Ordinary and succesful

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Summary

Human alterations of the earth's ecosystems have led to profound changes in the landscape structure, the CO_2 concentration of the atmosphere, the hydrology and the global nitrogen cycle. As a major consequence, nearly all plant and animal communities in the semi-natural landscape of Central Europe are subject to a decrease of species diversity. This applies also to more natural landscapes, such as salt marshes, where species numbers are declining. Three major processes currently alter the salt-marsh ecosystem: change of land use, anthropogenic nitrogen input, and sea-level rise.

In the past two decades, the most notable change of vegetation in several abandoned salt marshes of the Wadden Sea area was the spread of native clonal grass *Elymus athericus* (Poaceae). *E. athericus* is expanding at higher elevations of the salt-marsh gradient, now frequently dominating extensive areas. In addition, this species recently also invaded lower elevations. A consequence of this expansion is a decline of species diversity in the entire salt marsh.

There are two different, non exclusive models that could explain the loss of species diversity through changing environmental conditions: (A) The ecological Model: The new, supposedly more homogeneous and nutrient-rich conditions could favour species with a high phenotypic plasticity that are able to spread very fast by means of vegetative reproduction, and that are strong competitors. (B) The evolutionary model: Changes in the environment could alter the natural selection pressure leading to rapid genetic adaptation of populations. In this thesis I followed the two outlined explanation models, one purely ecological and one integrating evolutionary and ecological processes, that could explain the success of *Elymus athericus* in expanding and invading new habitats. Ecological experiments, demographic investigations of the life history and analyses of genetic population and clone structure with molecular markers provided insight into factors that promote or hamper the invasion of this species. Figure 1.3 provides an overview on the research strategy.

In Chapter 2 we approached model (A) by testing in a field experiment at the North Frisian coast of Germany whether *E. athericus* can extend its distribution under enhanced nitrogen availability and whether its invasion can be prevented by competition with *Atriplex portulacoides*, a clonal dwarf shrub. The reciprocal effects on both species were measured as vegetation cover and above-ground biomass. *Elymus athericus* extended its distribution into the lower salt marsh when *Atriplex portulacoides* was removed. The lower distributional boundary of *Elymus athericus* in this experiment is thus probably a

result of the competition with *Atriplex portulacoides*. Neither species showed a response to nitrogen fertilization. Improvement of nitrogen availability in concentrations of the annual atmospheric input had hence no detectable effect on plant zonation and growth.

A prerequisite for many experiments in this thesis is a proper characterisation of the gradient of inundation in salt marshes. In order to explain biological zonation, elevation above the Ordnance Sea Level is frequently used as an indicator of the abiotic gradient in intertidal ecosystems. This is based on the implicit assumption that tidal elevation is directly correlated with inundation frequency and/or duration. Despite the importance of inundation for tidal ecosystems, measurements have rarely been taken directly by measuring inundation at the site of investigation. We measured Mean High Tide (MHT) and flooding frequency at three sites on the Dutch Barrier Island of Schiermonnikoog (Chapter 3). To assess the scale dependence, we compared local measurements with the estimated inundation frequencies based on the official tide gauge at a distance of several kilometres. Locally measured MHT water levels differed among sites and were consistently higher than estimated MHT water levels. With this data we subsequently estimated the inundation frequency of vegetation plots and correlated it with species distribution. In an Analyses of Variance inundation frequency accounted for three times the variance in explaining different vegetation zones than elevation. The discrepancy in annual inundation frequency of the vegetation between sites was 300% for a given tidal elevation. Estimated and measured inundation frequencies reliably correlated at a small scale (meters), but not at a larger scale (hundreds of meters to kilometres). If inundation frequency is used as an explanatory variable, it will therefore be advisable to consider the scale dependence of the measurements, in particular if different sites are to be compared.

In the evolutionary model (B) I hypothesised that changes in the environment would lead to changes in the selection pressure acting upon populations. In one of the first analyses of the genetic population structure in salt-marsh species, we investigated population differentiation through isolation by distance, and among strongly divergent habitats (thereafter named low and high marsh, Chapter 4). We intended to test the impact of different selection regimes within these habitats. High and low marsh habitats were sampled at six sites throughout the Wadden Sea area. Contrary to our expectations, an analyses with polymorphic cross-species microsatellite primers revealed significant genetic differentiation already on a very small scale (<100 m to 5 km) and isolation by distance on larger scales (60 to 443 km). After Analyses of

Molecular Variance we found that 14% of the genetic variance could be explained by the differentiation between habitats, as compared to only 8.9% among six sites on a landscape scale. This suggests that strong abiotic and biotic differences between these habitats (e.g. in inundation frequency or presence of herbivores) represent different selection regimes, which result in restricted gene flow over distances as small as 80 m.

We were particularly interested in plant response to selection measured in life history traits. The selection pressure in salt marshes could lead to genetic habitat adaptation or adaptive phenotypic plasticity on a small spatial scale. We examined two times three populations of *E. athericus* from the low and high marsh by a reciprocal transplant experiment at three sites on Schiermonnikoog (Chapter 5). For each genet different growth and reproductive parameters were measured for adult ramets in each habitat and site. Population means in growth traits and vegetative reproduction mainly reacted by a plastic response to transplantation at all sites. A positive correlation of growth and reproductive traits indicated that there was no trade-off between these parameters but there was directive selection for longer shoots. However, if we analyse the genet separately plasticity was only beneficial for genets from the high marsh. Genets from the low marsh showed reduced reproductive output if they increased in growth traits after transplantation. Populations from the low marsh were superior to those in the high marsh in sexual reproduction, which indicated a genetic differentiation between habitats. The results were consistent over sites. We found no typical home site advantage at the population level but we did at the genet level, indicating ongoing evolution towards new population reaction norms. Possibly this indicates that the relatively young populations have not reached equilibrium but are still evolving. The evolutionary process in these young populations is probably constrained by small-scale temporal and spatial variation and thus limited predictability of the environment.

Alternatively selection could act stronger on other life history stages, such as germination or seedling survival, which we investigated in Chapter 6. Field experiments in salt marshes of different age and 'invasion status' on Schiermonnikoog revealed that germination rates are low. Hence, germination is probably the most critical life history stage in *E. athericus*. Accordingly, only low numbers of indigenous seedlings could be found. Once a seedling had emerged, between 35% and 80% survived during the first season, and 26% to 35% persisted until next spring. In two transplant experiments, survival and growth of seedlings depended on parent origin, which suggests habitat adaptation. We manipulated herbivory and competition in a factorial design, in order to disentangle which interactions are most important for explaining habitat adaptation. Differences in survival and growth among seed parent origin were only present when herbivory and competition with neighbouring species were allowed, which made maternal effects as predominant source for the observed differences unlikely. Superior seedlings originated from habitats with either intense herbivory or competition. We conclude that inherited life history traits resulting from different selection pressures in the parent populations can effect establishment at new sites.

In Chapter 7 we investigated the impact of management regimes of *E. athericus* to test their impact on the genetic population structure and adaptation. Since 1972 different management regimes (mowing, grazing, untreated control) have been applied experimentally to a salt marsh on Schiermonnikoog. We analysed life history traits in the field and tested their genetic basis in a common environment experiment. In addition, we tested genetic differentiation between management regimes using five polymorphic microsatellite markers. The analyses revealed significant differentiation between management regimes. In the common environment most life history differences observed in the field persisted. Plants invested less in growth if biomass had been repeatedly removed by grazing or mowing in the past. Moreover, ramets from grazed and mown plots invested more in vegetative reproduction. We interpret this as genetic adaptation to an environment where flowering is rare and clonal reproduction is advantageous. This is one of the first examples where experimental treatments lead to a genetic differentiation both visible in molecular markers and apparent in life history traits of a plant species.

In summary, I conclude that the success of *E. athericus* probably relies for a large part on its high rates of seedling establishment, a low adult mortality and the fact that this species is a strong competitor for light against other saltmarsh species. The importance of these features depends on the selection pressure in the actual habitat and modulated by rapid genetic habitat adaptation and adaptive plasticity. Intensive herbivory can reduce the abundance, while dense vegetation sward can hinder germination of *E. athericus*. This thesis shows that a combination of approaches from community ecology, population genetics and evolutionary biology can help to understand the population dynamics of an invasive species. The methods and results presented for *Elymus athericus* may serve as model system for other native or alien invaders.