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ART. VII.—*Ecological Studies in Victoria.—Part VI.—
Salt Marsh.*

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Salt Marshes exist at several points along the coast, but at Western Port there is a very strong development at the northern and north-western portions, with Mangrove on the seaward side. These marshes are not regularly washed by the tide, but only occasionally, by exceptionally high seas. During the summer the evaporation of water is high and glistening salt may be seen on the landward side. At this period, therefore, the concentration of the soil solution is greatest and this is the outstanding factor of the environment. The Mangrove, *Avicennia officinalis*, in contrast to the marsh, is right in the tidal water and twice each day its breathing roots are exposed to the air. The Mangrove marks the limit of the high tides. The junction between the Mangrove and the Salt Marsh is sharp, particularly where the fall away from the latter is well marked, as at Tooradin pier. Where the slope is very gradual the junction is not so well defined. This is seen at Bembroke and Hastings. However, in this latter case there is not a general mixing of the marsh flora with the Mangrove, but chiefly with *Salicornia australis*. Where the transition is gradual, some of the marsh plants are regularly covered by the tide, but the depth of water is not great. Although there is a transition zone in some cases, the true salt marsh community finishes as soon as Mangroves are met with, and in these studies the investigation has not been carried into the tidal zone.

On the landward or inner margin of the salt marsh, there is very frequently a narrow zone, devoid of shrub growth and often quite bare, on which in summer, salt is clearly visible. The bare areas of the zone have somewhat the appearance of the clay pans of the warmer parts of Australia. In parts, this zone is vegetated by *Mesembrianthemum australe*, and in others appears to have been formerly occupied by this plant. The reason for its death is not known. This zone is never broad and where present it is succeeded by the Swamp Ti-tree, *Melaleuca ericifolia*, association. This latter where present marks the landward limit of the salt marsh, whether the narrow *Mesembrianthemum* zone be present or not. The Swamp Ti-Tree is essentially a fresh water plant although it endures brackish water. At the northern end of Western Port the ti-tree formerly extended to the main Gippsland

Railway, approximately ten miles away. Along the north-west of Western Port the ti-tree occupies only a few feet between the marsh and sand hills. These sand hills might be regarded as dunes but although abutting on the sea, the flora is not that of the coast dunes. They bear instead typical heath vegetation dominated by Manna Gum, *Eucalyptus viminalis*.

PHYSIOGNOMY AND COMPOSITION.

The salt marsh is essentially a shrub community since the dominant plant *Arthrocnemum halocnemoides* is woody, amply branched and stands some three feet high. In this shrub the ultimate branchlets have a succulent cortex which withers as growth proceeds, leaving the woody axis unimpaired for conduction and for increase in diameter. These bushes do not form a closed canopy and between and beneath them lies the main portion of the vegetation. This latter consists of perennials which are also mostly succulent, but which more or less die down in the late autumn. Before doing so, *Salicornia australis* assumes a very bright reddish colour. Both *Suaeda maritima* and *Mesembrianthemum australe* also become brightly coloured. The lower stratum of vegetation forms a complete or almost complete soil cover and the association is therefore a closed one. *Salicornia australis* forms the major portion of the lower stratum partly because it is taller than the other constituent species but more particularly on account of the profuse branching of its aerial shoots, which if they bend over and reach the ground may root. *Selliera radicans*, which does not produce aerial shoots, but only runners or shallow rhizomes, may rightly be considered as constituting a ground or third stratum; but because it is not universally found and its erect leaves are not shaded by the low-growing species, it can be united with the other members of the second stratum. The effective covering of the soil, thus forming a closed community, is due to the rhizomic or runner habit of the plants of the second stratum, the peaty soil being interwoven with roots and rhizomes. In early winter the small rosettes of *Samolus repens* become very evident and appear to be individual plants. This species sends out leafy runners which ultimately root at the apices but not along the length, and form new plants. They also appear to arise from rhizomes. The rosettes send up one or more aerial flowering shoots.

COMPOSITION.

Although the salt marsh is densely populated with individuals the species population is small. A small number of species is a characteristic of a pioneer community, as in a fore dune, but there is the added fact that the individuals are widely separated. In such a community there is some outstanding adverse factor of the environment which is reflected in the sparseness of the individuals.

In the marsh, however, while there is a paucity of species, there is also an abundance of individuals which form a complete ground cover. This is somewhat the reverse of the usual conditions. Usually there is an intimate connection between the numbers of individuals present and number of species. This is not always the case, however, and an outstanding exception is that of the Ti-tree association of the Koo-wee-rup Swamp, where the soil is densely covered chiefly by one species. The salt marsh association provides another exception in regard to its floral composition for, one family, Chenopodiaceae, dominates it both structurally and systematically. This family is represented by four genera, each with a single species. In addition to the two very commonly occurring species, *Salicornia australis* and *Arthrocnemum halocnemoides*, there are *Atriplex paludosum* and *Suaeda maritima*. The genus *Atriplex* is represented on the coast by another species *A. cinereum*, which is perhaps best regarded as a strand plant. It has several species in the Mallee. *Atriplex paludosum* occurs only sparsely in the marsh and in four transects at widely separated places, this species did not occur in a single quadrat. *Suaeda maritima* is also sparse in the marsh itself but it occurs particularly where there is any sand and mostly towards the margins.

A striking feature of the association is the great lack of connection between its floral composition and those of the adjoining associations. When compared with the equally maritime association, the Sand Dune, there is a conspicuous difference. The dune flora does reflect the characteristic flora of the State since there occur the genera *Casuarina*, *Leptospermum*, *Acacia*, *Banksia*, and *Olearia*. All of these genera occur in the heathlands as well and in other associations, but not one has a representative in the marsh. On the other hand, the genera of the marsh, even species, are distinctly cosmopolitan. The genera *Suaeda*, *Salicornia*, *Statice*, *Frankenia* and *Samolus* are equally at home in European salt marshes as in Victoria.

The genera *Glyceria*, *Juncus* and *Atriplex* are represented both in dry land associations of the State and in the salt marshes of Europe. The species *Suaeda maritima* and *Juncus maritimus* are found both in our own salt marshes and those of Europe. The affinity, therefore, of the salt marsh is extra-Australian, while the two adjoining associations, Heath and Dune, are intensely Australian.

Along the landward margin of the marsh, occur a number of plants which swell the total number of species but which are not found, or only sporadically, in the marsh itself. These are listed as marginal in the table of species found in the Salt Marsh at Western Port (Table 1).

Of the families given in Table I. only one, Goodeniaceae, is characteristically Australian. This family is also represented on the coastal dunes but by a different genus.

TABLE I.—COMPOSITION OF SALT MARSH.

| | | | | | | | |
|-----------------|----|----|-----------------------------------|----|----|----|--------|
| Juncaginaceae | .. | .. | <i>Triglochin striata</i> | .. | .. | .. | o. |
| | | | <i>T. minutissima</i> | .. | .. | .. | m. |
| Gramineae | .. | .. | <i>Distichlis spicata</i> | .. | .. | .. | o. |
| | | | <i>Glyceria stricta</i> | .. | .. | .. | o. |
| | | | <i>Stipa teretifolia</i> | .. | .. | .. | o. |
| | | | <i>Sporobolus virginicus</i> | .. | .. | .. | m. |
| | | | <i>Lepturus incurvatus</i> | .. | .. | .. | o. |
| Cyperaceae | .. | .. | <i>Cladium filum</i> | .. | .. | .. | f. |
| Juncaceae | .. | .. | <i>Juncus maritimus</i> | .. | .. | .. | l.a. |
| Chenopodiaceae | .. | .. | <i>Atriplex paludosum</i> | .. | .. | .. | o. |
| | | | <i>Suaeda maritima</i> | .. | .. | .. | o. |
| | | | <i>Salicornia australis</i> | .. | .. | .. | v.c. |
| | | | <i>Arthrocnemum halocnemoides</i> | .. | .. | .. | v.c. |
| Amarantaceae | .. | .. | <i>Hemichroa pentandra</i> | .. | .. | .. | c. |
| Aizoaceae | .. | .. | <i>Mesembrianthemum australe</i> | .. | .. | .. | c. |
| Caryophyllaceae | .. | .. | <i>Spergularia rubra</i> | .. | .. | .. | m. |
| Malvaceae | .. | .. | <i>Plagianthus spicatus</i> | .. | .. | .. | m. |
| Frankeniaceae | .. | .. | <i>Frankenia pauciflora</i> | .. | .. | .. | r. |
| Umbelliferae | .. | .. | <i>Apium australe</i> | .. | .. | .. | v.r. |
| Primulaceae | .. | .. | <i>Samolus repens</i> | .. | .. | .. | c. |
| Plumbaginaceae | .. | .. | <i>Statice australis</i> | .. | .. | .. | o. |
| Gentianaceae | .. | .. | <i>Sebaea albidiflora</i> | .. | .. | .. | m.r. |
| Convolvulaceae | .. | .. | <i>Wilsonia humilis</i> | .. | .. | .. | r; la. |
| | | | <i>W. Buckhousei</i> | .. | .. | .. | o; la. |
| Goodeniaceae | .. | .. | <i>Selliera radicans</i> | .. | .. | .. | c. |
| Compositae | .. | .. | <i>Brachycome graminea</i> | .. | .. | .. | m.r. |

c = common; f = frequent; l.a. = locally abundant; m = marginal; o = occasional
r = rare; v.c. = very common; v.r. = very rare.

Only two of the genera have more than one species, while two families have more than one genus. It has been pointed out in previous papers of this series that one of the characteristics of an association is that the average number of genera per family always exceeds the number of species per genus. The values here are 1.4 and 1.1 respectively. Generic characters are not in general related to, or affected by the environment, hence there is theoretically, at all events, no barrier to the entry of any particular genus. A species on the other hand must be adapted to the particular environment or it cannot survive. Quite commonly the specific characters are an expression of the physiological adaptation to the environment. This, however, is not always the case, as is seen in grasses of the Marsh.

The frequencies of the marsh species, omitting the marginal ones, is expressed in Table II., which gives the percentage occurrences in 60 quadrats taken across the marsh, from the Ti-tree to the Mangrove, at three widely separated places. The quadrats were one square yard, distant sixteen feet from one another.

While the percentage frequencies give a measure of the occurrence of the species they do not necessarily convey any information regarding their distribution. The low frequencies of

TABLE II.—FREQUENCIES OF SPECIES IN SALT MARSH.

| Species. | | | | | | Percentage Occurrence. |
|-----------------------------------|----|----|----|----|----|------------------------|
| <i>Salicornia australis</i> | .. | .. | .. | .. | .. | 87 |
| <i>Arthrocnemum halocnemoides</i> | .. | .. | .. | .. | .. | 70 |
| <i>Samolus repens</i> | .. | .. | .. | .. | .. | 63 |
| <i>Hemichroa pentandra</i> | .. | .. | .. | .. | .. | 63 |
| <i>Distichlis spicata</i> | .. | .. | .. | .. | .. | 28 |
| <i>Selliera radicans</i> | .. | .. | .. | .. | .. | 25 |
| <i>Triglochin striata</i> | .. | .. | .. | .. | .. | 18 |
| <i>Wilsonia Backhousei</i> | .. | .. | .. | .. | .. | 15 |
| <i>Juncus maritimus</i> | .. | .. | .. | .. | .. | 12 |
| <i>Cladium filum</i> | .. | .. | .. | .. | .. | 10 |
| <i>Suaeda maritima</i> | .. | .. | .. | .. | .. | 5 |
| <i>Mesembrianthemum australe</i> | .. | .. | .. | .. | .. | 5 |
| <i>Stipa teretifolia</i> | .. | .. | .. | .. | .. | 3 |
| <i>Statice australis</i> | .. | .. | .. | .. | .. | 2 |

both *Mesembrianthemum australe* and *Statice australis* are due to different causes. The former is restricted to the landward side of the marsh and hence can only occur in quadrats taken on the edge. This species, therefore, will almost always occur in a transect. On the other hand *Statice australis* is sporadically distributed over the marsh and its low frequency is a measure of its sparse distribution. *Atriplex paludosum* is similarly distributed, but it did not occur in any of the quadrats. Both of these species occur as isolated plants, while other species, as *Selliera radicans*, form large colonies, due to their rhizomic habit. The high value for *Salicornia australis* is due to its universal distribution. It has a greater amplitude as regards the concentration of salt than any other species, for it passes from the fairly uniform concentration at the Mangrove margin, across the marsh, and into the ti-tree community for a short distance. *Mesembrianthemum australe*, which commences in the partially bare zone, associates with *Salicornia australis* for a short distance, but passes inland, far removed from salt influences, along with the ti-tree.

To the east of Tooradin where the Toomuc and Cardinia Creeks enter the bay, the marsh ends on its landward side in grassland. Here *Arthrocnemum halocnemoides* again may be regarded as marking the limit of the marsh, but the boundary is poorly defined. *Mesembrianthemum australe* here is much more common and extends well into the marsh. This is somewhat surprising for here the dominating shrub stratum is better developed, taller and closer together, thus casting a greater shade. There is beyond the marsh proper, as limited by the shrub stratum, a transition zone in which *Distichlis spicata*, *Salicornia australis* and *Mesembrianthemum australe* densely intermix and form a complete ground cover.

ENVIRONMENT.

It frequently happens that in an association one factor of the environment is so pronounced as to dominate all others. In the salt marsh the outstanding factor is the highly concentrated soil solution, compared with that usually found. Climate has but secondary effects. Wind, which is the cause of the moving sand in the coastal dunes, here is the force bringing the high seas over the marsh. Temperature also has a secondary effect in assisting evaporation in the summer period and thus concentrating the soil solution. As shown in Table III., there is no dearth of water, which has been derived, at least partly, from the sea, and rainfall therefore does not necessarily contribute to the needs of the plants. The same climatic conditions are being experienced by the other maritime associations, and so the differences between these plant communities cannot be ascribed to any climatic factor. The differences lie wholly in the soil. This is shown in Table III. The soil samples were collected in February during dry weather and when the salt was freely showing along the landward margin. The first sample was taken at the junction of the Swamp Ti-tree and the Marsh, and the last sample where the Mangrove commenced. It will be noticed that, although little rain had fallen for some time, the water content of the soil was high, right across the marsh. This is in striking contrast to the moisture content of other associations under similar climatic conditions at the same period of the year. (Patton 4, 5.) The variation in the moisture content calculated on the dry weight from 421 per cent. to 92 per cent. is due chiefly to the high and variable organic content of the soil. Since the chief constituent of the mineral soil is clay, the combination of clay and organic matter gives a high water holding capacity. Added to this, however, is the fact that the

TABLE III.—SOIL SAMPLES FROM TOORADIN SALT MARSH.

| Distance in Feet. | Moisture Content per cent. | Loss on Ignition per cent. | Gms. of NaCl in 100 gms. | | Equivalent O.P. in Atmos. | Remarks. |
|----------------------|----------------------------------|----------------------------------|-----------------------------|----------------------|---------------------------------|--|
| | | | Of Dry Soil. | Of Soil Moisture. | | |
| 0 | 92 | 44.3 | 4.000 | 4.35 | 30.8 | Edge of Ti-Tree Mesembrianthemum |
| 38 | 329 | 70.4 | 24.925 | 7.58 | 53.6 | Arthrocnemum and Salicornia |
| 86 | 268 | 36.6 | 18.100 | 6.75 | 47.6 | Salicornia |
| 141 | 421 | 62.5 | 22.425 | 5.33 | 37.7 | Salicornia and Hemichroa |
| 197 | 170 | 27.6 | 8.175 | 4.81 | 33.9 | Salicornia and Hemichroa |
| 255 | 173 | 25.7 | 9.450 | 5.46 | 38.6 | Arthrocnemum and Samolus |
| 317 | 116 | 14.7 | 5.575 | 4.81 | 33.9 | Salicornia Samolus Arthrocnemum Selliera |
| 385 | 180 | 26.0 | 6.775 | 3.76 | 26.6 | Salicornia and Samolus |
| 428 | 102 | 10.5 | 4.375 | 4.29 | 30.4 | Commencement of Mangrove |

area is flat and drainage is bad. In places there may be no, or almost no, mineral soil at all, the whole upper part consisting of peat. In this series of papers soil is defined as the medium in which roots find themselves, no matter what that medium may be. The definition is wide, but for ecological purposes it works well.

The chloride content of the soil, ascertained by titration against silver nitrate, has been expressed, in this and later tables, as sodium chloride. It will be noted that where the ignition loss is high, both the water and the salt content, calculated to dry weight, are also high. This is merely an expression of the fact that the greater the amount of peat, the greater amount of salt water present. The actual variation of the concentration of the soil solution, however, is not wide, as is shown by the amount of salt in 100 gms. of soil moisture. In the last column the corresponding osmotic pressures for the concentrations are given. In Table IV. are given the results of portion of another traverse at an area where the *Mesembrianthemum* zone on the inner or landward margin of the marsh was well developed. This zone bears *mesembrianthemum* in parts while other parts are bare. A sample of the soil from the ti-tree community was also collected.

TABLE IV.—ANALYSIS OF SOIL, SALT MARSH, TOORADIN.

| Distance in Feet. | Moisture Content per cent. | Loss on Ignition per cent. | Gms. of NaCl in 100 gms. | | Equivalent O.P. in Atmos. | Remarks. |
|----------------------|----------------------------------|----------------------------------|-----------------------------|----------------------|---------------------------------|--|
| | | | Of Dry Soil. | Of Soil Moisture. | | |
| -8 | 41.29 | 25.38 | .824 | 1.995 | 14.1 | Ti-Tree |
| 0 | 129.79 | 53.19 | 3.708 | 2.857 | 20.2 | Edge of Ti-Tree |
| 16 | 75.30 | 43.09 | 6.735 | 8.944 | 63.2 | { Getting bare |
| 48 | 60.78 | 41.62 | 11.370 | 18.707 | 132.2 | { <i>Mesembrianthemum</i> |
| 80 | 209.08 | 63.00 | 15.347 | 7.340 | 51.9 | { Quite bare |
| 112 | 310.91 | 59.51 | 19.158 | 6.162 | 43.6 | { True Marsh |
| | | | | | | { <i>Arthrocnemum</i> and <i>Salicornia</i> |

The high salt concentration and consequently high osmotic pressure of the bare areas is apparently the reason for the absence of vegetation. Yet these have been vegetated at least in part, for the soil, as the loss on ignition shows, contains a high percentage of organic matter and the remains of dead plants, in situ, can be seen. Both Tables III. and IV. indicate that the greatest concentration of salt is towards the landward margin, and that there is a decrease towards the sea. Within the marsh itself, the osmotic pressure of the soil with reference to common salt content only, is generally below 50 atmospheres. The concentrations in the marsh soil generally agree with the statement of Braun Blanquet (1) that in the uppermost layers of the *Salicornia* marshes in the Mediterranean region, the common salt content reaches 8 to 10 per cent. during the summer drought.

The marsh proper commences with the appearance of *Anthrocnemum halocnemoides* and from its first occurrence to the appearance of the Mangrove, the marsh is always moist and the soil contains a high percentage of organic matter. The amount of organic matter and clay in the soil is not uniform, the differences are largely due to very small differences in the elevation of marsh, the lower portions containing more mineral soil while the higher may consist of peat only. The peat may be described as fibrous, for when dried it distinctly has the appearance of a confused mass of threads. When fresh, it is exceedingly difficult to separate on account of the mass of long thick walled root hairs which ramify through it. How much of the peat horizon is living and how much dead it has not been possible to determine.

Halfway across the marsh, where the peat was well developed and where there was a full representation of the commonly occurring species, samples of the soil were taken every three inches from the surface to water level, which was just below twelve inches. In Utah, Harris (2) also found that in marsh areas bearing *Salicornia utahensis*, the water level was close to the surface. The top six inches of the marsh at Tooradin were very peaty and had, in addition, abundant living rhizomes and roots. The loss on ignition, therefore, is not a true indication of dead organic content. The living and dead matter almost ceased at six inches. There was a sharp line of demarcation between the peat and the clay soil below in which there were very few living roots. Braun Blanquet (1) remarks that it is easy to remove the upper layer of soil with the roots. The striking differences between these layers is seen in Table V. On account of the wide differences in organic content, the water content of the two upper samples was much higher than the two lower, in spite of the fact that the lowest was immediately above the water table.

TABLE V.—ANALYSIS OF SOIL SAMPLES TAKEN VERTICALLY IN SALT MARSH, TOORADIN.

| Depth Inches. | Moisture Content per cent. | Loss on Ignition per cent. | Gms. of NaCl in 100 gms. | | Osmotic Pressure in Atmos. | Remarks. |
|------------------|----------------------------------|----------------------------------|-----------------------------|----------------------|----------------------------------|---|
| | | | Of Dry Soil. | Of Soil Moisture. | | |
| 3 | 345 | 55.2 | 20.95 | 6.07 | 42.90 | } Fresh roots and rhizomes } Very peaty } Few roots } Dark clay |
| 6 | 347 | 49.1 | 21.27 | 6.13 | 43.30 | |
| 9 | 119 | 21.8 | 7.60 | 6.39 | 45.20 | |
| 12 | 99.5 | 20.4 | 6.35 | 6.38 | 45.10 | |

The results in Table V. indicate that despite wide differences between organic and water content of the samples, the concentrations of salt per 100 gms. of water are very similar. This means that the soil solution is approximately the same vertically through

the soil, due no doubt, to the proximity of the ground water. The osmotic pressures, corresponding to the common salt concentrations, are all below 50 atmos.

The strength of the soil solution is the outstanding feature of the environment and plants, if they are to succeed, must have a suction force greater than the osmotic pressure of the soil. A series of plants, taken over various portions of the marsh, at the same time as the soil samples, gave the suction pressures shown in Table VI. The method used for determining the suction pressures was by weighing small pieces of tissue before and after immersion in solutions of known concentrations.

TABLE VI.—SUCTION PRESSURES OF SALT MARSH PLANTS, TOORADIN.

| Species. | Suction Pressure. |
|--|-------------------|
| | Atmos. |
| <i>Selliera radicans</i> | 51.68 |
| <i>Hemichroa pentandra</i> | 47.88 |
| <i>Suaeda maritima</i> | 44.84 |
| <i>Salicornia australis</i> | 43.70 |
| <i>Mesembrianthemum australe</i> | 35.30 |

With the exception of the last, the pressures are comparable to the osmotic pressures of the soil solutions. Under the conditions existing when the samples were taken it would appear that the plants were just maintaining themselves. It is surprising to note that *Mesembrianthemum australe* had a lower value than the other species, in spite of the fact that it grows in the zone of greatest salt concentration. Although determinations were made on material of this species gathered at widely separated points, the suction pressures obtained never equalled those of the other species. The osmotic pressure of the sap was also very low. By Barger's method it was 34.2, and by the Freezing Point Determination, it was 37.0. The sap was extracted from material collected at several places.

It is possible that this plant, with its exceedingly high water content, does not depend on root activity for its water requirements during the period of high salt concentration in the soil. It continues to grow, even if detached, at the expense of the moisture stored in the leaves most remote from the growing point. If this be the case the water storage is definitely an adaptation which cannot be said of the other succulents.

During the winter, water lies freely on the marsh, and the concentration of the salt is greatly lessened, as shown in Table VII., but the moisture content does not greatly vary. In some cases the results are actually lower than in Table III. The samples were collected in June after rain had fallen.

TABLE VII.—ANALYSIS OF SALT MARSH SOIL IN WINTER.

| Distance in Feet. | Moisture Content per cent. | Gms. of NaCl in 100 Gms. | | Equivalent O.P. in Atmos. | Remarks. |
|----------------------|----------------------------------|-----------------------------|----------------------|------------------------------|----------------------------|
| | | Of Dry Soil. | Of Soil Moisture. | | |
| 0 | 129 | •226 | •175 | 1•24 | } Same as in Table III. |
| 38 | 374 | 9•888 | 2•644 | 18•69 | |
| 86 | 218 | 4•340 | 1•991 | 14•07 | |
| 141 | 464 | 8•035 | 1•732 | 12•24 | |
| 197 | 167 | 2•821 | 1•689 | 11•94 | |
| 255 | 183 | 3•255 | 1•779 | 12•57 | |
| 317 | 104 | 1•401 | 1•347 | 9•52 | |
| 385 | 168 | 2•266 | 1•349 | 9•53 | |

Braun Blanquet (1) states that in the Mediterranean areas after the autumn rain the salt may be almost completely leached out, and he quotes 0•15 per cent. It is doubtful if such a low figure would be reached on the Western Port Marshes. Even in the summer the water level is close to the surface and this must influence the salt concentration. In winter, when the seas are carried over the marsh, a fairly high concentration would be maintained.

ANATOMY AND PHYSIOLOGY.

Of the four commonly occurring species in the marsh shown in Table II. all are succulent, with the possible exception of *Samolus repens*, whose general appearance is markedly different from the others. Its thin stems and small coriaceous leaves are characteristic of xerophytic plants. Succulence is achieved by modifications of different plant organs. In some, as already mentioned, it is the cortex which is the organ of water storage, while in others, as *Mesembrianthemum australe*, the leaves are modified for that purpose. Succulents are the true possessors of the marsh, but the fact that non-succulents as *Distichlis spicata* are present is evidence that succulence is not a necessary modification. As, however, the succulents form by far the great majority of the population only these have been studied. The percentage of moisture present in the succulents is given in Table VIII. The moisture content is calculated to the oven-dry weight.

TABLE VIII.—MOISTURE CONTENT OF SPECIES IN SALT MARSH.

| Species. | Moisture Content per cent. |
|---|----------------------------|
| <i>Mesembrianthemum australe</i> | 1,202 |
| <i>Suaeda maritima</i> | 811 |
| <i>Salicornia australis</i> | 642 |
| <i>Selliera radicans</i> | 610 |
| <i>Hemichroa pentandra</i> | 615 |
| <i>Arthrocnemum halocnemoides</i> | 495 |
| <i>Samolus repens</i> | 358 |

From the succulents, the sap can be readily extracted by pressure, and in Table IX. are given the chloride contents, expressed as common salt, of the saps of several species. The saps were obtained in quantity from material collected at several places, so that they represent average samples. The suction pressures, given in Table VII., are dependent on the concentration of the cell solution, and in the marsh plants sodium chloride plays a most important part. The concentration of salt in the cell, while greater than that of sea water (3), is not as great as in the soil solution. The saps of the first and fourth were obtained at the same time as the soil samples given in Table III. The remainder were collected after rain had fallen, and therefore it is possible that the cell solutions are more dilute than when conditions were drier. In addition to the salt content of the cell saps (Table IX.), the salt content of the water in the marsh creek is also shown. This was collected at the same time as the soil samples of Table III.

TABLE IX.—SODIUM CHLORIDE CONTENT OF SALT MARSH SAPS AND SALT WATERS.

| Species. | In One Litre of Sap. | | O.P. of NaCl. in Atmos. |
|--------------------------------------|---------------------------|---------------|----------------------------|
| | Gms. of Cl ₂ . | Gms. of NaCl. | |
| <i>Salicornia australis</i> | 39.30 | 64.76 | 42.18 |
| <i>Arthrocnemum halocnemoides</i> .. | 35.80 | 59.00 | 38.38 |
| <i>Suaeda maritima</i> | 26.90 | 44.33 | 28.80 |
| <i>Mesembrianthemum australe</i> .. | 25.30 | 41.69 | 27.09 |
| <i>Selliera radicans</i> | 21.20 | 34.93 | 22.69 |
| Creek Water | 26.4 | 43.51 | 28.27 |
| Sea Water | 19.32 | 31.84 | 20.67 |

The sea water given (3) is taken from the ocean, where the concentration is said to vary but slightly. Along the marsh the concentration varied widely, being stronger than the ocean water near the marsh, and much more dilute if flood water is coming down the drainage channels. *Salicornia australis*, which had the highest chloride content, 39.30 gms. per litre of sap, was found by Barger's method to have an osmotic pressure of 47.1 atmospheres, by Freezing Point determination 47.5 atmos., and by density, assuming the sap to be a pure solution of common salt, 45.5 atmos. In Utah, Harris (2) found that in a sample of *Salicornia utahensis* which had an osmotic pressure of 43.9 atmos., there was a chloride content of 37.1 gms. per litre, but the highest pressure, 51.9 atmos., was associated with a low content of only 25.7 gms. of chloride.

As an abundance of sap was available, the opportunity was taken of comparing the rate of loss by evaporation from the expressed sap and from the plants themselves. The leaves of all the succulents have surprisingly thin cuticles when compared

with those of the plants of other maritime associations, the Sand Dune (Patton (5)) and the Mangrove. All these associations are subject to the same climatic conditions. The cuticle of *Samolus repens* is very much thicker than those of the succulents, a character in keeping with the general appearance of this plant. In Table X. are given the thicknesses of the cuticle in microns, together with the number of stomata per sq. mm.

TABLE X.—THICKNESS OF CUTICLE AND NUMBER OF STOMATA IN SALT MARSH PLANTS.

| Species. | Thickness in Microns. | Stomata per sq. mm. |
|---|--------------------------|------------------------|
| <i>Salicornia australis</i> | 4.4 | 55 |
| <i>Arthrocnemum halocnemoides</i> | 5.1 | 63 |
| <i>Suaeda maritima</i> | 5.3 | 32 |
| <i>Mesembrianthemum australe</i> | 5.1 | 33 |
| <i>Selliera radicans</i> | 5.7 | 55 |
| | { Upper | 53 |
| | { Lower | 62 |
| <i>Samolus repens</i> | 9.0 | 59 |
| | { Upper | |
| | { Lower | |

The plants given in Table X. may be grouped into three classes, the first two are leafless, the stomata being on the cladodes, the next two have cylindrical leaves with stomata all round and the last two are flattened, but have stomata on both faces. As the leaves of *Mesembrianthemum australe* had the highest water content, and also a very thin cuticle, it was suitable for experiments on water loss. Its osmotic pressure was close to that of a molar solution of common salt, although its chloride content (Table IX.) was appreciably lower. Experiments with single leaves, which had their bases sealed with a mixture of paraffin wax and vaseline, showed that the ratio of loss per unit area, compared with that from a free surface of water, was 1:12.3. When the leaves showed signs of shrivelling the water loss was rapid. Also leaves which were pigmented lost moisture more rapidly than those which were a normal green. Similar results were noted with other pigmented plants. The increased loss is probably due to the fact that the leaves are gradually dying.

As the transpiration from single leaves may be affected by the injury in breaking them off, a large healthy branch was used for comparison with the water loss from three similar containers, one with water, the second with mesembrianthemum sap, and the third with a molar solution of common salt. The branch had nineteen leaves, having an area of 88 sq. cms. All the experimental material was placed in a constant temperature room, the average temperature being 70 degrees F. The ratios of water loss from unit area are given in Table XI.

TABLE XI.—COMPARISON OF WATER LOSS.

| Material. | | | | | | | Ratio of Water Loss. |
|------------------------|----|----|----|----|----|----|----------------------|
| Water | .. | .. | .. | .. | .. | .. | 23 |
| Mesembrianthemum sap | .. | .. | .. | .. | .. | .. | 20 |
| Salt Solution 1.N | .. | .. | .. | .. | .. | .. | 19 |
| Mesembrianthemum plant | .. | .. | .. | .. | .. | .. | 1 |

It will be seen that the loss of moisture from the expressed sap does not differ greatly from the loss from pure water, but differs very greatly from that of the plant itself. The plant continued to grow for several weeks, the leaves at the base shrivelling in order of age. Experiments with shoots of *Suaeda maritima* gave similar results to those of Table XI., which show that the high salt concentration of the sap is not a protection against water loss. It may be noted here that the amount of evaporation varies considerably according to the type of container used, even though they be placed near one another, and the solutions are all at the same depth from the rim.

DISCUSSION.

The question whether a halophyte is a xerophyte or not is raised by the habitat in which these plants occur. Since the moisture content of the soil is high and the reservoir beneath is close to the surface, there does not appear to be any necessity for the plant to store water. It is quite possible, as stated by Schimper (6), that the high concentration of the soil solution may make it physiologically dry, which seems to be the case with *Mesembrianthemum australe*. The storage of water in this plant appears to be a provision against lack of supply when the soil concentration is high. Its own moderately low concentration, lower than that of the soil, and its ability to grow without an external water supply, both suggest xerophytism; but any protection against excessive transpiration is not shown save, perhaps, by the low number of stomata per unit area. In the marsh proper, the plants can in no way be considered xerophytes. The soil is always moist and the high concentration of the soil solution is offset by the high concentration of the cell sap. It may therefore be assumed that the plants do not suffer any disadvantage as regards water requirements. That the strength of the soil solution is not an adverse factor may be deduced from the lateness of flowering of the marsh plants, which occurs when the salt concentration in the soil is at or near its maximum. Generally, in Southern Victoria, October is the month of greatest floral activity, but in the marsh the maximum occurs between November and February, while *Statice australis* is not in full flower until April. The small number of species and their apparent lack of

regularity of flowering makes it impossible to determine exactly the period of greatest floral activity. Even if it be assumed that the succulents utilize their storage of water for growth, flowering and seed production, no such explanation can be given for the non-succulents, particularly *Statice australis*, which is vegetatively active in the period of greatest salt concentration and flowers later. Although the great majority of the individuals are succulents, the presence of plants with a normal morphology, as the grasses, shows that succulence is not a prerequisite for existing in a Salt Marsh. I desire to thank Dr. Heyman, Chemistry Department, University of Melbourne, for the Freezing Point Determinations.

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