

Population biology of the annual grass *Triplasis purpurea* in relation to distance from shore on Staten Island, New York

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Abstract. Four populations of the native annual grass *Triplasis purpurea* were surveyed on coastal beaches along the south shore of Staten Island, NY, to determine the potential of this species to colonize shoreline habitats mostly devoid of other vegetation. If the species can establish and maintain dense populations, it may have conservation value for urban beaches disturbed by human activities. For two populations, survivorship, growth, and reproduction were monitored at different distances from shore to determine the ability of this species to maintain viable populations. At three sites, *T. purpurea* occurred in > 75 % of all quadrats and the highest density was 1195 plants/m² at 74 m from shore in one recently disturbed site. Density generally increased with increasing distances from shore at low tide (from ca. 40 - 90 m). Plants showed the greatest growth and reproduction at close distances to shore (30 - 40 m); part of this effect was due to density in one population, but when density effects were removed statistically, there still remained a decline in growth and reproduction with increasing distance from shore. Improved vigor nearest to shore may be due to continual sand deposition. Survivorship showed a Type I pattern, with low mortality throughout the growing season. By colonizing newly-deposited and continually shifting sands, *T. purpurea* can contribute to the earliest stages of ecological succession along disturbed beaches in eastern North America and may be valuable to the development and management of urban coastal plant communities.

Keywords: Coastal beach; Colonization; Psammophyte; Seed production; Survivorship.

Introduction

In coastal ecosystems, annual plants can be prolific seed producers and important to the colonization of bare dune substrates (Watkinson et al. 1979; Watkinson & Davy 1985; Symonides 1988; Hesp 1991). Although annuals are not generally critical to dune building (Woodhouse 1982), their abundance in the pioneer zone along coastal beaches (*sensu* Barbour et al. 1985; Hesp 1991) where natural or anthropogenic disturbance is widespread, contributes to the earliest stages of dune formation and ecological succession. Hence, native annuals could be valuable to the development and conservation of natural coastal communities.

Coastal habitats can contain plant and animal species unique to these systems with conservation value (Cook & Tanacredi 1990; Stalter 1993; Stalter et al. 1996). Unfortunately, in urban areas, the difficulty of preserving and managing coastal beaches is often compounded by the negative impact of recreational development, off-road vehicles, and other human-related activities (Burden & Randerson 1972; Liddle & Greig-Smith 1975; Hosier & Eaton 1980; McDonnell 1981; Carlson & Godfrey 1989; Bonanno et al. 1998). Along the southern coast of Staten Island, a borough of New York City, casual observations indicate that native annual grasses, especially *Triplasis purpurea* and *Cenchrus tribuloides*, provide considerable cover in areas impacted by human traffic that are mostly devoid of other vegetation (Cheplick & Demetri 1999; Cheplick & Wickstrom 1999).

As an initial step in exploring the role of *T. purpurea* in the colonization of coastal beaches in an urban ecosystem, *T. purpurea* populations and associated species were surveyed. The specific objectives of this research were (1) to determine the potential of *T. purpurea* to colonize beaches that are mostly devoid of other vegetation, (2) to determine what species were associated with, and could potentially impact, *T. purpurea* populations in the plant communities of the urban shoreline, and (3) to quantify the survivorship, growth, and reproduction of *T. purpurea* in two natural populations. Because *T. purpurea* abundance and growth appeared to be related to proximity to the shore (Cheplick pers. obs.), the population ecology of this species was examined in reference to distance from the shoreline measured at low tide when waves were calm. Because abiotic stresses such as salt spray and sand movement are most pronounced close to shore (Oosting & Billings 1942; Hesp 1991; Bertness 1999; Cheplick & Demetri 1999), it was hypothesized that (1) *T. purpurea* would reach maximum densities on parts of the beach farthest from shore and (2) its growth, survival, and reproduction would be greatest farthest from shore, provided intraspecific densities were not high enough to negatively impact these factors.

Material and Methods

Study species

The native annual grass *Triplasis purpurea* grows along the eastern seaboard of North America, ranging from Ontario, Canada and south to Florida and Texas (Hitchcock 1950; Duncan & Duncan 1987). Seed germination begins in late April to late May on Staten Island after natural stratification of seeds in the soil over winter (Cheplick 1996b). After seedlings emerge, growth occurs via tiller production and elongation during the summer. Axillary panicles with cleistogamous spikelets form along culm internodes in late August and the resulting seeds are completely enclosed within leaf sheaths (Chase 1918). Although most seeds mature on enclosed, axillary panicles (Cheplick 1996a), the tips of large tillers produce emergent terminal panicles with open, chasmogamous spikelets. Sheath-enclosed seeds are dispersed when parental culms break apart over winter, but many seeds remain *in situ* within the leaf sheaths, especially at the lower internodes of parental culms. Hence, dispersal is limited in this species (Cheplick 1996b, 1998).

Colonization potential

Four sites along the south shore of Staten Island were selected for the documentation of natural densities of *T. purpurea* (Fig. 1). The sampling procedure employed line transects with quadrats systematically placed at uniformly-spaced intervals of 2 - 9 m, depending on the area sampled. Because the beaches along the strandline varied in length and width, the distances from shore at which populations were sampled also varied, but at all sites six, equally-spaced distances were used. In all populations, six transects parallel to the shoreline were established at six distances. For each site, distance from shoreline was measured at low tide from the maximum extent of the water (on a calm day when waves were minimal) to each parallel transect. Also, at each site, the first parallel transect closest to shore where *T. purpurea* occurred was just above the maximum extent of water at high tide along the first dune ridge (Bertness 1999) which also runs parallel to shore. It should be noted that there are no fully developed foredunes at any site along the Staten Island shore and that the primary dune ridges (usually < 0.5 m height) can at best only be considered 'embryo dunes' (Bertness 1999). At three of the sites, the top of the primary dune ridge was located 25 - 45 m from the water at low tide; however, at Great Kills (GK), the first dune ridge (and associated plants) was much further back (58 m) because a gradually sloping beach resulted in a large distance between the low and high tide water's reach.

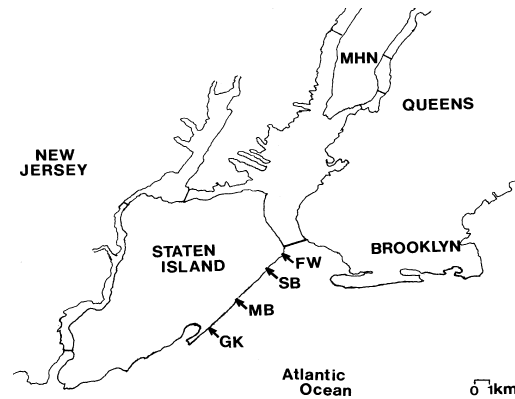


Fig. 1. Map of the New York City-New Jersey area showing location of the four study sites along the south shore of Staten Island (FW = Fort Wadsworth, SB = South Beach, MB = Midland Beach, GK = Great Kills). MHN = Manhattan.

All sites were similar in terms of their aspect along the Staten Island shore (Fig. 1) and their soils were of the Hooksan series, characterized by thick, sandy sediments (> 98% sand) that are 'excessively drained' and nutrient-poor (L.A. Hernandez, pers. comm.; report, Natural Resources Conservation Service, United States Department of Agriculture). All beaches sampled had at least a moderate level of human use for fishing, beachcombing, sunbathing and similar activities (Tanacredi 1983).

10 quadrats (35 cm × 27 cm) were equally spaced along each parallel transect at Midland Beach (MB), South Beach (SB) and Fort Wadsworth (FW), but in the smaller area occupied by the GK population, only six quadrats per transect could be utilized. On the day of sampling, all *T. purpurea* seedlings in each plot were counted and co-occurring species were recorded when present. Frequency was calculated as the number of plots in which a species occurred divided by the total number of plots examined (Bonham 1989; Bullock 1996).

The population at MB (40° 34' 4" N, 74° 5' 30" W), sampled on 6 June 1996, was at a moderately disturbed site and occupied a band ranging from 30 - 90 m from shore. Along each transect, 10 quadrats were spaced at 9-m intervals and transects were at 45, 54, 63, 72, 81, and 90 m from shore. Common co-occurring species included scattered *Ammophila breviligulata* and numerous *Cenchrus tribuloides*.

The SB population, sampled on 17 June 1996, was 3.1 km north of MB (Fig. 1) and on an open, sandy beach mostly devoid of other vegetation. 10 quadrats along each transect were spaced at 9-m intervals and transects were at 23, 32, 41, 50, 59, and 68 m from shore.

The FW population, sampled on 10 July 1997, was 1 km north of SB (Fig. 1) and occupied a rather narrow band (30 - 45 m) along a beach heavily laden with driftwood and human-generated garbage washed onto shore from

lower New York Bay. 10 quadrats along each transect were spaced at 2-m intervals and transects were at 33, 35, 37, 39, 41 and 43 m from shore. Common co-occurring species included *A. breviligulata* and *Spartina patens*.

The GK population, sampled on 25 June 1996, was 4 km south of MB (Fig. 1) and part of the Gateway National Recreation Area, U.S. National Park System (Tanacredi 1987). The *T. purpurea* plants had established a dense population on overturned sands recently disturbed during the construction of nearby beach facilities. Six quadrats along each transect were spaced at 2.5 m intervals and transects were at 58, 62, 66, 70, 74, and 78 m from shore. Co-occurring species included *A. breviligulata* and *C. tribuloides*.

Population biology

The *T. purpurea* populations at MB and FW were selected for further study. At MB, the same quadrats used to survey initial seedling densities to assess colonization potential (see earlier) were sampled every 2-3 weeks during the summer and fall of 1996, beginning 6 June. All *T. purpurea* individuals were counted on each sampling date in 10 quadrats per each transect at 45, 54, 63, 72, 81, and 90 m from shore. To obtain enough plants for survivorship estimation, 10 additional quadrats were established on 12 June at the two distances closest to shoreline where natural density was low (see Fig. 2).

As a non-destructive measure of plant size, total tiller length was recorded. This value represents the sum of the individual lengths from base to tip of all tillers of an individual. 'Mid-season size' on 27 June (plants had only a single tiller then) and 'late-season size' on 20 Aug. were estimated by total tiller length. In addition, the number of tillers was recorded in summer (20 Aug.) and autumn (7 Oct.). A single plant was measured per quadrat (60 quadrats, 10 per distance), but because on some dates there were no remaining plants in a particular quadrat, sample sizes per distance varied from 6 - 10.

At the end of the growing period (7 Oct.), the largest plant, selected to measure the maximum size and reproduction that could be achieved at a specific distance from shore, was collected from each quadrat and returned to the lab. Seeds were extracted from leaf sheaths and counted. After drying for at least 2 days at 60 °C (Bonham 1989), the dry mass of seeds and shoots were obtained.

The population biology of plants at FW was studied in a similar manner in 1997. The 60 quadrats established on 10 July (10 per transect) to assess colonization potential (see procedure described earlier) were used to investigate growth and reproduction at 33, 35, 37, 39, 41, and 43 m from shore. Because of the relatively late time when quadrats were set up, survival was not quantified

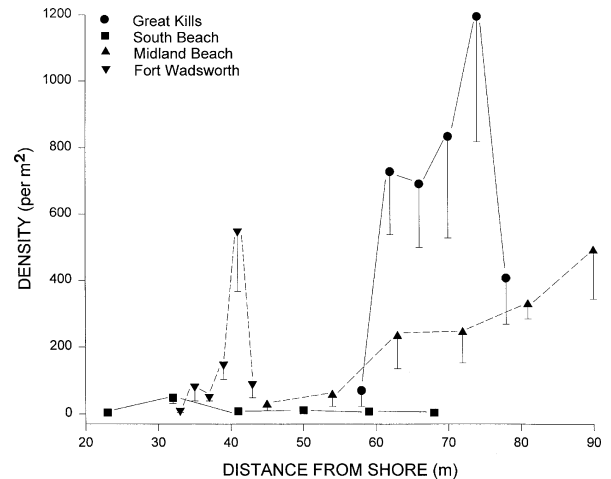


Fig. 2. Density of *Triplasis purpurea* in relation to distance from shore in four populations along the south shore of Staten Island, NY. The first point of each curve corresponds to the primary dune ridge (Bertness 1999) just above the maximum extent of water at high tide. Points show means and vertical lines represent SE. Sampling dates are given in Table 1.

for the earliest part of the growth period; however, final densities were recorded on 12 Sept. for comparison with densities recorded on 10 July. For all measured variables, one plant was randomly selected per quadrat and because all quadrats contained at least some plants on all dates, the sample size per transect was always 10. 'Mid-season size' was estimated by total tiller length on 15 July; the number of tillers was recorded in summer (15 July) and autumn (12 Sept.). As a measure of the maximum growth and reproduction achieved at the six distances from shore, the largest plant per quadrat was collected on 12 Sept. and returned to the lab. The number of seeds produced and dry seed and shoot biomasses were determined, as described earlier for MB plants.

Data analyses

To analyse the colonization potential of *T. purpurea* in relation to distance-from-shore, natural seedling densities in quadrats at FW, MB, and GK were subjected to one-way analysis of variance (ANOVA). Distance from shore was the fixed source of variation. Because the quadrats had been systematically placed, some quadrats contained no *T. purpurea*. To meet ANOVA assumptions, $\log_{10}(\text{density} + 1)$ transformation was necessary prior to analysis (Sokal & Rohlf 1981). This and subsequent analyses were performed using SAS, Version 6.08 (SAS Institute, Cary, North Carolina, USA). When *F*-ratios were significant, the Scheffé test was used to distinguish means (Day & Quinn 1989). Because of very low densities (0 - 13 per quadrat, many quadrats

with no plants) at SB (Fig. 2), density data for this population were not analysed.

Failure-time analyses were used to compare survivorship at six distances from shore at MB (Muenchow 1986; Fox 1993). PROC LIFETEST of SAS was employed, with distances as the STRATA. Life table survival estimates and standard errors were plotted as survivorship curves. Both Wilcoxon and log-rank statistics were output as tests of homogeneity of the survivorship curves over strata; however, because they gave similar results (not unusual; see Pyke & Thompson 1986), only Wilcoxon statistics are reported. Individual survivorship curves were subjected to *post hoc* pairwise comparison using the covariance matrix for the Wilcoxon statistics (details in Fox 1993).

Because censuses were only conducted on two dates (10 July, 12 Sept.) at FW, only one survivorship value is available per distance. Hence, a row by column test of independence was conducted using the *G*-test (Sokal & Rohlf 1981) to determine whether or not proportionate survival between the two dates depended on distance from shore.

The primary reason for collecting plants from MB and FW was to compare growth and reproduction across distances (not to compare populations). Moreover, data were collected on different dates and years in the two populations. Thus, data from MB and FW were analysed, and are presented, separately. Because density changes greatly with distance from shore at both MB and FW (Fig. 2), analysis of covariance (ANCOVA) was appropriate for the size and reproduction variables (Underwood 1997). The covariate, which was not always significant for every variable, was initial density. The fixed factor of interest was distance-from-shore. Type III sum of squares were used in all ANCOVAs (PROC GLM in SAS). Least square means (adjusted for the covariate) were generated (LSMEANS in SAS) and multiple comparisons of the means were computed (option PDIFF in SAS) (Dowdy & Wearden 1991). \log_{10} transformations of total tiller length, seed number, seed mass and shoot mass were sometimes necessary to meet normality assumptions and to deal with heterogeneity of variances (Dowdy & Wearden 1991; Underwood 1997). Means of \log_{10} -transformed variables were back-transformed for reporting (Sokal & Rohlf 1981). Tiller numbers are 'count data' and thus, were square-root transformed prior to analysis (Sokal & Rohlf 1981; Underwood 1997).

Results

Colonization potential

In three of the four populations, *T. purpurea* was the most frequently occurring plant, occurring in at least 75% of all quadrats (Table 1). At SB, where vegetation was sparse, frequency was only 28% and the mean density (over all distances) was only 14 plants/m². In contrast, early-season densities were extremely high at Great Kills, with a maximum of 1195 plants/m² at 74 m and a mean density (over all distances) of 655 plants/m². Although there were only six quadrats per distance and great variation among quadrats at GK (Fig. 2), density was significantly positively related to distance-from-shore ($F = 2.66$, $df = 5$, $P = 0.04$).

The population at Fort Wadsworth occupied a relatively narrow beach, but density showed a highly significant increase with distance ($F = 8.80$, $df = 5$, $P < 0.0001$). The Scheffé test revealed that this was entirely due to the markedly higher density at 41 m from shore (Fig. 2). Beyond 41 m, density became low again and was similar to the densities found closer to shore.

The population at Midland Beach showed a gradual increase in density with increasing distance from shore ($F = 5.36$, $df = 5$, $P = 0.0004$). The Scheffé test indicated that densities at the two farthest distances (81 and 90 m) were both significantly greater than densities at the two closest distances (45 and 54 m) from shore (Fig. 2).

Although *T. purpurea* is not exclusively coastal (Hitchcock 1950), records of associated species indicate that it can occur as close to shore (20 - 30 m) as other coastal species on Staten Island (Table 1), including the common seaside plants *Salsola kali* and *Cakile edentula*.

Plant species associated with *T. purpurea*

At GK and MB, *Cenchrus tribuloides*, a native annual grass, and *Bromus japonicus*, an introduced, weedy annual grass (Hitchcock 1950), were the most frequently

Table 1. Characteristics of four *Triplasis purpurea* populations along the shore of Staten Island, NY. Mean density is the grand mean over all six distances from shore. Maximum density is the highest density found at any distance from shore (see Fig. 2). Closest distance refers to the shoreline.

	Great Kills	Beach Midland	South Beach	Fort Wadsworth
Sampling date	25.06.96	06.06.96	17.06.96	10.07.97
No. quadrats	36	60	60	60
Frequency (% of quadrats)	86.1	75.0	28.3	83.3
Mean density (/m ²)	654.6	229.8	14.1	155.2
Maximum density (/m ²)	1195.8	488.9	48.7	548.1
Closest distance (m)	58.0	34.3	23.0	33.0

occurring species in the quadrats and had the highest average densities (Table 2). *Cakile edentula* was also relatively common at these two sites. Scattered clumps of perennials such as *Ammophila breviligulata* were found at all four sites, a *Cyperus* species was found at GK, and *Spartina patens* was relatively abundant at the farthest distances from shore at FW.

The two northernmost beaches, FW and SB (Fig. 1), had plant communities that were relatively depauperate in comparison with MB and GK (Table 2). Most associated plants were only recorded in one or a few quadrats and densities were often less than 1 plant/m².

Population biology

Survivorship from the early summer (6 June) to early autumn (19 Sept.) at MB was significantly heterogeneous over the different distances from shore (Wilcoxon $\chi^2 = 37.39$, $df = 5$, $P < 0.001$; Fig. 3). All curves were Deevey Type I (Deevey 1947), with low mortality throughout most of the summer and high mortality as plants became senescent in early autumn. Pairwise comparisons indicate that survival was significantly higher at 45 m ($P < 0.0001$) compared to other distances. Most other *post hoc* comparisons were not statistically significant, except that survival at 72 m was lower ($P < 0.05$) than that at 45, 54, 63, and 90 m (Fig. 3).

Survivorship was high at FW between mid-summer (10 July) and early autumn (12 Sept.), the only dates for which density data are available. However, survival between these dates depended significantly on distance from shore ($G = 22.96$, $df = 5$, $P < 0.001$). Survivorship was 80.0, 78.2, 85.7, 85.0, 92.9, and 95.3% at 33, 35, 37, 39, 41, and 43 m from shore, respectively.

The number of tillers produced by mid-summer (15 July) was not affected by either density or distance-from-shore at FW and MB, but by autumn, the number of tillers was significantly lower at increasing distances at FW (Table 3; Fig. 4a). However, tiller numbers in

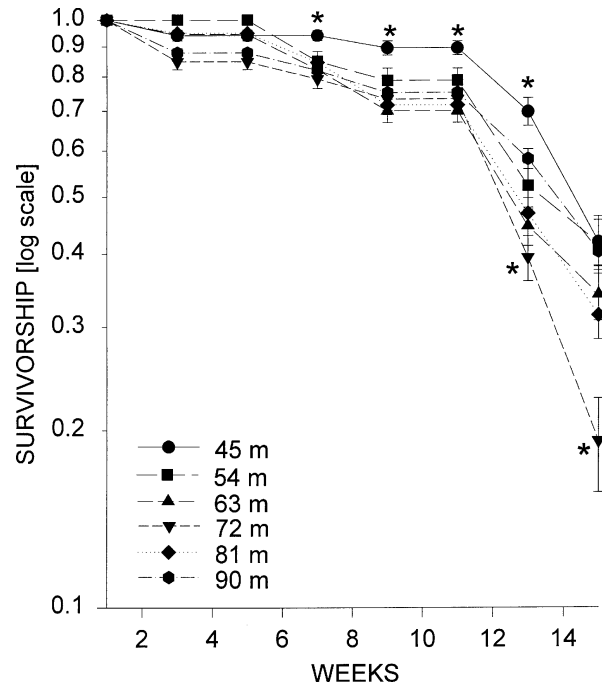


Fig. 3. Survivorship curves of *Triplasis purpurea* in quadrats at different distances from the shore of Midland Beach, Staten Island, NY during 1996. The starting point is 6 June; the final point is 19 Sept. An asterisk next to a symbol indicates that the curve at that distance is significantly different ($P < 0.05$) from three or more of the other curves.

autumn did not show a clear relationship to distance at MB (Table 3; Fig. 4b).

Mid-season size was lowest at 63 m at MB where mean (\pm SE) summed tiller length (adjusted for density) was 1.7 ± 0.4 cm; at 45 m, size was 3.5 ± 0.4 cm. At FW, there was a general decline in size with increasing distance from 15.2 ± 2.5 cm at 33 m to 7.6 ± 2.5 cm at 43 m, but this effect was not significant after adjusting for density (Table 3). Late-season size at MB exhibited a

Table 2. Density (per m²) and frequency (% of quadrats) of species associated with four *Triplasis purpurea* populations along the shore of Staten Island, NY. Species are ordered in the approximate order of their occurrence at the sites. NIQ = not in quadrats (but may be present at the site).

Associated species	Great Kills		Midland Beach		South Beach		Fort Wadsworth	
	Density	Freq.	Density	Freq.	Density	Freq.	Density	Freq.
<i>Cenchrus tribuloides</i>	18.5	50.0	27.3	41.7	NIQ	NIQ	<1.0	1.7
<i>Bromus japonicus</i>	23.8	41.7	16.2	13.3	NIQ	NIQ	NIQ	NIQ
<i>Cakile edentula</i>	1.8	11.1	6.5	13.3	NIQ	NIQ	<1.0	1.7
<i>Cyperus spec.</i>	14.1	25.0	NIQ	NIQ	NIQ	NIQ	NIQ	NIQ
<i>Ammophila breviligulata</i>	2.3	5.6	4.8	11.7	1.1	1.7	<1.0	1.7
<i>Spartina patens</i>	NIQ	NIQ	NIQ	NIQ	NIQ	NIQ	3.5	10.0
<i>Solidago sempervirens</i>	<1.0	8.3	<1.0	1.7	NIQ	NIQ	NIQ	NIQ
<i>Salsola kali</i>	NIQ	NIQ	NIQ	NIQ	<1.0	3.3	<1.0	1.7
<i>Artemisia vulgaris</i>	NIQ	NIQ	<1.0	3.3	NIQ	NIQ	NIQ	NIQ

Table 3. ANCOVA results for variables recorded on *Triplasis purpurea* at various distances from shore at Fort Wadsworth and Midland Beach, Staten Island, NY. The covariate was initial density.

Source of variation	Fort Wadsworth				Midland Beach			
	df	MS	F	P	df	MS	F	P
Summer tiller number								
Covariate	1	0.24	1.78	0.19	1	1.18	3.16	0.08
Distance	5	0.24	1.77	0.14	5	0.58	1.55	0.20
Error	53	0.13			38	0.37		
Autumn tiller number								
Covariate	1	0.98	2.35	0.13	1	0.45	1.09	0.30
Distance	5	1.30	3.11	0.02	5	0.66	1.60	0.19
Error	53	0.42			34	0.42		
Mid-season size*								
Covariate	1	6.28	0.10	0.75	1	0.89	0.01	0.92
Distance	5	85.06	1.41	0.24	5	366.41	3.68	<0.01
Error	53	60.51			38	99.49		
Seed number								
Covariate	1	0.91	6.67	<0.01	1	1348.53	0.96	0.33
Distance	5	0.61	4.46	<0.01	5	4119.64	2.92	0.03
Error	53	0.14			34	1409.53		
Total seed mass								
Covariate	1	1.27	7.55	<0.01	1	2761.32	1.30	0.26
Distance	5	0.62	3.70	<0.01	5	6834.11	3.21	0.02
Error	53	0.17			34	2128.90		
Shoot mass								
Covariate	1	0.63	8.11	<0.01	1	6.20 × 10 ⁴	1.58	0.22
Distance	5	0.28	3.67	<0.01	5	9.52 × 10 ⁴	2.42	0.06
Error	53	0.08			34	3.93 × 10 ⁴		

*Total tiller lengths on 15 July 1997 at Fort Wadsworth and 27 June 1996 at Midland Beach.

significant decline with distance ($F = 3.20$, $df = 5$, $P = 0.02$), from 73.2 ± 10.8 cm ($x \pm SE$) at 45 m to 16.3 ± 12.2 cm at 72 m.

At the end of the growing season, the number of seeds produced, and total seed and shoot dry mass were significantly affected by both initial density and distance at FW (Table 3). All three variables exhibited a reduction with increasing distance from shore (Fig. 5a). From 33 to 43 m, dry shoot mass per plant decreased from 896.4 ± 349.5 mg to 411.1 ± 125.9 mg. Although significant, regression of the \log_{10} number of seeds on density revealed that density explained only 21% of the variance in the number of seeds produced ($r^2 = 0.2060$, $P < 0.01$, $n = 60$).

At MB, the number of seeds produced, and total seed and shoot dry mass declined significantly with increasing distance from shore, but there was no detectable effect of density (Table 3; Fig. 5b). Dry shoot mass per plant was 492.4 ± 76.7 mg closest to shore (45 m), but only ranged from 146.9 ± 89.0 mg to 205.6 ± 68.9 mg further back from shore (72 - 90 m).

Maximum seed rain potential per unit area was estimated by multiplying the mean density at the end of the growing season by the mean number of seeds per plant. At FW, potential seed rain ranged from $5382/m^2$ at 33m to $29\,572/m^2$ at 41 m where densities were very high (Fig. 2). At MB where mean seed production per plant was lower (Fig. 5), potential seed rain ranged from $7079/m^2$ at 45 m to $1340/m^2$ at 72 m.

Discussion

Colonization potential and the beach plant community

Clearly, *Triplasis purpurea* has the ability to colonize coastal beaches along the south shore of Staten Island and maintain relatively dense populations in areas that are lacking other forms of plant cover. Duncan & Duncan (1987) remarked that *T. purpurea* primarily occurred on "dunes, especially in places devoid of other plants or nearly so." Stalter (1993) also noted that it was "typical" on "open primary dunes" in the southeastern United States. The high densities maintained by this native psammophyte, in conjunction with high survival, prolific seed production, and moderate tolerance of partial sand burial and salt spray (Cheplick & Grandstaff 1997; Cheplick & Demetri 1999), may make it suitable for the development and management of Atlantic coastal plant communities.

On the urban beach where human traffic is common, annual plants like *T. purpurea* and *Cenchrus tribuloides* (Table 2) can dominate the 'pioneer zone' and initiate the earliest stages of succession (Woodhouse 1982; Watkinson & Davy 1985; Bonanno et al. 1998). Careful conservation of such pioneer coastal areas may help preserve the rather specialized niches of the native annual plants found there. Fundamental concerns over the conservation of natural communities have become increasingly relevant in light of the continued worldwide urbanization and degradation of coastal ecosystems

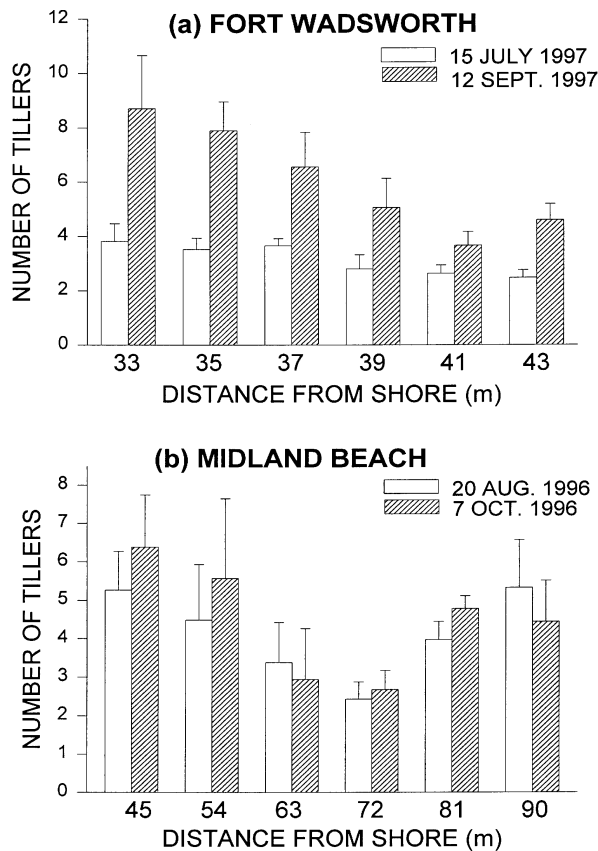


Fig. 4. Mean number of tillers per plant on summer and autumn sampling dates at (a) Fort Wadsworth and (b) Midland Beach, Staten Island, NY, in relation to distance from shore. Bars show means + SE. Note differences in scale of Y-axes between (a) and (b).

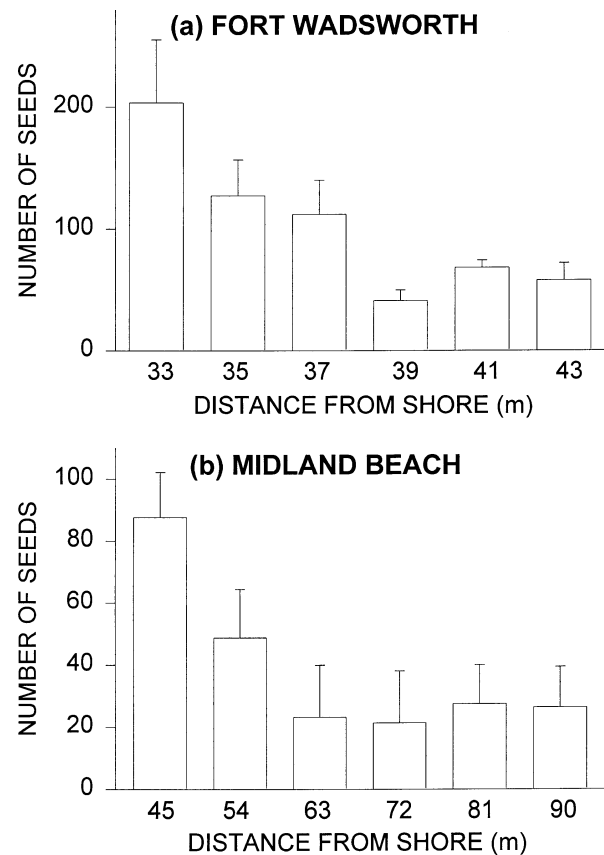


Fig. 5. The mean number of seeds matured per plant at (a) Fort Wadsworth and (b) Midland Beach, Staten Island, NY, in relation to distance from shore. Bars show means + SE. Note differences in scale of Y-axes between (a) and (b).

(Davis 1956; Ozturk 1999). Although it is unclear how the urban environment *per se* specifically affects *T. purpurea* and other native species, the restoration and management of urban coastal ecosystems generally focuses on the improvement of productivity and biodiversity (Tanacredi 1987; Cook & Tanacredi 1990; Stalter et al. 1996). Annual plants, including invasive species, can add to the biodiversity of the coastal vegetation (Castillo & Moreno-Casasola 1996) and should also improve the productivity of the pioneer zone where perennial cover is minimal.

In accordance with the hypothesis that *T. purpurea* would reach maximum densities on parts of the beach farthest from shore, densities of *T. purpurea* increased with distance from shore in most populations on Staten Island (on the different dates when they were sampled; Table 1). However, as one proceeds away from the shore, eventually a point is reached where the intrusion of established perennials prevents the establishment and maintenance of dense stands of annuals. Indeed, this is the reason for the drastic reduction in *T. purpurea*

density at the farthest distances from shore at Great Kills and Fort Wadsworth (Fig. 2). For example, in 10 quadrats at 43 m in the FW population, the density of shoots of the perennial grass *Spartina patens* was $21.2 \pm 8.3/m^2$. Although *S. patens* did not occur closer than 40 m and therefore its frequency and mean density on the entire beach was low (Table 2), at distances greater than 43 m it formed a solid cover together with other perennials such as *Panicum virgatum* (Cheplick pers. obs.). In such perennial-dominated areas further back from shore, it is likely that the low availability of suitable microsites limits seedling recruitment (Eriksson & Ehrlen 1992) of dune annuals (Watkinson 1990).

Although many perennials show the greatest abundances further back from the shore where *T. purpurea* becomes uncommon, the beach community contains scattered clumps of *Ammophila breviligulata* and *Solidago sempervirens* (Table 2) that could be potential competitors at some sites. However, more commonly *T. purpurea* is likely to compete with annual species. For example, at Midland Beach, the native annual grass

Cenchrus tribuloides was the most abundant associated species (Table 2) and Cheplick & Wickstrom (1999) demonstrated that this species can significantly reduce the growth and reproduction of *T. purpurea*. Introduced annuals such as *Bromus japonicus* (Table 2) and *Mollugo verticillata* (Cheplick pers. obs.) can be common on some beaches and might also affect *T. purpurea*, but these weeds do not occur close to shore. Despite moderate human traffic in the urban environment and the continually disturbed nature of the beach habitat (Watkinson et al. 1979; Woodhouse 1982; Carlson & Godfrey 1989), weedy colonizers were not common close to the Staten Island shore. This may be because inland ruderals, although adapted to disturbance, are unable to tolerate the stressful coastal environment; however, in some Atlantic coastal areas, ruderals contribute to the richness of sand dune plant communities (Castillo & Moreno-Casasola 1996).

Population biology

The pattern of survivorship shown by *T. purpurea* shows a Deevey Type I curve (Deevey 1947), a result that agrees with other studies of demography in coastal annuals (Mack 1976; Watkinson & Harper 1978; Jefferies et al. 1981; Symonides 1988). However, for any one annual species, demography can vary greatly in time and space (Keddy 1981; Mack & Pyke 1983; Symonides 1988; Watkinson 1978). At MB, there was a tendency for *T. purpurea* to show the greatest survival at the closest distances to shore (Fig. 3). It is possible that the relatively low levels of mid- to late season mortality experienced by *T. purpurea* populations in some habitats may not be critically important to between-year dynamics. This is because of natural mortality near the end of the growing season following reproduction and completion of the annual's life cycle (Cheplick 1996a). Indeed, the estimates of potential seed rain are underestimates, because they were based on the density of living plants at the end of the season, by which time a fairly large proportion of dead individuals had probably already set some seed. Thus, if the Type I curve is typical for this species, most individuals in a population will mature seeds regardless of their distance from the shore.

In contrast to survivorship, growth and seed production showed distinct trends in relation to distance-from-shore but they were opposite to the original hypothesis that these parameters would be greatest at the farthest distances. Although mid-season size, as assessed by tiller numbers and lengths, did not always show a significant pattern, by the end of the growing season, plant dry mass and seed production both were significantly lower at increasing distances from shore at MB and FW (Table 3; Fig. 5). Moreover, the ANCOVAs revealed

that this pattern was not exclusively due to simple changes in density. Clearly, there are other environmental factors beside intraspecific density that affect growth and reproductive fitness in this species.

Abiotic factors that vary spatially in coastal ecosystems include airborne salt spray, sand deposition, and soil nutrients and moisture (Oosting & Billings 1942; Boyce 1954; van der Valk 1974; Barbour et al. 1985; Hesp 1991). Glasshouse experiments with *T. purpurea* have shown that sand deposition stimulates growth and reproduction, but sea-water sprays primarily have detrimental effects (Cheplick & Grandstaff 1997; Cheplick & Demetri 1999). However, measured levels of salt deposited onto shoots at MB were relatively low compared to other coastal systems (Cheplick & Demetri 1999) and *T. purpurea* showed good tolerance of low to moderate levels of sea-water sprays. Thus, some of the improved vigor recorded nearest to shore may be due to increased deposition of fresh sand and the resulting influence this has on the physical environment.

In an exhaustive review of the effects of sand burial on coastal plants, Maun (1998) noted that burial increases the amount of nutrients and total soil volume into which roots can expand. An earlier glasshouse study revealed that *T. purpurea* shows much-improved tiller and seed production with increased soil nutrients in the form of mineral fertilizer (Cheplick 1996a). Although other factors could be involved (see Maun 1994, 1998 for discussion), sand accretion and the environmental changes that accompany it probably play a role in the promotion of purple sandgrass vigour along coastlines. In this regard, Stalter (21 June 1999, pers. comm.) has commented that, in the southeastern US, this species tends to inhabit areas of consistent dune accretion, but not areas where levels of salt sprays are normally very high.

Intraspecific density explained a small, but significant, proportion of the decline in seed production and shoot and seed dry mass in relation to increasing distance-from-shore at FW, but not at MB, possibly because fewer quadrats were available for analysis (Table 2). In the sand dune annual *Cakile edentula*, Keddy (1981) reported that at the seaward end of an environmental gradient, plants were large with a high density-independent reproductive output, but increased density and shortages of nitrogen at the landward end inhibited reproduction and reduced survivorship. Other examples exist of density-dependent reproduction in coastal annuals (Watkinson & Harper 1978; Jefferies et al. 1981). Clearly, both density-dependent and density-independent factors are likely to impact annual populations, and their relative importance undoubtedly varies in space and time, as found here for purple sandgrass.

Conclusions

In his nine-year study of the dune annual *Vulpia fasciculata*, Watkinson (1990) reported that its decline in abundance was “associated with a decrease in the local movement of surface-blown sand.” On sandy coasts, annuals like *Triplasis purpurea* are generally associated with the strandline, an area subject to frequent disturbance at high tides and during storms (Watkinson & Davy 1985; Hesp 1991; Maun 1998). Indeed, most annuals appear to have evolved in open, sunny habitats that “either experience or are created by frequent disturbances” (Bazzaz & Morse 1991). Because colonizing habitats consisting of freshly deposited sand are continuously available in most dune systems, the earliest stages of ecological succession are consistently represented (Watkinson et al. 1979) and annuals are a significant component of the pioneer community.

For conservation purposes, the maintenance of vigorous *T. purpurea* populations on coastal beaches is likely to depend on substrate disturbance, both natural (by sand movement) and human-induced. Herbarium specimens of purple sandgrass at the Staten Island Institute of Arts and Sciences (SIAS) indicate that the species was present on the south shore of Staten Island in the 1870s (Edward Johnson, SIAS, pers. comm.). The density, vigor, and reproduction of the populations examined here illustrate how this native species (and other coastal annuals like *Cenchrus tribuloides*) can contribute to the long-term diversity and productivity of native species in coastal, urban natural areas, a desirable outcome for park resource managers (Tanacredi 1987; Cook & Tanacredi 1990; Stalter et al. 1996). By colonizing newly-deposited and continually shifting sands, *T. purpurea* also contributes to the earliest stages of ecological succession along disturbed beaches.

Acknowledgements. We thank the Department of Parks & Recreation, City of New York, and the Division of Natural Resources, National Park Service at Gateway National Recreation Area for permission to conduct research at Midland Beach and Fort Wadsworth, respectively. Gordon A. Fox kindly provided details on performing failure-time analyses using SAS; Luis A. Hernandez provided valuable information on the soils found at the field sites; and Richard Stalter and three anonymous reviewers provided valuable comments on earlier versions of the manuscript. The research was supported by Grant 6 - 67182 from the PSC-CUNY Research Award Program to GPC and an Undergraduate Summer Research Fellowship from the Division of Science and Technology, College of Staten Island-CUNY, to H.D.

References

- Barbour, M.G., de Jong, T.M. & Pavlik, B.M. 1985. Marine beach and dune plant communities. In: Chabot, B.F. & Mooney, H.A. (eds.) *Physiological ecology of North American plant communities*, pp. 296-322. Chapman & Hall, New York, NY.
- Bazzaz, F.A. & Morse, S.R. 1991. Annual plants: potential responses to multiple stresses. In: Mooney, H.A., Winner, W.E. & Pell, E.J. (eds.) *Responses of plants to multiple stresses*, pp. 283-305. Academic Press, New York, NY.
- Bertness, M.D. 1999. *The ecology of Atlantic shorelines*. Sinauer Associates, Inc., Sunderland, MA.
- Bonanno, S.E., Leopold, D.J. & Hilaire, L.R. 1998. Vegetation of a freshwater dune barrier under high and low recreational uses. *J. Torrey Bot. Soc.* 125: 40-50.
- Bonham, C.D. 1989. *Measurements for terrestrial vegetation*. John Wiley & Sons, New York, NY.
- Boyce, S.G. 1954. The salt spray community. *Ecol. Monogr.* 24: 29-67.
- Bullock, J. 1996. Plants. In: Sutherland, W.J. (ed.) *Ecological census techniques: a handbook*, pp. 111-138. Cambridge University Press, Cambridge.
- Burden, R.F. & Randerson, P.F. 1972. Quantitative studies of the effects of human trampling on vegetation as an aid to the management of semi-natural areas. *J. Appl. Ecol.* 9: 439-457.
- Carlson, L.H. & Godfrey, P.J. 1989. Human impact management in a coastal recreation and natural area. *Biol. Conserv.* 49: 141-156.
- Castillo, S.A. & Moreno-Casasola, P. 1996. Coastal sand dune vegetation: an extreme case of species invasion. *J. Coastal Conserv.* 2: 13-22.
- Chase, A. 1918. Axillary cleistogenes in some American grasses. *Am. J. Bot.* 5: 254-258.
- Cheplick, G.P. 1996a. Cleistogamy and seed heteromorphism in *Triplasis purpurea* (Poaceae). *Bull. Torrey Bot. Club* 123: 25-33.
- Cheplick, G.P. 1996b. Do seed germination patterns in cleistogamous annual grasses reduce the risk of sibling competition? *J. Ecol.* 84: 247-255.
- Cheplick, G.P. 1998. Seed dispersal and seedling establishment in grass populations. In: Cheplick, G.P. (ed.) *Population biology of grasses*, pp. 84-105. Cambridge University Press, Cambridge.
- Cheplick, G.P. & Demetri, H. 1999. Impact of saltwater spray and sand deposition on the coastal annual *Triplasis purpurea* (Poaceae). *Am. J. Bot.* 86: 703-710.
- Cheplick, G.P. & Grandstaff, K. 1997. Effects of sand burial on purple sandgrass (*Triplasis purpurea*): the significance of seed heteromorphism. *Plant Ecol.* 133: 79-89.
- Cheplick, G.P. & Wickstrom, V.M. 1999. Assessing the potential for competition on a coastal beach and the significance of variable seed mass in *Triplasis purpurea*. *J. Torrey Bot. Soc.* 126: 296-306.
- Cook, R.P. & Tanacredi, J.T. 1990. Management strategies for increasing habitat and species diversity in an urban national park. In: *Ecosystem management: rare species and significant habitats*, pp. 248-250. New York State Museum Bull. 471.

- Davis, J.H. 1956. Influences of man upon coast lines. In: Thomas, W.L., Sauer, C.O., Bates, M. & Mumford, L. (eds.) *Man's role in changing the face of the earth*, pp. 504-521. University of Chicago Press, Chicago, IL.
- Day, R.W. & Quinn, G.P. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59: 433-463.
- Deevey, E.S. 1947. Life tables for natural populations of animals. *Quart. Rev. Biol.* 22: 283-314.
- Dowdy, S. & Wearden, S. 1991. *Statistics for research*. John Wiley & Sons, New York, NY.
- Duncan, W.H. & Duncan, M.B. 1987. *The Smithsonian guide to seaside plants of the Gulf and Atlantic coasts from Louisiana to Massachusetts, exclusive of lower Peninsular Florida*. Smithsonian Institution Press, Washington, DC.
- Eriksson, E. & Ehrlén, J. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia (Berl.)* 91: 360-364.
- Fox, G.A. 1993. Failure-time analysis: emergence, flowering, survivorship, and other waiting times. In: Scheiner, S.M. & Gurevitch, J. (eds.) *Design and analysis of ecological experiments*, pp. 253-289. Chapman & Hall, New York, NY.
- Hesp, P.A. 1991. Ecological processes and plant adaptations on coastal dunes. *J. Arid. Environ.* 21: 165-191.
- Hitchcock, A.S. 1950. *Manual of the grasses of the United States*, 2nd ed. (revised by A. Chase). United States Department of Agriculture Miscellaneous Publication 200, Washington, DC.
- Hosier, P.E. & Eaton, T.E. 1980. The impact of vehicles on dune and grassland vegetation on a southeastern North Carolina barrier beach. *J. Appl. Ecol.* 17: 173-182.
- Jefferies, R.L., Davy, A.J. & Rudmik, T. 1981. Population biology of the salt marsh annual *Salicornia europaea* agg. *J. Ecol.* 69: 17-31.
- Keddy, P.A. 1981. Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *J. Ecol.* 69: 615-630.
- Liddle, M.J. & Greig-Smith, P. 1975. A survey of tracks and paths in a sand dune ecosystem. II. Vegetation. *J. Appl. Ecol.* 12: 909-930.
- Mack, R.N. 1976. Survivorship of *Cerastium atrovirens* at Aberffraw, Anglesey. *J. Ecol.* 64: 309-312.
- Mack, R.N. & Pyke, D.A. 1983. The demography of *Bromus tectorum*: variation in space and time. *J. Ecol.* 71: 69-93.
- Maun, M.A. 1994. Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio* 111: 59-70.
- Maun, M.A. 1998. Adaptations of plants to burial in coastal sand dunes. *Can. J. Bot.* 76: 713-738.
- McDonnell, M.J. 1981. Trampling effects on coastal dune vegetation in the Parker River National Wildlife Refuge, Massachusetts, USA. *Biol. Conserv.* 21: 289-301.
- Muenchow, G. 1986. Ecological use of failure time analysis. *Ecology* 67: 246-250.
- Oosting, H.J. & Billings, W.D. 1942. Factors effecting [sic] vegetational zonation on coastal dunes. *Ecology* 23: 131-142.
- Ozturk, M. 1999. Urban ecology and land degradation. In: Farina, A. (ed.) *Perspectives in ecology*, pp. 115-120. Backhuys Publishers, Leiden.
- Pyke, D.A. & Thompson, J.N. 1986. Statistical analysis of survival and removal rate experiments. *Ecology* 67: 240-245.
- Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. W.H. Freeman, San Francisco, CA.
- Stalter, R. 1993. Dry coastal ecosystems of the eastern United States of America. In: van der Maarel, E. (ed.) *Dry Coastal Ecosystems: Africa, America, Asia and Oceania*, pp. 317-340. Elsevier, Amsterdam.
- Stalter, R., Byer, M.D. & Tanacredi, J.T. 1996. Rare and endangered plants at Gateway National Recreation Area: a case for protection of urban natural areas. *Landscape Urban Plan.* 35: 41-51.
- Symonides, E. 1988. Population dynamics of annual plants. In: Davy, A.J., Hutchings, M.J. & Watkinson, A.R. (eds.) *Plant population ecology*, pp. 221-248. Blackwell Scientific, Oxford.
- Tanacredi, J.T. 1983. Coastal zone management practices at an urban national park. *Environ. Manage.* 7: 143-150.
- Tanacredi, J.T. 1987. Natural resource management policy constraints and trade-offs in an urban national recreation area. In: Adams, L.W. & Leedy, D.L. (eds.) *Integrating man and nature in the metropolitan environment*, pp. 221-227. National Institute for Urban Wildlife, Columbia, MD.
- Underwood, A.J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge.
- van der Valk, A.G. 1974. Environmental factors controlling the distribution of forbs on coastal foredunes in Cape Hatteras National Seashore. *Can. J. Bot.* 52: 1057-1073.
- Watkinson, A.R. 1990. The population dynamics of *Vulpia fasciculata*: a nine-year study. *J. Ecol.* 78: 196-209.
- Watkinson, A.R. & Davy, A.J. 1985. Population biology of salt marsh and sand dune annuals. *Vegetatio* 62: 487-497.
- Watkinson, A.R. & Harper, J.L. 1978. The demography of a sand dune annual: *Vulpia fasciculata*. I. The natural regulation of populations. *J. Ecol.* 66: 15-33.
- Watkinson, A.R., Huiskes, A.H.L. & Noble, J.C. 1979. The demography of sand dune species with contrasting life cycles. In: Jefferies, R.L. & Davy, A.J. (eds.) *Ecological processes in coastal environments*, pp. 95-112. Blackwell Scientific, Oxford.
- Woodhouse Jr., W.W. 1982. Coastal sand dunes of the U.S. In: Lewis III, R.R. (ed.) *Creation and restoration of coastal plant communities*, pp. 1-44. CRC Press, Boca Raton, FL.

Received 5 August 1999;

Revision received 26 June 2000;

Accepted 26 June 2000.