

Dynamics and Processes of Barrier Island Vegetation

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ABSTRACT

The vegetation of barrier islands is molded by a complex of strong environmental influences associated with the maritime environment (particularly salt spray and sand movement); biotic influences (dispersal biology, ecophysiology, competition, herbivory) also play important roles in determining the distribution of species and communities. In this article, the role of these factors in barrier island ecosystems is examined by following a hierarchical approach to the understanding of ecological processes and dynamics. The biology of plant individuals is examined and related to the population processes of genetic differentiation and demography. Community-level processes, including competition, herbivory, and succession are examined as functions of individual and population-level processes. A similar approach is taken for ecosystem-level processes (nutrient dynamics, soil food webs, productivity). Evidence from these disparate levels of organization suggest that the methods evolved by plants for locating, acquiring, and retaining patches of suitable habitat, together with the need for a suite of physiological and biological adaptations to the environment appear to be primary factors in the ecology of barrier island vegetation.

I. INTRODUCTION

A. Scope of Review

Barrier islands have long been known for their distinctive vegetation. The grasses of the sand dunes, the maritime forests, the wind-pruned appearance of the trees, the distinctive zonation of communities and the specialized group of species capable of tolerating the shoreline environment have supplied subject matter for ecological study for as long as ecology has been a discipline. Indeed, the idea of succession, one of the key concepts of ecology, was initially developed through the study of sand dune vegetation (albeit lakeshore dunes, not barrier dunes) by Cowles.¹ An extensive literature has developed subsequently, much of it descriptive in nature, detailing the species and plant communities that occur not only on barrier islands, but on coastal dune systems throughout the world. The interest in coastal vegetation stems from the fact that these plants are subject to extreme physical constraints from salt spray, salt water, moving sand, and poor soil, a combination of limiting factors which sets coastal vegetation apart from other types of vegetation.

Because descriptions of coastal vegetation abound, including several very recent summaries,²⁻⁵ little attention is paid in this review to descriptions of vegetation types, patterns of zonation,

and species compositions. Rather, an attempt is made to relate what is known of ecological processes in barrier island plants and communities to current theoretical issues in ecology. This approach, I hope, will promote an understanding of the way in which abiotic and biotic factors interact in determining the nature of barrier island terrestrial vegetation, and the ways in which it changes through time.

Much of the research on plant form and function has been carried out on coastal dunes. However, many of the same species in these studies are also dominants on barrier islands. Furthermore, the environmental factors affecting the plants in beach and foredune environments are similar, whether the beach and dunes are on an island or are part of the mainland. Many papers describing coastal vegetation throughout the world do not distinguish the vegetation of barrier formations from mainland dune systems; the same plant communities are described for beach and dune habitats regardless of the presence of a lagoon or upland behind the dunes. Thus, the similarities of the environmental and ecological processes as well as the composition of the plant communities justify the use of research on coastal dune plants in this consideration of the dynamics of barrier island vegetation.

The processes to be considered form a hierarchy (Figure 1). The biology of plant individuals — establishment from a propagule, growth and mortality — sets the stage upon which interactions within and among species occur. Competition between plants, herbivory, and symbiotic or mutualistic relationships among species are thus dependent upon processes at the individual organism level. Competitive and other interactions among populations have a reciprocal influence on individuals through effects on reproduction, growth, and survival.⁶ Interspecific interactions in turn supply the causal mechanisms for successional changes in vegetation. Interactions among the communities of different trophic groups (plant-microbe, plant-herbivore, plant-pollinator, etc.) finally determine the kinds and intensities of ecosystem functions that occur at a site. This hierarchical approach to ecological processes provides both a framework for the very varied subjects included in this review, and also accords with the increasing stress placed by theorists on the role of individual-based processes in determining the nature of population, community, and ecosystem dynamics.⁷⁻⁹

B. Barrier Island Vegetation

Barrier islands are usually linear landscape elements, aligned

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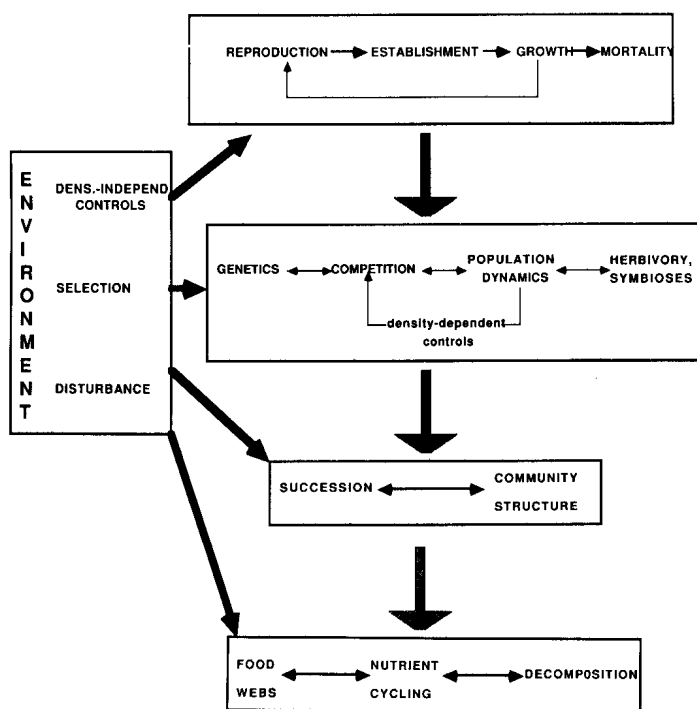


FIGURE 1. Hierarchical structure of ecological processes.

along the coast in response to the prevailing winds and currents. Because of the steep gradients of environmental factors that occur across barrier islands with increasing distance from the ocean, the vegetation is also usually more or less linearly arranged into belts parallel to the long dimension of the island (Figure 2). Although the species composition of the belts varies widely among geographic regions, the presence of the belts and their general characteristics are among the most striking and most well-defined aspects of the ecology of barrier islands.

Figure 3 shows a typical transect of vegetation types across barrier islands. The following features are common to this vegetation: (1) a zone of pioneer plants which colonize the beach, (2) a zone of dune-forming perennial grasses or forbs, (3) a zone, on dunes further inland, in which shrubs are substituted for herbs, (4) the development of a variety of types of vegetation in swales between series of dune crests, (5) the presence of maritime forest behind the dunes, (6) a fringe of salt marsh or mangrove swamp along the bay or lagoon behind the island. The development of each of these zones varies with local conditions: on narrow islands subject to frequent overwash, shrub thickets and forest vegetation are absent, pioneer communities are poorly developed on islands with high storm surges,¹⁰ and the extent of the various upland communities will vary with the height and nature of dune development and the history of disturbance. The size, shape, and extent of dune formations and the intervening swales thus affect the diversity of the interior zones. Nevertheless, the dominating linearity of

the major zones, reflecting the geomorphological development of each island, is a paramount feature of barrier island vegetation.

Figure 4 shows the relationship between island size and the number of species of vascular plants for some islands of the Atlantic and Gulf coasts of the U.S. Although the various floristic studies may not be equivalent in thoroughness or scope, the poor relationship between species richness and island size is nonetheless apparent. Species richness ranges between 300 to 500 species over more than an order of magnitude of island sizes; it falls off rapidly only for very small islands (under 1000 ha). A similar relationship of species richness to island size occurs among the barrier islands of the Wadden Sea⁴ (along the coasts of The Netherlands, Germany, and Denmark) with a lower range of species numbers (100 to 400) being found on islands below a threshold size (<1000 ha) than found on moderate to large islands (250 to 647 species on islands from 10,000 to 20,000 ha). Variation among the Wadden Sea islands was attributed to island age, disturbance history (both natural disturbance regimes and the history of human use), amount of topographic diversity, and soil quality (primarily the amount of calcium in the dune sands). A lack of relationship between species richness and island size has also been found for some oceanic island systems.²⁰ A lack of relationship between distance from the mainland and species richness is also suggested by the data in Figure 4: Cape Hatteras, much of which is 40 km from the mainland, has as many species as does Plum Island, which is separated from the mainland by only 1 to 2 km of open water. Distance from the mainland is not an important determinant of species richness on some ocean islands, as well.²⁰ Although storm frequency, topography, latitude, island shape, habitat diversity, island age, and soil quality are all likely to be important in determining barrier island species diversity, their relative importance has not yet been quantitatively assessed.

The species pool found on barrier islands is, in part, a subset of the vegetation of the nearby mainland areas. Padre Island, Texas supports 216 species; a wildlife refuge on the mainland coast opposite the island supports 451 species.¹⁷ This contrast must reflect the wider variety of habitats included in the mainland refuge. In a comparison of mainland and island dune habitats in Mississippi, Huguley and Eleuterius²¹ found a slightly greater species richness on the mainland dunes (70 vs. 55 species) and a greater similarity between the two island dune sites (73%) than between either island site and the mainland site (52 to 58%). Wallops Island, Virginia, and the peninsular Wallops Mainland share 52% (255 species) of their species; the 116 species unique to the islands are mostly dune plants, while the 117 species found only on the mainland are forest and swamp plants.²²

However, barrier islands also support endemic species. In a survey of the vegetation of Florida barrier islands, Johnson and Barbour³ recorded 246 species occurring in 43 sites; 18

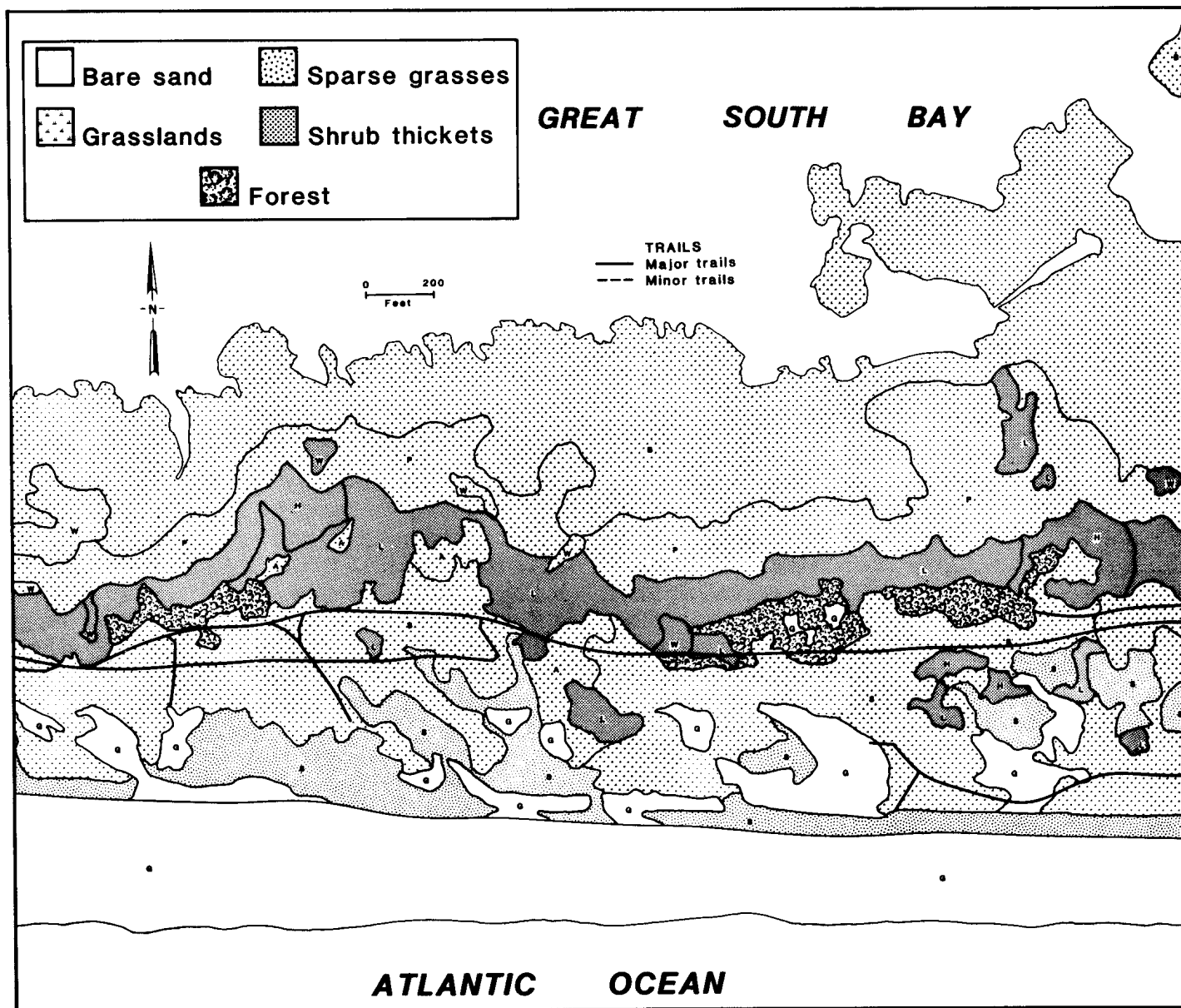


FIGURE 2. Linear arrangement of plant communities on Fire Island, New York.

are endemic to the coast (both island and mainland). Of the 99 species native to Padre Island, two are endemic.¹⁷ Of the 1007 species recorded for the 40 island and mainland coastal sites in the Wadden Sea,⁴ 337 (33%) are found only on the islands. These are mostly (94%) herbaceous plants, and they are most commonly found in grassland or dry waste areas, freshwater wetland habitats, acidic moors and bogs, and the interior of woodlands.

Another major source of species diversity on barrier islands is human impact, both through the influx of exotic species, and the loss of diversity through habitat destruction. On Padre Island, 54% of the currently recorded species are attributed to human introduction,¹⁷ on Wallops Island 23% of the flora is

introduced,²² and in the Wadden Sea islands, 423 species (not including the 1007 mentioned previously) are introduced.⁴ Similar figures could be obtained from most barrier island floras. Although the extensive destruction of barrier island habitats for human use has been well documented,^{23,24} the impact of this loss of habitat on species richness and the persistence of rare species remains unknown.

C. Barrier Island Environments

1. Extent and Occurrence of Barrier Islands

Barrier islands are found throughout the world, varying in their extent with sea level changes, tidal range, geomorphic features of the off-shore and onshore environments, and cli-

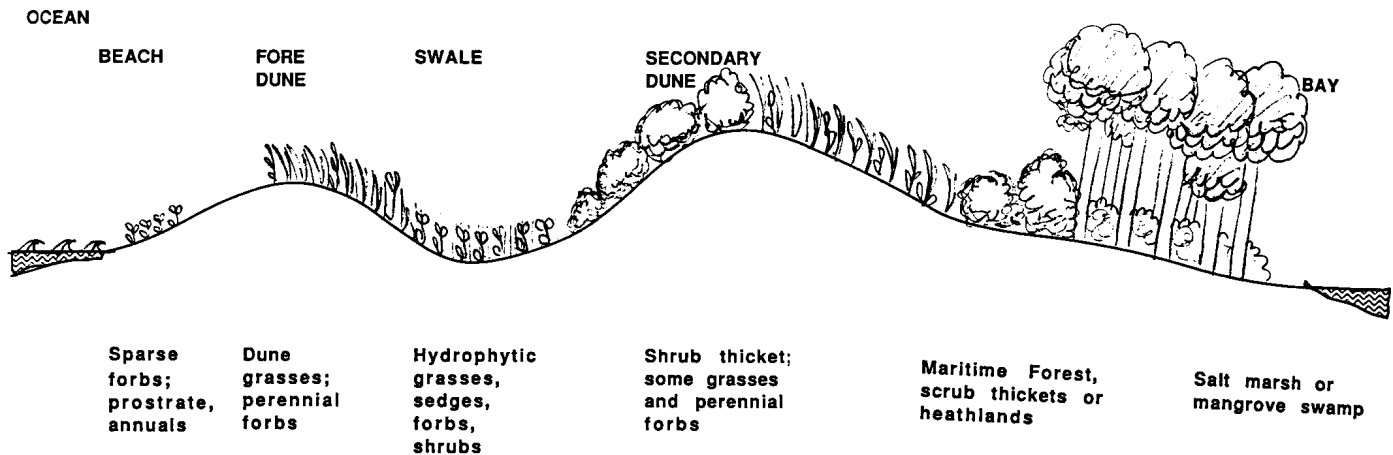


FIGURE 3. Typical array of plant communities on a transect across a hypothetical barrier island.

mate.²⁵⁻²⁷ They account for 10 to 15% of the world's shorelines, including chains along the North and South American coasts, Africa, Australia, India, and Sri Lanka, and also are found on the coasts of the Arctic, Baltic, Mediterranean, Black, and Caspian Seas. However, the most extensive barrier island chain is found along the Atlantic and Gulf coasts of North America (5000 km of coastline). Areas of extensive barrier island development coincide with zones of low to moderate tidal range along coasts of low profile, with gentle offshore gradients and an abundant supply of sediment. The morphology of barrier islands varies greatly, depending not only on geomorphic and climatic factors, but also on the nature of the dune vegetation and its mode of interaction with moving sand.²⁸ Barrier islands are almost continuously changing in shape and location, a feature which serves to distinguish these landforms from most others, and which is of major importance to the plants that try to grow on them. Barrier islands are relatively new geomorphological features (rarely more than 6000 to 7000 year B.P.), having developed as a result of the rise in sea level following the end of the last glaciation. Sea level rise continues to be the dominant force affecting both the morphology of islands and their migration towards the mainland. Thus, compared to coastal dune systems that may have been in place for several times as long, there has been less time available for soil development, species immigration, and evolutionary adjustments of local populations to the barrier island environment.

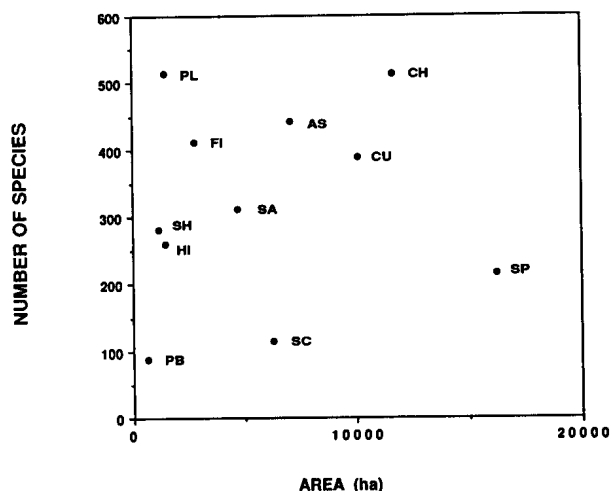
2. The Physical Environment

Many studies of barrier island vegetation have included a characterization of the soils, climate, aerosol chemistry, and sand movement — the physical features that distinguish coastal environments from inland ones and are most important to the vegetation. Table 1 illustrates the gradients across a hypothetical island for a variety of the physical factors. The foredune environment is harsh: soils have very low contents of nitrogen, nutrient cations, organic matter and associated water-holding

capacity and cation exchange capacity, there are high wind velocities and large amounts of sand movement, and high rates of salt spray deposition. The principal determinant of soil quality in the dune environments is the amount of calcium, which in turn reflects the geological origin of the sediments that are feeding the barrier island system; coralline-derived beach sands can consist of >99% CaCO_3 ,²⁹ whereas siliceous sands may contain <0.1% carbonate. A high carbonate content maintains alkaline pH conditions, often over 8.0, in the foredunes, with relatively slowly decreasing values in rear-dune and interior habitats. In dune systems derived from low-carbonate sands, soil pH may be circumneutral on the foredunes, and usually decreases rapidly to highly acidic conditions (pH 3 to 4) in the maritime forest soils. Dune soils are almost always very low in organic matter, nitrogen, phosphorus, and potassium;³⁰⁻³⁴ increases in available nutrients and water-holding capacity may occur as organic matter increases in interior soils. A lens of fresh water is often within reach of tap-rooted plants, which can thus avoid the water stress imposed by limited soil water. The fresh water aquifer follows the Ghyben-Herzberg principle, in that the depth to the fresh water/salt water transition zone is approximately 40 times the height of the water table above sea level;^{35,36} however, the actual depth will vary with ocean overwash, tides, and the presence of confining beds of clay (Figure 5).

Salt spray is both a source of stress and mortality³⁷ and a primary source of nutrients to barrier island vegetation. Gradients of salt spray inland from the ocean are steep, and vary greatly with wind conditions, distance, topography, and height of the vegetation.³⁸⁻⁴⁰ Salt deposition can vary at a given site more than two orders of magnitude with changes in windspeed and direction.³⁸ Above a critical windspeed (5.5 to 7.9 m/s), a sharp increase in bubble formation on the ocean surface results in parallel increases in salt deposition.⁴¹ Deposition decreases rapidly with distance from the ocean, following an exponential or power function.⁴¹ Salt derived from ocean spray

(A) NORTH AMERICAN ISLANDS



(B) WADDEN SEA ISLANDS

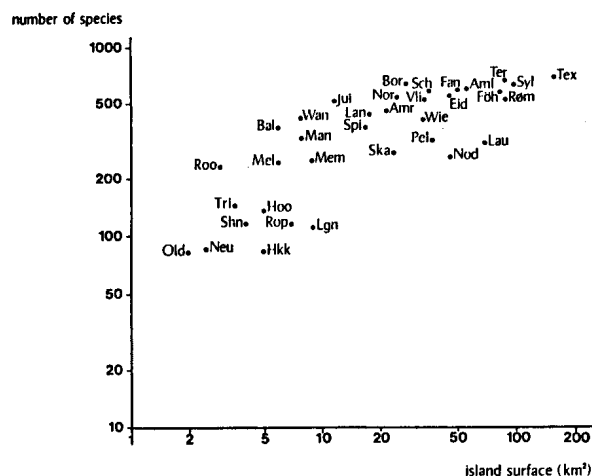


FIGURE 4. Relationships of species richness to barrier island size for two groups of islands. (A) Selected Atlantic and Gulf Coast islands (FI - Fire Island;¹¹ CH - Cape Hatteras;¹² AS - Assateague Island;¹³ HI - Horn Island;¹⁴ SC - St. Catherine's Island;¹⁵ CU - Cumberland Island;¹⁶ SP - North Padre Island;¹⁷ SA - Sanibel Island;¹⁸ PL - Plum Island;¹⁹ PB - Petit Bois Island.¹⁴ (B) Islands of the Wadden Sea (From Dijkema, K. S. and Wolff, W. J., Wadden Sea Working Group Report. No. 9, 1983. With permission. See for full names of islands.)

can be detected up to several km inland of the shore,⁴² and even at these distances, the amount of deposition varies 2- to 3-fold with the degree of exposure.⁴³ However, most of the salt from ocean spray is deposited within 500 m of the water. On a 700-m-long transect across a barrier island, Martin³⁸ recovered 50% of the total salt deposited within the first 60 m, and over 90% was deposited within 300 m. Local topography (number, size, and placement of dunes) will affect the rate of decrease in deposition with distance.⁴⁰ Height above the soil surface is another critical variable; deposition may decrease up to 90% between trapping surfaces at 1 m height and those at 0.1 m height, and deposition within a plant canopy may be only one third of the deposition at the surface of the

canopy may be only one third of the deposition at the surface of the canopy.³⁹ Given these sources of variation, it is not surprising that estimates of salt deposition vary from <1 to >200 mg salt/dm²/d.⁴⁴

Sand movement is an equally variable yet critical aspect of the barrier island environment. On a yearly basis, accretion or erosion of sand from foredunes varies with position on the dune, the transgressive or regressive nature of the island, the angle of the island with respect to prevailing winds and currents, and the frequency, intensity and seasonality of storms.^{23,27} Measured rates range from as little as +2.5 cm/yr⁴⁵ on Cape Cod foredunes to as much as -144 cm/yr on the Outer Banks of North Carolina,³¹ with most values falling in a range of about 10 to 50 cm per year net change (erosion or accretion). Windward surfaces often erode while the apex and lee slopes of the same dune receive the sand as accretion, and the swale at the base of the dune remains static in level.⁴⁶ Figure 6 illustrates the range of variation in sand movement with dune position over a three-year period for a single dune; monitoring of a sequence of six dunes in the same site revealed that variations among dunes, with respect to the same dune position, was equally great (up to 1.5 m of sand movement difference between the minimum and maximum values observed for a given dune position).⁴⁷ The migration of the whole dune superposes an additional pattern of sand movement on the yearly erosion and accretion. As swales are overtaken by moving dunes, vegetation is killed, while the exposure of new swale habitat in the wake of the moving dune provides sites for colonization.⁴⁸ The importance of sand movement to barrier island vegetation varies equally on a geographic scale; tropical islands frequently lack dunes and moving sand.^{26,49}

On a larger spatial scale, the constantly changing geomorphology of most barrier islands, both in response to storms and in response to prevailing winds, tides and currents, is a major factor in determining the zonation and composition of plant communities. Washover events drastically rearrange vegetation patterns^{28,50,51} as well as the topography of the island cross-section, and the importance of washover events (distance of penetration inland and frequency at a given location) can vary greatly within an island.²³ Plant response to washover varies greatly both between and within species, and plant growth form interacts with geomorphic processes in turn to affect the frequency and intensity of overwash. Annual erosion rates also vary widely on within-island, between-island, and between-region scales; on the North American Atlantic coast, an annual mean erosion rate of 1.5 m/yr includes values exceeding 30 m/yr.

Washover events are coupled with the inland migration of barrier islands in response to sea level rise.⁵² Washover events carry large amounts of sediment over the dunes onto the back-barrier marshes, and sediment is also accumulated along the marshes near inlets. As the marshes are built up by sand accumulation and the dunes are rebuilt along the ocean shore, the whole island moves inland. As long as the rate of sea level

Table 1
Representative Ranges of Values Observed in the Literature of Soil Chemical and Physical Attributes for Different Points Across a Hypothetical North Temperate Barrier Island

Parameter	Foredune	Swale	Rear dunes	Forest/heath
pH	7—9	5—6	5—8	4—5
% Organic matter	0—0.1		0.1—6	5—12
Soil texture	coarse sand, 99.9%			fine sand, 99.0%
Sand movement, cm/yr	7—60		0.1	
Soil moisture, % capacity	1—2	25—50	1.2—1.5	1—6
Cation exchange capacity, meq/100 g	10—15	15—30		4—20
Salt Spray, mg/dm ² /d	50	10—15	10—20	5—8
Total N, ppm	0.1—30	0.8—60	2—100	12—1,450
PO ₄ , ppm	0—110	103—133	6—112	6—18
K, ppm	6—50	6—25	1—13	1—144
Ca, ppm	70—38,000	45—230	220—4,640	920

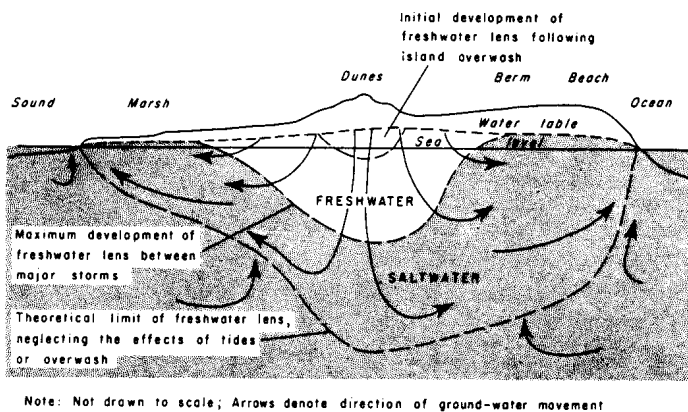


FIGURE 5. Relationship of the freshwater lens beneath a barrier island to island topography and to the underlying salt water. (From Winner, M. D. Jr., *U.S. Geol. Surv. Wat. Res. Invest.*, 78-52, 1978.)

rise does not exceed the rate of marsh and dune development, the island will retain its form, but will slowly move inland. Psuty⁵² has estimated that islands can be expected to migrate laterally about 200 units per unit sea level rise. Sea level rise may also cause a narrowing of barrier island formations, if there is a sufficiently high dune formation to insulate the interior of the island from the inundation and erosive readjustment of the beach profile. In the case of migrating islands with low or interrupted dunes, the implications for plants include frequent periodic disturbances creating newly exposed habitat for colonization, and a concomitant migration of habitat zones in step with the movement of the island. In the case of islands undergoing narrowing without migration, the effect on the vegetation will be a loss of habitats — especially beach and fore-dune areas, as well as salt marsh areas on the bayside — and,

possibly, an increase in salt stress on the remaining vegetation, as salt spray encroaches further inland.

The controls exerted over vegetation patterns by sand movement, salt spray and soil quality have been frequently demonstrated since the initial classical ecological studies of barrier island (and other coastal dune) vegetation.^{38,39,53-56} Modern analyses⁵⁷⁻⁵⁹ have used ordination and clustering methods to relate vegetation patterns to complex-gradients of environmental factors. The ordinations repeatedly identify salt spray and sand movement (the two sometimes expressed as distance inland from the beach or a topographic measurement), soil moisture (separating dune crest and swale environments), and soil quality as primary factors distinguishing different types of vegetation.

The ecological ramifications of the physical processes briefly described here are dealt with next, in terms of their influence on individual plant biology, population dynamics, and community processes.

II. ECOLOGICAL PROCESSES AND DYNAMICS

A. Biology of Individual Species: Reproduction

In order for vegetation to develop on an island, seeds or other propagules must disperse to the island from mainland habitats and disperse within the island to new habitats, must germinate, and seedlings must become established and survive through reproductive age. That these phases of plant establishment are often subject to the highest mortality rates of any phase of plant growth, and therefore are likely to limit the presence and abundance of species in a given habitat has been postulated frequently.⁶⁰⁻⁶⁴ The strong gradients of physical con-

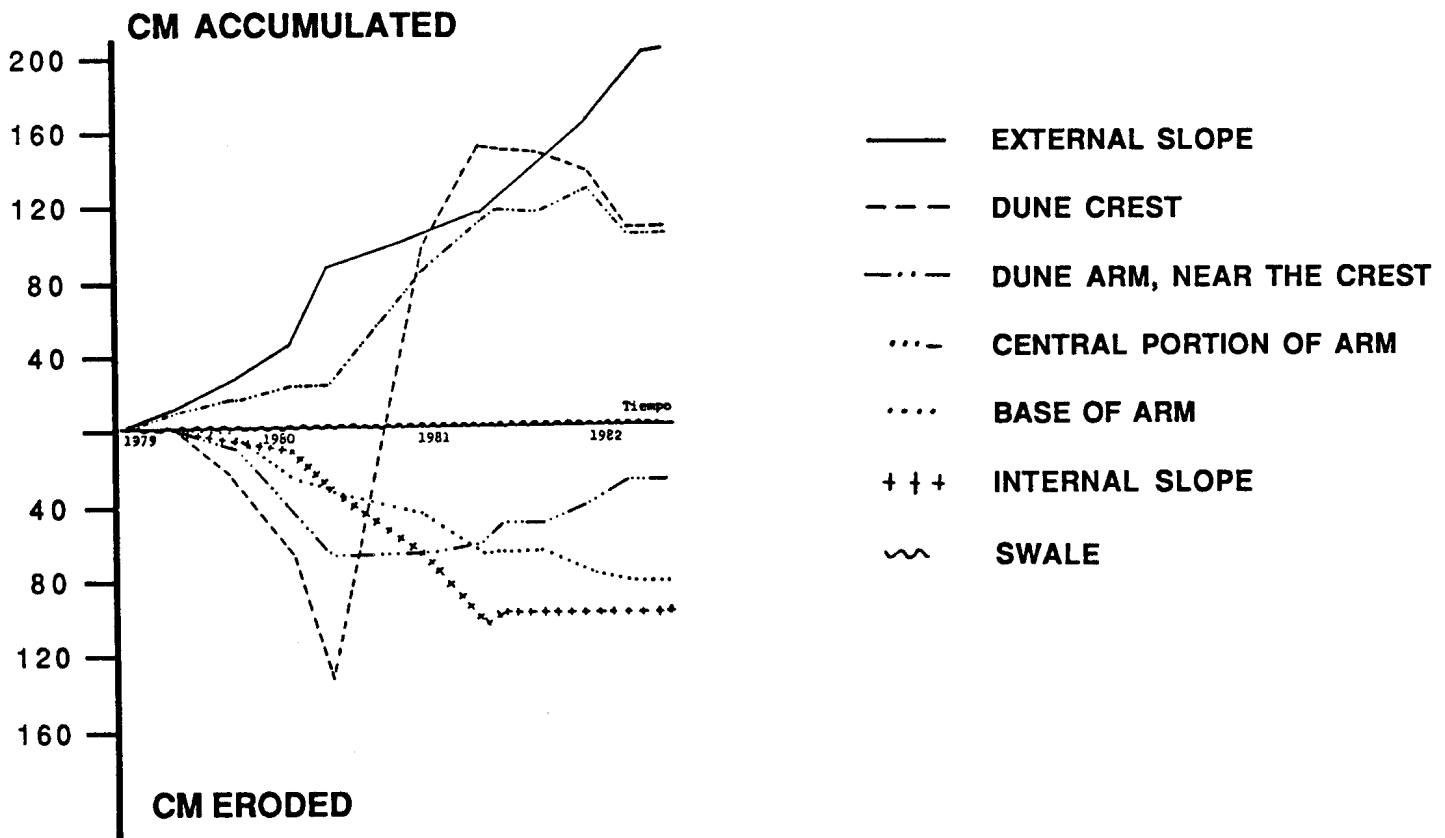


FIGURE 6. Patterns of sand movement at 7 sampling points across a coastal primary dune near Jose Cardel, Veracruz, Mexico. (From Moreno-Casasola, P., *Biotica*, 7, 577, 1982. With permission).

ditions across barrier islands could be expected to impose mortality and other limitations on seed dispersal, viability, germination, and seedling establishment in a differential way across the transect inland from the ocean.

1. Seed Dispersal

Despite the interest of plant geographers⁶⁵ and ecologists^{66,67} in dispersal to islands, there has been relatively little attention paid to the dispersal ecology of barrier island plants. Seeds disperse to barrier islands over an intervening lagoon or bay; they disperse within islands across strongly contrasting habitat types and environmental conditions. Methods of dispersal, and the role of dispersal in the biology of species are likely, therefore, to vary markedly among habitats on these islands.

Ocean transport of floating seeds could be expected to be important at least for strandline and foredune species. Ridley,⁶⁵ in his extensive analysis of sea dispersal, pointed out that seeds must not only be able to float for long periods of time, but also remain viable after prolonged immersion in seawater. He noted that sea-dispersed plants were the first to colonize barren islands, and he suggested that several widely distributed beach species, including *Ligusticum scoticum*, *Cakile maritima*, *Honckenya peploides*, and *Mertensia maritima*, have travelled

around the Arctic by sea. Darwin⁶⁸ initiated the study of the effect of sea water on seeds; he reported that *Crambe maritima* and *Beta vulgaris* could germinate following 37 and 100 d, respectively, in sea water. Most (65 to 70%) of the seeds of *Cakile maritima*, *Salsola kali*, and *Pancreatium maritimum* can germinate following 40 d in sea water.⁶⁵ *Pancreatium* actually remains afloat longer in sea water than freshwater.⁶⁹ *Sesuvium portulacastrum*, a common pan-tropical beach species, also has been reported to depend on ocean-dispersed seeds.⁴⁹ Co-occurring beach species may have very different capacities for ocean-mediated dispersal; *Atriplex laciniata* and *Salsola kali* float only briefly (<8 and 22 d, respectively), compared with *Cakile maritima* and *Atriplex glabriuscula*, which can both float for 30+ d.⁷⁰

Seeds that can float for long periods of time have a wide variety of morphological adaptations for this purpose. *Honckenya peploides* seeds, which can remain afloat for over a year have spongy albumen within the embryo. *Lathyrus japonicus* has modified cotyledons, and *Vigna lutea*, has a cavity between the cotyledons.⁶⁵ In *Rubus crispus*, tubercles on the perianth segments of the coastal variety *littoreus* enable the seeds to float at least 72 h in sea water, whereas the inland forms without the tubercles cannot float.⁷¹ Much of the ocean-mediated dis-

persal of coastal plants involves the spread of vegetative material (stems and rhizomes); species listed by Ridley as dispersing in this way include *Paspalum vaginatum*, *Spartina* spp., *Elymus arenarius*, *Sporobolus virginicus*, and *Ammophila arenaria*. *Ammophila breviligulata* caryopses can float in fresh water for 10 d, while fragments of rhizomes float for about 6 d.¹³⁵ Thus, many strandline and foredune species have adaptations that promote buoyancy in salt water above that observed for plants from inland environments, but there is still considerable variability among strand and dune species in their ability to float, and therefore for long-distance dispersal to be mediated by ocean transport.

Aside from ocean-mediated long-distance dispersal, however, much of the dispersal of seeds in beach habitats involves local movement of propagules over short distances. Much of the research on strandline ecology has concerned *Cakile* spp., both in Pacific coastal dune environments and Atlantic barrier island environments. The fruit of *Cakile* consists of a two-segmented fruit (silicle); the proximal segment (which often is sterile) usually remains attached to the parent plant, while the distal, larger segment becomes detached. On gravel bars of Atlantic coast barrier environments, the large majority of seedlings are found in close proximity to the parental plants, forming dense clusters (up to 9.5×10^5 seedlings). Although some individuals do become established at least 25 cm distant from the parents, the majority of seeds from distal fruits do not move this far from the parent.⁷² The proximal fruit segment, because of its adhesion to the parental plant, does not disperse at all. No movement of seeds from either fruit occurs between bare shingle and wrack habitats. On a sand dune habitat by contrast, there is considerable movement of the distal segments.⁷³ During the winter, winds move the seeds along the beach and up the face of the primary dune, where their movement is stopped by the swards of *A. breviligulata* at the dune crest. The wind-borne fruits are also stopped by lines of *Zostera* wrack along the upper beach. Thus, despite the ability of *Cakile* to float in seawater and thus be dispersed widely along a sandy beach, Keddy's studies indicate that most fruit dispersal is localized near the parent plant or within 15 m inland. Barbour⁷⁴ also reported that in one study at Bodega Head, California, over 90% of the seedlings remained within 1 m of the parent plant.

Retention of seeds in close proximity to the parents has been reported for other sand dune species. *Lithospermum carolinense*, although not a barrier island species, is a perennial herb typically found on inland sand dune habitats. Nutlets fall within 48 to 74 cm of the parent plant; the action of gravity and rodent foraging occasionally moves seeds 1 to 2 m from the parent.⁷⁵ Once a population of plants is established, such localized dispersal results in highly aggregated populations. The topography and vegetation in the immediate vicinity of each plant have a significant effect on both the distance and direction of dispersal.⁷⁶ The English coastal dune annual, *Vulpia fasciculata*, is similar: 79% of caryopses are found within

10 cm of the parent, and the maximum distance of primary dispersal observed was 36 cm.⁷⁷

Secondary dispersal by wind, water, and animal activity can move seeds away from the parent after they are shed. As with *Cakile*, winds account for some secondary dispersal of *V. fasciculata* through the movement of the fallen spikelets along the ground. The amount of this secondary movement is proportional to the density of the parent population.⁷⁶ Wind moves fallen spikelets of *Uniola paniculata*⁷⁸ and *Iva imbricata*⁷⁹ in the vicinity of the parents, and concentrates them in small depressions, especially on the lee slopes. High waves move fruits of *Cakile edentula* landward from the beach, and concentrate them in drift lines.⁸⁰ Seasonal flooding of the interdune swales also moves the spikelets of *Uniola* into aggregations in the wrack at the water line. Ghost crabs (*Ocypode albicans*) move seeds and spikelets into their burrows, thereby dispersing the seeds away from the parents and aggregating them in favorable sites for germination. Other dune species, such as *Andropogon littoralis* and *Solidago mexicana*, also are aggregated by ghost crab collection and burial in the burrows.

Although some species produce seeds with the typical adaptations for wind dispersal (e.g., *Erigeron canadensis*, *Solidago sempervirens*, *Gnaphalium obtusifolium*⁷⁹), the more common pattern is the primary placement of seeds near the parents, and secondary movement up to a few meters away by agents that also aggregate them. Sites of organic matter accumulation or slightly better soil moisture conditions are likely to be "safe sites".⁶² Thus, the local environment of the parent apparently signals the continued existence of suitable habitat for the offspring, so that long-distance dispersal is not favored. Watkinson⁷⁷ suggested that the small dispersal distances typical of the winter annuals of the English coastal dunes reflected the fact that plants growing near parents were likely to successfully reproduce, whereas dispersal over greater distances was likely to bring the seeds into unfavorable microenvironments, such as dune swales. Weller⁷⁵ proffered a similar interpretation for *Lithospermum*, a long-lived perennial, as did Zedler et al.⁸¹ for *Cirsium rhotophilum*. Although the physical environment of the dunes may undergo frequent small changes from year to year, some suitable microsites within the dunes are likely to be predictably available, varying only in their particular location with respect to parent populations. Similarly, the juxtaposition of the varied habitats of dunes and swales is also predictable. Localized dispersal will thus permit species to remain within the appropriate habitat type, and to take advantage of small-scale openings and disturbances, while avoiding movement into nearby unsuitable habitats. Such a situation has been specifically demonstrated for the annuals of the dry dune habitats on English coastal dunes; dispersal occurred mostly within populations with a patch size of 16 to 24 cm, thus keeping seeds from dispersing into adjacent wet swale areas.⁸² In *Polygala vulgaris*, neighborhood areas are typically 1.7 to 8.3 m², with the ant-dispersed seeds moving no more than 2

m.⁸³ Dunes and swales are likely to be frequently confounded only on islands with frequent washover events. Thus, the dispersal patterns of herbaceous plants in dune environments support the hypothesis that selection here is for the occupation of suitable small patches of habitat, and not for the avoidance of competition with parents or other vegetation, or the occupation of new habitat distant from the site of the original population.

The persistence of dispersed seeds as a seed bank in the dune soils has been considered by only a few investigators, and these studies have been based on coastal dune systems. In all cases, seed banks in dune soils were found to be small to nonexistent. Fore-dune soils on Lake Michigan have virtually no seeds, and dune forest soils have only a very small pool (3 seeds per soil sample).⁸⁴ For those dune annuals that have been examined, near-100% germination removes all seeds from the soil each year.^{77,85} In the coastal dunes near Veracruz,⁸⁶ seven species of perennials produced a seed bank of 213 to 629 seeds/m², with larger concentrations on the lee and side slopes of the parabolic dunes. These seed pools are comparable to salt marsh seed pools, but are one to two orders of magnitude smaller than those of other herbaceous ecosystems.⁶⁴ The lack of seed pools for the annual species and the presence of a seed pool for the perennial plant community contrast with the more commonly observed presence of large seed banks for short-lived species, and smaller seed reserves of long-lived species.⁸⁷ If the sparse data presented here can be used to predict patterns, they would suggest that seed bank size would increase with distance from the strand, as perennial herbaceous species are added to the flora along the "typical" temperate zone barrier island transect. The paucity of seed banks in the dune floras probably also reflects the instability of the soil; continual deposition and erosion of fresh sand would both bury seeds too deeply for emergence, or remove them entirely. Thus, habitats with substantial substrate movement may select against the evolution of long-term dormancy mechanisms.

Dispersal in the strand and fore-dune environments involves the movement of vegetative structures, such as fragments of rhizomes and stems, as, or more, commonly than it does the movement of seeds. Such dispersal has been noted, for example, for *Paspalum vaginatum*, *Spartina* spp., *Elymus arenarius*, *Sporobolus virginicus*, and *Ammophila arenaria*.⁶⁵ In many parts of the North Atlantic coast, wrack deposits are extensive from large off-shore populations of *Zostera* and macrophytic algae, and continuous lines of *A. breviligulata* sprouts arise from fragments embedded in the organic matter. On South Atlantic beaches, wrack deposits are more sparse, and *Uniola* sprouts from vegetative material are found only occasionally.⁸⁸ On lakeside dunes, 99.98 and 99.99% of *A. breviligulata* plants at two sites were derived from water-dispersed fragments (density of 20/m²), rather than seed germination (density of 0.004/m²).^{89,90} *Uniola paniculata*, in contrast, relies on seeds for the establishment of new populations, and more rarely disperses through the sprouting of rhizome or stem fragments.⁷⁸

The dispersal biology of plants in barrier island communities other than the strand and fore-dunes has received virtually no attention. This is perhaps not surprising since the woody plant communities, and their environments, appear more similar to mainland environments, and do not seem to pose the striking problems of existence evident on the strand and fore-dunes. The frequency of dispersal syndromes associated with obvious morphological features was explored in several barrier island floras by using descriptions of dispersal syndromes of particular species^{65,67} and descriptions of the fruits in regional floras to estimate the relative importance of different modes of dispersal on barrier islands (Table 2). Dispersal syndromes clearly identifiable from known habitat (e.g., submerged aquatics) and fruit morphology (e.g., plumose appendages or wings, fleshy tissues, etc.) were distinguished; plants with seeds or fruits lacking any obvious morphological adaptation for dispersal were lumped as "other", without regard to their potential for dispersal in animal guts, in adhering mud, etc. The wide variety of dispersal syndromes found in barrier island floras (Table 2) suggests that the species diversity and species composition of barrier island vegetation may be more strongly limited by other factors (for example, physiological constraints related to environmental stress and paucity of habitat types) than by the ability of seeds to reach the islands. The periodic attachment of some barrier islands to the mainland following closure of inlets may also permit some species to occupy barrier formations that would otherwise be unable to colonize an island because of a lack of suitable method for long-distance dispersal over water. Mechanisms for long-distance dispersal are currently viewed as ancillary results of selection for local dispersal abilities.⁶⁶ The fact that most of the herbaceous plants of barrier islands fall in the "other" category argues that the ability for long-distance dispersal has not been a requirement for species to reach these islands.

Berry-bearing trees tend to be as or more common than wind-dispersed trees on these islands. In mainland temperate forests, berry-bearing trees tend to be less common (10 to 25% of trees) than wind-dispersed species (29 to 38%), and a variety of other dispersal modes are observed that are rare or absent from the barrier islands.⁶⁶ However, the most abundant tree species of many of the Atlantic and Gulf coast islands — oaks and pines — include nut-bearing (animal-dispersed) and wind-dispersed species. Thus, animal (bird) transport of fleshy fruits contributes disproportionately to the total species diversity of the tree stratum on these islands, but not to the community structure (relative abundance of species) of most maritime forest communities. The *Ilex*-dominated forests of Fire Island, New York and Sandy Hook, New Jersey are exceptions in that most of the dominant species bear fleshy fruits.

The shrub/vine communities are dominated by berry-bearing species (67 to 88%). The shrub stratum of inland temperate forests is similar; 85 to 100% of shrub species are berry-bearing,⁶⁶ and the preponderance of fleshy fruits on shrub species

Table 2
Distribution of Dispersal Syndromes in the Floras of Several Atlantic Coast Barrier Islands: Number of Species and Percentage in Each Dispersal Category

Site (Ref.)	Total no. SPP	Plant type	Berries	Wind	Animal adhesion	Nuts	Other	Water ^a
Fire Island, NY (11)	405	Tree	7(26.9)	14(53.8)	0	5(19.2)	0	0
		Shrub/vine	40(78.4)	4 (7.8)	0	0	7(13.7)	0
		Herbs	13 (4.1)	51(14.6)	18 (5.6)	0	237(74.3)	9 (2.8)
Assateague, VA (13)	419	Tree	13(41.9)	12(38.7)	0	6(19.4)	0	0
		Shrub/vine	33(84.6)	4(10.3)	0	0	2 (5.1)	0
		Herbs	5 (1.4)	58(16.6)	18 (5.2)	0	259(74.2)	9 (2.6)
Cape Hatteras, NC (12)	513	Tree	9(25.7)	9(25.7)	3 (8.6)	11(31.4)	4(11.4)	0
		Shrub/vine	45(67.2)	4 (6.0)	1 (1.5)	0	17(25.3)	0
		Herbs	16 (3.9)	85(20.8)	20 (4.9)	1 (0.2)	28(68.7)	6 (1.5)
Horn Isl., MS (14)	260	Trees	3(50.0)	1(16.6)	0	0	1(16.6)	1 (6.6)
		Shrub/vine	15(88.2)	0	0	0	0	2(11.8)
		Herbs	6 (2.5)	34(14.1)	22 (9.1)	165(68.6)	9 (3.7)	0
Petit Bois Isl., MS (14)	87	Trees	0	1	0	0	0	0
		Shrub/vine	7(87.5)	0	0	0	0	1(12.5)
		Herbs	5 (6.4)	14(17.9)	2 (2.6)	54(69.2)	3 (3.9)	0

^a Includes only species specifically described as dispersing in seawater.

is generally recognized.⁹¹ The commonly-held supposition that barrier island floras are highly dependent on bird-mediated seed dispersal is thus only partly supported by these data. Shrub communities are abundant because of the constraints of salt spray, shifting sand, storm effects, and other environmental constraints. If it is the case that most shrub species bear bird-dispersed fruits, the fact that shrub-dominated communities are largely bird-dispersed tree species, however, does support an important role for birds in determining the composition of barrier island floras. Bird-dispersed trees and shrubs are also disproportionately represented in the scrub and forest communities of the South African coastal dunes.⁹² These patterns suggest that the association of bird-dispersed communities with barrier islands may be related to the high proportion of shrub-dominated vegetation common in coastal habitats, rather than to the role of birds in bringing seeds to islands.

Although the herbaceous flora is dominated by small, generalized seeds, all major dispersal syndromes are represented, and occur at similar frequencies on the several islands surveyed in Table 2. The species in the "other" category undoubtedly include species dispersed by vertebrates through ingestion and adherence in mud; also species whose seeds are dispersed by ants may be included. About 5% of the herbaceous plants are in genera listed by Beattie⁹³ in his compendium of ant-dispersed taxa, suggesting that myrmecochory should be included among the dispersal syndromes present on barrier islands. It is also likely that many of these generalized fruits are dispersed by a variety of modes — gravity, water, wind, animal ingestion or movement, as was illustrated for *Cakile* spp. above.

The frequency with which different dispersal modes occur on barrier islands can be expected to vary with the zonation of the vegetation. On the dunes of the Yucatan coast, Espejel⁹⁴ found that about 45% of the beach species were ocean-dispersed, wind-dispersal was most common (about 25% of the flora) in sheltered fixed dunes and on dune tops, and animal-dispersed plants were most characteristic of slacks, fixed dunes, and ruderal areas. This distribution corresponds well to the theoretical expectation that wind dispersal predominates in arid habitats, whereas animals, gravity, and other factors are more important in moist or wet habitats.⁶⁶ Shrub-dominated communities will have a preponderance of animal-dispersed plants, because of the tendency, discussed previously, for shrub species in general to produce fleshy fruits. Maritime forests are more diverse in dispersal biology; a mixture of dispersal types are present on most islands.

2. Seed Survival

In a few studies, the fate of seeds has been followed between seed production and seed germination. In a population of *Uniola*,⁷⁸ 70% of the ovules aborted, and this provided a site for the invasion of various fungal infections. At least 18 species of insects were collected feeding on the fungal tissue as well as floral tissue. Bird predation on mature *Uniola* seeds accounted for up to 80% of total seed set, and predation by mice and other small mammals on spikelets on the ground caused additional mortality (amount unspecified). Only 2.7% of the seed set survived the fall and winter, and was available for germination. Maun⁸⁹ noted that in *Ammophila breviligulata*,

failure of seed set could account for 20 to 39% reduction in potential seed production. Insect herbivory can reduce the seed set by *Salix repens* by as much as 50%.⁴⁸

3. Seed Germination

As in the studies of dispersal, the literature on seed germination and seedling establishment of barrier island and coastal dune species is concentrated on strandline and foredune species, with a decreasing abundance of studies on species progressively further from the beach. The implicit assumption in much of the work on seed and seedling biology has been that these aspects of the biology of strand and dune plants control individual species population dynamics. It is also implicitly assumed that the mortality caused by salinity, dessication, sand movement and other stresses during these stages of plant development act as a filter controlling the diversity of the vegetation.

Table 3 summarizes the conditions required for germination for a variety of beach and dune plants. For many of the species studied, alternating temperatures enhance germination; for some species (e.g., *Iva imbricata*, *Uniola paniculata*), they are required. Ignaciuk and Lee⁷⁰ point out that such a requirement ensures that the seeds are not buried too deeply, since the diurnal fluctuation of temperature decreases rapidly with depth. The need for stratification of the seeds is more variable; some, like *Iva imbricata* and some populations of *Uniola paniculata*, require stratification; others, like *Physalis viscosa* or *Spinifex hirsutus*, germinate without pretreatment. Low-temperature stratification appears to be relatively uncommon among the species studied, however. Seneca and his co-workers have documented clines in the stratification requirements for *A. breviligulata* and *U. paniculata*. In *Ammophila*, northern populations required at least 15 d exposure to 4°C to get 63% germination, whereas 73% of seeds from North Carolina populations germinated with no cold pretreatment.⁹⁸ Similarly, seeds from Florida populations of *U. paniculata* had no requirement for cold pretreatment, whereas seeds from Virginia and North Carolina need 30 d at 4°C to achieve 90% germination.⁹⁵ In contrast, there is no geographic variation in germination requirements of *Cakile maritima* along the California coast.⁷⁴

Angevine and Chabot,⁶⁰ in their review of seed germination syndromes, suggested that several alternative strategies can be adopted by plants to avoid conditions dangerous to seedlings. Seeds can avoid competition by using long-term dormancy and maintenance of viability to "wait" until appropriate conditions arise, or they can disperse widely and germinate immediately, thus taking advantage of widely separated patches of suitable habitat. Although these syndromes have been verified in other groups of plants,⁸⁷ they do not appear to have much validity for the strand and dune plants examined so far. As the examples discussed illustrate, many of them combine poor dispersal ability (or the lack of any apparent mechanism for long-distance

Table 3
Germination Requirements of Seeds

Species	Requirements/conditions	Ref.
<i>Physalis viscosa</i>	Light enhanced; no stratification	79
<i>Erigeron canadensis</i>	Light enhanced; no stratification	79
<i>Iva imbricata</i>	Light enhanced; requires stratification at 4°	79, 239
<i>Solidago sempervirens</i>	Light enhanced; variable temp. enhances	79
<i>Cakile maritima</i>	Light-inhibited	44, 70
<i>Uniola paniculata</i>	Variable cold stratification with latitude; alt. temp	96, 97
<i>Ammophila breviligulata</i>	Variable stratification with latitude; variable temp enhances	95, 98
<i>Abronia maritima</i>	Alternating temperature enhances; low salinity	99
<i>Calystegia soldanella</i>	Alternating temperature enhances; low salinity	99
<i>Panicum amarulum</i>	Alternating temperature	95
<i>Cakile edentula</i>	Cold stratification; alternating temperature	80
<i>Atriplex glabriuscula</i>	Alternating temperature	70
<i>Atriplex laciniata</i>	Alternating temperature	70
<i>Salsola kali</i>	Temp. 30°C; stimulated by NaCl at low temp.	70
<i>Spinifex hirsutus</i>	Alt. temp.; light-inhibited; no stratification	100
<i>Croton punctatus</i>	Alt. temp.; scarification	79
<i>Strophostyles helvola</i>	Scarification only	79
<i>Pancratium maritimum</i>	No stratification; light-inhibited, tolerates low salinity	69
<i>Ammophila arenaria</i>	Alternating temperature; stratification enhances germination	101
<i>Atriplex leucophylla</i>	Optimum temperature 25°C, temperature range varies geographically	102

dispersal) with low long-term viability (as evidenced by the absence of seed banks in the soil) and few dormancy mechanisms (at least with respect to temperature and light).

Soil salinity is frequently cited as one of the factors most likely to limit seed germination on barrier island (or other coastal) environments. Table 4 summarizes the results of a variety of studies through the adjustment of the reported salinities to units of mmol NaCl/l (from percent NaCl and percent seawater), and the values for 50% and 100% reduction in germination interpolated from the figures or tables published. Temperature conditions and the rinsing of seeds in freshwater following their immersion in salt water strongly affects the response of many species. Most driftline and dune species can germinate in water with some salt content, but most cannot tolerate salinities approaching those of seawater. The characteristic dune-building grasses of the Atlantic and Gulf coasts, *A. breviligulata*, *U. paniculata*, and *P. amarulum*, are among the species most sensitive to salt. Dune species likely to be flooded by overwash, including *S. patens*, *S. valerandi*, *C. littorale*, are more tolerant of salt. Members of the Cheno-

Table 4
Effects of Salinity on Seed Germination Expressed as Percent Reduction in Germination. Salinity in mmol NaCl/l. (Seawater is approximately equal to 600 mmol NaCl/l.)

Species	Salinity at 50% reduction	Salinity at 100% reduction	Comments	Ref.
<i>Ammophila breviligulata</i>	70—128	120—170	Geographic variation	95, 98
<i>Cakile maritima</i>	60—300; 900 ^a	240—600	Less effect at higher temp.	70, 104, 105
<i>Plantago coronopus</i>	62	250	Less effect at higher temp.	103
<i>Uniola paniculata</i>	90	257		95
<i>Panicum amarulum</i>	170	342		95
<i>Samolus valerandi</i>	180	250		103
<i>Scrophularia nodosa</i>	180	250		103
<i>Digitalis purpurea</i>	180	250		103
<i>Atriplex glabriuscula</i>	100—300; 240 ^a	600—900; 900	Less effect at higher temp.	
<i>Atriplex laciniata</i>	240—300; 900	600—900; 900		
<i>Centaurium littorale</i>	250	N.D.		103
<i>Elymus arenarius</i>	300; 300	600; 900		105
<i>Pancratium maritimum</i>	375	500		69
<i>Salsola kali</i>	450; 900	900; 900	Enhancing effect at low temp.	70, 105
<i>Suaeda maritima</i>	300; 300	900; 900		105
<i>Spartina patens</i>	513	685		95

^a Exposure to saltwater followed by rinsing in freshwater before germination test.

podaceae that colonize the beach, particularly *S. kali* and *S. maritima*, are among the most tolerant of salt. Species vary also in their tolerance of salt water for long periods of time. *C. maritima* tolerates up to 5 d of immersion before germination decreases, but *Atriplex* spp. and *S. kali* can tolerate over 30 d immersion.⁷⁰

Woodell¹⁰⁵ distinguished three types of response of seeds to salinity. A Type I response, characteristic of dune and driftline species rarely exposed to inundation, involved sensitivity to salt, including only a partial recovery in freshwater. A Type II response, characteristic of dune species most commonly found in hollows or other areas subject to overwash, involved greater resistance to salt, and a complete recovery after re-immersion in fresh water. A Type III response, more characteristic of salt marsh than dune or driftline species, involved enhanced germination following exposure to salt water and return to fresh water. She concluded that tolerance to salt exposure, and the stimulation of germination by initial exposure to salt, was directly related to the likelihood that a given species would be inundated in its natural habitat. The coupling of salt-induced delay in germination followed by successful germination following re-immersion in fresh water observed by Woodell for many species may reflect a mechanism whereby germination is delayed until exposure to freshwater (presumably through rainfall) reduces soil salinity.

Sand movement is also frequently considered to be a limiting factor on seed germination and establishment in coastal environments. Tyndall et al. compared the ability of seedlings of several species to elongate to the likelihood of their being buried by sand.¹⁰⁶ The seedlings of *C. edentula*, the only spe-

cies found on the beach, were covered by an average of 5.4 to 5.5 cm of sand, but could elongate to 19.0 cm under optimal laboratory conditions. The dune species, *U. paniculata* and *S. patens*, were unable to elongate either on towels or under sand sufficiently to emerge from 5 to 6 cm of sand deposition. A sand-flat species, *Triplasis purpurea*, was able to elongate 5.5 cm under sand under the experimental conditions, but was never observed on the beach. The authors concluded that seed burial probably acts as an important, but not the sole, filter determining species diversity of the strand community through its prevention of germinating seeds from reaching the surface.

Similar findings have been reported for other groups of species. The optimal depth of burial for *Elymus canadensis*, *C. edentula* and *A. breviligulata* (2 to 4 cm) was similar to the observed depth of burial of naturally occurring seedlings (3.49 to 3.84 cm).¹⁰⁷ Other dune species, including *Spinifex hirsutus*,¹⁰⁰ *U. paniculata*,⁷⁸ and *Vulpia fasciculata*⁷⁷ emerge from 1 to 5 cm of burial, with emergence decreasing to zero as burial increases to 10 to 15 cm. *A. breviligulata*, however, can survive these higher levels of sand accretion.¹⁰⁸ Species whose seedlings can emerge after burial usually have heavier seeds than species without this ability,^{79,99,107,109,110} Survival also may vary with the proportion of the seedling buried, rather than the absolute amount of sand accretion.⁸⁰ The ability of seedlings of a species to survive sand deposition is clearly a primary factor in determining its likelihood of long-term membership in the flora of the barrier island habitats subject to mobility of the sand. However, the ability of seeds to germinate and emerge after burial should be distinguished from the ability of established seedlings to tolerate burial, elongate and re-merge. For

example, the studies summarized above suggest that *A. breviligulata* seeds are not highly tolerant of burial, but that once established, the seedlings are highly tolerant of burial (see also the following). No species of the beach or foredune environments — those habitats with a maximum of sand movement — can emerge from the common amounts of annual deposition (20 to 100 cm), and even the amounts of sand deposition over the winter season are usually greater than the depths from which these species can emerge. Therefore, even though species typical of environments with large amounts of sand movement have large seeds permitting emergence after burial, their survival must depend on separation of the times of seed germination with the periods of frequent and intense sand-moving storms. In other words, successful germination and establishment must either occur rapidly after shedding of seed, before large amount of sand movement occur, or must be timed to coincide with seasons of low sand mobility. This analysis also suggests that the germination ecology of beach populations may differ from those of stable dune populations, in that reworking of beach sands, movement of seeds in the waves, and deposition in driftlines may obviate the need to emerge from large amounts of sand deposition. Thus, seeds of *Cakile* spp., which can float in seawater and retain its viability at least for short times, could be kept at a manageable depth for successful germination in beach environments by repeated burial, erosion, and local water transport in the surf to new positions in the drift line. Dune populations, however, will be dependent on germinating before excessive amount of sand deposition can occur.

Having germinated, seedlings must survive a variety of mortality factors in order to become established plants. Table 5 summarizes sources of seedling mortality that have been identified either qualitatively, through casual observation, or quantitatively, through experiments or measurements, for some of the dominant strand and dune species. The primary role of sand movement in the strand and dune environments is clear. Large amounts of sand movement can either bury seeds too deeply for the seedlings to emerge, or can completely remove seeds or seedlings through erosion. Small amounts of erosion frequently cause death through dessication, because of the exposure of the immature root system. In *A. breviligulata*,¹⁰⁸ when the sand level falls below the coleoptilar node (with as little as 1 cm change in elevation), the weak mesocotyle is likely to break; in addition, insufficient adventitious roots form to absorb water. Water stress imposed by the low water capacity of the surficial sands is also identified as a stressor by several authors. Other sources of mortality include herbivory, which can account for 12% of observed seedling death and trampling.

The moisture content of the substrate must be within narrow limits to avoid mortality from dessication or from fungal attack. Excessive moisture can promote fungal infection and mortality from damping-off, as Keddy^{72,73} found for *C. edentula* seedlings in some sites and years. Damping-off was particularly

associated with seedling germination in wrack; in one site, seedlings in bare shingle had a survival rate of 80 to 97% whereas seedlings in wrack had a survival rate of 36 to 67%. For other species, however, wrack provides sufficient additional moisture to allow seedling survival. For *A. arenaria*, sites of slightly greater available moisture than the usual quality of the surface sand are crucial for seedling survival.¹¹² Thus, in the beach and dune environments, seedlings evidently are dependent on finding microsites with moderate amounts of sand movement and levels of soil moisture that are high enough to support plant growth but not so high that they encourage fungal infection.

B. Individual Species Biology: Plant Growth and Life History

Once plants have become established from seeds or vegetative tissues, new plants grow under the joint control of environmental factors and biotic interactions with individuals of the same and other species. In reviewing the data on growth, reproduction and death of barrier island plants, and the morphological, physiological, and genetic determinants of these parameters, I focus on the issue of whether particular patterns are apparent among these species that reflect the environmental constraints of barrier island habitats, and that distinguish barrier island vegetation from non-coastal vegetation.

1. Growth Patterns: Plant Architecture and Morphology

The structure of plant individuals reflects both long-term evolutionary response to environmental factors and short-term plastic responses to local environmental conditions. The response of dune-forming grasses to variations in environmental conditions has been extensively analyzed; the morphology and biotic responses of other species have received less attention. The biology of *Ammophila*, has, in particular, received extensive analysis, including studies of *A. arenaria* in Europe^{46,101,117-125} and western North America,¹²⁶⁻¹²⁹ and studies of *A. breviligulata* on lakeshore coasts and barrier island coasts in North America^{75,89,95,98,108,130-137} and many references in the dune stabilization literature.¹³⁸⁻¹⁴⁰

Many of the dominant species of both the foredune grasslands and the backdune scrub vegetation are clonal, spreading through vegetative growth of tillers or rhizomes. This growth habit not only produces a "bud bank" in the soil that is analogous to a seed bank, but allows the plant to explore the space around it. These features are well illustrated by the patterns of clonal growth of *A. breviligulata*^{89,134,136} (Figure 7). An initial plant, produced from seed or from the germination of a dormant bud on a rhizome fragment, sends out several plagiotropic (lateral) rhizomes in all directions; these primary rhizomes, usually about 1 m long, can be up to 3.9 m long, and contain about 15 dormant buds per meter. Average lateral spread is 2 to 3 m/yr.¹⁴⁰ These buds are capable of producing up to three

Table 5
Sources of Seedling Mortality

Species	Source of mortality	Habitat	% of population killed	Ref.
<i>Cakile edentula</i>	Sand movement (erosion and burial)	Lakeshore	4.5	80
	Dessication		32	
	Herbivory		9	
	Total		86—95	
<i>C. edentula</i>	Damping-off	Gravel bar-shingle	3—20%	72
		Gravel bar-wrack	33—67	
<i>C. edentula</i>	Damping-off	Barrier beach	0—35	73, 112
		Sand dune	Density and year-dependent; higher on strand	
<i>C. maritima</i>	Herbivory	Dune	12	74
	Herbivory	Strand	0	
	Total	Dune	100	
	Total	Strand	95	
<i>Cakile maritima</i>	Drought	Foredune	91	110
<i>Ammophila breviligulata</i>	Micro-erosion near seedling	Lakeshore	7	107
	Dessication		93	
	Total		100	
<i>Ammophila breviligulata</i>	Drought	Lakeshore	100	80
<i>Ammophila breviligulata</i>	Sand burial, erosion		90—100	79
<i>Ammophila arenaria</i>	Rabbit grazing	Coastal dunes	1	101, 111
	Dessication	Coastal dunes	N.D.	
<i>Lithospermum caroliniense</i>	Dessication	Lakeshore	0.80—67.8	75
<i>Vulpia fasciculata</i>	Herbivory	Fixed dunes	0—5	77
<i>Vulpia fasciculata</i>	Wind-drag dessication	Coastal dune	12—28	113, 114
	Total		7—41	
<i>Ptelea trifoliata</i>	Dessication	Lakeshore	63.2	115
	Trampling		22.1	
	Miscellaneous		14.7	
	Total		89.5	
<i>Solidago sempervirens</i>	Burial/erosion	Strand	Near 100	79
<i>Erigeron canadensis</i>	Burial/erosion		Near 100	79
<i>Physalis viscosa</i>	Burial/erosion		Near 100	79
<i>Strophostyles helvola</i>	Salt spray		Near 100	79
<i>Erigeron canadensis</i>	Burial/erosion		Near 100	79
<i>Xanthium strumarium</i>	Blowing sand, dessication	Beach	N.D.	116
<i>Salix repens</i>	Drought	Dune slack	100	48

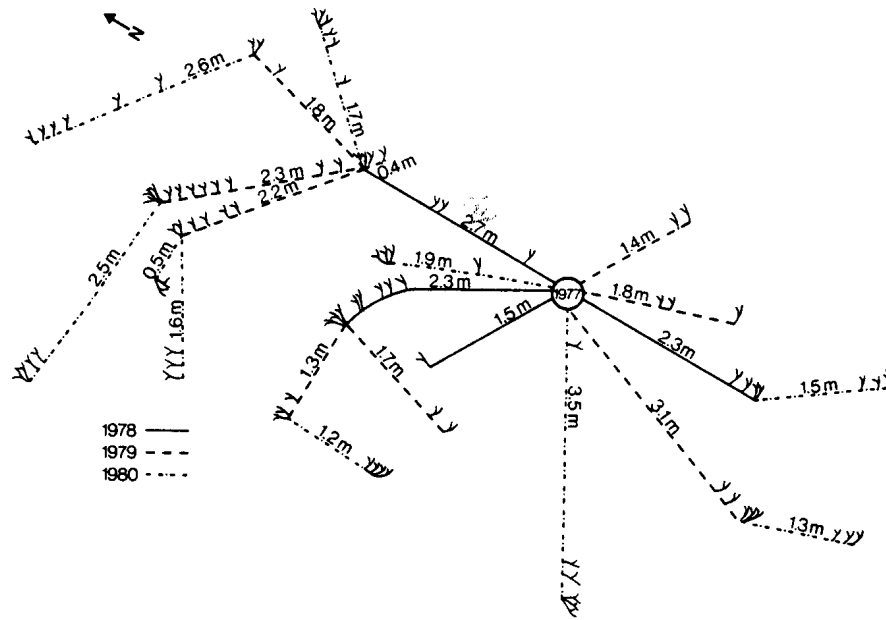


FIGURE 7. Patterns of rhizome growth of *Ammophila breviligulata* over a three-year period, from a single plant. Rhizome length in meters. (From Maun, M. A., *Can. J. Bot.*, 63, 113, 1985. With permission).

secondary rhizomes, as well as a shoot. However, most buds remain dormant, with a maximum of 41% of the nodes producing new rhizomes. The number of ramets (new shoot plus associated roots) produced is very variable, ranging from 8 to 81% of the nodes, and resulting on average in 10 to 13 ramets per clone per year. Most of the germinating buds are located in the distal portion of rhizome, as the proximate portion rapidly becomes brittle. Secondary rhizomes are usually shorter than the primary rhizomes, and, although they start growth in June (well after the beginning of the growing season in April), they show the most growth in autumn. All rhizomes grow laterally, but at the beginning of the next growing season, they become orthotropic (erect) and produce a new shoot. The result of this pattern of growth is an increase in area occupied by a plant of about 9.5 m²/yr, and an increase in total rhizome length of about 14 m/yr. Wave action is effective in cutting the rhizomes into pieces 10 to 80 cm long, with two to five buds per fragment. With at least two buds on a fragment, there is a high rate of success (100%) in the establishment of at least one ramet per fragment.

Ammophila arenaria grows in a slightly different way. A newly established plant sends out a long horizontal rhizome with many dormant buds (approximately 9.6/m along a mean of 2.2 m primary rhizome length per plant.¹¹⁸ Some of the buds produce leafy shoots; sand accumulation around these shoots stimulates the production of vertical rhizomes, extending upwards towards the sand surface.¹¹⁷ About 8.7% of total seasonal growth is devoted to rhizomes, and of this, 98.2% consists of vertical rhizomes (containing 96.9% of the bud bank).^{128,129} Like *A. breviligulata*, vertical rhizomes can pen-

etrate up to a meter of sand. Buds on the vertical rhizomes are more prone to development into leafy shoots, resulting in a tussock of *Ammophila* shoots. Clumps occupy an area on average 20 to 40 cm² in dimension.¹¹⁹ Vertical rhizomes occasionally branch, producing more tillers per rhizome tip and a larger clump. Clumping at a somewhat larger scale (80 to 160 cm) appears to be attributable to environmentally-determined survival of seedlings or sprouts from rhizome fragments. Cyclic variations in the length of internodes may occur on the rhizomes, with buds following longer internodes being more likely to produce leafy shoots. As the system of vertical rhizomes and dense leafy shoots develops, the original horizontal connection between clumps dies. In vigorous young populations on mobile dunes, there are co-occurring high rates of tiller birth and death,¹²² producing a high flux rate; in populations on the oldest dunes, there may be slower rates of turnover. Rhizome fragmentation is, like in *A. breviligulata*, an effective means of dispersal and initiation of new individuals.¹²³ *Agropyron junceiforme* and *Elymus arenarius*, two other dune-forming grasses of northern Europe, have similar clonal growth forms, but with shorter, shallower roots and rhizomes that can only survive amounts of sand deposition up to 30 cm per year.⁴⁶

Small differences in resource allocation can result in large differences in growth form. *Elymus mollis* (*sensu* Hitchcock and Cronquist¹⁴¹) a co-occurring dune grass on the Pacific coast of North America, has a clonal growth form similar to that of *A. arenaria*. It devotes a slightly larger fraction of its total growth to rhizomes (11.6%), and only 32.2% of these are vertically oriented. The bud bank is approximately equally distributed between vertical and horizontal rhizomes. As a re-

sult of these differences, *Elymus* clones are more spatially extensive, while *Ammophila* clones consist of dense tussocks. The dense growth of *Ammophila* tillers produces a larger above-ground biomass with greater leaf area, and permits it to exclude other species (including *Elymus*).^{128,129}

A slightly different pattern of clonal growth in dune grasses is found in *Carex arenaria*, a plant commonly found near the base of dunes in Britain.¹⁴² This plant produces two kinds of rhizome structures: both types consist of four nodal units in a linear array. In one type the internodes are long, and in the other, the internodes are very short (0.5 to 1.0 mm), producing clustered tillers. On each nodal unit, there are two buds, one producing an aerial shoot and rhizome unit system, and the other either remaining dormant or producing a second shoot/rhizome unit. The linear extension of both long and short units produces an advancing front that colonizes new areas in an annular pattern, while the remaining population becomes senescent. The clones thus have an overall age-structure of juvenile, adolescent, mature and senile phases, and the whole population moves across the habitat.¹⁴³ The other dune grasses lack this internal population structure; older tillers remain vigorous and the population spreads rather than travels. Although there are considerable variations among the age-classes in the population dynamics of shoots and rhizomes, all phases are characterized by a rapid turnover (similar high birth and death rates) of tillers, and this flux occurs every month of the year. Dormant buds form a large pool in the soil (up to 840/m²), with 60% of all bud sites occupied by dormant buds. Rhizome units can survive for at least seven years. The linear spread of the rhizomes results in an efficient exploration, occupation, and subsequent infilling of space (Figure 8).

Arctostaphylos uva-ursi, one of the common low-growing woody shrub species of the secondary dunes,^{144,145} is one of the few woody clonal species of barrier islands whose clonal architecture has been investigated. Remphrey et al.¹⁴⁶ analyzed the growth patterns and form of this plant both on stabilized sand dunes and also in boreal forest. A patch is composed of shoot complexes, each complex in turn composed of different kinds of shoots. Colonizing complexes, found on the periphery of the patches, consist primarily of dominant shoots that are long (8 to 12 cm), and are decumbent (mostly between 0 and 20° elevation angle); these complexes also contain some non-dominant short, erect shoots (2.3 cm long and elevation angle 71 to 90°). Maintenance complexes within the clone consist mostly of these short, erect shoots. Colonizing complexes often have a high order of branching, and lateral branches predominate over linear, monopodial growth forms. Basal burls, consisting of dormant clusters of lateral buds, also serve as a source of maintenance shoot complexes.^{147,148} Shoots can produce leaves from buds formed during the current season in addition to buds formed during the previous season;¹⁴⁹ this ability to produce new leaf tissue in response to favorable environmental conditions permits an opportunistic, exploitative growth strat-

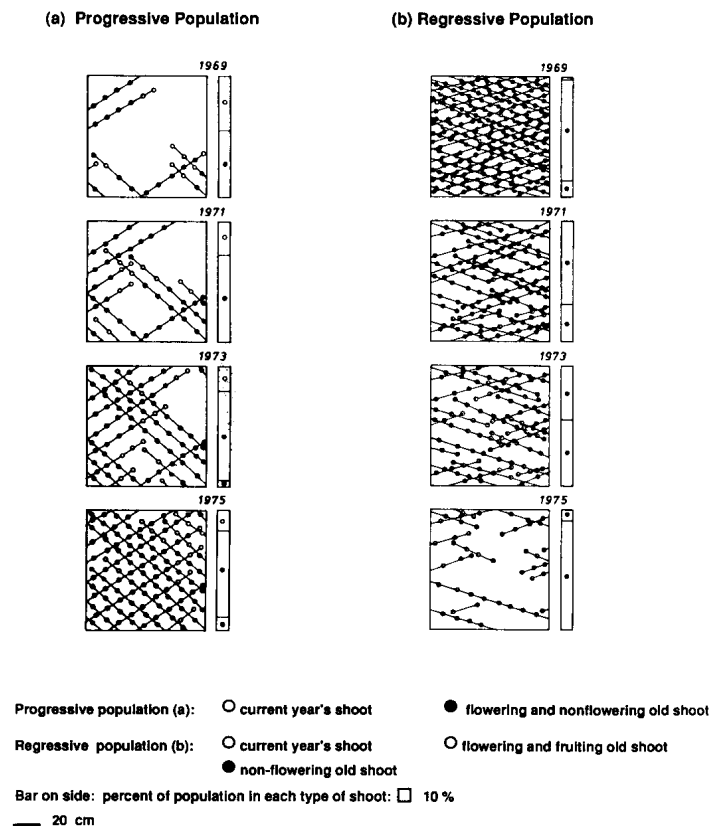


FIGURE 8. Patterns of clonal expansion and regression in *Carex arenaria*. The lines connect individuals on the same rhizome. The vertical bar indicates the percentage of the total population in each kind of shoot. (a) progressive population, (b) regressive population. (From Symonides, E., *Ekol. Pol.*, 27, 191, 1979. With permission.)

egy. The underground architecture of the plant also has a highly ordered morphology, with "woody frame units" arranged in a branched, hierarchical sequence. Colonizing units, associated with colonizing complexes of shoots, produce a primary woody frame, and minor units, associated with maintenance shoot complexes, are produced within the primary frame and help fill in the space between colonizing units. The roots branch repetitively, produced up to eight orders of branching. The frame units are horizontal, and successive layers of frame are connected by short, inclined structures.

The plant population studied in a boreal forest habitat had a significantly different growth pattern, with less compact patch development, more upright stems, and more linear, monopodial growth. The variation in plant architecture between the sand dune and forest sites was attributed to environmental factors (possibly light intensity), rather than genetic differentiation, because more linear, upright plants were found at the perimeter of the sand dune site, in a forested ravine. In the sand dune habitat, the net result of these branching patterns are a centrifugally expanding compact prostrate mat, which does not show features of central death, peripheral regenera-

tion, and migrating or arcuate form. The continuous reorientation of vertical shoots to a more decumbent position permits the plant both to survive sand deposition, and to continue to spread (and form a new tier within the below-ground woody frame) after burial. Modeling studies of this growth pattern¹⁵⁰ demonstrate that it is very effective in covering an area and in exploring and utilizing the space within that area.

There are several potential advantages of rhizomatous growth for the acquisition and utilization of resources spread out in a sparse and discontinuous manner. As discussed previously with respect to seed dispersal, patches of suitable habitat in beach and dune environments are small, and strongly contrasting habitat types (e.g., xeric dune slope and hydric swale) are in close proximity. In some clonal plants, directed growth of rhizomes can lead to expansion of the clone in more favorable microenvironments.¹⁵¹ Lovell and Lovell¹⁵² have reviewed this ability of vegetative structures to discover and utilize patchily distributed microsites of suitable or superior habitat. Under conditions of low resources (nutrients and/or water), rhizomes are often long, with little branching or ramet initiation; in pockets of improved conditions, adventitious rooting will contribute to the production of vigorous ramets and increased branching of the rhizome or stolon. Local sites of high nutrient availability may, in turn, affect whether a bud gives rise to a new rhizome or a shoot. These features of rhizomatous spread are well documented for "guerilla" species⁶² — species with long internodes on the rhizomes or stolons, that can extensively explore habitat space. The value of such spatial exploration for nutrient acquisition has been demonstrated for several dune species (including *Carex arenaria*,^{153,154} *Fragaria chiloensis*,¹⁵⁵ and *Hydrocotyle bonariensis*),¹⁵⁶ in which the growth and nutrient content (N, P, and carbon compounds) of new ramets is subsidized by the older ramets. Rhizomes can thus cross unsuitable areas, and new shoot/root complexes can become well established without the need to be initially self-sufficient. In contrast, species forming dense, compact clusters — "phalanx" species⁶² — evidently rely on the ability to intensively use the available resources for pre-empting a site, reserving it from season to season. Many of the shrub species common to rear dune and swale habitats are probably similar to *Arctostaphylos* in belonging to this class of clonal plant.

The clonal growth patterns of the barrier island species that have been studied in detail seem to fall into these two groups of patterns. The herbaceous clonal perennials found on the primary dunes, and other sites of mobile sand, have linear rhizome systems, which Bell and Tomlinson¹⁵⁷ suggest is adaptive for the linear distribution of the habitat. It also permits both rapid and very extensive exploration of the physical habitat. The long rhizomes, with their large populations of dormant buds, are also well-designed for fragmentation into many small pieces, each of which can act as a propagule. Furthermore, the severe limitations on establishment and growth of the foredune and strand environment, imposed by shifting sand, salt spray,

and frequent catastrophic disturbance from storms, limits the number of competing plants which can occupy the site; thus, foredune herbs using a "guerilla" pattern of clonal spread are not likely to be competitively excluded by other plants. In addition, the very low level of nutrients available in the beach and dune soils may also favor an exploratory growth pattern, so that nutrient resources over a large area can be utilized. The growth pattern of *Arctostaphylos* and other shrubs produces compact patches which appear adapted to intensively utilize the habitat, and efficiently explore only the local environment of the plant. Species diversity is higher in the more sheltered habitats, thus increasing competitive pressure for space acquisition and retention. Such a pattern has been described for the plants of Japanese coastal dunes: clone size is greater in species growing in the unstable beach and foredune habitats than in species found on the fixed dunes.¹⁵⁸ Thus, the backdune environment appears to favor intensive utilization of the local environment, rather than the extensive exploration seen on the mobile dunes. The increased nutrient availability characteristic of the more developed soils of the more stable sites may permit plants to survive in patches of habitat that are small compared to the areas utilized by the exploratory species.

Root morphology and growth has been studied in sand dune habitats (mostly lakeside and coastal areas) by a small number of investigators, primarily in descriptive studies. Waterman¹⁵⁹ examined the morphology of a variety of species on the dunes of Lake Michigan. He noted that many dune species had enlarged root tips, with increased parenchyma which he attributed to the mechanical resistance of the sand. He observed that the roots of many, but not all species followed veins of organic matter through the soil. This was true, for example, of *Prunus pumila*, whose lateral roots followed the paths of decaying rhizomes through the soil, and whose shoot size was proportional to the amount of contact between the roots and local deposits of organic matter. The roots of *Lathyrus japonicus* also preferentially exploited layers of organic matter in the sandy soil. In contrast, the long roots of both *A. arenaria* and *Artemisia caudata* showed no association with organic matter deposits.

Root morphology could be expected to vary with the degree of substrate stability. However, the detailed investigations that have been carried out report strongly contrasting patterns. On a sequence of coastal dunes in Japan,¹⁵⁸ root depth was greatest in the most unstable habitats (those most prone to erosion and/or accumulation of sand) (Figure 9a). On the most unstable beach and foredune environments, root systems were composed of long laterals and associated adventitious roots (no tap roots) that uniformly filled the soil column to >100 cm depth. In more stable habitats (semi-fixed and fixed dunes), plants were more shallowly rooted (root depth roughly declining as the habitat became more stable), and a greater diversity of morphological types occur; a concomitantly greater degree of spatial separation between the roots of co-occurring species

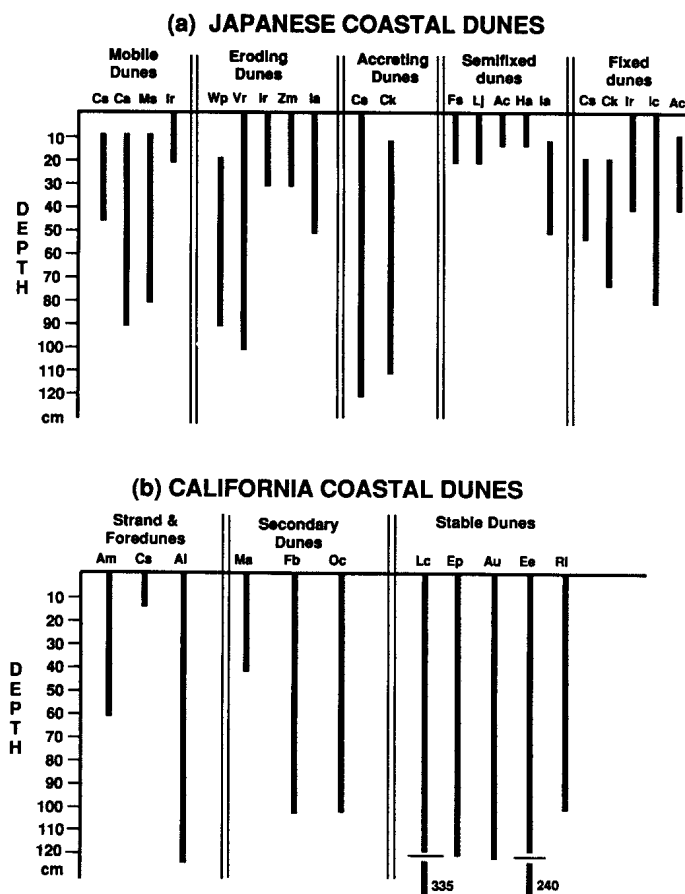


FIGURE 9. The distribution of roots with depth in two dune systems. (a) Japanese coastal dunes; (b) California coastal dunes. The bar represents the maximum vertical extent of roots of each species. Key to species: (a) Ac, *Artemisia capillaris*; Ck, *Carex kobomugi*; Cs, *Calystegia soldanella*; Fs, *Fimbristylis sericea*; Ha, *Heteropappus arenarius*; Ia, *Ischaemum anthe-phroides*; Ic, *Imperata cylindrica*; Ir, *Ixeris repens*; Lj, *Linaria japonica*; Ms, *Messerschmidia sibirica*; Vr, *Vitex rotundifolia*; Wp, *Wedelia prostrata*; Zm, *Zoysia macrostachya*. (b) Am, *Abronia maritima*; Cs, *Convolvulus soldanella*; Al, *Atriplex leucophylla*; Ma, *Mesembryanthemum aequilaterale*; Fb, *Fran-seria bipinnatifida*; Oc, *Oenothera cheiranthifolia*; Lc, *Lupinus chamissonis*; Ep, *Eriogonum parviflorum*; Au, *Abronia umbellata*; Ee, *Ericameria eri-coides*; Ri, *Rhus integrifolia*. ([a] from Yano, N., *Jour. Sci. Hiroshima Univ. Ser. B. Div. 2*, 9, 139, 1962.; With permission. [b] data adapted from Purer, E. A., *Ecol. Monog.*, 6, 1, 1939.)

was observed. In contrast, the perennial forbs and shrubs of the southern California coastal dunes¹⁶⁰ have the reverse relationship between rooting depth and habitat stability (Figure 9b). In the most unstable (maximum erosion/accumulation) habitats, the prostrate plants are very shallowly rooted, without extensive taproots. In the somewhat more stable habitat of the primary dune and dune slack, root systems are more extensive and include tap roots extending to 1 m depth; these species tended to be decumbent to low-growing erect shrubs. In the most protected parts of the stable dunes, erect, taller shrubs have taproots extending to 2 m depth, and extensive root/rhizome systems projecting laterally up to 5 times the canopy

diameter. On western tropical dunes, the most common shrub of the protected rear dune habitats, *Coccoloba uvifera*, also has deep and widely spreading roots.²⁹ In another study of California pioneer beach plants, De Jong¹⁶¹ found that the co-occurring native perennials had a wide range of root systems, from shallow fine roots in *Atriplex leucophylla* to the deeply tap-rooted *Abronia maritima*. Differing patterns of water and nutrient availability in different coastal habitats, related to differences in climate and sand mineralogy, may contribute to these differences in patterns of root development.

These few studies of root form in coastal environments suggest that there exists a great diversity of rooting strategies that can be found in each type of habitat in a dune system. If there are general relationships between environmental variables and the form of plant root systems, they have yet to be clearly demonstrated.

2. Growth Patterns: Response to Sand Burial

Burial by sand and plant growth have an interactive relationship: the form, growth rate, and survival of a plant depend on its response to burial, but this response in turn determines the size, shape and stability of the dunes that are built around it.^{28,46,88,158,162.}

Table 6 summarizes the research that has specifically addressed the effects of sand burial on established plants. Moreno-Casasola⁵⁷ gives a more comprehensive list of species which have been reported tolerant of sand burial, most without confirmation by experiment or detailed observation. Species tolerant of extensive burial usually have extensive rhizomatous growth, and produce both vertical and horizontal rhizomes. Alternatively, stems are capable of elongating and growing vertically to emerge from moderate amounts of deposition.^{99,163} Internode length is plastic, so that the plants can adjust their growth to the prevailing conditions. The plants have an ability to produce adventitious roots near the sand surface from buried stems and/or elongating rhizomes. Growth is stimulated in many species by intermediate amounts of sand burial. The non-rhizomatous forbs which tolerate burial can evidently withstand small amounts, compared to *Ammophila* spp., and other dune-forming grasses. Rhizome vigor, size, and growth rate are critical parameters in determining the amount of sand deposition that can be tolerated. Presumably the non-rhizomatous forbs listed in Table 6 use stored reserves in the root or stem, and the low amount of sand accretion tolerated by them (at least as reported) probably reflects the lower energetic reserves available to them. The non-rhizomatous plants in Table 6 are annuals; their period of active growth coincides with low seasonal rates of deposition, and thus their lower reserves would be adequate for the sand deposition they are likely to experience during the growing season. Perennials must have larger reserves to counter the larger amounts of sand deposition during the fall and winter storm season, and thus the ability of a rhizome system to store food would be necessary. Although a

Table 6
Plant Responses to Burial in Sand

Species	Response	Ref.
Mosses		
<i>Barbula fallax</i> , <i>Bryum pendulum</i> , 18 others	Species from mobile dunes emerge from up to 3 cm deposition, others killed.	164, 165
Grasses		
<i>Ammophila breviligulata</i>	Increases in biomass, leaf area, density, rhizomes, flowering; survives up to 100 cm deposition	56, 79, 107, 132, 133, 136, 166, 167
<i>Ammophila arenaria</i>	Increases in vertical rhizome growth, leafy shoot	117, 169
<i>Uniola paniculata</i>	Increase in density and height; survives 20 cm deposition; moderate deposition aids seedlings	78, 79, 132
<i>Spartina patens</i>	Increase in rhizomes, density, growth, up to 15 cm; Recovers from up to 30 cm; upright form survives more deposition than decumbent form	88, 132, 162, 167, 171
<i>Corynephorus canescens</i>	Some growth response; adventitious root production	170
<i>Agropyron</i> spp.	Survives 60 cm deposition; horizontal rhizomes turn upwards	46, 169
<i>Eragrostis pilosa</i>	Survives shallow burial	172
<i>Festuca rubra</i>	Increased growth of tillers and roots	173
<i>Spartina alterniflora</i>	Survives 22 cm deposition; survival reflects initial density and cover	167
Forbs		
<i>Solidago sempervirens</i>	Survives up to 56 cm; recovery independent of initial population size	79, 168, 172
<i>Erigeron canadensis</i>	Low survival at 5 cm deposition	79
<i>Oenothera humifusa</i>	No seedling survival of sand deposition	79
<i>Atriplex laciniata</i>	16 cm deposition stimulates growth	174
<i>Atriplex glabriuscula</i>	8 mm per week stimulates growth	174
<i>Cakile maritima</i>	4 mm per week stimulates growth	174
<i>Salsola kali</i>	12 mm per week stimulates growth	174
<i>Artemisia stellaria</i>	Growth stimulation; survives 59 cm deposition	167
<i>Lathyrus japonica</i>	Survives 43 cm deposition	163, 167

variety of woody shrubs grow in habitats subject to some sand movement, only *Rosa rugosa* appears to have been experimentally studied.¹⁷⁵ Like the perennial herbs, it is capable of producing adventitious roots just below the new soil surface. The response to sand burial of *Arctostaphylos uva-ursi*, whose clonal growth patterns were described above, has not been specifically investigated; however, Remphrey et al.¹⁴⁶ noted that its ability to withstand sand accretion was related to its production of horizontal roots with short, oblique connections between successive layers of the root "frame", and the capacity of colonizing shoots to root at the nodes. Other shrub species growing in these environments are also probably capable of rooting at the nodes. Thus, species that tolerate, or benefit from, sand burial are characterized by substantial underground food reserves in rhizomes or roots, the production of horizontal and vertical roots or rhizomes with highly variable internode lengths, the presence of a large and plastic bud bank, and the ability to produce adventitious root systems just below the new sand surface.

The reasons for the stimulation of growth by burial seen for many of these plants has yet to be completely elucidated. Hypotheses include the effects of added plant nutrients, changes

in soil aeration and moisture status, pH, microflora, changes in plant physiology, natural senescence of the plants, patterns of root growth and root function, and changes in biomass allocation patterns. No clear mechanism has yet been identified, however, for any of the species studied.

3. Growth Patterns: Morphological Variation Within and Among Species

Morphological changes in individual plants in response to barrier island environments have been described for a few species. Commonly, morphological differences between coastal populations and inland forms have been ascribed to the effects of salt deposition. In a classic study by Chrysler,¹⁷⁶ the leaf anatomy for several species growing on the coast of Cape Cod was compared with populations found inland at Lake Michigan. He found that the maritime individuals had leaves that were 14 to 158% thicker than the inland individuals, due to the enlargement of the palisade layer. In addition, the outer walls of leaf epidermal cells in maritime individuals were 1.5 to 2 times as thick as those of inland plants, and had rougher or hairier surfaces. Cartica and Quinn¹⁷⁷ examined the leaf morphology of *Solidago sempervirens* in more detail on a gradient

across a barrier island from the primary dune to the bay. They found, like Chrysler, that there was a gradient of leaf thickness from oceanside to bayside, and that this gradient could be reproduced in the greenhouse by spraying plants with different amounts of salt; they therefore concluded that the differences in leaf thickness observed in the field were due to environmental effects rather than genetic differentiation of populations. There was no gradient, however, in stomatal and trichome densities. Several coastal species from southern Australia similarly showed an increase in succulence in near-shore populations compared with inland plants.¹⁷⁸

Rozema et al.¹⁷⁹ described several morphological syndromes common to the dune plants of northern Europe. The dune grasses (*Elytrigia junceiformis*, *Ammophila arenaria*, *Elymus arenarius*, *Festuca rubra*) as well as some of the forbs, have a suite of xeromorphic features, including ability to roll the leaves, leaf pubescence, an epicuticular wax layer, and sclerophylly. Similar general features were described by Waisel.¹⁸⁰ The distribution of three species of *Elytrigia* among salt marshes, foredunes, and inland ruderal environments is correlated with the amount of epicuticular wax (61.2 $\mu\text{g}/\text{cm}^2$ leaf surface in *E. junceiformis*, the dune species, 20.6 $\mu\text{g}/\text{cm}^2$ in *E. pungens*, the salt marsh species, and 18.0 $\mu\text{g}/\text{cm}^2$ in *E. repens*, the inland species);¹⁸¹ not only the quantity of wax but also the quality varied among these species.¹⁸² Espejel⁹⁴ compared morphological features of the stems and leaves of 238 taxa from the Yucatan coastal dune system, and found that nearshore habitats were dominated by herbaceous plants that frequently were succulent, pubescent, or armed, and had simple or linear leaves, whereas plants of the sheltered fixed dunes were also herbaceous, but lacked succulence, pubescence, or other leaf adaptations. The vegetation of the slacks was mostly woody, with leaf adaptations such as pubescence, sclerophylly and reduction or dissection. On sandy coasts in Japan,¹⁸³ the plants nearest the ocean tend to be vines or rhizomatous prostrate species; erect annuals are found farthest from the water. Species with the ability to emerge after burial are mostly found on the dunes, and their frequency in the vegetation at a site corresponds to the amount of sand movement. These studies thus support the idea that beach and dune plants, at least, have an identifiable suite of morphological features, either characteristic of the species as a whole or characteristic of its coastal populations.

Barbour et al.^{44,184} have found less clearcut patterns, however, in an extensive study of strand plants from the Gulf of Mexico. Perennial, non-succulent forbs were the most common plant type (46% of the flora), and perennial grasses were next most abundant (29%), with woody perennials almost as common (26%). There was considerable diversity in leaf anatomy, with both classical C4 forms (23% of the flora) and classical C3 forms, but also modifications of both forms, and a group of eight species that had a previously undescribed leaf anatomy (characterized by large cavities). The distribution of leaf char-

acteristics around the Gulf only partly conformed to the expectation that hotter, drier regions would be dominated by species with C4 metabolism and structural adaptations (such as small leaf size, pubescence, succulence, sclerophylly) that reduce heat load and transpiration, while cooler regions should have a predominance of C3, broad-leaved species. However, the hottest region (southern Texas) had less cover by C4 species and more cover by broad-leaved forbs than did the coolest region (Panhandle region), which had a surprising dominance of sclerophyllous leaves. The stable beaches of the Louisiana coast, which were expected to support a high cover of woody erect plants (presumably less capable of coping with extensive sand burial than rhizomatous herbs), in fact had the lowest cover by woody sclerophylls. A survey of plants from sites around the perimeter of North America similarly showed few correlations of climate and growth form. On a local scale, however, there were clearer correlations of habitat and growth form. Species found only on the beach were prostrate forbs, either succulent plants with C3 metabolism or pubescent plants with C4 metabolism. Species found only on inland portions of the primary dune were glabrous forbs; grasses were found on all parts of the beach to dune transect. Species normally found in exposed microsites were herbs with succulent or pubescent, large leaves; those in protected microsites were woody, erect and rigid, nonsucculent, and had small glabrous leaves. Grasses showed much less differentiation by microsite than did the forbs and shrubs. Barbour and his co-workers conclude that the relationship between growth form and environment — both regional climate and local microclimate — is not as strong as might be expected.

4. Physiological Ecology and the Growth of Plants

Several recent reviews of the physiological ecology of barrier island species^{44,174,179} illustrate and discuss the wide variety of physiological adaptations that have been observed in coastal plants, and the reader is referred to them for comprehensive discussion of the nature of physiological processes in coastal plants. As in the subjects covered, much of the relevant work has been done on plants from coastal dune environments, rather than strictly on barrier islands, and the assumption is being made that the physical conditions of the beach and foredune of barrier islands is similar to that of coastal beaches and foredunes.

Table 7 summarizes the major environmental factors to which barrier island species show adaptations, and lists several major contributions to the study of each observed response to the environmental factors. Barbour et al.⁴⁴ have included in their paper reference to the older literature. Most of the studies involve analysis of the effect of single environmental factors on selected aspects of physiological function, and few attempt to relate the physiological behavior of coastal species to multi-resource gradients, or to assess the implications of interactions between environmental factors for growth, competitive fitness,

Table 7
Literature Describing Physiological Adaptations to Environmental factors

Environmental factor	Physiological response	Ref.
Salt stress (spray or soil)	Resistance or tolerance	38, 44, 78, 130, 174, 179, 181, 187, 188, 189, 190
	Leaf surface changes	182
	Induced growth and other physiological responses	191, 192, 193, 194, 195
Drought and water stress	Tolerance of low water potential	30, 44, 102, 161, 196, 198, 127
	Inorganic ion accumulation	191
	Organic ion accumulation	127, 197, 199, 198, 200
	Utilization of ground-water lens	201
	Limits on growth	106, 202
	Avoidance through deep rooting	127
Light, temperature (control of photosynthesis)	Carbon metabolic pathway	44, 174, 195, 203, 202
	Gas exchange, photosynthesis rate	129, 195, 203
Nutrient limitations	Association with N-rich microsites	204, 205
	Soil limitations on growth (N,P,K)	44, 125, 128, 174, 206, 207, 209, 210, 205, 128
	Nutrient translocation and storage	171, 196, 211, 128, 202
	Nutrient uptake	212, 211, 205, 213
	N-use efficiency	129

susceptibility to mortality factors, or other dynamic processes.¹⁸⁵ Similarly, there have been few attempts to relate physiological limits on carbon gain in the different environments of the coastal dunes to patterns of species occurrence, patterns of biomass accumulation, or patterns of species interactions.¹⁸⁶

Two themes emerge from these studies, plus the thoughtful review of Barbour et al.⁴⁴ First, success in the coastal environment is a function of interacting adaptations to complexes of environmental factors. For example, although tolerance of salt spray is in general characteristic of beach and dune plants, many authors have noted that distributions of plants in the field often differ from those suggested by the results of controlled studies of salt spray tolerance. *Euphorbia polygonifolia*, *Rhus radicans*, *Parthenocissus quinquefolia*, and *Hudsonia tomentosa*, common to mid-Atlantic barrier islands, all are highly sensitive to salt spray, yet are found on lee slopes of the primary and on the secondary dunes.¹⁴⁵ These species are all prostrate or low-growing, and they are usually found in microsites with lower spray loads, and in amongst the taller stems of *Ammophila* that shield them from spray impaction. Thus, they avoid salt spray rather than tolerate it. However, by avoiding spray

through the adaptation of growth form these species must possess adaptations to survive mobile sand, and, presumably to tolerate the low water-holding capacity of the soil (either through the development of deep taproots or the physiological tolerance of high tissue water potentials). Conversely, several species from the barrier islands of North Carolina can withstand greater amounts of experimentally applied salt spray than the amounts characteristic of the particular environment in which each grows.¹⁹⁰ *Myrica pensylvanica*, for example, can grow equally well with and without salt spray; among the species studied (including *Uniola*, *Cakile edentula*, *S. patens*, and *Triplasis purpurea*), although some experience a diminution of above-ground growth with experimentally applied salt spray, there is no change in below-ground growth, and no mortality. The ability of shrubs to develop low-growing (pruned) growth forms adds to the salt-spray tolerance of the shrub species. Thus, physiological responses to salt spray include not only tolerance of high levels of salt in and on leaves, but also plasticity of growth form, and tolerance for low nutrient and low soil water conditions.

The interactions that have been demonstrated among nutrition, salt tolerance, and water relations offer additional examples of the way in which interactions among physiological factors control growth. Soil moisture controls the production of nitrate reductase in *A. arenaria*²¹¹ and apparently nitrate is acquired during wet periods and is stored during dry periods (up to 169 $\mu\text{g N-NO}_3/\text{g}$). Salt tolerance in *Cakile maritima* is related to the induction of nitrate reductase in high-nitrate environments (such as rotting litter on the beach); the lack of such induction of enzyme in *Elymus arenarius* may explain its lower salt tolerance.²⁰⁴ *Salsola kali* is not only salt-tolerant, but growth in saline media (up to 150 mM NaCl) increases if nitrogen is supplied (at 14-35 mM NO_3).¹⁹² This nitrogen-dependent salt stimulation results from the production of compatible osmotic solutes, which are high in nitrogen and are important in the maintenance of cell turgor. *Cakile*, which does not produce these nitrogenous osmotica, can maintain turgid cells in the absence of salt, but *Salsola*, which requires salt stimulation to produce large quantities of the osmotic solutes, experiences low cell turgor at low salinity, and a concomitant decrease in growth. Pavlik, in a series of comparative studies of *A. arenaria* and *Elymus mollis*, had demonstrated that addition of nitrogen alters not only growth patterns but also water relations and photosynthetic rates.^{126,127} These studies illustrate the need for coordinated investigation of the interactions of limiting factors (salt, nutrients, and water availability) in both understanding the nature of physiological adaptations to the barrier island environment and to understand the implications of these stresses for patterns of growth and species interactions.

Second, the wide diversity of physiological adaptations observed in coastal plants is suggestive of a diversity of microhabitats on a small spatial scale as well as a diversity of possible mechanisms of adaptation. For example, small variations in

the elevation of the dune surface results in ecologically significant variation in the depth to the water table and soil moisture availability; the variation in rooting depth of beach, dune and swale species combined with this spatial heterogeneity results in a diversity of patterns of plant water relations. Shallow-rooted species such as *C. maritima* may tolerate lower water potentials, greater daily and seasonal changes in water potential, and lower pre-dawn potentials during the dry portion of the year, than do deep-rooted plants such as *Abronia maritima*, which shows little sign of water stress throughout the season despite a complete lack of rainfall.^{44,203} Au³⁰ recorded a wide range of mid-day and predawn water potentials for 16 species from Shackleford Bank, North Carolina; herbaceous species tended to have lower mid-day potentials (-0.5 to -1.2 MPa) than did the woody species (-1.2 to -1.5 MPa), and the woody species tended to have a greater diurnal change in potential than did the herbaceous species; however, there was still considerable variation within groups. In general, the failure of Barbour et al.⁴⁴ to discern correlations between physiological traits and dune habitats suggests that a broad range of physiological systems in barrier island plants permit survival in an equally broad range of microhabitats within each major habitat zone. Thus, patterns of physiological adaptations resemble patterns of seed dispersal and growth form, in that the ability to utilize diverse microhabitats in close proximity to each other is apparently a critical aspect of survival in coastal habitats.

C. Population Processes

1. Genetic Variation Within Species

Given the strong environmental gradients that exist across barrier islands, and the equally marked differentiation between barrier island and non-coastal environments, genetic differentiation could be expected to arise between populations of plants. It has been well established that strong selection pressures can counteract gene flow among plant populations, and permit considerable differentiation and isolation of populations in close proximity to each other but subject to differing selective forces.^{82,214} The data on seed and seedling biology, growth form, and ecophysiology have all suggested that coastal populations may well fit this description. As noted previously, many beach and dune species have low seed dispersal distances, and given limitations in the abundance of insect pollinators, pollen dispersal distances also are probably small for barrier island plant populations (at least for plants not adapted for wind-mediated pollination). This has indeed been demonstrated for *Polygala vulgaris* in Britain, in which less than 25% outcrossing occurs in populations of at most 50 individuals.⁸² The clonal nature of many of the perennial herbs and shrubs also could act to reduce pollen dispersal distances, by promoting within-clone pollination events. Thus, between the existence of pronounced gradients of varying selection pressures and the trend towards low gene flow attributable to restricted seed and pollen dispersal, barrier island environments

would seem likely to present an excellent opportunity for the genetic differentiation of plant populations. Differentiation between island and mainland habitats would seem even more likely, given the barrier to pollen and propagule movement imposed by the salt marsh and lagoon areas between an island and the coast.

Table 8 summarizes the studies in which genetic variation within and among barrier islands (and coastal) sand dune habitats has been studied. There are two patterns evident among the studies of within-island variation. For some species, e.g., *S. sempervirens* and *A. breviligulata*, genetic variation cannot be demonstrated, but rather there is strong phenotypic plasticity in growth pattern, leaf morphology, and reproductive biology. Other species, notably those which can occupy the entire range of habitat types within the barrier island/coastal system, do show evidence of genetic variation in morphological, physiological, and reproductive traits. These species, including *S. patens* on the North American Atlantic coast, and *F. rubra* and *A. stolonifera* on Wadden Sea islands and the British coast, are outbreeding perennials, and occur in the bay-side salt marshes, in the swale systems within the islands, and on the ocean-side foredunes. In some cases, e.g., *F. rubra*,²²¹ the pattern of variation suggests a cline or gradient of genetically-determined characters across the island (in this case salt tolerance and growth rate); in others (e.g., *S. patens*^{219,229}), the pattern suggests the evolution of discrete ecotypes among the populations. The potency of the environmental gradients is particularly apparent in the case of *Dactylis glomerata*. This grass was introduced from inland habitats, where it is native, into the coastal dunes of England after World War II, as seeds mixed in hay brought in for cattle. During the approximately 25 years between introduction and the time of the study,²²⁰ physiological and morphological traits underwent significant genetic change. Beachside plants showed an increasing tolerance to lack of soil water; under drought conditions, they could better maintain their net assimilation, relative growth rates, and leaf area, and they could produce higher root:shoot ratios than could plants from nearby inland populations.

The plants characterized by extensive phenotypic plasticity and little genetic differentiation in Table 8 come from more uniform sets of habitats than do the more genetically diverse species. *Ammophila* spp. and *S. sempervirens* are found only on soils derived from dune sands; although they may occur on mobile foredunes and stabilized rear dunes or bay-side dunes, they do not occur in the saturated soils of swales, nor in the saline soils of the salt marshes. The species that show genetic variation are found in this wider range of edaphic conditions. Thus, phenotypic plasticity in barrier island plants is evidently associated with restriction to a single habitat type, albeit one broadly defined, whereas genetic variation accompanies the ability to occupy a variety of habitat types. Schlichting,²³⁰ in a review of the evolution of phenotypic plasticity, found that the phenomenon was characteristic of species subjected to large

Table 8
Tests of Genetic Variation Within and Among Plant Populations of Barrier Islands and Other Coastal Habitats

Species	Type of contrast	Results	Ref.
<i>Solidago sempervirens</i>	Across barrier island	Phenotypic variation in leaf morphology, resource allocation fecundity; no genetic variation	177, 215
<i>Ammophila breviligulata</i>	Across lakeshore dune field	No genetic component to decline in vigor across transect	216
<i>Ammophila breviligulata</i>	Coastal vs. lakeshore	Genetic differences in germination, seed salt tolerance, light and temperature response of seedlings; no differences for seedling salt tolerance	98
<i>Ammophila arenaria</i>	Across coastal dune field	High phenotypic plasticity; amount of plasticity may be genetic; genetic variation in shoot height	217
<i>Phleum arenarium</i>	Across coastal dune field	High phenotypic plasticity; no genetic component to fruit variation; low isozyme variation	218
<i>Spartina patens</i>	Across barrier island	Genetic variation in morphology, reproduction, salt tolerance; differences in genetic structure of populations	219, 229
<i>Dactylis glomerata</i>	Across coastal dune field	Genetic differences in relative growth rate, water use, net assimilation, root:shoot ratio	220
<i>Festuca rubra</i>	Across barrier island	Genetic differences in salt tolerance, growth rate, salt exclusion, proline production, drought tolerance, shoot and leaf morphology	221, 222, 223
<i>Agrostis stolonifera</i>	Across barrier island	Genetic differences in leaf wax properties	182
<i>Rumex crispus</i>	Beach vs. inland sites	Genetic differences in fruit morphology and ability to float	71
<i>Atriplex leucophylla</i>	Between sites: coastal dune latitudinal transect	Genetic differences in morphology, growth form, seed germination, water relations, photosynthesis	102
<i>Cakile maritima</i>	Between sites; coastal dune latitudinal transect	No genetic differences in seed germination, seedling growth	74
<i>Cakile maritima</i>	Coastal vs. lakeshore	Genetic differences in salt tolerance	189
<i>Abronia maritima</i>	Between sites: coastal dune latitudinal transect	Genetic differences in seed weight, % seed set; ability to float in seawater; ability to emerge from sand burial	99
<i>Uniola paniculata</i>	Between sites: coastal and barrier island geographic transect	Genetic differences in flowering and seed set; seed germination; no differences in thermoperiod, salt tolerance of seedlings	97, 224, 225
<i>Lathyrus japonicus</i>	Between sites: barrier island latitudinal transect	Genetic differences in respiration rates; thermal properties of NAD malate dehydrogenase	226, 227
<i>Ceratodon purpureus</i> , <i>Aulacomonium palustre</i> , <i>Polytrichum commune</i>	Barrier island vs. inland sites	No genetic differentiation among populations	228

amounts of environmental variability. The frequent yet irregular changes in dune topography attributable to erosion, accretion, and storm damage, promote fluctuation in sand accretion and salt spray, which are the two most strongly marked environmental variables within the dune habitat. There is likely to be more fluctuation in these variables within a dune system

than there would be between dune, inland swale, and salt marsh habitats. Thus, it seems possible that selection pressures within dune (sandy soil) habitats may act differently on plant populations than selection pressures among dune and non-dune habitats within islands. The former pressures, associated with high variability in environmental conditions, promote high pheno-

typic plasticity and low genetic variability, whereas the latter, associated with variation among more stable habitat types, promote genetically based variation among populations.

The presence of extensive clinal genetic variation on geographic transects is not surprising, as it reflects adaptation of populations to local environmental conditions. For example, Johnson⁹⁹ related the presence of heavier seeds in northern populations of *Abronia maritima* to two factors: (1) cooler climates during the germination/seedling establishment phase necessitate larger reserves for the plant in order to survive, and (2) more frequent disturbance from overwash in southern populations necessitates a reserve of lighter, more numerous seeds to locate new habitats. Similarly, Seneca²²⁵ showed that the seeds from the more northerly populations of *U. paniculata* from North Carolina required cold pretreatment for germination, but southern populations (from Florida) did not. *A. breviligulata* populations from Michigan lakeside dunes produce seeds with a need for cold stratification, greater sensitivity to temperature range, greater sensitivity to short daylengths and lower tolerance for substrate salinity than the seeds from North Carolina barrier island populations⁹⁸ (see Section II.A.3). An exception to the frequent demonstration of clinal genetic differences is the study of *C. maritima* populations from the California coast,⁷⁴ in which no genetic differences in seed and seedling behavior were found. This lack of genetic differentiation may reflect the fact that this species was introduced to California c.1935, and its current distribution along the coast has occurred over only 30 years;²³¹ thus, there may not have been sufficient time in which genetic change could occur.

2. Demography and Population Dynamics

Some aspects of plant demography — seed population, dispersal, establishment, and survival — were discussed as aspects of individual species biology. Considered together with adult mortality patterns, these facets of species behavior determine the dynamics of the plant populations. The literature is limited to the intensive studies on the small number of species that have constituted the bulk of the discussion thus far. Three aspects of demography of barrier island populations are considered here: (1) the causes and patterns of mortality of established plants, (2) the role of density-independent factors versus density-dependent factors in this mortality, and (3) the identification of factors which limit population size.

Mortality of established seedlings and adult individuals results from the same principal causes as the mortality of new seedlings: primary factors are drought and the movement of sand, and, secondary factors include herbivory from mammals and/or insects. *Lithospermum carolinense*,⁷⁵ *Lupinus arboreus*,²³² *Xanthium strumarium*,¹¹⁶ *Vulpia fasciculata*,^{114,233} and a variety of shrub and tree species from the Frisian Islands of the Wadden Sea²³⁴ all experience significant mortality during periods of limited soil moisture. In contrast, most mortality in a shingle and wrack shoreline population of *C. edentula*, re-

sulted from outbreaks of salt marsh caterpillars; insect predation was also a major source of mortality for *Cirsium rothophilum*⁷⁶ and *Lupinus arboreus*,²³² both plants of the California coastal dunes. Grazing by rabbits has been identified as the dominant source of mortality for annuals²³⁵ and for woody shrubs and trees in both coastal and barrier island dunes in Europe and England²³⁶ (See Section II.D.2.6 next). Mortality from other sources may be exacerbated by drought.

The survivorship curves resulting from this mortality take several forms (Figure 10). For some annuals, mortality conforms to a Deevey Type I mortality curve, in which plants suffer little mortality from seedling emergence until flowering.²³⁷ Others, however, experience high levels of mortality (60 to 70%), with most of the mortality occurring immediately after emergence, and in some cases (e.g., *C. edentula* and *A. arenaria*) the conformance to a Type I curve varies among years and sites. For other species (e.g., *Xanthium strumarium*), the Type I curve is modified by an initial period of high mortality at the time of seedling emergence, followed by high survivorship of established seedlings until flowering is completed. Type I mortality curves are usually associated with an annual life-cycle and an unstable habitat.^{64,237} The dispersal patterns discussed (Section II.A.1) suggest, however, that there is often a premium on remaining in close proximity to the parents, because the parental site is likely to continue to be suitable; this hypothesis implies that Type I mortality pat-

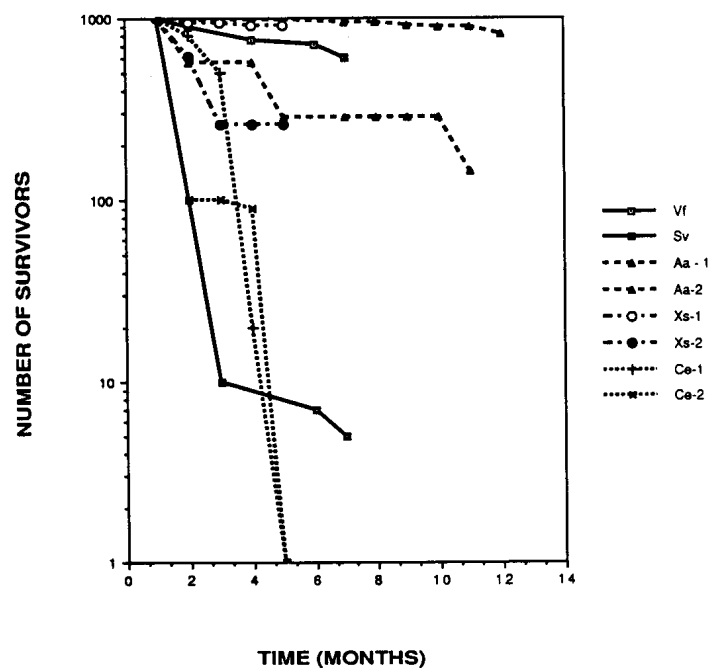


FIGURE 10. Representative survivorship curves for herbaceous annuals and perennials of the dunes. Vf, *Vulpia fasciculata*,²³⁵ Sv, *Spergula vernalis*,²³⁵ Aa-1 and -2, *Ammophila arenaria*, from 2 study plots in the same site;¹¹¹ Xs-1 and -2, *Xanthium strumarium*, from 2 study plots in the same site;¹¹⁶ Ce-1 and -2, *Cakile edentula* from a dune crest and the beach, respectively.⁷³

terns are not necessarily restricted to species of evanescent habitats. Symonides²³⁶ has noted that on Polish dunes, survivorship of grass seedlings was greater for individuals growing near parents, especially in years of drought; the tussocks of established plants conserved soil moisture and protected against blowing sand. The variability in mortality patterns among dune annuals, then, may reflect factors other than the likelihood of habitat change, including relationships between species' phenologies and the seasonal patterns of storm-driven sand movement, soil drought, and insect activity and between-year variability in all these factors. In contrast to the dune annuals, perennial species commonly have survivorship patterns that more closely resemble Type III patterns, with high mortality rates for seedlings followed by very low mortality of adults.^{116,239,240}

The size of the plant populations results from the balance among the life history traits and demographic factors described. The factors that set the size of a given population, and maintain it for a given site, may include environmental effects independent of the size of the population (density-independent factors), and/or processes whose intensity varies with the size of the population (density-dependent factors). It might be assumed that frequent physical disturbance and extreme environmental conditions from sand movement and salt spray cause density-independent mortality factors to dominate population dynamics near the ocean, and that density-independent regulation of population size would decrease in relative importance with distance from the shore. Density-dependent factors, reflecting intra- and interspecific competition, herbivory and other biotic interactions, might conversely be expected to increase with distance from the shore and diminution of extreme physical conditions.

Keddy,¹¹² in his studies of the population biology of *C. edentula*, has specifically sought evidence of density-dependent mortality in different shoreline and dune habitats. He found that both density-dependent and density-independent effects varied in importance along a transect from the leading edge of the vegetation on the beach of a barrier split to the landward side of the primary dune, and also varied with the life-stage of the plants. In the seaward (beach) populations, density-independent forces were the major source of mortality; in the landward populations, both density-dependent and density-independent mortality occurred. Density-dependent mortality characterized both the seedling establishment phase and the established plant growth phase in the landward site only. Reproductive output, however, varied with density in the seaward populations, but not in the landward populations. Density-independent limits on reproductive output in landward populations reduced the total reproduction in these habitats below that necessary for maintaining the population, and thus persistence of the landward populations depended on seed dispersal from the seaward sites.²⁴⁰

Watkinson and Harper¹¹⁴ similarly investigated density-dependence in the population biology of *Vulpia fasciculata*, a

plant of the English coastal dunes. They found little evidence for density-dependent mortality, but did find that reproduction decreased with increasing plant density over a threshold value (Figure 11). Mortality attributed to a combination of dessication, grazing, and wind-drag exerted strong controls on population size, but regardless of the plant density. The low population density of many dune annuals has been proposed as a reason for the lack of density-dependent effects in mortality rates, and the lack of evidence for self-thinning.²³⁷ Similarly, reproduction and growth varied with density in *Xanthium strumarium*, but mortality did not.¹¹⁶

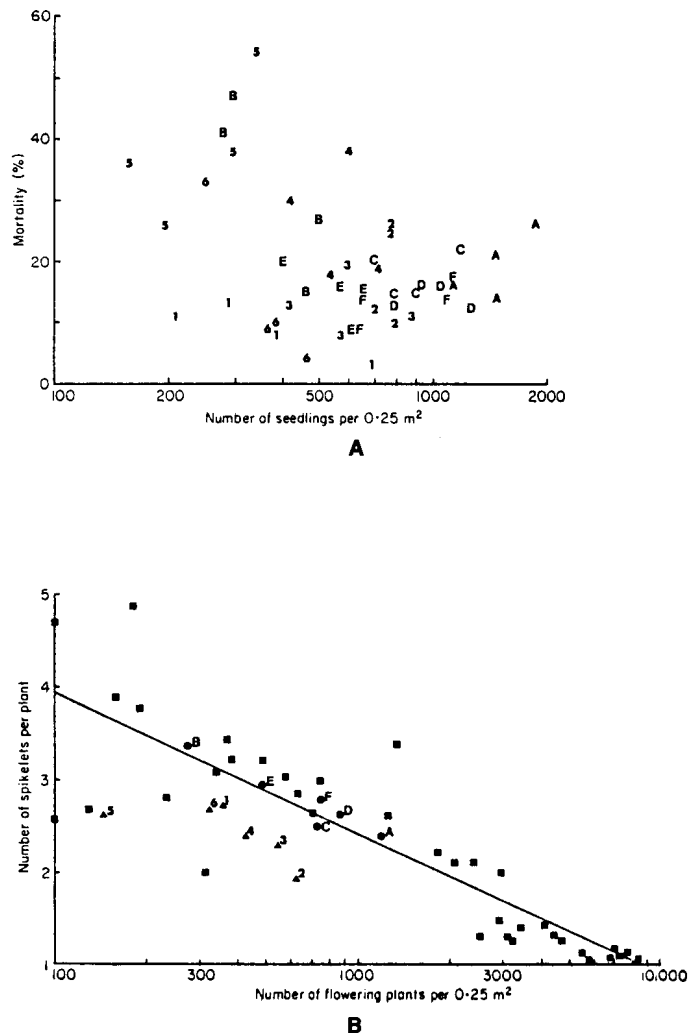


FIGURE 11. Relationships of (A) mortality and (B) reproduction to seedling density in *Vulpia fasciculata*. (From Watkinson, A. R., and Harper, J. L., *J. Ecol.*, 66, 15, 1978. With permission.)

Population size in dune plants not only reflects mortality and reproductive rates, and their sensitivity to density, but other limiting factors in the environment. Numerous investigators have stressed the role of nutrient limitation in many populations^{46,112,125,206} and in patterns of growth and reproduc-

tion in many species.¹²⁷⁻¹²⁹ Weather, and the microclimate associated with different facies of the dune system have been implicated as controlling factors in the population biology of *Lithospermum carolinense*.¹⁰⁸ The presence and density of other species has been identified as a facilitating factor (*Lupinus arboreus*,²³² and as an inhibitory factor (*Cakile edentula*⁷³). Internal patterns of resource allocation in *Ammophila breviligulata*¹²³ play a role in determining the abundance of new stems, and thus help determine population growth patterns in different habitats.

Strong²³⁸ argued that the effect of density on life history parameters actually occurs as a gradient. A linear reduction in function (survival, growth, reproduction) with density corresponds to the classical concept of density dependence. However, relationships between density and life-history parameters are characterized as much by their variance and dispersion as by the existence of linear correlations. "Liberal" population regulation (described by Strong as the result of multiple influences on population size, each operating with a wide variance in level of effect) is postulated to be characteristic of intermediate population levels, and to consist of variable but generally low levels of response to density. The response to density can be further characterized as an interaction of multiple factors plus a stochastic factor. The data reviewed suggest that this approach may be a more useful one for barrier island plant populations than simply a search for evidence of density effects on survival and reproduction. The variety of limiting factors on population size, such as nutrient effects (see Section II.B.5), competing vegetation,^{73,232} weather,⁷⁵ herbivory (see Section II.D.2.b), and the physical environmental factors summarized in Table 4, suggests that barrier island populations of a given species will occur over a wide range of densities, both in space (in different microhabitats) and in time, and that the density-dependence of specific mortality factors and of reproductive function will also therefore vary widely. In fact, the studies of *C. edentula* in different habitats, and over several years, illustrates the variation in mortality and reproductive patterns that can occur. Therefore, it would be more useful to characterize species by the range of density-dependent relationships observed. The studies reviewed together suggest a consistent lack of relationship between mortality and density, although many of the causes of mortality involve biotic effects (e.g., grazing, resource extraction, competition) that can act in a density-dependent manner. If density-dependence is a function of population size, as Strong suggests, then it follows that sand dune populations rarely achieve the minimum density necessary for the exertion of density-dependent effects.

D. Community Processes

1. Competitive Interactions

Since Hutchinson's seminal paper "Homage to Santa Rosalia (or, why are there so many kinds of animals?)"²⁴¹ was published in 1959, competition has been specifically identified

as a dominant process responsible for the structure of plant (and animal) communities. Debate concerning the occurrence of competition in natural communities, and its importance relative to other processes (such as predation, the response to exogenous disturbance and physical environmental constraints) has dominated the dynamics of ecological thinking ever since.²⁴² Barrier island environments, being prone to high levels of physical disturbance, might be expected to support communities in which physical processes exert sufficiently great control over community structure that competitive processes rarely occur.²⁴³ Barrier island environments are also temporally varying, with storms and the sand-moving effects of normal weather causing constant change in the physical environment. Wiens²⁴⁰ has argued that in such environments, competition is likely to be less important as a structuring force than other factors. However, competition for soil resources (and for light) has been proposed as a primary driving force in plant community structure.²⁴⁵ Thus, current theory makes contradictory predictions concerning the importance of competition in barrier island communities. Therefore, it is necessary to first establish whether competitive interactions occur among barrier island plants, and then to ascertain the temporal and spatial patterns of such interactions.

There have been only a small number of direct investigations of competitive processes in barrier island communities. Silander and Antonovics²⁴⁶ explored interspecific interactions on the Outer Banks of North Carolina by selectively removing species from a series of plots on a transect across the island, and noting the change in cover of the remaining species. Figure 12 displays some of their results. In some cases, presumptive evidence of competition was found as species increased in cover following the removals; for example, in the high marsh, *Fimbristylis spadiacea* increased in the absence of *S. patens*, and vice versa. Other interactions were not reciprocal: *Hydrocotyle bonariensis* increased slightly following the removal of *Muhlenbergia capillaris* in the swale, but the latter species decreased greatly following the removal of *Hydrocotyle*. A given species could have contrasting effects on different co-occurring species: the removal of *Spartina* in the swale caused a large decrease in *Muhlenbergia*, a very small decrease in *Hydrocotyle*, and a large increase in *Eragrostis*. Of the 48 interactions between species pairs reported, 14 involved decreases in cover following removal of a dominant, 17 involved increases of 10 to 50% in cover, and 9 involved increases of over 50%. Thus, interactions among dominant and sub-dominant species in communities across the barrier island were complex. Competition occurred together with possibly facilitative relationships, few pair-wise relationships were reciprocal, and few species had uniform effects on all co-occurring species.

Competitive relationships have also been directly examined among the winter annuals of the coastal dunes of Wales.^{247,248} These studies utilized artificially planted populations of species

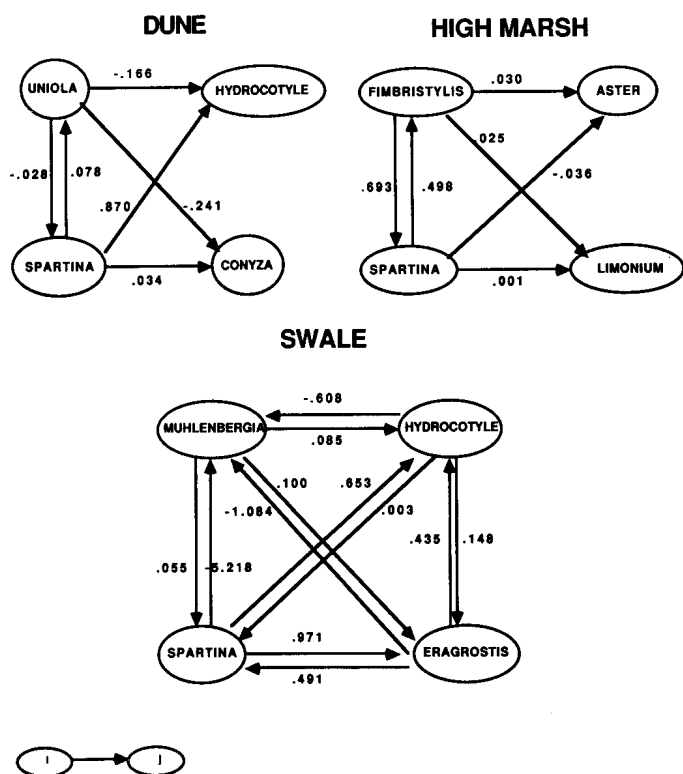


FIGURE 12. Competitive relationships among species in dune, swale and marsh habitats. Coefficient is $(C_{i(j)} - C_i)/C_j$, where $C_{i(j)}$ is the cover of species i after removal of species j , C_i is the initial cover of species i , and C_j is the initial cover of species j . (Data from Silander, J. A. and Antonovics, J., *Nature*, 298, 557, 1982.)

mixtures and single species grown at varying densities. Competitive interactions reflected the relative size of the plants: the largest species, *Vulpia fasciculata* and *V. membranacea* responded primarily to their own densities, whereas the smaller species (*Mibora minima*, *Phleum arenarium*, *Aira caryophylla*, *A. praeox*, and *Cerastium atrovirens*) responded to the presence of larger individuals of other species, as well as to their own species. A larger perennial species (*Festuca rubra*) had suppressive effects on the growth of all the annuals.²⁴⁸ The results from species combinations grown in the greenhouse accurately reflected the patterns of occurrence in the field. Sixty-nine percent of the variance in the weight of a given plant (in the greenhouse) was attributable to characteristics of the neighboring plants (weight, distance, and dispersion); this was attributed to competition for nutrients.²⁴⁷ Thus, these studies in the coastal dunes demonstrated not only that competitive relationships occur, and that they reflect the relative size, vigor, and spatial arrangement of individuals, but also that the patterns discerned in experimental greenhouse mixtures explained the patterns of occurrence in field sites.

There is also indirect evidence of competitive interactions among barrier island plants. The displacement of *C. edentula* ssp. *californica* by *C. maritima* in Pacific coast beach and

foredune habitats has been attributed to competitive interactions.^{74,231} The competitive superiority of *C. maritima* is apparently related to its superior ability to set seed, despite its poorer growth when grown together with *C. edentula* ssp. *californica* in experimental cultures.⁷⁴ In fact, the restriction of all *Cakile* species to the strand and foredune areas on both Atlantic and Pacific coasts has been attributed to its failure to survive in competition with *Ammophila* spp. on the basis of observation and unreported experiments.^{73,74}

Differential use of resources and response to environmental conditions has been associated with competitive relationships. Co-occurring annuals in the dunes of the Wadden Sea islands have species-specific patterns of nutrient uptake and use that could reflect competitive interactions.²⁰¹ *Phleum arenarium* is capable of concentrating a large amount of nitrogen from the very nitrogen-poor soils, and has rapid and large rates of translocation of N, K, and especially P. *Erodium glutinosum* also takes up large quantities of nitrogen, but is not as effective at translocating nutrients. *Aira praecox* and *Saxifraga tridactylites* lack the ability to concentrate nutrients from the dune soil. Co-existence of California beach plants has been ascribed to differences in root morphology and concomitant differences in diurnal and seasonal water relations.^{102,203} The ability of the introduced species *A. arenaria* to displace the native grass *Elymus mollis* (*sensu* Hitchcock and Cronquist¹⁴¹) on Pacific coastal dunes may reflect a complex pattern of differences in water and nutrient use, photosynthetic efficiency, and growth-pattern.^{127,128,198} *Ammophila arenaria* tolerates higher water deficits, maintains higher rates of light-saturated photosynthesis at lower leaf nitrogen contents, and directs its photosynthate into the production of new blades and tillers. *Elymus* devotes a greater amount of its net production to root and rhizome growth, which results in a more extensive, diffuse growth form than that of *A. arenaria*. The historical increase of *Ammophila* and decline in *Elymus* thus corresponds to different patterns of resource use and growth.

These studies provide some circumstantial evidence that competitive interactions not only occur in herbaceous barrier island communities, but may be widespread and important in structuring those communities. Although it has been argued that differences in the way in which resources are used does not necessarily imply competition between the species,²⁴⁹ when such differences are coupled with historical patterns of species' replacement they become more compelling (although still circumstantial). The emphasis on individual species biology, and the response to the dominating forces of sand movement and salt spray has, perhaps, deflected direct experimental investigations of species interactions in these environments. Nevertheless, these studies and the findings of Silander and Antonovics are mutually consistent in indicating that competition is an important structuring force in barrier island communities, even in the most disturbance-prone habitats.

The data reviewed in Sections II. A. and B give an inkling

of possible mechanisms of competition. Differential use of resources, as described, has been implicated as a competitive mechanism through circumstantial relationships. Another potentially important mechanism involves the ways in which space is acquired and retained through clonal growth and/or seed dispersal. For example, the growth patterns of *Arctostaphylos* clones, described above, may effectively exclude other species from a given site and reduce the neighborhood effects of other plants. The more exploratory clonal growth pattern of *A. breviligulata* or *Carex arenaria* may be less effective at excluding other species, but may exert competitive effects through reduction in soil resources available to co-occurring species. Plant growth rates are strongly influenced by competitive interference,²⁴⁷ as are reproductive rates (see Section II.C.2).

Other aspects of competition — competitive hierarchies and the frequency of occurrence of competitive interactions in different barrier island habitats — have received even less attention. The data of Silander and Antonovics²⁴⁶ suggest that competitive rankings of co-occurring species may be quite complex, and include transitive, intransitive, and competitive-cooperative networks. Given the shortages of water and nutrients in the soil, the amount of physical disturbance, and the gradient of these factors that is found from ocean to bay, barrier islands would seem to present excellent opportunities to test the relative importance and frequency of competition as a structuring force in communities, and to study the competitive mechanisms of plants with different life-history strategies growing in the same environment.

2. Plant-Animal Interactions

a. POLLINATION

In one of the few studies to address the role of insularity on the ecology of barrier island plants, Spears²⁵⁰ has compared the pollination biology of two species growing on islands off the coast of western Florida with mainland populations, in order to determine whether lowered density or diversity of pollinators occurs on barrier islands, and whether such lowered pollinator resources are correlated with decreases in reproductive success on islands compared to mainland habitats. The species studied included *Centrosema virginianum*, a perennial herbaceous vine with a highly specialized flower, and *Opuntia stricta*, a perennial succulent with a large, unspecialized flower. Both species grow in the *Uniola*-dominated dune community. Pollen dispersal was indeed diminished on the islands, compared with the mainland population, and fruit set was also diminished on the island farther from the mainland and not connected to it by a bridge. Bumblebees (*Bombus* spp.), the main pollinator of *Centrosema* on the mainland, did not appear on the islands, and the bees present on the islands were less capable of manipulating the specialized flower. Pollinator visits were more variable in occurrence on the far island. The data supported the hypothesis that the availability of pollinators may limit reproduction in barrier island plants. The extensive vegetative,

clonal growth common to many barrier island strand and dune species must be considered, however, in evaluating the reproductive biology of barrier island plants, since changes in the size and form of clones can affect insect-visitor behavior patterns, pollen movement patterns, and seed set per inflorescence.²⁵¹

b. HERBIVORY

That herbivory has a role potentially as important as competition in the structuring of communities is well established.²⁴² Because no studies have specifically addressed the role of herbivory in community dynamics, its importance relative to other factors, such as competition, dispersal, edaphic factors, and disturbance from storms is hard to evaluate for the barrier island communities. The available data consist primarily of qualitative accounts of the presence and activity of herbivorous insects and mammals, and a few more detailed studies of the effects of mammalian grazing on plant communities. Because of the extensive use of barrier islands by humans, and the associated presence of livestock, horses, and feral animals, it is highly likely that herbivory has played a much more important role in structuring the communities existing today than might be observed on barrier islands with no history of human use.

Accounts of insect herbivory mention a wide variety of insect species and an equally wide range of estimated effects on growth, mortality and reproduction. In one population of *U. paniculata*, 15 species of beetles and 3 species of sucking bugs were collected feeding on pollen grains, stigmatic tissue, the lemma and palea, and fungal tissue also growing in the spikelet; they played "a fairly important role in their effect on seed production".^{78,101} Huiskes⁹² listed 11 species of insects known to feed on *A. arenaria*; the best-studied (*Meromyza pratorum*, a fly) can infest 9 to 20% of the tillers.²⁵² Pine forests of Merritt Island, Cumberland Island, and undoubtedly other barrier islands of the southeast U.S. support large populations of bark beetles (*Ips* spp.).^{16,253} Several other forest insect pests (pine tip moth, *Rhyacionia frustrana*, and eastern juniper bark beetle, *Phloeosinus dentatus* have also been reported on Cumberland Island. Differential effects in adjacent habitats have also been found. On an open shingle beach, 37.9% of a population of *C. edentula* was killed by herbivory by salt-marsh caterpillars (*Estigmene acrea*), whereas on mats of wrack within the shingle habitat, only 15% of the plants were killed.⁷² *C. maritima* suffered greater damage from unknown herbivores in dune populations (12% of young seedlings killed) than on the beach (no seedling mortality);⁷⁴ herbivory is frequently mentioned as a source of seedling mortality for other species (Table 5; Section II.A.3).

Grazing by mammals, both native and introduced, has probably been one of the most important factors structuring barrier island vegetation in historical times. Small rodents feed on dune grasses and forbs,²⁵⁴ and may vary their choice of plant part or plant species with seasonal changes in nutritional quality

of the vegetation.^{254,255} The histories of Shackleford Banks, (North Carolina, U.S.), and Cape Cod (Massachusetts, U.S.) are typical. Shackleford Bank was almost completely covered with maritime forest at least until 1853; livestock grazing and clearing and burning greatly reduced the maritime forest, and permitted extensive erosion.³⁰ The stabilized dunes of the Province Lands of Cape Cod supported a diverse forest of beech, oak, pine, birch, and sassafras in pre-colonial times; extensive livestock grazing effectively prevented the regeneration of these forests after they were cut by the colonists.²⁵⁶ Similar histories have been recounted for many of the islands along the southeast Atlantic coast.^{5,54,55} A similar land-use history has been documented for the barrier islands of the Wadden Sea.^{4,257} Other introduced mammals may be locally important: on Core Banks and Portsmouth Islands, North Carolina, nutria (*Myocastor coypus*) feed extensively on *Uniola*, causing increases in dune erosion because of the large decreases in plant cover in overgrazed areas.²⁵⁸

The role of herbivory in structuring plant communities has been most extensively explored in Europe, where large populations of rabbits and the advent of myxomatosis have stimulated research on the question. Rabbit grazing prevents *Vulpia fasciculata* from outcompeting other winter annuals on the Welsh dunes²⁴⁷ in experimental plots; in long-term study plots, diversity of forbs has decreased since the reduction of rabbit populations from myxomatosis.²⁵⁹ Conversely, in dunes artificially planted with *Ammophila*, rabbit grazing permits the *Ammophila* to outcompete other herbaceous plants, and species-rich grasslands develop only in the absence of grazing.²⁶⁰ On the Dutch Frisian Islands, moderate levels of grazing are associated with the highest species diversity, and decreases in diversity are associated with rapid changes (either increases or decreases) in the amount of grazing.²⁶¹ Loss of *Crataegus-Betula* woodland area in the Dutch coastal dunes has been ascribed in part to rabbit grazing²⁶² because of decreases in recruitment and resultant changes in plant population dynamics. Similar changes in recruitment and population structure have been found for the *Ilex*-dominated forest on Fire Island, New York.²⁶³ Rabbit grazing can alter geomorphic processes through its effects on the interaction between vegetation and sand movement; high young dune landscapes have arisen from older dune systems as a result of grazing in coastal Netherlands.²⁵⁷

Thus, there is ample evidence that herbivory is one of the important forces structuring plant communities on barrier islands, and that it can act through effects on many aspects of plant life cycles and species interactions. Its importance relative to other processes, however, remains to be defined.

3. Succession

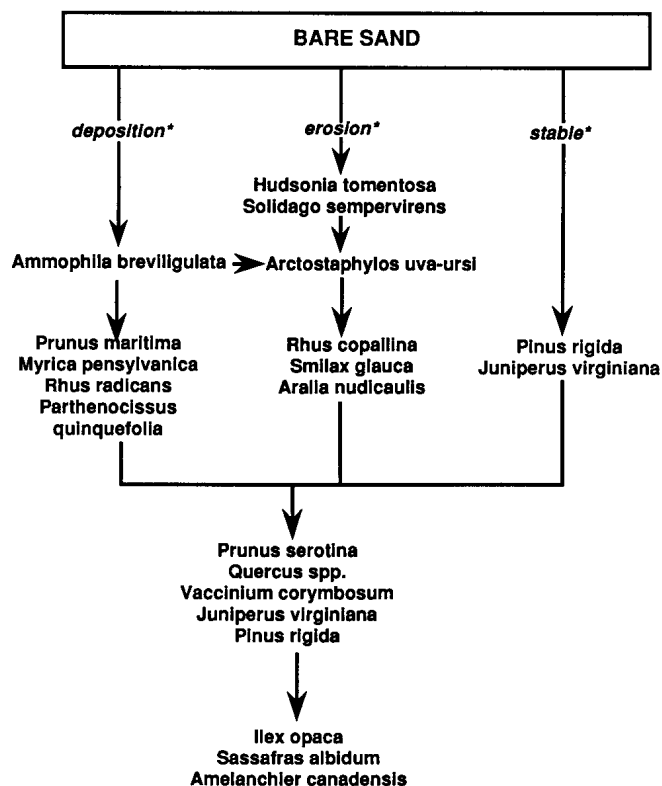
Whether barrier island vegetation changes in species composition and community structure in predictable, directional ways over time remains one of the major areas of controversy

in barrier island ecological research. The idea of succession on barrier islands was initially based on the striking zonation of vegetation across barrier islands. The spatial sequence of community types is assumed to apply to temporal sequences at any given location. Although the notion of a temporal sequence of vegetation change has been frequently criticized,^{38,50,55,61,264-466} it still persists, in part because such changes in vegetation have indeed been documented in a variety of sites, and over a range of time-scales from years to millenia.²⁶⁷

Figure 13 shows three representative successional diagrams that have been developed for barrier islands; the examples have been chosen from a range of barrier island types on the East and Gulf coasts of North America. The diagrams are all based on observations of current spatial patterns of vegetation. The complexity of the diagrams varies in part with the actual complexity of the vegetation and with the interest of the author in recognizing variants of vegetation types. All the diagrams share the same general features: bare sand beach is colonized by pioneer herbaceous species; as a foredune develops, they give way to other types of herbaceous vegetation which in turn is taken over by shrub thickets that may develop into forest stands. Variants of each general class of vegetation occurs relative to topography and disturbance history. The role of physiographic change is highlighted in the diagrams; successional pathways follow different courses depending on topographic changes caused by erosion (deflation) and accretion. Eleuterius¹⁴ (Figure 13c) has differentiated changes in vegetation initiated by erosion and by accretion from changes occurring without such major disturbances. Persistent large-scale flooding reverses the directions of many of the arrows in the diagram. On the outer banks of North Carolina, (Figure 13b), bare sand subject to accretion gives rise to grassy dunes, whereas if no accretion occurs, a different grassland association develops. The pattern of vegetation development will vary also with the position of a site relative to the ocean. On Fire Island (Figure 13a) bare sand on the beach is colonized by the typical community of annual herbs (*Salsola kali*, *Euphorbia polygonifolia*, *Cakile edentula*; not included in the diagram but described by Art¹⁴⁶), followed by the development of *A. breviligulata*-dominated dunes. Bare sand within the dune/swale habitat, however (e.g., sand deposited during a washover), may be directly colonized by shrubs²⁶⁶ or trees.

The question remains, however, how frequently and under what conditions do temporal sequences of vegetation change occur that resemble the spatial sequences so amply documented. Following the planting of *A. breviligulata* on the North Carolina Outer Banks, a high primary dune developed in place of the low hummocky dunes, and the open grassy flat communities gave way to dense grassland and shrub thickets.²⁶⁸ Water table level changes due to sea level rise caused moist forest vegetation at Nag's Head, North Carolina, to sequentially change into wet meadow and then aquatic vegetation.²⁶⁹ Changes in water table depth related to human impacts (infil-

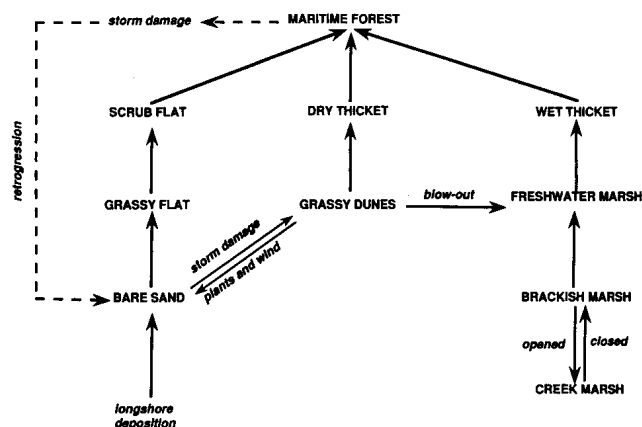
(A) FIRE ISLAND, NEW YORK



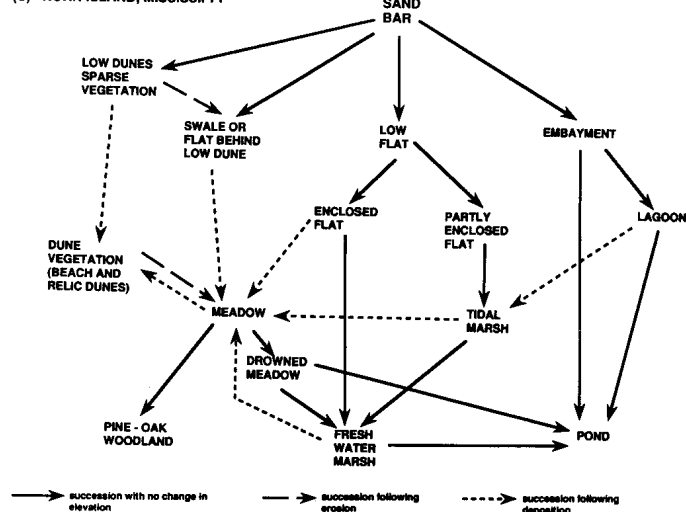
* Initial conditions only

FIGURE 13. Representative diagrams of successional pathways of barrier island vegetation. (A) Fire Island, New York, (B) Shackleford Banks, North Carolina, (C) Horn Island, Mississippi. (From [A] Art, H. W., *Nat. Park Serv. Sci. Monog. Ser. 7*, 1976; [B] Au, S. F., *Nat. Park Serv. Sci. Monog. Ser. 6*, 1974; [C] Eleuterius, L. N., *Nat. Park Serv. Coastal Field Res. Lab.*, 1979. With permission).

(B) SHACKLEFORD BANK, NORTH CAROLINA



(C) HORN ISLAND, MISSISSIPPI



spatial patterns recorded with respect to topography. Doing^{10,273} has described the range of these patterns for beach and foredune communities worldwide, as well as with respect to varying dune morphologies in the Netherlands. Depositional sites and erosional sites have differing vegetation, even if the sites are in close proximity.^{274,275} Washover deposits are colonized by different groups of plants, depending on the grain size of the deposits.²⁷⁶ In mobile dune systems in England and Wales, a cyclic sequence of vegetation change can occur, with alternating *Ammophila* colonization of new dune surfaces and *Salix* colonization of new slacks exposed by the movement of the dune.⁴⁸

These observed temporal changes in vegetation can be reconciled with the apparent stability of vegetation zones by postulating that on barrier islands, successional change (taken here as any sequential pattern of change in plant community composition over time) occurs episodically, over a wide range of time scales, in response to changes in physiography or other

disturbances. While physiographic conditions are stable, particularly with respect to distance from the ocean, elevation, and the height of the dunes between a given point and the ocean, vegetation patterns remain more or less stable. Increases in diversity,^{167,277,278} species substitutions, or differentiation of the vegetation into a complex of related types may occur with respect to variation in microsite conditions and soil development, but the general patterns of community zonation will persist. However, as described in Section I.C.2, since sea-level rise is the dominant (and increasingly important) force molding barrier islands, most barrier islands are experiencing episodic changes in form that precipitate vegetative readjustment. Successional sequences to be expected from the building of successive sets of dune lines (regressive islands) will be less common than vegetative adjustments to encroachment of the ocean over existing beaches and dunes (transgressive islands) because of the dominance of erosive conditions on most barrier island coasts. The point is that physiographic change, ranging from erosion of dunes and frequent overwash events to the accretion of extensive fields of parallel dunes will determine the rate and extent of successional change.

The mechanisms of succession have received little attention on barrier islands, and the applicability of modern theories of succession has not been evaluated. These theories posit that change in vegetation with time results from the interplay among physical environmental conditions, individual species life histories, and interactions among species.^{7,8,279} Certain patterns of species interaction have been particularly identified with successional change;⁹ these include facilitation (the promotion of growth of a second set of species by an earlier set of species), inhibition (the prevention of growth of a second set of species by the earlier set), and tolerance (lack of either stimulatory or inhibitory effect of the initial set of species on a subsequent set). Competitive interactions have been invoked to explain the occurrence of both inhibitory and tolerant successional patterns. In particular, competition for different relative amounts of a series of limiting resources (e.g., light, soil nutrients, water) is further proposed as a basis for successional change;^{6,280} according to this concept, as the ratio of soil resources to light changes over time, different groups of species, adapted to the different ratios of these resources, follow each other through a series of competitive exclusions. Huston and Smith⁸ have taken this one step farther, claiming that such competitive interactions simply reflect inverse correlations between life history parameters (for example, plant form, life-span, number and size of propagules, frequency of seed-set, etc.) and physiological traits (for example, nutrient and water use efficiency, photosynthetic capability under high and low light conditions). Together, suites of life-history and physiological traits predispose different species to competitive success under slightly different environmental conditions, thus leading to species replacement as environmental conditions change.

Life history and physiological traits that might be important

in successional processes on barrier islands are given in Table 9 (this list is not exhaustive, but merely suggestive); many of these traits have been discussed in Sections II.A, B, and C. Some of the described successional patterns can be related to differential qualities of these traits. For example, competitive interactions within the dunes appear to be related to aspects of space acquisition and retention plus the need to tolerate mobile sand and salt spray. Thus not only growth rates but also growth forms, and the relative rates of growth of plant parts are likely to figure prominently in determining the outcome of competitive interactions. Under fore-dune conditions of high sand movement and salt spray, species will be favored that have clonal growth based on rhizomatous patterns that are extensive, rather than intensive, and that involve rapid vertical as well as horizontal rhizome growth. Large seeds permitting emergence from deep sand, tolerance of salt spray, and high nitrogen and water use efficiency, will also favor species over those without this combination of adaptations. On stabilized dunes, competition for space retention substitutes for competition for space acquisition on mobile dunes: more intensive patterns of rhizome growth leading to the establishment of large compact clones will be competitively superior. Characteristics of seed biology permitting tolerance of salt water and moving sand should be replaced by characteristics promoting survival in more dense vegetation; these might include production of larger numbers of smaller seeds, equipped with dispersal mechanisms for occupying small openings in the vegetation, and seedling tolerance of lower light levels. The inverse relationship between height growth and salt spray tolerance may imply an increasing role for competition for light; as shrub thickets get higher, competitive success may increasingly depend on the ability to tolerate shading within the thickets (both shade-tolerance of species, and the ability of individuals of a species to produce sun-leaves and shade-leaves to maximize photosynthesis within a dense canopy). Changing water table heights and soil moisture contents will add further physiological parameters to the complex of traits determining competitive outcomes at a given site. As environmental conditions vary both in space and time across an island, it is apparent how the complex of communities included in successional diagrams (Figure 13) and described in studies of zonation patterns, could arise through competitive displacements along a multi-dimensional gradient of growth forms, physiological tolerances, physiological capacities, and demographic parameters.

Successional changes in barrier island environments may involve other kinds of species interactions in addition to competitive ones. A succession initiated on bare beach sand is the kind of primary sere associated with facilitative interactions.^{9,281} In the studies of interspecific interactions of Silander and Antonovics,²⁴⁶ several herbaceous perennials of the fore-dune decreased in abundance in the absence of the dune-forming grasses; thus, the dune-forming species may facilitate the invasion of other species, including the perennial and woody

Table 9
Life-History and Physiological Traits Possibly
Mediating Competitive Interactions Leading to
Successional Change

Life-history traits	Physiological traits
Lifespan (annual, short- or long-lived perennial)	Salt effects on growth (stimulation, inhibition, tolerance; salt spray and saline soil)
Age- or stage-specific mortality rates	Salt effects on seed germination
Growth form (erect, decumbent, prostrate, trailing, etc.)	Seedling response to sand burial
Plant height	Seed germination requirements (temp., light)
Seed size	N, P use efficiency
Dispersal biology	Nutrient translocation and storage
Size of "individual" (genet or clone)	Water use efficiency and drought tolerance
Reproductive biology (balance of sexual and vegetative)	Carbon allocation (above- vs. below-ground)
Clonal morphology and rate of spread	Tolerance to flooding
Rooting depth and distribution	Carbon metabolism (C3 or C4 pathway)
Presence of buried buds	Shade tolerance

species that form the next stage of a successional sequence. *Salsola kali*, an important colonizing species of the beach, has been found to facilitate the establishment of later-stage grasses in other harsh habitats.²⁸¹ *Myrica* spp., major shrubs of the rear dunes and dune slacks throughout the Atlantic coast, are known to fix nitrogen through actinomycete symbionts of the roots.²⁸² Other (inland) species of *Myrica* have been found to affect competing species through enrichment of soil nitrogen,²⁸³ but no such evidence has been found for the shrub species of *Myrica* found along the North American Atlantic Coast in coastal or non-coastal environments.²⁸⁴

In summary, successional processes on barrier islands are episodic, and are closely tied to the physiographic processes that determine island shape and stability. Successional patterns described for coastal dune sequences suggest that the change from pioneer herbs to fully developed forest may take hundreds or thousands of years; the process is intimately related to the course of soil development.^{56,285,286} On barrier islands, less time has been available for soil development, since barrier islands are rarely more than 6 to 8000 years old, than in many coastal dune systems which have been dated to tens or hundreds of thousands of years. If island habitats remain stable for long periods of time (millenia), soil development and thus succession to maritime forest can occur; successional patterns will be truncated or prevented in sites with frequent major disturbances (e.g., the complete overwash once per hundred years demonstrated for Fire Island, N.Y.²⁶⁶). Local changes in environmental conditions (blowouts, dune growth, water table level changes) will cause changes in community composition as different combinations of life-history and physiological traits confer a competitive advantage to the species present. The tight

relationship between geomorphology and succession indicates that the occurrence of succession, and the pathways followed, will be as variable as the kinds of barrier formations that can occur. The species-based processes that form the mechanism of successional change, however, are likely to be similar on all barrier islands, and deserve more critical field investigation.

E. Ecosystem Processes

In order to limit the scope of the discussion, only those aspects of ecosystem ecology directly affecting or affected by plant function are considered.

1. Nutrient Inputs and Outputs

The importance of salt spray as a source of cationic nutrients in maritime ecosystems has been well established in studies both on Atlantic coast barrier islands, and several coastal dune sites.²⁸⁷⁻²⁸⁹ Despite the frequently demonstrated importance of salt spray as both a source of cationic nutrients and as a source of stress, and the strong vertical and horizontal gradients of input (see Section I.C.2), there has been little study of relative effectiveness of different leaf morphologies and plant growth forms in trapping and/or avoiding salt spray. Long narrow leaf shapes accumulate more spray per unit area than rough-surfaced, irregular canopies.³⁸ Thus, grassland ecosystems on barrier islands may have higher cation accumulation rates per unit leaf area than shrublands whose species have rounded, even-topped canopies. More comparative studies of spray capture by different plant species are needed, however, before the consequences of leaf and plant form for nutrient capture (and excessive salt deposition) can be evaluated.

Nitrogen, unlike the cationic nutrients, is in low supply, and is generally viewed as a primary limiting factor for plant growth.^{33,125,156,207} The rate of mineralization of organic nitrogen that accumulates in dune soils may have as important a limiting role as does the input of N to the ecosystem.²¹⁰ Nitrogen-fixing organisms play a potentially important role in supplementing the nitrogen budget of coastal ecosystems. Three sources of nitrogen fixation have been identified as suppliers of potentially significant amount of N, including free-living microbes associated with plant roots, bacterial symbionts of leguminous plants, and actinomycete symbionts of *Myrica* and related species. Some nitrogen fixation can occur in proximity to plant roots.²⁹⁰⁻²⁹² In experimental studies of microbial activity in the rhizosphere, it has been shown that *Azotobacter* inoculation increases plant growth, with a concomitant increase in soil nitrogen in pots containing plants,²⁹⁰ while *Bacillus* strains isolated from the rhizosphere of *A. arenaria* fix N at a (maximal) rate of 130 $\mu\text{m C}_2\text{H}_4/2$ ml culture per hour.²⁹² Some species of grass from inland sand dune habitats have sand grain sheaths (rhizosheaths) with which nitrogen fixation (up to 6 $\mu\text{m C}_2\text{H}_4/\text{g d wt/h}$) is associated.²⁹³ There is some question, however, whether significant amounts of N are fixed in natural ecosystems.²⁹⁴ Nodulated legumes may fix N at up

to $2.83 \mu\text{m C}_2\text{H}_4/\text{g fw/h}$,²⁹⁴ which is available to other plants for uptake²⁹⁵ and contributes to ecosystem nitrogen cycles.²⁹⁶ The actinomycete associates of *Myrica pensylvanica* from north Atlantic barrier island habitats can fix nitrogen at rates up to $5.03 \mu\text{m C}_2\text{H}_4/\text{g fw/h}$.²⁸² Thus, plant-associated nitrogen fixation apparently occurs and contributes to plant nitrogen requirements and ecosystem function, at least under some conditions.

Other inputs of nitrogen to the plant community include aerosol and precipitation inputs. Representative values for such inputs include 0.2 ppm organic nitrogen (up to 0.47 ppm total N) in rainfall and snow samples in near-coastal sites in New Zealand,²⁹⁷ 1–5.5 ppm $\text{NH}_4\text{-N}$ in precipitation and fog on the Pacific coast²⁹⁸ and 1.6 kg/ha in bulk precipitation plus 2.5 kg/ha in spray plus fog.²⁹⁴ These inputs can be compared, for example, with aerosol inputs measured over an inland site subject to acidic deposition in southern California, in which 1.9 kg total Kjeldahl N/ha/yr was recorded²⁹⁹ (47% of the total N input to the chaparral ecosystem during a 25-year rotation), or inputs to eastern inland forests of 2.5 kg/ha per year aerosol N plus 6.5 kg/ha per year precipitation N.³⁰⁰ It is thus likely that the aerosol inputs of N to barrier island ecosystems are at least equal, and probably greater in relative importance to the overall nitrogen economy than the inland systems that have been studied. More detailed study of the interaction of leaf and plant morphology in the capture of aerosols would help clarify the relative roles and quantify the absolute inputs of above-ground versus below ground nitrogen inputs to barrier island ecosystems.

Inputs and dynamics of phosphorus have received scant attention. Aside from a number of values for the quantities of phosphate in dune soils (Table 1), and studies of the effects of phosphate added as fertilizer on plant growth, there is no data on the sources, pools and sinks of phosphate in barrier island or comparable coastal ecosystems.

The dominant processes governing the loss of nutrients from barrier island ecosystems are leaching and volatilization from fire. The importance of leaching was clearly shown in the early studies of dune soil development.^{30,39,56,289,301} In dunes with an initially moderate carbonate content (5%), most is lost from the top decimeter of soil within 300 to 400 years.⁴⁶ Actual concentrations and rates of loss vary widely, depending on the rate of input of calcium in shell fragments, the type of vegetation, and the amount and acidity of precipitation. Sodium also is rapidly leached; for example, on Bodie Island, North Carolina, the turnover time for sodium in the soil is 11 to 37 d, depending on soil depth and position on the dune; salt deposited in spray in March has leached below 60 cm by May.^{31,79} Potassium also is leached; in English dunes, about 22 kg/ha per year are lost in leaching, compared with 32 kg/ha per year input in spray and precipitation.³⁰² However, on Fire Island, N.Y., groundwater loss of potassium was lower, compared to throughfall inputs, than the input:output ratios for sodium,

calcium and magnesium, suggesting an important role for plant uptake in the dynamics of this element.¹⁴⁵ Plant uptake was also implicated in the retention of calcium, magnesium, and potassium in a coastal shrub ecosystem (*Baccharis pilularis*), in which sodium, a non-essential element, was strongly leached.²⁸⁹ The relative effectiveness of plant uptake and other immobilizing ecosystem processes in retaining soil nutrients against the strong tendency towards leaching loss in the sandy soils is, however, essentially unquantified.

The importance of fire in barrier island plant communities has frequently been documented^{271,303,304} but no studies have specifically addressed the role of fire in nutrient dynamics. However, the role of fire in nutrient input and output processes has been frequently examined (reviewed by Boerner³⁰⁵). Nitrogen and sulfur are easily volatilized and cations may be lost in convection of ash; the remaining ash may settle out and contribute to nearby ecosystems, or become a source of available cations to the regenerating vegetation. Leaching and runoff losses of the mineralized cations may also occur. In ecosystems developed on nutrient-poor substrates, much of the nutrient pool is located in above-ground biomass and the forest floor; fires can thus remove a large fraction of the nutrient pool. Rapid resprouting of shrubs and trees and nutrient uptake by the surviving root systems help conserve mobilized nutrients and trap cations entering in precipitation. It is likely that the nutrient-conserving mechanisms described for other nutrient-poor ecosystems apply at least to the shrub and maritime forest ecosystems of barrier islands. It is less likely that responses to fire observed in grasslands developed on rich prairie soils provide a model for the response of dune grasslands developed on poor sandy soils.

2. Nutrient Dynamics and Soil Ecology

The role of the plant community in structuring the soil ecosystem has been the focus of several studies, primarily on the coastal dunes of Europe and western North America; little work on soil ecology has been done on barrier islands. Dune plants promote a rhizosphere flora much richer than the surrounding bulk soil, and the composition of the rhizosphere flora varies with plant species.^{306,307} *Atriplex babingtonii*, a plant of the English foreshore, supports a bacterial flora 1.4×10^3 times the flora of the open sand, while *A. arenaria* support a flora 200 times that of the open sand. Differentials in rhizosphere and nonrhizosphere populations of fungi are even greater (7- to 290-fold increase, depending on plant species). Microbes heavily colonize the surface of the roots of dune grasses (*Amphiphila arenaria*, *Agropyron junceiforme*, and, to a lesser extent, *Festuca rubra*), and actually invade the epidermal and cortex cells, lysing cells and causing partial sloughing of the outer cell layers of the root.³⁰⁸ The species diversity of fungi colonizing above-ground litter also varies with plant species.³⁰⁹

The fungal flora also varies across vegetation zones and on dune systems with different calcium contents.³¹⁰ Diversity in-

creases inland on the gradient, reaching a maximum on semi-fixed dunes. On beach and foredunes, fungal mycelia are restricted to pockets of organic matter, but are more widespread on the primary dune. Few species are restricted to the dune habitat. Fungi inhabiting feces also vary in community composition and abundance along vegetational gradient; variation in the microclimate associated with the development of the vegetation in different sites along the gradient is correlated with variations in diversity and abundance of the coprophilic fungi.³¹¹

The soil microflora interacts with plants in promoting soil development in dune ecosystems. Hyphae of both saprophytic and endomycorrhizal fungi help bind sand grains into aggregates through the excretion of amorphous polysaccharides, which in turn serves as a substrate for colonization by bacteria, actinomycetes, and algae.³¹²⁻³¹⁴ The presence of a diverse microflora enhances the process of aggregation. The degree of soil aggregation increases along the vegetation gradient: during the summer, soil aggregates (mg/kg soil) increase from 5 in the foredunes to 40 on the mobile dune slope, 300 on the dune crest, and 1260 on young fixed dunes.³¹³ The aggregates contain a variety of fungal species, including mycorrhizal species, and various bacteria including some thought to be nitrogen-fixing. There is an interactive effect between plant root growth and aggregate formation;³¹⁵ in the absence of plants, bacteria are the main aggregate-formers, while fungi become dominant in the presence of roots. The total amount of aggregation, and concomitantly the abundance of all microfloral species, also increases dramatically in the presence of roots.

Vesicular-arbuscular mycorrhizae (VAM) are an important component of the fungal flora. They have been identified on many of the grass species of the dunes, and their abundance (in amount of mycelium and percent infection) is at a peak in the stable dunes.³¹⁶ Growth of *A. arenaria* and *A. repens* is increased by infection. On American barrier island foredunes,³¹⁷⁻³¹⁹ several mycorrhizal fungal species are present,³²⁰ and different plant species support different groups of fungal species. Infection levels range from 10% for *Panicum virgatum* in Maine to 90% for *Uniola paniculata* in Georgia.³¹⁸ The level of infection increases inland, in proportion to the amount of vegetation cover. In North Atlantic areas, spore density is roughly correlated with the percent cover of *Ammophila*, but not with the cover of less abundant species; similarly, in more southern sites (Florida), spore density in unvegetated dunes is only 6% of that in dunes vegetated by *Uniola*.³²⁰ On the Dutch dunes (mainland and barrier island), the perennial grasses similarly show a high percentage of VAM infection (30 to 60%) that increases inland from the foredunes, but the annual forbs and grasses do not support mycorrhizae.³²¹ Low winter temperatures may limit fungal growth in the annual species, which germinate and grow primarily during this season. In other cases, e.g., pioneer plants on the beach, lack of infection may be dependent on movement of sand containing fungal spores into the site.³²²

In similar fashion, plant community composition affects the faunal component of the soil community. Both species diversity and abundance of nematodes increases on the gradient from beach to stable dunes, and there is change in trophic structure of the nematode community along the gradient.³²³ In primary dune soils, and the proportion of bacterivores rises to 27% in parallel with soil organic matter and soil acidity.³²⁴ Within a given site, differing groups of species of nematodes can be found beneath different plant species.³²⁵ Soil arthropod diversity also varies in response to plant species composition.³⁰⁹ In California coastal dunes, macroarthropod diversity declines as *A. arenaria* cover declines (following a hypocycloid relationship), and increases with decreasing amounts of bare ground in areas of native vegetation. Slobodchikoff and Doyen³²⁶ speculate that the prostrate mat plants characteristic of the native vegetation may supply more food, because of their patterns of root growth, than does the introduced *A. arenaria*.

The role of root-microbe-faunal interactions in regulating nutrient cycling has become a major theme of ecosystems theory,³²⁷ and the scanty evidence compiled here suggests that there are strong interactions between plants and the nutrient-processing soil communities of barrier island ecosystems. Root exudates and fine-root production stimulate the development of soil microbial populations and promote the development of soil structure from the loose beach sand. Thus, community development and successional change may be a function of these interactions, insofar as microbially-mediated nutrient cycling processes and soil genesis are important factors in community composition.

3. Net Production

There have been surprisingly few ecosystem-level studies of primary production in barrier island communities. Art's classic study of the maritime forest of Fire Island, New York^{145,288} is the only study of a complete community; a number of other studies have measured productivity for individual species, or simply have given total site biomass values.

Total site biomass values for the grassland communities of the dunes are fairly similar over a wide range of geographic locations. Peak above-ground biomass values were 400 g/m² and 110g/m² for one-year-old and ten-year-old stands of *Ammophila arenaria*, respectively, in coastal dunes in Sweden. Total biomass, including roots and rhizomes, was 581g/m² and 718 g/m², respectively, reflecting an increasing allocation of biomass to below-ground structures in older populations.¹²³ *A. breviligulata* populations from the foredunes of Lake Michigan were reported to be 183 g/m² above ground (347 g/m² total).¹³⁶ The prior two estimates were made solely on samples of *Ammophila*, and thus do not give estimates of total site biomass. Fore-dune communities of *Ammophila* and *Uniola* in North Carolina ranged from 370 g/m² estimated total biomass on the front of the fore-dune to 830 g/m² total biomass on the rear of the fore-dune.²⁸⁷ Total site biomass values for a range of sites in dune grasslands of the Netherlands³²⁸ ranged between <100

g/m² and >800 g/m². Total above-ground biomass for strand communities in California and Texas are 98 to 121 g/m² for two sites in California and 149 g/m² in Texas.⁴⁴ These values are in the low to intermediate range for temperate grasslands (range 100 to 1500 g/m², approximate mean 500 g/m²).³²⁹ Although above-ground *Ammophila* biomass decreases with distance from the ocean,^{121,123} other species increase in abundance; the effects on total site biomass and site productivity will vary with the growth forms of the species that replace the grass. Total site biomass patterns will obviously vary with the amount of bare ground, the invasion of shrub species into grassland communities, and the density of the vegetation. The variation in total site biomass with vegetation type across a barrier island is illustrated in Figure 14. These data, for Fire Island, N.Y.,³³⁰ show that as expected, total site biomass increases as the proportion of woody vegetation and the height of the vegetation increase.

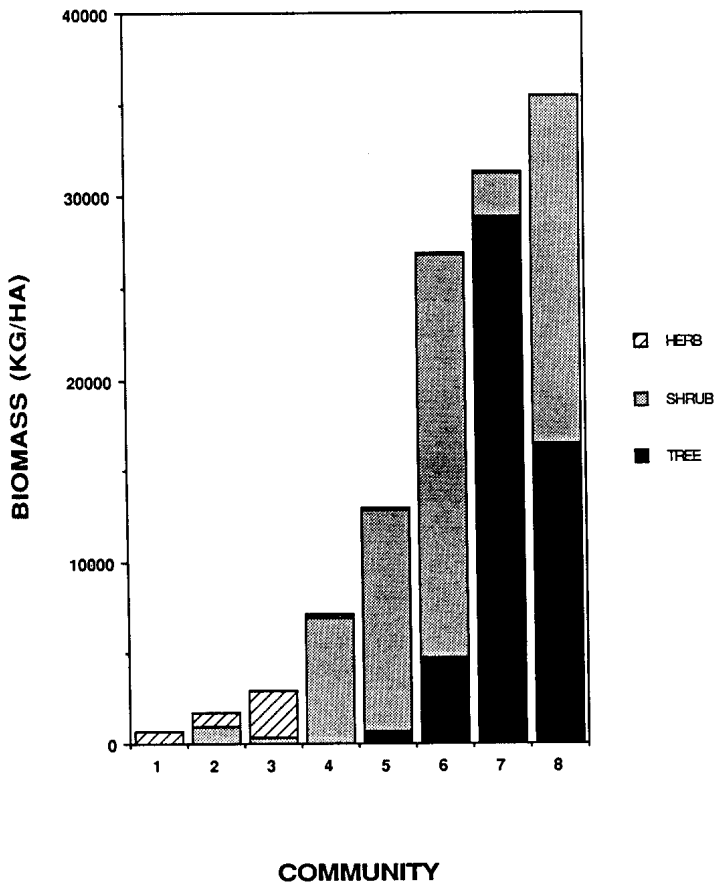


FIGURE 14. The standing crop biomass in different communities on Fire Island, NY, and its distribution among plant life-forms. Community types: 1 - *Ammophila* - dominated grassland; 2 - grass-shrub mixture; 3 - *Arctostaphylos*-low shrub mixture; 4 - shrubland of *Myrica*, *Rhus*, others; 5 - tall shrub thicket of *Myrica*, *Rhus*, others; 6 - tall shrub thicket of *Amelanchier*, *Vaccinium*, others; 7 - pine forest; 8 - broad-leaved forest. Data from Reference 330.

The study by Art¹⁴⁵ of the *Ilex opaca* forest on Fire Island, N.Y., provides a picture of the biomass and production relationships of a maritime forest. The total biomass of 17,083 g/m² was partitioned into 5673 g/m² branch and bark (35%), 5125 g/m² roots (30%), 647.4 g/m² leaves (3.8%) and the remainder in stems. Compared to inland forests, there is larger allocation of biomass to both roots and branches. The total plant biomass, however, is smaller than many mainland temperate forests; those with comparable or smaller biomass are open woodlands or those from very nutrient-poor sites. Net production in the forest was 1123 g/m² per year, a value comparable to those of other temperate forests. Sixty-six percent of the net production, and 72% of the total biomass is contributed by the dominant species, *Ilex opaca*. Litter fall in the forest is 557 g/m² per year, similar to the values for other mainland temperate forests. These data suggest that maritime forests may have a different physical structure than mainland forests, with relatively larger amounts of branches and roots, possibly owing to the effect of salt spray on growth form. The difference in physical structure does not seem to correspond, however, to differences in function, as measured by net primary production and litterfall.

III. DISCUSSION

A. General Patterns in the Ecology of Barrier Island Vegetation

Barrier island vegetation is molded by a complex of abiotic factors which decrease sharply in intensity from ocean to bay. Certain aspects of the response of the plants to these factors have been studied in great detail in a few species; other aspects have received virtually no study. A few generalizations can be drawn, but these statements should be interpreted as much as heuristic statements for future research as conclusions based on the available information.

Plants occupying the beach and foredunes are distinguished by several adaptations: (1) the ability to utilize ocean water for seed dispersal, (2) the tolerance — and in some cases stimulation — of seed germination and growth with respect to brief exposure in salt water, (3) the adaptations to survive sand deposition, including large seeds, deep root growth, and the capacity to elongate in step with sand accretion, (4) growth forms (prostrate habit, wide horizontal leaves) that minimize salt deposition, and (5) a high degree of phenotypic plasticity, rather than genetic differentiation among populations.

The acquisition and retention of space recurs as a theme in the consideration of many aspects of the ecology of individual species. Seed dispersal distances are small, suggesting that unlike the situation in many inland communities, there is an advantage to retaining space occupied by the parental individuals. Clonal growth is a common feature of both herbaceous perennials and woody plants. Patterns of clonal spread in mo-

bile habitats are usually extensive, "guerilla" types, in which space is explored and covered rapidly, but not densely. In more stable habitats (fixed dunes, swales), intensive, "phalanx" growth patterns are common, and space acquired is densely occupied to the exclusion of other individuals of the same or other species. Thus, competitive interactions may revolve about the ability to occupy space, rather than obtain soil nutrients, water, or light, as in mainland habitats.

Succession also reflects the space-acquiring habits of barrier island species. The extensive propagation of root/rhizome systems in dune sand by pioneer species fosters the development of nutrient-cycling food webs in the soil; this may in turn facilitate the establishment of other species, including those of later successional communities. Likewise, the sand-trapping abilities of different dune-forming species is a function of their patterns of clonal spread, and the size and shape of the dunes produced by the plants has a profound effect on the nature of the vegetation that joins and succeeds the pioneers.

A high degree of within-habitat, small-scale heterogeneity is another feature that is apparent in many of the studies reviewed here. In traversing a dune, the amount of sand movement, the amount of aerosol deposition, the depth to water table, soil quality, and the microclimate can vary drastically over short distances. Thus, movement of propagules or growth of rhizomes over distances on a scale of meters can expose the individual to a varying array of environmental conditions. Even with a given location on a dune, small irregularities provide significantly different conditions for plant growth, as is evidenced by the reliance by several species on such irregularities for seed germination and seedling establishment. Small dispersal distances, compact growth forms, and the ability to translocate nutrients and water to subsidize growth of rhizomes past poor sites and into more hospitable sites are all responses to such small-scale habitat heterogeneity.

Contrary to expectation, biotic factors, including herbivory, intraspecific and interspecific competition, play a prominent role in all barrier island habitats. Biotic controls on population and community dynamics are generally thought to decrease in importance as disturbances become more frequent and severe, and as the physical habitat becomes more harsh. However, no such trend could be discerned for the communities along the ocean-to-bay gradient. It has been frequently observed that no one environmental factor can explain the vegetation patterns of barrier islands; the missing factor(s) may include the biotic interactions that are usually presumed to be of minor importance in habitats subjected to frequent physical disturbance. An evaluation of the relative importance of biotic and abiotic controls on population and community processes in communities along the gradient must await more extensive research.

B. Areas for Future Research

Throughout this review, I have indicated where additional data are needed to appraise the applicability of current ecological theory to barrier island ecology. The need for com-

parative studies of processes in contrasting community types, and the need for studies addressed to theoretical issues has been obvious. Beyond this, however, are several general themes for future research on barrier island vegetation, which can serve to unify research on a variety of individual topics.

1. There is, at present, insufficient data to assess the role of insularity on the ecology of barrier island vegetation. Do barrier island communities differ in their structure and function from equivalent mainland, or inland communities? The evidence of differences in tree form, sources of nutrient input, distribution of seed dispersal syndromes within the flora and pollination ecology described above suggests that many barrier island communities may differ from mainland communities for a wide range of ecological processes. Does the species diversity of barrier islands differ from that of mainland coastal sites or barrier spit formations (peninsulas)? Again, the meager data suggest an affirmative answer, but little more. Are chains of barrier islands similar to oceanic archipelagoes in their species diversity patterns? How does distance from the mainland affect the diversity of barrier islands? The list of questions that could be addressed from this point of view could include essentially all aspects of ecological dynamics included in this paper.
2. Barrier island communities, from the beach through the interior to the bay, cross sharply defined gradients of environmental factors, yet it is not possible, with the available information, to compare the relative importance and mode of action of either biotic or abiotic forces in community structure and dynamics among these communities. Comparative studies of ecological processes under such varied conditions of disturbance and physical stress would help define the ecological dynamics of barrier island vegetation; they also would provide an ideal opportunity to study the interplay of disturbance, competition, herbivory (i.e., predation), dispersal biology, population genetics, and individual ecophysiology.
3. Barrier islands are ideal locations in which to investigate the interactions among different communities across the landscape. Several examples can be cited to illustrate some possible kinds of between-community effects. The movement of propagules from beach populations of *C. edentula* inland to the dunes permits persistence of the species in the dune community. Blowing sand may transport spores of mycorrhizal fungi and other components of the soil ecosystem that are essential for nutrient cycling processes. Sulphate emissions from fringing salt marshes may significantly affect the biogeochemistry of interior shrub and forest communities. Strong winds, extensive movement of sand, and a shallow groundwater table all provide means for the transfer of material, energy, and nutrients between communities.
4. Barrier island vegetation is under tremendous pressure

from the human populations that compete for space in the coastal zone. The impacts of these people (trampling, off-road vehicle use, building on primary dunes, pollution, introduction of exotic species, etc.) have not been reviewed here because of limitations of space. The response of the ecological processes considered here to such disturbances should have high priority for research.

5. Coastal plant communities will be the first to be affected by the projected increase in sea level resulting from the rise in global CO₂. Although several studies have addressed the impacts of sea level rise on the coastal wetlands³³¹ and on coastal geomorphology^{52,332} the effects on barrier island vegetation have received no attention. Aside from an increase in erosion and washovers caused by storms, sea level rise may cause the water table to rise in the inland portions of the island, increasing the amount and diversity of swale habitat at the expense of drier habitat. The resulting changes in species diversity, community structure, and ecosystem function are likely to be profound.

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