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## WATER AND SALINITY RELATIONS OF CALIFORNIAN BEACH SPECIES

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### SUMMARY

(1) Plant and soil-water variables were monitored at monthly intervals for a year on two Californian beaches.

(2) Plant xylem-sap tensions were greater in plants at the warmer, drier, southern California site than in plants at the cooler, wetter, northern California site, but did not approach levels typical of extreme xerophytes. The species *Atriplex leucophylla* (Moq.) D. Dietr. and *Cakile maritima* Scop. had the greatest seasonal changes in dawn xylem-sap tension, whilst *Abronia maritima* Nutt. ex Wats. and *Ambrosia chamissonis* Less. had low dawn xylem-sap tensions throughout the year.

(3) Measurements of soil-water concentration and soil-water potential showed that the sand at 100 cm depth remained relatively moist throughout the year, but during rainless periods it dried out at shallower depths. The soil water-table depth varied little throughout the year and the salinity of water below it was always less than 3% that of seawater. The concentration of salt in sand generally decreased inland from the ocean. Calculated soil osmotic potential was between 0 and –10 bar at 100 cm depth, but substantially less at shallower depths.

(4) Evidence is presented to explain the source of water available to beach plants during extended rainless periods. Field phenology and growth patterns are discussed in relation to the seasonal course of water relations and temperature.

### INTRODUCTION

The water and salinity relations of coastal beach and dune vegetation have been the subject of study and speculation for many years. Beach plants have often been classified as xerophytes on the basis of their morphology (Kearney 1904; Harshberger 1908; Oosting 1954; Chapman 1976), but Martin & Clements (1939) and Zohary & Fahn (1952) have shown that their transpiration rates are higher and their cell-sap concentrations are lower than those of desert xerophytes. Chapman (1976) also classified beach plants as halophytes, but Kearney (1904) questioned whether beach plants were halophytes because of the low salt content of the beach sand he obtained from several coasts.

The source of soil water in beaches is also uncertain. The water-holding capacity of typical beach and dune sand ranges from 1.5 to 6.0% on a dry mass basis (Salisbury 1952; Oosting 1954; Ranwell 1972; Van der Valk 1974). On the basis of transpiration rates, leaf area and root volume, Salisbury (1952) calculated that the amount of moisture

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stored in dune sand could supply enough water to sustain plant growth for only 4–5 days. Nevertheless, plants on maritime beaches and dunes continue to grow through rainless periods for several weeks, and beach sand is usually quite moist within a few decimetres of the surface. Several possibilities have been considered in attempts to explain the source of this water. Kerner in 1865 (as cited in Olsson-Seffer (1909a)) thought it might move up through the sand by capillarity. Olsson-Seffer (1909b) and Willis *et al.* (1959) proposed that ‘internal dew formation’ takes place along a temperature gradient in the sand as water vapour moves up from below. Salisbury (1952) proposed that internal dew formation occurs from atmospheric water vapour. There is little evidence to support any of these hypotheses.

The purpose of this research is to describe the seasonal patterns of water and salinity relations of selected beach species on the Pacific coast of California, and to elucidate the sources of water available to plants in this zone during rainless periods. For this purpose, two study sites were selected; a cooler, relatively wet site on the northern coast of California and a warmer, drier site on the southern coast.

### THE STUDY SITES

The northern site is near the Bodega Marine Laboratory of the University of California (latitude 38°20'N, longitude 123°04'W), on a long narrow beach facing north-west and subject to almost continuous direct wind and wave activity from the north-west. The beach slopes up gently for approximately 30 m and then gives way to a steep, 3–5-m high, uninterrupted foredune. The steep foredune is primarily stabilized by an introduced species, *Ammophila arenaria* (L.) Link. On the vegetated part of the beach at the base of the foredune—the primary zone of research in this study—four taxa provide a sparse cover. Three species, *Abronia latifolia* Eschs., *Ambrosia chamissonis* Less. and *Atriplex leucophylla* (Moq.) D. Dietr., are native perennials, and the fourth, *Cakile maritima* Scop., is an introduced annual.

The southern site is on Trancas Beach near Malibu, California (latitude 34°02'N, longitude 118°51'W). The long axis of this beach runs east–west, and the predominately onshore wind and waves come at an angle from the south-west. In contrast to the northern site, the vegetated portion of this beach is nearly level, and the foredune consists of relatively low aggregated hummocks formed by beach species. The beach and foredune hummocks at this site are dominated by *Abronia maritima* Nutt. ex Wats., *Ambrosia chamissonis*, *Atriplex leucophylla* and *Cakile maritima*\*

### METHODS

Each site was visited for a minimum of 1 day a month for 12 consecutive months from January 1975 to January 1976. On each visit, plant xylem-sap tensions were measured at dawn, midday and dusk with a pressure bomb (Scholander *et al.* 1965). At each time, a minimum of three determinations was made per species sampled.

At dawn and dusk of each visit, sand samples of 150–200 g were taken at each of two locations within the hummocks on the vegetated part of the beach. At each location duplicate samples were taken with a sand auger from 10, 30 and 100 cm depth, for a total of eight samples per depth on each sampling day. The samples were sealed in soil cans and transported to the laboratory, where water content was determined gravi-

\* For convenience, species are referred to in many subsequent places by their generic name only.

metrically. The concentration of salt in the sand was determined. A 50-g aliquot of oven-dry sand was placed in a rubber-stoppered 125-ml Erlenmeyer flask and 25 ml of distilled water added. The flask was shaken for 0.5 h on a mechanical shaker, allowed to stand for a minimum of 24 h, and shaken again. After the second shaking the particulate material was allowed to settle, and the clear solution was decanted into an electrical conductivity cell. The factor 0.64 was used to convert conductivity ( $\mu\text{S cm}^{-1}$ ) at 20 °C to 'salt' or 'salinity' in  $\mu\text{g g}^{-1}$ . During the last 8 months of the field study, additional sand samples were taken at a depth of 30 cm near the leading edge of the vegetation, and also well up on the foredune, to determine if a salinity gradient existed across the beach.

Seasonal changes in water-table level and salinity were determined with miniature wells. A 2.5-cm-diameter steel tube, perforated with small holes near a plugged end, was driven into the sand to some depth below the water table. Each month, water-table depth was measured and water samples were taken to the laboratory where electrical conductivity was measured.

Soil, air and leaf temperatures were measured at 0.5-h intervals throughout the daylight hours with thermistors and a 12-channel Wheatstone Bridge recorder. Soil temperatures were measured at the surface, and at 10, 30 and 100 cm depth. Air temperatures were measured at 10 cm above the sand surface with a thermistor that was shielded from direct and vertically reflected radiation. Temperatures of one or two leaves of each species were measured with 0.61-mm-diameter tissue-implantation thermistors, which were imbedded in the mesophyll and left in position throughout each sampling day.

Rainfall records were obtained from the Bodega Marine Laboratory on the north coast, about 0.5 km from the study site, and from the Zuma Canyon Patrol Station (station 450, Los Angeles County Flood Control District) in the south, about 2 km from the study site.

During the latter part of the study, several additional variables were measured. In April 1975, two Wescor PT-51 soil psychrometers were installed at 10, 30 and 100 cm depth at each site within an *Atriplex leucophylla* hummock. Readings were taken during the early morning and late afternoon of each sampling day.

In June 1975, an experiment was set up to determine the source of sand moisture during the rainless summer period at the northern site. Two 100 × 100 × 60 cm holes were dug within the pioneer zone of the beach vegetation at the base of the foredune. In one hole, the bottom and sides, up to within 10 cm of the surface, were lined with a large sheet of plastic (0.13 mm thick) to prevent horizontal and vertical movement of water. The other hole was a control. Both were refilled with sand. Neither 'hole' had plants growing in it at the start of the experiment, though there was nothing in the control to prevent lateral roots growing into it during the experiment. Two Wescor PT-51 soil psychrometers were placed at the same depth (50 cm) in each hole before it was refilled with sand. Monthly measurements of soil-water potential were made from July to December 1975. This experiment was repeated, with duplicates, at the northern site in the summer of 1976.

A mechanical analysis of sand size-distribution at each site was made using standard soil sieves and a mechanical shaker. Sand samples were taken at 10, 30 and 100 cm depth during February 1975, and mean sand size-distributions were calculated for each site.

Field notes on germination, growth and phenology were made throughout the year. Photographs of a specific section of each site were taken on each visit and later compared, to ascertain periods of maximum vegetative and reproductive activity. Seedlings of each species were noted as they appeared and marked for identification on subsequent visits.

Specific seedlings of *Cakile* and *Atriplex* were also photographed regularly throughout their initial establishment period.

## RESULTS

### *Rainfall*

The mean annual precipitation at the northern site for 1968–75 was 82.3 cm. At the southern site it was 39.2 cm for 1965–75. Figure 1 shows the summer-dry, winter-wet precipitation pattern for both sites during 1975.

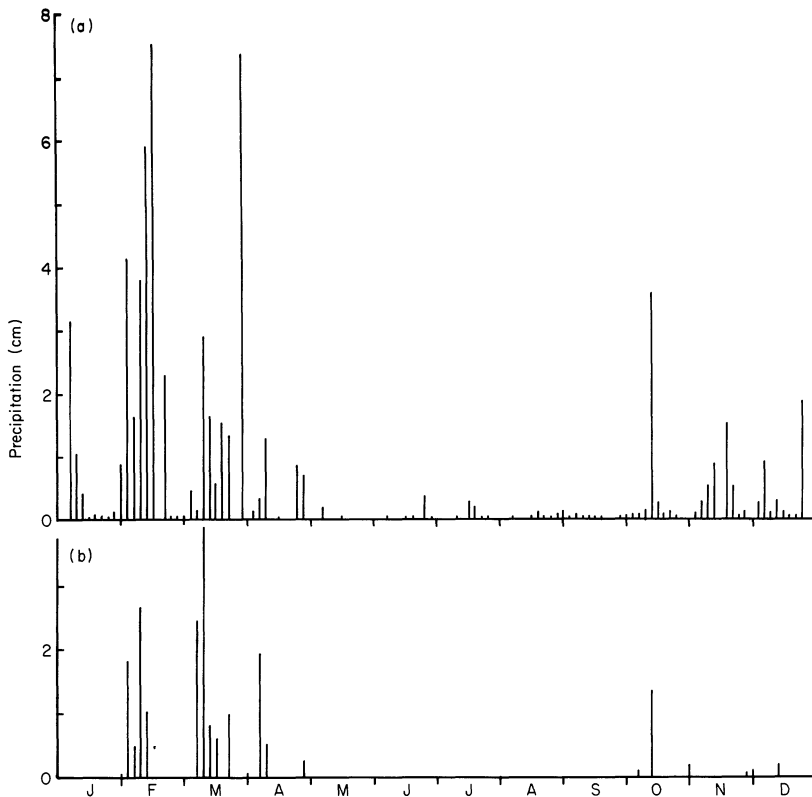


FIG. 1. Precipitation in 3-day periods during 1975 at the study sites on the Californian coast. (a) Northern site, (b) southern site.

### *Temperature*

The results of the leaf and air temperature measurements are summarized in Table 1. The mean temperature during daylight is calculated from measurements at 0.5-h intervals throughout the 3 sampling days in a given season. The mean of the six highest such measurements for each sampling day were also averaged over each season to give the mean 'maximum' temperature, also shown in Table 1.

At the northern site, leaf temperatures were generally 1–2 °C higher than air temperature at 10 cm above the sand surface, but at the southern site there was no consistent

TABLE 1. Seasonal mean air and leaf temperatures (°C) at the two sites on the Californian coast: (a) during daylight, (b) 'maximum' (= six highest instantaneous measurements in a day); asterisks indicate means calculated with incomplete data

	Winter		Spring		Summer		Autumn	
	Mean daylight	Mean max.	Mean daylight	Mean max.	Mean daylight	Mean max.	Mean daylight	Mean max.
Bodega (northern site)								
Air (10 cm)	9.9	12.3	12.0	14.2	15.0	17.7	13.2	14.9
<i>Abronia latifolia</i>	10.6	13.9	13.4	16.8	17.7	23.1	13.2	17.4
<i>Ambrosia chamissonis</i>	10.7*	13.3*	14.3	18.0	16.7	20.7	13.7	17.6
<i>Cakile maritima</i>	11.2	14.5	13.8	17.2	16.9	20.9	14.4	18.5
<i>Atriplex leucophylla</i>	11.4	15.1	15.5	18.7	16.3	19.7	14.5	17.9
Trancas (southern site)								
Air (10 cm)	14.1	17.0	15.8	19.2	21.1	25.1	18.0	21.0
<i>Abronia maritima</i>	14.2	18.5	15.1	19.1	22.7	28.1	18.1	21.7
<i>Ambrosia chamissonis</i>	13.7	16.8	15.6	20.7	21.5	25.7	17.9	20.7
<i>Cakile maritima</i>	13.4*	16.4*	16.6	20.5	23.0	28.8	—	—
<i>Atriplex leucophylla</i>	13.5	16.0	15.4	18.8	20.9	24.4	18.2	21.0

difference, and leaf temperature was often slightly below air temperature. This may be a result of the more upright habit of the southern plants when compared with the northern plants. The northern site was always cooler than the southern one, the difference in daylight temperature regimes being most pronounced in the summer months. Some of the differences in leaf temperature between species at a given site may be due to slight differences in microclimate, leaf orientation or leaf succulence. Some of the leaves were as much as 2 m apart, and orientated with slightly different exposures to wind and solar radiation. At the southern site, the succulent, entire-leaved *Abronia* had higher leaf temperatures than the dissected, succulent-leaved *Cakile* or the less succulent-leaved *Ambrosia* or *Atriplex*. In general, the temperature regime at both sites is cool and exhibits very little seasonal variation.

Figure 2 shows the range of temperature measured at various levels in the soil during the daylight hours on each sample day. On a daily basis, temperature in the upper layers of the sand fluctuated greatly, but at the 100 cm depth remained relatively constant due to the low thermal conductivity of sand. There was, however, a detectable seasonal change in temperature at 100 cm depth.

Temperature in the upper 30 cm tended to be lower than temperature at 100 cm in the early-morning hours and during the second half of the year, when temperature changes at depth lag behind surface temperature changes.

#### *Sand texture*

As shown in Table 2, the sand particle-size distribution at the sites differs chiefly in that the southern site has an average of 20% more in the 0.5–1.0-mm fraction and 17% less in the next smaller fraction. The ranges are given to indicate variations in size distribution at different depths.

#### *Phenology and growth*

At the southern site plants of all four taxa made most growth in the winter and spring. Although plants of *Ambrosia* and *Cakile* began to turn yellow and lose leaves in the summer and autumn, those of *Atriplex* and *Abronia* made a moderate amount of growth

*Water relations of beach plants*

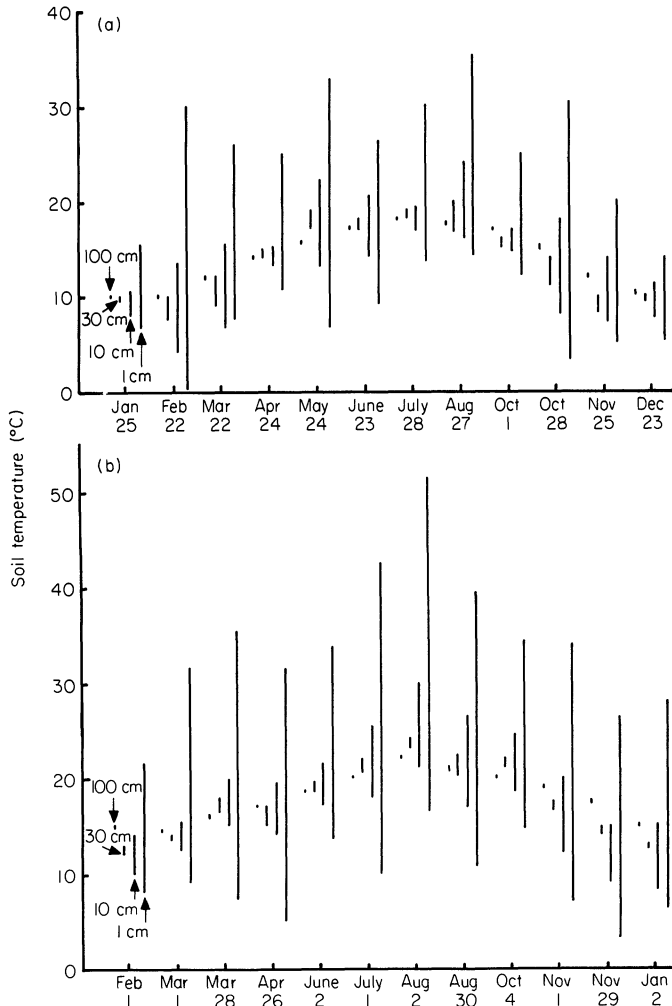


FIG. 2. Range of soil temperature at four depths at the study sites on the sample days indicated in 1975. (2 January at the southern site is the only sample day in 1976.) (a) Northern site, (b) southern site.

TABLE 2. Particle-size distribution (% mass) of sand from the two study sites of the Californian coast; the results are averaged from four samples at each of three depths (10, 30 and 100 cm)

	Particle-size categories (mm)				
	> 1.00	0.50-1.00	0.25-0.50	0.10-0.25	< 0.10
<b>Bodega (northern)</b>					
Mean	0.7	5.6	79.8	13.5	0.3
Range	0.3-1.7	3.4-10.0	76.4-81.9	11.5-14.8	0.1-0.4
<b>Trancas (southern)</b>					
Mean	1.1	25.4	62.0	11.2	0.3
Range	0.6-1.9	12.9-38.4	52.7-73.8	6.8-14.3	0.3-0.3

during this period. The periods of maximum flower and seed formation in all species occurred in late spring and summer, but flowers or seeds of both were present in some stage of development throughout the year on plants of *Abronia*, *Atriplex* and *Cakile*.

At the northern site most of the growth of all four species occurred in spring and summer. All species flowered in late spring, summer and early autumn, but flowers were present on some *Cakile* plants throughout the year.

At both sites, but particularly at the southern site, some plants of *Cakile* died in the late summer and autumn, while others survived and continued to flower throughout the winter. Continued observation of *Cakile* at both sites indicates that it is a facultative annual and can survive for more than 1 year if conditions are favourable, as Barbour (1970) has suggested.

At the southern site, plants of all four taxa germinated after the late autumn and winter rains, whereas at the northern site *Cakile* was the only species observed to germinate before spring. Seedlings of *Cakile* and *Atriplex* were numerous at both sites, but *Ambrosia* and *Abronia* seedlings were rare. At the southern site, most plants of *Cakile* died before the autumn but several newly-established plants of *Atriplex* survived into the following year. At the northern site fewer seedlings of either *Atriplex* or *Cakile* became established, but several of each survived and carried on into the following year. In the south all seedlings of *Ambrosia* and *Abronia* that were noted died before summer, while in the north seedlings of *Abronia* did survive and become established. Observations in subsequent years at the southern site suggest that *Ambrosia* and *Abronia* can only become established at this site in years when there are late spring and early summer rains.

#### *Soil moisture and water potential*

Figure 3 shows the seasonal changes in soil moisture determined gravimetrically for the northern and southern sites. The annual fluctuation of soil moisture appears to be greater at the finer-textured northern site, but this is partly caused by a few samples taken immediately following tidal inundation and rain (March 22 and April 24), during which time the sand was probably above field capacity. At 10 cm, the concentration of soil water was least during the rainless summer period. The soil water concentration at greater depths was consistently greater than at 10 cm, but generally remained below 4% during the summer months.

The seasonal course of soil-water potential measured with soil psychrometers at each site during the latter part of the study period is shown in Fig. 4. Water potential is higher at greater depth and only slight seasonal changes occur there. At both sites very low water potential at 10 cm ( $-30$  to  $-85$  bar) contrasts with soil-water potential seldom less than  $-15$  bar at 30 and 100 cm.

Table 3 shows the mean and range of salt concentration (by mass) in sand of samples from both beaches during the last 8 months of the field studies. Salinity varied greatly from month to month throughout the year, particularly at the front and back stations. At the leading edge of the vegetation, mean salinity was generally higher than just a few metres inland in the main hummocks of the pioneering species. However, the mean salinity on the face of the steep foredune at the northern site was higher than that slightly more seaward. Perhaps the steep foredune intercepts more salt spray than the lower areas on the gently sloping portion of the beach, whereas the leading edge of vegetation is covered more frequently by the sea.

Assuming that all the salt contained in a given sand sample is dissolved, the salt concentration in the soil water can be calculated and converted to osmotic potential by comparison with sea-water values. Figure 5 shows the seasonal variation in calculated soil-osmotic potential at the northern and southern sites. Calculated soil-osmotic potential at 30 cm is generally much more variable than at 100 cm, both seasonally and within given sample days. At the northern site, the calculated osmotic potential at 100 cm has a



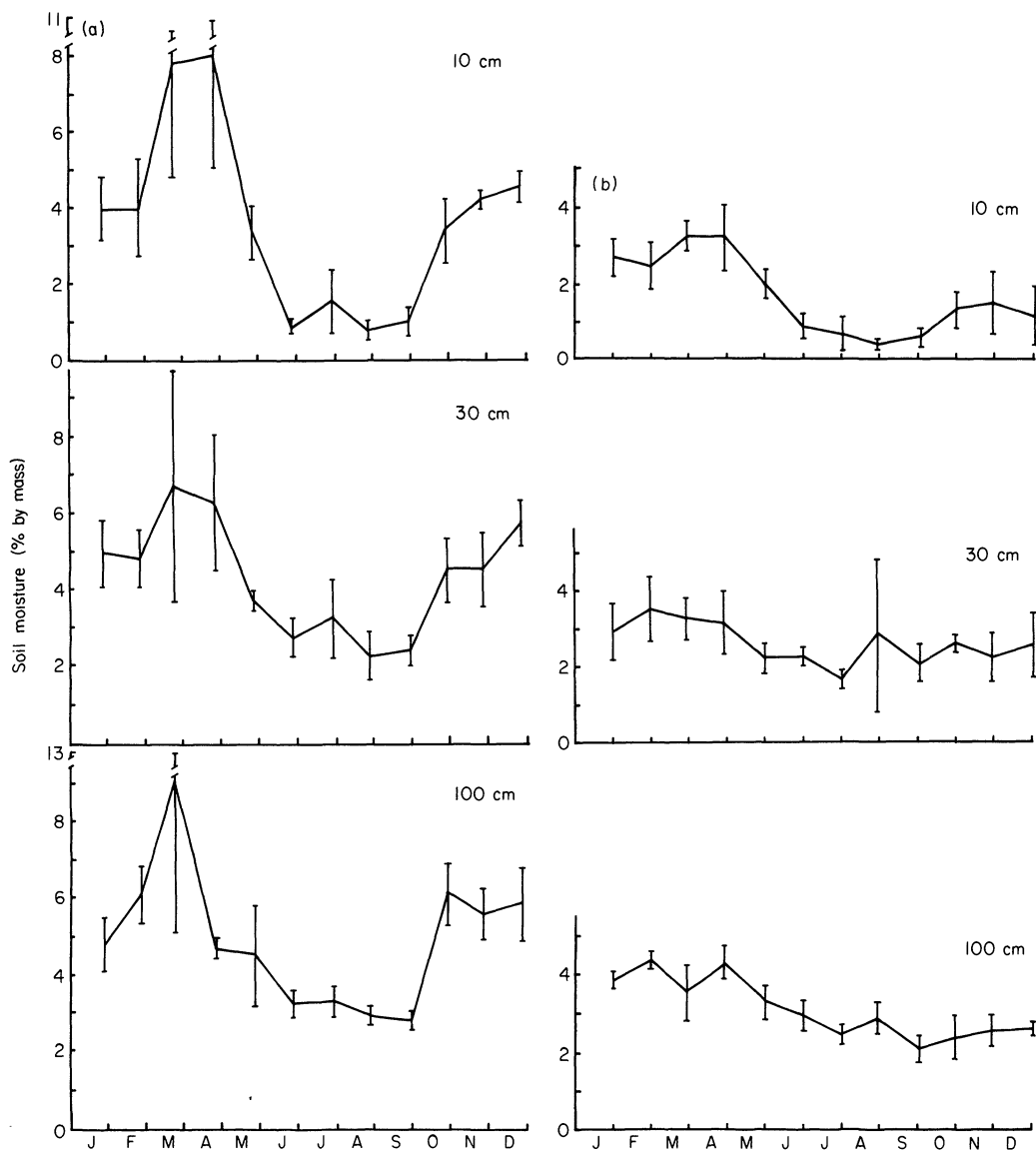


FIG. 3. Soil moisture at three depths at the study sites in 1975. Vertical bars indicate  $\pm 1$  SD,  $n = 8$ . (a) Northern site, (b) southern site.

TABLE 3. Salt concentration (% mass) in dry sand at a depth of 30 cm at four locations in each study site from May 1975 to January 1976

	Leading edge	Hummock front	Hummock back	Foredune
Bodega (northern)				
Mean	0.06	0.04	0.03	0.05
Range	0.02-0.19	0.02-0.06	0.02-0.06	0.02-0.09
Trancas (southern)				
Mean	0.08	0.04	0.03	0.04
Range	0.03-0.13	0.01-0.10	0.01-0.11	0.01-0.17

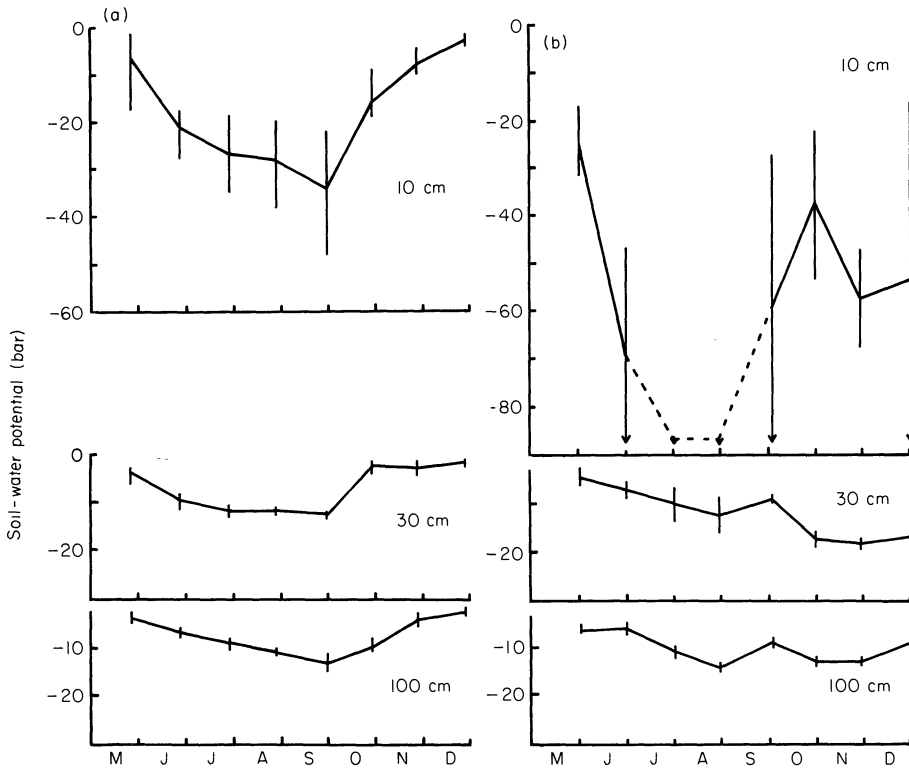


FIG. 4. Soil-water potential at three depths at the study sites on the Californian coast during the last 8 months of 1975. Vertical bars show the range. The broken line indicates measurement periods during which readings were beyond the capabilities of the instrument used. (a) Northern site, (b) southern site.

winter and spring maximum and a late summer minimum. At the southern site it is more difficult to distinguish a pattern of seasonal variation at 100 cm. It is clear that at either site, deeper-rooted plants would be exposed to higher and less variable soil-osmotic potential than shallow-rooted plants.

The large variation in calculated soil-osmotic potential is partly a result of the multiplication of two measured variables, but may indicate that salt and water are not distributed homogeneously at any given depth throughout the seemingly homogeneous sand.

#### *Water-table level and salinity*

The seasonal course of water-table depth and salinity for both study sites is given in Fig. 6. Neither the water-table level nor the salinity changed substantially throughout the year, but the salinity of the water was greatest at both sites during the winter and spring and least during the summer and autumn. The salinity at both sites was  $< 1000 \mu\text{g g}^{-1}$ , which is about 3% of that of sea water.

#### *Water movement experiment*

Figure 7 shows the results of the experiment to detect water movement up to the upper layers of sand from the wetter layers below. On June 23, within 2 weeks after the

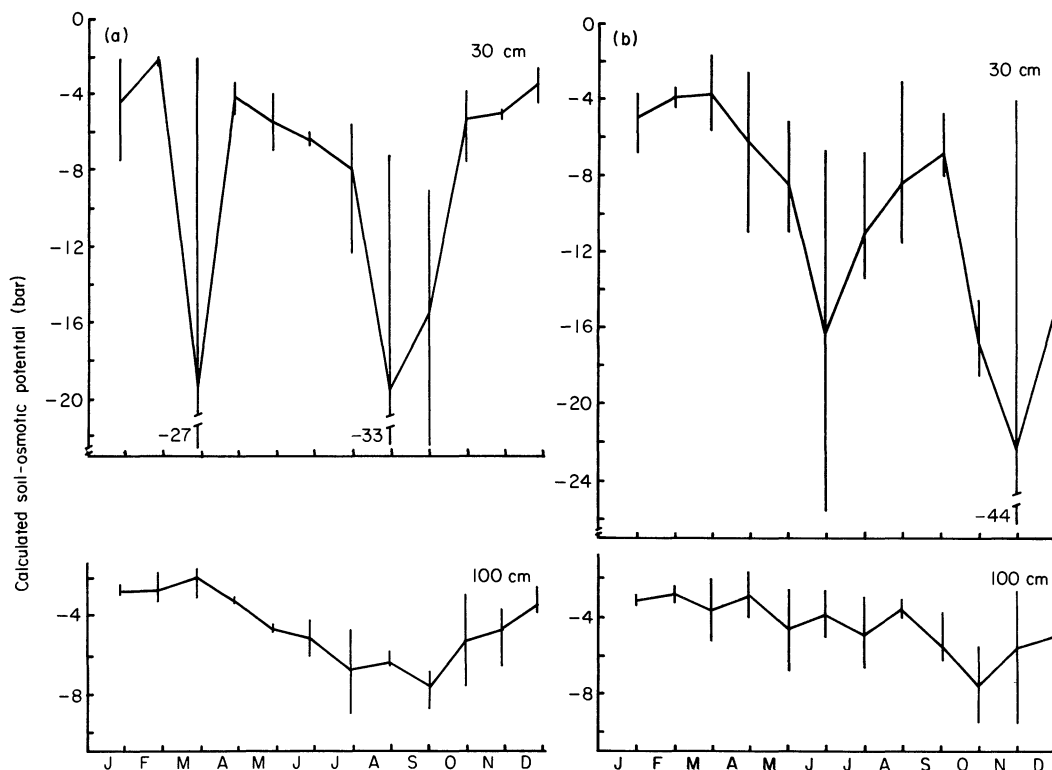


FIG. 5 Calculated soil-osmotic potential in 1975 at two depths at the study sites on the Californian coast. Vertical bars show the range. (a) Northern site, (b) southern site.

experiment was set up, the water potential of the sand above the barrier was more negative than the soil-water potential in the control without the barrier. On 10 October 1975 it rained, and by October 28 the water potential above the barrier increased dramatically because the plastic lining prevented drainage. The fact that the water potential in the control had not risen on 28 October is unexpected. The sand-water potential in the control was somewhat higher than at 30 and 100 cm in undisturbed sand (Fig. 4). This may be a result of disturbing the original structure of the sand in the control, or it may be the result of having removed live roots from the vicinity of the psychrometers. There was no new plant growth on the surface of the 'holes' during the experiment. Nevertheless, sand-water potential above the plastic was substantially lower than in the control throughout the rainless period, indicating that water moves up from below when the barrier is not present.

During the following summer, this experiment was repeated at the northern site with four holes, two with plastic barriers and two controls; soil psychrometers were placed both above and below the plastic. On 2 July 1976 the mean water potential above the plastic, below the plastic and in the control were  $-36$ ,  $-3$  and  $-10$  bar respectively. The sand was substantially drier during the summer of 1976 than during that of 1975, but the water potential in the controls was consistently less negative than in the plastic-lined holes. Furthermore, the water potential *below* the plastic was consistently less negative than in the controls, indicating that the plastic barrier did prevent the upward movement of water in these holes.

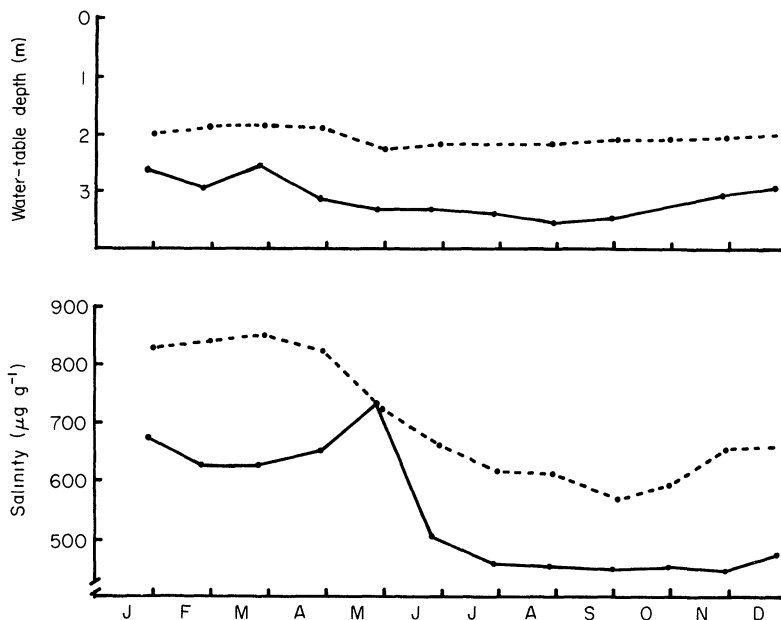


FIG. 6. Seasonal variation in the water-table depth and salinity in 1975 at the northern (—) and southern (---) sites. Note that the salinity scale has suppressed zero.

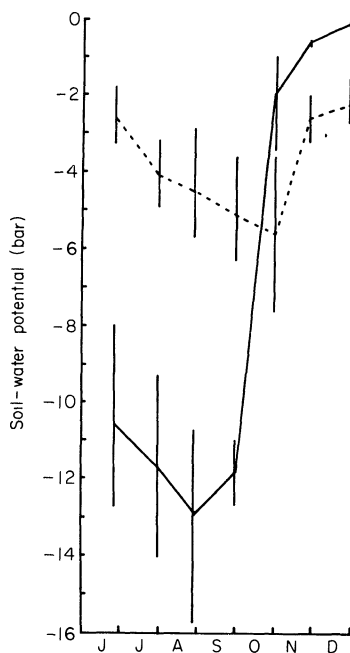


FIG. 7. Soil-water potential at a depth of 50 cm in the plastic-lined 'hole' (—) and the unlined control (---) of the water-movement experiment (see text). The experiment began 2 weeks before the first measurement. The vertical bars show the range.

## Plant xylem-sap tensions

Figures 8 and 9 show the seasonal and diurnal course of xylem-sap tension in *Atriplex leucophylla* and *Cakile maritima* at the northern site, and of *Atriplex leucophylla*, *Cakile maritima*, *Abronia maritima* and *Ambrosia chamissonis* at the southern site. Periodic

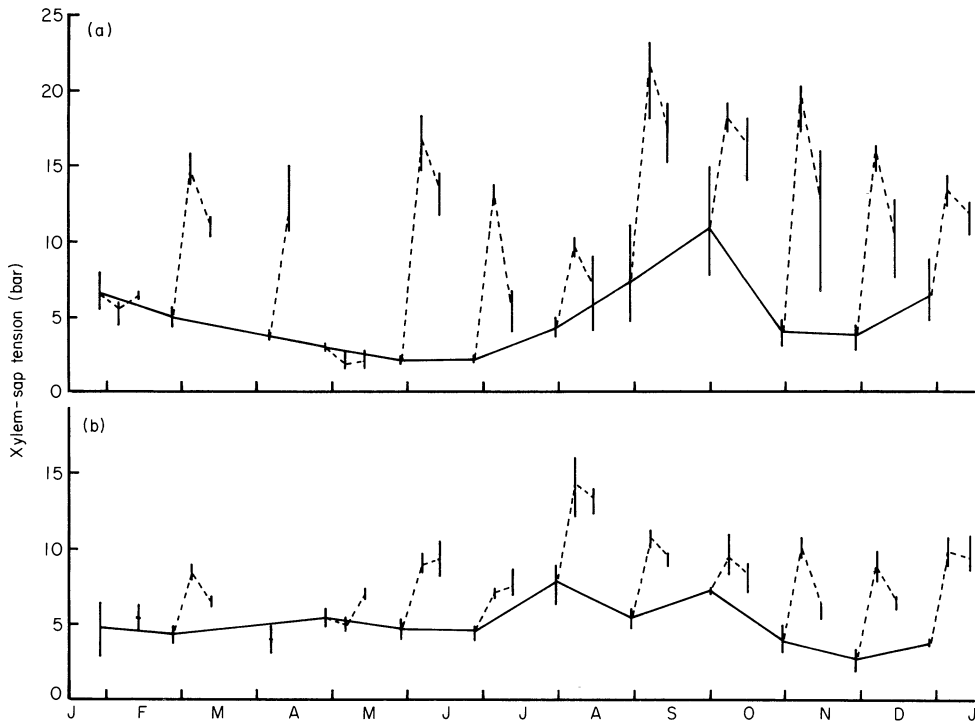


FIG. 8. The seasonal (—) and daily (---) course of xylem-sap tension for (a) *Atriplex leucophylla* and (b) *Cakile maritima* at the northern site during 1975. The daily measurements were at dawn, midday and dusk. The vertical bars show the range.

measurements of xylem-sap tension in *Abronia* and *Ambrosia* at the northern site indicated that these species generally had smaller tensions than did *Cakile* at this site. Dawn xylem-sap tensions at the cooler and wetter northern site were generally lower than at the warmer and drier southern site. The fluctuations in xylem-sap tension during any given day depended strongly on the conditions of the day and on the species. At both sites, mean tensions in *Atriplex* often increased by 10–12 bar between dawn and mid-day, whereas diurnal changes in mean xylem-sap tension in *Cakile* rarely exceeded 5 bar.

At the northern site, dawn xylem-sap tensions of *Atriplex leucophylla* were relatively low during the winter and spring, but gradually increased during the summer and autumn months until rain fell in October. At the southern site, mean dawn xylem-sap tensions were depressed during the warm, dry summer months, and then abruptly increased in the autumn even though the midday xylem-sap tensions during the summer period were among the highest measured. Preliminary investigations suggest that this species may take advantage of early morning fog and dew to alleviate water stress temporarily during this period.

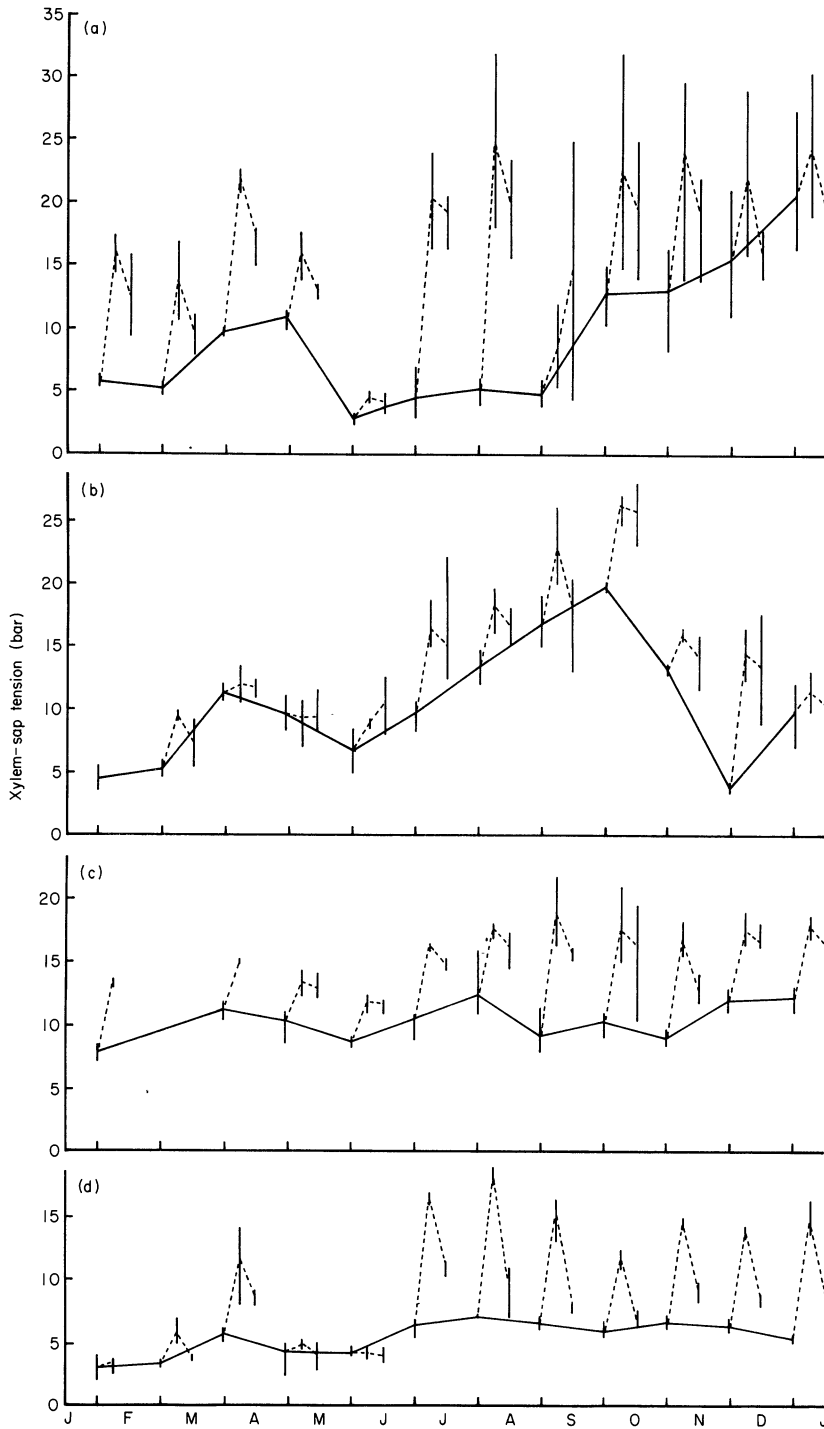


FIG. 9. The seasonal (—) and daily (---) courses of xylem-sap tension for (a) *Atriplex leucophylla*, (b) *Cakile maritima*, (c) *Abronia maritima* and (d) *Ambrosia chamissonis* at the southern site during 1975 and January 1976. The daily measurements were at dawn, midday and dusk. The vertical bars show the range.

In contrast to the responses at the northern site, *Cakile* in the south had a marked seasonal pattern of dawn xylem-sap tension, with tension being greatest in early autumn but decreasing after October. The drop in tension after October, however, may be an artefact, resulting from a sampling problem with this species. Because it is a facultative annual, most individuals die toward the end of the summer. The plants sampled in November may represent a select group of individuals that survived the dry summer because of locally abundant water supplies trapped in buried organic matter, or because of deeper root systems than those of other individuals of the same species.

*Abronia* and *Ambrosia* showed no distinct seasonal trends in dawn xylem-sap tensions at the southern site. The mean dawn xylem-sap tensions for *Abronia* were between 7.5 and 12.5 bar throughout the entire year, while the mean dawn tensions of *Ambrosia* ranged from 3.0 to 7.0 bar. The daily increases in xylem-sap tension between dawn and midday were similar for both species, but by dusk sap tensions were often very close to dawn values in *Ambrosia* whereas *Abronia* recovered more slowly.

## DISCUSSION

Ocean beaches are popularly considered to be either xeric or saline habitats, or both, for vascular plants, and beach taxa are generally accepted as being either halophytic or xerophytic. However, these ideas appear to be naïve and partially incorrect.

Although the amount of water held by beach sand relative to its own weight at any given time is extremely low, the water potential of beach sand at depths below 30 cm is generally greater than  $-15$  bar. The mean dawn xylem-sap tensions measured on the four species found on each of the beaches studied only exceeded 15 bar four times during the entire year.

How is it possible that beach plants can maintain such low dawn xylem-sap tensions, and how does the sand remain moist when the summer months are virtually rainless? The data suggest that water moves upward from at least 100 cm depth, possibly from the relatively non-saline water table, and that the species studied absorb this upward-moving water at different depths, thus showing different seasonal patterns of water relations.

The experiments with the plastic barrier clearly show that if water is prevented from moving upward, the sand above the barrier rapidly dries out and does not become rehydrated unless it rains. This would not be expected on the basis of Salisbury's (1952) hypothesis regarding internal dew formation from atmospheric water vapour, but is consistent with the ideas of Olsson-Seffer (1909a) and Willis *et al.* (1959) that water may move upward from the water table. Salisbury's experiments did not preclude the possibility that water came from below, because he did not prevent the upward movement of water. Thus the results of my experiments are consistent with Salisbury's experimental results but not with his interpretation. Willis *et al.* (1959) have previously questioned Salisbury's hypothesis on the basis of the temperature gradients they measured in dune sands. They contend that it is unlikely that the soil temperatures at the place of maximum dew formation fall below the atmospheric dew point.

There are several mechanisms which might drive water upward. Kerner's early hypothesis of movement by capillarity was questioned by Olsson-Seffer (1909a), because '... the rise of water by mere capillary action' in typical dune sand is too slow to account for the amount of water present in dune sand. Olsson-Seffer (1909a) proposed that water moves upward as vapour along a temperature gradient, and condenses in the upper layers when temperatures are cooler there. He called this phenomenon 'internal dew

formation in the soil'. The temperature ranges at various levels depicted in Fig. 2 are consistent with this possibility. At some time during most days the temperature was lower in the upper than in the lower sand levels. Willis *et al.* (1959) also measured similar temperature gradients in sand dunes in England.

Another possibility is that the water may move upward as liquid along a water-potential gradient. Since water potentials were more negative in the upper layers of sand, the necessary direction of travel for water would be upward from the areas of less-negative water potential. It is not possible from this study to determine if either of these phenomena could account for movement of water in sufficient *amount* to sustain plant growth and maintain the levels of moisture reported here. However, it is important to note that the water-holding capacity of sand is so small that it would take only very small amounts of water per unit volume to maintain the sand at water potentials between  $-10$  and  $-15$  bar. Further work clearly needs to be done to establish the hydrodynamics of the beach sand habitat.

Each beach species appears to have a unique 'strategy' with regard to the existing resources of water on the beach. At the one extreme, *Ambrosia chamissonis* exhibits very little seasonal fluctuation in dawn xylem-sap tension, maintains relatively low tensions and by dusk is able to recover almost completely from the maximum midday tensions. At the other extreme, *Atriplex leucophylla* exhibits marked seasonal patterns of dawn xylem-sap tension, develops relatively high midday tensions on clear days, and recovers more slowly from high midday tensions. Excavation of roots at the southern site revealed that *Atriplex* has an extensive development of very fine shallow roots ( $< 40$  cm deep) and a relatively small taproot, whereas *Ambrosia* usually has one central taproot extending down more than 100 cm before producing extensive fine branches.

*Abronia maritima* and *Cakile maritima* seem to be intermediate to the above species with regard to water relations. *Abronia maritima* is perennial and has a relatively deep tap-root. It also shows little seasonal change in dawn xylem-sap tension. However, dawn tensions are nearly double those of *Ambrosia* throughout the year, and recovery to dawn tension levels is slower than in *Ambrosia*. *Cakile maritima* usually has most of its roots in the upper 50 cm of sand (on one occasion roots were found that penetrated deeper than 100 cm). Perhaps the pattern of xylem-sap tension of this annual species depends on how long it has had to extend its roots down to the wetter levels of sand. Although there are differences in the life form and physiology of these taxa (De Jong 1978), at least some of the differences in patterns of xylem-sap tension may be explained by rooting patterns and, in particular, by rooting depth.

My observations regarding the root systems of *Ambrosia chamissonis* and *Abronia maritima* agree with those reported by Martin & Clements (1939), but differ from those reported by Purer (1936). Purer reported that these taxa had rather shallow, truncated root systems. Perhaps her excavations were in areas of a higher water table: she mentions that roots were found to be only a 'few inches' from what she reported to be a salty water table. Purer also reported that *Atriplex leucophylla* has few branch roots but has a large tap root extending deeper than *Abronia* or *Ambrosia*, whereas my excavations revealed extensive shallow roots and a relatively small tap root.

There were, unfortunately, too few plants in the immediate area of the northern study site to allow the measurement of xylem-sap tensions of *Abronia latifolia* and *Ambrosia chamissonis* throughout the entire year. However, from the data on *Atriplex leucophylla* and *Cakile maritima* as well as the periodic measurements on *Abronia latifolia* and *Ambrosia chamissonis*, it is clear that the northern site plants were under less water stress



than those on the southern site. This might be explained by the lower temperature, higher rainfall and the finer-textured sand that characterize this site.

The phenological patterns of the species studied appear to be partially influenced by temperature and water relations. At the northern site the period of maximum growth tends to occur later than in the south, probably due to lower temperatures in the north. On the other hand, growth tends to decrease earlier in the summer at the southern site. In *Cakile* and *Atriplex* this is probably caused by increased water deficits, but the same explanation does not appear to hold for *Abronia* and *Ambrosia*, which have little seasonal variation in xylem-sap tensions.

The loss of leaves by the semi-deciduous *Ambrosia chamissonis* in the summer and autumn months may be of advantage by reducing water loss during the drier part of the year, and may also help to explain the non-seasonality of its xylem-sap tension.

The inability of the *Ambrosia* and *Abronia* seedlings to survive the summer at the southern site, where there is a lack of spring and summer rain, may result from insufficient moisture to enable them to extend their roots deep enough to tap permanent water in sufficient quantities. *Atriplex* and *Cakile* appear to be able to survive with higher xylem-sap tensions, and thus are able to establish and survive the rainless summers even in dry years.

With regard to beach salinity and the halophytic nature of beach taxa, the present study has shown that even the drift-line zone of the beach habitat is not highly and continuously saline. The sand at the leading edge of the vegetation generally contained higher concentrations of salt than did sand farther inland in the middle of the zone of pioneering beach species.

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