

EFFECTS OF NaCl ON THE ION UPTAKE AND GROWTH OF *ATRIPLEX* *VESICARIA* HEWARD

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Summary

Atriplex vesicaria, a xerophytic perennial pasture species of inland Australia, was found to have an extraordinary high tolerance to saline water cultures; seedlings were successfully established in solutions up to 1M NaCl.

The internal salt levels of the mature leaves, when calculated on a leaf water basis, maintained a positive gradient to the culture solution concentrations of about 12 atm over the whole NaCl range. It is shown that the main centres of NaCl accumulation were in the rapidly developing young leaves, but that sufficient NaCl absorption occurred in the mature leaves to maintain comparable levels of chlorine concentration. Only sodium levels increased with leaf maturation, possibly as a response to the Donnan effects of organic anions.

Relatively low levels of NaCl were found in the roots and it was apparent for this species that the NaCl absorption mechanism of the root system serves mainly in uptake and transport of ions to the leaves.

To explain K⁺ and Na⁺ uptakes in *Atriplex* species, two different mechanisms are suggested for the absorption of alkali cations; firstly, a sodium mechanism where K⁺ ions can compete when Na⁺ concentrations are low, resulting in "luxury" uptake levels of potassium; and secondly, a potassium mechanism which is completely independent of competition from Na⁺ ions. From K/Na ratios of less than unity for uptake from equimolar solutions, it is concluded for the leaves of *A. vesicaria* that a majority of alkali cation carriers must be eminently suitable for sodium absorption, even though a smaller proportion may be completely specific for potassium.

Functionally, luxury potassium levels are considered to be substituting for sodium and not the reverse. Apart from trace-element effects, the specialized sodium uptake of the Chenopodiaceae is looked upon as primarily osmoregulatory in function and not nutritional.

I. INTRODUCTION

This work continues a study on the comparative physiology, within the one genus, of a typical halophyte, *Atriplex hastata* L., found in coastal salt-marsh and strand communities, and a typical xerophyte, *A. vesicaria* Heward, which is not normally found on saline soils (Osborn and Wood 1923). The work on *A. hastata* has already been presented (Black 1956a) and the autecologies of the two species have been fully discussed (Black 1956b).

Hitherto high internal salt levels have been chiefly associated with halophytes, and species required for high sodium or chlorine studies have usually been drawn from this ecological group. However, many halophytes have morphological or systematic connections with xerophytes; the genus *Atriplex* is such a wide-spanning group.

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Physiological similarities between halophytes and xerophytes were postulated early by Schimper (1903) but these claims fell into disfavour as useful generalities when they failed to explain later experimental facts obtained from studies of divergent ecological mechanisms (Braun-Blanquet 1932, p.192). More recently Magistad (1945) noted the apparent close relationships between many salt-tolerant and drought-resistant plants.

It is probable that among the varied forms which xerophytes are known to take, there are many where a degree of salt tolerance is either absent or plays no important part in their ability to resist, endure, or evade drought periods. However, for the xerophytic *Atriplex* species, where (1) it is known that many have a high salt content in the leaves (Wood 1925; Beadle, Whalley, and Gibson 1957); (2) the genus includes many known halophytes, and (3) their soils often have only a small margin below the borderline of salinity, it would appear that their salt-uptake properties play an essential part in their drought resistance.

II. METHODS

(a) *Growth Media*

The basic culture solution, solution 1 of Hoagland and Arnon (1938), was prepared from A. R. reagents and distilled water; NaCl was added to give the series 0, 0.006, 0.02, 0.05, 0.1, 0.2, and by 0.1 increments to 1.0M. Na⁺ and K⁺ were equimolecular in the 0.006M NaCl solutions. The solutions were aerated with a hand bubbler at weekly intervals when water losses were replaced. The 4-l. enamelled cans were covered with drilled sheets of glass which had white paste-board covers on their upper surfaces. In the equilibrium experiment the NaCl concentrations were in two series, A and B.

(b) *Plant Culture*

The seeds were collected at Fowler's Gap (approx. 70 miles north of Broken Hill, N.S.W.) from bushes with the typical bladder type of fruit. Young seedlings at the cotyledon stage were taken from sand cultures and set out in NaCl treatments up to 0.2M. The plants required for the higher NaCl concentrations were moved up the series at 2-4-day intervals.

The tolerance of these seedlings to NaCl was greater than those of a different seed batch used for preliminary trials (Black 1956a) as seedlings were progressively established in solutions up to 1M NaCl. Even at this stage it appeared that it might be possible to use higher concentrations, but as many plants had already died in the higher concentrations and there was a limited number of plants available, no concentrations higher than 1M were used. The plants were thinned out to one per can, except the duplicate plants of the three highest NaCl treatments.

(c) *Sampling*

The sampling and harvesting of the equilibrium experiment was carried out in November after 20 weeks of growth in the water cultures. The plants were brought into the laboratory early in the morning, and healthy full-sized leaves

without petioles were removed from about the fourth or fifth node pair from the terminal buds. Young leaves, with the petioles removed as much as possible, were cut from the first pair of nodes from the terminal buds. These ranged from one-quarter to two-thirds of the length of the mature leaves. These samples were weighed fresh, and then washed for $1\frac{1}{2}$ min in distilled water to remove surface chlorides. The stems were cut at the cotyledon scars, and the roots rinsed three times with distilled water. It was not possible to obtain a sufficiently accurate fresh weight for the root systems.

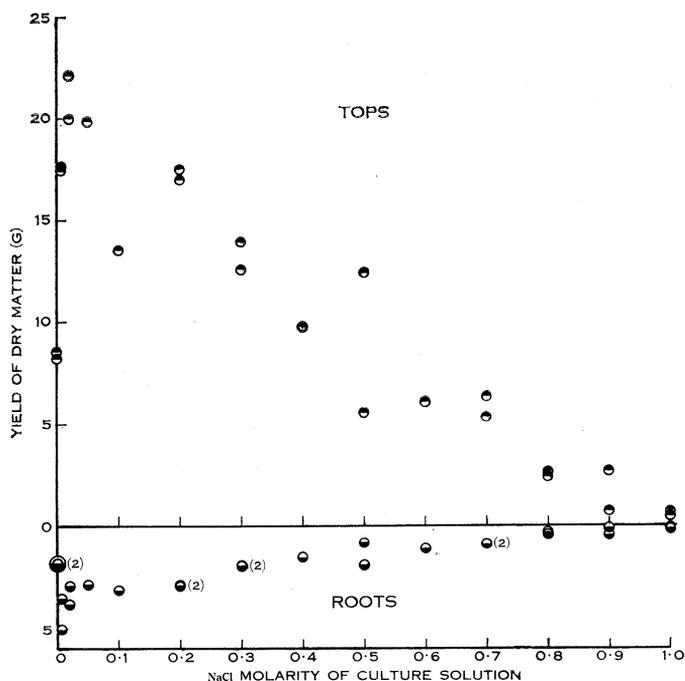


Fig. 1.—Dry matter yields of the roots and tops of *A. vesicaria* plants from the NaCl series, plotted against external NaCl concentrations.

All plant parts were dried overnight in a forced draught oven at 80°C and then weighed oven dry. The water content/dry matter (W/D) ratios were calculated for the leaf samples. Samples of all nutrient solutions were analysed for chlorides.

In the dynamic accumulation experiment single plants were grown in 0.006M NaCl culture solutions for 16 weeks. Immediately after the initial sampling in November, all plants were removed from their cans, their root systems thoroughly rinsed with distilled water, and were then placed in 0.1M NaCl culture solutions. Plants 1 and 2 were sampled for young and mature leaves while plants 3 and 4 had portions of their root systems sampled. Sampling was carried out in the glass-house early each morning and each leaf sample was collected randomly from the plant, although no stem was sampled of young leaves more than once. Sampling was continued over a period of 10 days from the culture solution transfer.

(d) Analysis

The samples of young and mature leaves, and the younger portions of the root systems, were all ground in a pestle and mortar. Portions of these samples were dried in an oven at 100°C for 2 hr. The oven dry weight was then determined,

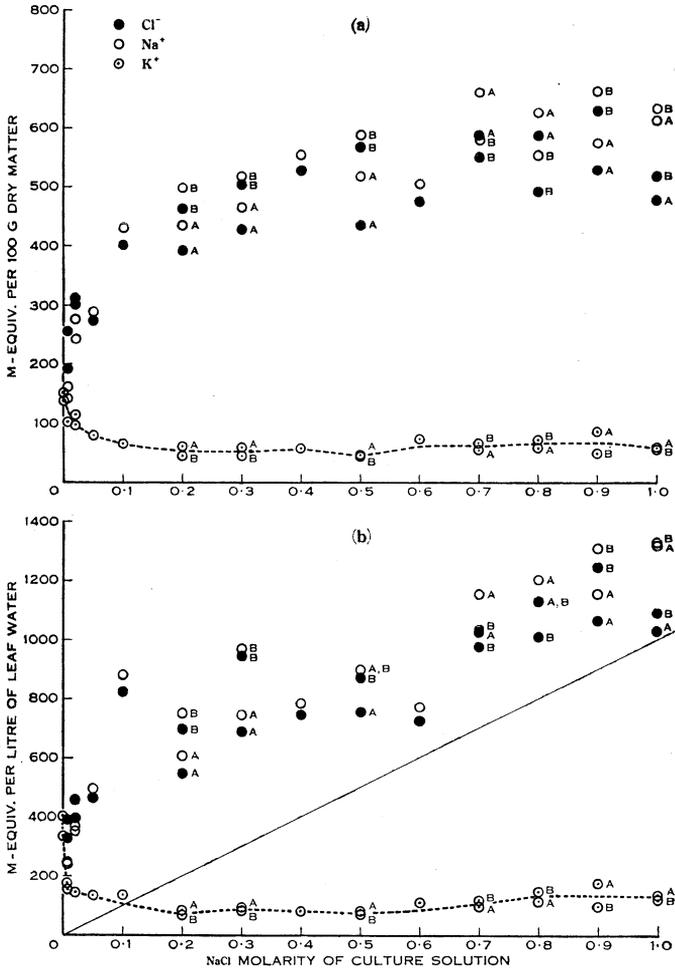


Fig. 2.—Na⁺, K⁺, and Cl⁻ contents of young leaves of *A. vesicaria* plotted against external NaCl concentration. Na⁺ and Cl⁻ contents for 0 NaCl treatments for the two series of plants respectively are (a) Na⁺ = 2.6, 3.4; Cl⁻ = 9.1, 8.5; (b) Na⁺ = 7.6, 7.5; Cl⁻ = 26.7, 18.9.

and the material boiled for 1 hr in distilled water in a ratio of approximately 1 : 500. After cooling and filtering, the extract was made up to a known volume at about 1 : 1000.

Sodium and potassium concentrations were determined using a low temperature flame photometer. Chlorides were measured by the electrometric method of

Best (1929) except that an arithmetical correction technique was applied in order to obtain greater accuracy in the analysis of the "0 NaCl" plants and the repeat extractions.

Three repeat extractions were done on the residues of high-salt mature leaves, and two on high-salt root samples, in order to check the effectiveness of the extraction procedure. For the mature leaves, chloride averaged 0.2, sodium 0.9, and potassium 2.1 per cent. of the values for the initial extractions. The corresponding values for the root samples were, chlorine 1.3, sodium 2.6, and potassium 3.0 per cent. These percentages were considered to be small enough to neglect, as they fell within the random errors involved in the plant culture and analytical methods used.

III. EQUILIBRIUM EXPERIMENT

(a) Growth and Salt Tolerance

The dry matter yields of the roots and tops of the plants from the NaCl series show an almost linear decrease in growth for increasing external NaCl concentration (Plate 1; Fig. 1). The stimulating effect on growth of low external NaCl concentrations (Fig. 1) has been considered in more detail (Black 1956b, p.73).

A measure of the relative salt tolerance of *A. vesicaria* and *A. hastata* can be obtained by comparing the yields at various high external NaCl concentrations, as the yields of the two species at low external concentrations were closely comparable (Black 1956a). For instance, with *A. vesicaria*, top yields of 5 g and over occurred right up to the 0.7M culture level, whereas with *A. hastata* such yields ceased abruptly after the 0.3M culture level. *A. vesicaria* appears to have a greater tolerance of highly saline water cultures than *A. hastata*, in spite of the fact that only the latter species is an ecological halophyte.

(b) Analytical Results

(i) *Young Leaves*.—The sodium and chlorine levels in the young leaves of all plants lay very close to each other when plotted as equivalents (Fig. 2), although sodium was always present in slight excess except in treatments below 0.02M NaCl.

The relationship between internal and external NaCl concentrations was more linear when the internal NaCl levels were plotted on a leaf water or "cell sap" basis (Fig. 2(b)). This was because the W/D rose rapidly from a minimum of 3.42 (0 NaCl, series A) to a maximum of 7.87 (0.02M, series A), and thereafter fell to a minimum of 4.65 (1.0M, series A). All internal NaCl concentrations were greater than the corresponding external concentrations (Fig. 2(b)), and the concentration differences were greater at the lower end of the series.

(ii) *Mature Leaves*.—The chlorine equivalents on a dry matter basis for the mature leaves (Fig. 3(a)) were in general slightly lower than for the corresponding young leaves (Fig. 2(a)), the differences being greatest for the low-salt plants. This effect is similar to that already shown for *A. hastata* (Black 1956a). These differences for the high-salt plants of *A. vesicaria* were largely eliminated when the chlorine levels were plotted on a leaf water basis (Figs. 2(b), 3(b)) because, for these

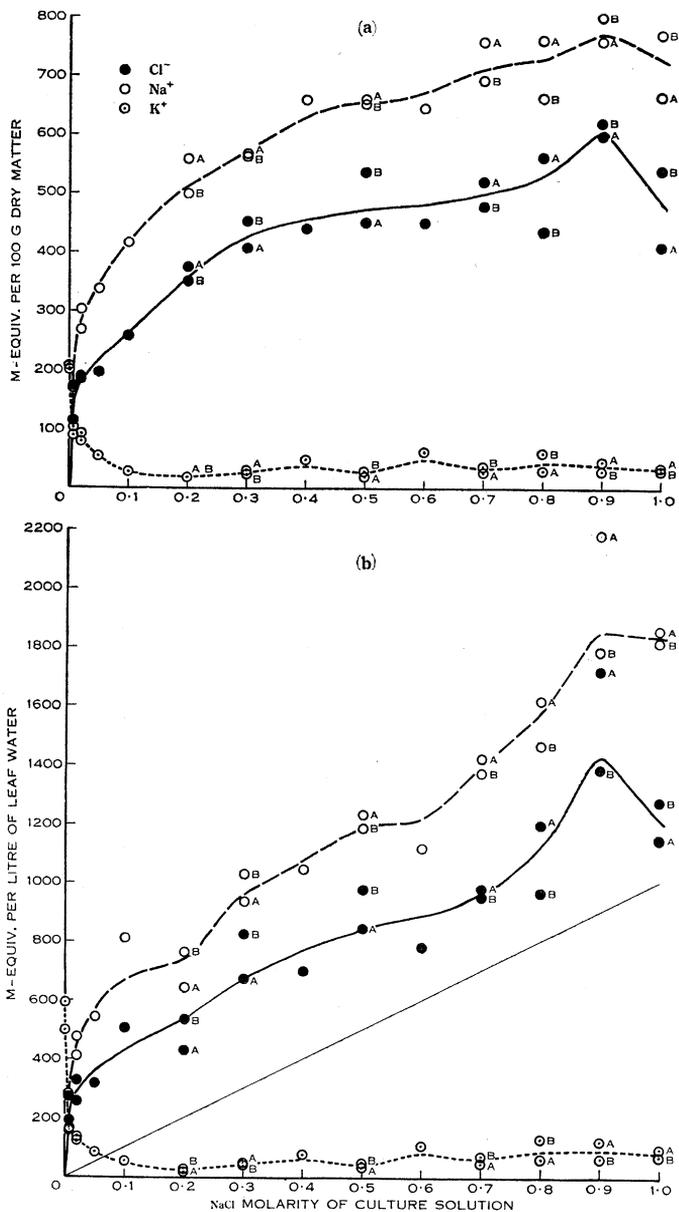


Fig. 3.—Na⁺, K⁺, and Cl⁻ contents of mature leaves of *A. vesicaria* plotted against external NaCl concentration. Na⁺ and Cl⁻ contents for 0 NaCl treatments for the two series of plants respectively are (a) Na⁺ = 6.8, 8.1; Cl⁻ = 3.3, 1.8; (b) Na⁺ = 20.0, 19.7; Cl⁻ = 9.9, 4.3.

plants, the moisture contents of the young leaves were consistently higher than for the mature leaves.

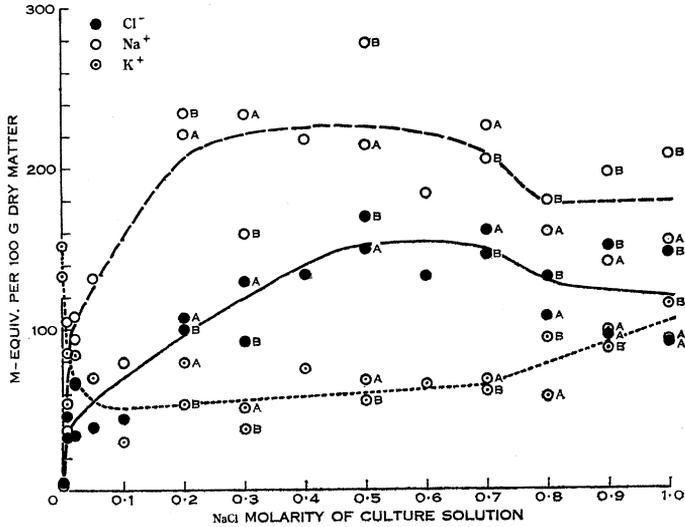


Fig. 4.— Na^+ , K^+ , and Cl^- levels of young samples from root systems of *A. vesicaria* plotted against external NaCl concentration.

The sodium equivalents lay consistently above the chloride levels in the mature leaves (Fig. 3), and generally above the sodium levels in the corresponding

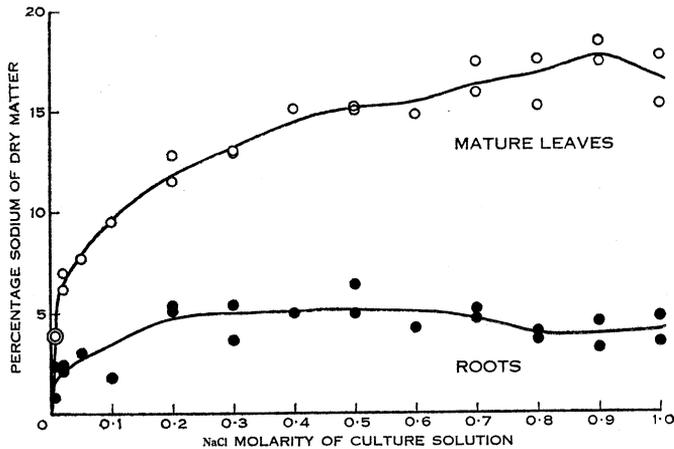


Fig. 5.—Comparative sodium levels of the mature leaves and roots of *A. vesicaria*. Percentage sodium contents for 0 NaCl treatment for mature leaves = 0.16, 0.19; for roots = 0.07, 0.07 for the two series of plants respectively.

young leaves (Fig. 2). However, the potassium levels in the mature leaves were always below those of the young leaves with the notable exception of the 0 NaCl treatment (Fig. 12).

The more linear relationship shown by plotting the internal Na^+ and Cl^- concentrations on a leaf water basis (Fig. 3(b)), were due to W/D trends similar to those noted for the young leaves; also internal ion concentrations were greater than the corresponding external concentrations.

(iii) *Roots*.—Here the sodium levels as equivalents were consistently above the chlorine levels, except in the 0 NaCl treatments (Fig. 4). This is a different situation to that shown for *A. hastata* (Black 1956a) where chlorine levels were dominant in at least the central portion of the range. There was a lowering of the internal sodium and chlorine levels for the three highest NaCl treatments (Fig. 4).

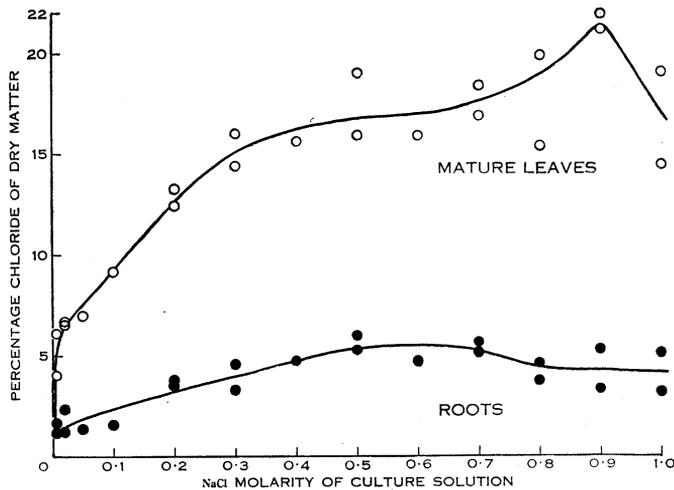


Fig. 6.—Comparative chlorine levels of the mature leaves and roots of *A. vesicaria*. Percentage chlorine contents for 0 NaCl treatment for mature leaves = 0.12, 0.06; for roots = 0.17, 0.18 for the two series of plants respectively.

Both the sodium and chlorine levels in the roots were considerably lower than the corresponding levels in the mature leaves (Figs. 5 and 6). This situation for chlorine was the exact opposite to that shown for *A. hastata* (Black 1956a). The differences tended to be greatest in the high-salt plants of *A. vesicaria* where the salt-uptake mechanism of the roots appeared to be more readily damaged by the high external NaCl concentrations.

IV. DYNAMIC ACCUMULATION EXPERIMENT

(a) *Young Leaves*

Over the sampling period, the sodium and chlorine levels of the young leaves rose rapidly (Figs. 7(a), 7(b), 7(d), 7(e)). This clearly indicated a high level of NaCl absorption as the final uptakes were close to those of the 0.1M treatment of the equilibrium NaCl series (Fig. 2).

The potassium levels were not significantly altered over the 10 days (Figs. 7(a), 7(d)) but the water relations effects were consistent and of interest. They

commenced as an immediate and significant drop in the W/D ratio which was most apparent in the samples collected 1 day after the transfer treatment; then followed a rapid recovery to about the original value from the third day on (Figs. 7(c), 7(f)).

(b) *Mature Leaves*

On a dry matter basis a slow absorption of NaCl was indicated over the sampling period, more particularly by the chlorine determinations (Figs. 8(a), 8(d)). The moisture content of the mature leaves dropped immediately and apparently

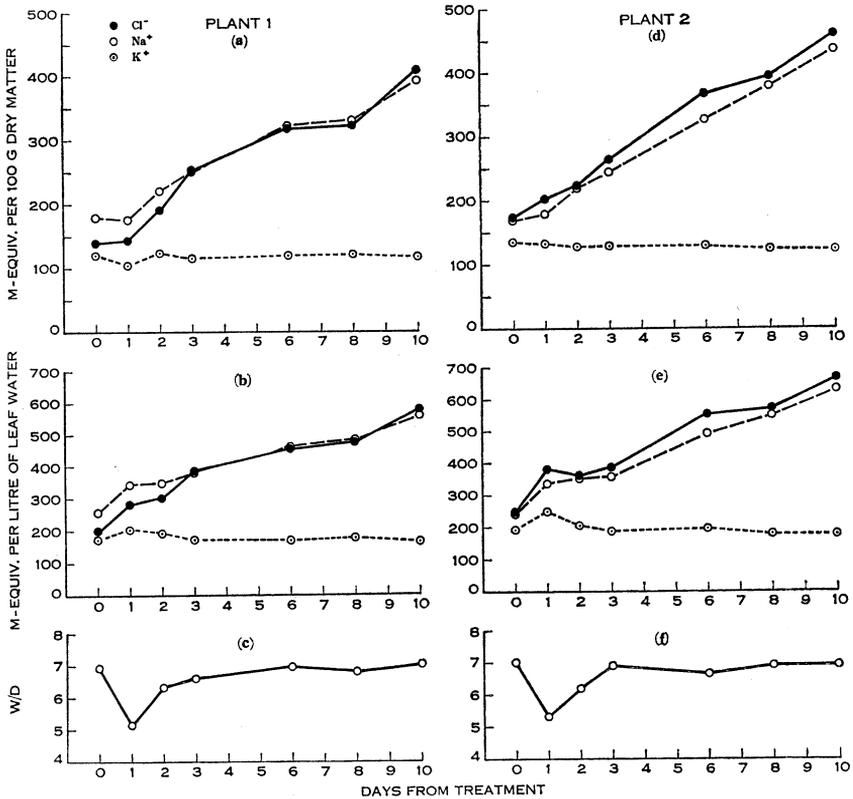


Fig. 7.—Salt accumulation in the young leaves of two *A. vesicaria* plants transferred at time 0 from a 0.006M to a 0.1M NaCl culture solution.

permanently (Figs. 8(c), 8(f)). This, of course, further increased the internal salt concentrations (Figs. 8(b), 8(e)). This mechanism was probably the main protection of the mature leaves against the suddenly increased external osmotic tension.

These results show that the salt-uptake mechanism of the mature leaves can do little more than maintain the high internal salt levels brought about in the developing leaves.

(c) *Roots*

The sodium and chlorine levels shown for the root systems over the sampling period (Figs. 9(a), 9(b)), probably did not change significantly, owing to the larger sampling errors involved in this material. Nevertheless, the results show that the

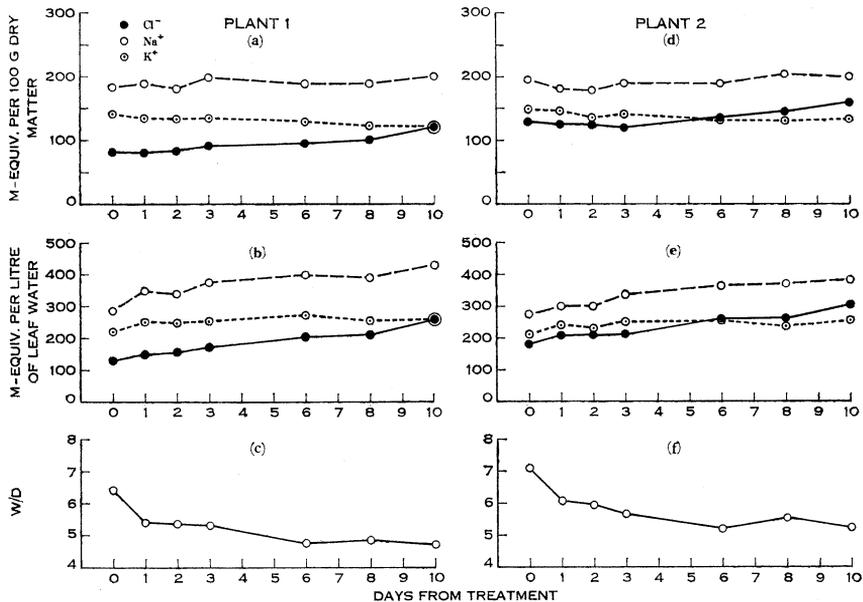


Fig. 8.—Salt changes in the mature leaves of two *A. vesicaria* plants transferred at time 0 from a 0.006M to a 0.1M NaCl culture solution.

NaCl contents did not greatly increase in the roots, although a rapid absorption rate must have been taking place to supply the demands of the young leaves (Fig. 7).

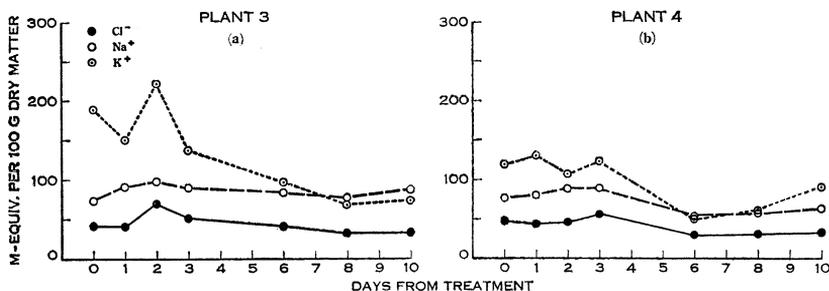


Fig. 9.—Salt changes in the roots of two *A. vesicaria* plants transferred at time 0 from a 0.006M to a 0.1M NaCl culture solution.

The NaCl absorption into the roots apparently had disturbing and depressing effects on the potassium contents (Figs. 9(a), 9(b)). This was the only occasion in this experiment, when mutual competition effects between Na⁺ and K⁺ appeared.

(d) *Individual Ions by Weight*

The plotting of the same results on a dry matter basis, and for the individual ions studied (Fig. 10), illustrated more clearly the different responses of the plant parts. The results for potassium (Figs. 10(a), 10(d)) showed that a marked depression of internal levels occurred only in the roots. However, the sodium results

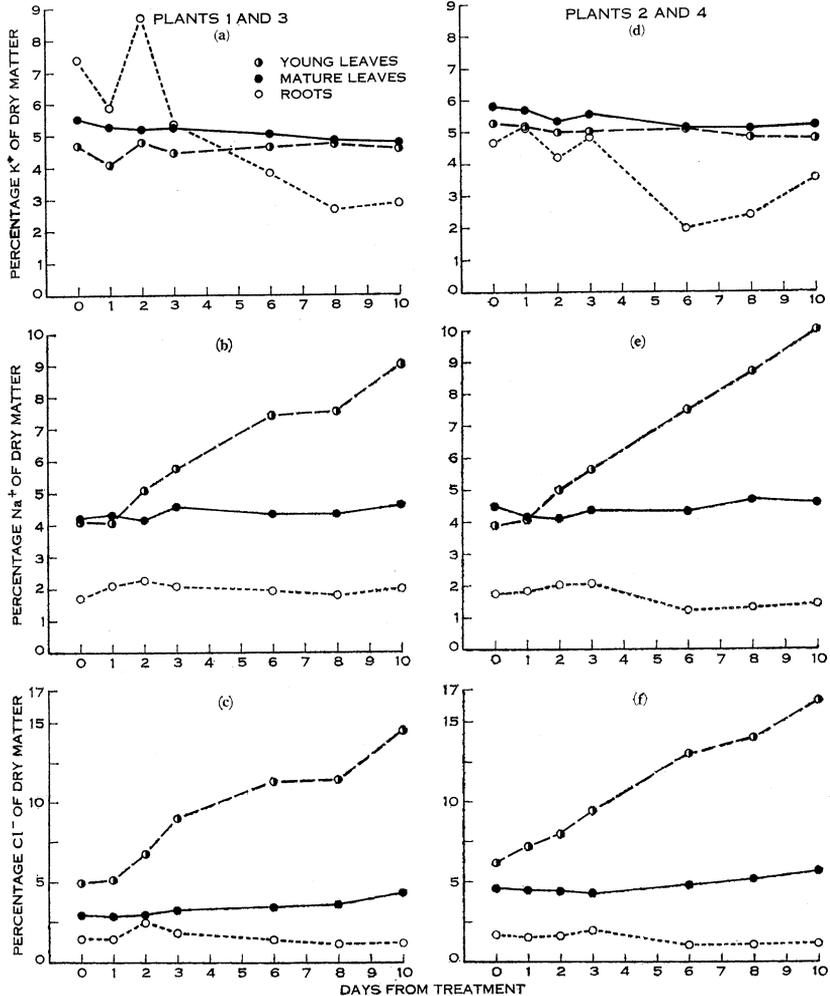


Fig. 10.—Responses of individual ions by weight for the young leaves, mature leaves, and roots of four *A. vesicaria* plants transferred at time 0 from a 0.006M to a 0.1M NaCl culture solution. Plants 1 and 2 were sampled for leaves, and plants 3 and 4 for roots.

(Figs. 10(b), 10(e)) showed that an increase of internal levels occurred only in the young leaves.

This indicated that the adsorbed Na⁺ ions causing mutual competition and reduced potassium absorption at the root surfaces, were either insufficient to increase

root sodium levels, or were removed by the rinsing procedure at sampling. The reduction of root potassium levels after the third day would result from the movement of potassium to the new growth which amounted to about two nodes on each stem over the 10 days.

The chloride percentages (Figs. 10(c), 10(f)) indicated a rapid uptake of the ion into the young leaves and a much slower uptake into the mature leaves.

V. GARDEN PLOT TRIAL

(a) *Plant Culture and Methods*

The following is a brief summary of some results from a garden plot trial. These are given to form a comparison with the results obtained from water cultures, and to point out agreements and anomalies in the plant responses under a completely different set of conditions.

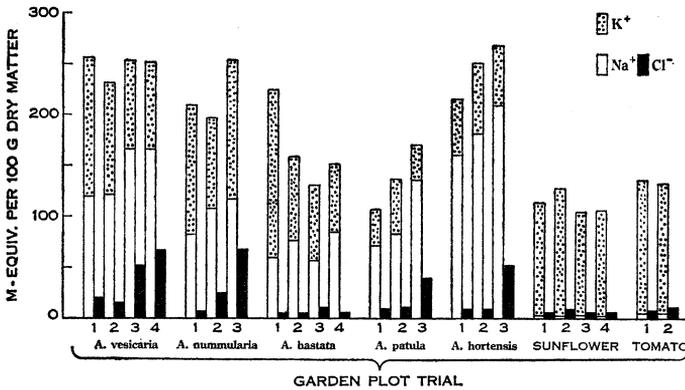


Fig. 11.—Cation and anion levels of Na^+ , K^+ , and Cl^- for the mature leaves collected from various species grown in a garden soil.

Plants of *A. vesicaria*, *A. nummularia* Lindl., *A. hastata*, *A. patula* L., *A. hortensis* L., sunflower (cv. Russian Giant), and tomato (cv. Burwood Prize) were randomized in a plot running east and west behind the Botany School, Sydney. Seedlings were set out at times to allow for a full vegetative growth by a sampling date in January. No fertilizers were used but the plot was kept cultivated for weed control. The *A. hortensis*, sunflower, and tomato plants had all flowered by the sampling date while the other *Atriplex* species were still only in vegetative growth. Samples of mature leaves were collected and analysed using the same techniques as for the water-culture experiments.

The results indicated that the NaCl levels in the soils were higher towards the western end. The cation and anion levels were thus recorded with the plants being numbered from east to west (Fig. 11).

(b) *Results*

The chloride results show that the two xerophytic *Atriplex* species, *A. vesicaria* and *A. nummularia*, were able in some cases to take up comparatively large concentrations of NaCl , although the highest of these (2.4 per cent. Cl of dry matter)

were about half the chlorine levels of the 0.006M NaCl culture solutions (Figs. 3(a), 6). These in turn were below the lower range of leaf chloride percentages (about 9 per cent. Cl of dry matter) for field specimens of *A. vesicaria* as determined by Wood (1925).

On the other hand, a lower absorption capacity was indicated for *A. hastata*, where the chloride levels were comparable to those for the sunflower and tomato plants. However, two higher chloride levels occurred in *A. patula* and *A. hortensis* plants; these species are ecologically and anatomically fairly close to *A. hastata*.

The cation-anion balances (Fig. 11) clearly illustrated the high selectivity of all the *Atriplex* species for the sodium ion. Nevertheless, potassium levels were usually comparable to those of the sunflower and tomato plants. Thus *Atriplex* species, generally, appear to have a higher capacity than most plants for absorbing monovalent cations.

VI. DISCUSSION

(a) NaCl Accumulation and the Donnan Equilibrium

Assuming salt concentrations expressed on a leaf water basis to be a measure of the mean cell sap concentrations, the results show that chloride concentrations of both young and mature leaves are approximately linearly proportional to the external concentrations, but exceeded the external concentrations by a more or less constant amount, which for the mature leaves was about 300 m-equiv/l (12 atm osmotic pressure) over the whole NaCl range (Fig. 3(b)).

Somewhat similar results have been described by Ashby and Beadle (1957) who found for two other xerophytic *Atriplex* species, *A. nummularia* and *A. inflata* F.Muell., that the cryoscopic osmotic pressures of expressed sap from their plus-salt plants were about 16 atm greater than the culture solutions. However, a different physiological response has been shown for *A. hastata* (Black 1956a) where mature leaf chloride concentrations were consistently below culture solution levels and Donnan effects appeared to dominate the equilibrium ion balance for culture solutions above 0.2M NaCl.

In the present equilibrium experiment, there is little indication of a Donnan effect in the young leaves (Fig. 2) because the total cation equivalents (Na⁺ and K⁺ plus other nutrient ions) is approximately equal to the chlorine equivalents. In the mature leaves (Fig. 3) the total cation is considerably in excess of chlorine equivalents indicating that the excess cations are held by a Donnan system, probably involving immobile organic anions.

Information about the processes involved in maintaining an approximately constant chlorine level in the leaves with time and maturation comes from the data for the dynamic experiment. In plants transferred from 0.006M to 0.1M NaCl, the salt content of the young leaves increased rapidly (Fig. 7) correcting the leaf water deficits caused by the osmotic pressure of the 0.1M solution. Apart from a very small increase in chlorine, the salt content of the mature leaves did not alter during the 10 days of the experiment (Fig. 8).

If it is assumed that the movement of salt from roots to leaves is via the xylem, then the rate of influx of ions into both young and old leaves should be

similar. Since the salt content of the old leaves does not increase, then either there is no influx of salt into mature leaves or the influx is balanced by an efflux possibly via the phloem. In field trials (Table 1) the rate of transpiration of old leaves was found to be similar to that of young leaves suggesting that an influx of salt into old leaves would occur. It is concluded that the influx in the young leaves greatly exceeds efflux and that as the leaves age, efflux gradually becomes more significant. The rapid retention of NaCl within the mesophyll tissues of the young leaves indicates a high capacity for accumulation.*

TABLE 1
RELATIVE TRANSPIRATION RATES OF YOUNG AND MATURE LEAVES OF *A. VESICARIA**

Water loss determined by weight of cut shoots from winter growth of field plants at Fowler's Gap, N.S.W. Trial carried out from 1 to 2 p.m. on an overcast day but with medium wind

Type of Leaf	Percentage Leaf Water Lost over First Hour (mean \pm S.D. of 5 shoots)
Young leaves (terminal buds and first two pairs of nodes)	10.8 \pm 0.8
Mature leaves (shoots 3-6 cm long after removal of tips)	12.3 \pm 1.1

* Same variety as used for water cultures.

No doubt these processes were also operative in the plants of the equilibrium series. The approximately constant NaCl concentration from young to mature leaves implies a rapid accumulation rate in the young growing leaf, but no net uptake once maturity was reached. The salt then must be leaving the mature leaf at a rate to balance the intake.

For the dynamic experiment, the relative rates of chlorine absorption and retention for the three organs studied were young leaves \gg mature leaves $>$ roots (Figs. 10(c), 10(f)). For the absolute amounts of chlorine absorbed per organ, the relative uptake of young leaves would have been even further ahead because of appreciable growth (in the order of 100 per cent. increases) over the last 7 days of the sampling period.

(b) Cation Selectivity

Mutual competition effects were shown by the plant sodium and potassium levels for the treatments above 0 NaCl (Figs. 2, 3, 4, 12), though the effects were complicated by near potassium depletion in the culture solutions supporting the biggest plants. These took up approximately 21 m-equiv. of potassium per plant from the initial total supply of 24 m-equiv.

* The biological mechanism for concentrating both ions of a salt against a concentration gradient utilizing energy from metabolism. This is accumulation as defined by Robertson (1951).

As with *A. hastata* (Black 1956a), competition was most marked when potassium levels were plotted on a leaf water basis (Figs. 2(b), 3(b)). This was because for the two series, A and B, the W/D ratio of the young leaves rose from 3.4, 4.5 for the 0 NaCl treatments to 6.5, 5.9 for the 0.006M treatments, and the W/D ratio of the mature leaves rose from 3.4, 4.1 to 6.2, 5.9 respectively; some of the higher NaCl treatments produced even higher W/D ratios.

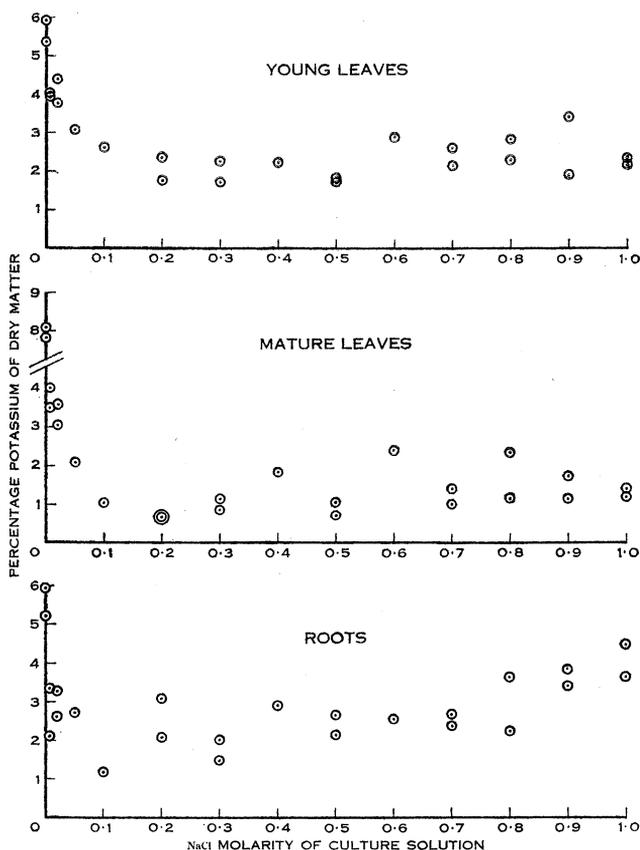


Fig. 12.—Potassium percentages of dry matter of *A. vesicaria* plants plotted against external NaCl concentration for young leaves, mature leaves, and roots.

The evidence for both *A. vesicaria* and *A. hastata* suggests that the uptake of potassium into these plants can best be considered as resulting from two different mechanisms. Firstly, there is a “luxury” uptake, where the potassium is completely exchangeable with sodium, and which is reduced to zero at high NaCl levels. Secondly, there is a specific uptake which, although it may vary somewhat according to potassium availability, is completely independent of the sodium-uptake mechanism. Bange (1959) has postulated a similar selective absorption of potassium and sodium for maize seedlings based on two distinct carrier systems.

The salt-accumulation process needed to maintain potassium levels in plants subjected to high NaCl treatments must require a highly specific active transport mechanism. Collander (1941), working with a number of species including *Atriplex*, was able to distinguish between the competitive properties of two groups of monovalent cations: K^+ , Rb^+ , Cs^+ , as distinct from Na^+ and Li^+ . Within the groups competition was complete; between the groups, only partial. Epstein and Hagen (1952), working with excised barley roots, studied similar effects and concluded the existence of several distinct binding sites of which one group binds K^+ , Rb^+ , and Cs^+ in preference to Na^+ and Li^+ .

TABLE 2

POTASSIUM AND SODIUM CONTENTS OF *A. VESICARIA* PLANTS GROWN IN CULTURE SOLUTIONS INITIALLY CONTAINING EQUIMOLAR CONCENTRATIONS (0.006M) OF POTASSIUM AND SODIUM
Values expressed as m-equiv/100 g dry matter

Plant Designation	Young Leaves		Mature Leaves		Roots	
	Potassium	Sodium	Potassium	Sodium	Potassium	Sodium
A	103	162	102	169	54	37
B	101	142	89	169	86	105
1	119	178	141	183	—	—
2	134	169	148	195	—	—
3	—	—	—	—	189	74
4	—	—	—	—	119	76
Mean K/Na ratio	0.70		0.67		1.53	

In studies of the cation-exchange capacities of cereal roots, Lundegårdh (1954) determined the following order of adsorption densities for the alkali elements on cation carriers. This was $(H^+) > K^+ > Cs^+$ and $Rb^+ > Li^+ > Na^+$. From equimolar solutions (0.0025M) of chlorides he found an absorption ratio for K/Na of 24. He stated, "The slow entrance of Na is obviously caused by a low percentage of carriers suitable for this ion."

Collander (1941) determined similar K/Na ratios for glykophytes, when these were grown in culture solutions containing equimolar concentrations of potassium and sodium (0.004M). However, he showed that halophytes took up a great deal more sodium than these, although the K/Na ratio still remained greater than unity. Comparable results for *A. hastata* agreed with this finding (Black 1956a).

Potassium and sodium levels in six *A. vesicaria* plants grown in culture solutions initially containing equimolar concentrations (0.006M) of potassium and sodium are presented in Table 2. Culture treatments were exactly the same for all plants, but the reduced growth period allowed for the latter (plants 1-4) probably accounts for their generally somewhat higher ion uptake.

These results in Table 2 clearly show that the leaves of *A. vesicaria* absorb larger quantities of sodium than potassium from equimolar concentrations. The results for the root samples are less satisfactory, but nevertheless indicate remarkably low K/Na ratios. K/Na ratios of less than unity for the leaves indicate that *A. vesicaria*, a xerophyte, is more highly specialized with respect to sodium absorption than the halophytes that have been examined to date.* Thus in the leaves of this species a majority of the alkali cation carriers must be eminently suitable for sodium absorption, even though a smaller proportion may be completely specific for potassium.

(c) Conclusions

It is difficult to form conclusions on the functional value to *Atriplex* species of their high selectivity for the sodium ion even though it is now known to be an essential micronutrient for *A. vesicaria* (Brownell and Wood 1957). Growth responses to sodium salts at macro levels by members of the Chenopodiaceae are quite commonly recorded (e.g. Keller 1925; van Eijk 1939; Black 1956b; Ulrich and Ohki 1956; Ashby and Beadle 1957). The usual explanation is that sodium partially substitutes for potassium in metabolism and that this may benefit the chenopodious plant specially when potassium supply is deficient.

Ashby and Beadle took a different attitude to explain their 0.4 and 0.6M KCl treatments which were very toxic and led to extraordinary high luxury uptakes of nearly 30 per cent. potassium of dried leaf material. They claimed an antagonism function for sodium which they supposed would reduce these lethal potassium concentrations. Though perhaps true enough for these experimental conditions, a better interpretation of these results, and those of this paper, would be to recognize the specialized sodium uptake of the Chenopodiaceae as an essential part of an osmoregulatory mechanism, important to both halophytic and xerophytic members. In a low-sodium growth medium, the non-specific sodium carriers of the active transport mechanism would combine with K⁺ ions and bring about a luxury uptake of potassium which could become toxic in a high-potassium medium. Thus, for these conditions, the excess potassium in the plant should be looked on as substituting for sodium, and the whole competitive interaction (as so well brought out by the osmotic pressure determinations of Ashby and Beadle) considered as osmoregulatory in character and not nutritional.

Heterogeneity of alkali cation carriers can also explain the apparent contradiction of higher potassium uptakes for high-potassium culture solutions than sodium for high-sodium solutions of these authors and the lower potassium uptakes of the equimolar culture solutions described here (Table 2). In the former case, all the alkali cation carriers would be available for potassium absorption, whereas against high-sodium culture solutions only the Na⁺ carriers could function, the K⁺ carriers being involved in maintaining nutritionally essential potassium levels. Only in equimolar solutions would a direct balance of absorption capacities for the two elements be involved.

* Sutcliffe (1957) has obtained K/Na ratios of <1 for red beet root tissue under conditions conducive to high accumulation rates.

VII. ACKNOWLEDGMENTS

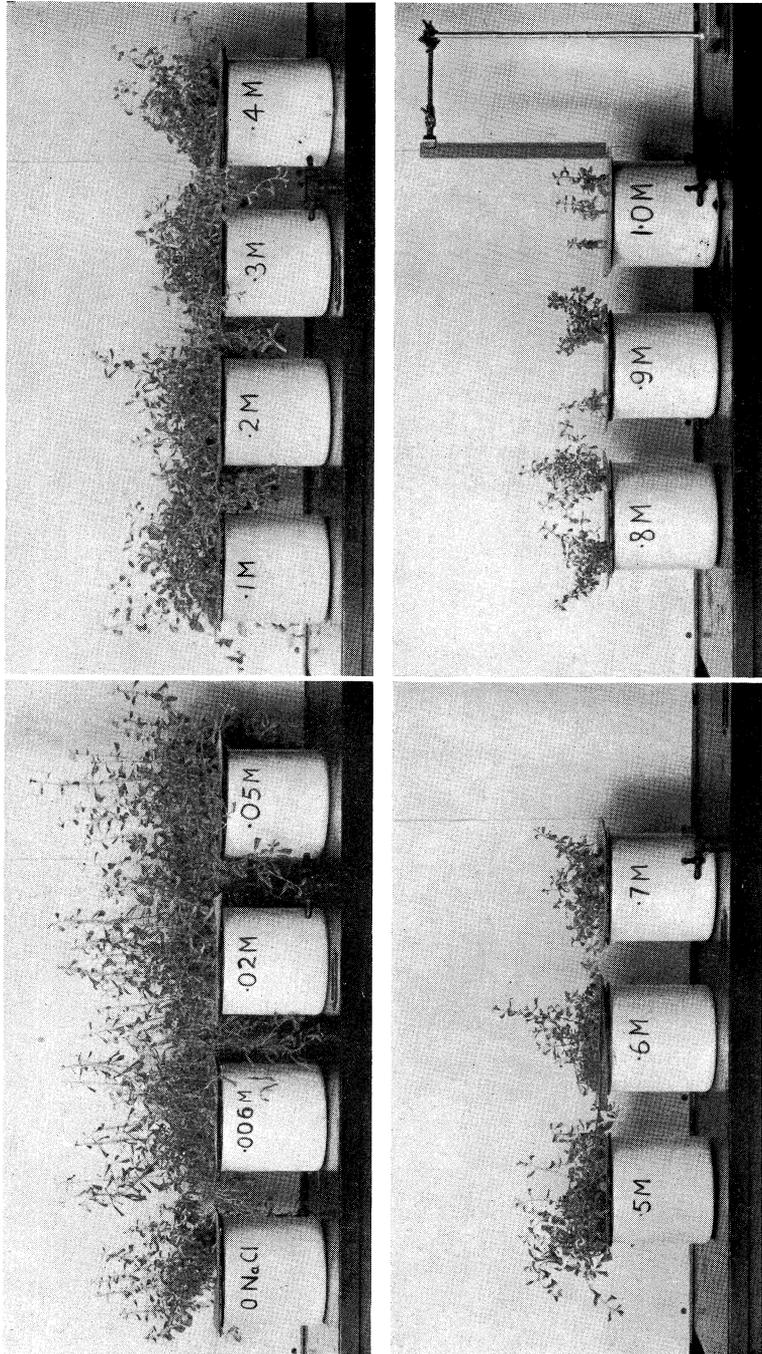
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