

Cordgrass Biomass in Coastal Marshes

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1. Introduction

Cordgrasses (Genus *Spartina*) are one of the most abundant and geographically wide spread halophytes, due to natural and human-mediated dispersal. *S. alterniflora* Loisel, *S. patens* (Aiton) Muhl., *S. spartinae* (Trin.) Merr. ex Hitchc. and *S. cynosuroides* (L.) Roth are native from coastal salt marshes along the East Coast of the American continent, *S. foliosa* Trin. is native to South Californian salt marshes, *S. densiflora* Brongn. and *S. argentinensis* Parodi grow naturally in South American salt marshes and *S. maritima* (Curtis) Fernald, *S. versicolor* Fabre, *S. x townsendii* Groves and *S. anglica* C.E. Hubbard are autochthonous species from European estuaries (Fabre, 1849; Moberley, 1956). Cordgrasses have been introduced to distant salt marshes where they usually behave as invaders. For example, *S. densiflora* colonizes as an alien species the West Coast of North America from San Francisco Bay to British Columbia, the West Coast of Morocco and the Gulf of Cadiz at Southwest Iberian Peninsula (Bortolus, 2006).

Cordgrasses are able to colonize contrasted environments throughout the intertidal gradient such as low marshes and salt pans, and along river channels such as sand spits at river mouths and brackish wetlands landwards. These different coastal marsh habitats show high abiotic and biotic environmental heterogeneity and cordgrasses exhibit a high level of phenotypic plasticity (e.g. Thompson, 1991; Thompson et al., 1991; Trnka & Zedler, 2000; Castillo et al., 2005a). Moreover, some *Spartina* species have developed ecotypes during the process of adaptation to different environmental conditions (e.g. Seliskar et al., 2002; Álvarez et al., 2010). It is also frequent that invasive and native *Spartina* species hybridized. Hybrids may become new allopolyploid species such as *S. anglica* (Schierenbeck & Ellstrand, 2009) and they can develop transgressive traits (e.g. Castillo et al., 2010).

Salt marshes are among the most productive ecosystems in spite of a low plant species richness due to a very stressful environment related with long flooding periods and high salinities (Adam, 1990). Living in this extreme environment, cordgrasses are able to develop dense tussocks, clumps and prairies that may accumulate very high below- and above-ground biomass.

The biomass of cordgrasses plays a very important role in the functioning of salt marshes and estuaries. For example, it controls the development of ecological succession, organizes space occupation of other plants and animals, and plays a key role in estuarine food webs. This chapter analyses inter- and intra-specific variations in the biomass of cordgrasses growing in coastal marshes all around the world.

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Fig. 1. Small cordgrass (*Spartina maritima*) grows on intertidal mudflats in European salt marshes where it forms continuous prairies with its coalescent clumps that colonize bare sediments with long rhizomes.

2. Sampling cordgrass biomass

Cordgrasses colonize surrounding sediments by successive series of rhizomes, which is reflected in concentric and alternating rings of live and dead shoots with low and high densities and usually in central die-back areas that may remain occupied by necromass. This clonal growth has been described for cordgrasses such as *S. maritima* (Caldwel, 1957; Castellanos et al., 1994) and *S. densiflora* (Castillo et al., 2003). Sediments without vegetation or colonized by other plants are found between expanding *Spartina* clumps prior to their coalescence.

Abiotic factors such as topography, oxygen concentration in sediments, drainage, photoperiod or salinity determine a high degree of environmental heterogeneity at large, medium and small scales (microhabitats) in coastal marshes, which influences the area occupied by expanding *Spartina* clumps. For example, growth of *S. anglica* and *S. maritima* rhizomes is limited by the interference of erosive banks that obstruct their horizontal expansion (Van Hulzen et al., 2007; Castillo et al., 2008b). In contrast, the production of aerial and subterranean biomass is stimulated by high accretion rates for *S. maritima* (Castillo et al., 2008a) and for *S. alterniflora* (Ford et al., 1999; Mendelssohn & Kuhn, 2003; Deng et al., 2008) due to an increase in soil fertility and marsh elevation, reducing nutrient deficiency and flooding stress. In this environment, it is usual to find several levels of rhizome corresponding with different sedimentation events. Thus, hydrologic and sedimentary processes are very important for the inter- and intra-marsh variability of *Spartina* marshes (Montalto & Steenhuis, 2004).

These biotic and abiotic processes usually produce an aggregated spatial pattern of *Spartina* biomass distribution, showing high spatial variability in biomass accumulation (Zedler, 1993). In this context, recorded values of biomass depend very much on the sampling method.

2.1 Above-ground biomass

The above-ground biomass of cordgrasses is usually sampled using plots that may be distributed randomly or regularly along radial transects from the edge of the *Spartina*

clumps to their centres. Randomly distributed plots are used for extensive and mature prairies where no clumps can be distinguished clearly. If this method is used for a *Spartina* population with isolated clumps, plots should be distributed randomly into the clumps, avoiding non-colonized areas, using stratified sampling. In contrast, radial transects are applied when isolated clumps are easy to distinguish (Castellanos et al., 1994; Nieva et al., 2001a).

The most frequent plot sizes are quadrants of 0.01 m² (10 cm side) (Buchsbbaum et al., 2009; Zhou et al., 2009a), 0.04 m² (20 cm side) (Castillo et al., 2008a; Culbertson et al., 2008; Buchsbbaum et al., 2009; Charles & Dukes, 2009), 0.09 m² (30 cm side) (Holdredge et al., 2010) and 0.25 m² (50 cm side) (Schmalzer et al., 1991; Darby & Turner, 2008a,b; Krull & Craft, 2009; Wang et al., 2009; Zhou et al., 2009b) (Table 1).

Larger plots normally show lower biomass values than smaller plots since they include both, areas with high and low shoot densities. However, heterogeneity of data series is usually lower with larger plots. In contrast, smaller plots coinciding with high shoot density areas record higher biomass values, however they may offer very heterogeneous data series when sampling high and low shoot densities. Castillo et al. (2008a) recorded above-ground biomass using quadrants of 0.04 m² and 1.00 m² in an expanding population of *S. maritima* and they obtained from two to five times less biomass using the larger plot size. Thus, the spatial scale to analyze cordgrass biomass has to be properly chosen since results are largely determined by it.

The above-ground biomass of cordgrasses also changes temporarily. Thus, higher biomass accumulation values normally coincide with the end of the growing season, which usually matches up with warmer months. For example, higher biomass accumulation in the Southwest Iberian Peninsula has been recorded for *S. maritima* and *S. densiflora* during autumn and the beginning of winter (Castellanos et al., 1994; Nieva et al., 2001). As well, *S. alterniflora* shows higher biomass accumulation at the end of the summer time in invaded Chinese marshes (Zhou et al., 2009a) and in Louisiana estuaries (Darby & Turner, 2008b). Aboveground necromass remains until it is removed by tides, currents or it is decomposed in situ (Schubauer & Hopkinson, 1984; Nieva et al., 2001a). Therefore, biomass records will change depending on the season of the year. More complete sampling would result from recording biomass variations throughout the year. However, recording maximum biomass accumulation at the end of the growing season seems to be a good method for comparing studies (Kirwan et al., 2009).

The above-ground biomass of cordgrasses may also be estimated by allometric relationships relating biomass with shoot density and shoot height (Castillo et al., 2008a; Tyrrell et al., 2008; Gonzalez Trilla et al., 2009). Anyway, when recording *Spartina* above-ground biomass it is important also to document processes that could affect biomass accumulation such as herbivory by vertebrates (i.e. cattle, deers or goose) or invertebrates (i.e. grabs and insects) or mechanical impacts such as tides and currents.

2.2 Below-ground biomass

Below-ground biomass studies are much less abundant than those reporting aerial biomass, however subterranean *Spartina* biomass plays very important functions in coastal marshes (Darby & Turner, 2008a,b; Turner et al., 2009) (Table 1).

Most of the roots and rhizomes of cordgrasses are accumulated close to the sediment surface due to their growth-form with superficial rhizomes parallel to the sediment surface and thin

roots, and to anoxic conditions in the sediments, especially at lower elevations, that limit root elongation (Padgett et al., 1998).

The below-ground biomass of *Spartina* species is usually sampled using cores of 20-30 cm long and 10-20 cm diameter that are driven into the sediments and removed containing the soil and the subterranean biomass (roots and rhizomes); 20-50% underestimates can be generated using this method (Johnen & Sauerbeck 1977) (Table 1). Then, cores are usually divided into sections to analyze below-ground biomass distribution with depth (Nieva et al., 2001a; Darby & Turner, 2008a,b; Michel et al., 2009; Zhou et al., 2009a,b). Normally, below-ground biomass is sampled at the same points where the above-ground biomass has been removed previously.

In-growth cores may be used to record below-ground biomass production. In-growth cores are created by removing a determined soil volume, which is replaced with root and rhizome-free sediment collected from an adjacent area. Then, ingrowth cores are removed seasonally, and subterranean biomass is sorted and dried to a constant weight. Total belowground production ($\text{g m}^{-2} \text{yr}^{-1}$) is calculated by adding together the total amount of live and dead biomass produced at the end of the one year study period (Gallagher et al., 1984; Perry & Mendelssohn, 2009).

Temporal changes in subterranean biomass of cordgrasses are not well established. However, *Spartina* below-ground biomass does not seem to show as clear a temporal pattern as the aerial biomass does, with higher accumulations at the end of the warmer season (Darby & Turner, 2008b).



Fig. 2. Sampling *Spartina versicolor* above-ground biomass along a transect in a representative tussock. Each transect was a belt of contiguous quadrants (10 cm radially \times 15 cm wide) across the radius of a tussock; every quadrant sampled a concentric ring around the tussock centre so that the results integrated the zones of different density within the clone.

3. Aerial biomass of cordgrasses

Spartina species are clonal plants and their ramet distribution and demography is a key factor determining the functioning of these species and their roles in plant communities (Suzuki & Hutchings, 1997). Some cordgrasses grow in dense tussocks (van Groenendael et

al., 1996) -“phalanx” growth species after Lovett Doust & Lovett Doust (1982)- and others in sparse clumps - “guerrilla” growth.

Despite the important presence in numerous ecosystems of clonal plants with “phalanx” growth, there have been few detailed studies of their growth strategy (Gatsuk et al., 1980; Bullock et al., 1996; Guardia et al., 2000). *S. argentinensis*, *S. densiflora*, *S. bakeri*, *S. patens* and *S. versicolor* forms dense tussocks that show a high occupation of available space inside tussocks by live shoots in expanding populations and by live and dead shoots in mature populations (Figueroa & Castellanos, 1988; Nieva et al., 2001b). These dense tussocks seem to show a high degree of physiological integration between ramets (Hester et al., 1994 for *S. patens*) reflected in very low mortality rates of young shoots (Pitelka & Ashmun, 1985; Maillette, 1992). Thus, interior areas of “phalanx” tussocks are not easily colonized by other species unless they develop central die-back areas (known as “monk’s tonsure”). On the other hand, high stem densities also favor the deposition of particles suspended in the tidal water, an additional source of nutrients (Adam, 1990).

S. alterniflora, *S. anglica*, *S. foliosa*, *S. maritima* and *S. x townsendii* are “guerilla” species. They grow in clumps with low shoots densities in comparison with “phalanx” species. These cordgrasses expand with long rhizomes from which a rapid development of aerial tissues is carried out after colonization of bare sediments mainly during warmer periods. Their growth rate seems to decrease when different clumps are close to each other due to higher levels of intraspecific competition between ramets (Castellanos et al., 1998; Li et al., 2009). Intraspecific competition may also inhibit seedling recruitment as has been described for *S. alterniflora* in Willapa Bay (Washington, USA) (Lambrinos & Bandos, 2008).

“Guerrilla” clumps frequently develop central die-back areas throughout their ontogenic development from expanding seedlings to mature tussocks (Turner et al., 2004). Clumps’ central areas are more elevated and show less shoot densities than peripheral zones of clumps. Thus, central areas may be colonized by more competitive species that are less tolerant to abiotic stress and that finally displace *Spartina* out by interspecific competition. For example, *S. maritima* facilitates the development of ecological succession by ameliorating anoxia at the centre of its tussocks, so other species such as *Sarcocornia perennis* subspecies *perennis*, *Sarcocornia perennis x fruticosa* and *Atriplex portulacoides* are able to colonize them and outcompete the small cordgrass (Castellanos et al., 1994; Figueroa et al., 2003).

Most *Spartina* species with a “phalanx” growth-form accumulate more above-ground biomass than cordgrass species growing in “guerrilla”. “Guerrilla” species expand faster by rhizomes (e.g. 0.13 m yr⁻¹ for *S. maritima* in European marshes following Castillo & Figueroa, 2008) than “phalanx” species (e.g. ca. 0.06 m yr⁻¹ for *S. densiflora* as reported by Nieva et al., 2005 and Kittelson & Boyd, 1997 in European and North American salt marshes, respectively). This faster colonization of surrounded sediment by “guerrilla” species has as a result a lower density of biomass in the occupied space. However, *S. patens* with high ramet densities shows low biomass values compare with *S. alterniflora* with “guerrilla” growth because its shoots are usually much thinner, having smaller leaves (Table 1).

Cordgrass above-ground biomass varies markedly between and within species depending on many different environmental factors and the growth form of each taxon. Minimum aerial biomass values have been recorded for “guerrilla” species growing in low marshes (ca. 100 g DW m⁻²) and maximum values (ca. 15000-30000 g DW m⁻²) have been recorded for “phalanx” species in brackish wetlands (Table 1).

Between “phalanx” growth species, *S. bakeri* accumulates ca. 400-700 g DW m⁻² in the western Atlantic coast of North America (Chynoweth, 1975; Schmalzer et al., 1991). *S.*

densiflora above-ground biomass accumulation changes markedly between different invaded marsh habitats in SW Iberian Peninsula. Thus, dense-flowered cordgrass shows its highest biomass values (higher than 15000 g DW m⁻²) at brackish marshes (Nieva et al., 2001a), with its photosynthetic apparatus being more efficient at lower salinities (Castillo et al., 2005b). In contrast, invading European populations of *S. densiflora* in middle salt marshes show aboveground biomass values ca. 14000 g DW m⁻² (with ca. 10500 shoot m⁻²). This value falls to ca. 400-600 g DW m⁻² in low salt marshes (with ca. 6000-7000 shoot m⁻²) (Nieva et al., 2001a; Castillo et al., 2008b) since *S. densiflora* is quite sensitive to long flooding periods (Castillo et al., 2000). In high marshes, *S. densiflora* accumulates intermediated biomass values between low and middle marshes (ca. 6000 g DW m⁻² with ca. 4000 shoot m⁻²) (Nieva et al., 2001a). Similar above-ground biomass values have been recorded also for South American native populations of *S. densiflora* (Vicari et al., 2002) and invasive populations in California (Moseman-Valtierra et al., 2009) (Table 1). In addition, mature tussocks of *S. densiflora* normally to show elevated wrack accumulation (ca. 800 g DW m⁻²) (Castillo et al., 2008b). Wrack accumulation may interfere with other species colonization of inner areas of *Spartina* clumps.

S. patens, another cordgrass with “phalanx” growth, accumulates between 100 and 500 g DW m⁻² of aerial biomass in North American Atlantic brackish marshes (Silander & Antonovics, 1979; Bertness, 1991; Buchsbaum et al., 2009) and *S. spartinae* accumulates between 200 and 500 g DW m⁻² in coastal marshes of Texas (MacAtee et al., 1979). *S. versicolor* also forms dense tussocks and colonizes brackish marshes in Europe where it accumulates ca. 3000 g DW m⁻² (unpublished data) since its shoots are much thicker and taller (ca. 60-95 cm) (Menéndez & Sanmartí, 2007) than those of *S. patens* (ca. 31 cm) (Silander & Antonovics, 1979) (Table 1).

Among cordgrasses with a “guerrilla” growth-form, *S. alterniflora* in western Atlantic low salt marshes accumulates between 100 and 1100 g DW m⁻². Changes in *S. alterniflora* biomass between populations are related mainly with its short and tall forms, varying its shoot height between 20 and 140 cm, also with a highly variable shoot density that changes markedly between 100 and 4000 shoot m⁻² (Craft et al., 1999, 2002, 2003; Proffitt et al., 2005; Culbertson et al., 2008; Darby & Turner 2008b; McFarlin et al., 2008; Sala et al., 2008; Tyrrell et al., 2008; Buchsbaum et al., 2009; Gonzalez Trilla et al., 2009; Krull & Craft, 2009; Michel et al., 2009; Holdredge et al., 2010). One year after invading Chinese marshes, *S. alterniflora* accumulated ca. 300-450 g DW m⁻² with shoot height between ca. 70-240 cm (An et al., 2007), accumulating in mature Chinese populations between 200 and 3700 g DW m⁻² (Wang et al., 2008; Li & Yang, 2009; Wang et al., 2009; Zhou et al., 2009a,b) (Table 1).

Above-ground biomass of *S. cynosuroides* and *S. maritima* shows similar values than those recorded for *S. alterniflora*, also showing very high inter-population differences. Thus, *S. maritima* accumulates ca. 1000 g DW m⁻² in low European salt marshes, however it can vary very much depending on the abiotic environment, increasing to ca. 1500 g DW m⁻² (Benito & Onaindia, 1991; Castellanos et al., 1994; Figueroa et al., 2003; Lillebo et al., 2006; Castillo et al., 2008a,b) (Table 1).

As we have shown above cordgrass above-ground biomass accumulation depends on clone architecture and shoot morphology. These traits show high intraspecific variation as described for *S. alterniflora* (Lessmann et al., 1997; Proffitt et al., 2005), *S. densiflora* (Nieva et al., 2001a; Castillo et al., 2008b), *S. maritima* (Sanchez et al., 1997; Castellanos et al., 1998; Otero et al., 2000; Castillo et al. 2005a; Castillo et al., 2008a,b) and *S. patens* (Silander &

Antonovics, 1979). Intraspecific changes in growth form may be based on phenotypic plasticity or genotypic differences. Thus, several species of *Spartina*, such as *S. alterniflora* or *S. maritima*, show clearly distinguishable tall and short growth forms (Shea et al., 1975; Mendelssohn, 1979; Anderson & Treshow, 1980; Howes et al., 1986; Pezeshki & DeLaune, 1991; Castillo et al., 2005a). Some studies have concluded that the observed variability in growth forms among *Spartina* populations may be the result of genetic differentiation (Gallagher et al., 1988; Sanchez et al., 1997; Proffitt et al., 2003), identifying ecotypes with different canopy heights and biomass accumulation (Lessmann et al., 1997; Daehler, 1999; Otero et al., 2000; Seliskar et al., 2002; Proffitt et al., 2005).

In contrast, other studies have attributed different growth forms to phenotypic plasticity in response to differences in environmental factors (Anderson & Treshow, 1980), such as the availability of nutrients (Dai & Wiegert, 1997; Wigand et al., 2003; Zhao et al., 2010), salinity (Phelger et al., 1971; Trnka & Zedler, 2000) or sediment anoxia (Castillo et al., 2005a). The consequence of this is that the different growth forms are ecophenes. In this context, an increase in shoot height is a commonly reported growth strategy for increased water depth in emergent plants (Grace, 1989; Vandersman et al., 1991; Insausti et al., 2001; Sorrel et al., 2002) including in the genus *Spartina* (Lessmann et al., 1997; Castillo et al., 2005a). Shoots might grow taller in response to sediment anoxia, a response possibly signaled by ethylene (Pezeshki et al., 1993), or in response to increased nutrient mobilization in the sediment under more anoxic conditions (Lenssen et al., 1999). Taller shoots would increase the effective photoperiod (i.e. average leaf emergence from tidal waters during daylight hours), a potent environmental factor in limiting the survival of *Spartina* clumps on low marshes, where a few centimeters of elevation in the tidal gradient may determine the lower distribution limit (Castillo et al., 2000). In addition, taller shoots may play a role in improving the oxygenation of rhizomes and roots via aerenchyma in anoxic environments, as in certain non-tidal wetland species (Sorrel et al., 2002); such internal ventilation might be associated with internal pressurization, as has been described for *S. alterniflora* (Hwang & Morris, 1991). Variations in canopy height of a dominant *Spartina* species can influence ecological functions and the structure of plant and animal communities in a marsh (Seliskar et al. 2002).

As we have reported previously, *Spartina* biomass accumulation depends also on abiotic environmental factors. In warmer locations at lower latitudes, cordgrasses lack a dormant period, sustaining high biomass accumulation rates. For example, created marshes of *S. maritima* in the Odiel Marshes (Southwest Iberian Peninsula) develop faster (within 2-4 years with maximum net aerial primary productivity of ca. 600 g DW m⁻² yr⁻¹ following Castillo et al., 2008a) than North American marshes of *S. alterniflora* (Craft et al., 1999, 2002, 2003; Edwards & Mills, 2005), which seems to be related to warmer winters in Iberian salt marshes. Thus, *S. alterniflora* productivity decreases with latitude and air temperature along the western Atlantic coast of North America (Kirwan et al., 2009). Other climatic factors such as rainfall that determinates erosion, salinity and flooding may also limit cordgrasses biomass accumulation (Gonzalez Trilla et al., 2009). Experimental results in the western Atlantic coast indicated that modest daytime warming increased total above-ground biomass for *S. alterniflora*, but not for *S. patens*. Warming also increased maximum stem heights of *S. alterniflora* and *S. patens* (ca. 8%). In addition, drought markedly increased the total biomass of *S. alterniflora* and the live biomass of *S. patens*, perhaps by alleviating waterlogging of sediments (Charles & Dukes, 2009). On the other hand, *Spartina* biomass

also depends on nutrient availability, especially nitrogen, as it has been reported for *S. alterniflora* (Darby & Turner, 2008a; McFarlin et al., 2008).

Biotic direct and indirect interactions also control biomass accumulation of *Spartina* populations. Thus, interspecific competition between two cordgrasses may limit their biomasses. Following the general theory of salt marsh zonation (sensu Pennings & Callaway, 1992 and Pennings et al., 2005): competitive dominants colonize higher elevation in the tidal frame displacing competitive subordinates to more stressful environments with long submergence periods or higher salinities. For example, invasive cordgrass such as *S. alterniflora*, *S. densiflora* and *S. patens* may displace indigenous cordgrasses (SanLeon et al., 1999; Chen et al., 2004; Castillo et al., 2008b). The outcome of competitive interactions changes depending on the abiotic environment. For example, *S. densiflora* invading European salt marshes displaces the native *S. maritima* at middle and high marshes but it seems to be displaced by small cordgrass at low salt marshes (Castillo et al., 2008b). In this sense, it has been described that the invasion of *S. densiflora* at North American salt marshes is limited by competition with native species (Kittelson & Boyd, 1997) and that *S. patens* competitively excludes *S. alterniflora* and forbs at New England salt marshes (Ewanchuk & Bertness, 2004).

Cordgrass biomass is also affected by competition with other coastal plants as reported along the North-eastern coast of the United States where the reed *Phragmites australis* Cav. is invading high marshes reducing local biodiversity with *S. alterniflora* remaining on the seaward edge of marshes where porewater salinities are highest (Silliman & Bertness, 2004). To the South, in Louisiana, the expansion northward of the tree *Avicennia germinans* (black mangrove) driven by global warming is replacing *S. alterniflora* marshes by mangroves (Perry & Mendelssohn, 2009).

Spartina biomass can be also influenced by interactions with marsh fauna. For example, deposit-feeding fiddler crabs (*Uca* sp.) increase *S. alterniflora* biomass accumulation growing on sandy sediment by enhancing nutrient deposition (Holdredge et al., 2010) and grazing by small grazers may carry out a top-down control on *Spartina* biomass dynamic (Sala et al., 2008; Tyrrell et al., 2008).

Above-ground biomass of cordgrasses may collapse very fast as a result of die-back processes related with long flooding periods and sediment anoxia, drought events or nutrient exhaustion (Webb et al., 1995; Castillo et al., 2000; McKee et al., 2004; Ogburn & Alber, 2006; Li et al., 2009). For example, *S. densiflora* invading populations in European salt marshes behave as perennial at middle and high marshes but they are biannual at low marshes. Biannual populations are composed of small tussocks that produce seeds and die, so populations disappear suddenly after two years (Castillo & Figueroa, 2007). *Spartina* shoots are semelparous (they die shortly after their first sexual reproduction event) and their mean shoot life span is about 2 years for species such as *S. densiflora* (Vicari et al., 2002; Nieva et al., 2005) and *S. maritima* (Cooper, 1993; Castellanos et al., 1998). In this sense, some studies predicted that fluctuating environments such as coastal marshes would promote semelparity (Bell, 1980; Goodman, 1984).

On the other hand, cordgrass biomass accumulation is affected negatively, even in the long term, by anthropogenic impacts such as oil spills and erosion (Culbertson et al., 2008), however biomass production may be stimulated by pollutants such as saline oil (Gomes Neto & Costa, 2009).

<i>Spartina</i> Species	Growth form	AGB (g DW m ⁻²)	BGB (g DW m ⁻²)	Location	Sampling method	Source
<i>S. alterniflora</i>	<i>Guerilla</i>	469		Louisiana, USA	50 cm quadrants	Hopkinson et al., 1978
		137	-	Oak Island, USA	24 cm long x 26 cm Ø cores	Ferrell et al., 1984
		400-1200	-	North Carolina coast, USA	50 cm quadrants	Cornell et al., 2007
		100-1100	-	Great Sippewissett, Massachusetts, USA	20 cm quadrants	Culbertson et al., 2008
		-	150-1200	Louisiana coast, USA	50 cm quadrants 30 cm long x 11 cm Ø cores	Darby & Turner 2008a
		100-900	300-2300	Louisiana coast, USA	50 cm quadrants 30 cm long x 11 cm Ø cores	Darby & Turner 2008b
		715-3477	-	Yangtze River Estuary, China	25 cm quadrants	Li & Zhang 2008
		150	-	Georgia coast, USA	50 x 25 cm plots	McFarlin et al., 2008
		450-950	-	Narragansett Bay, USA	10 cm quadrants	Sala et al., 2008
		100-1400	-	Wells National Estuarine Research Reserve, Maine, USA	Allometric estimation	Tyrrel et al., 2008
		1350	-	Yangtze River estuary, China	50 cm quadrants	Wang et al., 2008
		400	-	Plum Island Estuary, Massachusetts, USA	20 cm quadrants	Charles & Dukes, 2009
		1400	-	Altamaha River Mouth, Georgia, USA	50 cm quadrants	Krull & Craft, 2009
		-	6500	Patuxent River, Maryland, USA	20 cm long x 16 cm Ø cores	Michel et al., 2009
		200	-	Plum Island Sound, Massachusetts, USA	10 cm quadrants	Buchsbaum et al., 2009

		200-800	-	Bahía Blanca Estuary, Argentina	Allometric estimation	Gonzalez Trilla et al., 2009
		3700	-	Yangtze River Delta, China	40 cm quadrants	Li & Yang, 2009
		250-700	-	Yangtze River Estuary, China	50 cm quadrants	Wang et al., 2009
		700-768		Altamaha River, Georgia, USA	50 cm quadrants	White & Albert, 2009
		70-600	80-450	Jiangsu coastland, China	10 cm quadrants 30 cm deep digging	Zhou et al., 2009a
		2000	4500	Yancheng Natural Reserve, China	50 cm quadrants 30 cm deep digging	Zhou et al., 2009b
		900	-	Wellfleet, Massachusetts, USA	30 cm quadrants	Holdredge et al., 2010
<i>S. anglica</i>	<i>Guerilla</i>	320-1290	-	Ramalhete marsh, England	16-19 cm Ø	Neumeier & Amos 2006
<i>S. bakeri</i>	<i>Phalanx</i>	773	-	Merritt Island, Florida, USA	50 cm quadrants	Schmalzer et al., 1991
		429	-	Merritt Island, Florida, USA	33 cm quadrants	Chynoweth, L.A. 1975
<i>S. cynosuroides</i>	<i>Guerilla</i>	762-1242	-	Georgia, USA		Odum & Fanning, 1973
		394	-	Louisiana, USA	100 cm quadrants	Hopkinson et al., 1978
		840-1080		Essex, England	50 cm quadrants	Potter et al., 1995
		-	9400	Patuxent River, Maryland, USA	20 cm long x 16 cm Ø cores	Michel et al., 2009
		236-832	-	Altamaha River, Georgia, USA	50 cm quadrants	White & Albert, 2009
<i>S. densiflora</i>	<i>Phalanx</i>	400- 15000	1000-4500	Odiel Marshes, SW Iberian Peninsula	15 x 10 cm plots 20 cm long x 5.5 cm Ø cores	Nieva et al., 2001a
		475-725	-	Otamendi Natural Reserve, Argentina	10 cm quadrants	Vicari et al., 2002
		3800-30000	-	The Tijuana River National Estuarine Research Reserve, California, USA	50 cm quadrants	Moseman-Valtierra et al., 2009

<i>S. patens</i>	<i>Phalanx</i>	900	-	Louisiana, USA	56 cm Ø	Hopkinson et al., 1978
		400	-	Plum Island Estuary, Massachussets, USA	20 cm quadrants	Charles & Dukes, 2009
		100-120	-	Plum Island Sound, Massachussets, USA	10 cm quadrants	Buchsbaum et al., 2009
<i>S. maritima</i>	<i>Guerilla</i>	920-930	-	Ramalhete marsh, England	16-19 cm Ø	Neumeier & Amos 2006
		672-1427	1190-8694	Odiel Marshes, SW Iberian Peninsula	20 cm quadrants	Castillo et al., 2008a
		193-486 (T) 1063-4210 (M)	527-7189 (T) 850-3608 (M)	Tagus (T) and Mondego (M) estuary, Portugal	30 cm quadrants	Sousa et al., 2008
		209-490	1510-4268	Tagus Estuary, Portugal	30 cm quadrants	Caçador et al., 2009
		1085-1313	-	Mira River, Portugal	20 cm quadrants	Castro et al., 2009
<i>S. spartinae</i>	<i>Phalanx</i>	207-513	-	Texas, USA	50 cm quadrants	McAtee et al., 1979

Table 1. Growth-form ('guerrilla' or 'phalanx' after Lovett Doust & Lovett Doust (1982)) and mean above- and below-ground biomass (AGB and BGB, respectively; in g DW m⁻²) studied location, applied sampling method and source for some cordgrasses species (*Spartina* genus) colonizing coastal marshes.



Fig. 3. Clump of the hybrid *Spartina densiflora x maritima* surrounded by *S. densiflora* and *Sarcocornia fruticosa* in Guadiana Marshes (Southwest Iberian Peninsula).

4. Subterranean biomass of cordgrasses

The knowledge of environmental factors determining BGB of cordgrasses is very important for salt marsh conservation and management, as it is a critical factor regulating ecosystem functions. Thus, it seems that it is the plant's belowground accumulation of organic, rather than inorganic, matter that governs the maintenance of mature salt marsh ecosystems in the vertical plane (Turner et al., 2004).

Spartina species usually accumulate 2-3 times much more subterranean than aerial biomass. Aerial : the subterranean biomass quotient of cordgrasses is usually lower than 1 (ca. 0.5) (Pont et al., 2002; Windham et al., 2003; Castillo et al., 2008a; Darby & Turner 2008b). Below-ground biomass in cordgrasses carries out very important and diverse functions such as storing of resources in its abundant rhizome system (Suzuki & Stuefer, 1999), fixing the plant to sediments in a very dynamic environment subjected to frequent and intense mechanical impacts (grazing, waves and currents) or exploring the sediments for nutrient uptake. In this sense, competition for nutrients has been identified as a relevant factor organizing salt marsh plant zonation (Brewer, 2003).

As in the case of aerial biomass, the subterranean biomass of cordgrasses varies markedly between and within species. *S. densiflora* accumulates ca. 1000-1600 g DW m⁻² at low marshes, and ca. 4500-6500 g DW m⁻² at middle, high and brackish marshes in the SW Iberian Peninsula (Nieva et al., 2001a; Castillo et al., 2008b). Below-ground biomass of *S. versicolor* is ca. 3500 g DW m⁻² at brackish marshes in the SW Iberian Peninsula (non-published data) (Table 1).

In the Atlantic Coast of North America, *S. alterniflora* growing on sandy sediments accumulates ca. 450 g DW m⁻² (Holdredge et al., 2010) and ca. 6500 g DW m⁻² in fine sediments (Michel et al., 2009). In Louisiana salt marshes, Darby & Turner, (2008a,b) reported a below-ground biomass for *S. alterniflora* between 150 and 2300 g DW m⁻². Subterranean biomass production of *S. alterniflora* in Louisiana salt marshes is about 440 g DW m⁻² yr⁻¹ (Perry & Mendelssohn, 2009) and ca. 4500 g DW m⁻² in invaded Chinese salt marshes (Zhou et al., 2009b). *S. cynosuroides* accumulates between 760 and 1240 g DW m⁻² in Georgia and Louisiana marshes (Odum & Fanning, 1973; Hopkinson et al., 1978) and ca. 9400 g DW m⁻² in high marshes in Maryland, USA (Michel et al., 2009). *S. maritima* accumulates in the sediments between 400 and 8700 g DW m⁻² at low salt marshes that it usually colonizes (Castellanos et al., 1994; Figueroa et al., 2003; Castillo et al., 2008a; Sousa et al., 2008; Caçador et al., 2009).

Spartina below-ground biomass accumulation seemed to be favored by sediment accretion (Castillo et al., 2008a) and cordgrass subterranean biomass influences soil elevation rise by subsurface expansion, organic matter addition and sediment deposit stabilization (Ford et al., 1999; Darby & Turner, 2008a). Sedimentation may also increase the aeration of sediments, favoring root development (Castillo et al., 2008a). Thus, well-drained soils led to more-uniform vertical distribution of BGB for *S. alterniflora* and *S. patens* (Padgett et al., 1998; Saunders et al., 2006).

However, fertilization with nitrogen and phosphorous usually increases *Spartina* above-ground biomass, the addition of these nutrient seems to reduce root and rhizome biomass accumulation (Darby & Turner, 2008a). In view of this result and the importance of subterranean cordgrass biomass for marsh functioning, eutrophication is an important threat to salt marsh conservation.



Fig. 4. *Spartina maritima* prairie, a cordgrass with “guerilla” growth from, starting to be outcompeted by *Sarcocornia perennis* subspecies *perennis* in Odiel Marshes (Southwest Iberian Peninsula).

5. Cordgrass biomass and ecosystem functioning

Salt marshes fulfill many functions, such as biodiversity support, water quality improvement, or carbon sequestration and they are floristically simple, often dominated by one or a few herbaceous species (Adam, 1990). In this context, cordgrasses are especially important since they are dominant species in many coastal marshes all around the world.

Cordgrasses are commonly used for salt marsh creation, restoration and protection (Bakker et al., 2002; Fang et al., 2004; Konisky et al., 2006; An et al., 2007; Castillo et al., 2008a; Castillo & Figueroa, 2008). In addition, cordgrasses are also used as biotools for phytoremediation (Czako et al., 2006). Primary productivity and biomass accumulation are important indicators of success for salt marsh creation and restoration projects (Edwards & Mills, 2005). Although plant biomass accumulation is a key factor in the functioning of *Spartina* dominated marshes, other ecological attributes, such as species richness and distribution, benthic infauna density or soil nutrient reservoirs, may develop at different rates than cordgrass biomass in restored wetlands (Craft et al., 1999; Onaindia et al., 2001; Craft et al., 2003; Edwards & Proffitt, 2003).

Below- and above-ground biomasses are key functional traits that play very important roles in the ecological behavior of cordgrasses. Thus, *Spartina* biomass influences on the carbon content of marsh sediments (Tanner et al., 2010), the marsh carbon stock (Wieski et al., 2010), marsh methane emissions (Cheng et al., 2010), salt marsh microbial community (First & Hollibaugh, 2010; Lyons et al., 2010), grazing (Burlakova et al., 2009), sediment dynamic (Neumeier & Ciavola, 2004; Salgueiro & Cacador, 2007; Li & Yang, 2009), etc.

Cordgrass biomass affects the emergent of the habitat structure, facilitating succession development by providing a base for habitat development (Castellanos et al., 1994; Figueroa et al., 2003; Proffitt et al., 2005; Castillo et al., 2008b). For example, *S. maritima* in European low salt marshes, *S. alterniflora* in western Atlantic low salt marshes and *S. foliosa* in Californian low salt marshes are important pioneers and ecosystem autogenic engineers

(Castellanos et al., 1994; Castillo et al., 2000; Proffitt et al., 2005). Thus, sediment deposition develops with the establishment of these foundation cordgrasses at low marshes, which yields abiotic environmental changes such as decreasing anoxia and flooding period (Castellanos et al., 1994; Craft et al., 2003; Bouma et al., 2005; Castillo et al., 2008a; Castillo et al., 2008b).



Fig. 5. Clump of the hybrid of *Spartina foliosa x alterniflora* colonizing a mudflat, where the native *Spartina foliosa* is not able to survive, in San Francisco Bay (California).

On the other hand, biomass production by cordgrasses plays a very important role in the nutrient cycle of coastal marshes. *Spartina* species add organic matter to the sediments that they colonize (Craft et al., 2002; Lillebo et al., 2006) and even to adjacent bare sediments by necromass exportation in the form of dead leaves and shoots (Castillo et al., 2008a).

Although cordgrasses are essential for healthy marsh functioning in their native distribution ranges, some of them are very aggressive when introduced to exotic environments. For example, *S. alterniflora* invades salt marshes in China, Europe and the Pacific coast of North America from the Atlantic coast of America. *S. anglica* is colonizing also Chinese and North American salt marshes coming from European marshes. *S. densiflora* is invading the Pacific coast of Chile and North America, African and European marshes from the Atlantic coast of South America (Bortolus, 2006) where it is a salt-marsh dominant of wide latitudinal range (Isacch et al., 2006). Once introduced by anthropogenic activities, exotic cordgrasses are able to invade contrasted marsh habitats due to their high capacity to colonize as pioneer species new formed environments and disturbed locations, showing a wide tolerance to abiotic stress factors such as salinity, anoxia or long flooding periods (Nieva et al., 1999, 2003; Castillo et al., 2005a). Moreover, *Spartina* species with "phalanx" growth develop very dense tussocks with tall canopy and high above- and below-ground biomass, avoiding the colonization of native species, stopping the development of ecological succession during very long periods and representing strong competitors (Figueroa & Castellanos, 1988). In addition, some invasive cordgrasses usually show an abundant seed production and long distance dispersion by tidal water and currents (Kittelson & Boyd, 1997; Nieva et al., 2001a; Castillo et al., 2003; Nieva et al., 2005; for *S. densiflora* in European and North American salt marshes). Alien *Spartina* usually modify the abiotic environment during their invasion faster

than native species. For example, the introduced *S. alterniflora* in Chinese salt marshes is significantly more efficient in trapping suspended sediment than the native *Scirpus* and *Phragmites* species (Li & Yang, 2009).

6. Conclusions

Cordgrasses usually are dominant species in salt marshes all around the world and they play very important roles in ecosystem functioning. Cordgrass biomass accumulation below and above the sediment surface determines energy and material flows in salt marshes.

Most cordgrasses show markedly spatial variations in their biomass accumulation pattern, depending on biotic and abiotic environmental factors and on their growth form (“guerrilla” versus “phalanx”, and “short” versus “tall” form). Thus, specific studies to evaluate the ecological roles of cordgrasses should be carried out for each specific location and for each taxon, analyzing both below- and above-ground biomass production and accumulation. In this context, it is very important to choose an appropriate sampling method adapted to our own goals and that would allow comparisons with previous studies.

Future research is needed specially to improve our knowledge about cordgrass below-ground biomass accumulation, dynamic and functions. The evaluation of the salt marsh ecosystem will be incomplete if based exclusively on what is happening aboveground, or as though what happens aboveground is a satisfactory indicator of what is driving changes belowground. Monitoring programs, for example, could be improved if belowground soil processes were included, rather than excluded, as happens frequently. Furthermore, it may be that because of the dominance of the changes in biomass pools belowground compared to aboveground, what happens belowground may be more influential to the long-term maintenance of the salt marsh than are changes in the aboveground components.



Fig. 6. Salt marsh invaded by the South American neophyte *Spartina densiflora* in Humboldt Bay, California.

Future studies should also analyze specifically the development and functions carried out by recently formed *Spartina* hybrids between native and invasive species invading salt marshes in San Francisco Bay and the South-west Iberian Peninsula. The comparison of the biomass dynamic for these hybrids with their parental species will help us to clarify their ecological roles and to prevent serious environmental impacts.

It is also important to study how invasive cordgrasses respond to intra-specific competition with native species by changing their biomass allocation, accumulation and production. In addition, finding and selecting ecotypes for native cordgrasses with different biomass accumulation patterns would be very useful to improve our technology for salt marsh restoration projects.

7. References

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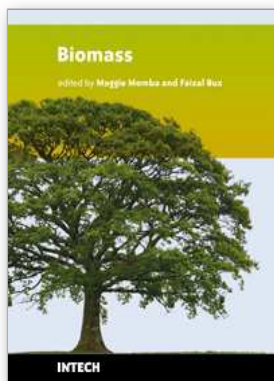
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Biomass

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Due to demands placed on natural resources globally and subsequent deterioration of the environment, there is a need to source and develop appropriate technology to satisfy this requirement. For decades mankind has largely depended on natural resources such as fossil fuels to meet the ever increasing energy demands. Realizing the finite nature of these resources, emphasis is now shifting to investigating alternate energy source governed by environmentally friendly principles. The abundance of biomass and associated favorable techno-economics has recently changed global perceptions of harnessing biomass as a valuable resource rather than a waste. To this end this book aims to make a contribution to exploring further this area of biomass research and development in the form of a compilation of chapters and covering areas of ecological status of different types of biomass and the roles they play in ecosystems, current status of biomass utilization and deriving energy and other value added products from biomass. In this context biomass can be defined as large plants and trees and different groups of microorganisms. This book will serve as an invaluable resource for scientists and environmental managers in planning solutions for sustainable development.

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