

DIVALENT CATION ABSORPTION AND INTERACTION IN *ATRIPLEX*

By C. B. OSMOND*

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Summary

The absorption of calcium and magnesium from solutions of chloride salts by *Atriplex* spp. and tomato was investigated. In *Atriplex* divalent cation uptake to leaves remained constant when external concentration was low (1–10 m-equiv/l) but thereafter uptake increased in proportion to concentration. This response was in contrast to that of tomato where divalent cation uptake was saturated at relatively low concentrations (10–20 m-equiv/l).

The absorption of calcium by *Atriplex* from solutions of low calcium chloride concentration was not affected by high levels of monovalent cations. Calcium uptake from concentrated calcium chloride solutions was reduced by high monovalent cation levels. High concentrations of calcium chloride increased the K^+/Na^+ ratio in leaves but did not alter total monovalent cation uptake.

The relatively low calcium content of *Atriplex* leaves in the field is due to the presence of high levels of sodium which depress potential calcium uptake.

The observations suggest that two processes of cation uptake were involved: a "specific" process, possibly metabolically dependent, operative at low concentrations; and a "luxury" process, possibly passive, operative at high concentrations.

I. INTRODUCTION

In the field, leaves of semi-arid members of the genus *Atriplex* contain high levels of salts, rising to 25% of dry weight in *A. nummularia* (Wood 1925). High sodium chloride levels found in these tissues were related to the predominance of sodium chloride in accompanying soils (Beadle, Whalley, and Gibson 1957). Soil calcium levels were also high, yet calcium represented only 10% of total cations. Ion activities in soils are difficult to assess and low leaf calcium may have been due to low calcium availability in the soil. Alternatively, selective uptake by the plants may be involved.

In water-culture studies, high levels of sodium, potassium, and chloride were absorbed by *Atriplex* species (Ashby and Beadle 1957; Black 1960). Whether this high uptake was confined to monovalent ions was not known. The present work reports similar studies on the absorption of calcium and magnesium from culture solutions as well as interactions between calcium and monovalent cations.

* Botany Department, University of New England; present address: Botany Department, University of Adelaide.

II. MATERIALS AND METHODS

(a) Field Samples

These were collected at a field station of the New South Wales Soil Conservation Service located at Fowler's Gap (70 miles north of Broken Hill) during September 1961. Mature leaves were taken from several bushes at each site and combined for analysis.

(b) Water-culture Experiments

Seed collected at Fowler's Gap was germinated between filter papers or in sand after removal of bracteoles, and transferred to culture solutions at the first leaf stage. After 2 weeks in the base culture solution, seedlings were grown in more concentrated solutions, the concentration being increased gradually at intervals of 2-3 days to allow osmotic adjustment.

In experiment 1 seedlings of *A. vesicaria*, *A. inflata*, and tomato were grown in plastic pots of 900-ml capacity without aeration. Solutions were kept at this level and changed weekly during the experimental period of 11 weeks (March-July 1961). The annual species, *A. spongiosa*, which grows rapidly and uniformly, was used in experiment 2. Treatments were applied for 28 days (October-November 1962) in 4-litre enamel pots with 6 hr aeration daily. In experiment 1 treatments were in triplicate but in experiment 2 in duplicate only. At harvest, healthy, fully expanded leaves from all four seedlings in each pot were combined for analysis.

Treatment additions of different cations were made as chloride salts in both experiments. *Atriplex* spp. were known to be tolerant of chlorides within the concentrations used. The composition of the base nutrient solutions and of the different additives was as follows:

	Cation	Concn. (m-equiv/l)	Anion	Concn. (m-equiv/l)
Experiment 1	Na ⁺	20	Cl ⁻	20
	Ca ²⁺	10	NO ₃ ⁻	15
	K ⁺	6	SO ₄ ²⁻	4
	Mg ²⁺	4	H ₂ PO ₄ ⁻	1
Experiment 2	K ⁺	5	NO ₃ ⁻	6
	Na ⁺	5	Cl ⁻	5
	Ca ²⁺	1	SO ₄ ²⁻	1
	Mg ²⁺	1	H ₂ PO ₄ ⁻	1
	NH ₄ ⁺	1		

In experiment 1, CaCl₂ was added so as to increase the calcium levels to 20, 40, 80, and 160 m-equiv/l, and MgCl₂ to make the magnesium levels up to 8, 14, 24, and 44 m-equiv/l. In experiment 2, CaCl₂ was added to some treatments to give calcium levels of 10 and 100 m-equiv/l. At each calcium level sodium or potassium chloride was added to 50 or 100 m-equiv/l, giving five K⁺/Na⁺ ratios of 0.05, 0.1, 1.0, 10.0, and 20.0.

Micronutrients, 0.5 ml/l (Arnon 1938), and 10 p.p.m. iron as Fe^{3+} -EDTA (Jacobson 1951) were added to all solutions.

(c) *Analytical Methods*

All samples were dried for 24 hr at 60–70°C, ground, and dry-ashed for 12 hr at 560°C. The ash was digested in boiling dilute HCl. Sodium and potassium were estimated with an EEL flame-photometer and calcium and magnesium by titration with EDTA using calcein as indicator for calcium and eriochrome black-T for calcium plus magnesium (Johnson and Ulrich 1959).

III. RESULTS

(a) *Ion Concentration in Field-grown Atriplex spp.*

The concentration of the principal cations in mature leaves of *Atriplex* spp. grown in the field is shown in Table 1. In *A. vesicaria* calcium levels were low relative to the concentration of monovalent ions, as previously noted by Beadle, Whalley,

TABLE 1
CATION CONCENTRATION OF THE LEAVES OF *ATRIPLEX* SPP.

Species	Sites Sampled	Cation Concentration (m-equiv/g dry wt.)			
		Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}
<i>A. vesicaria</i> (narrow leaf form)*	6	0.75 ± 0.19	0.36 ± 0.12	3.64 ± 0.41	0.51 ± 0.09
<i>A. vesicaria</i> (broad leaf form)*	6	0.91 ± 0.14	0.57 ± 0.10	3.58 ± 0.34	0.49 ± 0.09
<i>A. inflata</i>	2	0.68 ± 0.13	1.47 ± 0.33	—	—
<i>A. conduplicata</i>	2	0.84 ± 0.09	1.15 ± 0.12	—	—

* The narrow leaf and broad leaf forms of this species are characteristic of gilgai and calcareous soils respectively.

and Gibson (1957). Magnesium concentration was judged by these workers to be very low but the more sensitive technique used here shows it to be quite substantial. The $\text{Ca}^{2+}/\text{Mg}^{2+}$ ratio in perennial *A. vesicaria* was greater than unity but annual species usually contained more magnesium than calcium.

(b) *Water-culture Experiments*

In these long-term experiments ion concentrations have been expressed as milliequivalents of ion per gram dry weight of leaf tissue. Mature (fully expanded) leaves only were analysed. Chloride treatments had little effect on the growth of saltbushes, as measured by fresh weight of shoots, but growth of tomato in experiment 1 was depressed (Fig. 1).

(i) *Absorption of Divalent Cations*

In experiment 1 the calcium concentration of *Atriplex* leaves increased linearly with external supply when solutions contained high calcium chloride levels (10–160

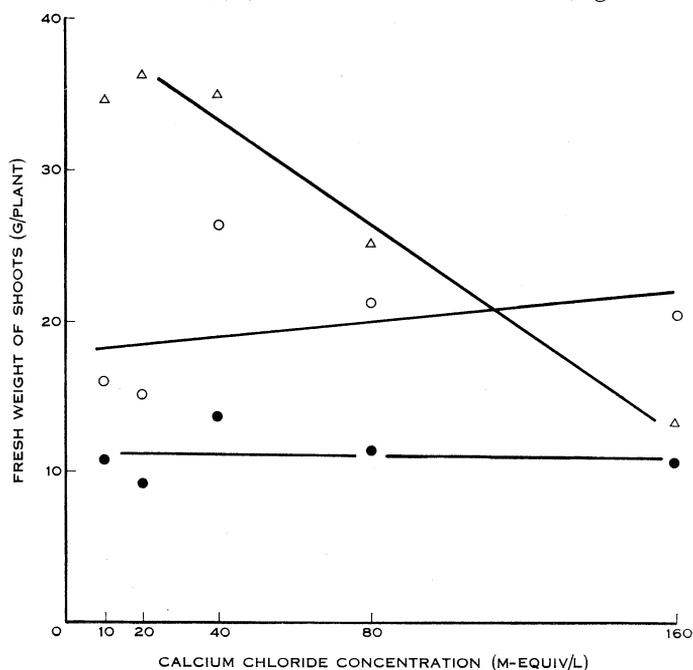


Fig. 1.—Growth of *Atriplex vesicaria* (○), *A. inflata* (●), and tomato (△) on culture solutions with added calcium chloride.

m-equiv/l) as shown in Figures 2(a) and 2(b). *A. spongiosa*, grown for a much shorter time during experiment 2, contained approximately the same calcium concentration

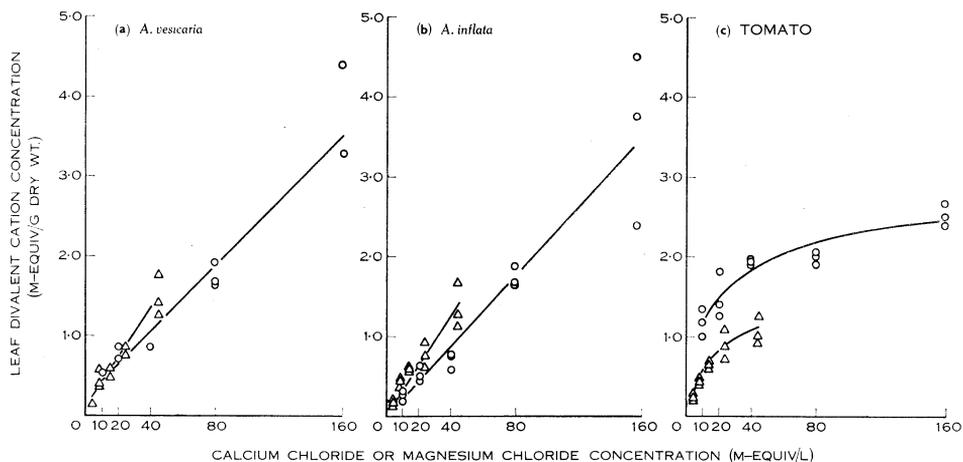


Fig. 2.—Leaf concentration of Ca²⁺ (○) and Mg²⁺ (△) in two *Atriplex* species and tomato grown in culture solutions with added calcium or magnesium chloride.

as the other *Atriplex* species (2.8 m-equiv/g dry wt. from 100 m-equiv/l solution). In contrast, when calcium chloride was increased from 1 to 10 m-equiv/l (expt. 2)

leaf calcium concentration did not increase (Fig. 3). In another experiment (Osmond, unpublished data), leaf calcium remained constant when calcium nitrate was supplied at 2, 5, and 10 m-equiv/l.

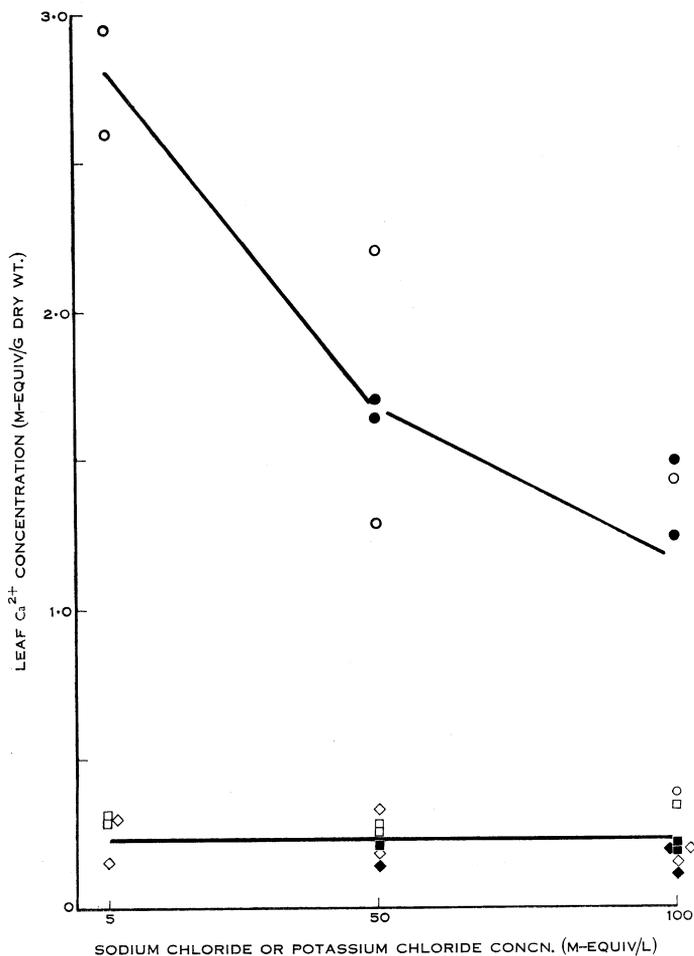


Fig. 3.—Leaf Ca^{2+} concentration in *A. spongiosa* grown in culture solutions with calcium chloride at 1 (\diamond , \blacklozenge), 10 (\square , \blacksquare), and 100 (\circ , \bullet) m-equiv/l and with sodium chloride concentrations of 5, 50, and 100 m-equiv/l (open symbols) or potassium chloride concentrations of 50 and 100 m-equiv/l (closed symbols).

Tomato absorbed more calcium from dilute calcium chloride solutions (10 m-equiv/l) than saltbush and less from concentrated solutions [Fig. 2(c)]. Between calcium chloride levels of 40 and 160 m-equiv/l, the calcium concentration of *Atriplex* leaves increased by 2–3 m-equiv/g dry weight but in tomato leaves by about 0.4 m-equiv/g dry weight only.

The magnesium concentration of leaves showed a similar pattern; *Atriplex* contained approximately equal amounts of calcium and magnesium whereas tomato contained twice as much calcium as magnesium. Magnesium level in *Atriplex* increased linearly over the concentration range tested but in tomato it increased more slowly at high concentrations (Fig. 2).

(ii) Ion Interactions

In experiment 2 leaf cation concentration (sodium plus potassium plus calcium) was more or less independent of solution concentration above 50 m-equiv/l and independent of substantial changes of ion ratio in solution. Figure 4 shows this for plants grown in solutions containing calcium chloride at 10 m-equiv/l.

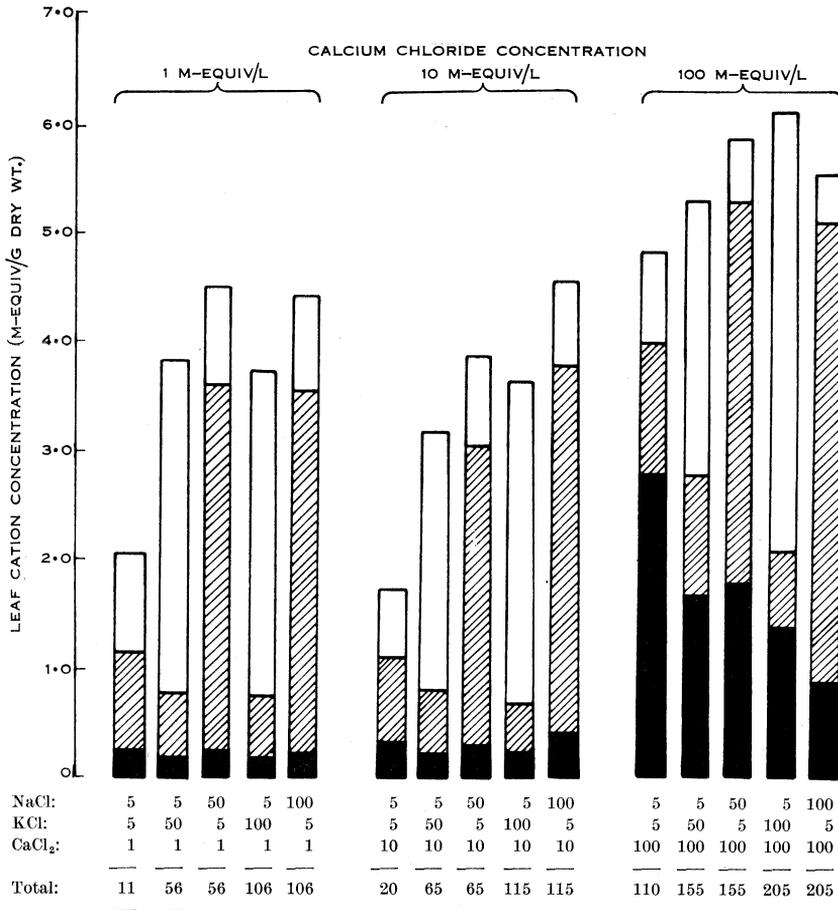


Fig. 4.—Cation absorption by *A. spongiosa* grown in solutions containing different proportions of Na⁺ (□), K⁺ (cross-hatched), and Ca²⁺ (■).

Similar results were obtained in the 1 m-equiv/l calcium chloride series but total cation uptake increased about 20% in the 100 m-equiv/l series. Plants grown on the base solution with a single salt added in high concentration (100 m-equiv/l) contained the same concentration of cations (i.e. sodium, potassium, and calcium

were about 3 m-equiv/g dry wt.). When monovalent cations were supplemented with calcium chloride at 100 m-equiv/l less calcium (Fig. 3) and slightly more sodium or potassium was absorbed so that total cation concentration remained unchanged. At low calcium chloride levels sodium and potassium chlorides had no effect on leaf calcium concentration (Figs. 3 and 4).

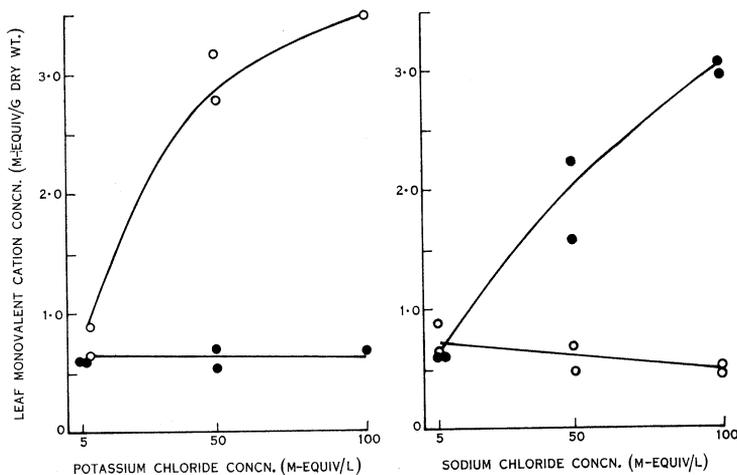


Fig. 5.—Concentration of K^+ (\circ) and Na^+ (\bullet) in the leaves of *A. spongiosa* grown in solutions with added potassium and sodium chloride.

The concentration of monovalent ions in mature leaves increased with external ion concentration (Fig. 5). Potassium level was only slightly depressed in the presence of much sodium chloride and leaf sodium level was similarly unaffected by potassium chloride concentration. Figure 6 shows the influence of 100-fold increase in calcium chloride concentration on the sodium and potassium level at five K^+/Na^+ ratios.

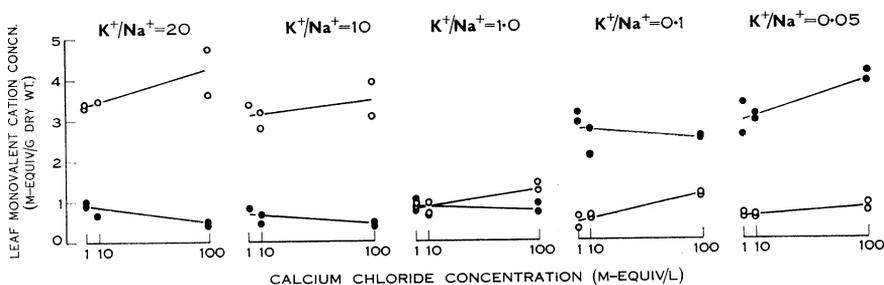


Fig. 6.—Concentration of K^+ (\circ) and Na^+ (\bullet) in leaves of *A. spongiosa* grown at different K^+/Na^+ ratios with increasing concentration of calcium chloride.

High calcium chloride level increased the potassium concentration of leaves grown in equimolar solutions or in solutions of low K^+/Na^+ ratio. A similar trend was noted at high K^+/Na^+ ratios but variation was large. Calcium depressed the concentration of sodium in leaves at K^+/Na^+ ratios of 0.1–20.0 but increased sodium level at a K^+/Na^+ ratio of 0.05.

These interactions at different calcium chloride levels affected the K^+/Na^+ ratio in leaves (Table 2). The ratio was primarily determined by the K^+/Na^+ ratio in solution. However, high calcium chloride levels increased this ratio at all but the lowest K^+/Na^+ ratio in the solution.

TABLE 2
EFFECT OF DIFFERENT CALCIUM CHLORIDE LEVELS ON
 K^+/Na^+ RATIO IN *A. SPONGIOSA* LEAVES

Solution K^+/Na^+ Ratio	Leaf K^+/Na^+ Ratio		
	CaCl ₂ 1 m-equiv/l	CaCl ₂ 10 m-equiv/l	CaCl ₂ 100 m-equiv/l
0.05	0.20	0.16	0.18
	0.19	0.16	0.18
0.10	0.11	0.18	0.43
	0.19	0.33	0.44
1.0	1.15	1.03	1.56
	0.86	1.44	1.57
10.0	3.91	5.19	5.92
	—	4.51	7.13
20.0	3.31	5.13	10.4
	3.76	—	7.96

IV. DISCUSSION

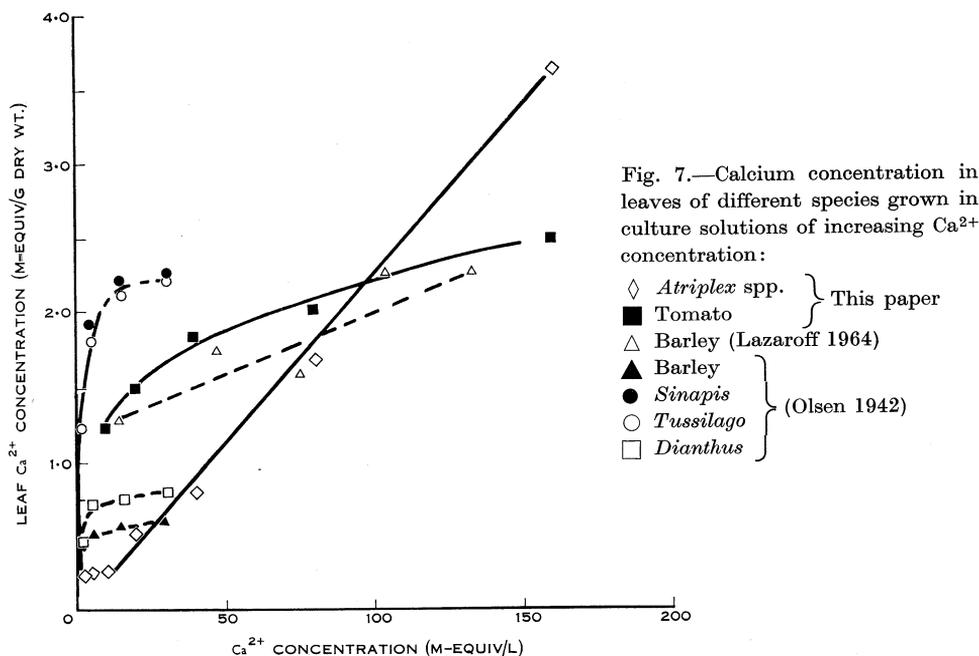
(a) Divalent Cation Uptake in the Field

It is difficult to establish ion activities in soils, especially in those supporting *Atriplex* which are often dry for long periods. However, these soils probably contain high levels of available calcium (Beadle, Whalley, and Gibson 1957; Osmond 1961). The ratio of soluble Ca^{2+}/Na^+ may approach 0.5 and calcium concentration at field capacity may range from 100 to 300 m-equiv/l. Exchangeable calcium is always high in these soils, between 65 and 90% of exchangeable bases (Osmond 1961). Thus calcium availability to plants under optimal growing conditions is unlikely to be limiting. The water-culture experiments show, however, that *Atriplex* absorbed high levels of calcium only when solutions were high in calcium but low in sodium or potassium. The low calcium content of *Atriplex* in the field is most likely due to the high soluble sodium in soils, not to low calcium availability.

(b) Divalent Cation Uptake from Culture Solution

These experiments show that mature leaves of *Atriplex* seedlings absorb calcium and magnesium to high concentrations from culture solutions. Calcium levels attained were comparable with sodium and potassium levels when these were provided at the same concentration. Clearly, *Atriplex* spp. do not discriminate against divalent cations.

Increases in ion concentration in mature leaves do not always reflect an increase in uptake from culture solution. Retranslocation of ions to other tissue and reduction in growth may increase leaf concentration without involving increased uptake from the solution (Greenway and Thomas 1965). However, in the present experiments, the divalent concentration of saltbush leaf tissue is taken to represent uptake via the roots because in most plants calcium is immobile (Biddulph, Nakayama, and Cory 1961) and the treatments had no drastic effects on growth. In tomato, reduced growth may have contributed to the small increase in divalent concentration at high levels of calcium. Similar effects of growth on leaf calcium concentration were observed in barley (Lazaroff 1964).



Divalent uptake in *Atriplex* differed from that of tomato and of other species (Fig. 7). The two principal differences were:

- (1) In dilute solutions (1–10 m-equiv/l) calcium uptake in *Atriplex* was saturated at a low level whereas in other species it increased rapidly with concentration.
- (2) In more concentrated solutions when calcium uptake in most species was saturated, calcium uptake in *Atriplex* increased in proportion to concentration.

Leaf ion uptake is due to absorption processes in the root and subsequent movement in the xylem. It is probable that transfer to the shoot involves processes similar to those responsible for ion uptake in root cortical cells and competition between the two processes is likely. At low concentrations, or in the presence of a large excess of competing ions, shoots absorb ions by processes independent of concentration or ion ratio (Pitman 1965). At higher concentrations when root

absorption processes are presumably saturated (Broyer 1950) and ion activity in the free space is greater, additional shoot uptake may occur. The considerable ion absorption by saltbushes may involve this component of shoot uptake, termed luxury uptake by Black (1960). The important question arises whether this uptake is merely an extension of the specific absorption or a different process altogether.

In *A. spongiosa* the absorption of calcium from dilute solutions was independent of concentration and insensitive to high levels of potassium or sodium chloride. It was similar to calcium uptake in barley at higher concentrations (Lazaroff 1964) and probably involves a specific absorption process. The additional calcium uptake by *Atriplex* at higher concentrations was depressed by high concentration of monovalent ions and probably involved different processes.

Monovalent cations were also absorbed by specific processes from dilute solutions in the presence of high levels of other cations. The specific uptake of potassium in the presence of sodium by saltbush is common to other species (Bange and van Vliet 1961). In most plants, however, sodium uptake is strongly depressed by high potassium levels (Heiman and Ratner 1961). That sodium absorption in *A. spongiosa* was insensitive to high potassium chloride levels is of particular interest because sodium is essential in these species (Brownell and Wood 1957).

Calcium influenced the specific absorption of sodium and potassium. When external levels of calcium chloride were sufficiently high to permit increased shoot uptake, potassium uptake was stimulated and sodium uptake depressed. Similar effects were found during the active absorption of sodium and potassium in excised cereal roots (Jacobson *et al.* 1961; Waisel 1962). Subsequent experiments with *A. spongiosa* leaf tissue (Osmond, unpublished data) show that calcium modifies the non-exchangeable, temperature- and inhibitor-sensitive sodium and potassium uptake in the same way. At least portion of ion uptake by barley shoots is similarly metabolically dependent (Barber and Koontz 1963; Greenway 1965). In *Atriplex* shoot absorption of cations from media of low concentration probably involves such a process.

The additional uptake of monovalent cations at high external concentration was not markedly affected by high calcium chloride levels. This luxury cation uptake by shoots has some characteristics of a physical process. At 100 m-equiv/l *A. spongiosa* absorbed approximately 2.5 m-equiv/g dry weight of calcium or monovalent cation in excess of that absorbed by the specific process. When monovalent and divalent cations were supplied together in high concentration, the more mobile monovalent cation was absorbed more readily, the total cation uptake remaining constant. At these high concentrations, passive processes are responsible for the bulk of shoot uptake in barley (Greenway 1965). Portion of this increased passive component may involve transpiration-mediated movement, and, for cations, exchange adsorption in the Donnan System as well (Jenny 1951). Biddulph, Nakayama, and Cory (1961) consider this to be a fundamental component of calcium uptake.

Further work on the nature of specific and luxury shoot absorption processes requires application of inhibitor and transpiration control techniques (Greenway 1965). If the luxury uptake of cations in *Atriplex* is largely a passive physical process,

perhaps involving exchange adsorption, it may explain the ability of these plants to absorb high levels of salt and maintain adequate turgor under conditions unfavourable to ion and water absorption by conventional processes.

V. ACKNOWLEDGMENTS

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