom.* **17**, 343-357

12. Demura, T., and Ye, Z. H. (2010) Regulation of plant biomass production. *Curr. Opin. Plant Biol.* **13**, 298-303

13. Risopatron, J. P. M., Sun, Y., and Jones, B. J. (2010) The vascular cambium: molecular control of cellular structure. *Protoplasma* **247**, 145-161

14. Szechyńska-Hebda, M., Czarnocka, W., Hebda, M., and Karpiński, S. (2016) PAD4, LSD1 and EDS1 regulate drought tolerance, plant biomass production, and cell wall properties. *Plant Cell Rep.* **35**, 527-539

15. Gonzalez, N., Vanhaeren, H., and Inzé, D. (2012) Leaf size control: complex coordination of cell division and expansion. *Trends Plant Sci.* **17**, 332-340

16. Dkhair, J., and Pareek, A. (2014) What determines a leaf's shape?. *EvoDevo* **5**, 47.

17. Zhong, R., and Ye, Z. H. (2007). Regulation of cell wall biosynthesis. *Curr. Opin. Plant Biol.* **10**, 564-572

18. Clode, P. L., Kilburn, M. R., Jones, D. L., Stockdale, E. A., Cliff, J. B.III, Herrmann, A. M., and Murphy, D. V. (2009) *In situ* mapping of nutrient uptake in the rhizosphere using nanoscale secondary ion mass spectrometry. *Plant Physiol.* **151**, 1751-1757

19. Pump, J., and Conrad, R. (2014) Rice biomass production and carbon cycling in 13CO2 pulse-labeled microcosms with different soils under submerged conditions. *Plant Soil* **384**, 213-229

20. Lau, J. A., and Lennon, J. T. (2011) Evolutionary ecology of plant–microbe interactions: soil microbial structure alters selection on plant traits. *New Phytol.* **192**, 215-224

21. Berg, G., and Smalla, K. (2009) Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiol. Ecol.* **68**, 1-13

22. Rodriguez, R. J., Henson, J., Van Volkenburgh, E., Hoy, M., Wright, L., Beckwith, F., Kim, Y. O., and Redman, R. S. (2008) Stress tolerance in plants via habitat-adapted symbiosis. *ISME J.* **2**, 404-416

23. Van Der Heijden, M. G., Bardgett, R. D., and Van Straalen, N. M. (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* **11**, 296-310

24. Kulmatiski, A., Beard, K. H., Stevens, J. R., and Cobbold, S. M. (2008) Plant-soil feedbacks: a meta-analytical review. *Ecol. Lett.* **11**, 980-992

25. Grover, M., Ali, S. Z., Sandhya, V., Rasul, A., and Venkateswarlu, B. (2011) Role of microorganisms in adaptation of agriculture crops to abiotic stresses. *World J. Microbiol. Biotechnol.* **27**, 1231-1240

26. Meena, K. K., Sorty, A. M., Bitla, U. M., Choudhary, K., Gupta, P., Pareek, A., Singh, D. P., Prabha, R., Sahu, P. K., Gupta, V. K., and Singh, H. B. (2017) Abiotic stress responses and microbe-mediated mitigation in plants: the omics strategies. *Front Plant Sci.* **8**, 172

27. Fahad, S., Hussain, S., Bano, A., Saud, S., Hassan, S., Shan, D., Khan, F. A., Khan, F., Chen, Y., Wu, C., and Tabassum, M. A. (2015) Potential role of phytohormones and plant growth-promoting rhizobacteria in abiotic stresses: consequences for changing environment. *Environ. Sci. Pollut. Res.* **22**, 4907-4921

28. Timmus, S., El-Daim, I. A. A., Copolovici, L., Tanillas, T., Kännaste, A., Behers, L., Nevo, E., Seisenbaeva, G., Stenström, E., and Niinemets, Ü. (2014) Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: enhanced biomass production and reduced emissions of stress volatiles. *PloS One* **9**, e96086

29. Selvakumar, G., Kundu, S., Joshi, P., Nazim, S., Gupta, A. D., Mishra, P. K., and Gupta, H. S. (2008) Characterization of a cold-tolerant plant growth-promoting bacterium *Pantoaea dispersa* 1A isolated from a sub-alpine soil in the North Western Indian Himalayas. *World J. Microbiol. Biotechnol.* **24**, 955-960

30. Khan, A., Sirajuddin, Zhao, X. Q., Javed, M. T., Khan, K. S., Bano, A., Shen, R. F., and Masood, S. (2016). *Bacillus pumilus* enhances tolerance in
rice (Oryza sativa L.) to combined stresses of NaCl and high boron due to limited uptake of Na+. Environ. Exp. Bot. 124, 120–129
31. Wu, C. H., Bernard, S. M., Andersen, G. L. and Chen, W. (2009) Developing microbe–plant interactions for applications in plant-growth promotion and disease control, production of useful compounds, remediation and carbon sequestration. Microb. Biotech. 2, 428-440
32. Gravel, V., Antoun, H. and Tweddell, R. J. (2007) Growth stimulation and fruit yield improvement of greenhouse tomato plants by inoculation with Pseudomonas putida or Trichoderma atroviride: possible role of indole acetic acid (IAA). Soil Biol Biochem. 39, 1968-1977
33. Viterbo, A., Landau, U., Kim, S., Chrenin, L., and Chet, I. (2010) Characterization of ACC deaminase from the biocontrol and plant growth-promoting agent Trichoderma asperellum T203. FEMS Microbiol. Lett. 305, 42-48
34. Mitter, B., Petric, A., Shin, M. W., Chain, P. S., Hauberg-Lotte, L., Reinhold-Hurek, B., Nowak, J., and Sessitsch, A. (2013) Comparative genome analysis of Burkholderia phytofirmans PsJN reveals a wide spectrum of endophytic lifestyles based on interaction strategies with host plants. Front. Plant Sci. 4, 120
35. Dimkpa, C. O., Merten, D., Svatoš, A., Büchel, G., and Kothe, E. (2009) Metal-induced oxidative stress impacting plant growth in contaminated soil is alleviated by microbial siderophores. Soil Biol Biochem. 41, 54-162
36. Berg, G. (2009) Plant-microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture. Appl. Microbiol. Biotechnol. 84, 11-18
37. Pauly, M., and Keegstra, K. (2008) Cell-wall carbohydrates and their modification as a resource for biofuels. Plant J. 54, 559-568
38. Wagner, A., Donaldson, L., Kim, H., Phillips, L., Flint, H., Steward, D., Torr, K., Koch, G., Schmitt, U., and Ralph, J. (2009) Suppression of 4-coumarate-CoA ligase in the coniferous gymnosperm Pinus radiata. Plant Physiol. 149, 370-383
39. Zhong, R., Lee, C., and Ye, Z. H. (2010) Evolutionary conservation of the transcriptional network regulating secondary cell wall biosynthesis. Trends Plant Sci. 15, 625-632
40. Rao, X., and Dixon, R. A. (2017) Brassinosteroid mediated cell wall remodeling in grasses under abiotic stress. Front Plant Sci. 8, 806
41. Xie, L., Yang, C., and Wang, X. (2011) Brassinosteroids can regulate cellulose biosynthesis by controlling the expression of CES genes in Arabidopsis. J Expt. Bot. 62, 4495-4506
42. Sánchez-Rodríguez, C., Ketelaar, K., Schneider, R., Villalobos, J. A., Somerville, C. R., Persson, S., and Wallace, I. S. (2017) BRASSINOSTEROID INSENSITIVE2 negatively regulates cellulose synthesis in Arabidopsis by phosphorylating cellulose synthase 1. Proc. Natl. Acad. Sci. 114, 3533–3538
43. Placido, D. F., Campbell, M. T., Folsom, J. J., Cui, X., Kruger, G. R., Baenziger, P. S., and Walia, H. (2013) Introgression of novel traits from a wild wheat relative improves drought adaptation in wheat. Plant Physiol. 161, 1806-1819
44. Gall, H. L., Philippe, F., Domon, J. M., Gillet, F., Pelloux, J., and Rayon, C. (2015) Cell wall metabolism in response to abiotic stress. Plants 4, 112-166
45. Moura, J. C. M. S., Bonine, C. A. V., De Oliveira Fernandes Viana, J., Dornelas, M. C., and Mazzafera, P. (2010) Abiotic and biotic stresses and changes in the lignin content and composition in plants. J. Integr. Plant Biol. 52, 360-376
46. Cho, S. K., Kim, J. E., Park, J. A., Eom, T. J., and Kim, W. T. (2006). Constitutive expression of abiotic stress-inducible hot pepper CaXTH3, which encodes a xyloglucan endotransglicosylase/hydrolase homolog, improves drought and salt tolerance in transgenic Arabidopsis plants. FEBS Lett. 580, 3136-3144
47. Guo, W., Zhao, J., Li, X., Qin, L., Yan, X., and Liao, H. (2011) A soybean β-expansin gene GmEXP2 intrinsically involved in root system architecture responses to abiotic stresses. Plant J. 66, 541-552
48. Dai, F., Zhang, C., Jiang, X., Kang, M., Yin, X., Lü, P., Zhang, X., Zheng, Y., and Gao, J. (2012) RhNAC2 and RhEXPA4 are involved in the regulation of dehydration tolerance during the expansion of rose petals. Plant Physiol. 160, 2064-2082
49. Fan, L., Linker, R., Gepstein, S., Tanimoto, E., Yamamoto, R., and Neumann, P. M. (2006) Progressive inhibition by water deficit of cell wall extensibility and growth along the elongation zone of maize roots is related to increased lignin metabolism and progressive stelar accumulation of wall phenolics. *Plant Physiol.* **140**, 603-612

50. Xu, J., Belanger, F., and Huang, B. (2008) Differential gene expression in shoots and roots under heat stress for a geothermal and non-thermal *Agrostis* grass species contrasting in heat tolerance. *Environ. Exp. Bot.* **63**, 240-247

51. Schmidt, R., Schippers, J. H., Mieulet, D., Obata, T., Fernie, A. R., Guiderdoni, E., and Mueller-Roeber, B. (2013) MULTIPASS, a rice R2R3-type MYB transcription factor, regulates adaptive growth by integrating multiple hormonal pathways. *Plant J.* **76**, 258-273

52. Deprost, D., Yao, L., Sormani, R., Moreau, M., Leterreux, G., Nicolaï, M., Bedu, M., Robaglia, C., and Meyer, C. (2007) The *Arabidopsis* TOR kinase links plant growth, yield, stress resistance and mRNA translation. *EMBO Rep.* **8**, 864-870

53. Gupta, B., Joshi, R., Pareek, A., and Singla-Pareek, S. L. (2017) Transgenic approaches to improve crop productivity via phytohormonal research: a focus on the mechanisms of phytohormone action. In: Mechanism of plant hormone signaling under stress. (pp.533-567), John Wiley & Sons, Inc., Hoboken, NJ, USA

54. Gonzalez, N., Beemster, G. T., and Inzé, D. (2009) David and Goliath: what can the tiny weed Arabidopsis teach us to improve biomass production in crops? *Curr. Opin. Plant Biol.* **12**, 157-164

55. Ghanem, M. E., Hichri, I., Smigocki, A. C., Albacete, A., Fauconnier, M. L., Diatloff, E., Martinez-Andújar, C., Lutts, S., Dodd, I. C., and Pérez-Alfocea, F. (2011) Root-targeted biotechnology to mediate hormonal signalling and improve crop stress tolerance. *Plant Cell Rep.* **30**, 807-823

56. Albacete, A. A., Martínez-Andújar, C., and Pérez-Alfocea, F. (2014) Hormonal and metabolic regulation of source–sink relations under salinity and drought: From plant survival to crop yield stability. *Biotechnol. Adv.* **32**, 12-30

57. Werner, T., Motyka, V., Laucou, V., Smets, R., Van Onckelen, H., and Schmülling, T. (2003) Cytokinin-deficient transgenic Arabidopsis plants show multiple developmental alterations indicating opposite functions of cytokinins in the regulation of shoot and root meristem activity. *Plant Cell* **15**, 2532-2550

58. Joshi, R., Sahoo, K. K., Tripathi, A. K., Kumar, R., Gupta, B. K., Pareek, A., and Singla-Pareek, S. L. (2017) Knockdown of an inflorescence meristem-specific cytokinin oxidase–OsCKX2 in rice reduces yield penalty under salinity stress condition. *Plant Cell Environ.* doi: 10.1111/pce.12947

59. Rivero, R. M., Kojima, M., Gepstein, A., Sakakibara, H., Mittler, R., Gepstein, S., and Blumwald, E. (2007) Delayed leaf senescence induces extreme drought tolerance in a flowering plant. *Proc. Natl. Acad. Sci.* **104**, 19631-19636

60. Peleg, Z., Reguera, M., Tumimbang, E., Walia, H., and Blumwald, E. (2011) Cytokinin-mediated source/sink modifications improve drought tolerance and increase grain yield in rice under water-stress. *Plant Biotechnol. J.* **9**, 747-758

61. Meitzel, T., Radchuk, R., Nunes-Nesi, A., Fernie, A.R., Link, W., Weschke, W., and Weber, H. (2011) Hybrid embryos of *Vicia faba* develop enhanced sink strength, which is established during early development. *Plant J.* **65**, 517-531

62. Merewitz, E. B., Gianfagna, T., and Huang, B. (2010) Effects of SAG12-ipt and HSP18.2-ipt expression on cytokinin production, root growth, and leaf senescence in creeping bentgrass exposed to drought stress. *J. Am. Soc. Hortic. Sci.* **135**, 230-239

63. Qin, H., Gu, Q., Zhang, J., Sun, L., Kuppu, S., Zhang, Y., Burow, M., Payton, P., Blumwald, E., and Zhang, H. (2011) Regulated expression of an isopentenyltransferase gene (IPT) in peanut increases yield under field conditions. *Plant Cell Physiol.* **52**, 1904-1914

64. Liu, M. X., Yang, J. S., Li, X. M., Mei, Y. U., and Jin, W. A. N. G. (2012) Effects of irrigation water quality and drip tape arrangement on soil salinity, soil moisture distribution, and cotton yield (*Gossypium hirsutum* L.) under mulched drip irrigation in Xinjiang, China. *J. Integr. Agric.* **11**, 502-511

65. Ke, Q., Wang, Z., Ji, C. Y., Jeong, J. C., Lee, H. S., Li, H., Xu, B., Deng, X., and Kwak, S. S. (2015) Transgenic poplar expressing *Arabidopsis* YUCCA6 exhibits auxin-overproduction production
Expression of an Arabidopsis molybdenum cofactor sulphurase gene in soybean enhances drought tolerance and increases yield under field conditions. *Plant Biotechnol. J.* **11**, 747-758

75. Wan, X. R., and Li, L. (2006). Regulation of ABA level and water-stress tolerance of Arabidopsis by ectopic expression of a peanut 9-cis-epoxycarotenoid dioxygenase gene. *Biochem. Biophys. Res. Comm.* **347**, 1030-1038

76. Tung, S. A., Smeeton, R., White, C. A., Black, C. R., Taylor, I. B., Hilton, H. W., & Thompson, A. J. (2008). Over-expression of LeNCED1 in tomato (*Solanum lycopersicum* L.) with the rbcS3C promoter allows recovery of lines that accumulate very high levels of abscisic acid and exhibit severe phenotypes. *Plant, Cell Environ.* **31**, 968-98

77. Zhang, S., Hu, J., Zhang, Y., Xie, X. J., & Knapp, A. (2007). Seed priming with brassinolide improves lucerne (*Medicago sativa* L.) seed germination and seedling growth in relation to physiological changes under salinity stress. *Aust. J. Agric. Res.* **58**, 811-815

78. Li, K. R., Wang, H. H., Han, G., Wang, Q. J., and Fan, J. (2008) Effects of brassinolide on the survival, growth and drought resistance of *Robinia pseudoacacia* seedlings under water-stress. *New For.* **35**, 255-266

79. Vardhini, B. V., and Rao, S. S. R. (2003) Amelioration of osmotic stress by brassinosteroids on seed germination and seedling growth of three varieties of sorghum. *Plant Growth Reg.* **41**, 25-31

80. Koh, S., Lee, S. C., Kim, M. K., Koh, J. H., Lee, S., An, G., Choe, S., and Kim, S. R. (2007) T-DNA tagged knockout mutation of rice OsGSK1, an orthologue of *Arabidopsis BIN2*, with enhanced tolerance to various abiotic stresses. *Plant Mol. Biol.* **65**, 453-466

81. Nguyen, D., Rieu, I., Mariani, C., and van Dam, N. M. (2016) How plants handle multiple stresses: hormonal interactions underlying responses to abiotic stress and insect herbivory. *Plant Mol. Biol.* **91**, 727-74
FIGURE 1. Plant microbe interactions for biomass enhancement. Schematic diagram representing the plant-associated bacteria that can promote plant growth by producing various volatile organic compounds, phytohormones, siderophores, biofertilizers and antioxidants that indirectly or directly benefit plant growth by induced systemic resistance, phytoremediation, systemic acquired resistance, ion chelation, nutrient acquisition and inhibition of reactive oxygen species to improve stress tolerance in host plants.
FIGURE 2. Complex transcriptional circuitry contributing towards secondary cell wall development in plants as influenced by abiotic stress. The secondary cell wall biosynthesis consists of two nodes: one is E2Fc mediated and the other one is through the BR signaling pathway. E2Fc is the master regulator of downstream transcription factors that act in a coordinated manner to further result in synthesis, transport and assembly of secondary cell wall components such as cellulose, xylan, and lignin. Similarly, brassinosteroid signaling also modulates various downstream genes leading to cell wall remodeling under stress. BR (BRASSINOSTEROID); BSK1 (BR SIGNALING KINASE); BSU1 (BRI1 SUPPRESSOR1); BZR1 (BRASSINAZOLE-RESISTANT1); CAD4 (CINNAMYL ALCOHOL DEHYDROGENASE 4); CESA4/7 (CELLULOSE SYNTHASE 4/7); FLY1 (FLYING SAUCER 1); GSK2 (GSK3/SHAGGY-LIKE KINASES); GUX2 (UDP-GLUCURONATE: XYLAN ALPHA-GLUCURONOSYLTRANSFERASE 2); IRX7/9 (IROQUOIS HOMEBOX 7); LAC4/17 (LACCASE 4/17); REV (REVOLUTA); SKP2A (S-PHASE KINASE-ASSOCIATED PROTEIN 2A); SND1/2/3 (STAPHYLOCOCCAL NUCLEASE AND TUDOR DOMAIN CONTAINING 1/2/3); VND 6/7 (VASCULAR-RELATED NAC DOMAIN 6/7); XTH (XYLOGLUCAN TRANSFERASE/HYDROLASE); EXP (EXPANSINS). In this complex process, various NACs (NAM-ATAF1,2-CUC2) and MYBs act as the key master switches that control cell wall deposition.
FIGURE 3. Schematic representation of cross talk between different phytohormone signaling pathways leads to higher biomass production in plants under stress conditions. ABA (ABSCISIC ACID); BIN2 (BR-INSENSITIVE 2); BR (BRASSINOSTEROIDS); CK (CYTOKININ); CKX2 (CYTOKININ OXIDASE 2); ERF (ETHYLENE-RESPONSIVE TRANSCRIPTION FACTOR); GA (GIBBERELLIC ACID); GA2ox6 (GA2 OXIDASE6); GSK (GLYCOGEN SYNTHASE KINASE); HDC/RXT (HISTONE DEACETYLASE COMPLEX/ REGULATION OF TRANSCRIPTION); IAA (INDOLE 3-ACETIC ACID); NCED (9-CIS-EPOXYCAROTENOID DIOXYGENASE); IPT (ISO PENTYL TRANSFRASE); SPL (SQUAMOSA PROMOTER-BINDING-LIKE PROTEIN). For brevity sake, only representative examples have been depicted.
Table 1: Representative list of abiotic stress responsive genes that have been genetically manipulated to improve the biomass production in plants

| S. No. | Target Plant          | Gene Name | Observed parameter/ Trait                                      | References |
|--------|-----------------------|-----------|-----------------------------------------------------------------|------------|
|        | **Plant Microbe Interactions** |           |                                                                |            |
| 1      | Solanum lycopersicum  | ACCD      | Improved plant growth in the presence of abiotic stresses     | (32)       |
| 2      | Brassica napus        | ACCD      | Improved salt tolerance and plant growth                       | (33)       |
|        | **Cell Wall Biosynthesis** |           |                                                                |            |
| 1      | Arabidopsis thaliana  | CesA1     | Higher cellulose accumulation and improved stress tolerance    | (40, 41)   |
| 2      | Arabidopsis thaliana, Oryza sativa | BRI1 | Enhanced drought tolerance with higher root and shoot biomass | (42, 43)   |
| 3      | Gossypium sp.         | Susy, UGPase | Enhanced drought tolerance, cellulose accumulation and total biomass | (44)        |
| 4      | Arabidopsis thaliana  | XTH3      | Enhanced xyloglucan biosynthesis and water stress tolerance    | (46)       |
| 5      | Glycine max           | EXPB2     | Improved root system architecture under water deficit         | (47)       |
| 6      | Rosa sp.              | NAC2, EXPA4 | Silencing of these genes resulted in reduced drought tolerance | (48)       |
| 7      | Zea mays              | CCR       | Inhibited wall extensibility under water stress                | (49)       |
| 8      | Arabidopsis thaliana  | MYB41, MPS | Enhanced salt stress and cell wall biosynthesis                | (51)       |
| 9      | Arabidopsis thaliana  | TOR1,2    | Regulation of organ and cell size, seed production and resistance to osmotic stress | (52)       |
| 10     | Medicago sativa       | MYB46     | Increased lignin deposition, secondary cell wall thickness and enhanced abiotic stress tolerance | (69)       |
|        | **Phytohormone regulation** |           |                                                                |            |
| 1      | Oryza sativa          | CKX2      | Increased panicle branching with more filled grains per plant and higher harvest index under salinity | (58)       |
| 2      | Arachis hypogaea      | IPT       | Enhanced biomass and yield under drought and salinity         | (60, 63)   |
| 3      | Medicago sativa, Arabidopsis thaliana | SPL8/9 | Enhanced biomass and tolerance towards salt and drought stress | (67)       |
| 4      | Arabidopsis thaliana  | HDC1      | Overexpression reduced NaCl and ABA sensitivity and showed increased biomass | (69)       |
| 5      | Solanum lycopersicum  | ABRC1     | Maintained growth and yield besides tolerating cold, drought and salt stress | (71)       |
| 6      | Nicotiana tabacum, Solanum lycopersicum | NCED1/3 | Enhanced biomass besides drought and salt stress tolerance | (75, 76)   |
| 7      | Medicago sativa, Arabidopsis thaliana | GSK1   | Stunted growth and abiotic stress sensitivity                  | (80)       |
Engineering abiotic stress response in plants for biomass production
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