

Plant responses to osmotic stress in the coastal zone of Marion Island

V.R. Smith

Institute for Environmental Sciences,
University of the Orange Free State, Bloemfontein 9301.

Leaf water potential and osmotic potential responses to changes in soil salinity are described for six Marion Island (sub-Antarctic) vascular species. These responses were associated with changes in leaf tissue and leaf sap chemical composition. Sodium is the dominant cation in the leaf sap of the shore-zone species and is readily taken up in response to increases in soil salinity. This appears to be reversible and leaf sodium levels are rapidly reduced following the initial increase. Species growing further inland, away from the direct influence of seawater and the heaviest deposition of salt spray, utilise magnesium and potassium ions in osmotic adjustment to enhanced salinity. Sodium uptake, forced by excessive substrate sodium levels appears not to be readily reversible. Salt-water treated plants exhibited lower Ψ and Ψ_{π} levels than plants treated with fresh-water and this corresponds with observations of plants from different osmotic environments in the field. Comments on the validity of the methods used to measure Ψ and Ψ_{π} are provided and the influence of possible errors is described.

Introduction

Tillaea moschata (Crassulaceae) and *Cotula plumosa* (Compositae) form a well-defined salt-spray community on the shore-zone of Marion Island (Huntley, 1971). Soils and plants of this zone are subject to sea water inundation and salt-spray, alternating with periods of intensive leaching by the high rainfall (> 2500 mm per annum). Soil water potential fluctuates rapidly between zero and -23 bars, approximately that of sea water.

The other island vascular species are able to withstand lesser degrees of salinity. The maritime tussock grass *Poa cookii* (Gramineae) occurs at sites heavily influenced by salt-spray but is more characteristic of coastal and inland areas influenced by seal and seabird manuring (Smith, 1976a, 1978). Another grass, *Agrostis magellanica* (Gramineae) dominates nutrient-poor, waterlogged mire peats in areas away from sea water inundation and heavy salt-spray deposition. However, sodium (6-12 ppm) and chloride (16-43 ppm) are the predominant ions in the soil solution of inland mire areas (Grobbelaar, 1974).

Acaena magellanica (Rosaceae) is characteristic of inland communities away from heavy salt-spray influence, although it is also found closer to the shore where rapid flow of fresh-water occurs through the substrate. *Blechnum penna-marina* (Polypodiaceae) forms a closed fernbrake carpet on well-drained slopes and is intolerant of salt-spray. Because the predominant prevailing winds are westerly, fernbrake occurs within 20 m of the south-eastern shore of the island. Following prolonged easterly storms (unusual) the fern fronds are killed and the carpet takes on a 'burnt' or blackened appearance. A similar effect occurs when inland fernbrake areas are colonized by gentoo penguins.

The above-mentioned plant species comprise at least 60 per cent of the vascular biomass in the island's low altitude

(< 300 m above sea level) vegetation. This paper presents differences between them in leaf chemical composition, water potential and osmotic potential as well as the responses of these parameters to soil salinity.

Methods

Leaf ash elements were determined by ashing ground (< 40 mesh), dried (105 °C) leaf material in a muffle furnace (450 °C, 1.5 hours; Smith, 1976b) or by the H₂O₂-H₂SO₄ digestion procedure (Allen *et al.* 1974). Concentrations of Ca, Mg, Na and K in the ash extract were determined by atomic absorption spectrophotometry. Leaf saps were obtained from fresh plant samples which were rinsed with distilled water, patted dry with tissue paper and placed in tightly stoppered glass tubes. The tubes were immersed in boiling water for one hour. On cooling, the sap was expressed from the tissue using a hydraulic press. The cation concentrations of dilutions of the sap were determined by atomic absorption spectrophotometry. Lanthanum nitrate suppressant was added to the sample solutions before Ca determinations. Chloride concentration of the sap was determined using a specific ion electrode.

Leaf water potential (Ψ) was measured on leaf discs by thermocouple psychrometry (Wescor C51 sample chamber in conjunction with a Wescor MJ 55 microvoltmeter). Leaf osmotic potential (Ψ_{π}) was determined in the same manner using filter paper discs saturated with leaf sap.

Sampling details are provided in the discussion.

Results and discussion

Leaf chemical composition

Concentrations of elements in the leaves and leaf saps of the six species under consideration are presented in Fig. 1. Considerable spatial, diurnal and seasonal variation occurs in these concentrations. However, the general ionic patterns in the leaves of the species are depicted in the figure. Sodium is the dominant cation in the two shore-zone species *Tillaea moschata* and *Cotula plumosa*, whereas K predominates over Na in the other island species. *Acaena magellanica* and *Blechnum penna-marina* accumulate approximately equal proportions (on a milli-equivalent basis) of Mg and K. Smith (1976b) demonstrated that Mg is the dominant cation in the exchange-suite of inland soils under these two species. Ca content in the island plants is low, reflecting the low soil Ca status (Smith, 1976b). It is interesting that *T. moschata*, the species most characteristic of saline, Ca-poor habitats, exhibits a fairly marked Ca accumulation in the leaf tissue.

Cationic patterns in the leaf sap of the species resemble those of the leaf ash.

Compared to the inland species, the two shore-zone species contain low leaf sap chloride concentrations, despite the large amounts of Na which accumulate. Na:Cl ratios (Table

1) in *T. moschata* and *C. plumosa* are significantly ($P=0,001$) larger than those of the other species. Cation (Ca+Mg+Na+K):Cl ratios in saps of these two species and *B. penna-marina* are also greater than in the saps of the other three species. This suggests that the shore-zone species prevent accumulation of Cl in their leaves whereas *B. penna-marina* avoids both Na and Cl accumulation.

The low Cl contents suggest that substantial levels of organic anions are produced in *T. moschata* and *C. plumosa* in order to neutralize the high Na leaf levels. In this context the possibility that *T. moschata* exhibits crassulaceous acid metabolism cannot be excluded. It is difficult to envisage the requirement of such an adaptive variant of the carbon fixation pathway under the island conditions of low temperature, high humidity and (generally) waterlogged soils, but it has been suggested that Na is essential in CAM plants (Flowers, Troke and Yeo, 1977) and Laetsch (1974) has proposed that β -carboxylation represents an adaptation for the synthesis of anions to counterbalance the accumulation of cations resulting from growth in saline habitats since CAM (and C₄) plants are often halophytes. *Mesembryanthemum crystallinum* exhibits CAM under saline (NaCl) conditions and C₃ metabolism in non-saline culture (Flowers *et al.* 1977). However, the relation between CAM and halophytism could be fortuitous. The succulent habit of CAM plants may have evolved to maximise the compartment where malate is stored (Woolhouse, 1978) and this feature will also enhance

levels to which Na can accumulate (on a dry weight basis) before osmotic relations of the leaf are adversely affected.

Effect of soil salinity on leaf chemistry

Ten litres of sea water or freshwater per m² were added to six pure stands of each species in the field according to the following schedule: days 1 and 3 — sea water added at 09h00, 10h00, 12h00 and 15h00 SAST (GMT + 2 hours); days 2 and 4 — freshwater added at 09h00, 12h00 and 15h00.

At 06h00, 18h00 and immediately before each water application, approximately 15-20 g (fresh weight) leaves were harvested from each stand. The samples were immediately rinsed thoroughly in running distilled water and dried at 105 °C for 24 to 36 hours. *Blechnum penna-marina*, *Poa cookii* and *Agrostis magellanica* stands were situated ca. 250 m inland while those of *Tillaea moschata* and *Cotula plumosa* occurred on the top of a coastal cliff 2-10 m from the shore. Most leaves of *Acaena magellanica* had senesced at this time (April 1978) so that this species was not included in the investigation.

The changes in Na concentration of the leaf ash over the four days are illustrated in Fig. 2. Considerable diurnal variation occurred and the data were also very variable within harvests. Sodium levels in *T. moschata* and *C. plumosa* increased markedly (c. 200 meq. kg⁻¹; $P=0,001$) within one hour of the first addition of sea water on day 1. Five hours

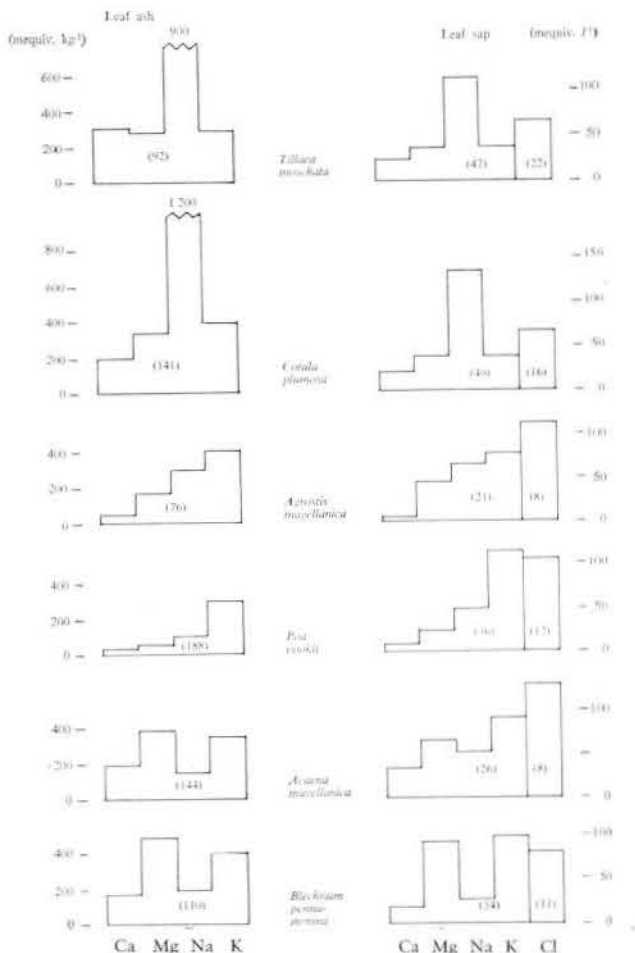


Fig. 1. Chemical composition of leaves and leaf saps in six island species. Number of samples represented indicated in parentheses.

Table 1
Na:Cl and Ca+Mg+Na+K:Cl ratios in the leaf saps of six plant species (calculated on mequiv. basis; ± standard deviation).

| | n | Na:Cl | Cation:Cl |
|------------------------------|----|------------|------------|
| <i>Tillaea moschata</i> | 22 | 1,7 ± 0,40 | 3,1 ± 0,62 |
| <i>Cotula plumosa</i> | 20 | 2,0 ± 0,49 | 3,4 ± 0,75 |
| <i>Agrostis magellanica</i> | 8 | 0,6 ± 0,13 | 1,7 ± 0,36 |
| <i>Poa cookii</i> | 12 | 0,5 ± 0,18 | 1,9 ± 0,48 |
| <i>Acaena magellanica</i> | 8 | 0,4 ± 0,14 | 1,8 ± 0,63 |
| <i>Blechnum penna-marina</i> | 11 | 0,3 ± 0,10 | 2,9 ± 0,64 |

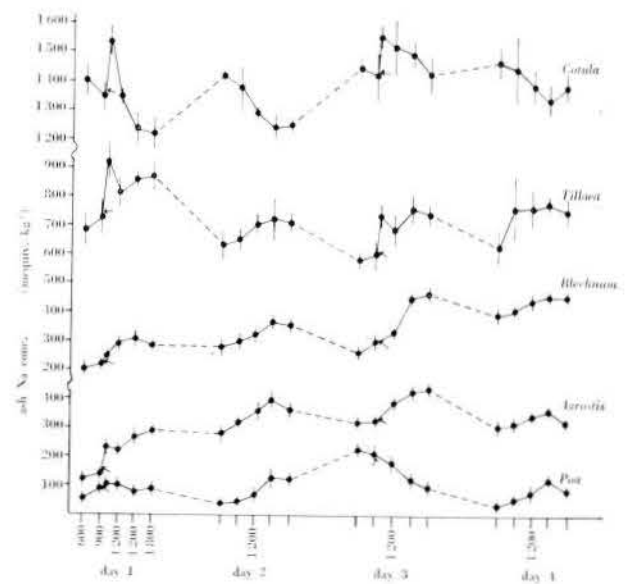


Fig. 2. Leaf ash Na values during alternating days of freshwater and sea water conditions. Arrows indicate times of first application of sea water on days 1 and 3. Vertical bars represent standard deviation of mean value (n = 6).

later the Na content of *C. plumosa* leaves had returned to the normal 16h00 value. Similarly, Na levels in *T. moschata* dropped sharply from the 10h00 peak; however, they increased again during the afternoon, resuming the normal diurnal pattern of leaf Na concentration for this species but at enhanced levels. During the night these levels decreased to normal morning values. Sea water treatment on the third day caused a similar response to that of day 1 in Na contents of both shore-zone species, but the initial response in *T. moschata* was smaller than on the first day and the daily pattern for this species was also displaced to lower Na values by c. 150 meq. kg⁻¹ relative to day 1.

The first sea water treatment also markedly increased the leaf Na content in *Agrostis magellanica*. The enhancement was of a longer duration than in the shore-zone species and the Na levels did not return to the 'pre-sea water' value within 48 hours. On the third day only a small response to sea water addition occurred and the Na concentrations returned to those of the second day within 24 hours. It appears that *Agrostis magellanica* can tolerate enhanced levels of Na in the leaves and is able to maintain these levels against further excessive increases. Smith (1977) postulated that the importance of Na in the leaves of *Agrostis magellanica* represents an (osmotic?) adaptation enabling the species to exploit the nutrient-poor mire areas.

Leaf Na contents of *B. penna-marina* increased slowly following sea water application on the first day. However, the effect was still apparent 48 hours later. Sea water addition on the third day caused a more pronounced uptake of Na into the leaves than occurred on the first day; again the levels did not recover within 24 hours. In contrast to *Agrostis magellanica*, *B. penna-marina* does not appear to be able to reduce excessively high leaf Na levels even after 48 hours and following replacement of saline with freshwater conditions. It is not known what internal levels of Na are toxic to *B. penna-marina* fronds or whether these levels were approached at the end of the trial. Certainly, Na contents in the leaves on the fourth day (400-450 meq. kg⁻¹) were much higher than those normally associated with this species (100-200 meq. kg⁻¹). Maximum values of 280-330 meq. kg⁻¹ have been found in dead, salt-burnt fronds but these are probably lower than the toxic concentrations due to post-mortem leaching by rain. None of the plant species on day 4 appeared to be dying, although the *B. penna-marina* fronds were slightly flaccid.

Leaf Na concentration responses for four of the species are depicted diagrammatically in Fig. 3. Idealized curves (cosine curves with 24-hour wavelengths) have been fitted to the data and they should not be regarded as representing the true diurnal variation, since no data points were available between 6 p.m. and 6 a.m. Rather, the curves indicate the difference in patterns of Na response to sea water application between the five species. *T. moschata* leaf Na levels recovered from both days of sea water treatment while *C. plumosa* showed less of a recovery from the second sea water application. In *B. penna-marina*, Na levels increased throughout the 4 days, apparently with no recovery to lower values. *Agrostis magellanica* showed a similar response to *B. penna-marina* on the first day of sea water application, but no response to the second day of this treatment. The changes in Na concentration of *Poa cookii* leaves during the four days could not be explained in terms of the sea water treatment (Fig. 2).

The behaviour of the other leaf cations during the changes in substrate salinity varied according to species and also between days 1 and 3. The various responses were all very

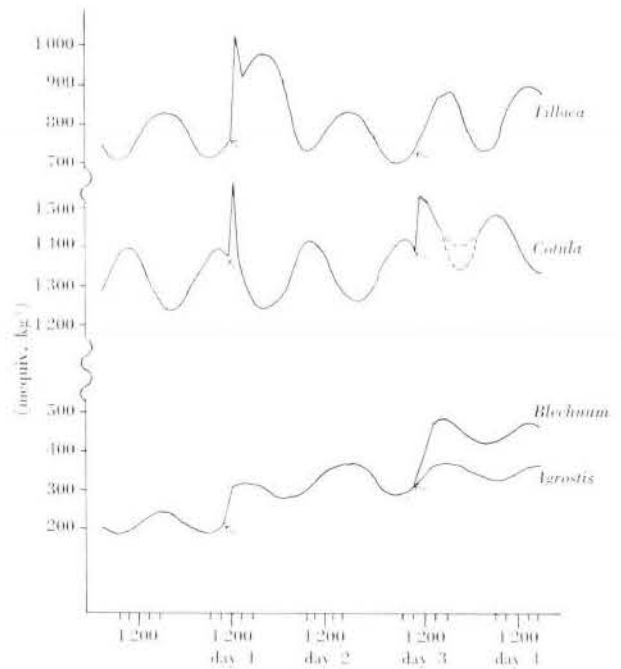


Fig. 3. Idealized representation of response of leaf Na content to alternating sea water and freshwater applications. Arrows indicate time of first sea water application on days 1 and 3.

much smaller than the changes in leaf Na concentrations, however, and within-harvest variability of the K and Mg data was especially great. Small, significant ($P=0.05$) increases in Mg, Ca and K occurred in *T. moschata* leaves between days 3 and 4, possibly resulting from salinity effects on day 3. The increase in Mg occurred immediately following sea water application and continued until 09h00 on day 4. In contrast, Ca and K contents began increasing during the night of day 3 and continued throughout the morning of day 4.

Sea water application also significantly decreased leaf ash K concentrations (data not shown) for the first 6-9 hours in *B. penna-marina*, representing an inverse response to changing Na levels. Mg values (not shown) in this species were inconsistent but showed a morning decrease to noon values, followed by a strong rise to the 18h00 levels. Sea water treatment appeared to lessen the afternoon increase but the effect could not be determined statistically.

Effect of sea water on leaf sap chemistry

Fibrous peat sods containing *T. moschata* and *C. plumosa* were saturated with sea water and placed in shallow plastic trays in the field. At noon on the second day leaf samples were taken for sap chemical analysis. The sods were then leached for 10 minutes with freshwater and replaced in the trays. Twenty-four hours later samples were again removed for leaf sap analysis (Fig. 4 a and b). The experiment was repeated using fresh plants (Fig. 4 c and d) and a further trial, in which freshly-collected sods were leached with freshwater for 2 days and then subjected to 24 hours of sea water treatment, was also performed (Fig. 4 e and f).

The results indicate that Na is the dominant cation involved in the response of the leaf sap chemistry to salinity changes, accounting for 65 to 79 per cent of the total cation concentration change in *T. moschata* and 68 to 129 per cent in *C. plumosa*. Mg levels also responded directly to salinity

changes (7-34 per cent of total cation change in *T. moschata* and 11-21 per cent in *C. plumosa*), whereas sap K and Ca responses were inconsistent (negative values in Fig. 4 indicate that the change in element concentration was opposite in direction to that of the total cation complement, hence percentage values for Na in excess of 100 per cent in some cases).

These responses are similar to those of isolated plants of the two species placed in deionized or sea water in the laboratory, and also to changes in leaf sap chemistry of plants in the field following severe sea water inundation at sites where rainfall leaching had predominated for several days. However, leaf sap concentrations of plants growing at increasing distances from the shore revealed another facet of the response of these plants to salinity levels (Fig. 5 a and b). *T. moschata* plants 45 m from the shore possessed substantially lower leaf sap total cation concentrations than did plants 5 m from the shore, due mainly to lower Mg levels. Plants growing 75 m from the shore had significantly lower cation contents than those at 45 m, but the decrease between these two localities was almost entirely due to depressed Na levels, Mg concentrations actually increasing. A similar pattern was evident for *C. plumosa*, that is, the difference in Na concentration between

plants from 5 and 45 m was smaller than that between plants from 45 m and 75 m from the shore and the Mg content increased between 45 and 75 m. Cation concentrations in the soil solution decreased markedly between 5 and 75 m but the ratios of cations to each other remained almost exactly constant, reflecting that of sea water (Na:Mg:K:Ca = 46:6:0.6:1.2). It seems likely that the response of *T. moschata* and *C. plumosa* leaf chemistry to salinity under natural conditions involved a qualitative aspect which was not apparent in the crude trials reported here, involving gross manipulations of salinity levels. Figure 5 also presents the differences in sap chemistry of *Blechnum penna-marina* (Fig. 5c) and *Acaena magellanica* (Fig. 5d) between plants from relatively saline (130 m from the shore) and non-saline (450 m inland) areas. In these species, Mg and K form the major components of differences in sap cation concentration between sites; Na only comprises a small percentage of these differences. Only small differences in total sap cation concentration were observed in *Poa cookii* plants from shore and inland regions in this study. However, manuring influences

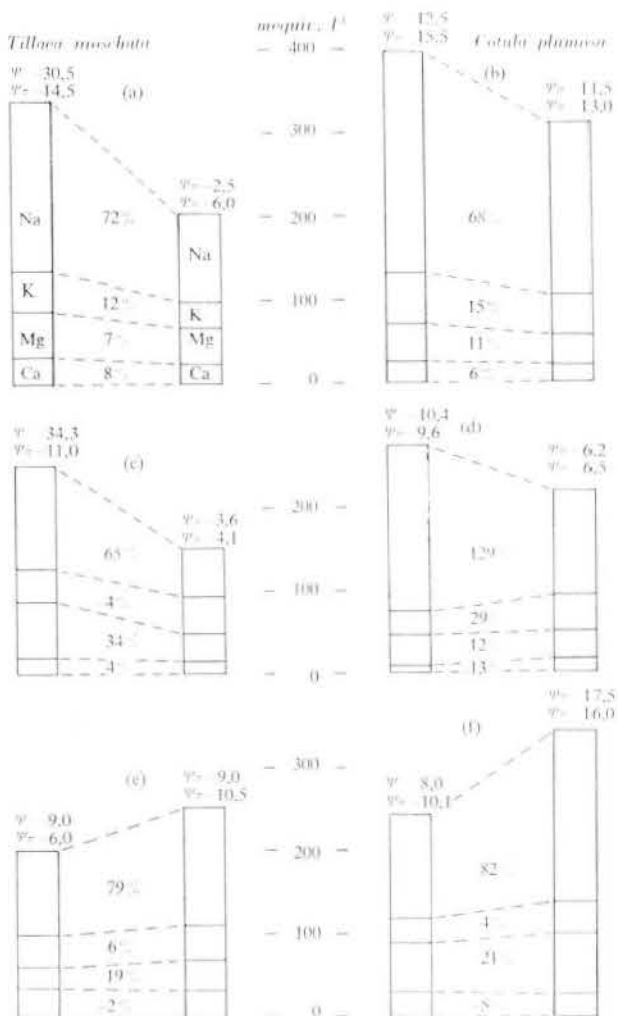


Fig. 4. Responses of leaf sap cation concentrations to changes in substrate salinity. Sequence of elements in all bar graphs is the same as that in (a). Values between bar graphs indicate the percentage contribution of the particular element to the total change in sap cation concentration, Ψ and Ψ_{π} values are in bars.

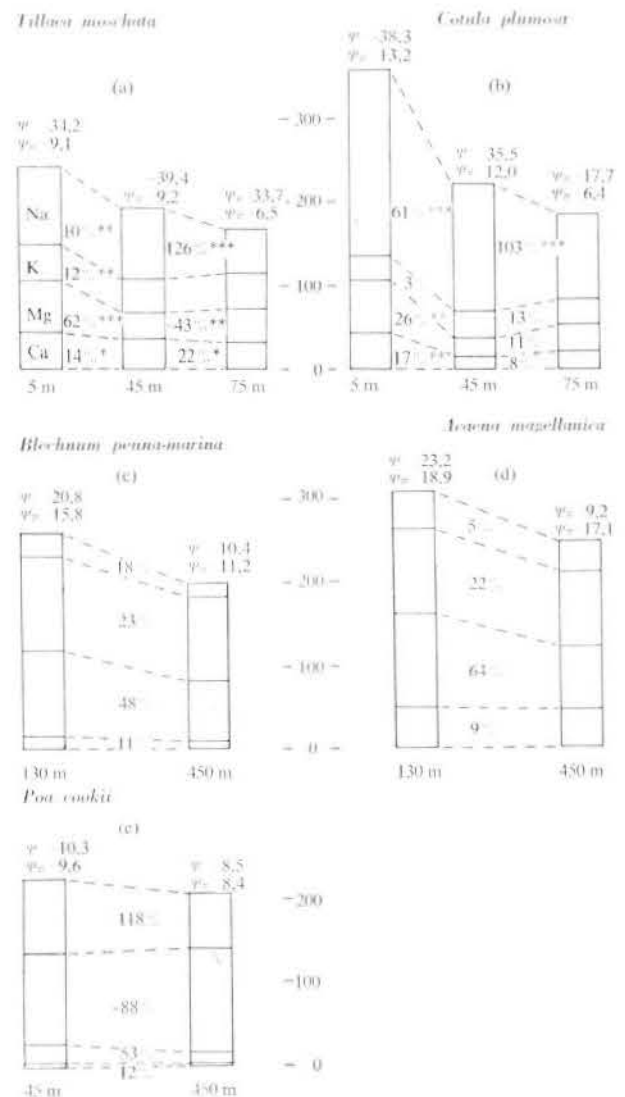


Fig. 5. Leaf sap cation concentrations of plants growing at different distances from the shore. These distances are indicated below each bar graph. Asterisks indicate that the change in element concentration was significant at $*P=0.05$, $**P=0.01$ and $***P=0.001$ ($n=6$). In (c), (d) and (e) only two samples from each site were collected.

Table 2
Ranges encompassing 100% and 85% of Ψ and Ψ_{π} values measured during 1972-73.

| | Ψ (bars) | | Ψ_{π} (bars) | |
|---------------------------|----------------|----------------|---------------------|----------------|
| | 100% | 85% | 100% | 85% |
| <i>T. moschata</i> | -3,6 to -39,4 | -10,2 to -33,3 | -2,1 to -14,5 | -9,1 to -13,7 |
| <i>C. plumosa</i> | -8,0 to -44,0 | -17,0 to -35,2 | -6,4 to -18,3 | -12,0 to -15,0 |
| <i>B. penna-marina</i> | -10,0 to -24,0 | -13,1 to -17,0 | -11,2 to -17,0 | -12,2 to -13,9 |
| <i>Acaena magellanica</i> | -9,7 to -37,4 | -14,9 to -24,4 | -13,0 to -18,9 | -14,9 to -18,4 |
| <i>P. cookii</i> | -4,5 to -43,1 | -15,0 to -21,8 | -8,4 to -17,6 | -12,0 to -16,3 |

by seabirds at the inland site masked the effect of decreasing salinity on leaf chemistry in this species.

Relationship between leaf water potential, osmotic potential and sap chemistry

The ranges of leaf water potential and osmotic potential values obtained during the 1972/73 growing season for plants from different sites and at various times of the day are presented in Table 2. These are similar to those reported for herbs and cultivated plants from mesophilic sites (Richter, 1976). Also provided in Table 2 are the ranges encompassing 85 per cent of the values in each species. Comparing these ranges, it is evident that the two shore-zone species generally exhibited lower (i.e. more negative) Ψ values than did the inland species. *Acaena magellanica* plants characteristically possessed lower Ψ_{π} values than the other species.

Sea water treatment markedly decreased leaf Ψ and Ψ_{π} of *Tillaea moschata* and *C. plumosa* (Fig. 4). Plants from freshwater environments possessed higher Ψ and Ψ_{π} values than did plants from saline areas (Fig. 5), and in *C. plumosa* these values increased with increasing distance from the shore. In *B. penna-marina* and *Acaena magellanica*, however, leaf Ψ responded to changes in atmospheric relative humidity rather than to the small changes in soil water potential. Ψ_{soil} only rarely fell below zero at inland sites under these plants, indicating that the water contents of the soils are saturated and above field capacity. $\Psi_{\text{atmosphere}}$, calculated from R.H. using a derivative of Raoult's Law, was related to Ψ in the two species as follows: *B. penna-marina* $\Psi = 0,013 \Psi_{\text{atm.}} - 11,280$, $r = 0,889^{***}$; *Acaena magellanica* $\Psi = 0,016 \Psi_{\text{atm.}} - 13,060$, $r = 0,800^{**}$. *B. penna-marina* fronds during 'dry', windy conditions (e.g. R.H. = 62 per cent) exhibited values as low as -21 bars without adverse effects, Ψ returning to higher values when the R.H. increased. Salt-burnt fronds of this species possessed similar values (-18 to -22 bars) before leaf death, suggesting that the effect of sea water and/or salt spray was due to ion-specific toxicity rather than osmotic phenomena.

In Figs. 4 and 5, it is evident that salt-water treated plants and those from saline environments possessed lower Ψ than Ψ_{π} , indicating a negative pressure potential ($\Psi_p = \Psi - \Psi_{\pi}$) or leaf cell plasmolysis. In fact, over 80 per cent of Ψ and Ψ_{π} values measured on the island plants corresponded to negative values. In Fig. 6, the calculated Ψ_p is plotted against Ψ for all estimates obtained during 1972/73. Highly significant straight lines of similar slope are found for four of the species. The line for *Poa cookii* is flatter but also significant ($\Psi_p = 0,661 \Psi + 8,716$; $r = 0,946^{***}$). The regression lines show that leaf cell plasmolysis occurs at Ψ values below the intercept on the abscissa, corresponding to -8 bars for *T. moschata*, $c.$ -13 bars for *C. plumosa* and *B. penna-marina*

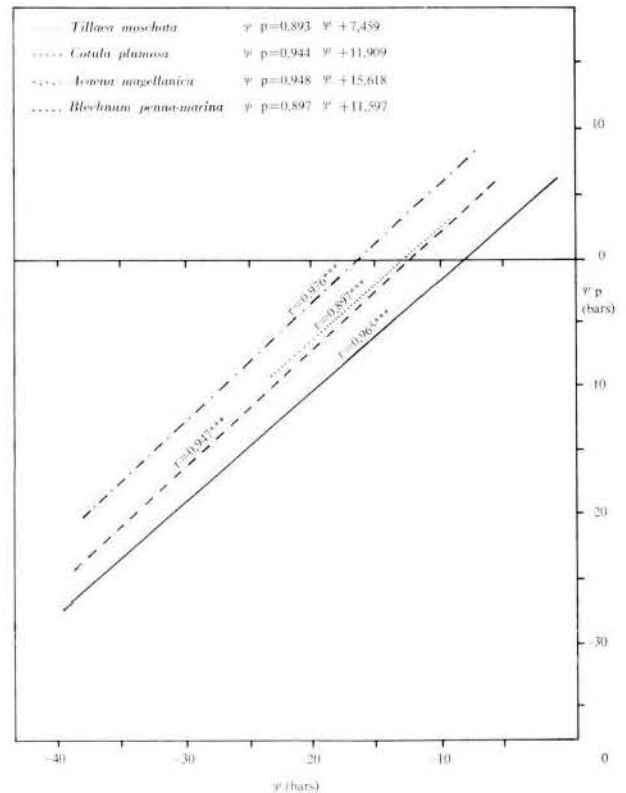


Fig. 6. Regressions of Ψ_p on Ψ for four of the species. r values significant at $P = 0,001$.

and -17 bars for *Acaena magellanica*. These values are much higher than those at which apple leaves begin to exhibit negative turgor ($\Psi = -34$ to -42 bars; Goode and Higgs, 1973), indicating that the island plants are markedly susceptible to osmotic stress and that *T. moschata* is especially vulnerable in this respect. However, the extent to which Ψ_{π} values of expressed sap correspond to the Ψ_{π} of the vacuolar sap *in situ* in the cells is open to question (Slavik, 1974), since during expression from the killed tissue the sap may become contaminated by xylem and phloem solutions, or filtered by passing through tissue structures and the compressed gauze pad of the hydraulic press apparatus. It is possible, therefore, that the observed values are erroneously high due to dilutions of the sap during expression, thus affecting the calculated Ψ_p values. In Table 3 the amounts of cations found in the sap are expressed as a percentage of the total amounts in the corresponding leaf tissue, calculated as:

$$\frac{\text{meq. l}^{-1} \text{ cations in sap} \times \% \text{ H}_2\text{O content of tissue}}{\text{meq. kg}^{-1} \text{ cations in leaf ash}}$$

Approximately 75 per cent of the total leaf cations and virtually all of the Na and K are expressed in the saps of the two shore-zone species. A similar percentage of the total leaf cations is found in *Poa cookii* leaf sap which, however, contains especially high Mg values. Lesser proportions of the leaf cations are found in the saps of the two inland species *B. penna-marina* and *Acaena magellanica*. Except for *P. cookii*, the percentages of total leaf Ca and Mg in the expressed sap are generally lower than those of Na and K, reflecting the structural properties of these elements in the leaves.

The high percentage recoveries of leaf cations in the expressed sap suggest that the sap extraction procedure was

Table 3

Cation contents (\pm standard deviations) of leaf saps expressed as a percentage of their corresponding contents in the total leaf tissues.

| | Ca | Mg | Na | K | Total |
|------------------------|-------------|--------------|--------------|--------------|-------------|
| <i>T. moschata</i> | 37 \pm 4 | 48 \pm 14 | 107 \pm 29 | 103 \pm 34 | 75 \pm 8 |
| <i>C. plumosa</i> | 44 \pm 8 | 68 \pm 15 | 84 \pm 18 | 88 \pm 25 | 73 \pm 12 |
| <i>B. penna-marina</i> | 53 \pm 18 | 69 \pm 8 | 65 \pm 6 | 60 \pm 1 | 62 \pm 1 |
| <i>Acaena</i> | | | | | |
| <i>magellanica</i> | 9 \pm 3 | 8 \pm 1 | 85 \pm 20 | 67 \pm 8 | 44 \pm 1 |
| <i>P. cookii</i> | 70 \pm 12 | 107 \pm 33 | 101 \pm 20 | 74 \pm 23 | 83 \pm 22 |

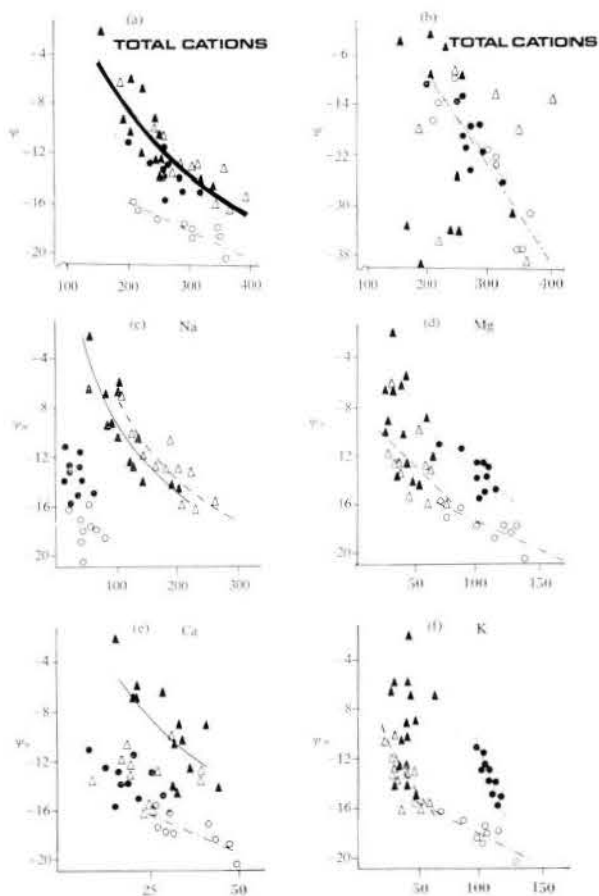


Fig. 7. Relationships between leaf sap cation concentrations and Ψ or Ψ_{π} . Only those regression curves (linear or logarithmic) significant at $P > 95\%$ are presented. — *T. moschata* and *C. plumosa* combined data, — *T. moschata* — *C. plumosa*, - - - *Acaena magellanica*, *B. penna-marina*. All concentrations (abscissae) are in milliequivalents per litre of sap.

efficient in this respect and that Ψ_{π} of the expressed sap $\approx \Psi_{\pi}$ of the vacuolar sap. However, in colloidal vacuolar saps the total *in situ* Ψ_{π} consists of solute and matric components (Nobel, 1974; Slayter, 1967) and most of the colloidal particles responsible for the matric component are filtered out during sap extraction. Ψ_{π} values obtained by the Ehlig (1962) procedure (measured directly on discs of killed tissue without sap expression; $\Psi_p = 0$, hence $\Psi_{\pi} = \Psi$) avoid these limitations and, in the island plants, were 0.2 to 4.2 bars lower than those of the expressed sap; this would serve to displace the regression lines to the left by the corresponding amounts in Fig. 6. However, these differences are too small to explain the widespread occurrence of negative Ψ_p values obtained for the island plants. Killing the tissue by rapid freezing (-15°C , expansion of propane/butane mixture) yielded higher Ψ_{π} values than heat killing.

Another source of error in Ψ_{π} measurements is due to the adsorption of water on the sample chamber walls because of saturated conditions provided by the wetted filter paper disc. Conversely, the measured Ψ values may have been erroneously low, perhaps due to differences between conditions during calibration (filter paper saturated with salt solution) and during leaf Ψ determination (relatively 'dry' discs of leaf tissue; Slavic, 1974). Salt secretion by the tissue during the equilibration (30 minutes) prior to Ψ measurement is known to cause spuriously low values (Klepper & Barrs, 1968). However the errors are most significant at high (> -10 bars) values, the maximum error occurring at full turgor, opposite to the situation in the island plants.

Negative turgor potentials are being increasingly reported for plants under natural conditions (Kappen *et al.* 1972; Turner, 1974) although these negative values are often ignored as being without ecological significance, or as being indicative of a substantial matric component of the total potential (Slayter, 1967). Slavic, (1974), pointed out that the reality of such values and their possible explanation is controversial. More recently, Richter, (1976), noting that more and more authors are reporting negative pressure potential values, suggested that a scrutiny of the occurrence, frequency and magnitude of negative turgor would be useful.

Whether or not the Ψ_{π} or the Ψ values are in error, an examination of the response of these parameters to leaf sap chemistry is instructive. In Fig. 7 the relationships between sap cation concentration and leaf Ψ and Ψ_{π} of all plants sampled at noon ± 1 hour during the 1972/73 growing season are presented.

The Ψ_{π} correlated well with total cation concentrations of the saps of all four species investigated (Fig. 7a), whereas Ψ correlated with total cation concentration only in *Acaena magellanica* and *B. penna-marina* (Fig. 7b). Sodium was responsible for most of the variation in Ψ_{π} for the two shore-zone species, while this ion did not correlate with Ψ_{π} in *B. penna-marina* or *A. magellanica*; Mg was the ion predominantly associated with Ψ_{π} changes in these latter two species. Significant correlations occurred between Ψ_{π} and sap Ca concentrations in *T. moschata* and *C. plumosa* and between Ψ_{π} and K concentrations in *B. penna-marina*, *C. plumosa* and *Acaena magellanica*.

The downward displacement of the regression line for *Acaena magellanica* relative to those of the other three species in Fig. 7a indicates that the sums of leaf sap Ca, Mg, Na and K plus their associated anions were insufficient to account for the measured Ψ_{π} values in this species. The Ψ_{π} values corresponding to the sum of the cation concentrations

Table 4

Percentages of the measured Ψ values accounted for by the Ca + Mg + Na + K + anion (Cl⁻) concentration of the corresponding leaf saps.

| | % |
|---------------------------|---------|
| <i>T. moschata</i> | 95 ± 22 |
| <i>C. plumosa</i> | 96 ± 14 |
| <i>B. penna-marina</i> | 72 ± 16 |
| <i>Acaena magellanica</i> | 60 ± 11 |

(assuming ideal solutions of Cl⁻ salts of these cations) were calculated for each data point in Fig. 7 and expressed as a percentage of the measured Ψ_{π} (Table 4). It is evident that most of the measured Ψ_{π} is accounted for by the leaf sap Ca + Mg + Na + K + anion concentrations of the shore-zone species, whereas the presence of other, undetermined solutes (and/or colloids exerting matric effects) is indicated in the saps of *A. magellanica* and *B. penna-marina*. Work on the role of sugars in maintaining Ψ_{π} values of these plants, as well as ultrastructure studies of the vacuoles and cells, is currently in progress.

Conclusion

Substantial amounts of Na accumulate in the leaves of Marion Island plants (Smith, 1977), representing a response to the dominance of this element in the soil solution. In view of this dominance, and that of chloride, the island plants may be described as saline-tolerant, rather than halophytic. The characteristic shore-zone species *Tillaea moschata* and *Cotula plumosa* possess especially high leaf Na levels; however, none of the species contains the high salt (NaCl > 10 per cent of dry weight) concentrations characteristic of many mangrove and salt-dune plants. Only *T. moschata* is halophytic, in the sense that it is restricted to areas subject to salinity levels, but this may be due to decreased competition by other species. An obligate requirement for saline conditions has not been demonstrated for *T. moschata*, and Huntley (1971) showed that NaCl is not required for successful germination of this species.

Most of the Na taken up from the soil solution is accumulated in the leaves of the island species, in contrast to typical glycophytes which exclude excessive ions from the leaves. However, the evidence available to date does not suggest that the plants are able to withstand osmotic stress by decreasing the osmotic potential of their leaves to any marked degree, so as to maintain turgor. In fact, in this respect, the plants appear to be extremely susceptible to osmotic stress and the data indicate that negative pressure potentials commonly occur in all species. Leaf wilting is extremely uncommon on the island, however, and further investigations into this phenomenon are planned.

Succulentism forms an obvious mechanism of salt-tolerance in *T. moschata*. In *C. plumosa* the development of a succulent, perennial stolon system with short-lived leaves and frequent abscission of salt-laden leaves during the growing season may represent an adaptation to saline conditions. End-of-season leaf abscission in *Blechnum penna-marina* and *Acaena magellanica* may also be important as mechanisms for ridding these perennial plants of excessive NaCl. However, the main factor enabling the survival of these two species is simply avoidance of moderately to grossly saline areas. *Poa cookii* neither avoids nor prefers saline sites and the chemical, Ψ and Ψ_{π} data do not

show obvious responses to salinity. In this species, increasing leaf sap Na concentration often caused increased Ψ_{π} , usually due to depressed Mg and K levels. There is also some evidence that less of the Na taken up by *P. cookii* roots is translocated to the leaves than occurs for the other island species.

The high humidity conditions prevalent on Marion Island (annual mean R.H. 80 per cent) may ameliorate salinity effects by decreasing transpiration and thereby minimizing the amounts of ions moved to the leaves with the transpiration stream. The predominance of Na and Cl in the soil solution may cause depressed uptake of other cations and anions and may be partly responsible for the low Ca and N contents of Marion Island plants. Future work will concentrate on these nutritional aspects of soil salinity.

Note added in proof: Subsequent studies have indicated that *Tillaea moschata* deposits salt on the leaf surface. The rinsing procedure adopted (stream of deionized water) may not have efficiently removed this salt, forming a source of error causing erroneously low water potential values and hence increasing the possibility of negative turgor potentials due to the assessment of $\Psi_p = \Psi - \Psi_{\pi}$. The occurrence of negative Ψ_p values in this species was therefore reinvestigated using a more thorough rinsing of individual leaves with subsequent testing of the rinse-water for chloride. In measurements over a 72 hour period on plants subjected to three treatments: (i) roots rinsed and placed in distilled water (ii) roots placed in 0.5 M NaCl solution and (iii) roots in soil solution — low salinity, ≈ 450 ppm Cl, the frequency of negative turgor values was found to be:

distilled water treatment $^{9/25} \Psi_p$ measurements negative

0.5 M NaCl treatment $^{23/27} \Psi_p$ measurements negative

soil solution treatment $^{10/26} \Psi_p$ measurements negative.

The most negative value measured was $c. -10$ bars and regression of the Ψ_p on the Ψ data yielded an abscissa intercept of $c. -16$ bars compared with -8 bars in Fig. 6. These results form part of a current investigation into the factors influencing plant water status on the island.

References

- Allen, S.E., Grimshaw, H.M., Parkinson, J.A. & Quarmby, C. *Chemical Analysis of Ecological Materials*. Oxford, Blackwell Scientific Publications, 1974.
- Ehlig, C.F. Measurement of energy status of water in plants with thermocouple psychrometer. *Plant Physiol.*, **37**, 288-290, 1962.
- Flowers, T.J., Troke, P.F. & Yeo, A.R. The mechanism of salt tolerance in halophytes. *Ann. Rev. Plant Physiol.*, **28**, 89-121, 1977.
- Goode, J.E. & Higgs, K.H. Water, osmotic and pressure potential relationships in apple leaves. *J. Hort. Sci.*, **48**, 203-215, 1973.
- Grobbelaar, J.U. *A contribution to the limnology of the sub-Antarctic Island Marion*. Unpublished PhD thesis, University of the Orange Free State, 137 pp., 1974.
- Huntley, B.J. Vegetation. In *Marion and Prince Edward Islands*, edited by E.M. van Zinderen Bakker, J.M. Winterbottom & R.A. Dyer, 98-160. Cape Town, A.A. Balkema, 1971.
- Kappen, L., Lange, O.L., Schulze, E.D., Evenari, M. & Buschbom, U. Extreme water stress and photosynthetic activity of the desert plant *Artemisia herba-alba* Asso. *Oecologia (Berl.)*, **10**, 177-182, 1972.
- Klepper, B. & Barrs, H.D. Effects of salt secretion on psychrometric determinations of water potential of cotton leaves. *Plant Physiol.*, **43**, 1138-1140, 1968.
- Laetsch, E.E. The C₁ syndrome: a structural analysis. *Ann. Rev. Plant Physiol.*, **25**, 27-52, 1974.
- Nobel, P.S. *Introduction to Biophysical Plant Physiology*. San Francisco, Freeman, 1974.
- Richter, H. The water status in the plant-experimental evidence. In *Water and Plant Life, Problems and Modern Approaches*, edited by O.L. Lange, L. Kappen & E.D. Schulze, 42-58. Heidelberg, Springer-Verlag, 1976.

- Slatyer, R.O. *Plant-Water Relationships*. Experimental Botany International Monograph Series, Vol. 2. London, Academic Press, 1967.
- Slavik, B. *Methods of Studying Plant Water Relations*. Ecological Studies 9. Berlin, Springer-Verlag, 1974.
- Smith, V.R. The effect of burrowing species of Procellariidae on the nutrient status of inland tussock grasslands on Marion Island. *J. S. Afr. Bot.*, **42**, 265-272, 1976a.
- Smith, V.R. Standing crop and nutrient status of Marion Island (sub-Antarctic) vegetation. *J. S. Afr. Bot.*, **42**, 231-263, 1976b.
- Smith, V.R. The chemical composition of Marion Island soils, plants and vegetation. *S. Afr. J. Antarct. Res.*, **7**, 28-39, 1977.
- Smith, V.R. Animal-plant-soil nutrient relationships on Marion Island (sub-Antarctic). *Oecologia (Berl.)*, **32**, 239-253, 1978.
- Turner, N.C. Stomatal behaviour and water status of maize, sorghum and tobacco under field conditions. II. At low soil water potential. *Plant. Physiol.*, **53**, 360-365, 1974.
- Woolhouse, H.W. Light-gathering and carbon assimilation processes in photosynthesis; their adaptive modifications and significance for agriculture. *Endeavour, New Series*, **2** (1), 35-46, 1978.

The limnology of Marion Island: Southern Indian Ocean

J.U. Grobbelaar

Institute for Environmental Sciences,
University of the Orange Free State, Bloemfontein 9300.

The lentic waters of Marion Island are small shallow lakes, crater lakes, lava-lakelets and wallows, originating from ice-scouring, volcanic activity and biotic influences. Sedimentation and vegetation encroaching from the shore influence the morphology of the water bodies. The lotic water types are mere intermittent rivulets. The water bodies are homothermal and polymictic but in calm conditions energy absorption by the surface water layer and by the benthic algal felts and periphyton raises their temperatures. The waters are dystrophic, with low alkalinity. Nitrogen and phosphorus are detectable only in biotically fertilized waters. The ionic dominance resembles that of sea water. There is very little primary production in the unfertilized waters, and even in the biotically fertilized water bodies there are no fish and the food chain ends with zooplankton.

Introduction

Biological research has been undertaken on the sub-Antarctic island Marion since 1965 and observations on the limnology were made during the first (1965-1966), second (1971-72), third (1972-73) and fourth (1973-74) biological expeditions. Huntley (1971) reported on a few general features of some water bodies and streams, as well as on physical and chemical measurements. The work done during the second and third expeditions was presented by Grobbelaar (1974a) as a PhD thesis. The chemistry and primary production have been reported by Grobbelaar (1974b, 1975 and 1978a), factors affecting the algal growth by Grobbelaar (1978b) and observations on the zooplankton by Kok and Grobbelaar (1978).

The freshwater types

Lentic waters

It is misleading to use the term 'lake' for water bodies on Marion Island as no lake per definition (Odum, 1971) occurs on the island and all are mere ponds or pools restricted to areas of low relief close to the sea. This is due to the lack of suitable lake basins, steep island slope and porosity of the lava rocks. The term 'lake' is, however, used for convenience

and indicates the larger water bodies.

Catchment areas of the water bodies are mainly restricted to their immediate surroundings and stream-fed ones are the exception. The water bodies are often clustered together in groups, e.g. Albatross, Skua, Swartkop Point and Kampkoppie Lakes.

The lentic waters have been classified into four types, i.e. (a) lakes, (b) crater lakes, (c) lava-lakelets, and (d) wallows. An additional distinction can be made between lakes which are: (a) situated on grey lava, (b) situated on black lava, (c) biotically influenced, and (d) not-biotically influenced.

Water bodies on the old grey lavas

There are a few lakes, of which the Albatross and Skua Lakes are the most notable (see Fig. 1). The old grey basalt was covered with glacial depositional landforms and the lake basins are formed in kettles or against moraines (K. Hall, personal communication). Most basins have a sandy-clayish bottom sediment and thicknesses of up to 2,5 m were measured.

A considerable degree of variation in form and size of these lakes is found and surface areas range between 100-32 600 m², with a mean of about 4 000 m². The lakes are all shallow, their maximum depth lying between 0,4 and 2,4 m, with a mean depth of approximately 1 m. None of the lakes has a profundal zone and the littoral zone extends over the entire basin. The basins are usually flat-bottomed with steep sides. Terrestrialization of the basins, mainly from the shores, can change the shapes, where the encroaching vegetation may, under extreme conditions, form a swinging mat or raft. The prevailing strong north-west winds produce waves which hinder terrestrialization and can lead to wave cutting. Three basic lake profile types thus result (see Fig. 2):

Type 1: Protected lakes where terrestrialization takes place along the whole circumference of the shore line.

Type 2: Exposed lakes with a north-westerly shore of peat and a south-easterly shore of rocks.

Type 3: Same as Type 2, except with a south-easterly shore of a sandy-scoria material.

The littoral and supra-littoral vegetation communities