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# Nitrogen, salinity, substrates and growth of gloxinia and chrysanthemum

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# 1 Introduction

In the nutrition of flower crops, most attention is paid to nitrogen. Schuffelen (1949) has pointed out that response of crops to fertilizer depends much more on nitrogen than on phosphorus and potassium. In floriculture, phosphate and potassium deficiencies hardly ever occur but nitrogen deficiency is quite frequent. Yield and quality of flower crops, therefore, depend largely on rate of nitrogen (Shanks *et al.*, 1955; Lunt & Kofranek, 1958; Eck *et al.*, 1962; Hogan & Shanks, 1965; Coorts *et al.*, 1964; Penningsfeld, 1960; Arnold Bik, 1960).

Another hazard to flower crops is salinity of the substrate or growing medium. Fertilizers inevitably raise electrolyte concentration in the substrate.

An excess of salts resulting from injudicious use of fertilizers commonly causes salt damage to flower crops. Farmyard manure, sometimes constituting 10 to 15% (v/v) of the substrate, is an important source of salts, especially of potassium and sodium. Accumulation of $Na^+$ and $Cl^-$ from irrigation water may likewise be considerable, particularly in the western Netherlands where in some regions the $Cl^-$ content of surface water approaches the critical level of 200 mg per litre.

The most common flowers have been classified in their order of salt tolerance (Lunt *et al.*, 1957; Kofranek *et al.*, 1953, 1956, 1958; Kohl *et al.*, 1956). The effect of salts is ascribed primarily to the osmotic pressure of saline solutions.

Nutritive elements are still applied to flowers primarily through the substrate. The substrate is much more closely controlled in floriculture than in agriculture. Thus for potted plants a limited volume of soil is used per plant. Without special care in the mixing of the substrate and the tending of individual plants, such crops could hardly be raised. Traditional potting composts have been developed over many years by trial and error. The components of these composts vary but all of them are rich in organic matter, undoubtedly because it improves the physical properties of the substrate (Dänhardt & Kühle, 1959; Bunt, 1961; Tepe, 1953). Peat especially improved the water-holding capacity of mixtures with clay (Arnold Bik, 1962).

Nitrogen, salt concentration and substrate composition can be considered the most important criteria in the nutrition of flower crops. They are closely interrelated. The influence of substrate on the two other factors is evident from the rise in critical salt levels with peat content. Because of the increase in moisture capacity, the actual concentration is less, thus alleviating the danger for the grower (Hösslin & Penningsfeld, 1949).

Furthermore, the relation between substrate and nitrogen can be observed in an

increasing response to nitrogen with peat content of the substrate (Arnold Bik, 1962). Moisture supply to the crop could well be involved in such a response.

So far, little attention had been paid to the relation between nitrogen nutrition and salinity. Such a relationship can be deduced from the following considerations.
1. Trials with different levels of nitrogen and moisture (Hamilton *et al.*, 1956; Hawthorn & Pollard, 1956; Richards *et al.*, 1958; Stanberry & Lowrey, 1965; Bauer *et al.*, 1965) show that response to nitrogen is greater when moisture level is optimum.
2. The availability of water to the plant decreases with increasing salt concentration as a result of a rise in osmotic pressure of the solution (Hayward & Spurr, 1943; 1944).

Both observations suggest that the response to nitrogen is reduced by increasing salinity.

However an understanding of any effect of salt on the response to nitrogen is hindered by the mutual antagonistic effects of ions. For instance it is known that $NO_3^-$ and $Cl^-$ compete with each other for entry into the plant (de Wit *et al.*, 1963).

The mutual dependence of substrate with nutrition and salinity is recognized by soil-testing experts working in the greenhouse districts of Holland. For instance, organic matter is taken into account for the interpretation of analytical data (van den Ende, 1952). However it is not entirely clear whether correction is on volume weight or on water-holding capacity of the soil sample.

Data on the relationships seem sparse. More information should ease advisory work on nutrition of flower crops. My research had the aim of clarifying these relationships.

I studied the influence of salt accumulation on efficiency of nitrogen and their dependence on factors which determine the salt concentration in the substrate. The factors were nitrogen application itself, application of sodium chloride and the type of the substrate. These variables were introduced in various combinations in the trials.

To evaluate the influence of salt accumulation on plant growth, two physiological aspects are usually distinguished (Bernstein & Hayward, 1958):
1. the effect of a non-availability of water, i.e. physiological drought, through the difficulty roots have in absorbing water against the high osmotic pressure (OP).
2. the specific ion effect by influx of salts into the plant and hence ionic antagonism and toxicity.

Originally workers on saline soils, especially in America, tended to consider the salt effect entirely as drought. This concept, known as the theory of osmotic inhibition or as the theory of physiological drought, derived from the assumption that the plant behaves like an ideal osmotic cell. It was based on two observations: the similarity in growth depression of plants between isosmotic solutions of different salts (Hayward & Spurr, 1944) and the additiveness of matric suction and osmotic suction of the soil solution in growth depression on saline soils (Wadleigh & Ayers, 1945). This view proved to be a simplification and had to be abandoned. Work by van den Berg (1952) and others led to the view that the specific ion effect is important in the influence of salinity. The concept of the plant as an ideal osmotic cell, opposed particularly by Walter (1955), was shown to be untenable by the discovery that the plant can adapt

to changes in OP of the substrate (Bernstein & Hayward, 1958; Bernstein, 1961; Lagerwerff & Eagle, 1962). Some time after transfer of roots to a saline substrate, the OP in the plant had risen by salt uptake by about as much as the rise in external OP, thus restoring the turgor pressure (TP) and the osmotic gradient between plant and medium.

This phenomenon led some people (Bernstein, 1961) to reject physiological drought. However, adjustment of TP as such is not sufficient to restore internal water balance. Such restoration would require an adjustment of diffusion pressure deficit (DPD) as well but that does not happen.

Slatyer (1961) showed by direct DPD measurements that a rise in external OP by addition of salt to the substrate induces an equivalent rise in both internal OP and DPD; the internal water balance deteriorates despite restoration of TP. Consequently, Aspect 1 can be maintained alongside acceptance of osmotic adaptation by the plant. This broader view of salinity allows the two aspects to be related.

The above is important in that the influence of salinity upon nitrogen response of the plant can theoretically be linked to an osmotic effect.

When gravity and the external gas pressure are ignored, the availability of water in soil or substrate to the plant is a function of the total suction $S_t$ (Wadleigh & Ayers, 1945). The following relationship exists between $S_t$, the matric suction $S_m$ and the osmotic suction of the soil solution or solute suction $S_s$ (Bolt *et al*, 1965):

$$S_t = S_m + S_s \tag{1}$$

Thus to study the influence of substrate salinity on plant growth, $S_m$ must be standardized as far as is possible. In trials with different substrates, this condition was met wherever possible.

In cultures on nutrient solutions, $S_m$ can be deleted from the above relationship. The availablity of water is then a function of $S_s$ only.

Since the water balance of the plant is involved in physiological drought, I gathered information on the water consumption of the plant.

To examine the specific ion effect, I studied cation and anion relationships in the plant material and, in one trial, the influence of 4 different salts on the nitrogen effect was compared.

# 2 Materials and methods

## 2.1 Plant material

*Gloxinia* (syn. *Sinningia*) cv. Schweizerland, a salt-sensitive species (Arnold Bik, 1962) was obtained from commercial nurseries as seedlings and *Chrysanthemum* cv. Giant Yellow Indianapolis, a salt-tolerant species (Kofranek *et al.*, 1953) as rooted cuttings. As there was little greenhouse space, the two species were grown at different times.

## 2.2 Types of trial

All 3 trials were of factorial design with 4 variables: rate of nitrogen; type of salt; rate of salt; type of substrate.

Trial 1 had 4 × 4 × 1 × 1 treatments; each treatment consisted of three replicate 8-litre plastic buckets of nutrient solution, each containing 3 plants.

Trials 2 and 3 had 5 × 4 × 3 × 1 and 6 × 1 × 2 × 3 treatments, respectively, each consisting of 6 replicate enamel pots containing 5.4 litre substrate and 3 plants. Nitrogen was supplied as ammonium nitrate. Each pot received $Ca(H_2PO_4)_2$ supplying 1200 mg $P_2O_5$; $K_2SO_4$ 2200 mg $K_2O$ for Trial 2, 1500 mg $K_2O$ for Trial 3; $MgSO_4$ 400 mg of MgO for Trial 2, 200 mg MgO for Trial 3; Sporumix A (a trace element mixture) 1080 mg and FeEDDHA (ethylenediamine-di-(0-hydroxyphenyl-acetate)) 0.5 g. The trials were in greenhouses, the first at Aalsmeer Research Station and the others at Eelderwolde, between 1964 and 1967.

*Trial 1: different concentrations of N and of NaCl in nutrient solutions* Nitrate N was supplied at 2, 8, 20 and 40 meq per litre. The buckets were fitted with lids, each with 3 round holes in which plants were held by a strip of plastic foam round the base of the stem and with a plastic tube through the centre almost to the bottom of the bucket for intermittent aeration (10 min in every 15). Nutrient solutions (Table 1) were made up with the assistance of Soilless Culture Section of the Organization for Applied Scientific Research (TNO) and were renewed every week for chrysanthemum and every 2 weeks for the slower growing gloxinia. After 2 or 3 weeks NaCl was added to the culture solutions: for gloxinia 0, 12, 36 and 72 meq per litre and for chrysanthemum twice as much because of its higher tolerance. For gloxinia the trial lasted from 13 April until 6 June 1966 and for chrysanthemum from 21 June until 26 July 1967.

Table 1. Ionic composition (meq/litre) of the nutrient solutions for the four concentrations of $NO_3^-$ before adding NaCl.

| $NO_3^-$ | $NH_4^+$ | $K^+$ | $Na^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $NO_3^-$ | $Cl^-$ | $H_2PO_4^-$ | $SO_4^{2+}$ |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 0.90 | 4.0 | 1.0 | 4.0 | 3.5 | 2.0 | 7.55 | 0.35 | 3.5 |
| 8 | 0.90 | 4.0 | 4.0 | 4.0 | 3.5 | 8.0 | 4.55 | 0.35 | 3.5 |
| 20 | 0.90 | 4.0 | 12.35 | 4.0 | 3.5 | 20.0 | 0.90 | 0.35 | 3.5 |
| 40 | 0.90 | 4.0 | 32.35 | 4.0 | 3.5 | 40.0 | 0.90 | 0.35 | 3.5 |

*Trial 2: different N rates and different types and rates of salt in pots* Nitrogen was supplied at 200, 1200, 2200, 3200 and 4200 mg per pot and NaCl, KCl, $Na_2SO_4$ or $K_2SO_4$ at 0, 40.4 and 84.4 meq per kg dry substrate. The compost substrate was made by mixing 3 parts by volume of peat moss with 2 of sand. The slightly acid peat moss was limed previously, 2.5 g per litre for gloxinia and 3 g per litre for chrysanthemum; the amount of chalk was lower for gloxinia than for chrysanthemum because of its greater sensitivity to lime-induced chlorosis. The pots were watered daily to 70% saturation. For gloxinia the trial lasted from 24 June until 10 August 1965 and for chrysanthemum from 18 August until 15 October 1965.

*Trial 3: different rates of N and of NaCl, and different substrates in pots* Nitrogen was supplied at 100, 400, 800, 1300, 1900 and 2600 mg N per pot for gloxinia and 200, 800, 1600, 2600, 3800 and 5200 mg N per pot for chrysanthemum, and NaCl at 0 and 6, and 0 and 12 g, respectively. As in Trial 2 peat moss was limed, before mixing with sand for gloxinia and clay soil for chrysanthemum in the proportions 3:7, 6:4 and 9:1. This sort of mixture is widely used in flower crops (Baker, 1957; Arnold Bik, 1965). For chrysanthemums the pots were replaced by plastic buckets holding 9.2 litre substrate and nutrients were added at double rate. The pots were watered daily to pF 1.8 for gloxinia and pF 1.6 for chrysanthemum. The trial lasted from 31 March to 8 June 1965 for gloxinia and from 9 April to June 1964 for chrysanthemum.

## 2.3 Observations

*Specific conductivity of saturation extract* ($EC_e$ in mmho $cm^{-1}$ at 25° C) was used as a measure of salinity (USDA Handbook 60; Richards, 1954). This method is being increasingly used for potting mixtures (Baker, 1957). It is based on extraction of the saturated substrate and is therefore a function of moisture capacity, i.e. of the ratio soil: water. In the culture solutions the specific conductivity (EC) served as a measure of salinity. Osmotic pressure was measured cryoscopically with an apparatus developed by Richards & Campbell (1948) and by a method of van den Ende & Koornneef (1961).

*Ions in the saturation extract* were estimated by methods described by Schuffelen *et al.* (1961), in particular $NH_4^+$, $K^+$, $Na^+$, $Ca^{2+}$, $Mg^{2+}$, $NO_3^-$, $Cl^-$, $H_2PO_4^-$ and usually also $SO_4^{2-}$.

*Moisture capacity and pF curves*, estimated, respectively, during preparation of saturation extracts and by Ir. P. Boekel (see Acknowledgments).

*Yield of dry matter* is a useful parameter of the quality of ornamentals (Lunt & Kofranek, 1958). In the hydroponic trials, aerial and 'underground' parts of the plants were harvested. In the trials with solid substrates, aerial parts of both species and tubers of gloxinia were harvested.

*Leaf colour* at harvest of gloxinia grown on solid substrates was rated on a scale: 2 = very light; 4 = light; 6 = normal; 8 = dark; 10 = very dark.

*Water consumption* was estimated by losses of nutrient solution each time culture solutions were changed in Trial 1 and by loss of weight, allowing for weight of plants, in Trial 2.

*Ions in the plant* were estimated as in soils but in addition to the ions, total nitrogen in dry matter (DM) was estimated.

# 3 Results of Trial 1: different concentrations of N and of NaCl in nutrient solutions

## 3.1 Salinity of the nutrient solutions

Table 2 gives osmotic pressure (OP) and specific conductivity (EC) of the nutrient solutions. For gloxinia the average increases in OP and EC with increasing NaCl concentration agreed quite well with those appearing in USDA Handbook 60 (Richards, 1954, figs 2 and 5).

For the various nitrate levels, the variations in OP and EC were a bit smaller for chrysanthemum than for gloxinia.

Table 2. Osmotic pressure (OP) at 0° C and specific conductivity (EC) at 25° C of nutrient solutions.

| NaCl | meq $NO_3^-$/litre | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| levels | 2 | | 8 | | 20 | | 40 | | average | |
| | OP | EC | OP | EC | OP | EC | OP | EC | OP | EC |
| meq/litre | atm | mmho/cm | atm | mmho/cm | atm | mmho/cm | atm | mmho/cm | atm | mmho/cm |
| Gloxinia | | | | | | | | | | |
| 0 | 0.6 | 1.7 | 0.7 | 2.0 | 1.1 | 2.9 | 1.8 | 5.0 | 1.05 | 2.90 |
| 12 | 1.1 | 3.0 | 1.3 | 3.4 | 1.6 | 4.2 | 2.3 | 6.2 | 1.58 | 4.20 |
| 36 | 2.2 | 5.9 | 2.3 | 6.2 | 2.6 | 6.9 | 3.4 | 8.8 | 2.62 | 6.95 |
| 72 | 3.7 | 9.7 | 3.8 | 10.0 | 4.2 | 10.9 | 4.8 | 12.6 | 4.13 | 10.80 |
| Chrysanthemum | | | | | | | | | | |
| 0 | 0.5 | 1.6 | 0.6 | 1.8 | 0.9 | 2.5 | 1.6 | 4.4 | 0.90 | 2.6 |
| 24 | 1.5 | 4.1 | 1.6 | 4.4 | 2.0 | 5.2 | 2.6 | 6.9 | 1.93 | 5.2 |
| 72 | 3.5 | 9.2 | 3.6 | 9.3 | 3.8 | 9.8 | 4.5 | 11.5 | 3.85 | 10.0 |
| 144 | 6.2 | 16.0 | 6.4 | 16.6 | 6.5 | 16.8 | 7.2 | 18.3 | 6.58 | 17.0 |

## 3.2 Nitrate concentration and yield of dry matter

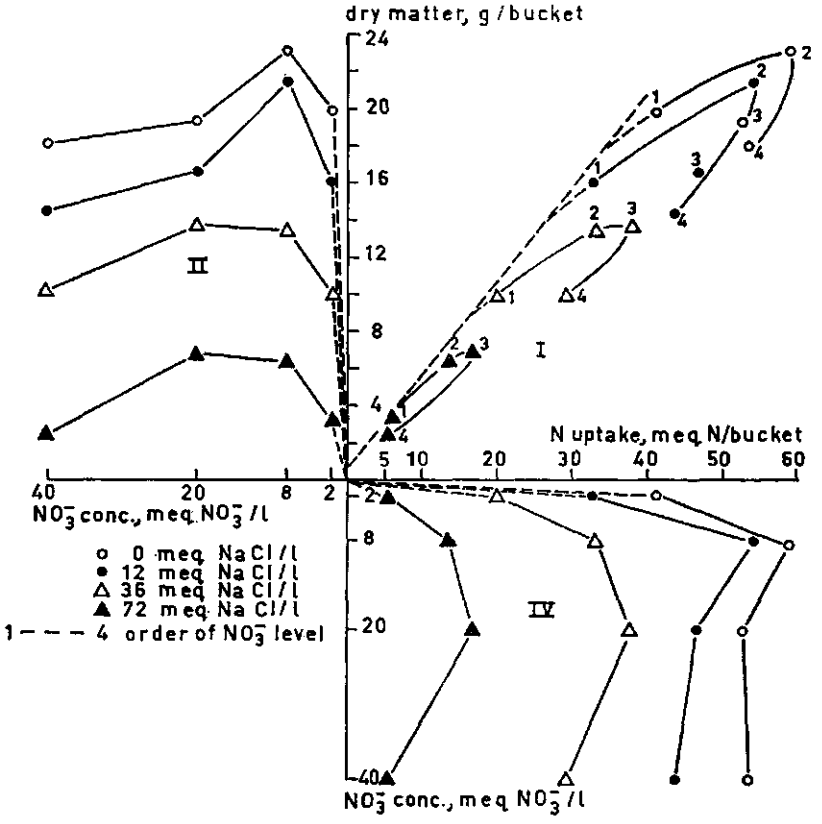
Table 3 shows the relative yield depression caused by NaCl.

The influence of a limiting factor (i.e. NaCl) on the response to nutrition can be clearly visualized in a quadrant graph as proposed by de Wit (1953) Fig. 1 shows such

Table 3. Yields of dry matter in water culture with various NaCl and $NO_3^-$ levels, as a percentage of those found with no NaCl.

| NaCl level | meq $NO_3^-$/litre | | | | |
|---|---|---|---|---|---|
| meq/litre | 2 | 8 | 20 | 40 | average |
| Gloxinia | | | | | |
| 0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| 12 | 83.8 | 93.0 | 86.0 | 80.0 | 85.4 |
| 36 | 52.3 | 58.3 | 71.0 | 56.1 | 59.4 |
| 72 | 17.3 | 27.8 | 35.2 | 13.3 | 23.6 |
| Chrysanthemum | | | | | |
| 0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| 24 | 89.0 | 92.3 | 81.7 | 83.3 | 86.6 |
| 72 | 64.6 | 70.1 | 65.3 | 63.4 | 65.9 |
| 144 | 42.0 | 48.0 | 45.2 | 45.8 | 45.2 |

Fig. 1. Relationship between nitrogen concentration, nitrogen uptake and yield of dry matter of gloxinia at four NaCl levels.



a graph for the gloxinia trial. The unfavourable effect of NaCl on yield is evident from the vertical arrangement of the curves in Quadrant II.

To evaluate the relationship between $NO_3^-$ and yield in Fig. 1, it should be realized that the plants were entirely dependent for their nitrogen nutrition on the nutrient solutions. Therefore if the nutrient solutions contain no nitrate, the increase in yield will be practically nil. Hence, after extrapolation to 0 meq $NO_3^-$ per litre, the four curves in Quadrant II will practically converge in the origin of the graph. This extrapolation is indicated in the graph with a broken line. An examination of the course of the curves starting from the origin elucidates their mutual interrelationship and focuses attention on the effect of NaCl as a factor limiting the response of plants to $NO_3^-$ nutrition. At higher rates of $NO_3^-$ all curves decline. For the two lower NaCl levels, the decline sets in after the second $NO_3^-$ level, for the two higher NaCl levels after the third $NO_3^-$ level.

The curves of Quadrant IV show a striking similarity with those of Quadrant II. NaCl exerted a depressive influence on uptake of nitrogen. The optima for uptake of nitrogen coincided with those for production of dry matter. Extrapolation of the curves to 0 meq $NO_3^-$ also results in close convergence at the origin. Since the plants were harvested at a stage when N uptake is strongly correlated with growth, it is difficult here to further investigate the relationship between nitrate concentration and nitrogen absorption.

A limiting factor will also manifest itself in the relationship between nutrient uptake and yield. Evidently, the efficiency with which the absorbed nutrients are utilized by the plant is strongly dependent on the existing environmental conditions.

The four curves in Quadrant I must converge at the origin after extrapolation to zero nitrogen absorption, since no nitrogen absorption will mean no production of dry matter. In the graph, these extrapolations were drawn arbitrarily, and are therefore indicated by broken lines.

The combination of curves thus obtained closely resembles those presented by de Wit (1953) to show the influence of a certain limiting factor on the relationship between nutrient uptake and yield.

The graph of Trial 1 shows that the four curves coincide in the range in which yield is proportional to nitrogen uptake. However, at increasing N uptake, the curve deviates sooner from this linear relationship, the higher the rate of NaCl. This implies that utilization of absorbed nitrogen by the plant was unfavourably affected by the presence of NaCl in the root environment.

It is striking that at higher rates of NaCl all four curves decline sharply both for yield and nitrogen absorption, especially for yield. This result in every NaCl series must be ascribed to a limiting factor other than NaCl. Significantly the maxima in the curves can be connected by a reasonably straight line through the origin. Hence for nitrogen a critical N content in dry matter exists which in this trial was about 2500 meq N per kg DM. When this critical value is exceeded, growth declines sharply. De Wit (1953) and de Vries & de Wit (1958) recognized the possibility of such a critical value.

The results of the chrysanthemum trial are given in Fig. 2. The responses of chrysanthemum to the treatments resembled those of gloxinia. Quadrant II shows that both the yield and yield relative to $NO_3^-$ concentration were adversely affected by NaCl.

The relative yields for this trial at different rates of NaCl are listed in Table 3. The large difference in salt tolerance between the two species is evident from the depression in yield at 72 meq NaCl. For gloxinia the depression was 76%, for chrysanthemum only 34%.

Quadrant IV shows that the relationship between nitrogen uptake and $NO_3^-$ concentration was disturbed by the presence of NaCl, as was found also for gloxinia.

The relationship between N uptake and yield of chrysanthemum (Quadrant I) agreed well with that observed for gloxinia. Also for chrysanthemum the utilization of absorbed nitrogen seemed to be lowered by NaCl. The higher portions of the curves also show a sharp decline. Hence, a critical N percentage seems to exist also for chrysanthemum. The maxima of the curves and the origin can be connected by a straight line indicating a critical content of 2350 meq N per kg DM.

Figure 3 shows that a distinct relationship does not always exist between nitrogen

Fig. 2. Relationship between nitrogen concentration, nitrogen uptake and yield of dry matter of chrysanthemum at four NaCl levels.

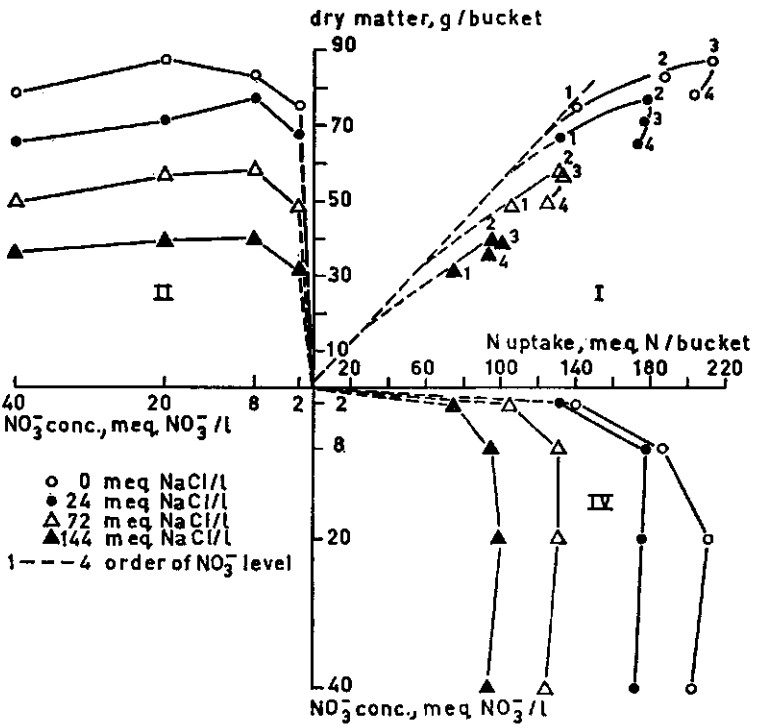
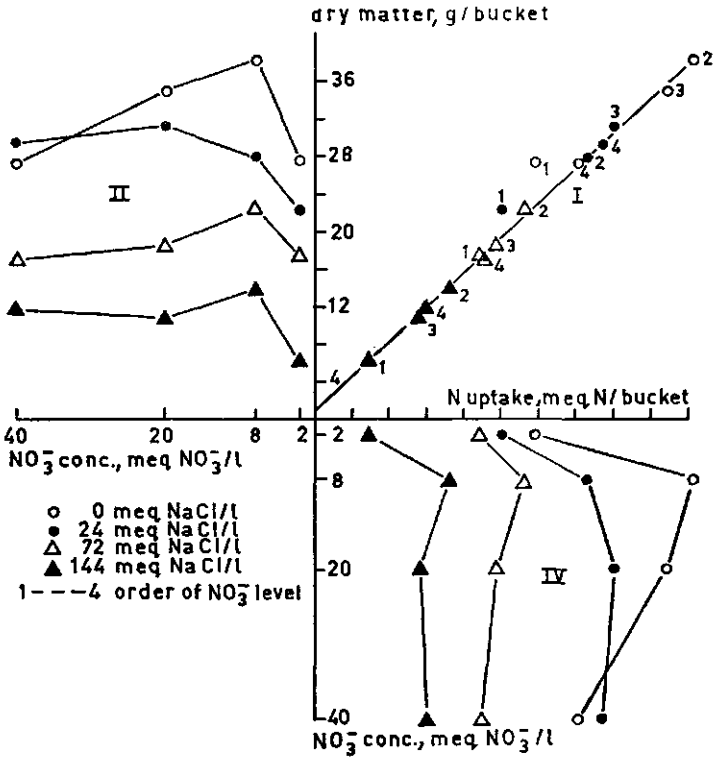


Fig. 3. Relationship between nitrogen concentration, nitrogen uptake and yield of dry matter of chrysanthemum at four NaCl levels (plants shaded against sunlight).




uptake, NaCl and yield. It summarizes the results of another chrysanthemum trial, in which treatments, season and duration were similar but the plants grew in a greenhouse permanently shaded against sunlight. The yields, being lower than those in the other trial, reflected the lower light intensities in this trial.

Quadrant I shows points that all lie on a straight line through the origin, except the points of the lowest rate of $NO_3^-$ for the first and second rates of NaCl. This straight line represents a nitrogen content of about 2640 meq N per kg DM, a value higher than that in full sunlight. The higher value indicates that the plants had a slight excess of nitrogen. The practical absence in this trial of the effect of NaCl on dry matter relative to nitrogen uptake can be ascribed to suboptimal lighting. It corroborates that the effect of a certain growth factor is greater the nearer the other factors are to optimum (Brouwer, 1960). In this trial, the effect of NaCl on the relationship between $NO_3^-$ application and yield of dry matter must be almost entirely ascribed to the effect of NaCl on nitrogen uptake relative to $NO_3^-$ application.

### 3.3 Nitrate concentration and water consumption

In figs 4a and 5a, the water consumption in each NaCl series is plotted against concentration of $NO_3^-$ for gloxinia and chrysanthemum, respectively. In shape these curves for both species closely resemble the curves relating $NO_3^-$ concentration and yield of dry matter (figs 1 and 2). The remarks made on the influence of NaCl on yield relative to $NO_3^-$ concentration hold also for the influence of NaCl on total water consumption relative to $NO_3^-$ concentration.

Table 4 gives total water consumption for the various treatments in percentage of that without NaCl.

By comparison of the data on reduction in water consumption with those on reduction in yield, a close correlation is again apparent. The reduction in water use and

Fig. 4. Relationship between total water consumption, nitrogen concentration and yield of dry matter of gloxinia at four NaCl levels.

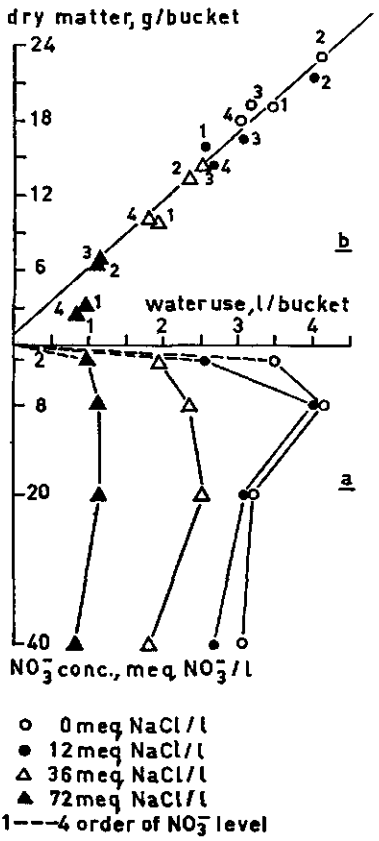



Fig. 5. Relationship between total water consumption, nitrogen concentration and yield of dry matter of chrysanthemum at four NaCl levels.

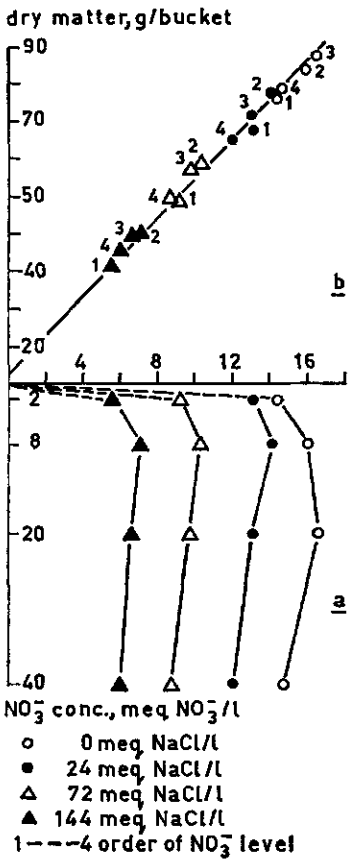


Table 4. Water consumption relative to that with no NaCl.

| NaCl level | meq $NO_3^-$/litre | | | | |
|---|---|---|---|---|---|
| meq/litre | 2 | 8 | 20 | 40 | average |
| Gloxinia | | | | | |
| 0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| 12 | 73.6 | 97.1 | 96.6 | 87.4 | 88.9 |
| 36 | 55.2 | 56.7 | 80.0 | 59.5 | 62.9 |
| 72 | 27.5 | 27.1 | 35.9 | 26.9 | 29.2 |
| Chrysanthemum | | | | | |
| 0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| 24 | 91.5 | 90.3 | 78.9 | 82.1 | 85.6 |
| 72 | 67.7 | 65.4 | 58.8 | 60.3 | 62.9 |
| 144 | 38.9 | 44.5 | 39.9 | 44.6 | 42.0 |

in yield at 72 meq NaCl per litre was about twice as much in gloxinia as in chrysanthemum.

In figs 4b and 5b, yield is plotted against total water consumption for gloxinia and chrysanthemum, respectively. In both graphs the points of all treatments (except two for gloxinia) lie on a straight line almost through the origin. Hence, for both species there was a linear relationship between yield and total water consumption. Both trials confirm the relationship derived by de Wit (1958) for both values from results of several pot trials in temperate regions.

In both trials, the transpiration coefficient (water consumption/DM) seemed independent of NaCl and $NO_3^-$ levels, and total ion concentration of the nutrient solution. The transpiration coefficients for the two species were remarkably similar: 185 for gloxinia and 186 for chrysanthemum. Only for the 1st and 4th $NO_3^-$ level of the 4th NaCl series of the gloxinia trial were much higher values obtained: about 330. For the first level, this high value must be ascribed to a lower net assimilation rate (NAR), being the rate of accumulation of dry matter per unit leaf area. This low NAR was caused by lack of a nutrient (de Wit, 1958; Watson, 1952; Middelburg, 1967), in this case, presumably nitrogen in the first place (Fig. 4b). For the 4th level root damage and disturbed root function presumably played a role.

The following consequences can be drawn from the observed relationship between yield and total water consumption:

Except in the two cases mentioned, the nutrient percentages of the plant material exceeded the level below which NAR and nutrient supply are positively correlated (de Wit, 1958). Thus, on account of the constancy of NAR in increment of dry matter per unit time, being leaf area × NAR, increment of dry matter was a linear function of leaf area.

The transpiration coefficient is determined by the factors transpiration and net assimilation. Both factors are influenced by the degree of stomatal opening. A reduction in stomatal opening leads to a relatively larger increase in total resistance to diffusion of water vapour from the leaf than to diffusion of $CO_2$ into the leaf (Slatyer & Bierhuizen, 1964). The result is a reduced transpiration coefficient if stomata are partially closed. As no higher transpiration coefficients (except two for gloxinia) occurred than those indicated by the straight lines in figs 4b and 5b, stomatal opening must have been normal for most of the trials in all treatments. This implies that the rate of transpiration per unit leaf area was the same for all treatments, so that a linear relationship may be assumed between transpiration and leaf area.

Hence, yield and transpiration are both functions of the leaf area. The nature of the correlation between both values is thus elucidated.

A study of the relationship between leaf growth and transpiration can shed light on the water balance of plants during the trial, thus promoting an understanding of the background of the observed yield differences.

However, the data on total water consumption will be of little help in this respect. At the time of observation water consumption and leaf area were already interrelated in such a way that cause and effect could no more be distinguished. For an insight into the water balance, only those data can be used that were collected in the period before leaf growth and transpiration were interdependent, that is shortly after the trial started.

Table 5 gives an impression of the influence of NaCl on water consumption during the period from the start to first renewal of the solution. To exclude possible effects of N, an evaluation of the influence of NaCl on transpiration in this initial period can be based on the data in the last column, representing the average of all $NO_3^-$

Table 5. Water consumption during the period from the start to the first renewal of the solution in percentage of that found with no NaCl.

| NaCl level | meq $NO_3^-$/litre | | | | |
|---|---|---|---|---|---|
| meq/litre | 2 | 8 | 20 | 40 | average |
| Gloxinia (14-day period) | | | | | |
| 0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| 12 | 82.2 | 65.0 | 92.0 | 101.3 | 81.0 |
| 36 | 94.7 | 46.6 | 78.8 | 95.4 | 74.0 |
| 72 | 55.3 | 33.5 | 57.2 | 62.2 | 49.0 |
| Chrysanthemum (8-day period) | | | | | |
| 0 | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| 24 | 88.6 | 88.6 | 87.3 | 95.8 | 90.0 |
| 72 | 77.3 | 78.9 | 72.8 | 69.9 | 74.8 |
| 144 | 55.7 | 64.0 | 66.5 | 60.8 | 61.7 |

levels. That column shows a distinct decrease in transpiration with increasing NaCl concentrations. NaCl exerted a much smaller negative effect on the transpiration of chrysanthemum than of gloxinia. At 72 meq NaCl, the reduction in water consumption was 25% for chrysanthemum, and 51% for gloxinia.

In the initial period before the actual trial began, the gloxinia plants grew up for a 14-day period on nutrient solutions differing only in $NO_3^-$ levels. This was done to increase the chance of survival of plants later exposed to NaCl. For this initial period, water consumption relative to that of the first $NO_3^-$ level was 100, 104, 94, and 95% with 2, 8, 20, and 40 meq $NO_3^-$ per litre, respectively.

For chrysanthemum, without an initial NaCl-free period, water consumption, averaged over all NaCl levels for the period before the solution was first renewed, was 100, 97.4, 95, and 91%, respectively. The data, which were not highly reproducible, tend to show that for both species transpiration was lowered with more than 8 meq $NO_3^-$ per litre.

It has long been known that a rise in osmotic pressure in nutrient solution depresses the transpiration rate (Lagerwerff & Eagle, 1962; Brouwer, 1963a; Oertli, 1967). It has also been shown that the decrease in rate of transpiration arises from an increase in suction tension (DPD) in the leaf (Slatyer, 1961; Ehlig & Gardner, 1964; Janes, 1966). The manner in which the transpiration rate is affected by variations in DPD, brought about by addition of NaCl to the nutrient solution, was elegantly shown by Brouwer (1963b) using bean plants. Initially, the rate of transpiration decreased slowly with increasing leaf suction (DPD or $S_l$). Later, when, apparently, the critical DPD level for closing of stomata has been exceeded, the rate of decline increased.

Therefore the observed reductions in transpiration of chrysanthemum and gloxinia are clear indications of corresponding rises in DPD in the leaves. However, on account of the equation OP = DPD + TP, these rises are inevitably associated with corresponding decreases in leaf turgidity. A decrease in TP of a leaf in turn induces a decrease in rate of leaf growth, primarily, as is assumed, through a depression of cell elongation (Shaw, 1952; Slatyer, 1967). The negative effect of rising DPD on the rate of leaf growth was convincingly shown by Brouwer (1963b) in his trial, already mentioned, with beans. A reduced rate of leaf growth results in a lower increment of dry matter.

Summarizing the effect of salinity on water balance of the plant, thus in Trial 1 NaCl and excess $NO_3^-$, through a deterioration in water balance, decreased relative leaf growth rate $R_A$ (increase in leaf area per unit area per unit time; Bouma, 1965) and, consequently, relative growth rate $R_W$ (increase in weight per unit weight per unit time).

From data on transpiration in the initial period and from the close positive relationship between leaf growth and yield of dry matter in gloxinia and chrysanthemum, the influence of NaCl and excess $NO_3^-$ – or, in general, the influence of salt – is reduced in the foregoing to an osmotic effect. Evaluation of ionic balances in the various trials can show whether specific ion effects must be taken into account.

The data on transpiration in the initial periods do not raise the impression that

at the various salt levels a complete osmotic adaptation has taken place in the sense meant by Bernstein (1961). The variations in transpiration between the NaCl levels turned out to be too large for such an adaptation. Brouwer (1963b) and Oertli (1966) in similar trials likewise could not find a complete adaptation of the internal OP to rise in external OP. Brouwer (1963a) believed that the plant is only partially capable of compensating the rise in 'solute suction', so that an osmotic effect will always remain.

Oertli (1966) expresses similar views. According to Greenway (1965a), salt absorption in growing cells does not always proceed rapidly enough for complete osmotic adaptation.

The smaller reduction in transpiration of chrysanthemum than of gloxinia under the influence of NaCl in the medium might indicate that chrysanthemum can better adapt. However, this conclusion seems to be contradicted by the fact that the salt accumulation is much larger in gloxinia than in chrysanthemum (Section 3.5). According to Greenway (1965b), a rapid osmotic adaptation is one condition for salt tolerance.

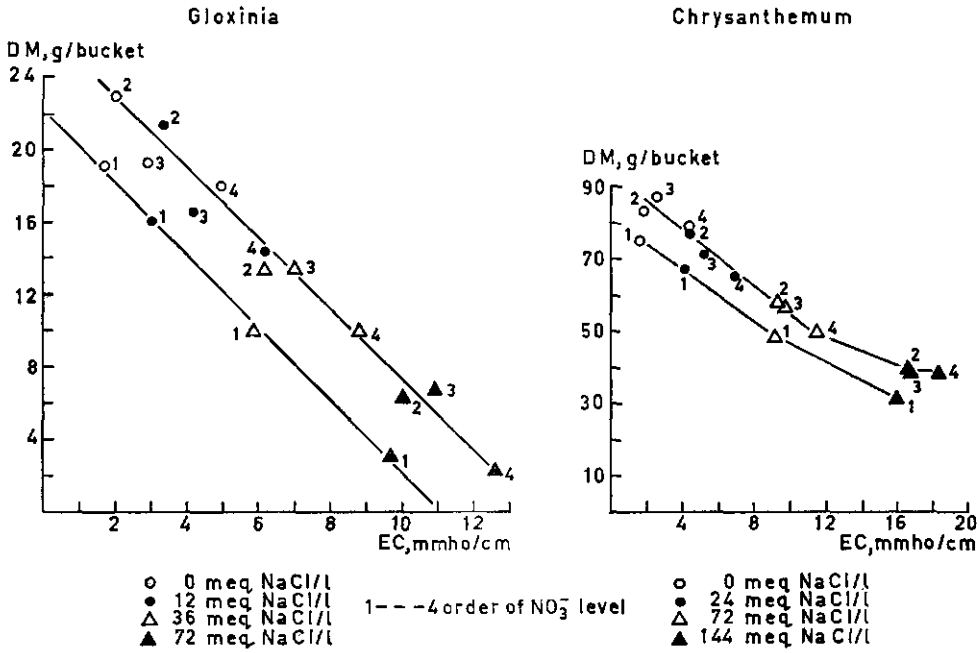
### 3.4 Salinity and yield of dry matter

Emphasis has already been placed on the interaction of $NO_3^-$ and NaCl in the medium on yield.

In Fig. 6, yield of gloxinia and chrysanthemum is plotted against EC of the nutrient solutions. The salinity caused by NaCl was responsible for the negative correlation over the entire EC range examined. At each NaCl level the salt effect of $NO_3^-$ is noticeable each time over a range of about 3 mmho per cm, corresponding with a $NO_3^-$ range from 2 to 40 meq per litre. At every rise in EC within this range, the yield tended to increase initially – against the general trend – but tended to decline beyond the optimum $NO_3^-$ level in conformity with the general trend. In the sub-optimum range, the nutritional effect of $NO_3^-$ apparently overshadowed the salinity effect, thus exhibiting another facet of the interaction between salinity and nitrogen. This interaction also accounted for the dispersion of points within each NaCl series. In the range between 1.5 and 12 mmho per cm two straight lines can be drawn, one through points representing the lowest $NO_3^-$ level and one through the points representing the other $NO_3^-$ levels. Both lines run virtually parallel.

In the range between 1.5 and 12 mmho per cm, decline in yield was linearly correlated with EC. For gloxinia, the reduction in yield per unit EC ($dP/dEC$) amounted to 2 g $mmho^{-1}$ cm, for chrysanthemum this value was 3.6 g $mmho^{-1}$ cm. These values have no general meaning, but apply to experimental conditions only. As was shown by Brouwer (1963a), the environmental factors, especially light intensity, are largely responsible for the reaction of a crop to salinity. Bean plants grown on nutrient solutions with different osmotic pressures by NaCl additions showed, in comparison with controls, a very strong reduction in dry weight and fresh-leaf weight in summer, whereas hardly any reduction was found in

Fig. 6. Relationship between yield of dry matter and EC of the nutrient solution.




winter. It must be remarked, however, that the yield of control plants was very low in winter.

The above was confirmed by the trials with chrysanthemum. In one of them, conducted under suboptimum light intensity (Fig. 5) but with otherwise the same treatments as in the chrysanthemum trial just discussed d$P$/dEC amounted to 1.98 g mmho$^{-1}$ cm. This value is over half that in the trial with normal light conditions.

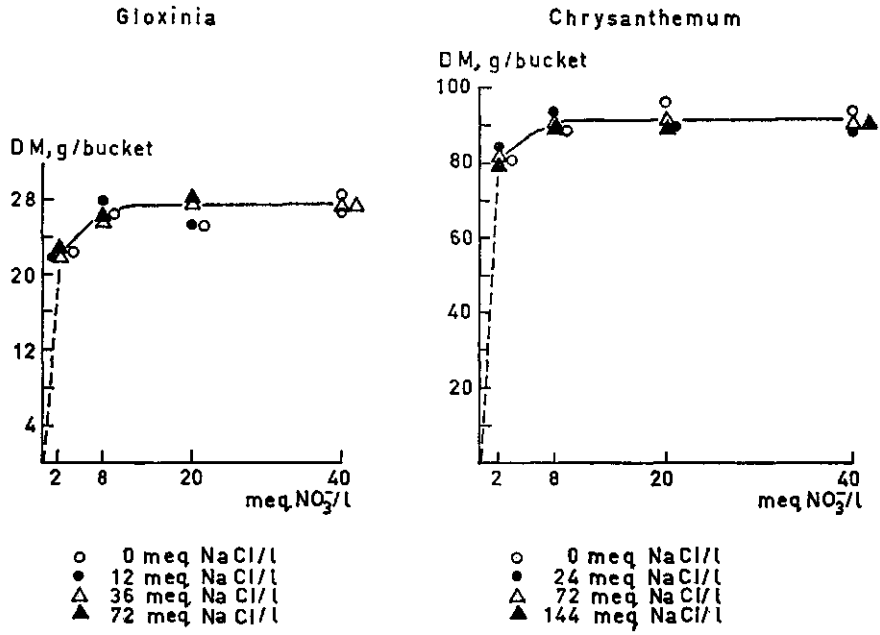
Furthermore, Fig. 6 shows that for chrysanthemum d$P$/dEC decreased at values of EC exceeding 12 mmho per cm.

Using the values obtained for d$P$/dEC and the corresponding EC values of the nutrient solution, yield of each treatment can be adjusted to an EC value of 0 mmho per cm. Plotting the adjusted yield against the $NO_3^-$ levels for both trials yields the relationships shown in Fig. 7.

Instead of four curves (figs 1 and 2) as found in the NaCl series, only one curve is obtained here. Furthermore, the decline in the curves beyond optimum $NO_3^-$ level has been replaced by a horizontal stretch. In addition, the one curve resulting from combination of four curves is typical in shape of a yield curve.

As correction for EC brought together the four NaCl curves into one yield curve, salinity was indeed the only factor disturbing the relationship between $NO_3^-$ level and yield in these trials and, at least within the EC range examined, NaCl and $NO_3^-$ in the medium were identical in salinity effect for either species. The specific ion effect did not therefore seem important in salinity in trials with either species. The decline

Fig. 7. Relationship between yield of dry matter and $NO_3^-$ concentration after adjustment to EC = 0.




in yield resulting from excess $NO_3^-$ presumably had the same physiological origin as that from NaCl (Section 3.3).

### 3.5 Ionic balance

The influence of $NO_3^-$ and NaCl on ionic balance in plants is shown in Fig. 8 for both species.

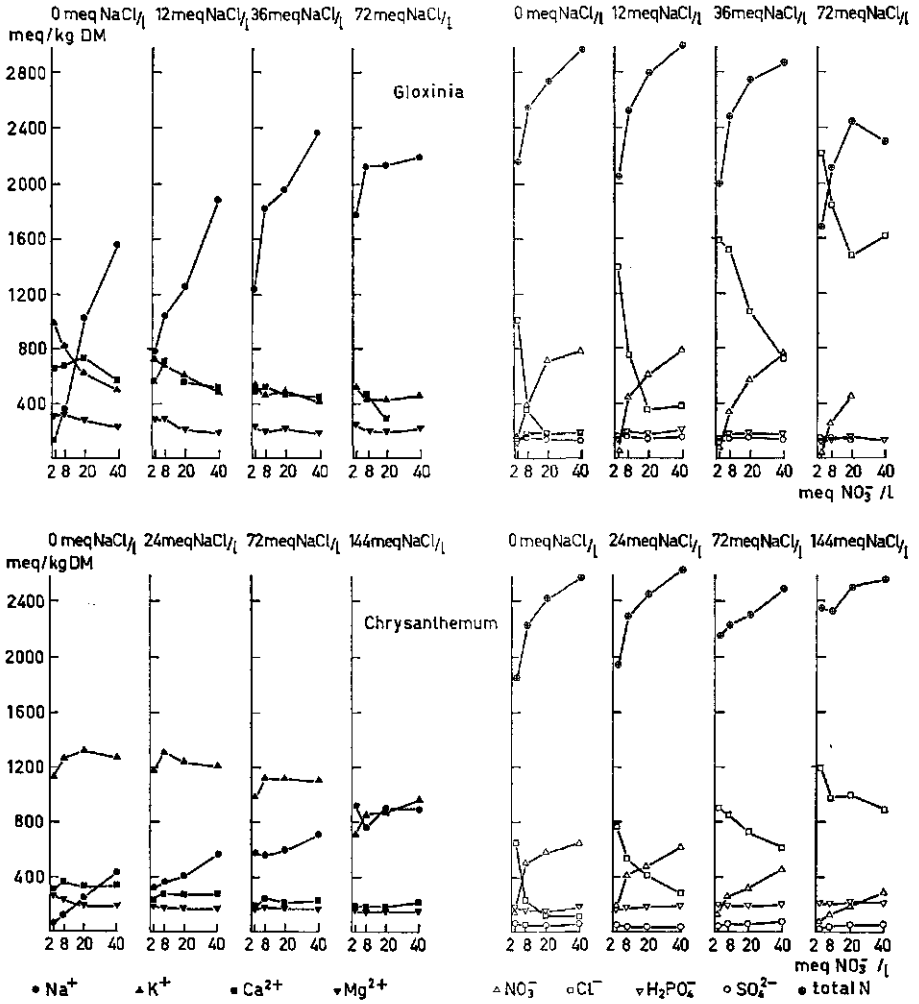
In the $NO_3^-$ range used, $K^+$, $Ca^{2+}$, and $Mg^{2+}$ were constant in the medium but $Na^+$ increased with $NO_3^-$. Of the anions, other than $NO_3^-$, $H_2PO_4^-$ and $SO_4^{2-}$ were constant; in the $NO_3^-$ range 2 to 20 meq per litre $Cl^-$ increased and in the $NO_3^-$ range 20 to 40 meq per litre it was constant (Table 1).

*Influence of NaCl on cations* $Na^+$ in the plant increased with NaCl in the medium. The increase of $Na^+$ was much sharper for gloxinia than for chrysanthemum.

With increasing NaCl in the medium $K^+$, $Ca^{2+}$ and $Mg^{2+}$ declined, again much more for gloxinia than for chrysanthemum. In order of increasing decline with rising NaCl in the medium, the three cations were for both species: $Mg^{2+}$, $Ca^{2+}$, and $K^+$.

*Influence of $NO_3^-$ on cations* Since $Na^+$ acted as compensating cation in the nutrient solution, $Na^+$ contents in the plant increased with rising $NO_3^-$ in the medium. Especially in gloxinia the increase of $Na^+$ was striking, which in turn was reflected by

Fig. 8. Ion contents of the plant as affected by $NO_3^-$ concentration of the nutrient solution at each NaCl level.




a similar sharp decline in $K^+$. Chrysanthemum behaved entirely differently, its $K^+$ content increasing, if only slightly, with increasing $NO_3^-$ in the medium.

$Ca^{2+}$ in gloxinia was not affected whereas $Ca^{2+}$ in chrysanthemum tended to rise somewhat. Finally $Mg^{2+}$ in both species declined with increasing $NO_3^-$ in the medium. Again the decrease in $Mg^{2+}$ was more pronounced for gloxinia than for chrysanthemum. For gloxinia the increase of $Na^+$ resulting from increased $NO_3^-$ levels in the medium seemed appreciably larger than the increase of $Na^+$ resulting from increased NaCl levels in the medium. Evidently in gloxinia an interaction between $Na^+$ uptake and the accompanying anion occurs, the $Na^+$ uptake being larger in the presence of $NO_3^-$ than in the presence of $Cl^-$. The competing action of $Na^+$ on the absorption of $K^+$, $Ca^{2+}$ and $Mg^{2+}$ as found in this trial seems

to coincide with the ordinary pattern of ion effects resulting from salinity (van den Berg, 1952; Bernstein, 1964; Greenway, 1963).

An indication of the cation selectivity of both species is provided by the contents of $K^+$, $Na^+$, $Ca^{2+}$, and $Mg^{2+}$, respectively, of the plants in the zero-NaCl series and averaged over all $NO_3^-$ levels:

gloxinia: 732, 772, 659, and 280 meq per kg DM

chrysanthemum: 1247, 215, 336, and 216 meq per kg DM

The dominance of $K^+$ in the cation balance of chrysanthemum, indicating its great preference for $K^+$, is quite evident. This finding agrees with the results of Lunt & Kofranek (1958) who reported a level of 1000 meq $K^+$ per kg DM in the leaves as the optimum $K^+$ level. There is a very wide margin between this content and the one at which symptoms of $K^+$ deficiency becomes evident, which is 150 meq per kg DM. In the chrysanthemum trial, the $K^+$ contents of the plant material in all treatments lay well above this critical level. There is, therefore, little reason to believe that in chrysanthemum the $Na^+ - K^+$ antagonism had resulted in $K^+$ deficiency.

Gloxinia did not show a great preference for any of the cations. In fact, the high level of $Na^+$ in the plants treated with $Na^+$ suggests rather an inability to resist the influx of any cation, than a preference for $Na^+$. Therefore the $Ca^{2+}$ content being twice as high as that of chrysanthemum does not necessarily reflect a special preference for $Ca^{2+}$. For gloxinia no critical levels of $K^+$, $Ca^{2+}$, and $Mg^{2+}$ have appeared in the literature. For all treatments the $K^+$, $Ca^{2+}$, and $Mg^{2+}$ contents were far above the minimum level mentioned by de Wit *et al.* (1963) for these elements, namely 200, 50 and 50 meq per kg DM respectively.

*Influence of NaCl on inorganic anions*[1] *and total N* The $Cl^-$ contents of the plant material examined increased with increasing NaCl levels in the medium. As for $Na^+$, this increase was more pronounced for gloxinia than for chrysanthemum. Furthermore, increasing NaCl concentration in the medium led to higher $H_2PO_4^-$ levels in gloxinia and lower levels in chrysanthemum. The $SO_4^{2-}$ contents were little affected. $NO_3^-$ levels in the plants decreased, surprisingly more so for chrysanthemum than for gloxinia. Wadleigh & Gauch (1942) also found this decline in $NO_3^-$ level in a trial with bean plants. A $Cl^- - NO_3^-$ antagonism might be involved (de Wit *et al.*, 1963; Lundegardh, 1959). For gloxinia, like $NO_3^-$, total N in plants decreased as well with increasing NaCl levels in the medium. This finding agrees with results of Wadleigh & Gauch (1942) and Kretschmer *et al.* (1953). Both findings suggest that the unfavourable influence of NaCl on the relationship between $NO_3^-$ level and N uptake, mentioned earlier for gloxinia, can at least partially be ascribed to $Cl^- - NO_3^-$ antagonism.

For chrysanthemum the matter is more complicated. In this species, increasing NaCl levels in the growth medium induced a rise in total N along with a sharp decline

1. The $SO_4^{2-}$ content is calculated from total S according to the method of de Wit *et al.* (1963).

in $NO_3^-$ N (see the first $NO_3^-$ levels of the four NaCl series in Fig. 8). These opposite tendencies indicate that organic N in the plant material rose. In this trial, N was taken up by the plants as $NO_3^-$. Since the synthesis of organic N is dependent on $NO_3^-$ depot in the plant (van Burg, 1962), $NO_3^-$ in the plant is thought to be an important criterion when judging whether N uptake by chrysanthemum or gloxinia has been adversely affected by $Cl^-$ – $NO_3^-$ antagonism. In the present case, such an adverse influence seems to have been present. Meanwhile it remains difficult to explain the rise in organic N found in chrysanthemum. This finding also conflicts with the results of Wadleigh & Gauch (1942) who found a decrease in protein N and soluble organic N with increasing NaCl in the medium of bean plants. In the chrysanthemum trial, the phenomenon was perhaps induced by the concentrating effect, accompanying the slower growth resulting from more NaCl in the medium (Greenway, 1965).

*Influence of $NO_3^-$ on inorganic anions and total N* $NO_3^-$ levels in the plants increased with increasing $NO_3^-$ levels in the medium. In gloxinia, this increase was almost twice as much as in chrysanthemum. The $Cl^-$ level decreased more in gloxinia than in chrysanthemum, along with the rise in $NO_3^-$. Although the $Cl^-$ – $NO_3^-$ antagonism would have played a role in lowering $Cl^-$ in the plant, this lowering, as it occurred in the range of 2 to 20 meq $NO_3^-$ per litre, must be primarily ascribed to the corresponding decrease of $Cl^-$ in the medium. The $Cl^-$ – $NO_3^-$ antagonism must be held responsible for the decrease in $Cl^-$ in the plants in the range of 20 to 40 meq $NO_3^-$ per litre, in that such a decrease occurred (for gloxinia, 3rd NaCl series; for chrysanthemum, 2nd, 3rd and 4th NaCl series).

$SO_4^{2-}$ contents of the plant material remained fairly constant; $H_2PO_4^-$ in the plants increased slightly with increases in $NO_3^-$ in the medium.

Total N in plants increased with rising $NO_3^-$ levels in the medium, for gloxinia much more than for chrysanthemum. For chrysanthemum, the rate of increase declined at higher NaCl levels, due to a rise in total N in the plants at the lowest $NO_3^-$ level. This latter finding could be an indication of a rise in concentration due to a depression in growth rate resulting from increasing NaCl levels in the medium (Greenway, 1965).

For gloxinia, the optima for $NO_3^-$ in the plant at the four NaCl series were 394, 446, 572, and 454 meq $NO_3^-$ per kg DM, respectively, those for total N in the plant 2556, 2525, 2756 and 2456 meq N per kg DM, respectively. For chrysanthemum, the $NO_3^-$ optima were 503, 424, 269 and 140 meq $NO_3^-$ per kg DM, respectively, and the total N optima were 2435, 2306, 2249, and 2356 meq N per kg DM, respectively. For both species, the optima for total N corresponded reasonably well with the saturation contents for N mentioned in Section 3.2. Chrysanthemum showed a distinct decrease in $NO_3^-$ optima with rising NaCl levels. Therefore, for an evaluation of the N level of the plant based on $NO_3^-$ in the plant, the $Cl^-$ level of the plant must also be taken into account. Beyond the optimum $NO_3^-$ levels in the medium, both $NO_3^-$ and total N in plants continued to increase. However, in such instances, the N absorption per plant decreased (figs 1 and 2). Based on the decrease in dry matter,

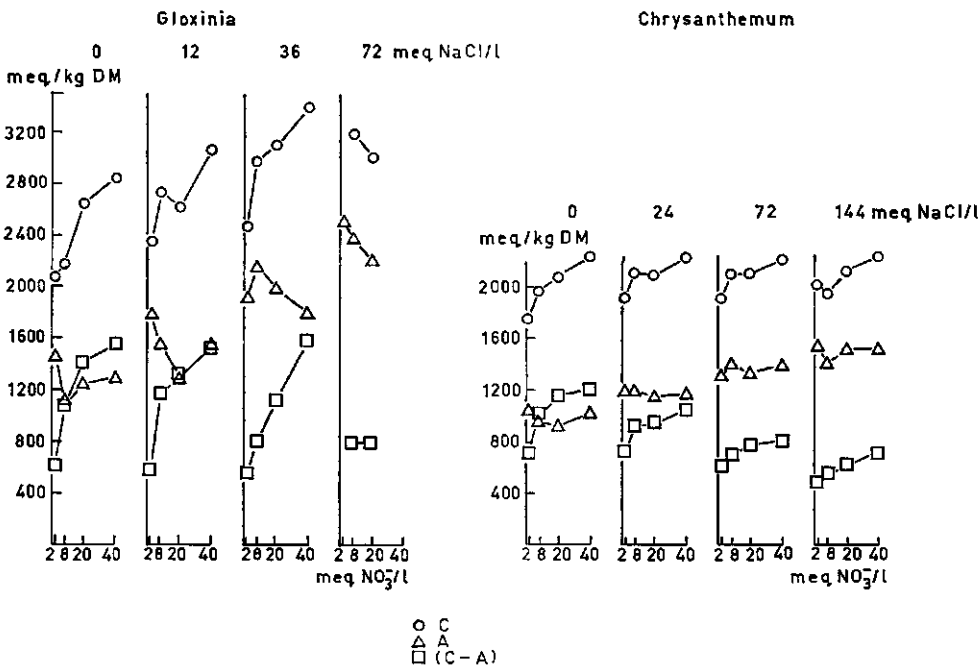
the conclusion must be drawn that a limiting factor other than N supply must have been involved. This could have been a disturbance of the internal water balance (Section 3.3) or a toxic effect caused by N excess.

*Total cations* Total cations C is equal to $K^+ + Na^+ + Ca^{2+} + Mg^{2+}$ (Fig. 9). Total cations C increased with NaCl level in the medium. The increase was very pronounced for gloxinia, but only small for chrysanthemum. For gloxinia, an increase in $Na^+$ absorption was mainly responsible for the increase in total cations C. For chrysanthemum, a decrease in uptake of $K^+ + Ca^{2+} + Mg^{2+}$ was almost compensated for by an increase in $Na^+$ uptake.

Total cations C increased with $NO_3^-$ level in the medium. The increase was large again for gloxinia, and smaller for chrysanthemum. This increase in total cations C was associated with a rise in $Na^+$ uptake by gloxinia, whereas for chrysanthemum, $K^+$ also contributed to the rise (Fig. 8).

For chrysanthemum it is furthermore striking that the rate of increase in total cations C with $NO_3^-$ level in the medium slowed down with increasing NaCl level in the medium. Since at 40 meq $NO_3^-$ per litre total cations C was constant for all four NaCl levels, the increase must be ascribed entirely to the increase in total cations C at 2 meq $NO_3^-$ per litre. An explanation for these changes in total cations C must

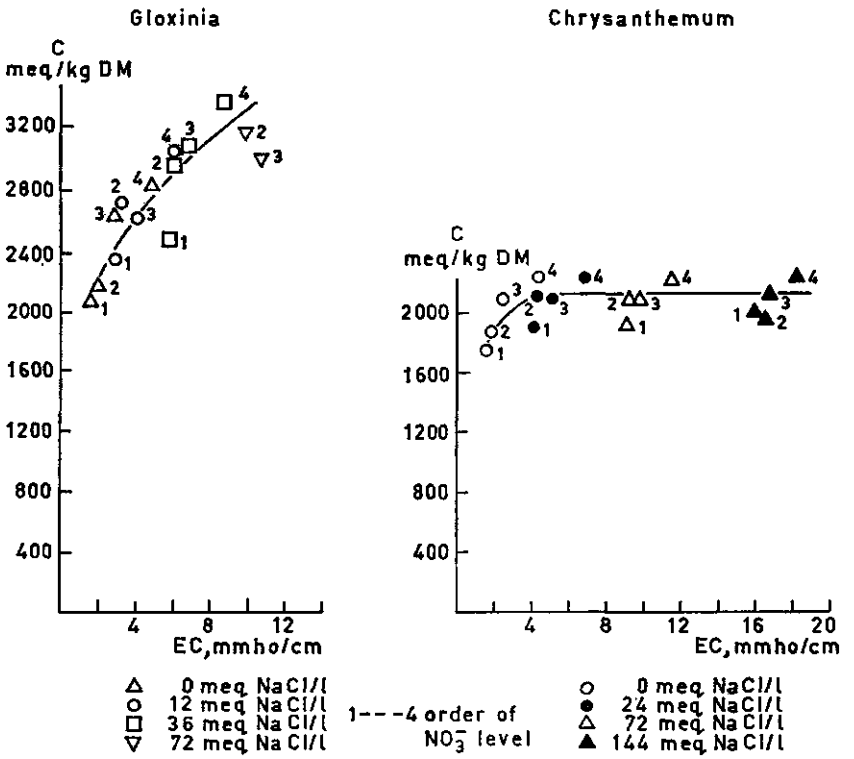
Fig. 9. Relationship between $NO_3^-$ concentration of the nutrient solution and total cations C, total inorganic anions A, and organic salts (C-A) in the plant at each of the four NaCl levels.



be sought in the behaviour of $Na^+$ inside the plant. At 2 meq $NO_3^-$ per litre, the rise in $Na^+$ with NaCl level in the medium was much more pronounced than at 40 meq $NO_3^-$ per litre, due to the much higher $Na^+$ concentration in the medium at 40 than at 2 meq $NO_3^-$ per litre (Table 1). These findings imply that chrysanthemum can exert some control over the $Na^+$ uptake and, hence, over total cations C in the plant. The maximum $Na^+$ concentration in chrysanthemum was near 900 meq per kg DM. Gloxinia apparently lacks this ability to regulate the uptake of $Na^+$. The $Na^+$ concentration in gloxinia can rise to 2400 meq per kg DM.

The difference in ability to regulate total cations C is even more evident in the relationship between total cations C and salinity (Fig. 10). Total cations C for gloxinia rose almost linearly with a rise in EC in the range of 1.5 to 12 mmho $cm^{-1}$. Total cations C in chrysanthemum rose markedly with an increase in EC from 1.5 to 4 mmho $cm^{-1}$ but then remained constant even up to 18 mmho $cm^{-1}$. For gloxinia the increase in total cations C between 1.5 and 12 mmho $cm^{-1}$ was 1300 meq per kg DM, for chrysanthemum 370 meq. For chrysanthemum it is striking that the increase in total cations C per mmho $cm^{-1}$ was larger in the $NO_3^-$ range than in the NaCl range. From this it can be concluded that the uptake of $Na^+$ proceeds more

Fig. 10. Relationship between EC of the nutrient solution and total cations C content of the plant.



rapidly with $NO_3^-$ than with $Cl^-$ as anion. The same was already found for gloxinia.

The difference in salt tolerance between chrysanthemum and gloxinia seems largely to be accounted for by a difference in ability to regulate the $Na^+$ concentration and total cations C inside the plant. In this connection it should be mentioned that van den Berg (1952) observed a good correlation between salt sensitivity of various agricultural crops and the rate of increase in total cations C under the influence of rising NaCl levels in the soil. Greenway (1962) concluded from a brief experiment with barley varieties of varying salt tolerance that the ability of a plant to regulate the ionic contents in its tissue is an important factor in the evaluation of its salt tolerance.

*Total inorganic anions* Total inorganic anions A is equal to $NO_3^- + H_2PO_4^- + SO_4^{2-} + Cl^-$ (Fig. 9). With increasing NaCl in the medium total inorganic anions A increased, more so for gloxinia than for chrysanthemum, as could be expected. This increase in total inorganic anions A resulted from the increase in $Cl^-$ inside the plant. It is remarkable that for chrysanthemum the influence of NaCl in the medium upon total inorganic anions A was larger than its influence upon total cations C. Chrysanthemum is clearly better equipped to resist a rise in $Na^+$ than in $Cl^-$ inside the plant.

With increasing $NO_3^-$ in the medium, total inorganic anions A for gloxinia tended to fall. For chrysanthemum, hardly any variation can be observed. For gloxinia, the decrease in total inorganic anions A resulted from a decline in $Cl^-$ inside the plant larger than the concurrent increase in $NO_3^-$. For chrysanthemum, the relative constancy of total inorganic anions A can be explained by the balance inside the plant between the decline in $Cl^-$ and the rise in $NO_3^-$. According to results of de Wit *et al.* (1963) with barley, total inorganic anions A should increase while $Na^+$ and $NO_3^-$ are rising in the medium. The absence of this phenomenon in Trial 1 must be ascribed to the compensating role of the anion $Cl^-$ in the medium.

*The organic salt content (C-A)* The content of organic salts inside the plant is equal to the (C-A) content (de Wit *et al.*, 1963).

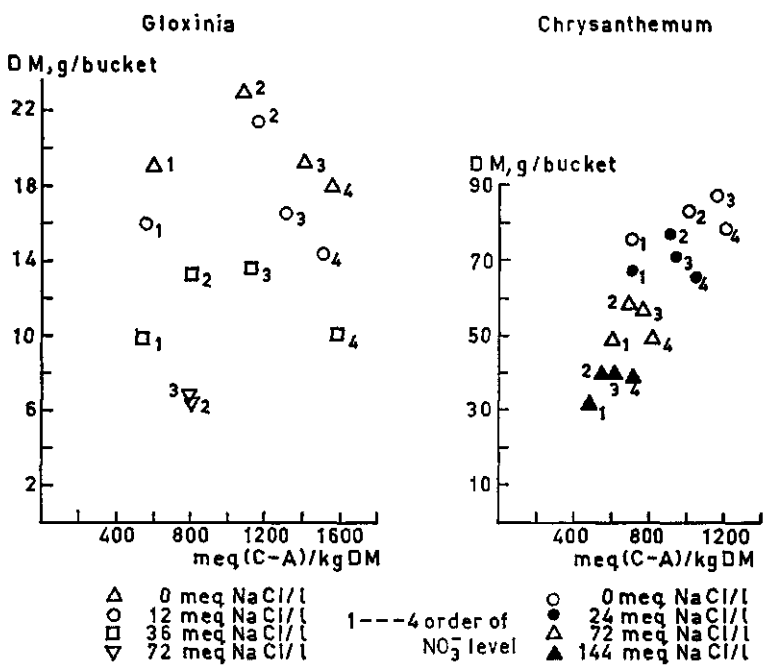
With rising NaCl levels in the medium, the (C-A) content of gloxinia decreased slightly, that of chrysanthemum decreased markedly (Fig. 9). The small influence of NaCl in the medium on the (C-A) content of gloxinia resulted from the sharp increase in $Na^+$ uptake giving rise to equally large increases in total cations C and total inorganic anions A. With chrysanthemum, this compensation of the increase in total inorganic anions A by a corresponding increase in total cations C was largely absent due to a much more strongly regulated uptake of $Na^+$, resulting in a much larger influence of NaCl on the (C-A) content of chrysanthemum than of gloxinia.

The (C-A) content increased with increasing $NO_3^-$ in the medium, more so for gloxinia than for chrysanthemum. The increase in the (C-A) value of gloxinia could be entirely accounted for by an increased $Na^+$ uptake. For chrysanthemum, the rise was caused by increased $K^+$ uptake as well. The smaller increase in the total cations C content of chrysanthemum in the $NO_3^-$ range with higher NaCl levels in the medium, as already referred to earlier, reflected itself in the course of the (C-A) content.

After extensive trials with various crops, de Wit *et al.* (1963) concluded that the (C-A) content of a plant species must be considered as an important growth criterion. Thus a normal (C-A) content is necessary for proper growth. It is however, no guarantee for proper growth, since other limiting factors might be involved. The validity of this concept was shown later by the investigations of van Tuil (1965). In Fig. 11 the relationships between yield and (C-A) content are given for gloxinia and chrysanthemum respectively. After what has already been said, it should not be surprising that gloxinia and chrysanthemum acted entirely differently in this relationship. For gloxinia, the optimum (C-A) content, as found under the given experimental conditions, was 1080 meq per kg DM, for chrysanthemum this value was 1160 meq per kg DM. Comparison of the four $NO_3^-$ series shows that the optimum (C-A) content of gloxinia was little affected by increases in NaCl level. The differences in yield that were found must, therefore, be ascribed to another limiting factor. With increasing NaCl level, the optimum value for chrysanthemum tended to decrease.

At first sight, chrysanthemum showed a good correlation between yield and (C-A) content. As mentioned earlier, an increase in (C-A) content of chrysanthemum was accompanied by a decrease in $Cl^-$ content of this species.

Fig. 11. Relationship between organic salts (C-A) in the plant and yield of dry matter.



### 3.6 Shoot : root ratio

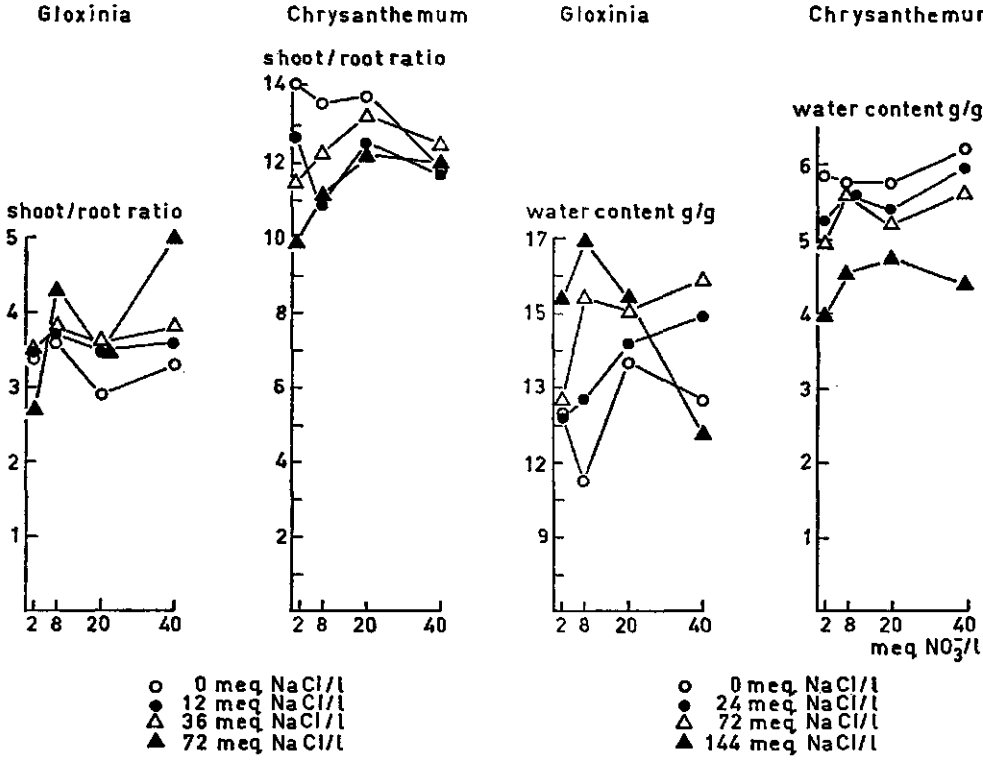
With increasing NaCl concentrations in the medium, the shoot : root ratio of gloxinia increased, that of chrysanthemum behaved rather irregularly: with a rise of NaCl in the medium from 0 to 24 meq per litre, the ratio decreased, from 24 to 72 meq NaCl per litre, the ratio increased again whereas another decline was found beyond 72 meq NaCl per litre (Fig. 12).

Some halophytes adapt themselves to saline conditions by lowering the shoot : root ratio (Sutcliffe, 1962). This adaptation apparently did not occur with gloxinia and chrysanthemum. Neither could confirmation be found of the rule that the ratio decreases with increasing solute suction in the root medium (Brouwer, 1963c).

It is generally accepted that the shoot : root ratio increases with a rising nitrogen supply (Brouwer, 1963c). This could indeed be found with gloxinia at all NaCl series, but only in the range of 2–8 meq $NO_3^-$ per litre. With chrysanthemum, the rule only held at the highest two NaCl levels in the range of 2 to 20 meq $NO_3^-$ per litre.

Fig. 12. Relationship between nitrogen concentration and shoot : root ratio (on dry matter basis) at the four NaCl levels.

Fig. 13. Relationship between nitrogen concentration and moisture content in aerial parts of the plant at the four NaCl levels.



### 3.7 Moisture in the plants

The water content of gloxinia, expressed in grammes of moisture per gramme dry matter distinctly increased with rising NaCl levels in the medium (Fig. 13). This finding might be explained as an attempt of gloxinia to adapt to an increasing salinity by increasing its succulence, as was also shown for the halophyte *Atriplex hastata* (Greenway, 1966).

According to Arnold (1955) succulence is not so much associated with accumulation of $Cl^-$ or NaCl but more with an increase in total salt in a plant.

Chrysanthemum behaved quite differently. Rising NaCl levels caused a steady decline in water content of this plant.

For both species, a slight increase in water content with increasing $NO_3^-$ levels in the medium could be noticed.

### 3.8 Conclusions

Increases in EC exert an adverse affect on increment of dry matter per unit nitrogen applied. This reduction in nitrogen effect is accounted for by a decrease in N utilization by the plant. This in turn can be attributed to a disturbance of the nitrogen metabolism caused by a rising suction tension in the leaf.

Yield of dry matter decreases practically linearly with increasing EC. The finding that after adjusting EC to zero the nitrogen curves converge into one single typical yield curve indicates the dominant role of the osmotic effect. However, the large influence of added NaCl on the ionic balance in the plant shows that the specific ion effect cannot entirely be neglected.

The larger salt tolerance of chrysanthemum than of gloxinia is based, at least partially, on the greater ability of the first species to prevent the influx of ions.

# 4 Results of Trial 2: different N rates and different types and levels of salts in pots.

## 4.1 Salinity of the substrate

Differences in $EC_e$ with N level and level and type of salt are given in Fig. 14. The various salts had different influences on $EC_e$. The average increase in $EC_e$ for each salt and for each amount of salt are listed for each species in Table 6.

Fig. 14. $EC_e$ values as affected by application of four different salts and five nitrogen rates.

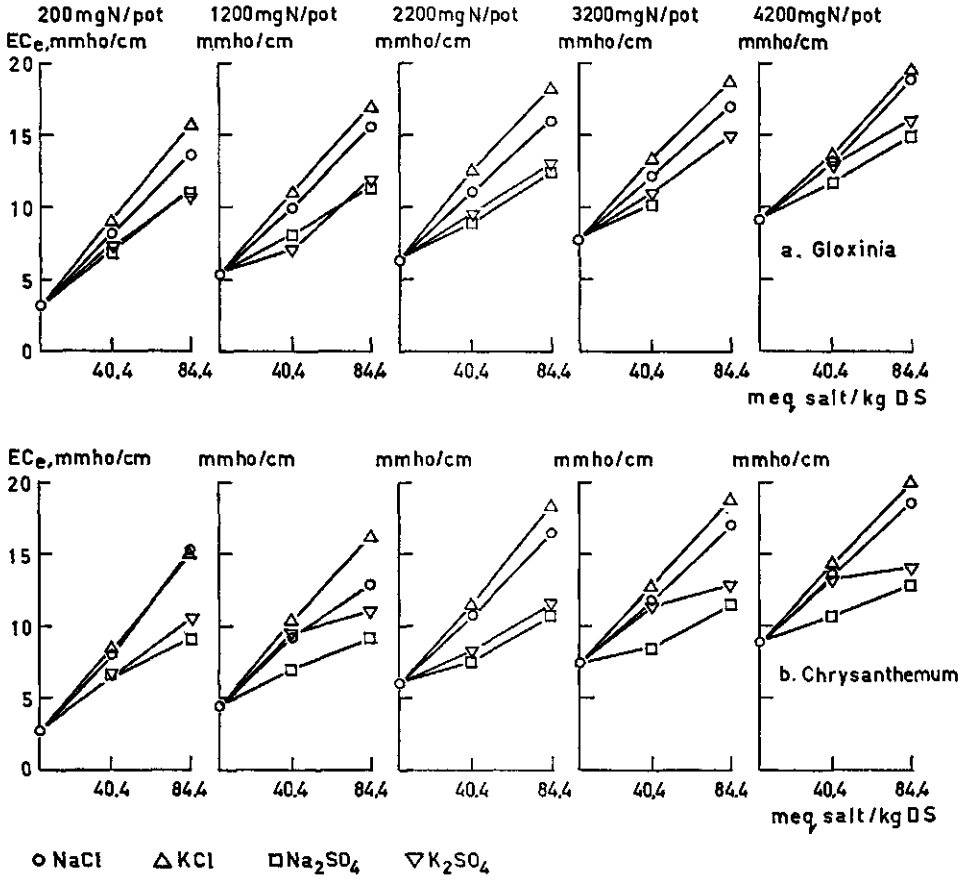


Table 6. Average increase in $EC_e$ (in mmho $cm^{-1}$) at 25° C for four types of salt and for 40.4 and 84.4 meq salt per kg DS (dry substrate).

| | NaCl | | KCl | | $Na_2SO_4$ | | $K_2SO_4$ | |
|---|---|---|---|---|---|---|---|---|
| | 40.4 | 84.4 | 40.4 | 84.4 | 40.4 | 84.4 | 40.4 | 84.4 |
| Gloxinia | 4.5 | 9.8 | 5.6 | 11.6 | 2.9 | 6.5 | 3.2 | 7.0 |
| Chrysanthemum | 4.8 | 10.1 | 5.6 | 11.8 | 2.2 | 4.8 | 3.9 | 6.2 |

The influence of the four salts on $EC_e$ decreased in the order: KCl, NaCl, $K_2SO_4$, $Na_2SO_4$. The equivalent conductivities of the salts at 0.1 *N* and 25° C are 128.96, 106.74, 108.80 and 89.98 mho $cm^2$ $eq^{-1}$, respectively (Hodgman, 1964; Sonneveld *et al.*, 1966). Except for $K_2SO_4$, this order of decreasing influence on $EC_e$ agreed with the order of decreasing equivalent conductivity, as to be expected. The anomalous behaviour of $K_2SO_4$ may be ascribed partially to precipitation of $SO_4^{2-}$ with $Ca^{2+}$ in the substrate solution and partially to adsorption phenomena.

The increments of N rate of 1, 2, 3 and 4 g of N per pot relative to the lowest level of N (0.2 g) corresponded on average to increases of $EC_e$ of 1.3, 2.6, 3.7 and 5.0 mmho per cm, respectively, in the gloxinia trial, and to increases of $EC_e$ of 1.0, 2.3, 3.5, and 5.0 mmho per cm. respectively, in the chrysanthemum trial.

### 4.2 Nitrogen rate and yield of dry matter

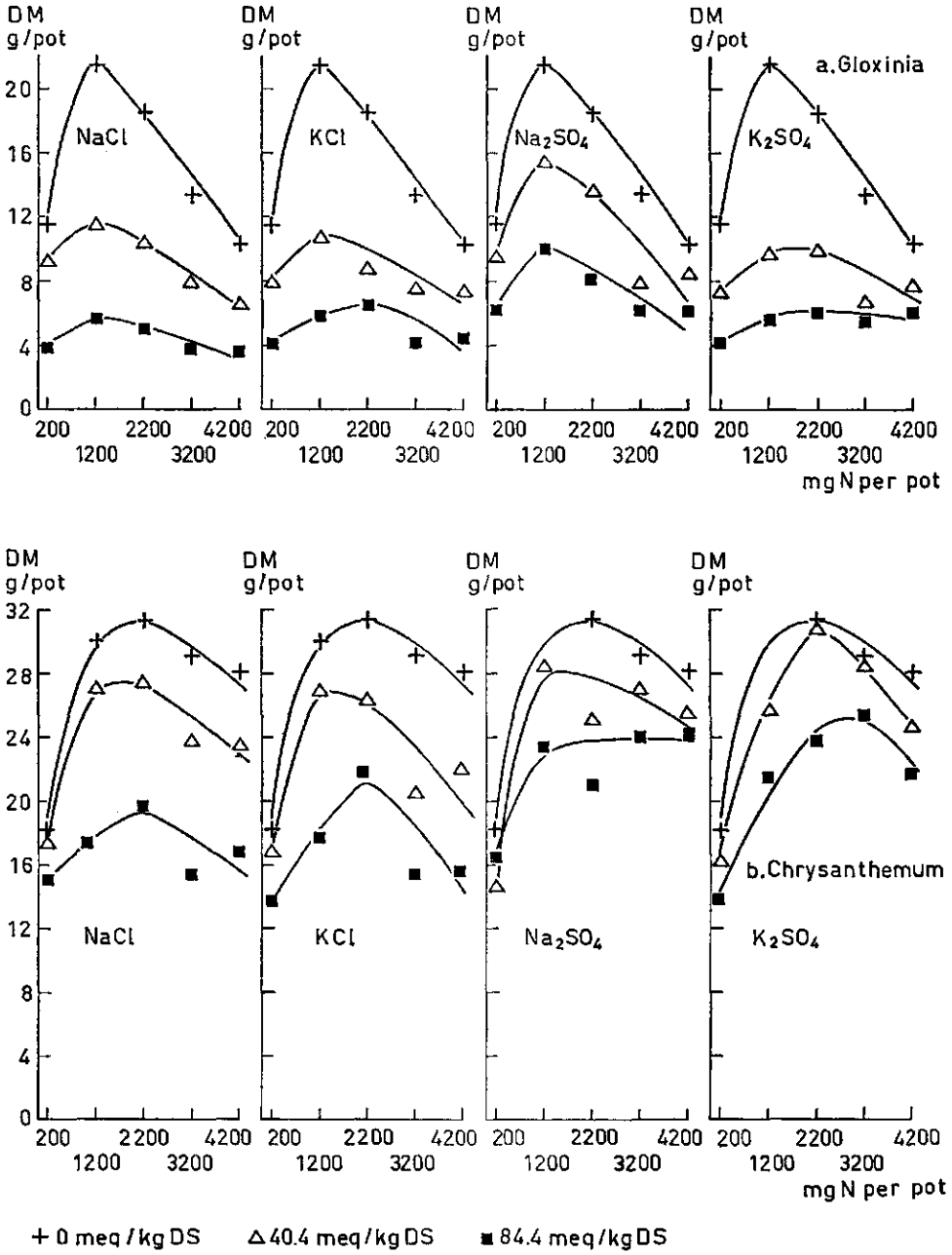
Fig. 15 gives the relationships between yield of dry matter and N rate for each type of salt at three rates for both species. All four salts distinctly suppressed yield of dry matter. This suppression increased with amount of salt added, but differed between the types of salt.

The mean reduction in yield of gloxinia and chrysanthemum for the two higher levels of salt of the four types are given in Table 7.

Table 7. Average percentage reduction in dry matter with 40.4 and 84.4 meq salt per kg DS relative to 0 meq salt for the four types of salt.

| | NaCl | | KCl | | $Na_2SO_4$ | | $K_2SO_4$ | |
|---|---|---|---|---|---|---|---|---|
| | 40.4 | 84.4 | 40.4 | 84.4 | 40.4 | 84.4 | 40.4 | 84.4 |
| Gloxinia | 42.0 | 70.3 | 44.5 | 66.2 | 26.8 | 52.3 | 45.0 | 63.0 |
| Chrysanthemum | 12.8 | 38.3 | 17.7 | 38.3 | 11.9 | 20.1 | 7.9 | 22.3 |

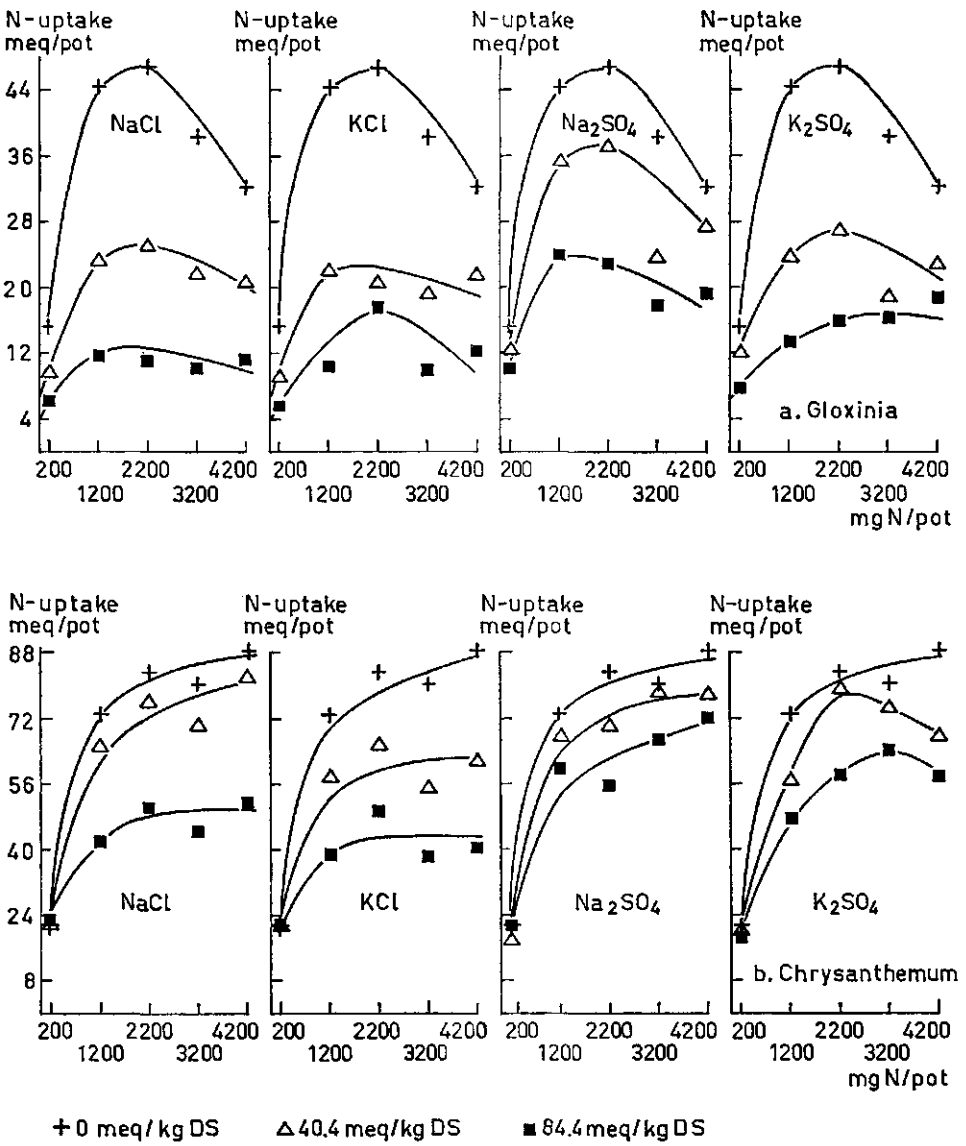
Fig. 15. Yields of dry matter as affected by nitrogen rate and to four different salts.



For gloxinia, the negative effect of $Na_2SO_4$ was smaller than that of NaCl, KCl, and $K_2SO_4$. The latter three hardly differed in effect. Thus, $K_2SO_4$ seemed more harmful than could be expected from its influence on $EC_e$ (Table 6). A specific ion effect might be involved.

For chrysanthemum, the sulphates were distinctly less harmful than the chlorides. The data in Table 7 confirm the earlier observation that chrysanthemum was much more salt-tolerant than gloxinia.

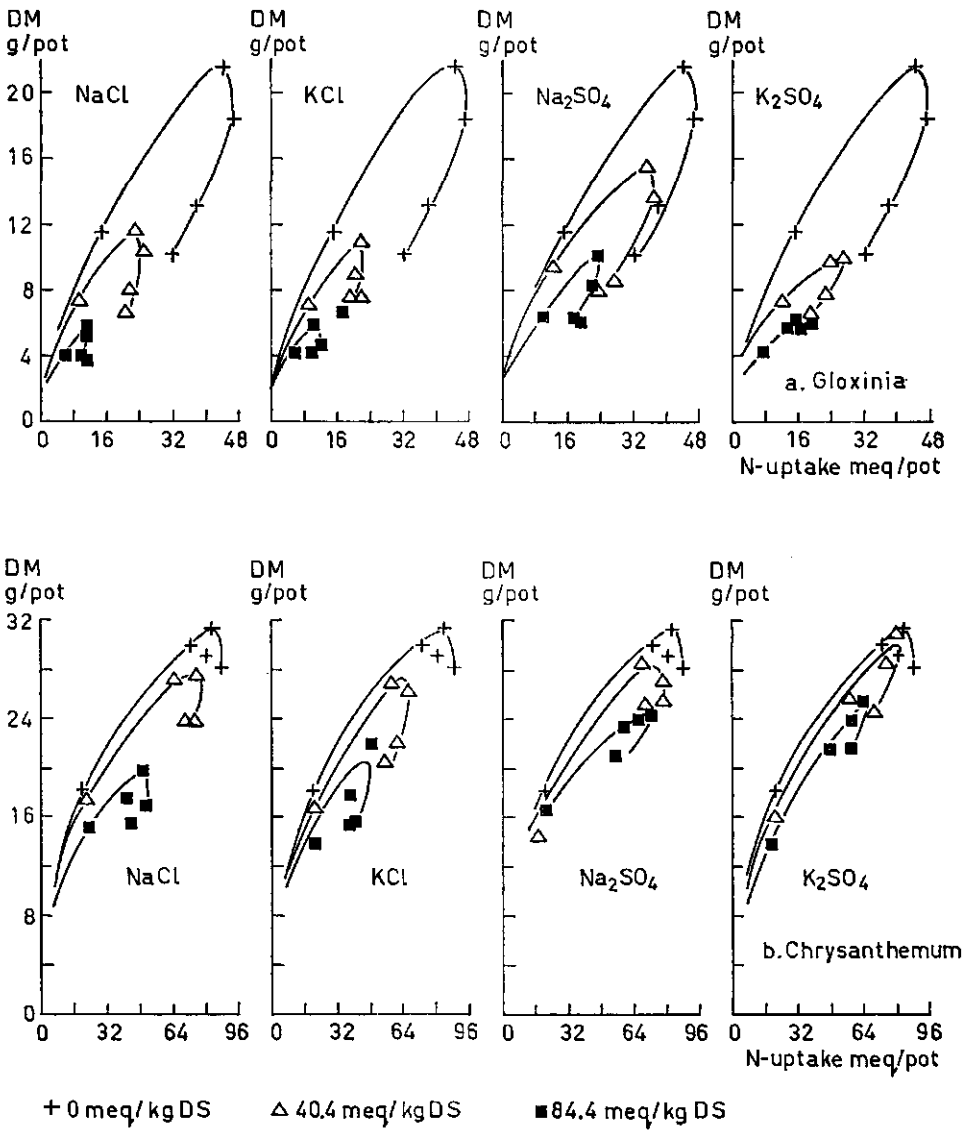
Fig. 16. Nitrogen uptake as affected by nitrogen rate and four different salts.



The shape of the curves in Fig. 15 shows furthermore that the effect of N rate decreased with increasing salt levels. The decrease seemed to depend not only on amount but also on type of salt. In this respect $Na_2SO_4$ affected the growth of gloxinia less than did the other three salts, which hardly differed from one another. Chrysanthemum was less affected by sulphates than by chlorides.

In practically all series, the curves relating N rate and yield of gloxinia had a peak

Fig. 17. Relationship between nitrogen uptake and yield of dry matter as affected by four different salts.



at 1.2 g N per pot, those for chrysanthemum had a peak at 2.2 g N per pot. The curves declined sharply beyond the optimum N rate.

Fig. 16 shows the effects of salt treatments and N rate on N uptake. Salts depressed uptake of N and reduced the positive effect of N rate on N uptake. The suppression of N uptake by the four salts paralleled that found for yield.

The influence of type and amount of salt on N utilization by gloxinia and chrysanthemum can be seen from the curves in Fig. 17. In principle, these curves are similar to those in Trial 1 with culture solutions (Quadrant I of figs 1 and 2). It can be observed that yield of both gloxinia and chrysanthemum per unit N absorbed decreased with level of salt in the substrate. The harmful effect of the salt again seemed to depend on the type of salt. The harmfulness of the various types of salt seemed similar to those observed in the relationships between N rate and yield and between N rate and N uptake.

The curves in Fig. 17 show the same sort of inflexion as in Trial 1. For each salt series the peaks of the curves can again be reasonably well connected by a straight line through the origin. The corresponding N contents (saturation contents) are 2060 meq N per kg DM for gloxinia and 2660 meq N per kg DM for chrysanthemum. The value for gloxinia is lower and that for chrysanthemum higher than in Trial 1. These differences are explicable by differences in culture, season, situation and form of N fertilizer.

Thus the results of Trial 1 are confirmed by those of Trial 2. The harmful effect of excess salt in the substrate on the relationship between N application and yield can also be related to a negative effect of the salt on utilization of N absorbed by the plant. In addition, this deleterious effect appears to be dependent on the nature of the salt.

### 4.3 Nitrogen rate and leaf colour of gloxinia

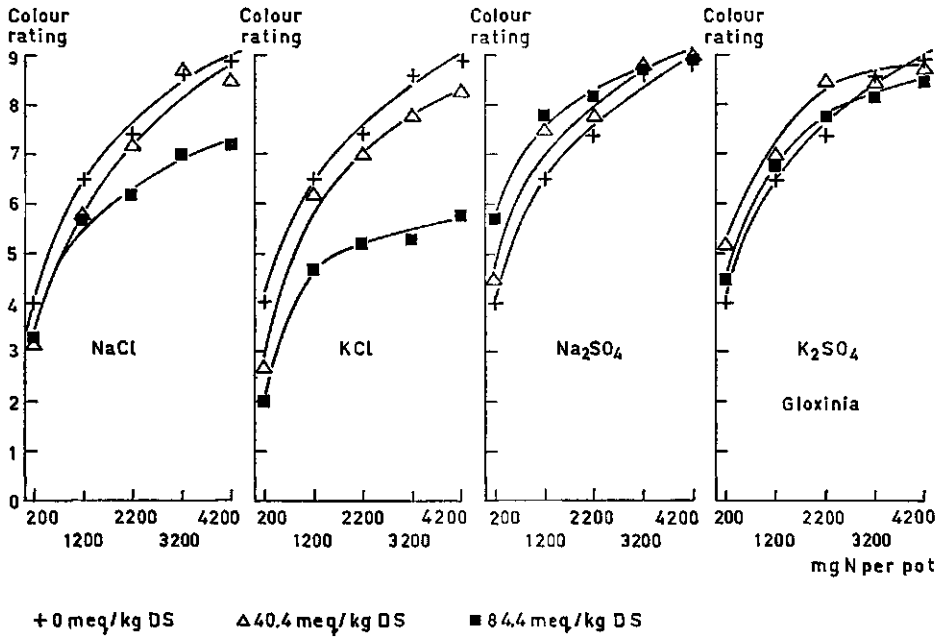
Since growers often experience difficulties with leaf colour of gloxinia, I examined the influence of the various treatments on this characteristic.

In Fig. 18, the ratings for leaf colour of gloxinia have been plotted against N rate for each type and level of salt.

The shapes of the curves show that leaf colour of gloxinia responded closely to nitrogen. At the lowest rate, the colour was too light. It increased rapidly with N rate. Salts, according to type, also had distinct effects, negative for chlorides, positive for sulphates. Of the two chlorides, KCl was more unfavourable than NaCl. There was close positive correlation between colour rating and $NO_3^-$ content of the plant (Fig. 22). The better leaf colour in the sulphate series can be ascribed to higher $NO_3^-$ contents, the poorer colour in the chloride series to lower $NO_3^-$ contents in the plant. As was concluded for Trial 1, the lower $NO_3^-$ contents in the presence of chlorides resulted from a $Cl^-$–$NO_3^-$ antagonism.

The poorer leaf colour in the KCl series than in the NaCl series was also associated with a lower $NO_3^-$ content of gloxinia in the KCl series than in the NaCl series. This

Fig. 18. Colour rating for gloxinia as affected by nitrogen rate and four different salts.




difference in $NO_3^-$ content must in turn be ascribed to the larger uptake of $Cl^-$ with $K^+$ than with $Na^+$ as accompanying cation. Specific ion effects can thus clearly manifest themselves in leaf colour.

### 4.4 Nitrogen rate and water consumption

Yield of dry matter was plotted against total water consumption in Fig. 19. Water consumption included evaporation as well as transpiration.

For each species, most points fell in a straight line. The slope of these lines and the intersection with the $x$ axis were the same for all salt series with each species. The relationship between water consumption and yield could, therefore, be indicated by a linear function. If $P$ is yield in g per pot and $W$ is water consumption in litres per pot, the following relationships existed between these two quantities:

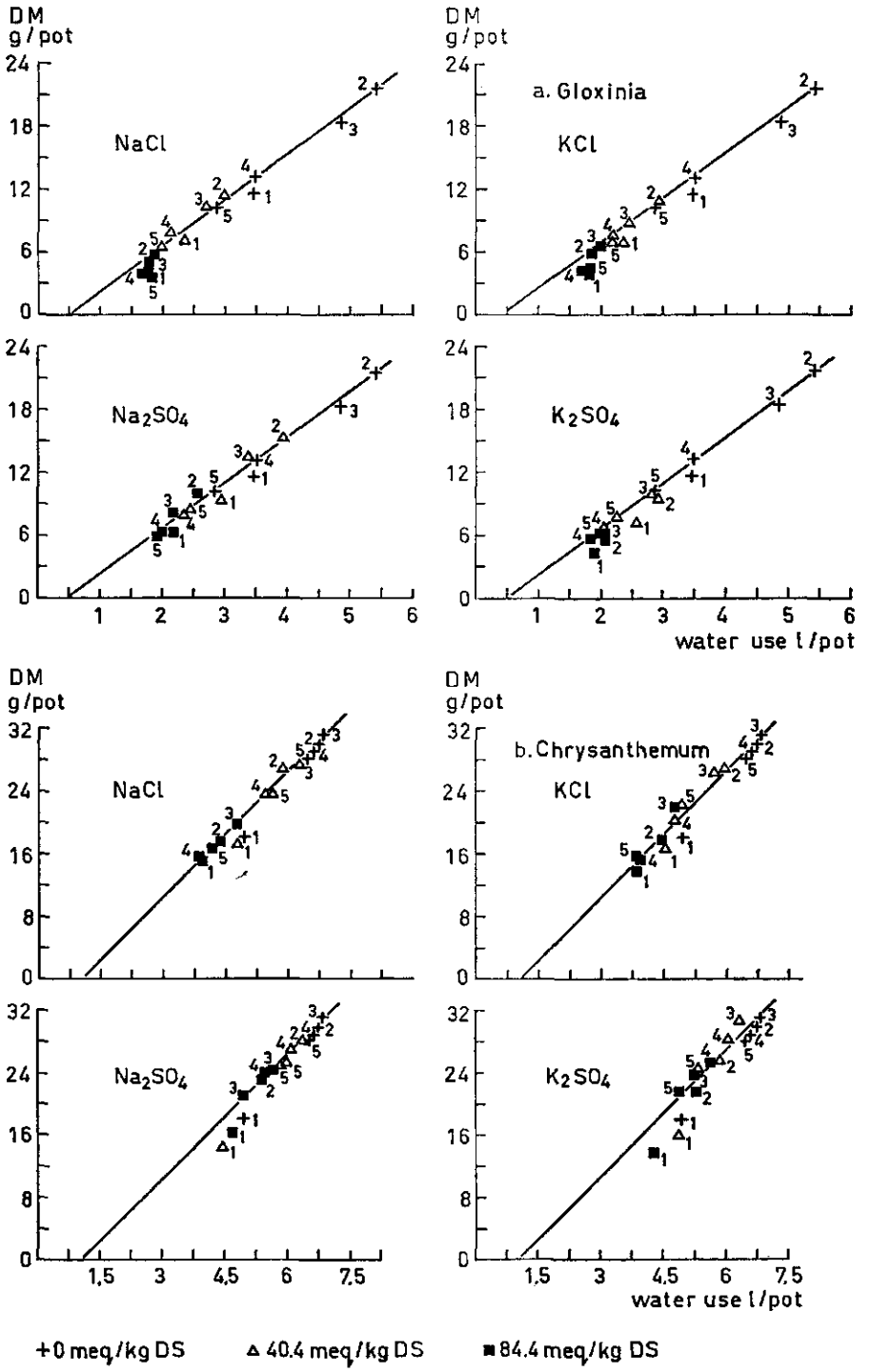
for gloxinia $P = 4.42\ W - 2.43$

for chrysanthemum $P = 5.37\ W - 5.64$

Evaporation $E$ in litres per pot could then be calculated from these relationships by substituting the value zero for $P$: $E$ was 0.55 for gloxinia and 1.05 for chrysanthemum. The lower value for gloxinia was explicable by the rosette gloxinia forms against the ground, so that the substrate was soon completely covered. Chrysanthemum grows upwards so that the leaves never cover the ground completely.

$E$ being known, $T$ (transpiration in litres per pot) could be found by subtracting $E$ from $W$:

Fig. 19. Relationship between yield of dry matter and water consumption in Trial 2.



$T = W - E$.

These equations relating $P$ and $W$, were converted into equations relating $P$ and $T$ by substituting $T + E$ for $W$:

for gloxinia $P = 4.42\ T$

for chrysanthemum $P = 5.37\ T$.

As the relationship between transpiration and yield was linear, the percentage reduction in transpiration with type and amount of salt equalled the percentage reduction in yield (Table 7).

The transpiration coefficient is the reciprocal of the regression coefficients from these relationships between $P$ and $T$. For gloxinia the coefficient was 0.226 litre per g DM, 21.5% higher than in water culture. For chrysanthemum the transpiration coefficient was 0.186 litre per g DM, similar to that in water culture.

The graphs show that, both for gloxinia and for chrysanthemum, the points for the lowest N rates without exception fell below the line, especially for chrysanthemum in the sulphate series. At higher N rates, the points approached or lay on the line, so that, at least in the lower N range, the water utilization improved with rate of N.

However water utilization greatly deteriorated with salinity and excessive rates of N, as can be seen most clearly in the NaCl and KCl series with gloxinia.

Except for these extreme treatments, the transpiration coefficient seemed to be independent of rate of nitrogen, of type and quantity of salt, and of $EC_e$.

To evaluate the influence of the various treatments on water balance of the plant, water consumption was compared between treatments over a short period early in the trial. In these trials, however, such data are only a rough guide because of the large contribution of evaporation to total water consumption during this early period. Variations in treatments, bringing about only small differences in $EC_e$, would hardly produce large differences in water consumption. Differences in salinity between treatments did, however, cause marked differences in water consumption.

At 0, 40.4, and 84.4 meq salt per kg DS (dry substrate), the average water consumption over the first ten days were 451, 433, and 428 ml per pot for gloxinia, and 698, 667, and 638 ml per pot for chrysanthemum, respectively. Thus transpiration decreased with increasing salinity.

An influence on water consumption of chrysanthemum over the first ten days was noticeable also for N rate. At all series, water consumption at the highest N rate was always less than at the lowest N rate. On average it was 705 and 672 ml per pot at 0.2 g N and 4.2 g N per pot, respectively. High N rates seemed to reduce transpiration as in water culture. Thus the influence on plant growth of salinity, including excess N, seems to be largely an influence of salt on water balance of the plant. The results of Trial 2 were similar to those in water culture.

### 4.5 Salinity and yield of dry matter

In Fig. 20 yield of dry matter for each N rate has been plotted against $EC_e$. In each graph, the distribution of the points proved that the negative relationship between yield and salt treatment can be reduced to a negative relationship between yield and $EC_e$. This general trend has been indicated by lines, drawn as accurately as possible through the points. The lines were exponential to almost linear for gloxinia, and linear for chrysanthemum. With suboptimum N, N rate influenced the $EC_e$-yield relationship. In the range 3-12 mmho $cm^{-1}$, the reduction in yield of gloxinia per unit increase in $EC_e$ ($dP/dEC_e$) was 0.74 g $mmho^{-1}$ cm for 0.2 g N per pot, and 1.81 g $mmho^{-1}$ cm for 1.2 g N per pot, being the optimum N rate.

In the same $EC_e$ range, $dP/dEC_e$ for chrysanthemum was 0.37 g $mmho^{-1}$ cm at 0.2 g N per pot, and 1.17 g $mmho^{-1}$ cm at 2.2 g N per pot, being the optimum N rate.

For both species, the effect of salinity seemed much larger at the N optimum than with suboptimum N. This again confirmed the general rule that the effect of a factor limiting plant growth is more pronounced, the nearer the other factors are to optimum (Brouwer, 1960).

Because of this important interaction between salinity and N rate, data about the effect of salt on different plants cannot be properly evaluated without considering nitrogen status. Furthermore, when studying salinity, plants must receive an optimum N supply. In some graphs in Fig. 20 the different salts showed a different distribution, with the same amounts of salt. These differences could result from specific effects associated with the nature of the salt but this cannot be proved as long as treatments differed in $EC_e$.

However, with these values of $dP/dEC_e$ yield can be adjusted to one $EC_e$ value for each rate of the four salts used. After such adjustment, a valid comparison – i.e. for equal amounts of N and salt, and for equal $EC_e$ values – was possible among types of salt. Significant differences remaining after such an adjustment can be ascribed only to differences in the properties of the salts.

Table 8 shows significant differences between types of salt in inhibition of yield, after adjustment of $EC_e$. The salts, in addition to their general $EC_e$ effects, often had specific effects on gloxinia. Thus the specific inhibition of growth of gloxinia was least for KCl and most for $K_2SO_4$. The other two salts were intermediate. The data did not indicate which of the other two salts, NaCl or $Na_2SO_4$, was more harmful.

There were far fewer pairs of comparable treatments with specific salt inhibition for chrysanthemum than for gloxinia. Hence chrysanthemum may be less sensitive to specific salt effects than gloxinia, as could be expected from the difference in salt tolerance between them.

For chrysanthemum, the specific inhibition by $Na_2SO_4$ was more than that by any of the other salts, which hardly differed among themselves. In two pairs a significant difference in inhibition was found between $K_2SO_4$ and KCl. Definite conclusions were hardly possible because of the variability of the results.

The influence of treatments on ionic composition of the plants was then examined as a possible clue to explain the specific salt effects.

Fig. 20. Relationship between $EC_e$ and yield of dry matter in Trial 2.

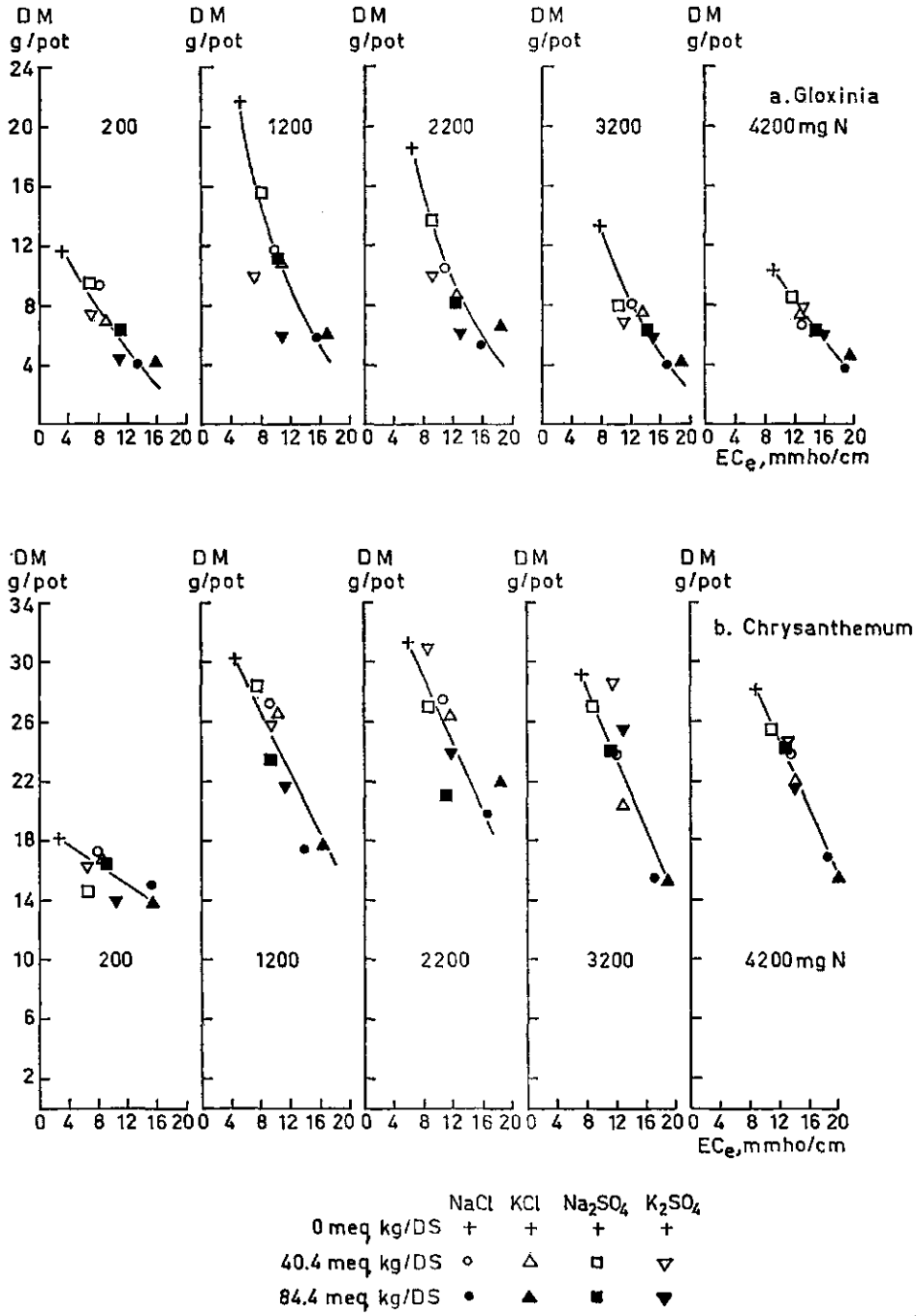


Table 8. Significant positive differences among various types of salts in their inhibition of yield of dry matter for each N rate and for two salt applications, after adjustment of $EC_e$ (P = level of significance).

| N level | 40.4 meq salt per kg DS | | 84.4 meq. salt per kg DS | |
|---|---|---|---|---|
| g/pot | pair of salts | P | pair of salts | P |
| Gloxinia | | | | |
| 0.2 | $Na_2SO_4$–$K_2SO_4$ | 0.05 | KCl –$K_2SO_4$ | 0.01 |
| 0.2 | — | — | $Na_2SO_4$–$K_2SO_4$ | 0.05 |
| 0.2 | — | — | KCl –NaCl | 0.01 |
| 1.2 | NaCl –$K_2SO_4$ | 0.01 | NaCl –$K_2SO_4$ | 0.01 |
| 1.2 | KCl –$K_2SO_4$ | 0.01 | KCl –$K_2SO_4$ | 0.01 |
| 1.2 | $Na_2SO_4$–$K_2SO_4$ | 0.01 | $Na_2SO_4$–$K_2SO_4$ | 0.01 |
| 2.2 | NaCl –$K_2SO_4$ | 0.01 | NaCl –$K_2SO_4$ | 0.01 |
| 2.2 | KCl –$K_2SO_4$ | 0.01 | KCl –$K_2SO_4$ | 0.01 |
| 2.2 | $Na_2SO_4$–$K_2SO_4$ | 0.01 | KCl –NaCl | 0.01 |
| 2.2 | KCl –$Na_2SO_4$ | 0.05 | KCl –$Na_2SO_4$ | 0.01 |
| Chrysanthemum | | | | |
| 2.2 | NaCl –$Na_2SO_4$ | 0.05 | NaCl –$Na_2SO_4$ | 0.05 |
| 2.2 | KCl –$Na_2SO_4$ | 0.05 | KCl –$Na_2SO_4$ | 0.01 |
| 2.2 | $K_2SO_4$ –$Na_2SO_4$ | 0.05 | KCl –$K_2SO_4$ | 0.05 |
| 3.2 | $K_2SO_4$ –$Na_2SO_4$ | 0.05 | — | — |
| 3.2 | $K_2SO_4$ –KCl | 0.01 | — | — |

## 4.6 Ions in substrate extracts

To assess the ionic balance of a plant, one must examine the chemical properties of the substrate as well as of the plant. For soils, the analytical data obtained from the saturation extract (SE) can be examined (Richards, 1954).

*pH* (Table 9) markedly declined with increasing N. This decline was undoubtedly due to acidification by $NH_4^+$ nitrogen from the ammonium nitrate.

The pH at the first N rate for chrysanthemum was about a unit higher than for gloxinia, because of the heavier liming for chrysanthemum. At the highest N rate, the pH did not differ much for the two species. A lowering of the pH by salt application is noticeable at the first and second N rates for chrysanthemum.

Only in the KCl and NaCl series did pH tend to rise at all between the third and fifth N level.

*Soluble inorganic N* (Table 10) means here the sum of $NH_4^+$ N and $NO_3^-$ N.

Soluble inorganic N in the SE increased almost linearly with rate of N. In general, these contents were a bit lower for chrysanthemum than for gloxinia, possibly due to

Table 9. Average pH values of the saturation extract for three salt applications at five N levels. Each value is an average for all four types of salt.

| | meq salt/kg DS | g N/pot | | | | |
|---|---|---|---|---|---|---|
| | | 0.2 | 1.2 | 2.2 | 3.2 | 4.2 |
| Glox. | 0 | 4.9 | 4.2 | 3.9 | 4.1 | 4.2 |
| Glox. | 40.4 | 5.1 | 4.4 | 4.1 | 4.1 | 4.3 |
| Glox. | 84.4 | 4.8 | 4.3 | 4.3 | 4.5 | 4.6 |
| Chrys. | 0 | 5.9 | 5.2 | 4.4 | 4.0 | 3.9 |
| Chrys. | 40.4 | 5.6 | 5.0 | 4.5 | 4.2 | 4.0 |
| Chrys. | 84.4 | 5.3 | 4.9 | 4.3 | 4.2 | 4.3 |

Table 10. Soluble inorganic N (i.e. $NH_4^+$ N + $NO_3^-$ N) (meq/litre) in the saturation extract at five N levels for the zero salt application and for two applications of chloride and sulphate. Each value is an average of sodium and potassium salt treatments.

| | Type of salt | Salt level | g N/pot | | | | |
|---|---|---|---|---|---|---|---|
| | | meq/kg DS | 0.2 | 1.2 | 2.2 | 3.2 | 4.2 |
| Glox. | — | 0 | 7.0 | 28.8 | 44.1 | 66.2 | 87.2 |
| Glox. | chloride | 40.4 | 7.5 | 26.7 | 42.2 | 59.4 | 73.0 |
| Glox. | chloride | 84.4 | 7.0 | 27.6 | 45.6 | 66.8 | 77.3 |
| Glox. | sulphate | 40.4 | 8.2 | 29.3 | 46.1 | 66.0 | 90.7 |
| Glox. | sulphate | 84.4 | 8.4 | 30.2 | 48.4 | 71.7 | 83.9 |
| Chrys. | — | 0 | 2.1 | 18.8 | 34.6 | 51.8 | 73.3 |
| Chrys. | chloride | 40.4 | 3.7 | 21.6 | 39.6 | 51.3 | 71.1 |
| Chrys. | chloride | 84.4 | 3.2 | 17.3 | 42.4 | 56.4 | 78.4 |
| Chrys. | sulphate | 40.4 | 1.1 | 16.5 | 32.7 | 48.1 | 70.6 |
| Chrys. | sulphate | 84.4 | 2.8 | 18.0 | 37.8 | 50.6 | 67.6 |

higher N loss by the heavier liming of chrysanthemum.

For gloxinia, N content was in general a bit lower in the chloride series than in the sulphate series, but for chrysanthemum higher. From the results reported in Section 4.2 it can be said that N rates giving 25-30 meq per litre SE for gloxinia and 33-40 meq for chrysanthemum were optimum.

*Percentage $NH_4^+$ N in soluble inorganic N* (Table 11) The form in which N is supplied ($NH_4^+$ or $NO_3^-$) is of great influence on the ionic balance in plants (Street & Sheat, 1958).

Table 11. $NH_4^+$ N as a percentage of soluble inorganic N in the saturation extract at five N levels without salt and for two levels of chloride and sulphate.

| | Type of salt | Salt level meq/kg DS | g N/pot 0.2 | 1.2 | 2.2 | 3.2 | 4.2 |
|---|---|---|---|---|---|---|---|
| Glox. | — | 0 | 0 | 0 | 6.5 | 21.9 | 30.5 |
| Glox. | chloride | 40.4 | 0.8 | 0.4 | 14.5 | 30.1 | 38.1 |
| Glox. | chloride | 84.4 | 3.7 | 6.7 | 34.0 | 43.4 | 46.4 |
| Glox. | sulphate | 40.4 | 1.0 | 0.7 | 7.0 | 20.6 | 28.3 |
| Glox. | sulphate | 84.4 | 1.9 | 1.8 | 9.3 | 21.2 | 29.0 |
| Chrys. | — | 0 | 0 | 0.5 | 0.4 | 2.9 | 16.4 |
| Chrys. | chloride | 40.4 | 3.7 | 0.9 | 0.5 | 3.1 | 18.0 |
| Chrys. | chloride | 84.4 | 5.7 | 0.9 | 4.5 | 17.9 | 34.1 |
| Chrys. | sulphate | 40.4 | 0 | 0.6 | 0.5 | 0.8 | 11.3 |
| Chrys. | sulphate | 84.4 | 0 | 0.7 | 0.7 | 1.3 | 12.0 |

Treatment had a distinct effect on percentage $NH_4^+$ N. Percentage $NH_4^+$ N rose sharply at the third N level upward. Chlorides of Na or K influenced percentage $NH_4^+$ N: with increasing concentration of $Cl^-$ in the medium, the balance between the two forms of nitrogen shifted towards $NH_4^+$. This positive relation between chloride and $NH_4^+$ N, evident for both species, might be associated with the cation concentrations, which were highest in the NaCl and KCl series as was also shown by the course of the $EC_e$ lines in Fig. 14. Increasing cation concentrations result in more free $NH_4^+$ in the medium. There may also be a negative influence of $EC_e$ and a toxic influence of chloride on the activity of nitrifying bacteria, already forced to operate in a medium too low in pH.

Sulphate did not alter percentage $NH_4^+$ N.

Percentage $NH_4^+$ N seemed to be much lower in chrysanthemum than in gloxinia. The heavier liming of chrysanthemum could be responsible for this.

*$Ca^{2+}$* (Table 12) The treatments strongly influenced free $Ca^{2+}$ in the substrate. $Ca^{2+}$ in the SE increased rapidly with increases in N level, as a consequence of the decline in pH. More $Ca^{2+}$ was released from the $CaCO_3$ added to the solution as pH decreased. The extra $H^+$ also exchanged with $Ca^{2+}$ on the adsorption complex. Similarly addition of salt increased free $Ca^{2+}$ by ion exchange: as $Na^+$ and $K^+$ increased in the solution, the balance shifted from adsorbed towards free $Ca^{2+}$. For both species, the content in substrate of free $Ca^{2+}$ was clearly higher in KCl than in NaCl solutions. This may be explained by the greater ability of $K^+$ than of $Na^+$ to release $Ca^{2+}$ from the exchange complex. At the higher N rates, especially with chrysanthemum, the content of free $Ca^{2+}$ was lower for the sulphates than without salt or with chlorides. The explanation lies in the low solubility of $CaSO_4$. At the

Table 12. The $Ca^{2+}$ contents of the saturation extract (meq/litre) at five N levels without salt and for two levels of chloride and sulphate.

| | Type of salt | salt level meq/kg DS | g N/pot 0.2 | 1.2 | 2.2 | 3.2 | 4.2 |
|---|---|---|---|---|---|---|---|
| Glox. | — | 0 | 20.3 | 35.2 | 41.5 | 41.4 | 39.7 |
| Glox. | chloride | 40.4 | 31.8 | 44.7 | 46.5 | 44.8 | 38.8 |
| Glox. | chloride | 84.4 | 38.1 | 49.7 | 42.2 | 39.1 | 40.5 |
| Glox. | sulphate | 40.4 | 27.5 | 34.3 | 36.9 | 37.9 | 39.6 |
| Glox. | sulphate | 84.4 | 27.2 | 29.4 | 30.9 | 32.0 | 32.1 |
| Chrys. | — | 0 | 18.5 | 29.2 | 42.9 | 50.8 | 52.7 |
| Chrys. | chloride | 40.4 | 29.5 | 40.7 | 50.5 | 57.7 | 58.6 |
| Chrys. | chloride | 84.4 | 37.3 | 43.0 | 59.5 | 55.5 | 51.0 |
| Chrys. | sulphate | 40.4 | 24.9 | 27.3 | 33.9 | 35.4 | 40.8 |
| Chrys. | sulphate | 84.4 | 25.4 | 26.1 | 30.0 | 32.6 | 34.1 |

Table 13. $SO_4^{2-}$ in the saturation extract (meq/litre) at five N rates without salt and with two levels of sulphate.

| | Sulphate meq/kg DS | g N/pot 0.2 | 1.2 | 2.2 | 3.2 | 4.2 |
|---|---|---|---|---|---|---|
| Gloxinia | 0 | 30.6 | 30.1 | 32.4 | 32.0 | 33.4 |
| Gloxinia | 40.4 | 72.0 | 53.7 | 54.0 | 55.7 | 58.1 |
| Gloxinia | 84.4 | 115.0 | 101.1 | 94.8 | 100.0 | 100.3 |
| Chrysanthemum | 0 | 28.8 | 29.5 | 27.4 | 27.7 | 27.5 |
| Chrysanthemum | 40.4 | 78.5 | 74.7 | 52.2 | 57.9 | 57.1 |
| Chrysanthemum | 84.4 | 106.0 | 104.9 | 82.9 | 76.0 | 76.0 |

higher contents of free $Ca^{2+}$, the solubility product of $CaSO_4$ was apparently exceeded when sulphates were added and gypsum would have been precipitated in amounts increasing with sulphate level. This precipitation of $Ca^{2+}$ as gypsum was reflected in the $SO_4^{2-}$ content of the SE (Table 13).

The content of free $Ca^{2+}$ with chrysanthemum was higher than with gloxinia because of heavier liming.

*$SO_4^{2-}$* (Table 13) Without salt series for both species, the contents of free $SO_4^{2-}$ were the same for all five N rates. The $SO_4^{2-}$ content was on average a bit lower with chrysanthemum than with gloxinia, because of heavier liming.

The $SO_4^{2-}$ content in the sulphate series decreased with increasing N levels

especially for chrysanthemum. For both species, the $SO_4^{2-}$ content at the lowest sulphate application was much lower for $Na_2SO_4$ than for $K_2SO_4$. This finding cannot be explained by differences in $Ca^{2+}$ content, since in both series this content was the same for each N level.

*$K^+$, $Na^+$ and $Mg^{2+}$* (Tables 14 and 15) As N rate increased, contents of the three cations, and of $Ca^{2+}$, increased in the SE. Again this behaviour is explicable from acidification during nitrification of $NH_4^+$.

This nitrification increased the concentration of $H^+$ as well as that of free $Ca^{2+}$ so that the equilibrium between the adsorbed and free phases of $K^+$, $Na^+$, and $Mg^{2+}$ shifted towards the free phase. The contents of these three cations with both species agreed well. The $Mg^{2+}$ content for chrysanthemum was a bit lower than for gloxinia, because of the higher pH for chrysanthemum. Although less $Mg^{2+}$ was added than $K^+$, $Mg^{2+}$ in the SE seemed to be about the same as or sometimes even more than $K^+$. This must be attributed to peat moss in the substrate which, like frozen decom-

Table 14. $K^+$, $Na^+$ and $Mg^{2+}$ in the saturation extract (meq/litre) at five N rates without salt.

| | Cation | g N/pot | | | | |
|---|---|---|---|---|---|---|
| | | 0.2 | 1.2 | 2.2 | 3.2 | 4.2 |
| Gloxinia | $K^+$ | 7.4 | 9.0 | 9.5 | 9.9 | 10.4 |
| Gloxinia | $Na^+$ | 2.0 | 2.2 | 2.3 | 2.3 | 2.2 |
| Gloxinia | $Mg^{2+}$ | 7.7 | 11.3 | 13.0 | 13.1 | 13.0 |
| Chrysanthemum | $K^+$ | 6.9 | 8.6 | 9.5 | 10.2 | 11.0 |
| Chrysanthemum | $Na^+$ | 2.0 | 2.2 | 2.3 | 2.5 | 2.6 |
| Chrysanthemum | $Mg^{2+}$ | 3.8 | 6.4 | 8.5 | 10.1 | 10.8 |

Table 15. $Na^+$ and $K^+$ (meq/litre) in the SE with two levels of those cations as chlorides or sulphates.

| | Gloxinia | | | | Chrysanthemum | | | |
|---|---|---|---|---|---|---|---|---|
| | meq $Cl^-$/kg DS | | meq $SO_4^{2-}$/kg DS | | meq $Cl^-$/kg DS | | meq $SO_4^{2-}$/kg DS | |
| | 40.4 | 84.4 | 40.4 | 84.4 | 40.4 | 84.4 | 40.4 | 84.4 |
| $Na^+$ | 40.8 | 81.4 | 41.6 | 82.7 | 42.5 | 85.0 | 37.4 | 70.9 |
| $K^+$ | 44.8 | 85.0 | 42.8 | 88.0 | 47.0 | 94.3 | 66.3 | 84.0 |

posed black sphagnum peat ('garden peat', Egberts & van der Kloes, 1960) is naturally rich in $Mg^{2+}$.

Contents of $K^+$ and $Na^+$ of equivalent K and Na treatments (applied as chlorides) were almost similar. Only the $K^+$ content for the KCl series for chrysanthemum was a bit higher than for other chloride series. As for the sulphates, the $Na^+$ content for the $Na_2SO_4$ series with chrysanthemum was lower than with gloxinia. The $K^+$ content at 40.4 meq $K_2SO_4$ per kg DS for chrysanthemum was anomalous.

For gloxinia, the chlorides and sulphates at equivalent levels yielded almost identical $Na^+$ and $K^+$ contents.

*$H_2PO_4^-$ and $Cl^-$* For gloxinia, $H_2PO_4^-$ contents were unaffected by treatment; the average value was 1.16 meq per litre. For chrysanthemum there was a slight upward trend with increasing N and hence with increase in acidity; the average value was 0.55 meq per litre. This low value, compared with that for gloxinia, must be attributed to the heavier liming.

Without salt and in the sulphate series, average $Cl^-$ in the SE was 1.15 meq per litre for gloxinia and 1.27 meq per litre for chrysanthemum.

Values for $Cl^-$ in the SE are given in Table 16.

There was close coincidence in $Cl^-$ content of the SE between types of salt and between gloxinia and chrysanthemum.

Table 16. $Cl^-$ (meq/litre) in the SE with two levels of NaCl or KCl.

| Salt rate | Gloxinia | | Chrysanthemum | |
|---|---|---|---|---|
| meq/kg DS | NaCl | KCl | NaCl | KCl |
| 40.4 | 48.9 | 50.6 | 49.7 | 50.3 |
| 84.4 | 102.5 | 104.4 | 104.4 | 106.2 |

## 4.7 Ionic balance

Figs. 21, 22 and 23 contain information on the influence of the treatments on the ionic balance of gloxinia and chrysanthemum.

*Influence of salt* The effects of the salts added to the substrate on the ionic balance of the plants can be found in Table 17. In general, the results seem to be as expected.

$Na^+$ in the plant increased with increasing $Na^+$ in the substrate, either as sulphate or chloride. These increases in $Na^+$ decreased $K^+$, $Ca^{2+}$, and, except after adding NaCl, $Mg^{2+}$.

Table 17. Effect of salts added to the substrate on ionic balance in the plant.

| Ion in the plant | Type of salt added | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | NaCl | | KCl | | $Na_2SO_4$ | | $K_2SO_4$ | |
| | glox. | chrys. | glox. | chrys. | glox. | chrys. | glox. | chrys. |
| $K^+$ | −− | (−) | +++ | ++ | −− | − | ++ | ++ |
| $Na^+$ | +++ | + | (−) | (−) | ++ | + | (−) | (−) |
| $Ca^{2+}$ | − | + | −− | (−) | −− | (−) | −−− | − |
| $Mg^{2+}$ | (+) | (+) | − | − | − | 0 | −− | − |
| $NO_3^-$ | −− | −− | −−− | −− | ++ | (+) | + | (+) |
| $Cl^-$ | ++ | + | +++ | ++ | (+) | 0 | (+) | (−) |
| $SO_4^{2-}$ | (−) | (+) | (−) | 0 | + | (+) | ++ | (+) |
| $H_2PO_4^-$ | (−) | 0 | (−) | (−) | (+) | 0 | (−) | (−) |
| Total N | (−) | 0 | − | − | (+) | 0 | (+) | − |
| C | ++ | + | ++ | + | + | (+) | + | + |
| A | +++ | ++ | +++ | ++ | + | (+) | + | (+) |
| C-A | −− | − | −− | − | (+) | (+) | + | + |

The symbols indicate the size of the effect: 0 none, (+) weakly positive, + moderately strongly positive, ++ strongly positive, +++ very strongly positive, (−) weakly negative, − moderately strongly negative, −− strongly negative, −−− very strongly negative.

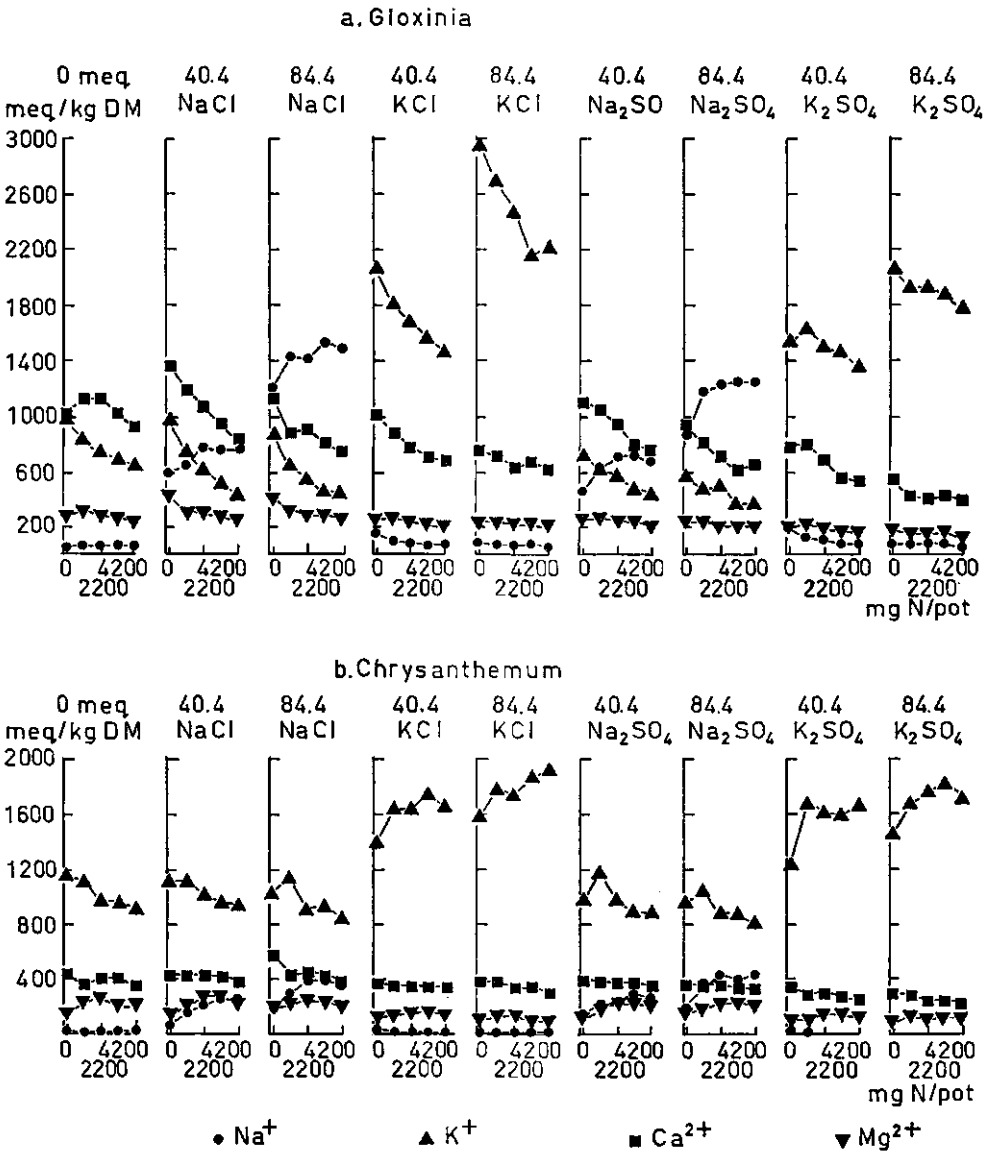
With increasing $K^+$ in the substrate, $K^+$ in the plant increased, and $Na^+$, $Ca^{2+}$ and $Mg^{2+}$ decreased. For gloxinia, the decrease in $Ca^{2+}$ seemed larger than that induced by $Na^+$, and larger for sulphates than for chlorides. Hence, the maximum decrease was with $K_2SO_4$. This strong suppression of $Ca^{2+}$ in the plant might explain why $K_2SO_4$ retarded growth of gloxinia so much more than other salts.

The $Cl^-$ content of the plant rose with increasing $Cl^-$, either as NaCl or as KCl, in the substrate. $NO_3^-$, $H_2PO_4^-$ and total N in the plant decreased with increasing $Cl^-$ in the substrate. Not only the chloride-nitrate antagonism, but also the increase in $NH_4^+$ relative to $NO_3^-$ in the SE (Section 4.6), resulting from addition of chlorides, must be held responsible for the decrease in $NO_3^-$ in the plant. A decline in $SO_4^{2-}$ in the plant by addition of $Cl^-$ was found only for gloxinia.

With increasing $SO_4^{2-}$ in the substrate, $SO_4^{2-}$ and, surprisingly, also $NO_3^-$ in the plant increased. For gloxinia, this rise in $NO_3^-$ was accompanied by a rise in total N. This effect of $SO_4^{2-}$ on $NO_3^-$ in the plant could not be accounted for by changes in $NO_3^-$ in the substrate resulting from addition of $SO_4^{2-}$, since the $NO_3^-$ concentration in the sulphate series was almost identical to that without salt (tables 10 and 11). This was also true for the $NH_4^+$ relative to $NO_3^-$ in the SE.

With increasing $Cl^-$ in the substrate, total cations C increased, but not so much as total inorganic anions A increased, so that the organic salt content (C-A) decreased.

Fig. 21. $K^+$, $Na^+$, $Ca^{2+}$, and $Mg^{2+}$ contents of the plant as affected by nitrogen rate and four different salts.




The suppressive effect of chloride on (C-A) in the plant was shown for barley and oats by de Wit *et al.* (1963).

With increasing $SO_4^{2-}$ in the substrate, total cations C rose. So did total inorganic anions A, but less strongly, so that the total effect was a rise in (C-A). De Wit *et al.* (1963) also found an increase in (C-A) of barley after addition of $K_2SO_4$.

*Influence of N rate* As mentioned earlier, $NH_4^+$ in the substrate rose with increasing N rate (tables 10 and 11). Because of competition between $NH_4^+$ and other cations for absorption by plant roots (Bange *et al.*, 1965; Dijkshoorn, 1964; de Wit *et al.*, 1963), at higher N rates the content of metallic cations in the plant must be reduced.

This was indeed usually so for most cations (figs. 21, 22 and 23). In all series, $K^+$ in gloxinia decreased sharply with increasing N, in the chloride series even more so than in the sulphate series. Despite their rise in concentration in the substrate, both $Ca^{2+}$ and $Mg^{2+}$ decreased in the plant, especially in the NaCl series (tables 12 and 14).

$Na^+$ in the plant increased in the $Na^+$ series, remained almost constant in the series without salt and decreased in the $K^+$ series.

The sharper rise in $NH_4^+$ in the substrate of the chloride series, resulting from increasing N rate (tables 10 and 11) undoubtedly contributed to the sharper decline of $K^+$, $Ca^{2+}$, and $Mg^{2+}$ in the plant in this series.

The negative influence of N rate on cations in the plant was less evident for chrysanthemum, as expected from the less pronounced increase in $NH_4^+$ in the substrate of chrysanthemum with increasing N rate.

Nevertheless, $K^+$ in chrysanthemum decreased distinctly with increasing N rate without salt and in the $Na^+$ series. In the $K^+$ series, however, there was an increase.

The behaviour of $Na^+$ in chrysanthemum was like that in gloxinia, only less pronounced.

$Ca^{2+}$ in the plant tended to decrease, whereas $Mg^{2+}$ increased slightly.

For both species, $NO_3^-$ in the plant increased with increasing N rate and thereby showed a close correspondence with the rise of $NO_3^-$ in the substrate. The rise of $NO_3^-$ in the plant was less sharp in the chloride series than without salt and in the sulphate series, partly because of competition from $Cl^-$ and partly because of the lower $NO_3^-$ levels in the substrate of the chloride series (tables 10 and 11).

In both gloxinia and chrysanthemum total N increased distinctly with N rate.

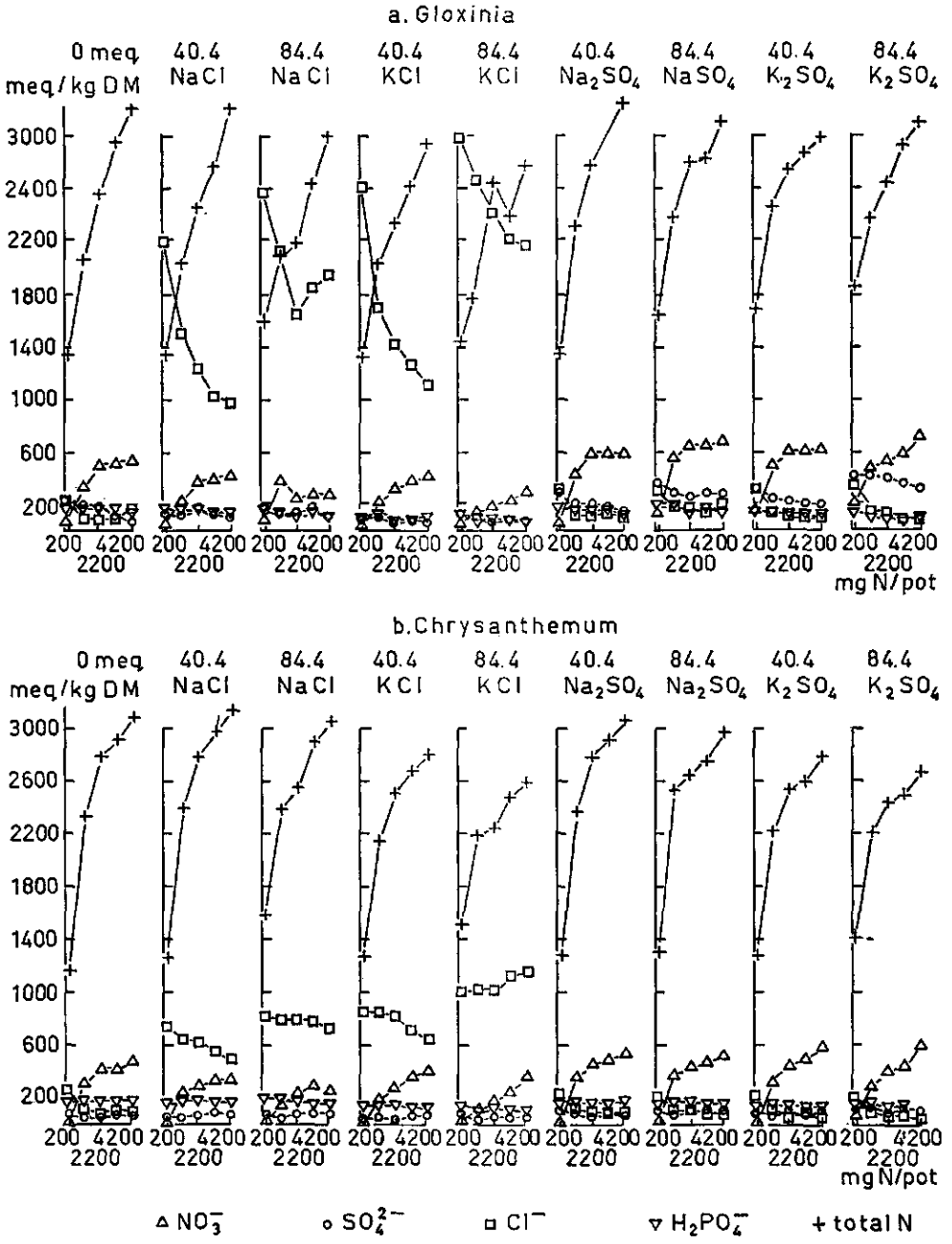
$Cl^-$ in the plant decreased in practically all series with increasing N rate as could be expected from the well known $Cl^-$–$NO_3^-$ antagonism. This decrease was especially large in the chloride series with gloxinia.

$SO_4^{2-}$ and $H_2PO_4^-$ in gloxinia declined slightly, and were hardly affected in chrysanthemum.

Total cations C in gloxinia decreased in all series with increasing N rate. Without salt and in the sulphate series, total inorganic anions A increased, resulting in a sharp decrease in organic salts (C-A). In the chloride series, however, total inorganic anions A declined, because of the earlier reported decline in $Cl^-$ which was not fully compensated by the increase in $NO_3^-$. In the NaCl series, the decline in total inorganic anions A was slightly less than that of total cation C, so that (C-A) declined slightly. The same was found with 84.4 meq KCl per kg DS. With 40.4 meq KCl per kg DS, the decrease in total inorganic anions A is a bit larger than that in total cations C, resulting in a small increase in (C-A).

Except without salt and the higher rate of NaCl, total cations C in chrysanthemum

Fig. 22. $NO_3^-$, $SO_4^{2-}$, $Cl^-$, $H_2PO_4^-$ and total N contents of the plant as affected by nitrogen rate and four different salts.



rose with increasing N rate. This is explicable by the increase in $Na^+$ and $K^+$ absorption in the $Na^+$ and $K^+$ series, respectively. However, total inorganic anions A rose to such an extend that in practically all series there was a decrease in (C-A) with increasing N rate.

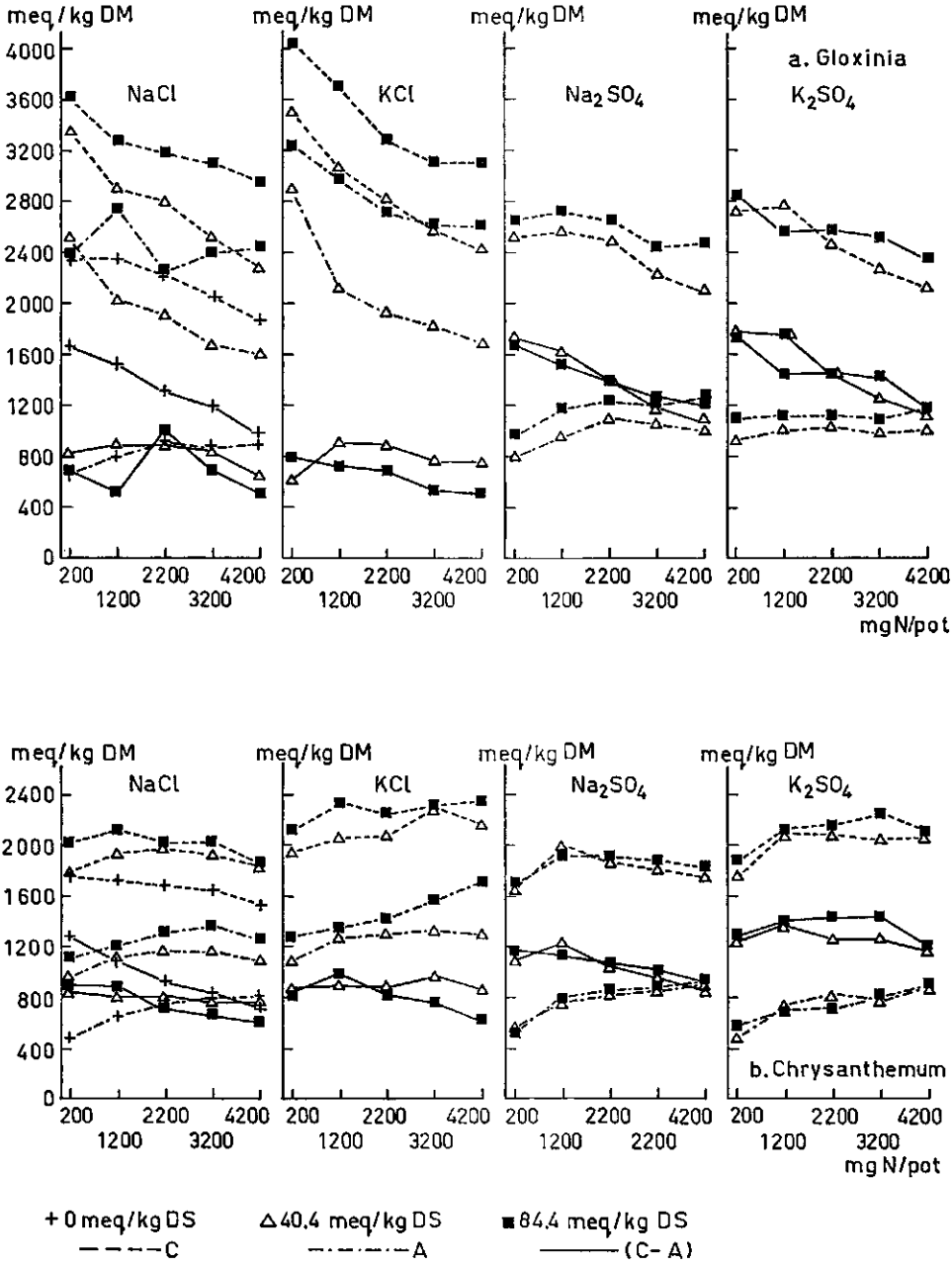
The observed decrease in (C-A) of both gloxinia and chrysanthemum with increasing N rate in last instance was associated with the rise in $NH_4^+$ concentration in the substrate. De Wit *et al.* (1963), Dijkshoorn (1964) and van Tuil (1965) already drew attention to the negative effect of $NH_4^+$ on the (C-A) content of the plant.

As in Trial 1, the general impression is that the ionic balance of gloxinia reacted much more sharply to changes in cation and anion concentrations in the substrate than did the ionic balance of chrysanthemum. The results of Trial 2 also confirmed the conclusions in Section 3.5 about the behaviour of the two species in uptake of various ions. Gloxinia readily absorbed all cations, both divalent and monovalent, without much selectivity. At optimum N rate, the contents of $K^+$, $Na^+$, $Ca^{2+}$ and $Mg^{2+}$ without salt were: 826, 65, 1130, and 321 meq per kg DM respectively. $Na^+$ was appreciably lower and Ca very much higher than in Trial 1 as would be expected from the very low content of $Na^+$ and the very high content of $Ca^{2+}$ in the substrate (tables 12 and 14). As $Ca^{2+}$ was deficient in gloxinia plants in the $K_2SO_4$ series of Trial 2, and about as high as in Trial 1, $Ca^{2+}$ level in the nutrient solution must have been a bit too low. Gloxinia, therefore, seems to need much more $Ca^{2+}$ than chrysanthemum. This could be a reason for the differences in salt tolerance between the two species (van den Berg, 1952).

At optimum N rate of the series without salt, the $K^+$, $Na^+$, $Ca^{2+}$, and $Mg^{2+}$ contents of chrysanthemum were: 984, 22, 415, and 217 meq per kg DM, respectively. Although $K^+$ was present in the substrate at about a quarter the concentration of $Ca^{2+}$, $K^+$ in the plant was twice as high as $Ca^{2+}$. This is another indication of chrysanthemum's preference for $K^+$. The $K^+$ content of the plant was much lower than in Trial 1. It was even a bit below the level of 1000 meq per kg leaf DM, mentioned as optimum by Lunt & Kofranek (1958). In Trial 2 the $K^+$ level in the plant could well have been a bit below optimum. The yields, corrected for $EC_e$, of the $K_2SO_4$ series with 2.2 and 3.2 g N per pot supported this assumption. The yields seemed to be a bit higher than for corresponding N rates of the series without salt (Fig. 20). As the difference in yield was small, $K^+$ could not have been much deficient. Such deficiency as there was would be the resultant of marginal $K^+$ rate, competition from $NH_4^+$ and perhaps the low pH of the substrate. According to Nielsen & Overstreet (1955), the uptake of $K^+$ decreases with decreasing pH. If there were such a $K^+$ deficiency, it becomes clear why the specific effect of $Na_2SO_4$ for chrysanthemum was largest (Section 4.5). According to Table 17, $K^+$ uptake by chrysanthemum was most strongly suppressed by $Na_2SO_4$, so that an already existing $K^+$ deficit would be aggravated.

In Section 3.5 the conclusion has been drawn that the greater salt tolerance of chrysanthemum than of gloxinia depends on a greater ability to regulate the cation

Fig. 23. Total cations C, total inorganic anions A, and organic salts (C-A) in the plant as affected by nitrogen rate and four different salts.

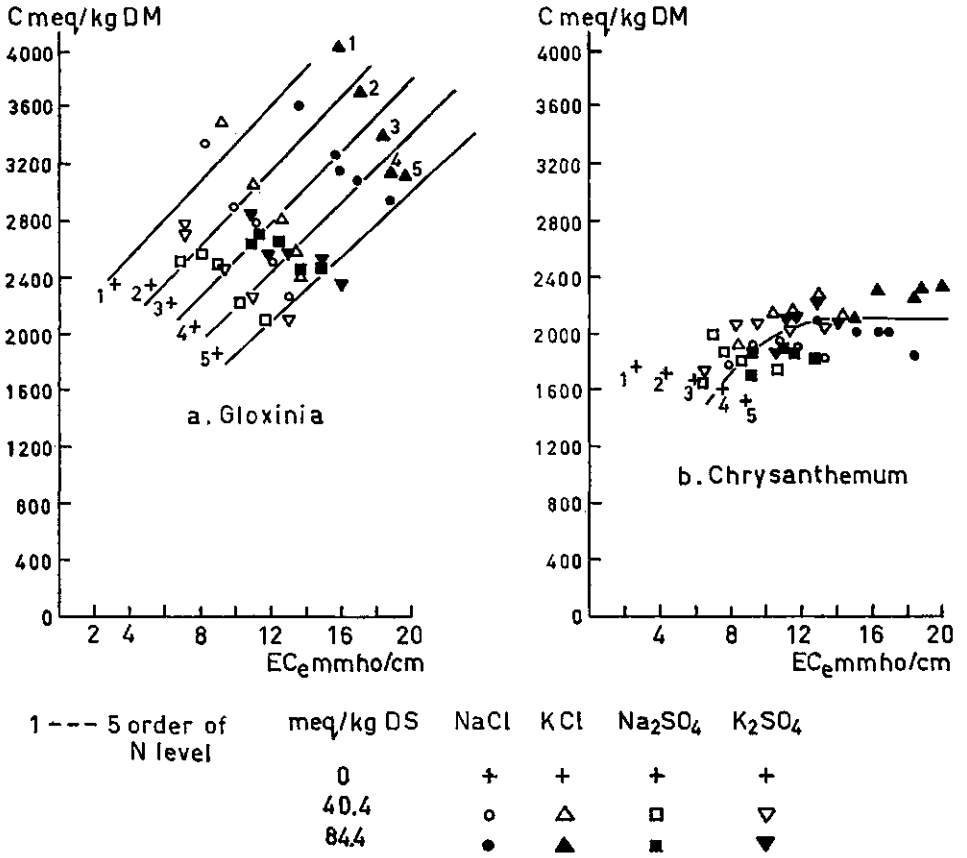


uptake. This is supported by Trial 2.

As in Trial 1, total cations C in gloxinia for each N rate increased linearly with increasing $EC_e$ (Fig. 24). The dependence on N rate of this relationship between total cations C and $EC_e$ resulted from the negative effect of N rate on total cations C. The largest variation in total cations C, from about 1800 to 4000 meq per kg DM, was in the range 9 to 16 mmho per cm. Fig. 24 also shows that the relationship between total cations C and $EC_e$ was not always positive. Within the N series, total cations C decreased with increasing $EC_e$. As stated before, this must be ascribed to the rise in $NH_4^+$ in the substrate. When N was present as $NO_3^-$ only, the relationship between total cations C and $EC_e$ was positive (Fig. 9).

As in Trial 1, total cations C in chrysanthemum increased hyperbolically with $EC_e$. However the influence of N rate on the relationship between total cations C and $EC_e$ was not quite as evident for chrysanthemum as for gloxinia. Between $EC_e$ values of 9 and 16 mmho per cm, total cations C varied from 1500 to 2300 meq per kg DM, a variation which was only slightly more than a third of that for gloxinia.

Fig. 24. Relationship between $EC_e$ and total cations C in the plant in Trial 2.



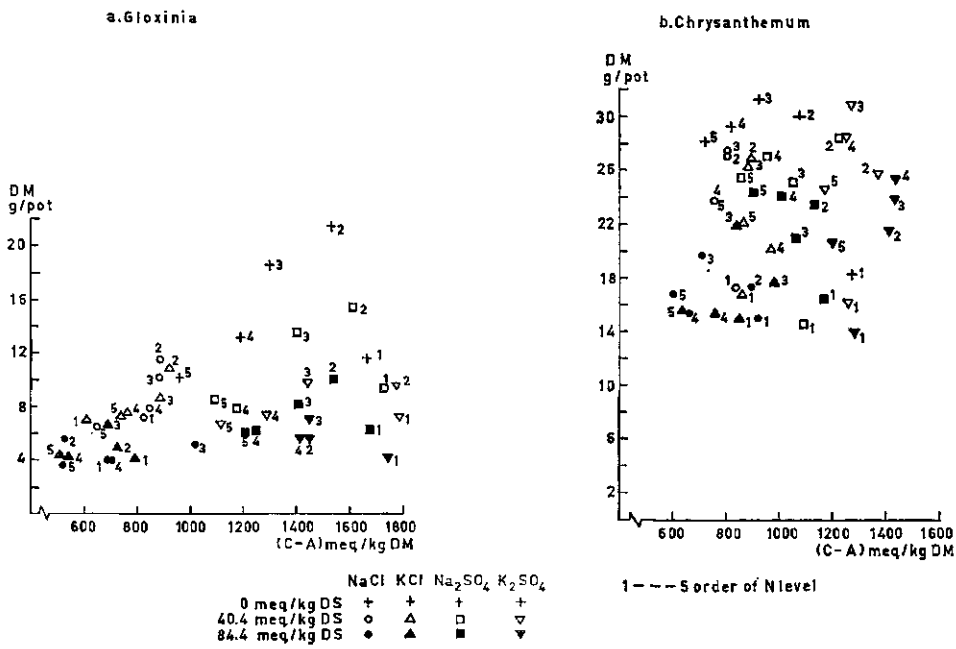
The linear relationship between total cations C and $EC_e$ for species like gloxinia permits the use of total cations C as a criterion of soil salinity so long as the form of the nitrogen supplied is taken into account. If the 'diagnostique foliaire' be used (Ulrich, 1943; Prévot & Ollagnier, 1956), this criterion could be important.

The greater ability of chrysanthemum than gloxinia to regulate the ionic balance was also evident in the amount of variation in organic salts (C-A). A review of all observations made for the two species (Fig. 25) shows that for gloxinia the value varied from 500 to 1800 meq per kg DM, for chrysanthemum from 600 to 1450 meq per kg DM.

Organic salts (C-A) at the highest yield of gloxinia in Trial 2 were 1530 meq per kg DM, considerably more than in Trial 1 (Fig. 11) mainly because of the much higher value of $Ca^{2+}$ and the much lower value of $Cl^-$ in the plant material, ensuing from more $Ca^{2+}$ and less $Cl^-$ in the substrate of Trial 2. As $Ca^{2+}$ in Trial 1 was probably too low, the (C-A) content in Trial 2 can be considered nearer the optimum for gloxinia.

For chrysanthemum, the (C-A) content at the highest yield was 920 meq per kg DM, considerably less than in Trial 1, because of a sharper decline in total cations C than in total inorganic anions A. The fall in total cations C resulted from decreases in $K^+$ and in $Na^+$, which were not fully compensated by increases in $Ca^{2+}$ and $Mg^{2+}$. The decrease in total inorganic anions A was caused by lower values of $NO_3^-$ and $Cl^-$. The suboptimum $K^+$ percentage in the plant, indicates that the (C-A) content

Fig. 25. Relationship between organic salts (C-A) in the plant and yield of dry matter.



was too low. A normal value for chrysanthemum seems to be that of the 3rd rate of N in the 1st $K_2SO_4$ series, which, after correction for $EC_e$, yielded more. There was about 1250 meq per kg DM, not much more than in Trial 1.

The distribution of values for organic salts (C-A) against yield was clearly influenced by three factors: the nature of the anion added, and the amounts of salt and of nitrogen added. For gloxinia, the points representing the sulphate series were central and right of centre, and those representing the chloride series were concentrated in the lower left corner. Values were lower, the higher the salt level. An additional shift to the left is noticeable in the chloride series. Finally increasing N rates tended to shift the points to the left. In the suboptimum N range, this shift was accompanied by an upward one, in the superoptimum N range by a downward one. The general result is a concentration of points representing the sulphate treatments with N deficiency in the lower right corner, and a concentration of points representing the chloride treatments with N excess in the lower left corner. This distribution pattern cannot be generalized. Deviations occur when N is applied as $NO_3^-$ only.

The graph clearly shows the strong influence of the form of N ($NH_4^+$ or $NO_3^-$) on ionic balance in plants.

### 4.8 Moisture in the plants

*Influence of salt* Chlorides and sulphates clearly had different influences on water content of gloxinia (Fig. 26). Chlorides increased, sulphates decreased moisture. This effect of chloride corresponded to that of NaCl in Trial 1. Chlorides interacted strikingly with N rate below optimum N rate: the lower the N rate, the higher the increase in moisture.

In contrast with gloxinia, there was a negative influence of chlorides on moisture in chrysanthemum. This negative effect increased with chloride level as in Trial 1. The chloride effect was smaller at lower than at higher N rates. Sulphates also lowered moisture, but less so than chlorides.

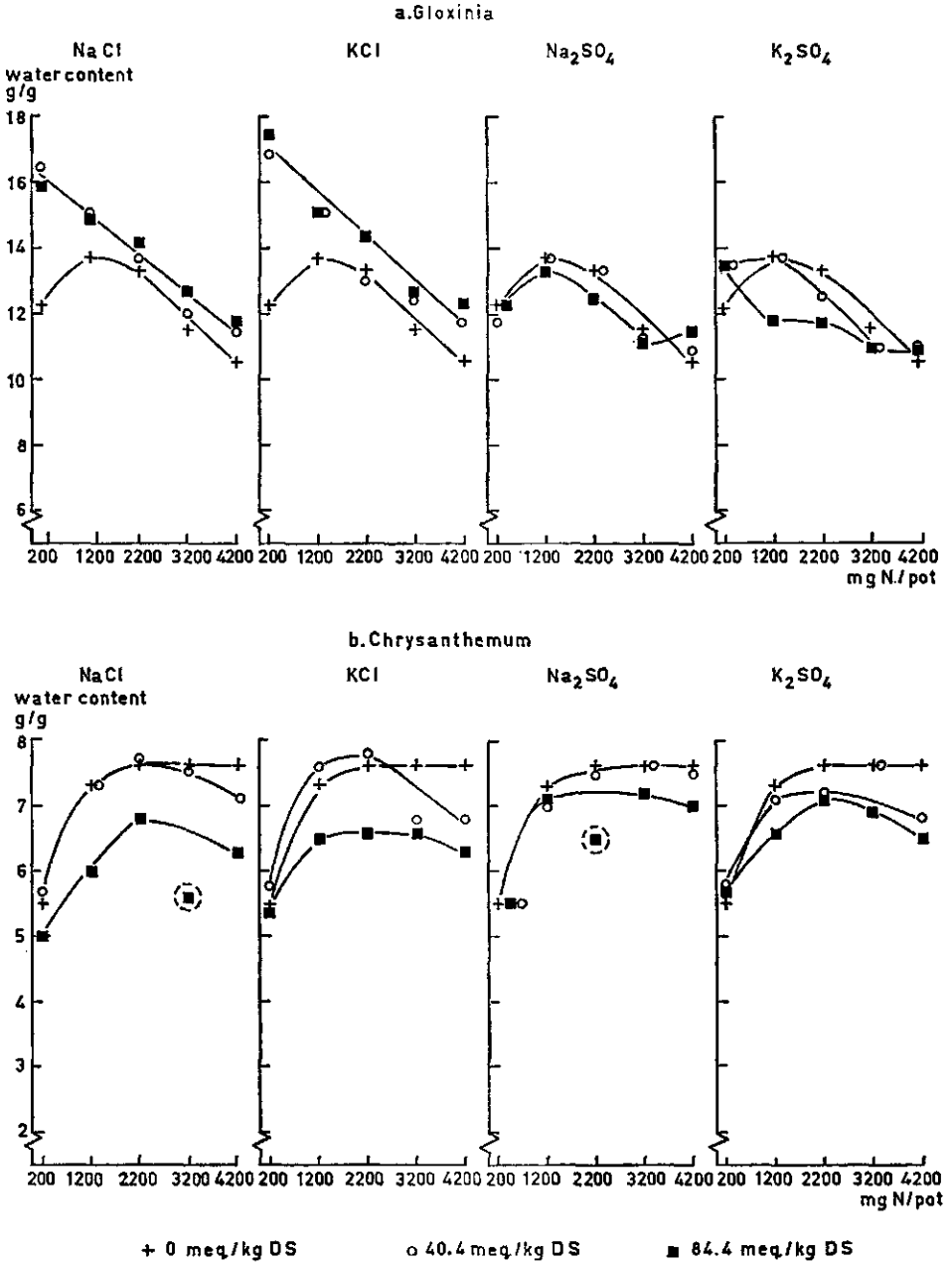
In Fig. 27, total cations C in gloxinia in all series have been plotted against the water content. The positive linear relationship between total cations C and moisture was evident and led to the conclusion that moisture in gloxinia was determined mainly by total cations C. The influences of type and amount of salt, and of form and rate of nitrogen were of minor importance, if any.

This result confirms the statement made by Arnold (1955) that succulence is correlated more with accumulation of total salt than with accumulation of $Cl^-$ or NaCl in the plant.

As already mentioned in Section 3.6, this behaviour of gloxinia in moisture holding can be looked upon as a protection against salinity.

*Influence of N rate* For gloxinia, in the suboptimum N range moisture increased with N rate. This relationship was not found in the chloride series, where moisture tended to decrease from the first N rate upwards. Above the optimum N rate, moisture

Fig. 26. Water content of the plant as affected by nitrogen rate and four different salts.



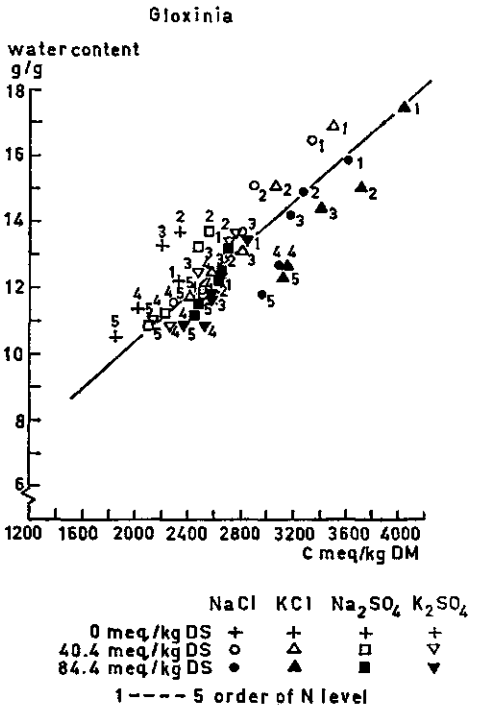



Fig. 27. Relationship between total cations C and water content of gloxinia.

decreased in all series.

For chrysanthemum, below optimum N rate, moisture clearly increased in all series with N rate. Above optimum, it remained constant in the series without salt, but tended to decrease in most of the other salt series.

### 4.9 Conclusion

The nitrogen effect was adversely affected by all four salts as for NaCl in Trial 1. In general the size of this negative effect seems proportional to the rise in $EC_e$, brought about by the addition of the salt. Again the lowering of the N effect by whatever salt can be attributed to a decreased N utilization.

The deleterious effect of $EC_e$ on yield of each species depended largely on the N rate. Therefore, for a proper evaluation of salt damage the N status of the crop must be considered.

The form of nitrogen in the substrate was of extreme importance for the ionic balance in the plant. High $NH_4^+$ contents distinctly decreased the organic salt content in the plant. A high $NH_4^+$ content of the substrate was promoted by using $NH_4^+$-containing fertilizers without sufficient lime to prevent the pH from declining to a level at which nitrification was inhibited.

The specific adverse effect of $K_2SO_4$ in gloxinia is related to a $Ca^{2+}$ deficiency induced by the combined actions of $K^+$ and $SO_4^{2-}$. Similarly, the specific harmfulness

of $Na_2SO_4$ for chrysanthemum is attributed to a $K^+$ deficiency brought about by the combined competitive actions of $NH_4^+$ and $Na^+$.

The results of Trial 2 confirm the difference found in Trial 1 in the ionic behaviour between the two species. Gloxinia, though exhibiting a high requirement for $Ca^{2+}$ seems to lack the ability to absorb this cation preferentially. However the high requirement of chrysanthemum for $K^+$ does go with a preferential uptake of $K^+$.

# 5 Results of Trial 3: different rates of N and of NaCl, and different substrates in pots

## 5.1 Salinity and moisture capacity of the substrates

The influence of type of substrate on $EC_e$ is based primarily on difference in moisture capacity. It can be expected that the rise in $EC_e$ resulting from addition of salt, if exchange phenomena are ignored, will be inversely proportional to moisture capacity. For the three substrates, henceforth called, in order of increasing content of peat moss, $S_1$, $S_2$ and $S_3$, these capacities were for gloxinia 437, 657, and 900 ml per litre substrate, respectively, and for chrysanthemum 420, 553, and 817 ml per litre substrate, respectively. These values were calculated from the weights of dry substrate per pot, the volume of substrate per pot and the SP values (Section 5.2 and Table 17). For gloxinia, moisture capacity of the substrate was a bit higher than for chrysanthemum, because of the differences in material mixed with the peat moss: for gloxinia sand and for chrysanthemum clay.

In Fig. 28, $EC_e$ is plotted against N rate for both species. The rise in $EC_e$ per unit N applied increased with decreasing moisture capacity.

The regression equations between $y$ ($EC_e$ in mmho per cm) and $x$ (N rate in g per pot) for the combinations of the three substrates and the two NaCl levels ($Z_1$ = without NaCl; $Z_2$ = with NaCl) were as follows:

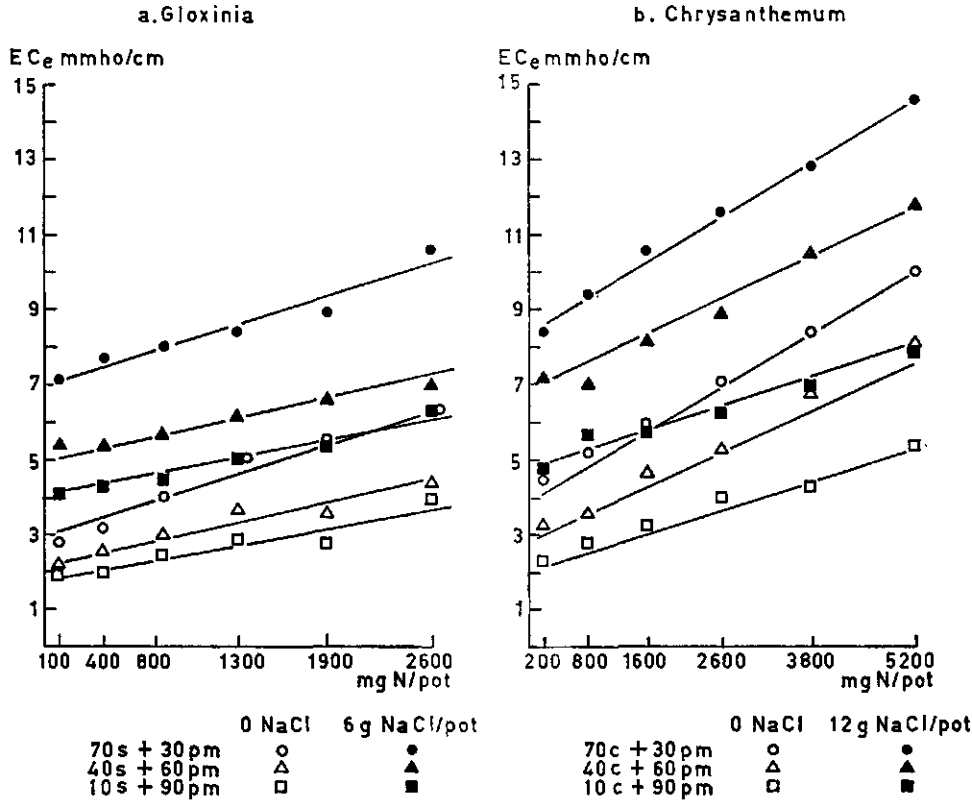
| N series | gloxinia | chrysanthemum |
|---|---|---|
| $S_1Z_1$ | $y = 1.272x + 3.02$ | $y = 1.152x + 3.92$ |
| $S_1Z_2$ | $y = 1.272x + 6.95$ | $y = 1.152x + 8.37$ |
| $S_2Z_1$ | $y = 0.907x + 2.16$ | $y = 0.916x + 2.86$ |
| $S_2Z_2$ | $y = 0.907x + 4.95$ | $y = 0.916x + 6.94$ |
| $S_3Z_1$ | $y = 0.751x + 1.79$ | $y = 0.636x + 1.98$ |
| $S_3Z_2$ | $y = 0.751x + 4.10$ | $y = 0.636x + 4.82$ |

For each substrate, the regression coefficients were the same because of identical moisture capacity and were thus independent of NaCl level.

Of the three substrates, the regression coefficients for gloxinia were in the proportion 100:71:59 for $S_1$, $S_2$ and $S_3$, respectively. Their proportional moisture capacities were 49:73:100. For chrysanthemum these values were 100:80:55 and 51:68:100, respectively.

The regression coefficients of the three substrates seemed to be almost inversely proportional to their moisture capacities.

Fig. 28. $EC_e$ as affected by nitrogen rate, NaCl level, and nature of substrate.




The regression equations also showed the increase in $EC_e$ caused by NaCl. For gloxinia, the increases were 3.93, 2.79 and 2.31 mmho per cm for $S_1$, $S_2$, and $S_3$, respectively. For chrysanthemum, respective rises were 4.45, 4.08, and 2.84 mmho per cm.

The proportional increases in $EC_e$ from NaCl of $S_1$, $S_2$ and $S_3$, respectively were for gloxinia 100:71:59 and for chrysanthemum 100:92:64. Especially for gloxinia, the reciprocity of the increase in $EC_e$ and moisture capacity was evident.

The graphs show clearly that the divergence between the substrate lines increased with NaCl. Between $S_1$ and $S_3$ of the series without NaCl, for instance, the difference in $EC_e$ increased with N rate. A further increase was caused by NaCl. The largest $EC_e$ differences between $S_1$ and $S_3$ were therefore found for the NaCl series at the higher N rate. High salt levels seemed to emphasize the substrate differences.

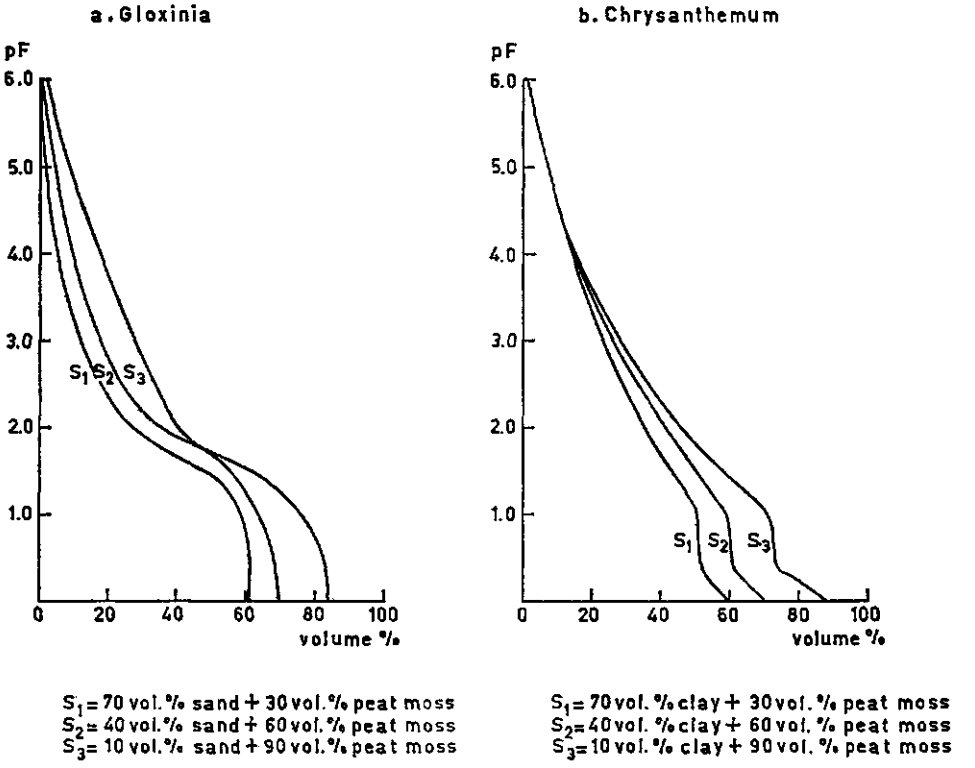
## 5.2 Moisture characteristics of the substrates

In the Introduction the need was mentioned of standardizing the pF in trials on salinity. Water was therefore added each day, except at weekends, to a certain minimum pF (for gloxinia, pF 1.8; for chrysanthemum, pF 1.6). Fluctuations in pF between irrigations by evapotranspiration could not, however, be avoided. The influence of matric suction was, therefore, not entirely eliminated. It is probably impossible to control this factor completely in the immediate vicinity of the root hairs (Ruf *et al.*, 1963). Especially with high evapotranspiration, pF in the rhizosphere could not be constant because water lost from the root zone through the roots to aerial parts would not be fully replenished (Janes, 1966). The deficit would be greater if the soil were drier. Water movement in the soil is therefore the limiting factor.

The pF curves of the substrates may indicate how far the results were affected by matric suction (Fig. 29). Its effects should appear from the shape of the pF curve at the pF value considered ideal.

For all three substrates of gloxinia, these curves deviated moderately from horizontal, so that water loss did not immediately cause a sharp rise in pF. As the three curves ran practically parallel in the range considered – $S_2$ and $S_3$ even coincided – the slight

Fig. 29. pF curves of the substrates used in Trial 3.



increases in pF were almost identical for the three substrates. Water losses were for gloxinia small anyway. During the last two weeks of the trial, the average daily water loss varied from 0.7 to 2.8 % (v/v). Thus the influence of matric suction seems to have been insignificant for gloxinia.

For chrysanthemum, pF was less controlled. The pF curves were, by comparison, steep in the experimental range and differed in slope. Besides chrysanthemum took much more water than gloxinia. During the last two weeks of the trial, average daily consumption varied from 3.6 to 8.8 % (v/v). Hence, matric suction could there be a major factor in the substrate effect.

The more favourable moisture characteristics of mixtures with sand than with clay were evident from the moisture volume between pF 1.0 and pF 2.0. For potted plants, including those grown on capillary benches, the range between pF 1.0 and pF 2.0 can be considered as the most important pF section. For $S_1$, $S_2$ and $S_3$ of the sand-peat mixture, these moisture volumes were 310, 300, and 380 ml per litre substrate; for $S_1$, $S_2$, and $S_3$ of the clay-peat mixture, they were 150, 180, and 250 ml per litre substrate, respectively.

As mentioned in Section 2.3 $EC_e$ was used as measure of salinity because comparisons of salinity are more meaningful when moisture capacity is taken into account. To qualify as an ideal criterion of salinity (i.e. a criterion independent of substrate), however, the quotient of percentage moisture (v/v) at saturation to that at normal pF, must be the same for different substrates.

For $S_1$, $S_2$ and $S_3$ of gloxinia, these quotients were 1.29, 1.40, and 1.91, respectively; for chrysanthemum 1.20, 1.35, and 1.77. Consequently, these figures indicate how many times larger were the electrolyte concentrations in normal soil solution than in the SE. Substrates rich in peat have $EC_e$ values too low relative to those low in peat and hence indicate too little salinity. $Ec_e$ as a measure of salinity though preferred to the usual salt determinations with a fixed soil-water ratio during extraction, is certainly not substrate-independent.

Table 18 listed some other physical properties, commonly measured in research on soil salinity (Richards, 1954). SP (saturation percentage) is percentage moisture

Table 18. Some additional physical properties of the experimental substrates.

| | substrate | bulk density g DS/100 ml | SP | FC | FAP | SP/FC | SP/FAP |
|---|---|---|---|---|---|---|---|
| Glox. | $S_1$ | 104.3 | 43 | 25 | 3.8 | 1.7 | 11.2 |
| Glox. | $S_2$ | 78.7 | 91 | 43 | 9.7 | 2.1 | 9.4 |
| Glox. | $S_3$ | 33.0 | 335 | 126 | 53.0 | 2.7 | 6.4 |
| Chrys. | $S_1$ | 107.6 | 44 | 32 | 12.0 | 1.4 | 3.6 |
| Chrys. | $S_2$ | 78.2 | 77 | 52 | 17.0 | 1.5 | 4.6 |
| Chrys. | $S_3$ | 28.0 | 320 | 165 | 47.0 | 1.9 | 6.8 |

(w/w) in saturated soil relative to oven-dry weight. FC (field capacity) is percentage moisture at field capacity (pF 2.0) relative to oven-dry weight. FAP (fifteen-atmosphere percentage) is percentage moisture at a moisture tension of 15 atm (pF 4.2) relative to oven dry weight.

For $S_1$ and $S_2$, SP and FAP almost agreed with the values listed by Richards (1954) for similar soils. For $S_3$, richer in peat, SP and FAP were slightly higher than values given by Campbell & Richards (1950) for peat soils in California similar in content of organic matter. The higher values are probably associated with the lesser decomposition of the peat in $S_3$.

According to Richards (1954), mineral soils, despite considerable variations in texture, have similar SP/FC and SP/FAP values: 2 and 4, respectively. Hence electrolyte concentrations of the soil solution of mineral soils at field capacity and at permanent-wilting point are 2 and 4 times as large, respectively, as those of saturation extracts.

Campbell & Richards (1950) found for SP/FAP of peat soils similar values, about 4.7.

According to Table 18, both quotients showed wider variations between substrates and therefore deviated widely from those listed by Campbell & Richards, presumably because of the diversity of the substrates of Trial 3. Anyway, the substrates did not confirm the rule that the ratio electrolyte concentration at FC to electrolyte concentration of the SE and the ratio electrolyte concentration at FAP to electrolyte concentration of the SE are constant.

Finally the aeration of the substrate is an important factor for growth. The pF curves for $S_1$, $S_2$, and $S_3$ at the standard pF values, show the following respective percentages air:

| | |
|---|---|
| for gloxinia: | 28, 22, and 37% (v/v); |
| for chrysanthemum: | 19, 22, and 23% (v/v). |

These air contents suggest that air supply was not a limiting factor.

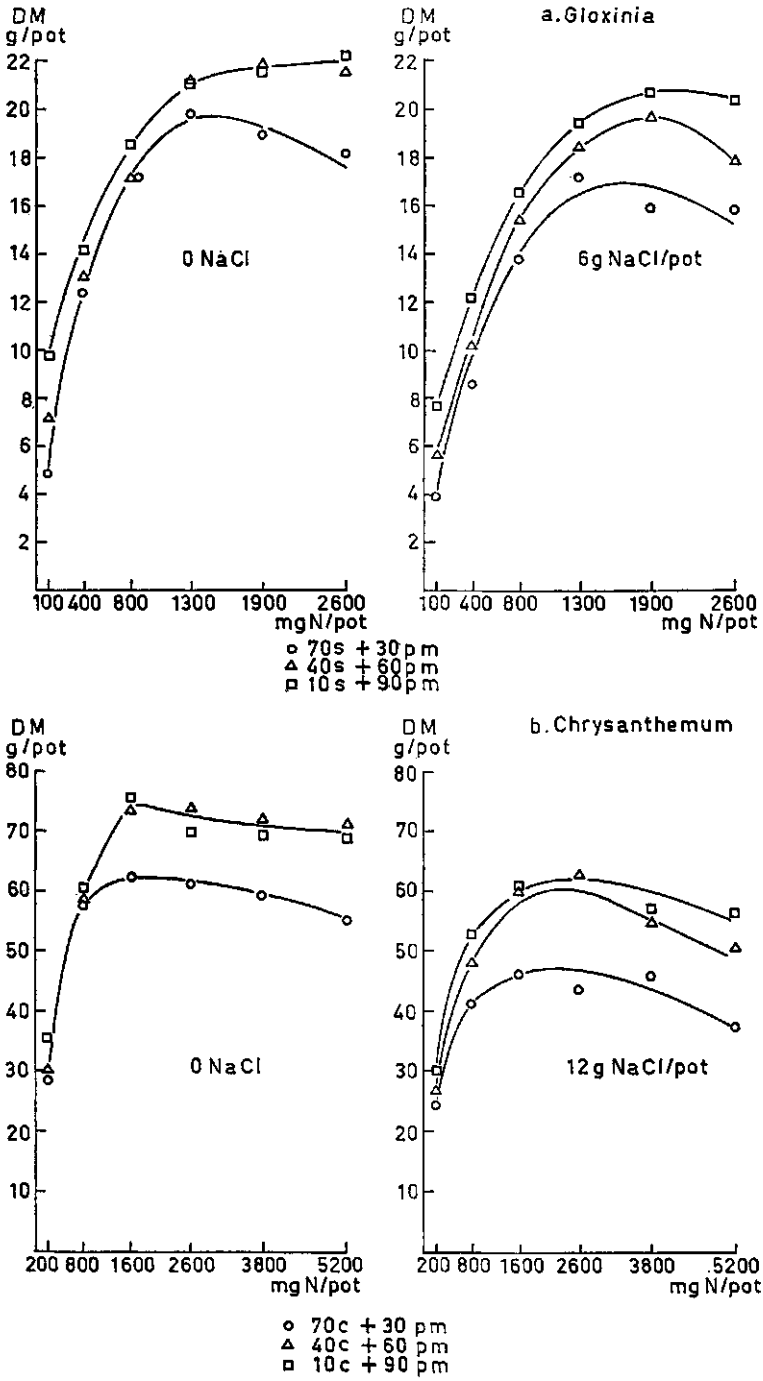
### 5.3 Nitrogen rate and yield of dry matter

In Fig. 30, yield of both species have been plotted against N rate at the two NaCl levels. For gloxinia, the group of curves is in principle like those in trials 1 and 2. The mutual arrangement and the individual positions of these curves conform with what can be expected from a negative effect of $EC_e$ and from the shapes of the corresponding $EC_e$ lines in Fig. 28a. The differences in shape and position of the curves for the various combinations of substrate ($S$) and NaCl ($Z$) are, therefore, caused by differences in $EC_e$. They are also responsible for the increasing divergence with N rate of the curves, which divergence is further spread by NaCl.

A new aspect brought out by this pattern is that the influence of substrate type on the effect of N rate on yield – through the relationship between type of substrate and $EC_e$ – can be reduced to an $EC_e$ effect.

This influence of substrate effect works in two ways. First, in the suboptimal

Fig. 30. Relationship between nitrogen rate and yield of dry matter as affected by nature of substrate at two NaCl levels.



range, the favourable effect of N is intensified by a rising peat content of the substrate. Secondly, above the optimum the detrimental effect of nitrogen excess is weakened by a rising peat content. Both aspects are well illustrated by the three substrate curves of the NaCl series in Fig .30a. As can be seen again in Fig. 28a, this course agrees with the divergence of the corresponding $EC_e$ lines. The foregoing also sheds more light on the important nitrogen-substrate interaction mentioned in the Introduction for trials with cyclamen and gloxinia (Arnold Bik, 1962). The presumption expressed there that this interaction can be interpreted as a matter of moisture supply finds support in the present results with gloxinia.

In the curves of Fig. 30a, at the series without NaCl, in the higher N range, the $S_2$ curve has a position almost identical to that of the $S_3$ curve. In view of the proximity between the corresponding $EC_e$ lines in Fig. 28a, this is hardly surprising. Equally expectedly the same curves of the NaCl series do not coincide.

According to the concept that $EC_e$ is the factor governing the N effect, rising $EC_e$ should actually result in lower N optima. In trials 1 and 2, many exceptions were found. For gloxinia, in Trial 3, the rule seems to hold only for the substrate series, and even then separately for both NaCl levels. The optimum for $S_1$ in the series without NaCl lay at 1.3 g N per pot, that for $S_2$ and $S_3$ at about 2.6 g per pot; in the NaCl series, the optima for $S_1$, $S_2$, and $S_3$ lay at 1.3, 1.9, and 2.6 g N per pot, respectively.

The average relative reductions in yield for $S_1$ and $S_2$ in comparison with average yield of $S_3$ for both NaCl levels were as follows:

| | |
|---|---|
| without NaCl, | 15.0 and 5.6%, respectively |
| with NaCl, | 22.8 and 10.5%, respectively. |

In agreement with the stronger divergence of the $EC_e$ lines in Fig. 28a, the yield reduction caused by NaCl seemed to increase as peat was decreased in the substrate. The interaction of salt with substrate for $EC_e$ also explains why the interaction between N and substrate was more pronounced in the NaCl series than in the series without NaCl.

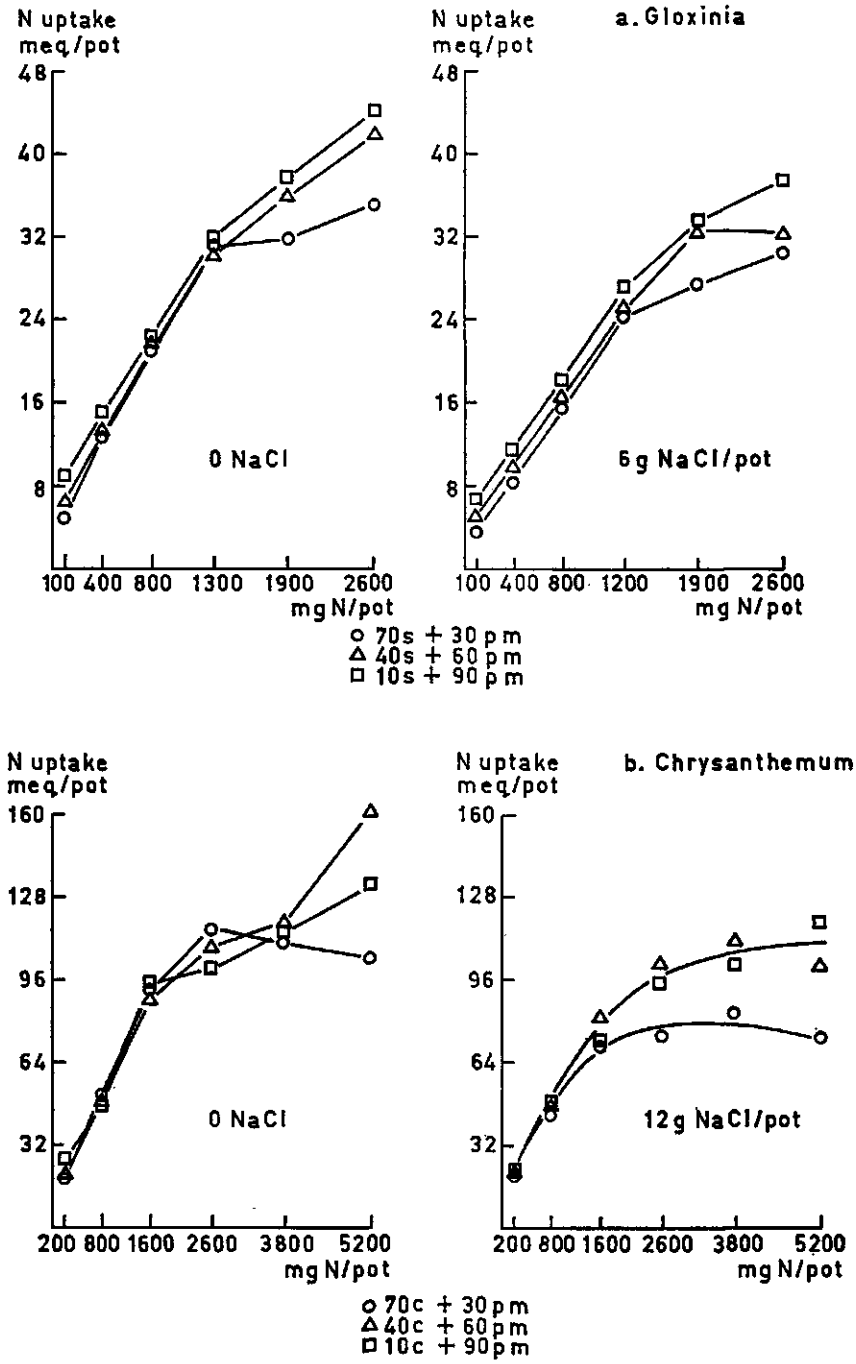
Another facet of the same interaction between NaCl and substrate fell into place when the average reduction in yield of the NaCl series relative to the average yield of the series without NaCl were compared for the three substrates. These reductions were 18.3, 14.7, and 10% for $S_1$, $S_2$, and $S_3$, respectively. In agreement with the larger distance between the $EC_e$ lines in Fig. 28a, the reduction in yield caused by addition of NaCl seemed to be accentuated by low contents of peat in the substrate.

The nitrogen rate-yield curves of chrysanthemum (Fig. 30b) largely show the same characteristics, although less regularly so than those of gloxinia. They also show a reasonable close agreement with the corresponding $EC_e$ lines (Fig. 28b).

Thus, the concept that the electrolyte concentration of the soil solution is the physico-chemical basis for the interactions between N and substrate and between salt and substrate is supported by the results with chrysanthemum as well.

The average yield depressions for $S_1$ and $S_2$ relative to the average yield of $S_3$ were as follows:

Fig. 31. Relationship between nitrogen rate and nitrogen uptake as affected by substrate at two NaCl levels.



without NaCl, 15.5 and 0%, respectively
with NaCl, 25.4 and 5.2%, respectively.

The average yield depressions for the NaCl series relative to the average yield for the series without NaCl were 26.5, 20.2, and 15.7%, for $S_1$, $S_2$, and $S_3$, respectively.

The results in both series show that the two facets of the interaction between NaCl and substrate reported for gloxinia, were also present for chrysanthemum. The yield depressions were larger for chrysanthemum than for gloxinia. In view of results of trials 1 and 2, the opposite was expected. The deviant results must be attributed to the considerably larger contribution of the matric suction because of the typical form of the pF curve resulting from the much larger water consumption of chrysanthemum. Later on, indications were obtained that the plants growing on $S_1$ did develop on a slightly drier substrate than did the plants growing on $S_2$ and $S_3$. The yield reduction of $S_1$ relative to $S_3$, therefore, exaggerated substrate effect.

The positions and the shapes of the curves of N rate against N uptake (Fig. 31a) for gloxinia can also be related to the corresponding $EC_e$ lines in Fig. 28a. In agreement with the results of trials 1 and 2, the relationship between N uptake and N rate was adversely affected by the rise in electrolyte concentration in the substrate. The sharp decline in the upper portions of the curves found in Trial 2 was here absent because of the usually lower $EC_e$. The substrate effect was relatively small. A noticeable difference in uptake between $S_1$ and $S_2$ was found between 1.3 and 2.6 g N per pot.

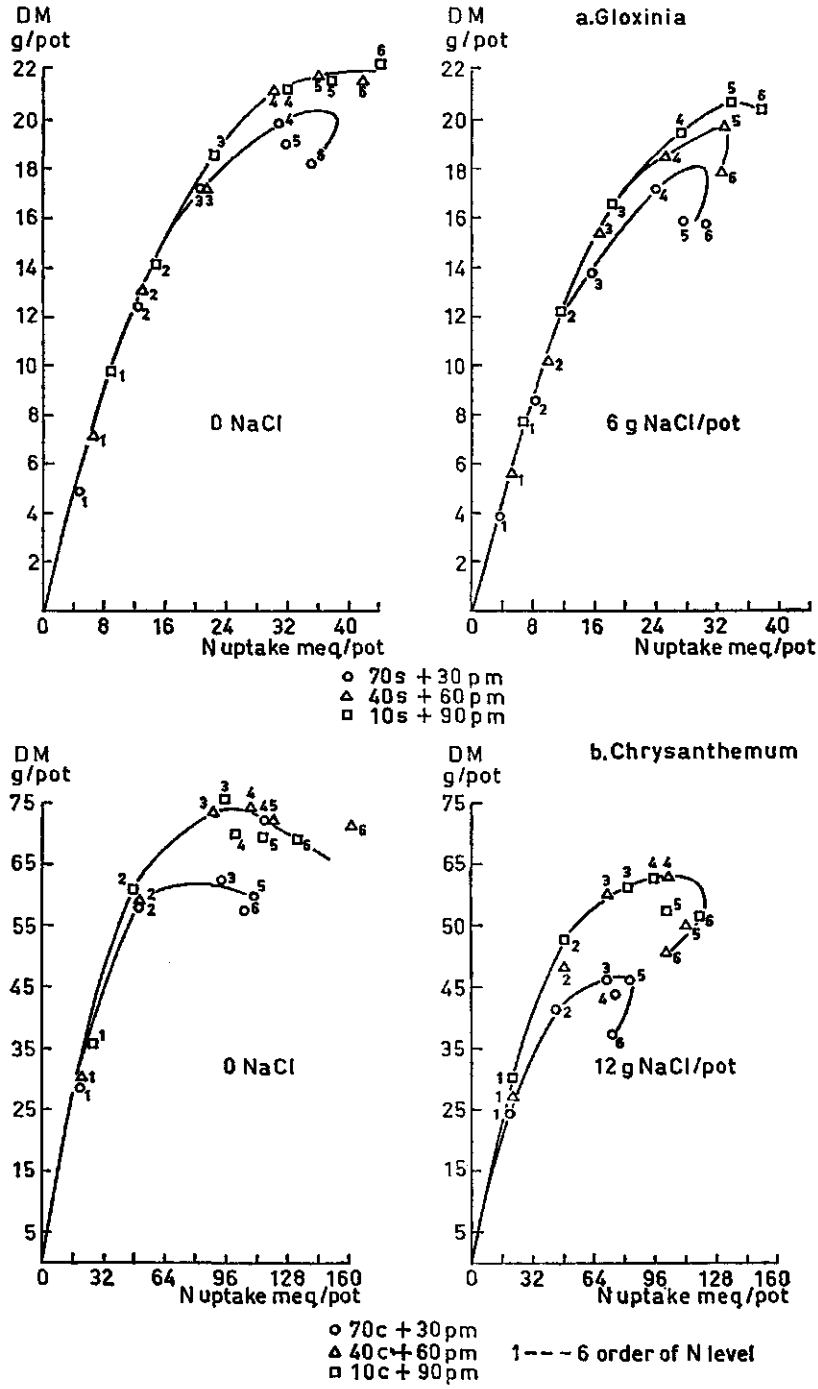
The curves of N rate against N uptake are much more irregular for chrysanthemum than for gloxinia (Fig. 31b). $EC_e$ had a suppressive influence again in the NaCl series. In fact, the $S_1$ curve deviated much earlier from a straight course than $S_2$ and $S_3$.

For gloxinia (Fig. 32a) and chrysanthemum (Fig 32b), the curves of N uptake against yield were characteristic of a situation in which $EC_e$ forms a limiting factor (sections 3.2 and 4.2). Decreasing the peat in the substrate, much like adding NaCl, depressed yield relative to N uptake. Therefore, the influence of substrate on the relationship between N rate and yield (mentioned in the Introduction), as well as the effect of salt on this relationship, seem to depend on the efficiency with which the plant utilizes N. The lowered utilization at rising electrolyte concentrations in the medium can be attributed to a deterioration in the water balance of the plant. Barnette & Naylor (1966) found with bermuda grass *(Cynodon dactylon)* that drought decreased protein synthesis and percentage protein in the leaves. Earlier, Petrie & Wood (1938), and Kemble & McPherson (1954) had found, that proteolysis and interruption of protein synthesis resulted from limited water supply of plants.

The $S_2Z_1$ and $S_3Z_1$ curves in Fig. 32a lack the sharp decline at the top, characteristic of all the other curves (sections 3.2 and 4.2). This must be ascribed to the low $EC_e$. As Fig. 28a shows the series have $EC_e$ values below 4.5 mmho per cm. Both curves look like those obtained by de Wit (1953) for oats.

The rather irregular shapes of the curves in the graphs of chrysanthemum may be related to manganese deficiency, undoubtedly caused by the high pH. Although the plants were sprayed with $MnSO_4$, this deficiency and the inadequate control of moisture must have disturbed the results.

Fig. 32. Relationship between nitrogen uptake and yield of dry matter as affected by substrate at two NaCl levels.



## 5.4 Salinity and yield of dry matter

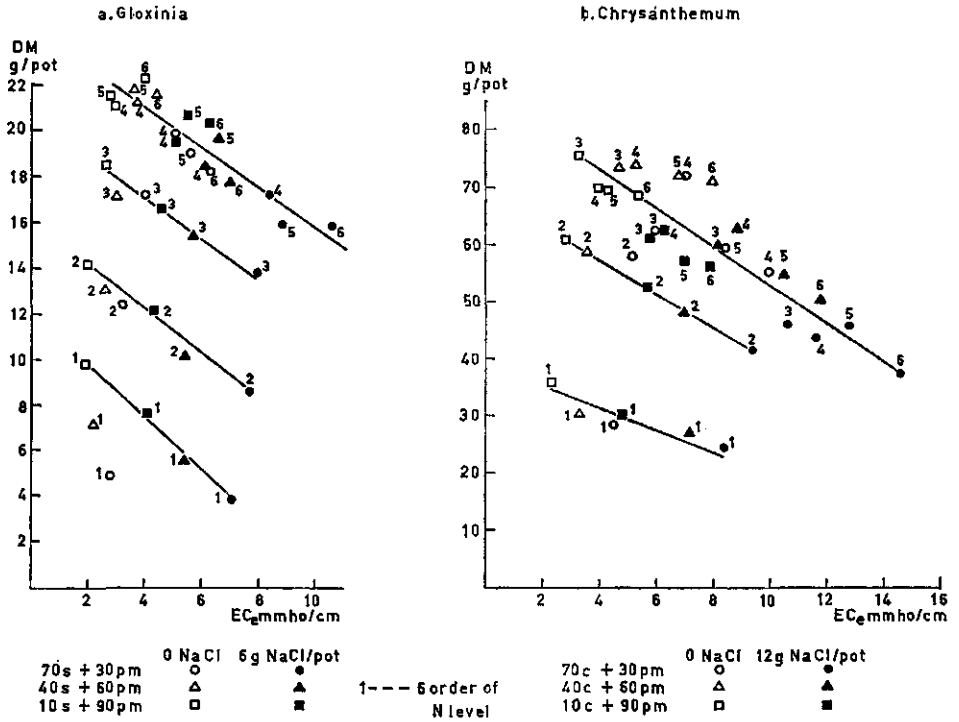
Fig. 33 shows the relationship between yield and $EC_e$ for gloxinia and chrysanthemum.

As in trials 1 and 2, there are two main influences: $EC_e$ and N rate. For gloxinia, the points of the *SZ* combinations for the first, second, and third N rate, respectively, are reasonably close to a straight line. Above the third N rate, the dependence on N rate becomes less clear. Now the points of the *NSZ* combinations are grouped around a straight line running almost parallel to the lines just mentioned. Almost the same situation can be found for chrysanthemum, except that the dependence of yields and $EC_e$ on N rate is restricted to the first and second N level. Furthermore, above the second N level, the *NSZ* points deviate more from a straight line than for gloxinia.

These results indicate that the relationship between yield and $EC_e$ was almost independent of the substrate type. In other words, the substrate effect could be largely reduced to $EC_e$ so that $EC_e$ is a useful and reasonably substrate-independent criterion of salinity. In practice, the objections to $EC_e$ as a substrate-independent criterion of salinity (Section 5.2) clearly are unimportant.

The limit of $EC_e$, above which, with ample N supply, yield started to decline, was

Fig. 33. Relationship between $EC_e$ and yield of dry matter as affected by nitrogen rate and substrate.



for gloxinia 4 mmho per cm and for chrysanthemum between 6 and 8 mmho per cm.

By covariance analysis of the results, the contribution of $EC_e$ to the substrate effect was estimated. After allowing for $EC_e$, substrate variance was reduced to 10.2% of the original value for gloxinia, and to 26.2% for chrysanthemum. In these calculations, the influence of N rate was ignored. $EC_e$, therefore, accounted for 90% of the substrate variance for gloxinia, and for about 74% for chrysanthemum. The reason for the lower value for chrysanthemum than for gloxinia, has already been discussed.

The high degree to which the substrate effect can be ascribed to $EC_e$ with gloxinia can also be demonstrated by adjusting the curves of N rate against yield of Fig. 30a to an $EC_e$ of 0 mmho per cm. As in Trial 1 (Fig. 7), they ought then to merge into one curve. The reference factor used, $dP/dEC_e$, being the reduction in yield per unit rise in $EC_e$, was derived from the linear relationship between yield reduction and $EC_e$ rise caused by adding NaCl. The factor amounted to 0.75 g $mmho^{-1}$ cm. In Fig. 34, the result of this modification matched expectation reasonably well. It therefore supports the evidence that the substrate effect can be fully or largely identified with an $EC_e$ effect, as long as pF is sufficiently constant and soil aeration is adequate.

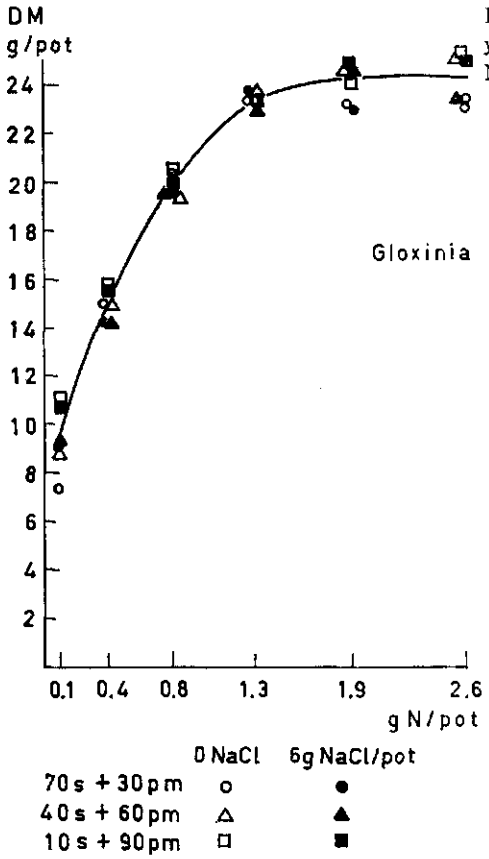



Fig. 34. Relationship between nitrogen rate and yield of dry matter as affected by substrate and NaCl level after adjustment to EC = 0.

The satisfactory results obtained with the reference factor based on NaCl level, emphasizes the importance of the osmotic component of salinity. However, since for gloxinia the total cations in the plant seemed to be a practically linear function of $EC_e$ (figs 10 and 24a), salt accumulation must also be considered a factor causing damage. This aspect of salinity has been examined by van den Berg (1952) and Greenway (1962).

### 5.5 Ions in substrate extracts

The chemical composition of the saturation extracts is shown in figs 35 and 36.

*Influence of substrate* As expected, most cations and anions and soluble inorganic N in SE decreased as peat contents of the substrates increased. $H_2PO_4^-$ was exceptional. This anion increased with peat content, presumably because of mobilization by complex-forming humic acids.

Furthermore, an influence of the clay in the substrates was distinguishable. For chrysanthemum, the remarkable rise of $Ca^{2+}$ with clay content indicates that the adsorption complex was highly saturated with $Ca^{2+}$, because of its high $CaCO_3$ content which also caused the high pH of all three substrates. Another remarkable feature was the increase of $K^+$ in the substrate with peat content for chrysanthemum, presumably because of preferential $K^+$ adsorption by clay.

The three substrates of gloxinia, in which sand constituted the mineral component, were much lower in pH. There pH rose with peat content because the $CaCO_3$ had been added not according to substrate volume, but to volume of peat moss. As peat moss in the substrate decreased, the amount of $CaCO_3$ per unit volume of substrate decreased, accentuating the decrease in pH caused by nitrification of $NH_4^+$. The increase in $NH_4^+$ with decreasing peat content for gloxinia must be attributed to the lower pH. With the much higher pH values for chrysanthemum, $NH_4^+$ was not present in the substrate.

*Influence of NaCl* As expected, $Na^+$ and $Cl^-$ in the substrate increased with NaCl level. These increases were accentuated with decreasing peat content. For $S_1$ and $S_2$ of gloxinia, $NH_4^+$ also rose with NaCl. For $S_1$ and $S_2$ of chrysanthemum $Ca^{2+}$ was on average markedly higher with NaCl than without it. The same was true of $Mg^{2+}$, especially with $S_3$. As the peat moss was rich in $Mg^{2+}$, the only surprise was that the rise in $Mg^{2+}$ after addition of NaCl did not occur for gloxinia. For $S_1$ and $S_2$ of chrysanthemum, $NO_3^-$ was appreciably higher with NaCl than without it, so that the clay must have contained a considerable amount of exchangeable $NH_4^+$.

*Influence of N rate* Because of rising moisture capacity, the increases in soluble inorganic N and in $NO_3^-$ in the substrate resulting from N application were depressed with increasing peat content of the substrate. With increasing N rate, $K^+$, $Mg^{2+}$ and

Fig. 35. $NH_4^+$, $K^+$, $Na^+$, $Ca^{2+}$, and $Mg^{2+}$ in the saturation extract as affected by nitrogen rate and substrate at two NaCl levels.

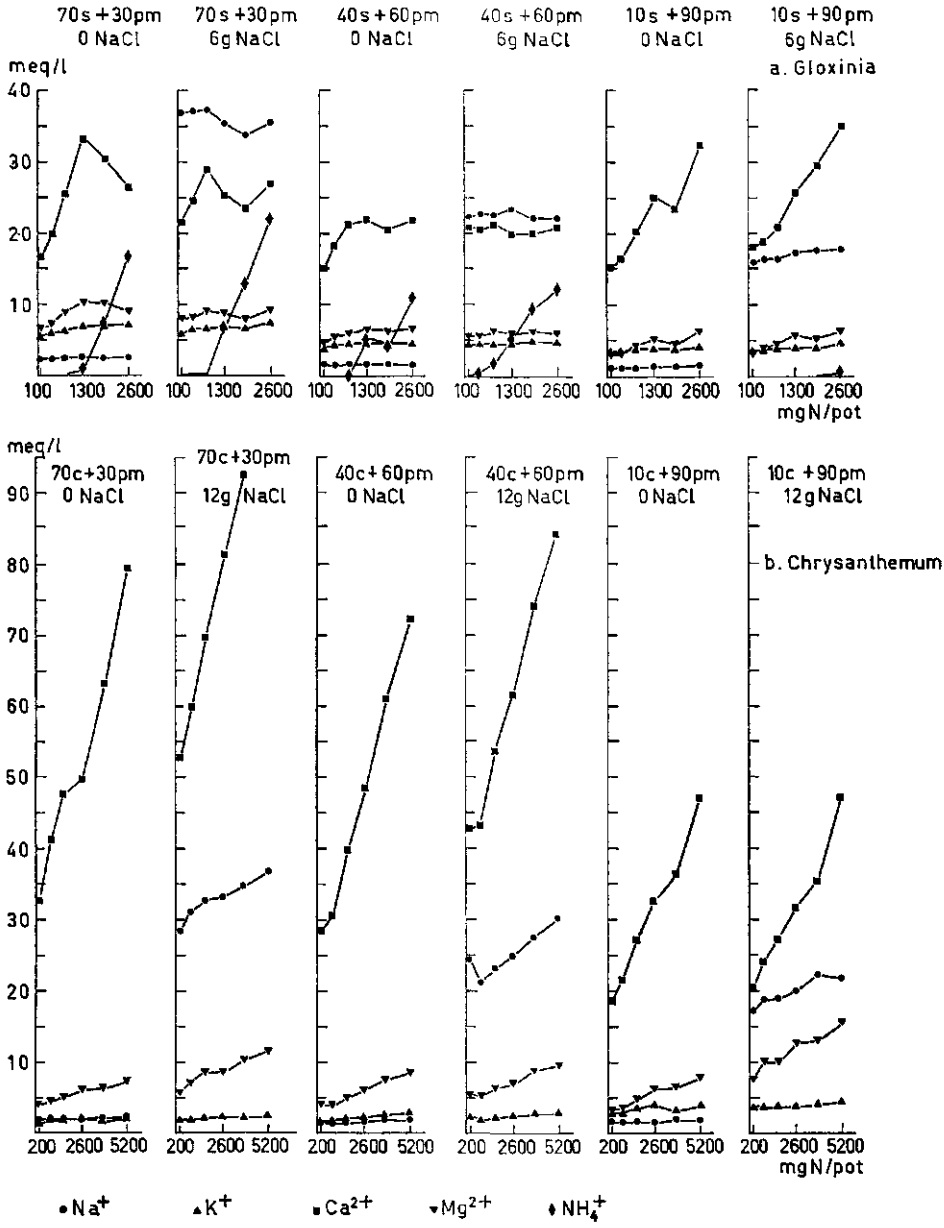
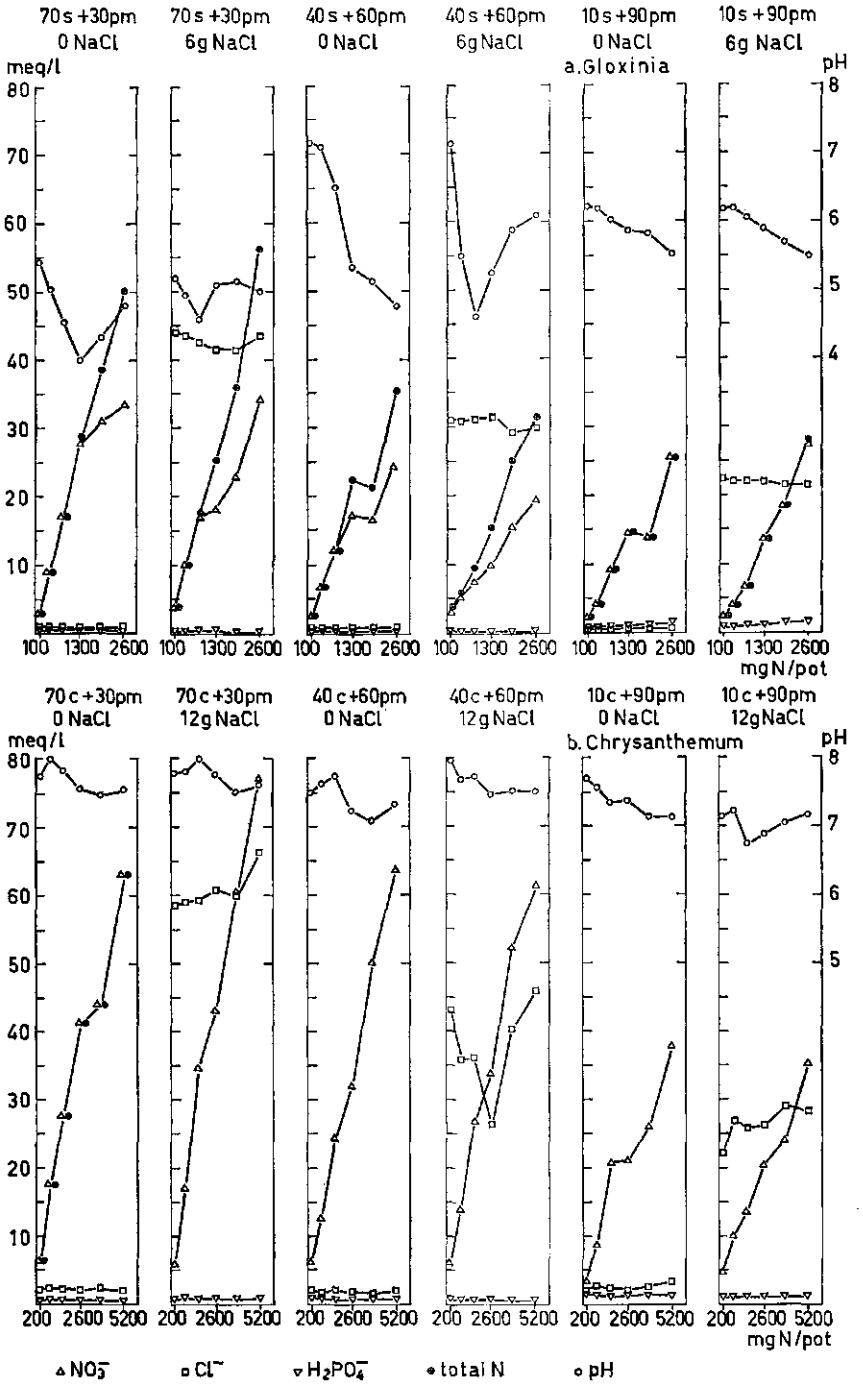


Fig. 36. $NO_3^-$, $Cl^-$, $H_2PO_4^-$, soluble inorganic N ('total N') and pH of the saturation extract as affected by nitrogen rate and substrate at two NaCl levels.



$Ca^{2+}$ in the substrate also increased. Especially the increase in $Ca^{2+}$ for $S_1$ and $S_2$ of chrysanthemum was striking. Furthermore, for $S_1$ and $S_2$ of gloxinia, $NH_4^+$ rose with higher N rates. For both species, pH seemed to decrease with increasing N rate.

The composition of the SE for the various treatments was comparable with that in Trial 2. In Trial 3, however, there was a bit less $K^+$ than in Trial 2 because of the lower $K^+$ rates in Trial 3 (Section 2.2). On average, $K^+$ was also clearly lower for chrysanthemum than for gloxinia, despite the almost equal rates per litre substrate, presumably because of preferential $K^+$ adsorption by the clay for chrysanthemum.

The much higher average level of $Ca^{2+}$ for chrysanthemum must also be attributed to the $Ca^{2+}$ introduced with the clay.

### 5.6 Ionic balance

The influence of the treatments on ionic balance of both species is shown in figs 37, 38 and 39.

*Influence of substrate* In gloxinia $K^+$, $Na^+$, $Cl^-$, $SO_4^{2-}$ and total inorganic anions A decreased with rising peat content; in chrysanthemum this was so for $K^+$, total cations C, and total N. However, $H_2PO_4^-$ increased for both. Usually, these differences in content paralleled those in the substrate.

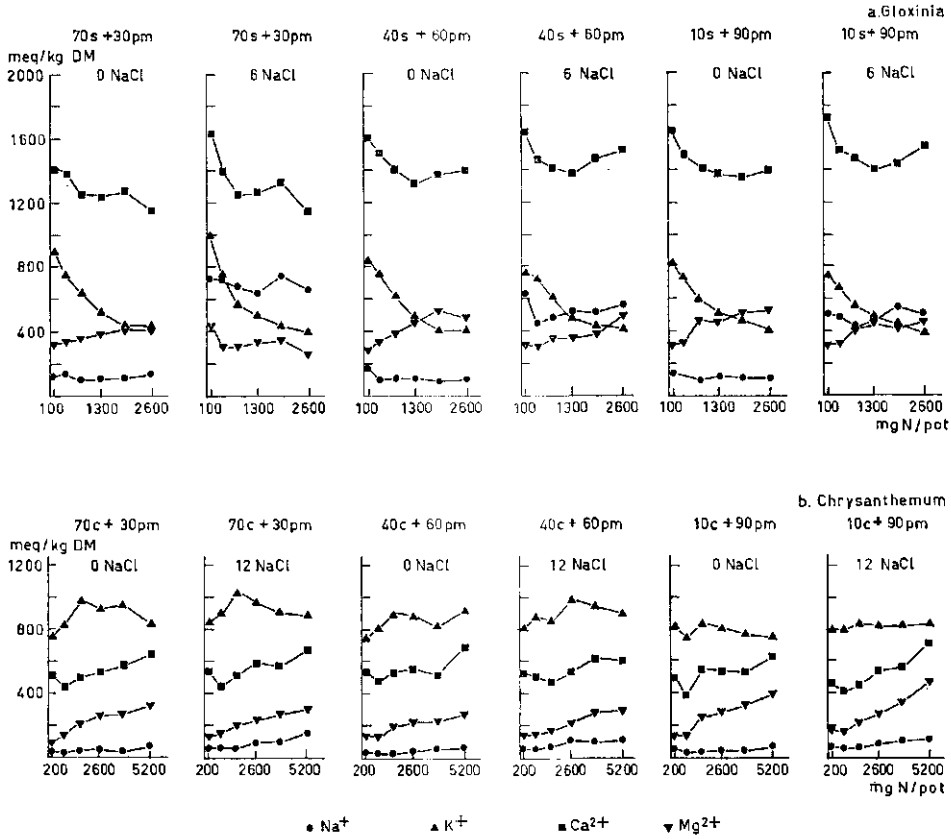
$K^+$ in chrysanthemum was an exception. It decreased with increasing peat content despite an increase in the substrate, perhaps by competition from $Mg^{2+}$. Reason for this assumption is the generally higher level of $Mg^{2+}$ in $S_3$ than in $S_1$ and $S_2$ because of the high content of $Mg^{2+}$ in peat moss.

In gloxinia, $Mg^{2+}$ generally increased with peat content, despite a decrease in $Mg^{2+}$ in the substrate. In both species, $Ca^{2+}$ increased with peat content. The increases in $Mg^{2+}$ and $Ca^{2+}$ caused the increases in total cations C and in organic salts (C-A) in gloxinia.

*Influence of NaCl* The influence of NaCl corresponded with that in Trial 2 (figs 21a, 22a, and 23a) in gloxinia but not in chrysanthemum. Although, both $Na^+$ and $Cl^-$ in chrysanthemum were higher with NaCl than without it, a decrease in other cations after adding NaCl was not found. $Ca^{2+}$ was unaffected; for $S_3$, $Mg^{2+}$ increased and for all three substrates, $K^+$ increased with NaCl. Unexpectedly, $NO_3^-$ and total N in the plant were on average markedly higher with NaCl than without it for all three substrates, perhaps because of $NO_3^-$ changes in the substrate (Fig. 36b). As $NO_3^-$ in the substrate was higher with NaCl than without it, at least for $S_1$ and $S_2$, the antagonism of $Cl^-$ to $NO_3^-$ uptake must have been outweighed by this $NO_3^-$ increase in the substrate.

The rise of $Na^+$ and $Cl^-$, especially in gloxinia, by addition of NaCl slowed down with increasing peat content.

Fig. 37. $K^+$, $Na^+$, $Ca^{2+}$, and $Mg^{2+}$ contents of the plant as affected by nitrogen rate and substrate at two NaCl levels.

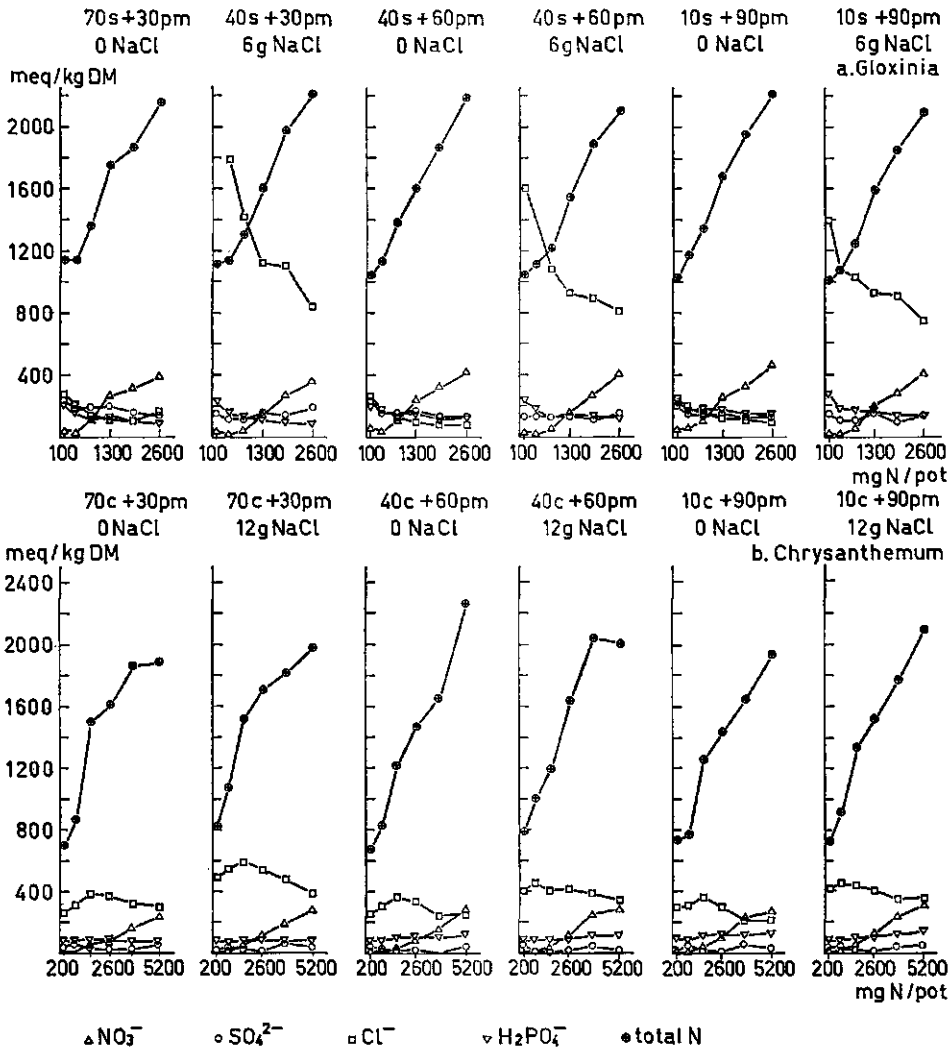



*Influence of N rate* The course of the ionic balance in gloxinia against N rate was comparable with that in Trial 2 (figs 21a, 22a and 23a).

For chrysanthemum, the course, however, showed important deviations primarily due to the different form of N in the substrate. In Trial 2, both $NO_3^-$ and $NH_4^+$ were present; in Trial 3 with chrysanthemum only $NO_3^-$ was present as in Trial 1. There, the compensating cation was $Na^+$; in Trial 3 $Ca^{2+}$, $Mg^{2+}$, $Na^+$ and $K^+$ together, but especially $Ca^{2+}$ and $Mg^{2+}$ functioned as compensating ions (Fig. 35b). This was clearly reflected in the changes in cations in the plant with rising N rate (Fig. 37b). $K^+$ in the plant tended to increase slightly, except with $S_3$. $Ca^{2+}$ and $Mg^{2+}$ increased sharply, $Na^+$ a bit less sharply. The result was a sharp rise in total cations C with increasing N rate. Since the rise in total inorganic anions A was less pronounced, organic salts (C-A) increased.

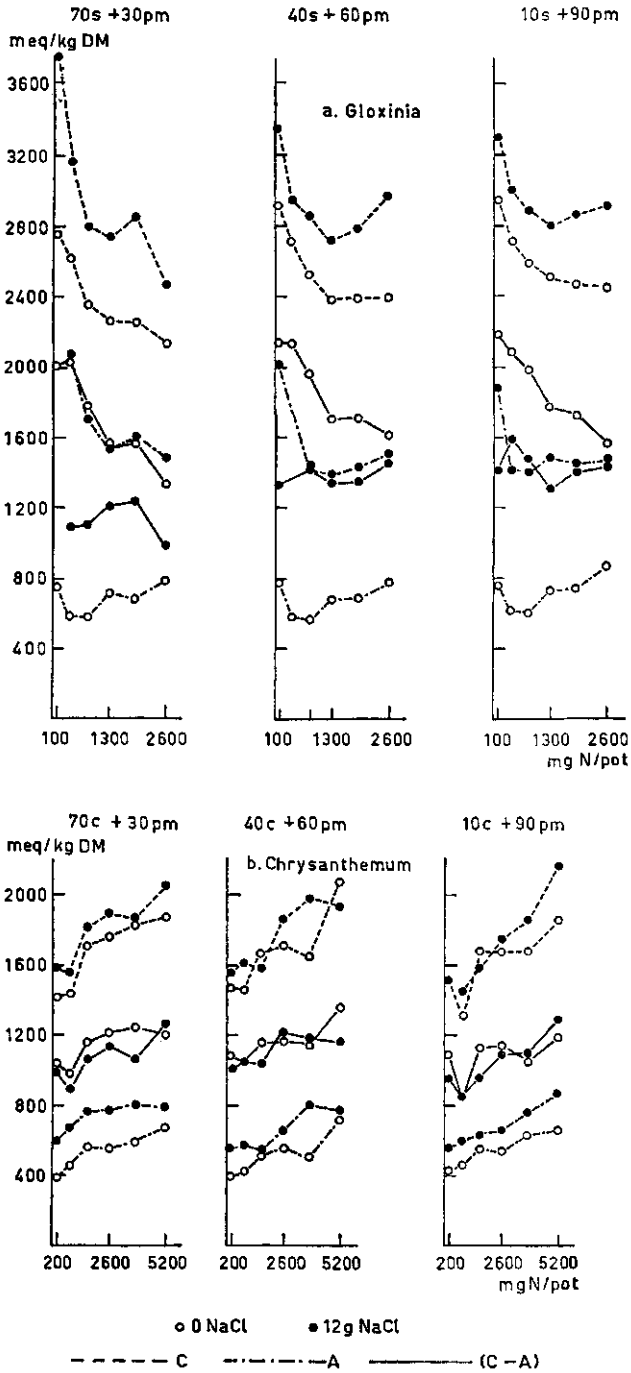
In chrysanthemum $Ca^{2+}$ and $Mg^{2+}$ were remarkably high with the optimum substrate $S_3$ but $K^+$ was remarkably low. Compared with the optimum treatment

Fig. 38. $NO_3^-$, $SO_4^{2-}$, $Cl^-$, $H_2PO_4^-$ and total N contents of the plant as affected by nitrogen rate and substrate at two NaCl levels.




without salt in Trial 2 (Section 4.7), in which incipient $K^+$ deficiency was presumed to occur, $K^+$ in chrysanthemum was even more deficient. This $K^+$ deficiency along with the Mn deficiency (Section 5.3) probably explains why the saturation levels for $NO_3^-$ and total N in chrysanthemum were already reached at 42 and 1260 meq per kg DM, respectively. An indication of $K^+$ deficiency was also obtained by comparing the quotient $K^+/(Ca^{2+} + Mg^{2+})$ of the optimum treatment of chrysanthemum in Trial 1 with that in Trial 3. In Trial 1, this quotient had a value of 2.52, in Trial 3 only 1.04. Despite $K^+$ deficiency, the (C-A) content for the optimum treatment was

Fig. 39. Total cations C, total inorganic anions A, and organic salts (C-A) in the plant as affected by nitrogen rate and substrate at two NaCl levels.



1127 meq per kg DM, a normal value for chrysanthemum. Compared with the optimum treatment of Trial 1 (Section 3.5), this value comprises higher contents of $Ca^{2+}$ and $Mg^{2+}$ and a much lower content of $NO_3^-$.

For the optimum treatment of gloxinia in Trial 3, the (C-A) content was 1573 meq per kg DM. This value was almost the same as in Trial 2 (Section 4.7). The corresponding value for total N content in the plant was 2228 meq per kg DM, a value according with that of the optimum treatment in Trial 2.

## 5.7 Conclusions

The influence of substrate on $EC_e$ depended entirely on the inverse proportionality between moisture capacity and $EC_e$. Accordingly, the increase in $EC_e$ per unit salt diminished with increasing peat content of the substrate.

The increase in N effect with peat content of the substrate was in fact an $EC_e$ effect like that in trials 1 and 2. Likewise, the reduction in effect of NaCl or of excess N with increasing peat content depended on the relationship between $EC_e$ and peat content of the substrate.

The relationship between yield of dry matter and $EC_e$ was almost independent of substrate. The usefulness of $EC_e$ as a criterion of salinity, even for different types of substrate, was thus confirmed.

From the finding that for gloxinia, after adjusting $EC_e$ to zero, only one typical yield curve remained, the conclusion can again be drawn that the substrate effect is largely an $EC_e$ effect. Moreover, this result indicated the importance of the osmotic component of salinity.

As can be seen for gloxinia, increasing peat contents of the substrate tended to decrease ion contents of the plant because of lower ion contents in the substrate.

The ionic balance of the plant, again, proved to be dependent on the form of N present in the substrate.

# 6 Practical applications

The trials have clearly shown the influence of osmotic suction of substrate moisture ($S_s$) on the interaction between N rate and vegetative growth. For this interaction, it is of little consequence to know which factors contributed to $S_s$.

The limitation of the nitrogen effect by $S_s$ – and hence, also of growth-rate – is mainly felt through its influence on the suction tension in the leaf $S_l$ or diffusion pressure deficit (DPD). $S_l$ is, therefore, the most valuable criterion of limitation by $S_s$, while percentage reduction in transpiration can be derived to indicate size of $S_l$.

A good indication of the dependence of $S_l$ on certain environmental factors, including $S_s$ and $S_m$ (matric suction), can be obtained from the following equation for water absorption ($W$) by plants as presented by Bierhuizen (1968):

$$W = \frac{S_l - S_t}{r_x + r_r + r_s} \qquad (2)$$

in which $r_x$, $r_r$ and $r_s$ are resistances to water movement in the xylem, the root, and the substrate, respectively. $S_t$ is total suction tension of the substrate, being the sum of $S_m$ and $S_s$. Bierhuizen's version of Eq. 2 did not specify the soil suction in the numerator; I selected $S_t$ because of the high content of electrolytes from fertilizers in greenhouse soils. Eq. 2 can readily be converted into the following relationship for $S_l$:

$$S_l = W(r_x + r_r + r_s) + S_t \qquad (3)^2$$

At equilibrium $S_l$ is constant because influx of water into the leaf equals efflux; $W$ then can be looked upon as transpiration rate. As such, $W$ is the sum of the weather factors light intensity, air temperature, wind velocity and relative air humidity.

Eq. 3 shows that in greenhouses, measures should be directed towards maintenance of the correct balance between as low as possible an $S_s$ value and as near optimum as possible a nutrient composition of the substrate solution. For this, the following practical measures are possible:

1. The substrate should have as high a moisture capacity as possible. Substrates rich in peat moss or 'garden peat', such as the mixture of 10% sand and 90% peat moss used for gloxinia in Trial 3 fulfil this requirement.
2. While the plant is growing most actively, the substrate should be as moist as possible

2. A similar relationship was also developed by Gardner & Ehlig (1962) and adapted by Rijtema (1965).

without endangering the air supply to the roots. In practice, moisture can be raised until air is 20% (v/v) of the soil. For sand and peat (10:90) substrate, this optimum corresponds to pF 1.4 (Fig. 29a). On days with high evapotranspiration, water may have to be added more than once a day. Automatic sprinklers controlled by a tensiometer would be ideal.

3. The types and rates of fertilizer added should be as effective as possible. They should be adapted to the specific requirement of the crop and the addition of superfluous electrolytes should be avoided.

4. Frequent application of dilute nutrient solutions ('liquid feeding') should be considered, preferably by machine or by irrigation systems. To ensure rapid growth, large single dressings with dry fertilizers should be avoided.

5. A rise in $S_s$ by application of irrigation water rich in minerals such as NaCl should be avoided.

For pot plants the measures are all the more necessary because of the restricted soil volume. To keep down $S_s$, further measures are appropriate for pot plants:

6. Plastic pots should replace clay pots, in view of the water loss through the porous clay pots (van der Zwaard, 1966).

7. Pot size should be adjusted to the normal leaf area of the plant. This would also simplify the proper cultivation of such plants in living rooms.

8. Water should be extremely low in salts, in particular NaCl. Use of water with an NaCl content considered fairly low (100-150 mg $Cl^-$ per litre) for plants in open soil, can be harmful for pot plants because of this salt's high osmotic coefficient (Robinson & Stokes, 1959), because of the hazard of accumulation with frequent watering and because the roots cannot escape from the unfavourable substrate. If surface, tap, or well water sufficiently low in NaCl is not available, pot plants should be watered with collected rainwater or demineralized water, perhaps mixed with other water of poorer quality.

9. To avoid salt accumulating in the surface layer by capillary rise, the substrate in the pots should be flushed at regular intervals. The pot should therefore not be filled to the brim with substrate.

Ideally the substrate solution should be controlled by percolating a nutrient solution continuously through the substrate. Such a system would also ensure a value of $S_m$ (matric suction) as low as possible. The limiting factor in such a system would, however, be the air supply, which in turn is dependent on the substrate composition.

Eq. 3 also shows that any possible harmful effect of $S_s$ can be compensated for by the other factors determining $S_l$. This suggests the following further measures:

10. $S_m$ should be kept down by Measure 2. The shape of the pF curve affects the daily fluctuation in pF resulting from moisture loss by evaporation. Hence, sand rather than clay should be used as the mineral material to be mixed with peat moss or 'garden peat' (Fig. 29).

11. Of the resistance factors in Eq. 3, $r_s$ is kept down by minimizing $S_m$ because it

increases exponentially with $S_m$ (Rijtema, 1965). Above pF 2.5, it increases even more rapidly. Root resistance $r_r$ increases sharply with imperfect aeration, with either lack of $O_2$ or accumulation of $CO_2$ in the root substrate (Slatyer, 1967). Avoidance of this undesirable situation is incorporated in Measure 2. The root resistance $r_r$ increases sharply with falling temperatures in the substrate (Brouwer & van Vliet, 1960). The substrate of physiologically active plants must therefore be kept at optimum temperature. Warming of irrigation water has already come into practice. With roses, forced after wintering in the cold, better results would be obtained by soil heating.
12. In the control of climatic factors, there is a dilemma, at least in summer: maintenance of water balance at the expense of photosynthesis, or maintenance of photosynthetic rate at the expense of water balance. For mesophytes, to which belong many pot plants, the problem does not arise, since the light intensity mostly is not limiting for photosynthesis. The most important measure here is the shading of plants against direct light. If they are not flowering and are not susceptible to fungal diseases, an extra sprinkling with water during bright sunshine can regulate both temperature and relative humidity. Since light intensity is practically always limiting for heliophytes in greenhouses (Bierhuizen, 1960), they should not be shaded against sunlight. The best solution for them would be air conditioning but this measure is still not economic (Bierhuizen, 1968). Effort could be directed towards regulating leaf temperature. In direct sunlight, the leaf can be far warmer than surrounding air, raising vapour-pressure deficit and sharply increasing transpiration. Cooling the leaf by wetting it with sprinklers is, according to Andersen (1969), the best way of avoiding excessive transpiration in bright sunshine. The advantage of his method is that photosynthetic rate is maintained.

Considering the specific ion effects mentioned before, the following measure should be borne in mind in manuring plants in pots or on benches:
13. Because of strong competition for absorption between $NH_4^+$ and $K^+$, $Ca^{2+}$, and $Mg^{2+}$, it is necessary, when using $NH_4^+$ fertilizers, to ensure a sufficient supply of $CaCO_3$ to the substrate. This $CaCO_3$ is needed not only to optimize pH but also to ensure the nitrification of $NH_4^+$. For the same reason, NaCl must be excluded from the substrate, a measure already recommended for other reasons.

# Summary

The study was on the harmful effect of salinity on N utilization in the flower crops gloxinia (a salt-sensitive mesophytic semi-shade plant) and chrysanthemum (a salt-tolerant sun plant). For solid substrates (trials 2 and 3) the specific conductivity of the saturation extract ($EC_e$ in mmho per cm at 25 °C) was used as measure of salinity (Richards *et al.*, 1954). In water culture (Trial 1), the specific conductivity of the nutrient solution (EC in mmho per cm at 25 °C) was used. The specific conductivity of the substrate also indicated osmotic suction $S_s$.

In solid substrates, the availability of water is dependent not only on $S_s$ but also on the matric suction $S_m$. To eliminate the influence of $S_m$, attempts were made to keep it constant.

In Trial 1, the yield of dry matter was studied at 4 nitrate concentrations and with 4 $EC_e$ values, the latter obtained by adding NaCl. Increases in $EC_e$ depressed yield increment per unit nitrogen. This reduction in N effect, being much larger for gloxinia than for chrysanthemum, represented a decrease in N utilization, attributable to a disturbance in nitrogen metabolism at rising suction tension ($S_l$ or DPD) in the leaf (Barnette & Naylor, 1966). This rise in $S_l$ with EC of the medium could be deduced from a decrease in percentage transpiration. Brouwer (1963) has shown that $S_l$ increases with NaCl concentration.

There was a practically linear negative relationship between yield and EC. After extrapolating EC to zero, the nitrogen curves coincided into one typical yield curve. Therefore the osmotic factor seemed dominant.

The large influence of NaCl on ionic balance in the plant showed that specific ion effects could not be neglected. Notable specific effects were for the cations, the antagonism of $Na^+$ to uptake of $K^+$, $Ca^{2+}$ and $Mg^{2+}$, and for the anions the antagonism of $Cl^-$ to $NO_3^-$. The organic salts (C-A) decreased appreciably with rising $Cl^-$ concentrations in the medium.

The two plants deviated in pattern of ion uptake. Chrysanthemum selectively absorbed $K^+$ and could to some degree control the entry of ions. Gloxinia showed no selectivity and could not prevent the entry of ions. This difference must partly account for the difference in salt tolerance between the species. Certainly some investigators (Bernstein & Ayers, 1953; Sutcliffe, 1962) looked upon selective uptake of $K^+$ as an indication of a species' salt tolerance.

Since salinity depresses water balance of plant through $S_s$, salt tolerance must also depend on the genetically determined osmotic characteristics of the plant. According

to Slatyer (1963) the osmotic pressure of mesophytic shade plants (e.g. gloxinia), is about 5 bar, for most crop plants (e.g. tomato and chrysanthemum) between 10 and 20 bar, and for halophytes (e.g. *Atriplex nummularia*) even 72 bar.

In Trial 2, on a solid substrate, the nitrogen effect was depressed by four different types of salt, as by NaCl in Trial 1. The depression seemed to be almost proportional to the increase in $EC_e$ caused by addition of salt. Only $K_2SO_4$ depressed yield of gloxinia more than could be explained by the increase in $EC_e$ caused by addition of the salt. As in Trial 1, the depression of the N effect by any salt could be attributed to a decreased N utilization.

The almost linear negative relationship between yield and $EC_e$ was clearly influenced by the N rate. At optimum N rate, the reduction in yield by $EC_e$ was much larger than at the lowest N rate. In assessing damage by salinity, the nitrogen status of the crop must be considered. Specific ion effects could be detected by correction for $EC_e$. $K_2SO_4$ exerted the largest specific harmful effect on growth of gloxinia. Chrysanthemum, which was usually much less affected by specific salt injury, suffered mostly from the specific effect of $Na_2SO_4$. Extremely important for the ionic balance in the plant was the increase in proportion of N as $NH_4^+$ with N rate (here given as ammonium nitrate). $NH_4^+$ competes strongly with other cations but according to van Tuil (1965) contributes much less than $NO_3^-$ to the content of organic salts. Increases in $NH_4^+$ in the substrate with N rate therefore accounted for the decreases in organic salts in almost all series.

For gloxinia, $K^+$ competed markedly with uptake of $Ca^{2+}$, for $K_2SO_4$ even more so than for KCl. The specific harmfulness of $K_2SO_4$ for growth was therefore essentially a $Ca^{2+}$ deficiency induced by $K^+$ and $SO_4^{2-}$ together.

The specific harmfulness of $Na_2SO_4$ for chrysanthemum can be ascribed to a decrease in $K^+$ in the plant by competition from $NH_4^+$ and $Na^+$ together.

The difference between species in pattern of ion uptake in Trial 1 was confirmed. Gloxinia seemed to have a high $Ca^{2+}$ requirement but unlike chrysanthemum's selectivity for $K^+$, could not absorb $Ca^{2+}$ selectively. According to van den Berg (1952) the salt tolerance of a crop is often associated with a specific $Ca^{2+}$ requirement. The results of Trial 2 support this opinion.

In Trial 3, the influence of different substrates proved to be based entirely on the inverse proportionality between moisture capacity and $EC_e$.

The shape of the pF curve and the daily water loss by transpiration indicate that, despite of attempts to standardize the moisture level, the influence of matric suction $S_m$ was considerable in the clay-peat substrates of chrysanthemum, although it had been eliminated in the sand-peat substrates of gloxinia.

The increase in N effect with increasing peat content of the substrates proved to be an $EC_e$ effect, as did also the lower negative effect of NaCl or of excess N with increasing peat content. These results also explained the significant interaction between nitrogen and substrate, reported elsewhere for gloxinia and cyclamen (Arnold Bik,

1962). The relationship between yield and $EC_e$ were almost independent of substrate. The usefulness of $EC_e$ as a criterion of salinity in trials with different substrates was thus confirmed.

For gloxinia, the curves of N rate against yield for each of substrate-NaCl series coincided into one typical yield curve when $EC_e$ was adjusted to zero. Therefore at uniform pF and with adequate aeration the substrate effect is actually an $EC_e$ effect so long as the substrate components do not exert any particular effect such as fixation of $K^+$.

Plant composition again showed that the form of N ($NH_4^+$ or $NO_3^-$) and, by its influence on nitrification, the $CaCO_3$ content of the substrate governed the ionic balance of the plant. In gloxinia total cations and total inorganic anions in the plant both decreased with increasing peat content, in accordance with the lower concentrations in the substrate. In chrysanthemum, this relationship was confused by the influence of the clay component of the substrate.

Trial 3 suggests that the effect of salinity was more an osmotic effect than a specific ion effect.

Practical measures for growers are suggested (Chap. 6) to minimize the harmfulness of salinity on the N effect and on the vegetative growth of pot plants and other ornamentals.

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