Sink or swim: submergence tolerance and survival strategies in Rorippa and Arabidopsis

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CHAPTER 1

With hope that variation will increase tolerance in every sense.

Introduction

Melis Akman
The external environment has a tremendous impact on organisms, shaping the distributions of the species, influencing their phenotypes and life cycles, as well as the accumulation and demise of genotypic variation through their evolutionary history. This is how new species evolve while others disappear, by means of Darwin’s law of natural selection.

Seven years before Darwin was born, another great scientist came to the realization that the variation in living organisms is shaped by the environment. This was the beginning of an era in which we started to understand how and why organisms are the way they are. Lamarck explains how species derived by various environmental conditions in these words in his *Hydrogéologie* (1802):

“After having produced aquatic animals of all ranks and having caused extensive variations in them by the different environments provided by the waters, nature led them little by little to the habit of living in the air, first by the water’s edge and afterwards on all the dry parts of the globe. These animals have in course of time been profoundly altered by such novel conditions; which so greatly influenced their habits and organs that the regular gradation which they should have exhibited in complexity of organisation is often scarcely recognisable.”

Although he excluded plants in his sentences, it is needless to say that his ideas also apply to plants. Terrestrial plants also evolved from aquatic ancestors approximately 500 million
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years ago and over 220 genera have returned to an aquatic environment (Cook, 1999). Yet, many terrestrial plant species lack adaptations to cope with excess water, and suffer from submergence caused by seasonal floods or excess rainfall. Thus, submergence stress acts as a strong selection force shaping plant distributions, leading to a gradient of plant species in flood prone areas (Silvertown et al., 1999; Vervuren, 2003).

It is sometimes not easy for non-biologists to realize that plants can get stressed and even “drown” under limiting oxygen levels under water. At the same time, a plant biologist cannot ignore the effects of excess water on plants and plant communities, especially in the landscapes that are typical for the Netherlands of which 25 percent is below sea level. Additionally, predictions for increasing number of floods worldwide (Milly et al., 2002; Durack et al., 2012) forces us to look more carefully at the environmental changes and their impact on plants.

Submergence is a compound stress, affecting plant functioning at several levels, which in turn can lead to severe tissue damage and eventually mortality. The most important problem imposed by submergence is decreased gas diffusion under water, disabling efficient gas transport into and out of the plant (Armstrong, 1980). Oxygen becomes limiting very quickly and oxidative phosphorylation is severely hampered (Voesenek et al., 2006). As a consequence, glycolysis is induced to produce ATP, which results in faster consumption of carbohydrates since the anaerobic pathway is far less efficient in terms of ATP production compared to aerobic respiration. Photosynthesis is also reduced since, like oxygen, carbon dioxide diffusion is not efficient under complete submergence (Mommer et al., 2005). In addition floods are often co-occurring with turbid waters in which light is only scarcely available, and this also leads to a further decrease in photosynthesis levels (Vervuren, 2003; Parolin, 2009). Together with faster carbohydrate consumption, this creates an energy crisis that can be lethal. In addition, accumulation of reactive oxygen species and toxic compounds such as organic acids, pyruvate and conversion of ethanol to acetaldehyde upon re-aeration also increases mortality (Jackson & Drew, 1984; Armstrong & Armstrong, 1999; Blokhina et al., 2003). The combined effects of these stresses resulting from various factors lead to severe tissue damage and if submergence prolongs, many plant species cannot sustain their cellular functioning and die.

In order to prevent crop failure as well as demise of natural plant populations in a changing world, it is essential to understand what makes that some plants thrive while others die. It is of fundamental importance to identify mechanisms that evolved in plants inhabiting flood-prone areas; adaptations that enable them to survive various flooding depths and durations, from partial waterlogging of roots to complete submergence, lasting days to months. The
challenge is to understand the functioning and mechanisms of these adaptations by studying both the intra- and interspecies variation accumulated in millions of years. Now, 200 years after Lamarck’s ideas on an earlier version of evolution theory, we are able to take up this challenge, thanks to the recent advances in genetics and genomics. While Darwin was working on his “Origin of the Species” and his theory of evolution (inspired by Lamarck), Gregor Mendel in the 1850s was experimenting with thousands of pea plants leading to a new discipline called Genetics that later transformed Darwin’s theory to the New Synthesis. A century later, from a modest one-page publication on the structure of DNA by Watson and Crick in 1953, to the discovery of DNA sequencing by Sanger in 1977, our understanding of genetics has progressed enormously. As a result, we are now capable of dissecting the mechanisms underlying phenotypic variation, seeing what Lamarck referred to as “scarcely recognizable”.

Aim of this thesis

The main aim of this thesis is to reveal the underlying physiological and molecular mechanisms that improve submergence tolerance in a variety of plant species adapted to various flooding conditions. For this purpose, we used an ecogenomics approach in which we integrate genetics, genomics, physiology, biochemistry and evolutionary biology. First, we investigated the mechanisms of extreme submergence tolerance in two Rorippa species, inhabitants of flood-prone areas. By comparing these two Rorippa species with two Rumex species showing similar patterns under submergence, we identified the similarities and differences between these two genera in submergence responses. Additionally, the model plant Arabidopsis enabled us to use the molecular resources to reveal the genetic basis of variation in submergence tolerance of two accessions in more detail.

Outline of the thesis

In the second chapter of this thesis, we investigated the extraordinary capability of Rorippa species for surviving months of submergence, achieved by escape and quiescence strategies. In long-term survival assays we investigated the costs and benefits of these strategies in two species, Rorippa amphibia and Rorippa sylvestris.

Subsequently, in Chapter 3, similarities and contrasting patterns between escaping and quiescent species of Rumex and the Rorippa were analyzed. We studied the changes in carbohydrate pools and if and how these are reflected in submergence tolerance. The expression patterns of the most likely regulators of these strategies, group VII ethylene response factors (ERFs), were also analyzed in these Rorippa and Rumex species.
In the 4th chapter, we used the molecular tools available for Arabidopsis and performed a quantitative trait loci analysis to reveal the genomic regions responsible for differential submergence tolerance in two Arabidopsis accessions.

Exploiting the opportunities in modern genetic research on model plants further, we performed an RNA-seq experiment in Chapter 5 to detect the differences in expression patterns of these two accessions under submergence and compared the results to the QTL analysis from the previous chapter. To conclude, the final chapter gives a summary of the main interesting findings from this thesis.