THESIS

IONIC BALANCE AND GROWTH OF CARNATIONS

Submitted by

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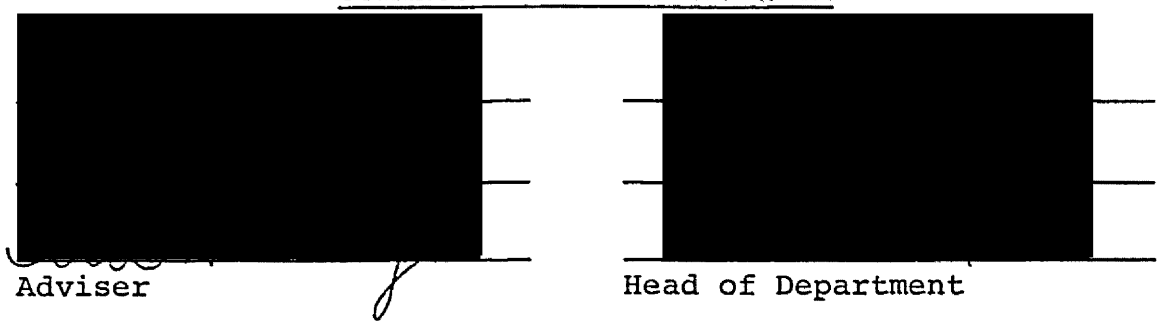

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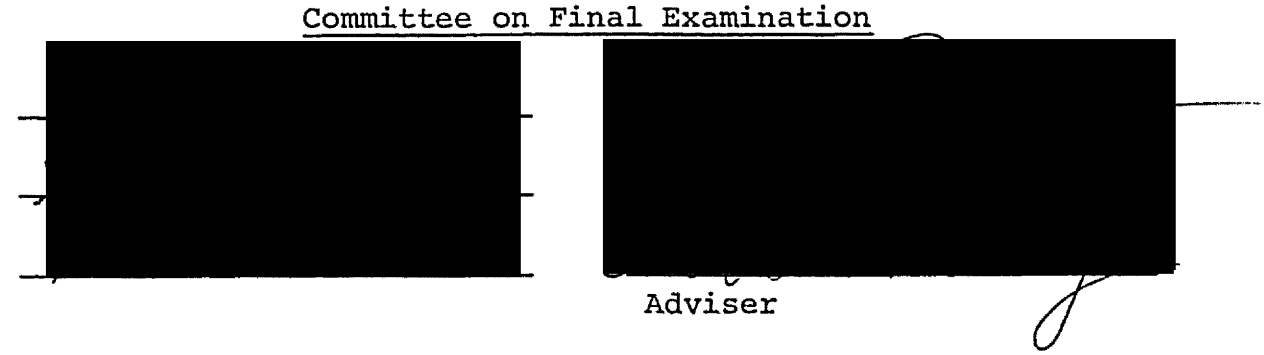

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ABSTRACT OF THESIS

IONIC BALANCE AND GROWTH OF CARNATIONS

A flow chart for diagnosing the nutrient status of carnation, Dianthus caryophyllus, was designed using the data from nutrient culture experiments. Diagnostic values for any specific ion were determined after considering the overall organic acid content, (C-A), of the plant and the level of the other ions in the plant tissue.

The optimum (C-A) content for the carnation was 1700-1900 milligram equivalents per kilogram dry matter. There was a highly significant correlation between increase in (C-A) content and plant yield. Changes in the (C-A) content with few exceptions were mainly due to changes in the cation (C) concentration of the plant tissue.

External factors affected the (C-A) content. Two levels of the external factors, light and CO_2, were studied. There was a significant increase in chloride uptake at the higher light level.

The total cation, magnesium, nitrate, and (C-A) concentrations in the tissue were significantly increased at the higher CO_2 level. Total cation uptake, total (C-A), and yield were increased at the higher CO_2 level. There was a decrease in chloride uptake at the higher CO_2 level.

There were probably three systems operating in cation uptake. 1. When potassium was in good supply, its presence suppressed the uptake of sodium rather effectively. 2. When the potassium supply was deficient, the four ions K, Na, Ca, and Mg competed for uptake. 3. Magnesium and calcium may have been taken up by a separate system in which they competed equally for uptake. Sodium enhanced the uptake of the other cations.

There was no apparent competition among anions for uptake. Sulfate and nitrate remained fairly constant in the plant tissue regardless of nutrient treatment. Phosphate was readily taken up, probably in luxury quantities. The chloride ion apparently was taken up over and above the normal inorganic anion uptake.

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I thank my parents whose moral support and financial aid helped me through this period.

James L. Green

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1 INTRODUCTION AND PERTINENT LITERATURE

1.1 Summary

The difference between the total cation and inorganic anion contents of the tissue, the (C-A) content, in most of the plant species studied was equal to the organic acid content of the plant. The relation between (C-A) content and plant yield was a positive linear relationship. Tissue analyses determining the (C-A) content was indicative of the nutrient status of the plant. For the few species studied, each had a characteristic (C-A) content associated with optimum yield.

The (C-A) content of the leaf tissue was affected by internal ion-uptake systems in the plant and by external environmental factors, e.g. nutrient solution composition, light, and carbon dioxide content of the plant atmosphere.

In this study the normal (C-A) content for the carnation plant and the qualitative and quantitative effects of external and internal factors on (C-A) content are reported. The following literature review provides a background for planning experiments to determine the (C-A) content of additional species.

1.2 Present Status of Carnation Tissue Analysis

1.2.1 Selection of sampling site

The chemical composition of the green leaf varies with the position of the leaf (Vickery, 1961). Prior to conducting comparative studies on the chemical composition of tissue in a given plant species, a sampling site must be standardized. The fifth leaf pair from the base of the main shoot was determined by Nelson and Boodley (1963) to be the best general area for sampling carnation tissue until primary lateral shoots developed seven pairs of leaves. Then the fifth pair of leaves from the terminal end of primary lateral shoots was sampled until flower buds became visible. At that time sampling was shifted to the same leaf pair on secondary lateral shoots. The same procedure was followed for sampling tertiary and quaternary lateral shoots. This procedure minimized physiological variation.

1.2.2 Seasonal effect on ion content

Seasonal variation of ion content of plant tissue in general was reported by Ulrich (1952). Seasonal variation in ion content of greenhouse-grown carnations was reported by Nelson and Boodley (1965). They found that the P and Mg ion concentrations in the tissue were constant throughout a two-year growth period. N, K, and Ca tissue concentrations were lowest during the months of June through August and increased during the winter.

Within the greenhouse environment, the main seasonal variations are probably daily total radiation and carbon dioxide content of the plant atmosphere, and possibly temperature. During the winter months in the greenhouse, the quantity and quality of daylight available was the limiting factor for plant growth, provided the temperature was controlled (Wijk and Businger, 1963). In a study on carnation nutrition, Goldsberry (1963) assumed that a nutrient solution containing a higher total ion concentration was required to avoid apparent deficiency symptoms as the CO_2 level was increased. Swasey, Shank, and Link (1966) over a four-year period found no indication of different fertilizer requirements with different CO_2 levels.

The literature related to the effect of light and carbon dioxide on stomatal movements and the postulated mechanisms of response was reviewed by Heath (1959), Ketellapper (1963), and Raschke (1965). The effects of light and CO_2 on stomatal aperture may be related to the ion content of the plant tissue by their effect on the transpiration rate of the plant. Transpiration rate decreased with partial closure of the stomatal apertures because of increasing CO_2 content of the air (Pallas, 1963). A level of 575 ppm compared to a level of 310 ppm CO_2 reduced the transpiration rate of corn by 23 percent (Zelitch, 1961). Chemical closure of the stomatal apertures also resulted in a reduction of transpiration (Thorn and Minshall, 1964; Zelitch and Waggoner, 1962; Stoddard and Miller, 1962).

The relationship between transpiration and nutrient-ion uptake has not been definitely established. Wide variations in the rate of transpiration had very little effect on the transfer of nutrients to the shoot and leaves of intact plants receiving a solution having a low nutrient-ion concentration. Under conditions of low transpiration and low water loss, the concentration of ions in the transpiration stream exceeded that in the external medium by as much as 100 fold. But the rate of transfer of ions to shoots varied closely with the rate of transpiration when the ion concentration of the external nutrient solution and the nutrient status of the plant were both high. Under these conditions the concentration in the transpiration stream was equal to or less than the concentration in the external nutrient solution (Russell and Shorrocks, 1959).

A high rate of transpiration presumably would favor the establishment of a steeper gradient of mineral-ion concentration across the root. In this way transpiration rates would indirectly influence the rate of movement of salts across the root and from the xylem elements of the roots to the leaves (Meyer, Anderson, and Bohning, 1960).

Lunt, Oertli, and Kohl (1960 a,b) and Wallace (1963) are in agreement that under some conditions transpiration rate can influence the rate of salt movement to leaves.

There may be a differential effect of transpiration on ion uptake with only certain ions being affected. Nitrate and potassium uptake were not influenced by the

transpiration stream movement in intact and decapitated tomato plants (Alberda, 1964). Bowling and Weatherley (1965) postulated that potassium uptake in Ricinus communis was divisible into 2 components: 1. an accumulation by cells of the root unaffected by transpiration, and 2. a passage through the root to the shoot via the vessels linearly related to the water movement of transpiration.

1.2.3 Genetic effect on ion content

Leaf samples from sixteen cultivars of the Sim, Littlefield, and miniature varieties of carnation were analyzed for nutrient content by Nelson and Boodley (1966). They were able to group the cultivars, grown under "similar nutrient regime," according to their nutrient content. The sixteen cultivars were divided into 3 groups corresponding to the 3 main varieties, Sim, Littlefield, and miniature. They concluded that it might be necessary to establish 3 sets of tissue nutrient standards to interpret tissue analyses of these three genetically different groups. Genetic variation must be considered in interpreting tissue analysis (Ulrich, 1952; Wit, Dijkshoorn, and Noggle, 1963).

1.2.4 Effect of nutrient supply on ion content

Because the plant exercises certain selective properties in ion uptake, the question may be raised as to the effect of the chemical composition of the nutrient solution on growth and development of the plant. The term "chemical

composition" comprises 1. concentrations of the component ions, 2. total ionic concentration, and 3. pH. In carnation nutrition, the relative anion proportions in the nutrient solution were important only within wide limits, but the relative cation proportions were very important. The total ion concentration was important within the limits of ± 0.2 atmospheres osmotic pressure. In many cases, the pH of the nutrient solution was important within the limits ± 0.2 pH units (Steiner, 1961).

The use of critical values to diagnose nutrient disorders was not always satisfactory because the range in plant tissue composition associated with deficient and normal plants frequently overlapped. The response of plants to a given nutrient depended upon the level of other nutrients (Watanabe, Lindsay, and Olsen, 1965).

The plant exercises ion-selectivity through the competitive ion uptake systems. Two competitive uptake systems for cations have been detected in grass (Wit, et al., 1963). A four-ion system operated in the uptake of K, Na, Mg, and Ca. A mono-valent ion system operated in the uptake of K and Na. The anions NO_3 and Cl competed during uptake by Gramineae (Wit, et al., 1963).

In addition to the effect of the ion composition of the nutrient solution, the total ion concentration of the solution is important (Steiner, 1961). In regulating plant growth, the total ion concentration was a greater factor in reducing growth of beans than was the effect caused by

specific ions (Magistad, Ayres, Wadleigh, and Gauch, 1943). However, Boyko (1967) found that plants in a physiologically balanced solution could withstand much higher osmotic pressures than plants in a solution of a single salt or an unbalanced solution.

Reduction of plant growth in solutions of high osmotic pressure was reported by Hagan, Vaadia, and Russell (1959), and Browver (1963). Carnation yield was reduced with each addition of soluble salts above a base level (White and Holley, 1957; Lunt, Kohl, and Kofranek, 1956).

1.3 Effect of Ion Content of the Tissue on Plant Growth

Studies involving effects of salt solutions on the ion contents of plant tissue, competitive phenomena among ions, selective ion uptake by growing plants, regulation of the (C-A) content, and yield were conducted by Wit, et al. (1963) on plantain, orchard grass, and rye-grass. Acknowledgment is due Wit, et al. (1963), Tuil (1965), and Noggle (1966), whose publications on nutrient studies of grasses served as a background for planning and interpreting this experiment.

A given plant species has an optimum (C-A) content which is one of the requirements for optimum yield. The (C-A) content is the difference between the total concentration in the plant tissue of the inorganic cations K, Na, Ca, Mg, and the total concentration of the inorganic anions NO_3,

H_2PO_4, SO_4, Cl (Wit et al., 1963). In most plant tissue the (C-A) is an estimate of the organic anion concentration (Tuil, 1965).

In small grains a lower than optimum (C-A) content developed when 1. availability of cations was low, 2. uptake of inorganic anions, e.g. Cl, that stayed as such in the plant was high, and 3. reduction of nitrates in the shoot proceeded at a low rate. Reduction of the (C-A) content was accompanied by a reduction of the growth rate.

A high (C-A) content occurred in the case of K shortage in the presence of any other cation, e.g. Na, that was readily taken up. Although other cations may have functioned as a positive charge in uptake, the K ion seemed to be the only one that accompanied the excess organic anions in their downward movement.

Ammonium fertilization resulted in a reduced growth rate of barley, oats, rye-grass and other plants (Wit, et al. 1963). This reduction was attributed to a stress on the (C-A) content induced by competition between NH_4^+ and other cations, e.g. K^+, and the release of H^+ ions during the transformation of NH_4^+ to organic nitrogen.

Within limits, the plant maintained the (C-A) content at a constant level. The plant responded to a stress on the (C-A) by a reduced growth rate maintaining status quo (Wit et al. 1963). Sixteen plant species, with one possible exception, had reduced growth rates with reduced organic anion concentration (Noggle, 1966).

Evidence for the dependence of organic-salt content on the salt supply has been available since the beginning of this century (Tuil, 1965). But its direct application to plant nutrition is comparatively recent. A review of the literature pertaining to the (C-A) content concept with special emphasis on the organic acids comprising the normal organic-salt content of perennial rye-grass, sugar beet, poplar, and birch is contained in Tuil's paper.

In general, the analysis of the organic anions showed that the anions of the water-soluble, non-volatile organic acids represented about 90 percent of the total organic salts (C-A), Tuil (1965). Malate and citrate constituted about 50 percent of the total organic anions in rye-grass. Other acid anions included succinate, malonate, glycerate, shikimate, quinate, and oxalate. Malate contributed mainly to the change in the organic-salt content. Chloride accumulated instead of organic acids, and mainly at the expense of malate. When ammonium was supplied in place of nitrate, the (C-A) content of the foliage was lower than normal, and chromatographic analysis showed that this was due to a fall in the oxalate content.

2 EXPERIMENTAL FACILITIES, METHODS, AND PROCEDURES

In general, the same facilities, methods and procedures were used throughout the experiments. Deviations from the general procedure are pointed out. The general procedures will be discussed in six sections: 1. growth chamber structure and control of plant environment; 2. experimental design of experiment 1 and experiment 2; 3. plant culture; 4. plant tissue analyses; 5. nutrient solution composition; and 6. technique for measuring stomatal aperture.

2.1 Chamber Structure and Control of Environment

Specific construction details and capabilities of the growth chambers are described in detail by Goldsberry (1963). The specific features of the chambers that are of concern in this study are:

2.1.1 Total solar radiation gradient within chambers

The chambers, covered with vinyl film, are oriented within the greenhouse in an east-west direction. Over a 46-day period, light measurements of total solar radiation were made using Sol-A-Meters located in chamber 1 (east end) and chamber 4 (west end). Light sensitive semiconductors

(photodiodes) on the surface of the Sol-A-Meter converted solar radiation into electrical energy with a ten times greater efficiency than would a thermopile. However, the sensitivity depended on the wave length of the solar radiation, and this fact limited the ability of the photodiode in measuring total global radiation (Wijk, 1963).

Daily measurable radiation in chamber 4 exceeded that in chamber 1 by 1.15 cal./cm^2. The measurable daily radiation in chamber 4 compared to chamber 1 was greater by 27 minutes. Measured radiation during midday in chambers 1 and 4 was approximately equal with chamber 4 receiving only 0.62 cal./cm^2 more radiation during the daily 5 hour period from 10:30 am to 3:30 pm.

In the design of experiment 1 (section 2.2) the light effect is taken into consideration with chambers 1 and 2 being designated as light level 1 and chambers 3 and 4 being designated as light level 2.

2.1.2 Temperature control among chambers

The temperature of all chambers was maintained at a day temperature of 68 F $\pm$ 3 F. The night temperature was maintained at 58 F $\pm$ 3 F.

2.1.3 Maintenance of CO_2 levels in the plant atmosphere

Confidence interval for the maintenance of CO_2 levels in experiment 1 are listed in Table 1. Maintenance of CO_2 levels in the plant atmosphere was accomplished by using the

TABLE 1.--Confidence intervals for the maintenance of CO_2 levels in the plant atmosphere

Chamber	95 Percent CI	99 Percent CI
1	495 ± 10 ppm CO_2	495 ± 13 ppm CO_2
2	864 ± 11	864 ± 15
3	854 ± 11	854 ± 15
4	455 ± 7	455 ± 9

TABLE 2.--Experimental design of the experiments:

Experiment 1
2 light levels (chambers 1 and 2, and chambers 3 and 4) to detect the light effect.
2 CO_2 levels within each light level (chambers 1 and 4 = 475±8 ppm CO_2, chambers 2 and 3 = 859 ppm ± 11 ppm CO_2).
14 nutrient treatments within each chamber.
2 pots/nutrient treatment/chamber.
2 plants/pot allowing for two harvest dates: 1 plant/pot harvested after 26 weeks of growth.
Experiment 2
4 replicates (chambers 1,2,3, and 4).
1 CO_2 level = 750 ppm CO_2.
8 nutrient treatments within each replicate.
5 plants/treatment/replicate.

injection and monitoring system described in detail by Goldsberry (1963). It was observed in experiment 2, that in order to maintain a constant level of 750 ppm CO_2 in all 4 chambers from 9:00 am to 4:00 pm, chamber 4 required a faster rate of injection of CO_2 than did chamber 1. The total CO_2 injection per chamber was not measured.

2.2 Experimental Design of Experiments 1 and 2

Experimental design of experiment 1 was quite different from that of experiment 2. Therefore, the design of the two experiments is considered separately, see Table 2.

Experiment 1 was designed to study the effect of 3 experimental variables on carnation growth: 1. nutrient solution treatment, 2. light level, and 3. CO_2 level. The effects of these three factors acting individually and interacting together were evaluated by use of 3-way analysis of variance.[1]

Experiment 2 was designed strictly to evaluate the effect of the 8 nutrient solution treatments. The light gradient within the chambers was removed from the analysis by considering each chamber as a complete block.

2.3 Plant Culture

Small cuttings of a single variety, Sim, were selected for rooting. Small cuttings were selected to minimize the "nutrient load" of the experimental plant material so

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[1]Tables of statistical analyses are not discussed in the test, but are presented to document treatment effects shown in the figures.

that imposed experimental nutrient solution effects would become effective sooner. A single variety was used to minimize the possible varietal effect on ion uptake.

The cuttings were rooted in a peat-perlite medium using standard procedures. Upon rooting, the cuttings were removed and planted into perlite. The use of perlite as a medium for plant growth has been evaluated by Wilson and Tunny (1965) who concluded that it was generally preferable to use media other than perlite. However, Morrison, McDonald, Sutton (1960) concluded that despite its low nutrient content, perlite could be used as a medium for plant growth. The empirical, physical, and chemical properties of perlite are described by Keller and Pickett (1954) and by the Perlite Institute (1962). Wet perlite has a pH of 6.6-8.0, a specific gravity of 2.2-2.4. It is soluble in hot concentrated alkali and in hydrofluoric acid, slightly soluble (less than 2 percent) in concentrated mineral acids, and very slightly soluble (less than 0.1 percent) in dilute mineral or concentrated weak acids. Perlite is considered to be a chemically inert medium and therefore ideal for a nutrient solution experiment.

Plants were watered daily until the root system of the previously rooted cuttings became established in the perlite. At that time, watering frequency was reduced to every other day. At each watering the pots were leached. Soluble salt readings and pH records revealed no salt

accumulation of pH shift: salt and pH readings of the leachate approximated those of the respective applied nutrient solutions.

In the experiments, reagent grade chemicals, plastic nutrient solution containers, pots, labels, etc. were used to minimize chemical contamination.

2.4 Nutrient Solution Composition

The nutrient solutions were formulated so that the variation among pH's was within the ±0.2 pH unit of tolerance established by Steiner (1961) except the mixed treatment of experiment 2. This specific treatment was designed to study the effect of pH upon ion uptake. The variation in the calculated atmospheres osmotic pressure was within the tolerance range ±0.2 atmospheres reported as critical by Steiner, except in the concentration series of experiment 1. (See Tables 15 and 19 for solution composition.)

In the replacement series, total ion content of the respective solutions was held constant. Within a solution, content of all ions other than the two replacing each other was held constant, and the sum of the two replacing ions was constant.

Experiment 2 was designed using the guidelines outlined by Homes (1963).

2.5 Tissue Analysis

All tissue analyses were determined by the Colorado State University Soil Testing Laboratory under the

supervision of Hunter Follett. The methods used in the determinations are listed in Table 23. Tissue analyses determined by the CSU methods are compared with the tissue analyses determined by the emission spectrograph at the Spectrographic Laboratory, N.Y.S. College of Agriculture on duplicate samples (Table 3). All tissue samples were collected, dried, and prepared as described by Boodley (1965).

All nutrient solution compositions are stated as milligram-equivalents per liter of solution (me/l.).

All tissue analyses are reported in milligram equivalents per kilogram dry matter (me/kgdm).

The term "ion content per plant" is used here to denote the value obtained by multiplying the milligram equivalent ions per kilogram dry matter by the kilograms fresh weight of the plant in consideration, or me/kg dm X kg fresh weight. The author realizes that a more meaningful and accurate ion content per plant could possibly have been obtained by multiplying the me/kg dm X kg dry matter. However, due to the fact that the plants were allowed to flower prior to the 26 week old harvest and only the fresh weight of the flowers was recorded, it was only possible to obtain the total fresh weight, including flowers for each plant. By comparing (Table 17) the average fresh weight and the calculated average dry weight, it can be seen that there is no difference between the ranking order of the treatment dry and fresh weights. Because the mean percent dry material was 20 percent, the me/kg dm X kg fresh weight is

TABLE 3.--Comparison of tissue analyses made by the CSU Soil Testing Laboratory and the Spectrographic Laboratory, N.Y.S. College of Agriculture, Ithaca, N.Y. Analyses for each ion were determined by the two laboratories on 18 duplicate samples, except for Fe and Zn which were determined on 12 duplicate samples

	Percent K	Percent Ca	Percent Na	Percent Mg	Percent P	ppm Fe	ppm Zn
CSU, mean	4.20	1.17	.11	.21	.395	52.9	14.9
NYS, mean	4.32	1.34	.14	.33	.512	61.3	19.2
Difference	-.12	-.17	-.03	-.12	-.116	-8.4	-4.3
Percent difference	2.78	12.70	21.4	36.3	22.6	13.7	22.4
CSU, std. deviation	1.41	.75	.10	.13	.499	2.75	2.75
NYS, std. deviation	1.29	.82	.08	.10	.632	3.97	3.97
Difference, std. dev.	.18	.09	.07	.17	.136	2.49	2.49
Paired T value	2.916	8.193	1.735	3.000	3.639	5.910	5.910
1 percent, T value	2.567	2.567	2.567	2.567	2.567	2.718	2.718
Null hypothesis	reject	reject	accept	reject	reject	reject	reject

approximately five fold too large. The relative comparisons are not affected because all are overestimated to approximately the same extent.

2.6 Technique for Measurement of Stomatal Aperture

The use of silicone rubber for replicating plant surfaces for examination by light microscopy was used successfully by Sampson (1961). The method was specifically adapted for use in making replicas of stomatal apertures to be measured microscopically by Zelitch (1961). Silicone rubber was first used in studying carnation stomatal apertures by Green (1966).

In this study, RTV 11 silicone rubber and a tin octoate curing agent, Nuocure 28, were used. The RTV 11 is available from the Silicone Products Department of the General Electric Co., Waterford, New York. The Nuocure 28 is available from the Nuodex Products Company, Elizabeth, New Jersey.

The leaf section and the leaf to be studied were standardized in a preliminary study. From the preliminary study it was concluded: 1. There was no significant difference in the number of stomates on the top compared to the number of stomates on the bottom of the leaf. 2. The greatest difference in stomatal aperture width induced by difference in CO_2 levels was detectable at the high light peak in the morning hours. 3. Plants growing in the higher light level had a higher ratio of stomates to epidermal

cells than did the plants growing in the lower light level 1. The ratio at light level one was 1 stomate: 2.37 epidermal cells, that at light level two was 1:2.62. 4. The most uniform leaf section for measurement of the stomatal aperture, was the number 3 leaf section (the leaf being divided into four sections with the number 1 leaf section that section at the point of leaf attachment to the stem). 5. The number 2 leaf pair (number 1 being the first leaf pair at the shoot apex whose leaves do not touch each other along their edges) was found to have the most uniform number 3 leaf section.

In this study, stomatal replicas were made of the stomates on the top surface of section number 3 of leaf number 2. Three-way analysis of variance was made to determine the effects of nutrient treatment, CO_2, and light on stomatal aperture. Data analyzed were the means of 15-30 stomatal aperture measurements per treatment in each chamber. Impressions were made at 10:00 am in all chambers. The results are reported in Table 4.

3 RELATION OF (C-A) CONTENT TO YIELD

3.1 Summary

Optimal growth in carnations was associated with the normal (C-A) content (1700-1900 me/kg dm). The change in (C-A) in the experiment was due mainly to change in the cation concentration of the plant tissue. There was a highly significant correlation between increase in (C-A) content of the tissue and increase in plant yield.

3.2 Results and Discussion

After uptake and partial conversion of the inorganic ions of the nutrient solution salts, there resulted an accumulation in the plant tissue of the inorganic cations: K^+, Na^+, Mg^{++}, and Ca^{++} and of the inorganic anions: NO_3^-, Cl^-, $H_2PO_4^-$, and $SO_4^=$. The sum of these cations and anions in milligram equivalents per kilogram dry material is given by C and A respectively. C equals the total salt cations in the plant tissue; A equals the inorganic salt content, and (C-A) equals the organic salt content of the plant material. In work of others in determining the (C-A), it was not necessary to account for the very low quantities of the other inorganic ions in the plant tissue (Tuil, 1966).

The uptake and subsequent tissue content of the salt cations occurred in amounts that, depending on the

composition of the nutrient solution, differed from the number of equivalents of the salt anion absorbed. In work of others, a positive (C-A) difference was associated with an uptake of OH^- (Tuil, 1965). The hydroxyl anions that balanced the excess cations absorbed were replaced in the plant tissue by organic anions formed by metabolic processes. When the (C-A) difference was negative, the hydrogen ions that balanced the excess salt anions absorbed were neutralized by the alkalinity produced by the metabolic breakdown of organic anions in the tissue. The pH of the plant tissue remained unchanged. The ions absorbed were present in the plant tissue as inorganic salts (A) and organic salts (C-A) of the salt cations (C), Ulrich (1941).

Total phosphorus was designated as inorganic phosphate in all the analyses. This eliminated the organic phosphates from the organic salts.

It is not essential in this paper to identify the balancing organic salts. Tuil (1965) in chromatographic investigations, showed that 90 percent of the (C-A) content consisted of the salts of the water-soluble, low-molecular plant acids. Malate formed the main constituent and varied to a much greater extent with (C-A) than did the other organic salts.

At suboptimal growth, the (C-A) of the carnation plant varied depending on nutrition and other factors (Table 6, Fig. 3). But optimal growth was invariably associated with a high organic salt content. There was a highly

TABLE 6.--The relation between yield and (C-A) content omitting treatments 6 and 12 (see figure 3)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	1552	538	506	-.0999	.2209	3	1) $b_1=b_2=$. . . accepted
2	1820	716	590	.0736	.0769	3	2) Significant differences among adjusted treatment means
3	1852	795	658	.2550	.5671	3	
4	1539	607	579	-.3823	.3662	3	3) $\bar{b}=0$ . . . rejected
5	1193	239	332	.4553	.3358	3	
7	1664	557	485	.9658	.9014*	3	
8	1717	654	564	1.1309	.8747	3	
9	1625	589	531	.4410	.9976**	3	
10	1312	581	633	1.3043	.8306	3	
11	1315	319	369	.1925	.6343	3	
13	919	300	489	.5037	.7156	3	
14	1006	257	415	.1305	.1178	3	
Ave	1459	513					
Among				.5480	.9026**11		
Within				.3490	.4821**36		
Total				.5220	.8369**47		

ANALYSIS OF COVARIANCE: predictor variable X = C-A, me/kg dm
dependent variable Y = grams fresh weight/plant

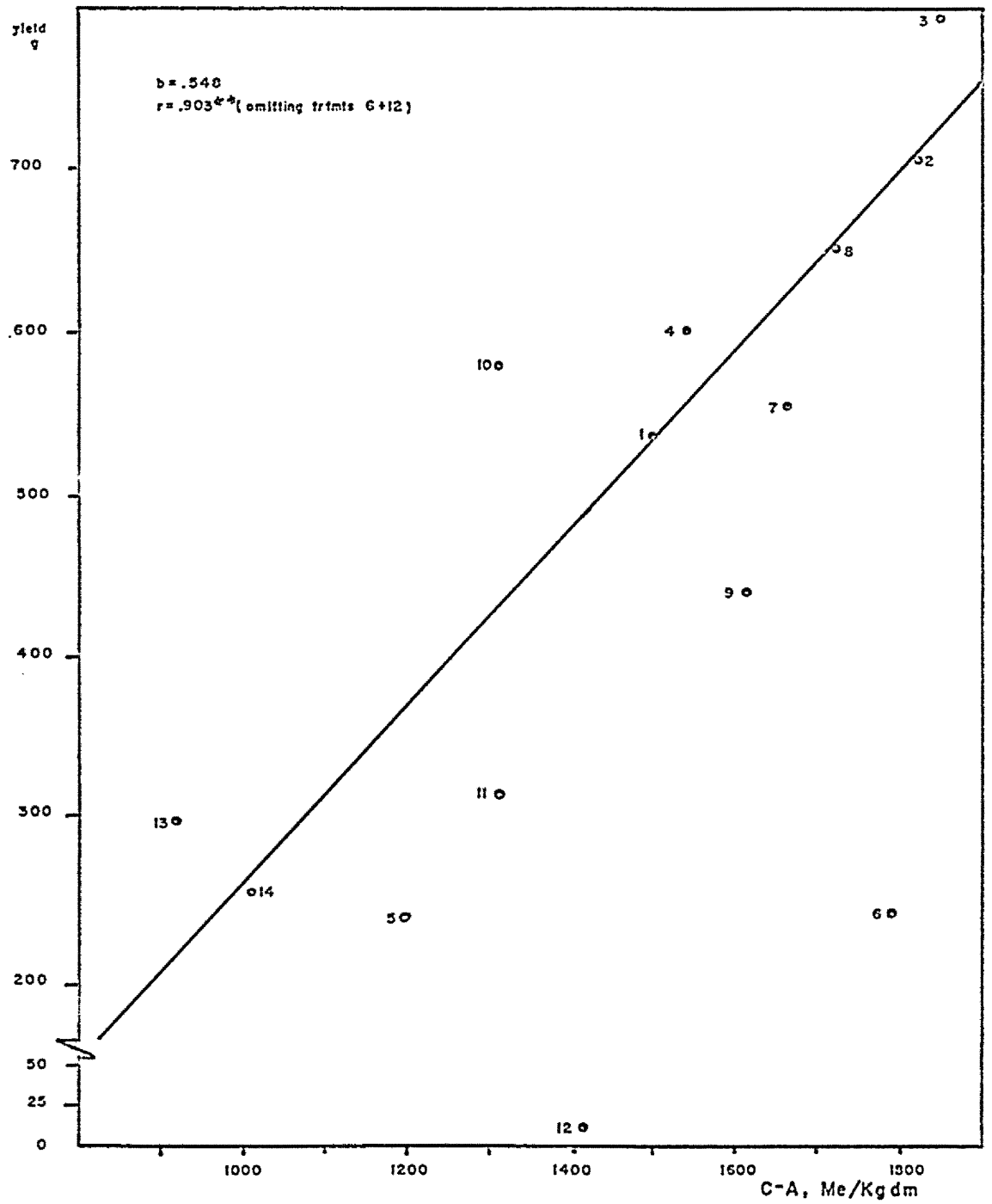


Fig. 3.--The relation between yield and (C-A) content of the carnation plant tissue.

significant correlation between increase in (C-A) content of the tissue and increase in plant yield (Fig. 3).

Variation in (C-A) content was mainly related to change in the cation concentration (C) of the plant tissue (Fig. 4a). Cation concentration was positively correlated with yield except in the case of extreme sodium imbalance (Fig. 4a, point 6). Inorganic anion concentration in the plant tissue (A) remained fairly constant (Fig. 4b). There was a significant negative slope relating yield and anion concentration. There was a highly significant correlation to this slope (Fig. 4b, slope = -9.12).

The correlation between total cation and total anion content per plant and yield is graphed in Figure 5. The difference between the cation salt content and the total inorganic anion content at any given yield is equal to the (C-A), Wit et al. (1963). Total cation content per plant was significantly related to yield in a positive linear relationship. Total inorganic anion content was also positively correlated to yield. This contrasted to the negative relation of inorganic anion concentration in the tissue to yield. The positive compared to negative slope may be explained by pointing out the difference between concentration of anions in the tissue and total uptake or content of anions per plant. The latter is the concentration of anions multiplied by the yield of the plant (section 2.5). Those plants which had the highest (C-A) content, usually due to low anion

TABLE 7.--The relation between yield and cation concentration of the plant (see figure 4a)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	1840	538	549	-.0882	.2214	3	1) $b_1=b_2=$. . . accepted
2	2169	716	648	-.0011	.0014	3	2) Significant differences among adjusted
3	2168	795	728	.1976	.4962	3	treatment means.
4	1851	607	616	-.3363	.4556	3	3) $\bar{b}=0$ . . . rejected
5	1460	239	340	.4569	.2899	3	
6	2333	246	139	-.4923	.8024	3	
7	1993	557	531	.7532	.8708	3	
8	2057	654	613	.9640	.8641	3	
9	1958	589	572	.3979	.9926**	3	
10	1661	581	635	.7921	.6005	3	
11	1659	319	373	.1238	.3872	3	
13	1485	300	396	.1007	.3275	3	
Ave	1886	512					
Among				.3259	.4812	11	
Within				.2377	.3881*	36	
Total				.3077	.4631**	47	

ANALYSIS OF COVARIANCE: predictor variable X = cations, me/kg dm
dependent variable Y = grams fresh weight/plant

TABLE 8.--The relation between yield and anion concentration of the plant (see figure 4b)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	287	538	558	-5.68	.196	3	1) $b_1=b_2=$. . . accepted
2	349	716	723	-31.98	.512	3	2) Significant differences among adjusted treatment means.
3	316	795	808	-1.24	.043	3	
4	312	607	622	-9.24	.496	3	3) $\bar{b}=0$ . . . accepted
5	267	239	262	-19.34	.351	3	
6	542	246	213	-17.81	.460	3	
7	329	557	567	30.17	.706	3	
8	340	654	662	24.26	.488	3	
9	333	589	599	21.99	.694	3	
10	349	581	588	-5.02	.192	3	
11	389	319	318	12.22	.931*	3	
13	567	300	263	.10	.022	3	
14	595	257	213	-.90	.060	3	
Ave	383	492					
Among				-10.62	.602*	12	
Within				2.06	.098	39	
Total				-9.12	.505**	51	

ANALYSIS OF COVARIANCE: predictor variable X = anions, me/kg dm
dependent variable Y = grams fresh weight/plant

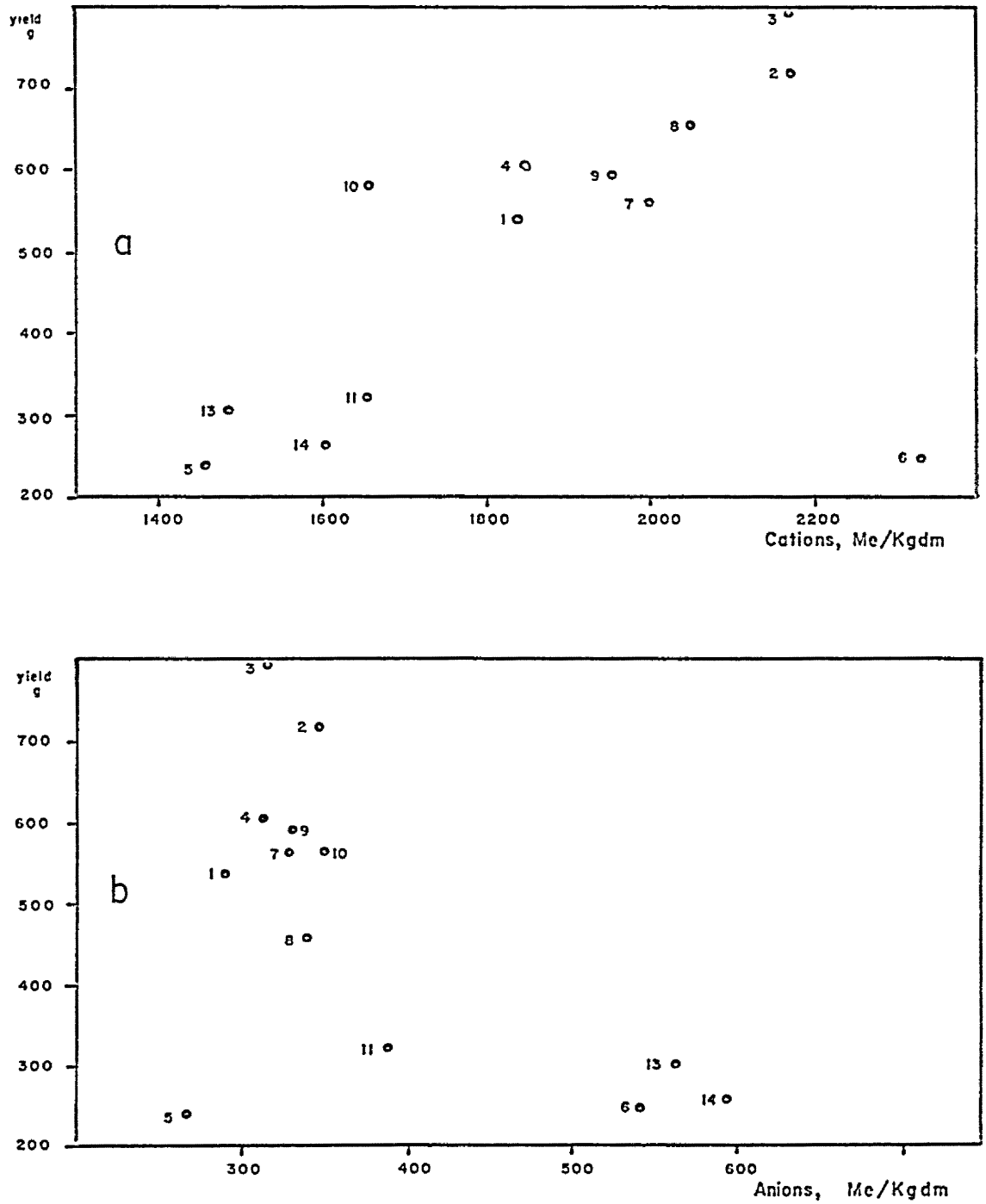


Fig. 4.--a. The relation between yield and cation concentration of the carnation plant. b. The relation between yield and anion concentration of the carnation plant.

TABLE 9.--The relation between yield and total cation content per plant (see figure 5)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	985	538	523	.4	.7858	3	1) $b_1=b_2=$. . . accepted
2	1552	716	483	.3	.9385*	3	2) Significant differences among adjusted
3	1729	795	494	.2	.8674	3	treatment means.
4	1122	607	540	.5	.8865*	3	3) $\bar{b}=0$ . . . rejected
5	349	239	469	.6	.9950**	3	
6	569	246	391	.5	.9946**	3	
7	1129	557	487	.4	.9933**	3	
8	1356	654	497	.3	.9961**	3	
9	1169	589	504	.2	.9967**	3	
10	971	581	572	.4	.9821**	3	
11	531	319	479	.4	.9149*	3	
13	448	300	492	.4	.9146*	3	
14	411	257	463	.6	.9992**	3	
Ave	948	492					
Among				.4	.9789**	12	
Within				.3	.9351**	39	
Total				.4	.9716**	51	

ANALYSIS OF COVARIANCE: predictor variable X = cation, me uptake/plant
dependent variable Y = grams fresh weight/plant

TABLE 10.--The relation between yield and total anion content per plant (see figure 5)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
Ave	178	488					1) $b_1=b_2=$. . . accepted
Total				3.34	.8954**	11	

ANALYSIS OF COVARIANCE: predictor variable X = anions, me uptake/plant
dependent variable Y = grams fresh weight/plant

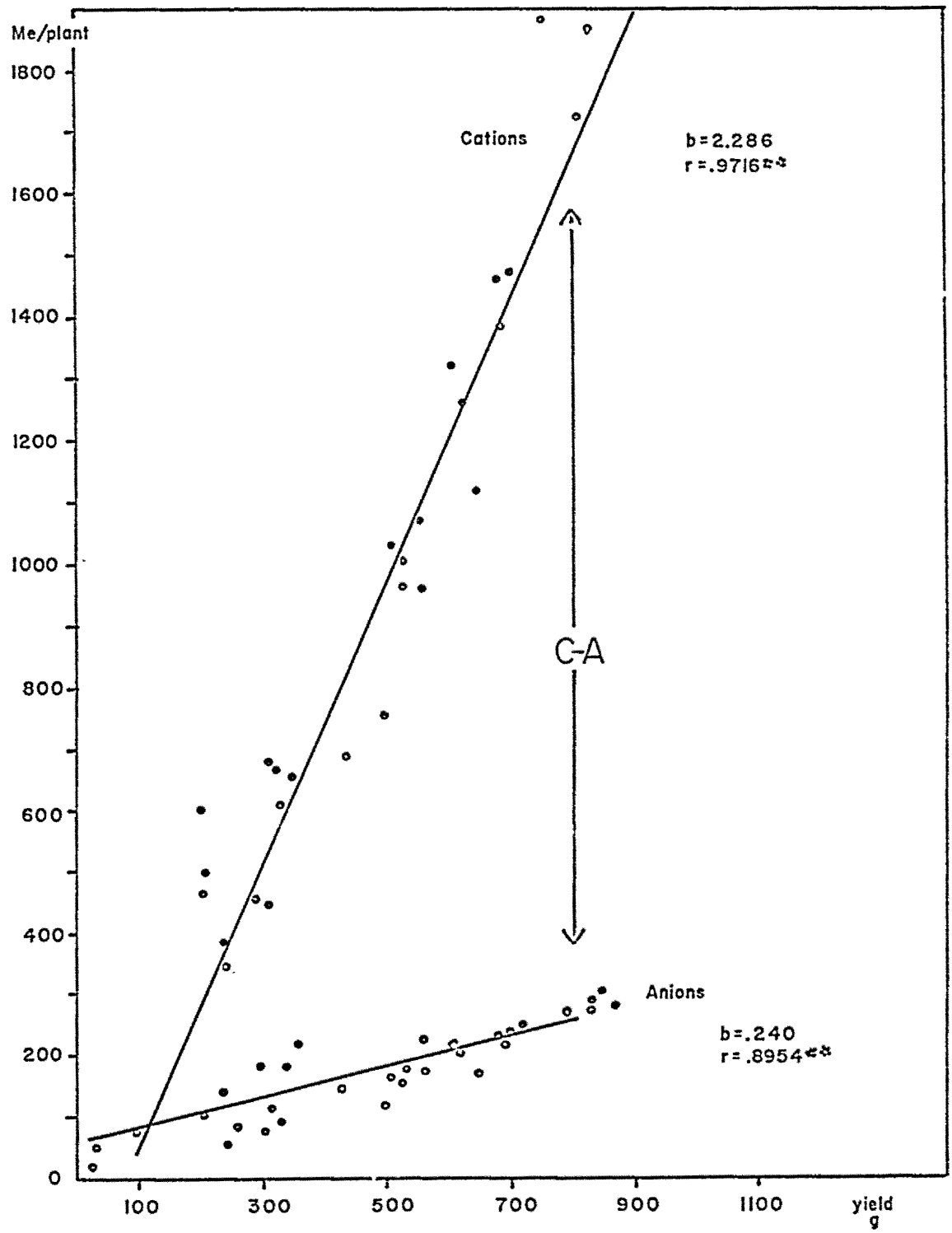


Fig. 5.--Correlation between total cation and total anion content per plant and yield.

concentration (A), had the highest yield and consequently high total anion content.

3.3 Conclusions

One of the prerequisites of optimal growth was a "normal" (C-A), organic salt content. But, depending on nutrition, a "normal" (C-A) was not always associated with optimal growth (Fig. 3, point 6). Factors in the external environment and in the applied nutrient solution composition need to be studied to determine their effect on the ionic balance of the plant and plant yield.

4 LIGHT, CO_2, AND NUTRIENT SOLUTION EFFECTS

4.1 Summary

The main effect of CO_2 on carnation growth was probably associated with the rate of transpiration, ion uptake, translocation, and possibly photosynthesis. The main effect of light on carnation growth was probably the influence on the photosynthesis rate.

4.2 General Effects of Light and CO_2

The solar constant for the solar energy falling on one cm^2 at normal incidence at the top of the atmosphere is 1.94 cal. cm^{-2} min^{-1} (Wijk and Ubing, 1963). The actual irradiancy at any altitude will be different due to extinction in the atmosphere.

During the winter months the quality and quantity of daylight available was the limiting factor for greenhouse-plant growth, provided the temperature was controlled, (Wijk and Businger, 1963). Photosynthesis rate increased with increasing CO_2 in the plant atmosphere until at a certain value the rate of influx of photons determined the photosynthesis rate (Kok, 1965). At higher intensities other factors begin to play a role and may set a ceiling for the attainable rate.

The efficiency of the chloroplasts in transforming solar energy is impressive. Though the exact figures are subject to controversy, it was demonstrated under special laboratory conditions that the photosynthetic process converted as much as 75 percent of the light that impinged on the chlorophyll molecules into chemical energy (Lehninger, 1961). On the other hand, the efficiency of energy recovery of a field of corn, given the random and uneven exposure of the leaves to sunlight and other conditions of nature, was considerably lower; on the order of only a few per cent (Lehninger, 1961).

The energetic efficiency of photosynthesis, considered as being the ratio of the chemical energy stored in the synthesized organic matter to the radiant energy absorbed in the chlorophyll, reached a maximum of 20-35 percent in the red region of the spectrum. The efficiency decreased rapidly in the near infrared, where it was practically zero at 0.75 microns, and more gradually in the visible part of the spectrum, where the efficiency per quantum of absorbed radiation remained approximately constant. An energetic efficiency of about 16 percent at 0.4 micron was considered as a fair estimate for optimum conditions. The overall energetic efficiency, e.g. the ratio of the chemical energy stored to the total radiant energy per unit of surface, was of the order of 1 to 3 percent over the entire growing season for the common agricultural crops (Wijk and Ubing, 1963).

Ten percent far-red plus red radiation were the most effective wavelengths for hastening flowering when carnation plants were grown entirely under artificial light (Vince, 1964). The amount of radiant energy contained in thermal radiation and its effect depends strongly on wave length of the radiation received.

Considering the energetic efficiency of the leaf to be 17 percent (Kok, 1965), 340 Kcal/m^2 are required during a 12 hour day to produce a mole, 30 grams, of carbohydrate/ m^2 leaf surface. This would be a requirement of 0.0472 cal/ cm^2/min^1.

Measurement of daily solar radiation in the chambers detected 18.31 cal/cm^2 in chamber 1 and 19.46 cal/cm^2 in chamber 4. This was 0.0412 and 0.0433 cal/cm^2/min^1 in chambers 1 and 4 respectively. Light may have been limiting the photosynthesis rate of the plants within the chambers. Not all species respond alike to light; Hesketh (1963) classed a group of species into three categories: those that showed no light saturation, those that were light saturated at about 1/3 full sunlight, and those that were saturated at about 1/10 full sunlight. The photosynthetic response of carnation to varying light has not been determined. It is not known whether the light supplied in this experiment was saturating, or if the plants were still responding to increases in light.

The CO_2 content of the earth's atmosphere is considered to be 300 ppm. In this experiment there were two

CO_2 levels: chamber 1 and 4 at 475 ppm and chambers 2 and 3 at 859 ppm.

Specific characteristics of the plants of experiment 1 were measured to determine the effect of light and CO_2 on plants grown under different light and CO_2 levels, and relations between nutrient solution treatments and light and CO_2 (Table 4). (For composition of the nutrient solution treatments, see Table 15).

4.3 Effects of Light, CO_2, and Ion Concentration on Yield

High light (level 2) and high CO_2 (level 2) both acted to increase the yield of the carnation plant (Table 4). However, they were not acting in conjunction. This is illustrated in Figure 1 where the deviations effected by light and CO_2 from the average yield are plotted. A large positive deviation from the average yield due to high CO_2 (C2) was usually accompanied by a slight positive deviation due to high light (L2) or even by a negative deviation. The same was true of the large positive deviations from the average yield attributable to high light. They were accompanied by a slight positive deviation due to high CO_2 or by a negative deviation. The high yield in the K-Ca replacement series, treatment 3, and the high yield in the K-Na replacement series, treatment 8 (treatments having optimum nutrient balance for their series) were induced by high light.

Nutrient treatments 2, 4, 7 and the concentration series (Fig. 1) were imbalanced solutions. In these

TABLE 4.--The effects of nutrient treatment,[1] environmental CO_2,[2] and daily total light[3] on ion content, yield, and stomatal aperture of the carnation plant as determined by three-way analysis of variance

	Nutrient Treatment	CO_2	Light Level	Nutrient Treatment[4] X CO_2
1. Cations, me/kg dm	**	**	ns	**
Cations per plant	**	*	ns	ns
2. Potassium, me/kg dm	**	ns	ns	**
Potassium per plant	**	*	ns	ns
3. Calcium, me/kg dm	**	ns	ns	**
Calcium per plant	**	*	*	ns
4. Magnesium, me/kg dm	**	**	ns	ns
Magnesium per plant	**	*	ns	ns
5. Sodium, me/kg dm	**	ns	ns	ns
Sodium per plant	**	ns	ns	ns
6. Anions, me/kg dm	**	ns	ns	ns
Anions per plant	**	ns	ns	**
7. Nitrate, me/kg dm	**	*	ns	**
Nitrate per plant	**	ns	ns	**
8. Sulfate, me/kg dm	**	ns	ns	ns
Sulfate per plant	**	ns	ns	*
9. Phosphate, me/kg dm	**	ns	ns	ns
Phosphate per plant	**	ns	ns	**
10. Chloride, me/kg dm	**	*	*	ns
Chloride per plant	**	**	*	**
11. Organic Nitrogen				
Org. N, me/kg dm	**	ns	ns	ns
Org. N per plant	**	ns	ns	*
12. (C-A), me/kg dm	**	**	ns	**
(C-A) per plant	**	**	ns	**

TABLE 4.--Continued

	Nutrient Treatment	CO_2	Light Level	Nutrient Treatment[4] X CO_2
13. Yield, grams fresh wt.	**	*	*	*
14. Percent dry matter	**	ns	ns	ns
15. Stomatal aperture	ns	**	ns	ns

* 5 Percent level of significance
**1 Percent level of significance

[1]13 nutrient solution treatments as described in Table 15 in the appendix.
[2]Two CO_2 levels: 475±8ppm and 859±11 ppm.
[3]Two light levels: level 2 having 27 minutes more measurable daily radiation than level 1. There was 1.15 cal/square centimeter greater total radiation daily in level 2 than in level 1.
[4]There were no other significant treatment interactions: Light X CO_2, Light X treatment, Light X CO_2 X Treatment were not significant.

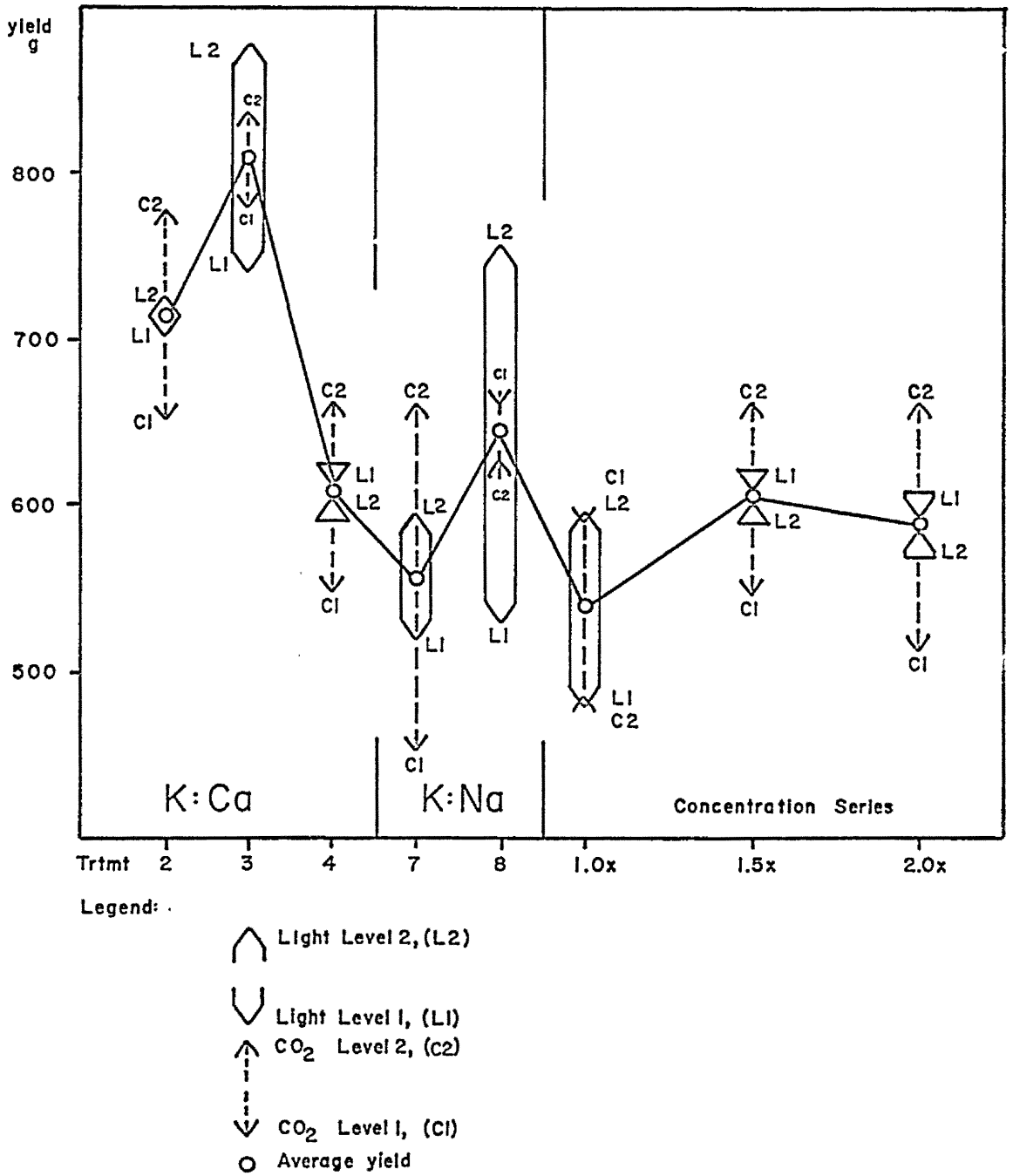


Fig. 1.--Deviations from average yield affected by light and CO_2. Light and CO_2 levels are defined in Tables 1 and 2.

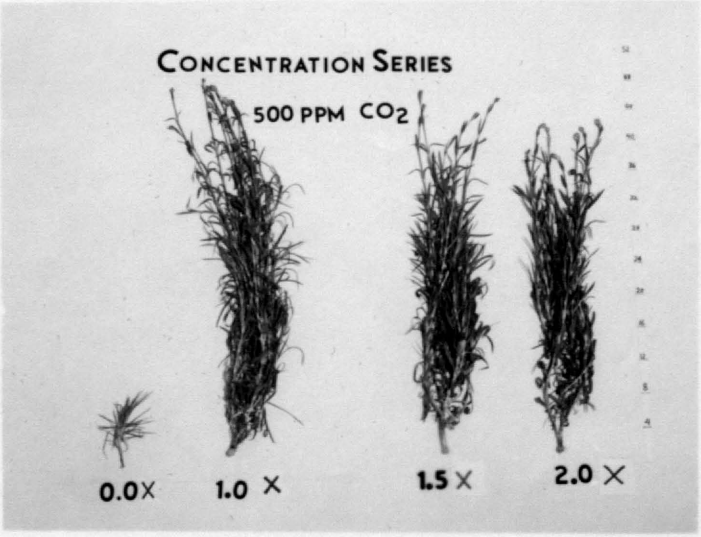
Fig. 2a.--Photograph of plants within the concentration series grown in 485±8 ppm CO_2 atmosphere.

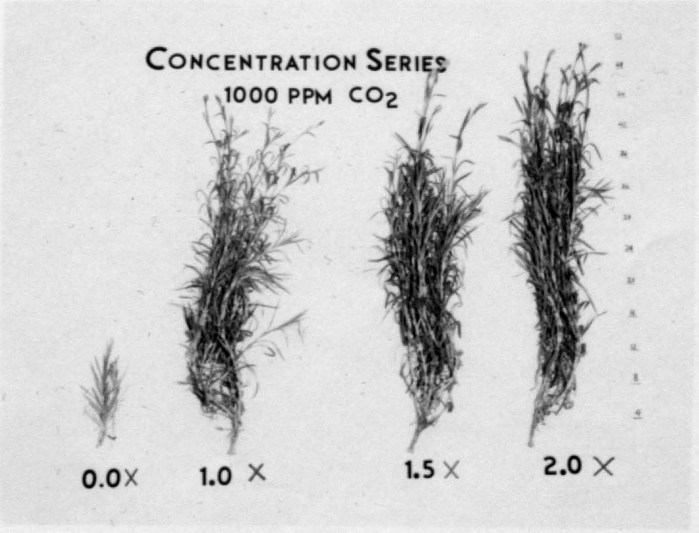
TABLE 5.--Composition of the nutrient solutions and yield of the plants in the concentration series of figure 2

Trt-mt #	Osm. pres.*	me/l K	Ca	Mg	Na	NO_3	SO_4	H_2PO_4	grams fresh wt. 475	855ppm CO_2
0.0X	0.000	-	-	-	-	-	-	-	31	21
1.0X	0.376	6.2	1.6	0.66	0.33	7.8	0.66	0.33	592	484
1.5X	0.576	9.5	2.5	1.00	0.50	12.0	1.00	0.50	551	664
2.0X	0.776	12.8	3.4	1.35	0.67	16.0	1.35	0.67	516	664

*atm.

Fig. 2b.--Photograph of plants within the concentration series nutrient experiment growing in 855±11 ppm CO_2 atmosphere.


CONCENTRATION SERIES
500 PPM CO_2
0.0X
1.0 X
1.5 X
2.0 X


CONCENTRATION SERIES
1000 PPM CO_2
0.0X
1.0 X
1.5 X
2.0 X

treatments the greater positive deviation from the average yield was due to the higher CO_2 level.

In the concentration series at the lowest ion concentration, low CO_2 and high light acted equally in causing a positive deviation from the average yield. At the higher ion concentrations, there was a reverse effect with high CO_2 and low light causing a positive deviation from the average yield (Fig. 2, Table 5).

High CO_2 compared to low CO_2 greatly reduced the stomatal aperture. Neither light nor nutrient treatment had an effect on stomatal aperture.

4.4 Effects of Light, CO_2, and Nutrient Solution on Ion Content

Chloride concentration in the plant tissue was the only ion concentration influenced by the light level. Chloride concentration increased with increasing light. Because higher light in general caused higher yields, there was a significant increase in the total chloride content per plant. This was also true of calcium content per plant (Table 4).

High CO_2 decreased the chloride concentration in the plant tissue. As in the concentration series, there was a positive deviation from the average yield due to high light accompanied by a negative deviation due to high CO_2. Or, high CO_2 and high light had opposite effects on the chloride uptake.

Magnesium was the only cation whose concentration in the plant tissue was significantly affected by the CO_2 level. Magnesium concentration in the tissue was higher at the higher CO_2 level. The total magnesium content per plant was higher at the higher CO_2 level.

There was an increase in the (C-A) content of the plant at the higher CO_2 level. An increase in the cation concentration at the higher CO_2 level was not accompanied by a change in anion concentration. The change in the (C-A) content was due mainly to this change in the cation content of the tissue.

4.5 Conclusions

4.5.1 CO_2 effect on yield

Optimum (C-A) is one of the prerequisites for optimum growth. The (C-A) was unchanged by the light level, but was significantly changed by the differential effect of CO_2 on ion uptake. The cation concentration (C) was significantly increased by an increase in magnesium concentration at the higher CO_2 level, and the inorganic anion concentration (A) was decreased by the decrease in chloride uptake at the higher CO_2 level.

The main effect of CO_2 was control of stomatal aperture and possible related effect on rate of ion uptake, transpiration, translocation and possibly photosynthesis. High CO_2 probably reduces ion uptake and stress on the transpiration rate: 1. at greater ion concentration of the

nutrient solution, there was a positive deviation from the average yield at the higher CO_2 level; 2. with suboptimal nutrient solutions, there was a positive deviation from the average yield at the higher CO_2 level; and 3. by reducing the transpiration, higher CO_2 may have functioned to reduce the uptake of the chloride ion.

4.5.2 Light effect on yield

The main effect of the higher light level was probably the increase in photosynthesis. There was no indication that the light difference was of a magnitude to effect the stomatal aperture and transpiration rate. But there was an unexplained increase in chloride uptake at the higher light level.

5 ION RATIOS AND COMPETITIVE UPTAKE

5.1 Summary

Maintenance of specific ratios among ions, not maintenance of a specific level of a given ion, was a prerequisite for optimum yield. When the plant was K deficient, the ion ratios were imbalanced. But the normal (C-A) content was maintained at a greatly reduced growth rate. There were competitive and enhancement effects among the cation constituents in the external nutrient solution treatments upon growth.

5.2 Results

Experiments on competitive and selective uptake by carnation plants were restricted to replacement series to avoid interaction between cation and anion uptake. Solution composition is described in section 2.4. Solution formulation is stated in Tables 15 and 19.

5.2.1 Maintenance of specific ion ratios

The relation of ion concentration in the plant tissue (me/kgdm) to the total ion uptake per plant (section 2.5) is graphically illustrated in Figures 6 and 10. The ion ratios within the plant tissue are stated in Table 24.

The effect of the ratios among the ions in the applied nutrient solution on the uptake of each of the ions by the plant can be seen in Figure 6b. The greatest effect was in the applied nutrient treatment having K:Ca = 12:0. Even though the potassium, magnesium, and sodium concentrations in the tissue were normal (Fig. 6a), the total uptake (Fig. 6b) of all cations per plant was greatly reduced due to the calcium imbalance in the applied solution. In this treatment there was a greatly reduced (C-A) content and yield (Fig. 3, point 5).

With the applied nutrient treatment having K:Na = 0:10, the plants were potassium deficient and the growth rate was greatly reduced due to the ion-ratio imbalance. A "normal" (C-A) content was maintained by plants in this treatment at a greatly reduced growth rate (Fig. 3, point 6).

In the NO_3:Cl replacement series the H_2PO_4, SO_4, and NO_3 concentrations in the tissue remained relatively constant (Fig. 10 a,b). The chloride content of the applied nutrient solution and the chloride concentration within the tissue had no apparent effect on the ratios of the other anions or upon their uptake. Chloride was apparently taken up by the carnation plant independently of all other anions. The chloride uptake did, however, greatly lower the (C-A) content by increasing the total anion content (A) of the plant tissue. The reduced (C-A) content was accompanied by a reduction in yield (Fig. 3, points 13,14).

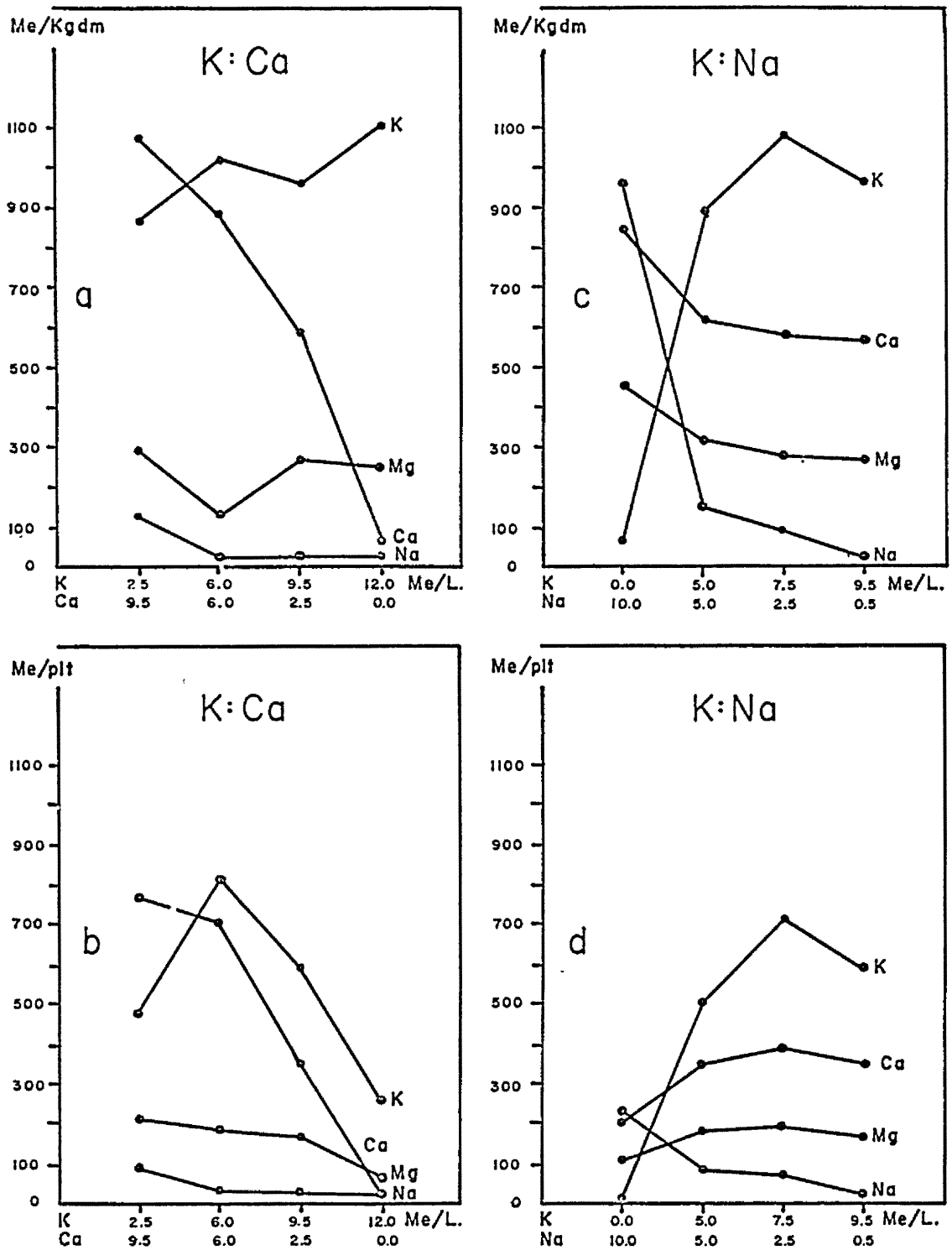
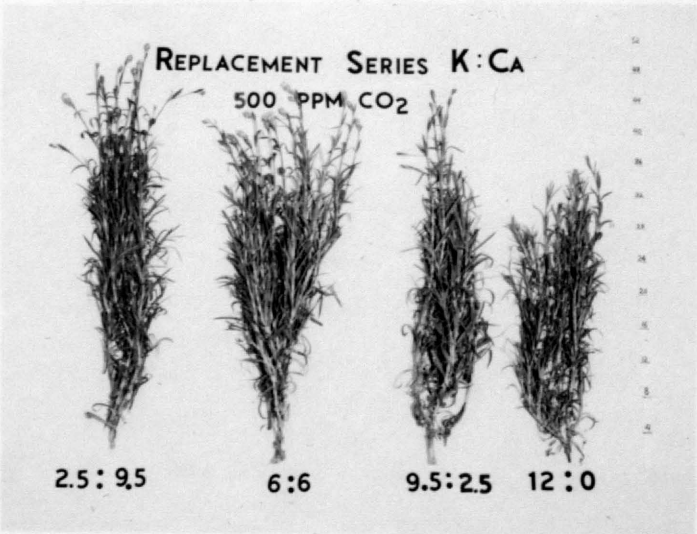


Fig. 6.--Cation replacement diagrams for the leaf tissue of carnation showing effect of replacement in the external nutrient solution on the plant tissue ion concentration and on the total ion content per plant. a. Effect of potassium-calcium replacement on cation concentration. b. Effect of potassium-calcium replacement on total cation content. c. Effect of potassium-sodium replacement on cation concentration. d. Effect of potassium-sodium replacement on cation content.

Fig. 7a.--Photograph of plants within the potassium-calcium replacement series grown in 485±8 ppm CO_2 atmosphere.

Fig. 7b.--Photograph of plants within the potassium-calcium replacement series grown in 855±11 ppm CO_2 atmosphere.


REPLACEMENT SERIES K:CA
500 PPM CO_2
2.5 : 9.5
6:6
9.5:2.5
12 : 0

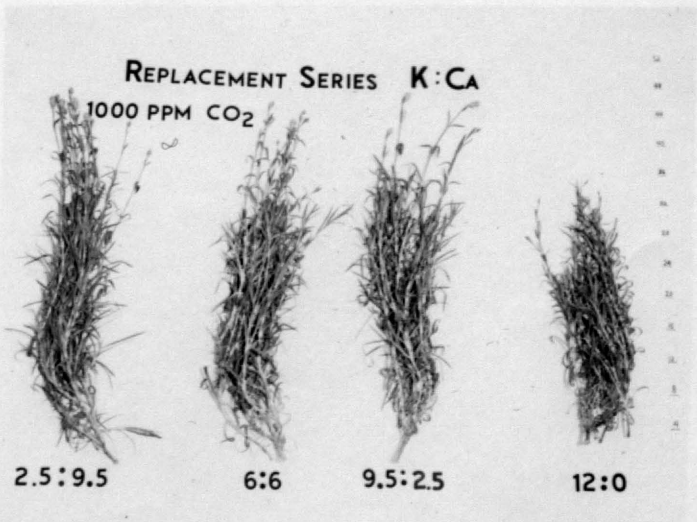
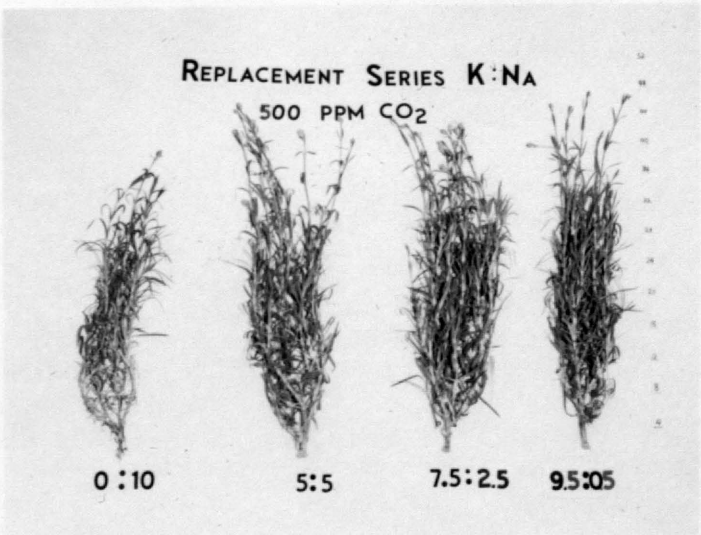

REPLACEMENT SERIES K:CA
1000 PPM CO_2
2.5:9.5
6:6
9.5:2.5
12:0

Fig. 8a.--Photograph of plants within the potassium-sodium replacement series grown in 485±8 ppm CO_2 atmosphere.

Fig. 8b.--Photograph of plants within the potassium-sodium replacement series grown in 855±11 ppm CO_2 atmosphere.


REPLACEMENT SERIES K:NA
500 PPM CO_2
0:10
5:5
7.5:2.5
9.5:05

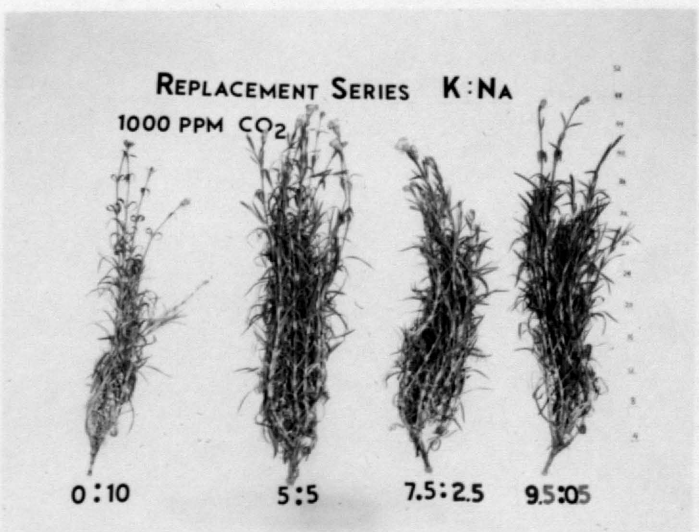
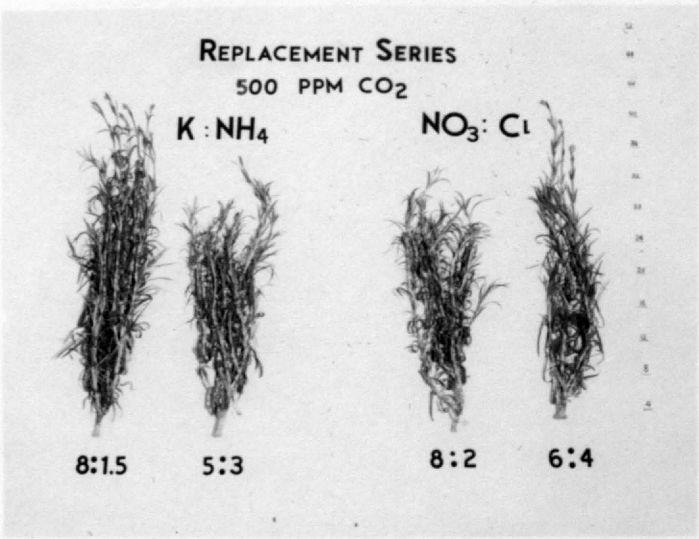
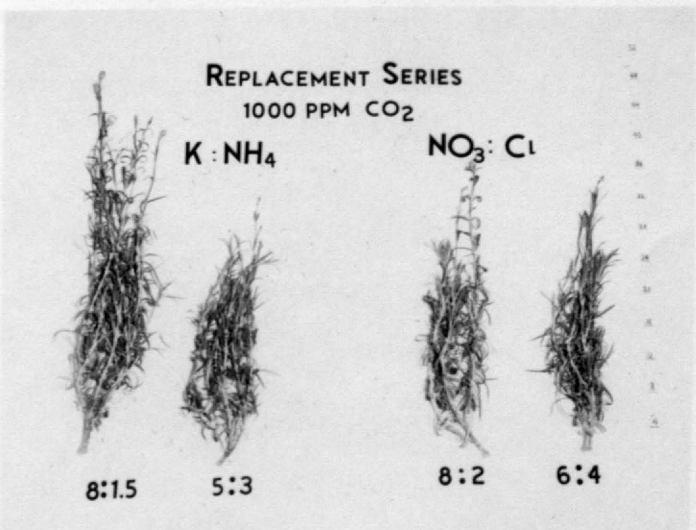

REPLACEMENT SERIES K:NA
1000 PPM CO_2
0:10
5:5
7.5:2.5
9.5:05

Fig. 9a.--Photograph of plants within the potassium-ammonium and within the nitrate-chloride replacement series grown in 485±8 ppm CO_2.

Fig. 9b.--Photograph of plants within the potassium-ammonium and within the nitrate-chloride replacement series grown in 855±11 ppm CO_2.


REPLACEMENT SERIES
500 PPM CO_2
K : NH_4
NO_3: Cl
8:1.5
5:3
8:2
6:4


REPLACEMENT SERIES
1000 PPM CO_2
K : NH_4
NO_3: Cl
8:1.5
5:3
8:2
6:4

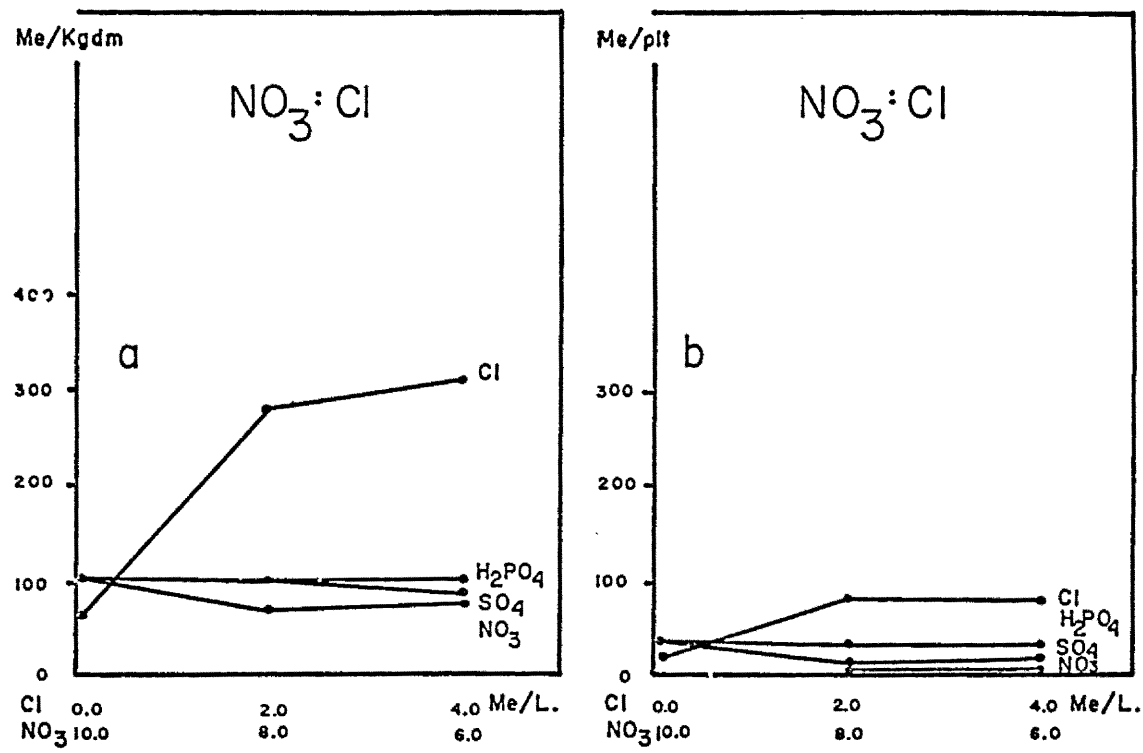


Fig. 10.--Anion replacement diagrams for the leaf tissue of carnation. Initial composition of the solutions is given in Table 15. a. Effect of nitrate-chloride replacement in the external nutrient solution on the Cl, H_2PO_4, SO_4, and NO_3 ion concentration in the plant tissue. See Figures 9a and 9b. b. Effect of nitrate-chloride replacement on the total anion content per plant.

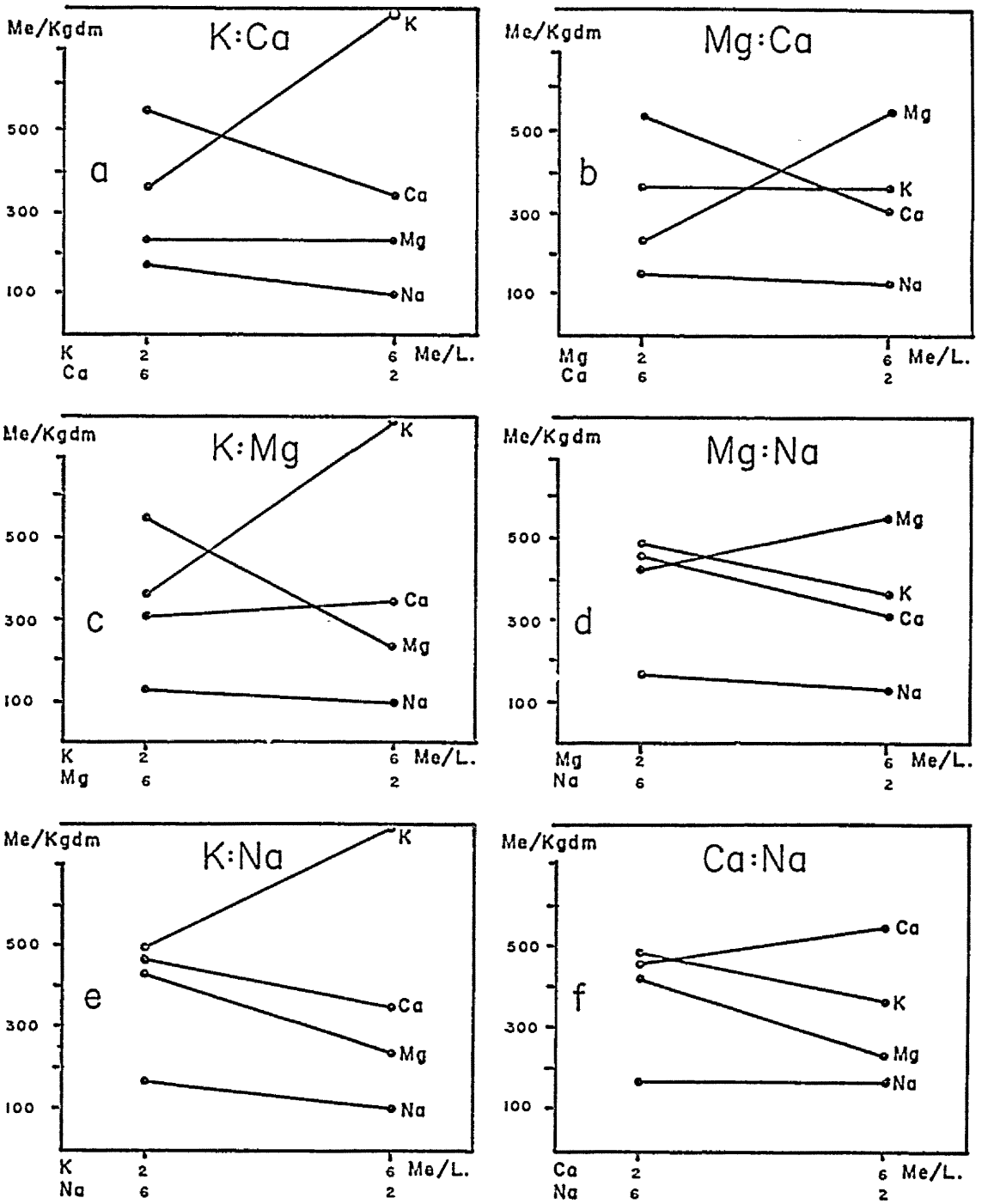


Fig. 11.--Cation replacement diagrams for the leaf tissue of carnation plants of experiment 2. Effect of replacement in the external nutrient solution on the concentration of K, Ca, Mg, and Na in the plant tissue. a. Effect of potassium-calcium replacement. b. Effect of magnesium-calcium replacement. c. Effect of potassium-magnesium replacement. d. Effect of magnesium-sodium replacement. e. Effect of potassium-sodium replacement. f. Effect of calcium-sodium replacement.

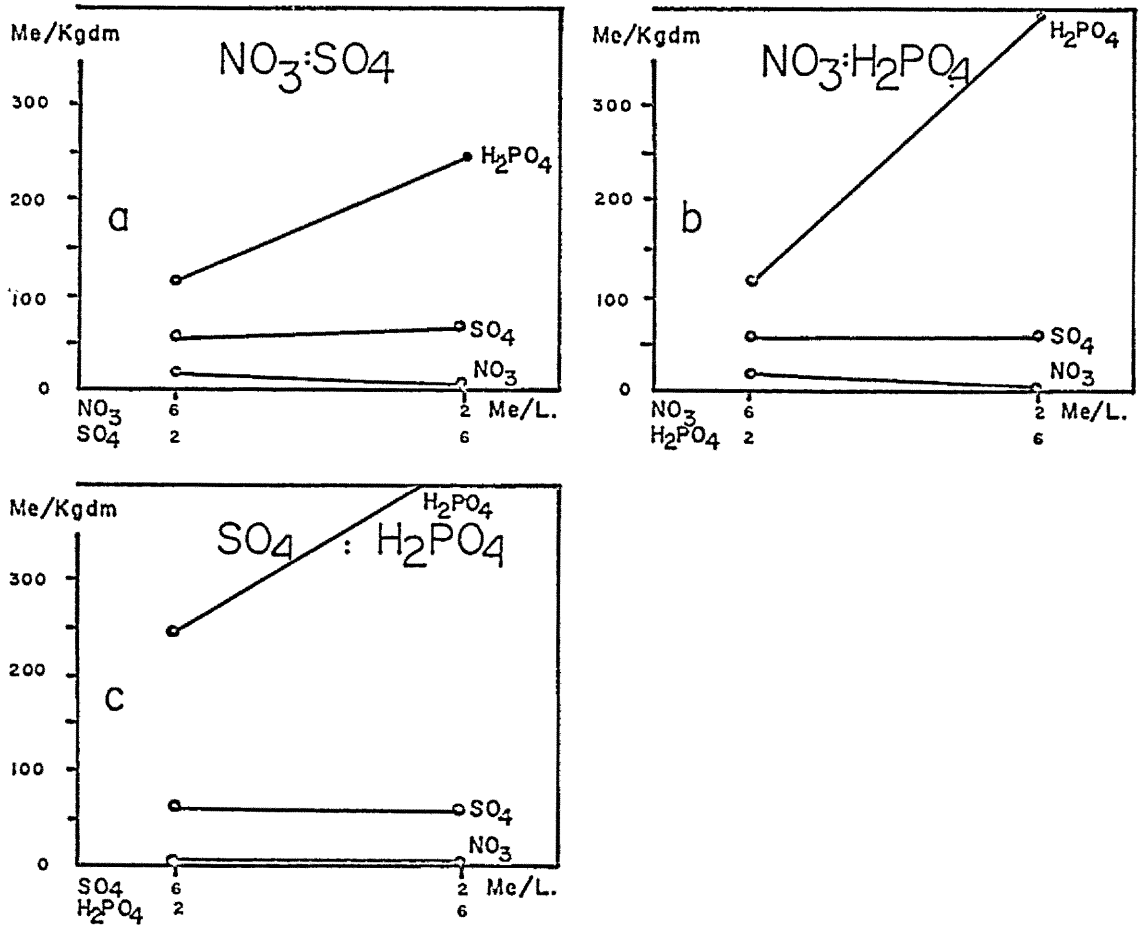


Fig. 12.--Anion replacement diagrams for the leaf tissue of carnation plants of experiment 2. Effect of replacement in the external nutrient solution on the concentration of H_2PO_4, SO_4, and NO_3 in the plant tissue. a. Effect of nitrate-sulfate replacement. b. Effect of nitrate-phosphate replacement. c. Effect of sulfate-phosphate replacement.

The $K:NH_4$ replacement series (Fig. 9 a,b) did not greatly change the ratios within the cation and anion groups (Table 24). With increasing NH_4 there was a decrease in the (C-A) content and plant yield (Fig. 3, points 10,11). The decrease in (C-A) was mainly due to an increase in inorganic anion concentration and a slight decrease in cation concentration.

There was a slight decrease in salt-cation content (C) when nitrate was supplied along with ammonium in the external nutrient solution (Fig. 15a, points 10,11). It appears that ammonium in the external nutrient solution increased the inorganic-salt content (A) at the expense of the organic salts. Ammonium in the absence of nitrate lowered the total salt content (C) at the expense of the organic salts with little or no effect on the inorganic-salt content (A). This explanation is consistent with the experiment of Tuil (1965).

5.2.2 Competitive uptake and enhancement effects

By replacing one ion with another while supplying all other ions at a constant level, the ability of one ion to be taken up to the same extent (replacement) as the other can be studied. Also, the effect of the concentration of one ion in the nutrient solution on the uptake of other ions in solution can be studied.

In the K:Ca replacement series (Fig. 6a,11a), even though the sodium and magnesium levels in the applied

nutrient solution were held constant in all treatments, there was a decrease of sodium concentration in the plant tissue with increase in potassium. This decrease in sodium with increase in potassium is also seen in Figures 11c and 11d.

Calcium when supplied at the same level as potassium in the applied solution was taken up by the plant to nearly the same extent as was potassium. Potassium and calcium are probably taken up independently as indicated by the constant horizontal line for potassium concentration in Figure 11b. The applied potassium was held constant in the nutrient solution and the potassium concentration in the plant tissue remained constant regardless of the level of applied calcium and the level of calcium in the plant tissue. If the two ions were competitive, potassium concentration in the tissue would be expected to increase with decreasing uptake (concentration) of calcium. In the carnation, potassium and calcium apparently do not inhibit, enhance, or in any other way affect each other's uptake. The ability of the carnation to absorb calcium as readily as potassium is different from that reported for gramineous plants, but in agreement with that for tobacco, citrus, and other dicotyledonous plants studied by Tuil (1965).

The enhancement effect of sodium on the uptake of potassium, calcium, and magnesium is illustrated in the K:Na replacement series (Figs. 6c,11e). A high ratio of sodium to the other cations compared to a low sodium ratio

(Figs. 11d,11e,11f) increased the concentration of the other cations in the plant tissue when these cations were at a constant level in the applied nutrient solution. This apparent enhancement effect is also seen in Figure 6c. There was a progressive decrease in calcium and magnesium concentration in the plant tissue as the sodium level in the applied solution decreased. As the potassium content of the nutrient solution was increased with subsequent decrease of the sodium content, potassium concentration in the plant tissue increased to a point and then decreased as the sodium content of the applied solution decreased (Fig. 6c).

There is probably a certain level at which sodium greatly enhances the uptake of the other cations. Sodium can become a problem, however, when the potassium level in the applied nutrient solution is extremely low (Fig. 6c). The sodium content increases slightly with decreasing potassium in the applied solution until the potassium level becomes deficient, then sodium rapidly replaces potassium in the plant tissue. The increasing sodium content with decreasing potassium content suggested that these two ions affected each other in a competitive fashion, independent of the other cations supplied.

There were probably three systems operating in cation uptake by the carnation plant. 1. When potassium was in good supply, it suppressed the uptake of sodium rather effectively. 2. When the potassium supply was deficient, the four ions K, Na, Ca, and Mg competed for uptake. 3.

Magnesium and calcium may have been taken up by a separate system in which they competed equally for uptake. The last uptake system is postulated because even though the calcium level was held constant in the applied nutrient solution (Fig. 11c), there was an increase in calcium concentration in the plant tissue when the magnesium in the applied solution was decreased.

When magnesium and calcium were held constant at 2me/liter in the applied solution (Fig. 11e), the lines for their concentration in the tissue were approximately parallel, suggesting that they are taken up by the same system at approximately equal rates.

There was no apparent competitive system involved in the uptake of chloride. Chloride appeared to be taken up over and above the normal inorganic anion uptake.

The sulfate concentration in the plant tissue remained constant regardless of the ratios and levels in the applied external solution. Phosphate concentration in the plant tissue increased linearly with increasing supply in the applied solution (Fig. 12b,c). Phosphate uptake and concentration in the plant tissue was greatly increased at a high level of sulfate in the applied solution (Fig. 12a).

The nitrate level was low in all of the treatments of experiment 2 (Fig. 12) compared to experiment 1 (Fig. 10). The low nitrate level in experiment 2 resulted in a stress on the (C-A) content associated with a lower cation content. This was probably due to the lower transport of nitrates

and organic anions to the top of the plant, resulting in the (C-A) content not being maintained at its normal value.

5.3 Discussion and Conclusions

A "normal" (C-A) content is only one of the prerequisites for optimal growth; the ion ratios in the nutrient solution affecting competitive ion uptake and the ions composing the (C-A) are critical.

The major fraction of the K was taken up through a system where the four cations K, Na, Mg, and Ca compete. Only a minor portion entered the plant through the system operative for the K and Na ions only. In the presence of ample potassium (the four-cation uptake system), sodium enhanced the uptake of the other cations in a noncompetitive way.

Potassium apparently had two functions in the plant. It was essential as such and it functioned as a positive charge in uptake accompanying organic anions translocation. As an essential element potassium could not be replaced by any other ion (Wit, et al., 1963). The cations K, Na, Mg, and Ca all functioned as positive charges and sodium was more readily taken up by the plant than was calcium or magnesium. When potassium was replaced by sodium in the nutrient solution the (C-A) content of the plant was maintained at approximately the same level (Fig. 15c, points 6 and 8). The high cation content associated with point 6 (Fig. 15a) was accompanied by a high anion content (Fig. 15b, point 6).

The high anion content was mainly the result of increased chloride and phosphate concentration in the plant tissue. In this treatment, there was a "normal" (C-A) that was not associated with an optimum yield.

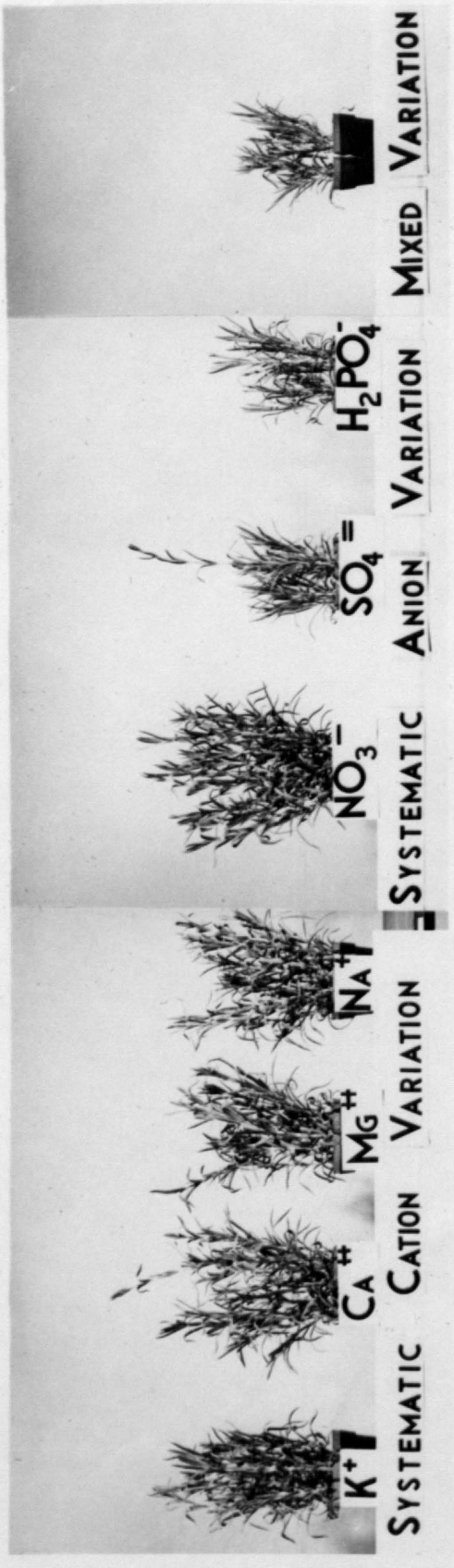
The mobility of sodium in the plant was less than that of potassium. Sodium moved readily upward, but was not able to move downward to the roots (Noggle, 1965). This resulted in an accumulation of organic salts in the leaf tissue and a consequent reduction in cation uptake because of the immobility of the organic anions (Noggle, 1965).

Other cations, even when absorbed in similar quantities, were unable to perform the specific functions of potassium because their rate of internal circulation was insufficient (Noggle, 1965). Partial substitution of other salt cations for potassium did not affect the ionic balance and growth as long as potassium remained present in sufficient amounts to perform its specific function.

Nitrate was readily absorbed and reduced before it was assimilated into organic compounds. Ammonium was also readily absorbed. Any difference in response to either form was therefore attributed to their different effects on the ionic balance of the plant. The ammonium ion probably competed with the potassium ion for uptake (Table 18, 10 and 11). When the ammonium ion was incorporated into protein its positive charge was released as H^+. The ammonium ion did not remain as a cation in the plant tissue.

Phosphate was readily absorbed by the plant and caused a stress on the (C-A) content because of the increased anion content of the tissue. Phosphate was probably taken up in luxury quantities.

Fig. 12d.--Photograph of plants within experiment 2. See Table 19 for composition of the treatment nutrient solutions and Table 20 for respective yields.


SYSTEMATIC CATION VARIATION
K+
Ca++
Mg++
Na+
SYSTEMATIC ANION VARIATION
NO3−
SO4=
H2PO4−
MIXED VARIATION

6 DESIGNING A FLOW CHART FOR USE IN DIAGNOSING THE NUTRIENT STATUS OF CARNATION

6.1 Summary

A flow chart for diagnosing the nutrient status of the carnation plant was designed using the data from experiments 1 and 2. The exit values for any specific ion were determined after considering the overall (C-A) content of the plant and the level of the other ions in the plant tissue.

6.2 Specific Requirements

The concentration ranges and the associated plant growth for the cationa K, Na, Ca, and Mg may be evaluated in figures 13b, 13d, 14b, and 14d.

The specific requirements of potassium concentration in the plant tissue range between 900 and 1100 me/kgdm. Deviations from this general concentration range in the tissue occurred in treatments, 2, 6, and 12. These points (Fig. 13b) are associated with treatments having a low supply of potassium in the applied nutrient solution.

The specific requirement of sodium concentration was in a narrow range between 25 and 150 me/kgdm. Deviation occurred in treatment 6 which was associated with an applied nutrient solution having a potassium deficiency.

The calcium requirement (Fig. 14b) had an optimum range around 800 me/kgdm. The overall range was from 50-1100 me/kgdm depending upon the composition of the applied solution.

The concentration range for magnesium in the plant tissue of experiment 1 ranged from 150-300 me/kgdm. In experiment 2 the concentration range for magnesium was similar to that of calcium. In experiment 1, the magnesium level in the applied solution was held constant at 1 me/liter; in experiment 2, it was varied from 2-6 me/liter. Further study needs to be done before a specific range for magnesium can be established.

The cation content of treatment 6 (Figs. 13, 14, point 6) was in the optimum range for all ions except Na and K. Because these levels were out of line, the yield of the plant was greatly reduced. To correct the imbalance, potassium must be supplied at a corrective level. With potassium deficient there was no control on the competitive uptake system for K and Na.

Total uptake of specific cations per plant was positively related to yield for all cations except Na (Figs. 13a, 13c, 14a, 14c).

The following milligram equivalent uptake per plant were associated with 1 gram of growth in experiment 1: 1.43 me K, 1.43 me Ca, 0.319 me Mg, and 0.043 me Na. This reduces to a ratio of 1K:1Ca:0.22Mg:0.03Na.

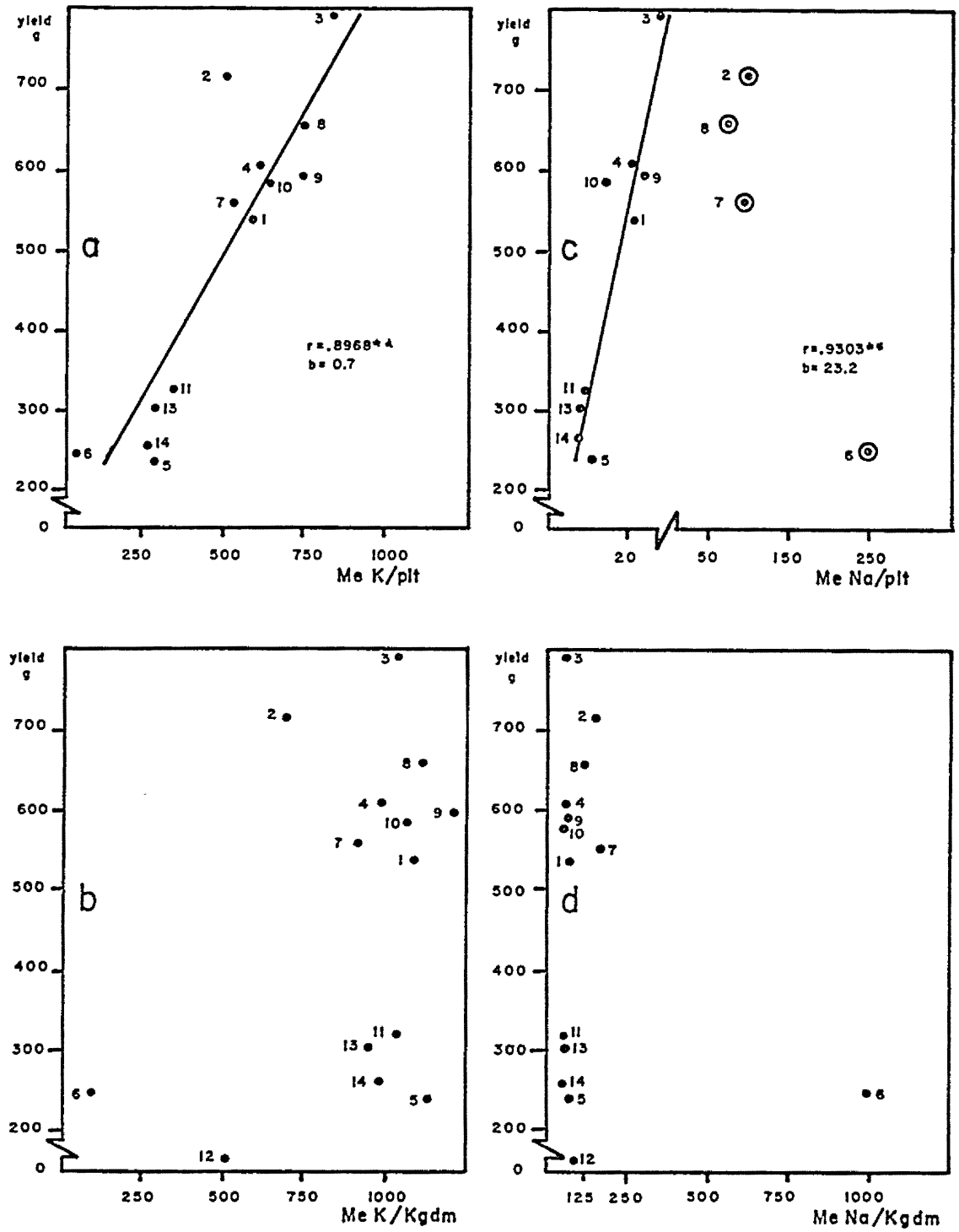


Fig. 13.--The relation between yield and cation content per plant, and the relation between yield and cation concentration within the plant. a. Relation between yield and potassium content. b. Relation between yield and potassium concentration. c. Relation between yield and sodium content. d. Relation between yield and sodium concentration.

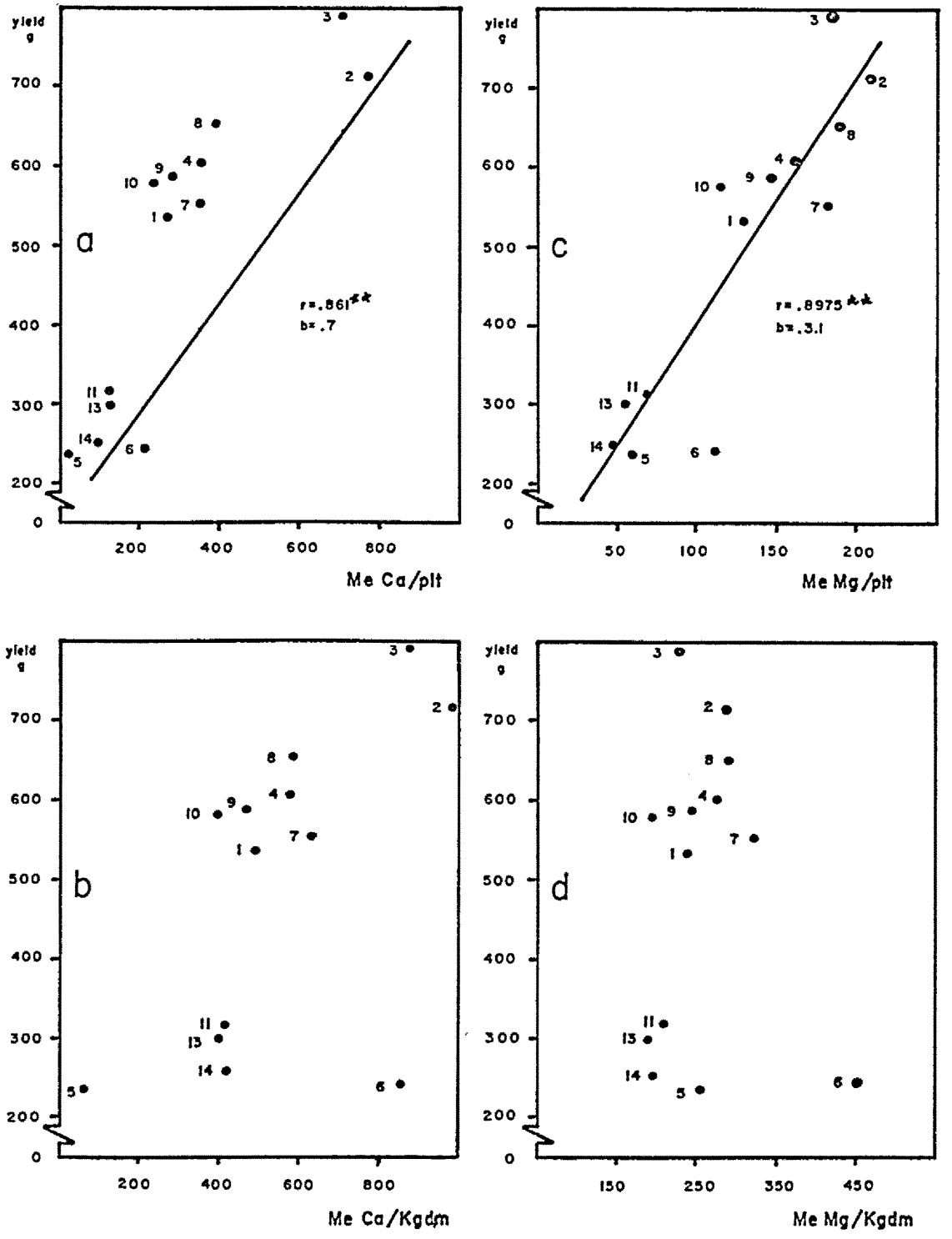


Fig. 14.--The relation between yield and cation content per plant, and the relation between yield and cation concentration within the plant. a. The relation between yield and total calcium content. b. Relation between yield and calcium concentration. c. Relation between yield and total magnesium content. d. Relation between yield and magnesium concentration.

The diagnostic values for the flow chart were determined after studying the graphs of Figures 15a,b,c, and in light of the discussion in the previous sections of this paper. An anion content greater than 400 me/kgdm always resulted in a stress on the (C-A) and a reduction in plant yield, see Figure 15b, and the lefthand side of the flow chart (Fig. 16). High anion concentrations were attributed to high chloride content (treatments 13 and 14), to replacement of the K by Na (treatment 6), and to high H_2PO_4 concentration.

The optimum (C-A) content of 1700 me/kgdm or greater was found in treatments 2, 3, 6, and 8. All of these treatments had high yields except #6 which had a low yield caused by K deficiency.

The (C-A) content ranging between 1400-1700 me/kgdm was found in nutrient treatments 1, 4, 7, 9. The main imbalance in these treatments was associated with a sub-optimal Ca content in relation to K and Na contents.

The remaining treatments having a (C-A) content less than 1400 me/kgdm were associated with a number of nutrient imbalances: 1. A general problem was high chloride content in the plant tissue. This resulted from high chloride supply in the external nutrient solution, or enhanced uptake due to Na and H_2PO_4 imbalances in the nutrient solution. 2. Luxury uptake of H_2PO_4 causing an increase in the inorganic anion concentration at the expense of organic anion production also resulted in a reduced (C-A) content. 3.

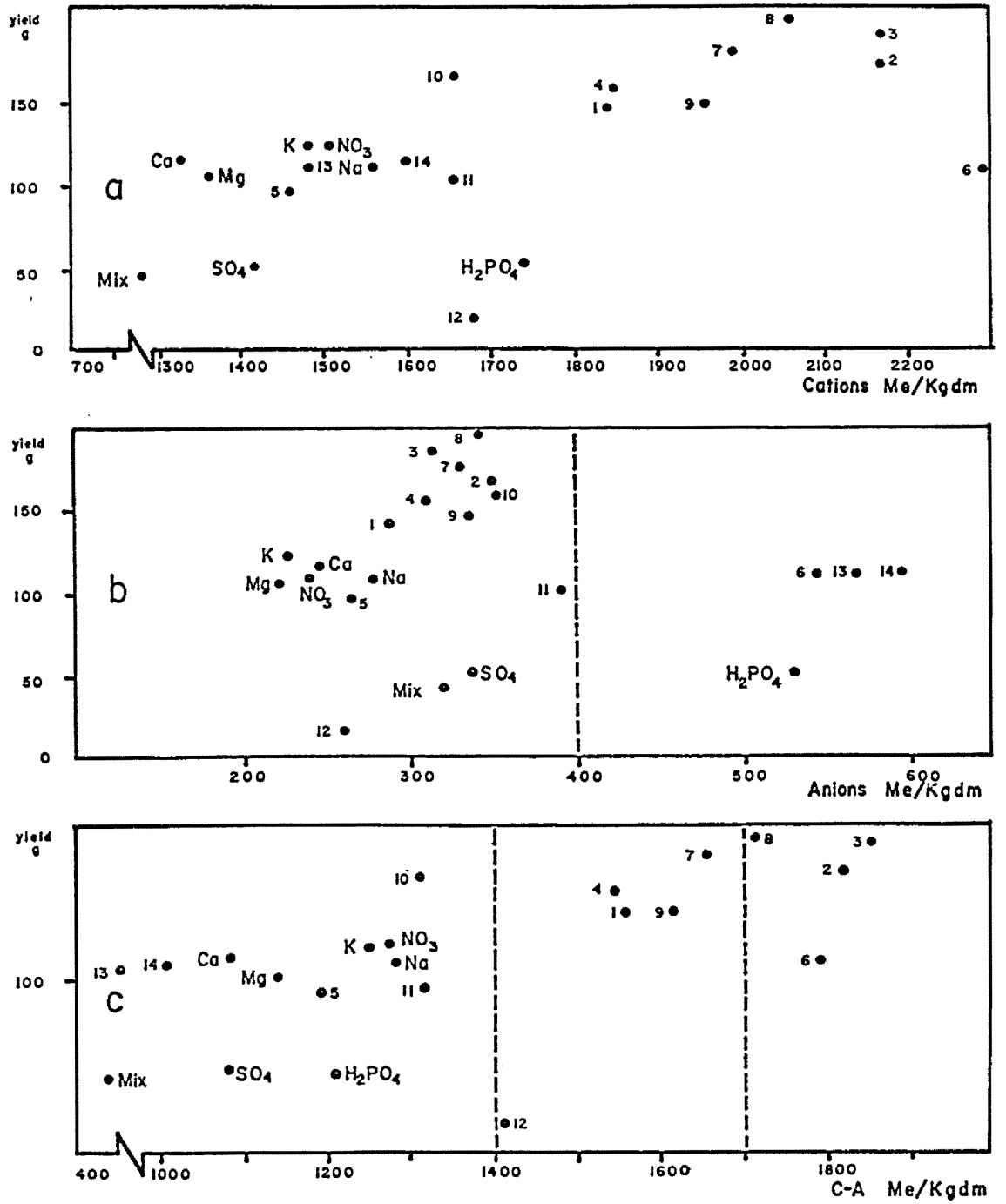


Fig. 15a.--The relation between cation concentration in the tissue and yield. b. The relation between anion concentration in the plant tissue and yield. c. Relation between (C-A) content of the plant tissue and yield. Points numbered 1-14 are results from experiment 1; other points are from experiment 2. Tissue analyses from experiment 1 are plotted against their respective plant weights after 12-week growth period. Tissue analyses from experiment 2 are plotted against their respective plant weights after 14-week growth period.

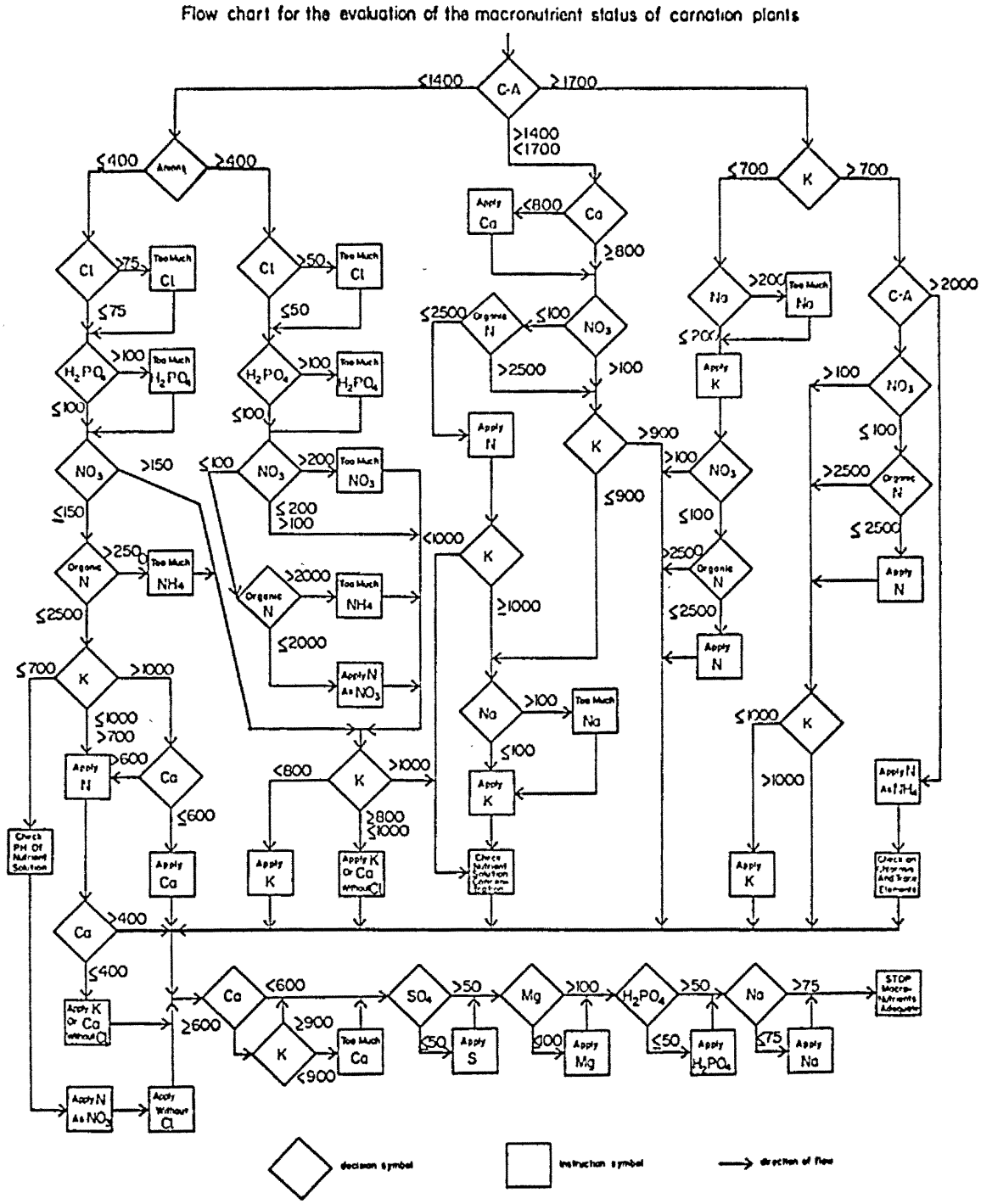


Fig. 16.--Flow chart for the evaluation of the nutrient status of carnation plants. All exit values are expressed in milligram equivalents per kilogram dry matter. H_2PO_4 refers to total phosphate. SO_4 refers to inorganic sulfate. Organic N is total nitrogen minus nitrate nitrogen expressed as milligram atoms per kilogram dry matter.

NH_4 replacement of nitrate and of other cations caused a reduced (C-A) and a reduced yield. 4. Extreme Ca deficiency in treatment 5 resulted in a reduced (C-A). 5. A low NO_3 supply resulted in a reduced (C-A) in all the nutrient treatments of experiment 2. 6. At acidic pH, 3.3, cation uptake was greatly reduced presumably by the competition of the H^+ ions. This resulted in a reduced (C-A) and consequent reduction in growth of the nutrient solution in experiment 2 labeled "mix."

6.3 Conclusions

A flow chart for diagnosing the nutrient status of the carnation plant has been designed using the data from the nutrient culture experiments. Diagnostic values for any specific ion were determined after considering the overall (C-A) content of the plant and the level of the other ions in the plant tissue.

The flow chart for carnation cannot be used on other crops. Wit, et al. (1963) have shown that the normal (C-A) content of the plant and the competitive ion uptake systems are different for other plant species. Construction of test flow charts for other plant species requires similar basic information as given here for carnation.

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A P P E N D I X

TABLE 11a.--The relation between yield and total potassium content per plant (see figure 13a)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	567	538	470	.6	.6548	3	1) $b_1=b_2$= . . . accepted
2	481	716	708	1.5	.9432*	3	
3	814	795	554	.5	.8555	3	2) Significant differences among adjusted treatment means.
4	587	607	525	.6	.8412	3	
5	263	239	383	.9	.9971**	3	3) $\bar{b}=0$ . . . rejected
6	16	246	564	.9	.1390	3	
7	509	557	529	.8	.9855**	3	
8	714	654	483	.7	.9958**	3	
9	720	589	414	.4	.9865**	3	
10	608	581	484	.8	.9911**	3	
11	322	319	422	.8	.9878**	3	
13	261	300	447	.6	.8851*	3	
14	248	257	412	.7	.9272*	3	
Ave	470	492					
Among				.7	.8968**	12	
Within				.7	.8954**	39	
Total				.7	.8963**	51	

ANALYSIS OF COVARIANCE: predictor variable X = K me content/plant
dependent variable Y = grams fresh weight/plant

TABLE 11b.--The relation between yield and potassium concentration of the carnation plant (see figure 13b)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	1063	538	486	-.2176	.3824	3	1) $b_1=b_2=$. . .accepted
2	673	715	802	-1.1229	.3412	3	2) Significant differences among adjusted treatment means.
3	1023	794	757	.3191	.3053	3	
4	965	607	590	.1604	.1790	3	3) $\bar{b}=0$ . . . rejected
5	1106	239	171	-1.7746	.6099	3	
6	66	246	547	-.3924	.2727	3	
7	897	557	563	1.3575	.8154	3	
8	1084	654	594	1.8092	.8673	3	
9	1205	589	487	.5588	.9574*	3	
10	1041	581	537	1.8186	.7407	3	
11	1007	319	287	.8354	.6930	3	
13	863	300	319	.1497	.3704	3	
Ave	916	512					
Among				.2127	.3388	11	
Within				.3539	.3431*36		
Total				.2230	.3350*47		

ANALYSIS OF COVARIANCE: predictor variable X = K, me/kg dm
dependent variable Y = grams fresh weight/plant

TABLE 12a.--The relation between yield and sodium concentration of the carnation plant (see figure 13d)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	39	538	732	-5.14	.2960	3	1) $b_1=b_2$. . . accepted
2	124	716	731	2.52	.8457	3	2) Significant differences among adjusted treatment means.
3	34	795	999	16.00	.7426	3	
4	33	607	814	16.38	.7625	3	3) $\bar{b}=0$ . . . rejected
5	37	239	437	9.55	.7492	3	
6	962	246	1478	-.67	.3543	3	
7	150	557	520	4.56	.7596	3	
8	97	654	727	16.57	.6574	3	
9	38	589	785	10.68	.5337	3	
10	24	581	807	-11.07	.3482	3	
11	25	319	541	6.79	.7604	3	
13	24	300	526	-4.52	.3987	3	
Ave	132	512					
Among				-.2740	.3848	11	
Within				2.0767	.3366*	36	
Total				-.2674	.3415*	47	

ANALYSIS OF COVARIANCE: predictor variable X = Na, me/kg dm
dependent variable Y = grams fresh weight/plant

TABLE 12b.--The relation between yield and total sodium content of plants in treatments 2,7, and 8 (see figure 13c)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
2	94	720	664	2.4	.9203*	3	1) $b_1=b_2=$. . . accepted
7	86	557	533	4.5	.9563*	3	2) Significant differences among adjusted
8	64	654	720	8.1	.9821**	3	treatment means.
Ave	80	637					3) $\bar{b}=0$ . . . rejected
Among				.2	.0544	2	
Within				4.0	.8823**	8	
Total				3.3	.7082**	10	

ANALYSIS OF COVARIANCE: predictor variable X = Na, me content/plant
dependent variable Y = grams fresh weight/plant

TABLE 12c.--The relation between yield and total sodium content of plants in treatments other than 2,6,7,8,12 (see figure 13c)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	22	551	411	43.4	.9780**	3	1) $b_1=b_2=$. . . accepted
3	27	795	566	14.3	.9255*	3	2) Significant differences among adjusted treatment means.
4	20	607	513	16.2	.9417*	3	
5	09	239	350	18.5	.9662**	3	3) $\bar{b}=0$ . . . rejected
9	22	589	449	15.8	.9235*	3	
10	14	581	606	31.7	.7874	3	
11	08	319	444	17.1	.9327*	3	
13	07	300	448	13.4	.4096	3	
14	06	257	415	22.4	.5677	3	
Ave	15	469					
Among				23.2	.9308**	8	
Within				18.6	.8092**	26	
Total				22.6	.9148**	34	

ANALYSIS OF COVARIANCE: predictor variable X = Na, me content/plant
dependent variable Y = grams fresh weight/plant

TABLE 13a.--The relation between yield and calcium, me content/plant (see figure 14a)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	268	538	575	1.4	.8922*	3	1) $b_1=b_2=$. . . accepted
2	773	716	215	.6	.8107	3	2) Significant differences among adjusted treatment means.
3	704	795	368	.5	.8657	3	
4	348	607	559	.3	.1259	3	3) $\bar{b}=0$ . . . rejected
5	16	239	544	13.9	.9624**	3	
6	209	246	346	1.1	.9444*	3	
7	353	557	503	1.3	.9927**	3	
8	387	654	564	1.2	.9956**	3	
9	281	589	612	1.2	.9952**	3	
10	235	581	654	1.8	.9555*	3	
11	133	319	500	.9	.6824	3	
13	123	300	492	1.7	.9111*	3	
14	107	257	466	1.3	.6431	3	
Ave	303	492					
Among				.7	.8610**	12	
Within				1.0	.8438**	39	
Total				.7	.8531**	51	

ANALYSIS OF COVARIANCE: predictor variable X = Ca, me content/plant
dependent variable Y = grams fresh weight/plant

TABLE 13b.--The relation between yield and calcium concentration of the plant (see figure 14b)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Coe. Coef.	df	Tests
1	498	538	564	.2650	.1496	3	1) $b_1=b_2=$. . . accepted
2	1082	716	540	-.2602	.2670	3	2) Significant differences among adjusted treatment means.
3	881	795	689	.4573	.5876	3	
4	579	607	605	-.7582	.8102	3	3) $\bar{b}=0$ . . . accepted
5	67	239	412	1.6306	.1226	3	
6	853	246	149	-.1722	.2287	3	
7	627	557	538	2.7031	.7802	3	
8	586	654	649	2.8869	.8697	3	
9	471	589	624	1.7317	.9618**	3	
10	401	581	640	1.6741	.4725	3	
11	415	319	373	.1102	.1925	3	
13	409	300	357	.4045	.2899	3	
Ave	572	512					
Among				.3836	.5449	11	
Within				.3435	.2301	36	
Total				.3818	.5040**	47	

ANALYSIS OF COVARIANCE: predictor variable X = Ca, me/kg dm
dependent variable Y = grams fresh weight/plant

TABLE 14a.--The relation between yield and magnesium, me content/plant (see figure 14c)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	130	538	534	2.9	.8921*	3	1) $b_1=b_2=$. . . accepted
2	207	716	498	2.3	.9346*	3	2) Significant differences among adjusted treatment means.
3	184	795	641	2.1	.8761	3	
4	166	607	501	3.4	.9833**	3	3) $\bar{b}=0$ . . . rejected
5	061	239	424	3.0	.9772**	3	
6	109	246	297	3.0	.9170*	3	
7	181	557	410	2.5	.9951**	3	
8	191	654	481	2.9	.9835**	3	
9	145	589	541	2.4	.9941**	3	
10	114	581	619	4.0	.9523*	3	
11	068	319	484	2.6	.8518	3	
13	057	300	496	4.2	.8933*	3	
14	050	257	471	4.6	.8036	3	
Ave	128	492					
Among				3.1	.8975**	12	
Within				2.7	.9392**	39	
Total				3.0	.9032**	51	

ANALYSIS OF COVARIANCE: predictor variable X = Mg, me content/plant
dependent variable Y = grams fresh weight/plant

TABLE 14b.--The relation between yield and magnesium concentration of the carnation plant (see figure 14d)

Nutrient Trtmt	Means X	Means Y	Adj. Y	Slope	Cor. Coef.	df	Tests
1	240	538	569	.6361	.1753	3	1) $b_1=b_2=$. . . accepted
2	289	716	687	2.0350	.4320	3	2) Significant differences among adjusted
3	230	795	837	1.9524	.5666	3	treatment means.
4	274	607	597	1.4900	.1395	3	3) $\bar{b}=0$ . . . rejected
5	250	239	258	1.7291	.7504		
6	452	246	21	-.8424	.7262	3	
7	319	557	491	5.1193	.9197*	3	
8	290	654	623	4.6607	.5740	3	
9	244	589	615	3.3307	.9567*	3	
10	196	581	666	2.2226	.2633	3	
11	212	319	383	.6217	.3649	3	
13	190	300	392	-.1856	.0664	3	
Ave	266	512					
Among				-.4473	.1675	11	
Within				1.2078*	.3336	36	
Total				-.2757	.0990	47	

ANALYSIS OF COVARIANCE: predictor variable X = Mg, me/kg dm
dependent variable Y = grams fresh weight/plant

TABLE 15.--Experiment 1: composition of the treatment nutrient solutions in milligram equivalents per liter. All solutions received 5ppm Fe Sequestrene 330, and 1 ppm boron per liter

Trt-mt	Milligram Equivalent/Liter								
	K^+	Ca^{++}	Mg^{++}	Na^+	NH_4^+	NO_3^-	$SO_4^=$	$H_2PO_4^-$	Cl^-
K-Ca Replacement									
2	2.5	9.5	1.0	0.5	000	12.0	1.0	0.5	000
3	6.0	6.0	1.0	0.5	000	12.0	1.0	0.5	000
4	9.5	2.5	1.0	0.5	000	12.0	1.0	0.5	000
5	12.0	0.0	1.0	0.5	000	12.0	1.0	0.5	000
K-Na Replacement									
6	0.0	2.5	1.0	10.0	000	12.0	1.0	0.5	000
7	5.0	2.5	1.0	5.0	000	12.0	1.0	0.5	000
8	7.5	2.5	1.0	2.5	000	12.0	1.0	0.5	000
4	9.5	2.5	1.0	0.5	000	12.0	1.0	0.5	000
$K-NH_4$ Replacement									
10	8.0	2.5	1.0	000	1.5	11.5	1.0	0.5	000
11	5.0	2.5	1.0	000	3.0	10.0	1.0	0.5	000
NO_3-Cl Replacement									
11	5.0	2.5	1.0	000	3.0	10.0	1.0	0.5	000
13	5.0	2.5	1.0	000	3.0	8.0	1.0	0.5	2.0
14	5.0	2.5	1.0	000	3.0	6.0	1.0	0.5	4.0
Concentration Series									
12 OX	tap water								
1 1X	6.2	1.64	0.655	0.328	000	7.84	0.66	.328	000
4 1-1/2X	9.5	2.5	1.000	0.5	000	12.00	1.0	0.5	000
9 2X	12.83	3.38	1.35	0.67	000	16.21	1.35	0.67	000

TABLE 16.--Experiment 1: yield after 12 week growing period

Trt-mt	Grams Fresh Weight/Plant								Ave. fr. wt.	Per-cent dm	Ave. dry wt.
	Ch 1		Ch 2		Ch 3		Ch 4				
1	114	119	105	157	189	127	191	150	144	17.4	25.1
2	143	116	145	195	214	133	204	183	167	16.5	27.6
3	178	148	169	244	213	149	184	214	186	16.6	30.9
4	137	124	183	160	199	197	108	130	155	16.0	24.8
5	063	117	059	097	086	196	142	085	095	16.7	15.9
6	090	138	086	134	118	095	108	106	110	17.3	19.0
7	077	160	187	111	171	294	196	184	177	16.9	29.9
8	156	121	164	209	217	217	269	213	196	15.5	30.4
9	099	115	164	168	242	177	146	167	147	18.4	27.0
10	125	168	154	167	216	191	177	123	165	16.4	27.1
11	056	098	100	095	138	105	087	117	100	18.8	18.8
12	012	010	015	014	018	016	013	020	015	25.9	03.9
13	129	092	110	114	109	133	104	092	110	18.0	19.8
14	108	121	101	101	158	110	101	104	113	19.1	21.6

TABLE 17.--Experiment 1: yield after 26-week growing period

Trt-mt	Grams Fresh Weight/Plant								Ave. fr. wt.	Per-cent dm	Ave. dry wt.
	Ch 1		Ch 2		Ch 3		Ch 4				
1	533	467	411	508	494	525	692	673	538	18.9	101.7
2	691	712	723	713	796	866	668	556	716	19.8	141.7
3	725	654	609	968	801	941	903	756	795	20.5	162.9
4	581	540	737	619	610	688	565	517	607	18.1	109.9
5	316	305	166	334	138	342	214	094	239	23.1	055.1
6	186	220	203	280	214	195	317	350	246	21.1	051.8
7	324	330	906	516	634	586	606	550	557	18.6	103.5
8	541	518	655	482	603	755	776	899	654	20.7	135.3
9	538	517	716	681	680	576	508	496	589	19.5	114.9
10	378	491	880	593	685	428	546	649	581	19.1	111.0
11	327	302	399	234	320	205	374	390	319	19.3	061.5
12	033	033	026	020	016	020	016	040	026	14.3	003.6
13	343	328	317	220	295	415	320	165	300	20.7	062.2
14	223	265	158	211	291	286	347	272	257	19.1	049.0

TABLE 18.--Experiment 1: tissue analyses of 26-week old plants. Values are expressed as milligram equivalents/kilogram dry matter. Each value is the mean of four individual analyses

Trtmt.	Milligram Equivalents/Kilogram Dry Matter											
	K	Ca	Mg	Na	Sum of Cations	NO_3	SO_4	H_2PO_4	Cl	Sum of Anions	(C-A)	Organic Nitrogen
1	1063	498	240	39	1840	94	86	73	34	287	1552	2065
2	673	1082	289	125	2169	109	100	91	49	350	1820	2491
3	1023	881	230	34	2168	111	83	78	45	316	1852	2266
4	965	579	274	33	1851	95	89	86	42	312	1539	2345
5	1106	67	250	37	1460	72	62	87	46	267	1193	1762
6	66	853	452	962	2333	97	110	193	143	542	1791	2791
7	897	627	319	150	1993	110	96	97	27	329	1664	2312
8	1084	586	290	97	2057	109	103	90	38	340	1717	2333
9	1205	471	244	38	1958	108	92	85	49	333	1625	2127
10	1041	401	196	24	1661	96	106	83	65	349	1312	2301
11	1007	415	212	25	1659	105	108	109	68	389	1270	2953
12	488	870	258	60	1676	3	116	35	106	260	1416	1520
13	863	409	190	24	1485	72	108	105	282	567	919	2469
14	959	419	196	26	1601	78	92	106	317	595	1006	2718

TABLE 19.--Experiment 2: composition of the treatment nutrient solutions in milligram equivalents per liter. All solutions received 5ppm Fe Sequestrene 330, 1ppm manganese sulfate, 1ppm boron

Trtmt	Milligram Equivalents Per Liter						
	K	Ca	Mg	Na	NO_3	SO_4	H_2PO_4
K	6	2	2	2	8	2	2
Ca	2	6	2	2	8	2	2
Mg	2	2	6	2	8	2	2
Na	2	2	2	6	8	2	2
NO_3	4	4	2	2	8	2	2
SO_4	4	4	2	2	2	8	2
H_2PO_4	4	4	2	2	2	2	8
Mix	2	2	2	2	8	2	6

TABLE 20.--Experiment 2: yield after 14-week growing period

Trt-mt	Grams Fresh Weight Per Plant							
	K	Ca	Mg	Na	NO_3	SO_4	H_2PO_4	Mixed
Ch 1	146.1	84.5	96.4	128.2	89.6	24.5	55.0	42.5
	94.9	100.4	110.0	126.8	133.6	10.6	38.1	42.4
	90.8	94.5	32.5	149.9	92.4	56.2	67.7	28.0
	205.3	85.7	98.3	58.0	108.0	28.1	48.0	53.8
	135.8	97.6	108.5	120.5	108.3	28.5	30.0	54.2
Ch 2	129.8	92.5	79.5	159.1	107.2	75.6	50.4	35.6
	108.6	155.6	117.6	109.6	123.2	48.6	40.9	49.2
	109.4	149.9	111.9	79.9	124.4	62.2	56.5	35.7
	85.6	140.7	101.4	85.0	162.1	46.3	61.8	56.4
	149.3	154.6	149.4	86.0	125.8	41.0	35.5	34.4
Ch 3	147.2	136.7	134.4	67.2	122.6	39.0	65.9	40.5
	128.5	111.6	101.8	101.9	47.7	55.0	42.3	35.6
	156.8	99.6	70.7	93.3	164.7	64.6	53.6	55.5
	110.8	91.7	115.1	102.5	157.3	68.4	43.3	28.8
	118.2	159.1	138.1	137.2	175.0	53.2	37.1	26.4
Ch 4	102.9	145.8	111.2	108.8	95.4	59.8	52.6	56.4
	82.8	127.8	127.8	111.4	158.0	39.4	47.8	33.6
	96.7	119.6	89.7	119.2	80.8	65.8	58.9	40.1
	147.0	96.7	100.4	101.6	167.4	77.8	51.0	31.0
	118.9	83.6	105.5	131.6	117.4	52.6	38.2	34.0

TABLE 21.--Experiment 2: yield after 14-week growing period

Trt-mt	Grams Dry Weight Per Plant							
	K	Ca	Mg	Na	NO_3	SO4	H_2PO_4	Mixed
Ch 1	24.6	14.5	17.2	22.4	16.0	17.9	10.8	9.8
	15.3	18.9	19.8	25.6	25.8	2.0	7.3	10.1
	15.4	15.2	14.4	25.8	16.1	13.0	12.8	7.1
	35.4	13.8	15.2	15.0	18.2	4.8	5.2	12.9
	22.8	15.6	18.6	29.1	19.0	5.3	10.0	12.2
Ch 2	23.5	16.3	13.6	27.0	17.1	14.9	9.5	8.6
	18.7	27.2	21.9	18.2	22.1	9.1	7.5	10.2
	13.4	29.6	18.6	12.8	20.7	11.2	9.5	8.1
	19.4	24.7	18.4	13.2	29.6	8.2	11.4	12.4
	25.2	27.0	28.3	23.9	21.8	7.8	6.5	7.2
Ch 3	24.8	26.9	21.7	10.9	21.5	7.8	11.5	9.8
	22.1	18.2	15.4	15.8	7.7	10.8	7.3	9.1
	27.7	18.5	10.0	14.7	29.0	13.2	11.0	12.7
	17.1	18.4	20.8	15.5	25.9	12.8	8.1	7.2
	19.3	25.3	25.8	23.8	29.2	9.5	7.5	8.0
Ch 4	15.2	26.2	18.8	16.9	16.6	10.8	10.6	12.8
	12.4	21.3	21.6	16.5	29.2	7.3	9.4	8.4
	13.4	20.3	14.3	20.5	13.8	12.2	11.5	7.8
	25.3	15.0	17.3	16.6	28.5	11.5	10.4	10.0
	19.4	12.6	17.8	7.4	20.4	14.0	9.6	7.9

TABLE 22.--Experiment 2: tissue analyses of 14-week old plants. Values are expressed as milligram equivalents/kilogram dry matter

Trtmt.	Milligram Equivalents/Kilogram Dry Matter											
	K	Ca	Mg	Na	Sum of Cations	NO_3	SO_4	H_2PO_4	Cl	Sum of Anions	(C-A)	Organic Nitrogen
K	798	345	238	100	1481	26	62	115	27	227	1254	1704
Ca	368	555	238	170	1332	17	70	110	47	244	1087	1503
Mg	368	311	551	130	1361	25	66	110	24	224	1137	1886
Na	496	465	427	170	1558	47	58	126	47	278	1280	2104
NO_3	591	471	353	91	1507	18	54	118	47	237	1269	1542
SO_4	831	393	140	52	1416	3	64	247	24	338	1079	1198
H_2PO_4	1023	481	189	48	1740	0	59	425	47	530	1210	930
Mixed	240	228	205	122	795	2	41	231	47	320	475	1349

TABLE 23.--Methods of tissue analysis used by the CSU Soil Testing Laboratory on the plant tissue analyses in this study

Nitrate-nitrogen content was determined by the phenoldisulfonic acid method described by Johnson and Ulrich, 1959.

Total phosphorus content was determined on 1-gram samples of ground plant material using the molybdovanadophosphoric acid procedure following a wet digestion with nitric perchloric acid mixture. Barton, 1948.

Calcium and magnesium were determined on the same digest as total phosphorus using the atomic absorption spectrophotometer.

Potassium and sodium were determined on the same digest as total phosphorus using the flame photometer.

Chloride was determined by the Mohr method of Johnson and Ulrich, 1959.

Inorganic sulfate was determined by the Bergh method described by Dijkshoorn, Lampe, and van Burg, 1960. A 2-gram sample was treated with 100 ml 20% HCL, evaporated to dryness on a waterbath, made up to 200 ml with water, filtered, then the sulfate was precipitated by adding excess Ba to an aliquot of the filtrate. After ignition in a platinum crucible the barium sulfate was weighed.

(C-A), as estimated by the ash alkalinity minus the nitrate content of the tissue, was determined by the method of Tuil, Lampe, and Dijkshoorn, 1964. A 0.5 gram sample of the air-dry powdered material was weighed and ashed in a porcelain crucible at 550 C for 3 hours. A free-flowing, grey ash was obtained which was moistened with a few drops of water and transferred with more water into a measuring flask. Ten or 20 ml of 0.1 N HCl were added (depending upon the expected alkalinity). The ash was dissolved and carbon dioxide was removed by boiling for a few minutes. After cooling, the volume was made up to 100 ml, the liquid was filtered and 50 ml of the filtrate were transferred to a small beaker. Glass and standard electrodes were inserted and the excess of HCl was titrated with standard 0.1 N NaOH under magnetic stirring up to pH 5. Ash alkalinity was calculated as: $4\ (1/2\ p\ N(HCl) - q\ N\ (NaOH))$ me/gram sample. P and q represent ml and N represents the normality of the standard HCl and NaOH, respectively.

TABLE 23.--Continued

A preliminary study to check the suitability of this method was conducted on 5 chrysanthemum tissue samples and 7 carnation tissue samples on which the (C-A) had previously been determined by analyses of the individual ions (Table 25).

There are discrepancies between the ash alkalinity value and the previously determined (C-A) on the order of 5-370 me/kg dm. Tuil, et al. (1964) reported discrepancies ranging from 200-400 me/kg dm. They attributed the discrepancies mainly to uncontrollable losses of Cl, the behavior of sulfur, analytical errors in the analysis of ionic constituents or incompleteness of the balance sheets used in previously determining the (C-A).

Further study and use will possibly reduce the discrepancies.

TABLE 24.--Experiment 1: relative ion concentrations in the plant tissue. Cation contents relative to K; anion contents relative to NO_3

Trt-mt	Relative Cations				Total cations to inorg. anions	Relative Anions			
	K	Ca	Mg	Na	C:A	NO_3	SO_4	H_2PO_4	Cl
K-Ca Replacement									
2	1.0	1.61	0.43	0.18	6.2:1	1.0	0.92	0.77	0.45
3	1.0	0.86	0.23	0.03	6.9:1	1.0	0.74	0.70	0.40
4	1.0	0.60	0.28	0.03	5.9:1	1.0	0.93	0.90	0.44
5	1.0	0.06	0.23	0.03	5.5:1	1.0	0.86	1.21	0.64
K-Na Replacement									
6	1.0	12.93	6.85	35.35	4.3:1	1.0	1.13	1.99	1.48
7	1.0	0.70	0.36	0.17	6.1:1	1.0	0.87	0.88	0.25
8	1.0	0.54	0.27	0.09	6.1:1	1.0	0.95	0.82	0.35
4	1.0	0.60	0.28	0.03	5.9:1	1.0	0.93	0.90	0.44
K-NH_4 Replacement									
10	1.0	0.39	0.19	0.02	4.8:1	1.0	1.10	0.86	0.68
11	1.0	0.41	0.21	0.03	4.3:1	1.0	1.03	1.03	0.65
NO_3-Cl Replacement									
11	1.0	0.41	0.21	0.03	4.3:1	1.0	1.03	1.03	0.65
13	1.0	0.47	0.22	0.03	2.6:1	1.0	1.50	1.50	3.92
14	1.0	0.44	0.21	0.03	2.7:1	1.0	1.18	1.36	7.63
Concentration Series									
12	1.0	1.78	0.53	0.13	6.5:1	1.0	38.70	11.70	35.30
1	1.0	0.47	0.23	0.04	6.4:1	1.0	0.92	0.78	0.36
4	1.0	0.60	0.28	0.04	5.9:1	1.0	0.93	0.90	0.44
9	1.0	0.39	0.20	0.03	5.8:1	1.0	0.86	0.79	0.45

TABLE 25.--Comparison of values for (ash alkalinity-nitrate) and (C-A). (C-A) was determined from balance-sheet values of the ionic constituents. All values are expressed as milligram equivalents/kilogram dry matter

Trtmt	Ash Alkalinity Minus Nitrate	(C-A)	Difference
Carnation			
3 (expmt 2)	1330.5	1137.4	193.1
4	1621.6	1279.9	341.7
4	1621.6	1279.9	341.7
6	1317.7	1078.7	239.0
6	1317.7	1078.7	239.0
8	657.6	474.9	182.6
8	657.6	474.9	182.6
Chrysanthemum			
3	1455.3	1450.5	4.8
3	1455.3	1450.5	4.8
6	1146.4	847.2	299.2
6	1216.0	847.22	368.8
8	1319.2	1107.1	212.1