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Thermal ecotypes in the green macrophyte *Valonia utricularis*

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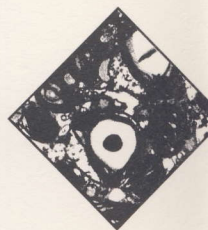
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Summary

The green macroalga *Valonia utricularis* (Roth) C. Agardh (Chlorophyta) has a world wide tropical to warm-temperate distribution, and also occurs in the Mediterranean. Annual temperature ranges at deep tropical localities are between 25 and 29°C but at warm-temperate localities seawater temperatures, especially in winter, are much lower (western Mediterranean 13-24°C). Since phylogenetic and distributional data suggest a tropical origin of the genus *Valonia*, the main question was how originally warm-adapted *V. utricularis* populations evolved the capacity to perform at the lower temperatures in the western Mediterranean and north-eastern Atlantic parts of the distribution. The main objective of this thesis was to examine intra-specific variation in thermal traits at the physiological level, and to identify temperature characteristics that are important in explaining the present distribution pattern of this species.

Pakker and Breeman (1996) described ecotypic differentiation among five Mediterranean/Canary Islands isolates and a Cape Verde Islands isolate of *V. utricularis*. The former group showed significantly lower temperature tolerance limits and increased growth rates at low temperatures. The first aim of this thesis was to investigate temperature requirements for survival, growth and reproduction in isolates from the entire biogeographic range of *V. utricularis*, i.e. including the Indo-Pacific region. I found two distinctive ecotypes; one ecotype included all northeastern Atlantic and Mediterranean isolates, the other all Indo-west Pacific isolates. Only minor variation occurred with the two groups. However, the isolate from the tropical Cape Verde Islands occupied an in between position. Subsequently, I analysed local adaptation,



selection pressure and trade-offs in the different *V. utricularis* populations. The results are discussed in a biogeographical context (*chapter 2*). As the next step, I analysed the physiological background of the observed ecotypic differentiation. I performed a detailed analysis of the temperature requirements of photosynthesis and paid special attention to the phenotypic plasticity of photosynthetic performance, i.e. the potential for temperature acclimation (*chapters 3, 4, 5*). In order to evaluate local adaptations and the evolutionary steps in the physiological adaptive processes, I also attempted to reconstruct the phylogenetic relationships among the different isolates. Unexpectedly, ITS sequence analysis gave no consistent results in *V. utricularis*, and this part of the investigation had to be abandoned (*chapter 6*).

Ecotypic differentiation in *V. utricularis* is characterised by an increased performance breadth, together with a minor overall shift towards lower temperatures in the Atlantic/Mediterranean compared to the Indo-west Pacific isolates (*chapter 2*). This can be interpreted as an adaptation to the broader annual temperature ranges in the warm-temperate region compared to the tropics. In addition, temperature requirements for reproduction were shifted towards lower temperatures in the Atlantic/Mediterranean isolates. Certain thermal traits, i.e. the lower and upper survival temperatures and with the temperature requirements for some growth, were correlated with lowest and highest local temperatures. However, there was no significant correlation between the temperature range for "good" growth and the annual temperature range at collection localities, indicating that optimal growth temperature is not important on the biogeographical scale.

The northern distribution limit of *V. utricularis* at the northeastern Atlantic coast at about 39°N (at the 13°C February and 17°C August isotherms) is probably set by a growth and/or reproduction boundary. The northern distribution limit in the Pacific at 26°N (at the 21°C February and 29°C August isotherms) may be set by low lethal winter temperatures (*chapter 2*). Thus, changes in thermal traits (i.e. survival, growth and reproduction) have enabled *V. utricularis* to extend its distributional range into warm-temperate regions in the northeastern Atlantic/Mediterranean. The development of cold-adaptation in the northeastern Atlantic/Medi-

terranean and its absence in the northwestern Pacific is possibly related to different impacts of Pleistocene glaciations in the two regions. The very similar temperature characteristics within each of the two groups (Atlantic/Mediterranean vs. Indo-west Pacific), compared to the strong differentiation between the groups suggests that ongoing selection at the northern distribution boundaries, both in the Atlantic and the Pacific, does not contribute to further variation. Ongoing gene flow probably restricts further differentiation.

Chapter 3 presents the results of a detailed investigation on the temperature dependence of photosynthesis in two isolates of *V. utricularis*, one from the western Mediterranean and one from the Indian Ocean. The optimal temperatures for photosynthesis, measured as the short-term temperature response, were shifted in the Mediterranean isolate by 7°C (33 vs. 26°C) towards lower temperatures, i.e. this isolate was more cold-adapted than the Indian Ocean isolate. In addition, the two isolates differed in their ability to acclimate in response to changes in growth temperature. The Mediterranean isolate had a high potential to acclimate to low temperatures, which was lacking in the Indian Ocean isolate. The Indian Ocean isolate was even strongly photoinhibited at the tested sub-optimal growth temperatures. Damage was also apparent from the ultrastructure of the chloroplasts. Chloroplasts were less densely packed and thylakoid structure was disorganised, which presumably contributed to the loss in PSII activity and a decrease in quantum efficiency of PSII. Acclimation was achieved in the Mediterranean isolate by an increase in photosynthetic efficiency. This isolate can reach optimal photosynthetic activity during seven months of the year. At the tropical site, temperatures are optimal for photosynthesis and growth during the entire year, so no selection pressure exists towards improved performance at low temperatures at this site. I concluded that acclimation to growth temperature plays a major role in the process of adaptation to the local temperature regime of the western Mediterranean. Acclimation potential was therefore investigated on a broader scale (*chapter 5*).

Due to acclimation, all tested isolates from the western Mediterranean can reach high photosynthetic capacity at local winter temperatures (*chapter 5*). This trait was also found at tempera-

tures beyond the local temperature range in isolates from the eastern Mediterranean and the Canary Islands. This might indicate close phylogenetic relationships with populations exposed to stronger selection pressure by low winter temperatures. All isolates from the Atlantic/Mediterranean share the characteristic of losing a significant amount of photosynthetic capacity when grown at 30°C. This is in accordance with very low or even no growth at this temperature, and with the lower local temperature maxima, which generally stay below 25°C in summer. None of the Indo-west Pacific isolates showed any ability to acclimate to sub-optimal growth temperatures. Acclimation potential may be considered to be redundant at the tropical Indian Ocean sites since these sub-optimal growth temperatures are, in all cases, outside the local annual temperature range. When grown at 30°C, the Indo-west Pacific isolates showed a photosynthetic capacity equal to that at 25°C. This is, again, in accordance with the high growth rates achieved at 30°C and the high local summer temperatures of 29°C at the collection localities. When acclimation responses of photosynthesis were absent (Atlantic/Mediterranean isolates at 30°C and Indo-Pacific isolates at <25°C), algae attempted to limit photodamage by down-regulating light absorption and/or up-regulating photoprotection *via* the xanthophyll cycle. This strategy was, however, only partially successful since chronic photoinhibition was detected in most of the isolates at these temperatures. In conclusion, the evolutionary response of the Atlantic/Mediterranean isolates is not just low temperature adaptation, but also the acquisition of phenotypic plasticity in response to a broader annual temperature range.

The objective of the study presented in *chapter 4* was to get more insight into the relationship between ecotypic differentiation and the occurrence of low temperature induced photoinhibition. The ability to cope with temporary strong low temperature stress was tested in nine isolates of *V. utricularis*. The northwest Atlantic/Mediterranean isolates showed superior chilling tolerance, compared to the Indo-west Pacific isolates. The former isolates possessed a substantial capacity for dynamic photoinhibition under low temperature stress, which can be considered as a necessary adaptation to the local low winter temperatures in the northern Mediterranean. In contrast, the tropical Indo-west Pacific isolates

had a generally low capacity for dynamic down-regulation of PSII reaction centres even under moderately low temperature stress. Again, this capacity would be redundant in the tropical Indian Ocean isolates. However, especially at the northern distribution limit in the northwestern Pacific (southern Japan) cold sensitivity restricts further northward extension.

Ecotypic differences are expected to involve primarily genotype by environment interactions and they were found in *V. utricularis* (chapter 7). Local thermal adaptation occurred, maximising the rate of photosynthesis and growth under the local temperature regime. The Mediterranean isolate outperforms the Indian Ocean isolate at low temperatures (13-24°C: Mediterranean environment) and, *vice versa*, the Indian Ocean isolate outperforms the Mediterranean isolate at high temperatures (25-28°C: Indian Ocean environment). The Mediterranean isolate is adapted to the local thermal regime at the expense of its capacity and performance at high temperatures. However, a clear tropical imprint is still present, as its performance would be better (growth) or at least similar (photosynthesis) under a tropical temperature regime.

The results presented in this thesis show for the first time that temperature acclimation responses are important in a biogeographical context. Low temperature stress as such is probably not sufficient to induce cold adaptation, as boundary populations were no better able to withstand cold-stress than those from the centre of the distribution. Instead, low temperature stress in isolation, i.e. under reduced levels of gene flow, appears to have played a decisive role in the development of cold adaptation. Such isolation occurred in the glacial eastern Mediterranean when gene flow from the tropical Atlantic was interrupted by a cold-water barrier near Gibraltar. The results of this thesis show that phylogenetic and physiological constraints played an essential role in shaping ecotypic differentiation over the distribution range of *V. utricularis*, which is probably valid for marine macrophytes in general.