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Title SELECTIVE INHIBITION OF ION ABSORPTION BY URANYL

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The research presented in this thesis evaluated the effects of uranyl (UO_2^{++}) upon the absorption of Li, Na, K, Rb, and Cl. Due to the biological importance of Na and K, these two ions were studied in the greatest detail.

The results of this research showed that, at UO_2^{++} concentrations above 1×10^{-1} milliequivalents per liter and pH's above 4.5, uranyl selectively inhibited K and Rb absorption but had essentially no effect upon Na and Li. Under these same conditions it was concluded that uranyl polymers such as $(UO_2)3(OH)_4^{++}$ were formed. It was suggested that these polymers produced the inhibition of K and Rb absorption.

When the pH was below 4.0 and the UO_2^{++} concentration below 1×10^{-2} millequivalents per liter the simple UO_2^{++} cation was the predominant form of uranyl. Under these conditions uranyl acted in a fashion similar to many of the other divalent cations in that it stimulated the absorption of K and Rb (and to some extent Na) from

single-alkali cation solutions. When K and Na were both in a test solution at pH 5, the simple UO_2^{++} cation stimulated K but slightly inhibited Na absorption.

By pre-treating root samples for thirty minutes in a 1 milli-equivalent uranyl solution the absorption of K could be greatly reduced and the absorption of Na stimulated. These effects of the UO_2^{++} could be completely reversed by subsequently treating the pre-treated tissues with EDTA for one hour.

The addition of UO_2^{++} to root tissues resulted in a slight reduction in the rate of respiration and produced a marked inhibition of K absorption but had no effect upon Na absorption.

The results of this study suggest that there are at least two carriers transporting Na and K. One of these carriers was inhibited by the higher uranyl concentrations at pH's above 4.5. This carrier shows a "preference" for K. The second carrier was unaffected by UO_2^{++} and showed a "preference" for Na. When only one of this pair of ions was present it could travel via either of the carriers. Competition of K with Na was greatest during absorption via the "UO_2^{++}-sensitive" carrier. Na competition with K was greatest during transport via the "UO_2^{++}-resistant" carrier.

It is suggested that UO_2^{++} may bind to a phosphate containing organic compound which is either the K carrier or a compound closely related to this carrier.

SELECTIVE INHIBITION OF ION ABSORPTION BY URANYL

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INTRODUCTION

The process by which ions enter living cells has been the subject of considerable controversy for many years. Systems ranging from simple diffusion, following Fick's law of diffussion (35), to the complex anion respiration concept of Lundegardh (47) have been proposed for ion transport. Part of this diversity of opinion resulted from failure to recognize that there are two separate phases of ion uptake.[1] The first phase is a rapid, non-metabolic diffusion into some space within the tissue. This space was called "apparent free space" by Briggs et al. (14). The second phase of this uptake is an active, energy requiring absorption[2] which is thought to be linked to the cells metabolic processes. When tissues which are low in a particular ion are placed in solutions containing this ion the absorption which occurs during the second phase of uptake usually exhibits a steady state rate.

The link between absorption and the cell's energy pool has been

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[1] In this thesis the word uptake will be used when referring to the total process of movement of ions into the tissue whether by active or passive means.

[2] Absorption will be used to refer to the active, metabolically mediated movement. Accumulation and transport have also been used when referring to the active metabolic uptake of ions.

shown by observing the effects of low temperature, anerobiosis and metabolic poisons upon the active steady state rate. Also observed during this phase of uptake is the synergism and antagonism of one ion upon the absorption of another (59). All of these observations have been used in identifying the nature of the mechanism of ion transport.

The Carrier Theory

During the last ten to fifteen years mechanisms which involve the use of "carrier" molecules have been discussed widely. The idea of a carrier was suggested by Pfeffer (60) and Lundegardh et al. (50). These workers envisaged an organic compound, located near the cell surface, binding with the ions and carrying them across the membrane of the cell. Lundegardh (50) suggested that this compound might be a phosphatide.

There are several lines of evidence which lead one to the conclusion that a carrier system is necessary to account for the observed facts concerning ion transport. Perhaps one of the strongest factors in favor of binding the ion to a carrier is the fact that metabolic energy is expended during the accumulation of ions across the semi-permeable membrane around the cytoplasm. This energy link was first proposed by Hoagland and Davis (31) and later expanded by Steward and Berry (82). Since that time numerous observations have

been made to support the conclusion that metabolic energy is required to accumulate ions within the cell. Spiegelman and Reiner (81) and Zscheile (94) have presented some thermodynamic approximations of the free energy required to accumulate ions against the observed concentration gradients found in the plant cell. According to Zscheile (94) approximately 4,000 calories per mole are required to meet the energy demands for transporting potassium across the membrane of Nitella cells. A number of workers (20, 45, 65, 68) have noted that only a metabolically produced compound could combine the transport of ions to the energy producing processes of the cells.

The second line of information that favors the movement of ions by carriers is related to the discrimination, that cells are known to exhibit, between similar ions such as K and Na. In plants, this selectivity is observed in such diverse tissues as Porphyra (19), Ulva lactuca (77), Valonia (58), roots from grain plants (6, 8, 22, 26, 30, 57), discs from beet root tissue (84), yeast cells, (43, 69) and Nitella cells (31, 94). It is conceivable that factors which alter the diffusion of ions through materials which are considered to be in the membrane (such as lipoproteins) could distinguish between such diverse ions as K^+ and Ca^{++} but it is difficult to envisage that a passive mechanism could discriminate against Na^+ in favor of K^+. Only a process linking the

ion to some organic compound could bring about this differentiation. Although occasional papers still appear which propose a mechanism other than a carrier for the movement of ions, the preponderence of information in recent years seems to favor the concept of carrier mediated ion absorption (48). Due to this general acceptance of the carrier hypothesis this thesis will consider that ions cross the membrane via some metabolically linked organic compound referred to as a "carrier".

Carrier Models

Among those accepting the carrier hypothesis there is considerable disagreement over the type of carrier system that will provide the necessary requirements for ion movement. Jacobson and Overstreet (40) have outlined the most important of these requirements. The following is a summary of their ideas concerning the nature of the carrier.

(a) It must be related to the oxidative metabolism of the plant.

(b) It must form a strong complex with a wide variety of inorganic ions; both cation and anion.

(c) It must account for the transport of ions of the same sign with a wide range of properties.

(d) It must break down easily on the inside of the cell to release the ion into the vaccuole, etc.

There have been many schemes proposed to account for the requirements listed above. Lundegardh (47) and Robertson (68) proposed that the mechanism was directly linked to the cytochrome-cytochrome oxidase system via what they called anion respiration. This idea has had considerable support but it has failed to show the reason for the specificity of ion absorption and also has failed to account for the separation between anion absorption and cation absorption that is known to occur in plants. Also this concept could not account for the effects of 2, 4-dinitrophenol (DNP) upon absorption and respiration. (This compound inhibits oxidative phosphorylation, inhibits absorption of ions and stimulates respiration (46).) To date it appears that most workers are convinced that the cytochrome-cytochrome oxidase system will not account for the observed facts.

Another area of controversy has arisen around the number of carriers (or mechanisms) that are responsible for moving ions across the cell membrane. Jacobson et al. (38), Conway (16), Hodges (32) and Moore (56, p. 42) have put forward the supposition that Na^+ and K^+ compete for the same ion carrier. On the other hand, Epstein and Hagen (22), Ariz (4), Fried and Noggle (23) and Bange (6, 7, 8) have concluded that there are two carrier sites which are responsible for the movement of the alkali cations.

Jacobson et al. (38) and Moore (56) base their conclusion upon the observation that different alkali cations are known to compete with each other, presumably at the binding site. Epstein and Hagen (22), Bange (6, 7), Tromp (87) and Fried and Noggle (23) concluded from kinetic analysis of the uptake data that a number of separate carriers were involved in the movement of these two ions.

Carrier Compounds

Not only is there disagreement over the scheme of ion absorption but also over the type of compound which serves as a carrier. The most commonly suggested organic molecule is an amino acid containing compound. The reason that the amino acids are implicated is that they are the most likely compound that could provide specificity and linkage to the metabolic activity of the cell (24, 83, 85). Tanada (86), Lansing and Rosenthal (44) and Hanson (28) have shown a connection between RNA and absorption. Their conclusions are based upon the results of experiments where the enzyme RNA'ase and ultraviolet light were used to manipulate absorption. RNA has been shown by Lansing and Rosenthal (44), Wachsman et al. (92), Hanson (28) and McLaren et al. (53) to be present in the surface layers of a number of cell types. Hokin and Hokin (33, 34) and Rothstein and Meier (74) have proposed mechanisms which involve the phosphatases as carrier molecules. Skou (79), Bonting et al.

(11), Whittam (93), Singer et al. (78), and Post et al. (63, 64) have isolated a Na-K ATPase from animal tissues that shows a strong parallel between the effect of oubain upon the ATPase and it's effect upon Na and K transport. Recently Hokin and Hokin (34) have shown that the phosphatidic acid system proposed by them fits the observations made on the Na-K-oubain sensitive ATPase. No matter which compound is suggested as the carrier, most of the observations have indicated that the compound in question is located in the cell membrane. Also it is interesting to note that most of these carriers are related to phosphate as well as to the proteins (33, 42, 64). Benson (10) states that the calcium effect discussed by Epstein (21) suggests that the phospholipids play a role in transport. MacFarlane (51) has shown that there are a number of phospho-lipo-protein compounds that can be extracted from the membrane fraction of bacteria. She has shown that these compounds are active in protein synthesis. This observation, along with those which connect the phospholipids with transport, could be a direct indication of the existence of the proposed link between protein synthesis and accumulation (83). This would also account for the suggested role that the phosphorylated compounds play in ion uptake (1, 11, 33, 34, 42, 63, 64, 74, 93). Recent work by Ahmed and Judah (1) has shown that the oubain sensitive, Na - K ATPase of brain tissues is located in the lipoprotein found in the microsome fraction of cell

homogenates. The microsome fraction is often contaminated with rather large amounts of membrane fragments resulting from the disruption of the cellular integrity (92). The fact that these recent observations show the presence in the membrane of compounds containing both protein and phosphate lend considerable support to the hypotheses which propose the presence of these compounds in the carrier molecule. The protein portion of the molecule would provide the specificity and the phosphate portion of the molecule would provide the link to the energy pool via ATP.

Inhibitors of Ion Absorption

Much of the identification of possible compounds and their links to energy sources in the cell has been accomplished with the aid of various inhibitors. For example, Tanada (85) inhibited K absorption with RNA'ase. Skou (79) inhibited both K influx and Na efflux with oubain, a known inhibitor of the Na-K ATPase. Many workers have used 2,4-dinitrophenol (DNP) to block the cells metabolic cycles. Loomis and Lipman (46) showed that this inhibitor uncoupled oxidative phosphorylation. Scott and Hayward (76) used phenylurethane, iodoacetate and arsenate to inhibit ion movement in sea lettuce, Ulva lactuca. Chloramphenicol, an inhibitor of protein synthesis was shown to inhibit ion absorption (85) but Hanson and co-workers (29) have recently shown that this compound not only

blocks protein synthesis but also inhibits oxidative phosphorylation much in the same way as DNP. In a review article Laties (45) pointed out that ion absorption could be inhibited by N_2, carbon monoxide, and low temperature. The interesting point of all of these compounds and methods is that they either affect all of the ions by inhibiting the metabolism of the tissues or else they are specific for inhibiting a certain reaction that affects all ions alike. There appears to be no good means of selectively inhibiting the movement of one ion while having little or no effect upon another ion.

In a preliminary report Mason et al. (52) noted that the addition of the uranyl cation (UO_2^{++}) appeared to differentialy inhibit Na and K absorption in barley roots. K absorption was inhibited; but uranyl had little or no effect upon Na absorption.

The Uranyl Cation

Uranyl is the polyatomic cation formed when hexavalent uranium is dissolved in water. This cation is the most stable form of uranium found in an aqueous media. Rabinowich (65, p. 349) has noted the extreme complexity of uranyl chemistry. The complexity stems from the many forms that this ion can attain as it polymerizes during hydrolysis. Rush et al. (75) have shown that these polymers vary with uranyl concentration and also pH. At low concentrations

(less than 1 X 10^{-2} milliequivalents per liter) or low pH's (less than pH 3.5) the majority of the uranyl is present as the simple UO_2^{++} cation. As the concentration increases or the pH increases polymerization between uranyl cations occurs. Rush et al. (75) report that polymers as complex as $(UO_2)_3(OH)_5^+$ can occur. At a concentration of one milliequivalent per liter and at pH's slightly greater than pH 6.0 a yellow precipitate of uranic hydroxide (65) appears. As the concentration of uranyl increases above one milliequivalent per liter the pH where the precipitate forms shifts to lower pH's.

Effects of Uranyl upon Absorption Mechanisms

A search of the literature reveals a scarcity of information concerning the effects of uranyl upon ion uptake. Ariz (3) used uranyl nitrate to inhibit chloride absorption. This observation must be accepted with some reservation since Lundegardh (49) has shown that nitrate will inhibit chloride absorption. Rothstein and Larabee (72), studying the uptake and metabolism of hexose by yeast cells, found that uranyl blocked glucose uptake but had no effect on the uptake of similar substrates. Rothstein and Hayes (70) also noted that uranyl reduced Mn uptake by yeast cells but concluded that this was due to a competition for a physical binding site on the cell surface. Although Rothstein concluded that uranyl physically blocked Mn uptake he also concluded that uranyl blocked glucose uptake by binding

to some compound in the cell surface, perhaps a phosphatase enzyme. Rothstein (71, 72) showed that UO_2^{++} inhibited the activity of a number of enzymes related to glucose uptake and metabolism. In contrast to this, Barron et al. (9) concluded that uranyl did not react with any of the enzymes in yeast cells but blocked glucose absorption by physically obstructing the passage of glucose into the cell.

The work of Ponz and co-workers (61, 62) tend to support Rothstein's conclusion that uranyl reacts with specific sites, located in the cell surface, that are active in moving carbohydrates across the membrane. They observed that uranyl inhibited intestinal absorption of glucose and glactose by loops of rat intestine but did not inhibit fructose and arabinose absorption. This effect could be overcome by washing the intestine with a solution of EDTA. They concluded that the uranyl probably complexed with specific enzymes located on the membrane of the cells. Kijima (43) also arrived at the same conclusion from his work with yeast cells. In this case, poly-phosphate was used to reverse the effects of uranyl.

The Site of the UO_2^{++} Effects

It has been hypothesized that the site of uranyl inhibition in yeast cells is very close to the surface of the cell if not on the actual surface. This conclusion was based upon studies of the reversal of the UO_2^{++} inhibition of glucose absorption. Hurwitz (36), Barron

et al. (9), Rothstein et al. (71) and Kijima (43) have all used polyphosphates to reverse the inhibition produced by uranyl. Judging from the rapidity of the reversal, Rothstein et al. (71) concluded that the site of action must be on or very near the actual surface of the cell.

Singer et al. (78) noted that UO_2^{++} markedly inhibited succinic oxidase, hexosemonophosphate oxidase and lysozyme. UO_2^{++} also had a slight effect upon cytochrome oxidase, phosphorylase, and hexokinase. In a review of the work of Singer and his associates, Rothstein et al. (71) concluded that Singer et al's. work presented further evidence that uranyl could not be entering the interior of the cell. He noted that the presence of UO_2^{++} in the interior of the cell would inhibit metabolism to a marked extent.

Barron et al. (9) showed, in the case of yeast, the UO_2^{++} did not alter respiration directly. Any inhibition of respiration could be accounted for in terms of the blocking of glucose entry into the cells. This was verified by the use of substrates whose absorption was not inhibited by UO_2^{++} and also by adding UO_2^{++} to glucose substrates at various time intervals after the initiation of the experiment. In the former case respiration was unaffected by UO_2^{++}. In the latter case glucose absorption was immediately blocked by the addition of the uranyl; but respiration continued for some time before the inhibition of glucose absorption markedly reduced the respiration rate.

They concluded that if uranyl were inhibiting respiration directly then the addition of UO_2^{++} should attack respiration sooner than was seen in these experiments.

Rothstein and Larabee (72) have presented a figure which shows the uptake pattern of UO_2^{++} by yeast cells. This curve is quite similar to the curve for Ca absorption by barley roots which was presented by Moore et al. (63). Moore and his co-workers (57) indicated that Ca apparently did not penetrate into the interior of the cell to any great extent. Jacobson et al. (38) noted that Ca blocked the absorption of Li but not K. The parallel between the interpretations of the effects of UO_2^{++} on yeast cells and Ca^{++} on barley roots led to a preliminary evaluation of the effects of UO_2^{++} upon the absorption of the alkali cations. This preliminary work suggested that UO_2^{++} was selective in inhibiting K and Rb absorption. The work which is presented in this thesis was initiated to evaluate the hypothesis that uranyl is a selective inhibitor of ion absorption by excised barley roots. It was also hoped that this study would aid in defining the mode of entry of ions into barley root tissue.

METHODS

In 1941 Ulrich (88) reported upon the use of excised root tissue from eteolated barley seedlings for uptake studies. This method, modified somewhat, has been used by numerous workers (6-8, 20-22, 37-41, 52, 56-57, 59, 66) since that time. Many of the current hypotheses concerning the nature of the ion absorption mechanism are based upon observations made during experiments which used Ulrich's techniques. The study reported in this thesis also used this technique so that comparisons with other work could be made.

Preparation of the Root Material

One hundred gram lots of barley seed, Hordeum vulgare, var. Trebei, were washed with distilled water then soaked for 24 hours in aerated distilled water. After soaking, the seed were rinsed with running distilled water than transferred to cheese cloth covered, stainless steel screens placed in plastic trays. After the seed were evenly spread over the surface of the screen a layer of cheese cloth was folded over the top of the seed. The cheese cloth was long enough to dip into the nutrient solution placed in the tray. After the seed were prepared, 3 liters of nutrient solution containing 0.1 millimoles each of $Ca(NO_3)_2$, KH_2PO_4, and $MgSO_4$ per liter were

added to the trays. The trays were placed in the dark in a light tight box; an aerator in the trays was attached to a filtered air supply; the trays were then covered with a piece of plate glass. The temperature was maintained at 25°C throughout the growing period. At the end of 72 hours the solution in the trays was changed. After six days, the tissue was harvested by cutting the roots from the seed at a point just below the screen. The roots were washed twice with distilled water and cut into approximately two centimeter lengths. After excising, the roots were placed in a dilute acid wash (distilled water adjusted to pH 4.0 with HCl) for twenty minutes. (This was done to avoid the effects of any adsorbed calcium or magnesium which might be present in the tissues. Jacobson et al. (39) have shown that there is enough adsorbed calcium in normal tissues to alter the uptake patterns of monovalent cations.) After twenty minutes in the dilute acid the roots were rinsed twice using six liters of distilled water for each rinse. At the completion of washing, the roots were placed in wet cheese cloth and centrifuged at 65 times gravity for five minutes. This was done in order to remove excess water and to insure a uniform reference for determining the fresh weight of the tissues. This procedure produced a uniform mass of about 85 grams of root material per tray. The entire lot of root material was thoroughly mixed during washing and again prior to weighing. The uniformity of this material can be shown by the comparison of

the analysis of duplicate check samples. This comparison revealed no significant differences in the Na or K content of the duplicate samples. (This observation is based upon statistical analysis of the duplicate checks from 15 experiments. See Appendix 1 for this data.) In order to reduce evaporational loss of water from the bulk lot of root material, the tray containing the roots was covered with several layers of cheese cloth during the weighing process. Jacobson et al. (39) presented conclusive evidence that a root to solution ratio of 1:1 or less was desireable in order to avoid problems resulting from leakage of various ions and organic compounds from the root material. These workers showed that with increasing root: solution ratios the amount of Ca lost from the cells is "sufficiently large to exert a strong effect on the absorption rates". In light of Jacobson et al's. work, a root to solution ratio of one gram of root material per liter of solution was maintained. Since the bottles were calibrated to hold 7 liters of solution, 7 grams of root material were weighed out on a torsion balance and placed into the solution. The time that the roots entered the solution was noted as the starting point of the time for the treatment.

Test Solutions

The particular solutions in the bottles were made up to fit the requirements of the experiment. In all cases, except where

indicated, the salts were present at 5 milliequivalents per liter for the alkali cations and 1 milliequivalent per liter for uranyl. The particular concentration of alkali cation was chosen because there is considerable information available in the literature for excised barley root studies which used this concentration (6-8, 20-22, 27, 30-31, 37, 41, 52, 56-57, 59). The source of the ions was reagent grade chloride salts of the various cations.

As the concentration of UO_2^{++} increased the hydrogen ion concentration also increased. This was the result of the hydrolysis of the uranyl salts in aqueous media (65). The liberated hydrogen ion caused the pH of the test solutions to range from about pH 5.4 at 1×10^{-3} milliequivalents of UO_2^{++} per liter to pH 3.5 at 1 milliequivalent per liter. In order to adjust the pH of these solutions to pH's higher than that resulting from the hydrolysis of the various salts in the solutions it was necessary to add hydroxides of the cations being investigated. Unless compensation were made for the added cation, the concentration of the alkali cations would vary from one uranyl concentration to the next. In order to offset these concentration changes the initial concentration of the alkali cation was below 5 milliequivalents per liter. The pH was then adjusted with standardized base using a micro-syringe to accurately measure the volume of base added. After the pH was adjusted the actual concentration of alkali cation was calculated. The difference between the

calculated concentration and 5.0 milliequivalents per liter was determined. An amount of standardized chloride salt of the particular alkali cation equal to this difference was then added to the solutions. This procedure resulted in equivalent treatments having the same concentration.

Temperature Control

After the solutions were prepared the bottles were placed in a constant temperature bath maintained at an average temperature of $24.7 \pm 0.5^{\circ}C$. The solutions were continuously aerated from a filtered air supply.

pH Control

At the beginning of the experiment the solutions were adjusted to the required pH using either standard HCl solutions or standard hydroxide solutions of one of the cations being investigated. During the experiment the pH was periodically checked and adjusted back to the desired value. All adjustments were made with standardized acids and bases in order to determine the changes in concentration resulting from this adjustment. In no case did the ion concentration change by more than $\pm$ 0.02 milliequivalents per liter as the result of the adjustment. The pH's ranged as follows during the experiments reported in this study.

pH	Average	Range
3.0	3.0 ± 0.05	2.90-3.10
4.0	4.0 ± 0.05	3.80-4.10
5.0	5.0 ± 0.15	4.75-5.30
6.0	6.0 ± 0.07	5.70-6.30

Length of the Absorption Period

At the end of the appropriate time periods the bottles were removed from the water bath and the roots collected on a nylon screen. The removal of the roots was timed so that the majority of the root material was out of the solution exactly at the time chosen. A record of the variation in the times was kept. The average time variation was determined to be ± 26 seconds. The absorption times for these experiments were chosen so that a measure of the active, steady state absorption could be obtained. This was desirable in order to avoid the difficulties in the interpretation of the uptake occurring during the initial period. Jacobson et al. (37) have pointed out some of the difficulties inherent in evaluating treatment effects occurring during this portion of uptake. In the tissues used in this study the "free space" was filled and the roots began to exhibit a steady state absorption prior to one hour and continued to accumulate ions at this rate for periods in excess of six hours. Figure 1 and 2, appearing later under the results portion of this thesis,

present data showing the presence of the steady rate. Once it was determined that a steady state rate occurred in the interval from one hour to six hours it was decided to use samples taken at these two times as a means of measuring this rate. By subtracting the content of the samples taken at one hour from the content of the samples taken at six hours a measure of the net rate was obtained. The majority of the results in this thesis are presented as milliequivalents of ion taken up per kilogram (fresh weight) per five hours.

Chemical Analysis

After the roots were removed from the bottle they were washed by slowly pouring three liters of distilled water over the tissue while the roots were still on the nylon screen. The roots were then placed into 125 milliliter Erlynmeyer flasks and dried overnight at 70°C. With the exception of the samples taken for chloride analysis the tissues were digested in nitric and perchloric acids. The digest was brought to volume in volumetric flasks and analyzed for the various ions in question. Na, K, Li, and Rb were determined with a Beckman Model DU flame photometer; Ca was determined with a Perkin Elmer Model 303 Atomic Absorption Spectrophotometer. (Due to the toxicity of uranium these instruments were placed so that the exhaust from their burners was drawn up through a well ventilated hood.) Uranium analysis was performed

by liquid scintillation counting using Bray's method (13).

Samples used for chloride analysis were placed in platinum crucibles rather than into Erlynmeyer flasks. The samples were then covered with 15 milliliters of 4 N. NaOH and dried overnight at 70°C. After the tissues were dry, the crucibles were placed in a muffle furnace for 5 hours at 500°C. The samples were allowed to cool then they were dissolved in 15 milliliters of distilled water; filtered; and brought to 100 milliliters volume. Aliquots of this solution were placed into beakers; acidified with nitric acid then potentiometrically titrated with standardized silver nitrate using a silver-silver chloride-glass electrode system (15, p. 99).

In the flame methods used for cation analysis uranium was found to have no effect upon the determination of the ion content of the tissues. In the chloride titration there was a slight effect of uranium upon the titration, but this effect was very small compared to the effects that uranium had upon the absorption of chloride.

There are a number of methods used in this thesis that appear in only one or two experiments. These will be presented with the discussion of the specific experiment. This was done in order to avoid the separation of the methods from the discussion as the technique has a direct bearing upon the interpretation of the results.

RESULTS AND DISCUSSION

Overstreet and Jacobson (59) have shown the benefit provided by using the antagonism and synergism between ions to study the mechanism of ion uptake. One of the most striking results of this type of study was that shown by Jacobson et al. (38) to occur with Li, K and Ca. Without Ca (or one of the other divalent cations studied by these authors) in the test solutions, Li and K were shown to compete with each other. But with Ca in the solution Li absorption was almost eliminated and K absorption was stimulated. This stimulation of K was similar to the typical Viets effect (90).

While investigating the role of polyvalent cations other than Ca a reference to the work of Rothstein (69) was encountered. Rothstein used the polyatomic cation of hexavalent uranium, uranyl (usually given the symbol UO_2^{++}), to produce a differential inhibition of glucose. The uranyl uptake curve presented by Rothstein and Larrabee (72) looks very similar to the uptake curve for Ca shown by Moore et al. (57). Moore et al. (57) suggested that the pattern of calcium uptake indicated that the majority of the Ca probably did not enter into the interior of the cell but was bound to the surface. Rothstein (69-74) also came to a similar conclusion concerning the uptake of uranyl.

Comparison Between Ca^{++} and UO_2^{++} Effects upon K and Li Absorption

Due to the similarity in the absorption patterns of these two cations, an experiment was set up to compare the effects of both Ca and UO_2^{++} upon the uptake of Li and K. Figure 1(a) shows that with the systems used in this experiment Ca behaved in a manner similar to that shown by Jacobson et al. (38). In contrast to Ca, the uranyl cation (Figure 1-b) had no effect upon Li uptake but eliminated the uptake of K by these tissues. This initial observation has been verified in a number of subsequent experiments.

Metabolic Nature of the UO_2^{++}-K-Li Interactions

Uranium, in contrast to Ca, is not widely distributed in nature. With the exception of a few indicator plants, uranium does not occur in any appreciable amounts in plant tissues (17). Due to the toxicity of uranium (78) one would expect that this element would either block both Li and K or else kill the tissues completely. The possibility of killing the cells is suggested by the work with animal intestinal tissues (91). When the tissue is contaminated with this element, cells containing the uranium are usually sloughed off by the organism and eliminated from the body. Such a poisoning of the root tissue would halt the metabolically medicated movement of

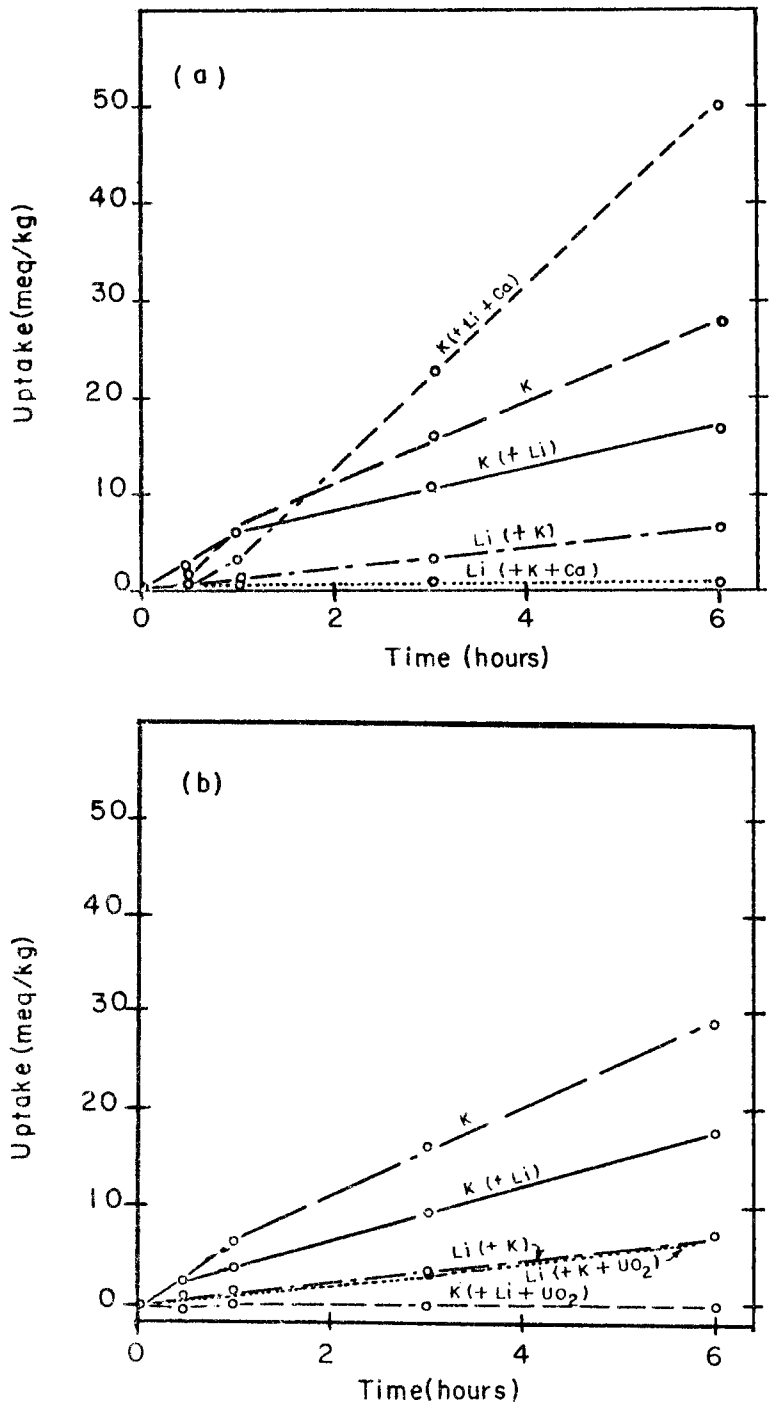

Figure 1. (a) The effects of Ca upon the absorption of Li and K from solutions containing 5 meq each of Li, K and Ca per liter.

(b) The effects of UO_2^{++} upon the absorption of Li and K from solutions containing 5 meq each of Li and K and 1 meq of UO_2^{++} per liter. (Appendix 2).

ions. If the uptake of Li is by a non-metabolic mechanism the uranyl could be eliminating K absorption by inhibiting metabolism and thus leave Li uptake unaffected.

An experiment was conducted to determine if the uptake of Li which was not affected by UO_2^{++} was linked to the cell's metabolism. DNP was used to inhibit the absorption mechanism of the cell and thus obtain some ideas of the nature of the Li uptake. (See Appendix 3 for this data.) This experiment revealed that Li was indeed accumulated by an active absorption process. The results of this experiment also strengthened the possibility that UO_2^{++} was selectively inhibiting K absorption. If this were the case then uranyl would provide a means of studying a portion of the absorption mechanism without interferences from another portion.

Effects of UO_2^{++} Upon Na and K Absorption

Since Na and K are closer in their chemical properties than Li and K a discrimination between these two ions would be more significant in identifying a true selectivity of inhibition. Also this would have more biological significance due to the role played by Na and K in animal physiology. Therefore an experiment was conducted to determine if perhaps uranyl would affect Na differently than K.

Solutions containing 5 milliequivalents each of K, of Na, or of K and Na per liter were used to evaluate the effects of UO_2^{++} upon the absorption of these ions by barley roots. The results of this experiment are shown in Figure 2. Figure 2(a) shows that UO_2^{++} reduced Na uptake by the same amount as did K. When both UO_2^{++} and K were present there was an additional reduction in Na uptake. Figure 2(b) shows that UO_2^{++} had the same effect upon K when it was present with Na as when it was present with Li. When only K and UO_2^{++} were in the solution the effect of the uranyl upon K uptake was not as great as when Na was present. The curve marked K + Na suggests that the majority of the effect of Na upon K uptake was in a reduction of the free space rather than in a reduction of the steady state rate of absorption. When K, Na and UO_2^{++} were all three present in the same treatment there was a slight loss of K from the tissues. This loss may well be due to the exchange of Na with K already present in the tissues.

Appendix 5 presents the results of 16 experiments in which the effects of one milliequivalent of UO_2^{++} per liter upon Na and K absorption were evaluated. Na and K were both present at 5 milliequivalents per liter. Statistical analysis (Appendix 6) of this data showed that the slight reduction in Na absorption that was produced by uranyl was not significant, but that the reduction in K absorption was significant at the one percent significance level.

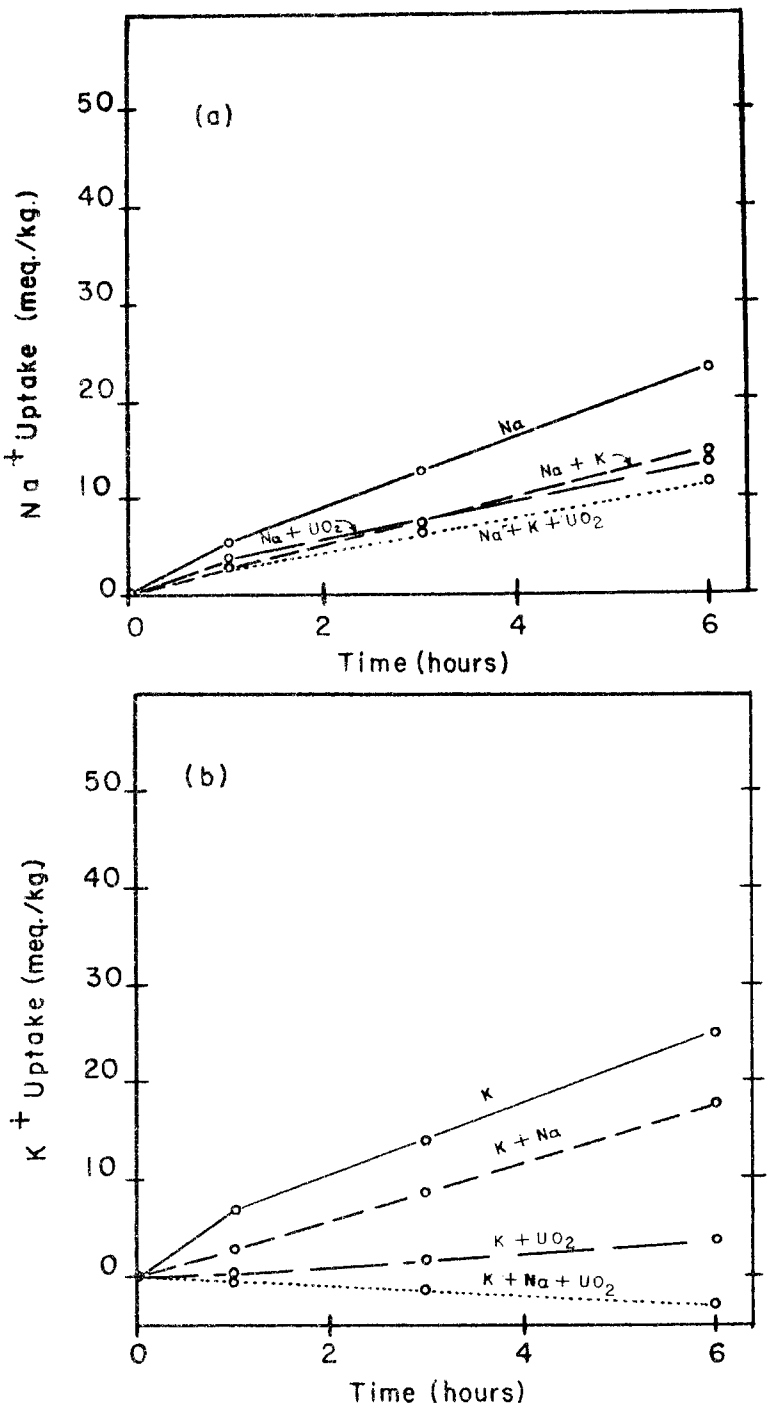

Figure 2. (a) Absorption of Na from solutions containing 5 meq per liter of Na and 5 meq per liter of K and solutions of the same composition plus 1 meq per liter of UO_2^{++}.
(b) Absorption of K from the same solutions shown in (a) above. (Appendix 4).

Effect of UO_2^{++}-pretreatment Upon Na and K Absorption

Rothsten, Frankel and Larrabee (71) showed that the pre-treatment of yeast cells with uranyl produced effects similar to those produced by placing the cells into the uranium solutions during the entire treatment period. In order to see if the effects of UO_2^{++} upon uptake would be comparable in UO_2^{++} pre-treated roots, a series of experiments was run to evaluate the effects of a thirty minute pre-treatment in a one milliequivalent per liter UO_2^{++} solution. This type of experiment would offer a more gentle method of treating the tissues than was available by placing the roots in the uranium solution for periods up to six hours. Secondly this technique would offer a means for determining the speed of the inhibition. The speed of inhibition would give some indication of the site in the tissues where the inhibition was occurring. (i. e. A rapid response would suggest that the site was close to the surface.)

In these experiments 7 grams of roots were placed in 500 milliliters of a one milliequivalent per liter solution of uranyl chloride for 30 minutes. These solutions were stirred periodically. At the end of the thirty minute period the roots were collected on a nylon screen and washed with one liter of distilled water. The roots were allowed to drain for one minute and then transferred to bottles containing the

test solutions. These solutions contained 5 milliequivalents each of Na and K per liter. From Figure 3 one can see that the pre-treatment was not as effective in inhibiting K absorption as was the presence of uranyl in the bottle, but the pre-treatment still produced a marked inhibition of K absorption. Na, on the other hand, was actually stimulated by the pre-treatment.

Analysis of the pre-treated tissues revealed that at the end of the pre-treatment they contained 7.3 milliequivalents of UO_2^{++} per kilogram. After six hours in the test solution (which contained no UO_2^{++} other than that lost from the pre-treated roots), the amount of UO_2^{++} in the roots had been reduced to 2.3 milliequivalents per kilogram. Considering the fact that this loss of UO_2^{++} is from a 7 gram root sample, the concentration of uranyl in the test solution would be approximately 4×10^{-3} milliequivalents per liter. Results of experiments presented in Appendix 21 show that this level of UO_2^{++} should either produce a slight stimulation of K absorption or else have no effect. The fact that the UO_2^{++} pre-treatment has almost the same effect as the presence of one milliequivalent of UO_2^{++} per liter suggests that it was the amount of UO_2^{++} retained in the tissues (2-3 meq. per liter) that inhibited K absorption and not the presence of the small amount of UO_2^{++} which diffused out of the tissues during the experiment. From this it is assumed that the portion of the accumulated uranyl that was affecting ion transport was bound tightly to the site of action.

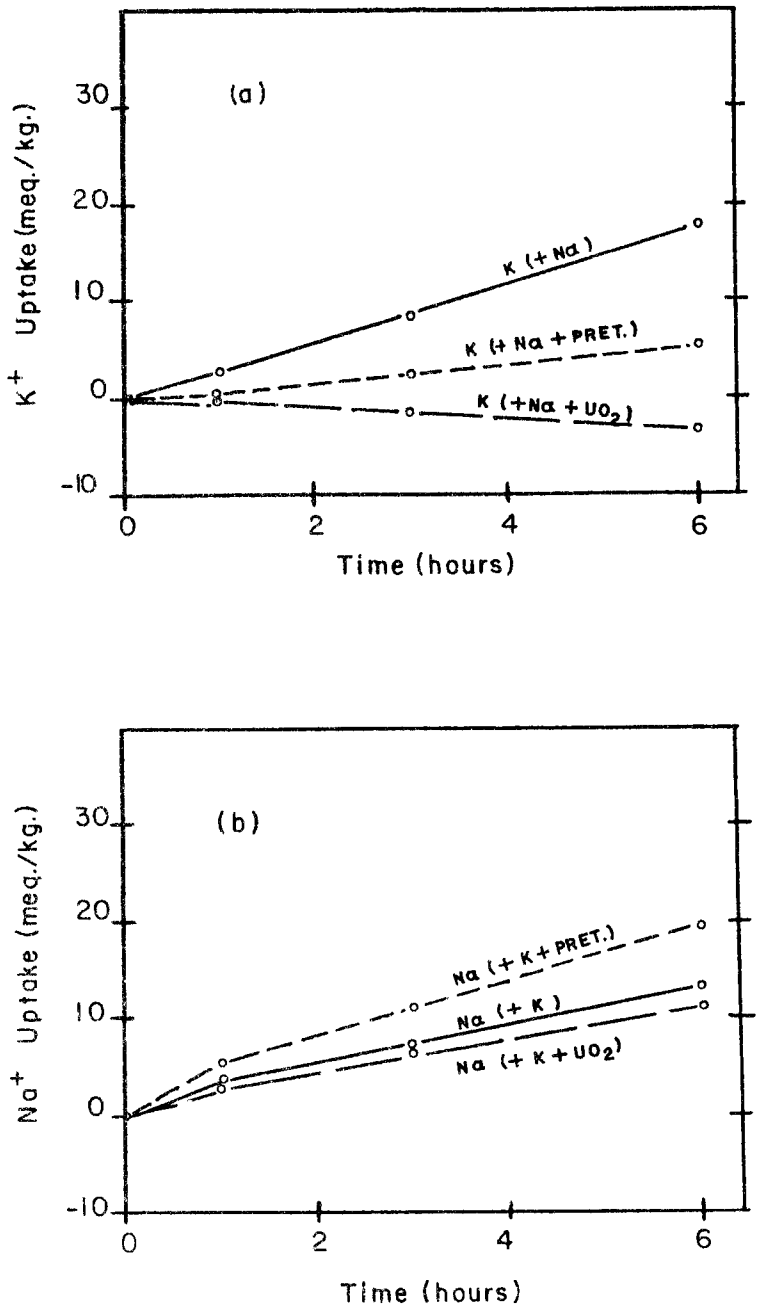

Figure 3. (a) Absorption of Na by UO_2^{++} pre-treated roots.
(b) Absorption of K by the same root tissue as in (a) above.
Solutions contained 5 meq each of Na and K per liter. Pre-treatment was for 30 minutes in 1 meq UO_2^{++} per liter. (Appendix 4).

Site of the UO_2^{++} Effects

Since the pre-treatment with uranyl was effective in selectively inhibiting K absorption in contrast to Na absorption a study to evaluate the speed of inhibition was conducted. The rapidity with which $UO2^{++}$ begins to affect the absorption of Na and K should give an indication of the location in the cell where UO_2^{++} was reacting. If the effects occur rapidly the site would most likely be at or very close to the surface; whereas a slower reaction would indicate that the site was more likely deeper into the cell.

In this experiment the tissues were pre-treated for time periods of 2, 10, 20, and 30 minutes in one milliequivalent UO_2^{++} per liter. Figure 4 presents the results of this experiment. Figure 4 shows that the 2 minute pre-treatment reduced the K absorption rate by approximately 43 percent. Beyond 2 minutes the increasing pre-treatment times produced a linear decrease in the rate of K absorption. The effect of the UO_2^{++} pre-treatment upon Na absorption was considerably different than the effect upon K absorption. Na was stimulated at all of the pre-treatment times. The majority of the Na stimulation occurred during the first 2 minutes and did not change to any great extent with increasing pre-treatment times.

In experiments similar to the one presented in Figure 4, roots were pre-treated for 4, 8, 15, and 30 minutes, then analyzed for their UO_2^{++} content. Figure 5 shows that the UO_2^{++} content of pre-treated tissues increased rapidly during the first four minutes of pre-treatment. At the time periods beyond four minutes UO_2^{++}

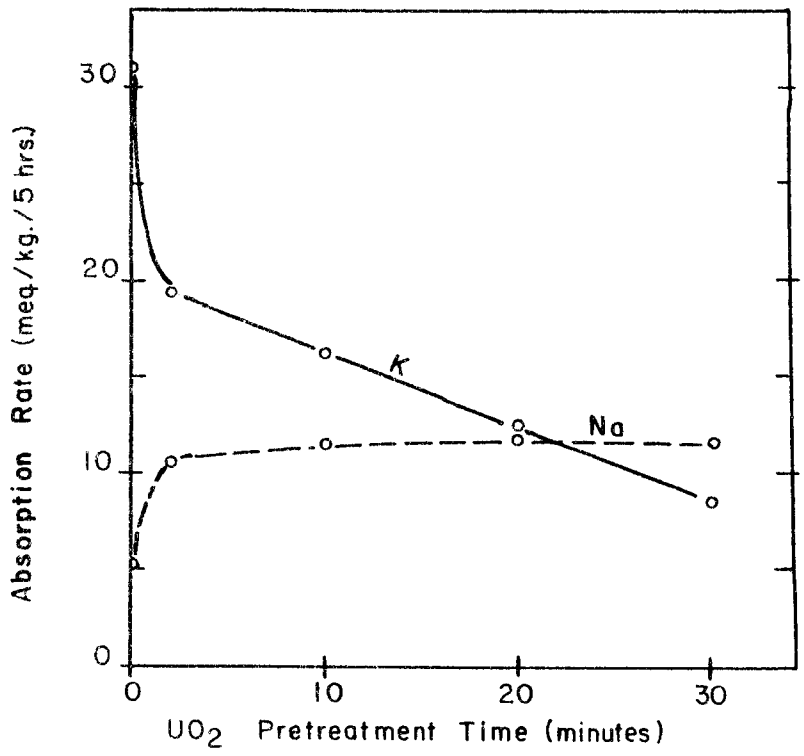

Figure 4. Absorption of Na and K from roots pre-treated with 1 meq UO_2^{++} per liter for various time periods. Na and K were both present at 5 meq per liter. (Appendix 7).

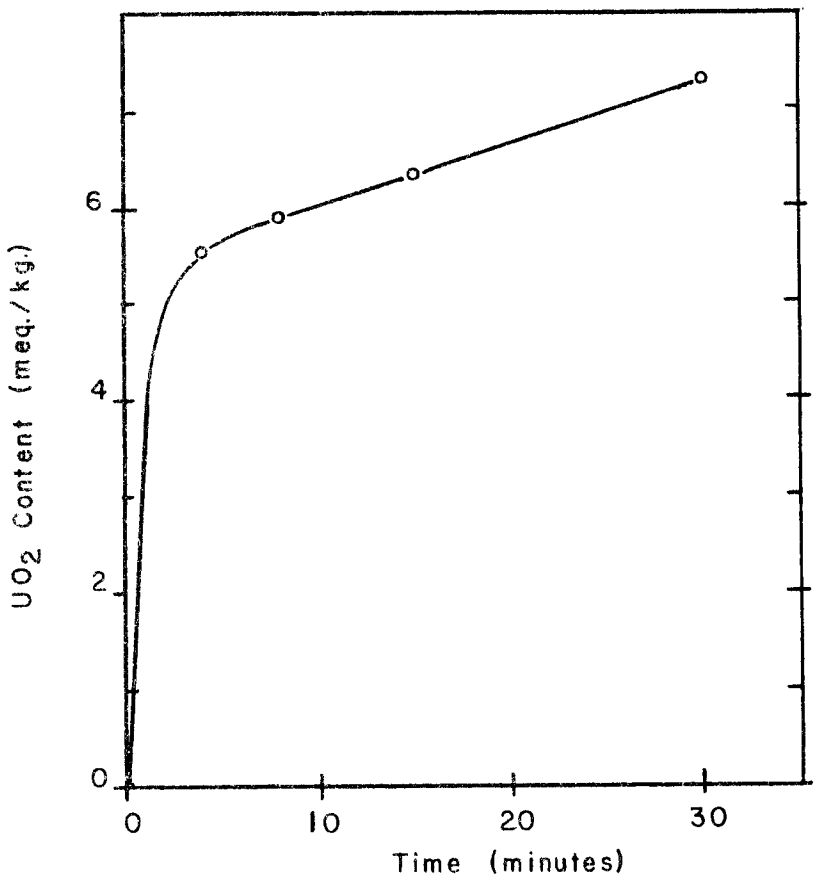

Figure 5. Uptake of uranium by roots treated for various time intervals in 1 meq UO_2^{++} per liter. (Appendix 7).

appears to have been taken up at a steady state rate. The fact that the effects of the UO_2^{++} pre-treatments were observed within the first two minutes that the tissues were in the UO_2^{++} suggests that the site of action was very close to the surface of the cell. This observation is in accord with the work on yeast cells carried out by Rothstein et al. (71) and Barron et al. (9).

Reversal of UO_2^{++}-pretreatment Effects

Rothstein and his co-workers (71-73) found that they could reverse the effects of the uranyl pre-treatment by placing the cells in a phosphate, a bicarbonate, or a citrate solution. In a paper by Ponz and Lluch (61) EDTA was shown to reverse the effects of UO_2^{++} in rat intestines poisoned by uranyl. In light of this work by Ponz and Lluch (61) and also Rothstein's work (71-73) an experiment was set up to evaluate the effects of various UO_2^{++} complexing agents upon uranyl pre-treated tissues. NaH_2PO_4 and Na_2CO_3 at 0.015 M, Na_2EDTA (ethylene-diamine-tetracetate) at 0.04 M and Na_2CyDTA (cyclohexane-diamine-tetracetate) at 0.006 M were used in this experiment.

Van Stevenick (89) has shown that EDTA will remove Ca from cells treated with this compound. He noted that this removal could cause the cells to become more permeable. The other compounds

used to complex uranyl also complex calcium to some extent. In order to offset any possible damage that may have resulted from the removal of Ca from the cells, 0.1 milliequivalents of Ca per liter was added to all of the treatments used in this experiment. After thirty minutes in the UO_2^{++} the tissues were collected on the nylon screen; washed with one liter of distilled water then transferred to 500 milliliters of the complexing solution. After thirty minutes in these solutions all of the treatments had given a partial reversal. Judging from the reductions in absorption shown by the tissues that were treated for one hour in the complexing agents, only the tissues treated with EDTA were still functional. (See Appendix 8 for the data on this experiment.) The tissues treated with EDTA had completely reversed the effects of the uranyl pre-treatment upon Na and K absorption. Uranium analysis of these same tissues showed that at the end of one hour in the complexing agent all of the uranium had been removed by the EDTA.

In order to verify this observation a second experiment was conducted using 0.03 N and 0.003 N EDTA as a complexing treatment. Root samples were pre-treated with UO_2^{++} for 30 minutes. Samples of these roots were then placed into solutions containing the EDTA for periods of 4, 8, 15, 30 and 60 minutes. These tissues were then removed from the EDTA solutions and washed. After allowing the roots to drain for one minute they were placed into

bottles which contained 5 milliequivalents each of Na and K per liter and 0.1 milliequivalents of Ca per liter. Figure 6 presents the results of the 0.03N EDTA treatment. At the end of one hour in 0.03N EDTA the absorption of the Na and K by the tissues was almost back to the level found in the control treatment. (The control absorption rates are represented by the horizontal lines shown in Figure 6.) Figure 7 shows the loss of UO_2^{++} from pre-treated roots subsequently treated with EDTA. From Figure 7 it is apparent that the major portion of the UO_2^{++} was in some location that was readily accessible to the EDTA. Apparently EDTA removed the uranyl from some site (probably close to the cell surface) that was closely linked to the transport of Na and K. The failure of the EDTA to completely reverse the effects of uranyl upon K absorption was probably related to the fact that a small amount of the UO_2^{++} was still present in the tissues. If this small amount of UO_2^{++} was actually the cause of the failure of the absorption mechanism to return to the control level then it would appear that the mechanism of K absorption is extremely sensitive to uranyl. This conclusion is supported by the fact that K absorption was reduced by 43 percent during the two minute pre-treatment shown in Figure 4.

The speed with which uranyl inhibited K absorption and also the rapid increase in uranium content shown in Figure 5 would suggest that some of the sites to which UO_2^{++} was bound were very

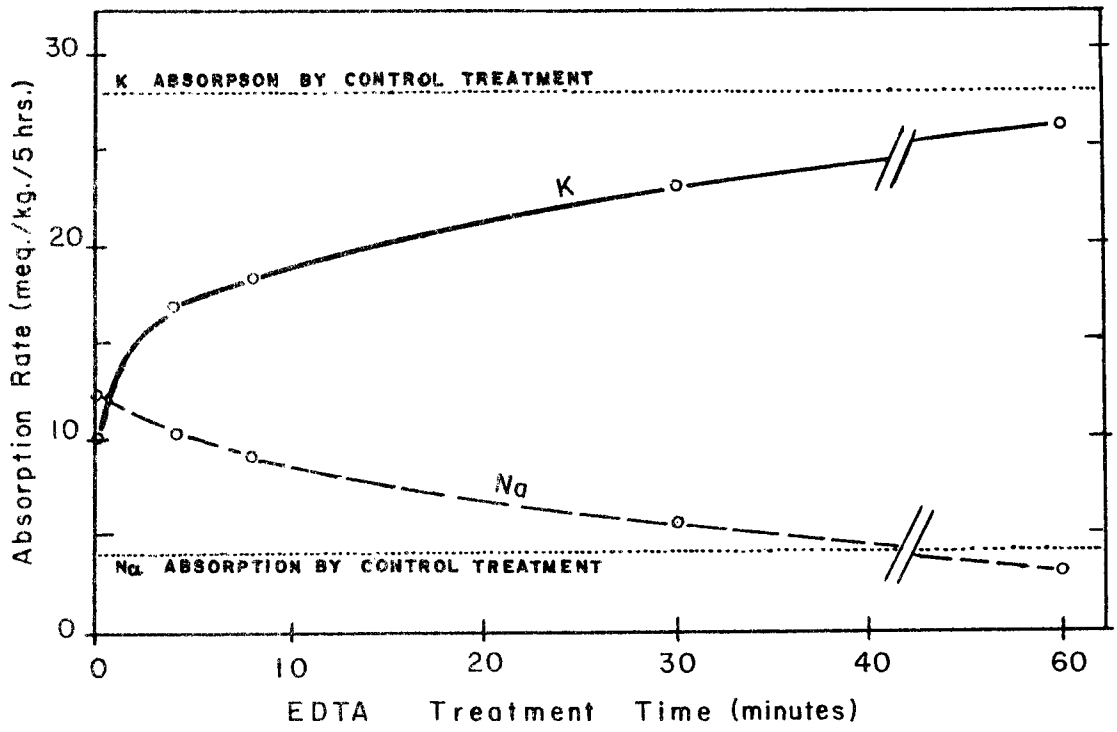

Figure 6. Absorption of Na and K by uranyl pre-treated roots subsequently treated with 0.03 N EDTA. The test solution contained 5 meq each of Na and K per liter and 0.1 meq of Ca per liter. (Appendix 9).

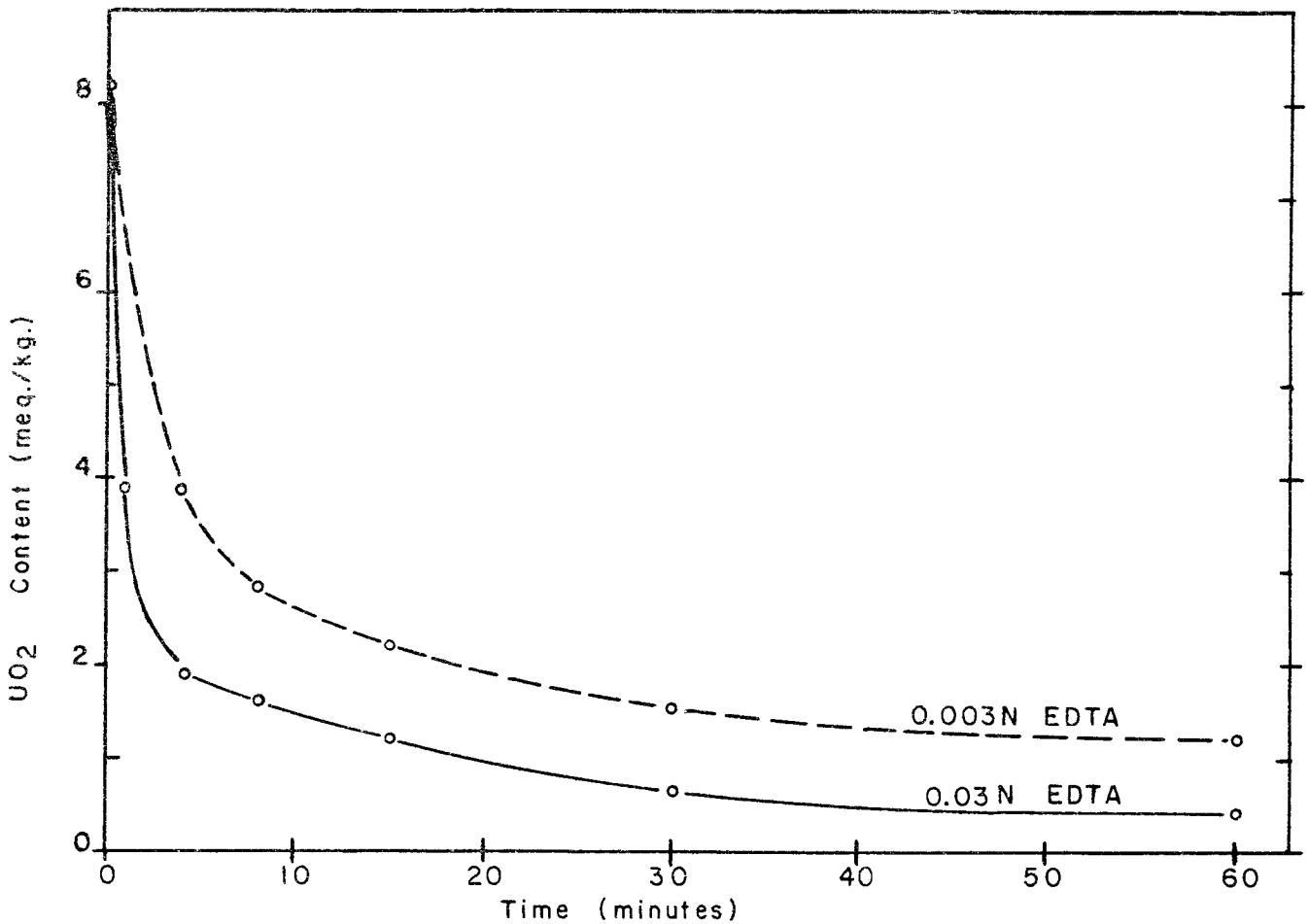

Figure 7. Uranium content of uranyl pre-treated roots after being placed in EDTA solutions for various time periods. Pre-treatment was for 30 minutes in 1 meq UO_2^{++} per liter. (Appendix 9).

close to the surface of the cell. Comparing the curve in Figure 5 and the curve in Figure 7 labeled 0.03 N EDTA it is apparent that the EDTA removed almost the same amount of UO_2^{++} in 4 minutes of pre-treatment as was taken up in that same time interval. If one estimates a four minute point on Figure 4 the effect of the uranyl in this time period was to reduce K absorption by almost 50 percent. These two observations suggest that UO_2^{++} must be attacking some site very closely related to the K absorption mechanism.

The Metabolic Nature of the UO_2^{++}-resistant Absorption

Inhibitors

One of the early concerns about the effects of UO_2^{++} upon the absorption of Na and K by these tissues was whether the uranyl-resistant uptake of Na was metabolically medicated or not. Work reported earlier where DNP was used to inhibit UO_2^{++}-resistant Li absorption suggested that uranyl was not affecting that portion of metabolism which supports Li absorption. In order to evaluate the role of metabolism in Na transport it was again necessary to resort to techniques that completely eliminate most of the uptake of ions. Use of DNP and low temperature were chosen as a means of blocking metabolic uptake. DNP inhibits absorption by uncoupling oxidative phosphorylation and low temperature by reducing the majority of all

metabolic functions in the tissues. By filling one of the water baths with ice a temperature of 0.5° C could be obtained. Table 1 shows that 5×10^{-5} M DNP caused a loss of K and reduced the Na absorption to zero. (The effects of the other DNP concentrations are presented in Appendix 10.) Table 2, presenting the results of the low temperature treatments, shows that both Na and K absorption were using energy produced by the cell's metabolic system. Both methods of inhibition show that the UO_2^{++}-resistant absorption of Na was metabolically mediated.

Table 1. Effect of 5×10^{-5} M DNP upon Na and K absorption. (Appendix 10).

Treatment	Control		UO_2^{++} Pret.		UO_2^{++} Pret. + DNP	
	K	Na	K	Na	K	Na
	(meq./kg./5 hrs.)					
K	29.0	----	12.8	----	----	----
Na	----	33.5	----	33.4	----	4.0
K + Na	20.7	17.1	5.4	25.8	-3.2	1.7

Table 2. Effect of low temperature (0.5°C) upon Na and K absorption by uranyl pre-treated roots. (Appendix 11).

Treatment	Rate of Absorption	
	Na	K
	(Meq./kg./5 hrs)	
Na + K	15.0	31.4
Na + UO_2^{++} Pret.	28.6	8.5
Na + K + 0.5°C	1.8	2.2
Na + K + UO_2^{++} Pret. + 0.5°C	2.4	0.0

Respiration Studies

The use of DNP and low temperature indicates that the portion of Na and Li absorption that was not inhibited by uranyl was metabolically mediated. The fact that the metabolism of UO_2^{++} treated cells was still adequate to move Na and Li suggests that UO_2^{++} was inhibiting absorption by some means other than a direct attack upon the metabolic functions of the cell. In order to more fully understand the effects of UO_2^{++} upon metabolism it was felt that a series of respiration studies should be carried out to obtain evidence which was more direct than that suggested by the DNP and low temperature experiments. A study of the effects of UO_2^{++} concentrations upon respiration was carried out in an attempt to determine if UO_2^{++} altered the respiratory patterns of the tissues. In Tables 3 and 4 the results of two experiments are presented.

In the first experiment standard Warburg techniques were used. One gram of root tissue was weighed out and loosely wrapped in a piece of cheese cloth. The tissue was then inserted into the Warburgh flask. Two milliliters of a solution containing 5 milliequivalents each of either Na, K or Na and K per liter were added to the flask along with an appropriate amount of uranyl to give the desired concentration of this ion. The pH of the solution was adjusted to pH 5.0 prior to the beginning of the experiment.

The Warburg vessel was placed into the water bath and allowed to come to equilibrium with the temperature of the bath before the experiment was begun. After 15 minutes in the water bath the stopcock was closed and a reading taken from the manometer. Subsequent to this initial reading, readings were made every ten minutes for a period of three hours. The data in Table 3 shows the rate of oxygen uptake by these tissues. Looking at the column marked Na and the one marked K one notes an increase in oxygen uptake for the K treated roots at 10^{-3} milliequivalents UO_2^{++} per liter and a reduction in oxygen uptake for the Na treated roots. However, when Na and K are both present there is a stimulation in oxygen uptake at this concentration.

Table 3. The effects of UO_2^{++} concentration upon oxygen uptake by excised barley roots using the Warburgh method for determining oxygen consumption. (Appendix 12)

UO_2^{++} Concentration	Oxygen Uptake		
	Na	K	Na + K
(meq./liter)		(microliters/hour)	
0	17.7	13.2	12.3
10^{-3}	13.9	17.7	15.8
10^{-2}	15.6	17.6	12.2
10^{-1}	15.2	12.3	11.5

At 10^{-1} milliequivalents UO_2^{++} per liter the pattern in the K column is reversed (i.e, K is inhibited). Data presented in

Appendix 17 indicates that these variations in the respiration pattern produced by UO_2^{++} approach a pattern similar to the pattern of ion absorption at different UO_2^{++} concentrations. This parallel between absorption and respiration can be interpreted in two ways. UO_2^{++} could be altering a portion of respiration and thus altering the absorption rate or else the respiration pattern could be a direct result of the effects of UO_2^{++} upon the absorption mechanism.

The first way seems to be less likely because it is hard to conceive of some mechanism that would inhibit a portion of respiration which acted to transport K and have little or no effect upon another portion which transported Na.

Handley and Overstreet (27) in their work with barley roots showed that any treatment which stimulated or suppressed ion absorption also had a similar effect upon the "salt respiration" of these tissues. Robertson (67), who originally proposed the term "salt respiration", defined it as "the term given to that increment of respiration which accompanies the entrance of a salt from the external solution". Handley and Overstreet (27) showed that there was a difference in the respiration depending upon the rate of entry of the cation used. With K or with Na the salt respiration was higher than with Ca. In these same tissues the rate of absorption of Na or of K was considerably greater than the rate of Ca absorption. Robertson (67) considered this "salt respiration" to result

from anion absorption but Handley and Overstreet (27) showed that cations can also produce a salt respiration. Using a "K-bentonite clay" system Handley and Overstreet (27) showed that the roots took up K and also produced the typical stimulation in respiration which occurs when ions are absorbed. In this case there was no anion that could be absorbed with the cation. From this they concluded that either cation, anion or both cation and anion absorption could stimulate respiration. Handley and Overstreet (27) suggested that any treatment which will hinder ion absorption will reduce the portion of respiration termed "salt respiration". Milthorpe and Robertson (55) also observed that reductions in ion absorption by barley roots resulted in a reduction in respiration.

Since the conditions of the Warburgh experiments are so different from the experiments where absorption was studied it was decided to use the technique developed by Handley and Overstreet (27) to evaluate the effects of UO_2^{++} upon respiration. This technique uses the same bottles used for the uptake study as a reaction vessel for determining respiration. In this method the same tissues are used for both respiration and absorption determinations thus provicing a more direct means of comparing these two processes. This method of determining respiration is based upon the Winkler method of oxygen analysis (77). Since this offers a better method for comparing the effect of uranyl upon ion absorption with the

effects upon respiration this method was used in the experiment presented in Table 4.

In this experiment the standard bottles used in the study were volumetrically calibrated to a point that would completely fill the vessel and still allow the bottle to be sealed with a rubber stopper. Solutions made up of the desired mixtures of Na, K, and UO_2^{++} were added to the bottles so that they were completely filled. The pH was adjusted to pH 5.0. This solution was then aerated for 18 hours prior to the experiment. The 18 hour time was chosen after evaluating the results of a preliminary experiment which showed that the water reached oxygen saturation after 12 hours of aeration. Just prior to the initiation of the experiment a sample of the solution was taken and placed in a BOD (Biological Oxygen Determination) bottle. This volume was replaced with solution of identical composition which had been treated in a fashion comparable to the solutions in the bottles. As soon as the sample was taken and the solution brought back to volume, 7 grams of root material were placed in the bottle. The bottle was then sealed being sure to exclude any air bubbles.

The samples taken at the initiation and during the experiment were titrated by the Winkler method for determining dissolved oxygen (77). This method was modified by using a commercial

phenylarsene oxide solution (PAO),[3] which was standardized at 0.0250 normal, to titrate the dissolved oxygen rather than the thiosulfate normally used in this method. PAO is considerably more stable than thiosulfate.

During the uptake period the bottles were periodically agitated by inverting them several times. This completely dispersed the root material throughout the solution. Handley and Overstreet (27) have shown that roots handled by this method will continue to take up ions in an active fashion for periods up to three hours. In order to measure the uptake of the ions, root samples were taken at one and three hours along with the solution samples. This was done by opening the bottle and rapidly taking a sample of the solution for pH determination and for oxygen determination. The roots were then collected on the nylon mesh screen in the usual fashion. The results of the absorption data are presented as milliequivalents per kilogram per 2 hours rather than per 5 hours.

The data presented in Table 4 show that there was some variation in the pattern of respiration, but the overall effects of UO_2^{++} upon respiration appear to have been relatively minor compared to the effects of UO_2^{++} upon ion absorption. The stimulation and other variations in respiration can again be accounted for by the

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[3] Obtained from Hack Chemical Corporation, Ames, Iowa. Lot No. 6501. Catalog number 1070.

relationship between ion absorption and salt respiration. In those cases where UO_2^{++} stimulated the absorption of the total salts (i. e. Na plus K) it also stimulated respiration.

Table 4. The effects of UO_2^{++} concentrations upon oxygen uptake by excised barley roots using Handley-Overstreet (28) technique for measuring oxygen consumption. Also included are the effects of UO_2^{++} upon Na and K absorption by these same root tissues. (Appendix 13)

UO_2^{++} Concentration	Oxygen Uptake	Ion Absorption	
		Na	K
(meq. /liter)	(mMoles/kg. /hr.)	(meq. /kg. /2 hrs.)	
0	20.1	4.9	6.7
10^{-3}	26.2	4.7	10.7
10^{-2}	30.1	4.6	6.5
10^{-1}	17.4	5.8	5.0
1	20.6	5.2	1.1

The overall conclusion to be drawn from the work upon respiration and metabolism is that the uranyl ion appears to have had an effect upon the ion absorption process per se and not upon those reactions which provide the cell with its energy sources. Both methods for evaluating respiration lead to the same conclusion.

Singer et al. (78) have shown that there are a number of enzymes that are vital to the cell's metabolic functioning that are markedly inhibited by UO_2^{++}. Probably the most important of these are succinic oxidase, cytochrome oxidase and

hexosemonophosphate oxidase. If UO_2^{++} were able to enter the cells one would expect the basal respiration (as opposed to salt respiration) to be materially reduced by UO_2^{++}. The fact that UO_2^{++} did not greatly reduce the respiration suggests that little or no uranium entered the cells of the root tissue.

Effects of UO_2^{++} Upon Chloride Absorption

In the treatments containing the higher UO_2^{++} concentrations it was noted that the pH continually decreased during the experiment. According to Hoagland and Broyer (30) this was an indication that the the cation was going into the tissues faster than the anion. In order to determine if this was the case, an experiment was carried out to determine the effects of uranium upon chloride uptake. Table 5 presents the results of this experiment.

Table 5. The effects of uranyl concentrations upon the absorption of chloride, Na and K by excised barley roots from solutions containing 5 milliequivalents each of Na and K per liter and 10 milliequivalents of Cl per liter. (Concentrations of Cl were adjusted so that they were all the same. Appendix 14.)

Treatment	Absorption Rate		
	Cl	Na	K
	(meq. kg. /5 hours)		
Na + K	29.8	15.8	16.8
Na + K + 10^{-3} meq. UO_2^{++}/l.	19.0	13.1	20.8
Na + K + 1 meq. UO_2^{++}/l.	2.9	14.3	0.7

Due to the limited number of platinum crucibles available for use in the dry ashing of these tissues it was necessary to limit the experiments to three uranyl concentrations. The data in Table 5 show that UO_2^{++} markedly reduced the uptake of Cl by these tissues.

The fact that UO_2^{++} has markedly reduced Cl absorption but has not eliminated cation absorption (particularly Na) is an important observation. Ulrich (88) has shown that when the cation-anion balance is upset by excess cation absorption the tissues will produce organic acid anions to restore the balance between cation and anion. If UO_2^{++} were attacking the metabolic processes of the cell, this probably would not occur. Since the laboratory equipment for determining organic acids was not available during this study there was no means to obtain direct evidence that organic acids were being produced. The only indication of what was happening must be reasoned from the following information.

Hoagland and Broyer (30) have shown that, under conditions where cation absorption exceeds anion absorption, H ion is released from the tissues to maintain a balance between cation and anion. Ulrich (88) has shown that under a similar imbalance between cation and anion absorption organic acids are produced by the cells. Hoagland and Broyer (30) noted that work which was underway in their lab (88) suggested that the source of the H ion released during

excess cation absorption was most likely the result of the increase in organic acids which occurred at the same time. They noted that Ulrich's (88) preliminary experiments showed an increase in organic acids in the same tissues that were releasing H into the solution. Thus the electrical neutrality of the cell and the solution was maintained. H balanced the anion charge in the solution and organic acid anions balanced the cation charge inside the cell.

Table 5 shows that at 1×10^{-3} milliequivalents UO_2^{++} per liter the sum of the cations was basically the same as the control but the Cl was reduced by 36 percent. At 1 milliequivalent UO_2^{++} per liter the sum of the absorbed cations was reduced by 55 percent as compared to a 90 percent reduction in Cl absorption. In order for the cells to maintain this great an imbalance between cation and anion there should have been organic acid anions formed.

Also in support of the hypothesis that organic acids were being produced is the fact that the pH of the test solutions containing the higher UO_2^{++} concentrations were observed to continually drop during the course of the experiment. (This drop was corrected by adjusting the pH back to the desired level after each time the pH check was made.) As was suggested by the work of Hoagland and Broyer (30) and Ulrich (88) this pH change was also an indication that organic acids were being produced in order to maintain the imbalance seen in Table 5.

Metabolic Nature of UO_2^{++} Uptake

Singer et al. (78) have shown that UO_2^{++} complexes with several of the organic acids which are involved in maintaining the above mentioned absorbed cation-anion imbalance. If UO_2^{++} were entering the cell the mechanism of organic acid production would most likely be completely inhibited and thus such an imbalance as is seen in Table 5 could not be maintained. Thus it seems most likely that UO_2^{++} was not entering the cells. This hypothesis is in some ways in opposition to that suggested by Figure 5. The apparent steady state portion of the UO_2^{++} absorption curve suggests that there was some metabolic absorption of this ion.

In order to further evaluate the possibility that UO_2^{++} was absorbed metabolically an experiment was set up to evaluate the effects of DNP upon UO_2^{++} uptake. Figure 8 presents data which shows the effect of DNP upon UO_2^{++} absorption. The control curve indicates a rather slow filling of the UO_2^{++} free space of these tissues then a leveling off of the curve to show no further uptake. Moore et al. (57) have interpreted a similar shaped curve to indicate that Ca did not enter barley root cells by a metabolically controlled pathway. The main differences between the UO_2^{++} control curve and the Ca curve shown by Moore et al. (57) is that the amount of UO_2^{++} taken into the cells was approximately four times as great as Ca.

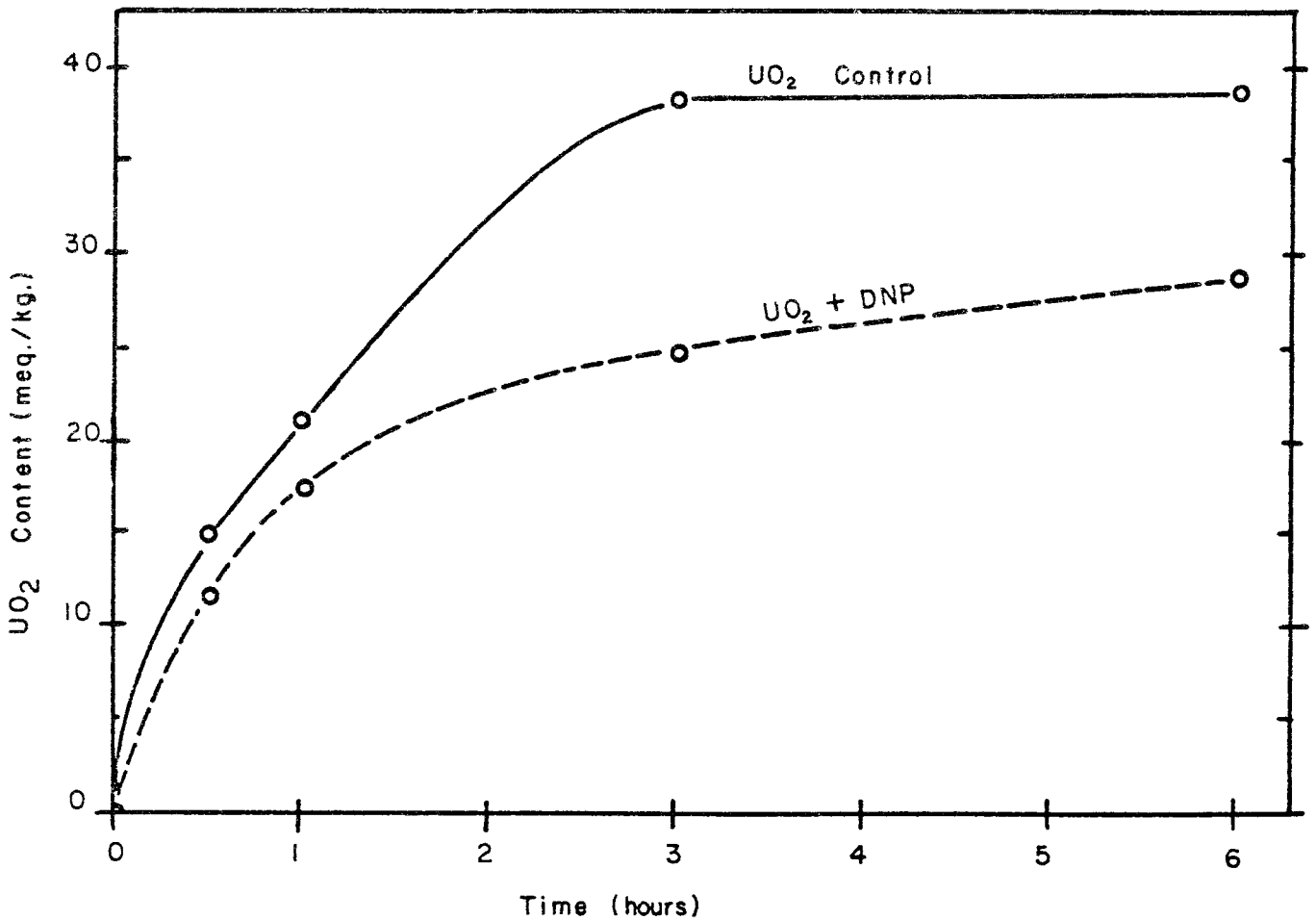

Figure 8. The effect of 5 X 10^{-5} M DNP upon UO_2^{++} uptake. UO_2^{++} was present at 1 meq per liter. pH was 5.0. (Appendix 15).

Also the time taken for UO_2^{++} to saturate the free space was considerably greater. Comparison between Figures 5 and 8 indicate that the change in slope seen in Figure 5 is different from that in Figure 8. In Figure 5 the change in the slope occurs at four minutes whereas the change in the slope of Figure 8 occurs at three hours. This discrepancy suggests that more than one reaction was occurring during the uptake of UO_2^{++}. The first change in slope, occurring very rapidly, may well have been the true free space and the second change, occurring at three hours, may indicate the saturation of some site on the surface of the cell.

The curve labeled UO_2^{++} + DNP shows that there was an effect of this metabolic poison but the general shape of the curve was not drastically changed. The change that does occur in the curve may indicate a number of possible mechanisms. (a) A portion of the UO_2^{++} may have been metabolically absorbed. (b) It may indicate that UO_2^{++} was binding with compounds that were being produced at or transported to the cell surface by a metabolically controlled process. (c) It may indicate a physical competition between DNP and UO_2^{++} for sites in the free space of the cells.

In light of the discussion on anion-cation balance it is hard to conceive of UO_2^{++} actually entering into the cytoplasm of the cell. A number of workers (9, 36, 71-72, 78) have suggested that cells most likely would not be able to survive with uranium present

inside the cytoplasm. Another factor to consider which suggests that uranium did not enter into the cell is the fact that EDTA was able to remove almost all of the UO_2^{++} which was taken up during the thirty minute pre-treatment. If it had been necessary for EDTA to enter the cells before the UO_2^{++} could be complexed the cells would most likely have lost their ability to absorb ions. Van Steveninck (89) has shown that this complexing agent will completely disrupt the membrane of the cell and thus destroy the permselectivity of the membrane. The fact that this did not happen can be seen in Figure 6 for K was actively taken up after treatments with EDTA.

The preceding discussion implies that either of the other two possible explanations seem more appropriate. The later of these two possibilities can be eliminated on the grounds that the time for the plateau to be reached was too long for most "free space" effects. In work presented with Ca (56, 57), and with K and Na (37) the free space was filled in the first hour that the roots were in the solutions. This delay suggests that the effects seen in Figure 8 were more complex than would be explained by a free space competition.

The second hypothesis (b) presented above seems to offer a better explanation for the two curves in Figure 8. Allen and Price (2) have shown that DNP will markedly reduce cytoplasmic streaming. If compounds which complex with UO_2^{++} are being brought to the

surface of the cell by streaming then DNP would appear to inhibit the portion of UO_2^{++} absorption which depended upon streaming to supply the sites of binding with this compound. Since DNP inhibits oxidative phosphorylations, the production of any compound that depended upon ATP for its energy source would also be inhibited by DNP. As was mentioned in the literature review, there are a number of phosphorylated compounds, found in the cell membrane, whose production is dependent upon ATP. Since UO_2^{++} readily complexes with phosphate the inhibition of this production of phosphorylated compounds could also reduce the apparent UO_2^{++} absorption.

An attempt to conclusively determine where UO_2^{++} was affected by DNP would be beyond the scope of this thesis. Only tentative hypothesis can be suggested which can account for the effects. Judging from the toxicity of UO_2^{++} (78), the time required to saturate the "free space", and the possibility that UO_2^{++} complexing compounds are being produced at or transported to the cell surface, it is hypothesized that UO_2^{++} is most likely reacting with sites or compounds in the cell membrane.

Loss of K from the Tissues

Uptake studies using tissues such as excised barley roots usually measure only the net uptake into the cells. The fact that an occasional loss of K from the cells was observed when the tissues

were treated with UO_2^{++} suggests that UO_2^{++} may make the cells "leaky" and thus offset the K which was being transported into the cells. The net result would appear to be a reduction in the absorption. In the case of compounds such as Na or Li, which initially are not present in the cells in any large concentration, this would not happen as there would be only a very small amount of the ion to leak out.

In order to determine if the K which was initially present in the barley roots would leak out in the presence of UO_2^{++}, an experiment was set up to compare the effects of UO_2^{++}, H_2O and Ca upon the retention of K. The distilled water treatment was used as a "control" treatment. The Ca treatment was included in order to determine if this divalent ion would have an effect upon the retention of K. Epstein (21) has suggested that Ca is essential for maintaining the integrity of the membrane. By including this ion it was hoped that any similarities between UO_2^{++} and Ca^{++} would be seen. By placing the tissues in solutions of UO_2^{++}, water and Ca for times up to 6 hours an indication of the effects of these solutions upon leakage could be obtained. Table 6 shows that at the end of 6 hours (the total time used for the uptake experiments) the maximum loss of K was 4.5 milliequivalents per kilogram in the UO_2^{++} treatment. This value is quite small compared to the reduction in K absorption produced by UO_2^{++}. Due to this fact is is assumed that uranium does not induce enough loss to materially alter the results obtained in the studies presented in this thesis. The results in Table 6 for distilled water are in agreement with Overstreet

and Jacobson's (59) observation that tissues in distilled water lost very little K except after extremely long time periods.

Table 6. Loss of K resulting from various treatments with solutions of Ca, UO_2^{++} and distilled water. Ca and UO_2^{++} were present at 1 milliequivalent each. pH was adjusted to pH 5.0.

Treatment Time	K Content		
	UO_2^{++}	H_2O	Ca^{++}
		(meq./kg.)	
0	17.1	17.1	17.1
2 minutes	17.1	17.1	17.1
5 "	17.1	17.1	17.1
10 "	16.9	17.1	17.1
20 "	16.9	17.1	17.1
30 "	16.4	17.1	17.1
1 hour	16.4	16.9	17.1
3 "	13.6	16.9	17.1
6 "	12.6	16.9	17.1
Total loss	4.5	0.2	0.0

The fact that Ca did not cause a loss of K from the tissues used in the experiment presented above suggests that the absence of Ca during the studies presented earlier may lead to erroneous conclusions. Initially Ca was left out of the solutions because the competition between Na and K is greatest in the absence of Ca (21, 66). Since the study of the inter-relationships between Na and K was one of the main purposes of this study, it was felt that Ca would only complicate the interpretation of the results. Rains et al. (66) have questioned the validity of interpreting the competition

patterns between Na and K if Ca is not present in the solutions.

Ca^{++}-UO_2^{++} Interactions

In order to know what effect Ca would have upon the selectivity of the UO_2^{++} inhibition of K, it was felt that it was necessary to evaluate the interaction between Ca and UO_2^{++}. Figure 9 presents the results of an experiment designed to evaluate what the effects of Ca at four concentrations would be upon the selectivity of the UO_2^{++} inhibition of K and Na. (Note: Due to the patterns of the interaction between UO_2^{++} and Ca it was necessary to reverse the axes of the two response surfaces so that the reader would be able to see the shape of the surface.)

Jacobson et al. (38) have shown that Ca stimulates K absorption and inhibits Na absorption under conditions similar to those used in this study. This pattern can be seen at the zero level of UO_2^{++}. In the presence of increasing UO_2^{++} the pattern was the same but the amounts of stimulation and inhibition were reduced.

As the level of Ca in the test solution increased the pattern of the UO_2^{++} effects upon Na and K changed. At all but the highest level of Ca the stimulation of K absorption produced by 10^{-2} and 10^{-3} milliequivalents of UO_2^{++} was present. However, the effects of the increasing Ca levels appeared to be reducing the influence of

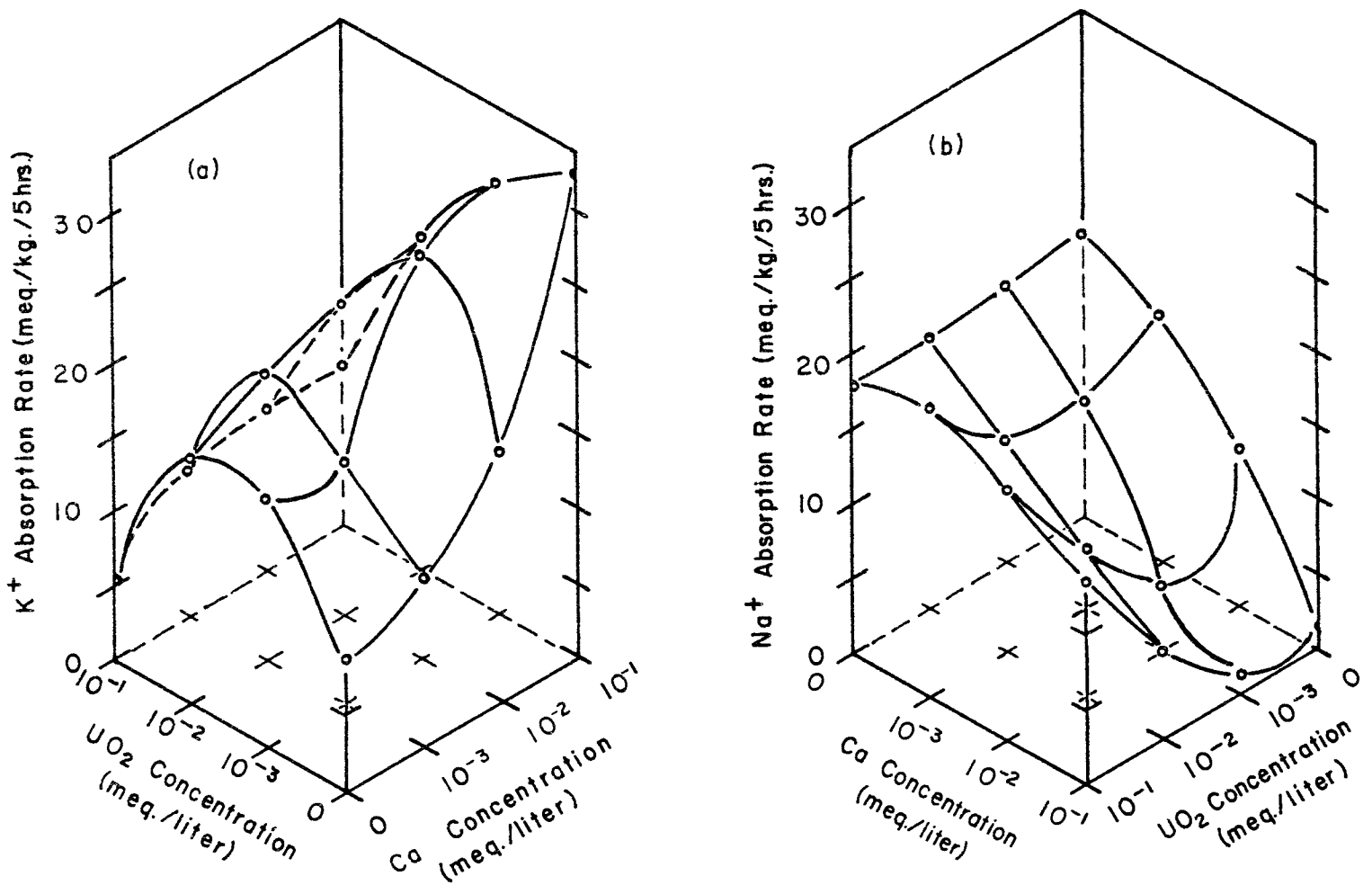

Figure 9. The effect of Ca and UO_2^{++} upon the absorption of (a) K and (b) Na from solutions containing 5 meq each of Na and K per liter. (Appendix 16).

the lower UO_2^{++} concentration. Beyond 10^{-1} milliequivalents of Ca the inhibitory effect of UO_2^{++} was all that was seen. The fact that low concentrations of uranyl stimulated K absorption when Ca was absent coupled with the fact that Ca at the 10^{-1} milliequivalent level eliminated the stimulation suggests that uranyl can act in much the same way as other polyvalent cations such as Ca, Mg, Mn, Sr, etc. (90).

Viets (90) has shown that Ca was the most effective cation among several other divalent cations used in his study for producing a stimulation of K. Thus one would expect that Ca should at least reduce the effects of other divalent cations if not eliminate their influence altogether. This may be suggested in Figure 9 by the fact that Ca eliminated the stimulation of K absorption produced by low UO_2^{++} concentrations. Another possibility to explain the fact that Ca eliminated the UO_2^{++} induced stimulation of K absorption may be related to a maximum amount of stimulation that can be produced by any of the divalent cations. No evidence has been found in the literature to suggest this as a possibility but this could explain the interaction of Ca and UO_2^{++}. As Ca increased in the absence of UO_2^{++} the level of K absorption increased. However, when UO_2^{++} was present the amount of Ca-induced stimulation was reduced. Also, as the level of Ca increased to 10^{-1} milliequivalents per liter this ion satisfied the root's divalent cation

requirement. When uranyl was added to the system containing the higher levels of Ca no stimulation was produced and the absorption of K was inhibited at all uranyl concentrations. Although Viets (90) work, mentioned above, lends more tangible support to the idea of Ca being "preferred" over UO_2^{++} the suggestion that there may be a maximum amount of divalent cation induced stimulation should not be ruled out as an explanation for the Ca-UO_2^{++} interactions seen in Figure 9.

The results of this experiment suggested that Ca did not alter the fact that UO_2^{++} selectively inhibited K absorption. In light of this and the desire to maintain a simple system (as far as the number of ions involved) it was decided to continue to leave Ca out of the test solutions. By leaving Ca out of the solutions the maximum competition between Na and K could be obtained. This would make it easier to see the effects of the various treatments upon the competition between these two ions.

The Effects of UO_2^{++} Concentration Upon Na and K Absorption

Figure 9 suggests that there are two effects of UO_2^{++} in the absence of Ca. One effect was the stimulation of K absorption and slight suppression of Na absorption at 10^{-3} milliequivalents UO_2^{++} per liter. The other effect was the marked suppression of K

absorption and the stimulation of Na absorption occurring at 10^{-1} milliequivalents UO_2^{++} per liter. In order to further evaluate this effect of UO_2^{++} concentration the results of another experiment were evaluated. In this experiment UO_2^{++} was varied from 0 to 1 milliequivalent per liter. Table 7 shows that in this experiment the two effects suggested above were again seen.

Table 7. The effects of UO_2^{++} concentration upon Na and K absorption from solutions containing 5 milliequivalents each of Na and K per liter. (Appendix 17)

UO_2^{++} Concentration	Absorption Rate	
	Na	K
(meq./liter)	(meq./kg./5 hours)	
0.0	16.4	13.9
1×10^{-4}	14.0	14.3
1×10^{-3}	12.4	17.2
1×10^{-2}	13.3	14.9
1×10^{-1}	19.3	5.5
1.0	12.7	0.0

UO_2^{++}-H Interactions

In an attempt to explain these phenomena, a search was made of the uranium chemistry literature. During this search it became apparent that under the conditions used in this study, there can be a number of forms of uranyl cations present. Rush et al. (75) evaluated the hydrolysis products occurring when hexavalent uranium is

dissolved in aqueous media. They noted that, as soon as uranium is dissolved, the hexavalent uranium cation is converted to the divalent uranyl cation, UO_2^{++}. The reaction[4] causes the pH of the solution to drop. If base is added to this solution to raise the pH, hydrolysis of the UO_2^{++} cation occurs. This hydrolysis, which results in the formation of polymers, is both pH and concentration dependent. In their work, Rust et al. (75) have shown that UO_2^{++} can have forms ranging from the simple cation UO_2^{++} (at low concentrations and at pH's less than 3.5) to the complex polymer $(UO_2)3(OH)_5^{+}$ (at high concentrations and at pH's from 3.5 to 6.0). One publication of their work (75) presents a detailed report of the forms present in their system. From curves presented in this publication there are four forms of uranyl which are likely to be present under the conditions used in the study presented in this thesis. These are: UO_2^{++}, $(UO_2)2(OH)_2^{++}$, $(UO_2)3(OH)_4^{++}$, and $(UO_2)3(OH)_5^{+}$. Of these forms there was only one form which occurred at the concentration where K was stimulated. This was the "simple" UO_2^{++} cation. At the concentrations where K is just beginning to be inhibited (near 10^{-2} meq. per liter) there are two forms present but only one of these showed a further increase with increasing concentration. This was the cation $(UO_2)3(OH)_4^{++}$.

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[4] $U^{+6} + 2H_2O \rightleftharpoons UO_2^{++} + 4H^{+}$

In light of the work of Rush et al (75) it was felt that a study of the effects of both UO_2^{++} concentration and hydrogen concentration should be undertaken in an effort to evaluate the interaction between H, UO_2^{++} and ion absorption.

Again a factorial experiment was used to obtain information concerning the interaction between two variables, H ion and UO_2^{++}. Figures 10, 11, and 12 present the results of this series of experiments. In the discussion of these figures the terms "threshold of depression" will be used to indicate that point on the curves where the particular curve changes from an increasing slope to a decreasing slope. The terms increase or stimulation will refer to an upward trend. The terms peak or maxima will be used when talking about a point on a particular surface where the surface reaches an upper limit.

When the pH of test solutions increases from acid to near neutral most cations exhibit an increase in absorption up to pH's considerably higher than those used in this thesis. Much of this increase is thought to be due to two factors (38). One is related to the fact that H ion appears to have a deleterious effect upon the cell membrane. The other factor is related to the competition between H and other cations. Anything which will ameliorate the effects of H will usually increase absorption. Thus by raising the pH the adverse effects of H are reduced. Also when cations, such

as the divalent Ca ion, are added to the test solution they compete with H and thus reduce its effectiveness in inhibiting absorption. Several workers (21, 30, 56) have also suggested that Ca, or other divalent cations, aid in stabilizing the cell membrane and thus its permselectivity.

K

The first experiment in this series evaluated the effects of UO_2^{++} concentration and pH upon the absorption of K from a solution containing 5 milliequivalents per liter of K. Figure 10 shows that at the zero and at the 10^{-3} levels of UO_2^{++} and pH 3 there was a loss of K from the tissues. This probably indicates that H was damaging the membrane so that it became leaky and thus allowed internal K to diffuse out. By increasing UO_2^{++}, the level of polyvalent cations reached a point where the adverse effects of H were not as great and absorption, rather than a loss, occurred. At pH 3 almost all of the uranyl was present at the UO_2^{++} cation (81). Thus the increase in absorption with increasing UO_2^{++} seen at pH 3.0 was most likely a "Viets type" effect resulting from the divalent cation.

The effect of UO_2^{++} became more complex as the pH increased. Rush et al. (75) have shown that the complex polymer $(UO_2)3(OH)_4^{++}$ begins to appear in the vicinity of pH 4.0 and 10^{-2} milliequivalents UO_2^{++} per liter. It is not known if this is the factor which caused

the decrease of K absorption (relative to pH 4.0 and 10^{-2} meq./liter) that occurred between 10^{-1} and 10^{-2} milliequivalents UO_2^{++} per liter. At this stage in our knowledge of ion absorption and UO_2^{++} chemistry it is the most likely explanation. According to Rush et al (75), this complex appears at lower concentrations as the pH increases. The threshold of the depression in K absorption also moved to the lower concentration as pH increased. This would support the idea that it was the uranyl polymer that caused the inhibition of K absorption.

Na

Figure 11 presents the results of an experiment where the effects of UO_2^{++} concentration and pH upon the absorption of Na (from a solution containing 5 milliequivalents Na per liter) were evaluated. This response surface is similar to Figure 10 in many respects. This surface is not as complex, mainly due to the absence of the "peak" at pH 4.0 and 10^{-1} milliequivalents UO_2^{++} per liter which was seen in Figure 10. The overall shape of both of these surfaces is quite similar. Also as the pH increases the typical increase in absorption was seen. As UO_2^{++} increased the suppression, which was suggested to be the result of the UO_2^{++} polymers, was also seen.

Na + K

Work presented earlier has led to the hypothesis that UO_2^{++} is selective in inhibiting K but has little or no effect upon Na. Close comparison between Figures 10 and 11 shows that UO_2^{++} had a greater effect upon K than upon Na. These differences are not as great as was seen when Na and K were both present in the test solutions. Since the proposal of the selective K inhibition hypothesis was based upon experiments where both Na and K were present in the same solution it was felt that it was necessary to investigate the effects of the UO_2^{++} concentration--pH interaction upon absorption from a solution containing both of these ions. Figure 12 presents the results of this experiment. (Na and K were both present at 5 milliequivalents per liter.)

Comparison between Figure 10 and Figure 12(a) reveals that the response of K absorption was the same in both the K-alone solution and in the K + Na solution. Interpretation of this surface would be the same as that given for Figure 10. The maximum absorption in both Figure 10 and 12(a) occurs at pH 6 and 10^{-3} milliequivalents UO_2^{++} per liter.

When one looks at Figure 12(b), however, it is obvious that Na responded quite differently in the K + Na solution as compared to the solution where Na was the only alkali cation that was

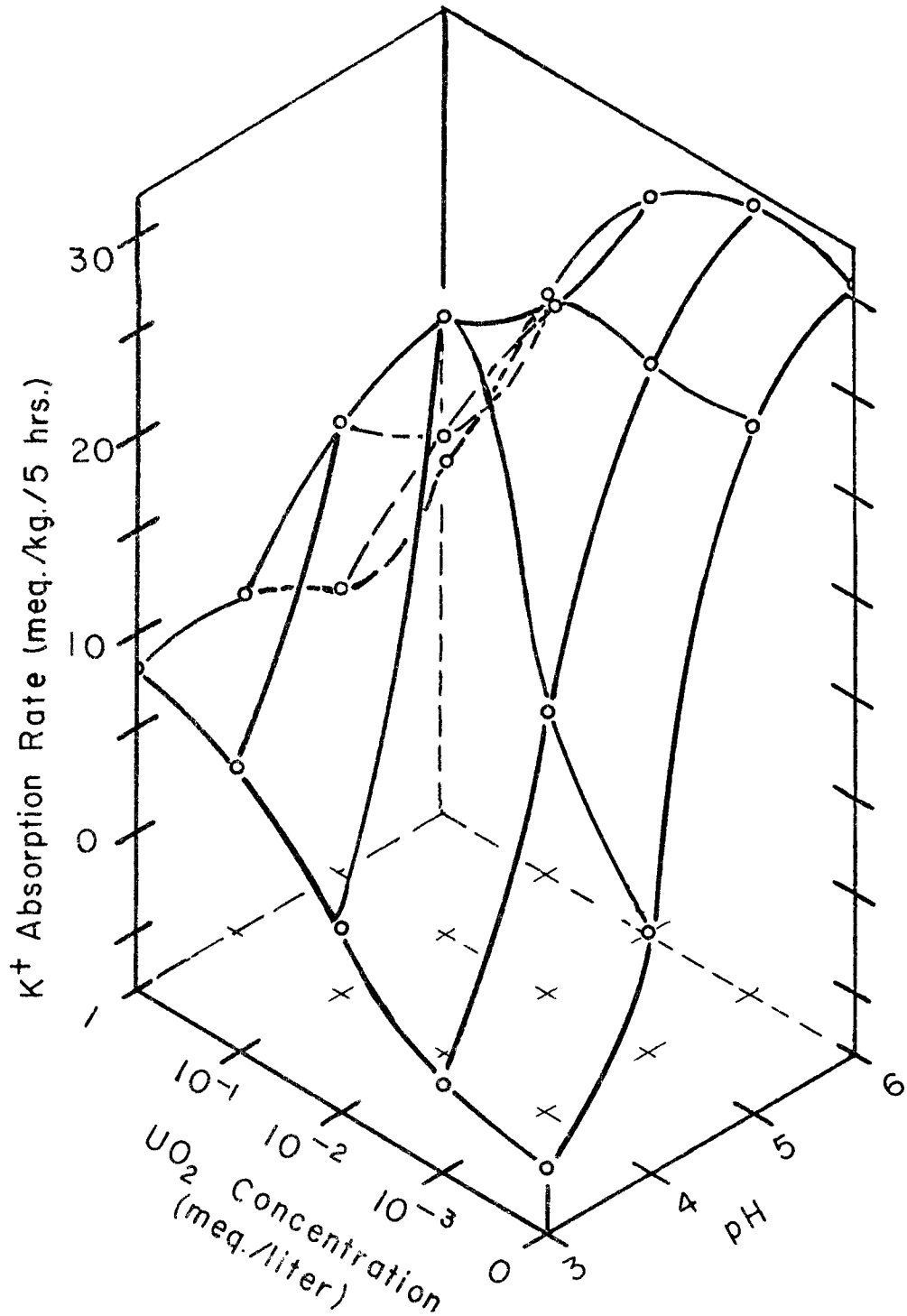

Figure 10. The effect of UO_2^{++} concentration and pH upon the absorption of K from a solution containing 5 meq of K per liter. (Appendix 18).

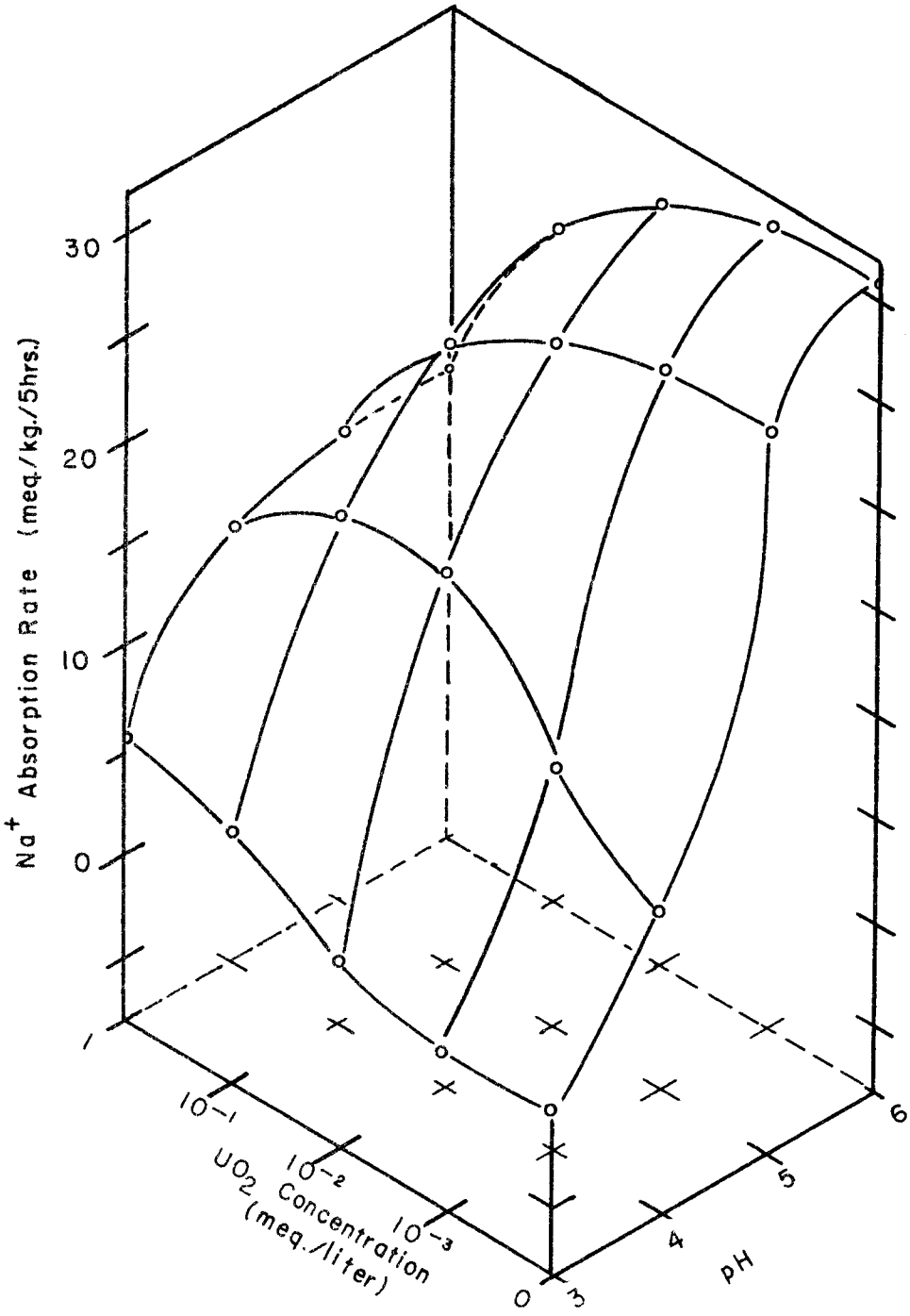

Figure 11. The effect of UO_2^{++} concentration and pH upon the absorption of Na from a solution containing 5 meq Na per liter. (Appendix 19).

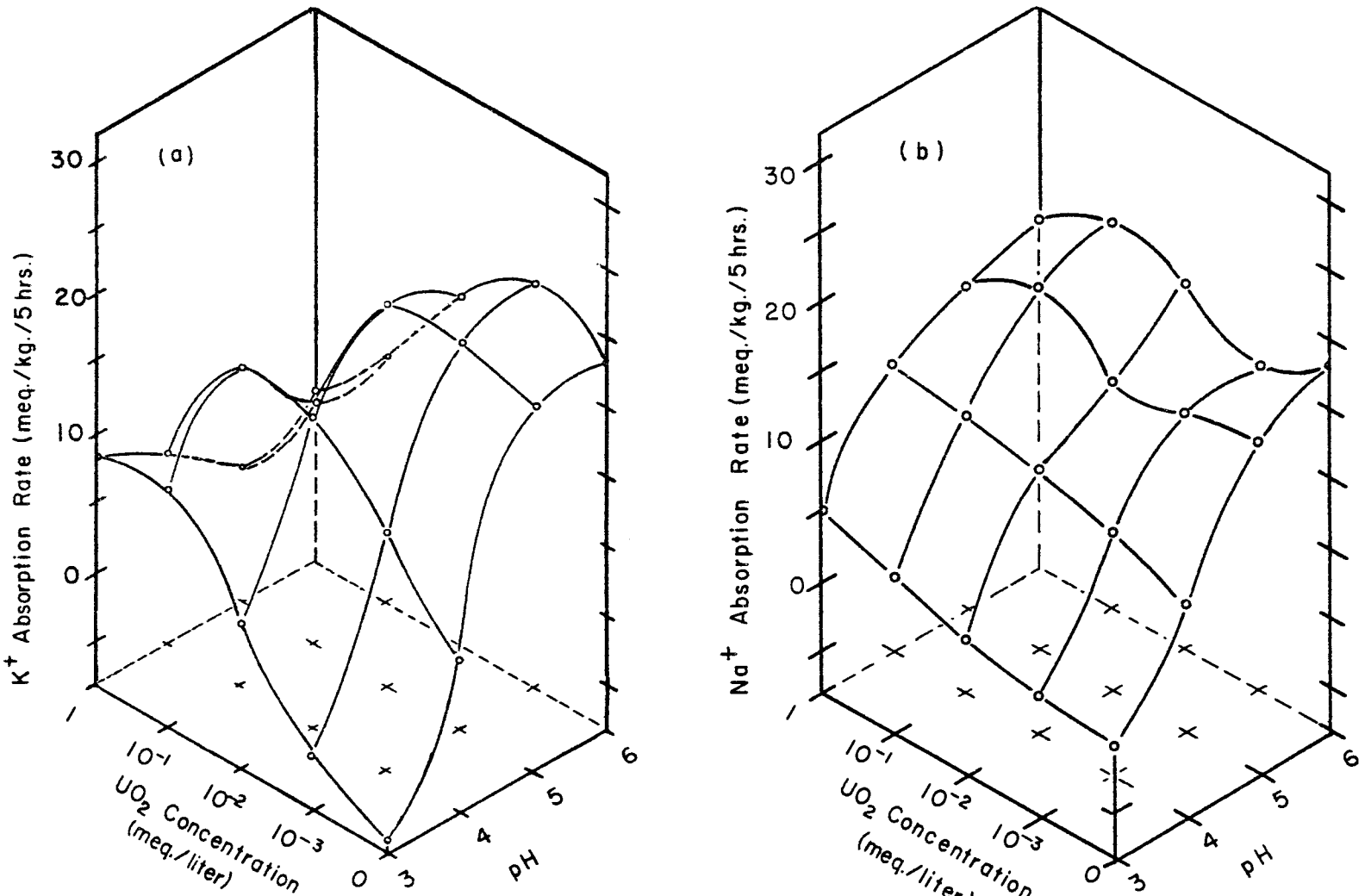

Figure 12. The effect of UO_2^{++} concentration and pH upon the absorption of (a) K and (b) Na from solutions containing 5 meq each of Na and K per liter. (Appendix 20).

present. The main effect of including K in the UO_2^{++} concentration-pH interaction with Na absorbtion was that the shape of the surface was flatter due to a reduction in the amount of stimulation produced at the low pH's by increasing uranyl concentrations. At pH 5 and pH 6 the low uranyl concentrations produced a slight inhibition in the absorption of Na. This is the same effect seen in Table 6. As the UO_2^{++} concentration increased there was a slight increase in the absorption of Na at pH 5 and 6. Comparing Figure 11 and Figure 12(b) one notes that the maxima in Na absorption occur at different places on these two surfaces. In Figure 11 the maximum is at pH 6 and the zero level of UO_2^{++}. In Figure 12(b) it is at 10^{-1} milliequivalents UO_2^{++} per liter and pH 6. This was a 100 fold difference in in the concentration where the point of maximum absorption occurred. This change in pattern suggests that there were to different factors affecting Na absorption when it was the only alkali cation present in the solution. First, there was the "Viets type" effect of the divalent cation, UO_2^{++}, upon the absorption mechanism. The other effect was the slight suppression then stimulation of Na absorption which occurred at pH 5 and 6. This variation in the absorption curve was masked with the Viets effect when Na was the only alkali cation in the solution. In fact it was only when K was present with Na that these effects were seen. The fact that K eliminated the Viets effect in Na absorption suggests that other than the slight stimulation and suppression of Na absorption by

UO_2^{++} seen at pH 5 and 6 there was essentially no effect of UO_2^{++} upon Na. If this was the case then the question arises; "How do you reconcile Figure 11 with Figure 12(b)?"

This question can be answered by considering the possibility that there were two absorption sites operating in the transport of these two ions. One of these sites was sensitive to UO_2^{++}. At low UO_2^{++} concentrations (at all pH's) absorption was stimulated via a Viets effect produced by the simple UO_2^{++} cation. As the concentration increased there was also an increase in the amount of polymerization of UO_2^{++} occurring with increasing pH. The resulting polymers apparently had a deleterious effect upon this UO_2^{++}-sensitive site. This would be the site that normally transports K. The second site was relatively unaffected by UO_2^{++}. This site normally transports Na. Other than the slight fluctuations seen in Figure 12(b) there was an over-all stimulation of Na absorption as UO_2^{++} increased but the effect was not great when compared to the effects seen in the absorption of K.

In Figure 11, with no added K in the solution, Na traveled via both a "UO_2^{++}-sensitive site" and a "UO_2^{++}-resistant site". Thus the absorption shown in Figure 11 was considerably greater than in Figure 12(b). In fact by looking at the actual values (Appendix 19 and 20) one notes that the maximum Na absorption is almost two-thirds greater in Figure 11 than the maximum absorption in

Figure 12(b). This increased absorption was most likely due to the movement of Na via the "UO_2^{++}-sensitive site." This same increase in absorption probably masked the absorption of Na by the site that was not greatly altered by UO_2^{++}.

UO_2^{++}, Na and K Concentration Interactions

In a series of experiments where the concentration of one of these two alkali cations was held constant at one concentration and the other cation varied through a range of concentrations, information was obtained that strengthens the hypothesis that there were two absorption sites operating in this system.

In Figure 13 results of an experiment are presented where K concentration varied from zero to 25 milliequivalents K per liter and Na was held constant at 5 milliequivalents per liter. The pH was 5.0 and UO_2^{++} concentration was 1 milliequivalent per liter. Figure 13(a) shows that there was a sharp reduction in Na absorption to a "base level" as the K concentration was increased. Once the "base level" was reached the effect of further increases in K concentration had a less marked effect upon the absorption of Na. At the same time Na was reduced by the increasing K concentration the K absorption rapidly increased (Figure 13-b).

The effect of the addition of UO_2^{++} to this system was to eliminate the portion of the curves where there was the greatest

competition between K and Na (13-a) and the greatest increase in K absorption (13-b). UO_2^{++} reduced the level of Na absorption to a "base level" that paralleled the level seen at the higher K concentrations. At 5 milliequivalents of K per liter (i.e. at equal concentrations of Na and K) the "control" and the "with UO_2^{++}" curves are almost identical. This is in agreement with Figure 2(a) where it was noted that at equal concentrations of Na and K both K and UO_2^{++} reduced Na absorption by the same amount.

In the experiment presented in Figure 14, K was held constant at 5 milliequivalents per liter and the Na concentration was varied. In this figure the effect of Na upon K was not as pronounced as in the reverse situation (Figure 13), but the competition is still seen. In Figure 14(a) the curves show that when UO_2^{++} was added to the system the result was again to eliminate a portion of the absorption of the ion that was held constant--in this case K. The UO_2^{++}-produced reduction in K absorption occurred throughout the range of Na concentrations but the effect was greatest at the lower Na concentrations. In Figure 14(b) UO_2^{++} did not have an effect upon Na absorption at the lower Na concentrations but above approximately 5 milliequivalents Na per liter, UO_2^{++} reduced the absorption of Na.

The results of the two experiments presented in Figure 13 and 14 support the two site hypothesis in the following way. The pattern of Na absorption seen in the "control" curve of Figure 13(a) shows

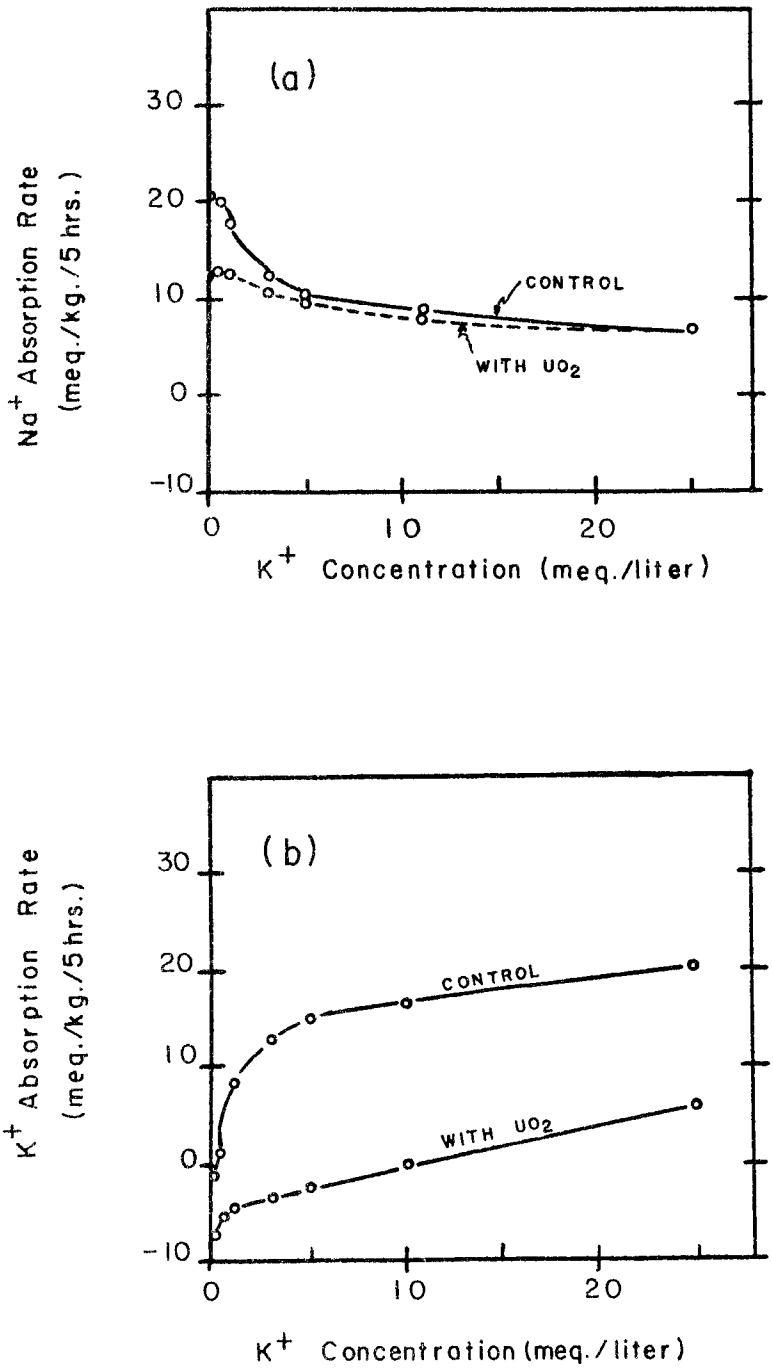

Figure 13. The effect of K concentration upon (a) Na absorption and (b) K absorption in the presence and absence of UO_2^{++}. Na was present at 5 meq per liter and UO_2^{++} was present at 1 meq per liter. pH was pH 5. (Appendix 21).

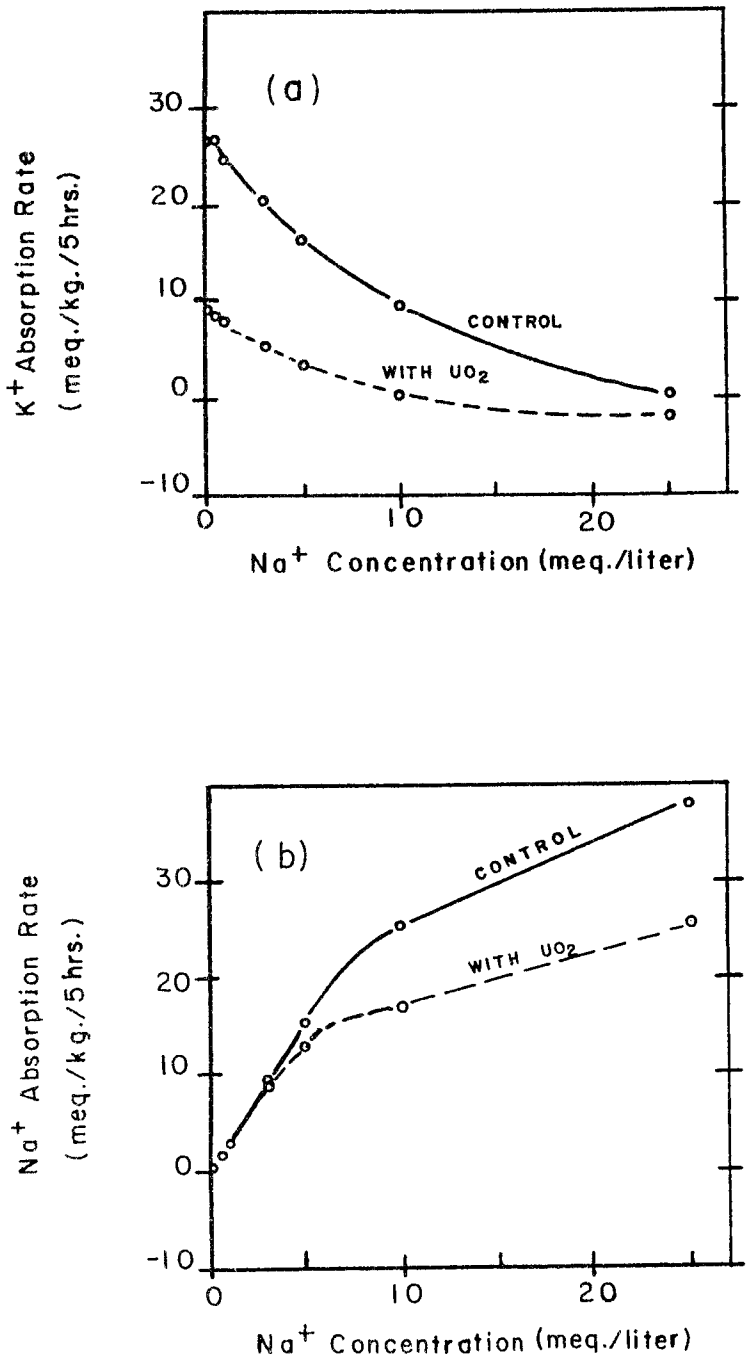

Figure 14. The effect of Na concentration upon (a) K absorption and (b) Na absorption in the presence and absence of UO_2^{++}. K was present at 5 meq per liter, UO_2^{++} was present at 1 meq per liter. pH was pH 5.0. (Appendix 22).

a marked reduction as K increases. At a point where K and Na are equal in concentration the competition becomes considerably less. This change in slope of the competition curve indicates the saturation of a site which shows a "preference" for K and the beginning of competition for a site which has "preference" for Na. In an earlier discussion it was suggested that the site over which K was transported was the UO_2^{++}-sensitive site. This is verified by the "with UO_2^{++}" curve in Figure 13(a). The portion of the curve representing the greatest Na-K competition was the portion eliminated by UO_2^{++}. The portion of the control curve representing the Na site is almost identical to the "with UO_2^{++}" curve. This interpretation can also be gleaned from Figure 13(b). In this figure K absorption increases rapidly with increasing K concentration. At equal concentrations of K and Na the slope of the curve changes. It is the first portion of the curve that shows the effects of UO_2^{++}. This is the same portion that is thought to be representative of the K site. The absorption of K via the UO_2^{++}-resistant site was not altered; in fact the rate of change with increasing concentration was constant at the higher K concentrations. This also suggests absorption by a site that was unaffected by UO_2^{++}.

In Figure 14(a), the pattern between Na and K does not show as sharp a break in the slope, but the change still occurred. In other words, there was a portion of the K absorption which was

more sensitive to Na and a portion which was less sensitive. The addition of uranyl to the system had the effect of greatly reducing the K absorption. The portion of the K absorption which was resistant to uranyl could be eliminated readily by Na at about 10 milliequivalents per liter. These data again suggest that Na and K were moving by way of two sites, one sensitive to uranyl which "favored" K and one relatively resistant to uranyl which "favored" Na.

In Figure 14(b) the steep portion of the curve represents absorption via the Na site. There was no effect of UO_2^{++} on this portion of Na absorption. In this figure it is only the absorption above 5 milliequivalents of Na per liter that shows the effects of UO_2^{++}.

Further evidence for a two site absorption is presented in Figure 15 and 16. Figure 15 presents data that evaluate the absorption of Na from a solution which contained 5 milliequivalents Na per liter, zero to 25 milliequivalents K per liter and 0 to 1 milliequivalent UO_2^{++} per liter. (The subscripts on the K and Na symbols represent the concentration of the respective ions) Figure 15(a) shows that the control curve (K_o) follows the same pattern seen in some of the earlier experiments. With no K in the solution there is a "peak" at both 10^{-1} and 10^{-3} milliequivalents UO_2^{++} per liter. When 1 milliequivalent of K per liter (K_1) was added to the solution the part of the Na absorption moving via the site which showed a

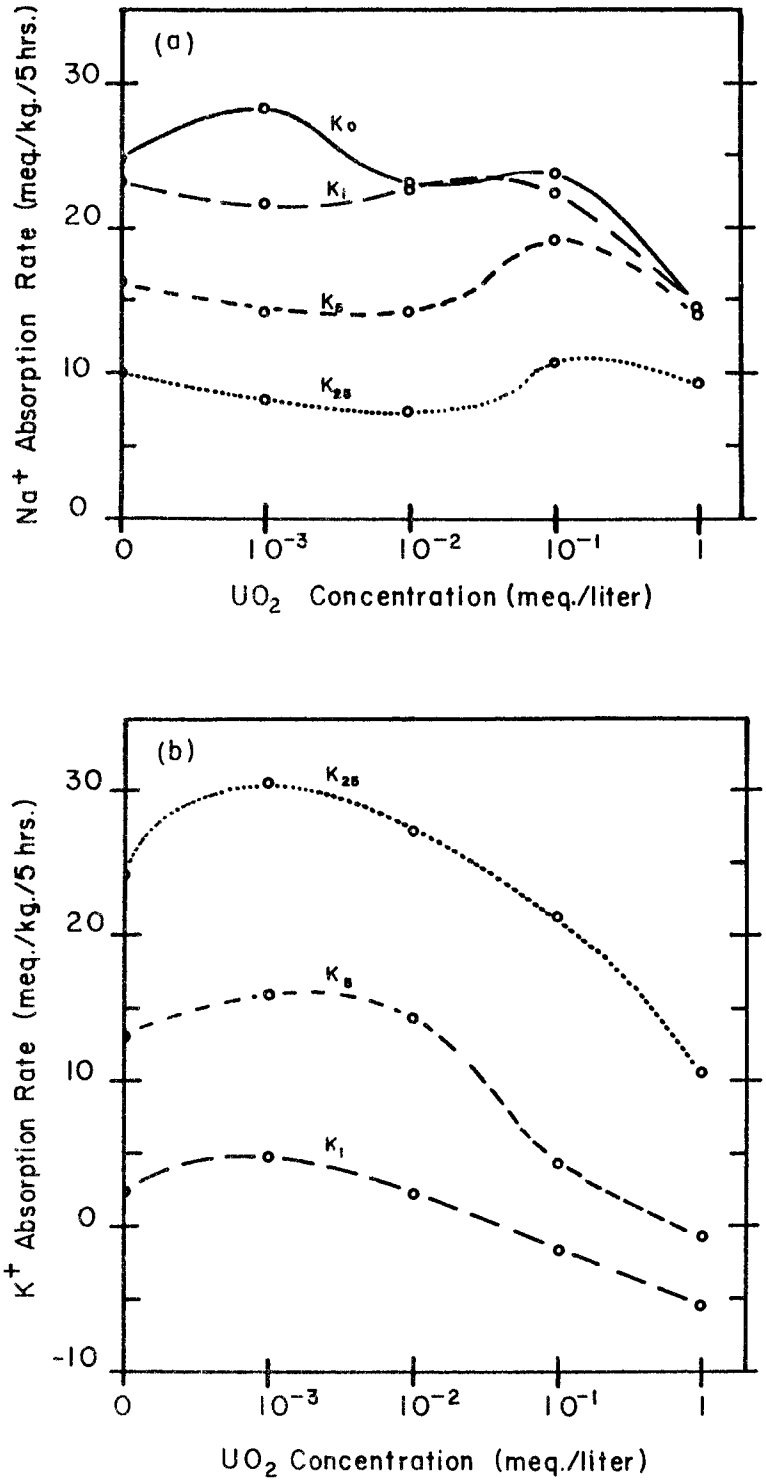

Figure 15. The effect of UO_2^{++} concentration and K concentration upon the absorption of (a) Na and (b) K. Na concentration was 5 meq per liter. pH was pH 5.0. (Appendix 23).

Viets effect was eliminated. Above 10^{-2} milliequivalents there is no change in the curve at this level of K. When the K concentration was increased to 5 milliequivalents per liter the absorption of Na at low UO_2^{++} concentrations was further inhibited by the presence of K. The portion of absorption at 10^{-1} milliequivalents UO_2^{++} per liter, which has been called the "UO_2^{++}-resistant" site, showed some effect on K. The value at 1 milliequivalent UO_2^{++} per liter still has not changed. When K was increased to 25 milliequivalents per liter (or 5 times the Na concentration) the Na absorption rate was reduced. The shape of the curves at K_1, K_5, and K_{25} are basically the same. Thus K appears to have eliminated the Viets effect on Na; but not the stimulation hypothesized to be the result of the complex uranyl polymers.

The K absorption curve, shown in Figure 15(b), indicates that it was the portion of absorption which was affected by low UO_2^{++} concentrations that showed the most rapid increase with increasing K concentrations. At K_5 there was a slight increase in abxorption followed by a loss at higher UO_2^{++} concentrations. At K_6 there was again a slight stimulation followed by a reduction with a depression threshold at about 10^{-2} milliequivalents UO_2^{++} per liter. Twenty-five milliequivalents of K per liter (K_{25}) showed a larger stimulation at the lower UO_2^{++} concentrations with a maximum still at 10^{-3} milliequivalents UO_2^{++} per liter. The entire absorption curve is considerably higher than at the K_1 or K_5 levels.

When the situation was reversed and Na concentration was

varied and K concentration was held constant at 5 milliequivalents per liter, the location of the effects of UO_2^{++} were reversed. Figure 16(a) shows that, as Na concentration increased, it was the absorption which was stimulated at 10^{-1} milliequivalents UO_2^{++} per liter that responded most to the increase in Na concentration. At equal Na and K concentrations (Na_5) the pattern shown previously in Table 6 is seen here--a slight decrease at 10^{-3} milliequivalents UO_2^{++} per liter and a stimulation at 10^{-1} milliequivalents UO_2^{++} per liter. When 25 milliequivalents Na per liter were added to the test solution the pattern of absorption shows two "peaks." The one at 10^{-3} milliequivalents UO_2^{++} per liter represents a slight Viets effect and the one at 10^{-1} milliequivalents UO_2^{++} per liter represents the stimulation produced by the uranyl polymers.

The results of increasing Na concentration, shown in Figure 16(b) was to reduce first the K absorption via the site which was stimulated by 10^{-1} milliequivalents UO_2^{++} per liter; then to markedly reduce the absorption via the site which produced the Viets effect.

These two figures suggest that there are two sites acting in the transport of Na and K. One of these sites was stimulated by low UO_2^{++} concentrations in much the same way that Ca produces the well known Viets effect (97). This site seems to have a preference for K. Throughout the remainder of this thesis this site will be called the "K-site." The second absorption site is stimulated by UO_2^{++} concentrations almost 100 times greater than the "K-site." This has been hypothesized to represent a stimulation produced by the complex uranyl polymer $(UO_2)3(OH)_4^{++}$. This site has a stronger affinity for

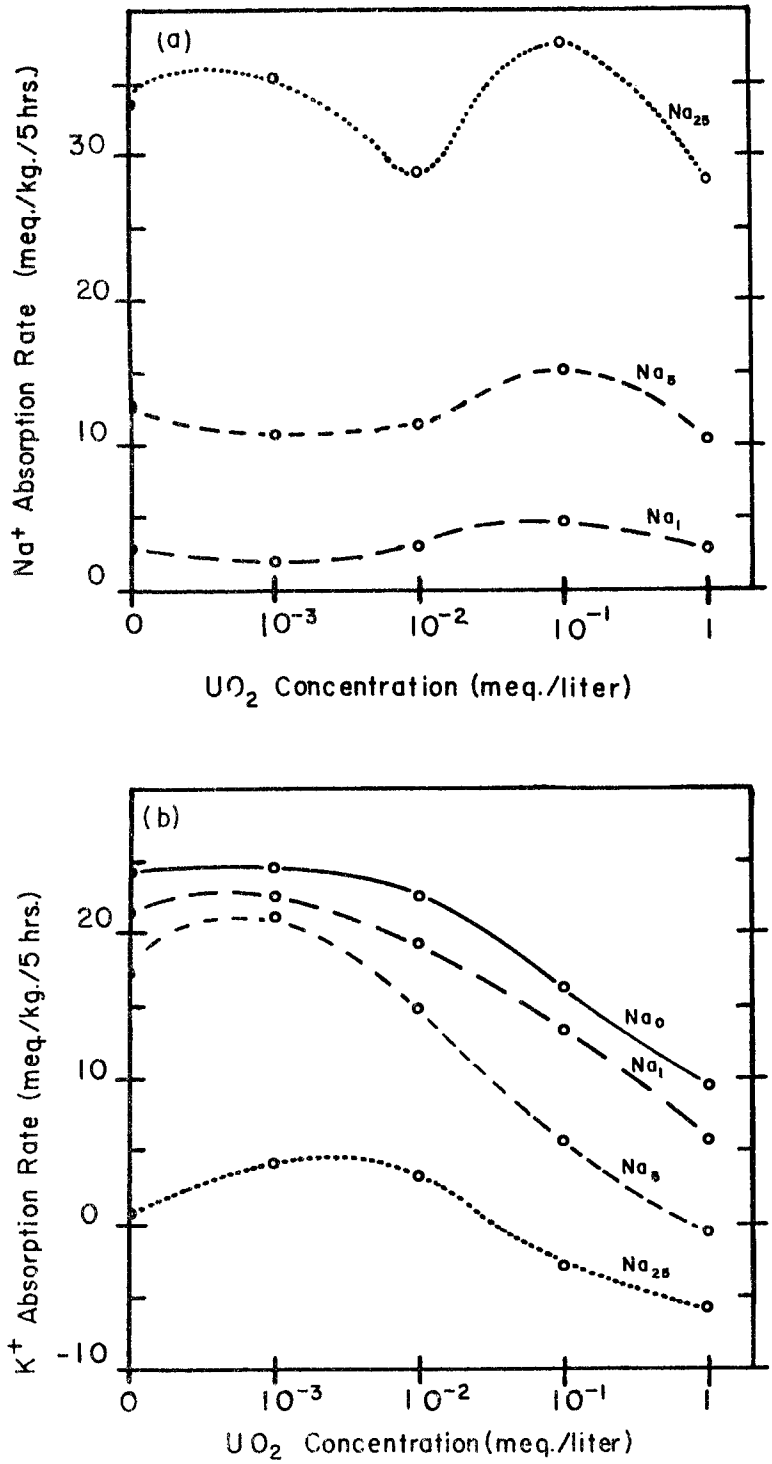

Figure 16. The effect of Na concentrations and UO_2^{++} concentrations upon (a) Na absorption and (b) K absorption. K concentration was 5 meq per liter. pH was pH 5.0. (Appendix 24).

for Na than for K. This site will hereafter be referred to as the "Na-site."

The use of the terms "K-site" and "Na-site" suggest that there are specific locations that are transporting the appropriate ion across the cell membrane. Although these sites are labeled "K-site" and "Na-site" they can transport either ion when the proper conditions are met (i. e., Na can travel via the "K-site" when there is no K present in the system). At this point in the thesis the stage has not been set to identify these sites as carriers. This will be done in the general discussion section appearing later. At this stage the only reason to use these terms is to simplify the discussion. This will avoid having to continuously refer to the points, where absorption is stimulated, by the cumbersome concentration terms.

The completion of this diversion into the effects of various concentrations of Na or K upon the absorption of the other ion sets the stage for completing the discussion of the response surfaces in Figures 10, 11, and 12. In Figure 10 the absorption of K represents transport via both the "K-site" and the "Na-site." Since the "K-site" was more active the absorption patterns exhibited by the response surface was that of the "K-site." When Na was added to the system the total absorption of K was reduced (Figure 12-a) but the shape of the surface is the same. In Figure 11 where Na was the lone alkali cation, the absorption was again the combination of both the "Na-site" and the "K-site." When K was added to this system, not only was the total Na absorption reduced (Figure

12-b) but also the shape of the response surface was changed. The shape of the response surface in Figure 12(b) represents primarily the absorption of Na via the "Na-site." There may, however, have been some absorption of Na still occurring over the "K-site."

In summary, uranyl appears to induce two effects upon the absorption of Na and K. How these effects are exhibited depends upon the ion combinations used in the test solutions. When both Na and K are present in the solution there appeared to be a Viets type stimulation in the absorption of K occurring at low UO_2^{++} concentrations. This was followed by an inhibition of K absorption at high UO_2^{++} concentrations. Na absorption, on the other hand, was suppressed by the low UO_2^{++} concentration but was stimulated or else was not affected by the high UO_2^{++} concentrations. This difference suggests that UO_2^{++} acts upon absorption in two different ways. The first action was the Viets effect supposedly resulting from the relatively simple UO_2^{++} cation. This effect was similar to that reported by Jacobson et al. (38) for the effect of other polyvalent cations upon Na and K absorption in mixed solutions. The second action was probably the result of the presence of the complex uranyl polymer $(UO_2)3(OH)4^{++}$ which occurs at uranyl concentrations above 1×10^{-1} and pH's above 4.5.

The Effects of UO_2^{++} Upon Other Alkali Cations

The effect of UO_2^{++} upon K and Li presented in Figure 1

suggests the need to evaluate the effects of UO_2^{++} upon other ions. In a preliminary report (52), which led up to the study presented in this thesis, Li, Na, K, Mg, and Mn were studied. In this previous study it was shown that the effects of UO_2^{++} upon Li were similar to the effects upon Na. Mg and Mn were both inhibited by the presence of UO_2^{++} in the test solution but Mn was not affected by a thirty-minute pre-treatment in one milliequivalent UO_2^{++} per liter.

Table 8 presents part of the data published in the preliminary report mentioned above (52). The table shows that Li and Na were affected in a similar fashion and K and Rb in a similar fashion. This suggests that perhaps Li was transported by the "Na-site" and Rb by the "K-site". In order to evaluate this possibility the results of a series of experiments are presented which investigated the effects of UO_2^{++} concentration and pH upon the absorption of Li, and Rb along with combinations of Li, Na, K, and Rb.

Table 8. Absorption of alkali cations by barley roots treated with uranyl chloride. (pre-treatment was for 30 minutes in 1 milliequivalent UO_2^{++} per liter. All alkali cations were present at 5 milliequivalents per liter. Uranyl was present at 1 milliequivalent per liter in the "+ UO_2^{++} treatment. pH was 5.0 (Appendix 25)

Ion	Control	+UO_2^{++}	UO_2^{++} Pret.
		(meq./kg./5 hrs.)	
Li	9.0	8.1	11.7
Na	24.4	15.7	26.6
K	27.8	7.7	18.5
Rb	20.0	7.7	15.4

In order to present the results of this group of experiments, an evaluation was made of Li alone, Li + Na, Li + K, and Li + Rb then a similar sequence of experiments was carried out for Rb.

Li

Figure 17 presents the results of an experiment which evaluated the effects of UO_2^{++} and H upon Li absorption from a solution containing 5 milliequivalents Li per liter. The most striking feature of this curve is the lack of any appreciable effect of UO_2^{++} upon Li absorption. As the hydrogen ion level decreased the absorption of Li increased. The absorption of Li appears to have exhibited no Viets (i.e. stimulation) effect at the lower UO_2^{++} concentrations. Also, absorption at the higher pH's and UO_2^{++} concentrations did not show a "peak" as was seen in Na absorption. There was a maximum absorption occurring at pH 6.0 and 10^{-1} milliequivalents UO_2^{++} per liter that was similar to that in Figure 12(b). The failure of Li to respond to UO_2^{++} may be related to the fact that the presence of a small amount of divalent cation (UO_2^{++} in this case) has been shown to suppress the absorption of Li (38). Jacobson et al. (38) have shown that Ca^{++} markedly inhibited Li absorption; moderately reduced Na absorption; and stimulated K absorption. The presence of the UO_2^{++} cation would thus be likely to either reduce Li absorption or else have no effect upon it.

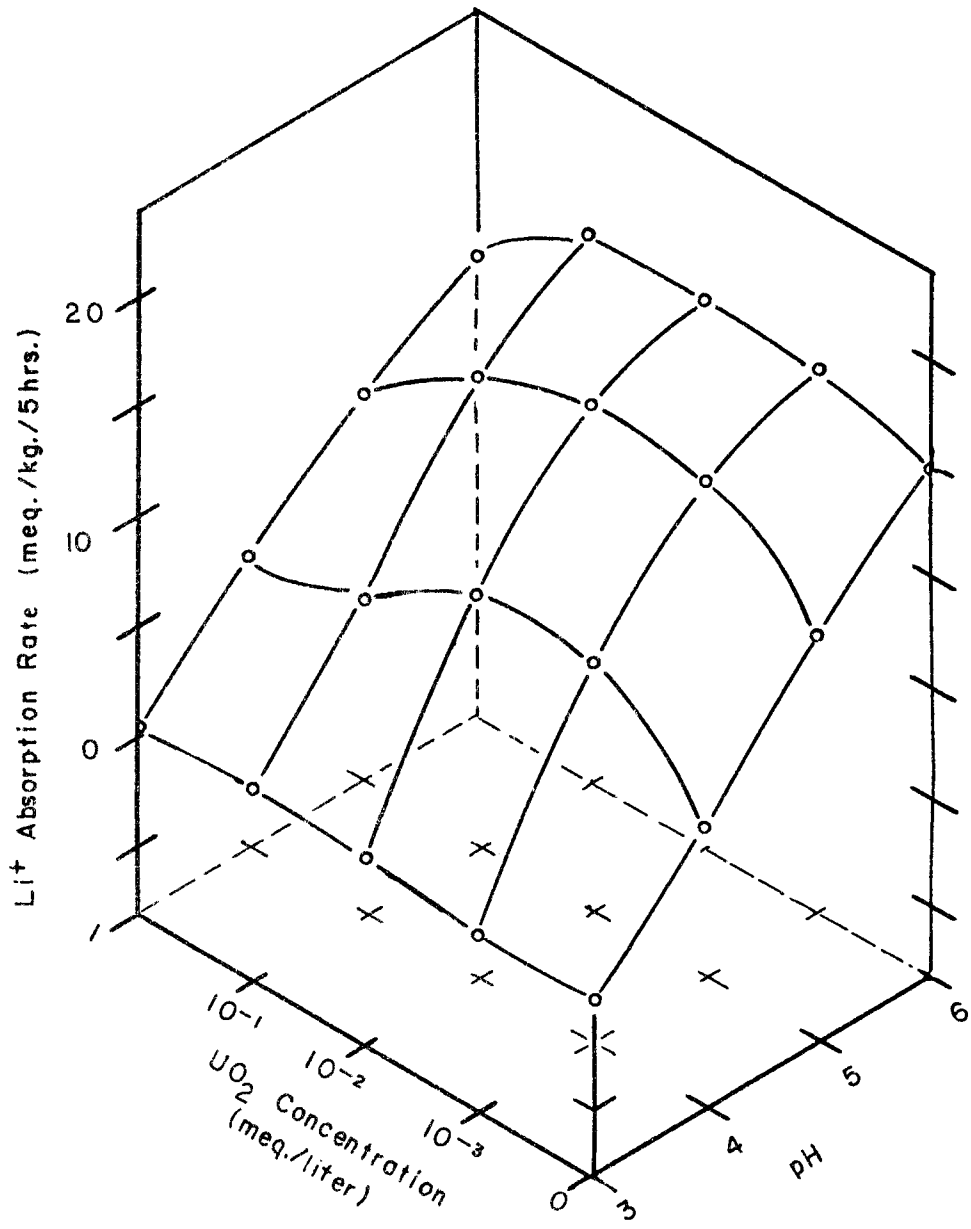

Figure 17. The effects of UO_2^{++} and pH upon the absorption of Li from a solution containing 5 meq Li per liter. (Appendix 26).

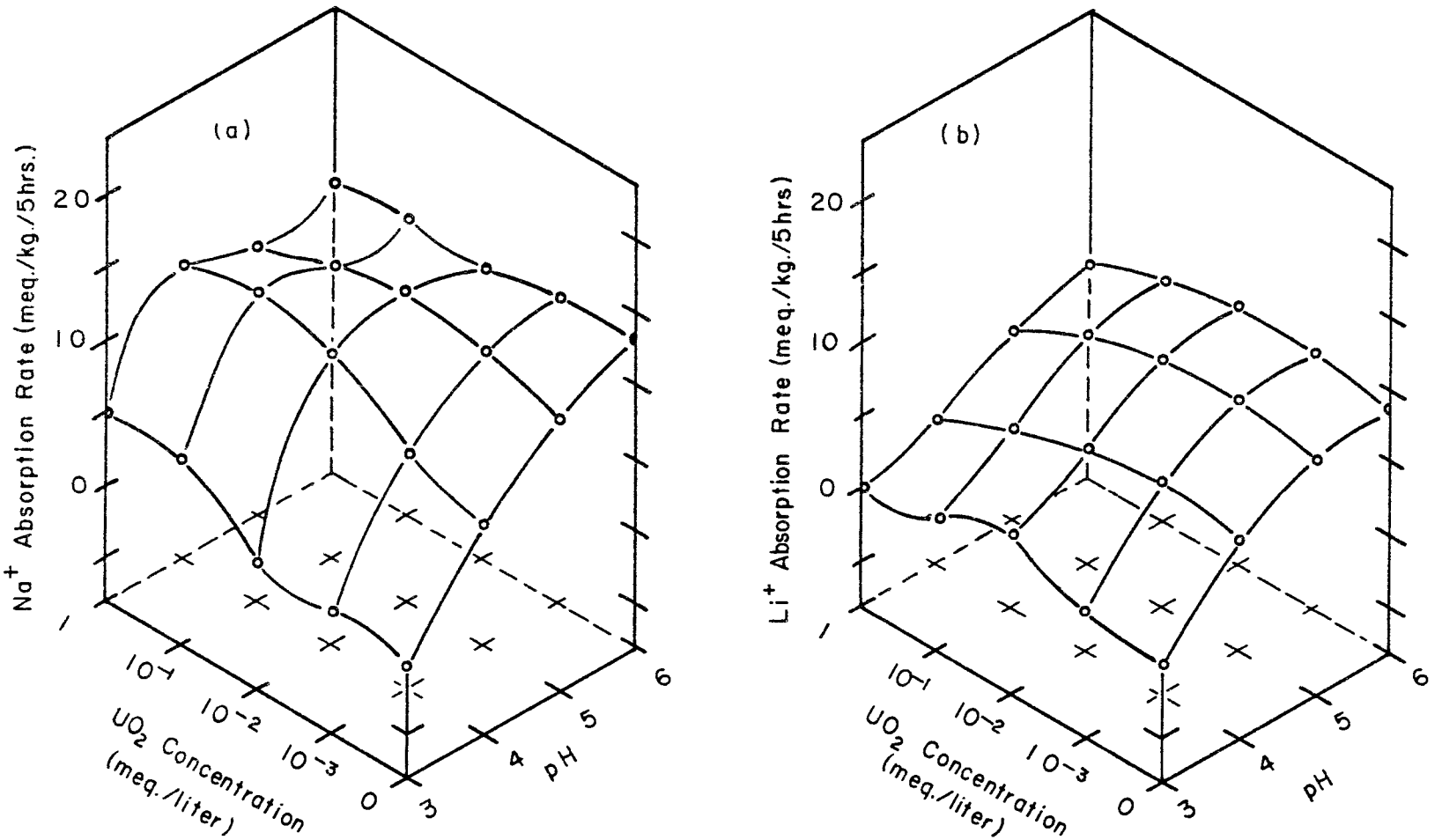

Figure 18. The effects of UO_2^{++} and pH upon the absorption of (a) Na and (b) Li from a solution containing 5 meq each of Li and Na per liter. (Appendix 27).

Since this effect was seen in the treatment where Li was the only alkali cation present it was felt that Li probably did not move via the "UO_2^{++}-sensitive", or "K-site". In order to determine if this was the case, absorption from solutions containing Li plus various other alkali cations were evaluated.

Li + Na

Figure 18 was obtained when the results of an experiment which evaluated the effects of UO_2^{++} and H upon the absorption of Li and Na were plotted. When Li and Na were together there appeared to have been very little change in the surfaces with the exception of the stimulation resulting from increasing pH. There is some suggestion in Figure 18(a) that Na absorption followed the K pattern. This is seen by looking at the slight peak occurring at pH 4 and 10^{-1} milliequivalents UO_2^{++} per liter. The fact that Li did not respond to UO_2^{++} in either this experiment or in the experiment presented in Figure 17 suggests that Li may not be able to cross the membrane via the site that was inhibited by high uranyl concentrations at pH 4, 5, or 6 (i.e, the "K-site"). If this were the case then one would expect Na to be the only ion of this pair that would move via the "UO_2^{++}-sensitive" site and thus the only ion of this pair to show any response to uranyl.

Li + K

When Li and K are combined in a treatment solution the parallel between Li and Na becomes more apparent. Figure 19(a) shows the marked effect of UO_2^{++} seen in the K surfaces presented earlier. This surface is shifted somewhat from the surfaces shown in Figure 10 and Figure 12(a), but there is still some similarity. The maximum absorption on this surface occurs at ph 5.0 and 10^{-1} milliequivalents UO_2^{++} per liter. Although different from Figure 12(a) the effect of the H-UO_2^{++} interaction still shifted the maximum of successive pH curves toward the lower concentrations and higher pH's.

Figure 19(b) is again a flat surface with only slight variation. The reason for the negligible effect of uranyl upon Li absorption response to UO_2^{++} may be related to the low absortpion of Li which occurred in these tissues. The low absorption rate would tend to mask any variations in the surface because these variations would be so small that they would not be apparent.

From the surfaces in Figure 19 it was not possible to define the two "sites" which were suggested as an explanation for Figure 12. The main conclusion here is that there was no Viets effect upon Li absorption and there is a Viets effect upon K absorption. Also there was no major suppression of Li but there was a

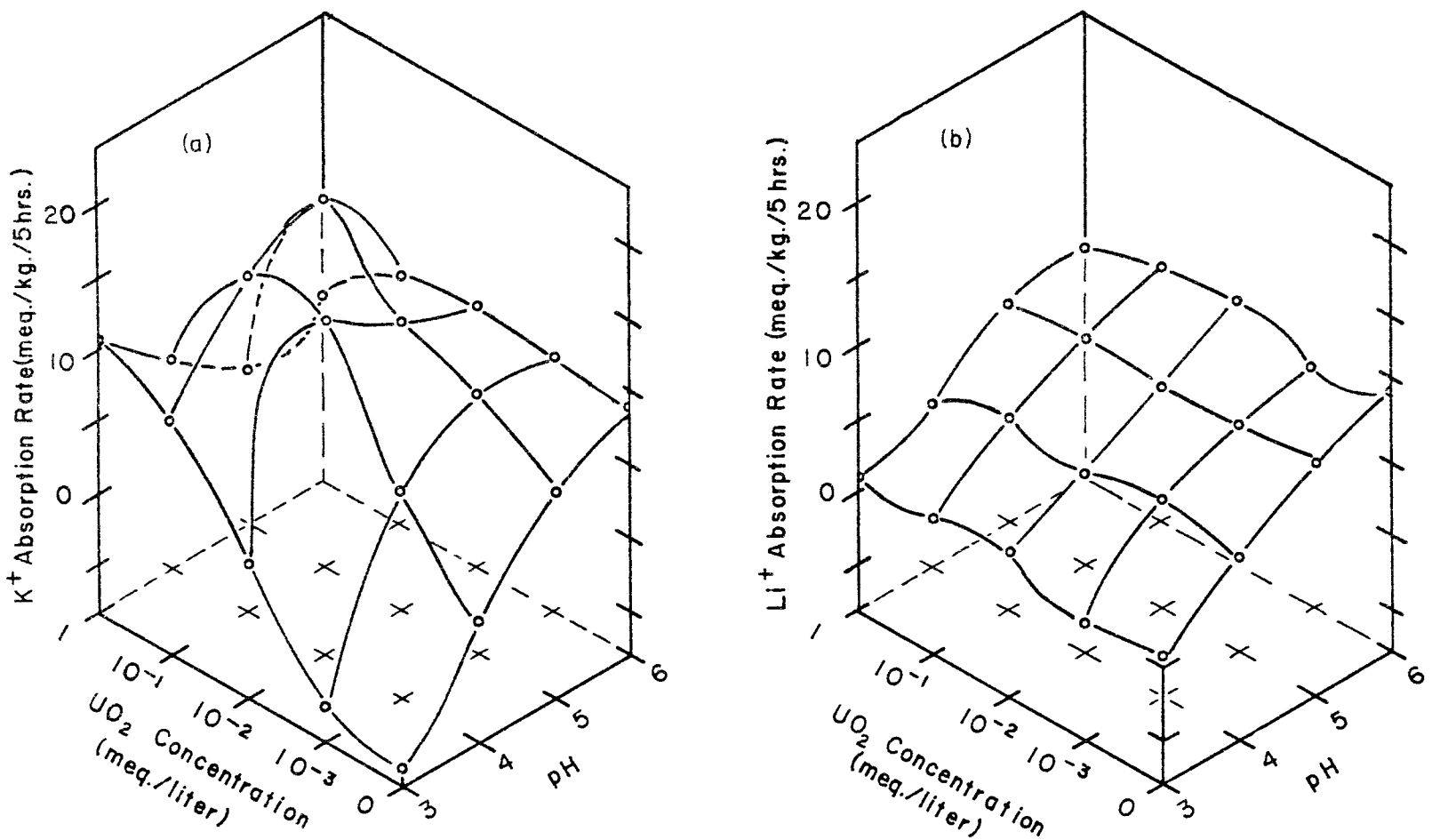

Figure 19. The effects of UO_2^{++} and pH upon the absorption of (a) K and (b) Li from a solution containing 5 meq each of Li and K per liter. (Appendix 28).

suppression of K absorption.

Li + Rb

The final surface to be presented in the Li series of experiments is Figure 20. In this experiment there was a slight Viets effect with Rb absorption and none with Li absorption. Comparing the 10^{-1} level with the 1 milliequivalent level in Figure 20(b) one sees that UO_2^{++} reduced Rb absorption. The effect of pH between zero and 10^{-2} milliequivalents UO_2^{++} per liter was the usual effect produced by the reduction in the amount of H ion in the system. The maximum of this curve occurs at pH 6 and the zero UO_2^{++} level.

Evaluating all of the Li surfaces the lack of response to UO_2^{++} is striking in light of the effects of this ion upon Na, K and Rb. With the exception of minor fluctuations, there was really little effect of UO_2^{++} upon Li no matter what other ion was added to the system. This agrees to some extent with the observation concerning the effects of UO_2^{++} upon Na but contrasts sharply with the effects upon K. Although there was some similarity between the Rb response surface in Figure 20 and the K absorption pattern the effects of uranyl upon Rb were such that it was hard to reach a definite conclusion concerning the Rb absorption pattern. Therefore, the results of experiments where Rb was evaluated will be presented before any decision will be made about the UO_2^{++} - Rb

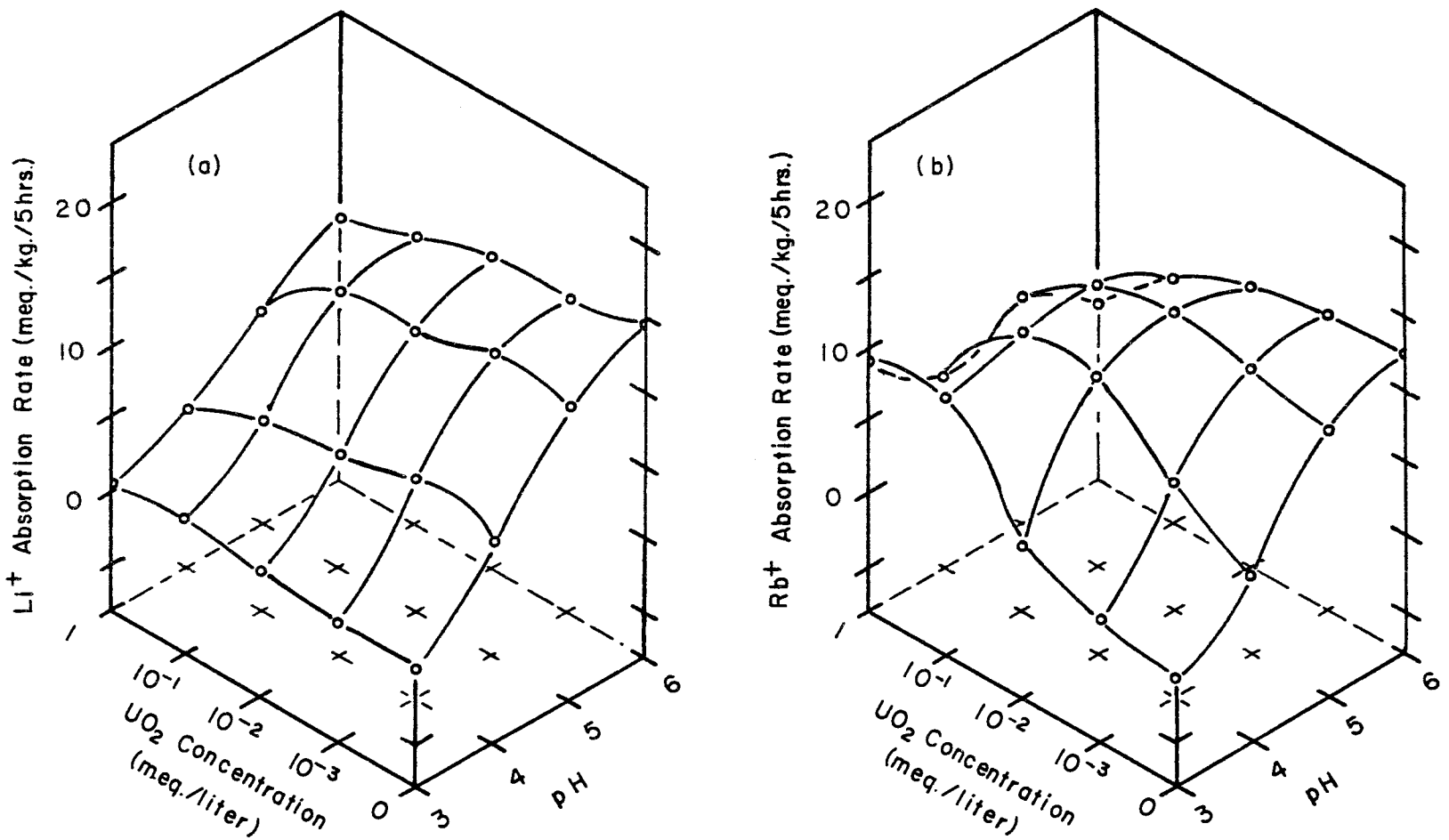

Figure 20. The effects of UO_2^{++} and pH upon the absorption of (a) Li and (b) Rb from solutions containing 5 meq each of Li and Rb per liter. (Appendix 29).

interaction.

Rb

Figure 21 presents results obtained during an experiment which evaluated the effects of UO_2^{++} and pH upon Rb absorption from a solution containing 5 milliequivalents Rb per liter.

This curve is somewhat intermediate between K and Na. At pH 3 there is a Viets type effect produced by UO_2^{++} throughout the range of UO_2^{++} concentrations. As the pH increases the maximum benefit of the Viets effect moves to the higher pH's and lower uranyl concentrations. The maximum absorption of Rb occurred at pH 6 and 10^{-2} milliequivalents UO_2^{++} per liter. This maximum occurred at the same pH and uranyl concentration as was found in Figure 10 and Figure 12(a) for K. There was a depression of Rb absorption produced by UO_2^{++} at pH 4, 5, and 6. The depression threshold occurred in the vicinity of 10^{-2} milliequivalents UO_2^{++} at pH 4 and 6 (see Appendix 30) and at 10^{-3} milliequivalents UO_2^{++} per liter at pH 5. This pattern is suggestive of transport via the same site as K transport.

Rb + Na

When Rb and Na were combined the resulting response surfaces are similar to Figure 12. Figure 22(a) shows that the

results of increasing pH was to increase the absorption rate of Na. UO_2^{++} slightly increased Na absorption at pH 3 and 4. At pH 5 and 6 there was a slight reduction in absorption at 10^{-3} milliequivalents UO_2^{++} per liter. Beginning between 10^{-3} and 10^{-2} milliequivalents UO_2^{++} per liter there was a pronounced stimulation which reaches a "peak" at 10^{-1} milliequivalents UO_2^{++} per liter. The 1 milliequivalent per liter treatment at pH 5 and 6 reduced the absorption rate of Na back to the level which occurred when UO_2^{++} was not in the system. This is basically the same surface that was seen in Figure 12(b). The maximum absorption in both Figure 12(b) and 22(a) occurs at pH 6 and 10^{-1} milliequivalents UO_2^{++} per liter.

The pattern of Rb absorption presented in Figure 22(b) is similar in many respects to the K absorption surface. In general, at the three lowest UO_2^{++} concentrations, decreasing the H ion concentration increases absorption. At pH 3 the effect of the uranyl concentration again served to protect the cells and thus increased the absorption of Rb. At pH 5 and 6 the rate of absorption was depressed from 10^{-2} to 1 milliequivalent UO_2^{++} per liter. A slight "peak", similar to that seen in Figure 10 and 12(a), appeared at pH 4 and 10^{-1} milliequivalents UO_2^{++} per liter. The overall pattern of this figure shows the Viets effect at low UO_2^{++} concentrations which was also seen in the K response surfaces. There was also an inhibition of Rb absorption produced at the higher UO_2^{++}

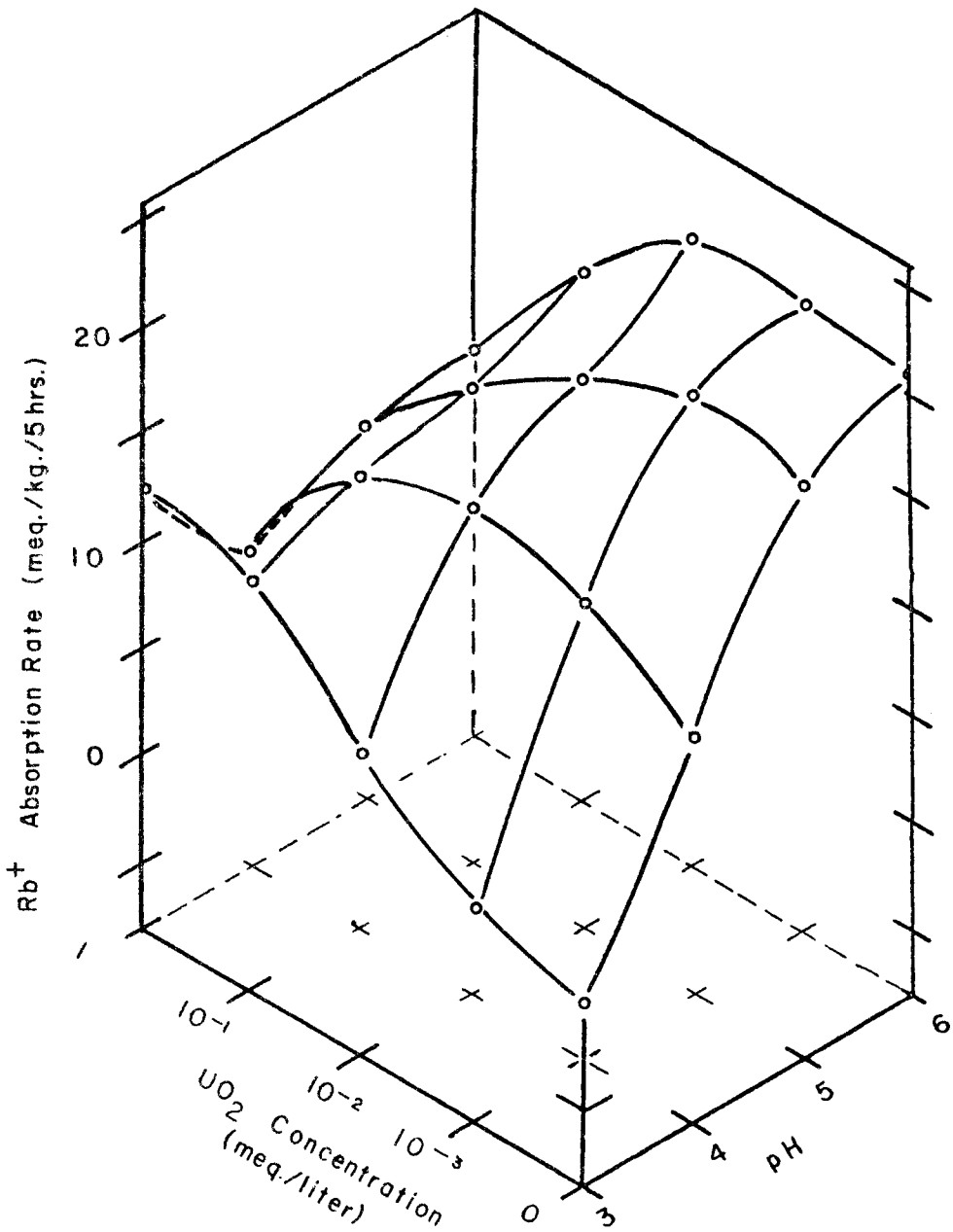

Figure 21. The effects of UO_2^{++} and pH upon the absorption of Rb from a solution containing 5 meq of Rb per liter. (Appendix 30).

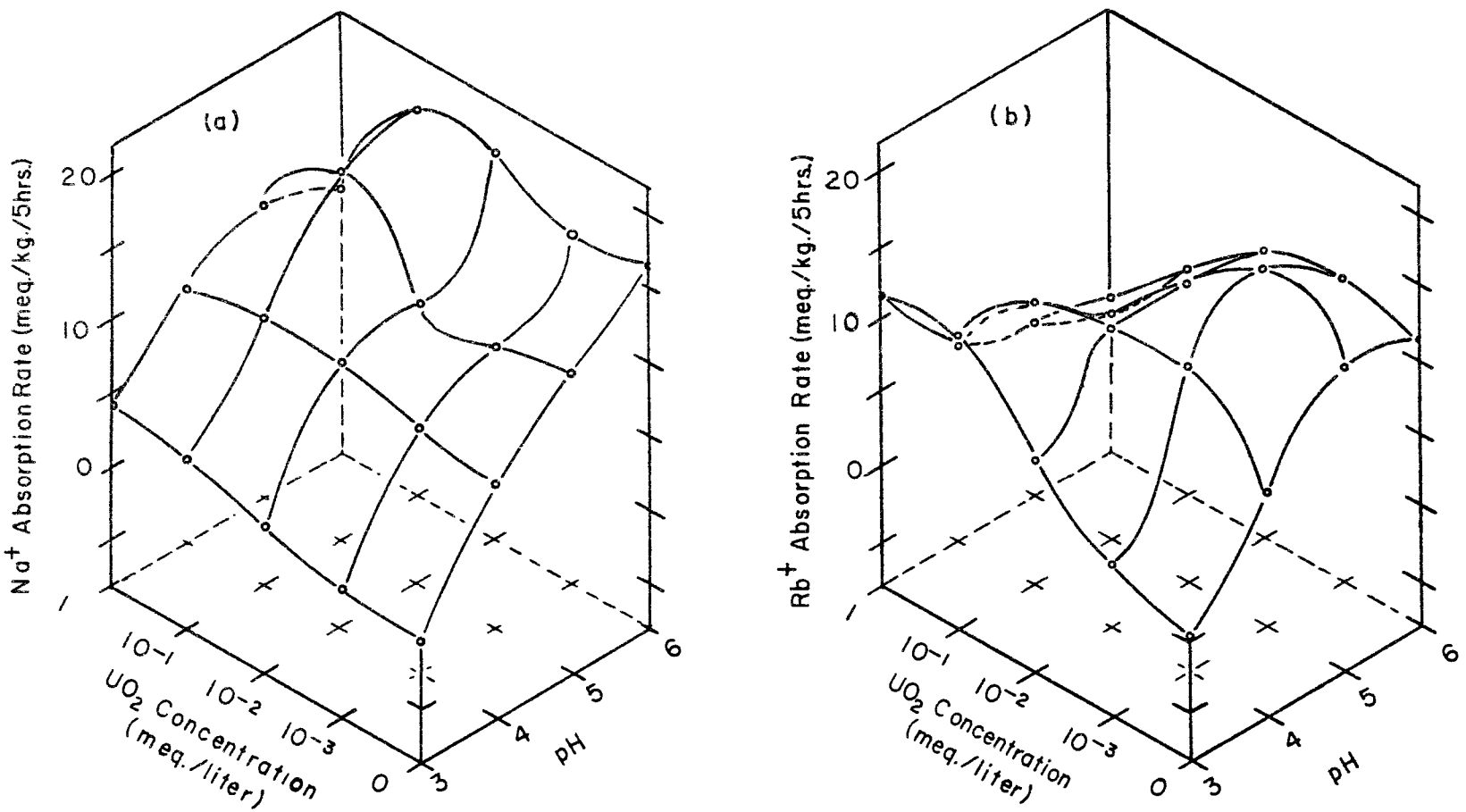

Figure 22. The effects of UO_2^{++} and pH upon the absorption of (a) Na and (b) Rb from a solution containing 5 meq each of Rb and Na per liter. (Appendix 31).

concentrations which paralleled that seen in the K absorption curves. The results presented in this figure strongly support the idea that K and Rb are affected in the same way by UO_2^{++}.

Rb + K

Figure 23 presents the results of an experiment where K and Rb were present at 5 milliequivalents each per liter.

Other than the fact that Rb absorption does not show as pronounced a response to uranyl and H as does K, these two surfaces are almost identical. There are "peaks" in both surfaces which occur at pH 6 and 10^{-2} milliequivalents UO_2^{++} per liter and at pH 5 and 10^{-1} milliequivalents UO_2^{++} per liter. The effect of 1 milliequivalent UO_2^{++} per liter at pH 5 and 6 was to depress the absorption of both of these ions. The general conclusion to be drawn from this figure is that K and Rb were again shown to respond in a similar fashion when treated with different uranyl concentrations and pH's. The fact that K absorption was somewhat lower in this experiment than in the experiments which produced Figure 10 and 12(a) suggests that Rb and K were competing with each other for the "K-site".

The results of the experiments where the effect of uranyl and pH were evaluated strengthen the hypothesis that UO_2^{++} selectively inhibits ion absorption.

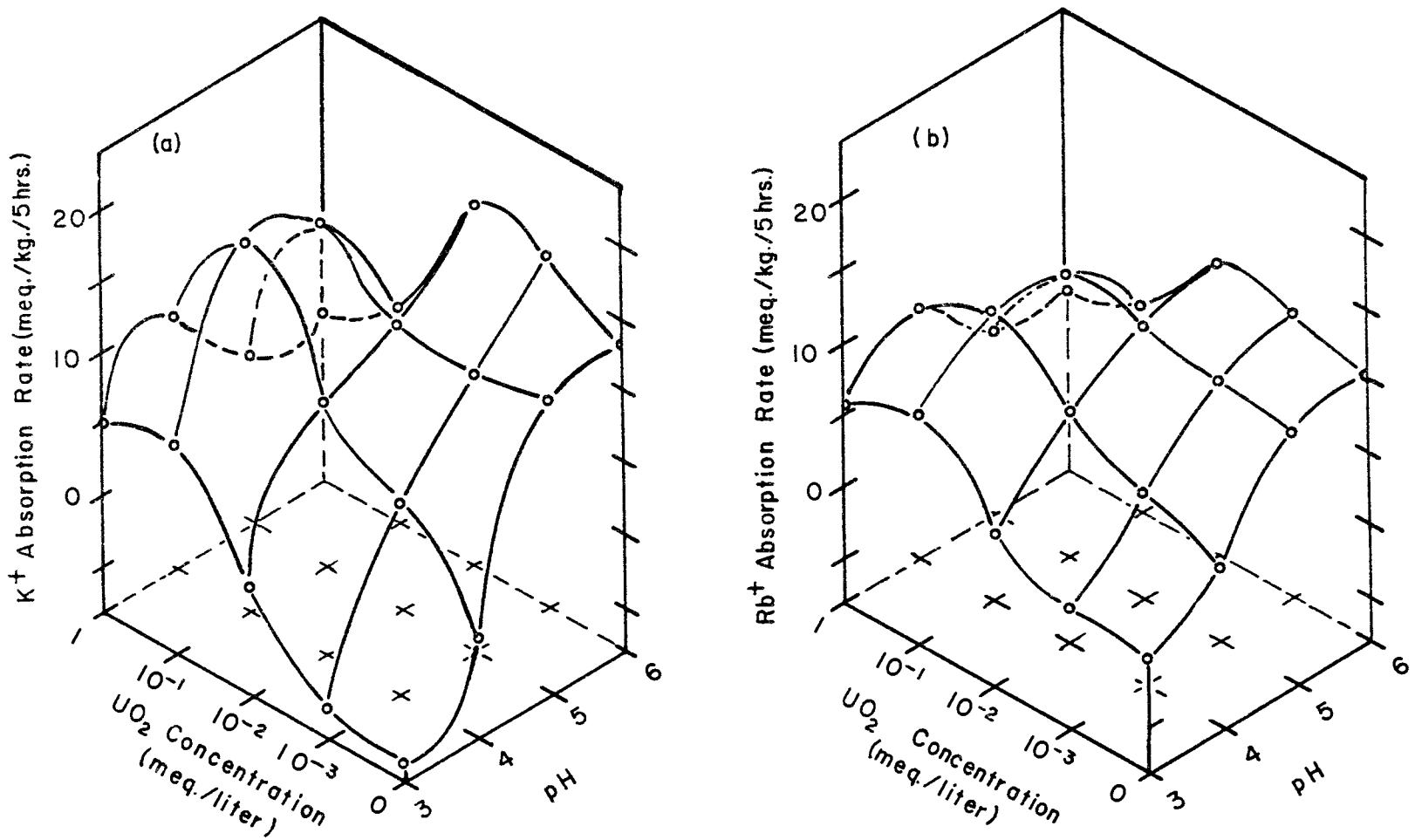

Figure 23. The effects of UO_2^{++} and pH upon the absorption of (a) K and (b) Rb from a solution containing 5 meq each of Rb and K per liter. (Appendix 32).

GENERAL DISCUSSION

In the presentation of the results of the various experiments conducted during this study a number of different methods have been used to evaluate the apparent selectivity of uranyl (UO_2^{++}) for inhibiting the absorption of certain of the alkali cations. The initial studies have shown that Na and K are affected differently by UO_2^{++}. In the presence of 1 milliequivalent UO_2^{++} per liter and at pH 5.0, Na was not affected by UO_2^{++} and K was markedly inhibited (see Appendix 6). Further evaluation indicates that Rb reacts in a fashion similar to K; and Li in a fashion similar to Na. Epstein (21) has noted the similarity of the absorption patterns between Na and Li and between K and Rb.

Selective Nature of UO_2^{++} Inhibition

The fact that, under the conditions mentioned above, UO_2^{++} selectively inhibits K and Rb but has little or no effect upon Na and Li is somewhat unique in ion absorption studies. Such an apparent selectivity has only been shown with one other cation. Jacobson et al. (38), Epstein (21) and Moore et al. (57) have shown that Ca will discriminate against Li and Na absorption in favor of K and Rb absorption. These workers noted that Ca would eliminate Li absorption, partially inhibit Na absorption and

stimulate K and Rb absorption. Jacobson et al. (38) concluded that Ca created a barrier at the cell surface which was "effective in blocking Li and H absorption". They concluded that the stimulating effect of Ca was the result of this ion blocking the absorption of the interfering ions. The effects of UO_2^{++}, in contrast to those of Ca, inhibited K and Rb absorption without having any effect upon Li absorption.

Jacobson et al. (38) and Rains et al. (66) concluded that the benefit of Ca was to ameliorate the deleterious effects of hydrogen and thus protect the cell membrane. They noted that at pH 4.0 Ca provided this protection to Na, K, and Rb but not to Li. Figures 10, 11 and 21 show that at low UO_2^{++} concentrations (10^{-3} and 10^{-2} milliequivalents per liter) and at low pH's (pH 3 and 4) the uranyl ion acted as many of the other polyvalent cations in that it too protected the cell membrane from hydrogen. This protection resulted in increased absorption of Na, K, and Rb. Above 1×10^{-2} milliequivalents UO_2^{++} per liter and above pH 4.0 the effects of UO_2^{++} are markedly different from the effects presented above. Under the conditions of higher pH and higher UO_2^{++} concentration K and Rb are markedly inhibited by uranyl. Li was unaffected and Na was either unaffected or slightly stimulated by the uranyl.

Rush et al. (75) have shown that there are a number of uranium cations which result from hydrolysis of uranyl. Work presented in

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Rush et al. (75) have shown that there are a number of uranium cations which result from hydrolysis of uranyl. Work presented in

this thesis suggests that the forms most likely to cause the effects seen in this study are UO_2^{++} (at the low concentrations and low pH ranges) and $(UO_2)^{++}_3(OH)^{++}_4$ (at the higher concentrations and higher pH's). Figure 10 shows that the impact of the polymers was sudden. This suggests that the transition from the beneficial forms of uranyl to the harmful polymers was a sharp transition.

Interpretation of the results suggests that the simple UO_2^{++} cation behaves in a manner similar to that shown by Viets (90) for Ca, Mg, Mn, Sr etc. This was verified by the experiment where Ca and UO_2^{++} were evaluated together. Looking at Figure 9 one notes that Ca eliminated the stimulation produced by the 10^{-2} and 10^{-3} levels of UO_2^{++}. Viets (90) has indicated that Ca was the most effective cation for stimulating K. Thus Ca, being the most effective divalent cation, would likely override the benefits of the UO_2^{++} cation. This would especially be true at the UO_2^{++}: Ca ratio of 1:1000 which is shown at the high Ca level in Figure 9. This observation implies that UO_2^{++} substituted for Ca and thus provided the protection for the membrane. As far as K, Rb and Na absorption was concerned this was true. However, in the case of Li there was no effect of UO_2^{++} upon absorption of this ion; but in contrast to UO_2^{++} Ca is known to eliminate Li absorption (38) at concentrations of Ca equal to the UO_2^{++} concentrations used in this study.

Thus at the lower pH's there are slight differences but strong

similarities between the effects of Ca and UO_2^{++} upon K, Rb and Na absorption.

When the pH was increased above about 4.5 and the uranyl concentration above 1×10^{-1} milliequivalents per liter the effects of the UO_2^{++} polymers became apparent. These effects upon K and Rb are directly opposite to the effects produced by Ca and the other di-valent ions studied by Viets (90) and by Jacobson et al. (38). Under these conditions UO_2^{++} inhibits K and Rb and has essentially no effect upon Li. In the case of Na there was a slight inhibition when Na was the only alkali cation in the test solution. When Na was in a mixed solution with Rb or K there was essentially no effect of UO_2^{++} upon Na absorption. This phenomenon was interpreted to indicate that the polymers identified by Rush et al. (75), are the ions which are affecting K and Rb absorption.

The above mentioned differences (Ca effect and the UO_2^{++} polymer effects) are not the only differences between UO_2^{++} and other polyvalent cations. Viets (90) showed that pre-treatments with Ca or any of several other ions would not produce a stimulation of K. On the other hand, pre-treatment with UO_2^{++} produced basically the same effect as did the presence of 1 milliequivalent of UO_2^{++} per liter in the solution. This is perhaps the most striking difference between UO_2^{++} and the other di-valent cations.

Epstein (20) has noted that there is a fraction of the ions taken

into root tissues which can exchange with other ions. These exchangeable ions, which are part of the free space uptake, are apparently loosely held in the tissue. By washing with distilled water after a pre-treatment with Ca the adsorbed ions were removed. Thus there were no di-valent cations available to form the "barrier" proposed by Jacobson et al. (38). In contrast to the "Ca-effect" the effect of UO_2^{++} was not reversed by distilled water rinses. In fact it was only after a relatively harsh treatment with EDTA that UO_2^{++} was removed from the tissues and its inhibiting effects reversed.

The above comparison between UO_2^{++} and the other divalent cations can be summarized by saying that: under conditions where the cation, UO_2^{++}, was the major form of uranyl this ion altered absorption in basically the same way as Ca, Sr, Mn, Mg, etc. However, under conditions which lead to the formation of uranyl polymers there was no similarity between the effects of UO_2^{++} and the effects of the other divalent cations.

UO_2^{++} and Possible Carrier Sites

The results of the UO_2^{++} pre-treatment experiments show that UO_2^{++} is unique among the polyvalent cations that have been studied in that the effect of UO_2^{++} could be carried over from the pre-treatment. Apparently UO_2^{++} was bound to some site in the cell in such

a way that it was removed only after treatment with EDTA. Rothstein et al. (71) made comparisons between the complexing constant for the yeast cell-UO_2^{++} complex and the constant for certain enzyme-UO_2^{++} complexes. He reasoned that the complexing constants of UO_2^{++} and organic compounds should be in the same order of magnitude as that found for UO_2^{++} and the yeast cells. Out of a large number of compounds studied there were two groups which formed strong complexes with UO_2^{++}. The first was the carboxyl group considered to be related to the proteins and the second was the phosphate groups in the polyphosphates such as ATP and ADP. Rothstein (73) found that UO_2^{++} bound to ATP was held 500 times more strongly than the UO_2^{++} which was bound to the proteins.

Hurwitz (36), working with the same system as Rothstein, concluded that the most likely explanation that could account for the UO_2^{++} inhibition of hexokinase in yeast cells was that a UO_2^{++}-ATP-enzyme complex was formed. This could occur by a linkage between the ATP and the enzyme thus altering the ability of this enzyme to function.

Hurwitz (36) also concluded that the UO_2^{++} cation was acting at or very close to the surface of the cell. This observation is supported by work presented by Rothstein (69-74) and Barron (9). The work presented in this thesis also suggests that UO_2^{++} was complexed to some site close to the cell surface. It has been shown

that there is an ATPase present in the so called membrane fraction of frog muscle (25) and human erythrocytes (1). Hokin and Hokin (33, 34) and Rothstein (73) have shown the presence of phosphatases in the membrane fraction of the cells. Benson (10) states that the effect of Ca upon the membrane selectivity (21) suggests a role for phospholipids in ion transport. Skou (79), Bonting et al. (11) and Whittam (93) have shown the presence of the Na-K, oubain sensitive ATPase in the "membrane" fraction of tissues. From these observations one would assume that UO_2^{++} was most likely binding with either ATPase itself or some polyphosphate that serves as a site for phosphate transfer from or to the adenosine phosphates. This site, most likely in the membrane, may be located on the actual carrier molecule or it may be closely interconnected with the carrier.

Work presented by Bowen and Kerwin (12) evaluated the effects of UO_2^{++} upon the myosin ATPase in the presence of different K concentrations. This data revealed that low levels of K gave a marked stimulation to the ATPase activity (measured by the amount of ATP split by the enzyme). At higher K concentrations the reaction returned to a level near that found at zero K. The portion of the activity which was most sensitive to the low K concentrations was also the portion of the ATPase activity which UO_2^{++} inhibited at the lowest UO_2^{++} concentrations used. This same portion of the

curve was also the area which was almost completely eliminated at the higher concentrations of UO_2^{++}. This observation combined with the two zones of sensitivity described in the discussion of Figure 15 and 16 suggests that the two "peaks" seen in these figures may be the results of UO_2^{++} acting on the ATPase in the cell. The current work in the animal fields which suggests a direct role of ATPase in Na and K transport also increases the importance of the possibility that UO_2^{++} was reacting with an ATPase.

The selective inhibition produced by UO_2^{++} could result from a number of processes which utilize the ATPase suggested above. This would account for the possible inhibition of UO_2^{++} uptake produced by DNP (Figure 8). By inhibiting oxidative phosphorylation DNP could reduce the phosphorylated compounds that UO_2^{++} was most likely binding to on the cell surface. One could speculate that these same sites were also related to a K stimulated ATPase system similar to that seen in myosin (12).

If UO_2^{++} was binding with a phosphorylated compound used for ion transfer then why didn't it affect both Na and K alike? There are a number of possibilities for this distinction. One is that the site for active Na absorption may be seated deeper into the cell than the site for K absorption. This has been suggested by Spanswick and Williams (80) in Nitella cells. In these large single cells K and Cl appear to be actively accumulated across the

plasmalema and Na actively accumulated across the tonoplast. Na is also actively extruded across the plasmalema in Nitella.

If such a system was working in barley root cells and K was actively accumulating at the plasmalema and Na at the tonoplast the fact that UO_2^{++} does not appear to penetrate very deeply into the cell suggests that one reason that Na was not inhibited may have been due to the distance of the Na transport mechanism from the site of action of UO_2^{++}.

Disagreement with this idea results primarily from the competition which exists between Na and K. Two sites as far apart (relative to cellular dimensions) as the tonoplast and the plasmalema would not appear to be in active competition with each other. Also, data in Figures 15 and 16 indicate that this is not the best hypothesis. In order to produce the stimulation of Na and the suppression of K in these figures, the sites of UO_2^{++} action must be intimately related with each other. Thus this idea of distance separation of the Na site and the K site does not seem to be the most likely alternative to explain the effects of UO_2^{++} upon Li, Na, K and Rb absorption.

UO_2^{++} and Proposed Carrier Models

During the last part of the discussion of the effects of UO_2^{++} upon Na and K the terms "Na-site" and "K-site" were used. This

was used at that time for convenience only. The observations that were made during this study could be the result of absorption by two carrier sites or it could be the result of configurational changes in a single carrier compound. This later refers to the changes in the shape of a molecule as the ionic environment changes. In the presence of one ion the carrier molecule would have one shape and accept one cation in preference to another. When another cation was present in the system then the carrier molecule would take on another shape that showed a "preference" for some other cation. Thus specificity would be the result of the configuration of a single type of compound rather than the result of different carriers for each ion.

Melchoir (54) has shown that Na and K induce changes in the shape of the ATP molecule. The Na ion caused the ATP molecule to coil around the cation to a much greater extent than K. The K ion was shown to be located at the bottom of a shallow saucer-like depression. This difference in shape was due to the size[5] and attractive energy of the two cations. Melchoir suggested that monovalent cations smaller than K were located inside the complex structure and those larger than K in a more exposed location.

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[5]Melchoir does not say if this was crystallographic size or hydrated size. Her data suggests that it is the former.

Askari and Franklin (5) have presented evidence of an AMP-deaminase reaction which exhibited similar changes in the properties of the enzyme. Here an organic compound was shown to change the shape of the enzyme. Their work showed that K stimulated the AMP-deaminase reaction whereas Na did not; but when ATP was added to the system both K and Na stimulated the reaction. These workers conclude that ATP produced changes in the alkali binding properties of the proteins prior to the dephosphorylation of the ATP molecule. This suggests that ATP and the monovalent cations can work together to alter protein structures.

If similar configurational changes occur in the ATP or the ATPase of the cell membrane then UO_2^{++} could conceivably force the more exposed K ion off of the ATP and leave the more protected Na complex in a relatively unaltered form. This type of effect would prevent binding of K and thus its transport.

The point to be made here is not so much what UO_2^{++} was altering as it is to show that the UO_2^{++} inhibition of K could well have been caused by changing the conformation of the molecule that was actually transporting ions in such a way that Na was "preferred" over K. Many of the observations which show that UO_2^{++} was selective in inhibiting K and Rb absorption could certainly be interpreted in light of a configurational change in a single carrier molecule. The divalent ion UO_2^{++}, which is prevalent at the low pH's

and low uranyl concentrations, could be acting in such a way that a "K preferred" configuration would be maintained in the carrier molecule. A similar configuration would be induced by Ca or some of the other polyvalent cations. The higher pH's and higher uranyl concentrations would contain a greater percentage of the complexes produced by hydrolysis of the UO_2^{++} cation. These complex polymers, due to their larger size, would produce a "Na-preferred" configuration and thus exclude K.

If such configurational changes did occur one would expect uranyl to completely eliminate the absorption of K because the carrier molecules would be in a Na-preferred configuration. The fact that, in many cases where Na and K were both in the same solution, uranyl completely eliminated K absorption would suggest that such a configurational change may well have taken place.

Figure 15 (b) suggests, however, that K may have been able to overcome the hypothesized configurational change. By increasing the K concentration to a point considerably greater than the Na concentration the effects of UO_2^{++} were reduced. This could result from the higher K concentration in the solution acting to maintain a configuration favorable to K transport.

Another explanation for Figure 15 (b) is that there were two carriers operating in this system. One carrier showed a preference for K and the other a preference for Na. Figure 13 (a) shows that

increasing K, in the absence of UO_2^{++}, reduced Na absorption rapidly up to a point where Na and K were of equal concentration. Above this point of equal concentration K still competed with Na but to a reduced degree. When UO_2^{++} was present at 1 milliequivalent per liter the portion of the Na transport that was most sensitive to K concentration was the portion eliminated by UO_2^{++}. This is in agreement with the observation made about Figure 2 which noted that K and UO_2^{++} both inhibited Na absorption by the same amount. If configurational change was the factor which provided selectivity then the normal discrimination of the transport system for K against Na would suggest that the carrier had a configuration which would accept K in preference to Na. The portion of the control curve in Figure 13 (a) between zero and 5 milliequivalents K per liter can be interpreted to support this idea. But if this was the case, why doesn't K eliminate Na transport completely at 5 milliequivalents K per liter? One might argue that this was the result of an "all or none" type of effect where a small portion of the cells or the transport sites are carrying Na and a portion K. As more and more K was added the effect became smaller because there was a smaller percentage of the cells (or sites) still transporting the single ion. This does not seem likely if our current interpretations of the uptake pattern-cell structure relationships are correct. The "non-metabolic" uptake, seen during the initial

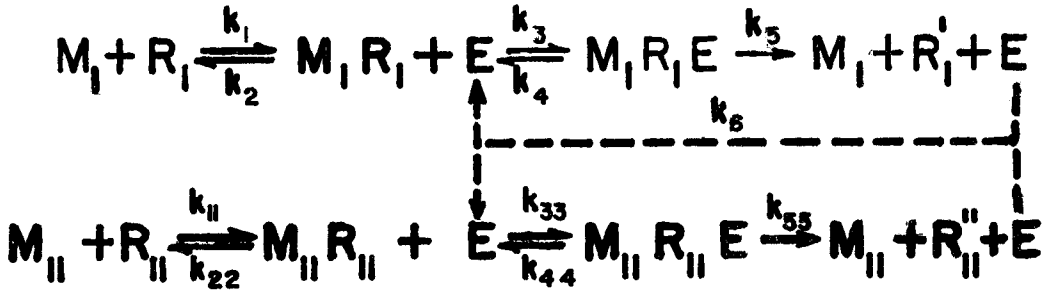
phases of uptake, is interpreted to indicate a rapid diffusion into the free space of the cells--the intercellular spaces, the cell walls, etc. This would lead to the majority of the transport sites being in contact with solutions of these ions in ratios of K^+: Na of as high as 5 : 1. It seems unlikely that such a system would operate under such a disproportionate relationship between the "preferred" ion and its "less-preferred antagonist".

A more logical, and certainly the easier to explain, hypothesis is that there are multiple carriers functioning in transport of ions. This idea of two carriers is supported in the literature with work from Ariz (4), Bange (6, 7), Bange and Overstreet (7), Epstein (20, 21), Epstein and Hagen (22) and Fried and Noggle (23). These workers have shown by kinetic analysis of experimental data that there is evidence to suggest that there was more than one site acting in the transport of the alkali cations. Epstein and Hagen (22) noted that there appeared to be a carrier with a "preference" for K, one with a "preference" for Na and a third carrier which would transport both ions. The competition between Na and K was interpreted to occur over the non-specific carrier. Epstein and Hagen (22) used curves similar to the control curve in Figure 13 (a) to develop their conclusions. The discrimination against Na that is normal in most plants was considered to be the result of Ca blocking the Na transport system (21).

If the multiple carrier concept is accepted, the hypothesis to explain Figures 13, 14, 15, and 16 would be similar to that of Epstein and Hagen (21). It is hypothesized that there are two carriers operating in the transport of Na and K. One shows a "preference" for K and one a "preference" for Na. When Na is the only one of these ions present uranyl will greatly reduce Na transport via the K carrier. At equal concentrations each ion will be essentially moving via its own carrier. In solutions where the K concentration is greater than the Na concentration there will be some competition of K for the Na carrier. When Ca or low concentrations of UO_2^{++} are present the Na carrier is inhibited and the energy that normally goes to this carrier will revert to the K carrier. When UO_2^{++} is present at a concentration or pH that produces the uranyl polymers the K carrier is inhibited and the energy for this carrier is reverted to the Na carrier and the Na absorption rate is thus increased.

Although in no way conclusive, the preponderence of the information presented in this study seems to support the multiple carrier hypothesis better than the conformational hypothesis. Actually, these ideas may not be as far apart as it first seems. Bange (7) in a recent paper entitled "The Carrier Theory of Ion Transport: A Reconsideration" suggests that the competition between ions is not occurring at the binding site but at a site further

into the transport sequence. He proposes the model indicated below then goes on to show its similarity to that proposed by Hokin and Hokin (33) in 1960. Bange concluded that specificity in this system is due to a relatively loose binding of the ion to proteins on the various molecules in this model.



Bange's model of ion transport
(M = ion; R = carrier; E = enzyme; k = constants)

In 1964, Hokin and Hokin (34) modified their scheme to take into account observations made by themselves and several other workers on the Na-K, oubain sensitive ATPase. In this modification they suggest that specificity depends upon the proteins which were attached to the various phospholipid which occurred in their system.

Are there such proteins attached to the phospholipids? MacFarlane (51) shows definitely that there are phospholipids which contain amino acids. She was able to isolate two fractions from bacterial membrane lipids which were ninhydrin sensitive. In one fraction alanine was the most prevalent amino acid present (although

there were traces of others). The second fraction contained alanine and lysine along with amino acid precurors glutamic acid and aspartic acid. MacFarlane points out that this finding may suggest part of the reason that ion transport and protein synthesis have been shown to be related.

Combining these observations one could conclude that there is one route for the transport of the alkali cations but that quite similar amino acid containing phospholipids act as the actual transport molecule. By altering the particular amino acid on the molecule the "configuration" of the molecule would be changed but also there would in reality be more than one carrier. The fact that one amino acid, alanine, was shown to be more prevalent than the others (51) would suggest that here is an indication for the reason that one ion is transported at a higher rate than others without excluding the presence of a specific carrier for each ion. Such a system would be extremely versatile, adapting to new environments as the need arose. The system would also be linked to the genetic processes via amino acid synthesis.

How would the UO_2^{++} data fit this? Perhaps Bange's model would suffice to explain how this could occur in such a system. By blocking the binding of K to an amino acid in the carrier (say R_1 in Bange's model equations) or by preventing the complexing between the enzyme and the M_1R_1 complex the UO_2^{++} polymers could inhibit

K absorption. Na absorption would be stimulated because there would be more enzyme present. Since Li, Na, K and Rb are similar ions they would be able to react with the same carriers although one carrier would be relatively more specific for a given ion.

Such a scheme would also account for the effects of Ca (and other polyvalent cations) upon the transport process. Assuming that Ca would react with the Na carrier, this ion would inhibit the Na transport and stimulate K transport. Under conditions where the simple UO_2^{++} cation was the only form of uranyl present the same effect would be seen because in this case uranyl would be acting as a divalent cation and thus inhibit Na.

It was suggested earlier that the configuration of amino acids can change depending upon the combination of ions present in the environment of the amino acid. Assuming that Bange's carrier system is located in the cell membrane, any change in the test solution would change the ionic environment around the cell surface and thus around the carrier. These changes in composition would cause the carrier molecule to assume different shapes depending upon the ions present in the test solutions. These changes would likely result in the inhibition of the transport of some ions while having no effect upon others.

Bange's scheme is just a model but the fact that it fits Hokin and Hokin's (34) scheme lends some validity to the ideas expressed

by this model. Judah and Ahmed (42) and Post et al. (64) have agreed with Hokin and Hokin's ideas as expressed in their more recent paper (34). It is not known if such a system is present in barley roots. The fact that UO_2^{++} has been shown to inhibit an ATPase and the fact that it reacts with the phosphates (which have been proposed as part of the carrier) suggests that a similar system may have been operating in the barley root system used in this study.

CONCLUSION

The only definite conclusion that can be reached as the result of this dissertation is that uranyl, at the higher concentrations used in this study, selectively inhibits K and Rb absorption via the "K-site" and has essentially no effect upon Na and Li absorption via the "Na-site". The variations in this pattern that were seen are the result of the interactions between the simple UO_2^{++} cation (occurring at low pH's and low uranyl concentrations) and the more complex uranyl polymers (occurring at higher pH's and higher uranyl concentrations). At the low pH's UO_2^{++} acts in a manner similar to many of the other divalent cations in that it protects the cell from the hydrogen ion. Also, under these conditions UO_2^{++} appears to inhibit Na absorption to some extent and stimulate K absorption when these two ions are both in the test solution. This UO_2^{++} effect is similar to the effect of Ca upon the transport of Na and K. It was also this form of uranyl that caused the response of Na to low concentration uranyl treatments. Under conditions where H was interfering with Na absorption, UO_2^{++} could compete with H and provide a stimulation to the portion of Na transport which moved over the K carrier. When K was high enough to prevent Na from moving via the K carrier there was essentially no effect of UO_2^{++} upon Na. The fact that the portion of the Na absorption that was the most

sensitive to UO_2^{++} was the portion that showed the greatest competition from K also supports the idea that the carrier which "preferred" Na was not inhibited by UO_2^{++}.

The nature of the carrier system was discussed in light of the effects of UO_2^{++} upon Na and K transport. No definite conclusion can be reached as to the presence of more than one carrier, however, the preponderance of the data presented in this dissertation fits into a multiple carrier pattern with fewer assumptions than does the idea of a single carrier. These carriers may be distinctly different organic compounds or in reality they may be quite similar compounds with different configurations. The data presented in this thesis could be used to support either of these latter hypotheses.

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APPENDICES

Appendix 1. Statistics for check sample analysis of 15 experiments.

	Na Content meq/kg		K Content meq/kg	
	R_1	R_2	R_1	R_2
	2.1	2.1	15.7	15.7
	1.1	1.1	13.6	13.6
	2.1	2.1	13.1	13.1
	1.4	1.4	15.7	15.7
	1.7	1.7	16.4	15.7
	0.7	0.7	13.6	14.3
	1.0	1.0	16.1	16.1
	0.4	0.4	15.4	15.4
	1.0	1.0	16.1	16.1
	1.0	1.0	18.0	18.0
	0.7	0.7	15.6	15.4
	0.9	0.9	16.4	16.9
	0.8	0.8	19.2	19.2
	1.0	1.0	16.0	16.0
	1.0	0.8	18.0	17.8
Mean	1.1		15.9	

Analysis of Variance for Na

Source of Variation	Sum of Squares	Degree of Freedom	M. S.	f
Experiment	6.928	14	0.495	353.71**
Duplicate	0.001	1	0.001	0
Error	0.019	13	0.0015	
Total		28*		

Analysis of Variance for K

Source of Variation	Sum of Squares	Degree of Freedom	M. S.	f
Experiment	74.20	14	5.300	56.38**
Duplicate	0.000	1	0.000	---
Error	1.22	13	0.094	
Total		28*		

* Lose 1 Degree of Freedom due to lack of between experiment duplication

**Significant at 1% level

Appendix 2. Conditions, treatments and results of Experiment U-1B. The pH was 5.0 ± 0.5; the temperature was 25.0° ± 0.5°C. Initial K^+, Li^+, Ca^{++} and UO_2^{++} content of the root material was 18.5, 0, 2.6, and 0 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. Composition				Uptake		
		Li^+	K^+	Ca^{++}	UO_2^{++}	K^+	Li^+	Ca^{++}
	hrs	meq/liter				meq/kg		
1	6	-0-	5.0	-0-	-0-	27.2		
2	3	-0-	5.0	-0-	-0-	18.0		
3	1	-0-	5.0	-0-	-0-	6.2		
4	1/2	-0-	5.0	-0-	-0-	0.7		
13	6	5.0	5.0	-0-	-0-	20.8	6.2	
14	3	5.0	5.0	-0-	-0-	9.8	3.1	
15	1	5.0	5.0	-0-	-0-	6.2	1.5	
16	1/2	5.0	5.0	-0-	-0-	2.5	1.0	
17	6	5.0	5.0	5.0	-0-	50.0	0.5	2.5
18	3	5.0	5.0	5.0	-0-	23.5	0.5	2.5
19	1	5.0	5.0	5.0	-0-	1.6	0.5	2.5
20	1/2	5.0	5.0	5.0	-0-	2.5	0.5	2.5
21	6	5.0	5.0	-0-	5.0	-0.2	7.2	
22	3	5.0	5.0	-0-	5.0	-0.2	3.1	
23	1	5.0	5.0	-0-	5.0	-0.2	1.5	
24	1/2	5.0	5.0	-0-	5.0	-1.1	1.0	

Appendix 3. Conditions, treatments and results of Experiment U-32. The pH was 5.0 ± 0.3; the temperature was 24.5°C. Pretreatment was for 30 minutes in 1 meq UO_2^{++}/liter for 30 minutes. The initial K^+ and Li^+ content of the root tissue was 10.7 and 0.0 respectively.

Trmt. No.	Trmt. Time	Soln. Composition				Tissue Content		Absorption Rate	
		K^+	Li^+	UO_2^{++}	DNP	K^+	Li^+	K^+	Li^+
	hrs	meq/liter			Moles/liter	meq/kg		meq/kg/5hr	
1	1	5.0	5.0	-0-	-0-	17.5	5.2	8.4	8.0
2	6	5.0	5.0	-0-	-0-	25.9	13.2		
3	1	5.0	5.0	Pret.	-0-	13.9	4.4	6.5	7.9
4	6	5.0	5.0	Pret.	-0-	20.4	12.3		
5	1	5.0	5.0	Pret.	$5x10^{-5}$	8.6	2.2	-3.2	1.7
6	6	5.0	5.0	Pret.	$5x10^{-5}$	5.4	3.9		
7	1	-0-	5.0	-0-	-0-		6.3		11.1
8	6	-0-	5.0	-0-	-0-		17.4		
9	1	-0-	5.0	Pret.	-0-		6.2		13.6
10	6	-0-	5.0	Pret.	-0-		19.8		
11	1	-0-	5.0	Pret.	$5x10^{-5}$		4.1		2.0
12	6	-0-	5.0	Pret.	$5x10^{-5}$		6.1		
13	1	-0-	5.0	1.0	-0-		4.7		8.2
14	6	-0-	5.0	1.0	-0-		12.9		
15	1	-0-	5.0	-0-	$5x10^{-5}$		2.2		0.3
16	6	-0-	5.0	-0-	$5x10^{-5}$		2.5		
17	1	5.0	-0-	-0-	-0-	17.5		29.0	
18	6	5.0	-0-	-0-	-0-	46.5			
19	1	5.0	-0-	Pret.	-0-	15.7		12.8	
20	6	5.0	-0-	Pret.	-0-	28.5			

Appendix 4. Conditions, treatments and results of Experiment U-5B. The pH was 5.0 ± 0.6; the temperature was 24.0° ± 1.0°C. Initial Na^+, and K^+ content of the root material was 1.2 and 16.2 meq/kg respectively. UO_2^{++} pretreatment was for 30 minutes in 1.0 meq/liter UO_2^{++}.

Trmt. No.	Trmt. Time	Soln. Composition			Uptake	
		Na^+	K^+	UO_2^{++}	Na^+	K^+
	hrs	meq/liter			meq/kg	
1	1	5.0	-0-	-0-	5.5	-1.9
2	3	5.0	-0-	-0-	13.0	-3.2
3	6	5.0	-0-	-0-	23.0	-4.3
4	1	5.0	-0-	1.0	4.0	-1.3
5	3	5.0	-0-	1.0	7.4	-4.3
6	6	5.0	-0-	1.0	12.5	-9.2
7	1	5.0	5.0	-0-	3.8	2.7
8	3	5.0	5.0	-0-	6.7	8.3
9	6	5.0	5.0	-0-	14.8	17.9
10	1	5.0	5.0	1.0	3.0	-0.2
11	3	5.0	5.0	1.0	6.7	-0.9
12	6	5.0	5.0	1.0	11.6	-3.2
13	1	-0-	5.0	-0-		7.2
14	3	-0-	5.0	-0-		13.8
15	6	-0-	5.0	-0-		24.3
16	1	-0-	5.0	1.0		-0.4
17	3	-0-	5.0	1.0		2.3
18	6	-0-	5.0	1.0		3.4
19	1	5.0	5.0	Pret.	4.8	0.6
20	3	5.0	5.0	Pret.	11.6	2.3
21	6	5.0	5.0	Pret.	18.6	4.5
22	1	5.0	-0-	Pret.	2.0	-14.3
23	3	5.0	-0-	Pret.	18.0	-7.9
24	6	5.0	-0-	Pret.	30.0	-10.9
25	1	-0-	5.0	Pret.		1.1
26	3	-0-	5.0	Pret.		5.1
27	6	-0-	5.0	Pret.		9.4

Appendix 5. Summary of experiments containing Na^+ and K^+ in the presence and absence of UO_2^{++}.

Exp. No.	Date	Na^+ Absorption Rate		K^+ Absorption Rate	
		Control	w/UO_2^{++}	Control	w/UO_2^{++}
		meq/kg/5hr		meq/kg/5hr	
U-22	5-28-64	7.5	14.2	15.0	-5.8
U-29	9-24-64	19.9	26.4	15.7	6.2
U-30	10-1-64	30.3	19.8	6.6	-2.8
U-34	11-5-64	13.6	20.6	18.0	2.3
U-37	11-19-64	19.0	12.4	17.7	3.1
U-38	11-25-64	8.7	10.3	28.1	-0.4
U-41	12-24-64	12.3	13.4	20.7	0.0
U-45	3-26-65	15.3	18.2	15.4	-1.1
U-46	4-8-65	13.5	10.6	19.3	1.9
U-47	4-15-65	16.4	12.7	13.9	0.0
U-48	4-22-65	12.6	10.7	20.1	2.0
U-52	6-4-65	16.3	14.0	13.1	-0.7
U-53	7-28-65	12.8	10.6	17.3	-0.4
U-54	8-5-65	21.0	13.4	14.2	0.0
U-61	1-9-66	16.0	15.0	18.0	1.8
U-63	1-13-66	16.0	13.6	10.9	-0.8
Average		15.7	14.7	16.5	0.3

Appendix 6. Statistical analysis of experimental data for experiments containing Na^+ and K^+ in the presence and absence of UO_2^{++}.

(a) Analysis of Na^+ data

Type of Total	Total	No. of Items	Observ. per Item	Total per Item
Grand	237,266.41	1	32	7,414.57
Experiment	15,299.80	16	2	7,649.90
Treatment	118,749.51	2	16	7,419.15
Observation	8,141.55	32	1	8,141.55
Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F Value**
Experiment	235.33	15	15.69	0.451
Treatment	4.58	1	4.58	0.132
Error	487.07	14[1/]	34.79	
Total	726.98	30[1/]	24.23	

(b) Analysis of K^+ data

Type of Total	Total	No. of Items	Observ. per Item	Total per Item
Grand	72,521.20	1	32	2,266.40
Experiment	5,098.81	16	2	2,549.40
Treatment	69,719.89	2	16	4,357.50
Observation	4,800.99	32	1	4,800.99
Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F Value**
Experiment	283.00	15	18.87	1.655
Treatment	2,091.10	1	2,091.10	183.269[2/]
Error	160.49	14[1/]	11.41	
Total	2,534.59	30[1/]	84.49	

1/ Lost one degree of freedom due to lack of experiment to experiment replication.

2/ Significant at 1/2 % significance level.

Appendix 7. Conditions, treatments and results of Experiment U-77. The pH was 5.0 ± 0.5; the temperature was 25.0°C. Initial Na^+ and K^+ content of the root material was 1.0 and 15.6 meq/kg respectively. Pretreatment was in 1 meq UO_2^{++}/liter.

Trmt. No.	Trmt. Time	Pretmt. Time	Soln. Composition			Tissue Content			Absorption Rate		
			Na^+	K^+	UO_2^{++}	Na^+	K^+	UO_2^{++}	Na^+	K^+	UO_2^{++}
	hrs	min	meq/liter			meq/kg			meq/kg/5hr		
1	1	-0-	5.0	5.0	-0-	4.3	19.0		14.7	17.0	
2	6	-0-	5.0	5.0	-0-	19.0	36.0				
3	1	-0-	5.0	5.0	1.0	4.0	18.0	13.7	13.8	0.0	34.7
4	6	-0-	5.0	5.0	1.0	17.8	18.0	48.4			
5	1	4	5.0	5.0	Pret.	5.8	21.0	1.52	17.8	14.0	-0.4
6	6	4	5.0	5.0	Pret.	23.8	35.0	1.13			
7	1	8	5.0	5.0	Pret.	5.8	20.8	1.74	17.8	13.2	-0.7
8	6	8	5.0	5.0	Pret.	23.6	34.0	1.02			
9	1	15	5.0	5.0	Pret.	6.0	21.0	2.28	18.0	10.0	-0.8
10	6	15	5.0	5.0	Pret.	24.0	31.0	1.50			
11	1	30	5.0	5.0	Pret.	6.4	19.5	3.21	19.6	9.0	-0.9
12	6	30	5.0	5.0	Pret.	26.0	28.5	2.31			
01	-0-	30	-0-	-0-	Pret.			7.3			
05	-0-	15	-0-	-0-	Pret.			6.3			
06	-0-	8	-0-	-0-	Pret.			5.9			
07	-0-	4	-0-	-0-	Pret.			5.6			

Appendix 8. Conditions, treatments and results of Experiment U-72. The pH was 5.0 ± 0.5; the temperature was 24.5° ± 0.5°C. Initial K^+ and Na^+ content of the root material was 15.2 and 1.2 meq/kg respectively. UO_2^{++} pretreatment was for 30 minutes in 1 meq UO_2^{++} per liter.

Trmt. No.	Trmt. Time	Complex Time	Complex Agent	Soln. Composition				Tissue Content			Absorption Rate	
				Na^+	K^+	Ca^{++}	UO_2^{++}	Na^+	K^+	UO_2^{++}	Na^+	K^+
	hrs			meq/liter				meq/kg			meq/kg/5hr	
1	1	-0-		5.0	5.0	0.1	-0-	2.7	22.0		2.1	30.0
2	6	-0-		5.0	5.0	0.1	-0-	4.8	52.0			
3	1	-0-		5.0	5.0	0.1	1.0	2.7	16.8	14.3	8.9	-1.3
4	6	-0-		5.0	5.0	0.1	1.0	11.6	15.5	20.2		
5	1	-0-		5.0	5.0	0.1	Pret.	4.0	16.8		10.4	9.4
6	6	-0-		5.0	5.0	0.1	Pret.	14.4	26.2			
7	1	60	Carb.[1]	5.0	5.0	0.1	-0-	7.5	15.2		1.8	25.8
8	6	60	Carb.	5.0	5.0	0.1	-0-	9.3	41.0			
9	1	60	Phos.[2]	5.0	5.0	0.1	-0-	4.2	21.0		0.6	28.0
10	6	60	Phos.	5.0	5.0	0.1	-0-	5.8	49.0			
11	1	60	CyDTA[3]	5.0	5.0	0.1	-0-	6.7	16.8		1.8	24.7
12	6	60	CyDTA	5.0	5.0	0.1	-0-	8.5	41.5			
13	1	60	EDTA[4]	5.0	5.0	0.1	-0-	6.4	18.5		2.1	22.0
14	6	60	EDTA	5.0	5.0	0.1	-0-	8.5	40.5			
15	1	30	Carb.	5.0	5.0	0.1	Pret.	9.0	8.5		17.5	13.5
16	6	30	Carb.	5.0	5.0	0.1	Pret.	26.5	22.0			
17	1	60	Carb.	5.0	5.0	0.1	Pret.	10.4	7.2		1.1	6.8
18	6	60	Carb.	5.0	5.0	0.1	Pret.	11.5	14.0			
19	1	30	Phos.	5.0	5.0	0.1	Pret.	7.2	21.0		4.4	22.0
20	6	30	Phos.	5.0	5.0	0.1	Pret.	11.6	43.0			
21	1	60	Phos.	5.0	5.0	0.1	Pret.	8.7	19.5		4.3	18.9
22	6	60	Phos.	5.0	5.0	0.1	Pret.	13.0	38.4			
23	1	30	CyDTA	5.0	5.0	0.1	Pret.	8.8	14.2		6.2	17.6
24	6	30	CyDTA	5.0	5.0	0.1	Pret.	15.0	31.8			
25	1	60	CyDTA	5.0	5.0	0.1	Pret.	11.3	15.3		1.7	1.2
26	6	60	CyDTA	5.0	5.0	0.1	Pret.	13.0	16.5			
27	1	30	EDTA	5.0	5.0	0.1	Pret.	9.5	15.7	0.8	2.8	27.8
28	6	30	EDTA	5.0	5.0	0.1	Pret	13.3	43.5	0.4		
29	1	60	EDTA	5.0	5.0	0.1	Pret.	12.0	13.0	0.4	2.7	30.0
30	6	60	EDTA	5.0	5.0	0.1	Pret.	14.7	43.0	0.4		

1/ 0.0148 M Na_2CO_3
2/ 0.0148 M NaH_2PO_4
3/ 0.0064 M NaCyDTA
4/ 0.0142 M NaEDTA

Appendix 9. Conditions, treatments and results of Experiment U-75. The pH was 5.0 ± 0.1; temperature was 24.5° ± 0.5°C. Initial Na^+ and K^+ content of the root material was 0.5 and 18.5 meq/kg respectively. Pretreatment was for 30 minutes in 1.0 meq UO_2^{++} per liter.

Trmt. No.	Trmt. Time	Time in EDTA	Soln. Composition					Tissue Content			Absorption Rate		
			Na^+	K^+	UO_2^{++}	Ca^{++}	EDTA	Na^+	K^+	UO_2^{++}	Na^+	K^+	
	hrs	min	meq/liter					meq/kg			meq/kg/5hr		
1	1	-0-	5.0	5.0	-0-	0.1	-0-	2.3	26.0		4.1	28.0	
2	6	-0-	5.0	5.0	-0-	0.1	-0-	6.4	54.0				
3	1	-0-	5.0	5.0	1.0	0.1	-0-	3.2	20.0	16.9	10.8	0.0	41.4
4	6	-0-	5.0	5.0	1.0	0.1	-0-	14.0	20.0	58.3			
5	1	-0-	5.0	5.0	Pret.	0.1	-0-	4.5	20.0	2.35	12.0	10.1	-0.4
6	6	-0-	5.0	5.0	Pret.	0.1	-0-	16.5	30.1	1.99			
19	1	4	5.0	5.0	Pret.	0.1	30.0	6.5	19.0		10.1	17.0	
20	6	4	5.0	5.0	Pret.	0.1	30.0	16.6	36.0				
21	1	8	5.0	5.0	Pret.	0.1	30.0	8.7	18.5		9.1	18.2	
22	6	8	5.0	5.0	Pret.	0.1	30.0	17.8	36.7				
23	1	15	5.0	5.0	Pret.	0.1	30.0	9.6	18.0		9.0	13.5	
24	6	15	5.0	5.0	Pret.	0.1	30.0	18.6	31.5				
25	1	30	5.0	5.0	Pret.	0.1	30.0	11.4	18.0		5.6	23.0	
26	6	30	5.0	5.0	Pret.	0.1	30.0	17.0	41.0				
27	1	60	5.0	5.0	Pret.	0.1	30.0	13.5	17.4	0.72	3.0	26.1	-0.4
28	6	60	5.0	5.0	Pret.	0.1	30.0	16.5	43.5	0.35			
29	1	4	5.0	5.0	Pret.	0.1	3.0	7.2	18.8		9.5	16.2	
30	6	4	5.0	5.0	Pret.	0.1	3.0	15.7	35.0				
31	1	8	5.0	5.0	Pret.	0.1	3.0	6.0	20.1		9.5	15.9	
32	6	8	5.0	5.0	Pret.	0.1	3.0	15.5	36.0				
33	1	15	5.0	5.0	Pret.	0.1	3.0	6.6	21.3		9.4	14.7	
34	6	15	5.0	5.0	Pret.	0.1	3.0	16.6	36.0				
35	1	30	5.0	5.0	Pret.	0.1	3.0	7.7	20.1		8.6	18.5	
36	6	30	5.0	5.0	Pret.	0.1	3.0	16.3	38.6				
37	1	60	5.0	5.0	Pret.	0.1	3.0	8.4	20.0		6.6	15.0	
38	6	60	5.0	5.0	Pret.	0.1	3.0	15.0	35.0				
03		-0-			Pret.		-0-	1.0	17.5	8.2			
04		4			Pret.		3.0	1.9	16.8	3.9			
05		8			Pret.		3.0	2.8	16.4	2.8			
06		15			Pret.		3.0	3.5	15.7	2.3			
07		30			Pret.		3.0	5.2	15.0	1.5			
08		60			Pret.		3.0	8.5	13.5	1.2			
09		4			Pret.		30.0	9.4	16.8	1.8			
010		8			Pret.		30.0	10.6	15.7	1.6			
011		15			Pret.		30.0	13.0	15.0	1.3			
012		30			Pret.		30.0	17.6	13.0	0.6			
013		60			Pret.		30.0	22.0	11.5	0.4			

Appendix 10. Conditions, treatments and results of Experiment U-41. The pH was 5.0 ± 0.2; the temperature was 25.0° ± 0.2°C. Initial Na^+ and K^+ content of the root material was 1.7 and 16.4 meq/kg respectively. Pretreatment was for 30 minutes in 1.0 meq of UO_2^{++} per liter.

Trmt. No.	Trmt. Time	Soln. Composition				Tissue Content		Absorption Rate	
		Na^+	K^+	UO_2^{++}	DNP	Na^+	K^+	Na^+	K^+
	hrs	meq/liter				meq/kg		meq/kg/5hr	
1	1	5.0	5.0	-0-	-0-	6.0	25.0	12.3	20.7
2	2	5.0	5.0	-0-	-0-	8.9	29.6		
3	4	5.0	5.0	-0-	-0-	14.3	36.4		
4	6	5.0	5.0	-0-	-0-	18.3	45.7		
5	1	5.0	5.0	-0-	$5x10^{-7}$	6.3	22.1	10.1	19.8
6	2	5.0	5.0	-0-	$5x10^{-7}$	8.9	28.6		
7	4	5.0	5.0	-0-	$5x10^{-7}$	13.4	35.0		
8	6	5.0	5.0	-0-	$5x10^{-7}$	16.4	42.9		
9	1	5.0	5.0	-0-	$5x10^{-6}$	5.7	18.6	6.4	20.9
10	2	5.0	5.0	-0-	$5x10^{-6}$	8.3	21.9		
11	4	5.0	5.0	-0-	$5x10^{-6}$	9.6	29.3		
12	6	5.0	5.0	-0-	$5x10^{-6}$	12.1	39.3		
13	1	5.0	5.0	-0-	$5x10^{-5}$	4.1	16.9	1.2	-8.6
14	2	5.0	5.0	-0-	$5x10^{-5}$	4.3	14.0		
15	4	5.0	5.0	-0-	$5x10^{-5}$	4.6	11.0		
16	6	5.0	5.0	-0-	$5x10^{-5}$	5.3	8.3		
17	1	5.0	5.0	1.0	-0-	5.7	18.9	13.4	0.0
18	2	5.0	5.0	1.0	-0-	8.3	18.9		
19	4	5.0	5.0	1.0	-0-	12.9	18.9		
20	6	5.0	5.0	1.0	-0-	19.1	18.9		
21	1	5.0	5.0	Pret.	-0-	8.3	17.6	21.0	6.0
22	2	5.0	5.0	Pret.	-0-	12.1	18.9		
23	4	5.0	5.0	Pret.	-0-	22.9	22.6		
24	6	5.0	5.0	Pret.	-0-	29.3	23.6		

Appendix 11. Conditions, treatments and results of Experiment U-40. The pH was 5.0 ± 0.1; temperature was variable. Initial Na^+ and K^+ content of the root tissue was 1.4 and 15.7 meq/kg respectively. Pretreatment was for 30 minutes in 1 meq UO_2^{++} per liter.

Trmt. No.	Trmt. Time	Temp. °C	Soln. Composition			Tissue Content		Absorption Rates	
			Na^+	K^+	UO_2^{++}	K^+	Na^+	K^+	Na^+
	hrs		meq/liter			meq/kg		meq/kg/5hr	
1	1	25.0	5.0	5.0	-0-	18.3	6.4	31.4	15.0
2	6	25.0	5.0	5.0	-0-	49.7	21.4		
3	1	25.0	5.0	5.0	Pret.	18.6	10.0	8.5	28.6
4	6	25.0	5.0	5.0	Pret.	27.1	38.6		
5	1	25.0	5.0	5.0	Pret.	18.6	10.0	8.5	28.6
6	6	25.0	5.0	5.0	Pret.	27.1	38.6		
7	1	0.5	5.0	5.0	Pret.	16.4	3.6	0.0	2.4
8	6	0.5	5.0	5.0	Pret.	16.4	6.0		
9	1	0.5	5.0	5.0	Pret.	16.4	3.6	0.0	2.4
10	6	0.5	5.0	5.0	Pret.	16.4	6.0		
11	1	0.5	5.0	5.0	-0-	16.4	3.6	2.2	1.8
12	6	0.5	5.0	5.0	-0-	18.6	5.4		

Appendix 12. Conditions, treatments and results of Experiment U-61. The initial pH was 5.0; temperature was 24°C.

Trmt. No.	Soln. Composition			O_2 Uptake	
	Na^+	K^+	UO_2^{++}	R_I	R_{II}
	meq/liter			ul/hr	
1	5.0	-0-	-0-	17.7	17.7
2	5.0	-0-	$1x10^{-3}$	13.3	14.6
3	5.0	-0-	$1x10^{-2}$	16.3	14.9
4	5.0	-0-	$1x10^{-1}$	15.7	14.4
5	-0-	5.0	-0-	13.3	13.1
6	-0-	5.0	$1x10^{-3}$	18.2	17.2
7	-0-	5.0	$1x10^{-2}$	18.1	17.0
8	-0-	5.0	$1x10^{-1}$	7.8	16.8
9	5.0	5.0	-0-	11.0	13.5
10	5.0	5.0	$1x10^{-3}$	14.5	17.1
11	5.0	5.0	$1x10^{-2}$	10.3	14.0
12	5.0	5.0	$1x10^{-1}$	10.8	13.2

Appendix 13. Conditions, treatments and results of Experiment U-70. The pH was 5.0 ± 0.1; temperature was 25° ± 0.5°C. The initial Na^+ and K^+ content of the roots was 0.9 and 19.5 meq/kg respectively.

Trmt. Code	Trmt. Time	Soln. Composition				Tissue Content			Absorption Rate		
		Na^+	K^+	UO_2^{++}	O_2^+	Na^+	K^+	O_2	Na^+	K^+	O_2
	hrs	meq/liter			mg/l	meq/kg		mM/kg	meq/kg/2hr		mM/kg/2hr
A	1	5.0	5.0	-0-	8.66	4.6	26.6	26.5	4.9	6.4	40.2
B	3	5.0	5.0	-0-	8.60	9.5	33.0	66.7			
C	1	5.0	5.0	$1x10^{-3}$	8.60	4.8	27.0	26.4	4.7	10.7	26.2
D	3	5.0	5.0	$1x10^{-3}$	8.55	9.5	37.7	52.6			
E	1	5.0	5.0	$1x10^{-2}$	8.53	4.8	28.3	18.5	4.6	6.5	30.2
F	3	5.0	5.0	$1x10^{-2}$	8.74	9.4	34.8	48.7			
G	1	5.0	5.0	$1x10^{-1}$	8.74	4.4	26.0	32.3	5.8	5.0	17.4
H	3	5.0	5.0	$1x10^{-1}$	8.74	10.2	31.0	49.7			
I	1	5.0	5.0	1.0	8.78	4.1	22.0	28.1	5.2	1.1	20.6
J	3	5.0	5.0	1.0	8.78	9.3	23.1	48.8			

Appendix 14. Conditions, treatments and results of Experiment U-69. The pH was 5.0; the temperature was 23.5°C. The initial Na^+ and K^+ content of the root tissue was 0.9 and 19.5 meq/kg respectively.

Trmt. No.	Trmt. Time	Meth. of Digest	Soln. Composition				Tissue Content			Absorption Rate		
			Na^+	K^+	Cl^-	UO_2^{++}	Na^+	K^+	Cl^-	Na^+	K^+	Cl^-
	hrs		meq/liter				meq/kg			meq/kg/5hr		
1	1	W.A.[1/]	5.0	5.0	10.0	-0-	4.7	27.1		15.8	16.8	
2	6	W.A.[1/]	5.0	5.0	10.0	-0-	20.5	43.9				
3	1	W.A.[1/]	5.0	5.0	10.0	$1x10^{-3}$	4.5	27.5		13.1	20.8	
4	6	W.A.[1/]	5.0	5.0	10.0	$1x10^{-3}$	17.6	48.3				
5	1	W.A.[1/]	4.99	5.0	10.0	$1x10^{-2}$	4.8	27.1		14.7	15.4	
6	6	W.A.[1/]	4.99	5.0	10.0	$1x10^{-2}$	19.5	42.5				
7	1	D.A.[2/]	4.9	5.0	10.0	$1x10^{-1}$			3.1			23.7
8	6	D.A.[2/]	4.9	5.0	10.0	$1x10^{-1}$			26.8**			
9	1	D.A.[2/]	4.0	5.0	10.0	1.0			3.1			2.9
10	6	D.A.[2/]	4.0	5.0	10.0	1.0			6.0			
11	1	D.A.[2/]	5.0	5.0	10.0	-0-			5.8			29.8
12	6	D.A.[2/]	5.0	5.0	10.0	-0-			35.6			
13	1	D.A.[2/]	5.0	5.0	10.0	$1x10^{-3}$			7.1			19.1
14	6	D.A.[2/]	5.0	5.0	10.0	$1x10^{-3}$			26.2			
15	1	W.A.	4.9	5.0	10.0	$1x10^{-1}$	4.7	23.8		18.8	8.7	
16	6	W.A.	4.9	5.0	10.0	$1x10^{-1}$	23.5	32.5				
17	1	W.A.	4.0	5.0	10.0	1.0	4.2	19.1		14.3	0.7	
18	6	W.A.	4.0	5.0	10.0	1.0	18.5	19.8				

1/ Wet Ashing

2/ Dry Ashing

** Cl - Contamination under platinum coating on crucible.

Appendix 15. Conditions, treatments and results of Experiment U-78. The pH was 5.0; temperature was 25.0°C. Initial Na^+ and K^+ content of the root material was 0.6 and 18.3 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. Composition				Tissue Content		
		Na^+	K^+	UO_2^{++}	DNP	Na^+	K^+	UO_2^{++}
	hrs	meq/liter			Moles/liter	meq/kg		
1	6	5.0	5.0	1.0	-0-	24.0	19.8	38.6
2	3	5.0	5.0	1.0	-0-	11.8	19.8	38.4
3	1	5.0	5.0	1.0	-0-	4.5	19.8	20.6
4	1/2	5.0	5.0	1.0	-0-	3.0	19.8	15.0
5	6	5.0	5.0	1.0	$5x10^{-5}$	5.3	9.4	28.8
6	3	5.0	5.0	1.0	$5x10^{-5}$	3.8	13.3	24.7
7	1	5.0	5.0	1.0	$5x10^{-5}$	2.5	17.0	17.8
8	1/2	5.0	5.0	1.0	$5x10^{-5}$	2.0	17.0	11.6

Appendix 16. Conditions, treatments and results of Experiment U-64. The pH was 5.0 ± 0.2; the temperature was 24.5°C. Initial Na^+, K^+, and Ca^{++} content of the root material was 0.8, 19.2, and 2.0 respectively.

Trmt. No.	Trmt. Time	Soln. Composition				Tissue Content			Absorption Rate		
		Na^+	K^+	UO_2^{++}	Ca^{++}	Na^+	K^+	Ca^{++}	Na^+	K^+	Ca^{++}
	hrs	meq/liter				meq/kg			meq/kg/5hr		
1	1	5.0	5.0	-0-	-0-	6.0	26.0	1.4	18.3	9.0	-0.2
2	6	5.0	5.0	-0-	-0-	24.3	35.0	1.2			
3	1	5.0	5.0	-0-	$1x10^{-3}$	5.8	26.0	1.4	16.8	11.5	-0.2
4	6	5.0	5.0	-0-	$1x10^{-3}$	22.6	37.5	1.2			
5	1	5.0	5.0	-0-	$1x10^{-2}$	5.4	27.4	1.4	10.4	16.6	-0.1
6	6	5.0	5.0	-0-	$1x10^{-2}$	15.8	44.0	1.3			
7	1	5.0	5.0	-0-	$1x10^{-1}$	3.4	27.5	1.7	1.8	32.5	-0.2
8	6	5.0	5.0	-0-	$1x10^{-1}$	5.2	60.0	1.5			
9	1	5.0	5.0	$1x10^{-3}$	-0-	6.0	27.5	1.4	17.8	17.5	-0.2
10	6	5.0	5.0	$1x10^{-3}$	-0-	23.8	45.0	1.2			
11	1	5.0	5.0	$1x10^{-3}$	$1x10^{-3}$	6.1	28.0	1.4	13.6	16.4	-0.2
12	6	5.0	5.0	$1x10^{-3}$	$1x10^{-3}$	19.7	44.4	1.2			
13	1	5.0	5.0	$1x10^{-3}$	$1x10^{-2}$	8.0	23.8	1.4	4.1	27.4	-0.1
14	6	5.0	5.0	$1x10^{-3}$	$1x10^{-2}$	12.1	51.2	1.3			
15	1	5.0	5.0	$1x10^{-3}$	$1x10^{-1}$	3.6	29.0	1.6	1.4	29.2	-0.1
16	6	5.0	5.0	$1x10^{-3}$	$1x10^{-1}$	5.0	58.2	1.5			
17	1	5.0	5.0	$1x10^{-2}$	-0-	5.0	27.7	1.4	18.5	16.8	-0.2
18	6	5.0	5.0	$1x10^{-2}$	-0-	23.5	44.5	1.2			
19	1	5.0	5.0	$1x10^{-2}$	$1x10^{-3}$	4.7	26.5	1.4	14.3	19.5	-0.2
20	6	5.0	5.0	$1x10^{-2}$	$1x10^{-3}$	19.0	46.0	1.2			
21	1	5.0	5.0	$1x10^{-2}$	$1x10^{-2}$	4.0	27.0	1.4	9.3	21.0	-0.1
22	6	5.0	5.0	$1x10^{-2}$	$1x10^{-2}$	13.3	48.0	1.3			
23	1	5.0	5.0	$1x10^{-2}$	$1x10^{-1}$	3.6	28.0	1.7	5.9	22.3	-0.1
24	6	5.0	5.0	$1x10^{-2}$	$1x10^{-1}$	9.5	50.3	1.6			
25	1	5.0	5.0	$1x10^{-1}$	-0-	4.6	26.0	1.5	19.2	5.5	-0.2
26	6	5.0	5.0	$1x10^{-1}$	-0-	23.8	31.5	1.3			
27	1	5.0	5.0	$1x10^{-1}$	$1x10^{-3}$	5.2	26.5	1.4	19.6	10.0	-0.1
28	6	5.0	5.0	$1x10^{-1}$	$1x10^{-3}$	24.8	36.5	1.3			
29	1	5.0	5.0	$1x10^{-1}$	$1x10^{-2}$	4.8	26.0	1.4	17.2	11.0	0.0
30	6	5.0	5.0	$1x10^{-1}$	$1x10^{-2}$	22.0	37.0	1.4			
31	1	5.0	5.0	$1x10^{-1}$	$1x10^{-1}$	4.0	24.0	1.5	13.0	10.8	0.3
32	6	5.0	5.0	$1x10^{-1}$	$1x10^{-1}$	17.0	34.8	1.8			

Appendix 17. Conditions, treatments and results of Experiment U-45. The pH was 5.0 ± 0.2; the temperature was 24.5 ± 0.5°C. The initial Na^+ and K^+ content of the root tissue was 0.4 and 15.4 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. Composition			Tissue Content		Absorption Rate	
		Na^+	K^+	UO_2^{++}	Na^+	K^+	Na^+	K^+
	hrs	meq/liter			meq/kg		meq/kg/5hr	
1	1	5.0	5.0	-0-	5.7	21.4	16.4	13.9
2	6	5.0	5.0	-0-	22.1	35.3		
3	1	5.0	5.0	1.0	3.9	17.1	12.7	0.0
4	6	5.0	5.0	1.0	16.6	17.1		
5	1	5.0	5.0	$1x10^{-1}$	4.9	19.0	19.3	5.5
6	6	5.0	5.0	$1x10^{-1}$	24.3	24.6		
7	1	5.0	5.0	$1x10^{-2}$	4.3	22.9	13.3	14.9
8	6	5.0	5.0	$1x10^{-2}$	17.6	37.8		
9	1	5.0	5.0	$1x10^{-3}$	5.7	21.7	12.4	17.2
10	6	5.0	5.0	$1x10^{-3}$	18.1	38.9		
11	1	5.0	5.0	$1x10^{-4}$	5.7	22.1	14.0	11.9
12	6	5.0	5.0	$1x10^{-4}$	19.7	34.0		

Appendix 18. Conditions, treatments and results of Experiment U-50. The pH was controlled to ± 0.2 pH units; temperature was 25.8 ± 0.5°C. Initial K^+ content of the root material was 16.4 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition		Tissue Content	Absorption Rate
			K^+	UO_2^{++}	K^+	K^+
	hrs		meq/liter		meq/kg	meq/kg/5hr
1	1	3.0	5.0	-0-	7.9	-5.0
2	6	3.0	5.0	-0-	2.9	
3	1	4.0	5.0	-0-	18.2	4.0
4	6	4.0	5.0	-0-	22.2	
5	1	5.0	5.0	-0-	23.6	26.4
6	6	5.0	5.0	-0-	50.0	
7	1	6.0	5.0	-0-	26.5	30.7
8	6	6.0	5.0	-0-	57.2	
9	1	3.0	5.0	$1x10^{-3}$	11.2	-3.9
10	6	3.0	5.0	$1x10^{-3}$	7.3	
11	1	4.0	5.0	$1x10^{-3}$	21.2	12.4
12	6	4.0	5.0	$1x10^{-3}$	33.6	
13	1	5.0	5.0	$1x10^{-3}$	25.4	26.8
14	6	5.0	5.0	$1x10^{-3}$	52.2	
15	1	6.0	5.0	$1x10^{-3}$	25.4	31.8
16	6	6.0	5.0	$1x10^{-3}$	57.2	
17	1	3.0	5.0	$1x10^{-2}$	14.3	1.1
18	6	3.0	5.0	$1x10^{-2}$	15.4	
19	1	4.0	5.0	$1x10^{-2}$	21.5	29.2
20	6	4.0	5.0	$1x10^{-2}$	40.7	
21	1	5.0	5.0	$1x10^{-2}$	26.7	26.2
22	6	5.0	5.0	$1x10^{-2}$	52.9	
23	1	6.0	5.0	$1x10^{-2}$	27.0	28.8
24	6	6.0	5.0	$1x10^{-2}$	55.8	
25	1	3.0	5.0	$1x10^{-1}$	20.0	6.3
26	6	3.0	5.0	$1x10^{-1}$	26.3	
27	1	4.0	5.0	$1x10^{-1}$	24.3	21.0
28	6	4.0	5.0	$1x10^{-1}$	45.3	
29	1	5.0	5.0	$1x10^{-1}$	23.7	17.0
30	6	5.0	5.0	$1x10^{-1}$	40.7	
31	1	6.0	5.0	$1x10^{-1}$	24.0	20.7
32	6	6.0	5.0	$1x10^{-1}$	44.7	
33	1	3.0	5.0	1.0	20.4	8.2
34	6	3.0	5.0	1.0	28.6	
35	1	4.0	5.0	1.0	21.3	8.7
36	6	4.0	5.0	1.0	30.0	
37	1	5.0	5.0	1.0	21.2	6.0
38	6	5.0	5.0	1.0	27.2	
39	1	6.0	5.0	1.0	20.0	1/
40	6	6.0	5.0	1.0	38.3 ppt	

1/ Due to ppt this value was estimated to be 7.3 meq/kg/5hr.

Appendix 19. Conditions, treatments and results of Experiment U-51. The pH was controlled to ± 0.15 pH units; temperature was 25.0° ± 0.5°C. Initial Na^+ content of the root material was 1.0 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition		Tissue Content	Absorption Rate
			Na^+	UO_2^{++}	Na^+	Na^+
	hrs		meq/liter		meq/kg	meq/kg/5hr
1	1	3.0	5.0	-0-	1.0	0.0
2	6	3.0	5.0	-0-	1.0	
3	1	4.0	5.0	-0-	4.3	6.4
4	6	4.0	5.0	-0-	10.7	
5	1	5.0	5.0	-0-	8.6	26.7
6	6	5.0	5.0	-0-	34.3	
7	1	6.0	5.0	-0-	10.0	31.4
8	6	6.0	5.0	-0-	41.4	
9	1	3.0	5.0	$1x10^{-3}$	1.7	-0.3
10	6	3.0	5.0	$1x10^{-3}$	1.4	
11	1	4.0	5.0	$1x10^{-3}$	5.4	11.2
12	6	4.0	5.0	$1x10^{-3}$	16.6	
13	1	5.0	5.0	$1x10^{-3}$	8.3	26.7
14	6	5.0	5.0	$1x10^{-3}$	35.0	
15	1	6.0	5.0	$1x10^{-3}$	9.7	30.3
16	6	6.0	5.0	$1x10^{-3}$	40.0	
17	1	3.0	5.0	$1x10^{-2}$	2.1	1.2
18	6	3.0	5.0	$1x10^{-2}$	3.3	
19	1	4.0	5.0	$1x10^{-2}$	6.6	17.1
20	6	4.0	5.0	$1x10^{-2}$	23.7	
21	1	5.0	5.0	$1x10^{-2}$	8.2	24.7
22	6	5.0	5.0	$1x10^{-2}$	32.9	
23	1	6.0	5.0	$1x10^{-2}$	8.7	28.5
24	6	6.0	5.0	$1x10^{-2}$	37.2	
25	1	3.0	5.0	$1x10^{-1}$	5.1	16.3
26	6	3.0	5.0	$1x10^{-1}$	21.4	
27	1	4.0	5.0	$1x10^{-1}$	2.7	4.2
28	6	4.0	5.0	$1x10^{-1}$	6.9	
29	1	5.0	5.0	$1x10^{-1}$	6.6	22.0
30	6	5.0	5.0	$1x10^{-1}$	28.6	
31	1	6.0	5.0	$1x10^{-1}$	7.1	24.3
32	6	6.0	5.0	$1x10^{-1}$	31.4	
33	1	3.0	5.0	1.0	2.9	5.8
34	6	3.0	5.0	1.0	8.7	
35	1	4.0	5.0	1.0	4.3	12.9
36	6	4.0	5.0	1.0	17.2	
37	1	5.0	5.0	1.0	4.6	14.0
38	6	5.0	5.0	1.0	18.6	
39	1	6.0	5.0	1.0	5.0	19.0
40	6	6.0	5.0	1.0	24.0	

Appendix 20. Conditions, treatments and results of Experiment U-62. The pH was controlled to ± 0.2 pH units; temperature was 24.0° ± 1.0°C. Initial Na^+ and K^+ content of the root material was 0.9 and 17.9 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition			Tissue Content		Absorption Rate	
			Na^+	K^+	UO_2^{++}	Na^+	K^+	Na^+	K^+
	hrs		meq/liter			meq/kg		meq/kg/5hr	
1	1	3.0	5.0	5.0	-0-	1.4	11.8	0.0	-7.3
2	6	3.0	5.0	5.0	-0-	1.4	4.5		
3	1	4.0	5.0	5.0	-0-	3.8	19.8	7.5	2.5
4	6	4.0	5.0	5.0	-0-	11.3	22.3		
5	1	5.0	5.0	5.0	-0-	5.0	23.8	16.0	18.0
6	6	5.0	5.0	5.0	-0-	21.0	41.8		
7	1	6.0	5.0	5.0	-0-	5.2	24.8	18.3	18.2
8	6	6.0	5.0	5.0	-0-	23.5	43.0		
9	1	3.0	5.0	5.0	$1x10^{-3}$	1.5	14.0	0.8	-4.0
10	6	3.0	5.0	5.0	$1x10^{-3}$	2.3	10.0		
11	1	4.0	5.0	5.0	$1x10^{-3}$	3.8	22.4	9.0	9.1
12	6	4.0	5.0	5.0	$1x10^{-3}$	12.8	31.5		
13	1	5.0	5.0	5.0	$1x10^{-3}$	4.7	25.7	14.8	19.8
14	6	5.0	5.0	5.0	$1x10^{-3}$	19.5	45.5		
15	1	6.0	5.0	5.0	$1x10^{-3}$	5.9	25.7	15.1	20.9
16	6	6.0	5.0	5.0	$1x10^{-3}$	21.0	46.6		
17	1	3.0	5.0	5.0	$1x10^{-2}$	1.6	17.8	1.9	2.2
18	6	3.0	5.0	5.0	$1x10^{-2}$	3.5	20.0		
19	1	4.0	5.0	5.0	$1x10^{-2}$	3.0	23.5	11.0	14.2
20	6	4.0	5.0	5.0	$1x10^{-2}$	14.0	37.7		
21	1	5.0	5.0	5.0	$1x10^{-2}$	4.0	24.4	14.0	19.3
22	6	5.0	5.0	5.0	$1x10^{-2}$	18.0	43.7		
23	1	6.0	5.0	5.0	$1x10^{-2}$	5.0	25.0	18.1	16.8
24	6	6.0	5.0	5.0	$1x10^{-2}$	23.1	41.8		
25	1	3.0	5.0	5.0	$1x10^{-1}$	1.6	21.0	3.2	9.0
26	6	3.0	5.0	5.0	$1x10^{-1}$	4.8	30.0		
27	1	4.0	5.0	5.0	$1x10^{-1}$	3.0	23.5	11.8	14.7
28	6	4.0	5.0	5.0	$1x10^{-1}$	14.8	38.2		
29	1	5.0	5.0	5.0	$1x10^{-1}$	4.1	23.7	18.1	9.3
30	6	5.0	5.0	5.0	$1x10^{-1}$	22.2	33.0		
31	1	6.0	5.0	5.0	$1x10^{-1}$	5.0	23.5	19.5	9.7
32	6	6.0	5.0	5.0	$1x10^{-1}$	24.5	33.2		
33	1	3.0	5.0	5.0	1.0	2.0	23.0	4.9	8.1
34	6	3.0	5.0	5.0	1.0	6.9	31.1		
35	1	4.0	5.0	5.0	1.0	3.4	22.2	12.6	5.9
36	6	4.0	5.0	5.0	1.0	16.0	28.1		
37	1	5.0	5.0	5.0	1.0	3.8	20.8	15.0	1.8
38	6	5.0	5.0	5.0	1.0	18.8	22.6		
39	1	6.0	5.0	5.0	1.0	4.0	21.0	17.0	4.0
40	6	6.0	5.0	5.0	1.0	21.0	25.0		

Appendix 21. Conditions, treatments and results of Experiment U-19. The pH was 5.0 ± 0.1; temperature was 23.0°C. Initial Na^+ and K^+ content of the root material was 3.3 and 15.1 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. Composition			Tissue Content		Absorption Rate	
		Na^+	K^+	UO_2^{++}	Na^+	K^+	Na^+	K^+
	hrs	meq/liter			meq/kg		meq/kg/5hr	
1	1	5.0	-0-	-0-	6.7	14.5	21.6	-1.3
2	6	5.0	-0-	-0-	28.3	13.2		
3	1	5.0	0.5	-0-	6.7	15.0	20.4	0.7
4	6	5.0	0.5	-0-	27.1	15.7		
5	1	5.0	1.0	-0-	6.2	15.0	17.1	9.2
6	6	5.0	1.0	-0-	23.3	24.2		
7	1	5.0	3.0	-0-	4.8	19.2	11.4	13.5
8	6	5.0	3.0	-0-	16.2	32.7		
9	1	5.0	5.0	-0-	4.2	19.3	10.4	15.2
10	6	5.0	5.0	-0-	14.6	34.5		
11	1	5.0	10.0	-0-	4.0	21.6	9.3	16.7
12	6	5.0	10.0	-0-	13.3	38.3		
13	1	5.0	25.0	-0-	3.3	25.7	6.7	20.1
14	6	5.0	25.0	-0-	10.0	45.8		
15	1	5.0	-0-	1.0	4.7	14.2	12.8	-7.5
16	6	5.0	-0-	1.0	17.5	6.7		
17	1	5.0	0.5	1.0	4.6	15.4	12.9	-5.0
18	6	5.0	0.5	1.0	17.3	9.6		
19	1	5.0	1.0	1.0	4.3	15.8	12.4	-4.6
20	6	5.0	1.0	1.0	16.7	9.6		
21	1	5.0	3.0	1.0	4.0	16.9	10.3	-3.3
22	6	5.0	3.0	1.0	14.3	13.6		
23	1	5.0	5.0	1.0	3.7	17.1	9.6	-2.1
24	6	5.0	5.0	1.0	13.3	15.0		
25	1	5.0	10.0	1.0	3.8	19.6	8.5	0.2
26	6	5.0	10.0	1.0	12.3	19.8		
27	1	5.0	25.0	1.0	3.2	22.3	6.7	6.0
28	6	5.0	25.0	1.0	10.0	28.3		

Appendix 22. Conditions, treatments and results of Experiment U-37. The pH was 5.0 ± 0.1; temperature was 25.0° ± 0.5°C. Initial Na^+ and K^+ content of the root material was 1.1 and 13.6 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. Composition			Tissue Content		Absorption Rate	
		Na^+	K^+	UO_2^{++}	Na^+	K^+	Na^+	K^+
	hrs	meq/liter			meq/kg		meq/kg/5hr	
1	1	-0-	5.0	-0-	1.1	20.9	0.0	26.5
2	6	-0-	5.0	-0-	1.1	47.4		
3	1	0.5	5.0	-0-	1.3	19.6	1.8	26.5
4	6	0.5	5.0	-0-	3.1	46.1		
5	1	1.0	5.0	-0-	2.1	21.9	3.6	24.5
6	6	1.0	5.0	-0-	5.7	46.4		
7	1	3.0	5.0	-0-	3.7	18.9	9.2	20.1
8	6	3.0	5.0	-0-	12.9	39.0		
9	1	10.0	5.0	-0-	7.9	19.3	25.7	9.6
10	6	10.0	5.0	-0-	33.6	28.9		
11	1	5.0	5.0	-0-	5.0	20.3	19.0	17.7
12	6	5.0	5.0	-0-	24.0	38.0		
13	1	25.0	5.0	-0-	13.1	18.1	37.9	0.6
14	6	25.0	5.0	-0-	51.0	18.7		
15	1	-0-	5.0	1.0	1.1	17.9	0.0	9.2
16	6	-0-	5.0	1.0	1.1	27.1		
17	1	0.5	5.0	1.0	1.3	17.4	1.8	8.3
18	6	0.5	5.0	1.0	3.1	25.7		
19	1	1.0	5.0	1.0	2.1	17.4	3.6	7.7
20	6	1.0	5.0	1.0	5.7	25.1		
21	1	3.0	5.0	1.0	2.1	12.9	9.3	6.5
22	6	3.0	5.0	1.0	11.4	19.4		
23	1	10.0	5.0	1.0	8.9	16.4	15.5	0.7
24	6	10.0	5.0	1.0	24.4	17.1		
25	1	5.0	5.0	1.0	4.0	16.9	12.4	3.1
26	6	5.0	5.0	1.0	16.4	20.0		
27	1	25.0	5.0	1.0	8.6	14.6	31.8	-1.5
28	6	25.0	5.0	1.0	40.4	13.1		

Appendix 23. Conditions, treatments and results of Experiment U-52. The pH was 5.0 ± 0.3; the temperature was 25.0°C. Initial Na^+ and K^+ content of the root material was 2.9 and 17.9 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. Composition			Tissue Content		Absorption Rate	
		Na^+	K^+	UO_2^{++}	K^+	Na^+	K^+	Na^+
	hrs	meq/liter			meq/kg		meq/kg/5hr	
1	1	5.0	-0-	-0-	15.7	11.5	3.6	24.8
2	6	5.0	-0-	-0-	12.1	36.3		
3	1	5.0	1.0	-0-	19.4	9.3	2.5	23.1
4	6	5.0	1.0	-0-	21.9	32.4		
5	1	5.0	5.0	-0-	23.6	7.7	13.1	16.3
6	6	5.0	5.0	-0-	36.7	24.0		
7	1	5.0	25.0	-0-	30.7	5.7	24.3	10.0
8	6	5.0	25.0	-0-	55.0	15.7		
9	1	5.0	-0-	$1x10^{-3}$	16.4	10.0	-4.7	28.5
10	6	5.0	-0-	$1x10^{-3}$	11.7	38.5		
11	1	5.0	1.0	$1x10^{-3}$	20.0	9.1	5.0	21.7
12	6	5.0	1.0	$1x10^{-3}$	25.0	30.8		
13	1	5.0	5.0	$1x10^{-3}$	24.3	7.1	16.0	14.3
14	6	5.0	5.0	$1x10^{-3}$	40.3	21.4		
15	1	5.0	25.0	$1x10^{-3}$	29.3	5.7	30.7	8.3
16	6	5.0	25.0	$1x10^{-3}$	60.0	14.0		
17	1	5.0	-0-	$1x10^{-2}$	16.0	10.9	-5.0	23.1
18	6	5.0	-0-	$1x10^{-2}$	11.0	34.0		
19	1	5.0	1.0	$1x10^{-2}$	21.4	8.9	2.2	22.8
20	6	5.0	1.0	$1x10^{-2}$	23.6	31.7		
21	1	5.0	5.0	$1x10^{-2}$	24.3	6.4	14.3	14.2
22	6	5.0	5.0	$1x10^{-2}$	38.6	20.6		
23	1	5.0	25.0	$1x10^{-2}$	28.6	5.0	27.1	7.4
24	6	5.0	25.0	$1x10^{-2}$	55.7	12.4		
25	1	5.0	-0-	$1x10^{-1}$	16.4	8.9	-8.1	23.7
26	6	5.0	-0-	$1x10^{-1}$	8.3	32.6		
27	1	5.0	1.0	$1x10^{-1}$	20.0	8.3	-1.7	22.4
28	6	5.0	1.0	$1x10^{-1}$	18.3	30.7		
29	1	5.0	5.0	$1x10^{-1}$	23.6	6.9	4.3	19.1
30	6	5.0	5.0	$1x10^{-1}$	27.9	26.0		
31	1	5.0	25.0	$1x10^{-1}$	28.0	4.7	21.7	11.0
32	6	5.0	25.0	$1x10^{-1}$	49.7	15.7		
33	1	5.0	-0-	1.0	15.7	6.9	-9.4	14.5
34	6	5.0	-0-	1.0	6.3	21.4		
35	1	5.0	1.0	1.0	17.9	6.3	-5.3	14.3
36	6	5.0	1.0	1.0	12.6	20.6		
37	1	5.0	5.0	1.0	20.0	6.0	-0.7	14.0
38	6	5.0	5.0	1.0	19.3	20.0		
39	1	5.0	25.0	1.0	24.8	4.6	10.9	9.4
40	6	5.0	25.0	1.0	35.7	14.0		

Appendix 24. Conditions, treatments and results of Experiment U-53. The pH was 5.0 ± 0.2; the temperature was 25.0°C. Initial Na^+ and K^+ content of the root tissue was 0.7 and 15.5 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. Composition			Tissue Content		Absorption Rate	
		Na^+	K^+	UO_2^{++}	Na^+	K^+	Na^+	K^+
	hrs	meq/liter			meq/kg		meq/kg/5hr	
1	1	-0-	5.0	-0-	0.6	24.3	0.0	24.3
2	6	-0-	5.0	-0-	0.6	48.6		
3	1	1.0	5.0	-0-	1.7	25.1	3.0	21.3
4	6	1.0	5.0	-0-	4.7	46.4		
5	1	5.0	5.0	-0-	4.6	22.1	12.8	17.3
6	6	5.0	5.0	-0-	17.4	39.4		
7	1	25.0	5.0	-0-	10.7	18.6	34.0	0.7
8	6	25.0	5.0	-0-	44.7	19.3		
9	1	-0-	5.0	$1x10^{-3}$	0.6	24.6	0.0	24.7
10	6	-0-	5.0	$1x10^{-3}$	0.6	49.3		
11	1	1.0	5.0	$1x10^{-3}$	1.7	24.3	2.3	22.8
12	6	1.0	5.0	$1x10^{-3}$	4.0	47.1		
13	1	5.0	5.0	$1x10^{-3}$	4.0	21.7	11.0	21.2
14	6	5.0	5.0	$1x10^{-3}$	15.0	42.9		
15	1	25.0	5.0	$1x10^{-3}$	10.7	20.0	35.4	4.1
16	6	25.0	5.0	$1x10^{-3}$	46.1	24.1		
17	1	-0-	5.0	$1x10^{-2}$	0.6	24.3	0.0	22.8
18	6	-0-	5.0	$1x10^{-2}$	0.6	47.1		
19	1	1.0	5.0	$1x10^{-2}$	1.4	23.6	3.2	19.3
20	6	1.0	5.0	$1x10^{-2}$	4.6	42.9		
21	1	5.0	5.0	$1x10^{-2}$	4.0	23.6	11.0	15.0
22	6	5.0	5.0	$1x10^{-2}$	15.0	38.6		
23	1	25.0	5.0	$1x10^{-2}$	10.7	20.0	28.9	3.4
24	6	25.0	5.0	$1x10^{-2}$	39.6	23.4		
25	1	-0-	5.0	$1x10^{-1}$	0.6	22.4	0.0	16.2
26	6	-0-	5.0	$1x10^{-1}$	0.6	38.6		
27	1	1.0	5.0	$1x10^{-1}$	1.4	22.6	5.0	13.1
28	6	1.0	5.0	$1x10^{-1}$	6.4	35.7		
29	1	5.0	5.0	$1x10^{-1}$	3.7	20.9	15.3	5.8
30	6	5.0	5.0	$1x10^{-1}$	19.0	26.7		
31	1	25.0	5.0	$1x10^{-1}$	10.0	19.3	37.9	-2.9
32	6	25.0	5.0	$1x10^{-1}$	47.9	16.4		
33	1	-0-	5.0	1.0	0.6	19.0	0.0	9.6
34	6	-0-	5.0	1.0	0.6	28.6		
35	1	1.0	5.0	1.0	1.4	19.0	3.0	6.0
36	6	1.0	5.0	1.0	4.4	25.0		
37	1	5.0	5.0	1.0	3.3	18.6	10.6	0.4
38	6	5.0	5.0	1.0	13.9	19.0		
39	1	25.0	5.0	1.0	7.9	17.1	28.5	-5.7
40	6	25.0	5.0	1.0	36.4	11.4		

Appendix 25. Conditions, treatments and results of Experiment U-43B. The pH was 5.0 ± 0.1; the temperature was 24.5° ± 0.5°C. Initial Na^+ and K^+ content of the root material was 0.7 and 13.6 meq/kg respectively. Pretreatment was for 30 minutes in 1.0 meq UO_2^{++} per liter.

Trmt. No.	Trmt. Time	Soln. Composition					Tissue Content				Absorption Rate			
		UO_2^{++}	Na^+	K^+	Li^+	Rb^+	Na^+	K^+	Li^+	Rb^+	Na^+	K^+	Li^+	Rb^+
	hrs	meq/liter					meq/kg				meq/kg/5hr			
7	1	-0-	-0-	5.0	-0-	-0-		22.1				27.8		
8	6	-0-	-0-	5.0	-0-	-0-		49.9						
9	1	1.0	-0-	5.0	-0-	-0-		17.4				7.3		
10	6	1.0	-0-	5.0	-0-	-0-		24.7						
11	1	Pret.	-0-	5.0	-0-	-0-		20.9				18.5		
12	6	Pret.	-0-	5.0	-0-	-0-		39.4						
13	1	-0-	5.0	-0-	-0-	-0-	9.3				24.4			
14	6	-0-	5.0	-0-	-0-	-0-	33.7							
15	1	1.0	5.0	-0-	-0-	-0-	4.3				15.7			
16	6	1.0	5.0	-0-	-0-	-0-	20.0							
17	1	Pret.	5.0	-0-	-0-	-0-	10.3				26.6			
18	6	Pret.	5.0	-0-	-0-	-0-	36.9							
19	1	-0-	-0-	-0-	5.0	-0-			6.5				9.0	
20	6	-0-	-0-	-0-	5.0	-0-			15.5					
21	1	1.0	-0-	-0-	5.0	-0-			2.7				8.1	
22	6	1.0	-0-	-0-	5.0	-0-			10.8					
23	1	Pret.	-0-	-0-	5.0	-0-			6.5				11.7	
24	6	Pret	-0-	-0-	5.0	-0-			18.2					
25	1	-0-	-0-	-0-	-0-	5.0				8.6				16.0
26	6	-0-	-0-	-0-	-0-	5.0				24.6				
27	1	1.0	-0-	-0-	-0-	5.0				4.3				8.6
28	6	1.0	-0-	-0-	-0-	5.0				12.9				
29	1	Pret.	-0-	-0-	-0-	5.0				9.1				14.5
30	6	Pret.	-0-	-0-	-0-	5.0				23.6				

Appendix 26. Conditions, treatments and results of Experiment U-57. The pH was controlled to ± 0.2 pH units; temperature was 25.0° ± 0.5°C. There was no initial Li^+ present in the root material.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition		Tissue Content	Absorption Rate
			Li^+	UO_2^{++}	Li^+	Li^+
	hrs		meq/liter		meq/kg	meq/kg/5hr
1	1	3.0	5.0	-0-	1.0	0.0
2	6	3.0	5.0	-0-	1.0	
3	1	4.0	5.0	-0-	3.1	4.6
4	6	4.0	5.0	-0-	7.7	
5	1	5.0	5.0	-0-	2.2	10.5
6	6	5.0	5.0	-0-	17.7	
7	1	6.0	5.0	-0-	7.8	14.8
8	6	6.0	5.0	-0-	22.6	
9	1	3.0	5.0	$1x10^{-3}$	1.2	0.0
10	6	3.0	5.0	$1x10^{-3}$	1.2	
11	1	4.0	5.0	$1x10^{-3}$	4.1	9.3
12	6	4.0	5.0	$1x10^{-3}$	13.4	
13	1	5.0	5.0	$1x10^{-3}$	6.9	14.4
14	6	5.0	5.0	$1x10^{-3}$	21.3	
15	1	6.0	5.0	$1x10^{-3}$	7.2	16.7
16	6	6.0	5.0	$1x10^{-3}$	23.9	
17	1	3.0	5.0	$1x10^{-2}$	0.8	0.4
18	6	3.0	5.0	$1x10^{-2}$	1.2	
19	1	4.0	5.0	$1x10^{-2}$	3.6	9.6
20	6	4.0	5.0	$1x10^{-2}$	13.2	
21	1	5.0	5.0	$1x10^{-2}$	6.2	15.3
22	6	5.0	5.0	$1x10^{-2}$	21.5	
23	1	6.0	5.0	$1x10^{-2}$	6.9	16.6
24	6	6.0	5.0	$1x10^{-2}$	23.5	
25	1	3.0	5.0	$1x10^{-1}$	0.7	0.7
26	6	3.0	5.0	$1x10^{-1}$	1.4	
27	1	4.0	5.0	$1x10^{-1}$	2.3	6.2
28	6	4.0	5.0	$1x10^{-1}$	8.5	
29	1	5.0	5.0	$1x10^{-1}$	3.8	13.7
30	6	5.0	5.0	$1x10^{-1}$	17.5	
31	1	6.0	5.0	$1x10^{-1}$	5.1	17.0
32	6	6.0	5.0	$1x10^{-1}$	22.1	
33	1	3.0	5.0	1.0	1.1	0.4
34	6	3.0	5.0	1.0	1.5	
35	1	4.0	5.0	1.0	1.5	5.2
36	6	4.0	5.0	1.0	6.7	
37	1	6.0	5.0	1.0	Lost due to ppt	1/
38	6	6.0	5.0	1.0	Lost due to ppt	
39	1	5.0	5.0	1.0	2.3	9.7
40	6	5.0	5.0	1.0	12.0	

1/ Due to ppt this value was estimated to be 13.0 meq/kg/5hrs.

Appendix 27. Conditions, treatments and results of Experiment U-60. The pH was controlled to ± 0.2 pH units; temperature was 25.0°C. Initial Na^+ and Li^+ content of the root tissues was 0.5 and 0.0 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition			Tissue Content		Absorption Rate	
			Na^+	Li^+	UO_2^{++}	Na^+	Li^+	Na^+	Li^+
	hrs		meq/liter			meq/kg		meq/kg/5hr	
1	1	3.0	5.0	5.0	-0-	1.5	0.6	-0.1	0.0
2	6	3.0	5.0	5.0	-0-	1.4	0.6		
3	1	4.0	5.0	5.0	-0-	5.0	2.6	6.7	5.9
4	6	4.0	5.0	5.0	-0-	11.7	8.5		
5	1	5.0	5.0	5.0	-0-	7.3	3.7	10.7	8.3
6	6	5.0	5.0	5.0	-0-	18.0	12.0		
7	1	6.0	5.0	5.0	-0-	7.7	4.0	13.3	9.2
8	6	6.0	5.0	5.0	-0-	21.0	13.2		
9	1	3.0	5.0	5.0	$1x10^{-3}$	2.0	0.6	0.5	0.8
10	6	3.0	5.0	5.0	$1x10^{-3}$	2.5	1.4		
11	1	4.0	5.0	5.0	$1x10^{-3}$	5.5	2.8	8.5	6.9
12	6	4.0	5.0	5.0	$1x10^{-3}$	14.0	9.7		
13	1	5.0	5.0	5.0	$1x10^{-3}$	7.0	3.5	12.3	9.4
14	6	5.0	5.0	5.0	$1x10^{-3}$	19.3	12.9		
15	1	6.0	5.0	5.0	$1x10^{-3}$	7.5	4.0	13.0	9.8
16	6	6.0	5.0	5.0	$1x10^{-3}$	20.5	13.8		
17	1	3.0	5.0	5.0	$1x10^{-2}$	4.0	1.0	0.5	3.0
18	6	3.0	5.0	5.0	$1x10^{-2}$	4.5	2.0		
19	1	4.0	5.0	5.0	$1x10^{-2}$	5.8	3.0	12.2	6.0
20	6	4.0	5.0	5.0	$1x10^{-2}$	18.0	9.0		
21	1	5.0	5.0	5.0	$1x10^{-2}$	6.7	3.4	13.4	9.3
22	6	5.0	5.0	5.0	$1x10^{-2}$	20.2	12.7		
23	1	6.0	5.0	5.0	$1x10^{-2}$	6.7	3.8	12.1	9.9
24	6	6.0	5.0	5.0	$1x10^{-2}$	20.8	13.7		
25	1	3.0	5.0	5.0	$1x10^{-1}$	3.0	0.7	5.0	1.1
26	6	3.0	5.0	5.0	$1x10^{-1}$	8.0	1.8		
27	1	4.0	5.0	5.0	$1x10^{-1}$	5.8	1.8	13.6	4.5
28	6	4.0	5.0	5.0	$1x10^{-1}$	19.4	6.3		
29	1	5.0	5.0	5.0	$1x10^{-1}$	6.2	2.7	12.1	7.8
30	6	5.0	5.0	5.0	$1x10^{-1}$	18.3	10.5		
31	1	6.0	5.0	5.0	$1x10^{-1}$	6.4	3.5	12.6	8.8
32	6	6.0	5.0	5.0	$1x10^{-1}$	18.0	12.3		
33	1	3.0	5.0	5.0	1.0	3.0	0.7	5.0	0.4
34	6	3.0	5.0	5.0	1.0	8.0	1.1		
35	1	4.0	5.0	5.0	1.0	4.4	1.0	12.1	2.0
36	6	4.0	5.0	5.0	1.0	16.5	3.0		
37	1	5.0	5.0	5.0	1.0	4.5	1.6	10.5	4.8
38	6	5.0	5.0	5.0	1.0	15.0	6.4		
39	1	6.0	5.0	5.0	1.0	5.1	2.0	12.1	6.4
40	6	6.0	5.0	5.0	1.0	17.2	8.4		

Appendix 28. Conditions, treatments and results of Experiment U-58. The pH was controlled to ± 0.1 pH units; temperature was 25.0°C. Initial K^+ and Li^+ content of the root material was 18.0 and 0.0 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition			Tissue Content		Absorption Rate	
			K^+	Li^+	UO_2^{++}	K^+	Li^+	K^+	Li^+
	hrs		meq/liter			meq/kg		meq/kg/5hr	
1	1	3.0	5.0	5.0	-0-	9.6	1.5	-7.1	0.7
2	6	3.0	5.0	5.0	-0-	2.5	2.2		
3	1	4.0	5.0	5.0	-0-	20.0	3.5	0.0	4.3
4	6	4.0	5.0	5.0	-0-	20.0	7.8		
5	1	5.0	5.0	5.0	-0-	24.8	4.3	6.0	8.1
6	6	5.0	5.0	5.0	-0-	30.8	12.4		
7	1	6.0	5.0	5.0	-0-	24.8	6.0	8.7	10.0
8	6	6.0	5.0	5.0	-0-	33.5	16.0		
9	1	3.0	5.0	5.0	$1x10^{-3}$	12.8	2.3	-5.8	0.2
10	6	3.0	5.0	5.0	$1x10^{-3}$	7.0	2.5		
11	1	4.0	5.0	5.0	$1x10^{-3}$	23.3	4.1	6.1	5.5
12	6	4.0	5.0	5.0	$1x10^{-3}$	29.4	9.6		
13	1	5.0	5.0	5.0	$1x10^{-3}$	25.8	4.9	9.9	7.6
14	6	5.0	5.0	5.0	$1x10^{-3}$	35.7	12.5		
15	1	6.0	5.0	5.0	$1x10^{-3}$	25.9	5.4	9.5	8.5
16	6	6.0	5.0	5.0	$1x10^{-3}$	35.4	13.9		
17	1	3.0	5.0	5.0	$1x10^{-2}$	17.5	2.0	1.2	1.8
18	6	3.0	5.0	5.0	$1x10^{-2}$	18.7	3.8		
19	1	4.0	5.0	5.0	$1x10^{-2}$	24.8	3.6	14.8	4.2
20	6	4.0	5.0	5.0	$1x10^{-2}$	39.6	7.8		
21	1	5.0	5.0	5.0	$1x10^{-2}$	25.8	4.4	11.7	7.4
22	6	5.0	5.0	5.0	$1x10^{-2}$	37.5	11.8		
23	1	6.0	5.0	5.0	$1x10^{-2}$	24.8	5.5	9.9	10.0
24	6	6.0	5.0	5.0	$1x10^{-2}$	34.7	15.5		
25	1	3.0	5.0	5.0	$1x10^{-1}$	21.0	1.5	8.0	0.9
26	6	3.0	5.0	5.0	$1x10^{-1}$	29.0	2.4		
27	1	4.0	5.0	5.0	$1x10^{-1}$	26.0	2.0	15.0	5.2
28	6	4.0	5.0	5.0	$1x10^{-1}$	41.0	7.2		
29	1	5.0	5.0	5.0	$1x10^{-1}$	15.0	3.0	17.3	7.7
30	6	5.0	5.0	5.0	$1x10^{-1}$	32.3	10.7		
31	1	6.0	5.0	5.0	$1x10^{-1}$	24.5	4.5	9.1	9.3
32	6	6.0	5.0	5.0	$1x10^{-1}$	33.6	13.8		
33	1	3.0	5.0	5.0	1.0	22.0	1.4	10.8	1.1
34	6	3.0	5.0	5.0	1.0	32.8	2.5		
35	1	4.0	5.0	5.0	1.0	22.5	2.5	6.2	3.0
36	6	4.0	5.0	5.0	1.0	28.7	5.5		
37	1	5.0	5.0	5.0	1.0	22.0	2.5	2.5	7.2
38	6	5.0	5.0	5.0	1.0	24.5	9.7		
39	1	6.0	5.0	5.0	1.0	22.0	2.7	4.5	7.5
40	6	6.0	5.0	5.0	1.0	26.5	10.2		

Appendix 29. Conditions, treatments and results of Experiment U-67. The pH was controlled to ± 0.1 pH units; temperature was 25.0°C. There was no initial Rb^+ or Li^+ in the root material.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition			Tissue Content		Absorption Rate	
			Rb^+	Li^+	UO_2^{++}	Rb^+	Li^+	Rb^+	Li^+
	hrs		meq/liter			meq/kg		meq/kg/5hr	
1	1	3.0	5.0	5.0	-0-	1.8	1.0	-0.8	0.0
2	6	3.0	5.0	5.0	-0-	1.0	1.0		
3	1	4.0	5.0	5.0	-0-	6.5	3.3	3.1	5.8
4	6	4.0	5.0	5.0	-0-	9.6	9.1		
5	1	5.0	5.0	5.0	-0-	8.7	4.5	10.3	12.2
6	6	5.0	5.0	5.0	-0-	19.0	16.7		
7	1	6.0	5.0	5.0	-0-	8.7	4.9	12.5	14.7
8	6	6.0	5.0	5.0	-0-	21.2	19.6		
9	1	3.0	5.0	5.0	$1x10^{-3}$	2.6	1.0	0.2	0.1
10	6	3.0	5.0	5.0	$1x10^{-3}$	2.8	1.1		
11	1	4.0	5.0	5.0	$1x10^{-3}$	7.4	2.9	6.6	6.9
12	6	4.0	5.0	5.0	$1x10^{-3}$	14.0	9.8		
13	1	5.0	5.0	5.0	$1x10^{-3}$	9.3	3.6	11.7	12.4
14	6	5.0	5.0	5.0	$1x10^{-3}$	21.0	16.0		
15	1	6.0	5.0	5.0	$1x10^{-3}$	9.0	4.3	12.0	13.6
16	6	6.0	5.0	5.0	$1x10^{-3}$	21.0	17.9		
17	6	3.0	5.0	5.0	$1x10^{-2}$	7.0	1.6	2.5	0.6
18	1	3.0	5.0	5.0	$1x10^{-2}$	4.5	1.0		
19	1	4.0	5.0	5.0	$1x10^{-2}$	8.4	2.2	11.1	5.7
20	6	4.0	5.0	5.0	$1x10^{-2}$	19.5	7.9		
21	1	5.0	5.0	5.0	$1x10^{-2}$	8.7	2.9	12.5	11.0
22	6	5.0	5.0	5.0	$1x10^{-2}$	21.2	13.9		
23	1	6.0	5.0	5.0	$1x10^{-2}$	8.5	4.3	11.1	13.1
24	6	6.0	5.0	5.0	$1x10^{-2}$	19.6	17.4		
25	1	3.0	5.0	5.0	$1x10^{-1}$	6.1	0.6	9.9	1.4
26	6	3.0	5.0	5.0	$1x10^{-1}$	15.0	2.0		
27	1	4.0	5.0	5.0	$1x10^{-1}$	8.3	1.8	10.7	4.8
28	6	4.0	5.0	5.0	$1x10^{-1}$	19.0	6.6		
29	1	5.0	5.0	5.0	$1x10^{-1}$	8.0	2.6	8.9	10.8
30	6	5.0	5.0	5.0	$1x10^{-1}$	16.9	13.4		
31	1	6.0	5.0	5.0	$1x10^{-1}$	7.4	3.4	10.7	11.8
32	6	6.0	5.0	5.0	$1x10^{-1}$	18.1	15.2		
33	1	3.0	5.0	5.0	1.0	6.5	0.5	9.3	0.6
34	6	3.0	5.0	5.0	1.0	15.8	1.1		
35	1	4.0	5.0	5.0	1.0	8.2	1.4	4.6	2.8
36	6	4.0	5.0	5.0	1.0	10.8	4.2		
37	1	6.0	5.0	5.0	1.0	7.1	1.5	4.1	10.0
38	6	5.0	5.0	5.0	1.0	13.2	9.1		
39	6	6.0	5.0	5.0	1.0	11.2	11.9	7.5	6.3
40	1	5.0	5.0	5.0	1.0	5.7	2.8		

Appendix 30. Conditions, treatments and results of Experiment U-56. The pH was controlled to ± 0.2 pH units; temperature was 25.0° ± 0.5°C. There was no initial Rb^+ in the root material.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition		Tissue Content	Absorption Rate
			Rb^+	UC_2^{++}	Rb^+	Rb^+
	hrs		meq/liter		meq/kg	meq/kg/5hr
1	1	3.0	5.0	-0-	3.1	0.5
2	6	3.0	5.0	-0-	3.6	
3	1	4.0	5.0	-0-	7.1	10.0
4	6	4.0	5.0	-0-	17.1	
5	1	5.0	5.0	-0-	9.7	18.9
6	6	5.0	5.0	-0-	28.6	
7	1	6.0	5.0	-0-	10.4	21.0
8	6	6.0	5.0	-0-	31.4	
9	1	3.0	5.0	$1x10^{-3}$	4.4	2.2
10	6	3.0	5.0	$1x10^{-3}$	6.6	
11	1	4.0	5.0	$1x10^{-3}$	7.9	13.5
12	6	4.0	5.0	$1x10^{-3}$	21.4	
13	1	5.0	5.0	$1x10^{-3}$	10.0	20.0
14	6	5.0	5.0	$1x10^{-3}$	30.0	
15	1	6.0	5.0	$1x10^{-3}$	10.7	21.4
16	6	6.0	5.0	$1x10^{-3}$	32.1	
17	1	3.0	5.0	$1x10^{-2}$	5.3	6.1
18	6	3.0	5.0	$1x10^{-2}$	11.4	
19	1	4.0	5.0	$1x10^{-2}$	7.7	14.6
20	**6**	**4.0**	5.0	$1x10^{-2}$	22.3	
21	1	5.0	5.0	$1x10^{-2}$	9.0	17.0
22	6	5.0	5.0	$1x10^{-2}$	26.0	
23	1	6.0	5.0	$1x10^{-2}$	9.6	21.5
24	6	6.0	5.0	$1x10^{-2}$	31.1	
25	1	3.0	5.0	$1x10^{-1}$	6.7	11.4
26	6	3.0	5.0	$1x10^{-1}$	18.1	
27	1	4.0	5.0	$1x10^{-1}$	7.9	13.5
28	6	4.0	5.0	$1x10^{-1}$	21.4	
29	1	5.0	5.0	$1x10^{-1}$	7.7	15.2
30	6	5.0	5.0	$1x10^{-1}$	22.9	
31	1	6.0	5.0	$1x10^{-1}$	7.7	16.6
32	6	6.0	5.0	$1x10^{-1}$	24.3	
33	1	3.0	5.0	1.0	6.6	12.7
34	6	3.0	5.0	1.0	19.3	
35	1	4.0	5.0	1.0	5.7	6.7
36	6	4.0	5.0	1.0	12.4	
37	1	5.0	5.0	1.0	5.0	9.6
38	6	5.0	5.0	1.0	14.6	
39	1	6.0	5.0	1.0	6.1	1/
40	6	6.0	5.0	1.0	24.7 ppt	

1/ Due to ppt this value was estimated to be 10.0 meq/kg/5hr.

Appendix 31. Conditions, treatments and results of Experiment U-68. The pH was controlled to ± 0.3 pH units; temperature was 25.0° ± 0.5°C. Initial Na^+ and Rb^+ content of the root material was 0.4 and 0.0 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition			Tissue Content		Absorption Rate	
			Na^+	Rb^+	UO_2^{++}	Na^+	Rb^+	Na^+	Rb^+
	hrs		meq/liter			meq/kg		meq/kg/5hr	
1	1	3.0	5.0	5.0	0.0	0.8	2.1	0.2	0.5
2	6	3.0	5.0	5.0	0.0	1.0	2.6		
3	1	4.0	5.0	5.0	0.0	3.0	5.8	8.0	7.3
4	6	4.0	5.0	5.0	0.0	11.0	13.1		
5	1	5.0	5.0	5.0	0.0	5.0	7.1	12.3	12.5
6	6	5.0	5.0	5.0	0.0	17.3	19.6		
7	1	6.0	5.0	5.0	0.0	6.4	6.8	16.8	11.5
8	6	6.0	5.0	5.0	0.0	23.2	18.3		
9	1	3.0	5.0	5.0	$1x10^{-3}$	1.0	3.3	0.9	2.5
10	6	3.0	5.0	5.0	$1x10^{-3}$	1.9	5.8		
11	1	4.0	5.0	5.0	$1x10^{-3}$	5.0	7.5	11.3	16.4
12	6	4.0	5.0	5.0	$1x10^{-3}$	16.3	23.9		
13	1	5.0	5.0	5.0	$1x10^{-3}$	3.0	7.0	9.0	12.7
14	6	5.0	5.0	5.0	$1x10^{-3}$	12.0	15.7		
15	1	6.0	5.0	5.0	$1x10^{-3}$	5.7	7.5	15.8	12.7
16	6	6.0	5.0	5.0	$1x10^{-3}$	21.5	20.2		
17	1	3.0	5.0	5.0	$1x10^{-2}$	1.2	4.8	2.0	6.2
18	6	3.0	5.0	5.0	$1x10^{-2}$	3.2	11.0		
19	1	4.0	5.0	5.0	$1x10^{-2}$	3.8	7.8	10.2	12.2
20	6	4.0	5.0	5.0	$1x10^{-2}$	14.0	20.0		
21	1	5.0	5.0	5.0	$1x10^{-2}$	5.3	7.8	11.2	12.2
22	6	5.0	5.0	5.0	$1x10^{-2}$	16.5	20.0		
23	1	6.0	5.0	5.0	$1x10^{-2}$	6.0	7.0	18.5	11.8
24	6	6.0	5.0	5.0	$1x10^{-2}$	24.5	18.8		
25	1	3.0	5.0	5.0	$1x10^{-1}$	1.2	5.5	3.5	12.0
26	6	3.0	5.0	5.0	$1x10^{-1}$	4.7	17.5		
27	1	4.0	5.0	5.0	$1x10^{-1}$	2.0	7.0	10.2	11.3
28	6	4.0	5.0	5.0	$1x10^{-1}$	12.2	18.3		
29	1	5.0	5.0	5.0	$1x10^{-1}$	4.0	5.8	17.0	7.6
30	6	5.0	5.0	5.0	$1x10^{-1}$	21.0	13.4		
31	1	6.0	5.05	5.0	$1x10^{-1}$	4.8	5.8	18.2	7.2
32	6	6.0	5.0	5.0	$1x10^{-1}$	23.0	13.0		
33	1	3.0	5.0	5.0	1.0	1.2	5.7	4.4	11.8
34	6	3.0	5.0	5.0	1.0	5.6	17.5		
35	1	4.0	5.0	5.0	1.0	3.0	4.6	9.1	5.0
36	6	4.0	5.0	5.0	1.0	12.1	9.6		
37	1	5.0	5.0	5.0	1.0	3.7	3.8	11.8	3.7
38	6	5.0	5.0	5.0	1.0	15.5	7.5		
39	1	6.0	5.0	5.0	1.0	4.4	4.6	1/	2/
40	6	6.0	5.0	5.0	1.0	19.0 ppt	11.0 ppt		

1/ Due to ppt estimated to be 2.4 meq/kg/5hr.

2/ Due to ppt estimated to be 10.0 meq/kg/5hr.

Appendix 32. Conditions, treatments and results of Experiment U-65. The pH was controlled to ± 0.2 pH units; temperature was 24.5° ± 0.5°C. Initial K^+ and Rb^+ content of the root material was 19.5 and 0.1 meq/kg respectively.

Trmt. No.	Trmt. Time	Soln. pH	Soln. Composition			Tissue Content		Absorption Rate	
			K^+	Rb^+	UO_2^{++}	K^+	Rb^+	K^+	Rb^+
	hrs		meq/liter			meq/kg		meq/kg/5hr	
1	1	3.0	5.0	5.0	-0-	10.9	1.3	-6.7	-0.2
2	6	3.0	5.0	5.0	-0-	4.2	1.1		
3	1	4.0	5.0	5.0	-0-	20.0	4.5	-0.2	2.9
4	6	4.0	5.0	5.0	-0-	18.8	7.4		
5	1	5.0	5.0	5.0	-0-	24.0	6.9	12.7	9.9
6	6	5.0	5.0	5.0	-0-	36.7	16.8		
7	1	6.0	5.0	5.0	-0-	25.5	6.9	13.3	10.4
8	6	6.0	5.0	5.0	-0-	38.8	17.3		
9	1	3.0	5.0	5.0	$1x10^{-3}$	13.4	1.5	-5.9	0.5
10	6	3.0	5.0	5.0	$1x10^{-3}$	7.5	2.0		
11	1	4.0	5.0	5.0	$1x10^{-3}$	22.6	5.0	4.4	5.6
12	6	4.0	5.0	5.0	$1x10^{-3}$	27.0	10.6		
13	1	5.0	5.0	5.0	$1x10^{-3}$	25.0	6.9	11.3	10.1
14	6	5.0	5.0	5.0	$1x10^{-3}$	36.3	17.0		
15	1	6.0	5.0	5.0	$1x10^{-3}$	25.0	6.9	16.5	11.9
16	6	6.0	5.0	5.0	$1x10^{-3}$	41.5	18.0		
17	1	3.0	5.0	5.0	$1x10^{-2}$	16.5	2.5	0.4	2.7
18	6	3.0	5.0	5.0	$1x10^{-2}$	16.9	5.2		
19	1	4.0	5.0	5.0	$1x10^{-2}$	24.0	5.2	9.8	8.1
20	6	4.0	5.0	5.0	$1x10^{-2}$	33.8	13.3		
21	1	5.0	5.0	5.0	$1x10^{-2}$	24.5	6.3	11.8	11.2
22	1	5.0	5.0	5.0	$1x10^{-2}$	36.3	17.5		
23	1	6.0	5.0	5.0	$1x10^{-2}$	25.0	6.5	17.0	12.3
24	6	6.0	5.0	5.0	$1x10^{-2}$	42.0	18.8		
25	1	3.0	5.0	5.0	1.0	20.0	3.2	5.0	5.8
26	6	3.0	5.0	5.0	1.0	25.0	9.0		
27	1	4.0	5.0	5.0	1.0	24.0	5.0	9.8	9.5
28	6	4.0	5.0	5.0	1.0	33.8	14.5		
29	1	5.0	5.0	5.0	1.0	24.0	5.4	3.8	4.6
30	6	5.0	5.0	5.0	1.0	27.8	10.0		
31	1	6.0	5.0	5.0	1.0	22.5	5.2	3.8	4.6
32	6	6.0	5.0	5.0	1.0	26.2	9.8		
33	1	3.0	5.0	5.0	$1x10^{-1}$	21.4	3.5	6.9	8.2
34	6	3.0	5.0	5.0	$1x10^{-1}$	28.3	11.7		
35	1	4.0	5.0	5.0	$1x10^{-1}$	21.8	3.6	17.9	12.4
36	6	4.0	5.0	5.0	$1x10^{-1}$	33.7	16.8		
37	1	5.0	5.0	5.0	$1x10^{-1}$	21.4	3.5	16.1	11.7
38	6	5.0	5.0	5.0	$1x10^{-1}$	37.5	15.2		
39	1	6.0	5.0	5.0	$1x10^{-1}$	21.4	3.9	6.8	6.4
40	6	6.0	5.0	5.0	$1x10^{-1}$	28.2	10.3		