

Expansion Patterns and Soil Physicochemical Characterization of Three Louisiana Populations of *Uniola paniculata* (Sea Oats)

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ABSTRACT

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The only three sizeable populations of *Uniola paniculata* (sea oats) on the Louisiana coast west of the Mississippi River delta were studied to determine if these populations were in a state of expansion or deterioration. The populations have become established in areas with a mean water-table depth of 129 cm, which although shallow is sufficiently deep to alleviate any signs of water-logging stress. Soil nutrient concentrations and pH were generally lower inside the populations compared to adjacent unvegetated areas. Despite very low sand accretion within the populations ($<0.1 \text{ m yr}^{-1}$), vegetative lateral expansion (lateral spread) exceeded 1 m yr^{-1} during years with mild weather conditions, whereas years with severe overwash events resulted in a net loss of population area. The mean rate of lateral expansion of the populations over three years was 0.58 m yr^{-1} with the greatest mean migration being to the northwest (away from the eroding coast) at a rate of 0.85 m yr^{-1} . Since seed production rates in these populations are very low, colonization of new sites is extremely improbable and any population expansion is believed to be solely the result of vegetative lateral expansion. The extremely limited distribution of this species along the Louisiana coast is best explained by its reliance on vegetative reproduction, which although at rates comparable to areas where *Uniola* is dominant, is often not sufficient to keep pace with the rate of coastline retreat along the highly erosional, low elevation Louisiana coast.

ADDITIONAL INDEX WORDS: Barrier island, coastal erosion, dune vegetation, vegetative spread, vegetative reproduction.

INTRODUCTION

Uniola paniculata L. (sea oats, hereafter referred to as *Uniola*) is usually the dominant dune grass along the Southeastern Atlantic and Gulf coasts of the United States (WAGNER, 1964; WOODHOUSE *et al.*, 1968). However, the distribution of *Uniola* along the Louisiana coast, particularly west of the Mississippi River delta, is very limited. Although *Uniola* is fairly abundant on the northern Chandeleur Islands east of the delta, only three sizeable populations of *Uniola* have been identified along the Louisiana coast west of the delta, all on the Caminada-Moreau coast (Figure 1). An inspection of herbaria suggests that *Uniola* in Louisiana may have been more common in the past; *Uniola* was collected from Timbalier Island in 1915 (MONTZ, 1981), although it was no longer

present when we initiated this study (it has since been reintroduced on the island; MENDELSSOHN and HESTER, 1988).

Many factors can influence the distribution and zonation of dune plant species. The effects of wind, with the accompanying salt spray (OOSTINGS and BILLINGS, 1942) and sand deposition (MARTIN, 1959), have been recognized separately and jointly (WAGNER, 1964) as important factors in the zonation of dune vegetation. *Uniola* is well adapted to the harshness of the barrier island environment and is often most abundant on the foreslope and crest of foredunes (WAGNER, 1964; WOODHOUSE *et al.*, 1968; VAN DER VALK, 1975; STALTER, 1976; OERTEL and LARSON, 1976). Woodhouse *et al.* (1968) suggest that *Uniola* dominates these exposed areas of the dune habitat because it is adapted to survive extremes of salt spray, evaporation and sand burial, and is thus able to outcompete other plant species.

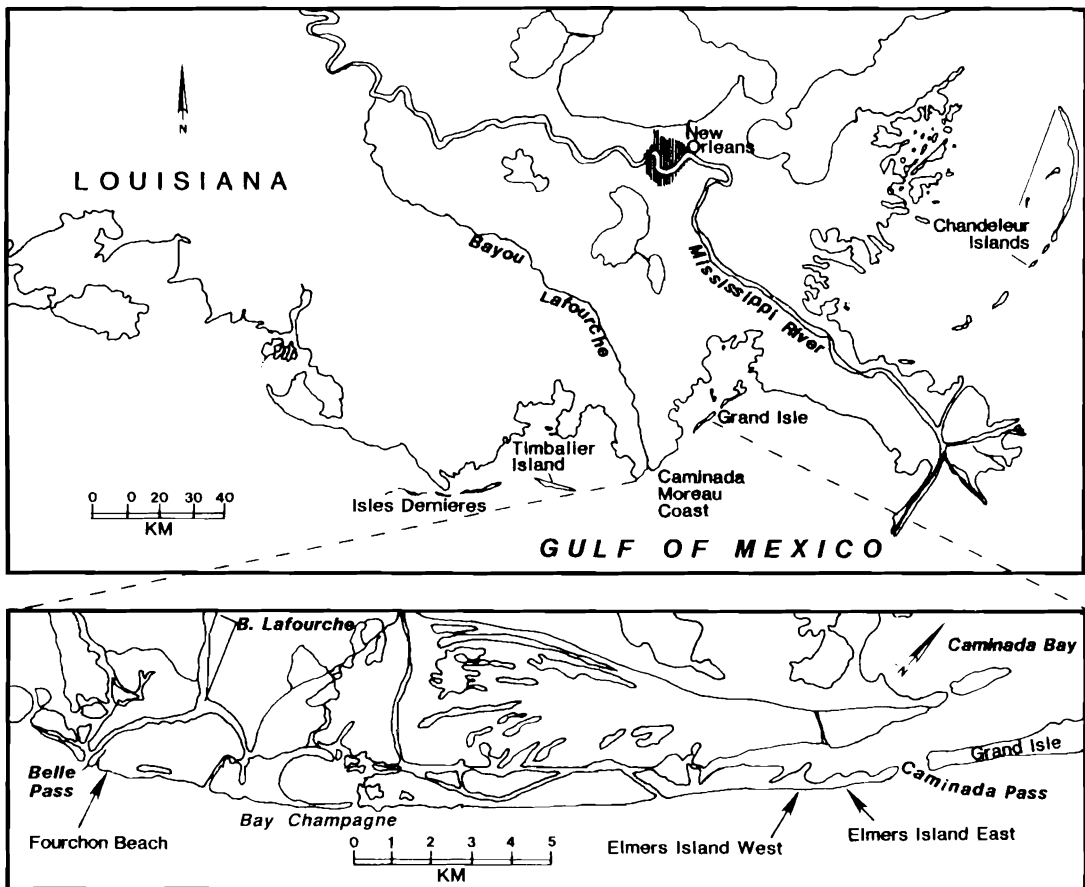


Figure 1. Regional map of the Caminada-Moreau coast indicating the locations of the three extant Louisiana *Uniola paniculata* populations west of the Mississippi River delta.

Seed production, germination, and seedling establishment are further factors that affect a species distribution. Northern populations of *Uniola* have been shown to have a cold treatment requirement to break dormancy, which decreases southward along its range from Virginia into Florida (WOODHOUSE *et al.*, 1968; SENECA, 1972; COLOSI, 1977). Louisiana populations do not exhibit enhanced germination response following cold treatment (HESTER and MENDELSSOHN, 1987). However, seed (caryopsis) production rates of Louisiana *Uniola* are extremely low, ranging from one to three orders of magnitude less than areas where it is dominant (HESTER and MENDELSSOHN, 1987).

Field observations by Wagner (1964) show a

strong association of *Uniola* seedlings with sites of moderate sand accumulation. Sites of extensive sand deposition (>15 cm) may result in seedlings having insufficient endosperm reserves to grow to the new sand surface, whereas areas of no sand burial subject the spikelets to desiccation and possible consumption by birds and small mammals (WAGNER, 1964). *Uniola* seed burial ranging from 5 to 15 cm of sand has been reported as most favorable for successful germination and seedling establishment (WAGNER, 1964; WESTRA and LOOMIS, 1966).

The reported maximum tolerable substrate salinity for *Uniola* seed germination is between 1.0% to 1.5% NaCl (SENECA, 1968), which is slightly lower than *Uniola* seedling substrate

salinity tolerance of 2.0% (SENECA, 1972). *Spartina patens* and *Panicum amarulum* are reported to have slightly higher germination and seedling salinity tolerances than *Uniola*, whereas *Ammophila breviligulata* is less tolerant (SENECA, 1968; 1972).

Louisiana's barrier islands have evolved as a consequence of delta abandonment and degradation of the various delta complexes of the Mississippi River and, thus, are highly erosional, sand-deficient environments characterized by low dune elevations, particularly west of the delta, which generally range from 1-2 m (PENLAND *et al.*, 1988; MONTEFERRANTE *et al.*, 1982). In a controlled study we demonstrated that the vigor of *Uniola* decreases and the plants show signs of stress if grown under the influence of a shallow water-table depth of only 0.3 m, whereas a deeper water-table depth of 0.9–2.7 m alleviates this stress without inducing drought stress (HESTER and MENDELSSOHN, 1989).

This field study was initiated at the same time as our above mentioned research, which addressed hypotheses of low sexual reproductive effort, and stressful effects of shallow water-table depth as possible factors affecting the distribution of *Uniola* in Louisiana. Therefore, this field research complements the other research by addressing the asexual reproductive success of this species, and was designed primarily to determine (1) if the existing populations of *Uniola* that occur west of the delta are in a state of gradual deterioration or expansion, and (2) what abiotic factors appear to be affecting their growth and distribution.

MATERIALS AND METHODS

Study Site

The field investigation was conducted along the Caminada-Moreau coast (Figure 1) where the three populations of *Uniola* are located. The beach orientation, as well as the predominant wind direction, are southeast (NOAA, 1981). Two of the populations are located towards the eastern end of the Caminada-Moreau coast on a spit known locally as Elmers Island (latitude 29° 11' 00" N, longitude 90° 03' 40" W). These two populations on Elmers Island will be referred to as Elmers Island East and Elmers Island West (Figure 1). The westernmost pop-

ulation is located on Fourchon Beach about two hundred meters east of the Belle Pass jetties (latitude 29° 5' 19" N, longitude 90° 13' 14" W) and will be referred to as the Fourchon Beach population (Figure 1).

Overall, the mean linear retreat of the Caminada-Moreau coast has been determined by HARPER (1977) to be 8.0 m yr⁻¹. The main forcing functions of the erosion in this area are a high frequency of tropical storms and cyclones, winter cold-front passages, and high subsidence rates combined with a limited local sediment supply (HARPER, 1977; PENLAND and BOYD, 1981; RITCHIE and PENLAND, 1989). Erosion rates exceed 15 m yr⁻¹ in the central area near Bay Champagne, where there is a divergence of longshore transport carrying eroded sand both to the east towards Elmers Island and towards the west into the Belle Pass jetties (HARPER, 1977; GAGLIANO *et al.*, 1981; PENLAND and BOYD, 1981). As a result, Elmers Island accretes up to 5 m yr⁻¹ along its eastern end (HARPER, 1977). However, the particular section of coast where the two Elmers Island populations are located has an estimated long-term erosion rate of 1 to 5 m yr⁻¹ (PENLAND and BOYD, 1981), and actually ranged from 0.8 to 3.0 m yr⁻¹ during the 1978–1984 period (RITCHIE and PENLAND, 1989). The westward longshore transport into the Belle Pass jetties has resulted in an average of 5.5 m yr⁻¹ of accretion on the eastern side of the jetties from 1969–78 (PENLAND and BOYD, 1981), and accretion of approximately 2.3 m yr⁻¹ from 1978 to 1984 (RITCHIE and PENLAND, 1989).

The unvegetated beach at Elmers Island is 20 to 30 m wide, and slopes upward to a vegetated dune ridge about 1.5 m high (MONTEFERRANTE *et al.*, 1982). In 1981 the Elmers Island East population was in line with a *Panicum amarum* dominated dune ridge. The Elmers Island West population was positioned further inland, about 12 m behind a discontinuous dune ridge in a relict washover fan.

The Elmers Island beach is generally unvegetated. The area immediately gulfward of the dune is sparsely vegetated with *Spartina patens*, *Ipomoea stolonifera*, *L. pes-caprae*, *Sporobolus virginicus*, and *Hydrocotyle bonariensis*. The dune ridge is more densely vegetated with the same taxa along with *Croton puncta-*

tus, *Iva imbricata*, and *Panicum amarum*, which tends to be dominant.

The beach at Fourchon, near Belle Pass, is much wider (about 60 m) due to sand accretion on the eastern side of the jetties. The *Uniola* population in this area is set back in close proximity to the dune ridge, which is 1.5–2.0 m high. The vegetation in this area is similar to that on Elmers Island except that there is more *Ipomoea* spp. and *Croton punctatus*, and less *Spartina patens* and *Panicum amarum*. Both Fourchon Beach and Elmers Island are subject to a high amount of human activity, primarily recreational fisherman who drive vehicles on the beach.

Sampling Schedule

Monthly field measurements were conducted on the three populations of *Uniola* from June through December, 1981, and then bi-monthly from February through June, 1982. These field measurements consisted of monitoring: (1) the sand accretion within each population; (2) the area (size) of each population; (3) the depth to the water table and surface water-table salinity under each population; and (4) soil nutrient and moisture analyses collected in June, July and November 1981. Monitoring of population area was extended to include two more annual measurements in June 1983 and June 1984, and a final measurement in February 1990.

Soil Nutrients, Moisture and pH

Soil samples were collected from two areas inside and two areas outside the geographic boundary of each population. Sampling was done in transects that ran parallel to the beach and through the approximate centers of each population. The two outside sampling areas were located 5–7 m from either edge of the population and the two inside sampling areas were evenly spaced across the width of the population. Samples were collected at surface (0–5 cm), 30 cm, 90 cm, and 150 cm depths.

Samples were analyzed for percentage soil moisture, total inorganic nitrogen ($\text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$), P, K, Ca, Mg, Na, Fe, Mn, and pH. Percentage soil moisture was determined as the percentage of the dry weight after oven drying.

Soil nitrogen was determined by extracting

20.0 g of dry soil with 20.0 ml of 2.0 N KCl. The nitrate-nitrite determination employed EPA method 353.2 (Colorimetric, Automated Cadmium Reduction). Ammonium was determined using EPA method 350.1 (Colorimetric, Automated Phenate) (U.S. EPA, 1979). The nitrate-nitrite and ammonium nitrogen concentrations were combined to yield the total inorganic nitrogen.

Phosphorus was extracted with Bray #2 (0.1 N HCl + 0.03 N NH_4F). Potassium, Na, Ca, and Mg were extracted using a 1.0 N, pH 7.0 ammonium acetate solution. Iron and Mn were extracted with 0.1 N HCl. Concentrations were determined using atomic absorption spectrophotometry.

Water-Table Depth and Salinity

Inside the geographic boundary of each population of *Uniola* two separate sections of 2 m long and 5 cm wide pvc tubing were driven into the sand until they penetrated the water table and were cleared of sand with a soil auger.

Surface water samples were drawn from these wells and conductivity determined using a Lab-Line Lectro Mho-Meter. Monthly precipitation data for the area was obtained from NOAA (1981–1982). The closest southeast station of Galiano, Louisiana was used from June–October 1981 at which time the new Golden Meadow, Louisiana station was used for the remainder of the initial year of study (through June 1982).

Sand Accretion

Within each population nine wooden stakes measuring 2 cm × 4 cm and 50 cm long were established in a cross pattern (lines running parallel and perpendicular to the beach) and then driven into the sand so that 20 cm remained above the sand surface. The heights of the stakes above ground level were recorded during each measuring period and were used as indicators of sand accretion or deflation for the nine different positions within each population. The stakes, per se, did not appear to have an effect on accretion since there was never evidence of increased accretion or deflation around the stakes.

Population area

Area measurements of a population were accomplished by measuring the distance from a stake established in the center of the population to the outer edge. Distance and compass bearing were recorded every meter, or whenever an obvious change in edge contour occurred (typically one measurement every 5–7°). Two types of edges were qualitatively defined as follows: (1) a dense edge where the density of *Uniola* was visually comparable with the density in the central homogenous area of the population (vegetative cover typically 75% to 100%); (2) a sparse edge, which delineated the outermost boundary of the population (vegetative cover typically 10% to 50%).

Data were plotted on polar coordinate graph paper. Area was determined by three replicate tracings with a digital planimeter. Since all three populations approximated a circular area, lateral expansion (lateral spread) was calculated as the change in average outer radius of the population over time. Each population was also partitioned into four polar quadrants: NE (0–90°), SE (90–180°), SW (180–270°), and NW (270–360°), and the area and lateral expansion similarly determined. We believe that this method of estimating rate of lateral expansion based on the area change was a good approach since (1) all area expansions observed in the populations were the result of vegetative tillering away from a population into unvegetated areas; there were no area increases due to seedling establishment, (2) it did not require the remeasurement of exact polar radii, which would have been limited in number, difficult to accurately relocate, and may not have represented a true overall change in the entire edge of the quadrant or population, and (3) agreement between the mean quadrant lateral expansion and the whole population lateral expansion over several initial time periods was high.

The 1990 area measurements required the establishment of a new center stake for each population since the original stakes could no longer be located. As such, only whole population area data are presented for the 1990 measurements since the unknown change in relative positioning of the populations prohibited any comparison of quadrant area change.

Biomass Parameters

In June 1982 three 0.25 m² quadrants were randomly sampled in both the inner (dense) and outer (sparse) areas of each population and stem density counts made prior to clipping the plots at the sand surface. Shoots were classified as live (having any amount of green tissue) or dead, and then dried at 65°C until constant weight was achieved and weighed.

Data Analysis

Analysis of variance (ANOVA; STEELE and TORRIE, 1980) was used to analyze the data and was conducted with S.A.S. (Statistical Analysis System) software (SAS INSTITUTE INC., 1985). The experimental design of the soil nutrient analysis was a split-split plot design of two replicates (COCHRAN and COX, 1957). The whole plots (location effect of soil from inside the populations compared to the soil in the adjacent outside areas) were arranged in a randomized block design that blocked on the three Caminada-Moreau *Uniola* populations. The effect of month was positioned on the first split (sub-plot). The effect of depth was positioned on the second split (sub-sub plot).

Analysis of the biomass parameters from the inner (dense) and outer (sparse) areas of the populations also involved a split-plot design. The split was on the inner and outer areas within each population.

Differences in the rate of lateral expansion between populations, quadrants, and years were analyzed by splitting on quadrants within populations. The 1990 data were not included in this analysis.

Analysis of the sand accretion data involved the use of a response surface model (the axes running parallel and perpendicular to the coast). Population, month, linear, and quadratic effects were tested.

RESULTS

Soil Nutrients and pH

With the exception of N and Mg, there was a tendency for locations inside the populations to be of lower average nutrient concentration and pH than locations outside the populations (Figure 2). This effect of location (across all popu-

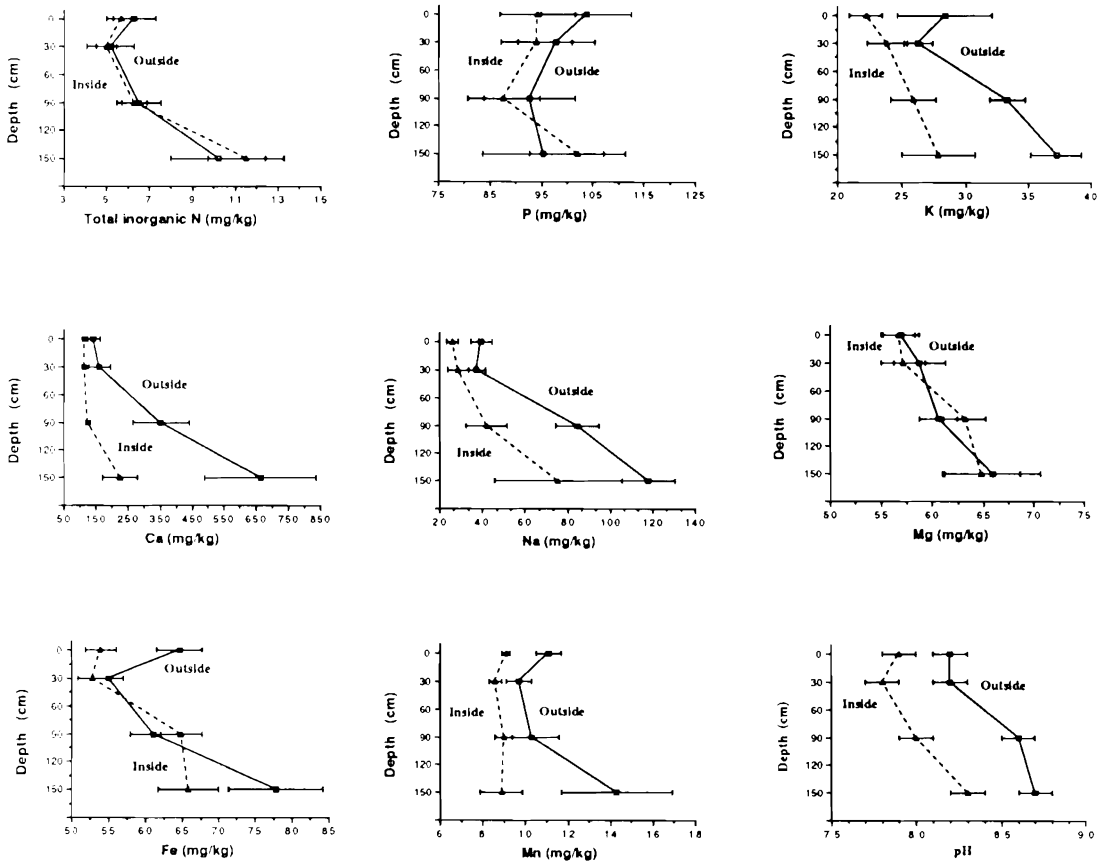


Figure 2. Depth profiles of mean soil N, P, K, Ca, Mg, Na, Fe, Mn (mg kg^{-1} dry soil), and pH from areas inside the three *Uniola paniculata* populations and the adjacent unvegetated areas (bar = standard error; $n = 12$).

lations and months) was significant for pH ($P < .01$), Ca, Na, and Mn ($P < .05$), and approached significance for K ($P = .054$).

The Fourchon Beach site had significantly lower P and Mg ($P < .05$) and significantly higher Fe and Mn ($P < .05$) than the other sites. Site differences in pH were significant at the .051 probability level with the Elmers Island West site averaging slightly higher than the others.

With the exception of P there was a trend of higher nutrient concentration with depth (Figure 2). Some nutrients, Mn, total inorganic N, and Fe in particular, showed a depletion at 30 cm before increasing in concentration with depth, whereas the concentrations of Ca and Mn inside the populations remained relatively constant with depth (Figure 2).

Water-Table Depth

The average depth of the water table under the three populations was 129 cm, with the Elmers Island East population (the most gulfward population) averaging the shallowest water-table depth of 123 cm (Figure 3). The water table was closest to the surface for all populations from February through April (Figure 3). The August water-table depth of 168 cm in the Fourchon Beach population was the deepest recorded for any of the populations. Rainfall above 200 mm month⁻¹ occurred in August 1981, February 1982 and April 1982 (Figure 3).

Water-Table Salinity

The upper surface of the water table under the three populations was generally of very low

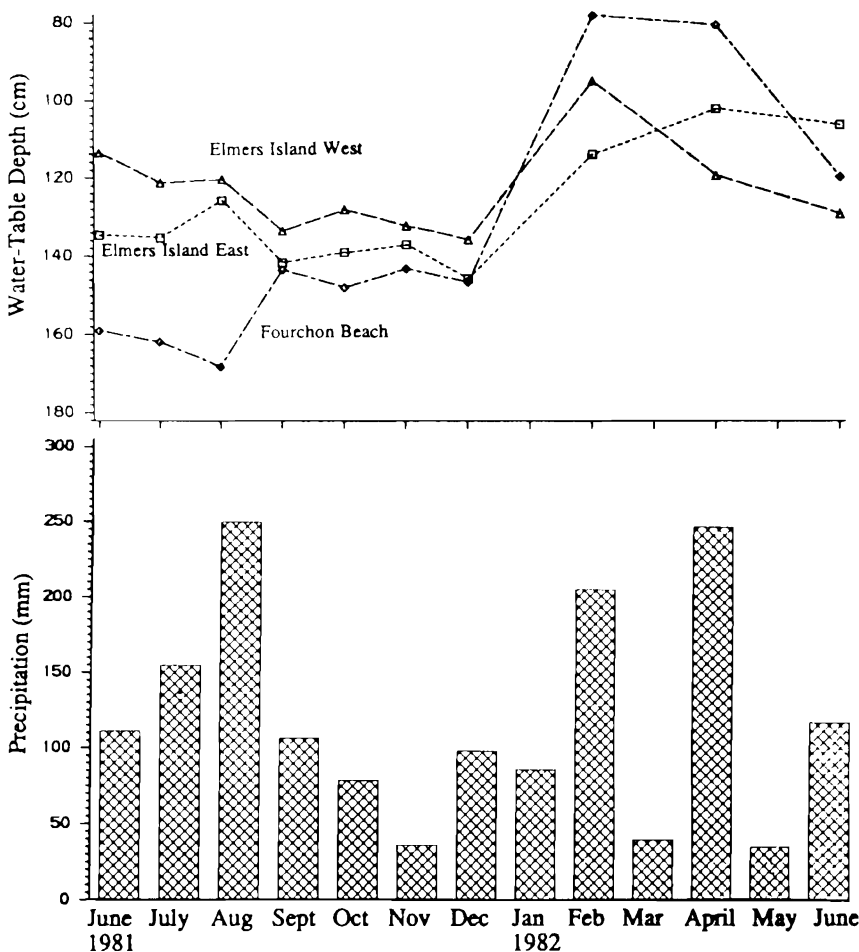


Figure 3. Monthly coastal precipitation and water-table depth under the three *Uniola paniculata* populations (n = 2).

salinity. However, the more gulfward positioning of the Elmers Island East population resulted in the most saline water-table surface (3.5 ppt) and, correspondingly, the greatest conductivity (6.2 mmhos cm⁻¹). The salinity and conductivity of the water-table surface under the Elmers Island West population was 0.4 ppt and 1.0 mmhos cm⁻¹, respectively, which was similar to the Fourchon population (0.5 ppt and 1.1 mmhos cm⁻¹, respectively).

Soil Moisture

Soil moisture data collected within the populations showed essentially no difference

among populations in the upper 30 cm of sand. Soil moisture values were all about 1% at the surface and about 4% at a depth of 30 cm. At the 90 cm depth soil moisture ranged from 4% at Fourchon Beach to 11% at Elmers Island West. At a depth of 150 cm the soil was essentially saturated for the Elmers Island East and West populations (about 23%) with the Fourchon Beach population having a soil moisture of 19%.

Sand Accretion

The three populations accreted a limited amount of sand, averaging only 7.4 cm yr⁻¹ (Table 1). Quadrant averages revealed that the

eastern quadrants (averaged across all populations) had more accretion than the western quadrants and that the accretion at the center of the populations was always low (Table 1).

Results from the response surface analysis of sand accretion showed that there were highly significant differences in sand accretion among populations. In the Elmers Island East population, most of the variation in sand accretion was explained along the NE-SW axis, which displayed a highly significant quadratic effect of less accretion in the center of the population. Higher accretion along the northeastern edge resulted in a significant linear effect along this axis.

In contrast, the Elmers Island West Population had highly significant linear and quadratic components along the NW-SE axis, rather than the NE-SW axis. In this case, the southeastern edge accreted a significantly greater amount of sand than the northwestern edge (Table 1). The effect of month was highly significant.

Similar to the Elmers Island East population, the Fourchon Beach population had a highly significant quadratic effect along the NE-SW axis. Although there was a tendency for higher accretion along the northeastern edge, the linear component of the NE-SW axis was significant only at the .06 probability level (Table 1). In this regard the Fourchon Beach population was unique since no particular edge accreted a significantly greater amount of sand than another.

Population Area and Lateral Expansion

Yearly Changes

The initial year of the study (1981–1982) proved to be an exceptionally good year in

terms of population expansion and resulted in the highest rates of lateral expansion (lateral spread) observed in the study, ranging from a mean population lateral expansion of 0.94 m yr⁻¹ for the Fourchon Beach population to 1.38 m yr⁻¹ for Elmers Island East (Figures 4–5).

The second year (1982–1983) was characterized by one tropical storm, a higher frequency of winter storms, and two severe overwash events (NOAA, 1982–83; *Weatherwise*, 1983). This resulted in highly significant ($P < .01$) lower rates of lateral expansion than either the 1981–1982 or 1983–1984 periods. The Elmers Island East population lost 27.09 m² in area, an average decrease of 0.86 m in lateral extent (Figures 4–5). The Fourchon Beach population lost 2.72 m² in area, which was only a decrease of 0.09 m in lateral extent. The Elmers Island West population managed to still gain 31.58 m² in area, which represented a 0.56 m yr⁻¹ rate of lateral expansion (Figure 4).

The 1983–84 winter was not as severe as the 1982–83 winter in terms of storm events, but was colder than normal with some extended periods of temperatures below freezing (NOAA, 1983–84). Although mean lateral expansion during this year of monitoring was not as high as the initial year, this difference was not statistically significant. All populations increased in area during this period, but the 1984 area of the Elmers Island East population was still less than it had been in 1982 (Figures 4–5).

The 1984–90 time interval was a period of high hurricane and storm activity. During this period a total of seven hurricanes and two tropical storms impacted the Louisiana coast (*Weatherwise*, 1985–90). The 1990 population area measurements showed major changes in population area compared to the previous years. The Fourchon Beach population was the

Table 1. Sand accretion rates of each quadrant within the three Caminada-Moreau *Uniola paniculata* populations (1981–1982; $n = 2$).

Quadrant	Sand Accretion (cm yr ⁻¹)			Mean ($n = 6$)
	Elmers Island East	Elmers Island West	Fourchon Beach	
Northeast (0–90°)	7.1 ± 7.1 ¹	7.1 ± 7.1	19.3 ± 17.3	11.2 ± 5.8
Southeast (90–180°)	4.5 ± 4.5	20.1 ± 15.0	10.7 ± 11.7	11.8 ± 5.8
Southwest (180–270°)	1.6 ± 0.6	2.7 ± 0.5	12.3 ± 0.2	5.5 ± 2.2
Northwest (270–360°)	1.6 ± 1.6	2.5 ± 2.5	9.1 ± 3.0	4.4 ± 1.8
Center Stake ($n = 1$)	1.0	2.5	0.0	1.2 ± 0.7
Population mean ($n = 9$)	3.4 ± 1.6	7.5 ± 3.7	11.4 ± 4.0	7.4 ± 1.9

¹Plus or minus (±) values are standard errors.

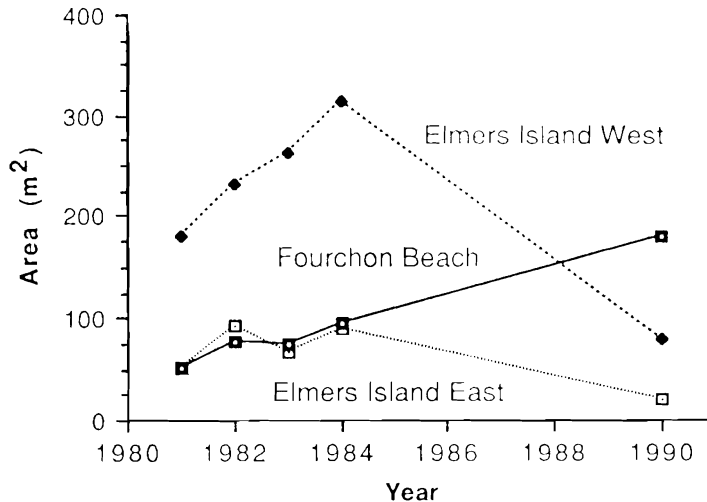


Figure 4. Yearly changes in total population area of each of the three *Uniola paniculata* populations.

only population to increase in area between 1984–90, and became the largest population (Figure 4). Elmers Island West decreased in area and was no longer positioned behind the discontinuous dune ridge, but rather became positioned in line with (and slightly in front of) the smaller dune ridge that remained. Elmers Island East managed to persist in front of the dune ridge with a much decreased area (Figure 4).

Population Differences

There was not a significant difference between populations in lateral expansion (1981–84), although Elmers Island West tended to have the greatest lateral expansion and was the only population not to decrease in size during the 1982–83 year (Figure 4). The interaction of population*year was significant at the .08 probability level, indicating that the populations were responding somewhat differently to the yearly conditions, particularly the 1982–1983 period (Figure 4).

The overall annual rate of lateral expansion (1981–1984 data) averaged across the three populations was 0.58 ± 0.22 m yr⁻¹. Individual mean rates of lateral expansion for each population were 0.44 ± 0.67 m yr⁻¹, 0.81 ± 0.14 m yr⁻¹, and 0.48 ± 0.30 m yr⁻¹ for the Elmers

Island East, Elmers Island West, and Fourchon Beach populations, respectively.

Quadrant Changes

When averaged over all populations and years (1981–84), there were no significant differences among quadrants in rate of lateral expansion. However, the southeastern (Gulf-facing) quadrants tended to have the lowest average lateral expansion, only 0.29 m yr⁻¹, whereas the northwestern quadrants exhibited the highest consistent rate of lateral expansion, 0.85 m yr⁻¹ (Figure 5). Moreover, the tremendous losses of area in the two Elmers Island populations between 1984 and 1990 are believed to have occurred predominately in the southeastern quadrants, although these amounts cannot be quantified (Figure 4).

The southeastern quadrant of the Elmers Island East population lost 22.23 m² of area (more than a 3 m loss in lateral extent) during the 1982–1983 season. During the same year, moderate losses in lateral extent occurred in the southwestern and northeastern quadrants of this population. Throughout the study the northwestern quadrant expanded at a rather consistent rate of 0.92 m yr⁻¹ (Figure 5).

Similarly, the northwestern quadrant of the Elmers Island West population also steadily

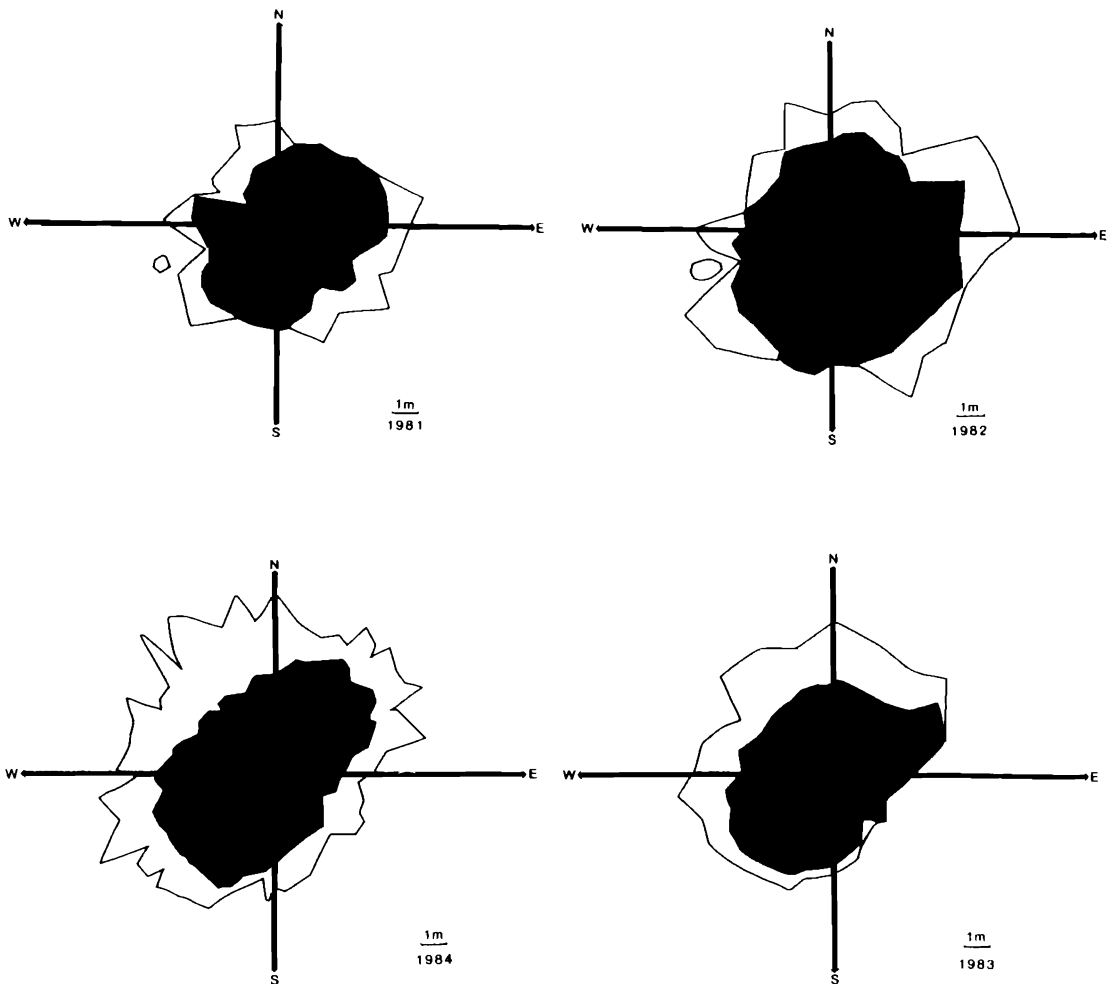


Figure 5. Population area of the Elmers Island East *Uniola paniculata* population from 1981 to 1984 showing overall net loss of area in the southeastern (gulfward) quadrant and net migration of population to the northwest, away from the eroding coast. Dark area represents homogenous central area of high stem density. Light area represents peripheral fringe of lower stem density.

increased at 1.32 m yr^{-1} , which was higher than any other 3-year quadrant average in this study. Both the southeastern and particularly the southwestern quadrants of the Elmers Island West population sustained small losses in area during 1982–1983; the southwestern quadrant lost 4.02 m^2 in area. The southeastern and southwestern quadrants of the Fourchon Beach population decreased in area and lateral extent during 1982–1983; the southeastern quadrant lost 0.61 m in lateral extent.

Biomass

All biomass parameters measured in the dense central areas of the populations had significantly greater values than those in the peripheral sparse areas (Table 2). Although the Elmers Island East population generally had the greatest biomass and the Fourchon Beach population the least, the only statistically significant population effect was the number of dead shoots m^{-2} ; the Fourchon Beach popula-

Table 2. Biomass parameters from the outer (sparse) and inner (dense) areas of the three Caminada-Moreau *Uniola paniculata* populations (June 1982; n = 3).

Location	Parameter	Population		
		Elmers Island East	Elmers Island West	Fourchon Beach
Outer (Sparse) Fringe	Live Shoots (m ⁻²)	46.7 ± 7.1 ¹	26.7 ± 5.8	26.7 ± 8.7
	Dead Shoots (m ⁻²)	4.0 ± 4.0	2.7 ± 1.3	0.0 ± 0.0
	Total Shoots (m ⁻²)	50.7 ± 4.8	29.3 ± 5.8	26.7 ± 8.7
	Live Aboveground Biomass (g m ⁻²)	78.5 ² ± 9.0	54.8 ± 6.5	35.3 ± 6.0
	Dead Aboveground Biomass (g m ⁻²)	26.0 ± 9.2	8.3 ± 1.0	17.1 ± 10.3
	Total Aboveground Biomass (g m ⁻²)	104.4 ± 18.1	63.1 ± 6.6	52.4 ± 15.7
	Live Shoot Weight (g shoot ⁻¹)	1.7 ± 0.1	2.2 ± 0.3	1.5 ± 0.3
Inner (Dense) Center	Live shoots (m ⁻²)	168.0 ± 44.2	106.7 ± 10.4	88.0 ± 15.1
	Dead Shoots (m ⁻²)	29.3 ± 12.7	38.7 ± 11.9	0.0 ± 0.0
	Total Shoots (m ⁻²)	197.3 ± 55.3	145.3 ± 20.7	88.0 ± 15.1
	Live Aboveground Biomass (g m ⁻²)	614.7 ± 185.4	264.4 ± 66.6	410.1 ± 109.5
	Dead Aboveground Biomass (g m ⁻²)	1054.7 ± 376.1	862.4 ± 130.5	332.1 ± 20.1
	Total Aboveground Biomass (g m ⁻²)	1669.3 ± 537.7	1126.8 ± 148.1	742.2 ± 101.8
	Live Shoot Weight (g shoot ⁻¹)	3.6 ± 0.1	2.4 ± 0.5	4.5 ± 0.4

¹Plus or minus (±) values are standard errors.

²All weights are dry weights.

tion had no dead shoots (Table 2). The population effect of number of live shoots and total shoots m⁻² was significant at the .07 and .06 probability levels respectively.

The total shoot density in the sparse areas ranged from 27 shoots m⁻² in the Fourchon Beach population to 51 shoots m⁻² in the Elmers Island East population with a corresponding total aboveground biomass range of 52 g m⁻² to 104 g m⁻² (Table 2). The dense central portion of the populations had a total shoot density range of 88 shoots m⁻² in the Fourchon Beach population to 197 shoots m⁻² in the Elmers Island East population, and a total aboveground biomass range of 742 g m⁻² to 1669 g m⁻², respectively (Table 2).

DISCUSSION

The observed differences in soil physicochemical properties between areas vegetated with *Uniola* and adjacent unvegetated areas appear to have little effect on the distribution of *Uniola*, since it readily invades these areas. Rather, the general trend of lower nutrient concentrations inside the populations appears to be the result of *Uniola* colonizing these areas and establishing an extensive root system, absorbing nutrients, providing organic matter, and stabilizing the substrate. As sand accumulates around the *Uniola*, the elevation of the popu-

lation increases and inundation becomes less likely. With time, the input and decomposition of organic matter inside the population tends to reduce the pH, and Ca concentrations tend to be lower, which has been suggested to be the result of leaching by organic acids (WAGNER, 1964; HOSIER, 1973). Thus, a more mature, vegetated substrate is generally expected to be characterized by lower pH and lower Ca concentration (WAGNER, 1964; HOSIER, 1973).

Overwash results in inundation of the sand surface, and depending on its severity may also erode the substrate around dune vegetation or redeposit sand and shell material on top of the vegetation, resulting in partial or complete burial. An overwash event generally has the effect of causing the substrate to regress to a younger stage of development, which is characterized by a high Ca concentration and a high pH (HOSIER, 1973). Higher cation concentrations would also be expected in areas subject to a higher frequency of sea water inundation. In this study the lower elevation unvegetated areas adjacent to *Uniola* not only had higher Ca concentrations and pH, but also higher concentrations of Na, K and Mn than the colonized substrate under the populations (Figure 2).

Site differences in soil nutrient concentrations revealed that the Fourchon Beach site had significantly lower soil P than the other sites (Table 2). The significantly lower P concentra-

tion combined with a slightly lower total inorganic N concentration may have been responsible for the lower density of *Uniola* in this population since *Uniola* responds readily to N and P additions through increased tiller production (WOODHOUSE and HANES, 1966; WOODHOUSE *et al.*, 1968; HESTER and MENDELSSOHN, 1990).

Although the three *Uniola* populations accreted an average depth of 7.4 cm yr⁻¹ of sand (Table 1), this is much less than what has been reported in other areas, particularly areas where *Uniola* is dominant. WAGNER (1964) reported that the most vigorous growth of *Uniola* on Bogue Bank, North Carolina occurred on steep dune slopes that accreted sand to a depth of 31 cm or more per year. The lower sand accretion of the Caminada-Moreau *Uniola* is interpreted to be the result of the relatively limited sand supply along the Louisiana coast (MENDELSSOHN *et al.*, 1991) and not some inherent difference in the ability of the *Uniola* in Louisiana to accrete sand.

The differences in the sand accretion rates between populations and quadrants are best explained by the positioning of the populations relative to a sand source and by the amount of fetch. For example, the Fourchon Beach population accreted the most sand apparently because it was located near the updrift side of the Belle Pass jetties, which served as a sand sink, and had a wide beach of dry sand. The Elmers Island East population accreted the least amount of sand and was the most gulfward population, which created a situation where the southeastern winds typical of the spring and summer months had a very limited fetch over dry sand before intercepting the population. The positioning of the Elmers Island West population behind a discontinuous dune ridge in a relict washover fan provided the southeastern winds with a very long fetch over dry sand through the dune depression before intercepting the population. The southeastern quadrant of this population accreted 20.1 cm yr⁻¹ of sand, which was more than any other quadrant in the study (Table 1).

Although other studies (WOODHOUSE *et al.*, 1968) have reported the cessation of growth and eventual death of *Uniola* in North Carolina when the sand supply was restricted or cut-off, the results of this study indicate that Louisiana *Uniola* can expand vegetatively at moderate

rates (about 1 m yr⁻¹ or greater) during fair weather with a mean sand accretion of less than 0.1 m yr⁻¹. WOODHOUSE *et al.* (1977) reported the vegetative lateral spread (expansion) of *Uniola* in North Carolina to be 0.6–1.0 m yr⁻¹. During years with favorable weather in this study, certain quadrants had lateral expansion values as high as 1.82 m yr⁻¹, whereas other quadrants lost as much as 3.19 m yr⁻¹ of lateral extent during years with high storm activity.

Observed increases in the vegetative growth of *Uniola* from moderate sand accretion is believed to be the result of nutrients adhering to freshly deposited sand and may involve a possible stimulatory effect of burial upon internode elongation (WAGNER, 1964). Sand movement may also aid in reducing the effects of nutrient leaching in the surface layers of sand (WILLIS *et al.*, 1959). Salt spray is another important source of nutrients in the dune system. Although direct foliar uptake of nutrients by the leaves of *Uniola* is probably of negligible significance to its nutrient budget, the leaves do intercept large quantities of spray, which is eventually washed off the leaves and become available for root uptake (BOYCE, 1954; VANDER VALK, 1977). In these Louisiana populations of *Uniola* it may be that salt spray combined with the acquisition of nutrients obtained from tillering into unvegetated areas is sufficient for relatively high rates of vegetative growth during favorable conditions. Therefore, although the limited sand supply in Louisiana may be of debatable importance in denying *Uniola* the opportunity for potentially heightened vigor, it is still certainly critical in restricting the amount of dune growth necessary to counterbalance storm surges on this subsiding coast.

The three populations have become established in areas where the water-table depth averaged about 1.3 m, which has been shown in a controlled study to be sufficient to alleviate any signs of waterlogging stress (HESTER and MENDELSSOHN, 1989). The observed high rates of overall population vegetative expansion during mild weather, and the fairly consistent high expansion to the northwest even during severe weather provide correlative evidence to support this. As such, although dune elevations in Louisiana are low, Louisiana populations of *Uniola* do not appear to be limited in their distribution by a shallow water-table depth in the dune habitat, which rarely

becomes shallow enough to stress the plants (MONTEFERRANTE *et al.*, 1982; HESTER and MENDELSSOHN, 1989).

Both the dense and sparse areas had similar expansion patterns and increased in area from 1981–84, indicating that these populations were in a state of expansion during this period; *Uniola* was expanding into new areas and also filling in the sparse areas within each population (Figure 5). When overwash events caused losses in area, the sparse area tended to be eroded away into the dense area, resulting in a scarp (Figure 5, 1983 panel). It therefore appears that Louisiana *Uniola* are capable of growing prolifically and spreading at high rates as long as the populations are not physically impacted by storm surges.

In addition to favorable conditions for vegetative growth, the success of a coastal plant growing on a rapidly eroding coast will be greatly influenced by its ability to colonize spatially distant sites either via seed production and dispersal or rhizome fragmentation. The rhizomes of *Uniola* are known not to fragment very easily, nor are they very mobile (WAGNER, 1964). Vegetative reproduction of *Uniola* is generally confined to radial expansion of an already established stand, whereas spatially distant sites are colonized only by seeds (WAGNER, 1964). Although Louisiana *Uniola* seeds exhibit fairly high germination rates under a variety of conditions, the seed production rates of these populations are extremely low, ranging from one to three orders of magnitude less than what has been reported in areas where *Uniola* is dominant (HESTER and MENDELSSOHN, 1987).

Given the very low seed production rates of these populations, successful seedling establishment must be highly unlikely. Even if a viable seed receives adequate soil conditions, successfully germinates, and emerges as a seedling, it still faces a fairly long establishment period of approximately two years, during which it is very vulnerable to storm damage (WAGNER, 1964; WOODHOUSE *et al.*, 1968).

The Louisiana coast is a storm-dominated, microtidal environment (*ca.* 36 cm diurnal tide) and the passage of an average of 10 to 30 cold front systems per year may elevate water levels up to 90 cm with waves often 2 to 3 m high, compared to average wave heights of 60 cm (BOYD and PENLAND, 1981). Tropical storms and

hurricanes have a recurrence interval of 1.6 yrs and 4.1 yrs, respectively (SIMPSON and LAWRENCE, 1971), and may raise water levels 2 to 7 m above mean sea level (BOYD and PENLAND, 1981). Measurements of overwash events on the Caminada-Moreau coast have shown that there is a regional overwash threshold of 1.42 m above mean sea level, which results in overwash of 75% of this coastline an average of 15 times per year (RITCHIE and PENLAND, 1988). Once every two to three years a level of 2.50 m will inundate most of the coast, and during hurricanes a level of 3 m will result in extensive inland flooding and destruction of barrier dune forms (RITCHIE and PENLAND, 1988).

The persistence of these established *Uniola* populations throughout the numerous storm and overwash events of the nine years of this study is remarkable, and it is obvious that successful seedling establishment is extremely improbable. *Spartina patens* is apparently able to remain a ubiquitous component of the barrier coast partly because of its salt tolerance and ability to grow through overwash deposits (GODFREY *et al.*, 1979), but also because its wide distribution in the dune and swale allows it to rapidly tiller from less impacted swale areas back onto the dune and into washover terraces (JEFFREY, 1984). *Panicum amarum* is sterile, but it does fragment and root very easily (CRAIG, 1976; DAHL, 1975), thus allowing it to colonize distant sites. The distribution of *P. amarum* in Louisiana is much more patchy than *S. patens*, but it remains a conspicuous component of the dune vegetation.

Although these Louisiana *Uniola* populations have demonstrated their resilience to overwash, if they must rely on vegetative lateral expansion as their primary means of propagation, then their longevity on a particular section of coast will ultimately be limited by the rate of coastline retreat in that area. Of the three populations, the Fourchon Beach population is the only population located in an area that has a history of accretion rather than erosion. As such, this population seems likely to persist the longest. In contrast, the present mean rate of coastline retreat from the southeast in the area of the Elmers Island populations (0.8 to 3.0 m yr⁻¹; RITCHIE and PENLAND, 1989), which approaches and exceeds the vegetative expansion of these populations

to the northwest at 0.9 to 1.3 m yr⁻¹, is expected to eventually overtake these populations. The 1990 data support these conclusions (Figure 4). The coastal position of the Fourchon Beach population in an area of historic accretion has allowed this population to continue to increase in area from 1984 to 1990, while the Elmers Island East and West populations decreased substantially (Figure 4). Although the areas of the Fourchon Beach and Elmers Island East populations were almost identical in 1981, the 1990 area of the Fourchon Beach population was approximately nine times greater than that of Elmers Island East (Figure 4). It therefore appears that in these areas of Louisiana where *Uniola* seed production rates are extremely low, the reliance on vegetative reproduction results in a very limited distribution controlled predominately by the rate of long-term coastline retreat in that area and episodic severe weather events.

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□ RÉSUMÉ □

Sur la côte ouest du delta du Mississippi, on a étudié les trois seules populations mesurables de *Uniola paniculata* pour déterminer si elles sont en expansion ou en régression. Ces populations sont établies dans des zones où la profondeur moyenne de la nappe est de 1,29m, ce qui malgré la faible profondeur est assez profond pour atténuer les signes de perturbation par exploitation de la nappe. Les concentrations en éléments nutritifs et le pH sont généralement plus faibles au sein des populations que dans les zones adjacentes non végétalisées. En dépit de la faible accretion sableuse dans les populations (moins de 0, lm/an), l'expansion latérale des végétaux (dispersion latérale) dépasse 1m/an lorsque les conditions climatiques sont tempérées, et présente un bilan négatif les années où se produisent de sérieux ennoyages. L'expansion latérale moyenne sur 3 ans des populations est de 0,58m/an et la plus grande migration séffectue vers le NW (s'éloignant de la côte en érosion) à la vitesse de 0,85m/an. Comme la production de graines est faible dans ces populations, la colonisation de nouveaux sites est peu probable, et toute population en expansion est considérée comme étant le seul résultat de l'expansion végétative latérale. La distribution très limitée de cette espèce le long de la côte de Louisiane s'explique par son lien avec la reproduction végétative qui, même là où *Uniola* domine, est souvent insuffisante à maintenir un équilibre avec le retrait du littoral fortement en érosion et faiblement élevé de la Louisiane. *Catherine Bousquet-Bressolier, Géomorphologie EPHE, Montrouge, France.*

□ RESUMEN □

Se ha estudiado las tres únicas poblaciones mensurables de *Uniola Paniculata* de la costa Oeste de Louisiana en el delta del Río Mississippi para determinar si dichas poblaciones se encontraban en estado de expansión de o regresión. Las poblaciones han quedado establecidas en áreas con una profundidad de agua media de 129 cm que, aunque somera, es suficientemente profunda como para mitigar cualquier signo de tensión por arrastre del agua. Las concentraciones de nutrientes en el suelo y el pH han sido en general menores dentro de las poblaciones que en las áreas adyacentes desprovistas de vegetación. A pesar de la pequeña tasa de sedimentación de arena dentro de las poblaciones (> 0.1 mm/año), la expansión lateral de la vegetación excedió el metro por año durante los años de clima suave, mientras que durante los años con fuertes rebases sobre la playa se produjo una pérdida neta de población. La velocidad media de expansión lateral durante tres años fue de 0.58 m/años, mientras que la máxima tasa de emigración de 0.85 m/año se produjo hacia el nordeste (en dirección opuesta a la costa en erosión). Como la producción de semillas en estas poblaciones es muy baja, la colonización de nuevas áreas es extremadamente improbable y se cree que cualquier expansión de las poblaciones se producirá tan sólo como resultado de la expansión lateral. La distribución extremadamente limitada de estas especies a lo largo de la costa de Louisiana se explica bien por su dependencia de la reproducción vegetativa que, aunque de tasa de crecimiento comparable con la existente en áreas donde la *Uniola* es dominante, es a veces insuficiente para compensar la regresión de la línea de costa a lo largo de la costa baja y altamente erosionable de Louisiana.—*Department of Water Sciences, University of Cantabria, Santander, Spain.*