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Distribution of Barrier Island Plants in Relation to Overwash Disturbance: A Test of Life History Theory

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ABSTRACT

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We document the relationships between the distributions of species and the pattern of "overwash" disturbance for plant species on Hog Island, a barrier island off the southern part of the Delmarva Peninsula (Virginia, U.S.A.). Overwash disturbance is the mortality of plants due to sand deposition during storms that create high waves that wash over the island. We analyzed the distribution of each of 95 species in relation to the pattern of overwash disturbance. We then used the results to test the hypotheses that, as one moves from areas of low overwash disturbance frequency to areas of high overwash disturbance frequency, (1) the number of annual and biennial plant species increases relative to perennial species and (2) the number of woody plant species decreases relative to herbaceous species. These hypotheses are derived from life history theory which predicts that early maturation and short lifespan are advantageous in highly disturbed environments. There were large differences among the plant species in their tolerances to overwash disturbance. As expected, there were fewer woody plant species than expected at random in areas of high overwash disturbance frequency. However, the hypothesis that annual plant species would be more common than expected at random in frequently disturbed areas was not supported. This result may be explained by advantages of clonal growth and reproduction in perennial plants, in areas of high overwash probability.

ADDITIONAL INDEX WORDS: *Life history, annual, biennial, perennial, herbaceous, woody, clonal, storm, washover, Hog Island, Delmarva Peninsula.*

INTRODUCTION

The barrier islands of eastern North America are long, narrow, low-lying islands running lengthwise off the coast at a distance of from several hundred metres to a few km. The surface material of the islands is sand. A dominant feature of barrier islands is the frequent occurrence of "overwash events", in which winter storms produce high waves that wash over the islands from the open ocean. These waves remove large quantities of sand from the beach face of the island and spread the sand into the interior of the island in "washover fans" (DOLAN *et al.*, 1979, 1987). The frequency of overwash varies over the surface of a barrier island. The frequency at any point depends on distance from the beach face (negative relationship) and elevation (negative relationship). The location and orientation of the beach face with respect to the typical storm track direction also influences overwash probability (DOLAN *et al.*, 1979; DOLAN and HAYDEN, 1981).

Overwash constitutes an important cause of disturbance to vegetation on a barrier island. The depth of sand deposited can amount to several cm; this can kill or injure plants, and bury seeds to a depth from which they can not germinate (SCHROEDER *et al.*, 1979; VAN DER MEIJDEN and VAN DER WAALS-KOOI, 1979; LEE and IGNACIUK, 1985). Different species have differing abilities to survive in areas of high overwash frequency (EHRENFELD, 1990). Patterns of vegetation distribution over an island are therefore highly variable in response to variability in overwash frequency over the island (SCHROEDER *et al.*, 1979; ZAREMBA and LEATHERMAN, 1986; ROMAN and NORDSTROM, 1988).

General theories have been proposed relating life history characteristics to survival in frequently disturbed areas (COLE, 1954; CHARNOV and SCHAFFER, 1973; STEARNS, 1976; IWASA and COHEN, 1989). Stated simply, the theories predict that species that have early maturation and short lifespans should survive best in frequently disturbed areas. The main idea is that if an individual is

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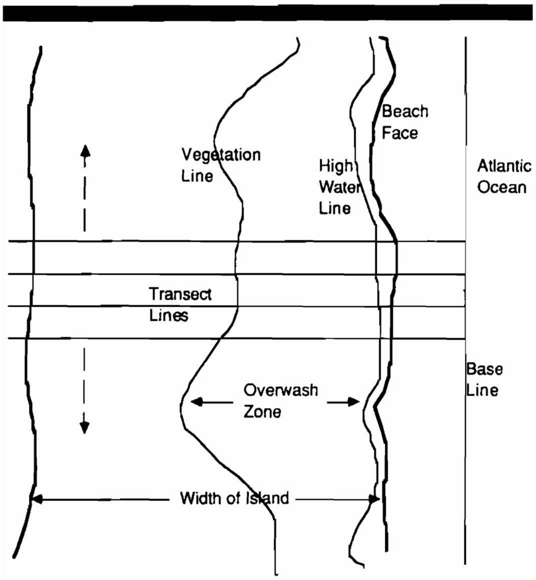


Figure 1. Illustration of method used by Dolan, Hayden and coworkers to measure overwash penetration distances. A portion of a barrier island is shown. The base line and transect lines are fixed. The overwash distance at a certain transect is the difference between the distance from the baseline to the vegetation line, and the distance from the base line to the high water line.

likely to be killed at any moment by a disturbance, it is most advantageous for that individual to produce as many offspring as possible, as quickly as possible (*i.e.*, early maturation). It will in general not be advantageous to put energy that could be used for reproduction into growth or storage for the future, since in a frequently disturbed area the future is very uncertain. For plants this idea can be more specifically stated as two hypotheses: as one moves from areas of low disturbance frequency to areas of high disturbance frequency (1) the abundance of annuals should increase relative to perennials (annuals have shorter lifespans) and (2) woody plants should decrease relative to herbaceous plants (woody plants on average mature later than herbaceous plants). Some empirical studies support these ideas (DYRNESS, 1973; JOENJE, 1985; WATKINSON and DAVY, 1985; COLLINS, 1987; HALPERN, 1988).

To test general hypotheses such as these it is necessary to examine the characteristics of a large number of species in different areas of varying disturbance frequencies. It is not possible to test them by study of only a small number of species because an individual species living in a frequently disturbed area is likely to have unusual or unique species-specific characteristic(s) that enable it to recover from the disturbance (*e.g.*, ELLISON, 1987). This can mean that each individual species will appear to be a "special case". General hypotheses such as those above are proposed to hold on average. In other words, if we look at a large number of species the general theory may hold for the majority of them, even though there will be exceptions due to species-specific unusual or unique attributes.

The aims of this paper are twofold. First, we wish to document the relationships between species distributions and pattern of overwash disturbance for plant species on Hog Island, a barrier island off the southern part of the Delmarva Peninsula (Virginia, U.S.A.). The overwash disturbance regime on the island is such that some parts of the island experience one or more overwash event(s) almost every year, while other parts virtually never experience overwash. We analyzed the distribution of each of 95 species in relation to the pattern of overwash disturbance. Our second aim is to use these results to test the two hypotheses stated above, namely that as one moves from areas of low overwash disturbance frequency to areas of high overwash disturbance frequency on Hog Island (1) the number of annuals increases relative to perennials and (2) the number of woody plants decreases relative to herbaceous plants.

ANALYSIS OF DISTURBANCE DATA

The calculations of the disturbance frequencies were based on a dataset compiled by R. Dolan, B. Hayden and co-workers over the past two decades during their studies of the geology and geomorphology of the Virginia barrier islands. Aerial photographs of the islands were used to determine the cross-island distance (m) of the penetration of overwash storm surge from the beach face of the island across the island, perpendicular to the length of the island. They used an orthogonal grid mapping system with grid transects spaced at 50 m intervals (DOLAN *et al.*, 1978). Measurements were recorded to the nearest 5 m, for each transect, of the distance from the baseline to the high water line and from the baseline to the vegetation line (*i.e.*, the overwash penetration line) (Figure 1).

The purpose of our analyses of the Dolan/Hayden overwash data was to develop an index of the disturbance probability at any point on Hog Island. The information consisted of a series of static "snapshot" views of the disturbance regime (*i.e.*, the aerial photography analysis). Therefore, we could not calculate the disturbance frequency *per se, e.g.*, in terms of the number of times per year that the sites experience a disturbance. Instead, we obtained an estimate of the likelihood that a site will be found in a "disturbed state", *i.e.*, it has recently been overwashed and covered with sand and has not yet had time to be recolonized by plants. For a particular series of photographs in the overwash data, the disturbed area is the area seaward of the "vegetation line" in the overwash data ("overwash zone" in Figure 1).

To calculate the index of disturbance probability we used the data in the Dolan/Hayden dataset on the overwash penetration for Hog Island. There were seven years of data—1949, 1955, 1962, 1967, 1975, 1977, 1988—with 288 transects covering the length of the island, for each year. Calculating an index of disturbance probability amounted to calculating the probability, at any point on each transect, of finding the vegetation line at or beyond (*i.e.*, farther from the ocean across the island, see Figure 1) that point. The procedure for developing the index was as follows. First we calculated the "overwash distance" (*i.e.*, the distance from the high water line to the vegetation line) for each transect for each year, by subtracting the baseline to high water line distance from the baseline to vegetation line distance (Figure 1). Initially we had thought that the overwash distance might conform to a standard distribution, with the mean distance varying spatially and the variance having some constant relationship to the mean. However, this did not turn out to be the case, probably due to peculiarities of the topography at different locations (ROMAN and NORDSTROM, 1988). It was not possible to find a relationship between the overwash probability distribution and some topographic measure(s) because fine-scaled information on topography is not available (all of the island is less than 5 m above sea level). Therefore, we were left with directly estimating the overwash distance probabilities, without relating them to any particular probability distribution.

There were seven data points for each transect (*i.e.*, seven years), which we felt would render too crude an estimate of the probabilities for the length of a transect (which can be over 1,500 m long). However, there is spatial correlation in the data; disturbance regimes along neighbouring transects are more similar than disturbance regimes along distant transects because neighbouring transects tend to be similar topographically, and are in similar positions relative to wave direction. Therefore we augmented the information for each transect by including the information from each of the four nearest (*i.e.*, two to the south and two to the north) transects. In this way we had 35 points for each transect. The index of disturbance probability for a particular point on a particular transect was then the fraction of overwash distances (of 35) that were less than or equal to the distance to the point. The total number of transects was reduced to 284 since the two southernmost and northernmost transects could not be included. The method of analysis and the results are shown in Figures 2 and 3.

ANALYSIS OF VEGETATION DATA WITH RESPECT TO OVERWASH PATTERNS

In the mid-1970's the Nature Conservancy commissioned a study of the vegetation distribution of Hog Island; the work was conducted by C. McCaffrey (MCCAFFREY, 1975). McCaffrey used a combination of aerial photographs and ground-truthing to produce vegetation maps. She identified plant "communities" as areas of vegetation that were visually distinguishable from other areas on the photographs. These "communities" are not necessarily discrete ecological communities since they were defined only on the basis that McCaffrey could tell them apart on the aerial photographs; we therefore refer to them as plant "assemblages". McCaffrey conducted ground surveys to determine the species composition and relative abundances of species within each assemblage.

There are two potential problems with the McCaffrey dataset. First, as a vegetation survey it is limited because of its subjective nature; it would be very unlikely that another person could independently come up with the same vegetation map. However, this did not pose a problem for our purposes because we were not ultimately interested in the pattern of assemblage distributions but in the pattern of species distributions. The data can be used to produce an estimate of the spatial distributions of plant species on Hog Island in 1975 (as described below), which is within the time span covered by the overwash data. The second potential problem with the data is that the assemblage distributions are very approximate because of the coarse spatial scale used by McCaffrey. However, the scale was sufficient for our needs because first, the accuracy is about the same as for the overwash data and second,

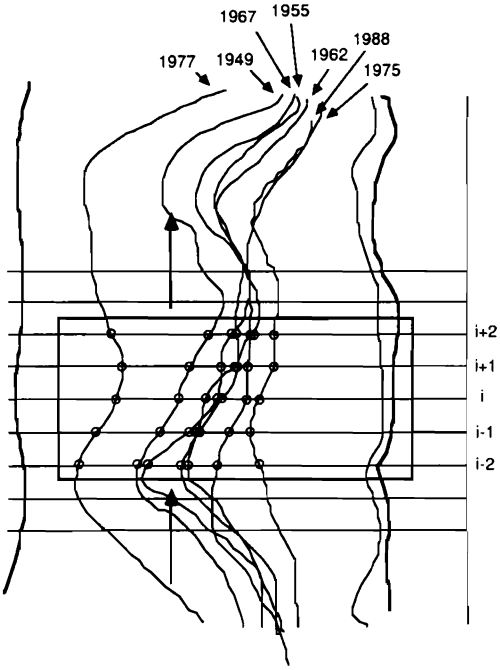


Figure 2. Illustration of our method of analysis of the dataset collected by Dolan and coworkers. Seven vegetation lines (see Figure 1) are superimposed. To estimate the distribution of overwash distances at transect i, we used the overwash distances from the seven years, for transects i − 2, i − 1, i, i + 1, and i + 2, resulting in 35 values for each transect. The box represents a "moving window" that is shifted up the length of the island, one transect at a time.

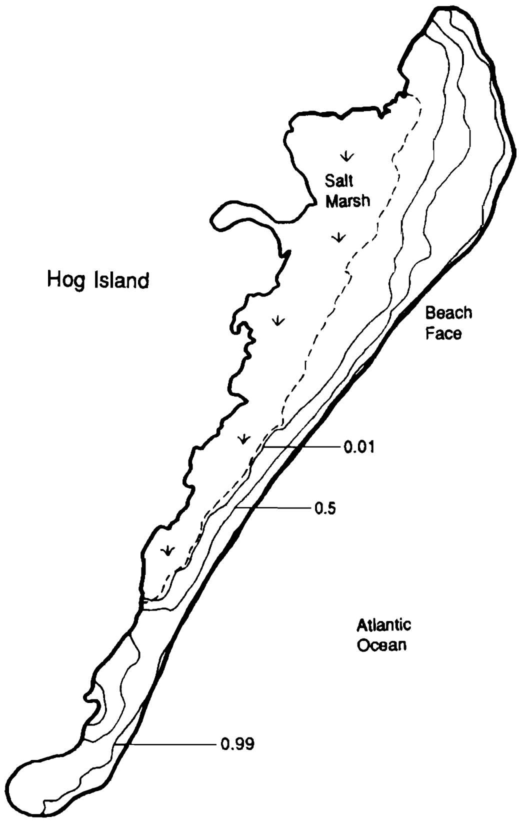


Figure 3. Illustration of the lines of equal index of disturbance probability, calculated for Hog Island. The index is an estimate of the probability that at any time the vegetation line (Figure 1) will be found at or beyond (*i.e.*, away from the beach face) the line. Shown are the lines of equal disturbance index for index values of 0.01, 0.5, and 0.99.

our interest was in broad patterns, not local variability.

The distributions of the plant communities were digitized by the Virginia Coast Reserve Long-Term Ecological Project at the University of Virginia. Each pixel in the data file represents a 2 m by 2 m square, and the value of the pixel represents the assemblage type present there. Each plant assemblage was characterized by McCaffrey (1975) by the relative abundances of all species in the assemblage. The measures of relative abundances were qualitative: "dominant", "abundant", "frequent", "occasional". We replaced her abundance categories with approximate percent cover estimates provided by C. McCaffrey (*personal communication*). There were 95 species in the plant assemblages on Hog Island.

The goal of our analysis was then to describe the relationship between the distribution of each species, as determined from the McCaffrey dataset, and the pattern of disturbance frequencies, as determined from the Dolan/Hayden dataset. To do this we had to first overlay the digitized vegetation map and the map of transects across the island. The disturbance frequency along each transect declines monotonically from the beach face across the island. The pattern of decline was determined from the analysis of disturbance data (above). To connect the disturbance pattern to the vegetation assemblage pattern we moved a pointer along each transect starting at the beach face in steps corresponding to the pixels in the vegetation data. At each point of transition into a plant assemblage, we assigned the disturbance index value at that point on the transect to that assemblage. This represents the highest disturbance value at which that assemblage is found on that transect.

To characterize each species with respect to the overwash disturbance regime in which it occurs we performed the following steps.

(1) We identified for each transect the disturbance index value for each point of transition into each assemblage type as the pointer moved from the beach face across the island.

(2) We constructed a frequency distribution for each assemblage for the disturbance index value at which the assemblage is found, by combining all transects that crossed into that assemblage. We chose 10 classes of disturbance index values for the frequency distributions: 0–0.1, 0.1–0.2, . . . , 0.8–0.9, 0.9–1.0.

(3) We constructed a frequency distribution for each species for the disturbance index in the following way

$$x_{s_i} = \frac{\sum_{c=1}^{C_s} a_c p_{c_s} d_{c_i}}{\sum_{i=1}^{10} \sum_{c=1}^{C_s} a_c p_{c_s} d_{c_i}} \qquad (1)$$

where x_{s_i} is the proportion of the total cover (for the whole island) of species s in disturbance index class i, C_s is the number of assemblages in which species s is found, a_c is the total area of assemblage c on Hog Island, p_{c_s} is the fraction of assemblage type c covered in species s and d_{c_i} is the fraction of transect points crossing into assemblage c that occur in a location that has a disturbance index value in disturbance index class i.

The results of the analysis are given in Figure 4. We categorized the 95 species on Hog Island, based on Figure 4, into one of four categories depending on their tolerances to high overwash disturbance frequencies. The four categories were (1) D− −: low disturbance tolerance, (2) D−: moderately low disturbance tolerance, (3) D+: moderately high disturbance tolerance and (4) D+ +: high disturbance tolerance. The plant species were also categorized as one of (1) annual or biennial (AB), (2) herbaceous perennial (HP) or (3) woody plant (WD). We then used the results to test the following two hypotheses: (1) Annual plants species are more numerous than expected at random in frequently disturbed areas; (2) woody species are less numerous then expected at random in frequently disturbed areas. The frequencies of each species type in each disturbance tolerance category are given in Table 1. Also given are the expected values and the cell χ^2 values for each combination, and the overall χ^2 value. The results do not support the hypothesis that annual plants species are more numerous than expected at random in frequently disturbed areas. However, the results do support the hypothesis that woody species are less numerous then expected at random in frequently disturbed areas.

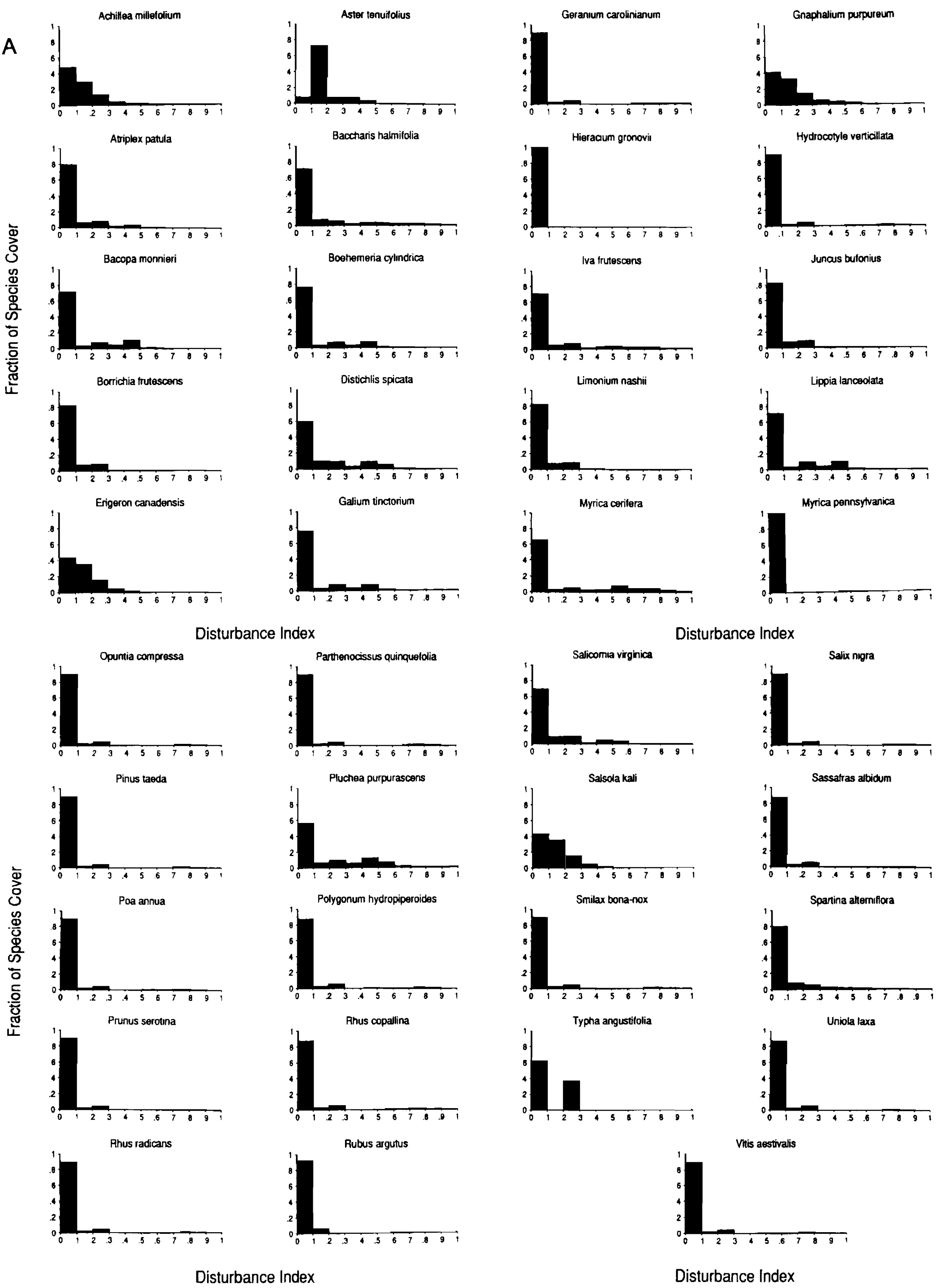
Table 1. *Frequency table for 95 species of plants on Hog Island. The species types are: annual or biennial (AB), herbaceous perennial (HP), and woody plant (WD). Disturbance tolerance categories are: low disturbance tolerance (D− −), moderate to low disturbance tolerance (D−), moderate to high disturbance tolerance (D+), and high disturbance tolerance (D+ +). In each cell the numbers (in order) are frequency, expected frequency, and cell χ^2. Note: the overall χ^2 value is 17.4, with significance level $p < 0.008$.*

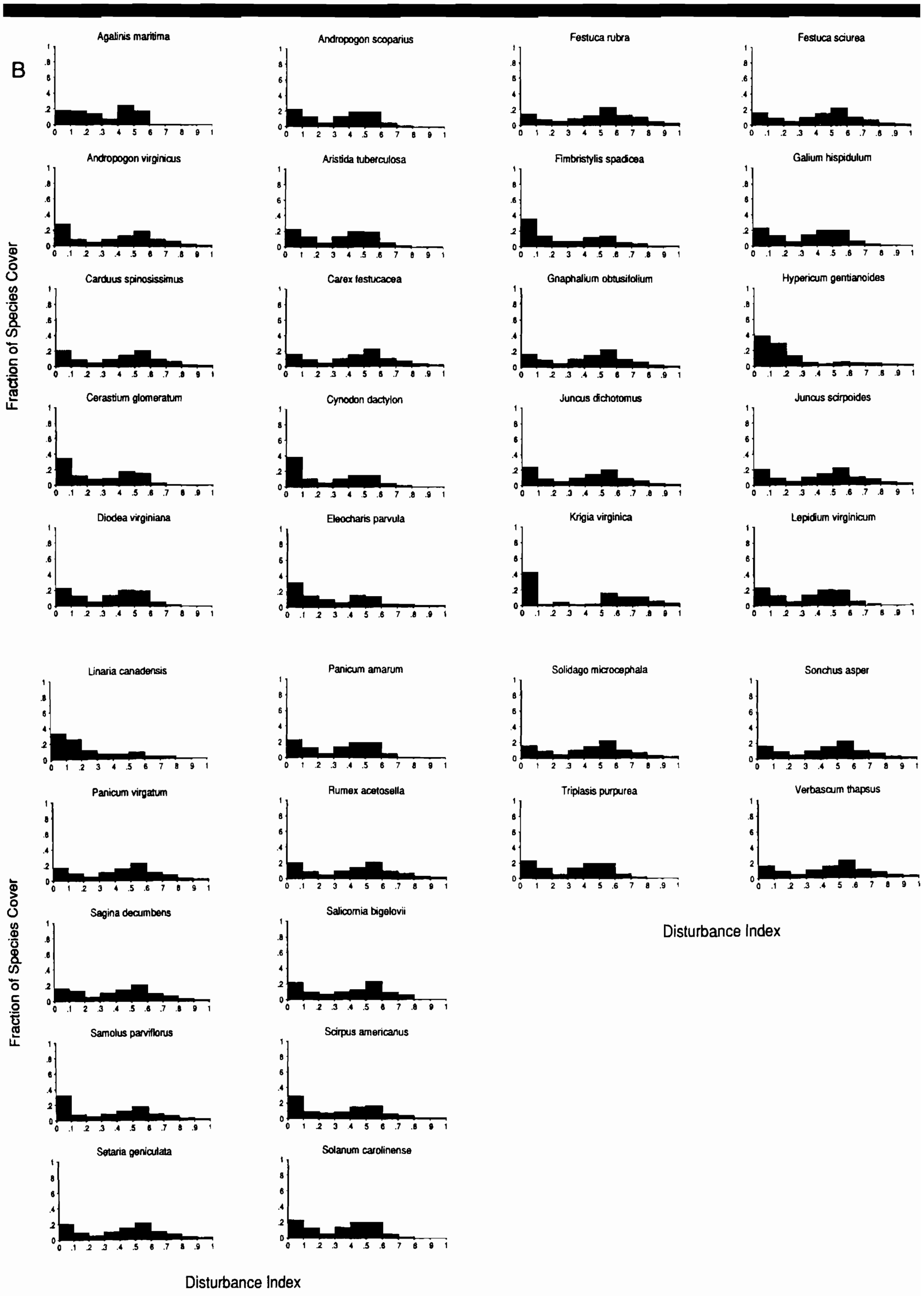
Disturbance Tolerance	Species Type AB	HP	WD	Total
D− −	8 12.7 1.76	17 18.9 0.18	14 7.4 5.91	39
D−	15 11.1 1.37	19 16.5 0.39	0 6.4 6.44	34
D+	6 5.9 0.00	8 8.7 0.06	4 3.4 0.10	18
D+ +	2 1.3 0.37	2 1.9 0.00	0 0.8 0.76	2
Total	31	46	18	95

DISCUSSION

As expected, woody plant species were less numerous than expected at random in frequently disturbed areas. This is consistent with the prediction from life history theory that organisms in highly disturbed areas exhibit early maturation. Woody plants generally mature at a later age than herbaceous plants. If a woody plant germinates in an area with a high disturbance probability, the seedling or sapling is likely to be destroyed in an overwash event before the plant has had a chance to reproduce. This result conforms with the findings of others that woody plants on barrier islands occur in areas of low overwash probability, generally on secondary dunes and on the landward side of the island, next to the lagoon (see EHRENFELD, 1990).

However, our second hypothesis from life history theory, that annuals are more numerous than


A
Achillea millefolium
Aster tenuifolius
Geranium carolinianum
Gnaphalium purpureum
Atriplex patula
Baccharis halmifolia
Hieracium gronovii
Hydrocotyle verticillata
Bacopa monnieri
Boehemeria cylindrica
Iva frutescens
Juncus bufonius
Borrichia frutescens
Distichlis spicata
Limonium nashii
Lippia lanceolata
Erigeron canadensis
Galium tinctorium
Myrica cerifera
Myrica pennsylvanica
Fraction of Species Cover
Disturbance Index
Disturbance Index
Opuntia compressa
Parthenocissus quinquefolia
Salicornia virginica
Salix nigra
Pinus taeda
Pluchea purpurascens
Salsola kali
Sassafras albidum
Poa annua
Polygonum hydropiperoides
Smilax bona-nox
Spartina alterniflora
Prunus serotina
Rhus copallina
Typha angustifolia
Uniola laxa
Rhus radicans
Rubus argutus
Vitis aestivalis
Fraction of Species Cover
Disturbance Index
Disturbance Index


B
Agalinis maritima
Andropogon scoparius
Festuca rubra
Festuca sciurea
Andropogon virginicus
Aristida tuberculosa
Fimbristylis spadicea
Galium hispidulum
Carduus spinosissimus
Carex testucacea
Gnaphalium obtusifolium
Hypericum gentianoides
Cerastium glomeratum
Cynodon dactylon
Juncus dichotomus
Juncus scirpoides
Diodea virginiana
Eleocharis parvula
Krigia virginica
Lepidium virginicum
Linaria canadensis
Panicum amarum
Solidago microcephala
Sonchus asper
Panicum virgatum
Rumex acetosella
Triplasis purpurea
Verbascum thapsus
Sagina decumbens
Salicornia bigelovii
Samolus parviflorus
Scirpus americanus
Setaria geniculata
Solanum carolinense
Fraction of Species Cover
Fraction of Species Cover
Disturbance Index
Disturbance Index
0
.2
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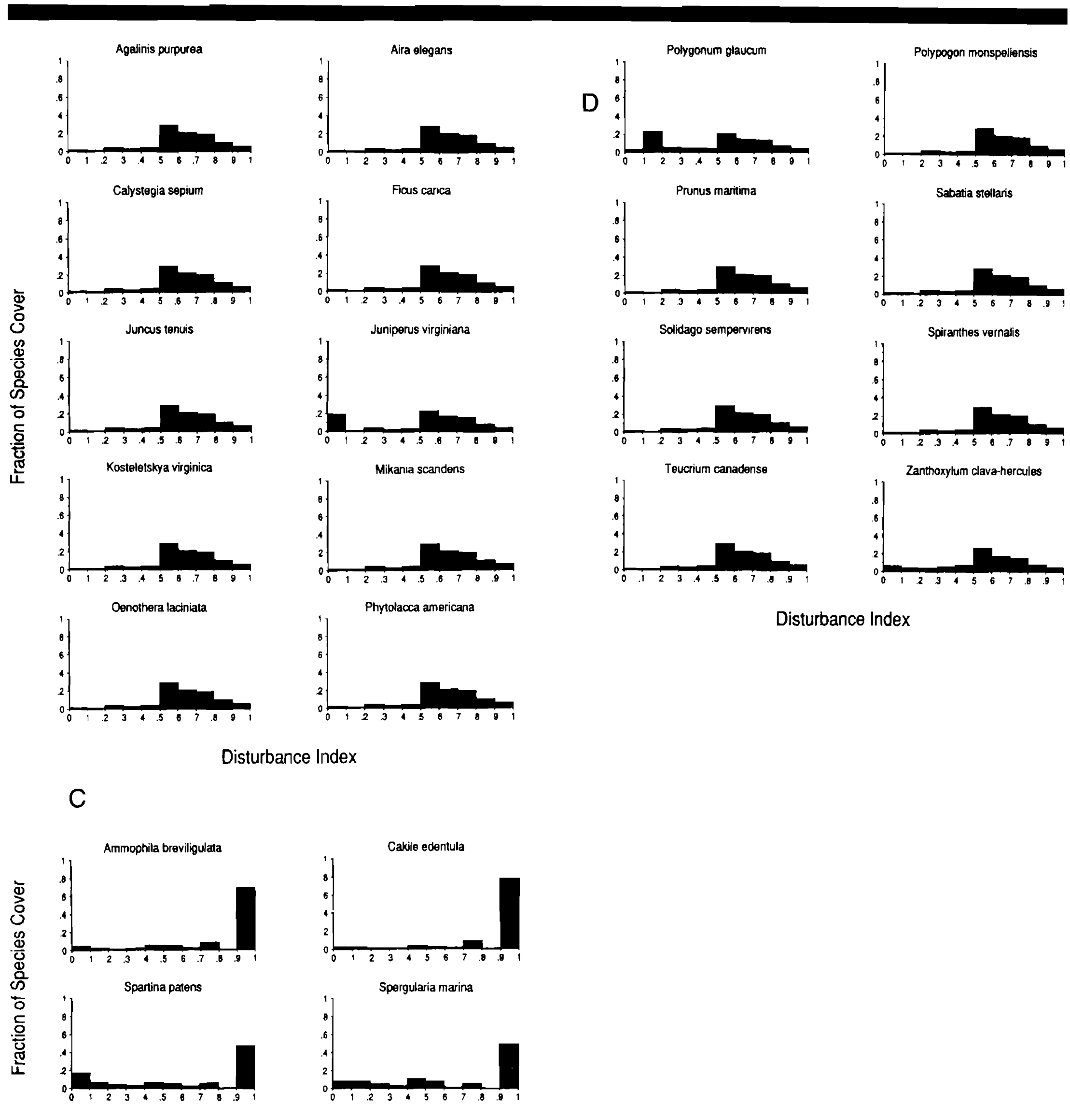

Figure 4. Approximate distributions of 95 plant species on Hog Island in relation to the index of overwash disturbance probability: (a) Species with low tolerance to overwash disturbance (D− −); (b) Species with moderate to low disturbance tolerance (D−); (c) Species with moderate to high disturbance tolerance (D+); and (d) Species with high disturbance tolerance (D+ +).

expected at random in frequently disturbed areas, was not supported by our analysis. Since perennials need to divert some energy into storage for survival to the next year, the seed set of annuals is normally much greater than that of perennials. If the adult is likely to be killed by overwash before the following year, the plant producing the largest seed set (*i.e.*, the annual) should be more successful in frequently disturbed areas.

A confounding factor that shaped this expectation is that much of the research on strandline ecology has been conducted on annual plants (*e.g.*, PEMADASA, 1974; WATKINSON, 1978; PAYNE and MAUN, 1984). This selection of study species has probably been partly due to the prevailing wisdom that annuals are disturbance-adapted. However, it is evident from our analysis that the fact that some annuals are disturbance-adapted does not necessarily imply that the annual lifeform in general is better adapted to disturbance than the perennial.

What is the reason for our unexpected result? We speculate that it is due to the fact that many of the perennial species that occur in highly disturbed areas of Hog Island and other barrier islands exhibit clonal growth and reproduction with extensive horizontal rhizomatous spreading (EHRENFELD, 1990). There are several reasons that these perennial species are well-suited to live in areas of frequent overwash disturbance. First, the vegetative "offspring" from clonal reproduction can be produced within one season whereas the shoots from seeds are not produced until the following season. In effect, this shortens the time to maturity, which, as described above, is advantageous in a frequently disturbed area.

The second advantage of clonal spreading in areas of high overwash probability is that the probability of mortality of a stem (whether a seedling or a clonal stem) is lower than that of a seed, when covered with the same depth of sand (EHRENFELD, 1990). Seed banks in dune soils are small to nonexistent. The assumption from life history theory, that an annual can produce more offspring within one year than a perennial does not hold if the perennial produces clonal shoots as "offspring", and the survival probability of these shoots is orders of magnitude greater than that of seeds. In fact, EHRENFELD (1990) notes that species that are tolerant of extensive burial usually have extensive rhizomatous growth. Also, clonal fragments are more likely to become established following sand burial than are seeds.

A third advantage of clonal reproduction relates to optimal dispersal distance in a highly disturbed environment. It is often assumed that in a patchy and frequently disturbed environment, organisms should disperse their offspring widely to maximize the likelihood that at least some of them will find suitable habitat (DEN BOER, 1981). At odds with this is the suggestion by WATKINSON (1978) that on barrier islands short-distance dispersal may be advantageous since plants growing near parents are likely to successfully reproduce, whereas dispersal over greater distances is likely to bring seeds into unfavourable microenvironments, such as dune swales. Since long-distance clonal spreading by perennial herbs and short-distance seed dispersal by annuals on barrier islands result in similar dispersal distances (SYMONIDES, 1979; MAUN, 1985; EHRENFELD, 1990), Watkinson's idea could apply equally well to both.

In summary, our analysis supports the idea that early maturation is advantageous in highly disturbed environments. However, it does not support the idea that short lifespan is advantageous; annuals were not more numerous and perennial herbs were not less numerous than expected at random in areas of high disturbance probability. We suggest that this result may be explained by the fact that many of the perennials in question grow and reproduce by clonal spreading which confers the following advantages in areas of high overwash probability: (1) early reproduction, (2) reduced probability of "offspring" mortality and (3) optimal dispersal distance.

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