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Biological basis of biological diversity: physiological adaptations of plants to heterogeneous habitats along a sea coast

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Abstract

To understand the mechanisms of adaptations to heterogeneous habitats along a sea coast, information is needed on the causal character of phenomena in the sequence: environmental factors » adaptive plant features » endogenous control mechanism. Abiotic conditions on the sea coast form a unique environment: sand burial, high temperature, soil salinity, soil flooding. The responses of coastal plants to these conditions are analyzed in order to define possible mechanisms of adaptation. Special attention is given to the cellular mechanisms of protection of photosynthetic machinery and antioxidative protection of cellular constituents. Hormonal and cellular control mechanisms of putative adaptive responses are analyzed. Several characteristics that may possess adaptive significance are discussed e.a. phenotypic plasticity and clonality, seed dormancy, mycorrhizal symbiosis.

Key words: adaptation, heterogeneous environmental conditions, hormonal and cellular regulation, mechanisms of cellular protection, plant conservation biology.

Introduction

In order to meet the targets of the Global Strategy for Plant Conservation, understanding the biology of rare plant species is of extreme importance. More than one third of the rare and endangered vascular plant species of Latvia listed in the Red Data Book occur in coastal habitats close to the Baltic sea. Understanding of the biology of these plants is required for successful development of models with protocols for plant conservation in Latvia. In addition coastal habitats are among most vulnerable zones throughout the world, therefore the information on coastal plant biology is of general interest.

Already in the 1980s there was a debate in the scientific literature for the necessity of establishing basic physiological mechanisms for survival of plants in the heterogeneous coastal environments (Ernst 1985; Lee, Ignaciuk 1985; Rozema et al. 1985). An excellent insight into the ecophysiology of early stages of coastal dune plants was given by Maun (1994). Despite the growing body of literature on the subject within the last decades our knowledge in this field is still incomplete (fragmented in ecological terms).

Some relationships in the coastal zone are more than obvious e.g. vegetation zonation in dune and salt marsh habitats, relative abundance of some species in contrast to the relative rarity of other species in the coastal zone etc. Both coastal sand dune and salt marsh habitats show a clear sequence of plant species along a transect from the beach to inland. The characteristic spatial distribution of plant species or zonation in sea-affected habitats was first considered as initial stages of succession (Odum 1969; Doing 1985). Knowing that similarities in coastal plant communities in different parts of world in part are due to specific environmental factors, emphasis has been given mainly to plant community analysis. Using this approach, habitat types in fore-dunes are described in terms of floristics, geomorphology, ecology and climate without analysis of the biological features of adaptive value.

Another approach tends to analyze zonation from the point of putative effective environmental factors. Recent studies suggest that salt marsh zonation can not be explained only on the basis of soil salinity and tidal regime (Silvestri et al. 2005). Root oxygen availability is considered to be of extreme importance. In addition to oxygen availability, nutrient disbalance or even toxicity of several ions should be considered.

There is a continuous debate in the scientific literature on whether plant community zonation in sand dunes is predominantly determined by salt spray or by sand burial (Maun, Perumal 1999; Wilson, Sykes 1999; Dech, Maun 2005). Again, possible adaptive life form characteristics and metabolic adaptations mostly have been disregarded. To move further it would be reasonable to quote here Osmond et al. (1987) "The survival of plants in any ecosystem depends on their physiological reactions to various stresses of the environment".

It becomes clear from the above that the nature of the relationships in a coastal vegetation can not be understood simply by means of statistical data analysis based on temporal and spatial distribution of individuals. We need to know the causal character of phenomena in the sequence: environmental factors » adaptive plant features » endogenous control mechanism. While relatively good information is available on the environmental factors, we lack here mostly knowledge on what lays between the perception of a certain signal and the resulting putative adaptive feature. The need for this type of knowledge clearly shifts plant conservation biology from ecological studies towards physiological investigations.

From a physiological point of view, the rarity of a certain plant species (both in terms of populations and individuals) might be the result of two alternative mechanisms. First, species well adapted to particular environmental conditions may become rare because of a decrease of availability of potential habitats. Second, species on the distributional border or with a patchy distribution might have suppressed adaptive potential, decreased fitness and consequently a decreased number of individuals in a particular habitat.

The aim of the present paper is to discuss the recent primary scientific literature relevant to the subject and to refer the reader to most important reviews in this respect for further reading. For better understanding, the most important relevant publications from the past decades are cited. Thus the present paper is not a comprehensive review on the enormously complex problem but rather an insight into the field of coastal plant conservation from the point of view of plant biology, with emphasis on recent literature.

Coastal habitats: heterogeneous, not stressful

Coastal habitats, both sand dunes and salt marshes, are often characterized as being "stressful". While the term has been used mostly to point out that environmental conditions there are outside the optimal range for majority of the plants, it does not mean that the plants growing in a coastal zone continuously face stress conditions. Common misconceptions in use of the term "stress" have been analyzed by Otte (2001). Therefore, instead of using the term "stressful", coastal habitats can be characterized as highly heterogeneous. According to Stuefer (1996) environmental "heterogeneity" may refer to various fundamentally distinct aspects of environmental variability including scale, contrast, predictability, temporality, spatiality etc. In respect to coastal habitats it is obvious that spatial and temporal variability of both resources and abitoic factors should be considered first. Thus in temperate sand dunes a patchy distribution of nutrients and water is spatially and temporally variable (Alpert, Mooney 1996).

In ecosystems, nutrient levels not only affect primary production, but also composition of species, dominance structure and, subsequently, vegetation succession (Di Tomasso, Aarssen 1989). On the other hand, the effects of nutrient availability on single plant species strongly depend on the presence of other species (Kiehl et al. 1997).

It is well known that coastal sand dunes are low in available phosphorus. However, the effect of mineral nutrients on growth of dune plants has been less studied than that for salt marsh species. The conditions differ in a driftline communities because of annual peaks of decomposition of algal litter and consequently the amount of available mineral nutrient. The response of annual driftline species *Salsola kali* to added phosphate was shown to be more pronounced than the response to nitrate (Lee, Ignaciuk 1985). However it was argued based on the experimental data that in conditions of sand dunes with severe abiotic conditions and limited water supply, plants are unable to respond to the increased availability of mineral nutrients (Houle 1997).

Other soil-related factors besides nutrient levels are also important for coastal plants. It is commonly accepted that vegetation composition on sand dunes is related to soil development. Thus grey dunes which have the largest spatial variability in soil pH, also support the highest diversity of plant species (Iserman 2005). In coastal wetlands, the main negative impact on plant physiology is related to flooding-initiated changes in soil chemistry e.a. soil reduction (Ponnamperuma 1972). Therefore, one of the possible problems facing plants on flooded soils is related to soil reduction-dependent changes in availability of mineral nutrients.

Plasticity and clonality

Plants in general can be characterized by a relatively high level of phenotypic plasticity. Coastal plants, in particular, have a higher level of adaptation in comparison with plants from less heterogeneous environments. Clonality is a manifestation of morphological and reproductive plasticity. Biochemical or regulative plasticity is seen as induced metabolic responses to changes in environmental conditions.

Clonal growth is manifested by the ability of plants to vegetatively produce potentially independent genetically identical daughter plant units (ramets). There are different ways how clonal growth is exhibited. Evolution of clonal plant life histories has been reviewed recently by Fischer and van Kleunen (2002). The most important question about the putative adaptivity of evolution of clonal traits (seen as an optimization of fitness in different environments) was discussed. It has been considered that all four clonal life history traits, namely (i) clonal plants can reproduce both generatively and vegetatively,

(ii) vegetative reproduction can be realized with spacers of different length, (iii) vegetative offsprings can be placed in the most suitable microhabitats, (iv) ramets of clonal plants can maintain prolonged physical and physiological integrity, affect plant fitness. It appears that phenotypic plasticity should have a special role in evolution of clonal life histories.

Clonal plants are extremely abundant in coastal plant communities. It is generally believed that this is mostly due to the fact that clonal growth/clonal integration provides adaptive means for resource capturing in the highly heterogeneous environment (Price, Marshall 1999). However, experimental evidence in support to the concept is still sparse or absent. It has been even argued that clonal integration is not necessarily advantageous in all habitat types (Kun, Oborny 2003). Potentials and limitations of concepts regarding the response of clonal plants to environmental heterogeneity have been reviewed by Stuefer (1996) therefore this aspect of clonality and plasticity in coastal habitats will not be analyzed in detail here. Rather several examples and discussion on possible control mechanisms will be given below.

It is generally believed that the degree of clonal integration, which is highly variable among different species, is related to the degree of environmental patchiness and therefore to average resource availability in a heterogeneous environment. However only limited experimental evidence so far is available to support this hypothesis (D'Hertefeldt, Jonsdottir 1999). The sand sedge *Carex arenaria* from sand dunes in temperate regions forms extremely long clonal fragments (up to 12 m) with older ramets containing only rhizome and associated roots. Extensive clonal integration in *Carex arenaria* with water and nutrients being taken up by older ramets and translocated acropetally while photosynthetically fixed carbon being translocated basipetally was found (D'Hertefeldt, Jonsdottir 1999).

Resource sharing between ramets in clonal plants can be modified by hormones, similarly to their action between separate organs of an individual non-clonal plant. Resource sensing by individual ramets can be expected, as resources are generally transferred from ramets situated in microsites with relatively abundant resources to those in microsites with relative shortage of resources. However sharing of carbon can be bidirectional in contrast to sharing of nitrogen that is mostly unidirectional towards younger ramets. Consequently, the existence of a tightly coordinated control system can be expected instead of gradient-driven transport mechanisms. Limited experimental evidence so far suggests the existence of hormonal control of resource sharing in clonal plants. Thus, application of exogenous indole-3-acetic acid modulates the degree of resource sharing induced by low light intensity or low nitrogen level (Alpert et al. 2002). However there is no evidence for shifting of resource flow by hormonal treatment in a situation when resources are abundant. In addition, no physiological mechanisms have been proposed for regulation of storage of resources in particular ramets of rhizomatous clonal plants.

Regarding the persistence of integration, clonal plants can be divided in to two large groups. Genet splitter species do not form persistent physiological integration. When established, a daughter ramet splits up from the genet. Clonal fragmentation in other clonal species (genet integrators) has been proposed, but there is insufficient evidence about how often this may happen in natural conditions and of its physiological importance. It has been proposed that clonal fragmentation may result from dieback of individual ramets due to abiotic or biotic stress factors or from physiological disconnection caused by internal or external factors (Kun, Oborny 2003). The two types of clonal plants clearly represent alternative ways of dealing with environmental heterogeneity.

In general, morphological plasticity of stoloniferous clonal plant species has been shown to be considerably higher than that of rhizomatous plant species (Dong et al. 1996).

In addition to physiological integration, a less studied aspect of clonal plant networks is related to intra-genet transport of non-resource agents. Very recently experimental evidence has been shown that induced systemic resistance against herbivores exists in a stoloniferous herb *Trifolium repens* (Gomez, Stuefer 2006). It appears that a plant systemic signal generated in response to generalist herbivore damage is transported through phloem following source-sink gradients. A similar systemic response within a genet has been proposed for pathogen resistance of clonal plants (Stuefer et al. 2004). There is, however, no information available so far on how clonality affects mycorrhizal symbiosis. It remains to be demonstrated also that adaptation of clonal plants to abiotic constraints can involve systemic control within a clonal network. If demonstrated, such a mechanism will give a completely new picture on abiotic adaptations in highly heterogeneous coastal habitats.

Seed germination and dormancy

Several patterns of germination have been characterized for dune plants (Maun 1994), which reflect different mechanisms of dormancy by means of delayed germination until the optimal conditions in the environment are met. Dormant but viable seeds in soil form a seed bank as a propagule reserve for establishment of species especially after heavy environmental disturbance (Luzuriaga et al. 2005). Seed banks are important for the spatial and temporal distribution of annual coastal plant species which mostly lack vegetative propagation characteristic for many perennial coastal plants.

Halophyte seed germination has been reviewed recently in great detail (Khan, Gul 2005). Adaptations to high salinity at the germination level are represented not by maintenance of germination ability at high salinity levels but rather by the recovery potential of germination after conditions of saline imbibition. Consequently, saline-enforced dormancy of seeds represent a selective advantage in conditions of fluctuating soil salinity, such as coastal salt marshes, thus allowing seedling recruitment from a viable seed bank. It has been shown that precipitation in a salt marsh considerably reduces soil salinity leading to increased seedling establishment (more than 50 %) of a number of salt-tolerant species (Shumway, Bertness 1992). On the other hand, the ability of seeds or fruits to float in sea water for prolonged periods of time may be important for dispersal of annual plant species on temperate beaches with major sand accretion (Lee, Ignaciuk 1985). In a study using a large number of coastal plant species it was revealed that species with higher germination at relatively low NaCl have a high recovery germination after high NaCl (Hanslin, Eggen 2005). Some exceptions of the rule have been described: the marsh/shingle boundary species *Limonium bulidifolium* was observed to germinate better in any salinity than in fresh water (Woodell 1985).

It is widely accepted that the species composition of a seed bank always differs from existing vegetation (Ungar 2001; Jutila 2003). Seed bank studies of salt tolerant plant species have shown that the size and species composition of a persistent seed bank in temperate coastal salt marshes are controlled mostly by the combined action of the degree of salt stress and tidal action (Ungar 2001). However, some highly salt-tolerant plant species do not produce a persistent seed bank in the conditions of a salt marsh. It appears that certain species-specific physiological characteristics of seed germination should be taken into account.

It has been shown recently that changes in salinity and water regime during seed dormancy affect seed response at the time of seed germination (Espinar et al. 2005). Thus, the annual fluctuations in salinity and the duration of flooding affect the persistence of seed banks as well as seedling recruitment from a bank. Salinity-enforced dormancy is thought to be dependent on the endogenous balance of hormones affected by high NaCl, since it is possible to counteract the inhibition produced by salinity by fusicoccin, ethephon, and nitrogenous compounds (Khan et al. 2003).

Another aspect of seed dormancy besides seed banks is related to seed dispersal. For plants from coastal areas, seed dispersal is mostly by wind-driven sand drifting as well as by sea water transport. Besides anatomical and morphological adaptations to water transport, potentially sea-dispersed seeds should have a considerably stable dormancy status to perform successful transportation without germination. It is most reasonable to argue that the high osmotic potential of the seawater preventing water uptake is sufficient for preventing germination. However other dormancy-resembling mechanisms should not be ruled out, as seeds of many plant species readily imbibe seawater without any visible signs of germination (Khan, Gul 2005). Alternatively, seeds of both glycophytes (*Medicago sativa*) and halophytes (*Atriplex lentiformis*) can imbibe salt water with similar consequences for mobilization of stored resources and initiation of radicle protrusion (Malcolm et al. 2003). Only at the stage of hypocotyl elongation and cotyledon spreading, glycophyte seedlings become flaccid and die while halophyte seedlings are protected by means of tissue succulence.

Seeds exposed on the surface usually have very poor germination (Zheng et al. 2005) probably due to seed desiccation and light exposure. The light-dependent inhibition of germination in coastal dune plants has been suggested as a surface-avoiding mechanism in sandy habitats (Thanos et al. 1994).

Sand burial

Wind-driven sand deposition leading to burial of plants is one of the main stress factors on foredunes. Sand accretion alters physical features of the microenvironment where plants grow. Moisture and nutrients increase together with decrease in soil temperature and aeration, and light intensity (Maun 1994). It is necessary to distinguish sand burial of established plants from the effects of the burial at the stages of germination and seedling establishment. In addition, seedling establishment from germinated seeds physiologically is a more complex problem than the germination itself.

In general, the optimum depth for successful germination and seedling establishment for sand dune species is 2 to 6 cm (Maun, Lapierre 1986; Chen, Maun 1999; Zheng et al. 2005). Seed size positively correlates with rate of seedling establishment. This may be because the emergence of a seedling primarily depends on the amount of energy contained in a seed. Seeds with higher energy reserves may have a better chance for establishment in less favorable conditions. Heavier seeds in habitats with a high probability of sand burial are an advantageous trait, since they have a better chance to emerge from a greater depth. It was observed that species with relatively light seeds had a high emergence rate only at a 0.5-cm depth while species with relatively heavy seeds emerged at a higher rate from relatively greater depths (Zheng et al. 2005).

Several life form characteristics that allow to survive sand burial are important for sand dune plants. Creeping growth along a sand surface is a characteristic for coastal plants well adapted both to heavy winds and sand burial. First, many plants with a clonal growth habit have life forms similar to climbing plants. Second, many herbaceous non-clonal plants have morphological adaptations that favour emergence from sand. Third, true climbing plants are well adapted to sand dune conditions.

Clonal plants growing on sand dunes have characteristics similar to those of true climbing plants – young branches of stolones or rhizomes act as searchers and explorers reaching for resources in the highly heterogeneous environment. For climbing plants, a juvenile phase might represent a self-supporting growth habit maintained by suppressed elongation growth due to suboptimal conditions, e.a. low light. Similarly, clonal growth by elongation can be significantly suppressed during periods when inadequate conditions prevail. Linaoid plants growing on open sand dunes with few climbing opportunities have adopted a modified growth strategy where older perennial stems form underground axes generating shorter-lived stems above the surface of the sand (Isnard et al. 2003).

A number of plants exhibit clonal features only after being buried by sand at an intensive rate. On burial *Honckenya peploides* forms numerous adventitious roots from a newly formed subvertical rhizome (Gagne, Houle 2002). At the end of the vegetation season, buried stems become rhizomes with numerous adventitious roots and buds. In the following spring overwintered buds develop morphologically distinct shoots with smaller regularly and densely positioned leaves, allowing efficient growth of the shoot through the thick layers of sand (Ievinsh, unpublished data). Formation of morphologically different shoots upon severe burial is characteristic also for other sand dune plants e.a. *Alyssum gmelinii* and *Salsola kali* (Ievinsh, unpublished data).

Several plant species well adapted to sand burial represent "obligate buried species", as a certain level of sand accretion is necessary to maintain optimal growth of these plants. An extreme example is represented by *Salsola kali*, in which shoot dry mass can be stimulated up to two times following 14 weeks of sand accretion with the rate of 12 mm week^{-1} (Lee, Ignaciuk 1985). Sand buried plants of the well-adapted dune plant *Cakile edentula* exhibit higher leaf chlorophyll concentration than unburied plants (Zhang 1996). Another coastal pioneer species *Triplasis purpurea* has been shown to increase both plant size and seed production after partial burial by sand (Cheplick, Demetri 1999). Increased fitness (both biomass and seed production) of buried plants depends not only on sand burial itself but rather from the cumulative effect of burial and improved moisture and nutrient status associated with it (Zhang, Maun 1992; Zhang 1996). In experiments where washed sand instead of natural sand was used for plant burial the growth increase of buried plants was only temporary.

Formation of new stem nodes is a prerequisite for burial-induced shoot elongation (Voesenek et al. 1998). Endogenously produced ethylene has been shown to be involved in stem elongation of buried plants by stimulating the process of stem node formation (Voesenek et al. 1998). Soil burial-stimulated internode elongation also seems to be regulated by ethylene (Suge et al. 1997). Other investigations report an increase of the length of existing internodes (Maun 1994). For grasses partial burial of seedlings stimulates growth of new leaves and tillers (Maun 1994).

However even typical sand dune species can negatively respond to sand burial. Burial was shown to significantly reduce the biomass of the embryonic dune and foredune species *Leymus mollis,* having high survival rates (87 %) during burial by 2 cm of sand per week for seven weeks (Gagne, Houle 2002). Another typical foredune species *Honckenya peploides* appeared to be completely intolerant to burial – no seedling survived high burial rates of 1.5 or 2 cm of sand per week (Gagne, Houle 2002).

Tolerant-to-burial coastal dune species exhibiting no burial-dependent increase in elongation can shift biomass accumulation from below-ground to above-ground parts during prolonged partial burial (Brown 1997). In addition, nitrogen allocation can be directed from roots to stem and leaves emphasizing the importance of resource allocation for burial tolerance.

Resistance to sand burial involves tolerance to periods of prolonged dark conditions. Another possible stress factor during sand burial is a reduction of gas diffusion. Therefore it can be proposed that some common metabolic resistance mechanisms exist between adaptation to sand burial and flooding. Even species from dune habitats exhibit different degrees of sand burial tolerance that can be related to light exclusion. In a study with 29 New Zealand dune species survival in complete darkness ranged from 19 to 140 days (Sykes, Wilson 1990). It was suggested therefore that dark survival of dune species often might be considered as a pre-adaptation.

As a physiological adaptation to survive sand burial an ability to maintain photosynthetic intensity while in the buried state as well as a capacity to restore photosynthetic activity after the burial have been demonstrated (Kent et al. 2005). Thus elasticity of photosynthetic response allows buried plants to quickly replenish carbohydrate reserves between two burial episodes. The exact mechanism of the ability to maintain photosynthesis in the buried conditions (low light intensity, low rate of oxygen diffusion) is not known. In the case of clonal plants, physiological integration might be one of the mechanisms. The formation of aerenchyma-like tissues might solve the problem by oxygen diffusion, but no experimental evidence so far has been published.

Mycorrhizal symbiosis play a role in plant adaptation to sand burial (Perumal, Maun 1999). Mycorrhizal plants of both *Agropyron psammophilum* and *Panicum virgatum* subjected to sand burial had a higher CO_2 exchange rate, leaf area and biomass in comparison with the respective non mycorrhizal plants.

As opposed to sand burial, wind-driven removal of surface sand layers should be considered in the coastal environment. This may have both positive and negative consequences for driftdline and dune plant physiology. For already established plants, sand removal leads to exposure of rhizomes and roots and eventual death of plants in the most severe situations. However clonal fragmentation as a result of sand erosion may have a positive effect on the dispersal of clonal plants. For seeds in a seed bank, removal of an uppermost sand layer may result in loss of burial-imposed dormancy and establishment of seedlings in favorable conditions.

Light, temperature, salt – protection of photosynthesis

Protection of photosynthetic machinery is a crucial in maintenance of plant fitness in conditions of suboptimal conditions. Sand dune habitats in temperate regions in summer are characterized by a high irradiance of incident and reflected light as well as by high substrate temperatures. On sunny days surface sand temperatures on south dune slopes can rise up to 50 °C (Maun 1981). Consequently high light stress in combination with heat stress are inevitable consequences of existence in sand dunes in summer.

Acquired thermotolerance as an ability of plants to survive otherwise lethal high temperature stress can be induced by a mild high temperature (for a review see Sung et al. 2003). In general acquired thermotolerance is associated with a well studied heat shock response through induction of synthesis of heat shock proteins (Schoffl et al. 1998; Queitsch et al. 2000). While acquired thermotolerance has been studied in different model systems in controlled conditions it is not known what mechanism can count for thermal tolerance in natural conditions. In the context of the present paper it would be important to understand if adaptation of dune plants to high substrate and air temperatures involves mechanisms similar to those for acquired thermotolerance. It is reasonable to suggest that different parts of a dune plant in conditions of full sunshine will be exposed to a temperature gradient with a different physiological consequences. In addition the effect of root zone heat stress or thermotolerance on protection of photosynthetic machinery should be considered.

Effect of moderate heat stress on photosynthesis has been recently analyzed and new mechanisms for damage and protection have been discussed (for a review see Sharkey 2005). It was argued that mainly thylakoid reactions are affected by heat stress because high temperature tolerance can be improved by altering thylakoid lipid composition.

As major damage during high temperature stress is associated with active oxygen species-dependent damage of cellular biomolecules (see Suzuki, Mittler 2006 for a recent review) one might assume that an enzymatic antioxidative system is an important constituent during both basal as well as acquired thermotolerance. Increased peroxisomal ascorbate peroxidase gene expression is a part of the heat shock response (Shi et al. 2001). Expression of this gene from barley in *Arabidopsis thaliana* resulted in enhanced thermotolerance at 35 °C suggesting that scavenging of H_2O_2 in peroxisome under heat stress is important for a general thermotolerance.

Experimental evidence for cellular regulation against heat stress-dependent oxidative damage has been shown for *Arabidopsis thaliana* (Larkindale, Knight 2002). Calcium as a main second messenger acting in concert with ethylene, abscisic acid, and salicylic acid protects plant tissues against oxidative damage during post-stress recovery. Thus these endogenous regulators are important for basic thermotolerance after short-time heat treatment. Other studies have shown that salicylic acid-dependent signaling can promote basal thermotolerance in *Arabidopsis thaliana*, while acquired thermotolerance does not depend on salicylic acid (Clarke et al. 2004). It appears that different endogenous signaling systems may be involved during control of different types of thermotolerance.

Besides light and heat, other environmental factors in coastal habitats can affect plant physiology through photosynthesis. Salt stress is generally supposed to have a depressive effect on photosynthesis. Salt stress inhibits photosynthesis mostly through photosystem II activity (Sharma, Hall 1991). Detailed investigations have shown that salt stress enhances photodamage of photosystem II by inhibiting the repair of photosystem II via suppression of transcription and translation of light-dependent genes (Allakhverdiev et al. 2002). Decrease of photosynthesis in salt stress conditions stimulates excess excitation energy which may cause photodamage to photosystem II in the case of limited energy dissipation. The dissipation of harmful energy is thought to depend on heat formation through the zeaxanthin/violaxanthin system at the antenna region of photosystem II (Gilmore 1997). However until recently mostly glycophyte species have been studied in this respect. Recent data suggests that for halophyte species photosynthetic machinery is extremely well adapted to conditions of high salinity.

Photosynthesis of the sand dune stabilizing obligate halophyte species *Cakile maritima* is impaired at high salinity (400 to 500 mmol l^{-1} NaCl) mainly through a stomatal limitation mechanism with no inhibitory effect on CO_2 fixation enzymes and only a minor suppressive effect on H^+-ATPase activity (Debez et al. 2006).

One of the strategies allowing to grow in a highly saline soil is increased tolerance of photosystem II against photoinhibition caused by a combination of high salinity and high light. As an extreme example, *Suaeda salsa* is an obligate halophyte with 200 mmol l^{-1} NaCl as an optimal concentration for growth. Even 400 mmol l^{-1} NaCl combined with full sunlight did not cause any significant negative effect on photosystem II photochemistry (Lu et al. 2002). The protective effect was not due to an increased amount of protective pigments, either as shown for other species under the effect of salinity (Qiu et al. 2003) or drought and light stress (Masojidek et al. 1991). Similarly, a facultative halophyte *Artimisia anethifolia* well adapted to grow in conditions of high salinity showed no signs of decrease in photosystem II photochemistry due to high salinity even in high light conditions (Lu et al. 2003a; Lu et al. 2003b). The results suggest that photosystem II of halophytes shows high resistance both to high salinity and to photoinhibition. As in *Suaeda salsa* (Qiue et al. 2003) the protective effect was not associated with an inducible increase in xanthophyle cycle activity. However, the violaxanthin/zeaxanthin cycle was involved in the protection against high light. As a result the CO_2 assimilation rate of halophytes is raised in conditions of high light but optimal salinity (Lu et al. 2003c).

Recent data suggest that obligate halophytes are better protected against heat stress than glycophytes. Studies on high salinity effects on halophyte photochemical aspects of photosystem II showed that salt-adapted plants maintain a high CO_2 assimilation rate even at extreme temperatures above 40 °C suggesting enhanced thermotolerance of halophytes (Wen et al. 2005). The increased thermostability is independent of the degree of salinity (Lu et al. 2003c). Regarding the mechanism, it was shown that the increased stability of the oxygen-evolving complex is responsible for thermostability of photosystem II during salt adaptation (Lu et al. 2003c). It is not clear however what molecular changes in the complex are involved. A rapid adaptation of photosynthesis to high temperature by salt treatment is of extreme physiological importance for sand dune species.

Increased activity of enzymatic antioxidants has been proposed as a mechanism for increased protection of photosystem II of salt tolerant species and cultivars (Meloni et al. 2003). In addition, the xanthophyll cycle may protect photosynthetic apparatus in the obligate halophyte *Atriplex centralasiatica*, which is well adapted to increased salinity by a high tolerance of photosystem II to salinity and photoinhibition (Qiu et al. 2003).

It is generally accepted that in conditions with limited CO_2 supply the C_4 pathway is advantageous over the C_3 pathway because of more efficient CO_2 use in C_4 plants. In this respect several species with induced shift between photosynthesis pathways have been described. One such species is the aquatic plant *Hydrilla verticillata*, which changes from C_3 to C_4 in conditions of dense vegetation (Reiskind et al. 1997). Operation of an inducible CO_2 concentrating mechanism allows to minimize photorespiration in conditions of limited CO_2 supply together with high temperatures and O_2 level. Also, in conditions of water stress C_4 plants have better adaptation capacity and better water use efficiency in comparison with C_3 plants. In part this may be related to several anatomical features and biochemical characteristics at the level of CO_2 fixation (Nelson et al. 2004). On the other hand, better tolerance against water stress exhibited in C_4 plants is related to better ability to withstand endogenous oxidative stress (Nayyar, Gupta 2006). In shifting sand dunes mostly C_4 species are present because of a higher net photosynthetic rate in conditions of high temperature and light intensity accompanied by water stress episodes and, consequently, limited CO_2 supply. Recent findings indicate that C_3 species in sand dunes may exhibit characteristics of C_4 photosynthesis (Niu et al. 2006).

A switch from C_3 to CAM photosynthesis is inducible in *Mesembryanthemum crystallinum* after salinity treatment (Adams et al. 1998). Likewise, with the other inducible features, CAM becomes inducible only at the adult stage. However, compatible solute biosynthesis can be induced by salt treatment at the early stages of development. Like C_4 plants, intermediate C_3/CAM species are more resistant to environmental stress than typical C_3 species (Miszalski et al. 1998). In particular, one such species *Sedum album* shows enhanced antioxidative protection due to a drought-induced shift from C_3 to CAM photosynthesis (Castillo 1996).

Cold and freezing stress responses and the related adaptations are not analyzed in the present paper mostly because they are not specifically expressed in the coastal zone. However, it should be noted that in many respects cellular adaptations to cold and freezing involves systems (e.a. osmoprotectants, enzymatic antioxidants etc.) which are common with other stress responses (e.g. heat, dehydration by water stress and freezing, high salt).

Salinity

It is commonly thought that all plant species growing in a saline environment are halophytes. While it is reasonable from an ecological point of view to designate plant species growing on saline soils as halophytes it does not make any sense from a physiological point of view. To accentuate physiological plant responses to salinity, designation as halophytes is unbiased only for plant species which attain optimum growth at a certain increased level of NaCl. Thus, obligate halophytes are competitive only in conditions of increased salinity. Subsequently, in addition to the above mentioned obligate or true halophytes, facultative halophytes are salt-tolerant species whose growth is not affected at a certain level of NaCl in a substrate. In contrast, glycophytes are plants susceptible to even a minor increase in NaCl concentration. It should be noted that the above system of classification does not impose any absolute NaCl levels for any of the types but instead can be used only in relative terms.

True or obligate halophytes exhibit increased growth rates and higher tissue biomass at moderate salinity levels in comparison with non-saline soils (Short, Colmer 1999). Optimal salinity levels for obligate halophytes are in the range of 50 to 300 mmol l^{-1} NaCl (Lee, Ignaciuk 1985). Dependency from high salt concentrations can be manifested also by stimulation of photosynthetic electron transport in chloroplasts by high chloride levels for obligate halophytic species (Critchley et al. 1982). However in contrast to salt marshes where sea water inundation causes increased soil salinity, sand dune plants receive NaCl mainly in the form of salt spray (Rozema et al. 1985). It is reasonable therefore to distinguish tolerance to soil salinity from tolerance to salt spray (Greipsson, Davy 1996).

Also, different mechanisms of salt tolerance might be responsible for the two types of salinity tolerance. Consequently, plants tolerant to high soil salinity may be susceptible to increased salt spray and vice versa.

In general, salinity tolerance mechanisms are described as cellular, organizational, and whole plant adaptations. For an extensive review of different salt tolerance mechanisms readers are directed to Shannon (1997). Physiologically these mechanisms are oriented towards restriction of ion accumulation in shoots. Mechanistically, this can be achieved by facilitation of ion transport systems (i) transferring Na^+ taken up in roots back to the external medium, (ii) sequestering Na^+ into the vacuole, (iii) transferring Na^+ to older leaves, (iv) excreting salt into salt glands or onto leaf surfaces. Other additional means include cellular osmotic protection due to adjusting of internal osmotic balance by accumulation of compatible solutes and protection against consequences of endogenous oxidative stress.

Salt exclusion at the root level at first seems to be the best solution to the problem of salinity. However a drawback with effective Na^+ exclusion from plant cells is related to the fact that Na^+ influx through the plasma membrane is passive in contrast to active efflux (Maathuis, Amtmann 1999).

Recent studies with an emerging model species for plant salt tolerance studies *Thellungiella halophila*, a close relative to *Arabidopsis thaliana*, indicate that limitation of Na^+ influx in leaves is the main mechanism of salt tolerance in *T. halophila* (Wang et al. 2006). A large proportion of Na^+ taken up into the roots is immediately transferred back to the external medium. Obviously, a high selectivity for K^+ over Na^+ exists in all major cation uptake channels in root membranes of *T. halophila*. Thus, *T. halophila* appears to be a typical "excluding" species not relying on cellular salt tolerance mechanisms.

Damage from high salinity at the cellular level is associated with three different mechanisms. Firstly, ion toxicity is caused by excessive accumulation of Na^+ and Cl^- ions in the cytoplasm leading to ionic disbalance. This can be counteracted by an increased transport intensity of the ions to vacuole. Secondly, even if the excessive ions are compartmented in the vacuole, the osmotic potential needs to be balanced according to a decreased external water potential, otherwise damage to macromolecules will occur. Thirdly, a high cellular NaCl concentration causes an increased formation of active oxygen species with possible oxidative damage of cellular constituents. The formation of active oxygen species under high salinity can be attributed mostly to action of NaCl on the photosynthesis machinery. Here, the photosynthetic electron transfer system is a most obvious candidate for an activator of oxygen during salt stress.

The capacity of transporters to discriminate between K^+ and Na^+ and to translocate them is a critical feature to allow accumulation of high ion concentrations facilitating salt tolerance. In contrast to glycophytes that exclude Na^+ in the shoot, halophytes allow high levels of Na^+ to be translocated to the shoot. Na^+ sequestration into the vacuole is a critical feature of salt tolerance if Na^+ has been taken up in the shoot (Niu et al. 1995). In general, halophytes have higher basal and inducible Na^+/H^+ antiporter activity than glycophytes, supporting the role of Na^+/H^+ antioprters in salt tolerance through Na^+ exclusion from cytoplasm to vacuole (Zhao et al. 2006). At the cellular level, Na^+/H^+ antiporters catalyzing exchange of Na^+ for H^+ across the tonoplast membrane results in removal of Na^+ from cytoplasm into vacuole. The expression of a vacuolar Na^+/H^+ antiporter *SsNHX1* in *Suaeda salsa* is increased by salt stress, suggesting an important role in salt tolerance

(Ma et al. 2004). The antiporter uses an electrochemical gradient of protons generated by vacuolar H^+-translocating enzymes, e.a. H^+-pyrophosphatase. By expressing the *SsNHX1* from *Suaeda salsa* it was possible to increase salt tolerance in rice (Zhao et al. 2006) and by expressing the H^+-pyrophosphatase gene *SsVP* from *Suaeda salsa* – salt and drought tolerance in Arabidopsis (Guo et al. 2006).

A recent detailed review on high-affinity potassium and sodium transport systems in plants relevant to this paper was produced by Roriguez-Navarro and Rubio (2006). Readers interested on a whole array of Na^+ tolerance mechanisms related to Na^+ transport are directed to an excellent review by Tester and Davenport (2003).

Osmotic adjustment is one of the major cellular protection mechanisms against the adverse effects of salinity, drought, and high and low temperature stress. All these stress factors are extremely important in the coastal zone. Consequently, the capacity to adjust osmotic potential in tissues to a certain degree reflects a plant's ability to withstand abiotic stress of the coastal zone in general. Different species accumulate various chemical substances as osmoprotectants. In general they belong to polyols and sugars (e.g. mannitol, trehalose), amino acids (e.g. proline), and to ammonium compounds (glycine beataine) (Nuccio et al. 1999).

An increased amount of osmoprotectants in plant tissues under high salinity is an inducible response and it is thought that the more salt-tolerant species have a higher degree of salinity-induced osmotic adjustment. By tracing changes of compatible osmolytes in leaf tissues of several halophytes throughout the growing season in natural conditions it was shown that the highest osmolyte concentrations coincide with the potentially most stressful period (Murakeözy et al. 2003). Thus the amount of cellular osmoprotectants, even of salinity-adapted plants, is a tightly controlled and inducible feature.

Another line of evidence on compatible osmolytes as cellular stress protectants comes from studies with genetically engineered plants forced to produce higher amounts of these substances. The amounts of glycine betaine accumulated in genetically engineered plants with increased tolerance to a variety of abiotic stressors suggested that the protective effect can not be attributed to osmotic adjustment (Sakamoto, Murata 2000). Rather, direct protection of membranes and macromolecules can be suggested. Glycine betaine are thought to protect an oxygen-evolving complex of photosystem II and native conformation of Rubisco protein in chloroplasts against adverse consequences of wide array of abiotic stress factors including salt, high and low temperature, and drought.

Additional water supply to maintain osmobalance is mediated by a group of channel forming proteins designated as aquaporins (Hill et al. 2004). A relationship has been established between salt tolerance of plants and the activity of aquaproins. However, the role of aquaporins in salinity tolerance of halophytic plants is not clear.

Ion sequestration into salt glands, salt hairs or onto the leaf surface is one of the possible salt avoidance mechanisms. Not all halophyte species are capable of secreting salt, and for the salt secreting species a particular intensity of the secretion is both species-specific as well as strongly dependent on environmental conditions. The efficient salt secretors e.g. *Spartina anglica*, can translocate as much as 60 % of the absorbed Na^+ onto the surface, in contrast to the halophyte *Armeria maritima* which can secrete only 4 % (Rozema et al. 1981). It is reasonable to assume that at increasing salinities plants can secrete relatively larger amounts of absorbed salt. Indeed, *Spartina anglica* in the above mentioned study was from the most saline habitat (Rozema et al. 1981). Also, increasing salinity stimulated

Na^+ and Cl^- secretion by salt glands of *Glaux maritima* (Rozema, Riphagen 1977). At maximum salinity a five-fold increase in the amount of secreted ions was noted with only a two-fold raise of the osmotic potential of the plant sap.

Further, dependence of the density of salt glands and salt hairs on external NaCl concentration can be expected. It may seem paradoxical, but an increase in medium salt concentration resulted in a decrease of salt hair density in the salt marsh species *Atriplex triangularis* (Karimi, Ungar 1989). In addition, the hair density was reduced also by low light and lack of aeration. In the genus *Zoysia* (Poaceae), salt gland density was not affected by external salinity (Marcum et al. 1998). However, salinity tolerance of a particular cultivar or accession was negatively correlated with shoot Na^+ level and positively correlated with leaf salt gland density and Na^+ secretion rate.

Many of the adaptive features leading to increased salt tolerance are inducible, e.i. they appear only when high salinity is present or the intensity increases in response to salt treatment. These include leaf or stem succulence (Rozema et al. 1985). Salt-inducible shoot succulence leading to massive inorganic ion accumulation, especially of Na^+ and Cl^-, accounts for exceptional salt tolerance of several coastal halophyte species (Naidoo, Rughunanan 1990).

One of the aspects of salinity-imposed cellular damage is associated with lipid peroxidation, indicating a harmful effect of endogenous oxidative stress-associated processes (Hernandez et al. 1995). Therefore it is logical to propose that plants with higher constitutively expressed or salinity-induced antioxidative enzymatic capacity will have higher tolerance to saline conditions. Indeed, a number of recent publications show that improved resistance to oxidative stress may improve growth at increased salinity (Jungklang et al. 2004; Sharma et al. 2005). Moreover, a causal relationship has been established between high or increased activities of antioxidative enzymes and the degree of protection from salt-associated oxidative damage (Mittova et al. 2004; Wahid et al. 2006). However, mostly salt-tolerant species or salt-adapted plants have been investigated in this respect. No studies so far on comparing antioxidative defense systems between obligate and facultative halophytes in conditions of high salt have been described. Only very recently, experiments were performed with an obligate halophyte *Suaeda salsa* in which growth is enhanced by NaCl up to 400 mmol l^{-1} (Zhang et al. 2005) as well as with another obligate halophyte *Crithmum maritimum* with an optimum NaCl concentration at 50 mmol l^{-1} (Amor et al. 2005). It appears that for *Suaeda salsa* the activity of chloroplastic superoxide dismutase increases after NaCl treatment in a concentration-dependent manner contributing to resistance of salinity-dependent oxidative stress (Zhang et al. 2005). Thylakoid-bound superoxide dismutase is thought to be responsible for scavenging of photogenerated superoxide radicals in close vicinity to photosystem II. Similarly, the intensity of lipid peroxidation at 50 mmol l^{-1} NaCl for *Crithmum maritimum* was lower than in control conditions, indicating better protection against endogenous oxidative stress by means of increased activities of superoxide dismutase, catalase, and peroxidase (Amor et al. 2005). An optimal NaCl concentration increased the activity of chloroplast antioxidative system enzymes, e.a. ascorbate peroxidase and glutathione reductase, for halophyte *Suaeda salsa* with no harmful effect on the intensity of lipid peroxidation or photosynthesis (Pang et al. 2005).

A detailed study with a true mangrove *Bruguiera parviflora* revealed that four of five antioxidative enzyme activities, namely, superoxide dismutase, ascorbate peroxidase,

peroxidase, and glutathione reductase, significantly increased after treatment with 400 mmol l^{-1} NaCl (Parida et al. 2004). Only the catalase activity decreased after the treatment. It was concluded that NaCl-dependent overproduction of H_2O_2 functions as a signal causing upregulation of enyzmatic antioxidants resulting in unchanged level of lipid peroxidation. Catalase as a target for salinity-induced oxidative stress has been shown also for potato plants (Fidalgo et al. 2004).

Other exogenous factors can affect plant tolerance to salinity. Thus, salt tolerance of coastal foredune leguminous plant species was shown to increase with mycorrhizal colonization (Tsang, Maun 1999). Increased tolerance was manifested as a higher content of chlorophyll and shoot dry mass in mycorrhizal plants in conditions of high salinity in comparison with non-mycorrhizal plants. Also, as mycorrhizal plants had a higher number of bacterial root nodules, the presence of mycorrhizal symbiosis improved the nitrogen status.

In respect to endogenous control mechanisms of salinity tolerance, a close relationship between salt stress tolerance of undifferentiated glycophyte tissues and ethylene production intensity has been shown (Alvarez et al. 2003).

When more realistic combined effects of salinity and following soil drying are concerned, even halophytic species with high tolerance to osmotic stress exhibit decreased tolerance with increased duration of stress conditions (Brown, Pezeshki 2006). It appears that drought magnifies the adverse effects of high NaCl on mineral nutrition, selectively decreasing nutrient uptake (Brown et al. 2006). A possible cumulative effect of different environment extremes should be considered in further studies. In addition, due to the presumably inducible nature of defense responses, acquired resistance mechanisms should be suggested.

Water – too little or too much

Strong variations between driftline, primary dunes, and salt marshes may exist in respect to water availability. A low soil water potential is a common situation in sand dunes. However, as many adaptive morphological and biochemical features are present in sand dune plants conferring relatively high tolerance to water shortage (Ripley, Pammenter 2004), water stress should not be considered as an important physiological problem. It is evident also from ecological studies that water availability is not among the main factors limiting plant distribution in coastal dunes (Monneveux, Belhassen 1996; Dech, Maun 2005). A physiologically more serious problem can occur in salt marsh habitats when flooding by sea water is followed by a prolonged drought period.

Rainfall is extremely important for maintaining an appropriate water balance both in sand dunes and in salt marshes It appears that in salt marshes rainfall in combination with salt water inundation are the most important factors affecting water-salt relationships in plants. In addition, other edaphic factors (e.a. soil redox potential, nutrient availability) depend on inundation by sea water (Pennings, Callaway 1992).

Coastal marshes are characterized by significant water level fluctuations varying from prolonged drought conditions to complete submergence. Both avoidance and tolerance strategies are therefore important as adaptive features for coastal marsh species. Investment in shoot elongation in an effort to reach the water surface can be viewed as an advantageous trait in this respect (Macek et al. 2006). The most tolerant plant species (e.g.

Eleocharis cellulosa) can withstand more than four months of complete submergence and completely recover afterwards (Macek et al. 2006). The ability to recover photosynthetic activity after prolonged submergence is of special importance, as significant depression of the photosynthetic rate during complete submergence is a general phenomenon for macrophyte species (Mauchamp et al. 2001). Depression of vegetative reproduction of clonal plants during conditions of submergence is documented (Vretare et al. 2001).

A completely different situation is evident when the rise of water level leads only to prolonged root zone flooding. Then conditions of anoxia are formed only in root tissues while there is an abundance of oxygen in shoot tissues. Consequently, adaptive strategies leading to improved aeration of submerged tissues can be expected. Here aerenchyma development in shoots and roots represent an induced feature allowing transport of atmospheric oxygen to submerged roots. A recent review summarizing regulation of aerenchyma formation has been published by Evans (2003). In addition, formation of adventitious roots with relatively high porosity facilitating internal aeration due to waterlogging has been described (McDonald et al. 2001; Li et al. 2006).

Severity of oxygen deprivation due to flooding and resultative anoxia injury may have a clearly seasonal character (Crawford 2003). In salt marshes, inundation by sea water is accompanied by a simultaneous reduction of oxygen concentration.

According to a recent review, generation of reactive oxygen species is characteristic for all physiological phases of oxygen deprivation, being most pronounced during reoxygenation (Blokhina et al. 2003). During post-flooding in conditions of oxygen abundance, the formrd oxygen radicals and acetaldehyde undergo oxidative chain reactions in general leading to destruction of membrane lipids (Crawford 2003). Thus, while tolerance to anoxia depends mostly on the degree of metabolic adaptation to anaerobic conditions, post-anoxia tolerance will depend mainly on enzymatic antioxidative capacity of the tissues expressed constitutively or induced by anoxia.

Regulation of adaptation to soil flooding at the level of sensing and signal transduction has been reviewed by Visser et al. (2004) and recently by Voesenek et al. (2006). New mechanisms of adaptation against consequences of flooding and submergence have been proposed (Pierik et al. 2005; Mommer et al. 2006). A recent review (Bailey-Serres, Chang 2005) summarizes also findings on low oxygen sensing in plants leading to physiological adaptation to oxygen deprivation. In the context of the present paper it should be noted that both reactive oxygen species as second messengers and ethylene as an endogenous hormone appear to be involved in the control of adaptation to hypoxia. Most importantly, aerenhcyma formation as an induced response to root zone flooding has been shown to be regulated by ethylene (Viser et al. 1997). Thus, a good theoretical basis has been formed to understand a complex physiological phenomenon of plant responses and adaptations to increased water level and oxygen shortage. This knowledge should be used in further experimental work aiming at understanding of particular adaptation mechanisms for different plant species from coastal habitats. Most importantly, the data analyzed so far in the context of flooding and submergence are mostly from fresh water species. There is a serious gap in a theoretical knowledge on complex adaptive mechanisms to flooding by a salt water. Only limited experimental evidence so far indicate that increased salinity leads to suppression of morphological adaptations against hypoxia (Rolletschek, Hartzendorf 2000). Possible interactions between waterlogging and salinity from the point of agriculture has been reviewed recently (Barrett-Lennard 2003).

Mycorrhizal symbiosis and other biotic interactions

The extent of mycorrhizal colonization of coastal plants to a great extent depends on a habitat type. In shifting dunes there is a limited abundance of mycorrhiza, which increase with dune stabilization (Siguenza et al. 1996). One of the reasons for poor mycorrhizal colonization of coastal plants is possibly related to high soil salinity. It has been suggested that in general mycorrhizal fungi have a lower salinity tolerance than halophytic plants (Johnson-Green et al. 2001). Therefore, in salt marshes mycorrhizal infection is negatively related with the frequency of inundation with sea water, increasing towards the upper reaches of salt marshes. Comparing the intensity of mycorrhizal infection between inland and coastal populations of one species, *Distichlis spicata*, coastal plants had only 9 % intensity of the mycorrhizal colonization in contrast to 28 % infection of inland plants (Allen, Cunningham 1983). These plants excrete salt through leaf salt glands and the intensity of mycorrhizal colonization seems to be independent on soil salinity.

Ascomycete species have been shown to be more resistant to moderate NaCl stress (50 to 200 mmol l^{-1}) than basidiomycete species (Bois et al. 2006). Higher ascomycete resistance to salt stress in part may be due to accumulation of proline or mannitol as osmoprotectants.

Increasing salt concentrations promote mycorrhizal hyphal growth while decreasing arbuscule and vesicle numbers (Tsang, Maun 1999). Regarding the particular effect of soil salinity on spore germination and subsequent hyphal growth, it appears that the NaCl effect is species specific (Juniper, Abbott 2004). In general, spores germinated in the presence of high NaCl (up to 300 mmol l^{-1}) exhibit increased hyphal growth after transfer to non-saline conditions.

Statistical evaluation of the degree of mycorrhizal colonization is often difficult due to the several factors (Hildebrandt et al. 2001). Firstly, the degree of colonization is not constant during a life cycle and has a pronounced seasonality (Siguenza et al. 1996). Secondly, a sharp gradient of environmental conditions in coastal areas can lead to a patchy distribution of spores and hyphae in the soil (Carvalho et al. 2004).

However, the above does not imply that mycorrhizal colonization is less important for coastal plant biology. On the other hand, mycorrhizal hyphae bind sand grains facilitating dune stabilization (Sutton, Sheppard 1976).

Possible physiological mechanisms of arbuscular mycorrhizal symbiosis-dependent protection of host plants against detrimental stress effects have been reviewed recently (Ruiz-Lozano 2003). A particular emphasis was given to mycorrhiza-enhanced cellular osmotic adjustment. While the researchers all believe that mycorrhizas in general have a positive effect on host plant physiology, no conclusive evidence has been shown so far. However, while expected positive results in controlled experiments dealing with a limited number of stress factors have been shown, the effect of mycorrhizal symbiosis on plant fitness tested in field experiments mostly have been unpredictable.

Recently it was shown that arbuscular mycorrhizal symbiosis has a stress-like effect on the salt marsh species *Aster tripolium* in the early stage of development (Neto et al. 2006). However, improvement of plant growth in flooded conditions during subsequent phases of development was shown. Regarding a possible mechanism of positive effect of symbiosis, the beneficial effect of mycorrhizal colonization on flooding-induced instability of proteins in the photosystem II complex increasing maximum photochemical efficiency was proposed.

In conditions of a heavy metal-contaminated salt marsh, mycorrhizal colonization was negatively correlated with the contents of Pb and Zn in plants while biomass was positively correlated with the degree of colonization (Carrasco et al. 2006). The beneficial effect of mycorrhizal colonization was related to the reduction of plant uptake of heavy metals, especially lead. However, the effect was reduced at high salinity.

In wetlands in general flooding is one of the main factors affecting mycorrhizal colonization in conditions where available inorganic phosphorus levels do not fluctuate significantly. The level of arbuscular colonization is positively correlated with the duration of the unflooded period (Ray, Inouye 2006). Therefore, the length of the unflooded period can be used to predict the level of mycorrhizal colonization. In studies where both flooding and salinity effects on mycorrhizal colonization of *Aster tripolium* plants were analyzed, it was shown that continuous flooding reduced both the degree of colonization and fungal growth (Carvalho et al. 2003). However tidal flooding decreased colonization only if combined with an intermediate salinity level. It appears that salinity has a more deleterious effect on mycorrhizal symbiosis than flooding, especially at the stage of initiation of the symbiosis.

From an agronomical point of view, several investigations report a positive effect of inoculation with arbuscular mycorrhiza on plant productivity in conditions of irrigation with seawater (Yano-Melo et al. 2002; Giri et al. 2003; Rabie 2005). The mechanism involved is believed to be associated with mycorrhiza-enhanced protection of photosynthesis, water use efficiency, and increase in cellular osmoprotectants (Ruiz-Lozano, Azcon 2000). Similar mechanisms of protection are likely to be present in native coastal plants infected with mycorrhizal fungi.

Biotic interactions, excepting mycorrhizal symbiosis, are a less studied aspect of biology of coastal plants. As in other habitats, plant-plant interactions in coastal habitats are expected. In ecological studies, the term "facilitation" has been widely used to describe positive interactions between plants when neighboring plants buffer one another from environment extremes. While the term has been used together with the another term, "competition", to explain secondary succession in salt marsh habitats (Bertness, Shumway 1993) it is quite clear that in addition to competition for resources, from the point of view of chemical ecology, both facilitation and competition are related also to the promotive or inhibitory effect of certain plant-derived chemicals.

Due to the lack of experimental evidence, plant-plant interactions among sand dune and salt marsh plants will not be further analyzed within the present paper. It should be noted though that in the light of ecological data on putative facilitation and competition (sensu Bertness, Shumway 1993) between coastal plants, experimental studies are clearly needed to understand the important aspect of coastal plant biology.

It seems to be somehow logical to assume that in highly heterogenous coastal environments biotic interactions play a minor role in plant biology than in more "predictable" habitats. Similar to that discussed above for mycorrhizal fungi, other microorganisms and arthropod herbivores are supposed to be less adapted to environment extremes. Seasonal changes in a microbial community in a salt marsh studied over a year revealed a higher microbial abundance in a late summer (Keith-Roach et al. 2002). The few available studies on the distribution of both pathogens and insect herbivores in coastal habitats indicate that both pathogens and phytophagous insects may have non-identical distribution patterns along an environmental gradient. It was hypothesized that mainly changes of host plant quality along the gradient account for different performance of the pests. The performance of a polyphagous stem borer *Agapanthia villosoviridescens* (Coleoptera) on *Aster tripolium* was negatively correlated with an increase of soil salinity (Hemminga, van Soelen 1988). In contrast, the monophagous leaf miner *Bucculatrix maritima* on the same species was not affected by environmental conditions (Hemminga, van Soelen 1992).

Herbivory in coastal habitats has been studied mostly in respect to plant succession both in sand dunes and salt marshes. Several experimental studies have evaluated the impact of herbivory on flowering and survival of salt marsh plants during different phases of succession (Dormann, Bakker 2000; Dormann et al. 2000). It was shown that species more tolerant to salinity were most significantly affected by herbivory. It has been even argued that well adapted plants contain higher concentrations of stress proteins, becoming more attractive to herbivores (White 1984). However it is well known that general stress proteins of adaptive nature may have antinutritive features as well. Therefore the above hypothesis does not seem to be suitable as an explanation of the phenomenon.

Some physiologically more useful information can be gained from studies that compare the effects of herbivory under different regimes of suboptimal abiotic factors. It was shown that in salt marsh plants, survival is affected much more by herbivores than by differences in abiotic conditions between marsh zones (Rand 2002). In general, the data on herbivore effects in salt marsh conditions suggest that herbivores have a major impact on plant survival and seed production. During long-term studies in coastal marshes of Louisiana it was established that under herbivore pressure flooding- and salinity-dependent reduction of species richness and biomass was further stimulated (Gough, Grace 1998).

Studies with a model species *Arabidopsis thaliana* in natural conditions of sand dunes showed that weevils have a strong effect on seed production in contrast to no significant effect of leaf-eating herbivores (Mosleh Arany et al. 2005). In tropical dunes burial by sand is thought to mask the negative effects of herbivores on leaf production (Bach 1998).

Physiological experiments in controlled conditions have shown that effects from biotic stress factors (both pathogens and herbivores) are strongly affected by suboptimal environmental factors. Both a cumulative negative impact as well as some level of induced resistance have been described, depending on the timing and intensity of stress factors (Inbar et al. 2001; De Bruin et al. 2002).

Conclusions and perspectives

On sand dunes and in coastal salt marshes both high level of morphological plasticity visible as environmental constraint-induced development of morphological adaptations as well as a high level of biochemical or regulative plasticity expressed as induced antioxidative protection and protection of physiologically critical macromolecules are of special importance for plants.

In the field of plant conservation biology where every particular rare or endangered species represents immensely high value, primary scientific data is of extreme importance. Consequently, new model species need to be established that represent different adaptation strategies of coastal plants. Several physiological questions of fundamental importance should be considered for further studies. These include measurement of general metabolic costs of different morphological and biochemical adaptations to coastal environment, hormonal and cellular mechanisms of regulation of induced responses etc. Physiological models need to be found for the study of biologically relevant characteristics beyond resource sharing for clonal plants of different life forms.

The potential of broader understanding of plant species biology in addition to reproduction data is far from being completely understood. The present review was intended at least to generate some general interest in this respect in hope for applied outcomes in the form of practical measures in plant conservation.

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Bioloģiskās daudzveidības bioloģiskais pamats: augu fizioloģiskās adaptācijas eksistencei heterogēnos jūras piekrastes biotopos

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Kopsavilkums

Lai izprastu augu adaptācijas mehānismus eksistencei heterogēnos jūras piekrastes biotopos, nepieciešams atklāt likumsakarības sekojošā secībā: vides faktori » adaptīvas augu īpašības » endogēnie kontroles mehānismi. Apbēršana ar smiltīm, augsta temperatūra, augsnes sāļums, augsnes appludināšana ir abiotiskie faktori, kuri veido unikālos apstākļus jūras krastā. Piekrastes augu atbildes reakcijas uz šiem faktoriem analizētas, lai aprakstītu iespējamos adaptācijas mehānismus. Īpaša uzmanība pievērsta šūnu aizsardzības mehānismiem fotosintēzes aparāta pasargāšanai un šūnas komponentu pretoksidatīvajai aizsardzībai. Analizēti iespējamo adaptīvo reakciju hormonālās un iekššūnas kontroles mehānismi. Papildus analizētas vairākas īpašības ar iespējamu adaptīvu nozīmi, piemēram, fenotipiskais plastiskums un klonalitāte, sēklu miera periods, mikorīzu simbioze.