INTRATUSSOCK TILLER DISTRIBUTION AND BIOMASS OF SPARTINA DENSIFLORA BRONGN. IN AN INVADED SALT MARSH

J. M. CASTILLO*, A. E. RUBIO-CASAL*, T. LUQUE*,
M. E. FIGUEROA*, F. J. JIMÉNEZ-NIEVA**
* Departamento de Biología Vegetal y Ecología, Facultad de Biología,
Universidad de Sevilla. Apartado 1095, 41080-Sevilla, España.
E-mail: manucas@us.es.
** Departamento de Ciencias Agroforestales, Facultad de Ciencias
Experimentales, Universidad de Huelva. España.

(Recibido el 9 de Octubre de 2002)

Summary. The interaction of clonal plants with the environment is strongly conditioned by their architecture. Despite their success regarding geographical distribution and capacity of colonization, there are few detailed studies on clonal growth of "phalanx" species. We analysed intratussock tiller distribution and biomass of the South American "phalanx" clonal alien, *Spartina densiflora*, in an invaded salt marsh located in the Gulf of Cadiz (SW Iberian Peninsula). Appearance of central die-back, necromass biomass and mean live tiller height showed a direct relationship with tussock size. Intra-tussock densities of live tillers (10000 tiller m^{-2}) and above-ground biomass (12000 g D W m^{-2}) were higher than in other *Spartina* species with "guerrilla" clonal growth. However, below-ground biomass values (4800 g D W m^{-2}) were similar. Clonal growth traits, as high densities of live large tiller and high below-ground biomass, together with an integrated clonal functioning would prevent the colonization by other species of *S. densiflora* tussocks in the studied European invaded salt marsh, in contrast with the facilitation processes described in its original habitat.

Resumen. Las interacciones de las plantas clonales con el medio ambiente están fuertemente condicionadas por sus arquitecturas. Sin embargo, son escasos los estudios detallados de la arquitectura de especies con crecimiento clonal en "falange", a pesar del éxito ecológico que poseen, reflejado en su distribución geográfica y capacidad de colonización. En este estudio analizamos la distribución de tallos y la biomasa de los clones de *Spartina densiflora*, una especie sudamericana clonal con crecimiento en "falange" invasora del Golfo de Cádiz (Suroeste de la Península Ibérica). La aparición de degeneración en el centro de los clones ("dye-back"), la densidad de necromasa y la altura media de los tallos vivos se relacionaron directamente con el tamaño del clon. Se registraron densidades de tallos vivos (10000 tallos m^{-2}) y valores de biomasa aérea (12000 g m^{-2}) muy elevadas en comparación con otras especies de *Spartina* con creci-

miento clonal en "guerrilla". Sin embargo, las altas densidades de biomasa subterránea (4800 g m^{-2}) fueron similares a las de otras especies. Características del crecimiento clonal de *S. densiflora*, como una densidad elevada de tallos altos y biomasa subterránea muy alta, junto con un funcionamiento integrado entre ramets, prevendrían la colonización del interior de sus clones por parte de otras especies, lo cual contrasta con los procesos de facilitación descritos en su hábitat original.

INTRODUCTION

Clonal plants have a wide geographical distribution and high ability to colonize very different environments (SILANDER 1985). Their interactions with those environments are determined -to a great extent- by their architecture (HARPER 1985, HERBER & HARA 1997). Since their architecture may change in time, individual plants of different age states may play different roles in a plant community. Thus, studies about shoot distribution in clonal perennial plants should pay intensive research, allowing substantial advances in our understanding of the functioning of these species, and of their roles in plant community structuration (SUZUKI & HUTCHINGS 1997).

At times, the density of live tillers decreases in the center of clones. This process has been called "central die-back" and it has been described in numerous species with a "guerrilla" (LOVETT DOUST & LOVETT DOUSTT, 1982) growth form (CALDWELL, 1957; ADACHI & al., 1996). Sometimes, central die-back is associated with the colonization of species that are characteristic from later succession (CASTELLANOS & al., 1994).

In contrast to "guerrilla"-type clonal plants, the phenomenon of central die-back has not been demonstrated in clonal plants with "phalanx" growth (LOVETT DOUST & LOVETT DOUST 1982). There have been few detailed studies of clonal species with "phalanx" growth (GATSUK & al., 1980; BULLOCK & al., 1996), even though they are common in many ecosystems (GROENENDAEL & al., 1996).

Spartina densiflora Brongn. is a South American clonal perennial species (MOBBERLEY, 1956), which has invaded some North American marshes (KITTELSON & BOYD, 1997) and began, probably in the 16th century, the invasion of the European continent from the Odiel Marshes (SW Spain) (CASTILLO & al., 2000). Nowadays, *S. densiflora* has colonized ten estuaries in South-western Europe and it is still spreading to other Spanish and Portuguese localities. In South-western European salt marshes, *S. densiflora* grows in very dense tussocks (FIGUEROA & CASTELLANOS, 1988), covering virtually all the space available, resulting in vast areas with low species biodiversity (NIEVA & al., 2001), locally known as "*Spartina* seas". This contrasts with the situation in *S. densiflora* and *S. argentinensis* Parodi -two very similar species- communities in South America, where species as *Rumex pulcher* L., *Solidago*

chilensis Meyen and *Neptunia pubescens* Benth. are positively associated with intra-tussock central die-back areas (CARNEVALE & al., 1987; LEWIS & al., 1990).

The main aims of this study are to analyse in detail the intratussock tiller distribution and biomass of *S. densiflora* tussocks in a SW European marsh and to determinate whether central die-back occurs. Finally, we discuss briefly possible influences of *S. densiflora* clonal architecture on invaded SW European marshes, in comparison with the role played by this cordgrass species in South America.

MATERIAL AND METHODS

The Odiel marshes are extended in 7185 ha on the Gulf of Cadiz, SW Spain (37º 08´ - 20´N, 6º 45 - 7º 02´W). They form one of the largest salt marsh complexes of the Iberian Peninsula (LUQUE & al., 2000). These marshes are located in a coastal area with Mediterranean climate and a mesotidal semidiurnal character. Mean tidal range is 2.10 m and mean spring tidal range is 2.97 m, 0.40 - 3.37 m above Spanish hydrographic zero (CASTELLANOS & al., 1994). The Odiel Marshes were declared a Biosphere Reserve by UNESCO in 1983, and include a Special Area for Birds Protection declared by the European Union. Their strategic position, at the Euro-African and Atlantic-Mediterranean crossroads, accentuates their great ecological interest.

In order to study the clonal architecture of *S. densiflora*, thirteen isolated tussocks of different sizes were sampled using a stratified random method at a low marsh habitat between October of 1996 and February of 1997. Sediment redox potential at the sampling site was -95 ± 26 mV (n = 5) at surface from 0-10 cm -it was determined with a portable meter and electrode system calibrated in the field (Crison pH/mV p-506). Sediment interstitial water conductivity was 2.0 ± 0.1 mS cm^{-1} (n = 5) -it was determined with a conductivity meter (Crison-522).

The area occupied by a tussock was considered as a circle. Larger tussocks were close to the maximum size this species reaches in SW European marshes. Tussocks were removed to a depth of 20 cm with a shovel. Almost all the below-ground biomass was removed, since 90% of *S. densiflora* subterranean biomass is found in the first 20 cm deep layer (NIEVA & al., 2001).

From each tussock, every tiller was cut, one by one, and the following variables were recorded: whether it was alive or dead, flowered or not, height of live tillers and distance from the tiller base to the geometric center of the tussock. Tiller densities were calculated in successive 1 cm wide concentric rings.

Each tussock was divided in above-ground dead and live biomass and below-ground biomass and each fraction was weighed with a precision balance (Denver Company Instrument), after achieving constant dry weight (DW) through a 48 hour treatment with a forced-air heat cabinet at 80 ºC.

Pearson correlation coefficient was calculated for correlation analysis between tussock traits. Outlier values were detected (using a standard residual method) and removed from data series before correlation analysis. Student´s test (T-test) for independent samples was used to compare tussocks traits (STEEL & TORRIE, 1960). Data were tested for variance homogeneity with Levene test, with a meaning level of 95%, and transformed by square root function when it was necessary. All statistical analyses were performed using the computer package "Statistica" version 5.0 Stat-Soft Inc. (1995).

Determination and nomenclature of plant taxons was carried out following to TUTIN & al. (1964-1980).

RESULTS

Intra-Tussock tiller distribution

The area of *S. densiflora* tussocks ranged between 12.6 and 3848.5 cm^2. Alive and dead tillers in *S. densiflora* tussocks were found in concentric rings of high and low density, which were alternating along tussock radius. This ramet distribution pattern reflected a growth way developed through successive tiller cohorts. In smaller tussocks only one high-density ring of living tillers was detected, increasing to three in larger ones (Fig. 1).

Alive tillers distribution along tussock radius varied with its size. In smaller tussocks the highest densities of live tillers were recorded in central areas, with mean values between 10000 and 30000 tillers m^{-2}. However, in larger tussocks the highest densities of living tillers, close to 10000 tillers m^{-2}, were found in intermediate areas, decreasing gradually towards central and outer zones (Fig. 1). On the other hand, living tiller density decreased with tussock radius following a logarithmic response (r = -0.66, p < 0.05, n = 13) (Fig. 2), oscillating between 1204 and 34843 tillers m^{-2} (Table 1).

Mean living tiller height increased linearly with tussock size (r = 0.89, p < 0.0001, n = 12) (Fig. 2). It was uncorrelated with living tiller density (r = -0.26, p < 0.39), with maximum values close to 75 cm and little intra-tussock variations (Table 1).

A distinct central die-back phenomenon was observed in larger tussocks. It was reflected as a linear decrease, with tussock size, in living tiller density in central areas – in the first 5 cm of tussocks with a radius larger than 10 cm -
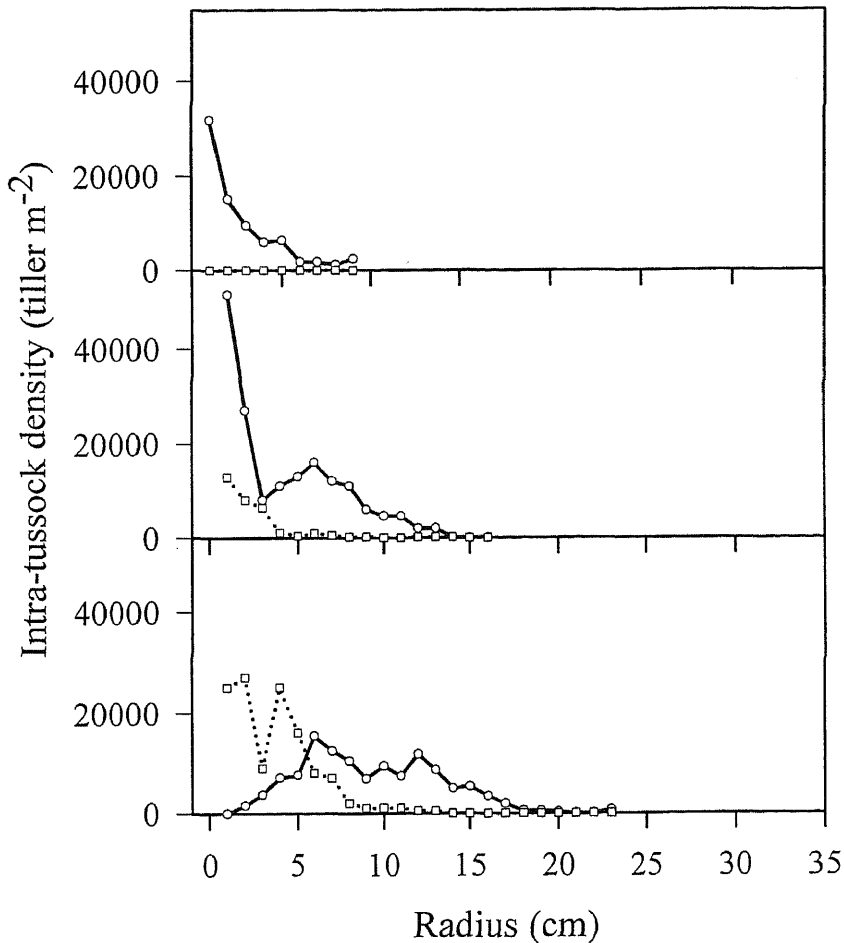
Fig. 1. Live (–O–) and dead (...☐..) tiller density (tillers m⁻²) along the radius for three different sized tussocks of *Spartina densiflora* in Odiel Marshes.

(r = -0.81, p < 0.05, n = 7). Thus, living tillers were always more abundant than dead ones (T-test = 5.73, df = 24; p < 0.0001), except in central areas of larger tussocks where dead tillers densities were higher (Figs. 1 and 2).

Flowered tiller density was not directly related with tussock size, with a mean of 1630 ± 351 flowered tillers m⁻² (Table 1). Flowered tillers showed the same distribution pattern with regard to the tussock radius than living tillers did. Thus, in smaller tussocks highest densities were recorded in the central areas (1000 and 8000 flowered tillers m⁻², respectively), whereas in larger tussocks the greatest number of flowered tillers was observed in intermediate areas (4000 flowered tillers m⁻²).

Tussock area	Live tillers density	Dead tillers density	Flowering tillers density	Total tillers density	Live tillers height	BGB/AGB
12.6	34843	0	0	34843	15.7 ± 8.0	0.3
28.3	4708	942	314	5650	12.3 ± 1.6	0.6
78.5	11649	201	0	11850	21.6 ± 1.7	0.7
113.1	17832	922	1845	18754	30.3 ± 1.3	0.7
201.1	15131	917	2017	16048	45.4 ± 1.8	0.5
254.5	7388	0	1705	7388	24.8 ± 3.1	0.8
530.9	12219	0	4035	12219	65.2 ± 1.5	0.3
706.9	9071	659	3481	9730	51.4 ± 1.8	0.3
1017.9	9317	5084	1563	14401	49.7 ± 1.1	0.5
1661.9	7100	4757	970	11857	54.3 ± 1.0	0.4
1963.5	7594	2767	1664	10361	64.6 ± 0.9	0.7
2290.2	8314	2155	2858	10469	75.2 ± 4.0	0.3
3848.5	1204	1758	734	2962	27.4 ± 1.8	1.1

Table 1. Area (cm^2), live, dead and total tiller densities (tillers m^{-2}), live tillers height (cm) and below-ground/live above-ground biomass ratio (BGB/AGB) of *Spartina densiflora* tussocks in Odiel salt marshes. (Mean ± SEM).

Dead tiller densities increased linearly with tussocks size ($r = 0.57$, $p < 0.05$, $n = 13$), with a maximum close to 5000 tillers m^{-2} (Table 1). For all tussocks, regardless of size, the highest densities of dead tillers were recorded in central areas -the oldest clone parts. In smaller tussocks dead tiller density was never above 2500 tillers m^{-2}, whereas in larger tussocks it was up to 15000 tillers m^{-2} in central areas (Fig. 1).

As in the case of living tiller density, total tiller density decreased with tussock size, showing a logarithmic response ($r = 0.67$, $p < 0.05$, $n = 13$), with values close to 10000 tillers m^{-2} in larger tussocks (Table 1). Maximum total tiller densities were recorded in central areas in every tussock, decreasing gradually towards their edge (Fig. 1).

Tussock Biomass

Above-ground dead and live biomass increased linearly with tussock radius ($r = 0.78$, $p < 0.005$, $n = 12$; $r = 0.72$, $p < 0.01$, $n = 12$, respectively), reaching values up to 3000 g DW m^{-2} in larger tussocks. On the other hand, above-ground total biomass increased with tussock size following a logarithmic curve ($r = 0.79$, $p < 0.05$, $n = 13$) (Fig. 2). Above-ground live biomass was uncorrelated with living tiller density ($r = -0.13$, $p < 0.66$; $n = 13$) and increased linearly
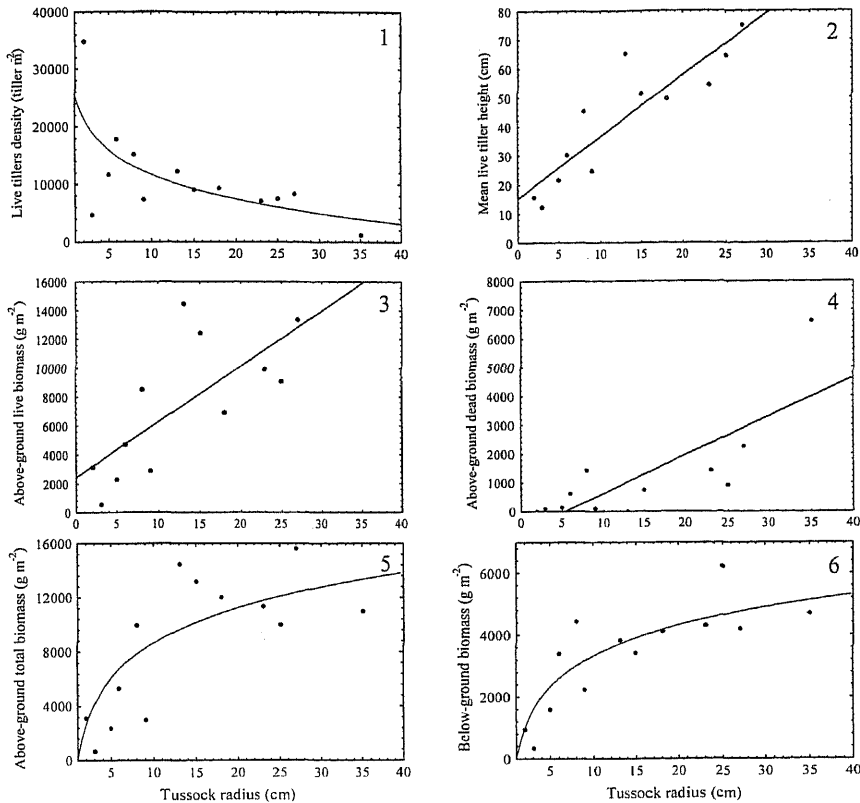
Fig. 2. Relationship between (1) live tiller density (tiller m⁻²), (2) mean live tiller height (cm), above-ground (3) live, (4) dead and (5) total biomass and (6) below-ground biomass (g DW m⁻²) with tussock radius (cm) of *Spartina densiflora* in Odiel Marshes. Regression ecuations: (1) $y = 25892.0 - 6168.5 \log(x)$; (2) $y = 15.1 + 2.1 x$; (3) $y = 2432.6 + 384.5 x$; (4) $y = -715.0 + 134.0 x$; (5) $y = 3751.5 \log(x)$; (6) $y = 1440.2 \log(x)$.

with mean living tiller height ($r = 0.93$, $p < 0.0001$; $n = 12$). Above-ground live biomass was higher than dead biomass in every tussock (T-test $= 4.59$, df $= 24$, $p < 0.0001$).

On the other hand, below-ground biomass increased with tussock size, showing a logarithmic response ($r = 0.86$, $p < 0.05$, $n = 12$) (Fig. 2). In larger tussock, it oscillated around 4000 g DW m⁻², reaching a maximum of 6234 g DW m⁻². The ratio below-ground biomass/above-ground live biomass oscillated between 0.3, recorded in the smallest and in the second highest tussocks, and 1.1, recorded in the highest one (Table 1).

DISCUSSION

This study shows in detail that, in a European marsh, *S. densiflora* grows in tussocks no bigger than 1 m in diameter, with high densities of large live tiller and high biomass densities, developing central die-back areas that remain occupied by high necromass levels.

S. densiflora tussocks colonize surrounding bare sediments by successive series of short rhizomes, which is reflected in concentric and alternating rings of live and dead tillers with low and high densities. This clonal growth has been described before for other species of the genus *Spartina* with guerrilla growth (CALDWEL, 1957; CASTELLANOS & al., 1994).

Intra-tussock live tiller densities and above-ground biomass recorded in this study for *S. densiflora* are considerably larger than values of other *Spartina* species with "guerrilla" growth, such as *S. alterniflora* Lois. (BERTNESS, 1991; DAI & WIEGERT, 1996), *S. anglica* Hubbard (OLIVER, 1925) and *S. maritima* (Curt.) Fernald (CARTAXANA & CATARINO, 1997; CASTELLANOS & al., 1998; COSTA & al., 2001). This clonal trait shows that *S. densiflora* is able to develop a more aggressive growth way than the other three *Spartina* species. Clonal physiological integration between ramets and stored resources in subterranean systems may contribute to a great extent to keep these high tiller densities (SUZUKI & HUTCHINGS, 1997), as it was pointed out before for *Spartina patens* (HESTER & al., 1994).

A clear central die-back has been observed with increased tussock size, recorded as a decrease in living tiller density in central areas. At the same time, an accumulation of dead tillers in central die-back areas happened. This provoked that total tiller density, however decreased with tussock size, showed always high values, close to 12000 tiller m^{-2}.

On the other hand, the high values of below-ground biomass recorded in this study are in agreement with BEGON & al. (1996) that pointed out the highly developed below-ground system of the genus *Spartina*, and they are similar to values recorded for *S. maritima* (CARTAXANA & CATARINO, 1997). This accumulation of below-ground biomass in perennial plants carries out different functions as store of carbohydrate reserves and fixation to the substrate in high-energy environments as tidal salt marshes (ADAM, 1990).

Above-ground live biomass was directly and linearly correlated with mean live tiller height, both variables increasing with tussock size. On the other hand, live tiller height showed low intra-tussock variation, which reflects allocation of assimilates to storage organs early in the growing season, avoiding intra-tussock ramet competition (SUZUKI & HUTCHINGS, 1997). This is supported by the recorded independence between live tiller density and both live tiller height and above-ground live biomass. It has been suggested that shoot density in

perennial clonal species is controlled externally rather than internally (DE
KROON, 1993). For example, differences in canopy architecture may regulate
the spectral composition of radiation that filters to the base of tillers (PORTER,
1989), which controls in some grasses the rate of tiller initiation (DEREGIBUS
& al., 1985). However, shoot density may also be restricted internally by the
production of buds. Thus, the high occupation of space by standing necromass
and rhizomes recorded in larger *S. densiflora* tussocks may affect intra-tussock
ramet emergence, by decreasing buds production. Clonal species behaving in
this way will often grow as dominant stands of vegetation, which can persist
for long periods (GRIME, 1979). Both hypothesis of external and internal con-
trol of intra-tussock tiller density are supported by the fact that during the first
year of sprout after fires, when standing biomass has been eliminated, the net
primary productivity of *S. densiflora* tussocks is higher than in populations not
disturbed by fire (NIEVA & FIGUEROA, 1997).

Below-ground biomass/above-ground live biomass ratio did not show a clear
pattern regarding tussock size; changes of this ratio with tussock size are
difficult to interpret at the light of this study. The highest value (1.1) was
recorded in the highest tussock that showed low density of short living tiller.
However, most of the tussock registered values close to 50 %, since both, above
and bellow biomasses, increased with tussock size. This value is lower than that
of other *Spartina* species (CARTAXANA & CATARINO, 1997; ORNES & KAPLAN,
1989). Thus, although *S. densiflora* below-ground biomass was similar to that
of other species of the same genus, the high above-ground biomass figures made
this ratio to be lower.

In South America, the original region of *S. densiflora* where it comes from,
it acts as a facilitator for the colonization of several species, enhancing diversity
of communities (LEWIS & al., 1985; CARNEVALE & al., 1987). Clonal traits
described in this study, as high densities of live large tillers -which would favour
necromass accumulation in central die-back areas- and high below-ground
biomass, together with an integrated clonal functioning, would prevent the
colonization by other species of *S. densiflora* tussocks. Inside *S. densiflora*
tussocks would dominate unfavourable conditions to growth, as lack of radiation
and soil depletion (LEWIS & al., 1990). MCCONNAUGHAY & BAZZAZ (1992)
point out that the simultaneous lack of space and light created severe conditions
for development. Similarly, MAULE & al. (1995) described as *Tradescantia
fluminensis*, an alien weed in New Zealand forests, forms a dense tussock,
preventing survival of native species. MCCONNAUGHAY & BAZZAZ (1992)
showed as the intense occupation of the below-ground space in perennial
grasslands is a key ecological factor limiting the growth of potential colonizers.
In general, it has been described as "phalanx" growth results in the occupation
of the original site for long periods and the obstruction of colonization by other

species (BEGON & al., 1996). The different roles played by *S. densiflora* in SW European and South American salt marshes may be related with intra-specific differences in clonal growth traits and/or to differences in community composition. So, above-ground biomass values presented in this study and in others works in European estuaries (FIGUEROA & CASTELLANOS, 1988; NIEVA & al., 2001) exceed those recorded in South American marshes of *S. densiflora* (SORIANO-SIERRA, 1990; SILVA & al., 1933).

Species combining capability of both, long-distance dispersal and short-distance spread, are among the most successful invaders (KORNAS, 1990; MAL & al., 1992). *S. densiflora* shows an aggressive clonal growth in a South-western European low salt marsh, which together with its high production of viable seeds (KITTELSON & BOYD, 1997), denotes a high invasive potential. Thus, *S. densiflora* grows covering virtually all the space available in vast areas of marsh, with very short distance between adjacent tussocks, contributing to decrease in biodiversity on European marshes (FIGUEROA & CASTELLANOS, 1988).

REFERENCES

ADACHI, N., I. TERASHIMA & M. TAKAHASHI (1996). Central die-back of monoclonal stands of Reynoutria japonica in an early stage of primary succession on Mt. Fuji, a Japanese volcano. *Ann. Bot.* **77**: 477-486.

ADAM, P. (1990). *Salt Marsh Ecology.* Cambridge University Press. Cambridge.

BEGON, M., J. L. HARPER & C. R. TOWNSEND (1996). *Ecology. Individuals, Populations and Communities.* Blackwell Science. Oxford.

BERTNESS, M. D. (1991). Zonation of Spartina patens and Spartina alterniflora in a New England salt marsh. *Ecol.* **72**: 138-148.

BULLOCK, J. M., J. SILVERTOWN & B. CLEAR HILL (1996). Plant demographic responses to environmental variation: distinguishing between effects on age structure and effects on age-specific vital rates. *J. Ecol.* **84**: 733-743.

CALDWELL, P. A. (1957). The spatial development of Spartina colonies growing without competition. *Ann. Bot.* **21**: 203-214.

CALLAWAY, R. M. (1994). Facilitative and interfering effects of Arthrocnemum subterminalis on winter annuals. *Ecol.* **75**: 681-686.

CASTELLANOS, E. M., M. E. FIGUEROA & A. J. DAVY (1994). Nucleation and facilitation in saltmarsh succession: interaction between Spartina maritima and Arthrocnemum perenne. *J. Ecol.* **82**: 239-248.

——, C. HEREDIA, M. E. FIGUEROA & A. J. DAVY (1998). Tiller dynamics of Spartina maritima in succesional and non-successional mediterranean salt marsh. *Plant Ecol.* **137**: 213-225.

CASTILLO, J. M., L. FERNÁNDEZ-BACO, E. M. CASTELLANOS, C. J. LUQUE, M. E. FIGUEROA & A. J. DAVY (2000). Lower limits of Spartina densiflora and S. maritima in a Mediterranean salt marsh determinated by different ecophysiological tolerances. *J. Ecol.* **88**: 801-812.

CARNEVALE, N. J., P. TORRES, S. I. BOCCANELLI & J. P. LEWIS (1987). Halophilous communities and species distributions along environmental gradients in southeastern Santa Fe Province, Argentina. *Coenoses* **2**: 49-60.

CARTAXANA, P. & F. CATARINO (1997). Allocation of nitrogen and carbon in an estuarine salt marsh in Portugal. *J. Coast. Conserv.* **3**: 27-34.

COSTA, M. J., F. CATARINO & A. BETTENCOURT (2001). The role of salt marshes in the Mira Estuary (Portugal). *Wetlands Ecol. Manage.* **9**: 121-134.

DAI, T. & R. G. WIEGERT (1996). Ramet population dynamics and net aerial primary productivity of Spartina alterniflora. *Ecol.* **77**: 276-288.

DEREGIBUS, V. A., R. A. SÁNCHEZ, J. J CASAL & M. J. TRLICA (1985). Tillering responses to enrichment of red light beneath the canopy in a humi natural grassland. *J. Appl. Ecol.* **22**: 199-206.

DE KROON, H. (1993). Competition between shoots in stands of clonal plants. *Plant Species Biol.* **8**: 85-94.

FIGUEROA, M. E. & E. M. CASTELLANOS (1988). Vertical structure of Spartina maritima and Spartina densiflora in Mediterranean marshes. In M. J. A. WERGER, P. J. M. VAN DER AART, H. J. DURING & J. T. A. VERHOEVEN (eds.). *Plant Form and Vegetation Structure*: 105-108. SPB Academic Publishing. The Hague.

GATSUK, L. E., O. V. SMIRNOVA, L. I. VORONTZOVA, L. B. ZAUGOLNOVA & L. A. ZHUKOVA (1980). Age states of plants of various growth forms: a review. *J. Ecol.* **68**: 675-696.

GRIME, J. P. (1979). *Plant Strategies and Vegetation Processes*. Wiley. Chichester.

GROENENDAEL, J. M. VAN, L. KLIMES, J. KLIMESOVÁ & R. J. J. HENDRIKS (1996). Comparative ecology of clonal plants. *Philos. T. Roy. Soc.* **351**: 1331-1339.

HARPER, J. L. (1985). Modules, branches, and the capture of resources. In J. B. C. JACKSON., L. W. BUSS & R. E. COOK (eds.). *Population Biology and Evolution of Clonal Organisms*: 1-33. Yale University Press. New Haven.

HERBER, T. & T. HARA (1997). Competition and spatial dynamics of clonal plants. In H. DE KROON & J. VAN GROENENDAEL (eds.). *The ecology and evolution of clonal plants*: 331-357. Backhuys Publishers. Leiden.

HESTER, M. W., K. L. MCKEE, D. M. BURDICK, M. S. KOCH, K. M. FLYNN, S. PATTERSON & I. A. MENDELSSOHN (1994). Clonal integration in Spartina patens across a nitrogen and salinity gradient. *Can. J. Bot.* **72**: 767-770.

KITTELSON, P. M. & M. J. BOYD (1997). Mechanism of expansion for an introduced species of cordgrass, Spartina densiflora, in Humbolt Bay, California. *Estuaries* **20**: 770-778.

KORNAS, J. (1990). Plant invasions in Central Europe: historical and ecological aspects. In F. DI CASTRI, A. J. HANSEN & M. DEBUSSCHE (eds.). *Biological invasions in Europe and Mediterranean basin*: 19-36. Kluwer Academic Publishers. Dordrecht.

LEWIS, J. P., M. B. COLLANTES, E. F. PIRE, N. J. CARNEVALE, S. I. BOCCANELLI, S. L. STOFELLA & D. E. PRADO (1985). Floristic groups and plant communities of southeastern Santa Fe, Argentina. *Vegetatio* **60**: 67-90.

——, S. L. STOFELLA, D. E. PRADO, E. F. PIRE, E. A. FRANCESCHI & N. J. CARNEVALLE (1990). Dynamics and development of floristic richness in the vegetation of a large depressed area of the Great Chaco. *Flora* **184**: 63-77.

LOVETT-DOUST, L. & J. LOVETT-DOUST (1982). The battle strategies of plants. *New Sci.* **95**: 81-84.

LUQUE, C. J., J. M. CASTILLO & M. E. FIGUEROA (2000). The Atlantic coast of Southern Spain. In C. R. C. SHEPPARD (ed.). *Seas at the Millennium: an Environmental Evaluation* **1**: 167-184. Elsevier Science Ltd. Oxford.

MAL, T. K., J. LOVETT-DOUST, L. LOVETT-DOUST, & G. A. MULLIGAN (1992). The biology of Canadian weeds. 100. Lythrum salicaria. *Can. J. Plant Sc.* **72**: 1305-1330.

MAULE, H. G., M. ANDREWS, J. D. MORTON, A. V. JONES & G. T. DALY (1995). Sun shade acclimation and nitrogen nutrition of Tradescantia fluminensis, a problem weed in New Zealand native forest remnants. *New Zealand J. Ecol.* **19**: 35-46.

MCCONNAUGHAY, K. D. M. & F. A. BAZZAZ (1992). The occupation and fragmentation of space: consequence of neighbouring roots. *Funct. Ecol.* **6**: 711-718.

MOBBERLEY, D. G. (1956). Taxonomy and distribution of the genus Spartina. *Iowa State College J. Sc.* **30**: 471-574.

NIEVA, F. J. & M. E. FIGUEROA (1997). Patrón de recuperación tras fuego en una marisma de Spartina densiflora Brong. *VII Congreso Latino-americano sobre Ciências do Mar. Resumos expandidos* **2**: 213-214. Instituto Oceanográfico da Universidades de São Paulo and Associação Latino-americana de Investigaores em Ciências do Mar. São Paulo.

——, A. DIAZ-ESPEJO, E. M. CASTELLANOS & M. E. FIGUEROA (2001). Field variability of invading populations of Spartina densiflora Brong. grown in different habitats of the Odiel marshes (SW Spain). *Estuar. Coast. Shelf S.* **52**: 515-527.

OLIVER, F. W. (1925). Spartina towsendii; its mode of establishement, economic uses and taxonomic status. *J. Ecol.* **13**: 74-91.

ORNES, W. H. & D. I. KAPLAN (1989). Macronutrient status of tall and short forms of Spartina alterniflora in a South Carolina salt marsh. *Mar. Ecol.-Prog. Ser.* **55**: 63-72.

PORTER, J. R. (1989). Modules, models and meristems in plant architecture. In G. RUSSELL, B. MARSHALL & P. G. JARVIS (eds.). *Plant canopies: their growth, form and function*: 143-159. Cambridge University Press. Cambridge.

SILANDER, J. A. (1985). Microevolution in clonal plants. In J. B. C. JACKSON, L. W. BUSS & R. E. COOK (eds.). *Population and evolution of clonal plants*. Yale University Press, New Haven.

SILVA, C. P., C. M. P. PEREIRA & L. P. P. DORNELES (1993). Espécies de gramíneas e crescimiento de Spartina densiflora, Brong. em una marisma da Laguna dos Patos, Rs, Brasil. *Caderno de Pesquisa (Sér. Bot.)* **5**: 95-108.

SORIANO-SIERRA, E. J. (1990). Ecosistemas de marismas, III. A produçao primária. *II Simposio de Ecossitemas da Costa Sul e Sudeste Brasileira: estructura, funçao e manejo*. ACIESP. Sao Paulo.

STEEL, R. G. D. & J. H. TORRIE (1960). *Principles and procedures of statistics*. McGraw-Hill Book Company. New York.

SUZUKI, J. & M. J. HUTCHINGS (1997). Interactions between shoots in clonal plants and the effects of stored resources on the structure of shoot populations. In H. DE KROON & J. VAN GROENENDAEL (eds.). *The ecology and evolution of clonal plants*: 311-329. Backhuys Publishers. Leiden.

TUTIN, T. G., N. A. BURGES, A. O. CHATER, J. R. EDMONDSON, V. H. HEYWOOD, D. M. MOORE, D. H. VALENTINE, S. M. WALTERS & D. A. WEBB (1964-1980). *Flora Europaea*. Vol. **1-5**. Cambridge University Press. Cambridge.