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Salt Marsh Vegetation: Latitudinal Gradients in the Zonation Patterns

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Summary. Zonation patterns of salt marsh vegetation were examined at latitudes ranging from 44° 40′ N at Halifax, Nova Scotia, to 58° 50′ N at Churchill, Manitoba. It was found that in all areas examined the landward boundaries of the species' zones were more nearly coincident (i.e., more clustered) than their seaward boundaries. A conspicuous latitudinal trend was found: the clustering of both landward and seaward boundaries increased with increasing latitude. Evidence that between-species competition influences the locations of zone boundaries was also obtained. Possible implications of the results in terms of a relationship between intrapopulation polymorphism and latitude are discussed.

1. Introduction

Salt marshes can provide a continuous gradient of conditions from extremely wet, inundated and saline to relatively mesic. This monotone gradient is the dominating environmental influence on the vegetation patterns (Adams, 1963), and usually causes obvious zonation. It is likely that, for each species, the locations of its upper and lower zone boundaries, besides depending on its tolerance limits for the abiotic factors that vary along the gradient, are also controlled to some extent by between-species competition. Comparative studies of the arrangements of the upper and lower zone boundaries might cast light on the interplay of these factors in determining zonation patterns. Further, a comparison of these patterns over a wide range of latitudes can not only add to the significance attached to any consistent observations, but might also provide evidence of a trend. Such latitudinal trends are clearly displayed by salt marshes in their species richness and in their numbers of visibly obvious vegetation zones. Thus on the south-east shore of Nova Scotia (at 45° N approximately) the marshes typically display four

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zones dominated by *Spartina alterniflora* Loisel., *S. patens* (Ait.) Muhl., *Carex paleacea* Wahl. and *Juncus balticus* Willd. respectively. In the marshes of James Bay (53° N approximately), however, *C. paleacea* dominates all but the upper and lower fringes.

This paper describes the results obtained, and conclusions drawn, from studies of the zonation patterns of eastern Canadian salt marshes at five different latitudes, ranging from 44° 40′ N to 58° 50′ N. Complete lists of the plant species encountered are given in Routledge (1975) and an abridged list in an appendix to this paper.

2. Data Collection

To compare the zonation patterns at various latitudes, data were collected from a total of fourteen marshes chosen from five different areas. Figure 1 shows the locations of the areas and Table 1 lists the areas and gives their latitudes and the names of the marshes studied at each.

Data collection in the Halifax area was carried out in the summer of 1973. The other four areas were visited in the summer of 1974.

The choice of marshes to investigate was made as follows. Accessible areas (in the geographic sense) at roughly equal intervals of latitude and where extensive salt marshes occur were chosen first; these are the places shown on the map in Figure 1. At each of these areas individual marshes were then selected that met certain requirements: a marsh was deemed suitable for study if it was inundated, at least on some tides, by salt or brackish water, if it showed little evidence of wave or ice erosion, and if it was (preferably) between 10 m and 100 m wide. (Only at Churchill, where many of the marshes are very wide, was it necessary to choose one wider than 100 m.) Within each area the marshes studied could, in the terminology of Cochran (1953), be considered a haphazard sample; for the purpose of the present analysis they were treated as a random sample of the marshes suitable for study in each area.

At each marsh several transects were observed in the following way. Fifty centrimetre wide belt-transects were laid across the marsh, running from the lower limit of the shrub or dune grass community (whichever was present) at the landward end to the lower limit of emergent vegetation

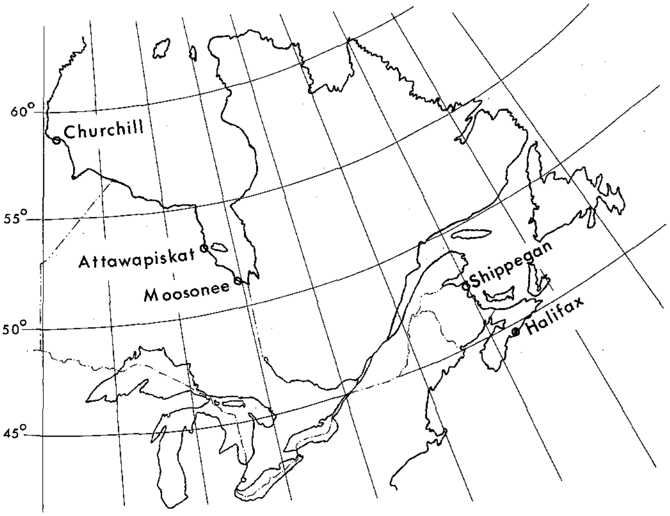

Fig. 1. The five areas at which salt marsh zonation patterns were investigated

Table 1. List of marshes studied

Area	Latitude	Marsh
1. Halifax, N.S.	44°40′N	a) Conrad Beach b) Lawrencetown Marsh c) Martinique Beach
2. Shippegan, N.B.	47°40′N	a) Lameque b) Inkerman Site 1 c) Inkerman Site 2
3. Moosonee, Ont.	51°20′N	a) Shipsands Island Site 1 b) Shipsands Island Site 2 c) Shipsands Island Site 3
4. Attawapiskat, Ont.	53°00′N	a) Attawapiskat Site 1 b) Attawapiskat Site 2 c) Attawapiskat Site 3
5. Churchill, Man.	58°50′N	a) Halfway Point b) Beech Bay

at the seaward end. To ensure their independence they were placed at least 10 m apart. In most marshes the transects were divided into contiguous metre-long quadrats (each a 1.0 m by 0.5 m rectangle) and the species of vascular plants present in each quadrat were recorded. In very wide (over 60 m) marshes, where it was impracticable to compile species lists for all the quadrats, quadrats for examination were taken at regular intervals along each transect. In one very narrow marsh (Lawrencetown) the transects were divided at 0.5 m intervals, giving contiguous square quadrats, to ensure that the quadrats should not be too large relative to the zone widths.

In each marsh the elevations of all quadrats relative to an arbitrary datum were observed to the nearest 1/100 foot (3 mm approximately) with a surveyor's level.

In order that as many marshes as possible might be sampled, it was necessary to simplify observations to the utmost. For this reason, only presences and absences of vascular plant species were recorded. No attempt was made to measure their abundances except to record when one or two species dominated a quadrat. Few taxonomic difficulties arose; when they did the policy adopted was that if a pair of species were indistinguishable without careful examination, with at least a hand lens, of nearly every individual specimen, they were lumped together into a single taxonomic unit.

The chief purpose of the observations was to provide data on the locations (both absolute and relative) of the zone boundaries of the several species within each marsh. The positions within a transect at which a particular zone's upper and lower boundaries cross it were taken to be the uppermost and lowermost quadrats in which at least one individual of the species concerned was found. Chance "outliers" may occasionally cause the width of a zone to be unduly large; conversely, chance absence of any individuals of a species from a place where it could grow may cause the width of a zone to be unduly small. However, the compilation of species lists is the quickest way of sampling vegetation and hence the way that produces the largest yield per unit effort. Our method of estimating the locations of zone boundaries is both objective and quick; it permits large samples, of numerous transects, to be examined and hence ensures that the effects of an error in any one transect will be small.

3. The Arrangement of Zone Boundaries

How are the zones of species arranged along an environmental gradient? Two conventional theories have long been debated (see, for example, Whittaker, 1967, and references therein). According to one, the species are grouped into relatively

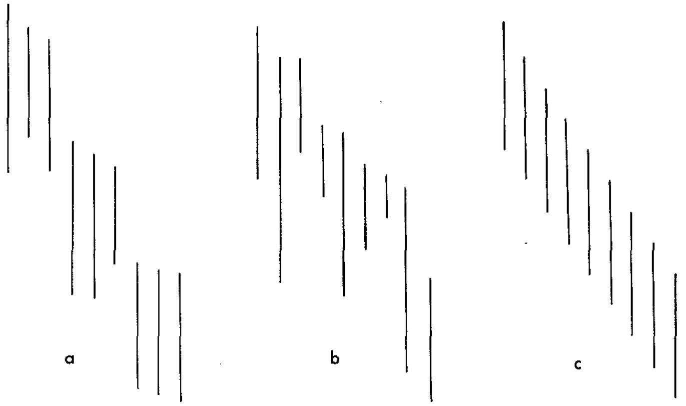

Fig. 2a–c. Three arrangements of species' zones. The gradient runs from top to bottom. Each vertical bar represents the segment of a transect that is intersected by a species' zone

distinct communities whose zones consequently occur in batches; according to the other, the several species' zones are located independently of one another. These two theories do not exhaust the possibilities, however. There is a third, that zones are more evenly spaced out along the gradient than they would be if they were at random. It is worth considering the arrangements of the boundaries of the zones that would accompany these three modes of organization.

Let us first look at the upslope boundaries of the species occurring in a transect. If the species were grouped into communities their upslope boundaries would be grouped correspondingly and would together form the upslope boundaries of the communities themselves (see Fig. 2a). If the ranges of the species were independent, then their upslope boundaries would be placed haphazardly along the gradient as in Figure 2b. And if their ranges overlapped regularly, as in Figure 2c, the upslope boundaries would be regularly spaced out along the gradient.

To distinguish among clustered, random, and regular boundary arrangements, Pielou (1975a, b) devised the following test. Consider any one transect. Let the number of quadrats in the transect (excluding the uppermost) be Q; let the number of species in these quadrats be k; and let the number of quadrats that are estimated to contain, and hence to be cut through by, at least one upslope boundary be U. (The uppermost quadrat, and the species in it, must be excluded from consideration since it is not known where these species' upslope boundaries occur.) Then, if the upslope boundaries are allocated at random to the quadrats,

$$\Pr(U=u)=p_u=\frac{\binom{Q}{u}\binom{k-1}{u-1}}{\binom{Q+k-1}{k}}, \qquad u=1,2,\dots,\min(Q,k). \tag{1}$$

Using this distribution, the following sign test can be constructed. For any transect, the median value of U given Q and k can be calculated. Given that the boundaries are at random, the probability that U exceeds this median is 0.5. For a collection of transects, let $\mathscr{U}$ be the number of times that U exceeds its expected median. Then, given random dispersal of the upslope boundaries within each transect, the distribution of $\mathscr{U}$ is binomial with $P=0.5$. A significantly low value of $\mathscr{U}$ is evidence that the number of quadrats cut by an upslope boundary is less than expected and hence that the upslope boundaries tend to be clustered. Conversely, a significantly high value of $\mathscr{U}$ is evidence that the number of quadrats cut by an upslope boundary exceeds expectation and hence that the boundaries are regularly spaced out.

In an entirely analogous manner we define D, the number of quadrats (excluding the last) cut by at least one downslope boundary. Likewise $\mathscr{D}$ is defined to be the number of transects for which D exceeds its median given random placement of downslope boundaries. A significantly low value of $\mathscr{D}$ is evidence that the downslope boundaries are clustered, and a significantly high value that they are regularly spaced out.

It should be observed that these hypotheses are not concerned with the position on the gradient of the zones of any particular species as such. Thus one would not, obviously, entertain the hypothesis that *Spartina alterniflora*, for example, was randomly placed; as is well known, its zone is always the one nearest the sea. The subject of the hypotheses is the arrangement of the boundaries per se, regardless of the species to which each belongs.

We shall also wish to intercompare the arrangements of zone boundaries in several different areas at different latitudes, in search of trends. This is easily done by calculating for each area the values of $\mathscr{U}$ and $\mathscr{D}$ for that area as proportions of the number of transects, say T, sampled there. Plots of $\mathscr{U}/T$ and $\mathscr{D}/T$ versus latitude can then be analysed for trends.

To illustrate the application of these procedures, we consider the data from the three marshes studied in the Halifax area. One of the transects in the first marsh contained $Q+1=24$ quadrats; excluding the uppermost quadrat from consideration, the number of species in the remaining Q was $k=14$. We now wish to find the expected median of D, the number of quadrats cut by downslope boundaries. By analogy with Equation (1), it is seen that

$$\Pr(D=d)=p_d=\frac{\binom{Q}{d}\binom{k-1}{d-1}}{\binom{Q+k-1}{k}}, \qquad d=1, \ldots, \min(Q,k). \tag{2}$$

Evaluation of these probabilities is most easily done by first calculating p_1 and then obtaining p_d for $d=2, \ldots, \min(Q,k)$ recursively, using the relation

$$\frac{p_{d+1}}{p_d}=\frac{(Q-d)(k-d)}{d(d+1)}.$$

It is then found that

$$\sum_{d=1}^{8} p_d=0.3737 \quad \text{and} \quad \sum_{d=1}^{9} p_d=0.6508$$

whence it follows that the expected median of D, say $M(D)$, is 8.5. The observed D for the transect was $\mathrm{Obs}(D)=11$. Thus $\mathrm{Obs}(D)>M(D)$ in this transect. Repeating these calculations for all the $T_1=19$ transects across the first marsh, it was found that $\mathrm{Obs}(D)>M(D)$ in $\mathscr{D}_1=15$ of the transects. The corresponding values for the second and third marshes in the Halifax area were

$$T_2=11, \mathscr{D}_2=7; \quad \text{and} \quad T_3=21, \mathscr{D}_3=17.$$

In this area as a whole, therefore, in the $T=\sum T_i=51$ transects examined, $\mathscr{D}=\sum \mathscr{D}_i=39$.

We now test whether $\mathscr{D}/T$ significantly exceeds its expected value under the null hypothesis, H_0, that downslope boundaries are arranged at random. According to H_0, $\mathscr{D}$ is binomially distributed with expectation $E(\mathscr{D})=0.5\ T=25.5$. Thus, since

$$\Pr(\mathscr{D}>25.5|H_0)<0.02\,\%,$$

we conclude, at the 0.02% significance level (one-tailed) that the downslope boundaries are regularly spaced in this area.

We now consider how $\mathscr{U}/T$, and $\mathscr{D}/T$, vary with latitude. Table 2 shows (on the left) the values of $\mathscr{U}/T$ and $\mathscr{D}/T$ for the individual marshes and (on the right) the values for the five different areas treated as single entities. These latter values are plotted against latitude in Figure 3. The final column in Table 2 gives the number of species found at each area in all transects in all marshes.

The results are noteworthy in two respects:

(1) Both $\mathscr{U}/T$ and $\mathscr{D}/T$ decrease monotonically with increasing latitude. The implication is that, as latitude increases, the boundaries of the species' zones become more and more clustered. This is true of both upslope and downslope boundaries.

(2) At all latitudes $\mathscr{D}/T>\mathscr{U}/T$, implying that upslope boundaries are everywhere more clustered than downslope boundaries. As already remarked, the downslope boundaries in the southernmost area studied (Halifax) showed a highly significant tendency to be regularly spaced. The upslope boundaries in the same area did not. The contrast between upslope and downslope boundary arrangements, with the upslope boundaries being the more strongly clustered, was found at all latitudes.

Table 2. Observed values of $\mathscr{U}$, $\mathscr{D}$, $\mathscr{U}/T$, $\mathscr{D}/T$, and of the numbers of species

Marsh	T	$\mathscr{U}$	$\mathscr{U}/T$	$\mathscr{D}$	$\mathscr{D}/T$	Area	T	$\mathscr{U}$	$\mathscr{U}/T$	$\mathscr{D}$	$\mathscr{D}/T$	No. of species[a]
Conrad Beach	19	8	0.42	15	0.78	Halifax	51	26	0.51	39	0.76	56
Lawrencetown	11	4	0.36	7	0.64							
Martinique Beach	21	14	0.67	17	0.81							
Lameque	15	4	0.27	6	0.40	Shippegan	27	10	0.37	14	0.52	53
Inkerman 1	5	2	0.40	4	0.80							
Inkerman 2	7	4	0.57	4	0.57							
Shipsands Is. 1	12	0	0.00	2	0.17	Moosonee	24	5	0.21	11	0.46	48
Shipsands Is. 2	8	5	0.62	7	0.87							
Shipsands Is. 3	4	0	0.00	2	0.50							
Attawapiskat 1	10	0	0.00	3	0.30	Attawapiskat	24	5	0.21	10	0.42	41
Attawapiskat 2	10	5	0.50	4	0.40							
Attawapiskat 3	4	0	0.00	3	0.75							
Halfway Point	12	0	0.00	4	0.33	Churchill	22	1	0.05	7	0.32	40
Beech Bay	10	1	0.10	3	0.30							

[a] Number of species found in all transects in all marshes in the area

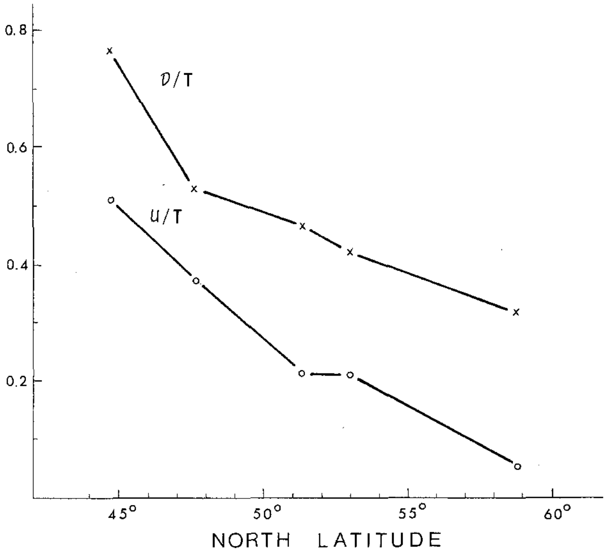

Fig. 3. The variation of $\mathscr{D}/T$ (x) and $\mathscr{U}/T$ (o) with latitude

The probabilities of obtaining these results by chance alone should be considered.

The probabilities of obtaining trends in either direction are Pr (a strictly monotone trend, as for $\mathscr{D}/T) = 2/5! = 0.017$; Pr (a monotone trend with one tie, as for $\mathscr{U}/T) = 4/5! = 0.033$.

These are the significance levels attained if we subject the results to two-tailed tests, or to one-tailed tests after observing the directions of the trends. Clearly we are justified in treating the trends as real and hence in concluding that the zone boundaries become more clustered as latitude increases.

Next we test the significance of the fact that $\mathscr{D} > \mathscr{U}$ consistently. A sign test at the 5% level does not reject the null hypothesis that $\Pr(\mathscr{D} < \mathscr{U}) = \Pr(\mathscr{D} > \mathscr{U}) = 0.5$ in favour of the two-sided alternative. The probability of obtaining the result departing most extremely from random expectation (i.e., either that $\mathscr{D} < \mathscr{U}$ consistently, or that $\mathscr{D} > \mathscr{U}$ consistently) is $2\ (0.5)^5 = 0.0625$. However, from the results on the left in Table 2, we see that in the 15 marshes considered individually $\mathscr{D} > \mathscr{U}$ in 13. The two-tailed probability of obtaining this result under the null hypothesis that $\Pr(\mathscr{D} < \mathscr{U}) = \Pr(\mathscr{D} > \mathscr{U})$ is 0.0064. Clearly we may conclude that upslope boundaries are more clustered than downslope boundaries at all latitudes.

We turn now to possible explanations for these observations. First consider the latitudinal trends. We begin by noting that the range of the tide determines the vertical extent of any salt marsh and hence, for a given angle of slope, its width. One might therefore expect zone boundaries to be more spaced out (that is, less clustered) the greater the tide range. If the tide ranges at the areas studied decreased with latitude we should immediately suppose that this could be the sole reason for the observed trend in $\mathscr{D}/T$ and $\mathscr{U}/T$ values. However, the actual trend in tide range is exactly the opposite: for the areas studied, the tide range increases monotonically from 1.4 m at Halifax to 3.4 m at Churchill. (These are mean ranges; the respective maximum ranges are 2.1 m and 5.2 m.) Thus the trend in tide ranges is such that it would be expected to obliterate, or even reverse, the observed trend in the vegetation's zonation pattern. This fact reinforces the ecological significance of the observed trend in zonation pattern.

One explanation of the trend is that, with increasing latitude, the zones of the various species become wider (relative to each marsh as a whole). Their boundaries would then become more nearly coincident with one another and with the borders of the marsh. A direct comparison of zone widths by Routledge (1975) shows that such a trend does indeed occur.

A possible cause for this is that plant populations growing in the harsh conditions of high latitudes exhibit greater within-species genetic variability than is found in low latitude populations of the same species. The result is that they can endure wider ranges of conditions and hence occupy wider zones. Another possible cause is that reduced between-species competition (perhaps because competing species are fewer) allows the species that are present to expand their zones. These points are discussed in more detail in Section 5.

It remains to explain the fact that upslope zone boundaries are everywhere more clustered than downslope zone boundaries. In all marshes there were more species at the landward than at the seaward end, and thus a large proportion of the upslope boundaries were concentrated at the landward end of a marsh. To say that downslope boundaries exhibited less pronounced clustering is a formal statement of the fact that, as one travels across a marsh from the land towards the sea, species steadily disappear from the community as the environment becomes steadily more marine and more inimical to "typical" angiosperms. Also, as we show in Section 4, between-species competition is at least partly responsible for the locations of many zone boundaries. These two facts together suggest the possibility that competition governs the locations of upslope boundaries whereas each species' downslope boundary occurs at a level on the marsh set by its physiological tolerance for submersion in salt water.

The situation may thus be parallel to (or, more strictly, antiparallel to) that described by Connell (1961 a, b) for two barnacle species on rocky shores; he showed that the upper limits for both species were set by physical factors whereas the lower limit of one of them (*Chthamalus stellatus*) was set by competition with the other (*Balanus balanoides*). Thus for these marine crustacea, physical stress determines their landward range limits whereas for terrestrial angiosperms it may be that physical stress determines the seaward range limits. (We thank Richard Bohrer for suggesting this parallel.)

4. Evidence for Between-Species Competition

The possibility that the widths of at least some species' zones were restricted by between-species competition was tested using data from Conrad Beach Marsh and Martinique Beach Marsh (see Table 2). The test (Pielou, 1975 a, b) does not enable one to judge which of the several species' zones are restricted by competition, but only whether at least some zones are so affected.

The test hinges on the following consideration. Obviously, if the locations of some zone boundaries on a smooth, continuous gradient are set by competition, there will be a tendency for pairs of competing zones to abut on each other rather than to overlap. Then the number of quadrats in a transect that are cut both by the upslope boundaries of some (one or more) species and by the downslope boundaries of others will exceed the number to be expected if all boundaries were mutually independent. As before, we estimate the boundaries of any species' zone to occur in, and cut through, the uppermost and lowermost quadrats in a transect that contain representatives of the species.

The Q, say, quadrats in any one transect (excluding the uppermost and lowermost) may be doubly classified as shown in the following 2×2 table, in which $a+b+c+d=Q$.

		Quadrat is cut by an upslope boundary	
		Yes	No
Quadrat is cut by a downslope boundary	Yes	a	b
	No	c	d

Given the null hypothesis of independence, the probability that the observed frequency in the Yes-Yes cell will be a is

$$p_a = \frac{\binom{a+b}{a}\binom{c+d}{c}}{\binom{Q}{a+c}}$$

with a taking values from $a_{\min} = \mathrm{Max}\,(0, |a-d|)$ to $a_{\max} = \mathrm{Min}\,(a+b, a+c)$.

Dealing with each transect separately, we now obtain the expected median value of a for the transect, say $M(a)$, from the relation

$$M(a) = \begin{cases} M & \text{if } \sum_{a_{\min}}^{M} p_a = 0.5 \\ M+0.5 & \text{if } \sum_{a_{\min}}^{M} p_a < 0.5 < \sum_{a_{\min}}^{M+1} p_a. \end{cases}$$

The hypothesis that competition is not affecting zone boundaries is equivalent to the assumption that

$$H_0\colon \Pr\{\mathrm{Obs}(a) < M(a)\} = \Pr\{\mathrm{Obs}(a) > M(a)\} = 0.5.$$

Now, for each transect, obtain A defined as

$$A = \begin{cases} 0 & \text{if } \mathrm{Obs}(a) < M(a) \\ 1 & \text{if } \mathrm{Obs}(a) > M(a); \end{cases}$$

and hence $\mathscr{A} = \sum A$, where the summation is over all T transects examined.

Then, under H_0, $\mathscr{A}$ is binomially distributed with expectation $E(\mathscr{A}) = 0.5\,T$.

Applying the test to the $T=40$ transects in the two marshes mentioned, it was found that $\mathscr{A}=30$, with a one-tailed probability, under H_0, of 0.001. The evidence that the locations of zone boundaries are dependent on between-species competition is thus highly significant. Unfortunately, the test is too crude to permit the intensity of the effect to be compared among latitudes.

5. Discussion

It is interesting to consider the relationship between hypotheses generated by the statistical study of vegetation patterns (such as ours) and conclusions on the same topics reached by the route of experimental genetics.

Geneticists are obtaining more and more evidence that genetic variability, especially that taking the form of enzyme polymorphism, is greater in populations living in heterogeneous or fluctuating environments than in those living in homogeneous or stable environments. For example, McDonald and Ayala (1974), experimenting with *Drosophila*, found "an overall positive correlation between environmental diversity and genetic polymorphism". Fewer studies have been made on plants. However, Babbel and Selander (1974) found that a species of *Lupinus* restricted to a narrow range of soils exhibited less genetic variability than a species of wider edaphic range; (but parallel studies on a pair of species of *Hymenopappus* did not give parallel results). Bryant (1974) in reviewing the adaptive significance of enzyme polymorphisms in a variable environment contrasts the two kinds of environmental variability, temporal and spatial. He found that, in the cases he examined, temporal variability is more important than spatial in sustaining enzyme polymorphisms; these polymorphisms provide the most readily detected (by electrophoresis) evidence of high genetic variability. Moreover the high level of genetic variability resulted in a high level of heterozygosity and it is probable that high heterozygosity per se is selectively advantageous in a harsh environment (Mayr, 1970, p. 137).

These considerations lead us to suggest that the phenomenon we observed, namely the increasing widths of the zones of salt marsh plants with increasing latitude, may be caused as follows: at high latitudes the climate is less stable (in its effects on the plants' physiology) than at low latitudes. In environments exhibiting more pronounced temporal variability heterozygosity, with overdominance, is selectively favoured, with the result that local populations of salt marsh plants tend to have high genetic variability. As a consequence of this, their edaphic amplitudes, or, which comes to the same thing, their tolerance ranges, are greater; that is, their zone widths are greater. The zone width of a species population constitutes visible evidence of the range of soil conditions, along the continuous gradient provided by a salt marsh, that the population is adapted to.

It will be seen that this argument attempts to distinguish causes from effects. Suppose we accept that the following phenomena tend to accompany one another:

(1) high temporal variability of the environment;

(2) high genetic variability in a population in that environment;

(3) high spatial variability in those parts of the spatial environment occupied by the population:

Then our suggestion is that the cause and effect sequence may be in the order given.

Another hypothesis that could account for the trend in zone widths is that the average width varies inversely with the number of co-occurring, and presumably competing, species present. As Table 2 shows, species numbers decrease monotonically with increasing latitude.

Work is continuing in an effort to judge the relative importance of these (and other) mechanisms that may explain the observed trend.

Appendix

The following list records the species found in all the marshes studied in any one area. Author's names will be found in the complete species lists in Routledge (1975). The numbers in parentheses refer to the areas, coded as in Table 1, where each species was found.

Triglochin maritima (1, 2, 3); *Festuca* spp. (1, 2, 3); *Puccinellia pumila* (1, 2); *P. lucida* (3); *Agropyron repens* (1); *Hordeum jubatum* (2); *Calamagrostis* spp. (5); *Agrostis stolonifera* (1); *Spartina alterniflora* (1, 2); *S. pectinata* (1); *S. patens* (1, 2); *Hierochloe ovata* (1, 2, 3); *Eleocharis*? *smallii* (3); *Eleocharis* sp. (4); *Scirpus americanus* (3); *Carex paleacea* (1, 2, 3, 4); *Juncus balticus* (1, 2); *Salix* spp. (3); *Rumex* spp. (3); *Atriplex patula* (1); *Atriplex* spp. (3); *Salicornia europa* (1, 3); *Stellaria humifusa* (5); *Stellaria* spp. (5); *Arenaria lateriflora* (1, 2); *Thalictrum polygamum* (1); *Ranunculus cymbalaria* (2, 3); *Parnassia palustris* (3); *Potentilla anserina* (1, 2); *Potentilla* spp. (3); *Lathyrus palustris* (1, 3); *Primula egalikensis* (3); *Glaux maritima* (2); *Limonium nashii* (1, 2); *Convolvulus sepium* (1, 2); *Rhinanthus borealis* (3); *Plantago maritima* (1, 2, 3); *Galium trifidum* (5); *Achillea millefolium* (1, 3); *Senecio congestus* (3); *Solidago sempervirens* (1, 2); *Aster novi-belgii* (1); *Hieracium* sp. (2); *Sonchus arvensis* (1).

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