Tuned to survive: Salt stress induced changes in Arabidopsis
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Summary

The arable areas suitable for high yielding elite crops are getting scarce due to decreasing availability of fresh water and increasing soil salinization. Majority of the plants are not able to grow in saline conditions and show severe growth reduction in response to salt stress. Plants produce many fast acting signals in response to salt stress, which are summarized in Chapter 1, leading to acclimation responses and growth reduction. Increase in Phosphatidic Acid (PA) is one of the very first responses to salinity stress. PA recruits its protein targets to the membrane, which undergo post-translational modifications or interact with molecular partners. SnRK2.4 is a PA target protein that is rapidly and transiently activated in saline conditions and is targeted to punctate structures in epidermal and cortex layers of the root. In Chapter 2, we show that PA-binding of SnRK2.4 is mainly accomplished through a number of basic amino acid residues in the abiotic-stress domain / PA-Binding Domain (PABD). Since PABD alone did not re-localize into punctate structures under any conditions studied, we excluded that the PA-binding alone is responsible for protein re-localization. The overexpression of a functional PABD resulted in reduced development of Lateral Roots (LRs) under control conditions, implying that PA-binding of SnRK2.4 is involved in initiation of growth arrest in response to salt stress.

Natural variation in salt stress tolerance within species can be a valuable resource for breeding purposes and identification of novel genes / alleles contributing to salinity tolerance. It is generally assumed that phenotypic differences between accessions are due to natural selection and genetic adaptations depending on the specific local conditions. However, since environmental data for readily collected accessions is lacking, the conclusions on local adaptations of those accessions remain tentative. In Chapter 3 a new Dutch population of Arabidopsis accessions was established and environmental data, including soil and plant ion accumulation, was collected. By re-growing collected accessions under controlled conditions we observed that lines from saline environments exhibited enhanced salinity tolerance as well as relatively low sodium accumulation under salt stress conditions. Observed differences in sodium accumulation suggest salt stress adaptation within the collected population of Dutch accessions.

Interestingly, the reduction of plant growth depends not only on severity of salt stress or plant genetic make-up, but also on tissue identity. Therefore, salt stress exposure not only leads to growth reduction, but also significant changes in plant morphology which might affect plant performance in saline conditions. In the model plant Arabidopsis thaliana we observed natural variation in rosette (Chapter 4) and Root System Architecture (RSA) size (Chapters 5 and 6) in control and salt stress conditions. In both shoot (Chapter 4) and root (Chapter 6) related phenotypes natural variation in saline conditions was correlated with the developmental differences between the accessions in control conditions. In order to examine salt-specific remodeling of plant morphology, in Chapter 5 the dynamics of RSA development in salt and control
conditions were described with simple quadratic growth functions (\textit{root-fit}). In Col-0 accession salt reduced the growth of Main Root (MR) more severely than the Lateral Root (LR) emergence or elongation. Reducing growth dynamics to organs-specific growth factors allowed us to normalize for the developmental differences observed between the accessions. By studying natural variation in growth dynamics using \textit{root-fit} we described four major strategies employed by different Arabidopsis accessions. Different RSA strategies were partially explained by natural variation in abscisic acid (ABA) sensitivity and corresponded to different Na$^+$/K$^+$ ratios in shoots of seedlings grown under mild salt stress.

Local adaptation to abiotic stress relies on multiple genes with small individual contributions. The genomic data available for Arabidopsis accessions now enables identification of candidate genes through Genome Wide Association Studies (GWAS). Study of shoot (\textit{Chapter 4}) and root (\textit{Chapter 6}) development under salt stress conditions revealed a number of putative candidate genes that could be involved in growth regulation under saline conditions. A number of identified putative loci were further confirmed by studying mutant lines and accessions showing altered transcription levels of putative candidate genes. The majority of the mutant lines showed either salt stress specific (HKT1, Ven-3, LRR-KISS) or developmental (Arabidillo2, KH-flowering locus, unknown protein) phenotypes. Low expression of LRR-KISS corresponded to salt stress induced decrease in rosette development. The allelic variation in promoter region of Arabidillo-2 suggested one Single Nucleotide Polymorphism responsible for down regulation of expression resulting in reduced root development. On the other hand, only enhanced expression of HKT1 was observed to reduce LR development under salt stress conditions. The role of allelic variation in identified candidate genes remains to be validated in the future studies, unraveling the molecular mechanisms controlling the transcriptional and post-transcriptional changes contributing to plant acclimation and salinity tolerance.

In \textit{Chapter 7} I discuss how the salt-induced changes in morphology can provide a framework for further studies. The dynamics of growth responses seem to be essential for dissecting individual aspects of salt stress physiology. The induction of growth arrest could be further used for identification of genes involved in early signaling responses due to osmotic effect of salt stress. The duration of quiescent phase and extent of growth recovery can be employed for identification of genes involved in plant acclimation and effective ion compartmentalization. The analysis of growth dynamics of individual plant organs will provide further understanding on how salt-induced changes in plant morphology affect physiology and contribute to salt stress tolerance.