SEASONAL SEED BANK PATTERNS OF AN ARTHROCNEMUM MACROSTACHYUM (CHENOPODIACEAE) COMMUNITY ALONG A COASTAL MARSH INUNDATION GRADIENT ON THE ARABIAN SEA NEAR KARACHI, PAKISTAN

BILQUEES GUL AND M. AJMAL KHAN

Department of Botany, University of Karachi, Karachi-75270, Pakistan.

Abstract

The seasonal variation of a seed bank was studied along an inundation gradient in a coastal marsh community dominated by Arthrocnemum macrostachyum (Moric.) C. Koch (Syn: Arthrocnemum indicum (Willd.) Moq.; Chenopodiaceae;) near Karachi, Pakistan. The distance from the Avicennia marina edge to mean high tide line (110 m) was divided into five zones. Density and height of the plants were higher in the middle marsh than in other areas. Plant cover and number of branches were lowest in the lower marsh and increased substantially in the next zone and there was no significant difference among other zones. Dry weight accumulation was highest in the lower-middle marsh. The size and composition of the seed bank was determined by monthly counting and identifying the seeds extracted from soil samples. A persistent seed bank flora was dominated by A. macrostachyum. The upper, upper-middle and middle marsh had seeds of five additional species viz., Atriplex stocksii Boiss., Suaeda fruticosa (L.) Forssk., Halopyrum mucronatum (L.) Stapf., Aeluropus lagopoides (L.) Trin. Ex Thwaites, Urochondra setulosa (Trin.) C.E. Hobbard and Cressa cretica L. from adjacent communities. Seed bank size was one of the largest in the samples collected immediately following dispersal ranging from $40,760 \pm 123$ seeds m⁻² in March to 917,135 ± 567 seeds m⁻² in July. Seed density then declined rapidly over two to three months. Size and diversity of the seed bank progressively increased from the lower to the upper salt marsh.

Introduction

The desert littoral marshes near Karaehi, Pakistan, are characterized by simplicity of structure and composition (Chaudhri, 1961). Monospecific patches of vegetation are common with or without minor associates (Khan, unpublished data). The zonation pattern is primarily controlled by tidal inundation, and salinity often correlates well with elevation and inundation (Zahran, 1973). The vegetation types from seaward to landward are mangrove (Avicennia marina), followed by muddy coastal marsh with Arthrocnemum macrostachyum (Karim & Qadir, 1979), and other communities dominated by Atriplex stocksii Boiss., Suaeda fruticosa (L.) Forssk. (Chenopodiaceae), Halopyrum mucronatum (L.) Stapf., Aeluropus lagopoides (L.) Trin. Ex Thwaites, Urochondra setulosa (Trin.) C.E. Hobbard (Poaceae), and Cressa cretica L. (Convolvulaceae) (Chaudhri & Qadir, 1958) which were present on adjacent low dunes.

Arthrocnemum macrostachyum is a woody, perennial, stem succulent halophyte that experiences spatial and temporal variation in soil conductivity (22 to 68 dS m⁻¹) and moisture (19 to 33%) (Gul, 1993). It produces non-dormant seeds during April and May, however, no germination has been recorded under natural field conditions at this location.

*Corresponding author and address: P.O. Box 8452, University of Karachi, Karachi-75270, Pakistan. E-mail: ajmal@botany.ku.edu.pk

Seeds are viable and germinate best under low salinity and high thermoperiod, which could also germinate at 1000 mM NaCl (Khan & Gul, 1998). Salinity-enforced dormancy (at concentration \geq 1000 mM NaCl) can be alleviated by application of GA₃ and kinetin (Khan *et al.*, 1998).

There are few studies on the seed bank of coastal communities, especially of subtropical shrub-dominated coastal marsh communities. Coastal shrubs and grasses produce large number of seeds, most of which disappear a few months after dispersal, but maintain a persistent seed bank despite a significant seasonal loss of seeds. In temperate areas, coastal salt marsh seed banks vary from 0 to 140,000 seeds m⁻² (Jefferies *et al.*, 1981; Jerling, 1984; Hartman, 1988; Ungar & Woodell, 1993, 1996), but they are usually fairly small. Low seed densities have been found in several subtropical Arabian Sea coastal communities near Karachi, Pakistan. Studies from Karachi have demonstrated that dominant perennial halophytic shrubs and grasses maintain a persistent seed bank (Gulzar & Khan, 1994; Aziz & Khan, 1996). Six different coastal dune communities had a very small seed bank of 30 - 260 seed m⁻² (Gulzar & Khan, 1994), while a coastal salt marsh community dominated by *A. macrostachyum* had a relatively large seed bank (11,000 seed m⁻²). *Cressa cretica* had a persistent seed bank with a maximum of 2,500 seed m⁻² after dispersal, which a few months later declined to 500 seed m⁻² (Aziz & Khan, 1996).

A number of hypotheses have been suggested to explain relatively small number of seeds in coastal salt marshes: loss of seeds because of coastal abrasion (Hutching & Russell, 1989), death due to environmental extremes beyond the range of tolerance (Ungar, 1995a,b), and composition of aboveground vegetation and its low seed production (Milton, 1939; Hutchings & Russell, 1989). Factors that could contribute to the distribution and maintenance of seeds in wetland soils include burial, inundation pattern (depth, duration and timing of water fluctuation), physical and chemical characteristics of the substrate and disturbance (Leck, 1989).

The role of seed banks in coastal communities of arid subtropical regions dominated by perennial halophytic shrubs is poorly understood. The present report describes the nature of the seed bank along a temporal and spatial gradient in an A. macrostachyum dominated coastal marsh community and determines the size of the seed bank along the inundation gradient and its relationship with the vegetation.

Materials and Methods

Study site: The study site is located in Manora Creek near Sands Pit about 10 km from Karachi, Pakistan (24° 48 N, 65° 55 E). Monthly mean ambient summer and winter temperatures are 36°C and 25°C, respectively. The monsoon season extends from June to September. Avicennia marina dominates the area which is daily submerged with seawater and from the A. marina edge to the mean high tide line the area is dominated by A. macrostachyum. Various communities are dominated by Atriplex stocksii, Suaeda fruticosa (Chenopodiaceae), Aeluropus lagopoides, Halopyrum mucronatum, Urochondra setulosa (Poaceae) and Cressa cretica (Convolvulaceae). Flowering and seed set of A. macrostachyum occur from May to July. A transect was laid from the A. marina to the high tide zone. The community along the transect was divided into five equal zones: 1. Lower marsh, 2. Lower middle, 3. Middle, 4. Upper middle and 5. Upper.

Table 1. Growth parameters of Arthrocnemum macrostachyum population growing at different zones of Arabian Sea coast salt marsh.

Growth parameters	Lower	Lower- Middle	Middle	Upper- Middle	Upper
Leaf biomass (mg plant ⁻¹)	70±11	149±16	129±7	126±15	127±18
Basal area (m ⁻²)	0.05±0.007	0.12 ± 0.04	0.14 ± 0.08	0.13 ± 0.05	0.14±0.06
Number of plant quadrat-1	4±1.1	18±2.4	23±3.9	12±2.2	7±1.2
Number of branches	20±3	55±5.3	77±10.2	58±3.9	73±2.2
Plant height (cm)	22±12.3	29±3.4	35±4.0	22±2.4	20±3.2

The vegetation in each zone was sampled using 20 sample points and the point-centered quarter method (Cottam & Curtis, 1956). Density, frequency and cover were measured and an importance value index calculated. To assess the size and species composition of the seed bank, 20 randomly selected soil cores were collected using a 1.5-cm diameter corer to a depth of 15 cm at monthly intervals from February 1994 to January 1995. Seeds were manually sorted immediately after collection with the help of a binocular microscope, identified by using a reference collection and counted. Because of the variety of dormancy mechanism in seeds of perennial sub-tropical halophytic shrubs a germination bioassay was not possible (Khan, 1993).

The results were analyzed using a three way ANOVA. A Bonferroni test was carried out to determine if significant (P< 0.05) differences occurred between individual zones (Anon., 1999).

Results

The aboveground vegetation in all of the five zones was dominated by a monotypic stand of A. macrostachyum (100% relative cover and frequency values). The lower marsh zone is bordered by Avicennia marina while the upper marsh zone border had Aeluropus lagopoides, Atriplex stocksii, Cressa cretica, Limonium stocksii and Suaeda fruticosa.

Leaf biomass was highest in the lower-middle marsh and dry masses of the plants from all other zones were not significantly different from each other. Cover of plants in the lower marsh was about 50% of that of the plant cover in all other zones, which were not significantly different from each other. Maximum density of plants was found in the intermediate zone. Number of branches per plant increased from the lower to middle marsh and then remained unchanged in the upper marsh. Plant height also peaked in the middle marsh and height of plants in the lower marsh was not significantly different from the height of plants present in upper marsh (Table 1).

A three way ANOVA indicated a significant ($P \le 0.0001$) effect of zone, species, month and their interactions on the seed bank (Table 2). The size of this desert coastal wetland seed bank was large. A maximum density of 917,135 seed m² of A. macrostachyum seeds occurred in July after dispersal and declined to 61,136 seeds m² after two to three months (Fig. 1). The seed bank was largest in the upper marsh (917,135 \pm 567 seeds m²) and decreased progressively towards the lower marsh (20,377 \pm 213). The seed bank in the lower marsh was 40,760 seeds m², immediately after dispersal and declined to 2035 seed m² after four months (Fig. 1). The seed banks of upper, uppermiddle and lower marshes were not significantly different from each other whereas the seed banks of lower-middle and lower marsh zone were significantly lower (Bonferroni test).

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Source	df	SS	F	P
Zone (Z)	4	205630	2184	0.0001
Species (S)	5	46718	1972	0.0001
Month (M)	11	35338	393	0.0001
S x Z	20	38975	35	0.0001
ZxM	44	29247	26	0.0001
SxM	55	42756	134	0.0001
SxMxZ	220	29111	8	0.0001

Table 2. Results of three way analysis of variance of characteristics by salinity, regulators and temperature on germination of Arthrocnemum macrostachyum.

Species richness in the seed bank also declined from the upper marsh to the lower marsh. The seed banks of upper and upper-middle zone contained six species, the middle zone had two, and the lower middle and lower zone had only A. macrostachyum seeds (Table 3,4, and 5). Arthrocnemum macrostachyum dominated all zones, with the seed bank size of the other species being much smaller but with similar seasonal distribution as that of A. macrostachyum. Species found in the seed banks of the upper and upper-middle zones were Aeluropus lagopoides, Atriplex stocksii, Cressa cretica, Limonium stocksii and Suaeda fruticosa, which are common in communities above the upper Arthrocnemum marsh zone.

Discussion

Low diversity and high density characterize the seed bank of A. macrostachyum community on the Arabian Sea coast. The seed bank of all zones was dominated by A. macrostachyum. Low species diversity could be attributed to high soil salinity (Aziz & Khan, 1996) and increased degree of inundation (Zahran, 1973; Leck, 1989), coastal abrasion (Hutchings & Russell, 1972), environments beyond the range of salt tolerance of seeds (Ungar, 1995a), or the composition of vegetation and seed production (Hutchings & Russell, 1989). In this salt marsh high salinity and frequent inundation seems to be more important.

Plants of the lower marsh, which are partially sub-merged, were short, with few branches and the aerial portion of most plants were broken or washed away due to wave action; however, below ground biomass was higher and seed production was low. The middle marsh had well-developed tall aerial shoots, plants with greater number of branches and higher cover in comparison to the lower marsh but had lower below ground biomass. Plants in the upper marsh showed a relatively reduced biomass, number of branches and height. It appears that seed production was lowest in lower marsh, highest in middle marsh and relatively lower in upper marsh.

The A. macrostachyum seed bank was very large in the upper marsh during July (917,135 seeds m⁻²) and the size of the seed bank progressively decreased from the upper to the lower marsh. This could be attributed to the following: 1. plants in the lower marsh produce a small number of seeds; 2. frequency of seed removal by tidal abrasion appeared higher in lower and middle marsh and was very low in upper marsh. It appears from our data that variation in the seed bank could be primarily due to twice daily inundation of the lower to middle marsh and a monthly inundation of upper middle and middle marshes.

Checies	Reh	Mer	Anr	Any May Inne Inly Ang Sent Oct	Inne	Inly	And	Sent	Oat	Nov	1	nel.
Shortes						,		3	3			
Arthrocnemum	101902	40760	40760	101902	336279	917135			101902	81500	101902	61136
macrostachyum	+223	±123	±112	±135	±234	±567	±145		±112	±430	±340	±120
Aeluropus logopoides	6112	2035	2035	0	4070	0		20377	19342	4070	0	0
	±75	1 68	±123		1 26				+214	±189		
Atriplex stocksii	0	8147	2035	2035	0	1387			4070	6112	2035	0
į		±124	±113	±125		±122			±123	±345	∓76	ŀ
Cressa cretica	4070	14265	20378	0	6112	10188	34642		2035	2035	0	4070
	±113	±438	±356		±432	±326			±346	±124		±54
Limonium stocksii	10188	0	6105	20376	14265	14265			6112	2035	9	0
	±340		±165	±367	±432 [′]	±435			±376	+234	,	
Suaeda fruticosa	0	0	4070	8147	0	0	27032		14265	4070	2035	0
			±214	±312					±467	±164	99∓	

Table 4. Season	asonal va	al variation in mean number of seeds m ⁻²	nean n	mber of	seeds m-2		r upper	middle m	(± SE) for upper middle marsh zone during 1994-95	during	1994-95.	
Species 2	Feb.	Mar.	Apr.	May		July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Arthrocnemum	61136	40760	34642	61137	203766	611363		201757	163000	40760	8	61138
macrostachyum	+223	±123	±112	±135				±123	±112	±340		±120
Aeluropus logopoides	0	0	4070	2035				6112	8145	0		2035
5.			±123	±231				±132	+214			1 39
Atriplex stocksii	6112	4070	0	0				2035	0	0		0
	+23	1 24						±54				
Cressa cretica	0	26495	0	24453	14265				2035	2035	4070	2035
		±427		±317					±46	±124	∓87	±154
Limonium stocksii	2036	0	14265	0					0	4070	2035	2035
	±37		±235				±123			74	∓34	1 23
Suaeda fruticosa	10188	0	4070	4070			14265	8147	10188	4070	2035	4070
	±814		+24	±32	±123		±112	±318	±315	±64	±56	∓76

TABLE S. SCREENING VALIDATION IN HIGHER HAMBEL OF SCREENING IN (1. 52.) FOR IMPORT, 10 W.C. IMPORT, MALE SOME CONTRACT IN THE STREET, MALE SOM	A. VALIALIO			I sectes III	(T C T)							
Species	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
						Mi	Middle					
Arthrocnemum	28530	34642	18342	42795	568588	407597	407597 185425 167083 163000	167083	163000	20377	10188	26300
macrostachyum	∓88	¥6 ∓	±54	±112	+324	±234	±213	±432	1 64	±12	1 21	1 58
Aeluropus logopoides	2035	0	2035	4070	0	6112	10188	14265	0	0	2035	0
	1 24		∓48	1 67		±34	∓786	±453			1 64	
						Lower	Lower Middle					
Arthrocnemum	0	14265	2035	79458	57066	20377	14265	18342	0	0	6112	0
macrostachyum		∓65	1 35	±123	96∓	±124	∓76	±43			171	
						Lo	Lower					
Arthrocnemum	2035	4070	0	0	0	20377	40760	14265	18342	10188	2035	2035
macrostachyum	13 4	±123				±213	±123	1 21	1 64	±42	∓16	∓8 7
						1176						

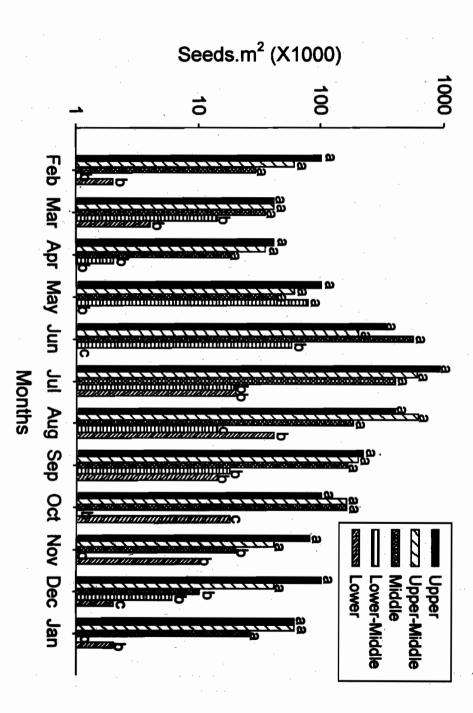


Fig. 1. Seasonal distribution (mean ± standard error) of Arthrocnemum macrostachyum seeds in upper, upper-middle, middle, lower middle and lower marshes zones in an Arabian coastal marsh. Bars with different letters are significantly different (P < 0.05), Bonferroni test

The size of the seed bank of a community dominated by Cressa cretica, on dry elevated sandy coastal areas near Karachi that were seasonally inundated with seawater reached its maximum (2500 seeds m⁻²) after dispersal, which is low in comparison to our data for the A. macrostachyum population. As noted by Harper (1977), seed bank composition varies with one species making up an overwhelming proportion of the seed bank. Size of the seed bank in coastal salt marshes elsewhere varied from 47 seed m⁻² to 130.000 seed m⁻² (Jerling, 1984; Hartman, 1988; Ungar & Woodell, 1993, 1996), British coastal marshes have no seed bank or only a small seed bank in the zonal communities (Milton, 1939; Jefferies et al., 1991; Hutchings & Russell, 1989). Investigations of eastern Pacific Ocean coastal marshes indicate that some communities may have large seed banks, with either temporary or persistent seed banks (Josselyn & Perez, 1981; Hopkins & Parker, 1984). In a Pacific Ocean zonal marsh community dominated by Salicornia virginica, the seed bank in October contained 700 to 3174 seed m⁻² (Hopkins & Parker, 1984). The dominant species made up 97% of the seed bank and there was a high correlation between the seed bank and the species within the plant community. Our data showed a great deal of spatial and temporal variation in the size of the seed bank. The large variation reported in the size of coastal seed banks may be a representation of the seed bank dynamics.

There was a close relationship between the seed bank and vegetation since A. macrostachyum seeds dominated every zone. However, the upper and upper-middle zones also had seeds from four other species present in adjacent communities. Other Arabian Sea coast communities also showed a close relationship between vegetation and seed bank flora (Gulzar & Khan, 1994; Aziz & Khan, 1996). Vegetation in all zones consisted of A. macrostachyum, and towards the landward edge of the upper marsh other halophytic communities are present on lower dunes. Few seeds from the adjacent communities were dispersed into the upper and upper-middle zones of the A. macrostachyum community.

Arthrocnemum macrostachyum is a shrub with an extensive woody rhizome system. It usually grows where part of the population is exposed to diurnal and lunar tidal inundation. Propagation occurs primarily through rhizomes, although it produces a large number of seeds and maintains a persistent seed bank. However, during five years of field observations, no successful establishment of seedlings was observed. During 1994, when the area received four times the average rainfall for four months, a number of other perennial halophytes (e.g. Suaeda fruticosa) were recruited through seeds, but no such recruitment was found for A. macrostachyum. The seeds are extremely salt-tolerant, and exposure to high salinity and temperature does not affect their viability (Khan & Gul, 1998). Most seeds promptly germinated under laboratory conditions when salinity was reduced.

Arthrocnemum macrostachyum could be categorized as one of the most salt tolerant species at the germination stage. Although high salinity induces dormancy in most of the seeds by inhibiting germination regulating compounds activity (Khan et al., 1998), a few seeds should still be able to germinate. We conclude that lack of recruitment through seeds in A. macrostachyum populations is not due to un-availability of seeds, or innate seed dormancy, but perhaps it is due to temporal loss of viability or dormancy induced by high salinity and temperature. The Arabian Sea coast populations maintain a persistent seed bank, which have a close relationship with the vegetation. The interesting question is why so many seeds are produced when recruitment from seeds is rare. Arthrocnemum

macrostachyum plants spread vegetatively by rhizome growth and once they are established the production of a large number of viable seeds is a means to produce sufficient genetic variability to allow the populations recruited into new open habitat when conditions are favorable. This study also shows that a large variation reported in the size of coastal seed banks could be due to the time and place of sampling and not the actual seed bank size.

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