Mineral Ion Composition and Occurrence of CAM-like Diurnal Malate Fluctuations in Plants of Coastal and Desert Habitats of Israel and the Sinai

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Summary. 1. The mineral ion composition and the occurrence of CAM-like diurnal malate fluctuations in species from 6 field locations in Israel and the Sinai were studied during the spring of 1974. The sites were a) a salt swamp near Acre on the Mediterranean Sea shore in the northern part of Israel, b) the high coast near Tel Aviv, c) the southern Dead Sea area near Sedom, d) the Negev highlands surrounding the ancient town of Avdat, e) the Wadi Paran in the southern Negev desert, and f) the Red Sea shore near the southeastern tip of the Sinai peninsula close to the Bedouin village of Nabek. The carbon assimilatory organs of the plants were analysed for Na^+, K^+, Cl^- and SO_4^{2-} as well as for malate at dawn and dusk.

2. Most species analysed are characterized by high levels of mineral ions (mainly Na^+ and Cl^-) often exceeding 300–400 µeq per g fresh weight, and by high Na^+/K^+ ratios in their tissues mainly ranging from 10 to 20. These typical halophytic attributes are particularly found in species of the Acre salt swamp, of the Dead Sea area and the Red Sea shore and in many species of the Negev highlands.

3. In plants occupying the Tel Aviv high coast habitats Na^+ and Cl^- are lower averaging 100 to 200 µeq per g fresh weight. The Na^+/K^+ ratio is about 5.

4. Numerous species mainly inhabiting the less saline loessial plains and wadis of the Negev desert contain only up to 100 µeq Na^+ and Cl^- per g fresh weight and are characterized by Na^+/K^+ ratios of about 1 and below.

5. The salt-accumulating species of the coastal habitats contain Na^+ and Cl^- in more or less equivalent amounts, i.e. halophytes of the "chloride type" in the terminology of Walter dominate these sites. In contrast, many

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Abbreviation. CAM = Crassulacean Acid Metabolism

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inland halophytes chiefly belonging to the Chenopodiaceae accumulate much more Na^+ than Cl^- and/or SO_4^{2-}.

6. The special feature of Na^+ contents which far exceed the sum of Cl^- and SO_4^{2-} distinguishes the inland Chenopodiaceae as a "physiotype" from members of other taxa. The Zygophyllaceae included in this study form a further "physiotype" which is characterized by higher Cl^- than Na^+ concentrations.

7. Five species of the Aizoaceae family investigated showed no special pattern of mineral ion content.

8. Certain species, especially some belonging to the Brassicaceae, showed a slight malate accumulation during the day.

9. CAM-like diurnal malate fluctuations were only observed in four species: the halophytic Aizoaceae *Mesembryanthemum crystallinum*, *M. forsskalii* and *M. nodiflorum* and the non-halophytic Asclepiadaceae *Caralluma* It is suggested that, among halophytes, the capability to perform CAM is generally restricted to members of the Aizoaceae.

Introduction

In a number of investigations it has been shown that salinity may exert a profound effect on photosynthetic behaviour in the halophytic Aizoaceae *Mesembryanthemum crystallinum*. Plants cultivated in a medium of low salinity normally perform C_3 photosynthesis. In contrast, plants treated with high salt concentrations (for example 400 mM NaCl) show features of CAM, i.e. exhibit a night-time net CO_2 fixation and malate accumulation, the malate again decreasing during the day (Winter, 1975; Winter and Lüttge, 1976). There is an associated increase in the assimilation/transpiration ratio (Winter, 1975)

CAM is also observed in non salt treated *M. crystallinum* when exposed to reduced water supply (Winter, 1974a, b). Therefore it has been suggested, that salinity regulates the photosynthetic patterns via its effect on plant water status. The change to CAM in *M. crystallinum* and the accompanying increase in assimilation/transpiration ratio support the widely accepted idea that CAM facilitates net carbon gain under ecological situations where water availability is reduced (Kluge and Fischer, 1967; Neales et al., 1968; Bartholomew, 1973; Meizner and Rundel, 1973; Szarek et al., 1973; Szarek and Ting, 1974).

These observations renewed an interest in the occurrence of CAM in halophytes, although earlier attempts had failed to demonstrate CAM in such species (Bennet-Clark, 1931; Bharucha and Rangnekar, 1957; Ranson and Thomas, 1960). An investigation of the relationship between CAM and salt tolerance was also encouraged by the coupling of salinity with soil dryness in many deserts (Walter, 1973a; Caldwell, 1974) and by the frequently observed succulence of many halophytes (Biebl and Kinzel, 1965; Jennings, 1968; Weissenböck, 1969). Leaf and stem succulence is generally associated with CAM and thought to represent a high capacity of the cell vacuoles for night-time accumulation of malate.

To extend our knowledge of the role of CAM among plants growing under saline and/or arid conditions, halophytes and non-halophytes of different habitats of Israel and the southern Sinai were surveyed in the field, using diurnal malate fluctuations as a CAM criterion. In addition, the mineral ion composition (Na^+, K^+, Cl^- and SO_4^{2-}) of the carbon assimilatory organs was determined to obtain information about the halophilic character and the salt tolerance of the species investigated.

Materials and Methods

The plant material was collected by one of us (K.W.) during a stay in Israel from the end of March to the middle of May 1974. This time includes the end of the rainfall season and the early dry period. Rainfall occurs in this part of the Middle East mainly from November to March. In the northern territories of Israel annual precipitation ranges from 500 to 1,000 mm, whereas in the southern desert regions rainfall hardly exceeds 100 mm per year. During the field work in Israel the day temperature maxima ranged between 25 °C and 30 °C and the minimum night temperatures were between 10 °C and 20 °C, in all cases depending on the particular place investigated. (The climatic factors are extensively described in a following paper.) Samples were taken of the dominant species of the plant communities of each region.

Leaves and sometimes carbon assimilatory stems were harvested at dawn and dusk, washed with distilled water and dried with blotting paper. After determination of fresh weight (3–10 g per sample), the samples were collected in polyethylene bottles (volume 50 ml) and covered with hot, distilled water. To kill the plant material the bottles were subsequently heated for 20 min in a boiling water bath. By this treatment the polyethylene became a little soft. The lids were screwed onto the bottles while being hot. During cooling a low pressure arose in the bottles and, as a consequence, they shrank slightly suggesting that they were air tight. After returning from each field trip the samples were stored in a freezer at −18 °C. The excursions took at most 3 days, but normally lasted only some hours. For $\delta^{13}C$ determinations plant material was dried at 70 °C in an oven.

For analysis the samples were transported to Darmstadt by air-freight. The plant material was homogenized and centrifuged and the residues washed twice with boiling distilled water. Aliquots of the combined supernatants (the total volume ranged from 30 to 60 ml) were used to determine malate enzymatically after Hohorst (1970), Na^+ and K^+ by flame photometry and Cl^- by electrometric titration. SO_4^{2-} was estimated after Kakac and Vejdelek (1963). A 1 ml extract was titrated with 0.1 N HCl to a pH of 4. Chloranilic acid barium salt ($C_6BaCl_2O_4 \cdot 3H_2O$) was added and the mixture heated for 5 min in a water bath. The total volume was then brought to 5 ml with 30% ethanol. After centrifugation the extinction of the supernatant was measured at 530 nm with a Zeiss PM QII spectrophotometer. Solutions of 1 to 30 mM Na_2SO_4 were used for calibration.

The oven dried plant tissue was used for $\delta^{13}C$ determinations in Lower Hutt (for methodical details see: Winter et al., 1976). The carbon isotope composition is expressed as $\delta^{13}C$ in $^0/_{00}$ with respect to Pee Dee belemnite limestone (PDB) where

$$\delta^{13}C = \left[\frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{Standard}} - 1 \right] \times 1,000.$$

The Plant Habitats

Site 1. Salt swamp on the flat coast of the Mediterranean Sea near Acre.

This area is an inundation saline (Zohary, 1962) which is formed by water of the Na'amen River and by seawater penetrating from the Mediterranean Sea.

Site 2. High coast of the Mediterranean Sea near Tel Aviv.

Four zones are distinguished above the water line (Waisel, 1972): The sand beach, the cliff, the plateau on the cliff top and the belt with sand dunes. The shallow soil of the cliffs and plateaus

is a sandy loam overlaying the "Kurkar" sandstone (fossile sand dunes cemented together by calcareous solutions) (Orni and Efrat, 1971). Soil salinity is predominantly aeolic in origin. Sprayed seawater evaporates and the remaining salt is blown inland. In addition, the cliff often receives windborne drops of seawater.

Site 3. The south-western foreshore of the Dead Sea near Sedom.
    The Dead Sea region is one of the main areas of Israel with a halophytic flora. The Dead Sea-water is well known for its extremely high salt content of nearly 30%. A vegetation transect of the site investigated shows a zonation which largely corresponds to that described by Zohary (1962) for this area.

Site 4. Surroundings of the ancient town of Advat in the central Negev highlands.
    The highland (500–800 m above sea level) contains numerous loessial depressions and dry river beds which flow to Wadi Zin. Dwarf shrubs are dominant elements of the vegetation. According to Evenari et al. (1971) 6 main habitats of the Negev highlands can be distinguished: 1) hilltops, 2) slopes, 3) loessial plains, 4) runnels in the loessial plains, 5) loessial wadis, 6) gravelly wadis. Soil salinity decreases in this sequence from about 2–4% per dry weight of soil on the hilltops to negligible amounts in the wadis (Tadmor et al., 1962). Furthermore, water available to plants increases in this sequence except for the gravelly wadis which store less water than the loessial wadis. Of the 6 habitats mentioned, the loessial wadis offer the most favourable conditions for plant life.

Site 4'. En-Avdat, a canyon of Wadi Zin about 5 km from Avdat, which stays partly wet throughout the year.

Site 5. Loessial, gravelly edge of Wadi Paran in the southern Negev (at the intersection between the wadi and the road from Mizpe Ramon to Eilat).

Site 6. Sandy flat coast near the south-eastern tip of the Sinai-peninsula at the Red Sea (Gulf of Eilat), about 18 km north of the Bedouin village of Nabek.
    In this region a saline ground water table is very near the soil surface. To some extent the water originates from the ground water stream of Wadi Kid, which comes down from central Sinai, forming a broad delta at Nabek. Another part of the water infiltrates from the sea. The vegetation of this area has been described by Evenari and Gutterman (1973).

Results and Discussion

1. Mineral Ion Composition

a) Plants with Halophytic Attributes

Amounts of Salts Accumulated. Most of the species listed in Table 1 show high leaf concentrations of Na^+ and Cl^-, sometimes exceeding 600–700 µeq per g fresh weight, which clearly establishes them as halophytes. One has to consider that the leaf material has been collected at the end of the rainy season when salinity in the upper soil layers is decreased. It can be expected that salt concentrations in the soil would increase during the rainless summer months, especially in the desert habitats. Therefore, in this season salt concentrations in the leaf sap may be still higher than reported here.

The highest salt concentrations of more than 300 to 400 µeq Na^+ per g fresh weight accompanied by variable amounts of Cl^-, are observed in species of the salt swamp near Acre, of the Dead Sea and the Red Sea area and in many species of the Negev highlands. K^+ contents of these plants are much lower than Na^+ contents, as is found in "salt accumulators" (Greenway and

Table 1. Water content (in percent of fresh weight and dry weight), fresh weight/dry weight ratio, Na^+, K^+, Cl^-, SO_4^{2-} and malate contents of leaves (and partly stems) of species from different sites in Israel and the Sinai. The mineral ion values and malate values are expressed as µeq per g fresh weight. FW=fresh weight, DW=dry weight

Species	Water content		FW/DW	Na^+	K^+	Cl^-	SO_4^{2-}	Malate	
	% FW	% DW						dusk	dawn
Site 1 (Acre)									
Inula crithmoides L. (Asteraceae)	91.9	1,123	12.3	203	9	392	29	4.4	4.0
Arthrocnemum macrostachyum (Moric.) Moris et Delponte (Chenopodiaceae)	89.9	894	9.9	455	43	490	43	1.6	< 1.0
Arthrocnemum cf. *fruticosum* (L.) Moq. (Chenopodiaceae)	89.3	836	9.4	440	48	537	78	< 1.0	2.0
Halimione portulacoides (L.) Aellen (Chenopodiaceae)	87.0	668	7.7	385	34	453	85	—	< 1.0
Plantago crassifolia Forssk. (Plantaginaceae)	90.7	981	10.8	128	22	235	94	1.4	1.2
Site 2 (Tel Aviv)									
Carpobrotus edulis L. (Aizoaceae)	93.6	1,466	15.7	164	5	280	21	5.0	11.2
Mesembryanthemum crystallinum L. (Aizoaceae)	94.7	1,809	19.1	308	10	175	28	9.8	56.8
Pancratium maritimum L. (Amaryllidaceae)	89.9	892	9.8	98	58	132	39	14.4	11.2
Crithmum maritimum L. (Apiaceae)	91.3	1,044	11.4	226	17	251	12	< 1.0	< 1.0
Anthemis leucanthemifolia Boiss. et Bl. (Asteraceae)	92.3	1,194	12.9	134	20	137	17	5.0	—
Artemisia monosperma Del. (Asteraceae)									
summer leaves	88.1	738	8.4	212	54	230	30	5.2	1.0
winter leaves	83.9	521	6.2	114	62	116	46	—	2.2
Atractylis flava Desf. (Asteraceae)	88.4	761	8.6	57	78	99	27	9.0	26.0
Diotis maritima (L.) Sm. (Asteraceae)	90.7	977	10.8	111	30	152	8	5.0	1.0
Inula crithmoides L. (Asteraceae)									
young leaves	91.9	1,134	12.3	268	5	359	45	7.2	7.6
old leaves	91.5	1,081	11.8	423	14	540	39	4.6	1.4

Table 1 (continued)

Species	Water content		FW/DW	Na$^+$	K$^+$	Cl$^-$	SO$_4$$^{2-}$	Malate	
	% FW	% DW						dusk	dawn
Senecio joppensis Dinsm. (Asteraceae)	– (succulent)	–	–	167	23	175	17	15.2	5.2
Cakile maritima Scop. (Brassicaceae)									
young leaves	92.5	1,225	13.2	146	24	156	22	11.2	3.2
old leaves	94.7	1,781	22.7	140	18	155	13	12.2	2.2
Silene succulenta Forssk. (Caryophyllaceae)	92.5	1,235	13.3	180	26	145	18	3.6	< 1.0
Salsola kali L. (Chenopodiaceae)	93.3	1,398	15.0	183	74	112	33	7.4	9.0
Reichardia tingitana (L.) Roth (Cichoriaceae)	92.4	1,216	13.2	175	24	195	17	5.8	6.6
Helianthemum stipulatum (Forssk.) Christens (Cistaceae)	83.1	491	5.9	74	25	89	20	1.8	< 1.0
Cyperus mucronatus (L.) Mab. (Cyperaceae)	81.2	433	5.3	182	37	177	13	10.2	7.6
Medicago marina L. (Fabaceae)	79.8	396	5.0	108	29	106	26	< 1.0	1.4
Oenothera drummondii Hook. (Onagraceae)	85.0	566	6.7	40	12	58	35	8.4	< 1.0
Plantago sarcophylla (Boiss.) Zohary (Plantaginaceae)	90.2	923	10.2	141	19	184	31	1.4	< 1.0
Limonium oleifolium Mill. (Plumbaginaceae)	82.9	487	5.9	138	37	180	153	16.8	21.2
Limonium sinuatum (L.) Mill. (Plumbaginaceae)									
upper leaves	79.7	392	4.9	161	27	125	85	18.4	1.4
lower leaves	83.9	522	6.2	168	28	99	104	16.0	18.0
Site 3 (Dead Sea)									
Aizoon canariense L. (Aizoaceae)	86.4	640	7.4	534	97	135	114	< 1.0	< 1.0
Mesembryanthemum forss-kalii Hochst. ex Boiss. (Aizoaceae)	92.1	1,170	12.7	474	74	486	40	16.0	125.6
Mesembryanthemum nodiflorum L. (Aizoaceae)	87.1	682	7.8	428	60	242	68	8.0	179.0

Table 1 (continued)

Species	Water content		FW/DW	Na$^+$	K$^+$	Cl$^-$	SO$_4^{2-}$	Malate	
	% FW	% DW						dusk	dawn
Arthrocnemum macrostachyum (Moric.) Moris et Delponte (Chenopodiaceae)	82.2	463	5.6	873	41	773	167	<1.0	<1.0
Anabasis setifera Moq. (Chenopodiaceae)									
leaves	80.6	416	5.2	902	69	110	123	8.0	21.8
stems	78.6	368	4.7	557	64	142	159	15.0	41.4
Atriplex halimus L. (Chenopodiaceae)	77.3	340	4.4	487	159	790	111	7.8	9.4
Salsola tetrandra Forssk. (Chenopodiaceae)	77.1	339	4.4	702	164	134	371	2.8	1.6
Seidlitzia rosmarinus Bge. (Chenopodiaceae)	−	−	−	687	56	72	225	11.8	21.6
Suaeda fruticosa Forssk. (Chenopodiaceae)									
young leaves	82.1	459	5.6	1,129	20	398	246	−	<1.0
old leaves	−	−	−	1,178	34	456	144	−	3.2
Suaeda monoica Forssk. ex J.F. Gmel (Chenopodiaceae)	80.6	417	5.2	733	83	283	188	9.0	3.4
Tamarix nilotica (Ehrenberg) Bge. (Tamaricaceae)	61.9	162	2.7	208	50	179	80	5.8	1.0
Nitraria retusa (Forssk.) Aschers. (Zygophyllaceae)									
young leaves	79.6	396	5.0	266	31	275	29	5.4	2.6
old leaves	81.5	442	5.4	259	27	375	66	<1.0	5.4
Site 4 (Avdat)									
Mesembryanthemum nodiflorum L. (Aizoaceae)	92.4	1,251	13.5	365	92	92	84	22.4	60.2
Caralluma negevensis Zoh. (Asclepiadaceae)	92.0	1,150	12.5	67	25	25	15	47.4	114.6
Artemisia herba alba Asso. (Asteraceae)	81.1	434	5.3	144	67	30	60	28.2	32.8
Gymnarrhena micrantha Desf. (Asteraceae)	87.6	714	8.5	142	62	111	49	20.6	−
Leontice leontocephalum L. (Berberidaceae)	80.3	411	5.1	8	70	1	20	38.4	12.8
Diplotaxis harra (Forssk.) Boiss. (Brassicaceae)	86.1	625	7.2	78	101	50	27	104.0	59.8

Table 1 (continued)

Species	Water content		FW/DW	Na$^+$	K$^+$	Cl$^-$	SO$_4^{2-}$	Malate	
	% FW	% DW						dusk	dawn
Moricandia nitens (Viv.) Dur. et Barr. (Brassicaceae)									
young leaves	84.7	562	6.6	68	48	60	29	50.8	39.2
old leaves	86.8	674	7.7	75	26	39	38	93.0	53.2
Reboudia pinnata (Viv.) Schulz (Brassicaceae)	88.5	779	8.8	86	86	64	<1	110.0	60.2
Gymnocarpos fruticosum (Vahl.) Pers. (Caryophyllaceae)	80.7	419	5.2	114	83	108	54	<1.0	6.2
Aellenia lancifolia (Boiss.) Ulbrich (Chenopodiaceae)	86.9	664	7.7	559	21	72	137	10.2	14.6
Atriplex halimus L. (Chenopodiaceae)									
young leaves	84.0	532	6.3	1,009	106	774	87	8.4	2.2
old leaves	82.4	482	5.8	711	74	461	114	<1.0	4.2
Chenolaea arabica Boiss. (Chenopodiaceae)	90.7	972	10.7	523	18	86	110	7.6	11.0
Halogeton alopecuroides (Del.) Moq. (Chenopodiaceae)	87.4	695	8.0	605	25	76	124	17.4	23.2
Hammada scoparia (Pomel) Iljin (Chenopodiaceae)	70.4	238	3.4	229	139	57	108	25.4	46.4
Noaea mucronata (Forssk.) Aschers. et Schweinf. (Chenopodiaceae)	76.2	325	4.2	94	117	67	85	—	36.2
Helianthemum kahiricum Del. (Cistaceae)	70.0	234	3.3	36	50	16	46	<1.0	—
Helianthemum ventosum Boiss. (Cistaceae)	73.2	275	3.7	37	47	32	—	5.4	6.0
Colutea istria Mill. (Fabaceae)	76.1	318	4.2	13	66	1	19	19.4	40.4
Erodium hirtum Willd. (Geraniaceae)	83.3	507	6.1	—	—	—	—	13.2	22.2
Reaumira hirtella Jaub. et Sp. (Tamaricaceae)									
highly saline habitat	85.6	608	7.1	655	16	310	331	15.0	8.0
less saline habitat	—	—	—	337	33	174	205	—	—
Reaumuria negevensis Zoh. et Danin (Tamaricaceae)									
young leaves	84.4	549	6.5	438	30	225	153	3.6	4.6
old leaves	78.8	409	4.8	315	34	101	236	<1.0	16.6

Table 1 (continued)

Species	Water content		FW/DW	Na$^+$	K$^+$	Cl$^-$	SO$_4^{2-}$	Malate	
	% FW	% DW						dusk	dawn
Thymelaea hirsuta (L.) Endl. (Thymelaeaceae)	61.2	158	2.6	72	54	47	29	13.4	5.4
Zygophyllum dumosum Boiss. (Zygophyllaceae)									
leaf blades	86.6	655	7.5	376	10	603	11	35.2	24.6
petioles	86.4	643	7.4	276	17	644	11	17.4	10.8
old petioles	86.9	675	7.7	232	15	533	11	63.2	10.4
Site 4′ (En-Avdat)									
Inula crithmoides L. (Asteraceae)									
young leaves	91.4	1,085	11.9	184	37	266	44	< 1.0	1.0
old leaves	90.0	903	10.0	238	10	399	45	< 1.0	< 1.0
Salsola tetrandra Forssk. (Chenopodiaceae)	84.4	540	6.4	625	68	144	324	9.0	15.0
Suaeda vera Forssk. ex J.F. Gmel var. *deserti* Zoh. et Baum (Chenopodiaceae)	89.8	890	9.9	651	30	168	151	11.6	—
Nitraria retusa (Forssk.) Aschers. (Zygophyllaceae)									
young leaves	82.3	467	5.7	258	20	226	26	12.6	35.2
old leaves	83.2	497	6.0	271	12	347	47	25.8	15.6
Site 5 (Wadi Paran)									
Centaurea lanulata Eig. (Asteraceae)	87.0	670	7.7	46	53	2	76	—	13.2
Diplotaxis acris (Forssk.) Boiss. (Brassicaceae)	91.1	1,050	11.5	36	127	44	15	67.4	33.0
Matthiola livida Del. (Brassicaceae)	89.9	886	9.9	34	68	1	< 1	5.0	—
Zilla spinosa (L.) Prantl (Brassicaceae)	85.0	570	6.7	11	64	12	11	71.8	59.8
Gymnocarpos fruticosum (Vahl.) Pers. (Caryophyllaceae)	83.8	535	6.4	48	68	40	—	—	< 1.0
Anabasis articulata (Forssk.) Moq. (Chenopodiaceae)	65.7	192	3.0	301	138	46	68	21.8	21.2
Hammada salicornica (Moq.) Iljin (Chenopodiaceae)	77.2	340	4.4	278	91	34	115	23.4	17.6
Reichardia tingitana (L.) Roth (Cichoriaceae)	92.4	1,203	13.0	161	63	131	56	< 1.0	4.0

Table 1 (continued)

Species	Water content		FW/DW	Na$^+$	K$^+$	Cl$^-$	SO$_4$$^{2-}$	Malate	
	% FW	% DW						dusk	dawn
Acacia gerrardii Benth. ssp. *negevensis* Zoh. (Mimosaceae)	70.0	233	3.4	17	40	6	–	12.4	8.0
Rumex vesicarius L. (Polygonaceae)	92.4	1,216	13.2	56	55	24	35	15.2	22.6
Ochradenus baccatus Del. (Resedaceae)									
leaves	70.0	233	3.3	24	75	1	42	21.2	12.8
stems	80.8	421	5.2	26	78	1	47	23.2	–
Haplophyllum tuberculatum (Forssk.) Juss. (Rutaceae)									
leaves	75.0	303	4.1	21	50	37	28	23.6	8.4
stems	70.2	235	3.4	25	69	19	53	11.0	12.0
Lycium arabicum Schweinf. (Solanaceae)	86.6	652	7.5	155	97	303	43	36.8	36.0
Site 6 (Nabek)									
Avicennia marina (Forssk.) Vierh. (Avicenniaceae)	67.3	206	3.1	467	165	383	242	< 1.0	6.0
Limonium axillare (Forssk.) Ktze. (Plumbaginaceae)	60.0	151	2.5	173	65	136	173	< 1.0	< 1.0
Salvadora persica L. (Salvadoraceae)	70.8	245	3.5	318	78	282	22	138.0	154.4
Nitraria retusa (Forssk.) Aschers. (Zygophyllaceae)									
young leaves	81.5	457	5.6	186	14	367	25	8.6	1.0
old leaves	86.5	647	7.5	282	9	520	8	6.8	2.0
Zygophyllum album L.f. (Zygophyllaceae)									
leaf blades	85.6	608	7.1	427	4	535	13	3.6	4.6
petioles	83.9	525	6.3	298	8	504	15	8.8	2.4
old petioles	84.2	545	6.5	458	8	642	< 1	3.8	2.6
Zygophyllum coccineum L. (Zygophyllaceae)									
leaf blades	89.9	922	10.3	508	16	528	4	2.6	4.6
petioles	–	–	–	299	17	590	3	< 1.0	3.0
old petioles	87.2	685	7.9	275	16	642	4	< 1.0	3.4

Osmond, 1970). The Na^+/K^+ ratio usually ranges from 10 to 20 and even reaches 56 in *Suaeda fruticosa* from the Dead Sea area.

The second highest salt level is found in the leaves of the high coast plants of Tel Aviv. Na^+ and Cl^- contents between 100 and 200 µeq per g fresh weight are common. The Na^+/K^+ ratio is approximately 5.

Pattern of Mineral Ion Content in Relation to the Habitats. Many species investigated accumulate about equivalent amounts of Na^+ and Cl^-. This applies mainly to plants of the coastal habitats (Acre, Tel Aviv, Nabek). A mixture of plants with different mineral ion patterns, as classified by Walter (1973a), does not occur at these locations. Walter distinguishes chloride-, sulphate- and alkali-halophytes depending on the kind of ions in the plants. Chloride-halophytes contain Cl^- as well as Na^+, sulphate-halophytes have high amounts of SO_4^{2-} as well as Cl^-, alkali-halophytes store much more Na^+ than Cl^- and/or SO_4^{2-} and compensate the surplus positive charge by synthesis of organic acids (Williams, 1960; Osmond, 1963). According to this classification, most of the coastal plants analysed can be termed chloride-halophytes (see also: Önal, 1964; Breckle, 1975). Cl^- clearly prevails over Na^+ in some species like *Carpobrotus edulis* and *Inula crithmoides* at the Mediterranean Sea shore and *Zygophyllum coccineum* and *Zygophyllum album* at the Red Sea shore.

The members of the inland plant communities show a different pattern of ion content. Numerous species of the Dead Sea area and of the Negev highlands in the surroundings of Avdat are characterized by high Na^+ but low Cl^- levels. *Anabasis articulata* and *Hammada salicornica* collected in Wadi Paran also belong to this type, to which the term alkali-halophyte is applicable. Considerable amounts of SO_4^{2-} occur in addition to Cl^-, however the two anions are not sufficient to maintain electrical charge balance (Table 2).

The sulphate-type halophyte appears to be realized in some salt-excreters, i.e. in the Tamaricaceae *Reaumuria hirtella* and *Reaumuria negevensis* (Avdat) and in the Plumbaginaceae *Limonium sinuatum*, *Limonium oleifolium* (Tel Aviv) and *Limonium axillare* (Red Sea shore). However, some salt excreted by these species may contribute to the salt contents shown in Table 1, even though the surface of the leaves had been thoroughly washed before ion determinations.

Pattern of Mineral Ion Content in Relation to Different Taxa. Kinzel and coworkers (Kinzel, 1969, 1972; Horak and Kinzel, 1971; Albert and Kinzel, 1973) have shown that a certain mineral ion composition is frequently better correlated with a certain taxon than with the mineral ion supply of the soil. The idea of the existence of different "physiotypes"[1] based on the pattern of internal mineral ion content is corroborated by our study, although unlike Kinzel and coworkers we discuss this aspect without consideration of Ca^{2+} and Mg^{2+} contents. *Suaeda vera* var. *negevensis* and *Salsola tetrandra* (Chenopodiaceae) contain more Na^+ than Cl^-, whereas the opposite is the case for *Inula crithmoides* (Asteraceae) and *Nitraria retusa* (Zygophyllaceae) yet these species grow adjacent to each other in the canyon En-Avdat. The majority of the "sodiophil-

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[1] "Physiotype" is defined by Albert and Kinzel (1973) as a special combination of physiological characteristics, which is typical for a certain taxon

Table 2. Na^+/Cl^- ratio and $Na^+/Cl^- + SO_4^{2-}$ ratio (expressed on the basis of equivalent amounts) in carbon assimilatory organs of some halophytes from the Dead Sea, from Avdat and from Wadi Paran

Species	Site	Na^+/Cl^-	$Na^+/Cl^- + SO_4^{2-}$
Mesembryanthemum nodiflorum	Dead Sea	1.8	1.3
Suaeda monoica	Dead Sea	2.6	1.6
Suaeda fruticosa	Dead Sea		
young leaves		2.8	1.8
old leaves		2.6	2.0
Aizoon canariense	Dead Sea	4.0	2.1
Salsola tetrandra	Dead Sea	5.2	1.4
Anabasis setifera	Dead Sea	9.5	2.3
Seidlitzia rosmarinus	Dead Sea	9.5	2.3
Sueda vera var. negevensis	Avdat	3.9	2.0
Hammada scoparia	Avdat	4.0	1.4
Mesembryanthemum nodiflorum	Avdat	4.0	2.1
Salsola tetrandra	Avdat	4.3	1.4
Chenolaea arabica	Avdat	6.1	2.7
Aellenia lancifolia	Avdat	7.8	2.7
Halogeton alopecuroides	Avdat	8.0	3.0
Anabasis articulata	Wadi Paran	6.5	2.6
Hammada salicornica	Wadi Paran	8.2	1.8

ic" inland halophytes included in this study are members of the Chenopodiaceae (see also Table 2): 12 of 15 species of this family collected in the Dead Sea area, in the surroundings of Avdat and in Wadi Paran belong to this "physiotype". Interestingly, nearly all of them are also distinguished by the C_4 pathway of photosynthesis (Winter, 1975). The mineral ion composition of Chenopodiaceae of other inland and desert areas often shows a pattern similar to that described here. Thus, in numerous species of the Curlew Valley (North Utah, USA) Na^+ content strikingly exceeds Cl^- and SO_4^{2-} (Wiebe and Walter, 1972). Wallace et al. (1973) report high amounts of Na^+ in leaves of many Chenopodiaceae of the northern Mohave and the southern Great Basin desert (USA). The Chenopodiaceae of another inland habitat, the region east of the Neusiedlersee in Austria, are also characterized by a rather specific mineral ion composition, which in this case corresponds to that of chloride-halophytes (Albert and Kinzel, 1973). However, in general, this type seems to be more typical for coastal members of this family. Thus, the Chenopodiaceae of various regions may differ in ion composition, yet within each region they may form a specific "physiotype" compared with other taxa.

The high Na^+/K^+ ratios of most of the halophytic species listed in Table 1 are consistent with the observation that, in halophytes, K^+ uptake is generally suppressed when the Na^+ level in the root medium is high (Flowers, 1972; Yeo, 1974; Winter, 1975). Nevertheless, it is very likely, that these plants still have a high selectivity for K^+ as compared with Na^+ and that K^+ is accumulated sufficiently even under such conditions (Rains, 1972). Even so, the roots of the "sodiophilic" Chenopodiaceae, mentioned in this paper, may have a cation uptake system

which has much less selectivity for K^+ over Na^+ compared with roots of glycophytes (Black, 1960). Collander (1937, 1941) supplied early evidence for differences in Na^+/K^+ selectivity between glycophytes and halophytes grown at low concentrations of both cations. Therefore, a more intensive study on Na^+/K^+ selectivity in halophytes may prove rewarding (Flowers, 1975), especially in the highly "sodiophilic" Chenopodiaceae described above.

The Zygophyllaceae *Zygophyllum dumosum*, *Zygophyllum coccineum*, *Zygophyllum album* and *Nitraria retusa* form a second "physiotype" among the plants studied. High amounts of Na^+ and Cl^- are accumulated but Cl^- exceeds Na^+. All specimens of *Nitraria retusa* consistently show this pattern of ion content, even though they had been collected for ion determinations at different localities, i.e. in the Dead Sea and the Red Sea area and in the canyon En-Avdat. Walter (1973a) indicates a similar surplus of chloride for *Zygophyllum iodocarpum* in central Australia. The electrochemical balance of this excess Cl^- over Na^+ plus K^+ is unknown. The mineral ion composition of the Zygophyllaceae *Peganum harmala* investigated in the arid Ebro-Basin (Spain) is however that of an alkali-halophyte (Moore et al., 1972; Walter, 1973b).

Abd El Rahman et al. (1975) presented data on ion contents in *Nitraria retusa* and *Zygophyllum album* from the area of Wadi El-Natrun (Egypt). In accordance with our results the authors emphasize that Cl^- contents are greater than Na^+ contents. When their values (p. 77, Fig. 3, data for April) given as mg per 100 g dry weight are recalculated on an equivalent basis their results indicate however an unusually high Cl^-/Na^+ ratio of 14 in *Z. album* and 13 in *N. retusa*.

The mineral ion composition of members of the Aizoaceae, included in our investigation, is not as uniform as demonstrated for the Zygophyllaceae and inland-Chenopodiaceae. *Mesembryanthemum crystallinum* collected at the Mediterranean Sea shore near Tel Aviv contains more Na^+ than Cl^-. *Carpobrotus edulis* occurring at the same habitat shows an inverse pattern. In *Mesembryanthemum forsskalii* (Dead Sea) Na^+ is electrochemically balanced by Cl^- whereas in *Mesembryanthemum nodiflorum* and *Aizoon canariense* Na^+ exceeds Cl^-. The leaves of *Carpobrotus edulis*, *Mesembryanthemum crystallinum* and *Mesembryanthemum nodiflorum* sampled in the field (Table 1) have similar proportions of Na^+, K^+ and Cl^- as specimens grown at high NaCl under controlled conditions (Winter, 1973a, 1975; Treichel and Bauer, 1974).

b) Plants with Non-Halophytic Attributes

The terms halophyte and "salt-accumulator" cannot be applied to all species included in this study. Particularly in plants occupying the less saline wadis and loessial plains of the Negev desert, Na^+ and Cl^- hardly exceed 100 µeq per g fresh weight and the Na^+/K^+ ratio normally is less than 1. This group comprises the perennial shrubs *Thymelaea hirsuta* and *Colutea istria* growing at the edges of Wadi Zin, the shrub *Moricandia nitens*, the therophyte *Reboudia pinnata* and the geophyte *Leontice leontocephalum* of the loessial plains in the surroundings of Avdat but also some slope inhabitants like *Diplotaxis harra*, *Helianthemum kahiricum* and *Helianthemum ventosum*. Nearly all members of the Wadi Paran community are also characterized by low salt contents of the

carbon assimilatory organs. This holds true for the annuals *Diplotaxis acris, Matthiola livida, Rumex vesicarius* and *Centaurea lannulata* as well as for the shrubs *Zilla spinosa, Haplophyllum tuberculatum* and *Ochradenus baccatus* and the tree *Acacia gerrardii negevensis*.

The low Na^+ and Cl^- concentrations in the leaves of the annuals are not surprising for two reasons: 1) they predominantly occupy habitats with low soil salinity (loessial plains, wadis), 2) their vegetative period is mainly confined to the rainy season (winter, early spring) when due to the high water content of the soil salinity is of minor importance. The latter aspect does not apply to the perennials mentioned above. It is a striking phenomenon that the habitats of these perennial "non salt-accumulators" are also occupied by "salt-accumulators", mainly Chenopodiaceae. Thus, in Wadi Paran *Zilla spinosa, Haplophyllum tuberculatum* and *Ochradenus baccatus* containing little Na^+ and Cl^- are found side by side with the Chenopodiaceae *Anabasis articulata* and *Hammada salicornica* which store high amounts of Na^+ in their carbon assimilatory organs. At the edges of Wadi Zin, *Colutea istria* and *Thymelaea hirsuta* are associated with *Atriplex halimus* ("salt-accumulator") and on a loessial plain close to Avdat, *Moricandia nitens* occurs together with *Hammada scoparia* ("salt-accumulator"). The reasons for this phenomenon may be more related to the high net salt uptake of the Chenopodiaceae rather than to salt excluding mechanisms (Greenway and Rogers, 1963) of the non salt accumulating species (Breckle, 1974). However, this aspect is still open for detailed investigations, especially since different root growth may be another important factor.

2. Occurrence of CAM-like Diurnal Malate Fluctuations

Four of the 75 species studied exhibit CAM-like diurnal malate fluctuations, accumulating large amounts of malate during the night: the halophytic Aizoaceae *Mesembryanthemum crystallinum, M. forsskalii* and *M. nodiflorum* and the Asclepiadaceae *Caralluma negevensis* (Table 1). CAM in these species is corroborated by $\delta^{13}C$ determinations. The $\delta^{13}C$ values listed in Table 3 are either intermediate between those of plants exclusively exhibiting C_3 or C_4 photosynthesis ($-22.7^o/_{oo}$, $-22.0^o/_{oo}$, $-18.4^o/_{oo}$) or indicate a C_4 like carbon isotope discrimination ($-17.2^o/_{oo}$, $-13.4^o/_{oo}$) (see: Troughton, 1971; Troughton et al., 1974).

Table 3. $\delta^{13}C$ values of species, from different sites in Israel, which showed indications of CAM based on malate levels at dawn and dusk

Species	Site	$\delta^{13}C$ ($^o/_{oo}$)
Mesembryanthemum crystallinum	Tel Aviv	−22.7
Mesembryanthemum nodiflorum	Avdat	−22.0
Mesembryanthemum nodiflorum	Dead Sea	−17.2
Mesembryanthemum forsskalii	Dead Sea	−18.4
Caralluma negevensis	Avdat	−13.4

In *Mesembryanthemum crystallinum* and *M. nodiflorum* CAM can be induced by high soil salinity (Winter and v. Willert, 1972; Treichel and Bauer, 1974; Winter, 1975). A similar behaviour could also be demonstrated for *Carpobrotus edulis* (Winter, 1973b; Treichel and Bauer, 1974). Our field measurements on *C. edulis* on the Tel Aviv high coast indicate only a small night-time malate accumulation and two specimens collected for $\delta^{13}C$ determination showed C_3 like $\delta^{13}C$ values of -26.0 and $-28.5^0/_{00}$ respectively. Therefore, under natural conditions *C. edulis* probably seldom makes use of its capability to perform CAM (see also Schütte et al., 1968; Mooney et al., 1974).

At present, it is unknown to what extent a shift between C_3 and CAM occurs in the CAM-Aizoaceae *Mesembryanthemum crystallinum, M. nodiflorum* and *M. forsskalii* during their life cycle in the field. The intermediate $\delta^{13}C$ values of $-22.7^0/_{00}$ in *M. crystallinum* and of $-18.4^0/_{00}$ in *M. forsskalii* and the large differences in $\delta^{13}C$ values between specimens of *M. nodiflorum* from Avdat ($-22.0^0/_{00}$) and the Dead Sea ($-17.2^0/_{00}$) may be interpreted as a result of such a shift. One may suggest that these annuals predominantly fix CO_2 by the C_3 pathway during the first weeks after germination. This period coincides with the humid time of the year. Later, when the plants are more developed and the drought season starts (the samples were taken in this drier season), a change from C_3 to CAM may take place (see also Mooney et al., 1974). Besides environmental factors (Winter, 1974c) the involvement of endogenous components such as leaf age in controlling the change from C_3 to CAM has been demonstrated for *M. crystallinum* (Winter, 1973c). The role of plant age in determining the balance between C_3 and CAM was apparent in experiments with *M. nodiflorum*. In spite of a 3 weeks treatment with 400 mM NaCl young plants showed no CAM-like CO_2 gas exchange pattern (Winter, 1974d).

The stem-succulent Asclepiadaceae *Caralluma negevensis* which grows in special niches in the Negev highlands near Avdat, is the only non-Aizoaceae among the CAM-species identified. Features of CAM in *C. negevensis* have already been detected by measurements of CO_2 gas exchange (Lange et al., 1975). The amplitude of the diurnal malate fluctuation is not as high as in the CAM-Aizoaceae investigated. *C. negevensis* shows no halophytic attributes in its Na^+/K^+ ratio.

In *Atractylis flava, Seidlitzia rosmarinus, Anabasis setifera, Hammada scoparia* and *Colutea istria* a slight night-time malate accumulation was observed. However, malate levels of parallel samples varied considerably and additional studies on photosynthetic pathways ($\delta^{13}C$ values, leaf anatomy) suggest the absence of CAM in these species. The accumulation of small amounts of malate during the dark in leaves of non-succulent C_3 plants like *Nicotiana tabacum* has already been shown by Schwarze (1933).

Gaur (1968) reported diurnal variations in titratable acidity in leaves of *Salvadora persica* growing in the Indian arid zone at Jodpur, which were interpreted as signs of CAM. Indeed, malate levels are rather high in leaves of *S. persica* specimens studied by us on the Red Sea littoral, but there are only insignificant differences between dawn- and dusk-values. A $\delta^{13}C$ value of $-25.0^0/_{00}$ obtained for our plant material clearly indicates the C_3 pathway of photosynthesis. Probably the high night temperatures, prevailing in the southern

Sinai throughout most parts of the year, prevent a dark net CO_2 uptake in *S. persica*, which nonetheless might have the potential to perform CAM as implied by Gaur (1968).

Some species analysed increase their leaf malate content during the day, for example *Senecio joppensis* and *Cakile maritima* (Tel Aviv), *Moricandia nitens, Diplotaxis harra, Leontice leontocephalum* and *Reboudia pinnata* (Avdat) and *Zilla spinosa* and *Diplotaxis acris* (Wadi Paran). Except *S. joppensis* (Asteraceae) and *Leontice leontocephalum* (Berberidaceae) this feature exclusively concerns members of the Brassicaceae family. The Brassicaceae can possibly be distinguished by this physiological characteristic as a "physiotype" from other families.

Conclusions

On the whole the malate contents are rather low in most of the salt accumulating species listed in Table 1. Many halophytes investigated here do have a distinct leaf succulence (see the data on water content and fresh weight/dry weight ratios in Table 1). Yet, CAM-like diurnal malate fluctuations were only observed in very few halophytic species, i.e. exclusively in the annual Aizoaceae *Mesembryanthemum crystallinum, M. forsskalii* and *M. nodiflorum*. It may be questioned wether our data can be regarded as representative for the occurrence of CAM in halophytes. This in particular, because temperature and/or precipitation conditions are unfavorable for CAM per se especially in the desert areas investigated (i.e. the Negev and the Sinai). Such climatic conditions may account for the absence of typical CAM-succulents (Cactaceae, Crassulaceae, Euphorbiaceae etc.) from these sites. Nevertheless, our results suggest that the role of CAM as an adaptive mechanism to highly saline conditions is mainly restricted to members of the Aizoaceae family. Thus, a detailed survey of the flora of South-Africa in which the Aizoaceae are abundant, may turn out to be highly rewarding. (The relationship between climatic factors and the relative distribution of C_3, C_4 and CAM type plants at the coastal and desert habitats screened in this study are discussed in a following paper.)

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