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### Shape up your root

*Novel cellular pathways mediating root responses to salt stress and phosphate starvation*

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## Summary

Increasing soil salinization creates harsh conditions for plant cultivation and contributes to a decline in arable areas worldwide. Most crops have high sensitivity to salt stress, which impairs their growth and productivity. Soil salinization often coincides with a decrease in the availability of inorganic phosphate (Pi), a crucial nutrient for plant growth and development. This means that in the field, plants subjected to salt stress suffer simultaneously from Pi starvation. The root is the first organ that perceives the changes in soil conditions and Root System Architecture (RSA) can be shaped by the environment. The importance of root responses to stresses and signaling components controlling RSA modulations with a focus on salinity and Pi deficiency are presented in **Chapter 1**. We also summarize the progress in studies of the influences of multifactorial stresses and present advances of using natural variation to dissect genetic components of stress responses.

RSA changes are phenotypic output of complex network of stress signaling pathways. A key step in stress responses is modulation of gene expression, which can occur through activation or repression of transcription, but also at post-transcriptional level, by control of pre-mRNA splicing or mRNA decay. **Chapter 2** presents an overview of mRNA metabolism pathways that participate in responses to osmotic and salt stress. This machinery targets a stress-specific subset of transcripts and we speculate that phosphorylation state of the 5' mRNA decapping complex can be responsible for this selectivity. In **Chapter 3** we present identification of VCS, a member of the mRNA decapping complex, as a direct phosphorylation target of SnRK2.4 and SnRK2.10 protein kinases, which are crucial components of early salt stress signaling. Since other SnRK2 protein kinases were also able to phosphorylate VCS, we suggest the existence of at least partial functional redundancy within the SnRK2 kinase family. Mutants of 5' mRNA decay components and SnRK2.4 and SnRK2.10 showed alterations in root growth in the presence of salinity, supporting the connection of these two pathways. Analysis of the salt-induced changes in transcriptome identified the aquaporin PIP2,5 and the auxin biosynthesis enzyme CYP79B2 as potential downstream components of the SnRK2 subclass 1 signaling pathways, possibly as a result of their effect on mRNA turnover.

Complexity of the plant environment urges the study of multiple concurrent stresses. Nutrients have been suggested to modulate impact of salinity. In **Chapter 4** we focus on the effect of Pi on root responses to salt stress. First, following the dynamics of root growth, Pi starvation was found to decrease the mild salt stress effect on growth rate of main and lateral root, while for high NaCl concentrations this effect was only observed for lateral roots. To get a more global picture of interaction of salinity and Pi deprivation we performed a detailed RSA quantification of changes made by salt, Pi starvation and their combination (double stress) at one time point. Similarly to the dynamics studies main and lateral roots responded in a different manner.

The effect of Pi starvation was masked by the salinity for all traits describing lateral roots, while the combination of Pi deprivation and salt stress had an additive effect on the main root.

Soil conditions differ worldwide and enforce a natural selection and genetic adaptations of plants, which are thought to result in interspecies phenotypic diversity. Natural variation is a valuable genetic tool for discovering genetic components guiding interactions with environment and facilitating breeding programs. We observed natural variation within *Arabidopsis* in modulation of RSA by salt stress, Pi starvation and their combination (**Chapter 4 and 5**). The model of the integration of signals from salt stress and Pi starvation was representative for a vast number of *Arabidopsis* accessions but at the same time we identified accessions with extreme responses, for example prioritizing responses of lateral roots to Pi starvation over salt (**Chapter 4**).

Exploring the genetic basis of the natural variation in responses to stresses can help us understand the evolution of phenotypic plasticity and be used to mapping loci controlling responses to stress. RSA data collected in **Chapter 4 and 5** were used for Genome Wide Association Studies (GWAS). A number of genetic loci was identified as putative components of root responses to salt stress, Pi starvation and their combination. Selected candidate genes were verified by studying their mutant lines or accessions with extreme expression of these genes. Sequence polymorphisms in the promoter region of *CIP111* correlated with its expression, which was in turn correlated with lateral root length under salt stress, as verified by knock-out mutants. LBD16 was identified as a salt-stress specific transcription factor, promoting lateral root formation in the presence of salinity.

Responses to the combination of salinity with low Pi availability were partly dependent on the phenotypic responses to the individual action of NaCl and Pi deprivation, which in turn were correlated with basal root development on control conditions (**Chapter 4 and 5**). Our results suggest that stress responses are controlled by the same genetic components as developmental processes, implying that plant interactions with environment require adjustment of the basal developmental processes.

In **Chapter 6** results of this thesis are discussed in a framework of gaps in our current understanding of plant responses to stress conditions and the new avenues for further research that are opened by the work described in this thesis.