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Synecology of beach vegetation along the Pacific Coast of the United States of America: a first approximation

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Abstract

Thirty-four beaches, located between central Washington and the Mexican border (approximately 47–33° N), were sampled for cover by replicate strip transects, and the results summarized by composite profile diagrams. The zonation patterns of twenty species revealed that the majority could be found in the leading (seaward) edge of vegetation, but most taxa increased in cover with increasing distance from mean tide line; that is, few species exhibited an ecological optimum in the most severe part of the vegetated beach. Even in the most inland portion of the beach plant cover and species richness were typically low (about five species, 20% cover). Cluster analysis revealed five groups of stands. The groups were poorly correlated with latitude, except for a major break at 37° N in central California. Regressions showed, as a first approximation, that community composition correlated with factors that reflect protection from disturbance by waves, man, or introduced taxa. Beach vegetation seems less well correlated with macro-climate than inland vegetation. However, the distribution limits of some species did correlate well with macro-climate.

Introduction

Attempts to summarize the phytogeography of North American Pacific coast beach vegetation have only recently been published (Breckon & Barbour, 1974; Macdonald & Barbour, 1974; Barbour, De Jong & Johnson, 1975). The objective of this paper is to build upon that base, and to extend our under-

standing to the synecological level. In meeting this objective, we shall describe the composition of selected stands of beach vegetation along the Pacific coast of the United States and correlate community traits with environmental parameters to indicate the most likely factors which determine the character of that vegetation. Our selection of community traits and environmental factors necessarily represents only a portion of the set of parameters which could have been chosen, hence the subtitle for this paper—a first approximation. Nevertheless, we think this analysis will permit synecological comparisons with other coastal vegetation.

'Beach' is here defined as that strip of land from mean tide line to just beyond the reach of storm waves or, if a foredune exists, to the top of the foredune. 'Strand' has often been applied to this same region, but some workers have used the term to include inland dunes as well as the beach proper. To avoid ambiguity, we have chosen the more intuitive term 'beach'.

The beach habitat is characterized by a maritime climate, high exposure to air-borne salts and sand blast, and a shifting, sandy substrate with low water-holding capacity and low organic matter content.

Description of beach vegetation

Selection of stands

Approximately 100 potential stand locations were selected prior to extensive field work. These ranged from the Olympic Peninsula, Washington, to the Mexican border (approximately 47–33° N latitude). They were chosen on the basis of aerial photography, literature references, suggestions from other workers, or from our own knowledge of the coast. All 100 sites were visited in 1973 and 1974, and thirty-four of them were selected for detailed sampling (Fig. 1).

These thirty-four stands shared a number of characteristics. They had a sandy substrate and
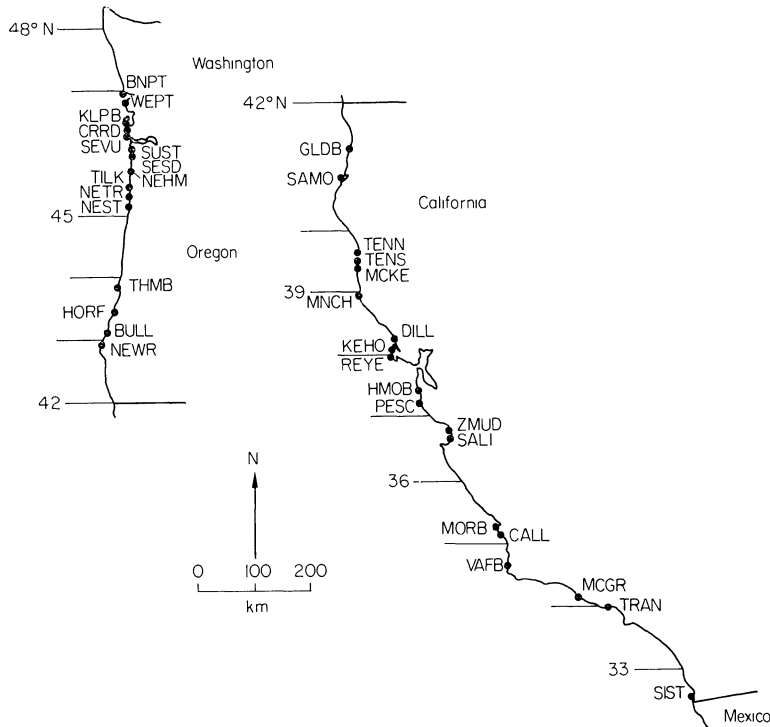
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Fig. 1. Location and identity codes for the thirty-four stands whose structure is discussed in text. The stands are numbered in other figures, stand 1 being the furthest north (BNPT), stand 34 the furthest south (SIST).

faced the open ocean (protected mud flats and cobble beaches were omitted). They had essentially a sealevel elevation (perched beaches were omitted). They exhibited some dune development behind them (narrow, cliffed beaches were omitted). They were located on beaches which had a continuous ocean front of at least 2 km (small pocket beaches along otherwise rocky coasts were omitted). Finally, selected beaches could not show the effects of severe human disturbance, although they could show high cover for such introduced plants as European beach grass (*Ammophila arenaria*). The last criterion made the inclusion of southern California beaches difficult, and this region is under-represented in our sample.

The stands shown in Fig. 1 fall into three 'eco-floristic' zones or subzones as defined by Breckon & Barbour (1974) and revised by Barbour *et al.* (1975). Those south of 34° 30′ are in the Dry Mediter-ranean zone,which is characterized by having relative-ly few species, many of which have inland, as well as maritime, distributions. Those north of that latitude are in the Temperate zone, which is characterized by the presence of many more species, some having endemic maritime distributions and others having

circumarctic-Beringian distributions. There are two subzones within this zone, and their dividing line is at 43°; the two subzones mainly differ as to the fraction of circumarctic-Beringian species. The stands were well-scattered through the zones, along some 2000 km of coast. The great majority were within 50 km of a neighbouring site, but distance between sites ranged from 5 to 200 km.

Sampling method

Each beach was sampled for cover with four to ten (usually ten) parallel 1 m-wide strip transects, spaced 10 m apart. This 40–100 m long portion of beach front was chosen by walking along 1–2 km of beach and subjectively selecting a representative portion. The transects were run inland at right angles to mean tide lines. They began at a base line, parallel to mean tide line and located between the water's edge and the leading edge of vegetation, and con-tinued inland to the top of the foredune or to the beginning of typically inland vegetation.

The percent cover for each species and of drift-wood or other jetsam was estimated for every square

metre along the strip transects, by flipping a 1 m²
quadrat frame up the transects. At the same time,
the difference in elevation between the two ends of
each quadrat (in the direction of the transect) was
measured by placing a non-rigid rectangular frame
on edge (Fig. 2). From this data, plus referral to
tide tables, we were able to compile a profile of the
beach from mean tide line and the absolute percent
cover of each species along that profile. In most
cases, the four to ten transects extended across
approximately the same length of beach; thus a
composite profile diagram of the beach and average
plant cover was prepared by summing comparable
quadrats and dividing by the number of transects
used (see Fig. 3). In three cases (beaches 8, 11, 12),
half the transects were considerably longer than the
other half, and in these cases we have prepared two
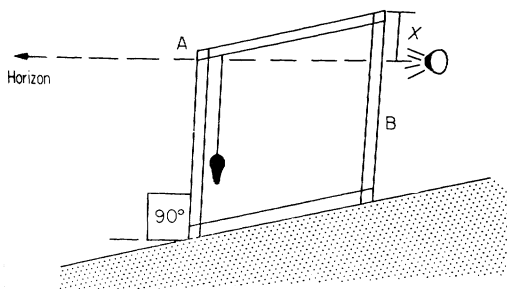composites, each representing five transects.

Fig. 2. Method of using a collapsible 1 m square quadrat
frame to measure the slope of incremental meter segments
along the transects. The bottom edge is placed along the
ground, and the sides are oriented perpendicular to the hori-
zon (by using a plumb-bob or approximation). One then
sights from point A to the oceanic horizon and extrapolates
that line back to side B of the quadrat to read the distance,
X, which reveals the cm of (in this case) rise.

It should be emphasized that the composite pro-
files produce three distortions that mask a very
heterogeneous plant cover and topography. The
cover, frequency, and topography are all evened out.
Thus, the composite profiles should be considered
schematic diagrams to permit comparison of
topographic profile, species composition, and cover
of different beaches at a glance.

In summary, the following measurements were
taken: (1) absolute percent cover per species for
each 1 m segment; (2) slope for each 1 m segment,
that is, rise/length × 100; (3) distance in metres
from mean tide line to the first vegetation; (4)
elevation in metres from mean tide line to the first

vegetation; (5) length in metres of the vegetated
portion of the beach; and (6) slope of the vegetated
portion of the beach. To save space, the profiles in
Fig. 3 only show vegetated portions of the transects.

In addition, substrate samples were collected
from a depth of 10 cm at the base of the first vegeta-
tion along every other transect. These were later
dried at 80–100°C for 24 h and passed through
sieves on a mechanical shaker for 20 min for
textural analysis into standard categories above
0·05 mm diameter (see Soil Survey Manual, 1951).
We found that the greatest variability from beach
to beach was in 'fine sand' (USDA definition,
0·25–0·10 mm diameter), and we will refer to this
category later in the paper.

Conductivity of the sand samples was also
measured (1:1 dilution) and converted to parts per
million total salt. Salt concentration for all sites
averaged 290 p.p.m. (447 μmhos), but it showed
such great variation within sites that we have not
attempted to find correlations between community
or topographic traits and soil salinity. Overall the
values ranged from 75 to 2800 p.p.m. If we assume
that field capacity of beach sand is 10% by weight,
then the soil solution at the leading edge of vegeta-
tion contains 750–28,000 p.p.m. salt. Most of these
samples were collected in the summer, but we need
more intensive, year-round sampling to reach any
general conclusions.

Transect summaries: composition, cover, zonation

There was considerable variation in length and
steepness of the vegetated portion of the beach
(Fig. 3). Beaches far to the north and south tended
to be long, with a gradual rise, whereas most of
those in Oregon and California tended to be short
and sometimes steep. In addition, there was a
positive correlation between latitude and distance
from mean tide line to the first vegetation (correla-
tion coefficient 0·73, 99% significance level). As
discussed later in the paper, beach length, steepness,
and distance from tide line do seem to affect com-
munity composition.

Beach communities were typically low in species
richness and cover. A total of thirty-two species were
encountered along the entire coast. Of these, twenty
were typical beach species, and twelve were inland
species generally occurring in only one or two of the
transects. The latter are lumped as 'Miscellany' in
Fig. 3. Three other taxa (*Malacothrix incana* and
subspecies of *Agoseris apargioides*) did occur on

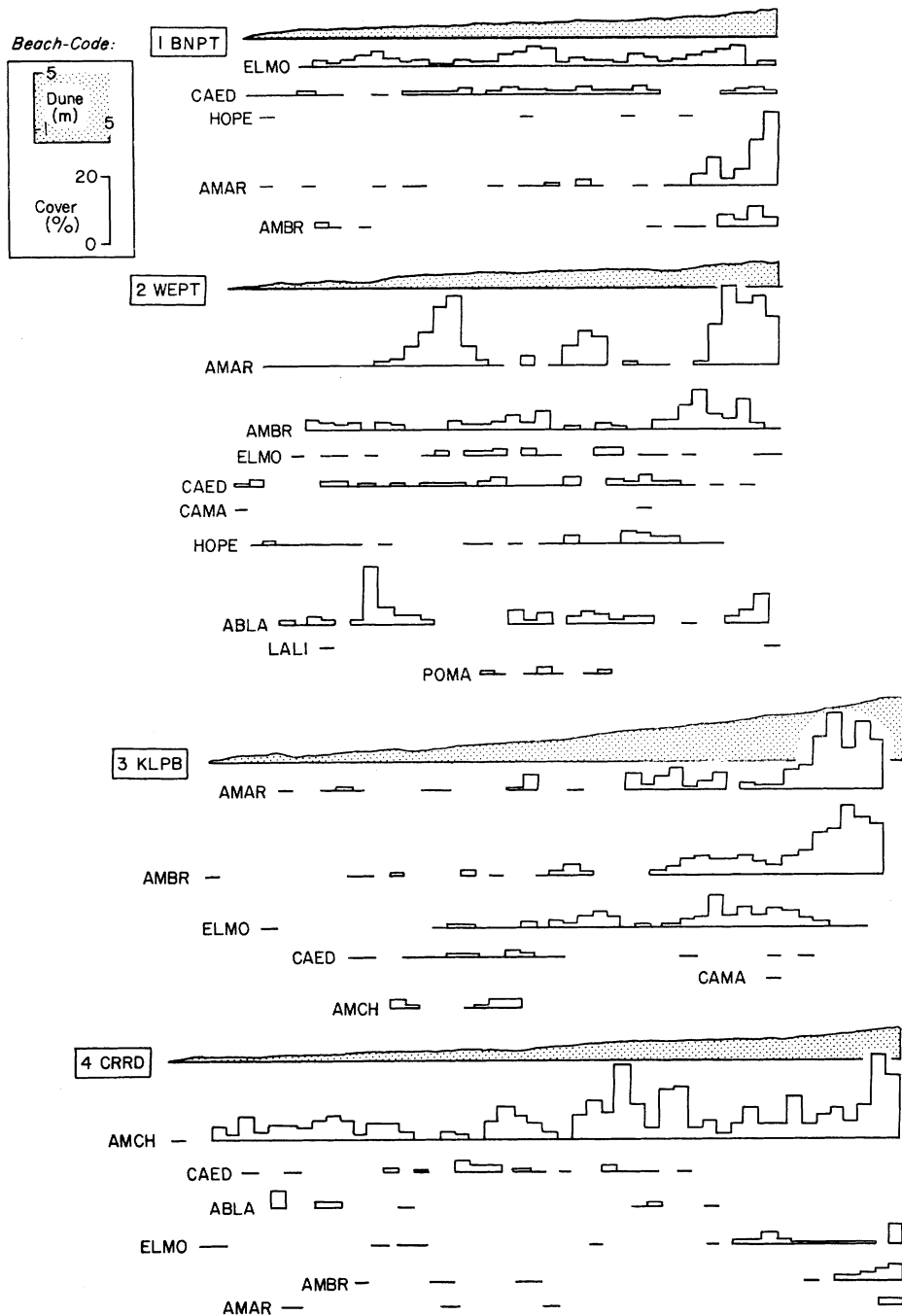**Fig. 3.** Beach profile and plant cover summaries. Most figures represent ten transects; those for A and B parts of beaches 8, 11, and 12 each represent about five transects. Beach locations, by code name, are shown in Fig. 1. Species identification is given in Table 1 (except Misc, which stands for typically inland species or unidentified species).
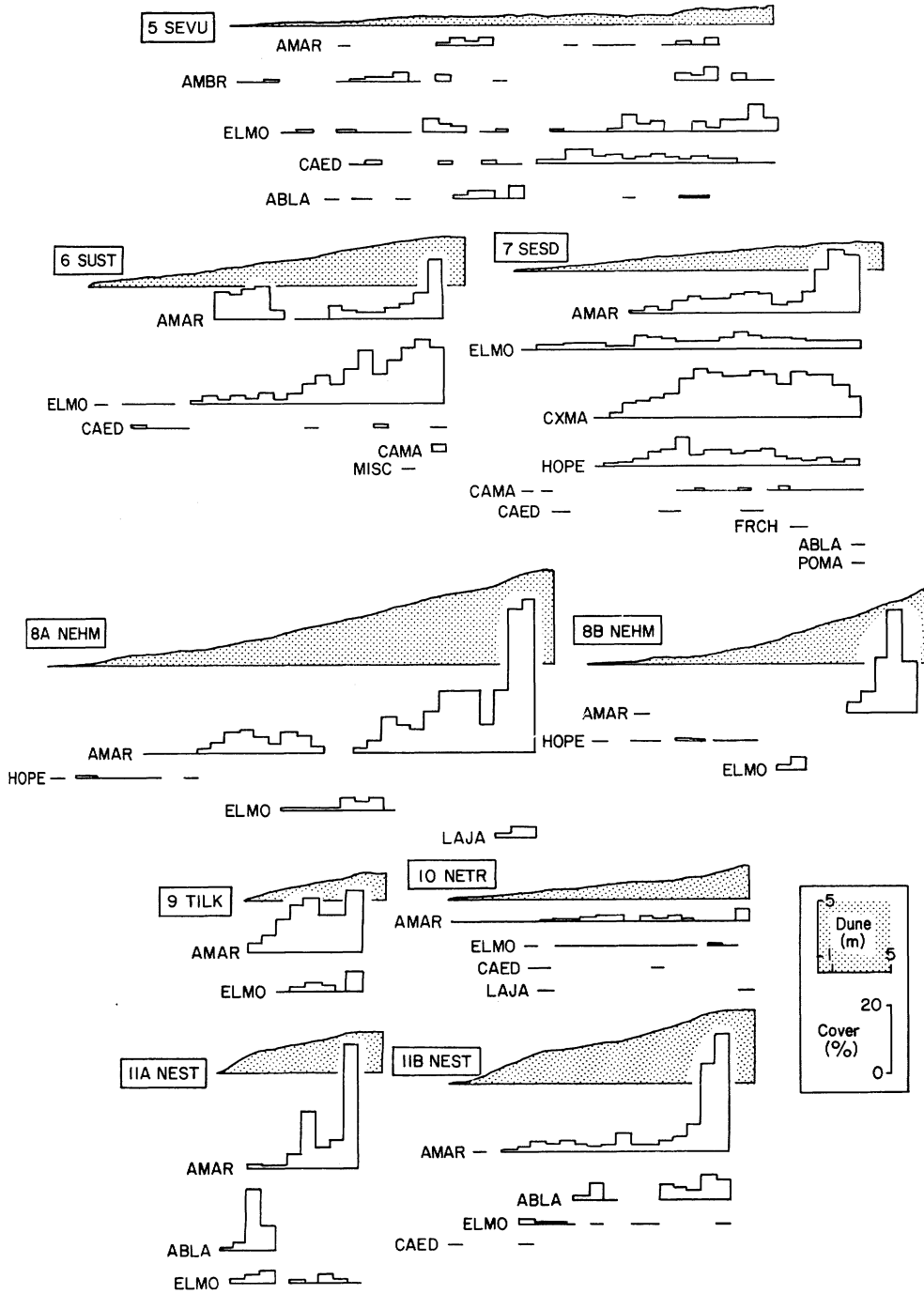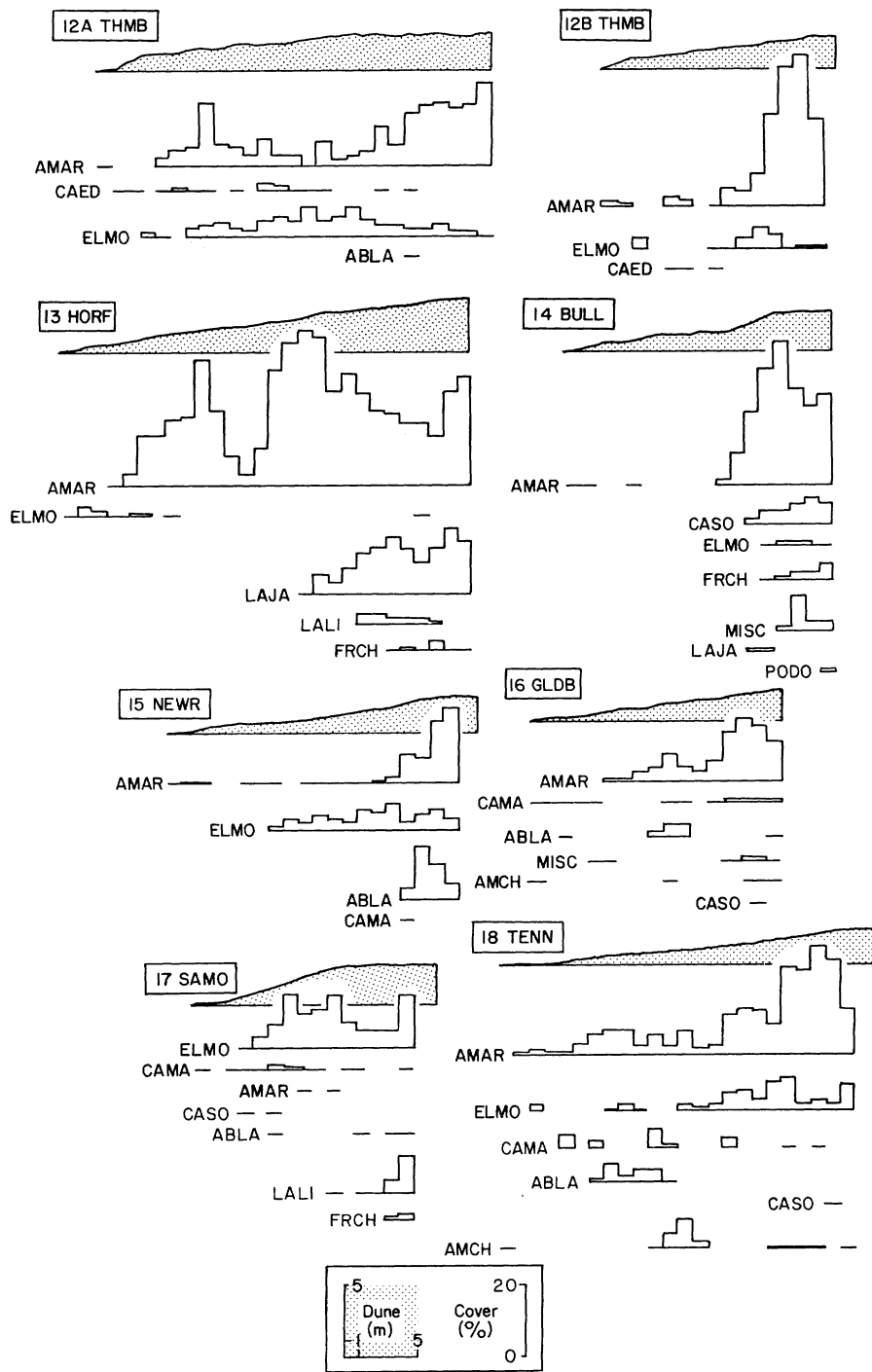
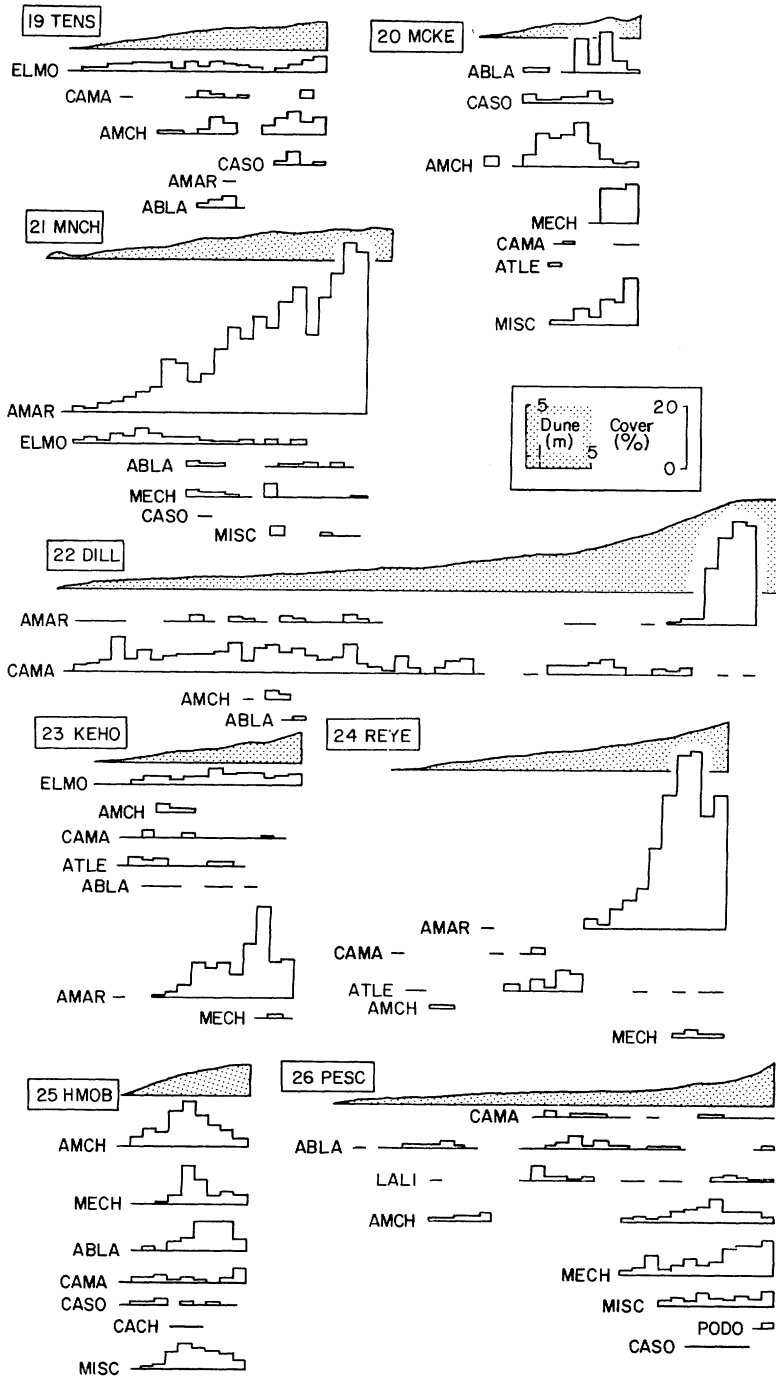**Fig. 3.** (*continued*)

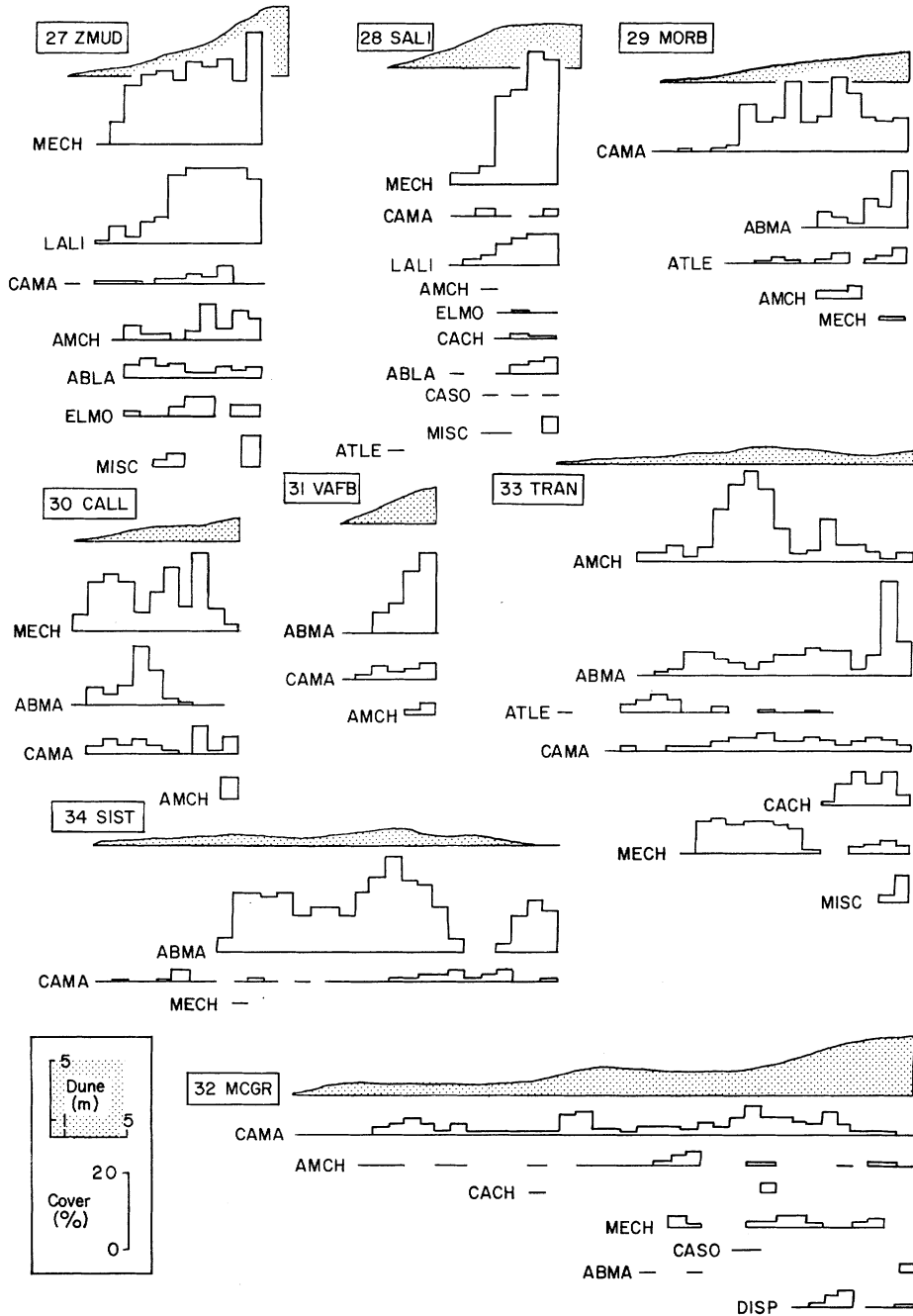Fig. 3. (*continued*)

Fig. 3. (*continued*)

Fig. 3. (*continued*)

the beach, but so sporadically that they were not sampled. Generally, about five species comprised the vegetation at any one beach, and of those only one or two contributed a significant amount of cover (usually *Ammophila arenaria* north of 38°, and *Mesembryanthemum chilense, Cakile maritima, Ambrosia chamissonis,* or *Abronia maritima* south of that latitude). Cover increased inland, considering the community as a whole, but this was not true for every species. In the first third of the vegetated portion of the beaches (closest to tide line), cover averaged less than 10%. In the most inland third, average cover was still generally below 20% and never more than 30%. (However, cover within any given 1 m² in this third often reached 100%).

Analysis of the cover for each third of the vegetated portion of the beach reveals that the twenty species exhibit a rough zonation (Table 1). Only

Table 1. Distribution patterns of species encountered on thirty-four beaches along the Pacific coast of the U.S.A., 47°–33° N. The first numerical column tabulates the percentage of beaches, on which the taxon was found at all, in which the taxon was in the seaward, leading edge of vegetation. The next three columns tabulate the percent of beaches which showed maximum cover for the taxon in the seaward first third of the vegetated beach, in the mid-third, or in the landward last third. The last three columns may not total 100 because taxa were sometimes so evenly distributed along a transect that their peak could not be assigned to any segment. Optima are underlined. Nomenclature follows Breckon & Barbour (1974)

Taxon	Present in leading edge	Cover peaks in		
		First third	Mid	Last
Abla, *Abronia latifolia*	14	24	24	<u>38</u>
Abma, *Abronia maritima*	40	0	<u>50</u>	<u>50</u>
Amar, *Ammophila arenaria*	31	0	16	<u>72</u>
Ambr, *A. breviligulata*	40	0	<u>100</u>	0
Amch, *Ambrosia chamissonis*	21	6	<u>53</u>	35
Atle, *Atriplex leucophylla*	33	<u>50</u>	33	17
Cach, *Camissonia cheiranthifolia*	0	0	33	<u>67</u>
Caed, *Cakile edentula*	27	9	<u>55</u>	0
Cama, *C. maritima*	43	9	<u>26</u>	22
Caso, *Calystegia soldanella*	0	11	11	<u>67</u>
Cxma, *Carex macrocephala*	0	0	<u>100</u>	0
Disp, *Distichlis spicata*	0	0	0	<u>100</u>
Elmo, *Elymus mollis*	20	8	24	<u>32</u>
Frch, *Fragaria chiloensis*	0	0	0	<u>100</u>
Hope, *Honckenya peploides*	20	<u>40</u>	20	20
Laja, *Lathyrus japonicus*	0	0	0	<u>75</u>
Lall, *L. littoralis*	0	0	0	<u>100</u>
Mech, *Mesembryanthemum chilense*	8	0	20	<u>70</u>
Podo, *Poa douglasii*	0	0	0	<u>100</u>
Poma, *P. douglasii* ssp. *macrantha*	0	0	<u>50</u>	<u>50</u>

eight species ever showed maximum cover in the first third, and of those only two (*Atriplex leucophylla* and *Honckenya peploides*) peaked in this zone more often than in any other zone. Four species tended to peak most often in the middle third, and of the remaining, ten species tended to peak in the most inland third.

Only a few species showed a very narrow pattern. *Ammophila breviligulata* and *Carex macrocephala* peaked in cover exclusively in the mid-third, and *Distichlis spicata, Fragaria chiloensis, Lathyrus littoralis,* and *Poa douglasii* peaked exclusively in the last third. All other species showed varying locations for peaks in cover, or exhibited no peak at all. Thus, the number of species with high cover increased as distance from tide line increased, and the fraction of the flora with narrow limitations also increased landward. Certainly the decline in species as one moves closer and closer to tide line correlates with our intuitive understanding of gradients in the severity of the habitat. This pattern of seaward attrition is a continuation of one that begins even further inland, in the dunes proper.

Although few species peaked in cover in the first third of the portion of the beach, some plants of most taxa were found at least once in the leading edge of vegetation (Table 1). This is not an artifact of recent erosion, for we excluded such beaches. Such a pattern of distribution may reflect great genetic variation in the populations, the role of chance in dispersal, or simply the occupation of locally favourable microsites in an otherwise severe part of the beach. Autecological investigations are necessary to decide which hypothesis is correct. In any event, there is no correlation between the frequency with which a species was encountered in the leading edge and where on the beach its cover peaked. *Cakile maritima,* for example, had the highest rate of occurrence in the leading edge (43% of the beaches on which it was present), yet its cover most often peaked in the mid-third; *Ammophila arenaria* was in the leading edge 31% of the time, yet it shows a strong cover peak in the last third; *Honckenya peploides* was found less often in the leading edge (20% of the time), yet it peaked in cover most often in the first third; and so on.

Analysis of beach vegetation

Cluster analysis: stand similarities

Cluster analysis is a term which applies to a large

class of numerical techniques which characterize the degree of relatedness among taxonomic entities or among stands of vegetation, as in this case. We have applied this approach to our thirty-four stands, using plant cover and a 'weighted pairs' method (Sneath & Sokal, 1973). A correlation coefficient of cover by species was calculated, via computer program, for all possible pairs of stands. A correlation matrix was constructed and this matrix was searched for the largest positive correlation coefficient. A dendrogram, showing the clustering of these first two stands at the level of their correlation coefficient was drawn, then the weighted average of the newly formed group was entered into a recalculation of the entire matrix, and the next highest correlation coefficient searched for. The dendrogram was drawn with these additional stands

entered, and the procedure repeated until finally all stands had been included in the dendrogram (Fig. 4). A value of $+100$ indicates identity, -100 indicates complete dissimilarity. There appears to be a major discontinuity between stands at the $+30$ level, and a dotted line has been drawn in Fig. 4 at that level, resulting in five clusters of stands (groups A–E).

The groups tend to separate by leading dominant. Group A stands, with two exceptions, are dominated by *Ammophila arenaria*. The exceptions are beach 3, dominated by closely related *A. breviligulata*, also introduced, and beach 7, dominated by *Carex macrocephala*. Group B stands are dominated by *Elymus mollis*, C by *Ambrosia chamissonis*, D by *Mesembryanthemum chilense*, and E by *Abronia maritima* or *Cakile maritima*.
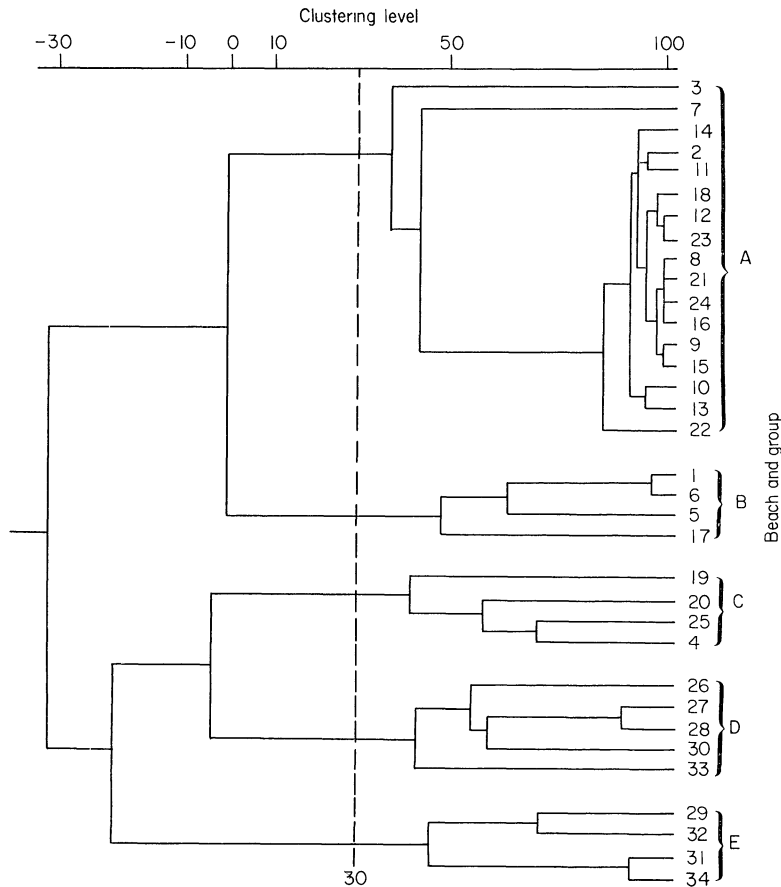
Stand numbers are assigned by latitude, with 1

Fig. 4. Dendrogram, showing stand relationships resulting from a clustering analysis. The thirty-four beach stands are identified by number; for further information on identity, see Figs 1 and 3. At the $+30$ similarity level (dotted line), five groups of stands are apparent (A–E).

Table 2. Regressions of community characteristics (*y*) on environmental factors (*x*), showing slope of the linear relationship and *y* intercept. Correlation coefficients (CC) and their significance level are also shown (a blank means significance below the 95 % level, hence non-significant in our discussion; significance levels were determined from Table 1 in Rohlf & Sokal, 1969). Regressions are based on twenty-four beaches, for those marked with an asterisk (*); all others are based on thirty-four beaches

y *x*	Slope	*y* Intercept	CC	Significance
Number of species (richness)				
Distance (m), mean tide line to leading vegetation	−0·01	7·94	−0·11	
Elevation (m), mean tide line to leading vegetation	0·80	4·75	0·22	
Length (m), vegetated part of transect	−0·02	7·80	−0·09	
Slope (%), vegetated part of transect	0·04	6·66	0·11	
Fine sand (%)	−0·004	7·31	−0·02	
Driftwood cover (%)	0·07	7·02	0·10	
Ammophila cover (%)*	−0·03	6·92	−0·08	
Disturbance	0·59	2·26	0·42	95
Total average species cover (%)				
Distance, tide line-vegetation	−0·11	23·59	−0·44	95
Elev., tide line-vegetation	2·10	9·97	0·22	
Transect length	−0·35	24·05	−0·50	99
Transect slope	0·35	11·58	0·36	95
Fine sand	−0·19	20·41	−0·32	
Driftwood cover	0·54	14·78	0·30	
Ammophila cover* (here, *y* = total cover − *Am.* cover)	−0·24	0·0	−0·31	
Disturbance	0·25	14·33	0·07	
Cover diversity (*H′*)				
Distance, tide line-vegetation	0·0003	0·43	0·06	
Elev., tide line-vegetation	0·05	0·29	0·24	
Transect length	−0·002	0·49	−0·10	
Transect slope	0·0003	0·45	0·01	
Fine sand	0·002	0·41	0·19	
Driftwood cover	−0·01	0·49	−0·35	95
Ammophila cover*	−0·01	0·52	−0·60	99
Disturbance	0·02	0·26	0·28	
Evenness (*J′*)				
Dist., tide line-vegetation	0·001	0·47	0·24	
Elev., tide line-vegetation	0·01	0·50	0·07	
Transect length	−0·002	0·58	−0·10	
Transect slope	−0·001	0·57	−0·06	
Fine sand	0·004	0·48	0·34	95
Driftwood cover	−0·02	0·60	−0·46	99
Ammophila cover*	−0·01	0·65	−0·63	99
Disturbance	−0·002	0·57	−0·03	

at the far north and 34 at the south; thus it can easily be seen that members of groups A, B, and C do not correlate well with latitude (except that, taken as a whole, groups A, B, and C include stands only north of 37°). Groups D and E do generally separate according to latitude, group D stands lying between 37° and 35°, group E stands lying between 35° and 32° 30′.

These breaks in community similarity at 35° and 37° do not quite coincide with geographic boundaries calculated by Breckon & Barbour (1974; revised by Barbour *et al.*, 1975). They placed zone and subzone boundaries at 43° and 34° 30′. We think that most of the discrepancy is due to their floristic, as compared to our vegetational, approach.

All species in their method were given equal weight and were assumed to have continuous distributions; species were weighted by cover in our method, and only those species actually encountered—rather than the potential species available—were entered into our calculations (our sampling procedure encountered only twenty of the thirty-five taxa they list as potential beach species between 47° and 33°).

The community shift at 37° strongly reflects the boundary between grass-dominated communities to the north and forb-dominated communities to the south. Although this latitude does not correspond to a major climatic shift (in the Koeppen sense), it may correlate with important isotherms. South of 37° average January temperature is above 10°C

5

and average July temperature is above 15°C (Durren-berger, 1974). These temperatures are thought to be critical in the transplanting of *Ammophila* (Brown & Hafenrichter, 1948). *Ammophila* can be artificially planted south of San Francisco, but we suspect that it cannot establish itself naturally there. The native dune grass, *Elymus mollis* shows a marked increase in cover and frequency north of 46° where Cfb (mesothermal, no seasonal rainfall pattern, Koeppen system) shifts to Csb (mesothermal, summer dry).

It is also worth noting that group A stands (*Ammophila*-dominated) show a higher clustering level than stands in any other group. *Ammophila*, as a leading dominant, exerts more control over community composition than any other dominant. In addition, Oregon and Washington beaches tended to be long and with a uniform orientation, where those in California were more localized and could face slightly different directions. Such differences could certainly affect stand homogeneity from site to site.

Although groups A, B, and C overlapped consider-ably in latitude, group B sharply differed from A and C in substrate texture. Group B (*Elymus*-dominated) stands averaged about 55% fine sand in contrast to about 10% fine sand for A (*Ammophila*-dominated) and C (*Ambrosia*-dominated) stands. But in view of the widespread, artificial planting of *Ammophila* for erosion control (Cooper, 1936, 1958, 1967), we do not really know what the textural difference implies. Attempts to separate the groups according to other environmental factors (as listed in the next section, Table 2) were unsuccessful.

The community shift at 35° does roughly corre-late with phytogeographic and climatic shifts at 34° 30′ (Barbour *et al.*, 1975). Climate changes there from Cs to BSs (semi-arid), and the percentage of species with inland-beach distributions increases.

The groups were analysed according to community characteristics such as species diversity. We calcu-lated species diversity by the standard Shannon & Weaver formula (Pielou, 1969):

$$\text{species diversity} = H' = \Sigma\, P_i . \log P_i$$

where

$$P_i = \frac{\text{av. absolute \% cover of species } P_i \text{ along transect}}{\Sigma \text{ av. absolute \% cover of all species}}.$$

H' is often calculated from species density, rather than cover, hence we have referred to H' as 'cover diversity' in Fig. 5. Throughout this paper, however,
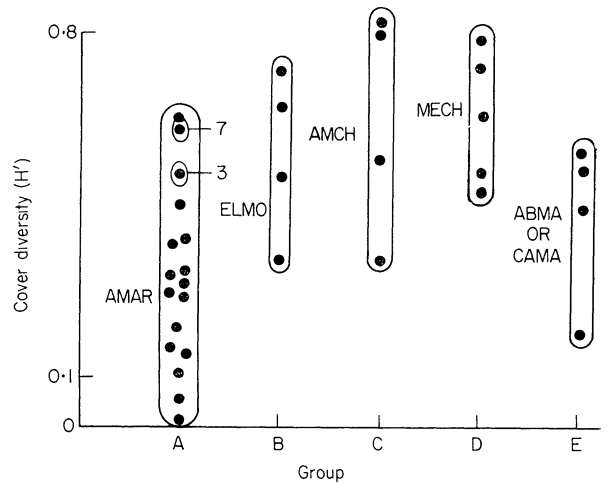

Fig. 5. Relationship between stand group, leading dominant, and species diversity. Stands sharing the same leading domi-nant are enclosed in the same space. Leading dominants are abbreviated according to the list in Table 1. Stands 3 and 7 in group A are discussed in text.

the terms H', 'cover diversity', and 'species diversity' will be taken as synonymous.

Mean H' for stands in group A is about 0·26; all other groups average twice or more that value. The effect of *Ammophila* on richness is apparent from casual field observation. We have unpublished data from adjacent plots at Point Reyes, California (approximately 38°), some dominated by *Elymus*, others by *Ammophila*, that show twice as many species on the *Elymus*-dominated beach. *Elymus*-dominated beaches have more open area and a gentler rise inland, perhaps offering less competition and a wider beach for other species to occupy.

Attempts to separate the groups according to other community characteristics (as listed in the next section, Table 2) were not as successful and are not illustrated.

Correlations between stand characteristics and environmental factors

We have seen that stand composition correlates very poorly, if at all, with latitude. This means that, within limits, the macro-climatic gradients in rainfall, frost, fog, sunshine, air and water temperature, and general degree of seasonality which occur between 47° and 33° (Breckon & Barbour, 1974) are not significant in moulding community structure. We hypothesize, therefore, that more local factors, such as the incidence of salt spray, mobility of substrate, presence of introduced species, and

protection from storm waves are much more important to this.

To some degree, this view is shared by many other workers. There is no unanimity among investigators as to which environmental factor is most important to the distribution of beach taxa, but the selections tend to be local, rather than climatic. Some have emphasized sand movement (Ranwell, 1972), some soil salinity (Seneca, 1969; Wagner, 1964), some nutrient deficiencies in the substrate (Art *et al.*, 1974; Morris *et al.*, 1974; van der Valk, 1974), and many others have emphasized salt spray gradients (Barbour *et al.*, 1973; Boyce, 1951 and 1954 and others whom he reviews; Oosting, 1945; Oosting & Billings, 1942; Stalter, 1974; Zohary & Fahn, 1952).

Unfortunately, at this stage of our research, we do not have data from the thirty-four stands which directly relate to such factors. However, we do have topographic and biotic measurements which indirectly relate to them. These measurements include distance from mean tide line to first vegetation, elevation of first vegetation above mean tide line, and length and slope of the vegetated portion of the beach. These factors can be interpreted as reflecting the degree of protection (or exposure) of the vegetation to sand abrasion, salt spray, or storm waves. The measurements at hand also include sand texture, cover by *Ammophila arenaria*, and a subjective scale of human disturbance. Sand texture may relate to the mobility of the substrate, that is, the finer the texture, the easier the sand may move. Conversely, the fine texture may indicate protection from the wind. *Ammophila* cover relates to disturbance by artificial plantings, as opposed to other forms of man-directed disturbance included in our subjective disturbance scale. This scale ranged from 3 (minimum disturbance) to 13 (highly disturbed, yet still capable of being included in the list of sample sites), and it was composed of five parts: proximity to population centres (scale of 1–3); accessibility to foot traffic (1–3); proximity to residential or recreational developments (0–1); indications of use by off-the-road vehicles or horses (0–2); and miscellaneous (1–4).

We have attempted to correlate several stand characteristics with the topographic, substrate, and disturbance factors listed above. The community characteristics are: total number of species; average percent cover per quadrat for all species over the vegetated portion of the beach; species diversity (*H'*, defined earlier in the paper); and species

evenness (*J'*, where

$$J' = \frac{H'}{H' \text{ max.}} = \frac{H'}{\log \text{ total no. spp.}}$$

as described by Pielou, 1969). Species diversity can be thought of as containing a richness component, which relates to numbers of species, and an evenness component, which relates to the uniformity in abundance or cover of those species (De Jong, 1975).

The numerical results of all these correlations are shown in Table 2. Only about one-third of the thirty-two correlation coefficients were significant at the 95% level or above, and even then the coefficients had an absolute value below 0·72. In other words, there was considerable variation not accounted for in these single-factor correlations. Nevertheless, each stand characteristic showed significant correlation with some environmental factor. Those significant correlations are discussed below.

Total cover was negatively correlated with distance from mean tide line to first vegetation, and positively correlated with the slope of the vegetated portion of the beach. That is, on short-steep beaches, colonizing beach species are probably eliminated by extreme storm waves every few years, leaving only the established dune species present; on long gradual beaches, new areas are exposed for colonization by dune species, producing less average cover per quadrat in our composite profiles.

Species diversity and evenness were negatively correlated with *Ammophila* cover, as expected. Species richness and cover (exclusive of *Ammophila*) were also negatively correlated with *Ammophila* cover, but not at the 95% significance level. The implication is that *Ammophila* eliminates some species and depresses others. This depression occurs in spite of the potential positive windscreen effect of *Ammophila* shoots on other species and, perhaps, increased soil nitrogen. Hassouna & Wareing (1964) have some evidence that *Ammophila arenaria* in Britain supports nitrogen-fixing bacteria in its rhizosphere. (We are currently investigating local populations of *Ammophila* for this phenomenon, but to date we have found no evidence to show *Ammophila* enriches surrounding sand in nitrogen.)

Species diversity and evenness were also negatively correlated with amount of driftwood cover. This is not what we expected, for we hypothesized that driftwood would create protected or nutritionally enriched microsites that could be colonized by addi-

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tional plants. Perhaps the result can be explained by the fact that we were unable to account for buried driftwood. Also, the surface driftwood which was sampled may represent a negative habitat factor— that is, recent submersion of the beach by storm waves.

The number of species surprisingly correlated positively with our 'disturbance scale'. This may indicate that our subjective system lumps too many factors together, or that the scale is too coarse. Certainly, our impression from southern beaches is that species number, cover, and diversity all decline with intensive human use. It should be emphasized here that *H'* was calculated from species lists which included miscellaneous, ordinarily non-beach, species (e.g. *Achillea, Hypochoeris, Aira, Erigeron, Grindelia*, and *Eschscholzia* species). The degree of disturbance we sampled may have created a more heterogeneous environment and permitted these species to invade.

The only stand characteristic to correlate with sand texture (percent fine sand) was evenness. This general lack of correlation indicates that substrate texture in sand grain size is not an important factor in species richness, cover, or diversity of beach vegetation, in contrast to its role in more inland vegetation. However, other textural categories, or humus content may be significant.

Barbour & Robichaux (1976) have recently taken biomass samples on California beaches and constructed regressions of cover on biomass, so that standing crop could be estimated from the transects shown in Fig. 3. Standing crop was not affected by latitudinal gradients, showing the azonal nature of the vegetation. It did correlate with leading dominant, however. Average transect standing crop ranged from 20 to 400 g m^{-2}, values similar to those of arid steppe and desert vegetation.

Summary and conclusions

Thirty-four beaches, located between central Washington and the Mexican border (approximately 47–33° N), were sampled for cover by replicate strip transects and the results summarized by composite profile diagrams. The zonation patterns of twenty species revealed that the majority could be found in the leading (seaward) edge of vegetation, but most taxa increased in cover with increasing distance from mean tide line. That is, few species exhibited an ecological optimum in the most severe part of the vegetated beach. We hypothesize that those species most commonly found in the leading edge, or those which peak in cover nearest to mean tide line, show a higher tolerance to such factors as incidence of salt spray, submersion by storm waves, or mobility of the substrate. We are currently conducting autecological studies to test this hypothesis.

Plant cover and species richness are typically low, even in the most inland portion of the beach (about five species, 20% cover at any given stand). Cluster analysis revealed five groups of stands, which showed differences in species diversity and in leading dominant. The groups correlated poorly with latitude, however, apart from a major break at 37° along the coast of central California which may be related to January or July isotherms. Regressions showed, as a first approximation, that some stand characteristics correlated with topographic and biotic factors that reflect the degree of protection from disturbance by wind, waves, man or introduced taxa. Beach vegetation and phytomass seem less well correlated with macro-climate than inland vegetation.

Acknowledgment

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