

AN ABSTRACT OF THE THESIS OF

ISHWAR PRASAD MURARKA for the DOCTOR OF PHILOSOPHY
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Title: THE EFFECTS OF NITROGEN, POTASSIUM, AND CHLORIDE
ON NUTRIENT COMPOSITION IN RUSSET BURBANK
POTATOES (SOLANUM TUBEROSUM)

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Abstract approved _____
Thomas L. Jackson

Three greenhouse experiments were designed to measure the effects of N, K and Cl on the nutrient uptake by Russet Burbank potatoes (Solanum tuberosum). A Deschutes sandy loam soil from Powell Butte area in Central Oregon, low in potassium, was used to study these effects.

Nitrogen applications produced significant increases in dry matter yield when applied in combination with at least 100 ppm of K. It was noted that the most significant changes in nutrient composition in the plant tissues occurred when 100 ppm N was added together with at least 100 ppm of K. Yield depressions were encountered when 600 or 800 ppm N was applied. Chloride application changed the nutrient composition without causing any significant effect on total plant growth.

Nitrogen application significantly increased all nitrogen components and uptake of Ca and Mg. Greatest increases occurred with the 100 ppm N rate. Nitrogen application caused significant reduction in Cl content and uptake. Potassium content was reduced by applied N, but K uptake was reduced only when excessive N applications reduced yields.

Potassium application significantly increased K content and uptake at all levels of N. Significant decreases in Mg content and uptake were obtained whenever K was applied. Small decreases in Ca content were also noted when K was applied. Potassium application reduced the contents of certain nitrogen fractions in the plants; but the total uptake of N was generally increased when K was added.

Nitrogen and K applications changed the milliequivalent sums of cations ($C = Ca + Mg + K + Na$), anions ($A = NO_3 + P + S + Cl$), and total anions ($TA = N + P + S + Cl$). Nitrogen addition increased all three sums, whereas K application decreased the three sums. There was no significant change in cation minus anion, (C-A), content as a result of K fertilization, indicating that a constant organic acid production was maintained independent of K level. However, N application reduced the (C-A) content, indicating a compensatory reduction in the organic acid contents when the anion uptake was not matched by an equal amount of cation uptake.

It was generally found that there was a higher accumulation

of inorganic ions in the stems than in the leaves. Specifically, more $\text{NO}_3\text{-N}$ was found in the stems whereas more protein-N was found in the leaves. The total anions, (TA), however, were comparable for both plant parts.

A very important finding was that the application of Cl reduced the level of $\text{NO}_3\text{-N}$ and total N found in the plants but did not change the amount of N found in the protein fraction. Almost all of the decreases in content and total uptake of N were presumably due to the antagonism in the accumulation of NO_3^- and Cl^- ions in the plants.

It appears that the uptake data provided a better index for evaluating the responses and effects of the applied nutrients than did the content data.

The Effects of Nitrogen, Potassium and Chloride
on Nutrient Composition in Russet Burbank
Potatoes (Solanum tuberosum)

by

Ishwar Prasad Murarka

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APPROVED:

Redacted for Privacy

Professor of Soils
in charge of major

Redacted for Privacy

Head of Department of Soils

Redacted for Privacy

Dean of Graduate School

Date thesis is presented March 29, 1971

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THE EFFECTS OF NITROGEN, POTASSIUM, AND
CHLORIDE ON NUTRIENT COMPOSITION IN RUSSET
BURBANK POTATOES (SOLANUM TUBEROSUM)

INTRODUCTION

It has long been known that the absorption and accumulation of each nutrient in a plant is dependent on the absorption and accumulation of other available ions. The differential rate of absorption and the differential intensity of the depressing effects of one ion upon the absorption of other ions depends upon the charge, relative size, and activity of the ions involved. Evidence is accumulating which suggests of the presence of proper proportions of nutrient elements. This idea then leads to the "Nutrient Element Balance" concept.

The axiomatic maintenance of electroneutrality during the process of ion uptake by plants has established the existence in them of cation and anion balance. The process of ion uptake shows selective absorption, and the ions are absorbed at different rates. It is through this selective absorption and differential uptake that the ionic balance and equilibrium is attained and kept in the plants. An accumulation of organic anions, excretion of H^+ or HCO_3^- ions, adjustment in the uptake of compensatory ions of opposite charge--all play important roles in the equilibrium within plants.

In many, but not all, plant species and under certain conditions, the milliequivalent sum of the cations per unit dry weight appears

to be constant. This implies that a decrease or increase in the concentration of one cation is equivalently compensated for by a corresponding increase or decrease in another cation. Wallace (1952) showed that this cation constancy was not a general phenomenon in alfalfa. He showed that the sum of the anions within plants varied as did the sum of the cations as the supply of K or Ca was varied. DeWit, Dijkshoorn and Noggle (1963), Noggle (1966), and Dijkshoorn (1958) explained that there is a balance between cations and the combined total of the inorganic anions plus the organic anions in the plants. If the ionic balance is a general phenomenon, it is anticipated that constant charge balance may also exist in the plants. With increased anion uptake there is a temporary disruption in the ionic balance; this equilibrium is maintained by an increased uptake of some cation or by decreased production of organic acid anions. Possibly K is the most common cation which is taken up in this situation. A competition between monovalent and divalent cations also favors the uptake of K over the other cations, provided the supply of K is not limiting.

Field experiments have shown high levels of $\text{NO}_3\text{-N}$ in potato petioles associated with high levels of K and relatively low levels of Ca and Mg. This data also showed that application of KCl reduced levels of $\text{NO}_3\text{-N}$ in potato petioles. These preliminary observations indicated that phenomena associated with cation-anion balance, especially K- $\text{NO}_3\text{-Cl}$ interrelationships, might be studied in potato plants.

Accordingly greenhouse experiments were conducted to seek answers to the following questions.

1) Will increasing NO_3 levels cause an increase in K levels in potato plants?

2) Will increasing K levels cause an increase in NO_3 levels in potato plants?

3) Will the Cl level affect the K- NO_3 relationships in potato plants?

4) Will the level of K and Cl affect the conversion of N to protein in potato plants?

5) Does a cation-anion balance exist in potato plants and does fertilization influence this relationship?

LITERATURE REVIEW

Ionic uptake and accumulation are selective mechanisms which maintain balance within a plant system. Metabolic and non-metabolic processes may be involved in allowing the plants to attain this balance. Several researchers have carried out work to explain the existence of cation-anion balance in different plant species and under varying conditions of anion and cation supplies. Antagonistic and stimulatory effects of the ions with one another are considered by various workers in trying to explain these phenomena.

Stimulatory and Antagonistic Effects in Ion Uptake

Viets (1944) was among the earlier workers who concluded that calcium accelerates K and Br accumulation throughout a wide range of Ca concentrations. He also indicated that Al, Sr, Mg and Ba were also able to produce the same effect. Accordingly the effect of polyvalent cations was related to increases in the respiration rate, loss of sugar, and rate and total capacity of salt accumulation.

Collander (1941) showed that different species of higher plants varied in their composition in regard to the different cations, and that selective salt absorption in higher plants is of complex nature. He showed that K, Rb and Cs ions were absorbed with equal rapidity and that they were the most copiously accumulated ions.

Harward et al. (1956) reported that the mineral nutrient content of potato leaves was affected both by the form of N and by Cl and SO_4 concentrations. The Cl content of the leaves was markedly increased in the presence of NH_4 .

Beeson, Lyon and Barrentine (1944) used nutrient medium and correlated the ionic absorption by tomato plants with variations in the composition of the nutrient medium. They showed a positive correlation between the nutrient uptake and nutrient supply. Also noted were negative correlations between the Ca supply to the K content and Mg content, and K supply to Mg content.

Italli (1938) in his work on cation equilibrium in plants in relation to the soil concluded that for Ca, Mg, K and Na the absolute amount present in the exchangeable form is not primarily the determining factor for the uptake of these ions by the plants, but rather it is the ratio to one, two or all three of the other cations.

McCalla and Woodford (1938) found that limiting the supply of one nutrient resulted in an increased uptake of another nutrient of the same ion charge or decreased the total uptake of nutrients absorbed as ions of the opposite charge. Despite relatively large differences in ratios of individual nutrients resulting from one limiting nutrient, there was a marked tendency to maintain a balance between total anions and cations.

Hooymans (1964) investigated the effects of Ca on the uptake

of the anion Br and the cations K, Rb, and Na. He noted the increases in Ca stimulated absorption of Br. Bromine absorption was stimulated to a lesser extent by increases in K, Na and Li. The effect of the Ca ion on K uptake was found to be inhibitory, stimulatory or neutral depending on the concentration of K present. At low K concentrations the uptake of K was inhibited by Ca, but at higher K concentrations this effect was not seen.

Lundegardh (1959) calls the mutual effects of anions in the process of salt accumulation to be synergistic or antagonistic. The synergistic effects commonly appear at low concentrations. He observed the antagonistic effects at high concentrations of nitrate and chloride.

Rains, Schmid and Epstein (1964) concluded that in barley roots Rb absorption declined with time in the absence of Ca and remained constant when Ca was present. Hydrogen ions showed competitive inhibition of Rb uptake.

Overstreet and Jacobson (1952) reviewed the intimacy of the absorption reactions and nutritional toxicity problems with the growing crops. In summary they state that metabolic activity was required for ion absorption and that the process is an exchange process. The ion accumulation is markedly selective and exhibit the influence of one ion of the culture medium upon another in absorption.

Moore, Overstreet and Jacobson (1961) investigated the uptake

of Mg and its interaction with Ca in excised barley roots. The results showed the metabolic nature of Mg uptake. The Mg absorption was blocked very effectively by small amounts of Ca. Moore (1964) discussed the interactions in the absorption process. These interactions were described to regulate ion absorption and as such are not competitive in nature. It was noted that Ca most often plays the regulatory role. The addition of Ca definitely enhanced absorption of K in acid systems. This stimulation may disappear as pH 7 is approached. Furthermore, a number of polyvalent cations exhibit this effect even more strongly than Ca.

Jacobson, Moore and Hannapel (1960) showed that H^+ ion concentrations influenced the absorption of monovalent cations in single salt solutions, and the absorption of K, Rb and Cs was enhanced by Ca at low pH. Lithium absorption was repressed by Ca at all pH values. The stimulating effect of Ca is considered to be essentially a blocking of the interfering ions. Jacobson et al. (1961) confirmed this influence of Ca on Na and K absorption. Changes in Na and K ratio had little effect on the sum of the absorption of the two ions.

Elzam et al. (1967) showed that in excised corn roots the sulfates or chlorides of Ca and Mg inhibited the uptake of K in the initial phases of transport but with lengthening of the time period Ca promoted K transport. Fisher (1967) reported that K and Mg ions reduced uptake of Ca by tomato plants.

Moore, Mason and Maas (1965) used barley roots to show that Ca was accumulated in the xylem against a concentration gradient over a wide range of ambient concentrations. This was taken as evidence for Ca uptake being a metabolically mediated process.

Mason, Moore and Maas (1966) reported that UO_2^{++} showed different effects on the various cations and that the absorption of certain cations was selectively inhibited by uranyl.

Elzam and Epstein (1965) reported that Cl absorption by excised barley roots was a linear function of time when Ca was present in solution but the rate of absorption was lower in the absence of Ca. Absorption of Cl was competitively inhibited by Br but was not affected by F and I. Absorption of Cl was inhibited by 2-4 Dinitrophenol, KCN, Na-azide, Na-arsenate and Na-amytal.

Middleton and Russel (1958) used short term and long term experiments to describe the interaction of cations in absorption by plant tissues. They showed that in the short term experiments the competitive power of the ions increased with the atomic number and the valence. Hence the presence of Sr inhibited the absorption of Rb in short periods. But in the 24 hour period experiments the absorption of Rb was greatly stimulated in the presence of Sr.

Epstein and Hagen (1952) used kinetic studies and concluded that the ion absorption process is characterized by a considerable degree of selectivity. Striking discrimination between Na and K was

noted. They related this selectivity in ion uptake to competition for the same binding sites of a carrier molecule. Epstein (1961) discussed the essential role of Ca in selective cation transport by plant cells. He emphasized the essentiality of Ca ions for the integrity of the selective absorption mechanism. He showed that Na interfered with K absorption when Ca was absent, but did not interfere with K absorption in the presence of Ca. Potassium and Rb are mutually competitive in the presence of Ca.

Work of Fried and Noggle (1958) illustrates multiple site uptake of individual cations by roots. At least two distinct carrier sites for each of the ions Rb, K, Na and Sr were indicated to be present. One site dominates at higher concentrations while the second site dominates at lower ion concentrations.

In measuring cation effects on chloride fluxes and accumulation levels in barley roots Jackson and Edwards (1966) concluded that maximum level of Cl accumulation occurred when the ion influx and efflux rates became equal. The Cl fluxes were independent of the simultaneous exchange flux of the cations, but depended on the nature and concentration of the salt solution from which they originated.

Johansen, Edwards and Lonergan (1968) reported the studies on the interactions between K and Ca in their absorption by intact barley plants. They showed that increasing K concentration in nutrient solutions of low Ca concentrations (250 and 2500 μM) depressed Ca

concentration and increased the K concentration in the plants. Increasing K from 20 to 200 μM depressed Ca absorption more than increasing K from 200 to 2000 μM . It was also observed that increasing solution K increased plant K but Ca concentrations in solution did not affect plant K.

Jackson and Stief (1965) reported that K and Na influx and efflux in barley roots involve a cation exchange that is independent of simultaneous exchange of the accompanying anion. Jackson and Adams (1963) observed that the cation absorption rates were independent of the identities, concentrations and rates of absorption of the anions of the external solutions.

Osmond (1968) reported that any small net influx of monovalent cation was balanced by chloride absorption. Also that the sodium influx and K efflux were reduced by low concentrations of Ca. Pitman (1964) showed that Cl uptake from solutions of $(\text{K}+\text{Ca})\text{Cl}$ was greater than that from KCl solution of the same Cl concentration. It was considered that Cl uptake limits K uptake by beet cells and that Ca acts to increase the Cl uptake.

Arisz (1964) has presented arguments for maintained non-permeability of the plasma membrane to cations and anions other than Cl. He has explained how an apparently unequal cation and anion uptake can be realized as a result of the simultaneous uptake of the combinations of other cations and anions containing either H^+ or HCO_3^- .

Hence he prefers to speak of permeability of the membranes to ion pairs rather than individual ions.

Cation-anion Balance and Organic Acid Contents of Plant Tissues

Shear, Crane and Myers (1946) emphasized that nutrient element balance is a fundamental concept in plant nutrition. The following quote from their paper explains this concept.

Because the cation:anion ratio within the leaf is a constant, it is evident that at a given concentration of anions any increased accumulation of one or more cations must be accompanied by an equivalent decrease in one or more of the cations. Conversely, at a given concentration of cations any increased accumulation of one or more anions must be accompanied by an equivalent decrease in one or more of the other anions. Variations in the accumulation of cations or anions, however, influence not only the accumulation of other ions of the same charge but may either increase or decrease the accumulation of oppositely charged ions. Therefore, though the cation:anion ratio remains a constant, the absolute level of both may be either increased or decreased by conditions which promote the accumulation of one or more ions of either charge. For this reason, an increased or decreased accumulation of one ion may not always be accompanied by an equivalent decrease or increase in the accumulation of one or more similarly charged ions. (p. 244)

Bear and Prince (1945) earlier reported that the number of milliequivalents of $K+Ca+Mg+Na$ per unit weight of the top portions of alfalfa plants that had been grown under uniform environmental conditions tended to be constant. They further observed that the nutrient cations replaced each other to a considerable degree in alfalfa

plants without interfering with the growth in any noticeable way.

Further studies by Bear (1950) showed that the milliequivalent total of N, P, S, Cl, and Si anions tended to be equally as constant as those of the cations even though the milliequivalents of the individual anions varied greatly. He showed that the ratios of the cations sum to the anions sum tended to be a constant. So the cation - anion equivalent relationship was given as

$$\frac{K+Ca+Mg+Na}{N+P+S+Cl+Si} = \text{constant}$$

This relationship was established irrespective of the environmental conditions. Replacement of the nutrient cations and anions and ion competition were suspected to have important effects on the nutritional value of the plants.

Wallace (1952) showed that the cation constancy was not a general phenomenon in alfalfa. He showed that the anion sum for the plants also varied as did the cation sum as the supply of K or Ca was varied. Dijkshoorn (1958a) studied the relationship of N, K and Cl to the mineral balance in perennial ryegrass. He noted increased anion and cation concentrations as a result of Cl fertilization. The cation to anion ratio, however, was not changed. Potassium altered the relationship of the individual cations with no effect on the total cation concentration. Increasing N content led to a decrease in the cation anion ratio. Dijkshoorn (1958b) further concluded that NO_3

accumulation occurred until a specific yield level was reached. At first there was gradual increase in the cation:anion ratio as the grass aged. After N depletion started the cation:anion ratio increase accelerated. The relationship between cation:anion ratio and nitrogen status was related to nitrogen metabolism.

Dijkshoorn (1962) considered the accumulations of both the cations and anions and showed that in cases of low cations to anions the deficit is balanced by H^+ ion uptake. He found a cation minus anion, (C-A), content of 1100 meq/Kg and an organic anion content of 1000 meq/Kg in perennial ryegrass. DeWit et al. (1963) studied the dependence of (C-A) content on the composition of the nutrient medium in which nutrition was varied without affecting growth. The results showed that a constant (C-A) content was maintained under such conditions. If the (C-A) content is reduced because of the low availability of cations, the stress on the (C-A) content is accompanied by a reduction of growth. They mentioned that an excessive cation (C) content or (C-A) content may occur in the case of K shortage in the presence of any other cation which is readily taken up. Although these other ions may function as a positive charge the K ion seems to be the only one which varied with the changes in excess organic anions.

Said (1959) showed that the ratio of cation (C) and anion (A) uptake may decrease with increasing nitrate metabolism. It was

assumed that the uptakes of cations and anions from neutral salts are directly coupled. Pucher, Vickery and Wakeman (1938) have shown, in tobacco grown under controlled fertilizer conditions, a large excess of positive ions over inorganic anions and this excess is balanced by the ether soluble organic acids.

Pierce and Appleman (1943) also showed a very high correlation between the excess inorganic cations and the ether soluble organic acids for 11 different plants species grown in the greenhouse under controlled solution culture.

Ulrich (1941) showed that in excised barley roots the shifts in relative cation and anion absorption changed the organic acid content of the roots and that these changes were reflected in the respiratory quotients. The R.Q. was less than one when organic acids were formed and greater than one when they decreased in amount. He then concluded that the acids were associated directly or indirectly with respiration. His data also showed that the organic acid adjustments to changes in the acid-base balance in the root cells were rapid. Kirkby and DeKock (1965) concluded that the ratio of cations:anions is not constant but is particularly dependent on the level of N supply, the form of N nutrition, and the age of the plant. Their results showed a cation:anion ratio varying between 0.2 and 1.0 with age of the brussels sprouts leaves.

Kirkby and Mengel (1967) found that the diffusible (unbound)

cation:anion ratios in all tissues of tomato plant were close to unity. They inferred that this balance was due to different cation species competing for the bulk of anions and vice-versa. In their experiments they also observed that the increase in supply of one ion species in the nutrient medium decreased the uptake of similarly charged ion species where there was no specific competition for a carrier site. Boawn et al. (1960) showed that N/K ratios were all above 1 and increased to 1.8 with added N. The sum of cations initially decreased and then increased with added N.

Briggs, Hope and Robertson (1961) in their discussion on metabolism, ion uptake, and accumulation pointed out that anions are produced by metabolic activity from neutral substances while cations from the external environment exchange for the hydrogen ions produced simultaneously with the anions. The first effect of metabolic processes is the accumulation process, and the second is the change in the organic acid anions of low molecular weight and the resultant change in the number of cations entering from the environment. The changes in the ionic environment are followed by relatively rapid changes in the metabolisms and consequent changes in the amounts of organic acids.

Nutritional Effects on Nitrogen Metabolism

Webster and Varner (1954) observed increases in protein

synthesis in cell free extracts when K was added. They further demonstrated the essentiality of K for the biosynthesis of peptide bonds.

Durzen and Steward (1967) showed an increase in glutamine in spruce and pine trees when K was low. Nason and McElroy (1963) concluded that K deficiency leads to increased residual carbohydrate content as a result of decreased protein synthesis.

Harper and Paulsen (1968) showed that the deficiency of the nutrients N, P, K, Ca, Mg, S and Fe decreased the specific activity of nitrate reductase from Triticum aestivum L. seedlings. Nitrate content was also decreased when N, P, K, Ca and Mg were deficient.

MacLeod and Carson (1969) reported that total N, protein N, nonprotein N and reduced N increased in mature grain when N concentration in nutrient culture solution was increased. Increased dry matter production was obtained with P and K concentration increases in the nutrient solution but the contents of all N fractions decreased due to these P and K concentration increases. Total protein N and non-protein N production were greater at higher rates of K and P principally because of the yield increases. Potassium appeared to have more effect on the nitrogen metabolism.

Cummings and Teel (1965) reported increased K content resulting in herbage with higher levels of true protein, less non-protein N and less malate. Steward et al. (1959) have shown that uptake of

nitrate and the further reduction and conversion of nitrogen to organic forms is restricted more than the protein synthesis under deficiency of certain mineral elements. In cases where K, Ca or S were deficient the conversion of organic nitrogen compounds to protein is more affected than the uptake of nitrate and the reduction following the uptake.

Sutcliffe (1960) used chloramphenicol antibiotic and showed a close relationship between the salt absorption and protein metabolism. Inhibition by chloramphenicol was attributed to a general effect on protein turnover and thereby on salt absorption because of the small turnover of the carrier protein molecules. Teel (1962) reported a marked accumulation of malate and soluble nitrogen compounds under low K regimes but with optimum potassium regimes increase in true protein synthesis was associated with declining malate and soluble nitrogen pools. Adams and Sheard (1966) showed that ammonia N increased as a result of K deficiency whereas sulfur deficiency increased nitrate and amide N both in orchardgrass and alfalfa plants. Of the 18 amino acids determined, arginine, glutamic acid and aspartic acid were increased by S deficiency but K had no effect. Leucine and lysine were increased in K deficient plants. Alanine was decreased by K deficiency. Glycine, valine, isoleucine, tryosine, phenylalanine, tryptophan, histidine and ornithine increased under conditions of K or S deficiency.

MATERIALS AND METHODS

Preparation of the Experimental Materials

A Deschutes sandy loam soil from Powell Butte in Central Oregon was used in the greenhouse experiments for this study. The soil was low in available K and as such provided an excellent material for these experiments. The soil was collected from the field and brought to the greenhouse where it was air dried and then screened through a three quarter inch iron mesh grate to remove stones and plant residue. Chemical analyses were carried out on a subsample from this soil by the Oregon State University Soil Testing Laboratory. The results of these analyses are shown in Table 1.

Table 1. Chemical analyses of the Deschutes soil

pH	P (ppm)	K (ppm)	Ca (meq/100g)	Mg (meq/100g)	Na (meq/100g)	CEC (meq/100g)
6.0	22	152	6.6	5.0	0.42	12.9

Six and one half pounds of the soil were weighed into plastic greenhouse pots measuring 7-1/2 inches in diameter and 6-1/2 inches in depth. One hole had been drilled in the bottom of the pots and short "Tygon" tubes were fitted in these holes so that the drainage water could be collected and returned to the pots. Each pot was separately incubated after adding six milliequivalents of Ca per 100 gram soil.

After the addition of freshly precipitated CaCO_3 the pots were thoroughly mixed and brought to field capacity with distilled water. Twenty-one days of incubation were allowed before the fertilizer treatments were applied.

Russet potato (Solanum tuberosum) buds were scooped out with a melon ball cutter to insure uniform seed pieces. These were then treated with "Capatan" and allowed to soak for a day prior to planting in greenhouse flats. These seeds were allowed to grow for ten days in the flats filled with agricultural grade "Perlite." Three seedlings were transplanted in each one of the fertilized pots used in the experiments. The plants were then allowed to grow for 30 days in the greenhouse, and were then harvested; the plants were starting to bloom and the first tubers were set at this time. The entire above ground portions of the plants were harvested and kept together for experiments I and II. The leaves were separated from the stems and petioles in experiment III. The plant material was dried in a force draft oven at 70°C for about a week and then finely ground with a laboratory "Wiley" mill. This ground material was used in the laboratory for chemical determinations.

The greenhouse temperature was kept between $80\text{-}85^\circ\text{F}$ during the days and about 50°F during the nights. Overhead fluorescent lights were used to provide supplemental light for growing the plants under a 16 hour day length period. A cooler system with an additional

turbulator ceiling fan was used to avoid the formation of air pockets in the greenhouse.

Experimental Design and Treatments

Experiments I and II were carried out in the summer of 1969, and experiment III was conducted during the summer of 1970. All three experiments were designed as factorials with treatments replicated four times in experiments I and II and three times in experiment III. The treatment levels were chosen to provide a wide range which was from growth limiting to abundant supplies of the nutrients. Experiment I used five levels each of N and K, Experiment II used four levels of N and K and two levels of Cl. Experiment III used five levels of N and four levels of K. The following table (Table 2) shows the list of the treatment levels used in these experiments.

Table 2. List of the treatment levels used in the three experiments

Experiment Number	Treatment	Rate (ppm)
I	Nitrogen as $\text{NO}_3(\text{N})$ Potassium (K) Chloride (Cl)	0, 100, 200, 300, 400 0, 50, 100, 200, 400 0
II	Nitrogen as $\text{NO}_3(\text{N})$ Potassium (K) Chloride (Cl)	0, 100, 200, 300 0, 50, 100, 200 100, 200
III	Nitrogen as $\text{NO}_3(\text{N})$ Potassium (K) Chloride (Cl)	100, 200, 400, 600, 800 100, 200, 400, 600 100

Potassium was applied as KNO_3 , KCl or KOH depending upon the K treatment in association with the other factors. Nitrogen treatment was applied either as KNO_3 or $\text{Ca}(\text{NO}_3)_2$. CaCl_2 or KCl was used as the source of Cl. Blanket application of 50 ppm P as H_3PO_4 , 30 ppm of S as MgSO_4 , and 5 ppm of Zn as ZnSO_4 were added to each pot. All fertilizer treatments were applied as solutions with the correct amounts measured for each pot. The pots were allowed to dry about five days after the fertilizer application and then were individually mixed.

Blocks in the greenhouse benches constituted the replications and were randomly assigned. Pots within a block were randomly placed with re-randomization three times during the period of plant growth so that the border effect and bench location sources of variations were minimized.

Plant Analysis

One-half gram of the dry, ground plant sample was weighed out and digested with HNO_3 and HClO_4 and brought to 100 ml volumes. Samples were diluted and Sr added for Ca and Mg determinations; K, Ca and Mg were measured using a Perkin Elmer Model 303 atomic absorption spectrophotometer. In experiments I and II, Na was determined by flame emission spectrophotometer but an atomic absorption unit was used in determining Na in experiment III. The

molybdevanadophosphoric acid colorimetric method by Jackson (1958) was used to determine P in the samples. Chloride was measured on sample extracts prepared with 0.02 M formic acid. Beckman silver electrodes together with fiber junction reference (Silver-Silver chloride internals) electrodes were used in recording the electrical potential of the sample extracts and then converting to percentage chloride values with the help of the standard curve obtained at the time of analysis.

A modified micro Kejhdaahl method, to include $\text{NO}_3\text{-N}$, was used to determine total N in the plant tissues (Johnson and Ulrich, 1959). Nitrate - N was obtained by the Devarda's alloy distillation procedure (Bremmer and Keeney, 1965). Protein - N was determined by the method of Steward and Porter (1969). The method consists of 70% boiling alcohol extraction followed by the micro-Kejhdaahl procedure on the remaining plant residue.

Statistical Analysis

Analysis of variance for factorial designs (Cochran and Cox, 1956) was employed in determining the effects of the treatments used in the study. Multiple regression analysis was carried out to obtain the functional relationships of the variables of interest. Most of the statistical analysis was done on the CDC 3300 computer at the Oregon State University Computer Center. Programs from the Statistical

Program Library (1969) were used. Additional computations were done on a desk calculator.

The models used in the regression procedure were chosen on the basis of relationships noted in the preliminary examination of the data. Equations in the forms of second degree polynomials constituted the chosen models, and are shown in the following:

Two different regression models were chosen for the three experiments. Model I was used in fitting the data from experiments I and III and model II was used in fitting the data from experiment II.

$$\text{Model I - } Y_i = b_0 + b_1 X_{1i} + b_2 X_{2i} + b_3 X_{3i} + b_5 X_{5i} + b_6 X_{6i} + e_i$$

$$\text{Model II - } Y_i = b_0 + b_1 X_{1i} + b_2 X_{2i} + b_3 X_{3i} + b_4 X_{4i} + b_5 X_{5i} + b_6 X_{6i} + b_7 X_{7i} + e_i$$

Where Y_i = response variables measured as dependent variables and were yield (g/pot), (meq/100g) or (meq/pot) of N, $\text{NO}_3\text{-N}$, Protein-N, Ca, Mg, K and Cl.

b_0 = constant of regression

$b_1, b_2, b_3, b_4, b_5, b_6, b_7$ = regression coefficients describing the changes in the response variables with the change in appropriate independent variable

X_{1i} = parts per thousand of applied N with values from the set 0, 0.1, 0.2, 0.3, 0.4, 0.6, and 0.8.

X_{2i} = parts per thousand of applied K with values from the set 0, 0.05, 0.1, 0.2, 0.4, 0.6.

X_{3i} = interaction variable transform for $X_1 \times X_2$ with variable values from the product set.

X_{4i} = parts per thousand of applied Cl with values from the set 0.1 and 0.2.

X_{5i}, X_{6i}, X_{7i} = polynomial variable transforms for X_1, X_2, X_4 respectively, to give the quadratic effects of the applied nutrients.

e_i = random error which is assumed to be NID $(0, \sigma^2)$.

Since stepwise multiple regression procedure was used, the fitted equations did not always contain all the coefficients of the two models.

RESULTS AND DISCUSSION

Plant Symptoms and Yield Responses to N, K and Cl Applications

In experiments I and II, the low levels of N and K were inadequate to meet the plant requirements and hence deficiency symptoms developed on the plants receiving such treatments. Experiment III was designed to exclude the growth responses; therefore, treatments were selected to provide conditions which adequately met the plant requirements for the two nutrients.

Deficiency symptoms were observed when low rates of N and K were applied in experiments I and II, regardless of the level of Cl. Normal plants were produced at the higher rates of applications of the two nutrients. Chlorotic and bronzed leaves were noticed on the entire lower half of the plants when both N and K were deficient. The severity of the symptoms was reduced when only one of the two nutrients was inadequate. When one or both of the nutrients were deficient, smaller plants were produced with the yellowing and/or bronzing of the leaves taking place as early as the seventh day after transplanting. No deficiency symptoms were observed at the highest rates of the applied nutrients. It was suspected that Cl applications may have increased the severity of N deficiency symptoms.

The yield data in Tables 3 and 4 show that there were highly

significant differences in dry matter production caused by N and K applications. In experiments I and II, the 100 ppm N rate accounted for most of the yield increases whenever K was not limiting. The subsequent higher rates of N application at any fixed rate of K were ineffective in further increasing the yields to any significant extent (Table 3). In experiment III, N application did not change the total dry matter production up to 400 ppm N application, but the 600 and 800 ppm N rates caused reductions in the yields. At these high rates of N applications the large amounts of salt added to the soil may have resulted in reduced vegetative growth and delayed maturity.

The increases in dry matter yields were large when K was applied. In all the experiments, the yields due to added K, increased until 200 ppm K was applied, beyond which the yield increases were smaller in magnitude (Tables 3 and 4). The average dry matter yield increased from 5.7 g/pot at zero K to 8.5 g/pot for 200 ppm K in experiment I. Similar increases were obtained for experiment II. The yields were higher for experiment III but the nature of the response to K application remained unchanged.

In experiments I and II, N application did not show significant yield increases when 0 or 50 ppm K was applied. However, when 100, 200 or 400 ppm K was applied, the responses to N application were large (Table 3). This was indicated by the significant and positive N x K interaction effect.

Table 3. The effects of N, K and Cl on dry matter yield (g/pot).

Experiment I

K(ppm) \ N(ppm)	N(ppm)					Ave.
	0	100	200	300	400	
0	5.33	6.15	5.75	5.54	5.49	5.7
50	5.42	6.64	6.43	6.26	6.45	6.2
100	6.38	6.79	7.63	7.14	7.81	7.0
200	6.54	8.15	9.05	9.50	8.99	8.5
400	6.58	9.11	9.23	9.46	9.79	8.8
Ave.	6.15	7.37	7.60	7.60	7.70	

Experiment II (with Cl)

K(ppm) \ N(ppm)	N(ppm)				Ave.
	0	100	200	300	
0	5.23	5.59	5.71	5.19	5.40
50	5.44	5.82	6.34	6.00	5.90
100	6.70	8.19	7.02	7.71	7.40
200	6.84	7.98	7.98	8.69	7.90
Ave.	6.10	6.90	6.80	6.90	

ppm of applied Cl		
0	100	200
6.8	6.7	6.6

All entries in the table for experiment I are averages for four observations.

All entries in the table for experiment II are averages for eight observations.

The remaining entries in the table are averages for 64 observations.

Table 4. The effects of N and K on dry matter yield (g/pot).

K(ppm) \ N(ppm)		100	200	400	600	800	Average
		<u>Experiment III</u>					
100	stems	3.99	4.26	4.51	4.21	3.12	4.02
	leaves	5.77	6.14	6.24	4.97	4.01	5.43
	total	9.77	10.40	10.73	9.17	7.13	9.44
200	stems	4.81	4.66	4.34	4.41	3.91	4.42
	leaves	6.11	5.91	6.05	5.43	4.87	5.67
	total	10.90	10.57	10.37	9.83	8.77	10.09
400	stems	5.37	4.71	4.42	4.87	3.84	4.64
	leaves	6.64	6.04	5.81	6.14	4.54	5.83
	total	12.00	10.77	10.23	11.00	8.37	10.47
600	stems	4.49	5.17	4.91	4.17	4.11	4.57
	leaves	6.50	6.61	6.27	5.02	5.34	5.95
	total	10.97	11.80	11.17	9.17	9.47	10.51
Average	stems	4.67	4.70	4.54	4.42	3.74	
	leaves	6.25	6.17	6.09	5.39	4.69	
	total	10.91	10.88	10.63	9.79	8.43	

All entries in the table are averages for three observations.

The highest yield of 9.8 g/pot was obtained with the 400 ppm N and 400 ppm K treatment combination in experiment I and the lowest yield of 5.3 g/pot was obtained from the check plot where N and K were not added. The 400 ppm N and K application rates were not included in experiment II; the highest yield of 8.7 g/pot was obtained from the 300 ppm N and 200 ppm K treatment combination. A yield of 5.2 g/pot was obtained for the check treatment in this experiment. In experiment III, the maximum yield of 12.00 g/pot was obtained with 400 ppm K and 100 ppm N treatment combination and the minimum yield of 7.1 g/pot was obtained from 800 ppm N and 100 ppm K treatment combination.

There was no significant yield response to Cl application (Table 3). This was obviously due to very small Cl requirements by higher plants. There was enough chloride present in the soil and as such no chloride deficiency was expected.

The responses to N and K applications observed in these experiments are primarily due to the limiting supplies of the two nutrients in the soil. The dependence of response to N application on applied K confirms that K was the most limiting nutrient. The extremes in the availability of the two nutrients created conditions limiting plant growth on the one hand and excess supplies for plant growth on the other hand.

Contents and Uptake of Mineral Nutrients
as Affected by N, K and Cl Applications

Nitrogen, potassium, calcium, magnesium and chloride are the five nutrient effects considered in the following discussion. Sodium was found in negligible amounts, and since there is no indication of its metabolic essentiality for potatoes it is not discussed in this dissertation. Phosphorous and sulfur remained unaffected beyond the dilution effect and are also not included in the present discussion. However, all three nutrients are included in the ionic balance considerations in the later section..

Throughout this thesis, the word content is used to denote concentrations of the nutrients; accumulation and uptake are used for the total amounts of the nutrients removed from the soil by the plants.

Experiments I and II were designed to measure the effects of N, K and Cl applications on the nutrient contents and uptake by the intact plants. Experiment III was designed to partition the effects of N and K applications on the nutrient contents and uptake by the leaves and the stems^{1/}. The two components were combined to obtain the total uptake.

^{1/} Stem is used to include all non-leafy plant tissues with the exception of the roots. This is done for ease of nomenclature.

Contents and Total Uptake of N

Table 5 shows the content and total uptake of N for the various treatments for experiments I and II. Statistical analysis of the data revealed that both N and K applications significantly affected the contents and total uptake of N in the plants. Also there was a significant N x K interaction effect on the total uptake of N by the plants in both the experiments. Since the N x K interaction effect was highly significant in these experiments, the N and K main effects are not discussed separately.

Generally the highest N contents were observed when K was not applied. As K applications were increased from 0 to 50, 100, 200 and 400 ppm in experiment I, the N contents were decreased (Table 5). However, the largest single increases in the N contents at all rates of added K (Figures 1a, b) were achieved with 100 ppm of added N. The effect of nitrogen on the N content was marked at all rates of applied K. A similar response was observed for experiment II (Table 5, Figure 1b).

Table 5 and Figures 2a and 2b show that N uptake was increased by application of both N and K in experiments I and II. The positive N x K interaction indicates that the decrease in N content was largely a dilution effect and that K application increased the total uptake of N by the plants. The growth responses, as depicted by dry matter

Table 5. The effects of N and K on the content and total uptake of N.

K(ppm)	N(ppm)	0		100		200		300		400		Average	
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment I													
	0	238.21	12.62	313.75	17.59	334.11	18.12	370.5	20.53	367.3	20.31	324.8	17.83
	50	219.64	11.15	303.93	20.06	343.22	22.05	362.0	22.76	381.3	24.59	322.0	20.12
	100	203.21	12.90	339.29	19.62	345.18	26.27	364.3	26.02	349.6	27.34	320.3	22.43
	200	190.89	12.46	266.97	21.54	322.50	29.18	326.6	30.96	342.0	30.65	289.8	24.96
	400	193.04	12.69	332.14	30.78	323.22	29.79	331.3	31.30	300.9	29.13	296.1	26.60
	Ave.	209.00	12.16	311.21	21.78	333.64	25.08	350.9	26.31	348.2	26.41		
K(ppm)	N(ppm)	0		100		200		300		Average			
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment II (with chloride)													
	0	237.5	12.37	319.0	17.59	328.5	18.69	355.0	18.60	310.0	16.81		
	50	213.3	11.51	310.1	17.91	335.9	21.41	359.9	21.57	304.8	18.10		
	100	187.1	12.59	260.1	21.19	327.0	22.95	325.6	25.05	275.0	20.44		
	200	178.6	12.19	273.3	21.74	312.9	25.02	316.1	27.41	270.2	21.59		
	Ave.	208.1	12.16	290.6	19.61	326.1	23.22	339.2	23.16				

In Experiment I, all entries in the table are averages for four observations.

In Experiment II, all entries in the table are averages for eight observations.

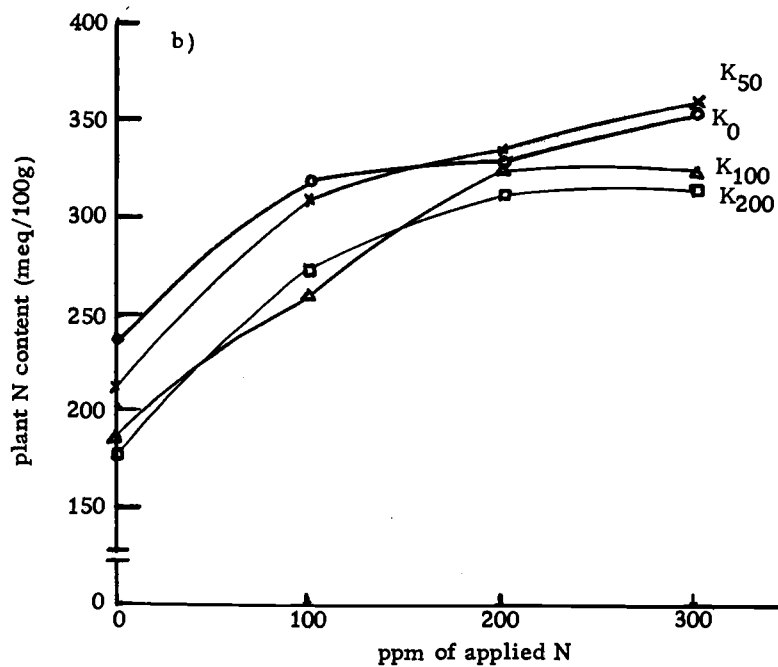
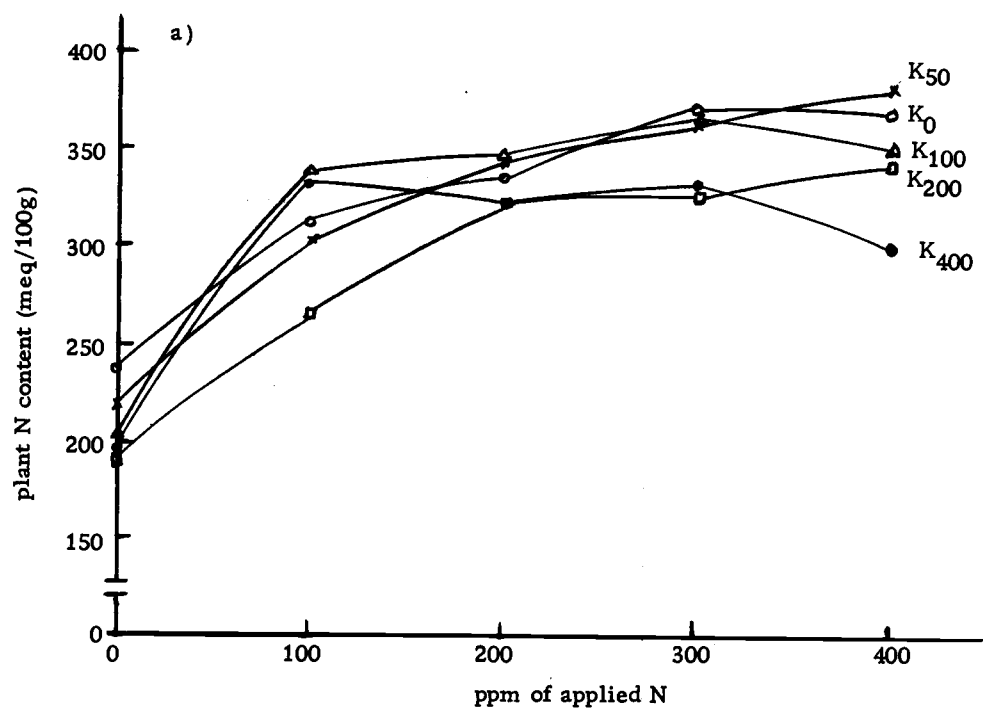


Figure 1. The effects of N and K on the content of N for (a) experiment I, and (b) experiment II.

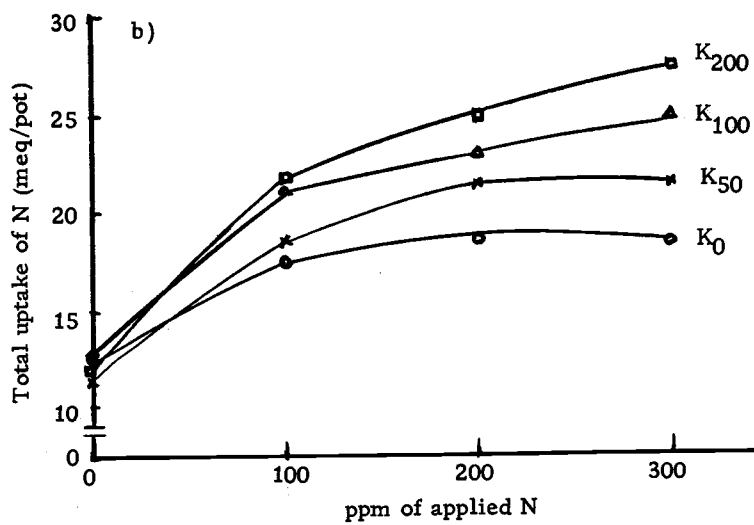
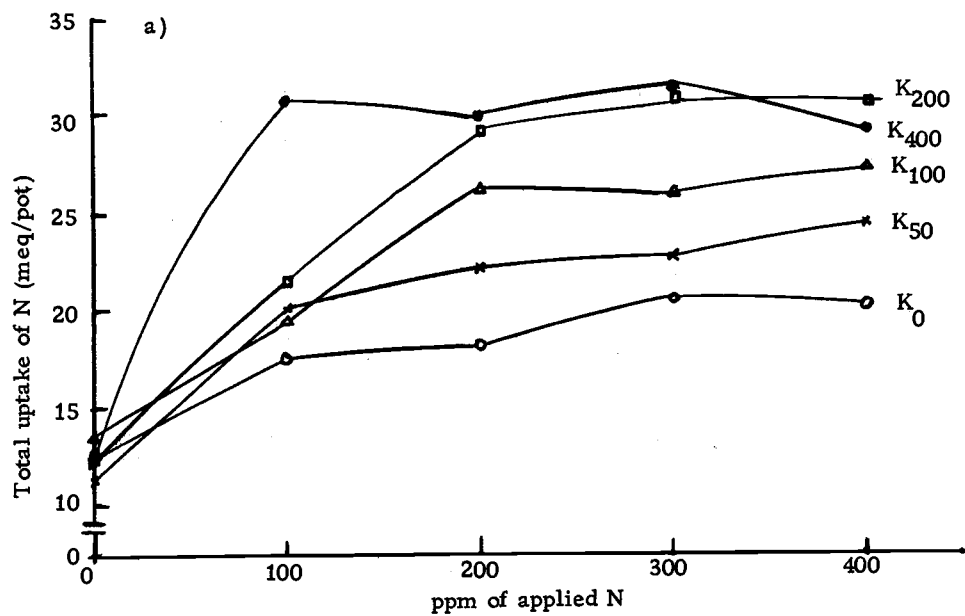


Figure 2. The effects of N and K on the total uptake of N for (a) experiment I, and (b) experiment II.

yields, also showed a positive interaction between N and K and supports the hypothesis that N utilization and uptake is enhanced by the sufficiency of K. It was previously mentioned that the dry matter yield increased most markedly when K supplies were increased with less conspicuous increases in dry matter production from increasing N application alone. This indicated that the severity of K deficiency was limiting plant use of N. The dependence of N uptake not only on the N supply but also on the K supply was significant in establishing the interaction between the two nutrients in the uptake process and in growth.

A definite antagonism between N and Cl affecting the contents and total uptake of N was observed. Chloride application significantly reduced the contents and total uptake of N in the plants (Table 7).

The N content and uptake for experiment III are presented in Table 6. Unlike the first two experiments K application showed no significant effect on the N contents in either the leaves or the stems. However, 100 ppm was the minimum K application. Nitrogen application produced highly significant increases in N contents in both the leaves and the stems (Table 6).

When total uptake of N was considered (Table 6) both N and K applications produced highly significant differences in the N uptake by the leaves and the stems. Application of K generally increased the total N uptake at all levels of N. Detrimental effects on the N

Table 6. The effects of N and K on the content and total uptake of N.

K(ppm) \ N(ppm)		100		200		400		600		800		Average	
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment III</u>													
100	Stems	149.76	5.98	192.38	8.19	195.62	8.80	204.05	8.58	240.00	7.54	196.36	7.82
	Leaves	259.52	14.98	282.62	17.32	283.57	17.68	292.38	14.52	322.86	12.93	288.19	15.49
	Total		20.96		25.51		26.48		23.10		20.47		23.30
200	Stems	135.00	6.47	192.38	8.94	202.14	8.77	199.05	8.79	238.57	9.31	193.43	8.46
	Leaves	259.05	15.78	299.53	17.64	287.62	17.38	293.57	15.94	305.47	14.81	289.05	16.31
	Total		22.26		26.58		26.15		24.73		24.12		24.77
400	Stems	128.57	6.89	199.05	9.38	178.57	7.90	196.67	9.59	249.76	9.62	190.52	8.68
	Leaves	259.76	17.24	292.15	17.64	286.90	16.66	290.24	17.84	310.24	14.09	287.86	16.69
	Total		24.14		27.02		24.56		27.43		23.71		25.37
600	Stems	146.67	6.57	191.91	9.95	186.13	9.16	214.53	8.95	238.34	9.77	195.52	8.88
	Leaves	260.24	16.87	294.29	19.44	284.29	17.83	300.00	15.07	297.86	15.92	287.33	17.03
	Total		23.44		29.38		27.00		24.02		25.68		25.90
Average	Stems	140.00	6.48	193.93	9.11	190.62	8.66	203.57	8.98	241.67	9.06		
	Leaves	259.64	16.22	292.15	18.01	285.60	17.39	294.05	15.84	309.11	14.44		
	Total		22.70		27.12		26.04		24.82		23.50		

All entries in the table are averages for three observations.

Table 7. The effects of Cl on nutrient contents and uptake by the plant tops.

Nutrient	ppm of applied chloride					
	0		100		200	
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
N	302.8	20.2	295.6	19.8	284.4	18.7
NO ₃ -N	84.2	5.8	74.3	5.0	59.7	4.0
Chloride	8.6	0.57	37.1	2.52	47.8	3.28
Potassium	67.3	4.6	70.5	4.7	73.4	4.9
Calcium	94.0	6.3	99.0	6.6	103.6	6.8
Magnesium	135.4	9.2	129.9	8.7	129.5	8.6

All entries in the table are averages for 64 observations.

uptake, when abundant to excess K was added, were not encountered. In fact, some increase in N uptake was obtained with even the highest K rate applied.

The lower rates of N increased the total N uptake but the total uptake of N decreased when 600 or 800 ppm N was applied. A decrease in dry matter production from the highest rates of N applications caused the decreases in total N uptake. Relatively smaller plants were produced with the application of 600 or 800 ppm N and this resulted in a higher N content but lower uptake of N.

The N content and uptake were lower for the stems in comparison with the leaves (Table 6). The difference in the N contents and uptake by the leaves and the stems was greatest at the 100 ppm N rate and the least at the 800 ppm N rate. This indicated that with increased N availability, nitrogen accumulated at a higher rate in the stems than the leaves.

High N requirements for several plant species are well established and response to N fertilization is commonly observed. Relationships between yield, N fertilization, and N content in specified plant part are used to predict the amount of N fertilizer required for optimum crop production. The N fertilization has an ultimate goal of higher crop production from the land. But, this is not achieved by liberal use of N fertilizers alone. The requirement for a balanced supply of the different essential nutrients is of equal importance to

obtain maximum yield. An adequate N supply is associated with vigorous growth and deep green color. Excessive quantities of N can prolong the growing period and delay maturity; this is most likely to occur when adequate supplies of some other nutrients are not present.

The results obtained from these experiments show that N fertilization increased the N content and uptake by the potato plants and produced yield responses. It was also found that when the K supplies were inadequate, the yield responses to N fertilization were limited. When excessive amounts of N were applied with the lowest rates of K the yield was depressed.

Nitrogen and K appear to interact in controlling the N uptake by potato plants. This interaction is present when N and K are in inadequate quantities. But once both N and K supplies are not growth limiting, the N and K effects appear to be independent in influencing the total uptake of N. However, Cl application appears to have an independent depressing effect on N uptake. This may present problem whenever N supplies are marginal and the depressing effects of Cl may be present. The effects of Cl application are better discussed in the next section when $\text{NO}_3\text{-N}$ content and accumulation are considered.

Contents and Accumulation of $\text{NO}_3\text{-N}$

Tables 7 and 8 show the contents and accumulation of $\text{NO}_3\text{-N}$

as affected by the applications of N, K, and Cl in experiments I and II. There were highly significant N x K interaction effects plus N and K main effects on the contents and the accumulation of $\text{NO}_3\text{-N}$ in experiment I. In experiment II, N effects were found to be significant when the content and accumulation of $\text{NO}_3\text{-N}$ were considered but K affected only the $\text{NO}_3\text{-N}$ content (Table 8). This significant effect of K in reducing the $\text{NO}_3\text{-N}$ content with little change in the accumulation was recognized as a dilution effect caused by increased vegetative growth.

Nitrate-N content and accumulation were affected in a similar manner by the N x K interaction in experiment I as were the content and total uptake of N. Nitrate-N content and accumulation increased with added N while added K generally decreased the $\text{NO}_3\text{-N}$ content but increased total accumulation of $\text{NO}_3\text{-N}$ (Table 8). However, K application had no effect on the content and accumulation of $\text{NO}_3\text{-N}$ in the plants at the zero level of applied N (Figure 3a,c). On the other hand N application still showed marked increases in the $\text{NO}_3\text{-N}$ content and accumulation even when K was not added (Figure 3a,c). Nitrate-N accumulation reached the highest values when either 400 ppm K were added with 100 or 200 ppm of N or when a 300 or 400 ppm N application was associated with 200 ppm K (Table 8).

In experiment II, both the contents and the accumulation of $\text{NO}_3\text{-N}$ were elevated with increased rates of N application (Table 8).

Table 8. The effects of N and K on the content and accumulation of $\text{NO}_3\text{-N}$.

K(ppm)	N(ppm)	0		100		200		300		400		Average	
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment I													
	0	35.0	1.8	103.9	5.7	107.9	5.7	135.0	7.5	120.4	6.8	100.4	5.5
	50	25.0	1.3	64.6	4.2	112.0	7.2	112.3	7.2	149.3	9.6	92.6	5.9
	100	20.4	1.3	84.3	4.9	108.9	8.3	118.9	8.5	94.8	7.4	85.5	6.1
	200	18.4	1.2	72.7	5.7	95.0	8.6	117.3	11.1	122.3	11.0	85.1	7.5
	400	19.5	1.3	112.0	10.1	114.3	10.6	94.3	9.0	96.1	9.1	87.2	8.0
	Ave.	23.6	1.4	87.5	6.1	107.6	8.1	115.6	8.6	116.6	8.8		
K(ppm)	N(ppm)	0		100		200		300		Average			
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment II (with Cl)													
	0	23.8	1.2	79.9	4.4	100.2	5.7	106.1	5.6	77.5	4.2		
	50	12.2	.7	79.1	4.5	85.0	5.4	106.2	6.4	70.6	4.2		
	100	7.8	.5	52.5	4.2	94.5	6.7	96.3	7.4	62.8	4.7		
	200	6.3	.4	52.6	4.2	88.0	7.0	85.0	7.4	58.0	4.8		
	Ave.	12.6	.7	66.0	4.3	91.9	6.2	98.4	6.7				

In Experiment I, all entries in the table are averages for four observations.

In Experiment II, all entries in the table are averages for eight observations.

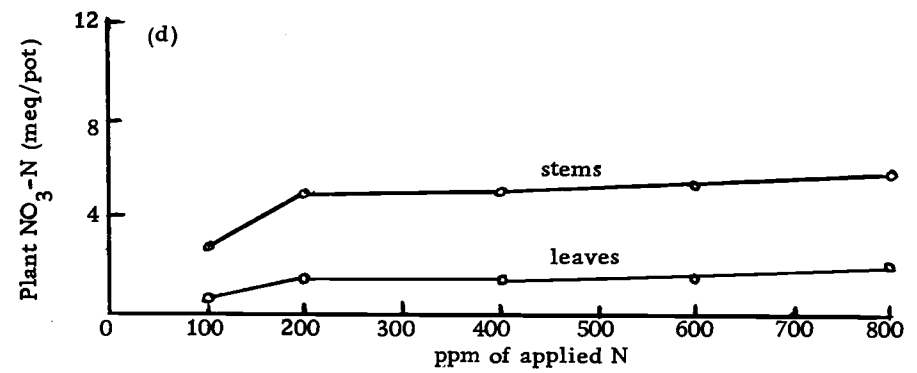
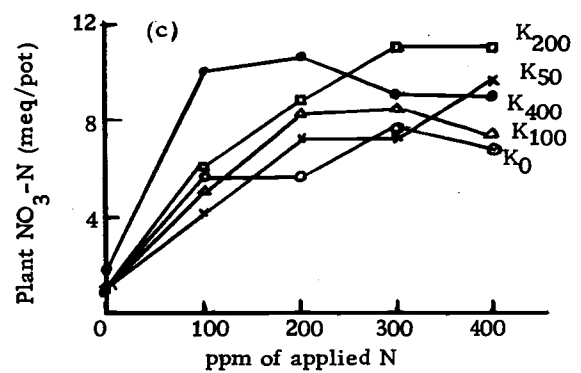
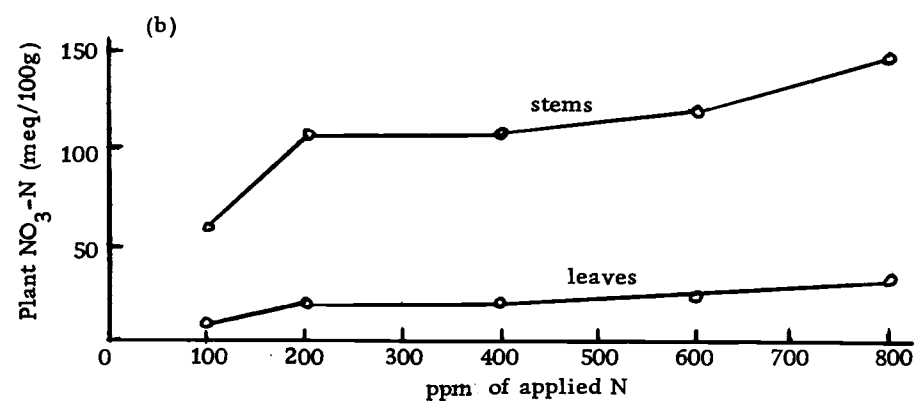
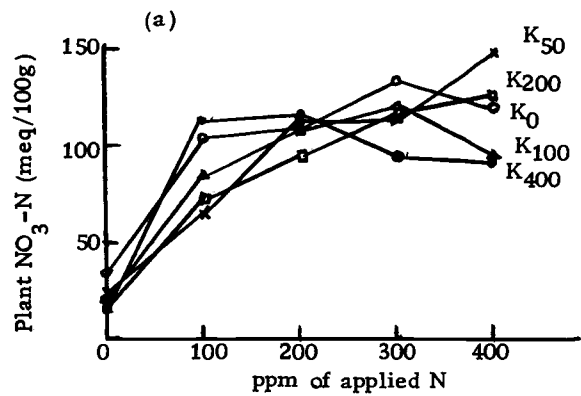


Figure 3. The effects of N and K on the content of NO₃-N for (a) experiment I, (b) experiment III, and accumulation of NO₃-N for (c) experiment I, and (d) experiment III.

One hundred ppm of N application, at all rates of K, showed the largest increases in the contents and the accumulation of $\text{NO}_3\text{-N}$; the subsequent higher applications showed little additional increase in $\text{NO}_3\text{-N}$ content for each added increment of N.

In experiment III, both the N and K applications significantly increased the $\text{NO}_3\text{-N}$ content and accumulation in the stems (Table 9). Nitrate-N content and accumulation in the leaves showed an increase due to N applications but K applications produced a variable response.

The $\text{NO}_3\text{-N}$ content in the stems remained unaffected when K was applied at the 100 and 400 ppm N rates, but K applications increased $\text{NO}_3\text{-N}$ contents in the stems with the 200, 600 and 800 ppm N additions (Table 9, Figure 3b, d). It appears that whenever a dry matter yield increase, due to K application, was obtained, the $\text{NO}_3\text{-N}$ content in the plants showed a decline. But $\text{NO}_3\text{-N}$ content seems to have increased when K application did not produce a growth response. However, the total $\text{NO}_3\text{-N}$ accumulation was increased with added K, which confirmed that K application indeed enhanced the nitrogen uptake.

When a comparison was made between the leaves and the stems for $\text{NO}_3\text{-N}$ content and accumulation, it was noted that the level of $\text{NO}_3\text{-N}$ in the leaves was about one fifth of that in the stems (Table 9, Figure 3b, 3d). It was previously mentioned that the content and total uptake of N were much higher in the leaves compared to

Table 9. The effects of N and K on the content and accumulation of NO_3^- -N.

K(ppm)	N(ppm)	100		200		400		600		800		Average	
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment III													
100	Stems	61.67	2.48	101.67	4.33	107.62	4.84	117.86	4.97	139.05	4.35	105.57	4.19
	Leaves	11.43	.66	23.81	1.45	23.33	1.45	21.19	1.06	32.38	1.30	22.43	1.18
	Total		3.14		5.78		6.29		6.03		5.65		5.38
200	Stems	52.86	2.52	103.33	4.80	110.24	4.79	115.95	5.13	142.14	5.56	104.91	4.56
	Leaves	9.76	.59	22.62	1.33	25.95	1.56	27.86	1.51	38.33	1.85	24.91	1.37
	Total		3.11		6.13		6.35		6.64		7.41		5.93
400	Stems	56.90	3.04	111.43	5.24	104.99	4.64	119.76	5.84	157.86	6.07	110.19	4.97
	Leaves	9.29	.61	20.31	1.21	17.14	.99	22.86	1.40	31.43	1.43	20.14	1.13
	Total		3.66		6.45		5.62		7.24		7.50		6.10
600	Stems	66.19	2.96	113.81	5.89	109.05	5.38	127.62	5.32	156.43	6.43	114.62	5.20
	Leaves	11.19	.73	19.46	1.32	20.00	1.25	28.81	1.45	41.19	2.21	24.19	1.39
	Total		3.69		7.21		6.63		6.77		8.64		6.59
Average	Stems	59.40	2.75	107.56	5.07	107.96	4.91	120.30	5.31	148.87	5.60		
	Leaves	10.42	.65	21.55	1.33	21.61	1.31	25.18	1.36	35.83	1.70		
	Total		3.40		6.39		6.22		6.77		7.30		

All entries in the table are averages for three observations.

the stems but much lower $\text{NO}_3\text{-N}$ content and accumulation were observed for the leaves. This would mean that the accumulation of $\text{NO}_3\text{-N}$ occurs in the non-leafy parts of the potato plants and that the petioles and stems would provide a better plant part to measure the $\text{NO}_3\text{-N}$ level in the plants for soil fertility evaluations.

The results also show that almost all of the increases in $\text{NO}_3\text{-N}$ accumulation (Table 9) occurred in the stems while the leaves showed a very small increase. It is important to recognize that excess $\text{NO}_3\text{-N}$ accumulation did not occur in the leaves which are the sites for protein synthesis and that the large amount of $\text{NO}_3\text{-N}$ absorbed was accumulated in the non-leafy parts of the potato plants.

The N absorbed by the plants from soil is principally in nitrate form. It is this inorganic form of N which can and does accumulate in substantial quantity in plants. The NO_3 is reduced to NH_3 followed by an incorporation into the organic forms. However, the organic forms of nitrogen predominate in the plants. Since the absorbed nitrate ions constitute the inorganic pool of nitrogen in the plants, any ionic competition or enhancement effects on nitrate uptake are of considerable importance in understanding the nitrogen nutrition of the plants.

It would appear that the accumulation of nitrate ions may be achieved by an increased availability of the ion. Also an absence of competition during the absorption will facilitate uptake of nitrate ion.

Increased nitrate availability can be attained either by an addition of the nutrient or by some stimulation provided by other means. There are instances where a cation causes an enhanced uptake of anion by the plants. There are a number of studies which indicated that K increases the nitrate content in certain plant species.

Sideris and Young (1946) reported that the $\text{NO}_3\text{-N}$ content of the basal leaf and stem sections of tomato plants was greater in the high K than in the low K cultures in the nitrate series. They explained that this increased $\text{NO}_3\text{-N}$ content was accompanied by higher concentrations of cations, i. e. K ions. More recently results obtained by Schneider and Clark (1970) show that K addition increased the accumulation of nitrate in pearl millet and sudangrass.

The results from experiments I and II also show that when the entire tops of the potato plants were considered, K application caused an increased accumulation of $\text{NO}_3\text{-N}$, but the content showed a decline as K application was increased. In experiment III, where stems and petioles were separated from the leaves, an indication was obtained that K application caused increases in $\text{NO}_3\text{-N}$ content in the stems. It appears that K- NO_3 relationship may be that of a compensatory cation-anion absorption phenomenon in the absence of competition from other ions and when the two nutrients are not growth limiting. The enhancement of one by the other may be caused by the necessity to maintain electrical neutrality in the potato plant. The metabolic

importance and the high requirements of the two nutrients combine together to give a causal relationship between the two in their uptake and absorption by the plants.

The Cl application showed a highly significant effect in reducing the $\text{NO}_3\text{-N}$ content and accumulation in the potato plants (Table 7). Almost all of the reduction in total N appeared to be due to the decrease in $\text{NO}_3\text{-N}$ accumulation as a result of Cl application. It is possible that the Cl effect on the $\text{NO}_3\text{-N}$ content and accumulation was primarily responsible for the observed lower N content and uptake (Table 7). The anions NO_3^- and Cl^- appear to compete during the uptake process. This competitive phenomenon has been observed by Lundegardh (1959) and DeWit et al. (1963). Lundegardh showed that in wheat plants NO_3^- and Cl^- ions in solution depress each other's uptake considerably. DeWit et al. similarly suggested the existence of competitive interaction between NO_3 and Cl uptake by perennial ryegrass. These studies support the observed competitive reduction of NO_3 uptake by Cl and vice versa. The results suggest that the two ions may be competing for accumulation in the plants.

Contents and Total Protein-N

The effects of treatments on the content and total protein-N are presented in Tables 10 and 11. It was discussed earlier that N and $\text{NO}_3\text{-N}$ contents increased with each successive increases in the

applied N but were reduced as the K and Cl applications were increased (Tables 5 and 6), however, the NO_3 -N content was low under nitrogen stress (at 0 N level). Protein-N content showed a similar relationship with N and K applications but remained unaffected by Cl additions (Table 12). Protein-N content was very low when N was not added but the application of 100 ppm N produced very marked increases in the protein-N content at all rates of applied K (Table 10). Further additions of N showed little additional increase in the protein-N content (Tables 10, 11 and Figures 4a, b).

The percentage of the N found in protein fraction decreased with each successive increase in applied N. About 75% of the total N was converted to protein-N at zero N level, but about 67% of total N was found as protein-N when the 100 ppm N was applied. At the highest rate of N application, i. e. 400 ppm in experiment I, approximately 60% of the total N was converted to protein. The NO_3 -N fraction increased from 10% of the total N at the zero N rate to about 30% at the 100 ppm N rate.

Potassium addition significantly decreased protein-N content (Table 10). Two hundred ppm K caused the maximum decrease in protein N content in experiment I but 100 ppm K was enough to produce a similar effect on protein-N content in experiment II (Table 10, Figures 5a, b). However the protein-N fraction as a percentage of the total N remained unaffected by added K.

Table 10. The effects of N and K on the content and total protein N in plant tops.

K(ppm)	N(ppm) 0		100		200		300		400		Average	
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment I</u>												
0	168.2	8.9	208.4	11.4	208.6	11.4	210.2	11.7	212.0	11.7	201.5	11.0
50	162.3	8.3	189.8	12.6	207.7	13.3	214.6	13.6	220.2	14.2	198.9	12.4
100	144.6	9.2	207.1	12.1	206.4	15.7	211.4	15.1	196.4	15.4	193.2	13.5
200	132.3	8.6	174.8	14.2	198.4	18.0	189.1	18.0	193.8	17.3	177.7	15.2
400	138.6	9.1	190.4	17.4	193.9	17.9	213.4	20.1	178.1	17.3	182.9	16.4
Ave.	149.2	8.8	194.1	13.5	203.0	15.2	207.8	15.7	200.1	15.2		
K(ppm)	N(ppm) 0		100		200		300		Average			
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment II (with Cl)</u>												
0	171.0	8.9	205.9	11.4	205.9	11.8	212.6	11.1	198.8	10.8		
50	161.8	8.8	197.4	11.4	217.2	13.8	219.6	13.1	199.0	11.8		
100	146.3	9.9	175.7	14.3	200.5	14.0	200.1	15.4	180.6	13.4		
200	136.9	9.3	180.6	14.5	196.1	15.7	187.1	16.3	175.2	13.9		
Ave.	154.0	9.2	189.9	12.9	204.9	13.8	204.8	14.0				

In Experiment I, all entries in the table are averages for four observations.

In Experiment II, all entries in the table are averages for eight observations.

Table 11. The effects of N and K on the content and total Protein-N found in plant tops.

K(ppm)	N(ppm)	100		200		400		600		800		Average	
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment III</u>													
100	Stems	76.67	3.06	83.81	3.55	82.38	3.72	84.47	3.59	90.72	2.84	83.81	3.35
	Leaves	219.05	12.65	234.76	14.39	230.24	14.33	235.00	11.68	249.05	9.97	233.62	12.61
	Total		15.70		17.95		18.05		15.27		12.82		15.96
200	Stems	71.43	3.43	84.28	3.92	80.24	3.46	85.24	3.75	85.24	3.31	81.29	3.57
	Leaves	215.48	13.33	245.95	14.49	223.25	13.47	235.48	12.79	239.76	11.66	231.98	13.11
	Total		16.56		18.41		16.94		16.53		14.97		16.68
400	Stems	70.00	3.76	84.28	3.97	76.33	3.37	78.33	3.82	84.76	3.27	78.74	3.64
	Leaves	214.76	14.26	243.57	14.71	231.19	13.42	238.95	14.48	240.71	10.93	233.24	13.56
	Total		18.02		18.68		16.78		18.30		14.20		17.20
600	Stems	75.24	3.37	82.62	4.28	76.43	3.73	82.38	3.43	83.27	3.42	79.99	3.65
	Leaves	214.53	13.89	235.48	15.59	223.81	14.04	238.10	11.96	236.43	12.63	229.67	13.62
	Total		17.25		19.87		17.76		15.39		16.05		17.27
Average	Stems	73.33	3.40	83.75	3.93	78.84	3.57	82.86	3.65	86.00	3.21		
	Leaves	215.95	13.48	239.94	14.80	227.12	13.81	236.13	12.73	241.49	11.30		
	Total		16.89		18.73		17.38		16.37		14.51		

All entries in the table are averages for three observations.

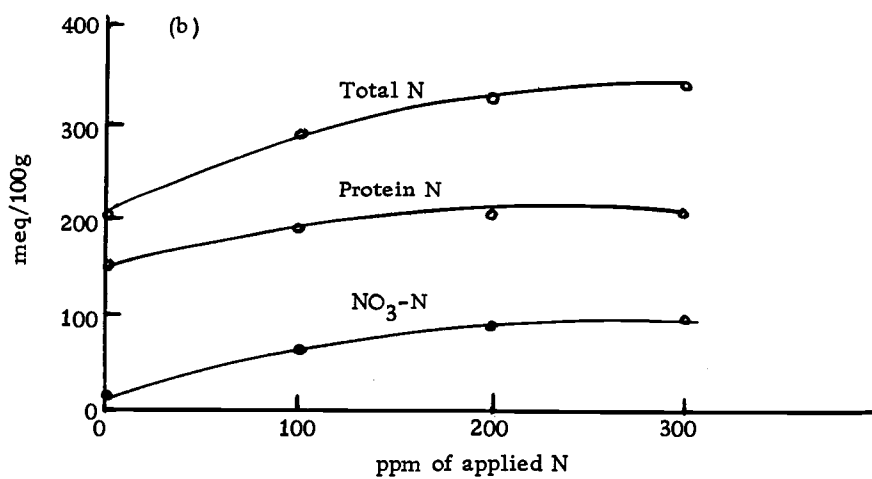
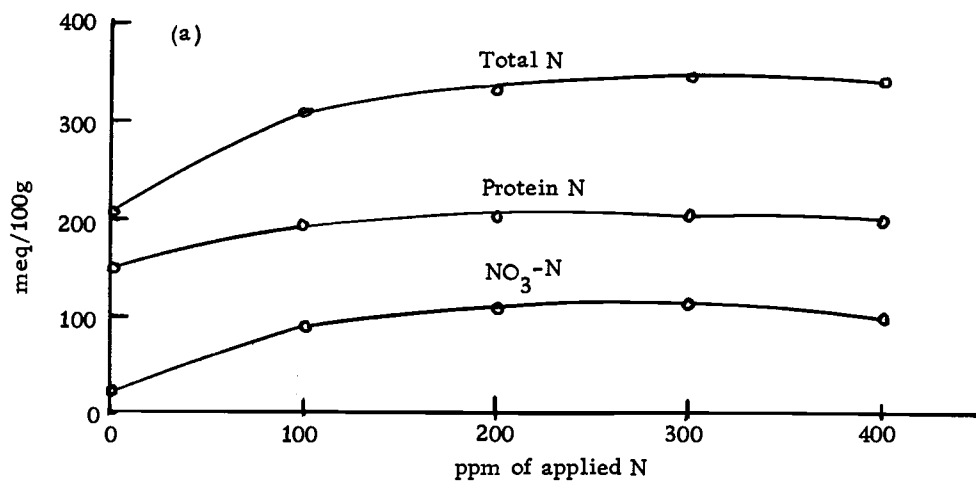


Figure 4. The effects of N on the contents of different N fractions for (a) experiment I, and (b) experiment II.

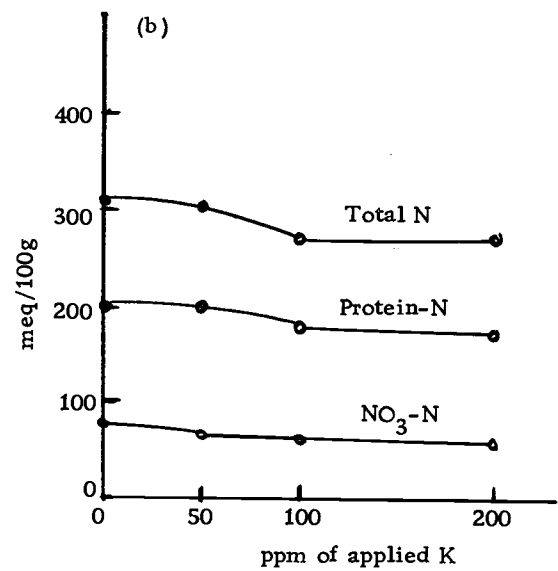
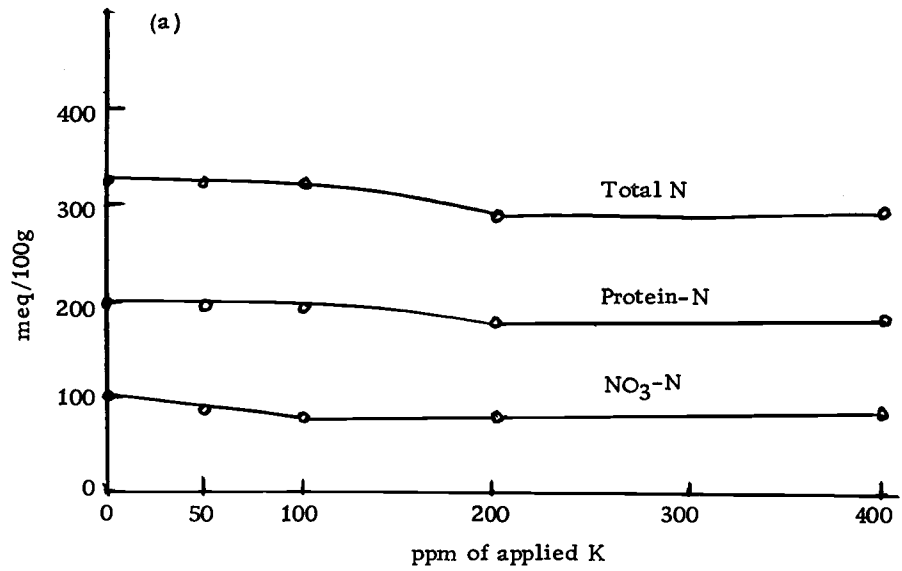


Figure 5. The effects of K on the contents of different N fractions for (a) experiment I, and (b) experiment II.

Results of these experiments show higher total N and protein-N contents when K was deficient (Figures 5a, b). While the content of total N was high, the K deficiency caused a reduction in dry matter yield and consequently a reduction in conversion of inorganic N to protein. The capability to metabolize protein must have been restricted by the K supplies limiting vegetative growth. It was observed that while the protein-N content decreased with added K, the total protein-N showed a highly significant increase (Tables 10, 11 and Figure 6a, b).

A highly significant N x K interaction effect on the total protein-N was obtained for these experiments. In the absence of significant interaction effect for protein-N content, it is considered that the growth restriction caused by the limited N and K supplies was removed only when both of the nutrients were applied. This would then allow for a higher N uptake and metabolic conversion to protein. Since this interaction was positive for the total protein-N, it is possible that the inadequate K supplies were limiting plant nitrogen utilization. In these experiments K was the most limiting nutrient and as such caused restricted growth until adequately supplied. More total protein was obtained by increasing levels of N when K supplies were also elevated (Figures 6a, b).

Weber and Varner (1954) have shown that K is required for the biosynthesis of peptide bond and that increased protein synthesis

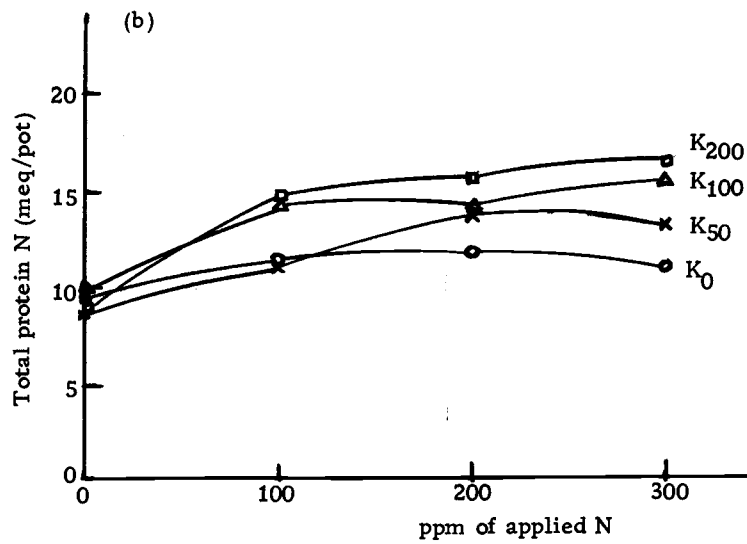
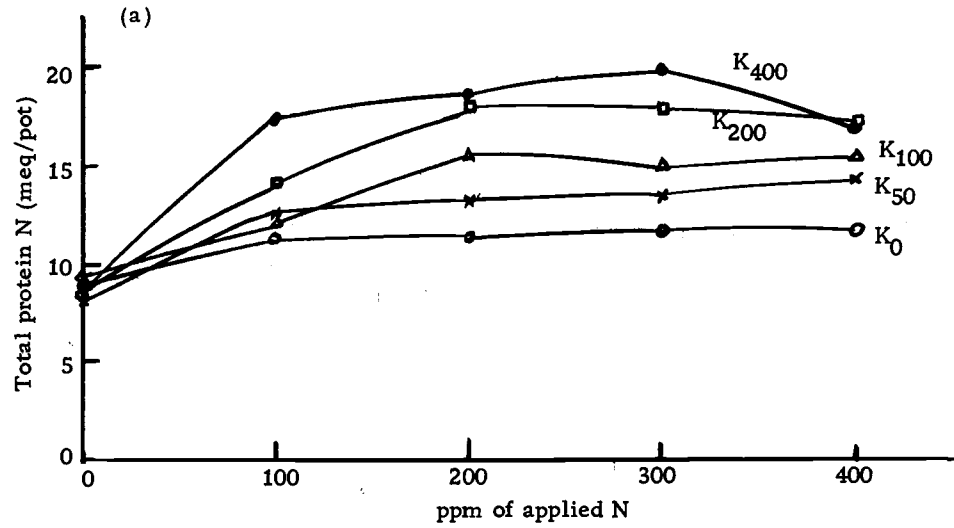


Figure 6. The effects of N and K on the total protein N for (a) experiment I, and (b) experiment II.

in a cell free extract with added K was obtained. If this is the case then the results obtained for these experiments confirm this effect that limiting the supply of K produces lower total protein in the plants (Table 10). Durzen and Steward (1967) showed that levels of nitrogenous compounds in spruce and jack pine responded markedly to application of nutrients. They showed that P and K deficiencies increased total soluble nitrogen, consisting of amino acids and amides, but reduced the conversion of these compounds to plant protein.

Steward et al. (1959) have shown that accumulation of $\text{NO}_3\text{-N}$ and the further reduction and conversion of nitrogen to organic forms is restricted more than the synthesis of protein under severe deficiency of certain mineral elements. However, in cases where K, Ca or S were deficient the conversion of organic nitrogen compounds to protein is affected more than the uptake of $\text{NO}_3\text{-N}$ and the reduction following the uptake. This seemed to be the case in these experiments where K deficiency did not limit the $\text{NO}_3\text{-N}$ accumulation but produced lower amounts of protein.

From experiment III, it was additionally found that the protein N content in leaves was about three times higher than in stems (Table 11). The nitrogen was effective in increasing the protein -N content in the leaves and the stems but the total protein-N was significantly increased only by the 200 ppm N rate. The 400, 600 or 800 ppm N applications reduced the total protein -N. This was primarily due

to the reduction in dry matter yields with these rates of N applications and could have been a salt effect. Potassium application increased total protein-N at all rates of N application. The protein-N content remained unchanged when K was added.

Table 12 and Figures 7a, b show the effect of Cl on content and total protein-N. Chloride application failed to show any significant effect on the content and total protein-N in potato plants. Significant reduction in NO_3 -N content and accumulation was obtained which was discussed earlier. The significant reduction in total N due to Cl application, was entirely the reduction shown by NO_3 -N (Figures 7a, b). This is a significant finding in establishing the non-interfering effect of Cl on protein synthesis. This is important because Cl often accompanies fertilizer K in rather large quantities.

Table 12. The effects of Cl on the content and amount of NO_3 -N, protein N and total N found in plant tops.

	parts per million of applied chloride					
	0		100		200	
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Total N	302.77	20.24	295.57	19.79	284.41	18.69
Protein N	189.63	12.61	189.26	12.65	187.56	12.30
NO_3 -N	84.23	5.78	74.25	5.02	59.73	3.99

All entries in table are average for 64 observations.

Contents and Uptake of Cl

Nitrogen applications produced significant reductions in Cl

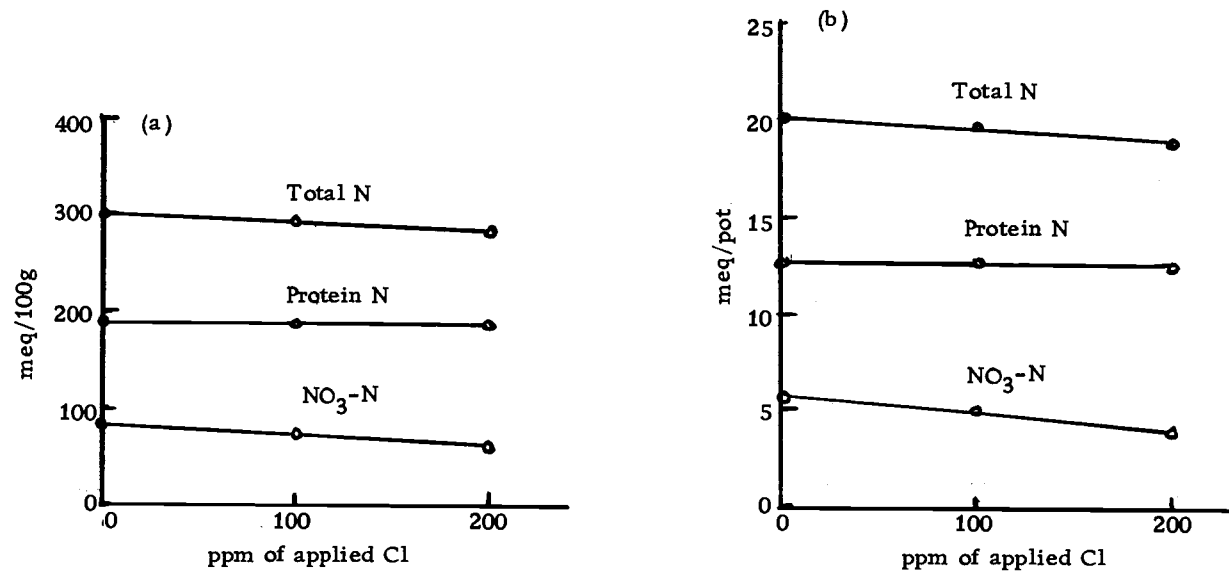


Figure 7. The effects of Cl on the (a) contents, and (b) amounts of different N fractions found in the plant tops.

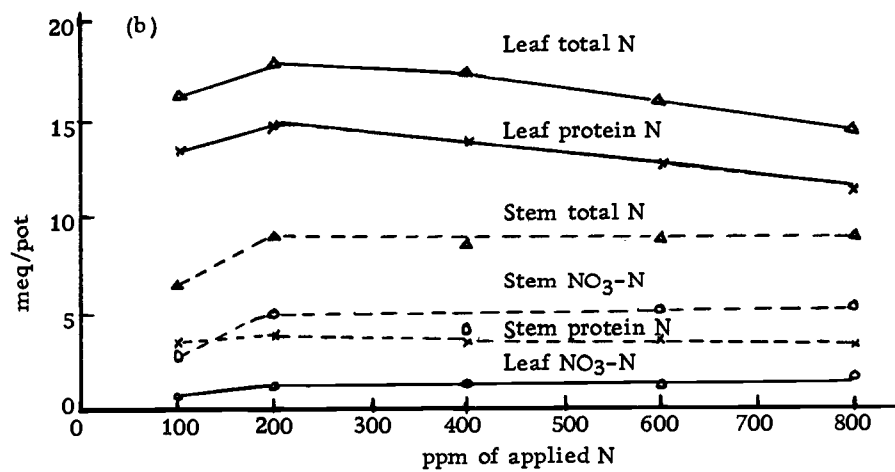
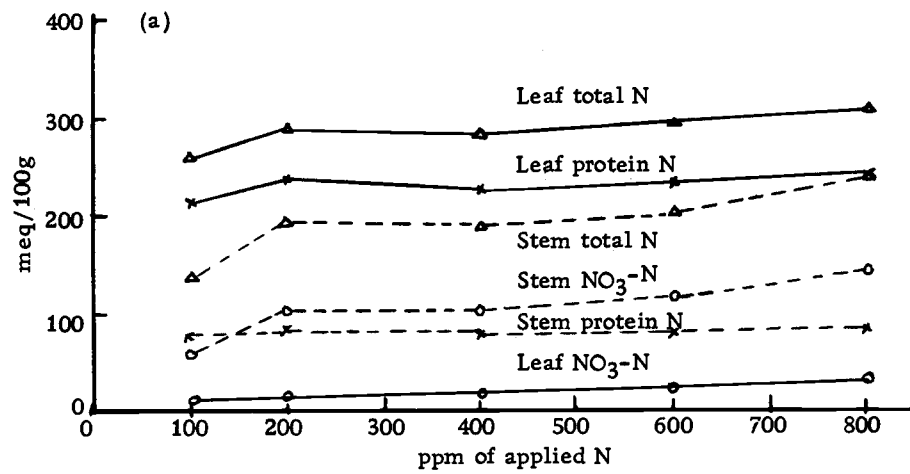


Figure 8. The effects of N on the (a) contents and (b) the amounts of different N fractions in leaves and stems.

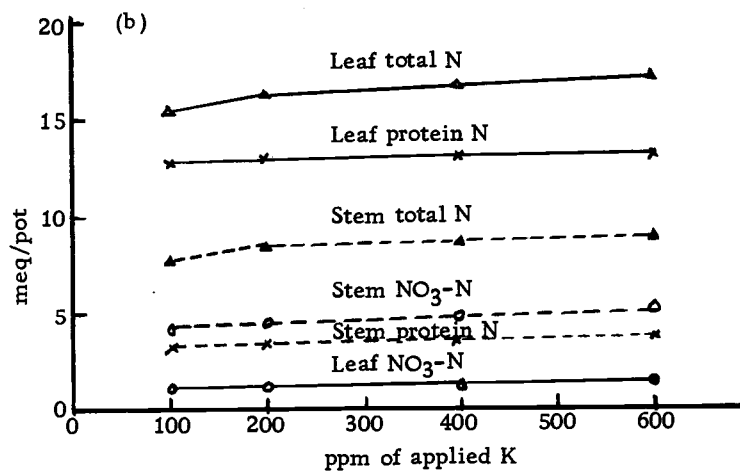
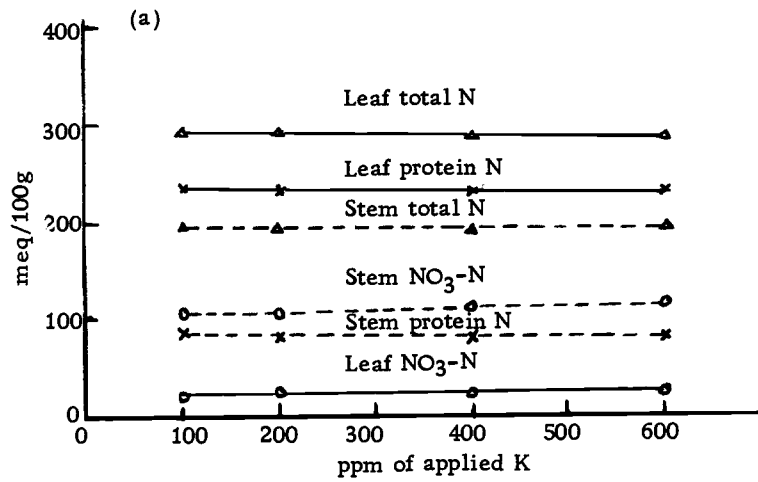


Figure 9. The effects of K on the (a) contents and (b) the amounts of different N fractions in leaves and stems.

content and uptake (Tables 13 and 14) in all three experiments. The Cl content was very low in experiment I but much higher Cl contents were obtained for experiments II and III (Tables 13 and 14) where Cl was added. In experiment I, a Cl content of 11.7 meq/100g found at zero N was reduced to 5.5 meq/100g when 300 ppm of N were added. In experiment II, the Cl content was 57.0 meq/100g at zero N and was reduced to 32.4 meq/100g by applying 300 ppm of N. A Cl uptake of 0.7 meq/pot at zero N was reduced to 0.4 meq/pot at 300 ppm N in experiment I. Similarly, a Cl uptake of 3.3 meq/pot at zero N was decreased to 2.3 meq/pot at 300 ppm N in experiment II. A total of 4.5 milliequivalent of Cl uptake per pot was obtained at 100 ppm N and was decreased to 1.6 meq/pot by the 800 ppm N application in experiment III.

The 100 ppm N application produced the largest decreases in Cl contents and uptake in experiments I and II, with the 200 ppm N rate producing the same effect in experiment III. The subsequent higher N applications produced a smaller but significant reduction in Cl content and uptake. The results for experiment III also show that the N effect was about the same for both stem and leaf Cl levels (Table 14).

Added K significantly increased Cl content in experiment II, where Cl was applied, but did not affect Cl content in experiment I (Table 13). However, Cl uptake showed significant increases due to K additions in both experiments I and II (Table 13). Since there

Table 13. The effects of N and K on the content and uptake of Cl.

K(ppm)	N(ppm) 0		100		200		300		400		Average	
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment I</u>												
0	13.2	.70	10.0	.62	7.9	.45	7.0	.39	5.4	.30	8.7	.49
50	12.2	.66	8.6	.57	5.6	.36	5.5	.34	6.0	.39	7.5	.46
100	11.6	.74	10.1	.64	6.2	.47	6.5	.47	5.8	.46	8.0	.56
200	11.3	.74	8.4	.68	8.0	.73	5.1	.48	5.2	.47	7.6	.62
400	10.4	.68	7.9	.72	5.9	.54	3.8	.36	5.2	.50	6.6	.56
Ave.	11.7	.70	9.0	.65	6.7	.51	5.5	.41	5.5	.42		
K(ppm)	N(ppm) 0		100		200		300		Average			
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment II (with Cl)</u>												
0	42.6	2.2	34.7	1.9	33.6	2.0	23.6	1.2	33.6	1.8		
50	48.7	2.7	45.3	2.6	34.0	2.1	32.2	1.9	40.0	2.3		
100	63.9	4.3	47.2	3.8	42.4	3.0	35.0	2.7	47.1	3.4		
200	60.7	4.1	46.5	3.8	50.4	3.9	38.7	3.4	49.1	3.8		
Ave.	57.0	3.3	43.4	3.0	40.1	2.7	32.4	2.3				

In Experiment I, all entries in the table are averages for four observations.

In Experiment II, all entries in the table are averages for eight observations.

Table 14. The effects of N and K on the content and uptake of Cl.

K(ppm)	N(ppm)	100		200		400		600		800		Average	
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment III													
100	Stems	53.99	2.15	43.20	1.83	32.40	1.46	26.76	1.12	24.51	.77	36.17	1.47
	Leaves	38.51	2.22	28.17	1.73	21.41	1.33	16.34	.82	16.34	.65	24.16	1.35
	Total		4.36		3.56		2.80		1.94		1.43		2.82
200	Stems	57.75	2.78	38.97	1.81	29.58	1.29	25.54	1.13	22.25	.86	34.82	1.57
	Leaves	35.21	2.15	26.95	1.59	21.41	1.29	17.09	.93	15.59	.75	23.25	1.34
	Total		4.93		3.40		2.58		2.06		1.61		2.91
400	Stems	47.89	2.58	35.21	1.66	30.97	1.36	24.32	1.18	25.54	.97	32.79	1.55
	Leaves	30.99	2.05	22.44	1.35	18.59	1.08	16.34	1.00	15.59	.71	20.79	1.24
	Total		4.63		3.01		2.44		2.19		1.68		2.79
600	Stems	50.24	2.26	37.09	1.92	32.40	1.60	23.29	.97	21.03	.86	32.81	1.52
	Leaves	28.17	1.83	22.44	1.49	18.59	1.17	17.09	.86	14.84	.79	20.23	1.23
	Total		4.09		3.41		2.77		1.83		1.65		2.75
Average	Stems	52.47	2.44	38.62	1.81	31.34	1.43	24.98	1.10	23.33	.87		
	Leaves	33.22	2.06	25.00	1.54	20.00	1.22	16.72	.90	15.59	.73		
	Total		4.50		3.44		2.65		2.00		1.59		

All entries in the table are averages for three observations.

was no Cl added in experiment I, the K stimulation of Cl uptake was limited in extent by the low levels of available Cl. But when Cl was applied in experiment II, the Cl uptake was greatly increased. The highest level of 0.62 milliequivalent Cl uptake per pot was obtained for 200 ppm K application in experiment I. However, the 1.8 milliequivalent Cl uptake per pot obtained at zero K level was increased to 3.8 meq/pot with the addition of 200 ppm K in experiment II.

In experiment III, the responses to K application were variable. The changes in Cl content and uptake were so small that it is difficult to establish a response pattern from K application.

The stems contained higher Cl levels than the leaves. A comparison between leaf and stem Cl levels showed that the differences were the highest at the 100 ppm N rate and the least at the 800 ppm N rate.

Chloride application significantly increased the Cl content and uptake by the potato plants (Table 7). The Cl content increased from 8.6 meq/100g at zero Cl level to 37.1 meq/100g at 100 ppm Cl rate and to 47.8 meq/100g at the 200 ppm Cl rate. Since yield response to Cl application was not obtained, it is logical to assume that the increases in Cl content and uptake were primarily due to increased accumulation within the plants.

Chloride is shown to be an essential element for plants, but it is required in very small quantities, therefore these high Cl levels

in the potato plants probably have no direct metabolic consequence. It is considered that the Cl uptake is a luxury consumption and provides a cation balancer. Russel (1961) has shown that the main function, for which Cl is not specific, is as an osmotic pressure regulator and a cation balancer in cell sap and the plant cells themselves. If this was the case then the increased Cl uptake due to K would appear to be a cation balancer.

The antagonism involving N and Cl applications has been reported by several different researchers. As mentioned earlier Lundegardh (1959) and DeWit et al. (1963) reported NO_3^- and Cl^- ions competing with each other for uptake by plants. It was also mentioned earlier that the NO_3^- -N accumulation in the potato plants was decreased by Cl application and increased by N applications. The results of these experiments further show that Cl uptake was increased when Cl was applied but decreased when N was added. These results then confirm that a NO_3^- -Cl competition is present when the two ions are considered in the uptake process. It is of importance to recognize that K application did increase Cl content while decreasing the NO_3^- content. Since all three ions involved are monovalent ions, it is thought that these ions present stimulation and competition of a monovalent system. The competition involves the two anions Cl and NO_3^- whereas the stimulation is present between the cation K and the anion Cl or NO_3^- .

Contents and Uptake of K

Tables 7, 15 and 16 show the K content and uptake for the three experiments. Both N and K applications produced highly significant differences in K content and uptake by the potato plants. Highly significant N x K interaction effects on K uptake were obtained for all three experiments, but K content showed this significant N x K interaction effect only in experiments I and II. A significant N x K x Cl interaction effect was noted for the K content and the K uptake in experiment II. Although such an interaction is difficult to explain in terms of cause and effect, it emphasizes the degree of interrelationships among the effects of applied nutrients on the K content and uptake. It was observed that Cl applications generally produced small but insignificant increases in both the K content and uptake in potato plants (Table 7).

In view of the fact that N x K interaction effect was highly significant, the N and K main effects are not discussed separately. When K was not applied, N application did not affect the K content and uptake in experiments I and II (Table 15, Figures 10a, b; 11a, b). The addition of N increased the K uptake when 200 or 400 ppm K was applied with K applications causing large increases in the K content and uptake at all levels of N (Table 15). The K content and uptake reached the highest values when 400 ppm K was applied together

Table 15. The effects of N and K on the content and uptake of K.

K(ppm)	N(ppm) 0		100		200		300		400		Average	
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment I</u>												
0	52.8	2.8	48.8	2.7	47.2	2.6	52.8	2.9	49.6	2.7	50.2	2.7
50	67.2	3.3	53.7	3.6	58.4	3.8	57.6	3.6	56.8	3.7	58.7	3.6
100	80.8	5.1	53.6	3.1	60.7	4.6	65.6	4.7	60.8	4.8	64.3	4.4
200	104.0	6.7	88.0	7.2	91.2	8.3	94.3	8.9	86.4	7.7	92.8	7.8
400	147.9	9.7	166.2	15.1	137.5	12.8	144.8	13.7	136.7	13.4	146.6	13.0
Ave.	90.5	5.6	82.1	6.3	79.0	6.4	83.0	6.8	78.1	6.5		
K(ppm)	N(ppm) 0		100		200		300		Average			
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment II (with Cl)</u>												
0	49.3	2.5	50.0	2.7	40.9	2.3	49.2	2.5	47.3	2.5		
50	74.8	4.0	63.3	3.6	51.6	3.2	62.8	3.8	63.1	3.7		
100	88.4	6.0	89.2	7.3	68.8	4.8	69.6	5.3	79.0	5.9		
200	113.6	7.8	93.2	7.4	97.6	7.8	88.8	7.7	98.3	7.7		
Ave.	81.5	5.1	73.9	5.3	64.7	4.5	67.6	4.8				

In Experiment I, all entries in the table are averages for four observations.

In Experiment II, all entries in the table are averages for eight observations.

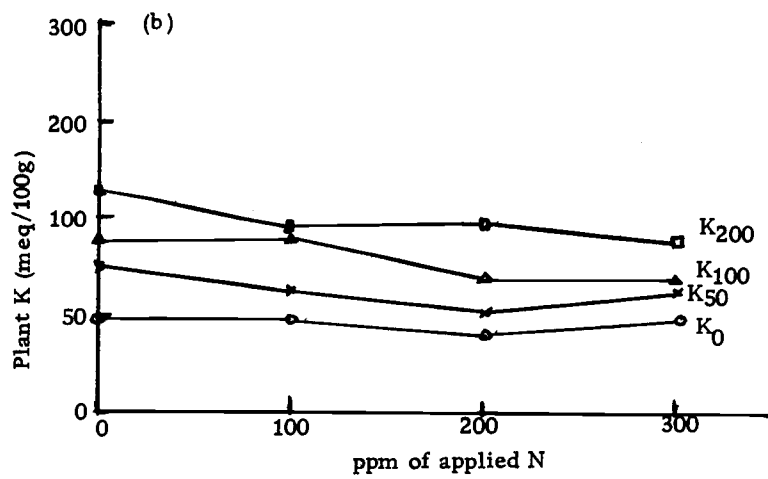
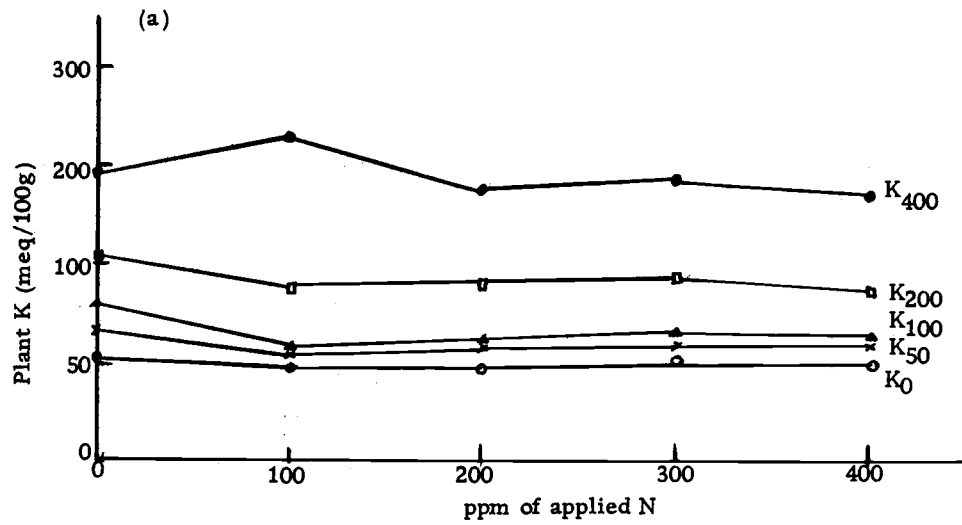


Figure 10. Effects of N and K on the K contents for (a) experiment I, and (b) experiment II.

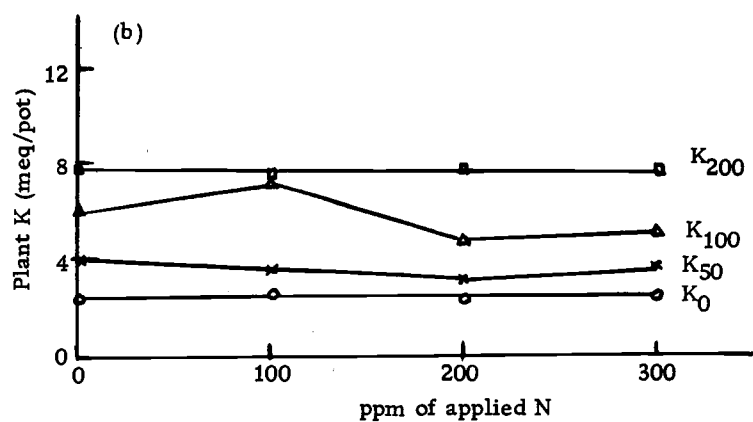
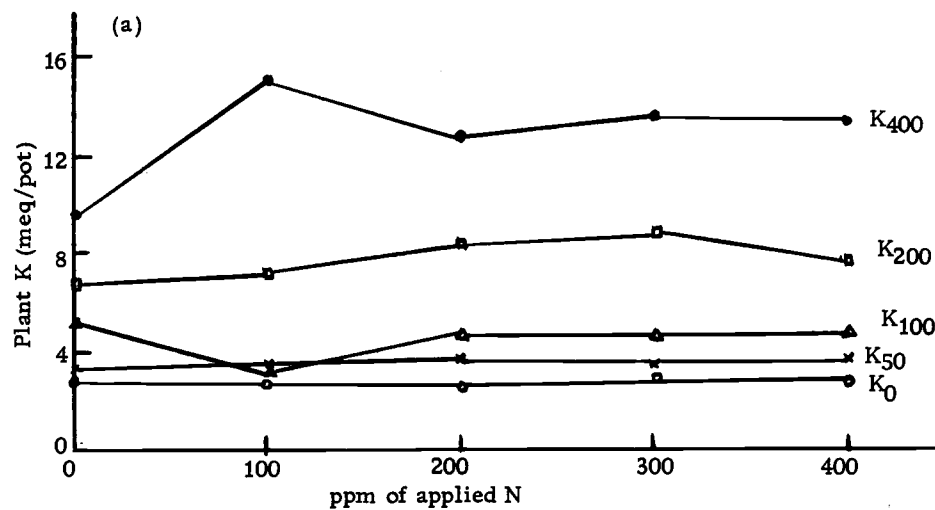


Figure 11. The effects of N and K on the K uptake for (a) experiment I, and (b) experiment II.

with at least 100 ppm N (Table 15, Figures 10a, 11a) in experiment I. The highest total K uptake of 20.6 g/pot was obtained for experiment III, when 600 ppm K and 200 ppm N were applied (Table 15).

In experiment III, the division of the plant material in stems and leaves further showed that K content was much higher in the stems than in the leaves, but the K uptake in the stems was only slightly higher than the leaves (Table 16). The smaller difference in K uptake in the stems and the leaves may be due to the higher dry matter yield of the leaves as compared to the stems. The increase in K content and uptake as a result of K application was similar in both the leaves and the stems (Table 16, Figures 12a, b). Nitrogen applications generally reduced the K content both in the stems and the leaves. The K uptake was increased slightly when 200 ppm N was applied but the subsequent higher N applications steadily decreased the K uptake in the leaves and the stems (Table 16, Figures 13a, b). It was evident that the reduction in K uptake by added N was more pronounced at low levels of applied K than at the higher levels of added K (Table 16). In this experiment, the higher rates of applied N reduced vegetative growth and as such the smaller amount of dry matter produced resulted in a reduction in total K uptake.

Potassium content and uptake were relatively restricted until 100 ppm K was added (Table 15). Potassium accumulation proceeded

Table 16. The effects of N and K on the content and uptake of K.

K(ppm)	N(ppm)	100		200		400		600		800		Average	
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment III													
100	Stems	101.45	4.04	105.71	4.50	87.81	3.95	89.51	3.77	102.30	3.20	97.36	3.89
	Leaves	74.17	4.28	66.50	4.08	62.24	3.91	60.53	3.01	67.35	2.69	66.16	3.60
	Total		8.32		8.58		7.86		6.78		5.89		7.49
200	Stems	134.70	6.45	150.67	6.99	118.50	5.14	104.01	4.58	122.76	4.76	126.13	5.59
	Leaves	99.74	6.08	94.63	5.58	85.25	5.15	76.72	4.16	79.28	3.84	87.13	4.96
	Total		12.54		12.57		10.29		8.74		8.60		10.55
400	Stems	175.62	9.41	189.26	8.90	164.54	7.28	153.45	7.47	170.50	6.55	170.67	7.92
	Leaves	124.47	8.26	132.14	7.98	117.65	6.84	110.83	6.82	109.97	4.99	119.01	6.98
	Total		17.67		16.88		14.12		14.29		11.53		14.90
600	Stems	196.08	8.79	209.72	10.86	183.29	8.99	186.70	7.80	196.91	8.10	194.54	8.91
	Leaves	147.49	9.58	147.48	9.73	129.58	8.14	125.32	6.29	138.11	7.37	137.60	8.22
	Total		18.38		20.59		17.12		14.09		15.48		17.13
Average	Stems	151.96	7.18	163.84	7.81	138.54	6.34	133.42	5.90	148.12	5.65		
	Leaves	111.47	7.05	110.19	6.84	98.68	6.01	93.35	5.07	98.68	4.73		
	Total		14.23		14.66		12.35		10.97		10.38		

All entries in the table are averages for three observations.

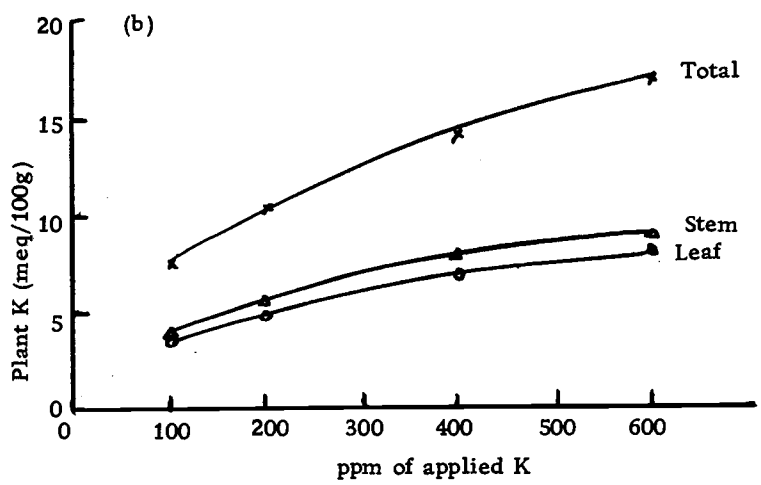
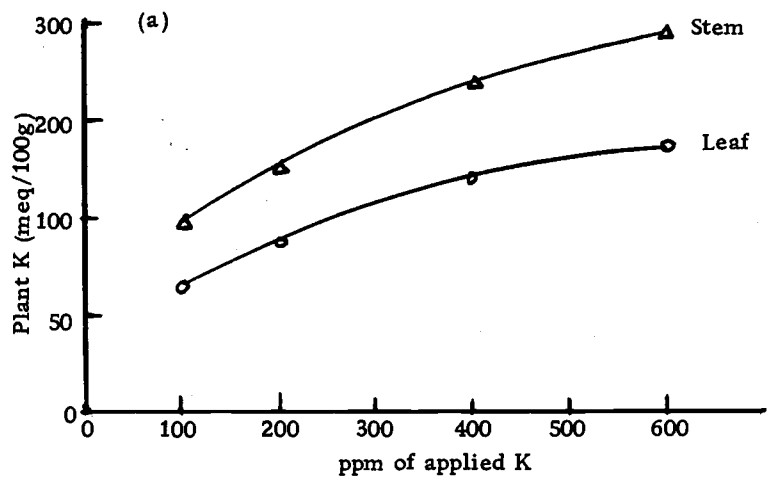


Figure 12. The effects of K on the (a) contents and (b) uptake of K in leaves and stems.

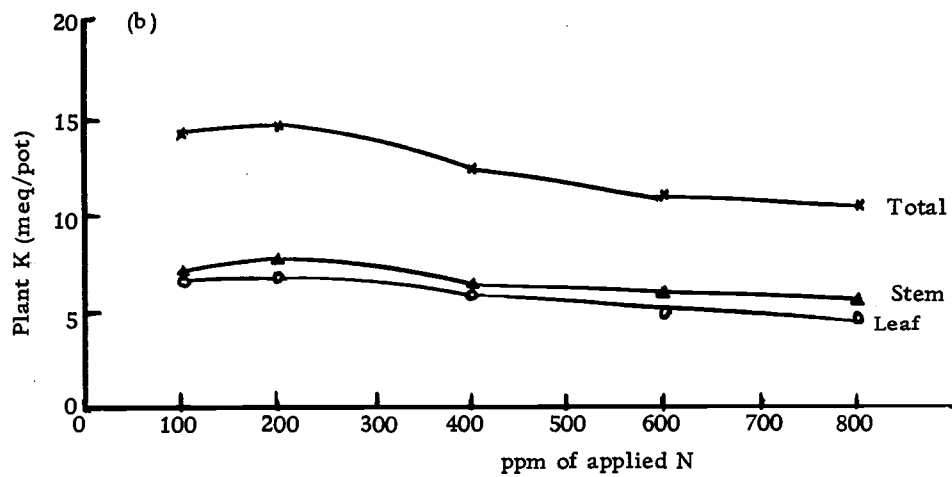
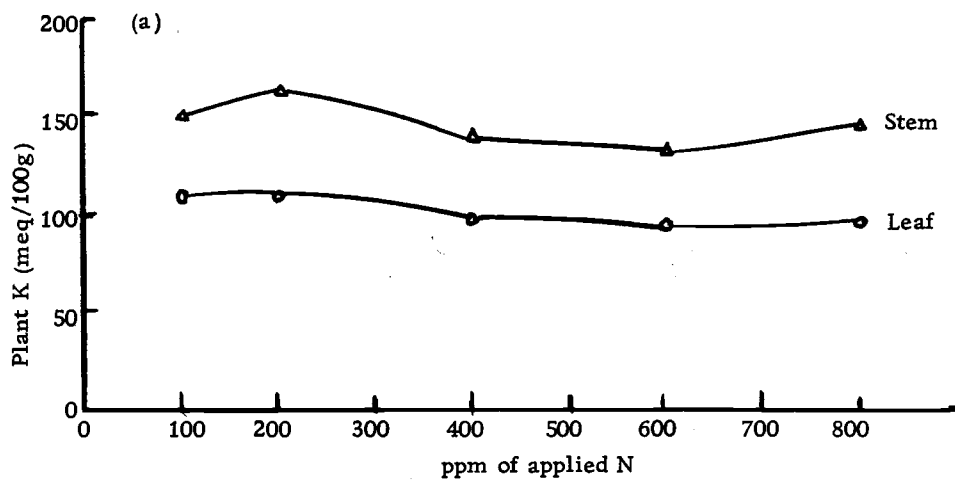


Figure 13. The effects of N on the (a) contents, and (b) uptake of K in leaves and stems.

at much higher rate when at least 200 ppm K addition was associated with the 100 ppm or more of added N (Tables 15 and 16). The lowest rates of K application were primarily used by the plants in removing the deficiency and the restriction on normal vegetative growth. The additional accumulation may in part constitute an increased K uptake to provide for the maintenance of the ionic equilibria in plants.

It is generally found that when the exchangeable K content of a soil is increased by the use of fertilizer or some other means, then the K content of crops is likewise increased subject to the condition that other factors are not limiting plant growth. It is to be assumed that the environmental conditions present do not restrict the plant's physiological and metabolic functions.

In a greenhouse study, Tucker and Smith (1952) found that addition of K fertilizer to the soil always resulted in an increase in the K content of red clover. An excessive absorption of K by alfalfa was reported by Bear and Prince (1945). Our observations from potato field experiments show an increase in K content of the plants due to K applications. The three greenhouse experiments also show a steady increase in the plant K content and uptake as a result of K applications. It is of further interest to note that the excessive K applications apparently were not detrimental to the potato plants.

Investigations on the effect of additions of N on the absorption of K by crops generally have indicated that a reduction in plant K

content often occurs with added N. This is especially true when soil K supply is limited. When N application increases dry matter production, then the decreases in K content are dilution effects caused by increased vegetative growth. Under these conditions higher total K uptake is generally encountered. This was true for experiments I and II where N and K applications both produced growth responses. But in experiment III, where N application did not increase yield, the content and uptake of K were decreased by the N applications. However, the minimum rate of applied N was 100 ppm which was sufficient for normal plant growth. Cowie (1942) reported that N and P applications enhanced K deficiency in potatoes grown on soils deficient in K. Lorenz (1944) also found that N applications decreased the K content of potato plants.

In view of the observed increases in the uptake of divalent cations following N applications, it is possible that a cation competition involving the divalent and monovalent ions especially K, Ca and Mg may be present. This competition could cause a reduction in K absorption. Also, it is not known whether the K absorption is reduced as a result of N addition. The net result still remains that the retention of K by the plants showed a decline. It is suspected, however, that the N effect on K absorption is an indirect effect and that more research needs to be done in this regard.

Contents and Uptake of Ca

Tables 17 and 18 show the Ca content and uptake results for the three experiments. Highly significant increases in Ca content and uptake were obtained from the application of N in all three experiments. Potassium application produced significant changes in Ca content and uptake in experiments I and II but the K effect on total Ca uptake in experiment III was not significant.

The maximum elevations in Ca content and uptake were obtained when 100 ppm N was applied with additional rates of N producing very little change (Tables 17 and 18). The Ca content in experiment I increased from 62.4 meq/100g at zero N to 90.9 meq/100g at 100 ppm N level with the Ca uptake increasing from 4.0 meq/pot to 6.3 meq/pot. A similar response was obtained for experiment II.

In experiment III, both the leaves and the stems showed marked increases in Ca content and uptake as a result of N applications (Table 18). The differences between the leaf and the stem Ca content and uptake were the highest at the 100 ppm N rate. The Ca content was twice as much and the Ca uptake was three times as much for the leaves as compared to the stems when the 100 ppm N was applied. But this difference was reduced as N application was increased.

Potassium application significantly decreased the Ca content but increased the Ca uptake by the potato plants (Table 17). The

Table 17. The effects of N and K on the content and uptake of Ca.

K(ppm)	N(ppm) 0		100		200		300		400		Average	
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment I</u>												
0	78.4	4.2	97.5	5.4	110.9	6.0	99.8	5.5	96.6	5.3	96.6	5.3
50	67.4	3.4	92.9	6.1	113.3	7.2	106.1	6.6	101.3	6.5	96.2	6.0
100	70.6	4.5	92.3	5.3	113.0	8.6	112.6	8.1	101.3	7.9	98.0	6.9
200	67.1	4.4	89.1	7.2	92.9	8.4	100.8	9.6	99.8	9.0	89.9	7.7
400	52.6	3.5	82.6	7.4	83.5	7.7	89.8	8.5	85.5	8.3	78.8	7.1
Ave.	67.2	4.0	90.9	6.3	102.7	7.6	101.8	7.7	96.9	7.4		

K(ppm)	N(ppm) 0		100		200		300		Average	
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment II (with Cl)</u>										
0	90.9	4.8	106.9	5.9	114.6	6.5	93.6	4.8	101.5	5.5
50	84.8	4.7	116.9	6.7	114.9	7.3	108.9	6.5	106.4	6.3
100	75.9	5.0	97.3	7.8	117.1	8.2	112.9	8.7	100.8	7.4
200	68.8	4.7	101.3	8.1	107.6	8.5	108.8	9.4	96.6	7.7
Ave.	80.1	4.8	105.6	7.1	113.6	7.6	106.1	7.4		

In Experiment I, all entries in the table are averages for four observations.

In Experiment II, all entries in the table are averages for eight observations.

Table 18. The effects of N and K on the content and uptake of Ca.

		N(ppm)		200		400		600		800		Average	
		100		meq/100g meq/pot		meq/100g meq/pot		meq/100g meq/pot		meq/100g meq/pot		meq/100g meq/pot	
K(ppm)		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
<u>Experiment III</u>													
100	Stems	41.67	1.66	50.83	2.15	65.83	2.94	73.33	3.09	70.33	2.21	60.40	2.41
	Leaves	98.33	5.66	98.33	6.01	117.50	7.27	110.83	5.52	125.00	5.02	110.00	5.90
	Total		7.32		8.16		10.20		8.62		7.23		8.31
200	Stems	40.83	1.96	48.33	2.24	65.33	2.82	80.83	3.55	90.00	3.51	65.07	2.81
	Leaves	92.50	5.65	93.33	5.50	108.33	6.56	114.17	6.20	125.83	6.13	106.83	6.01
	Total		7.61		7.74		9.38		9.75		9.63		8.82
400	Stems	35.83	1.92	45.83	2.15	57.50	2.52	70.00	3.42	95.00	3.67	60.83	2.73
	Leaves	82.50	5.47	86.67	5.23	95.83	5.56	110.83	6.80	130.00	5.89	101.17	5.79
	Total		7.40		7.38		8.08		10.21		9.56		8.53
600	Stems	38.33	1.74	46.67	2.41	64.17	3.11	62.50	2.60	94.17	3.87	61.17	2.75
	Leaves	72.50	4.72	84.17	5.55	98.33	6.17	98.33	4.94	130.00	6.96	96.67	5.67
	Total		6.46		7.96		9.28		7.54		10.83		8.41
Average	Stems	39.17	1.82	47.92	2.24	63.21	2.85	71.67	3.17	87.38	3.31		
	Leaves	86.46	5.38	90.63	5.57	105.00	6.39	108.54	5.87	127.71	6.00		
	Total		7.20		7.81		9.24		9.03		9.31		

All entries in the table are averages for three observations.

data further show that increases in Ca uptake were associated with increased yield from K applications and hence a decrease in Ca content due to dilution. Under limiting K nutrition, the Ca absorption was limited by less vegetative growth but when K supplies were restored to produce normal plants, the Ca absorption was also increased. The results from experiment III, show that K addition beyond 200 ppm rate did not affect Ca uptake either in the leaves or in the stems. However, the Ca content in the leaves and the stems showed a slight decline when K was added.

In experiment I, the Ca content was not affected by the N x K interaction effect but the Ca uptake was significantly affected by the N x K interaction effect. The presence of this effect for Ca uptake is related to the similar effect obtained for the dry matter production. Since Ca uptake and accumulation depends more on the plant growth, any interaction affecting the dry matter production could also influence the Ca uptake in a similar manner.

In experiment III, both the leaves and the stems showed a significant N x K interaction effect when Ca uptake was considered. In this experiment also, the dry matter yield was similarly affected by N x K interaction effect and hence the relationship between growth and Ca uptake is again considered to be a control for this observed effect.

It appears that the effects of N and K applications on Ca content and uptake were mostly encountered when both of the nutrients were

applied in quantities which produced normal plants. The changes encountered under excessive uses of N and K are considered to be very small and of no real significance from a physiological standpoint. It is considered that N, K and Cl applications did not change the Ca composition of potato plants to any great extent provided the three nutrients were present in adequate quantities to support optimum plant growth.

The relatively small changes in Ca content and uptake as a result of N, K and Cl additions may be the result of a disturbed ionic environment. A small adjustment may be seen when cation and anion supplies are changed which do not present any antagonism and/or stimulation per se. Moreover if cation constancy and ionic balance phenomenon are present in potato plants then an internal shift in the accumulating ions may result as a consequence of the changes in availability of the nutrients. Unless nutritional stress resulting in adverse effects on the metabolic functioning of plants is encountered, small changes in the ionic contents may present no more than an internal adjustment on retention of different ions which accomplishes equilibrium within the plants.

Contents and Uptake of Mg

Nitrogen application significantly increased Mg content and uptake in experiments I and II (Table 19). The greatest increase

Table 19. The effects of N and K on the content and uptake of Mg .

K(ppm)	N(ppm) 0		100		200		300		400		Average	
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment I												
0	148.5	7.9	180.8	10.3	180.8	10.0	167.9	9.3	166.9	9.3	169.0	9.4
50	99.8	5.0	138.5	9.1	155.8	10.0	150.6	9.5	151.0	9.7	138.8	8.7
100	95.0	6.1	171.5	9.9	139.8	10.6	135.0	9.7	132.5	10.3	134.8	9.3
200	74.2	4.9	102.3	8.3	107.5	9.7	117.9	11.2	121.0	10.9	104.6	9.0
400	46.5	3.1	66.9	6.1	76.7	7.1	86.5	8.2	84.4	8.2	72.2	6.5
Ave.	92.8	5.4	131.6	8.7	132.1	9.5	131.6	9.6	131.2	9.7		

K(ppm)	N(ppm) 0		100		200		300		Average	
	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment II (with Cl)										
0	144.4	7.6	177.9	10.0	182.2	10.5	160.6	8.5	166.3	9.1
50	109.5	6.0	148.2	8.7	148.3	9.6	145.8	8.8	138.0	8.3
100	90.0	6.1	111.9	9.1	126.1	8.9	130.1	10.0	114.5	8.5
200	66.4	4.6	104.1	8.3	114.0	9.1	115.7	10.0	100.0	8.0
Ave.	102.6	6.1	135.5	9.0	142.7	9.5	138.1	9.3		

In Experiment I, all entries in the table are averages for four observations.

In Experiment II, all entries in the table are averages for eight observations.

in Mg content and uptake were produced when 100 ppm N was applied. The subsequent higher N rates produced only small changes (Table 19). A Mg content of 92.8 meq/100g at zero N was increased to 131.6 meq/100g at 100 ppm N and a Mg uptake of 5.4 meq/pot at zero N was raised to 8.7 meq/pot by the addition of 100 ppm N in experiment I. A similar response was obtained for experiment II. A higher Mg content was generally found when K was not applied.

In experiment III, the Mg content in the stems increased with each increment of applied N irrespective of the level of applied K (Table 20). In contrast, the addition of N increased the Mg content in the leaves at all but 100 or 200 ppm of applied K. The application of 200 ppm N increased the Mg uptake by the stems and the leaves. There was no change in Mg uptake by stems or leaves when N rate was increased from 200 to 400 ppm N but application of 600 or 800 ppm N decreased Mg uptake for both stems and leaves (Table 20). This decrease in the Mg uptake was primarily a result of reduction in dry matter production from the excessive N applications.

Potassium application significantly reduced Mg content and uptake in experiment I (Table 19) but reduced Mg content at all N rates and the Mg uptake at 0 and 100 ppm N rates in experiment II (Table 19). In experiment I, the maximum reduction in Mg content and uptake was observed when 400 ppm K was added. The Mg uptake was reduced from 9.0 meq/pot at 200 ppm K to 6.5 meq/pot at 400 ppm

Table 20. The effects of N and K on the content and uptake of Mg.

K(ppm)	N(ppm)	100		200		400		600		800		Average	
		meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot	meq/100g	meq/pot
Experiment III													
100	Stems	101.67	4.07	121.11	5.14	127.78	5.75	133.06	5.59	137.22	4.32	124.17	4.97
	Leaves	101.67	5.85	111.95	6.90	103.33	6.43	93.90	4.69	98.33	3.94	101.84	5.56
	Total		9.92		12.04		12.18		10.27		8.26		10.53
200	Stems	74.44	3.57	94.44	4.37	103.33	4.50	110.28	4.86	110.83	4.32	98.67	4.32
	Leaves	88.33	5.39	99.45	5.87	94.44	5.70	83.33	4.53	95.28	4.65	92.17	5.23
	Total		8.96		10.24		10.19		9.38		8.98		9.55
400	Stems	55.83	3.00	58.89	2.76	73.61	3.24	76.94	3.75	82.22	3.13	69.50	3.17
	Leaves	70.84	4.69	71.95	4.35	70.28	4.08	78.89	4.84	77.78	3.53	73.95	4.30
	Total		7.69		7.11		7.32		8.59		6.66		7.47
600	Stems	38.61	1.74	50.83	2.64	53.33	2.62	58.33	2.43	67.78	2.76	53.78	2.44
	Leaves	56.94	3.70	59.44	3.94	61.94	3.89	63.89	3.21	64.45	3.44	61.33	3.63
	Total		5.43		6.58		6.51		5.64		6.20		6.07
Average	Stems	67.64	3.09	81.32	3.73	89.52	4.03	94.65	4.16	99.51	3.63		
	Leaves	79.45	4.91	85.70	5.26	82.50	5.02	80.00	4.32	83.96	3.89		
	Total		8.00		8.99		9.05		8.47		7.52		

All entries in the table are averages for three observations.

K and the Mg content decreased from 104.6 meq/100g at 200 ppm K to 72.2 meq/100g at 400 ppm K in this experiment.

In experiment III, both the leaves and the stems showed a significant reduction in Mg content and uptake when K was applied. The reduction of Mg by the addition of K was greater in the stems than the leaves. A significant NxK interaction effect was obtained for the Mg content and uptake in the leaves, Mg uptake in the stems, and the total Mg uptake. The NxK interaction effect was not significant for the stem Mg content. The presence of this interaction effect confirms that the two nutrients are interrelated in their effects on Mg absorption.

One hundred ppm Cl application produced a reduction in the Mg content and uptake but the subsequent higher Cl application did not have significant effect (Table 7). Since Cl reduced the uptake of N, this could have been an indirect N effect.

The depressing effect of K on plant absorption of Mg has been noted by many researchers. Walsh and Clarke (1945) related the Mg uptake in tomatoes to soil K:Mg ratios. When the ratio was sufficiently high, Mg deficiency occurred even though a large Mg supply was present in the media. Walsh and O'Donohoe (1945) showed that in potatoes, tobacco, sugarbeets, barley and mango plant tissues Mg deficiency coincided with an extremely high quantity of exchangeable K in the soil.

Prince, Zimmerman and Bear (1947) showed that the most important single factor influencing the Mg uptake by the plants is the quantity of available K. With abundant K supply the plant Mg levels are relatively low. Among most recent reports on K-Mg antagonism, Schneider and Clark (1970) showed that K significantly lowered Mg levels in pearl millet and sudangrass.

Results from experiments under consideration also show a highly significant antagonism between K and Mg. There are two possible explanations for this antagonism. If cation constancy and equilibrium is a general phenomenon then with the increase in K absorption there is a reduction in the uptake of other cations, notably magnesium. It is also possible that K could compete with Mg for the same sites in the absorption process and thereby reduce Mg uptake. In support of the second postulate Moore (1964) reported that K^+ and Mg^{++} compete for the same mechanism with K^+ being favored by the carrier by a factor of over 50 to 1.

The stimulation of Mg uptake from application of N was greatest with the 100 ppm N. This is related to the growth response obtained with this N rate. The higher rates of applied N produced smaller increases in Mg content of the stems but the leaf Mg content remained unchanged. The addition of N caused a decrease in K content and this could then mean that the N effect on Mg may be in part an indirect effect.

Table 21. Summary of analysis of variance for the variables investigated.

Source	Response Variables															
	Total N		Nitrate		Chloride		Potassium		Calcium		Magnesium		Protein N		Yield	
	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	g/pot	
<u>Experiment I</u>																
K	**	**	*	**	NS	**	**	**	**	**	**	**	**	**	**	**
N	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
K x N	**	**	**	**	NS	NS	**	**	NS	**	**	NS	NS	**	**	
<u>Experiment II</u>																
K	**	**	**	NS	**	**	**	**	*	**	**	NS	**	**	**	
N	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	
K x N	**	**	NS	NS	NS	NS	**	**	**	NS	**	NS	NS	**	NS	
Cl	**	**	**	**	**	**	NS	NS	*	NS	NS	NS	NS	NS	NS	
K x Cl	**	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	**	NS	NS	
N x Cl	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	
K x N x Cl	NS	NS	NS	NS	NS	NS	**	**	NS	NS	NS	NS	NS	NS	NS	

** Significant at .01 probability level

* Significant at .05 probability level

NS Not significant

Table 22. Summary of analysis of variance for the variables investigated. Experiment III.

Source		Response Variables														
		Total N		Nitrate		Chloride		Potassium		Calcium		Magnesium		Protein N		Yield
		meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	meq/ 100g	meq/ pot	g/pot
K	Stems	NS	*	**	**	*	NS	**	**	NS	NS	**	**	NS	*	**
	Leaves	NS	**	*	**	**	**	**	**	**	NS	**	**	NS	**	**
	Total		**		**		NS		**		NS		**		**	**
N	Stems	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
	Leaves	**	**	**	**	**	**	**	**	**	**	*	**	**	**	**
	Total		**		**		**		**		**		**		**	**
K x N	Stems	*	NS	NS	NS	NS	**	NS	*	*	**	NS	**	NS	NS	*
	Leaves	NS	**	NS	**	**	**	NS	**	NS	**	**	**	NS	**	**
	Total		*		NS		**		**		NS		**		**	**

** Significant at .01 probability level

* Significant at .05 probability level

NS Not significant

Additional Discussion on Ion Uptake

The effects of fertilization on ion uptake and accumulation by potato plants have been evaluated in these experiments. Fertilization with N, K and Cl showed significant effects on nutrient composition in the potato plants. The contents and uptake of Ca, Mg, N, K and Cl showed highly significant changes due to fertilization. However, S and P were adequately supplied and as such remained unaffected to any significant extent beyond dilution caused by increased vegetative growth. The interaction between N and K on the uptake and accumulation of N and K in the plants established a mutual metabolic dependence of the two nutrients when at limiting concentrations.

The rapid conversion of nitrate to organic forms following its uptake has some K mediated metabolic pathways. This necessitates that there be a sufficient uptake of K so that the conversion of nitrate to organic forms is not obstructed. The nitrogen is converted to amino acids and proteins which are then utilized in the growth functions within the plants. The increases in the vegetative growth produces more stems and leaves and result in higher uptake of other mineral nutrients which are utilized by the plants. Calcium and magnesium are two such cations which showed increased uptake as a result of N application.

Since there is a selective mechanism active in the ion absorption

process, the plants discriminate among the ions for their absorption and accumulation. At first the requirements of the plants are met by a balanced uptake of the nutrients. Then an additional uptake of the ions result in accumulation within the plant.

This was generally true in these experiments where the first additions of N and K were utilized in removing the growth restrictions due to the severe deficiencies of the two nutrients. It was during this period that the greatest increases in the nutrient uptake were achieved. As a consequence normal plants were produced and dry matter yield was also increased. But soon after the plants were adequately supplied with N and K, then the additional absorption of the excess supplies of N and K began, which was also due to the increased availability of the two nutrients. This presented interactions of ions in the absorption process.

There was competition between NO_3 and Cl ions in the uptake by potato plants. Application of one reduced the uptake of the other. Stimulation of Cl uptake by supplemental K was observed in these experiments. The antagonism between K application and Mg absorption was very marked. Increase in Mg and Ca absorption as a result of N application was also significant. A partitioning of potato plants into leaves and stems showed that fertilization effects were in general the same for both plant parts. However, the stems showed a greater accumulation of the absorbed ions. The combined concentrations of

the ions, however, are not much further apart.

Ionic uptake is generally followed by metabolic uses in the plants. Some of the absorbed ions are converted to organic forms and the others remain as inorganic ions and function as metal cofactors to enzymatic reactions. Nutrients like N and S are rapidly converted to amino acids and proteins and then assume metabolic roles within the plants. Phosphorous retains the ionic form of phosphate but combines with different metabolites of glycolysis cycle and also acts in high energy ATP functions. Calcium is the most important constituent of the middle lamella and forms stable compounds like pectates, oxalates, etc. Major proportion of Mg is present in ionic form but some of it is utilized in producing stable organic compounds. Chlorophyll is the most important compound containing Mg. Potassium and Cl are the remaining two ions of concern for the purpose of this study. These two ions are not known to form stable organic compounds within the plants. They are very mobile and remain in the ionic forms. But K is one common mineral ion which shows many diverse metabolic functions in the plants. In contrast Cl is required in very small quantities and its metabolic role is limited to one or two reactions. However, both K and Cl are most commonly encountered ions that accumulate in plants.

Information about the metabolic roles of the mineral nutrients in the plants portrays a picture of balance in uptake and accumulation

controlled by metabolic processes in the plants. The electroneutrality is maintained by the influx and efflux of the ions. This results in changes in the concentrations of individual ions. There are a few substitutions of some ions for the others. It is known that some of the ions are capable of substituting for other ions. Most commonly observed phenomenon relates to the mono-monovalent replacement of ions. Rubidium is shown to replace K and competitively inhibit K absorption. In di-divalent replacement series Ca-Mg are shown to compete with each other in the uptake process. A mono-divalent competition and replacement is also encountered between K and Mg system. A cation-anion competition is theorized but very little supporting evidence is currently available to substantiate this theory. Mono-monovalent anion competition is found in the absorption of Cl and NO_3 .

All these considerations present a complex array of events which all work together in giving a certain nutrient composition to plants. Changes in ionic environment and compensatory adjustments within the plants provide for an equilibrium condition for growth and development of the plants.

The results of these experiments show that nutrient uptake was not constant and that fertilization caused variations in the accumulation and the uptake of different ions. This indicates that the nutrients content in the potato plants, is not constant. Fertilization does

change the content of the individual ions, cause growth differences and allow for the higher or lower absorption of nutrients from the environment.

The Effects of N, K and Cl on the Cation-Anion Balance

The absorption of different mineral nutrients which constitute the ionic elements in the plants, was considered in the preceding discussion. It was evident that N, K and Cl fertilization was responsible for changing the composition of the plants with respect to different anions and cations. Stimulation and antagonism in ion uptake as a result of elevated N, K and Cl supplies were observed. It was seen that some of the nutrients were reduced in the plants while others were increased in their concentrations within the plant. Significant interaction between K and N was obtained and established the interdependence of the effects of the two nutrients.

Only cation and anion contents are considered for the purpose of this examination of the ionic equilibria in the potato plants. Tables 23-26 and Figures 14-16 show the results on the milliequivalent cation sum ($C = K + Na + Ca + Mg$), milliequivalent anion sum ($A = NO_3 + P + S + Cl$), milliequivalent total anions ($TA = N + P + S + Cl$), and the milliequivalent difference ($C - A$). All milliequivalent sums are per 100 grams of dry plant material. Total S and total P were used in the anion sums. Since most of the sulfur is taken up in the sulfate form,

Table 23. The effects of N on the contents of cation sum (C), anion sum (A), total anions (TA) and cations minus anions (C-A).

N (ppm)	A meq/100g	TA meq/100g	C meq/100g	(C-A) meq/100g	
<u>Experiment I</u>					
0	73.0	258.4	251.1	178.1	
100	131.2	353.7	305.4	174.2	
200	148.6	371.5	314.7	166.1	
300	154.1	387.2	317.2	163.1	
400	153.9	385.6	307.1	153.2	
<u>Experiment II (with Cl)</u>					
0	100.0	291.6	264.9	164.9	
100	141.3	366.7	315.9	174.6	
200	163.9	398.1	322.0	158.1	
300	160.3	403.1	312.1	151.8	
<u>Experiment III</u>					
100	stems	129.2	216.7	260.3	131.2
	leaves	78.9	305.3	277.9	199.0
200	stems	163.5	318.8	295.1	131.6
	leaves	79.1	346.2	287.0	207.9
400	stems	155.5	314.8	293.9	138.4
	leaves	75.4	341.0	286.7	211.3
600	stems	161.4	339.8	302.9	141.7
	leaves	77.8	355.1	282.4	204.6
800	stems	189.2	407.5	338.9	149.7
	leaves	87.7	381.3	310.9	223.2

In experiment I, all entries in the table are averages for 20 observations.

In experiment II, all entries in the table are averages for 32 observations.

In experiment III, all entries in the table are averages for 12 observations.

Table 24. The effects of K on the contents of cation sum (C), anion sum (A), total anions (TA) and cations minus anions (C-A).

K (ppm)	A meq/100g	TA meq/100g	C meq/100g	(C-A) meq/100g	
<u>Experiment I</u>					
0	153.0	373.2	316.6	163.9	
50	136.1	364.4	294.7	159.1	
100	124.8	361.5	297.9	173.1	
200	121.4	326.1	288.1	166.6	
400	125.8	331.1	298.3	172.5	
<u>Experiment II (with Cl)</u>					
0	148.2	381.4	315.8	167.5	
50	143.2	378.7	308.2	165.0	
100	139.0	352.0	295.2	156.1	
200	135.0	347.2	295.8	160.8	
<u>Experiment III</u>					
100	stems	159.7	319.9	284.3	124.6
	leaves	82.2	346.3	278.5	196.3
200	stems	156.1	314.7	292.6	136.5
	leaves	83.6	349.4	286.6	203.1
400	stems	159.2	316.9	303.8	144.6
	leaves	74.8	341.8	294.7	219.9
600	stems	163.9	326.6	312.2	148.3
	leaves	78.7	345.8	296.1	217.5

In experiment I, all entries in the table are averages for 20 observations.

In experiment II, all entries in the table are averages for 32 observations.

In experiment III, all entries in the table are averages for 15 observations.

Table 25. The effects of Cl on the contents of cation sum (C), anion sum (A), total anions (TA) and cations minus anions (C-A).

Cl (ppm)	C meq/100g	A meq/100g	TA meq/100g	(C-A) meq/100g
0	279.4	127.6	345.5	151.8
100	300.3	143.1	364.4	157.3
200	307.1	139.7	365.3	167.4

All entries in the table are averages for 64 observations.

Table 26. Summary of analysis of variance for the C, A, TA and (C-A) contents.

Source	A	TA	C	(C-A)	
<u>Experiment I</u>					
K	**	**	**	NS	
N	**	**	**	*	
K x N	**	**	**	NS	
<u>Experiment II</u>					
K	NS	**	**	NS	
N	**	**	**	*	
K x N	NS	**	NS	NS	
Cl	NS	NS	NS	*	
K x Cl	NS	**	NS	NS	
N x Cl	NS	NS	NS	NS	
K x N x Cl	NS	NS	NS	NS	
<u>Experiment III</u>					
K	stems	NS	NS	**	**
	leaves	**	NS	*	**
N	stems	**	**	**	*
	leaves	**	**	**	*
KxN	stems	NS	NS	NS	NS
	leaves	*	NS	NS	NS

** Significant at .01 probability level.

* Significant at .05 probability level

NS Not significant

the divalent ionic form was used in calculating the milliequivalents of sulfur. With total P, the monovalent H_2PO_4 ionic form was considered in the calculations.

Fertilization with N and K showed significant changes in the C, A and TA contents in the plants in experiments I and II. Nitrogen fertilization increased C, A and TA contents in experiments I and II (Table 23, Figures 14a, b). The 100 ppm of applied N, at all K rates, showed the biggest increases in the three sums (Table 23, Figures 14a, b). The average A content increased from 73.0 meq/100g at zero N to 131.2 meq/100g at 100N and the C content increased from 252.1 meq/100g at zero N to 305.4 meq/100g at 100 N in experiment I. The TA content showed an increase from 258.4 meq/100g at zero N to 353.7 meq/100g at 100 ppm N. Similar changes were noted for experiment II. Only small increases in the C, A and TA contents were obtained for the higher N applications. Since normal plant growth was reached with 100 ppm N rate and 100 or 200 ppm K additions, it is recognized that the low levels of the C, A and TA contents when N was not applied, are due to the growth limiting effects of the nutrients. The maximum yield increases were obtained when 100 or 200 ppm K was also applied with at least 100 ppm N giving rise to a dilution in ionic concentrations. It was at this point that the total cation sum was maximally reduced and that a corresponding lower concentration of anions was obtained (Tables 23, 24).

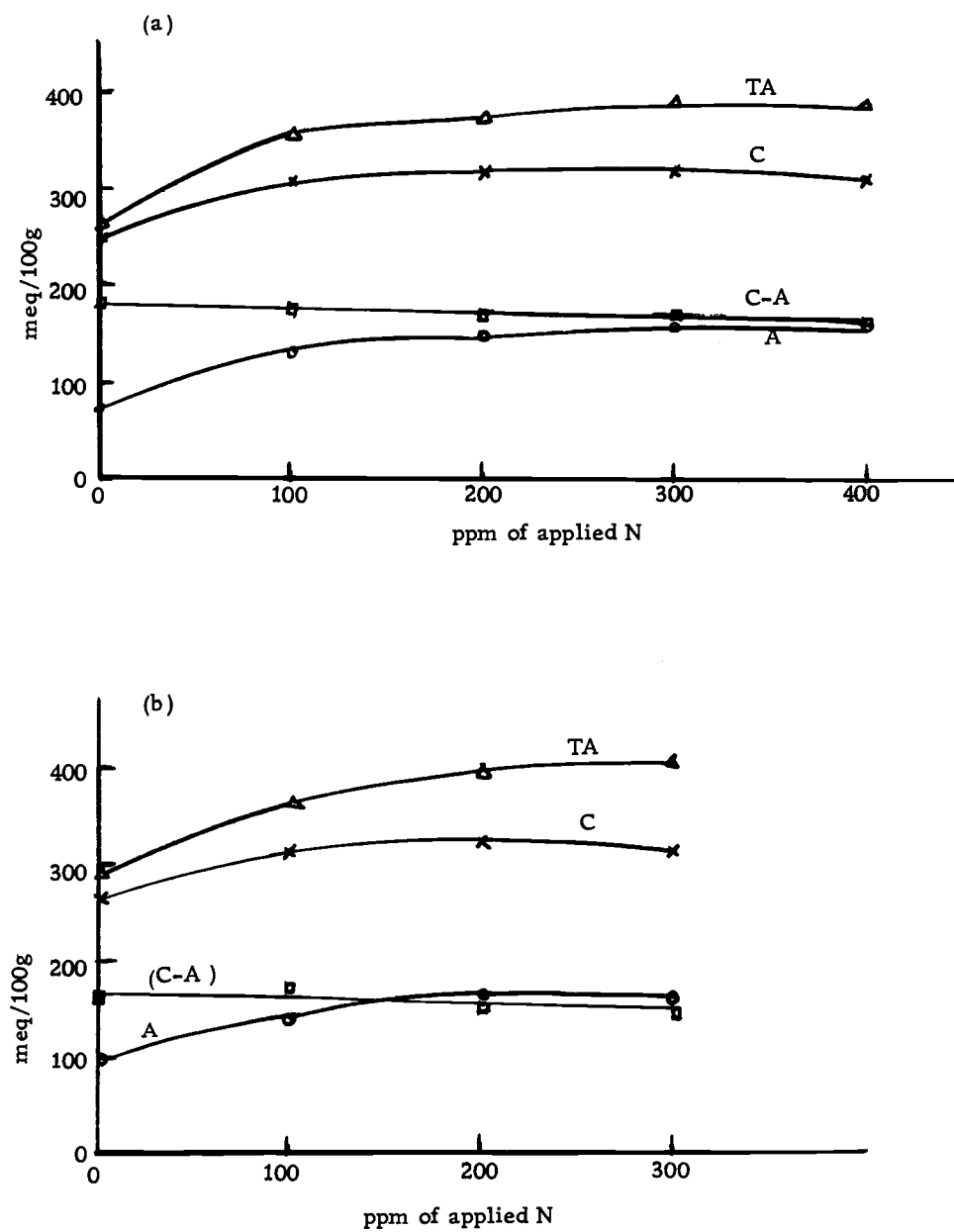


Figure 14. The effects of N on the C, A, TA and (C-A) contents for (a) experiment I, and (b) experiment II.

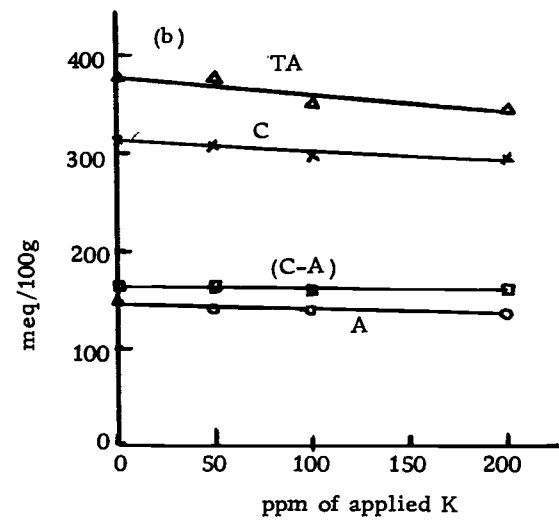
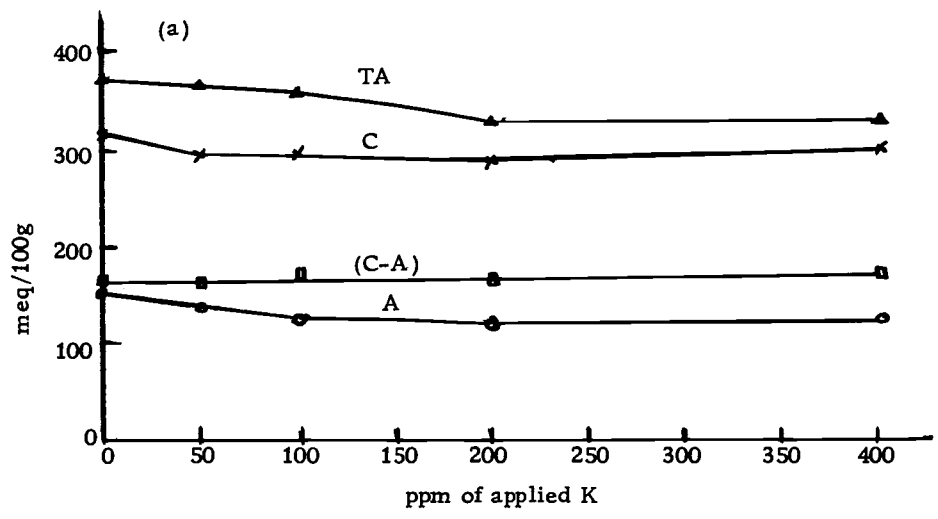


Figure 15. The effects of K on the C, A, TA, and (C-A) contents for (a) experiment I, and (b) experiment II.

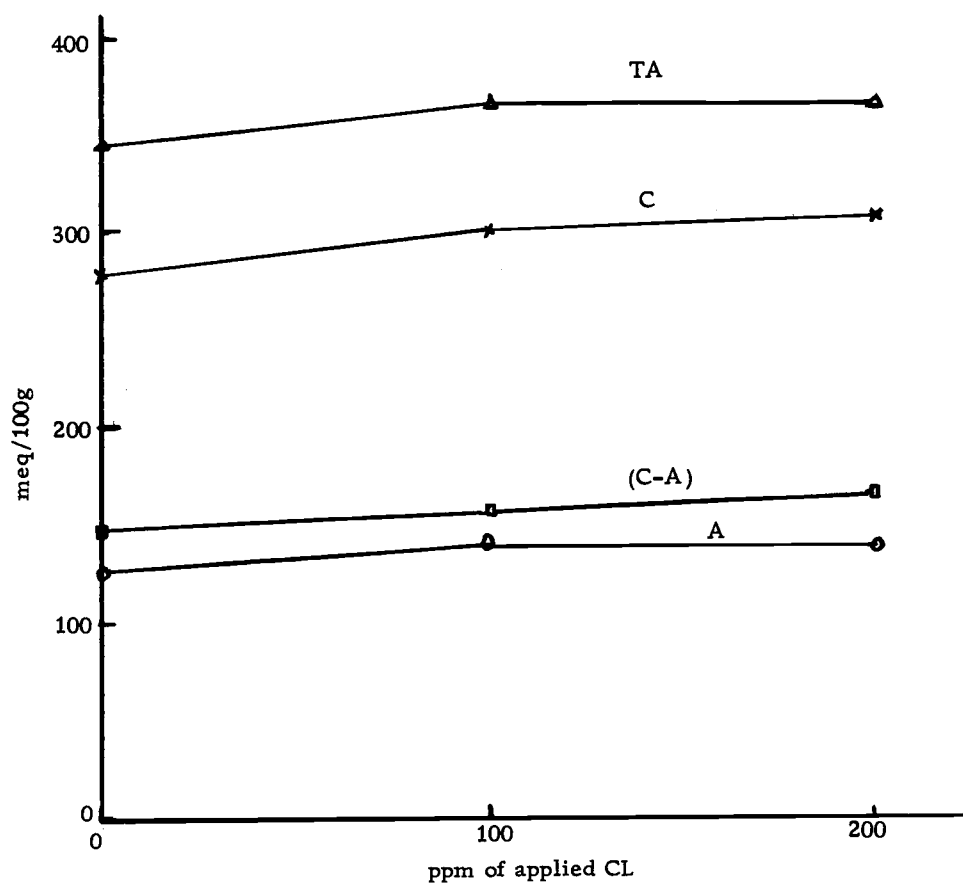


Figure 16. The effects of Cl on the C, A, TA, and (C-A) contents found in plant tops.

The presence of significant K effects on the C and A contents only confirm that fertilization did change the contents of the cations and anions and that the changes in the C and A contents were compensatory resulting in an insignificant K effect on the (C-A) content (Table 24, Figures 15a, b). The conclusion was drawn that the organic acid content, approximated by (C-A) content, in the plants remained unchanged as a result of K application and that the deficiency or sufficiency of K did not have any significant effect on the organic acid content in the plants. Any changes in the C content due to K applications were met with compensatory changes in the A content providing evidence for the existence of the ionic balance independent of K supplies.

With N fertilization there was a different adjustment within the plants. Since nitrogen is taken up as an anion and then converted to organic forms, N application naturally increases the anion content due to increased $\text{NO}_3\text{-N}$ uptake. In experiment I and II where (C-A) content decreased significantly due to the N fertilization, the increased uptake of the anions with added N was not matched with an equally increased cation uptake. This resulted in a decreased production of organic acid anions to maintain the equilibrium within the plants.

Dijkshoorn (1962) concluded that whenever cations are taken up more readily than the anions, organic acids in stoichiometric

quantities are accumulated to balance the excess of cations over the anions. When anion uptake is higher than the cation uptake, then organic acid anions are decreased in quantities equal to the excess anions. Fertilization was shown to change the contents of individual ions but did not appear to have disturbed the observed overall balance.

In experiment III, the C, A and TA contents were considered for the leaves and the stems separately. The highest rates of applied N and K were much in excess of the plant requirements. This was primarily done for the purpose of understanding the increased absorption of the ionic elements and effects on the equilibrium in the plant parts.

The leaves contained about one half as much A content compared to the stems but the TA and C contents were about the same for both plant parts (Tables 23 and 24). Due to much lower A content, the (C-A) content was higher for the leaves than for the stems. Since leaves are metabolically active growing tissues, much of the organic acid production probably occurs in this plant part. The stems contain much higher amounts of absorbed nutrient ions which are translocated to the leaves and the growing tips as growth progresses. This was evidently the case in obtaining a higher (C-A) content for the leaves and a lower (C-A) content for the stems.

One hundred ppm Cl application increased the A and TA contents but no further increase was obtained for the 200 ppm Cl addition

(Table 25, Figure 16). The C content also showed maximum increase when 100 ppm Cl was applied. However, the increase in C content was greater than the increase in A content, and this showed a small increase in (C-A) content due to added Cl. The excess C uptake necessitates the production of an increased amount of organic acid anions which then maintains the ionic equilibria in plants.

The work with the organic acid anions by Ulrich (1941) and Jacobson and Ordin (1954) have considered the function of acids in TCA cycle as the accumulating organic acid anions. Kirby and Mengel (1967) have taken into account the role of uronic acids in cell walls in this balance mechanism. Close proximity in the observed values of organic acids and the (C-A) content have been emphasized by DeWit et al. (1963), Dijkshoorn (1962), Said (1959), Pierce and Appleman (1943) and Patcher (1938). Kirkby and Mengel (1967) and Kirkby (1969) have reported that quite apart from N nutrition total cations are fairly well balanced by total anions.

The results from the published researches do indicate that fairly constant cation and anion contents are maintained in plants. This condition appears to be present for potatoes which are investigated in this present research. However, when a deficiency or limiting nutrient situation is encountered, the C, A and TA contents are much lower. Once both N and K were available in adequate quantities, the excessive supplies of the two nutrients produced no large

changes in the C and A contents. However, there was a reduction in the contents of individual ions whenever another ion of the same charge was increased.

Regression Relations and Response Functions

Multiple regression equations were obtained for each of the response variables by using the stepwise regression procedure. The results of this analysis are summarized in Table 27. The regression equations established the mathematical relationships of the response variables to the control variables. The analysis of the coefficients of regression show a significant linear effect of N and K. The quadratic effect was also found to be significant in most cases. Chloride application showed a significant quadratic effect with notable absence of the linear effect on several occasions. The K x N interaction effect contributed a significant proportion to account for the responses obtained. In general the positive linear effect was associated with a negative quadratic effect and a negative linear effect was accompanied by a positive quadratic effect, indicating that the response curves tended to level off as higher values of the independent variables were reached.

The R^2 column showed a wide range of values obtained for these experiments. There were several cases in which the R^2 values exceeded 0.90. Several other instances showed 70% or more of the

Table 27. Regression coefficients for the fitted response functions showing the effects of applied nutrients on the contents and amounts of the nutrients investigated.

Response variable	Expt No.	Plant part	Units of measurement	Constant of Regression (b_0)	Multiple regression coefficients for the independent variables							R^2
					X_1	X_2	X_3	X_4	X_5	X_6	X_7	
					N	K	N x K	Cl	N^2	K^2	Cl^2	
Yield	I	Entire	meq/pot	4.65	8.6024	17.5305	15.0938		-17.1786	-29.3375		.76
	II	Entire	meq/pot	5.29	5.4406	19.2849	25.7500		-17.6563	-49.5739		.51
	III	Stems	meq/pot	3.74	1.3854	4.8384			-2.9175	-5.4489		.52
		Leaves	meq/pot	5.86	0.9896	0.9703			-3.597			.65
		Total	meq/pot	9.44	2.3228	7.1980			-6.4625	-7.4204		.65
Total N	I	Entire	meq/100g	226.91	976.6392	-171.5212	-294.7238		-1535.7179	354.6429		.81
			meq/pot	9.38	86.8203	43.8496	33.3938		-148.0321	-71.8214		.81
	II	Entire	meq/100g	243.04	959.9405	-461.3225	354.3964		-1834.8516	928.7102	-372.026	.86
			meq/pot	12.46	70.7050	23.3204	137.1286		-157.6875	-93.8693	-36.8542	.74
			meq/100g	146.32	113.4169							.72
	III	Stems	meq/pot	6.24	9.1969		3.6800		-8.8891			.37
			meq/100g	265.93	52.8045							.52
		Leaves	meq/100g	15.09	9.0671	2.7822			-14.1259			.53
			meq/pot	19.71	19.4599	12.8885			-23.015	-11.6997		.37
Nitrate-N	I	Entire	meq/100g	29.84	641.6596	-88.8504	-225.6575		-984.7036	263.1993		.68
			meq/pot	0.3894	47.4387	12.0797			-75.5143	-13.3955		.70
	II	Entire	meq/100g	35.96	635.9171	-187.2633			-1175.2344	435.304	-493.3125	.81
			meq/pot	2.53	39.2039		45.3363	-10.489	-77.6016	-17.5191		.78
	III	Stems	meq/100g	58.22	141.0154		41.4645		-59.0188			.77
			meq/pot	2.45	8.5481		3.8448		-7.5839			.57
		Leaves	meq/100g	138.77	21.5046	-10.1756	24.2877					.63
			meq/pot	0.8259	1.5999	-0.5703	1.834		-1.221			.45
	Total	meq/pot	3.09	10.4697		4.6947		-8.8049			.60	

Table 27. Continued.

Response variable	Expt. No.	Plant part	Units of measurement	Constant of Regression (b_0)	Multiple regression coefficients for the independent variables							R^2
					X_1 N	X_2 K	X_3 N x K	X_4 Cl	X_5 N^2	X_6 K^2	X_7 Cl^2	
Protein-N	I	Entire	meq/100g	165.71	427.5997	-175.3345			-780.6143	299.606		.60
			meq/pot	7.23	44.0980	22.8244	29.1288		-83.9821	-38.2628		.74
	II	Entire	meq/100g	165.86	437.6513	-132.5118			-900.125			.66
			meq/pot	8.39	35.3126	23.1376	68.515		-87.0078	-83.7727		.58
		Stems	meq/100g	75.67	18.1923		-17.2781					.28
			meq/pot	3.00	2.1006	2.1461			-2.8627	-2.3354		.27
	III	Leaves	meq/100g	222.09	23.8865							.23
			meq/pot	13.49	4.0191		3.6665		-10.1431			.55
		Total	meq/pot	16.85	5.8871		4.3822		-13.0059			.53
Chloride	I	Entire	meq/100g	11.96	-33.9470	-3.7113			48.1000			.50
			meq/pot	0.5942	-1.3342	1.2153			1.6393	-2.2087		.33
	II	Entire	meq/100g	33.24	-68.0763	182.5484				-513.4801	408.125	.56
			meq/pot	1.04	-3.3888	19.5660		7.9688		-44.7443		.58
	III	Stems	meq/100g	65.65	-107.1758	-27.2015	12.4741		72.6583	21.4977		.89
			meq/pot	2.76	-4.4797				2.6974			.86
		Leaves	meq/100g	45.35	-72.4540	-28.9521	26.1185		45.7063	13.8113		.92
			meq/pot	2.62	-4.2677	-0.8605	1.3856		2.2833			.93
		Total	meq/pot	5.26	-8.7568		1.4146		4.9807	-1.1457		.92
Potassium	I	Entire	meq/100g	53.24	-50.8441	184.1319	-89.7275		100.8393	195.1251		.92
			meq/pot	2.28	5.2214	19.3034	15.8038		-13.3036	9.5654		.90
	II	Entire	meq/100g	51.19	-104.6144	411.8750	-283.6214		261.2188	-561.7983	94.1979	.77
			meq/pot	2.58	-1.4162	36.7602				-50.4545		.79
		Stems	meq/100g	86.72	-120.4765	367.4382			110.5699	-246.4544		.90
			meq/pot	3.06	-2.8396	21.9813				-17.0778		.87
		Leaves	meq/100g	60.76	-84.7289	259.5059			69.0148	-166.6227		.94
			meq/pot	3.03	-2.2941	18.0691	-3.958			-10.2644		.92
Total	meq/pot	5.80	-4.4296	40.9602	-6.1244			-27.3423		.94		

Table 27. Continued.

Response variable	Expt. No.	Plant part	Units of measurement	Constant of Regression (b_0)	Multiple regression coefficients for the independent variables							R^2
					X_1 N	X_2 K	X_3 N x K	X_4 Cl	X_5 N^2	X_6 K^2	X_7 Cl^2	
Calcium	I	Entire	meq/100g	72.76	269.8679					-499.1071	-115.0616	.69
			meq/pot	3.18	23.6253	16.5899	17.5888		-45.1214	-38.4779	.78	
	II	Entire	meq/100g	80.12	288.9765		505.8934	45.7031	-824.6094	-516.1788	.54	
			meq/pot	4.42	22.0804	15.2193	68.1650		-66.0547	-70.3807	.68	
	III	Stems	meq/100g	38.22	51.9040		44.4543			-29.6147	.76	
			meq/pot	1.52	4.0089		2.6374		-3.0687	-1.0310	.60	
		Leaves	meq/100g	98.35	33.286	-55.9985	69.8377				.72	
			meq/pot	5.50	2.7940		-5.1242		-4.1038	-3.7789	.23	
		Total	meq/pot	7.02	6.8029		7.7616		-7.1725	-4.8099	.43	
Magnesium	I	Entire	meq/100g	142.01	285.6538	-404.0867	121.67		-567.8857	370.5132	.84	
			meq/pot	6.78	26.6508		21.8292		-51.1393	-26.3658	.64	
	II	Entire	meq/100g	146.75	352.4307	-764.2908	490.3479		-938.8047	1781.3097	.81	
			meq/pot	7.42	28.0047	-14.5466	66.0022		-78.1172		.44	
	III	Stems	meq/100g	122.20	102.9299	-286.5794	-20.2615		-61.725	224.1545	.95	
			meq/pot	4.62	6.3263	-8.1817			-6.2750	4.3937	.86	
		Leaves	meq/100g	120.02	-15.3531	-14.1768	50.8001			55.3483	.83	
			meq/pot	6.87		-6.0224	4.9302		-3.7437		.71	
	Total	meq/pot	11.25	5.8898	-11.4591	5.7527		-9.8377		.82		

variation which was accounted for by the fitted models. However, few fitted equations produced R^2 values under 0.35. The poorest regression fit was obtained when only 23% of the variation was accounted for by the fitted model. On the other hand the best fitted regression equation showed a R^2 value of 0.95.

In general $N \times K$ interaction effect was significant in more cases analyzed by regression procedure, when compared to the analysis using ANOVA for factorial experiments. This was apparently due to the unequal spacing of the factor levels used in these experiments. The regression approach considered the quantitative values of the applied nutrients and accounted for the differences and interactions on that basis.

SUMMARY AND CONCLUSIONS

A series of greenhouse experiments designed to obtain a better evaluation of the effects of N, K and Cl on the nutrient uptake and composition of Russet Burbank potatoes were conducted in the summers of 1969 and 1970. The Deschutes soil selected for the purpose of this study was very low in available K.

The experiments were designed as complete factorial arrangement of N, K and Cl treatment combinations. The treatments were replicated four times in experiments I and II and three times in experiment III.

Entire plant tops were harvested in all three experiments after the plants were allowed to grow for 30 days and when tubers were starting to set. The leaves were separated from the stems and petioles for experiment III only. The plant tissues were analyzed for various elements using the established laboratory procedures. Statistical analysis was carried out to evaluate the significance of treatment effects.

The analysis of the results obtained from these experiments led to the following conclusions:

1. There was substantial response to 100 ppm N when applied in combination with 100 ppm or more of K. The yield increases were highly significant statistically.

2. Applications greater than 400 ppm N depressed yields when compared with 100 ppm N rate.

3. The maximum yield increases obtained were for the treatment combination employing 100 or 200 ppm K rates with at least 100 ppm N.

4. Maximum changes in nutrient composition occurred when 100 ppm of N and 100 ppm of K were applied.

5. Nitrogen application increased total N, protein N and $\text{NO}_3\text{-N}$ contents with the increases beyond the 100 ppm N rate being smaller. The total amounts of the different N fractions were also increased by the N applications up to 600 ppm of applied N. It was evident that the 600 or 800 ppm of applied N reduced the total amounts of the various N components in the potato plants when compared with the 200 or 400 ppm N rates.

6. Potassium application decreased the contents of the various N fractions but increased the total amounts of these fractions found in the potato plants. The decreases in the contents were largely a dilution effect caused by the increased vegetative growth due to applied K.

7. Chloride application decreased the contents of N and $\text{NO}_3\text{-N}$ and the total uptake of N by the potato plants but did not affect the protein-N fraction. The decrease in total N was a reduction in the $\text{NO}_3\text{-N}$ fraction presumably caused by an antagonism in uptake between the NO_3^- and Cl^- anions.

8. Potassium application increased conversion of nitrogen to protein when the total amount was considered. The greatest increase was obtained with the 100 ppm rate of applied K.

9. The stems showed higher accumulation of $\text{NO}_3\text{-N}$ with the leaves having a higher concentration of protein-N.

10. Chloride content and uptake were significantly increased when Cl was added. Potassium also increased Cl content and uptake in experiment II, the only experiment with Cl variable.

11. Potassium application produced marked increases in K content and uptake. The absorption of K was steadily increased with each successive addition of K.

12. Nitrogen application decreased K content but increased Mg and Ca contents. However, K uptake was increased by added N except when excessive uses of N depressed yields. The decreases in K content due to added N were primarily dilution effects.

13. Potassium application decreased the content and uptake of Mg by the potato plants. This effect was more pronounced at low rates of applied N.

14. Lowest anion and cation sums were obtained when N was not applied. But the C and A contents varied within a small range when N was applied. The (C-A) content was reduced with increasing rates of N application.

15. Potassium application caused a reduction in C and A

contents but did not change (C-A) content. This indicated that the organic acid content, approximated by (C-A), remained unaffected as K supplies were varied.

16. The stems showed higher accumulation of A and this produced lower (C-A) content in the stems than the leaves. This indicated that higher amounts of organic acids should be found in the leaves than the stems.

17. One hundred ppm of applied Cl produced a marked increase in C, A and TA contents with the 200 ppm Cl application giving little added effect.

18. The uptake data provided a better index to measure the responses due to the N, K and Cl applications.

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