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Zonal plant distribution and edaphic and micrometeorological conditions on a coastal sand dune

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Some edaphic and meteorological conditions were examined to detect environmental gradients from shoreline to inland at the Kado-ori coast, Ibaraki, Japan, in 1989. Zonal distribution patterns of coastal dune plant species, including three ubiquitous perennials, *Calystegia soldanella, Carex kobomugi* and *Ischaemum anthephoroides*, were described in relation to the environmental gradients. Environmental gradients were found in water availability, evaporative demand and soil-water salinity. Water availability, evaluated by thickness of capillary water layer, increased from 10 cm at 20 m to 48 cm at 85 m from the shoreline, reflecting the percentage of fine sand. Evaporative demand, which was evaluated by the evaporation rate from a wet black filter paper, decreased with increasing distance from the shoreline. Soil-water salinity was lowest (15 mmol/L) at 85 m from the shoreline and highest (90 mmol/L) at 30 m. On the coast, *C. soldanella*, a salt-tolerant perennial, was distributed mainly in the environmentally harsh area 40–60 m from the shoreline. *Ischaemum anthephoroides* and *C. kobomugi*, less salt-tolerant perennials, occurred mainly 70–80 m from the shoreline, where environmental conditions were more hospitable.

Key words: coastal dune plants; evaporative demand; soil-water salinity; water availability; zonal plant distribution.

INTRODUCTION

One of the major goals of plant ecology is to understand the processes that generate patterns in natural communities. With such an intent, many reports have shown apparent zonal plant distribution in coastal dune regions (Cowles 1899a,b,c,d; Boyce 1954; Olson 1958; Nobuhara 1967; Kachi & Hirose 1979; Maruyama & Miura 1981; Miura & Maruyama 1983; Nakanishi & Fukumoto 1987). Thus, it has been suggested that the coastal dune region is one of the best habitats for studying the process by which zonal plant distributions are generated. A typical zonal plant distribution pattern on most Japanese coast is that *Calystegia soldanella* Roem. et. Schult. (Convolvulaceae) and *Carex kobomugi* Ohwi (Cyperaceae) are distributed in more seaward sites than *Ischaemum anthephoroides* (Steud.) Miq. (Gramineae; Ishizuka 1961; Kachi & Hirose 1979; Maruyama & Miura 1981; Miura & Maruyama 1983). Some previous reports have shown that the plant zonal distribution patterns can be correlated with gradients of certain edaphic variables, as well as salt spray (Boyce 1954; Barbour 1978) and sand movement (Nobuhara 1967). Of those edaphic variables that show gradients from the shoreline to the inland, soil-water salinity (Kachi & Hirose 1979; Maruyama & Miura 1981; Miura & Maruyama 1983) and soil-water content (Kachi & Hirose 1979; Maruyama & Miura 1981) are two that have been often cited. It has been shown that the soil-water content increased and the soil-water salinity decreased with increasing distance from the shoreline (Kachi & Hirose 1979; Maruyama & Miura 1981; Miura & Maruyama 1983). Thus, correlations between patterns of zonal plant distribution and the environmental gradients in Japanese coastal dune regions can be summarized as follows: *Calystegia soldanella* and *Carex kobomugi* are distributed in more seaward sites with harsher environmental conditions than *Ischaemum anthephoroides*.

The studies mentioned above tended to examine not only sites with coastal dune plants alone, but also

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hind-dune sites covered with many inland species, including pine trees. Thus, it remained unclear whether there were environmental gradients within a dune area where zonation of coastal dune plants existed. To clarify the mechanisms that generate zonal plant distribution patterns of coastal dune plants, it is necessary to clarify the existence of gradients of environmental conditions from the shoreline to the inland in an area covered with coastal dune plants only.

Soil-water content has been used as a water condition in most of the previous studies (Kachi & Hirose 1979; Maruyama & Miura 1981; Miura & Maruyama 1983). In a region with sandy soils, the amount of available water is likely to be limited because of the low capacity to reserve capillary water (Maruyama & Miura 1981; Park 1985). In addition, soil surface temperature and air temperature near the soil surface tend to rise markedly because of the low specific heat of sandy soils (Matsuda *et al.* 1977). These high temperature conditions can result in high evaporative demand of the air surrounding coastal dune plants. Under such circumstances the water condition of coastal sand dunes must be evaluated, taking into consideration capillary water in the sandy soils and the evaporative demand of the air near the soil surface.

Ishikawa *et al.* (1991) showed that the order of salt-tolerance is *Calystegia soldanella* > *Carex kobomugi* > *Ischaemum anthephoroides*. This order must be related to the actual status of soil-water salinity in the vegetation zones dominated by these three species. Variability of the soil-water salinity within a growth season in the field should be examined because, in most cases, soil-water salinity was measured only once in a certain year.

In this study, we describe some environmental conditions, including soil-water availability (evaluated using the thickness of the capillary water layer), evaporative demand and seasonal fluctuation of soil-water salinity, on a coastal dune in northeast Japan. The distribution patterns of three perennial plants, *Calystegia soldanella*, *Carex kobomugi* and *Ischaemum anthephoroides*, which are ubiquitous on coastal dunes in Japan, were also measured. Environmental conditions that show apparent gradients from the shoreline to the inland were identified on the basis of the data obtained. Finally, the relationship between environmental conditions and distribution patterns of the three coastal dune plants is discussed with respect to the salt tolerance of the plants (Ishikawa *et al.* 1991).

STUDY SITE

Edaphic and atmospheric conditions were measured at the Kado-ori coast (36°02′ N, 140°38′ E), 40 km south-southeast of Mito, Ibaraki Prefecture. This coast is situated on Kashima beach facing the Pacific Ocean and extends approximately 80 km from north to south.

The coastal area at the Kado-ori coast is composed of a low, flat, beach plain spreading some 60 m inland from the shore, with a dune 8 m in height lying parallel to the shoreline, fringing the inland edge of the beach plain (Fig. 1). The beach plain is covered with sparse vegetation, whereas the dune is covered with dense vegetation. Further inland, there is a pine plantation about 50 m wide.

General meteorological features of the study site were taken from 11 year records (1978–88) at the Kashima Meteorological Observatory (35°53′ N,

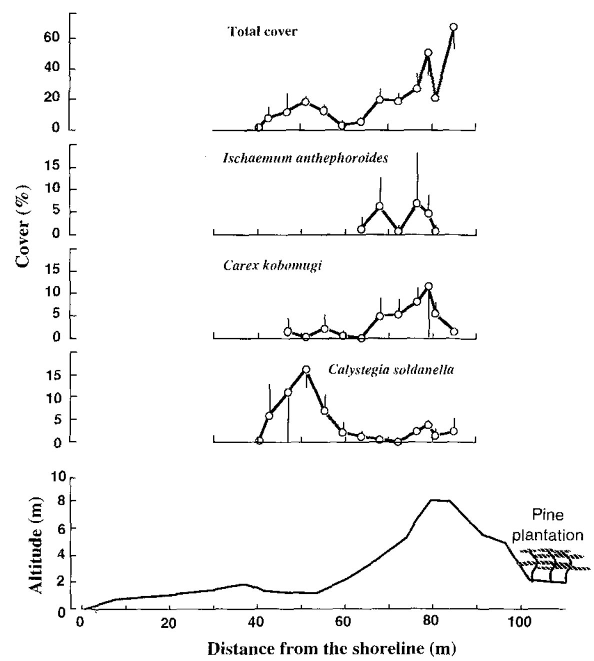

Fig. 1. Percent cover of total vegetation (upper) and each of the major three species at the Kado-ori coast as a function of distance from the shoreline. Topography of the study site is also shown in the lowest graph. The research was conducted on 12 July 1991. Vertical bars represent standard deviations ($n = 5$).

140°38′ E, and 37 m a.s.l.), 8 km south-southeast of the Kado-ori coast. Compared to the average values (1978–88) the meteorological conditions in 1989 and 1991, when most of the present study was conducted, were characterized by a warmer mean annual temperature (+1°C) and much higher annual precipitation (+700–900 mm; Table 1).

METHODS

Floristic data

A survey of the coastal dune vegetation was conducted on 12 July 1991. Investigation sites were selected along a transect running from the shoreline to the inland. At each site, five quadrats (0.5 m × 0.5 m) were arranged parallel to the shoreline at 2 m intervals. Photographs of these quadrats were taken and used for calculating percent coverage of each species.

Edaphic data

Investigations were made on 14 June, 9 and 13 August, 21 October, and 21 December 1989. The sand samples were collected at six depths: 0, 5, 10, 20, 40 and 60 cm. Soil-water content was determined by the weight difference between fresh and oven-dried (80°C for 7 days) sands. Soil-water salinity was measured using a sodium ion selective electrode (NA-115B, TOA Electric Co. Ltd, Tokyo, Japan) and a reference electrode (HS-305DS, TOA). The oven-dried sand was diluted with a buffer solution (ISA-NA, TOA) and Na^+ concentrations of the diluted buffer solution were measured by the electrodes. Actual NaCl concentration of soil-water in the field was calculated by adjusting the Na^+ concentration of the diluted buffer solution with the soil-water content. Total nitrogen content of the soil was measured by the Kjeldahl method. Particle size composition of the sand was estimated by sieving the sand collected on 21 December 1990. Water availability was evaluated by the thickness of the capillary water layer, because sandy soil has low capillary water-holding capacity. Thickness of the capillary water layer was estimated using a regression equation based on the data of Rode (1963). The regression equation used for the estimation was:

$$H = 8.89 \times X^{-0.93} \qquad (r^2 = 0.996) \quad (1)$$

where H and X are the thickness of capillary water layer in cm and the mean particle size in mm, respectively.

Evaporative demand

Evaporative demand was evaluated by measuring evaporation from sheets of black filter paper (Toyo Advan-tec., Tokyo, Japan; 9 cm diameter). Sheets of the filter paper were dipped into distilled water and placed either vertically, with the surface set parallel to the shoreline, or horizontally, at an average height of 5 cm from the soil surface.

Evaporation rates were calculated from the loss of

Table 1. Meteorological data obtained at the Kashima Meteorological Observatory (35°53′ N, 140°38′ E, 37 m a.s.l. and about 8 km south-southeast of the Kado-ori coast) in 1989 and 1991

	Month												
	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Annual
Precipitation (mm)													
Average	54	74	131	130	99	160	101	106	203	169	92	58	1260
1989	139	202	226	143	189	170	98	350	112	221	111	37	1998
1991	73	70	178	125	64	158	92	122	432	690	126	39	2169
Mean temperature (°C)													
Average	3.9	4.2	7.2	12.0	16.4	19.3	22.7	25.0	21.7	16.8	11.5	6.6	13.9
1989	6.9	6.3	8.3	14.1	16.0	18.6	22.5	25.3	23.7	16.3	13.0	7.5	14.9
1991	4.7	5.2	8.6	14.1	17.0	21.7	24.5	23.4	22.6	17.2	11.8	7.9	14.9
Duration of sunshine (h)													
Average	184.7	186.2	185.2	195.5	216.0	173.4	185.7	232.4	152.9	176.7	161.1	188.5	2025.9
1989	136.5	128.2	174.3	190.7	117.3	108.1	129.4	194.1	138.4	140.8	130.0	164.3	1752.1
1991	208.9	204.7	124.2	162.8	175.0	111.4	118.9	134.0	106.8	82.5	156.2	140.2	1531.2

Average values were calculated for 11 year records (from 1978 to 1988) at the Kashima Meteorological Observatory.

water from the filter paper during the 3 min exposure. These measurements were taken three times at each site. Air temperature 5 cm from the soil surface was measured simultaneously beside the sheets of the filter paper using a mercury thermometer (NO.1, Nihon Keiryo Inc., Tokyo, Japan). All measurements of evaporation rates were conducted during the period 13:30–14:30 h on a clear day (15 August 1991).

All statistical analyses were made using Super ANOVA (Abacus Concepts 1986) and Stat View II (Abacus Concepts 1986).

RESULTS

Vegetation

On the beach plain and on the dune at the Kado-ori coast, 12 species were found in the 12 July 1991 survey. Total vegetation cover increased with increasing distance from the shoreline (Fig. 1). *Ischaemum anthephoroides* was found only at sites 60–81 m from the shoreline. For *C. kobomugi*, percent cover increased with increasing distance from the shoreline, although it decreased at sites more than 81 m away. In contrast to these two species, percent cover of *C. soldanella* showed the highest value at 51 m, and then markedly decreased inland. In addition, patches of *Wedelia prostrata* were observed at sites 68 and 88 m from the shoreline, although this species was not found in the sample quadrats. *Elymus mollis* occurred only at sites between 40 and 50 m. The dune slopes from 80 m inland to the front of the pine forest were dominated by *Imperata cylindrica* var. *koenigii*. No plants were found in the area 0–40 m from the shoreline.

Edaphic data

Figure 2 shows variations of soil-water salinity, soil water content and soil total nitrogen content in relation to distance from the shoreline at the Kado-ori coast in 1989. Mean values of soil samples from 10 to 60 cm deep are shown because there was no marked difference among the soil depths. A typhoon had hit this coast on 6 August 1989. On each measurement day, NaCl concentrations at inland sites (60–85 m from the shore) were lower than 30 mmol/l even after the typhoon. In contrast to the inland sites, NaCl concentrations at sites within 60 m of the shoreline were higher than 30 mmol/l. At the site about 30 m from the shore, with no vegetation cover, NaCl concentrations always exceeded 70 mmol/l. On 9 and 13 August, NaCl concentrations exceeded 400 mmol/l, nearly the same as NaCl concentration of sea water (500 mmol/l), due to the typhoon. Although the soil-water content varied spatially and temporarily, ranging from 2 to 6%, there was no marked difference among the survey sites. Total nitrogen content of the soil also varied spatially and temporarily, ranging from 50 to 140 ppm, but was independent of the distance from the shoreline.

As shown in Fig. 3, the percentage of fine sand increased with increasing distance from the shoreline, whereas it was not affected significantly by soil depth (see also Table 2).

Figure 4 shows the percent composition of soil particles divided into four size classes. The percentage of fine sand increased with increasing distance from the shoreline (from 7% at 17 m to 91% at 85 m), whereas the percentage of coarse sand and gravel decreased.

The results of ANOVA of the effect of distance from the shoreline and soil depth on thickness of the capillary water layer is shown in Table 3. Thicknesses of the capillary water layer were significantly different ($P < 0.001$) among distances from the shoreline, but were not different among soil depths.

The mean thickness of the capillary water layer, calculated for soil samples of 10–60 cm deep, in relation to distance from the shoreline is shown in Fig. 5. The mean value increased with increasing distance from the shoreline, showing the highest value of 48 cm at 85 m, and the lowest value of 10 cm at 25.5 m.

Evaporative demand

Figure 6 shows the rates of evaporation from sheets of black filter paper and air temperature at the Kado-ori coast on 15 August 1991. Evaporation rates from both horizontally and vertically placed filter papers at sites 26 and 43 m distant from the shoreline were higher than those at sites at 68 and 85 m. Air temperatures at seaward sites were higher than those at inland sites by 3°C.

Table 4 shows the result of ANOVA of the effect of distance from the shoreline and orientation of filter paper on evaporation. The effects of distance from

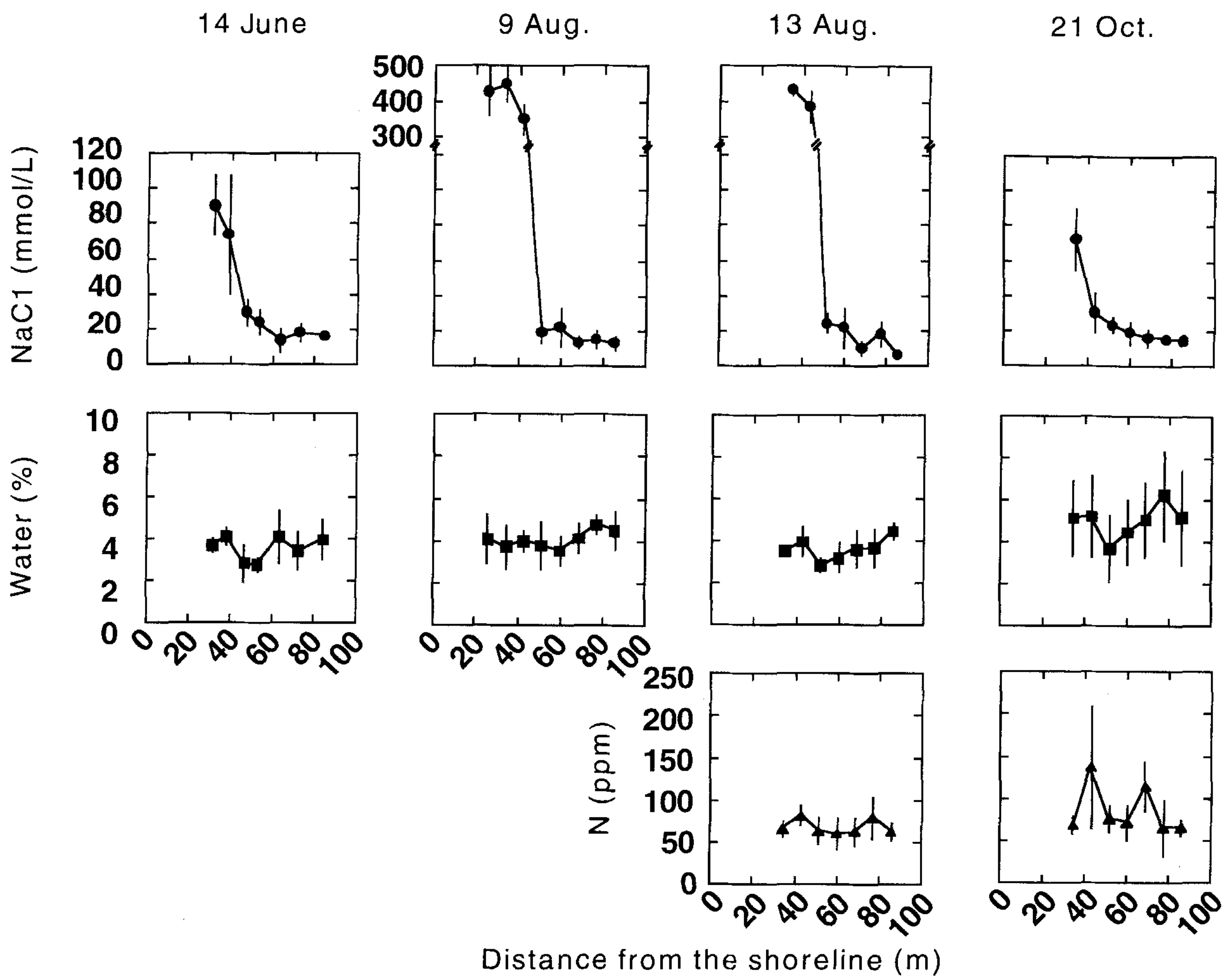

Fig. 2. Edaphic data of sands at Kado-ori coast as a function of the distance from the shoreline measured on various days in 1989. Values of soil-water salinity (NaCl, upper), soil water content (water, middle) and total soil nitrogen content (N, lower) were mean values of sands sampled from 10, 20, 40 and 60 cm depths. Vertical bars represent standard deviations ($n = 4$).

the shoreline, orientation and their interaction are statistically significant ($P < 0.001$, $P < 0.05$ and $P < 0.05$, respectively).

DISCUSSION

Environmental gradients

We have found clear environmental gradients from the shoreline to the inland at the Kado-ori coast. Water availability increased, and midday air temperature, evaporative demand and soil-water salinity decreased with increasing distance from the shoreline. These data suggest that growth conditions become more hospitable with increasing distance from the shoreline.

Although soil water content did not differ significantly among different distances from the shoreline, water availability significantly increased with increasing distance from the shoreline. This was caused by an increasing proportion of fine sand at inland sites beyond 60 m. Maruyama and Miura (1981) suggested that such a gradient of soil particle composition was caused by a prevailing seaward wind. However, the present results suggest that the topography of the dune system may also influence the soil particle composition, because the percentage of fine sand increased markedly at the seaward slope of the ridge beyond 60 m.

It is presumed that the higher evaporative demand at beach plain sites (26 and 43 m) was caused mainly by higher air temperatures, which could be attributed to the lower percentage of total vegetation cover.

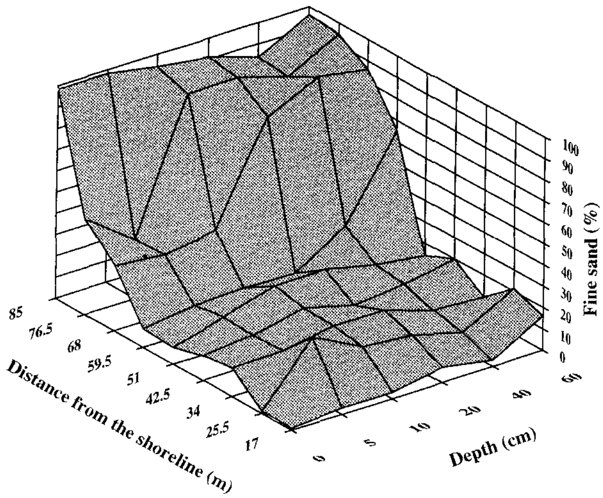

Fig. 3. Percent of fine sand of the soil as a function of the distance from the shoreline and soil depth. Soil samples were collected on 21 December 1989.

Table 2. Results of ANOVA on the effects of distance from the seashore and depth on percent of the fine sand

Source	d.f.	SS	MS	F	P
Distance from the seashore	8	21 781	2723	13.7	0.0001
Depth	5	568	114	0.6	0.7215
Interaction	1	821	821	4.1	0.049
Residual	39	7 776	200		

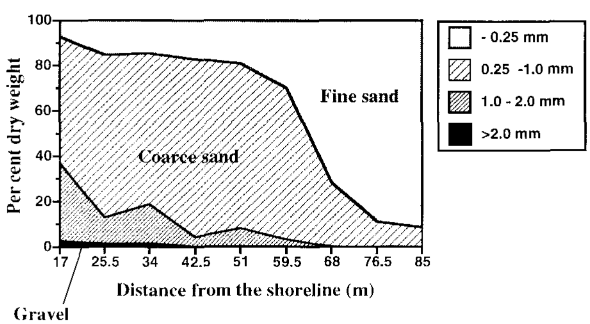

Fig. 4. Soil particle composition as a function of the distance from the shoreline. Values are means of soil sampled from 0 to 60 cm in depth on 21 December 1989 (n = 6).

Sodium chloride concentrations in the soil at the Kado-ori coast, which ranged from 20 to 90 mmol/L, were comparable to those reported for other Japanese coastal dunes. Kachi and Hirose (1979) and Maruyama and Miura (1981) showed that NaCl concentrations in coastal sands were about 50–85 mmol/L at seaward sites and 6–17 mmol/L at inland sites. Thus, it can be assumed that NaCl concentrations in the sands of Japanese coastal dunes generally fall into a range from 10 to 100 mmol/L, unless there is an extreme event such as a typhoon. It is notable that this range of soil-water salinity is enough to reduce growth rates in many plants (see review by Long & Baker 1987), including some dune plants (Ishikawa *et al.* 1991).

Table 3. Results of ANOVA on the effects of distance from the seashore and depth on thickness of capillary water layer

Source	d.f.	SS	MS	F	P
Distance from the seashore	8	3760	470	15.5	0.0001
Depth	5	91	18	0.6	0.7000
Interaction	1	149	149	4.9	0.0324
Residual	39	1178	30		

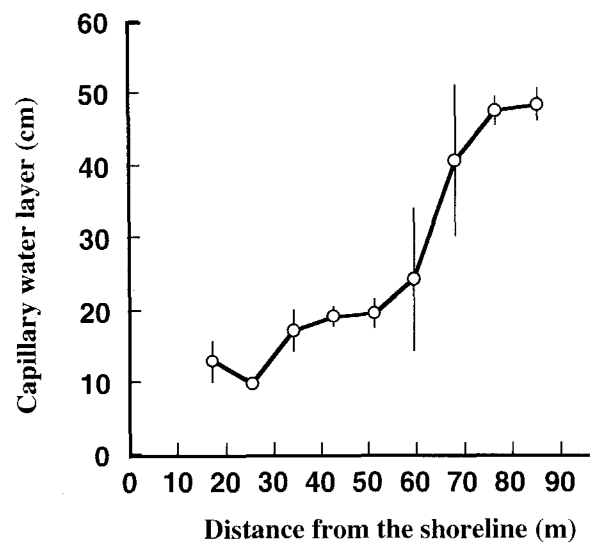

Fig. 5. Mean thickness of the capillary water layer of soil sampled on 21 December 1989 as a function of distance from the shoreline. These values were calculated from equation 1. Sands were sampled from 10 to 60 cm depth. Vertical bars represent standard deviations (n = 4).

Relationships between environmental gradients and plant zonation

The zonal distribution pattern of the three species at the Kado-ori coast was consistent with the general

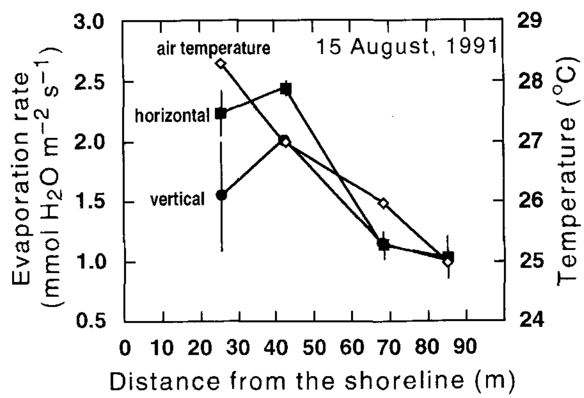

Fig. 6. Evaporation rates of horizontally (■) and vertically (●) placed black filter papers and air temperature (◇) 5 cm above the soil surface as a function of the distance from the shoreline. Measurements were conducted during a clear period of 13:30–14:30 h on 15 August 1991. Vertical bars represent standard deviations (n = 3 for evaporation rates; n = 1 for air temperature).

Table 4. Results of ANOVA on the effects of distance from the seashore and placement orientation on evaporation

Source	d.f.	SS	MS	*F*	*P*
Distance from the seashore	3	7.2	2.4	85.7	0.0001
Placement orientation	1	0.2	0.2	5.3	0.0366
Interaction	3	0.4	0.2	5.3	0.0116
Residual	14	0.4	0.03		

pattern in Japan (Kachi & Hirose 1979; Maruyama & Miura 1981; Miura & Maruyama 1983; Nakanishi & Fukumoto 1987). That is, *I. anthephoroides* was distributed at sites on the dune slope, whereas *C. soldanella* was distributed mainly on the beach plain. *Carex kobomugi* showed a general tendency towards distribution between the *C. soldanella* and *I. anthephoroides* zones. These distribution patterns can be related to the environmental gradients found in this study. That is, the beach plain sites where *C. soldanella* dominated had higher soil-water salinity, lower water availability and higher evaporative demand than the dune slope sites where *I. anthephoroides* dominated. *Carex kobomugi* dominated sites with intermediate environmental conditions. Such a correlation has also been reported for other Japanese coastal dune areas (Kachi & Hirose 1979; Maruyama & Miura 1981; Miura & Maruyama 1983).

Ecophysiological mechanisms for the distribution patterns of these three coastal dune plants have been already analyzed with respect to the salt-tolerance of the three plants. Ishikawa *et al.* (1991) reported that the reduction of relative growth rate by 100 mmol/l NaCl was 22% in *I. anthephoroides*, 18% in *C. kobomugi* and 5% in *C. soldanella.* Soil-water salinity of 100 mmol/l is almost similar to that at the seaward edge of the vegetation at the Kado-ori coast. Such species-specific differences in salt-tolerance must be one of the causes for the zonal plant distribution in coastal dune regions. Such a contribution of salt tolerance to the distribution pattern has also been suggested by laboratory and field experiments in salt marsh plant communities (Schat 1984; Snow & Vince 1984; Davy & Smith 1985; Bertness & Ellison 1987; Bertness 1988, 1991a,b; Pennings & Callaway 1992). These experiments in salt marsh plant communities clearly showed that salt tolerance was the most powerful determinant for generating zonal distributions of marsh plants in high-salinity environments.

The reason why *C. soldanella*, the most salt-tolerant among the three species, cannot dominate at inland hospitable sites such as the dune slopes is, however, still unclear. This must be studied more intensively, taking into consideration the effect of interspecific competition on zonal distribution. Some recent works on salt marsh plant communities (Snow & Vince 1984; Davy & Smith 1985; Bertness & Ellison 1987; Bertness 1988, 1991a,b) had suggested that the upper limits of distribution of the marsh plants are set by interspecific competition in relatively low-stress environments. Thus, it can be assumed that the distribution of *C. soldanella* at the inland hospitable sites is limited by competition with other superior competitors like *Carex kobomugi* and *Imperata cylindrica.*

The zonal plant distribution pattern of coastal dune plants should also be studied from the viewpoint of drought tolerance as gradients of soil-water availability and evaporative demand were found in this study.

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