ECOLOGICAL STUDIES ON THE VEGETATION OF COASTAL SAND BARS

II. SUCCESSION IN VEGETATION AND DEVELOPMENTAL PROCESSES OF DUNES*

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海岸砂洲植生の生態学的研究

II. 植生のサクセッションと砂丘の形成過程

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SYNOPSIS

The interrelated developments of vegetation and topography were studied on a sand bar less than 150 m in width at the seaward side of the tidal estuary of the Nanakita River, Miyagi Prefecture, North Honshu. Observations on the processes of beach formation revealed that the area under study has a series of surface ages ranging from nine to about 24 years in 1957. The results of the following surveys which were made at various parts of the bar, including those of actual changes during five years, were so interrelated each other that we can make a general picture of the developments: (a) Dispersal of seed and distribution and ecesis of seedling on a beach ridge emerged recently. (b)The number, distribution and growths of embryonic dunes formed during four years after the emergence. (c) Succession associated with the consolidation of the embryonic dunes forming the peculiar dune-and-channel pattern of the topography. It took less than nine years after the emergence. (d) Further developments of the vegetation, which consists of the changes associated with the increment in the relative height of the mobile dunes, and of those related to the stabilization of mobile dunes increasingly protected by the advancing foredunes. The results of gradient analyses of the vegetation, made along the above-mentioned environmental indices which are subject to the influences of the plant growths, served as a useful criterion for the interpretation of autogenic succession. In conclusion, it is emphasized that the interrelation between the vegetation and the dune topography on this sand bar should be regarded as a system of mutual interactions.

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* The expense of this study was defrayed in part by grants from the Scientific Research Expenditure Fund of the Ministry of Education in 1952, 1954 and 1955.

Since the classic works by WARMING (1881) and COWLES (1899), it has been accepted that the plant growths, chiefly of psammophytes, play an important role in initiating and establishing coastal dunes in humid regions (TANSLEY 1939 and STEERS 1946). They form *growing* barriers to the sand-transporting wind, and thus accumulate the sand to shape minute, incipient or *embryonic* dunes around them. The formation of these embryonic dunes, as well as their growth and fusion to build more or less continuous dune ridges along the shorelines, have been described by many authors (e.g., OLIVER 1913–29, LEMBERG 1933–35 and HEPBURN 1945). More recent studies by BAGNOLD (1941) and OLSON (1958) made a distinct progress towards a more quantitative approach to the problem, regarding the vegetation as a remarkable agent which increases the surface roughness constant, or the height of zero point in vertical distribution of wind velocities.

On the other hand, the topographic patterns of the dunes, which are thus established and modified by the work of vegetation, differentiate various minor habitats in relation to such influences as invasion of saline water by high waves or tides, salt spray and sand drift by wind, and moisture of dune soils influenced by the depth of the water table. As a result, the patterns of vegetation are largely related to and determined by the patterns of topographic conditions (OOSTING 1954, MARTIN 1959 and ISHIZUKA 1961). The topography and the vegetation in the dunes should, therefore, be considered as a system of mutual interactions in these habitats.

This report is an attempt to outline the processes of the above interrelations in the early stages of dune development and vegetational succession on the same area as in Part I of this study: the sand bar at the seaward side of the tidal estuary of the Nanakita River, 12 km east of Sendai City, North Honshu (ISHIZUKA 1961, Fig. 1).

In the preceding report, an investigation was carried out to elucidate the ages of the bar through some observations on the processes of beach formation. Four stations, numbered from 1 to 4, were selected successively from the north to the south on the sand bar (Figure 1). By a comparison of three editions of topographic maps of the area, an estimation was obtained at two points of the bar. The youngest, northernmost part of the bar, on which Station 1 was selected, was formed by the blocking of the outlet of the Nanakita River by the storms and the floods caused by the Ione Typhoon of 1947. On the other hand, it was also concluded that the beginning of the development of the dune and the vegetation at Station 4, which is located at the southern part of the bar, did not commence before 1933. Between these two extremes, the bar was inferred to have grown successively from the south to the north, through the gradual shifting of the outlet of the Nanakita River to the north. This inference was drawn from the trends in the movement of the outlet during four years, and from a general survey of the developmental stages of both the dune and the vegetation. Some verbal evidences from the inhabitants also support this conclusion.

In this paper, evidences of the parallel developments of vegetation and topography were collected by three separate procedures: observation of seed dispersal, distribution of seedlings and their ecesis on a part of the sand bar immediately after the emergence; field observations on the developments during the period from 1952 to 1957 at Stations 1 and 3; and comparisons of vegetational and topographic patterns among the four stations in 1957, based upon the above-mentioned presumption that these stations represent successive developmental stages. In comparing the compositions of the vegetation of the various stages, the results of topographic gradient analysis in the previous paper served as useful criteria for interpretation. Finally, the results of the three separate procedures were interrelated with one another, and a general scheme of the developments was integrated as the development of the topography-vegetation system.

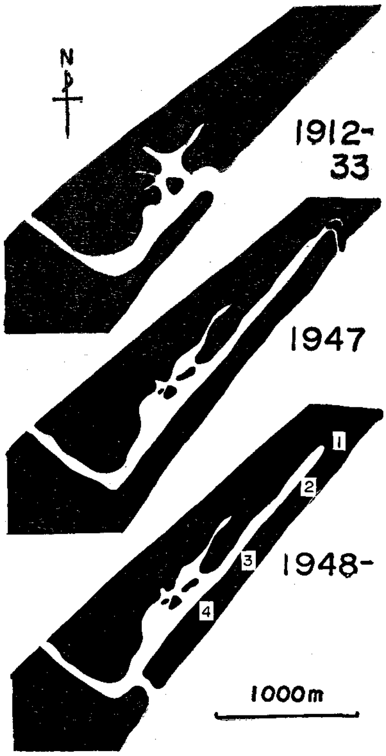

Figure 1. Maps of the area surrounding the tidal estuary (white in color) of the Nanakita River, illustrating the topographic changes since 1912. They are based on three editions of topographic maps published by the Geographical Survey Institute, formerly the Ordnance Survey of the Japanese Army. Numbers 1 to 4 in the bottom map indicate the stations surveyed in this study.

METHODS

Surveys were made at Stations 1 and 3 in 1952 and at all of the four stations in 1957. The detailed procedure was described in the previous paper. In each survey, the cover of each species was estimated in a great number of grid quadrats of 5 m× 5 m in size, and levelling of the land was carried out to construct a topographic map of each station with contour lines of 20 cm intervals. In the survey of Station 1 in 1952, when the vegetation was still extremely sparse, and there were only small and scattered embryonic dunes on the landward slope of the bar, the principal species inducing each of the embryonic dunes were recorded, and the lengths of both major and minor axes of these dunes were measured to the nearest 10 cm. Instead of estimating plant cover, the products of these two lengths were then taken as indicators of the dune areas formed by each species.

For the purpose of describing the topographic development in an objective way, the topographic analysis devised by TERADA (TERADA 1930) and used by YAMADA (YAMADA 1955) based on a statistical treatment of the contour lines was made on the data of the topographic maps of the stations.

In the summer of 1958, a beach ridge, which had a length of 300 m or so, a width of 50 to 80 m, and was practically devoid of vegetation, existed attaching to the southern end of the bar and facing the outlet at that period. It was presumed to have been made by the wandering of the outlet during the preceding year. For an investigation of the migration and establishment of the vegetation, a rectangular area of 70 m×50 m was selected in its middle part, and numbered as Station 0 (Figure 2, *a*).

The probable source of the seeds carried on to this bare sand bar, as well as the patterns of their distribution, was inferred by a combination of two analyses, namely, of the tidal drifts thrown up by the sea on the shore, and of the buried seed population in the sand. At Station 0, 13 quadrats of 1 m×1 m were laid transversely across the bar. The drifts in each quadrat were all collected and sifted out by a 1 cm-mesh sieve, and then assorted into two parts, namely, marine and non-marine, according to their probable sources. The marine drifts were chiefly composed of sea algae and eelgrass, and the non-marine chiefly of various land plants. The buried seed population was examined by AWANO and IIZUMI's method (AWANO and IIZUMI 1956). A preliminary survey was carried out on the depth of germination of various dune plants in the field. It revealed that they all germinate at depths between 2.0 and 7.0 cm, a mean depth of 4.0 cm being given for 76 seedlings of six species. Therefore, soil samples of 1,000 cc, 10 cm×10 cm×10 cm in size, were taken from the ground. After they were air-dried and well mixed, a half of each sample was added to 1,000 cc of 50 per cent solution of Na_2CO_3 (specific gravity 1.54), and the seeds risen up to the surface after stirring were collected and identified. The identification was made by comparison with the known specimens of the author and of Dr. IIZUMI, or by the descriptions of KONDO *et al.* (1933–44) and HEINISCH (1955).

GENERAL TRENDS IN THE DEVELOPMENT OF THE TOPOGRAPHY

1. *Topographic patterns*

Immediately after its emergence, the sand bar has a low, flat, simple and smooth topography forming a beach ridge less than 2 m high (Station 0, Figure 2, *a*).

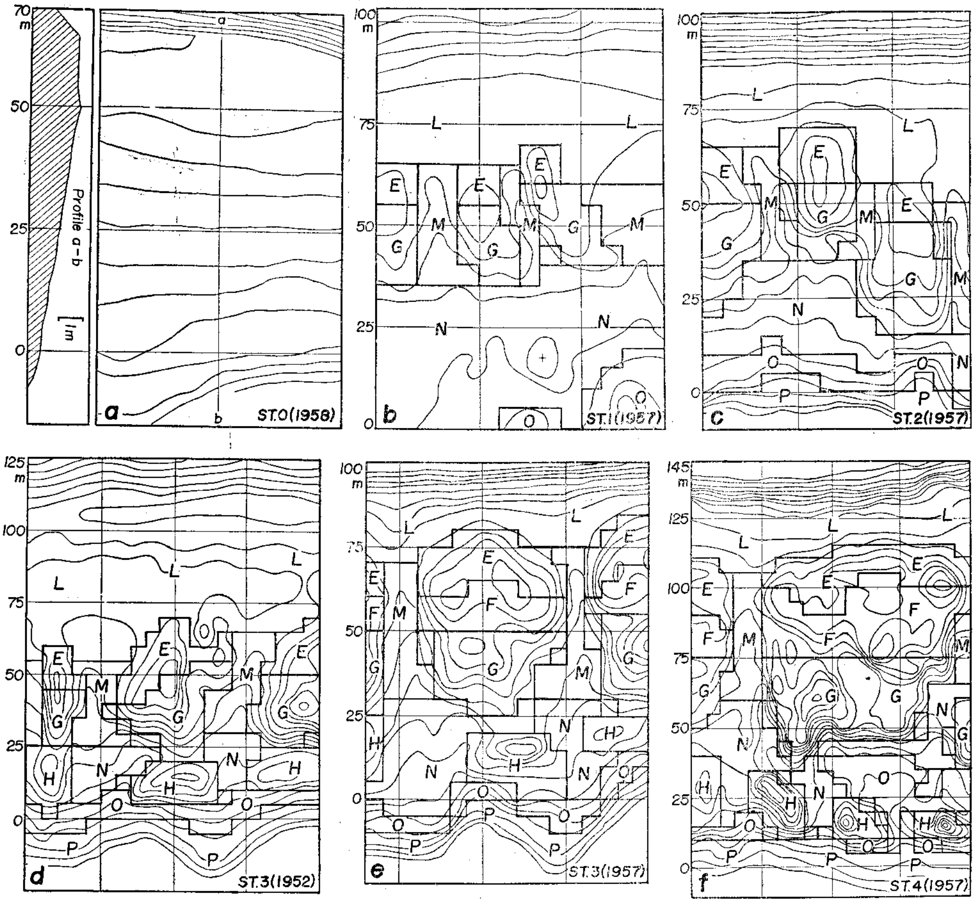

Figure 2. Topographic maps of the stations, contours at intervals of 20 cm. The open sea occupies the upper part in each map, while the estuary the lower. The topographic units are marked by capital letters (see Table 5).

The crest lies near the open sea, from which the bar slopes down to the sea at a slight inclination of 4° to 8°. The other, inner slope down to the estuary is rather extensive and extremely flat, inclining at an angle of only 1° or so. This form itself suggests its mode of construction to be due to the deposition by the onshore surfs. It was really observed at Station 0 soon after a storm that the waves from the open sea had washed all over the surface of the bar. Four years after the emergence of the bar, namely, at Station 1 in 1952, there were many minute and scattered embryonic dunes formed by the growths of dune plants and only 5 to 30 cm high on the landward slope. The general topography of the fresh beach ridge, however, had not been altered by them (Figure 3).

In 1957, there had already been built up larger dunes at the same station by the growth and consolidation of former embryonic dunes (Figure 2, *b*). They are located side by side on the middle part of the flat slope facing the lagoon, and

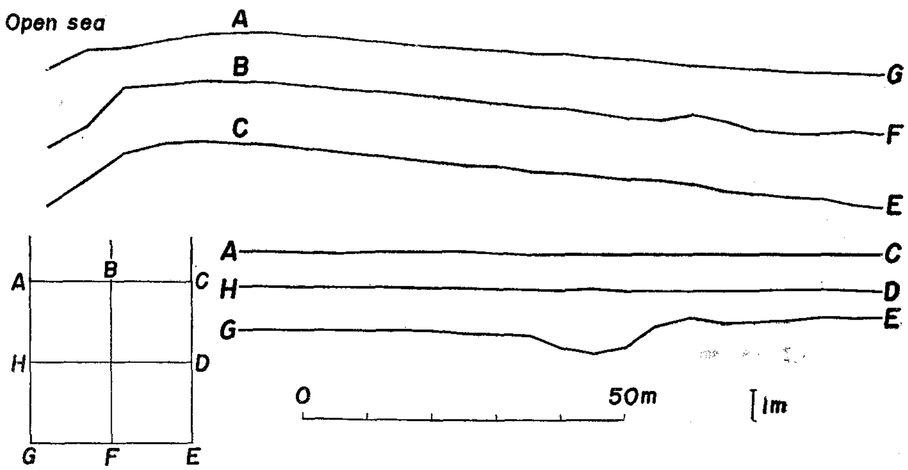

Figure 3. Topographic profiles at Station 1 in 1952 along the lines in the grid on the lower left.

interposed by wave channels in a form of shallow valley, through which pass the tidal flood during storms.

This dune-and-channel pattern of the topography keeps essentially unaltered during further development. There are, however, some marked modifications as follows (Figure 2, *c-f*):

(a) A gradual increase is seen in area and height of the dunes. The dune extension takes place in the form of advance to the crest of the bar, thus finally the original crest is covered with lower dunes (Figure 2, *e* and *f*). The process is well illustrated for the five year's changes ranging from 1952 to 1957 in the topography of Station 3 (Figure 2, *d* and *e*).

(b) The length and the depth of the wave channel increases in accordance with the development of the dunes. Judged from the various transverse profiles of the bar, the level of the channel floor roughly represents the original surface of the fresh beach ridge, although slight vertical erosion seems to have occurred on the floor of the part much narrowed by the dunes. After stormy days, low escarpments are often cut off on the side of the channels (Phot. 1).

(c) Small, cuspate deltas are often made on the place where the flood tides cross the bar and leave sand on the beach of the estuary (Figure 2, *d* and *e*). These aspects are observed most frequently at the middle parts of the bar.

(d) A line of dunelets is newly formed along the inner, estuarine shoreline. They tend to be oval in shape, with the long axes running parallel to the shorelines (Figure 2, *d-f*).

(e) The number of wave channels for a definite length of the bar decreases from the north to the south, with the result of increases in the width of the main row dunes. In view of the fact that some channels are invaded by dune plants accumulating sand on their floor, the trend of decrease is likely due to the filling-up of the previous channels.

(f) The erosion by wind may be negligible for the dune topography, except for a few minute blow-out areas in the oldest, southernmost parts of the bar.

2. *Topographic analysis*

It has been shown that the development of the topographic patterns is rather complicated. However, a trend of progressive development is clearly indicated by

Table 1. The results of the topographic analysis made on the 1957 maps of the stations. *The relative height of the dunes* is the height of the 5 m × 5 m quadrats measured from the bottom of wave channels nearest along the long axis of the bar, and expressed by the number of contour lines of 20 cm intervals. *The inclination of the slopes* is measured by the number of the contour lines in the quadrat

	Stations	St. 1	St. 2	St. 3	St. 4
Percentages of the areas	Outer beaches and channels (L, M & N)	75	50	34	28
	Inner beaches (O & P)	7	18	16	18
	Dunes (E, F, G & H)	17	31	47	50
	Not determined (R)	1	1	3	4
Relative height of the dunes	External slope of the main row dunes (E)	1.4	1.9	2.4	2.1
	Top and landward slope of the main row dunes (F & G)	1.6	2.6	2.9	3.1
	Inner row dunelets (H)	—	—	1.7	2.8
Inclination of the slopes	Outer beaches and channels (L, M & N)	0.6	0.9	0.9	1.0
	Inner beaches (O & P)	1.3	2.1	2.5	1.6
	Dunes (E, F, G & H)	1.2	1.7	2.0	2.2

the results of topographic analysis shown in Table 1. The area covered by the dunes continuously increases from 17 per cent of the total area of Station 1 which is nine years old in 1957 after its emergence, to 50 per cent in the southernmost, oldest site of Station 4 which is presumed to be about 24 years old. The decrease in the areas of outer beaches and channels indicates the dune extension into them. Both the relative height and inclination of the dunes show a marked increase during the development.

DEVELOPMENT OF THE VEGETATION

Based upon the above description, three stages can be distinguished in the development of the topographic patterns. They are:

(1) The stage of a bare and fresh beach ridge, on which no dunes are yet formed. On this sand bar, the stage continues for a period less than five years

after its emergence. From the standpoint of vegetation, it is the stage of migration and ecesis.

(2) The establishment of dune-and-channel pattern of the topography. It starts with scattered embryonic dunes, and leads finally to their consolidation to form the main row dunes. At Station 1, it required about five years.

(3) Further development and modification of the topography.

The vegetational changes were also found to be characteristic to each of the stages. Therefore, the framework of the following description is also based upon them.

1. *Migration and ecesis at Station 0*

Seed dispersal. A wide variety of plant and animal remains are washed ashore and piled in small heaps on the beaches. Like plant growths, the drift also acts as an obstacle to the wind, and it is gradually buried beneath a low heap of sand (Phots. 3 and 4). Being thrown up by surfs at high tides, the drifts from the open sea are distributed irregularly in dots or arranged in quite irregular rows mainly on the area near the crest line (Phot. 2). On the other hand, on the landward slope of the bar, the drifts tend to form more or less regular lines parallel to the shore. The probable cause of this regularity lies in that the remains from the estuary are collected and deposited by tides and rather weak waves during a rise of the water of the estuary. This type of drift line is most frequently seen close to the estuary shore (Phot. 3).

Seedling counts made at Stations 0 and 1 both revealed the fact that a great

Table 2. Composition of the buried seed population in the sand. It is expressed as the mean number of seeds per a 1,000 cc soil sample (10 cm×10 cm×10 cm). June and July, 1958, at Station 0

	Sand from the tidal drifts			Bare sand
Distance from the estuarine shore	10–15	25–35	35–50	10–35
Occurrence of the seedlings	+	+	–	–
Number of samples	3	3	2	3
Elymus mollis	2.3	0	0	0
Carex Kobomugi	1.0	0.5	0	0
Ixeris repens	3.7	0	0.5	0
Ischaemum anthephoroides	2.7	1.0	0	0
Carex pumila	2.7	0	2.0	0
Glehnia littoralis	0.3	0	0	0
Calystegia Soldanella	0.7	0	0	0
Chenopodiaceae (mainly of *Suaeda maritima*)	10.0	4.0	5.0	1.0
Total of the strand plants	23.3	5.5	7.5	1.0
Seeds of the inland plants*	113.0	31.0	32.0	13.0

*Mainly of the seeds of gramineous and cyperaceous plants.

majority, sometimes more than 90 per cent, of seedlings is found on the drift just mentioned (Phot. 4). Results of the analysis of buried seed population (Table 2) suggest a clear explanation for it. The sand of the drift lumps contains four to ten times as many seeds per unit area as the sand from the bare flats. The seeds are most numerous in the drifts closest by the shore of the estuary. Moreover, more than 80 per cent of the seeds are derived from inland species, which are seldom found on any part of the sand bar. Except a few anemochores, e. g., *Ixeris repens* and *Phragmites communis*, which might be brought by wind and caught by the debris, most seeds probably are carried in the hydrochoric and estuarine way.

An analysis of the remains in the tidal drifts also supports this inference. In Table 3, it is found that the drifts on the estuarine shore of the bar, on which

Table 3. The composition of the tidal drifts in 1 m×1 m quadrats laid in Station 0. The crest of the beach ridge lies at 60 m from the estuarine shore. See the text for further explanations

Distance from the estuarine shore (m)	Total fresh weight (g)	Per cent of the dry weight			Number of seedlings in quadrat
		Land origin	Sea origin	Not determined	
5	372	82	13	5	0
5	902	50	44	6	0
10	676	85	14	1	25
10	397	88	11	2	18
16	715	90	9	1	0
29	150	96	4	0	0
30	253	82	17	1	1
32	440	91	8	1	0
39	256	54	45	1	0
43	1003	27	72	1	0
48	4064	32	65	3	0
53	246	26	72	2	0
55	206	19	79	2	0

many seedlings grow, consist for the most part of various remains of land plants. This composition suggests that the remains are once thrown into the river or the estuary, and then transported and deposited by the water onto this area. On the contrary, the drifts near the crest line are chiefly composed of the remains of sea algae and eelgrass, indicating that they are carried and thrown up by the water of the open sea.

Distribution, composition and ecesis of the seedlings. During spring and summer months, there are frequently observed many seedlings of strand plants germinating on the landward slope of the bar. In each spring, the seedlings of *Suaeda maritima* grow abundantly in turfs on the intertidal zone of the old and protected beaches near Station 4. On the bare sands of a newly formed beach ridge, however, the seedlings are confined to the main body of the bar. They are most frequently found on the tidal drifts at supratidal zones of the estuarine beaches, and are almost dune plants. Conforming to the description by TANSLEY (1939, p. 848), there are considerable fluctuation in the abundance of the seedlings every year. It is most probable that these seedlings are the sole source in the initiation of vegetation upon the bare sand. The possible regeneration from rhizomes, which were cut off, thrown up and buried under the bare sand, was seldom observed.

In early July, 1958, a seedling count was performed at Station 0. As shown in Figure 2, *a*, a base line parallel to the long axis of the bar was set on the estuarine beach. The station was then divided into several rectangular areas according to the distance from the base line. The seedlings in each of the rectangles were recorded and the results are summarized in Table 4. The seedlings are most abundant in two

Table 4. Distribution and composition of the seedlings at Station 0, expressed as their numbers. July 8th, 1958. See the text for further explanations

Distance from the base line set nearby the estuarine shore (m)	−15–0	0–10	10–20	20–30	30–45
Elymus mollis	83	68	14	12	8
Carex Kobomugi	8	15	1	2	0
Ixeris repens	15	52	2	3	0
Ischaemum anthephoroides	15	22	1	7	9
Glehnia littoralis	2	2	2	0	0
Zoisia macrostachya	0	0	11	0	0
Calystegia Soldanella	39	53	16	15	17
Linaria japonica	0	1	0	0	0
Salsola Komarovii	4	2	0	0	0
Atriplex Gmelini	0	1	0	0	0
Phragmites communis	0	1	0	0	0
Total	166	217	47	39	25

rectangles close to the estuary, where a conspicuous drift line existed (Phots. 3 and 4). The species list reveals that, although the seeds of inland plants take the major portion of the buried seed population, the seedlings are almost solely composed of strand plants. *Elymus mollis*, *Calystegia Soldanella* and *Ixeris repens* hold the majority of the seedling population on the drift line. *Elymus* and *Calystegia* occur occasionally on bare sands between 10 m and 45 m in distance from the base line. From 45 m onwards, no seedlings were found.

Only several days after this survey, an exceptionally high tide occurred during the storm caused by the 11th Typhoon of 1958, which struck the area on July 23rd. The bar was then completely washed by surfs from the open sea. As the result, the greater part of the tidal drifts and of the seedlings were either washed away or buried under the sand. On the former drift line at the estuary beach, however, considerable numbers of seedlings, which were for the most part well-grown individuals of *Elymus*, survived the flood. A visit to the station in the following spring revealed that the *Elymus* plants had succeeded in their colonization, attaining a height of 20 cm or so and were already accumulating a heap of sand around them.

2. *Developments associated with the construction of the dune-and-channel pattern of the topography at Station 1*

As stated previously, the stage continues for the period between 1952 and 1957 at Station 1. The following descriptions are, therefore, based on a comparison between the surveys made separately in the two years.

Patterns of embryonic dunes in 1952. On the upper half of Figure 4, the distribution of the embryonic dunes in 1952 is illustrated along the transverse section of the bar. Similar to the seedling count at Station 0, an area of 100 m × 100 m was divided into ten rectangles according to the distance from the base line set close by the estuarine shore. The area of the embryonic dunes was estimated as the products of their lengths of major and minor axes. It is used as a measure of plant cover, since the vegetation was extremely meagre.

The total area of the 809 incipient dunes is less than 13 per cent of the whole area of the station. They are aggregated on the lower part of the landward slope, and around the crest line the area remains almost devoid of vegetation. The relative composition indicates a characteristic trend in the distribution of each species. As a result, the area may be divided into three distinct zones. *Carex Kobomugi* is the only species colonizing on the outer area near the crest. The inner, estuarine shore is occupied by dunes formed by *Elymus*, while *Carex pumila* occurs occasionally. The zone between the two is occupied by *Ixeris* and *Elymus*. The species density in the 100 m × 10 m rectangles shows a continuous decrease from ten at the estuarine shore, to only two at the crest line.

The distribution of sizes of the incipient dunes are summarized in Figure 5. The sizes, as well as the forms, of the young dunes vary according to the inducing species (NUMATA 1949) and location. *Carex Kobomugi* is conspicuous in forming the most minute but numerous dunes (Phot. 5), and in having its optimum zone of dune formation at the middle part of the landward slope of the bar. *Ixeris* forms more extensive, but lower dunes. *Elymus* forms most extensive, highest dunes of the three at the area near the estuary (Phot. 6). It suggests that the *Elymus*-dunes are the oldest ones in this zone, since *Elymus* is the only species which completed colonization at the estuarine beach of the bare sand bar, as shown in the foregoing section.

To find the pattern of the embryonic dunes along the *longitudinal* section of the bar, the rectangle at the middle (50 to 60 m from the base line) of the landward

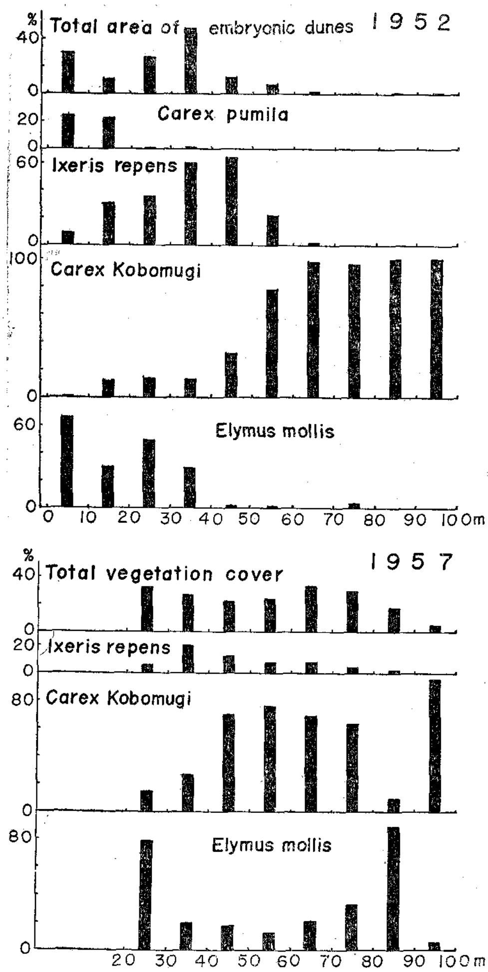

Figure 4. Comparison of the coverage of plants in Station 1 between 1952 and 1957. Abcisse gives the distance from the estuarine shore (0 m) to the crest line (100 m). In 1952, the figures are based on an estimation of the area of embryonic dunes, and in 1957 on ordinary cover estimation. The total area of embryonic dunes, as well as the total vegetation cover, is expressed as percentages of the rectangles examined. Coverages of the species are expressed as relative values to the totals.

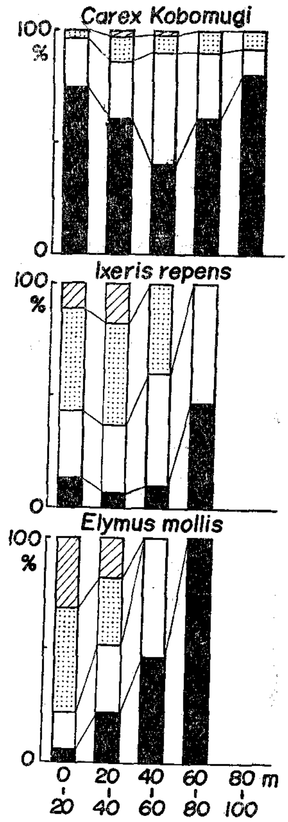

Figure 5. Size class distributions of embryonic dunes induced by three species in Station 1 in 1952. Each column represents the total area of the dunes induced by each species in 20 m × 100 m rectangle. They are arranged in a series along the transverse line of the bar from the estuarine shore (0 m) to the crest line (100 m). The columns are divided in proportion to the size-distribution of the dunes as follows : solid black : dunes less than 0.09 sq. m in area; white : from 0. 10 to 0. 99 sq. m ; dotted : 1. 00 to 9. 99 sq. m ; hatched : more than 10.00 sq. m.

slope was divided into 5 m × 5 m grid quadrats, and the dunes were measured and charted within each of them. The results reveal the area to be of striped patterns of vegetation arranged perpendicular to the long axis of the bar. The vegetation peculiar to the intermediate zone, namely, those chiefly composed of *Ixeris* and *Carex Kobomugi*, lies in narrow stripes of 10 to 15 m widths. Here, the embryonic dunes cover more than 20 per cent of the ground. These vegetation of the intermediate zone are interposed by the vegetation peculiar to the area nearer the crest, in which minute dunes of *Carex Kobomugi* are formed very sparsely and the incipient dunes cover an area less than five per cent of the quadrats. Tidal drifts thrown up from the open sea are scattered here in low heaps. The widths of these nearly bare stripes are somewhat larger (15 to 20 m). There were five or six sets of such striped pattern within a distance of 130 m measured parallel to the long axis of the bar. It is most probable that these patterns have been formed by invasions of surfs at past storms, which had the destroying effects upon the colonized plants, carrying and depositing drifted organic materials. During further development, it is likely that some of the bare stripes give rise to the formation of the wave channels, while the embryonic dunes in the vegetated stripes grow and fuse to form consolidated dunes.

Vegetational changes up to 1957. By 1957, the bar at Station 1 had attained its proper dune-and-channel pattern of topography by the consolidation of former embryonic dunes (Figure 2, *b*). The topographic changes go together with considerable changes in the vegetation. By comparing top and bottom of Figure 4, the following changes are to be pointed out :

First, it is concluded from the distribution of the total vegetation cover that a remarkable advance of the vegetation took place toward the crest line. This was accomplished chiefly by the growths and consolidation of former incipient dunes of *Carex Kobomugi*, which had been scattered very sparsely in the outer zone in 1952. The main body of consolidated dunes are now covered by this species and *Ixeris*. The total cover of vegetation on the dunes is more than 20 per cent of the ground.

Secondly, a marked colonization of *Elymus* took place inside the *Carex Kobomugi* zone at 80 m to 90 m. It is found on the external, seaward slope of newly consolidated dunes. The establishment of *Elymus* is thought to have an important effect for protecting the growing incipient dunes of *Carex* and *Ixeris* from the destruction by surfs from the open sea. Judged from the mode of distribution, *Elymus* is more tolerant to temporal increase of soil salinity than *Carex* and *Ixeris*.

Lastly, the former, intermediate zone inhabited chiefly by *Ixeris* became inconspicuous. The outer zone of *Carex Kobomugi* now passes directly into the inner zone of *Elymus*. It is also an outcome of the development of the embryonic dunes in this zone. The dunes, which were originated as separate sand accumulations induced by *Carex* and *Ixeris*, grow now into larger dunes, covered by evenly mixed vegetation.

The role of the seedlings. During the spring and the summer of 1952, numerous seedlings were found at Station 1. Seedlings were counted in June and September respectively. Alike the results at Station 0, the seedlings were also almost confined to the tidal drifts. In June, more than 5,000 seedlings were distributed in the area from the estuarine shore to the crest line. They were remarkably abundant on the middle part of the slope. The count in September revealed that the seedlings, which were somewhat more evenly distributed, were less than a half of those in June. In both of the counts, *Ixeris* was the most abundant, *Carex Kobomugi* being the second. *Ixeris* holds more than half of the seedlings on most parts of the slope, while *Carex* takes the major part on the crest.

Observations during the following autumn showed that most of the seedlings, chiefly of *Ixeris* and *Carex*, had succeeded in their establishment on the tidal drifts. They were observed to persist until the following spring, and thus increase the number of incipient dunes. Although *Elymus* seedlings were comparatively rare around the crest line, there were some which held their ground and gave rise to the aforementioned invasion.

3. *Further developments of the vegetation*

Types of the successional trends. In the foregoing chapters, the types of the vegetational changes were elaborated from independent series of field observations. After the construction of the dune-and-channel pattern of the topography, a more deductive approach is possible by the use of the results of the topographic gradient analysis in Part I of this study. The vegetation had been analysed along the gradients of two indices, which were inferred to indicate the main emvironmental gradients on the bar: the relative height of the dunes showing the position to the flooded water at specially high tides, and the total vegetation cover indicating the stability of the sand. From the viewpoints of the present report, these two indices should be expected to increase due to the influences of the vegetational growths during the course of succession. Therefore, the gradients of each species in the analysis, obtained according to the increase of each index, should be regarded as yardsticks for the *autogenic* developments of the vegetation. Especially, it will serve to distinguish the essential trend from stand-to-stand, or year-to-year fluctuations.

Based upon the above considerations, two types of the gradients were distinguished from the results of gradient analysis. They are as follows:

Type A, or the changes due to the stabilization of the sand by plant growths. The results of the analysis (Part I, Figure 10) indicate that the increase of total vegetation cover would be accompanied by the following changes of the vegetation: a decrease in the relative importance of *Carex Kobomugi*, and increase of such dune plants as *Ischaemum anthephoroides*, *Calystegia Soldanella*, *Lathyrus maritimus* and *Linaria japonica*, and an increase of vegetational diversity represented by the species density in the quadrats.

Type B, or the changes due to the increment in the height of the dunes. The results of the observation (Part I, Figure 9) indicate an increase of *Carex Kobomugi* in contrast to a decrease of *Elymus*. It is accompanied by slight increases of the diversity and the stability. From the results of two-dimensional representation of the analysis (Part I, Table 3), the changes are peculiar to the areas with intermediate values of the stability, the total vegetation cover being 20 to 30 per cent or so. The values were given for the vegetation on the main row dunes but not for their landward slopes.

In the foregoing section, the observation indicated the third type of vegetational change, which is related to the consolidation of the embryonic dunes. It is *the Type C trend, or the invasion of Elymus into the almost bare sand flats* nearby the crest, where only *Carex Kobomugi* has colonized making extremely sparse embryonic dunes. It is to be noted that the change of species is probably caused by the delay in the first colonization of *Elymus*, independently of the environmental change effected by the past plant growth working upon the topography.

Changes during the period of 1952 to 1957 at Station 3. As stated previously, two surveys were conducted at Station 3 in 1952 and in 1957 separately. The two maps, *d* and *e* in Figure 2, illustrate a marked change of the topography in the form of the advance of the main row dunes on to the crest areas. On the contrary, the dunelets along the estuarine shore, as well as the landward halves of the main dunes, maintain the same topography in the two maps. There were no fixed quadrats or points set up during the period. However, the features last mentioned enable us to surerimpose the former topography in 1952 on the 1957 map, and thus to pursue the changes more exactly.

In Table 5, the topographic changes are followed up as the transformation of the topographic units, which had been defined in the previous paper (Part I, Table 1). By a closer examination of the table, it is evident that the advance of the main row dunes causes the transformation of the former outer beaches (Unit L) either into the seaward slopes (E) or into the tops (F) of the dunes, while the former seaward slopes (E) are converted into the dune tops (F) or the backslopes (G). On the other hand, there are also remarkable changes in the topography of the low-lying areas along the estuarine shore. The former supratidal zone of the estuarine beach (unit O) is now transformed into the channels (N), while the intertidal zone of the beach (P) into the supratidal (O). Moreover, an advance of the tidal flood deltas is observed as the increment in the area of the intertidal zone (P). It is most probable that the above changes are the results of the action of the tidal floods, which crossed the bar at the time of some exceptionally high tides during the years between the surveys.

The data in Table 6, in which the vegetational changes are referred to by the

Table 5. Topographic changes at Station 3 during 1952 to 1957. The changes are indicated by the percentage of the transformed topographic units. For instance, it is indicated in the leftmost colum that only nine per cent of the topographic unit E in 1952 remained the same in 1957, while the other 69 per cent were converted into Unit F, 19 per cent into G, and three per cent into M. Unit X denotes that the area was lower than the intertidal zone of the estuarine beach in 1952

Topographic units set on the 1957 map	Topographic units set on the 1952 map: E	G	H	L	M	N	O	P	R	X
Seaward slope of main dunes (E)	9	0	0	47	3	0	0	0	0	0
Top of main row dunes (F)	69	6	0	5	9	0	0	0	0	0
Backslope of main row dunes (G)	19	81	9	0	0	0	0	0	33	0
Inner row dunelets (H)	0	0	78	0	0	4	11	0	17	0
Outer beaches (L)	0	0	0	37	0	0	0	0	0	0
Channels, outer parts (M)	3	6	0	11	63	0	0	0	17	0
Channels, inner parts (N)	0	0	6	0	11	96	46	11	33	0
Estuarine beach, supratidal (O)	0	0	0	0	0	0	39	33	0	0
Estuarine beach, intertidal (P)	0	0	0	0	0	0	0	56	0	100
Not determined (R)	0	8	6	0	14	0	4	0	0	0
Total	100	101	99	100	100	100	100	100	100	100

Table 6. Vegetational changes at Station 3 during 1952 to 1957. The topographic units in the uppermost line are those set on the 1952 map. Therefore, there are indicated the changes in the *same area*, irrespective of the transformation of the topographic units. The relative importances of every species are expressed by the summed dominance ratios (NUMATA 1958). See Table 5 for the symbols of the topographic units

Topographic units set on the1952 map	E		G		H		L		M		N		O		P	
Year of survey	1952	1957	1952	1957	1952	1957	1952	1957	1952	1957	1952	1957	1952	1957	1952	1957
Suaeda maritima	0	0	0	0	0	0	0	0	0	0	0	0	235	17	300	182
Carex pumila	0	0	2	0	36	4	0	0	0	0	12	0	57	13	8	0
Elymus mollis	296	263	70	128	300	263	158	300	80	300	300	300	148	300	156	300
Ixeris repens	272	134	236	152	154	143	184	40	74	63	52	73	121	57	49	4
Carex Kobomugi	238	262	300	300	162	202	300	61	300	123	98	60	67	50	8	0
Zoisia macrostachya	35	149	58	144	69	25	0	2	8	15	7	7	98	20	0	11
Glehnia littoralis	33	54	77	116	46	91	120	6	8	5	18	38	13	29	0	0
Ischaemum anthephoroides	7	58	41	126	60	273	0	0	0	15	27	90	36	63	0	0
Calystegia Soldanella	35	20	67	78	250	142	126	0	15	0	38	27	68	11	0	0
Lathyrus maritimus	4	57	4	127	64	79	0	0	0	0	7	21	38	11	0	0
Linaria japonica	0	0	8	71	16	16	0	0	0	0	12	11	36	14	8	0
Percentage of unstable zones	94	97	95	85	82	53	100	72	100	81	93	89	92	61	100	61
Percentage of quadrats with less than five species	78	75	62	35	22	15	100	98	100	97	75	63	61	68	92	100
Relative height of the dunes*	2.1	3.4	2.9	2.8	2.8	1.7	—	—	—	—	—	—	—	—	—	—

*Expressed as the number of contour lines of 20 cm intervals.

changes of relative importances, reveal the existence of a clear correlation between the developments of the topography and the vegetation.

(a) In the areas of the consolidation of the embryonic dunes, namely, in the outer beaches (Unit L) and in the outer parts of the channels (M), a marked colonization of *Elymus* occurred. As the result, the relative importance of *Carex Kobomugi* decreases compared with the increase of *Elymus*. It is the Type C trend of the foregoing section.

(b) On the seaward slopes of the main row dunes (Unit E), a decrease of *Elymus* occurs with the increase of *Carex Kobomugi*, as the result of the increment in the dune height (Type B trend).

(c) As stated previously, the topography of the backslopes of the main row dunes (Unit G) and the inner dunelets (H) remained roughly unaltered until 1957. Concerning these relatively stable and increasingly protected areas, the data indicate the occurrence of the Type A change on the backslopes. On the inner dunelets (H), however, the changes are somewhat more complicated. A decrease of *Elymus* occurs compared with the increase of *Carex Kobomugi*, while the increase of *Ischaemum* and *Lathyrus* is conspicuous. It is likely that these changes indicate the occurrence of a trend intermediate between the Types A and B.

(d) On the estuarine beaches of the Units O and P, a decrease of the halophyte, *Suaeda maritima*, is observed in contrast to the increase of *Elymus*, associated with the increase of the total vegetation cover. They are the results of the above-mentioned accretion of the tidal flood deltas. It is to be noted that the vegetational changes here are caused *allogenically* by the changes of the topography, the effects of vegetational reaction being negligible.

Comparison of vegetation among the four stations. In 1957, surveys were made at the four stations 1 to 4, which represent a series of surface ages ranging from nine to about 24 years. It appears quite natural to expect that the successional trends during these years would be detected by comparing the floristic compositions among the same topographic units of the four stations. It must, however, be taken into account that such an assumption may be admitted when the topography remains unaltered. If there were significant transformations of the topographic units, the results of the comparison among the same topographic units would show discrepancies with the actual succession on the same areas, such as was described in the above section.

The comparisons were made, as shown partly in Table 7, of the relative importance of each species, as well as the vegtational diversity and the stability, arranged in order of the stations. Stand-to-stand fluctuations were rather conspicuous, but, supported by the results of the foregoing sections, the trends were inferred as follows:

Table 7. Comparisons of dune vegetation among the same topographic units of the four stations. The relative importances of every species are expressed by the summed dominance ratios

Topographic units	Seaward slopes of main row dunes(E)				Dune-tops (F)		Backslopes of main row dunes (G)				Inner row dunelets (H)	
Station	1	2	3	4	3	4	1	2	3	4	3	4
Carex pumila	0	0	0	0	0	0	0	11	0	57	0	91
Elymus mollis	281	296	300	300	276	61	138	275	221	131	277	181
Ixeris repens	53	24	49	100	139	123	128	132	138	182	146	153
Carex Kobomugi	152	172	57	161	276	300	300	210	258	179	225	135
Zoisia macrostachya	11	0	0	86	51	70	80	8	163	44	18	44
Glehnia littoralis	0	0	2	37	50	37	15	24	108	67	94	58
Ischaemum anthephoroides	0	0	0	0	42	104	4	180	149	275	227	295
Calystegia Soldanella	0	0	0	0	21	18	0	87	71	81	136	108
Lathyrus maritimus	0	0	0	0	0	46	0	18	113	265	72	231
Linaria japonica	0	0	0	0	0	0	0	2	0	14	14	41
Percentage of unstable zones	100	100	95	100	97	100	100	90	87	73	90	24
Percentage of quadrats with less than five species	100	100	100	100	81	88	93	64	30	32	17	7
Relative height of the dunes*	1.4	1.9	2.4	2.1	3.2	3.3	1.6	2.6	2.7	2.8	1.7	2.8

*Expressed as the number of contour lines of 20cm intervals.

(a) Areas which show Type A trend in successive stations: backslopes of the main row dunes (Unit G), the inner dunelets (H), the inner parts of the channels (N), and the bayshore beaches (O and P). On all of these habitats, the stability increases towards Station 4. On the dunes, it is associated with the increase of *Ischaemum*, *Calystegia*, *Lathyrus* and *Linaria*, and the decrease of *Carex Kobomugi*. The increase of *Carex pumila* and *Suaeda* are observed respectively on the supratidal (Unit O) and on the intertidal (P) zones of the inner beaches. They agree with the expected trends drawn from the results of gradient analysis on the bayshore beaches (Part I, Figure 10).

(b) Areas showing Type B trend: the tops of the main row dunes (Unit F). Comparing Station 3 with Station 4, the relative importance of *Elymus* decreases in Station 4 in contrast to the increase of *Carex Kobomugi*. The relative height of the dunes is slightly larger in the latter station.

(c) Areas showing Type C trend: the outer parts of the channels (Unit M). The colonization of *Elymus* becomes progressively conspicuous towards Station 4.

(d) Areas with little or no significant changes: the outer beaches (Unit L) and the seaward slopes of the main row dunes (E).

The results of the foregoing two sections are summarized in Table 8. As expected, considerable discrepancies arise between the actual succession and the trend indicated by the comparison among the stations. They are found in the outer beaches, the

Table 8. A comparison of the successional trends, between the actual changes at Station 3 and the supposed changes from station to station. The cross (x) indicates that there were no significant trends, while the asterisk (*) that was there observed an increase of *Elymus* against the decrease of *Suaeda*, as the result of the allogenic increment in the area of the tidal flood deltas. See the text and Table 5 for other symbols

Topographic units	L	E	F	G	H	M	N	O	P
Actual changes	C	B	—	A	AB	C	A	*	*
Trends shown by the comparison among the stations	x	x	B	A	A	C	A	A	A

seaward slopes (Units L and E), and in the estuarine beaches (O and P). Observations made on the topographic changes at Station 3 (Table 5) reveal that there were marked transformation of the topographic units on these areas, either by consolidation and growth of the dunes (Units L and E), or by allogenic increment in area of the tidal flood deltas (O and P). On the other hand, the two results coincide with each other on the backslopes (Unit G), on the inner dunelets (H), and on the channels (M and N). The survey at Station 3 also indicates that the original topography remained relatively unaltered in these habitats, and that the area is increasingly protected by the advance of the foredunes.

DISCUSSION AND CONCLUSION

1. *Development of the topography-vegetation system*

In this research, practical observations of the actual changes are confined to five years, a rather short period compared with the estimated surface age of about 24 years at the oldest Station 4. Neverthless, they can be integrated into a general scheme illustrating the development of the topography-vegetation system on the bar. The scheme is summarized in Figure 6 chiefly concerning the development of the dunes.

The results, along with those of Part I of this research, revealed on the one hand that the vegetational patterns represented at each of the stages are largely related to and determined by the patterns of the topographic conditions. On the other hand, it is also clearly indicated in this paper that the plant growths act upon the topography. They act a leading part in initiating, consolidating and developing the dunes. It was shown, after the establishment of the dune-and-channel pattern of the topography, that the vegetation remarkably modifies the dunes, in the dune advance to the crest of the bar, and in the increment in the height of the dunes. The stabilization of the mobile dunes is made also by the reaction of the plant growths in areas increasingly protected by the advancing foredunes. These effects of the vegetation are to be referred as the *topographic reactions*.

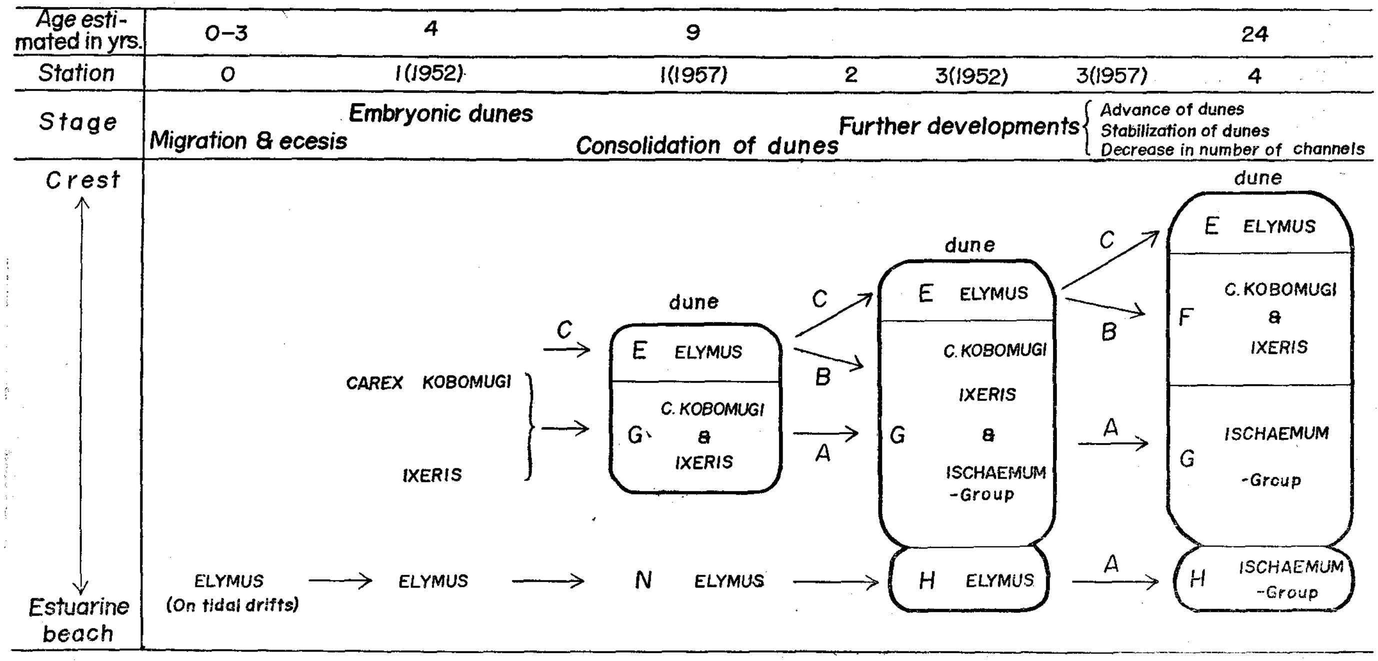

Figure 6. The development of the topography-vegetaton system on the sand bar. The plant names indicate the dominant species on the topographic units denoted by the symbols (see Table 5). The capital letters A, B and C indicate the types of the successional trends, which are described in the text in pp. 152 and 153. *Ischaemum, Calystegia, Lathyrrus* and *Linaria* are collectively called here as the *Ischaemum*-group.

As the next process, these topographic changes bring about the successional changes of the vegetation. The succession proceeds towards a readjustment of vegetational patterns, to fit them to the newly modified patterns of the topographic conditions. In these manners, the development of the topography-vegetation system comprise a system of mutual interactions.

MAJOR (1951) stated that the topography of an area is one of the *state factors* of an ecosystem, by which the inner processes of the system are ordained, and which are independent from the effects of the inner processes. On coastal sand bars, it is evident from the present research that a role of state factors is played by the original and general topography of the beach ridge. MAJOR admits, however, that there are several topographic processes which are subject to the reaction of vegetation, such as the formation of the high moors and the coastal sand dunes, and the vegetational control of erosion on slopes. It is well known that some surface forms develop under the influences of the plants, e.g., the regeneration complex of the high moors (OSVALD 1923 and YOSHIOKA 1954), and the various surface forms (*Strukturboden*) in the arctic and high altitude tundra formed by the effects of solifluction (WATT and JONES 1948, WILSON 1942, TAYLOR 1955 etc.).

The modification of microtopography by vegetation is often accompanied by vegetation mosaics, as clearly exemplified in the pattern of the regeneration complex of the high moor. WATT (1947) emphasized that the mosaic, or his *unit pattern*, is the reflection of the order and the funciton in a plant community. According to his opinion, we can describe the vegetation as a *working mechanism* by studying the strucutre and the change of the patterns.

The vegetational arrangements on each of the main row dunes, which are illustrated in Figure 6 schematically, show the character of such an organization in dune developments. The advance of the dunes is caused by *Elymus* in the front, whereas *Carex Kobomugi* invades and accumulates the sand on the dune-tops thus established. The landward slopes of the dunes become gradually protected by the advancing foredunes, where invading *Ischaemum*, *Calystegia*, *Lathyrus* and *Linaria* stabilize the sand. These arrangements are larger in scale than WATT's unit patterns, though they have a similar character in their nature.

The rate of dune development. The observations at Station 1 revealed that, under favorable conditions, consolidated dunes with a height of one meter or so may be established within nine years after the emergence of a beach ridge. The topography of Station 4 indicates that the height may increase to nearly 2 m during 24 years of development.

These results are comparable with the reports of the succession at the Far Point, a shingle beach newly formed by 1921, stretching from the end of the compound recurved spit of Blakeney Point, England, TANSLEY (1939) described, citing unpublished informations of F. W. OLIVER, that there were only a few scattered *Agropyron* and *Ammophila* dunes in 1928. In 1928, heavy seeding of *Ammophila* took place. Until 1937, there developed continuous dunes whereof crests were 2.5 m high above the beach, owing mainly to the growths of the seedlings derived from the seeds of 1928.

The formation and the fate of the channels. On this sand bar, the wave channels between the dunes are the peculiar feature of the topography. It is concluded that the channels are built up, i. e., originated from the surfaces of the past beach ridge, being constricted by the dunes. It is observed also that channels decrease in number per unit length of the bar, since the dune plants invade them during the years without specially high tides and consequently accumulate the sand to fill them. Such features and processes are observed occasionally on other sand bars of recent origin.

In the report on the vegetation and the topography of the offshore bars of New Jersey, U. S. A., MARTIN (1959) suggested that the sand is transported by the surfs across the bar through the channels, so that they take the leading part in the landward retreat of the bar. These processes are also observed in the present research showing an increase in the area of the tidal flood deltas on the estuarine shore. However, the above-mentioned mode of the construction of the channels appears to be quite different from MARTIN's descriptions. He reports that the channels are erosion features, originated as blow-outs of the already established dunes. It is his opinion that there exists a cyclic change between the filling-up and the formation of the channels.

2. *The use of gradient analysis for the study of vegetational succession*

So far, the successional trends were often assumed directly from the zonal arrangements of plant communities, which are observed on bogs, shores of the lakes and salt marshes. OOSTING (1954) is skeptical over the application of such procedures in the study of succession on sandy coasts. In his comments on the works of DAVIS (1942), GOODING (1947) and others, he indicates that the zonation is normally held in stability by topographic conditions, provided that there occurs no secular, large-scale change by the action of the topographic agents. In the present research, the succession was surveyed in the earlier stages, that were presumed to be less than 24 years after the emergence of the beach ridge, and the existence of actual developmental interrelations was proved between the vegetation and the topography.

In order to derive the trends of succession from the viewpoints of vegetational continuum, gradient analyses were first made in this study along the indices of environmental factors that are subjected to the reaction of the plant growths, instead of the state factors of an ecosystem such as the altitude or the soil moisture gradient adopted by WHITTAKER (1952, 1956 etc.). The trends were then inferred as statistical ones, rather than interrelations among the individual stands. This method of the inference of the successional trends, along with the more empirical one by the climax adaptation numbers by CURTIS and MCINTOSH (1951) and BROWN and CURTIS (1952), serves to improve the interpretation of succession in its objectivity and accuracy.

The results of this study indicate that the successional trends are multilateral. They are differentiated into several distinct types according to the conditions of colonization of the species populations, such as the distribution and germination of the seeds, ecesis of the seedlings, topographic reactions of plant growths acting in stabilizing and accumulating the sand, and the allogenic transformation of the topographic conditions. The environmental gradients across the sand bar, determined by the initial topography of a beach ridge, act a major role in delimiting the above processes. The type of the trends observed in each habitat varies according to its topographic conditions, instead of universal trend applicable everywhere in the area. This conclusion well accords with the opinions stated by WHITTAKER (1953), that the succession is a statistical process consisting of the overlapping of independent changes of species populations, each individually reacting to the effects of the environmental conditions.

3. *Early processes of the succession*

At Station 0, surveys were made concerning the compositions of the buried seed population and of the tidal drifts, as well as concerning the number, distribution and the ecesis of the seedlings. The results enabled us to form a preliminary account of the earliest processes of the plant colonization.

The analysis of the buried seed population and of the composition of the tidal drifts revealed that the seeds are distributed mainly by tides of the estuary, and are cast up on the shore during high tides mingled with various organic remains, chiefly composed of those of the land plants. At the supratidal zones of the estuarine beach, the drifted remains are arranged in regular lines, and are gradually buried in a low lump of sand. A great majority of seedlings are confined to this type of tidal drifts. These results well accord with the description of SALISBURY (1952) on the colonization of the dune-face vegetation of England. He further denotes that the decaying organic debris have the significance to the seedlings and/or to the seeds in supplying nutrients and in increasing the water-retaining capacity of the soils.

On the other hand, the seedling count further indicated that the species composition is quite different from that of the buried seed population. The seeds of the inland plants, which takes the great majority of the buried seeds, appear to lose their viability under the present conditions. This fact may show the tolerance of the strand plant seeds to the sea water (YOSHII 1916 and MONTFORT and BRUNDRUP 1927).

These results of the field surveys demand further comparative researches concerning the tolerance of strand plant seeds to sea water, especially regarding their buoyancy, germination and viability, as they were summarized and indicated by CHAPMAN (1960). The factors delimiting the growth and the survival (LAING 1958) of the seedlings also deserve attention.

The successful colonization in Station 1 shows a marked contrast to the rather unsuccessful one at Station 0 in 1958. The difference was chiefly caused by the exceptionally high tide in 1958. It is to be fully realized that the development of these littoral vegetation depends on the environmental conditions maintaining for some years without severe disturbances. The vegetation of the earliest stages, therefore, are essentially migratory in nature, as it was pointed out by CRAMPTON (1912), TANSLEY (1939) and NOBUHARA (1962). Topographic differneces in the width of the bar may play an important role in determining the rate of colonization, since the sea water cast up by surfs at high tide is absorbed rapidly into the sand when it flows down the landward slope rather slowly. It also deserves attention that the succession begins restricted to the supratidal zone of the estuary beach. It is mainly due to the combined effects of the decrease of disturbing waves toward the estuary shore and the hydrochoric, estuarine dispersal of the migrating seeds.

4. *Interrelations between Elymus mollis and Carex Kobomugi*

A change of dominance from *Elymus mollis* to *Carex Kobomugi* was observed in the process of succession on the already established mobile dunes (Figure 7). It was indicated that the change is probably caused by the decrease in the influence of tidal floods which relate inversely to the incretment in the relative height of the dunes. After the visit of an exceptionally high tide, it is occasionally observed that *Carex Kobomugi* growing on the seaward slopes dies when flooded with the sea water, while *Elymus* seldom does.

On the sandy coasts of western Europe, a remarkably similar interrelation is well known between the more salt-tolerant *Agropyron junceum* and *Ammophila arenaria*, one of the commonest dune plants. It is frequently reported that *Agropyron* colonizes as the first pioneer onto the bare sands, and accumulates the sand to form lower foredunes in a few years, whereas *Ammophila* usually predominates the vegetation of the higher, main dunes (BENECKE and ARNOLD 1930–31 and TANSLEY 1939). In northern Europe, *Elymus arenarius*, which is close to *E. mollis* taxonomically (MIYABE 1891), is widely distributed. Like *E. mollis*, *E. arenarius* is highly salt-tolerant. From the study of LEMBERG (1933–35) in plant succession on the dunes in the sandy coasts of Finland, it is likely that the interrelation between *E. arenarius* and *Ammophila arenaria* is similar to the above-mentioned to a considerable extent.

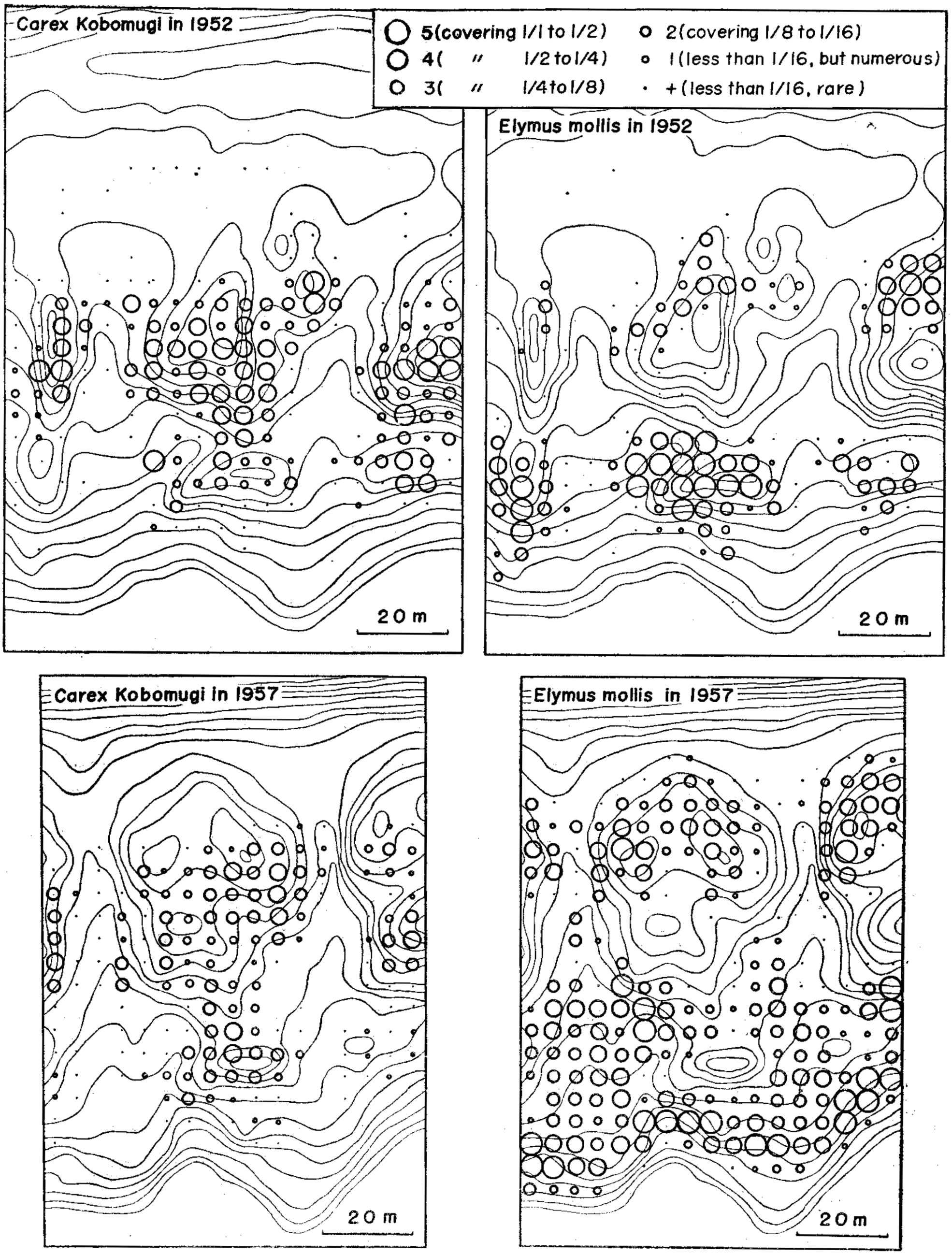

Figure 7. Maps illustrating the changes in the distribution of *Carex Kobomugi* and *Elymus mollis* in Station 3 during the period from 1952 to 1957. Sizes of circles on the maps indicate cover degrees estimated by the Hult-Sernander scale of the Uppsala School, as illustrated at the top right of the figure. In 1952, the channels among the dunes were almost devoid of vegetation. In both of the years, *Carex* occupies the tops and the backslopes of the main row dunes, while *Elymus* is mainly distributed on the seaward slopes and on the low-lying areas of the channels and the estuarine beaches. Neverthless, it is to be noted that the topographic changes during the years brought about a transition of dominance from *Elymus* to *Carex* on the areas of the seaward slopes and the inner row dunelets of 1952.

SUMMARY

1. The interrelated developments of vegetation and sand dune topography were studied on a sand bar at the seaward side of the tidal estuary of the Nanakita River, Miyagi Prefecture, North Honshu. It has a length of 2 km, a width less than 150 m, and supports a natural, meagre cover of vegetation which seldom develops beyond the unstable or semi-stable dune vegetation. Sand beaches fringe the outer as well as the estuary shorelines of the bar. The observations on the processes of beach formation revealed that the area under study shows a series of ages ranging from nine to about 24 years in 1957. The results of surveys made at various parts of the bar, including field observations in changes during five years at two stations, are so interrelated with each other that we can make a general picture of the developments.

2. Observations of the development of the topography show that, under favorable conditions, consolidated dunes with a height of less than one meter may be established within nine years after the emergence of a beach ridge. The height may reach to nearly 2 m during 24 years' development. The dunes are arranged in a row on the flat slope facing the estuary, and interpose among them wave channels in the form of shallow valleys, through which pass the tidal floods during storms.

3. Dispersion of seeds and distribution and ecesis of the seedlings were surveyed on a beach ridge, which was just born, and was practically devoid of vegetation. The results reveals that the seeds are mainly dispersed on the estuarine shore by high tides mingled with various organic remains which were chiefly derived from the land plants. A great majority of the seedlings is confined to drift lines on the estuarine shore. In spite of the disturbances of an exceptionally high tide in the summer, some seedlings of *Elymus mollis* were observed to establish themselves within a year.

4. Unless there occur severe disturbances of exceptionally high tides, numerous embryonic dunes are formed on the landward slope of the beach ridge, within five years after its emergence. In this stage, only *Carex Kobomugi* colonizes very sparsely on the area near the crest line, while *Elymus* forms larger dunes nearby the estuary. The zone intermediate between the two areas above-mentioned is densely dispersed by dunes induced by *Ixeris repens.*

5. Nine years after the emergence, these embryonic dunes had been consolidated into larger dunes, and the peculiar dune-and-channel pattern of the topography was brought about. The colonization of *Elymus* near the crest is likely to play an important role in protecting the embryonic dunes inhabited by *C. Kobomugi* and by *Ixeris* from the disturbances of waves for their growth and consolidation.

6. In a previous report of the present author, gradient analyses of the same vegetation were made along the two indices of environmental factors, namely, the

relative height of the dunes and the stability of the sand. These indices are both subjected to the influences of plant growths in these habitats. Therefore, the trends of further autogenic succession were inferred in this research from the behaviour of each species given along the increase of the indices. In the stages after the consolidation of the dunes, it was well illustrated that the inferred trends served as useful criteria or yardsticks in the interpretation of autogenic succession.

7. A change of dominance was observed from *Elymus* to *C. Kobomugi* in the process of succession on the mobile dunes. The change likely resulted from the decrease in frequencies of the temporal influence of the waves or the tidal floods, since it is largely related to the increment in the relative height of the dunes.

8. In areas increasingly protected by the advancing foredunes, the moblie dunes tend to be stabilized by the plant growths. The increase of the total vegetation cover of the dunes are accompanied by a remarkable change in floristic ccmposition, namely, a decrease in the relative importance of *C. Kobomugi*, as well as an increase of such dune plants as *Ischaemum anthephoroides*, *Calystegia Soldanella*, *Lathyrus maritimus* and *Linaria japonica*. The vegetational diversity also rises.

9. The results were integrated into a general scheme illustrating the development of a topography-vegetation system on the sand bar (Figure 7). Here, the main cause of the dune development lies in the influence of the vegetation upon the topography, while the trends of vegetational succession represented at each habitat are largely related to and determined by the topographic conditions. The interrelation between the vegetation and the dune topography on this sand bar should, therefore, be regarded as a system of mutual interactions. The gradients of topographic conditions across the bar, determined by the initial form of a beach ridge, act as the *state factor* of the ecosystem in delimiting the type and the rate of the above processes.

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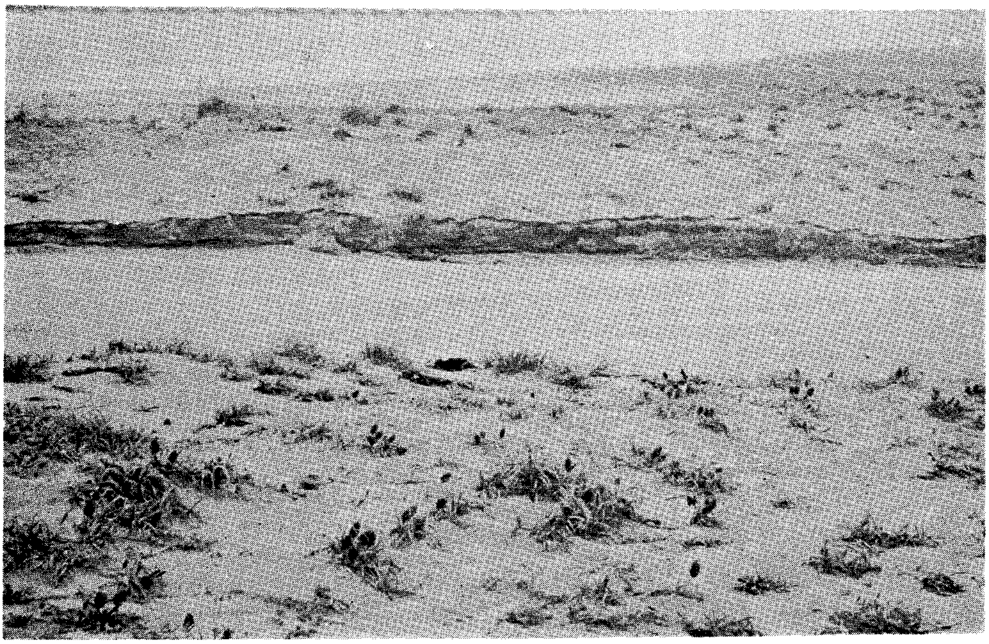
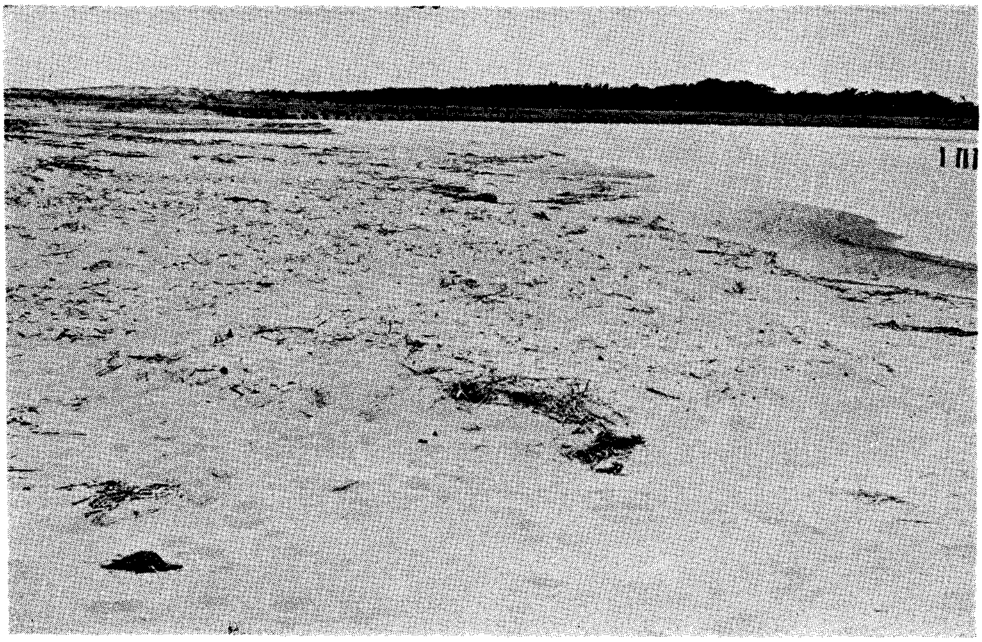
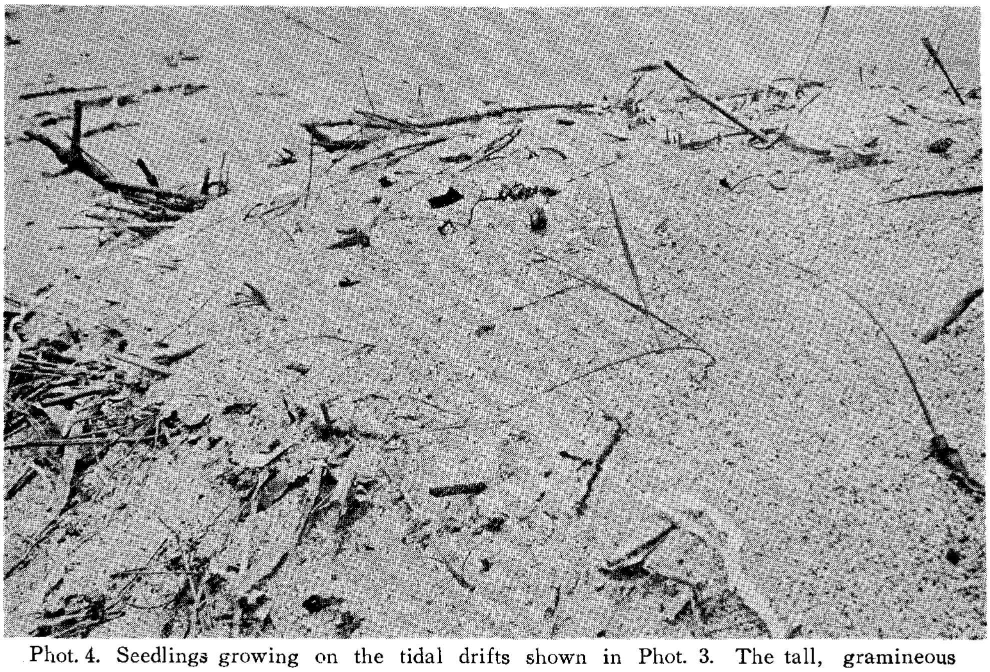


Phot. 1. Part of a channel after the storm caused by the 11th Typhoon of 1958, which struck the area on July 23rd. Low escarpments are cut off on the side of the channel by tides which flowed across the bar from the open sea (left) to the estuary (right).

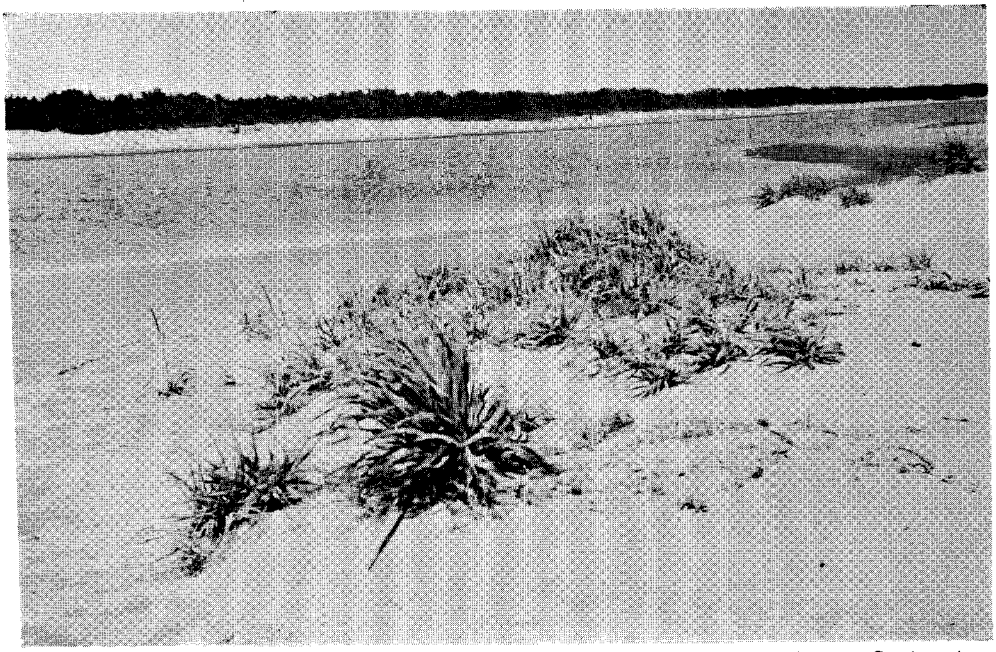
Phot. 2. Tidal drifts thrown up by surfs from the open sea. They are distributed irregularly in dots on the beach around the crest of the bar. Station 0, July 10th, 1958.



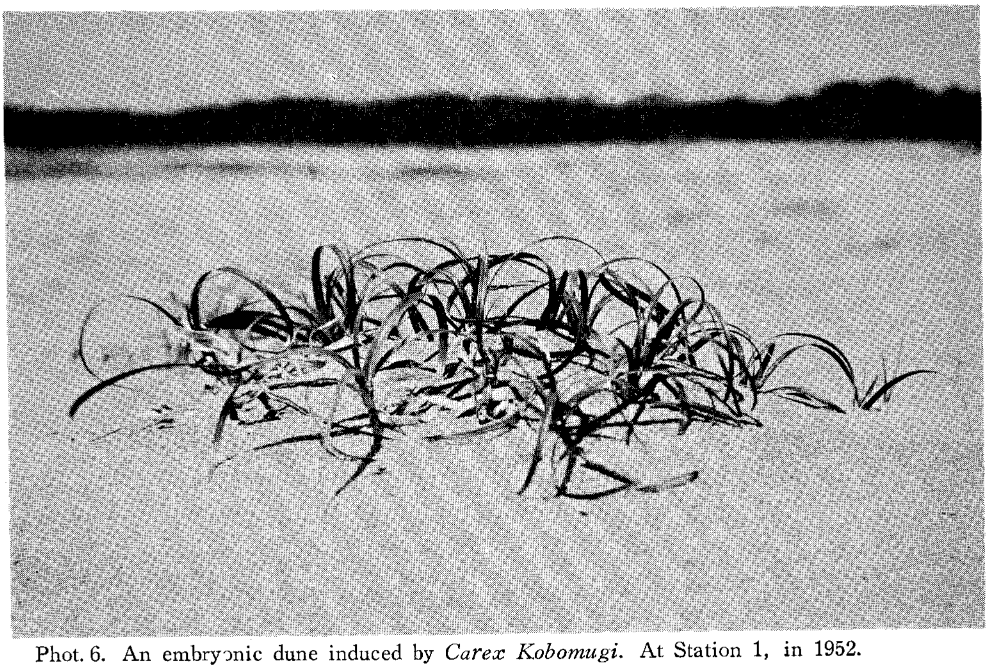
Phot. 3. Drift line at the estuarine shore of Station 0. July 10th, 1958. The difts are here arranged in wide and continuous belt lying parallel to the shore, and are buried under low heaps of sand.



Phot. 4. Seedlings growing on the tidal drifts shown in Phot. 3. The tall, gramineous seedlings, which are most numerous, are *Elymus mollis*. There also are seedlings of *Carex Kobomugi*, *Ixeris repens*, *Calystegia Soldanella* and *Salsola Komarovii*.



Phot. 5. Embryonic dunes induced by *Elymus mollis* on the estuarine beach near Station 1 in 1952.



Phot. 6. An embryonic dune induced by *Carex Kobomugi*. At Station 1, in 1952.