Coastal Salt Marshes

Structure and Function of Plant Communities

Maria Sarika and Andreas Zikos

Contents

Abstract

Coastal marshes are intertidal wetlands, highly diverse in species and habitats. They reduce wave heights and the rates of lateral erosion, thus promoting shoreline protection and stabilization. Halophytic colonizers adapted to the stressful conditions caused by prolonged saltwater flooding contribute to vertical accretion of coastal salt marshes and enhance the processes that ensure their functionality and lastingness. This review seeks to summarize the current evidence demonstrating that structure and function of halophytic plant communities play a crucial role in the evolution, dynamics, and ecological functions of coastal marshes. We indicate the key physical processes involved in coastal salt marsh

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development (e.g., sediment transport and deposition, hydrodynamic regimes) and how they are decisively affected by the halophytic vegetation, the development of which in turn is governed by numerous physical factors (e.g., flooding regime, soil salinity and oxygen availability). We also discuss how the coupled relationship of the salt marsh biotic, morphological, and physicochemical components affects the spatial distribution and zonal organization of plant communities along the environmental gradients as well as the provided ecosystem services. In our review it is pointed out that vegetation characteristics (e.g., density, biomass production, canopy architecture) are directly related to the vital benefits that a coastal salt marsh can offer to society and that wealthy salt marsh vegetation development enhances significantly fundamental ecosystem functions such as shoreline protection and stabilization. A short overview of the main vegetation types of the European coastal salt marshes is also given, primarily on the alliance level.

Keywords

Vegetation dynamics · Habitats · Ecosystem services · Threats

1 Introduction

Coastal salt marshes are dynamic intertidal ecosystems periodically flooded with saline or brackish water and dominated by halophytic grasses, herbs, and low shrubs. These ecosystems experience tidal regimes ranging from micro-tidal to macro-tidal and are widely distributed in middle and high latitudes worldwide, except Antarctica. In the tropics and subtropics, salt marshes are largely replaced by mangroves. Highest astronomical tide is approximately the upper elevation limit of their occurrence while they rarely lie below mean high water neap tide level (Adam 2002; Weis et al. 2017). They occur in sea-to-land transition zones, on sheltered soft shores typical of deltas, estuaries, and tidal inlets, ensuring the stability and maintenance of diverse habitat types through a variety of ecological services (Valiela et al. 2002; Boorman 2003; Doody 2008). High biodiversity and primary production levels characterize coastal marshes which act not only as protective buffers reducing the wave energy and shoreline erosion (Belluco et al. 2006; Gedan et al. 2011; Tempest et al. 2015) but also as unique shelter for many birds, plants, and other wildlife species that have adapted to this particular environment (Boorman 2003; Townend et al. 2011; Gedan et al. 2011). Because of their high conservation value, many habitats found in coastal salt marshes have been included in the European Habitat directive (92/43/EEC), while many salt marshes have been denominated as National Nature Reserves, Special Conservation Areas, Areas of Outstanding Natural Beauty, Sites of Special Scientific Interest, and/or Special Protection (Townend et al. 2011). However, these coastal systems, even though they are of high value to human societies, due to the many ecological services they provide, are among the most vulnerable and threatened habitats on a global scale

(Scapini 2010; Barbier et al. 2011). Most coastal salt marshes are threatened by erosion or drowning, and their protection is not a simple matter, as they are an integral part of a highly sensitive dynamic system regulated by biotic and abiotic processes. Salt marsh deterioration is motivated by the same processes that drive their development, and therefore a thorough understanding of this balance is required to protect and preserve these important systems (Townend et al. 2011).

In the present chapter, the current knowledge on the development, nature, importance (ecological services), and major threats of coastal salt marshes and on the crucial role that the vegetation has in their evolution, stabilization, conservation, and functioning is summarized. The main vegetation types of the European coastal salt marshes are described in short.

2 Development and Maintenance of Coastal Salt Marshes

The physical factors regulating the development of coastal marshes within their geographical range are tide, waves and currents, sediment deposition, erosion, freshwater influx, nutrient supply, and shoreline topography (Lefeuvre et al. 2000). The combined action of erosion and sediment deposition determines shoreline topography at a given time. Increased sediment vertical accretion and subsequent surface elevation alter coastal micro-topography giving genesis to intertidal salt marshes, the presence of which influences the duration, frequency, and depth of tidal floods as well as several physicochemical variables of the sediment such as moisture, organic content, salinity, and redox potential (Silvestri and Marani 2004; Veldkornet et al. 2016). Mud accumulates in the higher elevations of the tidal area because tidal flow rates are sufficiently low to allow fine particulate matter to settle only close to the high water mark, i.e., the highest level that the sea reaches. Thus sediment surface gradually rises within the tidal frame, allowing vegetation to establish in the zone between mid-neap tide level and high water spring tide level (Davy 2002). On the other hand, duration of the alternating submergence and exposure phases that coastal systems experience due to tidal range fluctuation is a crucial factor in the successful establishment of plants and in particular of the pioneering annual species (Cutini et al. 2010). Although colonization of mud or sand flats by pioneering vascular plants is considered to be one of the main mechanisms involved in the development of coastal marshes, the role of microalgae appears to be equally important as they promote sedimentation and, consequently, vertical elevation of the vegetated surface, thereby contributing to the stabilization of pioneer communities and to the arrival of new plant species (Adam 2002). The plants that initially colonize the tidal flats trap and strengthen the sediments through their root systems, facilitating the arrival of other plant species which further stabilize the soil (Fig. 1) (Silvestri et al. 2005). Salt marsh vegetation is capable of modifying its natural environment by damping down the energy of waves and tidal currents. At the same time, it promotes sediment accumulation, which gradually raises the elevation of vegetated platform on the upper shore (Fig. 2). The more the marsh is topographically elevated, vegetation development is further favored, and greater

Fig. 1 *Halocnemum strobilaceum* stabilizing the soil. (Photo A. Zikos)

Fig. 2 Vegetation promotes sediment accumulation and thus rise of the vegetated platform (Vourkari, Greece). (Photo A. Zikos)

protection against erosion is ensured (Temmerman et al. 2005; Belluco et al. 2006). It is thought that salt marshes are consolidated by the root systems of plants and plant communities seem to control at least partially their vertical accretion (Davy 2002; Silvestri et al. 2005).

2.1 Relative Sea Level and Sediment Availability

Coastal salt marshes occupy areas that are usually affected by tidal action, so any modification of tidal frame that may result either from a change of the relative sea level or of the tidal range may have significant repercussions on the marshes. Relative sea level changes can be caused by both changes in global sea levels and changes in land levels. A fall in relative sea level causes coastal marshes to rise above the tide line and thus terrestrial communities taking the place of those that originally existed in the marsh (Adam 2002). The effects of rising sea level vary with local conditions. The sediment supply to a coastal system can potentially increase following a rise in sea level. As the depth of the water increases, increasingly large waves will come closer to the shores, and the whole system will become more active. Although this can undoubtedly benefit systems growing by sediment accumulation (accreting systems), it can nevertheless cause drastic changes in the pattern of shores and creeks with direct effects on salt marshes, especially when critical natural processes are limited in any way (Boorman 2003). In such a case salt marshes can be maintained or even expanded only if the relative sea level rise is equal to or lower than the sediment accretion (Shepard et al. 2011). Sediment availability critically influences the ability of salt marshes to survive a possible rise of relative sea level as it is widely recognized that reduced deposition rate is currently the major factor impeding coastal salt marsh development (Boorman 2003). Various human activities are responsible for changing sediment supply. The construction of dams and the abstraction of water for irrigation, industry, and urban consumption reduce the flow of rivers and thus their ability to carry sediment downstream. Additionally, interventions with offshore engineering projects, such as changing the course of the delta channels by embankments or artificially constructed walls that regulate water levels, can also alter the sediment movement, thereby reducing deposition rates within the marsh (Adam 2002). When the required sedimentation does not take place, the marsh can retain a stable position in relation to the shifting tidal frame only if topography of the surrounding area allows it to move inland (Boorman 2003). Coastal salt marsh position changes within the tidal frame may also be stimulated by tidal range changes. Over various time periods, the range of the tide varies within predictable limits, but there are also permanent displacements that may be related to either estuary shape changes (on a local scale) or meteorological and oceanographic factors (on larger scales) (Adam 2002). Both uplifting and sinking of coastal marshes and the subsequent substantial change in the shoreline topography may also be caused by earthquakes. Groundwater extraction can also lead to the sinking of salt marshes and to the reduction of freshwater inputs, affecting nutrient, and salinity regimes.

2.2 Sedimentation, Erosion, and Vegetation Dynamics

The sedimentation process occurring in salt marshes relies mainly on the inflow of fine sediments transported horizontally through the estuarine systems (inorganic or allochthonous supply) rather than to organic production. The evolution of this process depends on the complex interaction between the time the tidal waters cover the marsh (known as hydroperiod), the distance that they travel within the marsh, the flow over the marsh surface and through vegetation, and the dynamic of settling and trapping. From the aforementioned physical constituents, hydroperiod is considered to be a key determinant of sedimentation although it generates diametrically opposite effects within the marsh. This is because greater hydroperiod increases not only the hydrodynamically induced sedimentation but also plant stress, thereby reducing organic productivity. Hence the influence of hydroperiod varies along the marsh, with the inorganic sedimentation dominating the lower marsh, giving way to the organic in the higher marsh. It is a common belief that hydroperiod variations ensure the balance of allochthonous marshes and their ability to respond directly to fluctuating rates of sea level rise and tidal range changes, enabling them to continuously adjust the rate of vertical accretion. Sedimentation rate can be also enhanced by subsidence, but when minerogenic sediment supply is limited and organic matter is the main feeder, the marsh will not be able to cope with the accelerating rise of sea level (Townend et al. 2011). In most marshes, sediment import takes place both through the tidal flow from the seaward side as well as through rivers or the catchment area. Factors affecting the retention and adsorption of sediments on the salt marsh surface include both changes of river flow in the upper estuaries and the extent of mud flat re-mobilization during the tidal flood. The amount of sediment available for accretion can be greatly increased by turbulence caused by wind or waves, at that stage (Adam 2002; Boorman 2003). Tidal asymmetry is also crucial for sediment delivery in the marsh, and often bibliographic data emphasize the importance of the period between flood and ebb phases, referred to as “stand of the tide” or “slack water,” for the deposition of fine sediments. It is interesting to note that during this period of slack water, the two phases complement each other as the flood that dominates before the onset of low tide (ebb phase) facilitates the import of fine sediments, while the peak tidal velocity observed during the ebb phase encourages the export of coarser sediments. It is generally accepted that inorganic or minerogenic contribution to salt marsh vertical accretion is supported by processes that increase the local concentration of suspended sediments. Therefore, the combination and interaction of a variety of processes like coastal erosion rates, biological activity, proximity with maximum turbidity point of estuary, and changes in tidal regime govern sediment availability (Townend et al. 2011).

Rising sea levels erode the seaward edges of the marshes, enhancing the potential accretion and the development of salt marsh vegetation at the upper levels of the marsh (Adam 2002; Boorman 2003). Coastal erosion is a common natural process, caused mainly by the energy of large wind waves. During the storms, erosion acts as part of the self-regulating potential of the land that is periodically flooded by tides (tidal flat) as well as that of the overall marsh, maximizing resilience and dissipation of wave energy across the shore. The erosion of seaward marsh edges could be considered as a source of sustained regeneration, which provides material for redistribution on muddy substrate (during storms) or to the surface of the marsh (during tides), resulting in low or no net erosion when there are no other constraints (Townend et al. 2011). In intact non-disturbed systems, this process induces the movement of the whole coastal salt marsh toward the land side, but often human interventions such as sea wall construction prevent the natural development of a new marsh landwards, eventually causing the loss of the entire system. Marshes only survive when sedimentation rates are equal to or greater than erosion rates (Adam 2002).

Vertical accretion through deposition and stabilization of sediments induces vegetation growth which in turn protects the marsh from erosion by reducing water flow over the marsh surface, thereby promoting further sediment accretion. The settlement and consequently deposition rate are influenced by changes in the flow regime which are enhanced by entrapment of sediments in the vegetative canopy. This is a property of vegetation morphology resulting from its size and density in relation to the flow field. Some species (e.g., *Spartina alterniflora* and *Phragmites australis*) (Fig. 3) collect sediment even on their shoots and leaves, increasing deposition up to 50% (Townend et al. 2011). Therefore the rates of deposition and thus the ability of the system to resist erosion depend not only on sediment supply and tidal duration but also on the extent to which the water flow is sufficiently impeded to facilitate sediment deposition (Tempest et al. 2015; Belluco et al. 2006). As the water passes through the vegetation, the damping of the flow enhances settling and reduces the possibility of vertical erosion of the marsh platform, even in the event of huge waves and may lead to increased accretion (Townend et al. 2011). Conversely, high sediment deposition rate can significantly affect negatively the growth and establishment of several salt marsh plants (Boorman et al. 2001). This dynamic balance between deposition rate

Fig. 3 *Phragmites australis* (Photo A. Zikos)

and vegetation establishment that ensures the development and survival of the salt marsh can be disturbed if the environmental processes involved in vegetation growth and sediment accretion are hindered or degraded. Any loss or weakening of vegetated surface may be the beginning of local erosion, which may affect much larger areas over time. However natural disturbances often have only local impacts since the lost vegetation patches recover long before damage is further extended, while at the same time, salt marsh heterogeneity and biodiversity are enhanced (Adam 2002). At high latitudes, winter ice can negatively affect large areas of salt marsh vegetation, while in warmer temperate locations, high summer temperatures along with high evapotranspiration rates promote extremely high soil salinity that prevents the colonization by vascular plants. Bare, unvegetated areas of various sizes referred to as "rotten spots" or "salt pans" are common feature of the subjected to thermal stress, hypersaline soils (Adam 2002; Bertness and Pennings 2002).

2.3 Freshwater Input

Tidal exchange and adequate freshwater supply are crucial for the sustainability of coastal salt marshes. Macrophyte germination and growth are supported by the freshwater which lowers the salinity of sediments and prevents dry, hypersaline conditions that would inhibit vegetation development (Voldkornet et al. 2016). For many decades, rivers all over the world have been regulated (dams for water storage, hydroelectric power plants, etc.) so that not only the amount of freshwater entering the estuary has drastically decreased but also its seasonal and intra annual fluctuation (Lemly et al. 2000). Until recently, however, the effects of river flow modification on estuaries and related ecosystems had not been taken seriously, as it was widely believed that freshwater entering estuaries is wasted. Reduced inflows along with the impact of artificial barriers constructed across a river or estuary to prevent flooding usually lead to significant changes in both estuaries and their associated salt marshes. On an even larger scale, flood barriers alter the shape and function of estuaries, converting them from saline tidal systems into brackish lakes with consequent changes of the plant and animal communities. It is also known that the groundwater extraction underneath the salt marsh is responsible for the sudden sinking or gradual subsidence of the soil surface. In contrast, where groundwater is shallow or even flows into the marsh through springs, a reduction of the flow may cause a change in species composition. Sometimes increased water supply such as rainwater discharge from nearby urban areas may result in replacement of the halophytic communities of the salt marsh by assemblages more typical of brackish or freshwater marshes (Stevenson et al. 2002).

3 Salt Marsh Ecological Services and Major Threats

Salt marshes support a wide range of functions that provide the biosphere with vital benefits known as "ecosystem services." The supply of raw materials and food, coastal protection, erosion control, water purification, conservation of fishing areas, carbon retention, tourism, recreation, education, and research are among the valuable goods that the coastal marshes offer to humanity (Barbier et al. 2011). One of the most important benefits provided by salt marshes is their role in protecting coastlines. Three salt marsh ecosystem functions are directly associated with coastal protection: wave attenuation, floodwater attenuation, and shoreline stabilization. Salt marshes act as a natural barrier against erosion, flooding, and storms, thereby reducing the effects of these natural phenomena that threaten shorelines (Weis et al. 2017, Shepard et al. 2011, Chirol et al. 2018). According to Gedan et al. (2011), even small marshes attenuate wave energy and inhibit erosion processes, providing significant shoreline protection and stabilization (Fig. 4). As coastal marshes and their vegetation are established and evolve, they provide vertical restraint structures, induce sediment stabilization, and elevate the tidal zone, thereby weakening the action of the incoming waves by reducing their velocity, height, and duration. In addition, they help reduce the height and duration of storm surges by absorbing and retaining larger amounts of water than the mud flats that are not covered by vegetation (Barbier et al. 2011). The painful consequences (human losses and economic impact) of extreme events such as hurricanes and tsunamis can be significantly reduced if the natural functions of coastal salt marshes are preserved or restored (Gedan et al. 2011). At the same time, they function as natural filters trapping sediment, nutrients, microbes, waste water effluents, and contaminants. When water from rivers, terrestrial runoff, rain, or groundwater enter the marsh, it passes through the emerging vegetation, and its flow is slowed due to friction with the upright parts of the salt marsh plants and the baffling effect caused. Lower water speed increases the sedimentation of particles suspended in the water, facilitating nutrient uptake by the plants. This natural water filtration taking place in coastal marshes is a valuable service that benefits both human health and neighboring

Fig. 4 Salt marsh vegetation protects the shore from waves and erosion (Vourkari, Greece). (Photo A. Zikos)

ecosystems, such as seagrasses which can be degraded due to the increased nutrient and pollutant supply (Barbier et al. 2011). It has been experimentally demonstrated that the organic matter produced in the coastal marshes is washed into the groundwater and then released seawards through runoff, where it feeds the food webs of the sub-tidal zone (Lefeuvre et al. 2000). These two adjacent landscape units are strongly linked through tidal exchanges with deeper waters, through ground and stream water transport between terrestrial and estuarine systems, but also through biogeochemical transformations. Retention of significant amounts of land-derived nitrogen in the coastal salt marshes due to the high denitrification processes occurring there is such a biogeochemical transformation that affects the structure of communities in the sub-tidal ecosystems (Valiela et al. 2002). However, it has been recognized that, at least along the European coasts, the organic matter export from salt marshes and the nutrient budget in the adjacent sea waters depend on latitude, tidal range, plant communities, and geomorphology of each individual system (Lefeuvre et al. 2000).

It is generally accepted that coastal marshes ensure ideal living and feeding ground for young fish, helping and enhancing the production of economically important and ecologically sustainable fisheries. The complex and tightly structured salt marsh vegetation creates habitats that are virtually inaccessible to large fish, thus providing important shelter areas where young fish, shrimp, and shellfish can safely feed and survive (Lefeuvre et al. 2000; Barbier et al. 2011; Garbutt et al. 2017). Many other beneficial species inhabit coastal salt marshes, further enhancing the services that these ecosystems can provide for tourism, recreation, education, and research. Ducks and a variety of migratory coastal birds use coastal marshes during their migration, other overwinter there, while long-legged birds favor shallow waters, especially in summer. However, the continuous loss of coastal marshes changes the coherence of estuarine food webs (Barbier et al. 2011; Weis et al. 2017).

The role of coastal marshes in the global carbon cycle is also of great importance as they constitute a major portion of the terrestrial biological carbon reservoir. Studies have shown that salt marshes sequester ten times more carbon than peat lands, thus contributing significantly to reducing global warming (Chmura et al. 2003). Because of the anoxic conditions prevailing in the marsh soils, part of the carbon temporarily bound to the plants is shifted from the short (10–100 years) to the long-term (1000 years) carbon cycle in the form of buried, slowly decomposing biomass, that is, peat, thus increasing the capacity of the salt marsh to store carbon. This cycle-shifting capability is possessed by few ecosystems of the world as in most of them carbon does not move into the long-term cycle but recycles rapidly (Barbier et al. 2011).

Over the past century, the services provided by the coastal marshes have been degraded due to the large-scale conversion that these ecosystems have undergone for the benefit of agricultural, industrial, and urban development (Nichols et al. 2007). According to Barbier et al. (2011), critical ecosystem services, such as the percentage of sustainable fisheries (33% decline), habitat availability suitable for young fish survival (69% decline), and filtration and detoxification services provided by the submerged vegetation, the wetlands, and the organisms that feed on suspensions

(63% decline), have been affected globally due to degradation of coastal salt marshes. They also report that in many cases biological invasions, decline of water quality and lack of coastal protection from flood events and thunderstorms are likely to be intensified by loss of biodiversity, ecosystem functions, and coastal vegetation. Adam (2002) reports that intense grazing of waterfowl such as geese affects negatively salt marsh vegetation by destroying the above- and belowground plant biomass and its recovery usually takes many years, even if grazing is completely prevented. As a result, erosion may begin before vegetation returns to the marsh area. Shipwreck debris or other floating materials of varying origin that are washed ashore during major tidal events such as equinoctial tides are often deposited in coastal marshes and may also kill the underlying vegetation. This drift material, which today consists mainly of non-biodegradable plastics, is deposited at any level in the marsh where it may remain for years. Large areas of salt marsh vegetation may also be lost following frequently repeated movement of recreational vehicles or the crossing of pipelines and power lines. The deep tracks and grooves created on the salt marsh surface as a result of these actions modify the drainage patterns. Through submergence or the development of hypersalinity, vegetation is weakened or lost completely in large areas of the marsh, and extensive erosion begins. Coastal marsh loss can also be initiated by the erosive action of waves on the edges of the marshes during thunderstorms. Strong waves can weaken the marsh edge, making it vulnerable to the action of normal waves henceforth. Human interventions such as settlings and channel redirection or other mechanical works further maximize the effect of wave action on coastlines that host wetland networks (Adam 2002). Fernandez-Nunez et al. (2019) report that although a coastal salt marsh could potentially accrete vertically following a possible sea level rise, lateral erosion caused by either anthropogenic or natural factors can significantly affect the pioneer zone and may induce loss rates higher than the accretion rates, resulting in the total loss of the marsh.

Despite the fact that in recent years the enormous value of these systems has been recognized worldwide, the rate of their loss is still increasing, mainly due to urban development and climate change (Chirol et al. 2018). Although salt marsh losses are difficult to calculate and quantify accurately due to lack of data (Duarte et al. 2008; Foster et al. 2013), it is estimated that the decline of coastal wetlands globally in the last 150–300 years is around 25–50% with a current global salt marsh loss rate of 1–2% annually (Duarte et al. 2008). According to the Intergovernmental Panel on Climate Change, the most important climate-dependent threat to salt marshes, i.e., the accelerated sea level rise, will range from 0.26 to 0.98 meters in the year 2100. Scientists predict that rising sea levels by 1 meter will eliminate 46% of Earth's coastal wetlands. Some wetlands will withstand and adapt to this rise, but others, especially those where sedimentation is cut off through embankments or seawalls, will not be able to survive (Day et al. 1995). The destabilization of belowground biomass due to a rise in the nutrient content (eutrophication) and its consequent increased decomposition seems to be an additional stressor that is likely to exacerbate the effects of rising sea levels on salt marshes, contributing to their loss (Weis et al. 2017). The severity of the effects of sea level rise will vary from region to region and will depend not only upon the magnitude of the relative increase in sea level but also on the processes affecting the ability of salt marshes to grow vertically and/or to migrate inland, the shoreline morphology, and human interventions (Weis et al. 2017). However, it is known that the smaller the tidal zone, the greater the risk of sea level rise. Thus in coastal regions where the amplitude of tidal range is low (<1 m), for example, in the Mediterranean Basin, the effects of sea level rise are likely to be particularly severe. In contrast, sea level changes have a milder effect on coastal areas with a high tidal range due to greater sediment transport and accretion (Nichols et al. 2007).

The ability of coastal wetlands to cope successfully with upcoming climate change and sea level rise may be adversely affected by current anthropogenic pressures (land use change, degradation of estuarine systems, hydrological modifications, rapidly expanding coastal infrastructures, seabed alteration, degradation of sediment delivery and freshwater input, eutrophication, vegetation disturbance, pollution) which seriously affect the integrity of these systems as well as the services they offer to coastal protection and human society (Barbier et al. 2011; Shepard et al. 2011; Weis et al. 2017). The risk appears to be particularly significant in areas with large populations and high levels of development. This dynamic and complex interaction of stressors is ultimately the most common threat to coastal ecosystems. The present human interventions carried out locally or in the wider watershed area that are irrelevant to climate change seem to be the main causes of environmental degradation of coastal systems currently (Nichols et al. 2007). Finally, the ways in which humans usually deal with coastal natural hazards (including storms, hurricanes, tsunamis) and sea level rise have further significant negative implications on sustaining coastal vital resources and ecosystems. Decisions made today for coastal management may have long-term consequences that will last even in future centuries. It is therefore necessary to evaluate the dynamics of natural systems, before any intervention or modification of coastal zones, so as to conserve the natural benefits and ecosystem services provided by salt marshes (Nichols et al. 2007; Shepard et al. 2011).

4 Coastal Salt Marsh Vegetation

Halophytic vegetation is key element of the intertidal systems dynamics. According to Adam (2002), various combinations of salt marsh plant assemblages and vegetation types occur along a wide range of spatial scales from the individual sites to the global patterns. Thus coastal salt marshes throughout the world can be distinguished in a number of major categories of broad concept based on their vegetation diversity, which in turn express the diversity of regional environmental and climatic conditions (for details, see Table 1 in Adam 2002). These major salt marsh categories are characterized by specified combinations of plant species. The largest of all types, in terms of total area it occupies, lies on the North American Atlantic and the Gulf of Mexico coasts and is characterized by the extensive mono-dominance of the species *Spartina alterniflora*. Depending on continental geography, the temperate salt marshes are further distinguished in several subgroups (see also Table 1 in Adam 2002) that may reflect geographic isolation and evolution (Adam 2002). Although the variation within these subgroups reflects the diversity of climatic conditions, overgrazing has led to changes in the coastal wetland ecosystems of northern Europe in such a way that the underlying climatically defined pattern is not always clear (Adam 1990).

It has long been recognized that physical processes and factors, such as salt marsh vertical accretion, salinity, flooding, and nutrient availability, regulate spatial arrangement and structure of salt marsh plant communities. In recent decades, however, experiments have shown that competition or facilitation relationships occurring among the salt marsh plant species play an equally critical role in regulating spatial arrangement and structure of plant communities (Barbier et al. 2011). The salt marsh plant communities consisting of only a few flood-tolerant species that are able to develop and reproduce in highly hypoxic and hypersaline soils generate along the gradients of elevation and salinity a network of emergent vegetation organized into recurrent zonation patterns (Belluco et al. 2006; Weis et al. 2017). In a tidal system, halophytes are not randomly distributed. They are organized in diverse communities arranged in the form of intermittent patches within discrete salt marsh zones, according to their physiological response to the gradient of environmental factors as well as their competitive ability and susceptibility to herbivory (Adam 2002; Bertness and Pennings 2002; Hladik and Alber 2014; Weis et al. 2017; Lee and Kim 2018). In such systems spatial zonation of vegetation strongly depends on the tidal cycle which can itself generate topographic and environmental gradients from sea to land. Therefore plants with different tidal tolerances occupy a different niche within the tidal frame, and it is obvious that the individual response of plants to the strong abiotic pressures ultimately determines the complex interactions between them along the elevation gradient (Davy 2002). At the marsh level, the development of plant communities in clearly separated zones is of particular interest. Although each species is distributed within characteristic elevation limits, the zonation of salt marshs (normally into low, mid, and high marsh) rather reflects the behavior of a few dominant species (Fig. 5). At a local level and on an even more detailed scale, spatial variation in species occurrence due to micro-topography can also be observed; for example, species occurring on creek banks may differ from those that thrive in inter-creek basins. Thus, many plant species grow in mosaics and are not distributed in discrete zones (Fig. 6) (Adam 2002).

4.1 Zonation

In salt marshes, the landward diminishing influence of the sea causes strong vegetation zonality at a local scale. Spatial distribution of plant assemblages can be roughly seen as a series of zones parallel to the coast, with the youngest at the lowest elevations near the sea and the oldest at the edge of the upper salt marsh. Within these zones, depending on micro-relief and flooding periodicity, a variety of

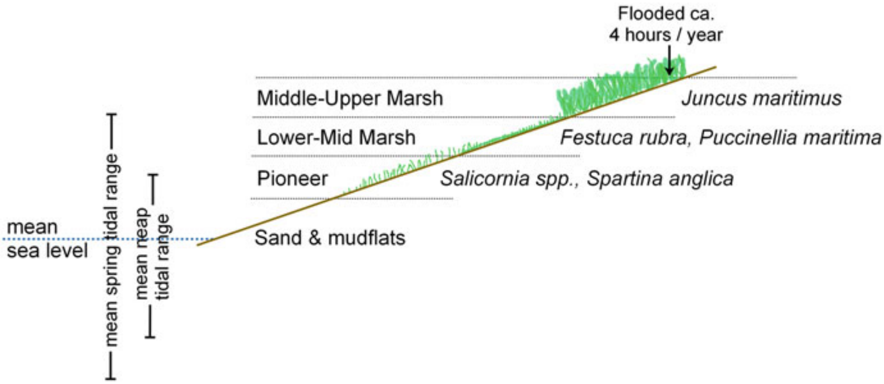

Fig. 5 Typical zonation pattern of a salt marsh in Northern Europe (van Beijma et al. 2014, reptinted with permission)

Fig. 6 Mosaic of salt marsh plant communities at local level (Spercheios delta, Greece). (Photo A. Zikos)

specialized habitats occurs, and the vegetation often forms distinct mosaics. Salinity and soil oxygen availability are limiting factors that reduce species richness. Low species number and monospecific stands characterize most vegetation types found in coastal marshes (Cutini et al. 2010). As a general rule, vegetation zonation in the salt marshes of higher latitudes, like the Atlantic coasts, is determined by the duration of flooding, while in the Mediterranean Basin, the most significant drivers are soil salinity and the summer drought (Dítě et al. 2019b). However, the evolution and dynamics of salt marsh vegetation are quite complex processes, which are strongly correlated to salt marsh morphology through a multifactorial interaction of biological and physical processes. Physicochemical (tidal cycle, salinity, and micro-topography) and biotic factors (inter- and intraspecific competition) interact within a cycle of eco-geo-morphological feedback that decisively influences the physiology and the distribution patterns of salt marsh plants (Silvestri et al. 2005). The development of the salt marsh plant distribution patterns is interconnected with reproduction, germination, establishment, and growth mechanisms, the operation of which directly depends on a series of physiological needs broadly related either to an adequate input of energy and vital substances (e.g., light, water, oxygen, salt ions, macronutrients, and micronutrients, etc.) or to a limited influence of stressing factors (e.g., soil salinity and waterlogging, toxic substances in soils, sudden thermal changes, inter- and intraspecific competition) (Silvestri and Marani 2004; Silvestri et al. 2005).

The interpretation of salt marsh vegetation zonation patterns and their correlation to variations of the physical environment has been the subject of many experimental studies over the last decades (Pennings and Callaway 1992). Recent researches focusing on salt marsh plant zonation patterns demonstrate that they are determined by both abiotic and biotic factors. These two environmental components play a crucial role in determining whether a species will be able to establish in a salt marsh, and for this reason, targeted studies essentially seek to decipher how the interaction of these constituents governs and delimits the upper and lower boundaries of the development of salt marsh plant (Lee and Kim 2018). Lee and Kim (2018) suggest that the lower borders of tidal salt marsh plant development are set by abiotic factors (elevation, salinity, flooding duration and frequency, redox potential, nutrient availability, soil moisture and chemistry, latitude, topographical and climatic factors), while the upper ones are determined by biotic factors (competition, facilitation, trade-off between competition and facilitation, physiological adjustment, seedling recruitment, emergence and growth strategy, herbivory). The competitive displacement and the physiological tolerance to stressors have long been recognized as the most decisive factors in generating salt marsh vegetation zonation (Pennings and Callaway 1992). Pennings et al. (2005) mention that the competitively superior plants occupy the least stressful higher elevation zones of the salt marsh, displacing the competitively inferior plants to the lower stressful zones. This view is also confirmed by Hladik and Alber (2014) who report that the distribution of plants in coastal salt marshes is generally explained by the stress-to-competition hypothesis. According to this hypothesis, species with physiological tolerances but low competitiveness are restricted to low elevations, while those occupying the upper elevations are characterized by low physiological tolerances but high competitiveness.

Among the abiotic factors, flooding frequency and duration have a pronounced role in the configuration of vegetation zonation, but many experimental studies suggest that salinity and soil moisture, among other environmental factors, are also vital (Silvestri and Marani 2004; Silvestri et al. 2005; Lee and Kim 2018). It has long been proven that up to a point there is a positive correlation between elevation and salinity, with the latter touching the maximum just above the mean high sea level and falling again at low concentrations beyond it. This spatial variability of salt concentration along the elevation gradient attributed to the longer evaporation periods that the higher elevation areas experience when the marsh is not flooded confirms also the direct link between halophyte species distribution and topographic elevation. At very high elevations, above the average upper sea level, soil salinity tends to decrease as the flood frequency and the associated salt influx weaken progressively. Zonation can thus be partly attributed to the correlation between soil salinity and elevation, since plants' tolerance to salinity is greatly species dependent (Adam 1990; Silvestri et al. 2005). In addition, the spatial heterogeneities of soil properties and the interaction between the evapotranspiration models and subsurface water flow have a particularly important role in the configuration of zonation patterns (Silvestri et al. 2005). Oxygen sufficiency is another crucial factor for plant growth. Depending on the topographic features and the given soil type, the availability of oxygen is determined by the frequency and duration of flooding. Flooding regime also affects root respiration, germination, and seedling growth, as well as soil chemical processes, possibly causing conditions that inhibit plant growth (Silvestri et al. 2005).

The main mechanisms involved in organizing the plant zonation patterns in coastal salt marshes seem to have a global reach, but the importance of particular factors rather varies geographically due to variations in the physical environment (Penning et al. 2005). It is widely accepted that within the range limits of abiotic factors, competition and facilitation are the main biological processes promoting the evolution of zonation standards as their action shifts along the physical stress gradients (Lee and Kim 2018). An increasing tendency to recognize the value of facilitative interactions has followed the wording of the stress gradient hypothesis. According to this hypothesis, in communities that are under high abiotic stress or high herbivory pressure, competition is less intense, and the interaction between plants becomes facilitative (Batriu et al. 2015). Halophyte vegetation studies conducted at low and high latitudes suggest that the dynamic balance (trade-off) between competition and stress tolerance, that is responsible for the development and stabilization of zonation patterns, is universal (Pennings et al. 2005). There are also studies highlighting the importance of historic factors for coastal marsh vegetation assemblages in humanized landscapes (Batriu et al. 2013). Relevant works confirm that any activities changing the physical stress gradient or influencing the competitive ability of plant species may alter the zonation of marsh plant communities (Bertness and Pennings 2002).

4.2 Development and Structure

Primary colonization of mud flats by plants is the first step in the development of salt marsh vegetation and the marsh itself. Few individuals of halo-tolerant plant species, scattered on the mud flats, comprise the pioneer salt marsh vegetation zone. The marine boundary of this zone, which can vary considerably from season to season and from year to year depending on tidal regime, is crucial for the establishment of primary colonizing plants, as the germination process requires little or no tidal disturbance. Elevation of the tidal frame is therefore one of the primary physical factors controlling the distribution of salt marsh species and communities since seedlings' ability to extend roots to a sufficient depth to anchor firmly and withstand safely to tidal action is directly influenced by the frequency and duration of the flood (Silvestri et al. 2005; Min 2015). Boorman (2003) reports that even small spatio-temporal changes in the patterns of tidal flow and sedimentation can have significant influence on the ability of halophytes to colonize the pioneer zone. Additionally, according to the same author, experimental results have shown that increased sedimentation enhances root and shoot growth rates, promoting the germination process of several pioneering species.

Plant communities in the pioneer zone are very simple in structure. Diverse halophyte species may coexist within this zone but they usually occur in the form of relatively large clusters of a single species rather than in mixed stands of more complex structure. Vegetation layering is almost non-existent, and the ground cover is limited. The fundamental biological and physical processes that take place in the zone of pioneer communities are related to sediment trapping and soil surface reconstruction (building up of the soil surface). As the establishment of plants colonizing the marine edge of the marsh becomes permanent, the shoots or individuals gradually increase, so that the soil is completely or partially covered with vegetation. The process evolves either with the help of pioneer annuals such as *Salicornia* and *Suaeda* species or with perennials such as *Spartina* spp., whose increasing development leads to the formation of a closed or nearly closed canopy. This in turn leads to higher sedimentation rates due to the protection that the vegetation cover provides and the onset of maturity of pioneering plant assemblages. These modifications allow new, less flood-tolerant plant species to settle in the marsh. The arrival of such species signals the transition to the next stage of salt marsh development, which is associated with the development of lower marsh vegetation. In the lower salt marsh zone, plant communities are more diverse and more stable than the pioneer ones as, in addition to the annual colonists, some perennial species are also abundant. Perennial plants such as *Tripolium pannonicum* subsp. *tripolium* (Fig. 7) and *Puccinellia maritima* are considered classic colonizers of the lower salt marsh zone where they spread rapidly representing largely the typical vegetation of this area. The former of these two species, besides of coping with the harsh conditions of lower marsh through high seed production, it can also behave as a biennial or short-lived perennial. The stoloniferous *Puccinellia maritima* although not as tall and inundation-tolerant as *Tripolium pannonicum* subsp. *tripolium* is a dynamic colonizer of bare muddy areas at levels higher than those usually occupied by the pioneer plant communities, where it forms extensive swards. Various other salt marsh perennial species grow sequentially within this vegetation zone usually fairly quickly, especially the sub-shrub *Halimione portulacoides* (Fig. 8) and woody shrubs of genus *Sarcocornia* (Fig. 9) (Boorman 2003).

The arrival and establishment of long-lived perennial plant species with basal leaf rosettes and low seed production such as *Limonium vulgare* (Fig. 10), *Plantago maritima*, and *Triglochin maritima* indicate that the salt marsh development has progressed to the next stage, which is related to the development of middle marsh communities. Less flood-tolerant but much more competitive species of the high marsh may also invade the zone of middle marsh communities, where most of the

Fig. 7 *Tripolium pannonicum* (Photo K. Goula, used with permission)

Fig. 8 *Halimione portulacoides* (Photo A. Zikos)

Fig. 9 *Sarcocornia perennis* (Photo A. Zikos)

Fig. 10 Purple flowering *Limonium* sp. is related, among other species, to the development of the middle marsh (Spercheios delta, Greece). (Photo A. Zikos)

pioneer and lower salt marsh species often survive, usually as scattered individuals. Generally the establishment of plant communities that typically colonize the higher salt marsh sectors represents the next step of salt marsh sequential development which takes place only when the vegetation platform elevates gradually from the middle marsh zone to the less saline terrestrial borders. High salt marsh species such as *Schoenoplectus litoralis*, *Juncus maritimus*, *Juncus gerardi*, and *Phragmites australis* dominate the upper salt marsh parts. Species composition however varies depending on the continent, geographical location, and soil nature (Adam 2002; Lee and Kim 2018). Damp-loving species such as *Juncus gerardii* and *J. maritimus* are involved in the development of the upper marsh zone in wet areas. Less humidity demanding species such as *Elytrigia atherica* and *Festuca rubra* contribute to the development of the upper salt marsh in dry areas. Within the dense stands of mature communities of the upper salt marsh, intense competition impedes the invasion of pioneer and lower marsh species. Toward the landward edges of the upper salt marsh zone, the presence of non- or marginally salt-tolerant species demonstrates the development of transition communities. Depending on the vegetation that develops in contact with the upper edges of the marsh, there is a range of transition communities. Among the most commonly encountered ones are those of damp grasslands and brackish wetlands, the former developing where land slants upward gradually, the latter along the line of freshwater seepages (Boorman 2003).

Species diversity, though varying within the zonal halophytic assemblages, has an increasing tendency from the shoreline toward the inland that seems to follow the drought increase. It has been already mentioned that in highly stressed habitats, such as the intertidal and supra-tidal mud flats and the lower saline edges of the marsh, plant communities have a very simple structure and uniform composition. Because they are exposed to factors negatively affecting plant growth (frequent/intense inundations, saline water table, sea spray), these pioneer communities usually consist of one or two dominant halophytes that due to their high adaptation to stressful conditions can make optimum use of the resources available in saline, often shallow and waterlogged soils, thus achieving abundant growth. These plants have also high osmotic potential and specialized mechanisms of salt uptake, transport, and secretion (El-Gharreb et al. 2006; Lee and Kim 2018). It is clear that survival in extreme conditions such as frequent flooding and high salinity demands adaptations which, due to genetic diversity, cannot be achieved by all plants so that they can cope successfully with a marsh environment (Whittaker 1972). Hence, due to low competition, only plants with high adaptation abilities survive in such environments where they successfully establish with high biomass, high dominance, but low species richness. Experimental research has demonstrated that stress negatively affects individual survival and colonization capacity, thus leading to a negative correlation between species diversity and total plant cover (El-Sheikh and Abbadi 2004). As a general rule, the most humid and saline sites are characterized by abundant growth of only one or two halophyte species, while the drier and less saline sites have the highest diversity but the lowest species abundance (El-Gharreb et al. 2006). However, the diversity of plant species in salt marshes has been shown to be negatively correlated not only with soil moisture and salinity but also with organic matter, clay, and minerals (El-Sheikh and Abbadi 2004).

The gradual increase of species diversity from the pioneering to the lower salt marsh communities induces a progressive development of the vegetation structure. With the development of more mature vegetation in the lower marsh, the structure of communities is beginning to acquire a three-dimensional organization pattern

Fig. 11 Three-dimensional organization pattern of salt marsh vegetation. (Photo A. Zikos)

resulting from the spatial arrangement of species as some of them are prostrate (both rosette species and creeping grasses), others are rising vertically (such as *Tripolium pannonicum* subsp. *tripolium* or the woody *Halimione portulacoides*), and others lie in between them (Fig. 11). Although these three structural elements are encountered in most of the lower and middle salt marsh areas, at any one particular point of the marsh, the occurrence of only one or two of the aforementioned elements is a frequent phenomenon. When the salt marsh perennials develop at high densities, they usually form monospecific stands with bare or almost bare ground below them. However, very often they are arranged in a distance sufficient for the development of an under story layer. Vegetation structure in the mature marsh resembles that of the lower but also differs significantly in that it exhibits greater species diversity and better development of all structural elements (Boorman 2003). Numerous previous studies have shown that plant communities inhabiting the higher zone of salt marshes, which essentially represents a transitional zone between saline sites and terrestrial habitats, are particularly rich in species. The theory of spatial and temporal heterogeneity could explain the high species diversity of this transitional zone, as it is an ecotonic area in which characteristics of both terrestrial and wetland habitats are prevalent. In such a case, the local variation of soil properties around individual plants could lead to an even higher level of species diversity, as the heterogeneity of the environment meets the requirements of various plant species within a community (Whittaker and Levin 1977; El-Sheik and Abbadi 2004; El-Gharreb et al. 2006).

4.3 Function

Halophytic vegetation crucially affects the dynamics of coastal areas lying within the tidal range (Belluco et al. 2006). It is well documented that coastal wetland plants

Fig. 12 Aboveground plant biomass (pictured *Juncus subulatus*), reduces water flow velocity and erosion and enhances salt marsh vertical accretion. (Photo A. Zikos)

interact in a variety of ways with water and sediment, positively affecting wave attenuation (slowing down water flow) and coastal stabilization (facilitating sediment deposition), natural processes that mitigate hazard and give the system the ability to adapt to climate change (Gedan et al. 2011; Shepard et al. 2011). Plant roots stabilize the soil, while the aboveground biomass significantly reduces the flow velocity of water entering the marsh due to wind-induced waves, impeding erosion and sediment resuspension (Fig. 12). Often the biomass produced by the halophytes contributes largely to the local flux of soil, thereby allowing marsh accretion to progress at the same rate as soil compaction, subsidence and sea level rise. On the other hand, soil conditions determining vegetation type and growth are shaped by tidal forcing, groundwater flow, and local topography, the latter one being the result of erosion and deposition processes (Silvestri and Marani, 2004; Silvestri et al. 2005; Gedan et al. 2011). The structure of the vegetation, and in particular the vertical and horizontal distribution of biomass, is a critical canopy characteristic that controls waves and tidal flow properties. When vegetation interacts with tidal currents and/or waves, flow velocity and water turbulence are drastically reduced. Processes involved in landscape evolution such as erosion, transport, and deposition of sediments are influenced by plant-flow interactions that in turn affect flow velocities and directions, as well as turbulence. On the coast, these interactions that absorb the wave and tidal flux energy act as an “environmental filter” affecting the geomorphology of the landscape over years and decades (Tempest et al. 2015). Although abundant data from modeling, observational, and field studies indicate that wetland vegetation reduces erosion and damage caused by storm surges or even small tsunamis, Gedan et al. (2011) found that this ecosystem service is context-dependent and exhibits nonlinear characteristics across space and time. However, the results of a meta-analysis carried out by Shepard et al. (2011) show that the significant positive effect of vegetation on wave mitigation and coastline stabilization is a reality across a range of geographic and hydrodynamic contexts. It has been proven that ecosystem services, especially wave attenuation and shoreline stabilization, are much more effective in large marshes that sustain dense and productive vegetation than in degraded or severely altered salt marsh areas. Because the vegetation density and biomass production of the salt marsh often vary seasonally depending on plant growth, it is likely that a temporal or even spatial variation in service provision across the marsh exists. It is estimated that wave attenuation rates in the first 10 meters, though variable, frequently exceed 50%, emphasizing the importance of seaward marsh edge in maintaining a minimum salt marsh elevation and preventing marsh plant drowning. The influence of vegetation on soil aeration is another strand of water-soil-vegetation interactions. According to Marani et al. (2006), there are two possible feedback mechanisms: (i) surface accretion promoted by vegetation enhances soil elevation and soil oxygen content which, in turn, induce biomass production; (ii) plant transpiration improves sediment aeration, enhancing also biomass production. It is likely that plant transpiration plays a vital role in the initial colonization of mud flats. Pioneer vegetation best adapted to hypoxic conditions is firstly established in suitable environments, contributing to the creation of permanently aerated soil layers where more sensitive species can subsequently invade. In this way the vegetation is expanded and stabilized, and by favoring sedimentation, it enhances the transition to a marsh system (Marani et al. 2006).

Both composition and richness of plant species are key elements for ecosystem structure and functions such as productivity, nitrogen dynamics, and canopy architecture. However, it has not yet been clarified which and how many species have to be present in each location in order to compose vegetation suitable to attract wildlife. For example, it is well known that bird diversity and the survival of lizards, rodents, and arthropods are directly related to the diversity of canopy architecture (foliage height, layering, cover, plant volume diversity) and that the diversity of the arthropods is partly related to plant diversity. However, for most ecosystems, we do not yet know which and how many plant species provide the essential canopy characteristics. Faunal diversity depends to a large extent on a variety of benefits provided by vegetation, including food, protection from predators, resting and nesting sites, and the possibility of meeting potential mates or competitors. On the other hand, these benefits depend at least in part on the physical arrangement of the aboveground plant parts (canopy architecture). Since several years ago, it is thought that increasing species richness could lead to an increase of canopy height, cover, or layering. Recent research has shown that species-rich plant assemblages have higher cover percentage and greater canopy stratification than species-poor assemblages and that by increasing the space occupied by plants both above- and belowground, sunlight and nutrient uptake, and thus productivity and nutrient retention also increases. The role that plant species diversity plays in the ecosystem functioning is the subject of a constant debate between two schools of thought, each one expressing a different approach. One of the approaches argues that a clear interdependence between diversity and ecosystem functioning exists, while the other one considers that ecosystem functioning is not necessarily driven by diversity but rather by the dominant species, and the composition of functional types (Keer and Zedler 2002). Keer and Zedler (2002), who studied the effects of species composition and richness on ecosystem functioning using a model with eight native halophytes, report that their data on canopy architecture support both aforementioned views.

5 Classification of European Coastal Salt Marsh Vegetation

According to the European Nature Information System (EUNIS), European coastal salt marshes fall into the habitat type A2.5 "Coastal saltmarshes and saline reedbeds" (Davies et al. 2004). For the assessment of this habitat by the European Environment Information and Observation Network (Eionet – a partnership network of the European Environment Agency and its 39 members and cooperating countries), it has been divided into four broad categories, namely, (a) arctic, (b) Baltic, (c) Atlantic, and (d) Mediterranean and Black Sea coastal salt marshes (Eionet Forum). These categories and the related data cited for them in the corresponding EIONET fact sheets are adopted in the descriptions that follow. Other bibliographical sources used additionally are mentioned separately.

The distinction between the **arctic** and the northern Atlantic region is not sharp but rather gradual. Arctic regions are characterized by low temperatures, long lasting ice cover, and an extreme seasonal fluctuation of solar radiation. According to Dijkema et al. (1984), the boundary between arctic and Atlantic maritime plants is placed approximately at the 65th–70th parallel north. Following this definition, arctic salt marshes occur in Iceland, Norway (including the arctic islands), and the European Russia, but not within the European Union (EU28). In arctic marshes, plant coverage is usually low, and there are large open areas of bare sediment. A good indicator to distinguish arctic from northern Atlantic salt marshes are plant communities of the order *Puccinellietalia phryganodis* (class *Juncetea maritimi*) and in particular of the alliances *Puccinellion phryganodis* and *Caricion glareosae*, characterized by the high abundance of circumpolar halophytic species (Walker et al. 2018; Dítě et al. 2019a). *Puccinellion phryganodis* refers to the vegetation of Boreo-arctic coastal lower marsh saline sectors where inundation by the sea lasts longer. The associations belonging to this vegetation type colonize flat areas covered in fine mud that is constantly moist, even during lowest tides, and are characterized by the species *Puccinellia phryganodes* and *Carex subspathacea* (Mucina et al. 2016; Dítě et al. 2019a). The alliance *Caricion glareosae* is typically found in Boreo-arctic coastal upper marsh saline sectors usually flooded by brackish water, on sandy or gravelly substrates, sometimes also on water-logged soil (Dítě et al. 2019a).

It forms associations that include the species *Agrostis stolonifera*, *Carex glareosa*, *C. mackenziei*, *C. salina*, *Festuca rubra*, *Plantago maritima* × *borealis*, and *Stellaria humifusa*.

Both the alliances *Puccinellion phryganodis* and *Caricion glareosae* occur along the shores of the North Atlantic and Arctic Ocean and are characterized by perennials species. There are however formations of the order *Therosalicornietalia* (class *Therosalicornietea*), dominated by annual species, including *Salicornia pojarkovae*, endemic to the Coasts of the White Sea (Russia) and Barents Sea (Norway) (Loconsole et al. 2019). They develop on fine muddy sediment of the mud flats and are considered pioneer communities. They can be assigned to the Habitat Type 1310 ("*Salicornia* and other annuals colonizing mud and sand") of the EU Habitat Directive 92/43. The rest of the plant communities of the arctic salt marshes cannot be assigned to any of the EU Habitat Types, since they occur only in the arctic biogeographical regions outside of the EU28 borders. The arctic, Atlantic, and Baltic coastal salt marshes have several plant species in common, some being dominant in all three regions. For this reason, vegetation units that typically occur at low and high tide mark areas of the Atlantic seaboards of Europe have also been recorded from the arctic salt marshes. This vegetation belongs either to the *Festucion maritimae* or to the *Armerion maritimae* alliances, both assigned to the order *Puccinellio maritimae-Salicornietalia*, class *Juncetea maritimi*.

The **Baltic** Sea is a brackish sea (Dijkema 1990), with a pronounced salinity gradient from approx. 20‰ in the southwest part (near the North Sea) to approx. 2–5‰ in the Gulf of Bothnia to the north and in the Gulf of Finland to the east. Salt marshes present along its shores are characterized by small tidal fluctuation (microtidal systems). Meteorological tides are higher than astronomical tides (Ibañez et al. 2002). Season and prevailing weather conditions are the main driving forces for water level fluctuation, discharge from rivers, storms, wind force, air pressure, and drifting ice having a major role. The fluctuation of water level from year to year can vary considerable (Ericson 1981). Low water level in spring is of high importance for the establishment of the vegetation on the lower marsh (Dijkema 1990).

In the tidal flats of the SW parts of the Baltic Sea and the adjacent parts of the North Sea (Danish, German, and western Swedish coast), the species *Salicornia dolichostachya* forms a pioneer zone located below mean water level. Further east this zone is replaced by a brackish reed belt dominated by *Bolboschoenus maritimus* (Fig. 13) and *Schoenoplectus lacustris* subsp. *glaucus*. *Tripolium pannonicum* subsp. *tripolium* is also an important species in this area (Dijkema 1990). At least one *Juncus maritimus* community has been recorded from the southern Baltic coast (Piotrowska 1974). Further north and east, toward the Bothnian Sea and the Gulf of Finland, the abundance of non-halophytic species increases, due to a drop in salinity. At the Baltic Sea shores, the halophytic *Eleocharis parvula* community develops; however it is replaced by a non-halophytic *Eleocharis acicularis* community, in the Gulf of Bothnia and the Gulf of Finland (Dijkema 1990).

The communities found in the lower salt marsh belts of the western part of the area belong predominantly to the *Festucion maritimae* alliance, and they are dominated by the species *Puccinellia maritima* (Dijkema 1990). The halophytic species

Fig. 13 *Bolboschoenus maritimus* (Photo A. Zikos)

Tripolium pannonicum subsp. *tripolium*, *Plantago maritima*, *Triglochin maritima*, *Spergularia media*, *Salicornia europaea*, and *Limonium humile* also occur here. Toward the east and the north, the drop of salinity allows less salt-tolerant communities to form, dominated by species such as *Agrostis stolonifera*. However there are also real halophytic communities of the *Scirpion maritimi* alliance (order *Bolboschoenetalia maritimi*, class *Phragmito-Magnocaricetea*), like the *Eleocharis uniglumis* community or communities dominated by *Carex paleacea* and *C. halophila* (Dijkema 1990). The subspecies *Puccinellia distans* subsp. *distans* and *P. distans* subsp. *borealis*, as well as the species *Spergularia marina*, also form communities in the lower marsh. These fall into the *Puccinellio maritimae-Spergularion salinae* alliance (order *Puccinellio maritimae*-*Salicornietalia*), which comprises vegetation of grass-rich saline swards of hypersaline supratidal habitats (Mucina et al. 2016). The lower belt of the marsh is particularly pronounced in the northern part of the Bothnian Gulf. The uplift of the land that takes places in this area creates bare ground that is ideal substrate for such pioneer species.

The upper salt marsh sector in this biogeographical region is dominated by *Juncus gerardi* communities, belonging to the alliance *Armerion maritimae*. The *Juncetum gerardii* Warming 1906 association is the most important community of the shores of northern Europe (Dijkema 1990). Other species that occur in the upper belt of the Baltic coastal marshes are *Festuca rubra*, *Agrostis stolonifera*, *Blysmopsis rufa*, *Vicia cracca*, *Argentina anserina* subsp. *groenlandica*, *Carex glareosa*, *C. nigra*, *Trifolium fragiferum*, *Lotus tenuis*, and *Calamagrostis neglecta* (Dijkema 1990). Due to the salinity gradient and the influence of freshwater, in many cases, true halophytes and more freshwater indicating species mix. It is noteworthy that the Bothnian Gulf is one of the few areas of northern Europe, where endemic taxa evolved, after the last Ice Age. Such taxa are, for example, *Deschampsia cespitosa* subsp. *bottnica* and *Euphrasia bottnica*. A high number of arctic-boreal species have their southernmost occurrence in this area, for example, *Puccinellia phryganodes*. Most vegetation types of the marshes around the Baltic and Bothnian Sea can be included in the priority EU habitat type "Boreal Baltic coastal meadows" (1630), while those at the German and Polish Baltic coast in the habitat type 1330 "Atlantic salt meadows (*Glauco-Puccinellietalia maritimae*)."

Atlantic salt marshes occur in the western coast of Europe, from central Portugal to the coasts of Denmark in the North Sea, the British Isles, the western coast of Sweden, and parts of southern Iceland and southern Norway. In the southern part of Portugal (south of the Mondego river estuary), the marshes have a strong Mediterranean character and are considered as such. The Atlantic salt marshes are predominantly macro-tidal systems. In this area, some of the most extensive salt marshes of Europe are found. To cite just one example, the average tidal range in Mont Saint-Michel Bay (France), the second highest in Europe, is approximately 11 m (with a maximum of more than 15 m), creating an intertidal zone of 240 km^2 (Lefeuvre et al. 2000).

The vegetation of these salt marshes varies according to climate, sediment type, frequency, and length of inundation. Starting from the sea and moving inland, toward the upper marsh, a zonation of more to less halophytic communities is observed. On the mud flats of the Atlantic salt marshes, pioneer communities of *Salicornia* species are common. These species-poor communities consist primarily of summer-annual taxa and are thus ephemeral (Beeftink 1977). They are assigned to the order *Therosalicornietalia*. According to the Interpretation Manual of European Union Habitats (European Commission 2013), these formations are included in the habitat type "*Salicornia* and other annuals colonizing mud and sand" (habitat code 1310). Apart from the annual communities, perennial pioneer communities of *Spartina* species, belonging to the alliance *Spartinion glabrae* (order Spartinetalia glabrae, class Spartinetea maritimae), also occur (Beeftink 1977; Bakker et al. 1993). This alliance gathers species-poor pioneer communities of perennial cord grasses occurring in temperate seas of Europe and North America (Mucina et al. 2016) and falls into the EU habitat type 1320 "*Spartina* swards (*Spartinion maritimae*)." *Spartina* species usually form dense monospecific swards creating a narrow belt slightly below mean high tide water level. They occur predominately on waterlogged mud under conditions of accretion. This vegetation type is the most erosion resistant one of the tidal flats (Beeftink 1977). Both the abovementioned pioneer habitat types promote further sedimentation, creating suitable conditions for *Puccinellia maritima* arrival and establishment. *Puccinellia maritima* reaches around mean high tide water level sufficient coverage to enhance maximal sedimentation (Bakker et al. 1993). Its communities are dominant in the lower marshes of the Atlantic coast. They are classified into the EU habitat type 1330 "Atlantic salt meadows (*Glauco-Puccinellietalia maritimae*)" and the alliance *Festucion maritimae*. The dominant vegetation in this belt of the marsh is at first a short prairie (*Puccinellia maritima*) but is later replaced by taller species like *Halimione portulacoides* and *Elytrigia atherica* (Lefeuvre et al. 2000). In the southern part of the Atlantic salt marshes (Southwestern France, northern Spain, and Portugal), Atlantic-Mediterranean floristic elements,

Fig. 14 *Triglochin barrelieri* (Photo K. Goula, used with permission)

like *Frankenia laevis*, *Hornungia procumbens*, *Triglochin barrelieri* (Fig. 14), *Parapholis incurva*, and *Spartina maritima* also participate in the communities.

The upper parts of the Atlantic salt marshes get inundated by the sea less frequently and for shorter periods. Communities that fall into the alliance *Armerion maritimae* are dominant here (Beeftink 1977). Characteristic species are *Juncus gerardi*, *Festuca rubra* subsp. *litoralis*, *Agrostis stolonifera*, *Armeria maritima*, *Elytrigia atherica*, *Juncus maritimus*, *Plantago maritima*, *Glaux maritima*, *Limonium vulgare*, *Hordeum marinum*, and *Artemisia maritima* (Beeftink 1977). In areas where the influence of freshwater is prevalent, formations of the *Scirpion maritimi* alliance, most frequently dominated by *Bolboschoenus maritimus*, occur.

Mediterranean coastal salt marshes show a higher variability compared to that of the Arctic and temperate coastal areas. This can be attributed primarily to the high variation in salinity and flooding regimes in small areas, due to the micro-topography of the region (Ibañez et al. 2002). Coastal salt marshes of the Mediterranean region are predominantly micro-tidal systems, having only small water level fluctuation; however some macro-tidal systems also exist (see below).

The Mediterranean climate is characterized by dry, hot, prolonged summers, while the winters are moderately cold and wet. Maximum sea level and rainfall are recorded in fall and a secondary maximum in spring (Ibañez et al. 2002). Evapotranspiration during the prolonged summer drought puts a strong drought stress on the plants and affects soil salinity in the marshes and thus the distribution of vegetation assemblages. In most areas, river discharge into the sea is rather low. Some exceptions do exist, like the Po and Rhone river estuaries (Ibañez et al. 2002). The once largest, as far as water discharge is concerned, Nile River, on the African shores of the Mediterranean, has nowadays very low discharge due to the construction of the Aswan High Dam and water usage, primarily for agriculture and human needs (Wahby and Bishara 1981).

The majority of the Mediterranean coastal salt marshes occur in deltaic formation. These deltas usually protrude into the sea and are rather small, in contrast to the estuaries of the Atlantic Europe, that are mostly large areas in coastal indentations, dominated by tides. Deltaic systems exhibit a high diversity of habitats. The most extended deltaic areas of the Mediterranean are that of the rivers Ebro (Spain), Rhone (France), Po (Italy), Nile (Egypt), and Danube (Romania). Important marsh areas can also be found in coastal lagoons, as, for example, in the northern Adriatic (Venice and Marano-Grado) and in the Languedoc region of southern France. Since most salt marshes of the area are micro-tidal systems, maximum meteorological tides are higher than astronomical ones (Fig. 15). Weather conditions and their seasonal variation are decisive for the flooding regime of the marshes. In many cases, the marshes are inundated only during severe storms and not regularly as a result of astronomical tidal action (Ibañez et al. 2002).

As mentioned before, some macro-tidal systems also exist in the Mediterranean. A good example of such is the salt marsh located in the northern Adriatic, between the lagoons of Marano and Grado (Géhu et al. 1984). The lower belt of these marshes is very similar to those found on the Atlantic coast, dominated by *Spartina* swards (EU habitat type 1320). Further up, prostate *Sarcocornia* communities develop (Fig. 16), replaced upward by erect *Sarcocornia* communities. In the upper marsh, *Arthrocnemum* communities dominate (Fig. 17). In the gaps of bare ground, seasonal pioneer vegetation of annual *Salicornia* species may occur. Halophytic communities of hemicryptophytic tall *Juncus* species form the transitional zone between the marsh and upland vegetation (Ibañez et al. 2002). Mediterranean-climate macro-tidal salt marshes do not exhibit a simple monotonic gradient of physical factors from sea inland, but rather an interaction between flooding and salinity is found. This interaction creates a zone of superior habitat in the middle marsh, where both factors are moderate (Pennings and Callaway 1992; Ibañez et al. 2002).

The more typical Mediterranean micro-tidal salt marshes can be found all over the basin, including the southern European coasts. In these systems no tidal mud flats are normally present between the open sea and the marshes. *Spartina* swards, readily abundant in macro-tidal marshes of the Atlantic, are practically absent. In many marshes, a hypersaline aquifer is found in shallow depths underneath the soil surface. Where shallow hypersaline groundwater is present, salt marshes can develop in supratidal areas. The elevation range of these supratidal marshes has a positive correlation with the drought intensity. The coastal salt marsh plant communities around the Mediterranean basin show similarities in structure; however

Fig. 15 The coastal wetland area of Schinias National Park (Greece) is a typical Mediterranean salt marsh, seasonally flooded due to the weather conditions and not as a result of astronomical tides. (Photo A. Zikos)

differences attributed to geographical range and climatic variation are observed (Ibañez et al. 2002). In the typical Mediterranean marshes, although a rough zonation from the sea toward the upper marsh is visible, rather than a clear spatial sequence of communities, a mosaic of different vegetation/habitat types is more common (Fig. 18).

This mosaic comprises communities of shrubby *Chenopodiaceae* species and tall halophytic *Juncus* communities. In general, salt marshes dominated by shrubby *Chenopodiaceae* (belonging to the genera *Sarcocornia*, *Arthrocnemum*, *Suaeda*, *Halocnemum*) are the most common marshes across the Mediterranean. In the lower marsh, *Sarcocornia perennis* communities are found around mean sea level (Ibañez et al. 2002). In the middle marsh, the *taller Sarcocornia fruticosa* communities develop. *Arthrocnemum macrostachyum* dominated stands are usually encountered in the upper salt marsh belt, but in drier areas in the eastern Mediterranean, this species is partially replaced by *Halocnemum strobilaceum* (Ibañez et al. 2002). These species-poor shrubby communities, dominated by members of the

Fig. 16 *Sarcocornia perennis* community. (Photo A. Zikos)

Fig. 17 *Arthrocnemum macrostachyum* (Photo A. Zikos)

Chenopodiaceae family, can be classified into the habitat type 1420 “Mediterranean and thermo-Atlantic halophilous scrubs (*Sarcocornetea fruticosae*).” They belong to the order *Salicornietalia fruticosae* (class *Salicornietea fruticosae*) and primarily to the alliances *Salicornion fruticosae* and *Arthrocnemion glauci*. The *Juncus* communities (Fig. 19) fall into the *Juncion maritimi* alliance of the *Juncetalia maritimi* order (class *Juncetea maritimi*) and can be classified into the EU habitat type 1410 “Mediterranean salt meadows (*Juncetalia maritimi*).” This habitat includes salt

Fig. 18 Mosaic of shrubby *Chenopodiaceae* and halophytic *Juncus* communities in a Mediterranean salt marsh. (Photo A. Zikos)

Fig. 19 *Juncus maritimus* (Spercheios delta, Greece). (Photo A. Zikos)

meadows in the Mediterranean basin, colonized by hemicryptophytes, tolerant of saline soils, on wet and temporarily inundated sites. They develop on the upper part of the marsh. Dominant species are *Juncus maritimus*, *J. acutus* (Fig. 20), *J. subulatus* (Fig. 21), and *J. heldreichianus*.

In areas not flooded for the whole summer, annual halophytic communities, dominated by *Salicornia* and *Suaeda* species (class *Therosalicornietea*, EU habitat type 1310), may exist, usually in depressions between the communities of perennials mentioned before. In the driest areas, where hypersaline periods are very long, salt flats, also known as salt pans, are common (Fig. 22) (Ibañez et al. 2002). These can either be completely bare of higher plants or temporarily covered by ephemeral

Fig. 20 *Juncus acutus* (Photo A. Zikos)

Fig. 21 *Juncus subulatus* (Lesvos, Greece). (Photo A. Zikos)

assemblages of annuals (class *Therosalicornietea*), during the period of the year when the conditions are suitable for these plants to grow (Dítě et al. 2019b).

The salt marshes of the Black Sea have both similarities with and differences from the Mediterranean ones. First of all, Black Sea has a lower salinity than the Mediterranean; evapotranspiration is less than in southern Mediterranean regions and the climate more continental. Salt marshes of the Black Sea demonstrate a lower variability than those of the Mediterranean. In the Black Sea, monospecific stands of *Juncus maritimus* or *J. acutus* are very common. Shrub communities dominated by the species *Halocnemum strobilaceum* (Fig. 23) occur at the northern Black Sea

Fig. 22 Areas completely bare of higher plants, due to hypersaline conditions are known as salt pans. (Photo A. Zikos)

Fig. 23 *Halocnemum strobilaceum* (Photo A. Zikos)

shores of Romania and Ukraine. Some salt marshes on the shore of the Black Sea, especially those at the Danube delta and the Razim-Sinoe lagoons, host communities dominated by *Salicornia perennans* (order *Therosalicornietalia*), *Puccinellia distans* subsp. *limosa*, and *Juncus gerardi* (order *Puccinellietalia*) that are more similar to those found in continental inland salt marshes.

The concepts and nomenclature of all the abovementioned syntaxa follow the hierarchical floristic classification system proposed by Mucina et al. (2016). For detailed information on all high rank vegetation units occurring in the European coastal salt marshes, the reader can refer to the same system. The nomenclature of the abovementioned plant taxa is according to the Euro+Med (2006) online database.

6 Conclusions

Coastal marshes are dynamic but also sensitive ecosystems arising at interfaces between sea and land and offer important ecosystem services such as coastal protection, food provision, and carbon sequestration. The origin and viability of coastal marshes as well as their ability to provide high value ecological benefits depend on the delicate equilibrium of abiotic and biotic factors that act at local scale, among which the relative sea level, erosion, sediment availability, and vegetation dynamics are of high importance (Silvestri and Marani 2004; Day et al. 2011). When the equilibrium governing the cooperative feedback of the abovementioned processes is disturbed, the same processes lead to reduction or loss of these systems (Townend et al. 2011). One of the major limiting factors regulating salt marsh development and sustainability is the relationship between relative sea level (duration and frequency of tidal flooding) and sediment accretion (deposition, decomposition, subsidence, compaction) at nay given time (Weis et al. 2017). It is widely recognized that the ability of salt marshes to withstand a potential rise of relative sea level is closely related to sediment supply as it has currently been confirmed that reduced deposition rate inhibits the development of salt marshes. A salt marsh can effectively cope with a possible sea level rise only if the relative sea level rise is equal to or lower than sediment accretion (Boorman 2003; Shepard et al. 2011). Although it is widely argued that vertical accretion of coastal marshes through sediment accumulation is enhanced in the context of rising sea level, lateral erosion due to either anthropogenic or natural factors may significantly affect the structure of the pioneer zone, thereby causing higher salt marsh loss rates (Fernandez-Nunez et al. 2019). However, vertical accretion enhances vegetation development which in turn impedes drastically erosion and sediment resuspension (Tempest et al. 2015; Belluco et al. 2006). As the vegetated platform rises vertically through sediment accumulation, the resulting environmental conditions increasingly favor the growth of a dense vegetation layer that in turn increases deposition rates, reduces water flow, and stabilizes the soil (Townend et al. 2011). Biomass produced by the halophytes contributes to the local retention and stabilization of the soil, thus enabling the rate of accretion to keep pace with soil compaction, subsidence, and rising sea levels.

It is therefore obvious that coastal wetland vegetation is strongly involved in the development of coastal marshes, supports vital functions of these ecosystems, and effectively promotes important ecological services such as wave mitigation and coastline stabilization. The dynamics of coastal flat terrain lying within the tidal frame are influenced by the halophyte communities. The development of the salt marshes in these localities is directly linked to the coupled balance between vegetation colonization and geomorphology (sediment accretion). This complex eco-geomorphological relationship governs the spatial distribution of halophytes and generates distinct zonation patterns along the elevation and salinity gradients, within which various salt marsh plant communities (annual and perennial succulents, sedges, rushes), consisting either of a single species or of a specific species combination, are typically organized in the form of intermittent patches (Silvestri and Marani 2004; Belluco et al. 2006; Weis et al. 2017). According to literature data

(Penning et al. 2005), these patterns can be used for the separation of the marsh into 3 zones (low, mid and high marsh). While the main mechanisms responsible for organizing zonation patterns operate in the same way on a global scale, the importance of the involved individual factors seems to vary geographically due to variations in the natural environment (Penning et al. 2005). Within the limits of the range of abiotic factors, competition and facilitation are recognized today as the main biological forces causing the patterns of the zonation sequence, as their action shifts along the gradients of physical stresses such as salinity, duration, and frequency of flooding, and availability of nutrients and oxygen (Barbier et al. 2011; Lee and Kim 2018).

Based on the specified plant species combinations and the vegetation types they host, coastal salt marshes around the world can be divided into six major categories, while several continental subgroups that reflect the diversity of regional environmental and climatic conditions are further distinguished (Adam 2002). The diversity of the dominant plant assemblages occurring in the salt marshes of European coasts allows the classification of the homonym salt marshes into four main types related to the biogeographic regions of the arctic, Baltic, Atlantic, and Mediterranean-Black Sea (Eionet Forum).

References

Adam, P. (1990). *Saltmarsh ecology*. Cambridge, UK: Cambridge University Press.

Adam, P. (2002). Saltmarshes in a time of change. *Environmental Conservation, 29*(1), 39–61.

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs, 81*(2), 169–193.

Batriu, E., Ninot, J. M., Rovira, P., & Pino, J. (2013). Plant communities partially reflect environmental gradients in humanized landscapes: A case study in the Llobregat delta marshes. *Phytocoenologia, 43*(3-4), 183–191.

Batriu, E., Ninot, J. M., & Pino, J. (2015). Interactions between transplants of *Phragmites australis* and *Juncus acutus* in Mediterranean coastal marshes: The modulating role of environmental gradients. *Aquatic Botany, 124*, 29–38.

Beeftink, W. G. (1977). The coastal salt marshes of Western and Northern Europe: An ecological and phytosociological approach. In V. J. Chapman (Ed.), *Wet coastal ecosystems* (pp. 109–155). Amsterdam: Elsevier.

Belluco, E., Camuffo, M., Ferrari, S., Modenese, L., Silvestri, S., Marani, A., & Marani, M. (2006). Mapping salt-marsh vegetation by multispectral and hyperspectral remote sensing. *Remote Sensing of Environment, 105*, 54–67.

Bertness, M. D., & Pennings, S. C. (2002). Spatial variation in process and pattern in salt-marsh communities in Eastern North America. In M. P. Weinstein & D. A. Kreeger (Eds.), *Concepts and controversies in Tidal Marsh Ecology* (pp. 39–59). Dordrecht: Kluwer Academic Publishers.

Boorman, L. A. Saltmarsh Review. An overview of coastal saltmarshes, their dynamic and sensitivity characteristics for conservation and management. JNCC Report 2003; No. 334.

Boorman, L. A., Hazelden, J., & Boorman, M. (2001). The effect of rates of sedimentation and tidal immersion regimes on the growth of saltmarsh plants. *Continental Shelf Research, 21*, 2155–2165.

Chirol, C., Haigh, I. D., Pontee, N., Thompson, C. E., & Gallop, S. L. (2018). Parametrizing tidal creek morphology in mature saltmarshes using semi-automated extraction from lidar. *Remote Sensing of Environment, 209*, 291–311.
Chmura, G. L., Anisfeld, S. C., Cahoon, D. R., & Lynch, J. C. (2003). Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochem Cycles, 17*(4), 1111. https://doi.org/10.1029/2002GB001917.
Cutini, M., Agostinelli, E., Acosta, T. R. A., & Molina, J. B. (2010). Coastal salt marsh zonation in Tyrrhenian Central Italy and its relationship with other Mediterranean wetlands. *Plant Biosystems, 144*(1), 1–11.
Davies, C. E., Moss, D., & Hill, M. O. (2004). *EUNIS habitat classification revised 2004*. Copenhagen: European Environment Agency.
Davy, A. J. (2002). Development and structure of salt marshes: Community patterns in time and space. In M. P. Weinstein & D. A. Kreeger (Eds.), *Concepts and controversies in Tidal Marsh Ecology* (pp. 137–156). Dordrecht: Kluwer Academic Publishers.
Day, J. W., Pont, D., Hensel, P. F., & Ibañez, C. (1995). Impacts of sea-level rise on deltas in the Gulf of Mexico and the Mediterranean: The importance of pulsing events to sustainability. *Estuaries, 18*(4), 636–647.
Day, J. W., Kemp, G. P., Reed, D. J., Cahoon, D. R., Boumans, R. M., Suhayda, J. M., & Gambrell, R. (2011). Vegetation death and rapid loss of surface elevation in two contrasting Mississippi delta salt marshes: The role of sedimentation, autocompaction and sea-level rise. *Ecological Engineering, 37*, 229–240.
De Bakker, J. P., Leeuw, J., Dijkema, K. S., Leendertse, P. C., Prins, H. H. T., & Rozema, J. (1993). Salt marshes along the coast of the Netherlands. *Hydrobiologia, 265*, 73–96.
Dijkema, K. S. (1990). Salt and brackish marshes around the Baltic Sea and adjacent parts of the North Sea: Their vegetation and management. *Biological Conservation, 51*, 191–209.
Dijkema, K. S., Beeftink, W. G., Doody, J. P., Gehu, J. M., Heydemann, B., & Rivas-Martinez, S. (1984). *Salt marshes in Europe*. Strasbourg: Report Council of Europe.
Dítě, D., Dítě, Z., Hájková, P., & Šuvada, R. (2019a). Vegetation and ecological characteristics of the northernmost salt marshes of the European continent. *Nordic Journal of Botany, 37*(7), 1–11.
Dítě, Z., Šuvada, R., Eliáš, P., Píš, V., & Dítě, D. (2019b). Salt marsh vegetation on the Croatian coast: Plant communities and ecological characteristics. *Plant Systematics, 305*(10), 899–912.
Doody, J. P. (2008). *Saltmarsh conservation, management and restoration* (pp. 219). New York: Springer.
Duarte, C. M., Dennison, W. C., Orth, R. J. W., & Carruthers, T. J. B. (2008). The charisma of coastal ecosystems: Addressing the imbalance. *Estuaries and Coasts, 31*(2), 233–238.
Eionet Forum. Reports on European Red List of habitats. Online Source. https://forum.eionet.europa.eu/european-red-list-habitats. Accessed December 2019.
El-Ghareeb, R. M., El-Sheikh, M. A. E., & Testi, A. (2006). Diversity of plant communities in coastal salt marshes habitat in Kywait. *Rediconti Lincei-Science Fisiche e Naturali, 17*(3), 311–331.
El-Sheikh, M. A. E., & Abbadi, G. A. (2004). Biodiversity of plant communities in the Jal Az-Zor National Park, Kuwait. *Kuwait Journal of Science and Engineering, 31*, 77–105.
Ericson, L. (1981). Aspects of the shore vegetation of the Gulf of Bothnia. *Wahlenbergia, 7*, 45–60.
Euro+Med. (2006). Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. Published on the Internet http://ww2.bgbm.org/EuroPlusMed/. Accessed December 2019.
European Commission. (2013). Interpretation manual of European Union habitats. *EUR, 28*, 1–144. European Commission: DG Environment.
Fernandez-Nunez, M., Burningham, H., Díaz-Cuevas, P., & Ojeda-Zújar, J. (2019). Evaluating the response of Mediterranean-Atlantic Saltmarshes to Sea-Level Rise. *Resources, 8*, 50. https://doi.org/10.3390/resources8010050.

Foster, N. M., Hudson, M. D., Bray, S., & Nicholls, R. J. (2013). Intertidal mud flat and saltmarsh conservation and sustainable use in the UK: A review. *Journal of Environmental Management, 126*, 96–104.
Garbutt, A., de Groot, A., Smit, C., & Pétillon, J. (2017). European salt marshes: Ecology and conservation in a changing world. *Journal of Coastal Conservation, 21*, 405–408.
Gedan, K. B., Kirwan, M. L., Wolanski, E., Barbier, E. B., & Silliman, B. R. (2011). The present and future role of coastal wetland vegetation in protecting shorelines: Answering recent challenges to the paradigm. *Climatic Change, 106*, 7–29.
Géhu, J. M., Scoppola, A., Caniglia, G., Marchiori, S., & Géhu-Franck, J. (1984). Les systèmes végétaux de la côte nord-adriatique italienne. Leur originalité à 1'échelle européenne. *Colloques phytosociologiques, 8*, 485–558.
Hladik, C., & Alber, M. (2014). Classification of salt marsh vegetation using edaphic and remote sensing derived variables. *Estuarine, Coastal and Shelf Science, 141*, 47–57.
Ibañez, C., Curcó, A., Day, J. W., & Prat, N. (2002). Structure and productivity of microtidal Mediterranean coastal marshes. In M. P. Weinstein & D. A. Kreeger (Eds.), *Concepts and controversies in Tidal Marsh Ecology* (pp. 107–136). Dordrecht: Kluwer Academic Publishers.
Keer, G. H., & Zedler, J. B. (2002). Salt marsh canopy architecture differs with the number and composition of species. *Ecological Applications, 12*(2), 456–473.
Lee, J. S., & Kim, J. W. (2018). Dynamics of zonal halophyte communities in the salt marshes of the world. *Journal of Marine and Island Cultures, 7*(1), 84–106.
Lefeuvre, J. C., Bouchard, V., Feunteun, E., Grare, S., Laffaille, P., & Radureau, A. (2000). European salt marshes diversity and functioning: The case study of the Mont Saint-Michel bay. *France. Wetland Ecology and Management, 8*(2-3), 147–161.
Lemly, A. D., Kingsford, R. T., & Thompson, J. R. (2000). Irrigated agriculture and wildlife conservation: Conflict on a global scale. *Environmental Management, 25*, 485–512.
Loconsole, D., Cristiano, G., & De Lucia, B. (2019). Glassworts: From wild salt marsh species to sustainable edible crops. *Agriculture, 9*, 14; https://doi.org/10.3390.
Marani, M., Silvestri, S., Belluco, E., Ursino, N., Comerlati, A., Tosatto, O., & Putti, M. (2006). Spatial organization and ecohydrological interactions in oxygen-limited vegetation ecosystems. *Water Resource Research, 42*, 1–12.
Min, B. M. (2015). Distribution properties of *Phragmites australis* and *Phacelurus latifolius* in the tidal-flat of Suncheon Bay. *Journal of Ecology and Environment, 38*, 5765.
Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J. P., Th, R., Čarni, A., Šumberová, K., Willner, W., Dengler, J., Gavilán García, R., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, F. J. A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovič, M., Schaminée, J. H. J., Lysenko, T., Didukh, Y. P., Pignatti, S., Rodwell, J. S., Capelo, J., Weber, H. E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S. M., & Tichý, L. (2016). Vegetation of Europe: Hierarchical floristic classification system of vascular plant bryophyte lichen and algal communities. *Applied Vegetation Science, 19*(1), 3–264.
Nicholls, R. J., Wong, P. P., Burkett, V. R., Codignotto, J. O., Hay, J. E., McLean, R. F., Ragoonaden, S., & Woodroffe, C. D. (2007). Coastal systems and low-lying areas. In M. L. Parry, Canziani OF, J. P. Palutikof, P. J. van der Linden, & C. E. Hanson (Eds.), *Climate change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 315–356). Cambridge: Cambridge University Press.
Pennings, S. C., & Callaway, R. M. (1992). Salt marsh plant zonation: The relative importance of competition and physical factors. *Ecology, 73*, 681–690.
Pennings, S. C., Grant, M. B., & Bertness, M. D. (2005). Plant zonation in low-latitude salt-marshes: Disentangling the roles of flooding, salinity and competition. *Journal of Ecology, 93*, 159–167.
Piotrowska, H. (1974). Maritime communities of halophytes in Poland and the problems of their protection. *Ochrona Przyrody, 39*, 7–63. (in Polish).

Scapini, F. (2010). Mediterranean coastal areas at risk between conservation and development. In F. Scapini & G. Ciampi (Eds.), *Coastal water bodies. Nature and culture conflicts in the Mediterranean* (pp. 1–20). London, New York: Springer Dordrecht, Heidelberg.
Shepard, C. C., Crain, C. M., & Beck, M. W. (2011). The protective role of coastal marshes: A systematic review and meta-analysis. *PLoS One, 6*(11), e27374. https://doi.org/10.1371/journal.pone.0027374.
Silvestri, S., & Marani, M. (2004). Salt-marsh vegetation and morphology, modeling and remote sensing observations. In S. Fagherazzi, M. Marani, & L. Blau (Eds.), *The Ecogeomorphology of Tidal Marshes, Coastal Estuarine Stud* (Vol. 59, pp. 5–26). Washington: American Geophysical Union, Coastal and Estuarine Monograph Series.
Silvestri, S., Defina, A., & Marani, M. (2005). Tidal regime, salinity and salt marsh plant zonation. *Estuarine Coastal and Shelf Science, 62*, 119–130.
Stevenson, J. C., Rooth, J. E., Kearney, M. S., & Sundberg, K. L. (2002). The health and long term stability of natural and restored marshes in Chesapeake Bay. In M. P. Weinstein & D. A. Kreeger (Eds.), *Concepts and controversies in Tidal Marsh Ecology* (pp. 709–736). Dordrecht: Kluwer Academic Publishers.
Temmerman, S. T. J., Bouma, G., Govers, Z. B., Wang, M. B., Vries, D., & Herman, P. M. J. (2005). Impact of vegetation on flow routing and sedimentation patterns: Three-dimensional modeling for a tidal marsh. *Journal of Geophysical Research, 110*, F04019. https://doi.org/10.1029/2005.JF000301.
Tempest, J. A., Möller, I., & Spencer, T. (2015). A review of plant-flow interactions on salt marshes: The importance of vegetation structure and plant mechanical characteristics. *WIREs Water, 2*, 669–681.
Townend, I., Fletcher, C., Knappen, M., & Rossington, K. (2011). A review of salt marsh dynamics. *Water and Environment Journal, 25*, 477–488.
Valiela, I., Cole, M. T., McClelland, J., Hauxwell, J., Cebrian, J., & Joye, S. B. (2002). Role of the salt marshes as a part of coastal landscapes. In M. P. Weinstein & D. A. Kreeger (Eds.), *Concepts and controversies in Tidal Marsh Ecology* (pp. 23–38). Dordrecht: Kluwer Academic Publishers.
van Beijma, S., Comber, A., & Lamb, A. (2014). Random forest classification of salt marsh vegetation habitats using quad-polarimetric airborne SAR, elevation and optical RS data. *Remote Sensing of Environment, 149*, 118–129.
Veldkornet, D. A., Pots, A. J., & Adams, J. B. (2016). The distribution of salt marsh macrophyte species in relation to physicochemical variables. *South African Journal of Botany, 107*, 84–90.
Wahby, S. D., & Bishara, N. F. (1981). The effect of the River Nile on Mediterranean Water before and after the construction of the High Dam at Aswan. In *Proceedings of a Review Workshop on River Inputs to Ocean Systems*. Proceedings of a review workshop held at FAO headquarters, Rome, Italy from 26 to 30 March 1979. New York: United Nations, pp. 311–318.
Walker, D. A., Daniëls, F. J. A., Matveyeva, N. V., Šibík, J., Walker, M. D., Breen, A. L., Druckenmiller, L. A., Raynolds, M. K., Bültmann, H., Hennekens, S., Buchhorn, M., Epstein, H. E., Ermokhina, K., Fosaa, A. M., Heidmarsson, S., Heim, B., Jónsdóttir, I. S., Koroleva, N., Lévesque, E., MacKenzie, W. H., Henry, G. H. R., Nilsen, L., Peet, R., Razzhivin, V., Talbot, S. S., Telyatnikov, M., Thannheiser, D., Webber, P. J., & Wirth, L. M. (2018). Circumpolar arctic vegetation classification. *Phytocoenologia, 48*, 181–201.
Weis, J. S., Segarra, K. E.A., & Bernal, P. (2017). Salt marshes. In United Nations, Division for Ocean Affairs and Law of the Sea, Office of Legal Affairs editor. *The first global integrated marine assessment. World assessment I* (pp. 887–892). Cambridge: Cambridge University Press.
Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon, 21*, 213–251.
Whittaker, R. H., & Levin, S. A. (1977). The role of the mosaic phenomena in natural communities. *Theoretical Population Biology, 12*, 117–139.