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Growth and yield of barley (*Hordeum vulgare* L.) as affected by salinity and mixed ammonium and nitrate nutrition

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GROWTH AND YIELD OF BARLEY (*Hordeum vulgare L.*) AS AFFECTED BY SALINITY AND MIXED AMMONIUM AND NITRATE NUTRITION

by

Arshad Ali

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Arshad Ali entitled Growth and Yield of Barley (Hordeum vulgare L.) as Affected by Salinity and Mixed Ammonium and Nitrate Nutrition.

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Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

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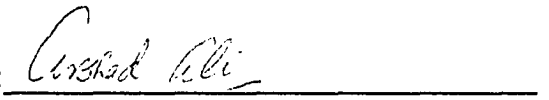
SIGNED: 

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ABSTRACT

Absorption and utilization of N by plants has been shown to be affected by the N form supplied and salinity. This study was conducted to determine the growth and N uptake of barley grown in modified Hoagland-Arnon nutrient solution containing different NH_4^+-N / NO_3^--N ratios and various salinity levels in the growth chamber. The first experiment was conducted to study the N uptake rate at five different NH_4^+-N / NO_3^--N ratios and three salinity levels (0, 6 and 12 bars). No ^{15}N was applied in this experiment. The second experiment was conducted with the same objectives with modification in the salinity levels based upon the results of experiment 1. The salinity levels were 0 and 8 bars. The third experiment was similar to the second experiment except the duration of the study that was 45 days instead of 30 days. The NH_4^+-N / NO_3^--N ratios were 0/100, 25/75, 50/50, 75/25 and 100/0. The total N concentration in all treatments was 100 ppm. Solutions were sampled after every 15 days during all experiments and analyzed for ammonium and nitrate concentration. For the short term ^{15}N uptake study (experiments 2 and 3), either ammonium labelled ^{15}N or nitrate labelled ^{15}N was added to each NH_4^+-N / NO_3^--N treatment for 6, 12, and 24 hours period on the last day of experiment 2 and 6, 12, and 18 hours period on the last day of experiment 3.

Mixed N nutrition resulted in greater accumulation of whole plant-N than plants receiving only NO_3^- or NH_4^+ as the source of N. Labelled nitrate recovery was highest in the 50 % NH_4^+ treatment. The same trend was evident from the solution sample analysis. In all the three experiments, plants produced significantly higher dry matter

yields when grown with mixed N nutrition than with NH_4^+ or NO_3^- alone. Total dry matter production, nitrogen uptake, root and shoot N contents, ^{15}N content and water uptake decreased with increasing salinity levels in all the three experiments. The plants fed with $^{15}NO_3^-$ source inhibited nitrate uptake more severally under saline conditions than the NH_4^+-fed plants under similar conditions. Salinity and N nutrition interaction was found significant in all experiments.

CHAPTER 1

INTRODUCTION

Nitrogen is unique among the essential mineral elements in that plants can utilize it in both anionic (NO_3^-) and cationic (NH_4^+) forms. Although most species can grow with either form, it has been well documented that supplying plants with mixtures of NO_3^- and NH_4^+ often results in better vegetative growth and enhanced nutrient accumulation than either form alone (Haynes and Goh, 1978: Hageman, 1984). Increases of up to 50 % in both growth rate and yield as a result of controlled ammonium addition to nitrate supply have been reported by Cox and Reisenauer (1973) and Reisenauer (1978) for wheat. Nitrogen assimilating enzymes distribution studies by Lewis, James and Hewitt (1982) indicate that the separation of nitrate and ammonium assimilation into shoot and root compartments may be responsible for these effects in young barley plants. Supply of N in solution entirely as NH_4^+ or NO_3^- has been shown to inhibit plant growth when compared to plant growth in solution containing 25 or 50 % of either N form. The use of ammonical fertilizers along with nitrification inhibitors may result more of mixed N (i.e. both NH_4^+ and NO_3^-) nutrition than is normally available to plant roots.

Weissman (1951) reported that dry weight, total protein content, and protein concentration, for young wheat seedlings (*Triticum aestivum L.)* grown in solution culture, were all higher in leaves of plants grown on NH_4^+ and NO_3^- than on either form alone. Comparing plant growth in solutions with various NH_4^+/NO_3^- ratios to those

containing all NO_3^-, Gashaw and Mugwira (1981) reported that 31-day-old wheat, rye (*Secale cereale L.*) and triticale (Triticosecale, Wittmack) plants were all heavier when grown with N mixtures containing 25 or 50 % NH_4^+ than when grown with 100 % NO_3^-.

Saline environments are usually characterized by a high NaCl content, which exerts both osmotic and specific ion effects on plant growth and development. Plants can be affected by high contents of Na^+ and Cl^- in their root zone through the reduction of the cell water potential, by direct toxic effects of accumulated salts within the plant on the protoplasm, and by inhibition or stimulation of absorption of other ions by plants (Epstein, 1962 and 1972; Greenway, 1973).

Among agricultural crops, Barley (*Hordeum vulgare L.*) is considered a highly salt tolerant plant and is grown as a major crop under both saline and non-saline conditions. There is a substantial difference in the yield and productivity of barley under these different conditions. This may be due to detrimental effects of salinity through the inhibition of water and nutrient uptake by plants. Even under normal (non-saline) conditions, the most common nutrient deficiency in the production of barley is nitrogen. Under saline conditions this problem may be more pronounced.

The mechanisms by which salinity adversely affects plant growth and development are still being challenged where nutrient (particularly nitrogen) uptake and metabolism are concerned. Inhibition of nitrogen metabolism in plants and low N uptake rate by bean plants induced by excess salt or by water deficit as reported by Frota and Tucker (1972, 1978a and 1978b) and Saad (1979), may be the most important factors responsible for abnormal plant metabolism and reduction in the rate of growth and yields.

There is a need for better definition of the conditions determining the influences of the form of nitrogen supplied and NH_4^+ to NO_3^- ratio on the growth and yield of barley. The complete explanation for the reduced growth rate and productivity of plants must, however, await further investigations. The objective of this study was to determine the effects of salinity and mixed N nutrition on dry matter yield, N partitioning and long and short term N uptake by barley plants grown under controlled conditions.

CHAPTER 2

LITERATURE REVIEW

Nitrogen is the mineral element that is required in the greatest amounts by plants (Bloom,1988) and is considered to be a major limiting factor to plant growth. Dry plant material contains about 2 to 4 % N (Mengel and Kirkby, 1987). Nitrogen (N) is used by plants for amino acids and purine and pyrimidine bases, the nitrogenous building blocks of proteins and nucleic acids, respectively (Lehninger, 1982). Ammonium (NH_4^+) is a reduced form and nitrate (NO_3^-) is a highly oxidized form of N. Most plants are able to use either NH_4^+ or NO_3^- as their sole source of N. Higher plants can not utilize atmospheric N_2 unless they are associated with N fixing bacteria (Salsac et al., 1987).

2.1: Nitrogen Nutrition of Plants

2.1.1: Uptake Mechanisms

The majority of plants absorb N as ions in the form of NO_3^-, NH_4^+, NO_2^- or amide. Nitrate and NH_4^+ ions are the two dominant forms absorbed (Haynes and Goh, 1977; Lehninger, 1982; Salsac et al., 1987).

2.1.1.1: NH_4^+ Uptake

From a thermodynamic point of view, plants do not need metabolic energy for NH_4^+ uptake, which is accompanied by a transient or even continuous depolarization

of the plasmalemma (Bertl et al., 1984; Ullrich et al., 1984). The literature indicates similarity between the uptake of NH_4^+ and other monovalent cations, particularly K (Dejaegere et al., 1984; Haynes and Goh, 1978). Ullrich et al.(1984) reported the NH_4^+ uptake rates were much higher in N-starved plants. This result is consistent with the assumption of an NH_4^+ uniport by Bertl et al. (1984). In contrast to these findings, Mengel et al. (1976) demonstrated that the uptake of NH_4^+ was not affected by K under reducing conditions. These authors suggested that under reducing conditions, N may be absorbed mainly in the form of ammonia by diffusion. Whether NH_4^+ uptake is an active process is still an open question (Mengel and Kirkby, 1987).

2.1.1.2: NO_3^- Uptake

The NO_3^- uptake mechanism is still controversial. The NO_3^- / H^+ cotransport with excess protons is the most supported hypothesis (Ullrich, 1987). Many workers believe that NO_3^- absorption is an active and energy requiring process (Heimer, 1975; Mengel and Kirkby, 1987; Swader, 1975) with NO_3^- moving against an electrochemical gradient.

Nitrate absorption by NO_3^- depleted plants exhibits an early lag (induction) period followed by a more rapid rate of absorption (Haynes and Goh ,1978). This apparent induction period has been observed in many plants, including corn *(Zea mays L.)* (Jackson et al., 1973), barley (Blevins et al., 1974; Raju and Mukhopadhyay, 1976; Rao and Rains, 1976b), cotton (*Gossypium hirsutum*), tobacco (*Nicotiana rustica*) (Minotti et al., 1968), wheat (Ashley et al., 1975; Jackson et al., 1972; Minotti et al., 1968, 1969b),

and in tobacco cell cultures (Hemier, 1975; Heimer and Filner, 1971). The reported induction period of the nitrate transporter varied from species to species ranging from few to several hours (Breteler and Nissen, 1982; Goyal and Huffaker, 1986; Jackson et al., 1972; Neyra and Hageman, 1975; Rao and Rains, 1976a). The rate of uptake after induction appears to be dependant on a critical internal NO_3^- concentration, which is affected by external concentration (Neyra and Hageman, 1975).

Studies have shown that the mechanism of NO_3^- uptake is complex. At low NO_3^- concentration (less than 0.001 M), uptake fits a single Michaelis-Menten equation (Haffaker and Rains, 1978). At higher concentration, a dual mechanism of absorption become apparent so that Michaelis-Menten kinetics is not followed. The second mechanism is probably the functional one which leads to NO_3^- accumulation in plants grown in fertilized media. Goyal and Huffaker (1986) also reported a dual NO_3^- transport system, whereas only single systems were found for transport of NO_2^- and NH_4^+. Huffaker and Rains (1978) reported that plants which have efficient mechanisms for NO_3^- absorption appear to have relatively low K_m values and consequently, have a high affinity for NO_3^- in soils of low fertility.

Many researchers believe NO_3^- uptake and NO_3^- reductase activity (NRA) are closely related under normal conditions (Brunetti et al., 1972; Lycklama, 1963). Both processes are subject to regulation by the same substances (Haynes and Goh, 1978): induction by NO_3^- and NO_2^-, and inhibition by NH_4^+ and amino acids (Schloemer and Garrett, 1974). The increase in the rate of NO_3^- uptake in *Zea mays* roots (Neyra and Hageman, 1975) and *Triticum durum* (Brunetti et al., 1972) parallels the induction of

NR. Some studies (Schloemer and Garrett, 1974; Swader et al., 1975), however, showed evidence that NRA and NO_3^- uptake is not linked. Recently, Schuster et al.(1989) did an extensive study on effect of N sources, light, and a plastidic factor on the appearance of NR. They found four different forms of NR, two appeared in the presence of NO_3^- and the other two were found in the presence of NH_4^+. This indicates that NO_3^- and NR are not completely associated.

2.1.2: Factors Affecting Uptake of NH_4^+ and NO_3^-

2.1.2.1: Concentration of NH_4^+ and NO_3^-

The most important factor affecting the uptake of NH_4^+ is its concentration in the root environment (Munn and Jackson, 1978). Increasing the supply of NH_4^+ in a medium may increase its uptake to a point of toxicity in the plant (Bloom, 1988).

Nitrate uptake increases with increased external supply of NO_3^-. When the NO_3^- supply is high, it will be absorbed in excess of the needs of plants and accumulate internally. The external supply of NO_3^- is probably the most important environmental factor controlling the accumulation of NO_3^- in plants (Maynard et al., 1976).

2.1.2.2: NH_4^+ and NO_3^- Nutrition

The NH_4^+: NO_3^- ratio in a medium is an important factor for uptake of N (Mills et al., 1976). The inhibitory effect of NH_4^+ on NO_3^- absorption has been well documented (Jackson, 1978). The inhibition in ryegrass, wheat, and apple was correlated with a substantially reduced uptake of NO_3^- by the plants (Haynes and Goh, 1978). Frith

(1972) showed that apple plants grown in NH_4NO_3 solution had lower NRA than those grown in other NO_3^- solutions without NH_4^+, concluding it is likely that NH_4^+ has two modes of inhibition: one on the actual uptake and another one on the NRA, presumably on NR resynthesis. In general, there are three ways in which NH_4^+ can become inhibitory for NO_3^- uptake: (1) repression of the formation of new NO_3^- carrier and NR; (2) inhibition of the carrier and/or NR either by NH_4^+ or by one of its metabolic products; and (3) physical inhibition of the NO_3^- uptake by a severe reduction of membrane potential (Ullrich, 1987). Other evidence suggests that NH_4^+ does not depress NO_3^- uptake in Lemna minor L. (Orebamjo and Stewart, 1975), wheat (Lycklama, 1963) and rice (Shen, 1969).

The inhibitory effect of NO_3^- on NH_4^- uptake has been investigated by Deignan et al. (1988), who postulated that the inhibitory effect of NO_3^- on NH_4^- uptake in wheat was more pronounced than the reciprocal inhibitory effect.

Plants differ in their abilities to acquire NH_4^+ and NO_3^- from a medium and in their tolerance of NH_4^+. Species of annual range grasses (*Avena, Bromus,* and *Lolium*) were shown to differ in ability to absorb NO_3^- from a nutrient solution (Huffaker and Rains, 1978). Bromegrass (*Bromus inermis L.)*, corn, soybean (*Glycine max Merr.*), and sorghum (*Sorghum bicolor L.*) also have been shown to differ in their capacity to absorb NO_3^- (Warncke and Barber, 1974). Differences for NO_3^- acquisition within species have been observed for barley (Smith, 1973), corn (Hoener and Deturk, 1938) and wheat (*Triticum aestivum)* (Brunetti et al., 1972). Differences among species and cultivars with respect to NO_3^- accumulation have been documented by Maynard et al. (1976).

Results obtained by Krajina et al. (1973) illustrate the different responses of different species. Of the four species of seedling conifer studied, two did best with NO_3^- (*Pseudotsuga menziesii* and *Thuya plicata*) while one did best with either NH_4^+ or a combination (*Tsuga heterophylla)* and one did best with NH_4^+ (*Pinus contorta*). These preferences reflect the habitats in which these plants have evolved. *P. menziesii* and *T. Plicata* are found naturally in soils where nitrification takes place while *P. contorta* and *T. heterophylla* commonly occur where nitrification does not actively occur (Krajina, 1969). Those plants which did best with nitrate exhibit symptoms of Mg and Ca deficiency when supplied with NH_4^+ (Krajina et al., 1973), whereas *P. contorta* showed no such deficiencies under the same nutrient regime.

Many *Solanaceous* crops, including tobacco (*Nicotiana tabaccum)* (McCants et al., 1959), potato (*Solanum tuberosum)* (Davis et al., 1986) and tomato (*Lycopersicon esculentum)* (Cox and Reisenauer, 1977; Green and Holley, 1973) have been reported to grow best with NO_3^-. There are also numerous other reports on a variety of plants with respect to their responses to different N forms. Bean, sweet corn (Maynard and Barker, 1969), pea (*Pisum sativum)*, cucumber (*Cucumis* sativus) (Barker and Maynard, 1972; Maynard and Barker, 1969), potato (Polizotto et al., 1975), tomato (Wall, 1940), and viburum (*Viburnum plicatum)* (Dirr, 1975) have been found to have increased growth as the proportion of NO_3^- to NH_4^+ increased. Carnation (*Dianthus caryophyllus)* (Schekel, 1971), rose (*Catharanthus roseus)* (Loyola-Vargas et al., 1986), apple (*Pyrus malus)* (Green and Holley, 1973), corn (Below and Gentry, 1988) and sunflower (*Helianthus annuus)* (Weissman, 1964) showed superior growth when both NH_4^+ and NO_3^- were

given. Azalea (*Rhododendron spp.)*(Cox and Seeley,1984), blueberry *(Vaccinum spp.)* (Peterson et al., 1988), rice (Peterson et al., 1988; Ravindra and Pandey, 1978), and cranberry (Greidanus et al., 1972) grew well with all N as NH_4^+.

Many researchers have reported that the combination of NH_4^+ and NO_3^- at certain ratios gave the highest growth rate and yield in several crops, including carnation (Green et al., 1978), radish *(Raphanus sativus)* (Ota and Yamamoto, 1987, 1989) and wheat *(Triticum aestivum)* (Cox and Reisenauer, 1973, 1978). A mixture of NH_4^+ and NO_3^- produced the greatest growth and protein production for the majority of species; the optimum ratio probably differs for different species and may change with age of the plant (Michael et al., 1970). Soon and Miller (1977) reported that dry weight, total protein, protein per unit weight and protein percentage of total N were all greater in leaves of sunflower fed with NH_4^+ and NO_3^-. Alleviation of inhibitory effects of NH_4^+ on radish growth by the addition of NO_3^- at more than 10 % of the concentration of NH_4^+ was observed (Ota and Yamamoto, 1987, 1989). The yield and growth enhancement were believed to have resulted from the reduced energy requirement in using NH_4^+ instead of NO_3^- in protein synthesis.

2.1.2.3: Medium pH

The pH of the growing medium exerts a profound effect on N uptake (Haynes and Goh, 1978). A most important difference between NH_4^+ and NO_3^- uptake is in their sensitivity to pH. Ammonium is taken up best at a neutral pH and its uptake is depressed as the pH falls (Mengel and Kirkby, 1987). A more rapid NO_3^- uptake

occurs at low pH values (Rao and Rains, 1976b) and above pH 6 NO_3^- uptake rate decreases (Rao and Rains, 1976a). Minotti et al. (1969a) reported that high acidity does not affect NO_3^- uptake until the pH falls below 4.5. However, Rao and Rains (1976a) observed no decline in NO_3^- uptake at pH values as low as 4.0. These workers suggested that reduction in NO_3^- uptake at high pHs may be due to the competitive effect of OH^- ions suppressing the NO_3^- uptake transport system. Michael et al. (1965) found that the uptake rates of both NH_4^+ and NO_3^- by various plant species were equal at a pH of 6.8. At pH 4.0, however, the uptake of nitrate was higher than that of NH_4^+. Findenegg et al., (1989) found that the accumulation of NH_4^+ in the plant increased as solution pH increased over the range of pH 4.0 to 7.0.

Many researchers (Barker et al., 1966a, 1966b; Tolley-Henry and Raper, 1986) have shown that the control of the pH results in the elimination of physiological responses caused directly by NH_4^+ and NO_3^- per se. Peet et al., (1985) and Rufty et al., (1983) working with tomato and soybeans, respectively, concluded that plants can effectively utilize either NH_4^+ or NO_3^- as long as the root zone pH is controlled. Wander and Sites (1956) found that pH affects the cation exchange capacity of rough lemon seedling roots. The maintenance of a neutral pH in the root environment favors the detoxification of NH_4^+ in the roots and limits its transport to the shoots. Many of the favorable growth responses of plants to NH_4^+ nutrition have been observed under conditions where the pH of the soil was alkaline (Lorenz et al., 1974). Even when all of the N is ammoniacal, nearly normal growth can be obtained if the pH of the medium is buffered near neutrality (Barker, 1967; Bloom, 1988; Sander and Barker, 1978; Tolly-

Henry and Raper, 1986). Tolly-Henry and Raper (1986) tested the hypothesis that the reduction in growth of NH_4^+ fed soybean is a consequence of increased acidity rather than N stress alone. The authors proved that increased acidity of one pH unit (from 6.1 to 5.1) could reduce dry matter accumulation by 40 % within 14 days. These results along with McElhanon and Mills (1978) suggested that the adverse effects of NH_4^+ on plant growth occur after absorption. However, Mengel and Kirkby (1987) pointed out that many plant species can tolerate high levels of NH_4^+ at acid to neutral pH values because the higher H^+ concentration depresses the NH_3 concentration. Several species, including wheat (Breteler and Smith, 1974), sugar beet (Breteler, 1973), and rice (Dijkshoorn and Ismunadji, 1972), grew well at NH_4^+ levels up to several mM provided that the pH was between 4 and 6.

2.1.2.4: Other Ions

Interaction among ions, that is antagonism between similar charges and attraction among opposite charges, is reported in the literature. Many researchers have reached a similar conclusion that uptake of NH_4^+ and NO_3^- is affected by other ions. Calcium and Mg^{++} contents in plants were low when NH_4^+ was the sole N source (Barker and Maynard, 1972). Phosphorus and S concentrations have increased relative to those in plants grown with NO_3^--N (Blair et al., 1970). Increasing the supply of Ca or K generally accelerates the uptake. The effect of cations on NO_3^- uptake may be to counter the negative charges on the roots' cell wall so that NO_3^- may migrate more

closely to the plasmalemma and its uptake sites than they could in the absence of these ions (Elzam and Epstein, 1965).

Ali et al. (1985) observed that the N metabolism of rice was impaired by the limited supply of minerals when plants were fed with NO_3^-, but not when they were fed with NH_4^+. Ali et al. (1987) reported that in wheat the influence of K on the absorption of NO_3^- was stronger than on the absorption of NH_4^+. They also observed that the influence of K was stronger in the translocation of N from roots to shoots compared to Ca and Mg. Several workers (Cram, 1973; Glass and Siddiqi, 1985; Kafkafi et al., 1982; Smith and Fox, 1977; Weigel et al., 1973) noted an interaction between uptake of Cl and NO_3^- ions. These workers suggested that NO_3^- and Cl ions are mutually inhibitory for the uptake of the other ion.

2.1.2.5: CO_2, Light and Carbohydrate

NH_4^+ Uptake: Ammonium uptake by plants shows a wide diurnal variation (Van Egmond, 1978). The diurnal pattern can be disturbed by providing continuous light or by supplying glucose to the nutrient medium during darkness. Ammonium uptake is greater in light than in darkness and increases with increasing light intensity (Van Egmond, 1978). The decline in NH_4^+ uptake in darkness is due to the depletion of carbohydrate reserves in roots (Reisenauer, 1978). Plants well supplied with carbohydrates are better able to utilize NH_4^+ than are energy starved plants. Seedlings and germinating seeds are sensitive to NH_4^+, because of their low carbohydrate contents

and inabilities to assimilate NH_4^+ rapidly enough to prevent its internal accumulation (Barker and Mills, 1980).

Reduction of carbon supply to the roots, by ringing bean (*P. vulgaris)* to remove the phloem, resulted in less N uptake than in intact plants, and NH_4^+ uptake was reduced more than that of NO_3^-. Additions of sucrose and malate increased NH_4^+ uptake more than NO_3^- (Michael et al., 1970).

NO_3^- Uptake: Huffaker and Rains (1978) have shown NO_3^- uptake to be greater in the absence of CO_2 than in its presence in the atmosphere. The effects of CO_2 on NO_3^- uptake were greater at high light intensities than at low intensities (Huffaker and Rains, 1978). The competition between CO_2 reduction and NO_3^- uptake may be for energy or reducing power generated by light or due to stomatal closure in the presence of CO_2. This results in a lessening of transpiration and water flux through the roots to shoots which causes a greatly diminished rate of NO_3^- uptake (Minotti and Jackson, 1970). Supplying an energy source such as glucose in the nutrient solution aids the maintenance of uptake activity by excised roots (Minotto and Jackson, 1970). Thus, a continual supply of energy appears to be essential for maintenance of NO_3^- uptake.

Nitrate reductase is activated by light (Jordan and Huffaker, 1972). Since activation of NR and stimulation of NO_3^- uptake are red/far-red reversible, phytochrome may be involved in metabolizing an inducer or in mobilizing NO_3^- from a storage pool to a metabolic pool (Jones and Sheard, 1975).

Seasonal solar radiation influences the NH_4^+:NO_3^- ratios required by plants. Under low radiation conditions carnation may be grown with 1/3 NH_4^+, while under high

radiation conditions NO_3^- alone provides the best growth (Green and Holley, 1973). For the flowering of chrysanthemums, Crater et al. (1974) recommended NO_3^- during the fall and winter months and NH_4NO_3 for the rest of the year. Hewitt (1970) observed that plants were more tolerant to low light conditions when fed with NO_3^-. Ta et al. (1981) observed growth of rice (*Oryza sativa)* in the summer was better with NO_3^- than NH_4^+. However, the growth of these plants in the autumn was better with NH_4^+ than NO_3^-, suggesting that seasonal climate conditions, such as light intensities, may be very important in determining the response of the plants to NH_4^+ and NO_3^-. Zornoza et al. (1987) reported similar results in pepper (*Capsicum anuum)*, suggesting a light intensity-N form interaction that favors NO_3^- nutrition for pepper at high light intensities. In tomato (*Lycopersicon esculentum)*, reduced light level (33 % of incident light) decreased NH_4^+ accumulation in shoots (Magalhaes and Wilcox, 1983). Barua and Dey (1986) found that in young leaves the NRA was consistently higher under 50 % sunlight than under full sunlight. Michael et al. (1970) observed that young potatoes attached to parent tubers took up both NH_4^+ and NO_3^-. When the tuber was removed, NO_3^- uptake increased. These authors also found that girdled bean took up less total N, but NO_3^- uptake exceeded NH_4^+ uptake. Kirkby and Hughes (1970) also concluded that plants containing larger quantities of carbohydrates assimilated NH_4^+ more rapidly.

2.1.3: Properties of N Assimilation

2.1.3.1: Processes of N Assimilation

Nitrogen metabolism is a complex process. When NO_3^- is absorbed by the plant, it must be reduced to NH_4^+ before it is further assimilated. But NH_4^+, once absorbed, can be used immediately in the synthesis of amino acids and other organic compounds (Haynes and Goh, 1978).

It is established (Beevers and Hageman, 1972; Hewitt et al., 1976; Losada and Guerrero, 1979) that the assimilatory NO_3^--reducing system consists of only two metalloproteins, namely NR and nitrite reductase(NiR), which catalyze the stepwise reduction of NO_3^- to NO_2^- to NH_4^+. This process require 8 electrons, which are delivered by the reductase enzymes from NADH or NADPH formed during photosynthesis. Both enzymes are suited for electron transfer since NR contains riboflavin (FAD) and Mo^{+3}, and NiR contains Fe^{+2} (Salisbury and Ross, 1978).

Ammonium, either the end product of NO_3^- reduction or absorbed from the medium, is incorporated into organic compounds to produce glutamine and finally 2 glutamates. The two major routes known to be responsible for the conversion of NH_4^+ into alpha-amino-N are: the glutamate dehydrogenase pathway, and glutamine synthetase-glutamate synthetase pathway (Lea and Miflin, 1979; Salisbury and Ross. 1978).

Since the reduction of NO_3^- costs a large amount of energy, a greater yield is expected for plants which assimilate NH_4^+ directly rather than reduce NO_3^- and assimilate NH_4^+. However, literature shows that plants supplied with NH_4^+ experience decrease in yield between 15 to 60 % (Salsac et al., 1987).

Carbohydrate metabolism is directly related to N assimilation, since carbohydrates are used as a source of carbon as well as respiratory energy for reductive amination. Nitrate reduction can take place in both green and non-green tissues, since sugar produced by photosynthesis migrates from chloroplast to cytoplasm and provides NADH during glycolysis (Haynes and Goh, 1978). In dark conditions, both photosynthetic and non-photosynthetic cells are able to assimilate NO_3^- and can use carbohydrates or other reduced compounds for the reduction of NO_3^- and NO_2^- (Losada et al., 1981).

In the case of NO_3^- assimilation, production of NH_4^+ is metabolically regulated by the oxidation of co-enzymes for the reductase. In NH_4^+ assimilation, however, there is relatively less control, which may lead to a rapid depletion of carbohydrates (Kirkby, 1968; Kirkby and Hughes, 1970). If this happens, ammonium begins to accumulate with ensuing toxic effects. In the presence of adequate carbohydrate supplies, NH_4^+ absorption-assimilation should proceed at a faster rate than that of NO_3^-.

2.1.3.2: Sites of NO_3^- Assimilation

The approaches used to determine the sites of inorganic N assimilation into organic N are analyses of sap collected from a root or xylem (Haynes and Goh, 1978; Shelp, 1987b) and the metabolic activities of the roots and leaves of plants, particularly NRA. Both methods have shown that there are genetically determined differences between species in the extent to which NO_3^- is assimilated in roots and shoots (Stewart et al., 1987). Nitrate reduction in higher plants is not restricted to the leaves, but also

takes place in roots, embryos, cotyledons, scutella, aleurone cells, pollen grain, and etc. (Beevers and Hageman, 1972; Haynes and Goh, 1978).

In the Roots: The xylem of many woody plants contains all its N in organic form. It is assumed that NO_3^- reduction in these plants takes place entirely in the roots, Nitrate reductase activity has been demonstrated in the roots of apple trees supplied with NO_3^- (Frith, 1972). The lack of NRA in leaves has also been reported for several non-woody plants, suggesting that in such plants NO_3^- reduction in the roots must be of paramount importance (Routley, 1972). These include many species of Ericaceae such as blueberry (*Vaccinium angustofolium L.*), cranberry (*V. macrocarpon Ait.*), and many species of Rhododendron (Dirr, 1974; Routley, 1972; Townsend, 1970). The capacity of root tissue to assimilate NO_3^- is related to its carbohydrate content (Minotti and Jackson, 1970).

In the Leaves or Shoots: In general, those plants that do not have the ability to reduce NO_3^- in their roots translocate N into the leaves in the form of NO_3^-, and reduce it there. Some plants have xylem sap containing 95 to 99 per cent of its N as free NO_3^-, and NRA cannot be detected in the roots (Wallace and Pate, 1967). These plants accumulate more NO_3^- than plants which reduce the majority of NO_3^- in the roots (Haynes and Goh, 1978). In the leaves of C_4 plants, NO_3^- reduction appears to occur predominantly or exclusively in the mesophyll cells (Losada et al., 1981; Moore and Black, 1979).

In the Roots and Shoots (or Leaves): When fed with NO_3^- Many herbaceous species are capable of maintaining active NR in both roots and shoots and both NO_3^- and organic N are found in their xylem sap (Pate, 1971). For example, in broccoli (Brassica

oleracea) NO_3^- reduction occurred in both roots and shoots, as shown by composition of phloem exudate and xylem sap (Shelp, 1987b).

An ^{15}N investigation in barley indicated that the shoot is the main organ of NO_3^- assimilation and the root is the major organ of NH_4^+ assimilation (Lewis and Chadwick, 1983) when 100 % NO_3^- or 100 % NH_4^+ were fed, respectively. Combined root and shoot assimilation was evident when both are fed to plants. Lewis et al. (1982) and Murphy and Lewis (1987) found similar results in barley and in maize.

Generally the movement of nitrogenous substances from the root to leaves occur mainly in the xylem (Pate, 1973) even though Martin (1971) showed that in kidney bean (*Phaseolus vulgaris L.*) it takes place both in the xylem and in the phloem, especially with NH_4^+.

2.1.3.3: Sites of NH_4^+ Assimilation

In contrast to NO_3^- assimilation, which occurs in both root and shoot, NH_4^+ assimilation takes place only in the root system (Raven and Smith, 1976; Stewart et al., 1987). The shoot is supplied with a mixture of amino acids, amides and organic acids which can be incorporated into cell material (Raven and Smith, 1976).

2.1.4: Effects of NH_4^+ and NO_3^- on Plant Performance

2.1.4.1: Effects of NH_4^+ and NO_3^- on Physiological Processes

Ammonium-fed plants have higher concentrations of total N (Kirkby, 1968), free NH_4^+, amides and free basic amino acids (Ikeda et al., 1974; Kirkby, 1968; Macleod and Carlson, 1965; Polizotto et al., 1975; Wander and Sites, 1956; Yoshida,

1969). Wander and Sites (1956) found a higher percentage of N in NH_4^+ than in NO_3^- grown rough lemon seedlings; but the total N utilized as shown by dry weights of leaves was greater when NO_3^- was used. Ammonium applied during the fruiting stage of tomato resulted in the rapid development of blossom end rot of fruit, due to the inhibitory influence of NH_4^+ on Ca uptake (Wilcox et al.,1973). Contents of organic acids such as malic acids were significantly lower in NH_4^+ fed plants (Dijkshoorn, 1973).

Excessive NH_4^+ accumulation in tomato (Maynard et al., 1968; Wall, 1940) and resultant toxicity symptoms (Barker et al., 1967; Maynard et al., 1968; Wall, 1940) can be reduced or eliminated by increasing K concentrations. Nelson and Hsieh (1971) found that the critical NH_4^+: K ratio in fresh chrysanthemum tissue, indicative of NH_4^+ toxicity, ranged from 0.025 to 0.026. Barker et al. (1967) explained the NH_4^+-K relationship in terms of protein stability. Potassium is bound to protein and since NH_4^+ and K share many similar properties, they may substitute for one another. When NH_4^+ replaces K, H-bonding with adjacent OH^- group in the protein molecule is possible. If this occurs, the tertiary structure changes leaving the protein molecule open to proteolytic action.

Ideally, NH_4^+ should be the best source of N, for it should be used more efficiently in the plant than would NO_3^- (Barker and Mills, 1980). However, when sufficient N is supplied to meet the goals of maximum production and N is supplied only in the NH_4^+ form, the toxic reactions of accumulation of uncomplexed NH_4^+ override the potential increased yield. With NH_4^+ nutrition, much of the energy production of the plant must go into carbon skeletons for the incorporation of NH_4^+ and its detoxification.

This process diverts energy and carbohydrates away from growth. Other hypotheses explain the decrease in plant growth caused by NH_4^+ nutrition in terms of lack of mineral ions or insufficient water for growth. The activity of NH_4^+ assimilating enzymes leads to a significant increase in soluble reduced N (Chaillou et al., 1986; Viets et al., 1946). However, this increase cannot compensate for the lack of mineral ions and organic ions (Chaillou et al., 1986). Ammonium nutrition leads to insufficient water uptake due to decreased solute concentration in the vacuoles (Viets et al., 1946). The increased uptake of P, SO_4, and Cl never can compensate for the deficit of organic anion synthesis (Chaillou et al., 1986). Raven (1985) studied the cost-benefit of various physiological processes. The computed photon cost of growth with N_2 fixation and the processes associated with the regulation of pH are 9 % higher than those of growth with NH_4^+. The cost of growth with NO_3^- depends on the location of NO_3^- reduction and the mechanism of OH^- disposal, and it is 5 to 12 % more than that for growth with NH_4^+ as N source.

Ammonium-fed plants contain high levels of free NH_4^+, amide, glucosamine and free basic amino acids, such as lysine and arginine, in comparison with NO_3^- fed plants (Takaki et al.,1968). Rice plants grown with NH_4^+ contain higher levels of asparagine than those grown with NO_3^- (Yoneyama and Kumazawa, 1975). Ikeda et al. (1974) reported serine accumulation in the leaves of NH_4^+ grown tomato. Increases in the amino acids and amines in NH_4^+-fed plants are the results of the detoxification of NH_4^+ by amino acid synthesis with organic acids as the source of carbon. Unlike NO_3^-, NH_4^+ requires no reduction; it is toxic, and must be combined with a non-nitrogenous

compound in order to synthesize such harmless and useful nitrogenous constituents as amino acids, amines or guanidino compounds (Barker et al., 1967).

The production of organic acid anions in NO_3^- fed-plants ensures that an ionic imbalance does not occur. Because the main anion absorbed (NO_3^-) is rapidly reduced to organic compounds, plants generally contains higher levels of free inorganic cations than free inorganic anions, Ionic balance within the plant is achieved by the production of organic acid anions, such as malate and citrate depending on the species (Haynes and Goh, 1978).

High levels of NO_3^- may lead to deficiencies of trace elements (Haynes and Goh, 1978). Nelson and Selby (1974) found that under NO_3^- nutrition, Sitka spruce (*Piceasitchensis*) and Scotch pine (*Pinus sylvestris*) developed moderate chlorosis which was associated with higher organic anion content compared with NH_4^+-grown plants. It was suggested that the chlorosis caused by NO_3^- nutrition could be explained by the competitive chelation hypothesis (Wallace, 1971), whereby the excess organic anions produced under NO_3^- nutrition compete for Fe-bonding sites in the cells, interfering with the function of the Fe. Colegrove and Roberts (1956) observed a better growth of azalea (*R. obtusum*) var. Hexe in NH_4^+ than in NO_3^- . Ammonium reduced the uptake of other cations, decreasing tissue pH while NO_3^- increased base absorption, increasing tissue pH. The increased pH caused inactivation of Fe in the plant; thus Fe chlorosis and other deficiency symptoms appeared. The yield and growth enhancement were suggested to result from the reduced energy requirement in using NH_4^+ instead of NO_3^- in protein synthesis, and increased photosynthetic capacity in wheat (Cox and Reisenauer, 1973).

Ammonium nutrition compared with NO_3^- nutrition generally leads to early flowering. This has been observed in apple (*Pyrus malus*) (Grasmanis and Leeper, 1967), carnation (*Dianthus caryophyllus* L.) (Green et al., 1973), chrysanthemum (*Chrysanthemum morifolium L.*) (Tsujita et al., 1974) and china aster (*Callistephus chinensis*) (Haynes and Goh, 1977). The reason for early flowering in NH_4^+-fed plants is unknown but probably involves interaction since flowering is hormonally controlled (Evans, 1971).

Sharma and Sirohi (1987, 1988) found that there were no significant differences in activities of ribulose 1, 5-biphosphate carboxylase and glycolate oxidase, and $^{14}CO_2$ assimilation in wheat with respect to the forms of N supplied. However, Hall et al. (1984) observed higher activities of those two enzymes per unit leaf area in barley and wheat grown with NH_4^+ than those grown with NO_3^-. The activities of NR and phosphoenolpyruvate carboxylase were higher in plants grown with NO_3^- than in those grown with NH_4^+ (Sharma and Sirohi, 1988).

2.1.4.2: Effects of NH_4^+ and NO_3^- on medium pH

Plants grown in either NH_4^+ or NO_3^- regimes change the pH of their medium. Media containing NO_3^- become more alkaline and those with NH_4^+ more acidic. These results have been reported for a variety of plant species. Maynard and Barker (1969) observed pH values as low as 2.8 with NH_4^+ nutrition in nutrient solutions or in sand culture. External pH changes are believed to be due to excretion of H^+ ions by the plants upon NH_4^+ uptake, and OH^- or HCO_3^- ions upon NO_3^- uptake. The mechanism of

internal pH control and H^+ and OH^- ion fluxes are complicated (Raven and Smith, 1974). The assimilation of NH_4^+ in the cell cytoplasm produces at least one H^+ ion per NH_4^+ ion; assimilation of NO_3^- produces almost one OH^- ion per NO_3^- ion (Raven and Smith, 1976). Hydroxyl ion excretion upon NO_3^- uptake has been observed by Eisele and Ullrich (1975).

The anion and cation balance in NH_4^+ and NO_3^--fed *Ricinus communis* was examined by Van Beusichem et al. (1988). Excess anion over cation uptake was equivalent to net OH^- efflux in NO_3^--fed plants, and the total charge from NO_3^- and SO_4^{2-} reduction equated to the sum of organic anion accumulation plus net OH^- flux. In contrast, a large H^+ efflux in NH_4^+-fed plants was in close agreement with excess cation over anion uptake. Again, this H^+ efflux equated to the sum of net cation assimilation plus organic anion accumulation.

2.1.4.3: Effects of NH_4^+ and NO_3^- on Uptake of Other Ions

The high levels of cations in leaves of NO_3^--fed plants result from two separate processes: ion uptake and ion translocation (Jackson and Williams, 1968). Jackson and Williams (1968) postulated that the rise in the rhizosphere pH as a consequence of the relatively rapid NO_3^- uptake favorably produced conditions for cation uptake. Plants grown with NH_4^+ alone contain lower concentration of Ca, Mg and K, and higher levels of P and S than those grown with NO_3^- alone (Haynes and Goh, 1978). The pH shift caused by NH_4^+ or NO_3^- will alter the solubility and availability of P. Ammonium caused a decrease in the pH, increasing the availability of P (Blair et al.,

1970). Furthermore, lowered rhizosphere pH caused by NH_4^+ increased the ratio of $H_2PO_4^-$ to HPO_4^{2-} ions (Soon and Miller, 1977). The $H_2PO_4^-$ ion is absorbed several times faster than HPO_4^{2-} and, in addition, HPO_4^{2-} salts have a tendency to precipitate on the root surface (Miller et al., 1970).

There is some evidence that NO_3^- enhances translocation of cations (Blevins et al., 1974; Jackson and Williams, 1968; Wilcox et al., 1973) and NH_4^+ inhibits cation translocation (Polizotto et al., 1975). Polizotto et al.(1975) found in potato that, in addition to inhibiting water uptake, NH_4^+ nutrition produced lower Ca and Mg concentrations in the collected exudates than did NO_3^--fed plants. Fertilization of tomato with NH_4^+ resulted in reduced shoot and root contents of Ca, Mg, K, P, and NO_3^-, and solution pH had little effect on tissue ion concentration (Pill and Lambeth, 1977).

Blair et al. (1970) also reported higher levels of P and S in an NH_4^+ treatment and higher Ca, and Mg in a NO_3^- treatment in corn indicating a predominately cation-anion balance effect. Magalhaes and Wilcox (1983) observed that NH_4^+ suppressed K, Ca and Mg accumulation in shoots, increased P contents, and markedly reduced K, Ca, and Mg per unit of root surface. Murtadha et al. (1988) observed symptoms of Ca deficiency on young leaves of sorghum grown in solutions containing a high proportion of NH_4^+ and low levels of Ca, but not when NO_3^- or urea were used with low levels of Ca. These workers postulated that a reduction in Ca concentration in these plants was partially a result of reduced solution pH exerting antagonistic effects on Ca absorption or releasing Ca from cell wall anionic sites. The tissue levels of N, P, Mn, Cu, Zn, and B of broccoli were increased more by NH_4^+ than by NO_3^- nutrition, whereas the reverse

is true for Ca contents, and Mg and K were only slightly affected (Shelp, 1987a). Barker and Ready (1989) described a depression of leaf and stem K in NH_4^+-fed tomato. Other workers (Barker and Maynard, 1972; Barker et al., 1966a) also described that plants grown with NH_4^+ were lower in K, Ca, and Mg than those grown with NO_3^-. This depression of cation accumulation may be due to competition between NH_4^+ and other cations. Ammonium depression of accumulation of divalent cations is greater than that of monovalent cations (Barker and Maynard, 1972).

2.1.4.4: NH_4^+ Toxicity

The toxic effects of NH_4^+ on different plant species have been well documented (Kirkby, 1968; Nelson and Hsieh, 1971; Wander and Sites, 1956). Plants that have evolved in soils in which NO_3^- is the primary form of inorganic N available have little tolerance for high levels of NH_4^+ (Barker and Mills, 1980). Ammonium ions are readily absorbed by plant roots, but they must not be absorbed more rapidly than they can be utilized in the cell; otherwise, toxicity occurs (Maynard and Barker, 1969). Toxicity from NH_4^+ occurs when the NH_4^+ remains in the root in large quantities and when NH_4^+ is the dominant form of inorganic N present in acidic media (Maynard and Barker, 1969).

Most cultivated plants exhibit some intolerance to NH_4^+ nutrition (Pardo, 1935). Plants of Ericaceae, which have been evolved or are grown in acidic peaty soils, do best with NH_4^+ (Greidanus et al., 1972). Onions have a tolerance to NH_4^+ nutrition due to

their ability to assimilate NH_4^+ into amides in the roots and bulb (Maynard and Baker, 1969).

Studies indicate that some calcifuge species are adapted to, or at least tolerate, a N supply predominately in the form of NH_4^+ (Ingestad, 1971, 1976). Kirkby (1969) also found that most calcifuges growing naturally in acid soils, where little nitrification takes place, are adapted to use NH_4^+ better than NO_3^-.

Maynard and Barker (1969) reported that roots of NH_4^+-grown plants were poorly developed and brown; but, addition of $CaCO_3$ was effective in overcoming this adverse effects. Cox and Reisenauer (1973) reported that roots were short and thick in NH_4^+-fed wheat. Maynard and Barker (1969) generalized that NH_4^+ toxicity is characterized by an immediate restriction in growth rate, and then by wilting, marginal necrosis and interveinal chlorosis of terminal leaves, followed by death of the entire plant. Germinating seeds are severely damaged and impaired in further growth by NH_4^+ ions (Barker et al., 1970). Chlorosis followed by necrotic leaf spots and stem lesions was observed in tomato (Barker et al., 1967a, 1967b; Maynard et al., 1968; Puritch and Barker, 1967). Interveinal chlorosis and marginal necrosis of poinsettia leaves were observed with NH_4^+ treatment (Boodley, 1970; Bryne and Hasek, 1979; Gaffeny et al., 1982). Ammonium-grown broccoli were stunted and exhibited signs of marginal necrosis on the old leaves, accompanied by an accumulation of NH_4^+ (Shelp, 1987a). Nonparasitic rots, corkiness, and other damage to roots have been associated with the accumulation of NH_4^+ in fumigated or steam sterilized soils (Uljee, 1964). Similar lesions on the stem

of tomato and eggplant (Barker et al., 1967; Puritch and Barker, 1967) are symptoms of NH_4^+ injury which occurs when K is insufficient in the medium (Barker, 1978).

Ammonium toxicity produced other symptoms including leaf roll of potato (Polizotto et al., 1975), necrotic leaf spots and thickened, leathery leaves of chrysanthemum (Nelson and Hsieh, 1971), necrosis in viburnum (Dirr, 1975), dramatically increased number of necrotic spots in poinsettia (Nell and Barrett, 1985) and symptoms of Mo deficiency (Smith, 1957) or Fe or Mn deficiency (Wander and Sites, 1956) in lemon seedlings. Reduced root growth and/or discoloration has been reported in pea and cucumber (Barker and Maynard, 1972), lemon seedling (Wander and Sites, 1956), citrus (Smith, 1957) and chrysanthemum (Nelson and Hsieh, 1971). Excess NH_4^+ reduced root and shoot growth in poinsettia (Boodley, 1970), potato (Polizotto et al., 1975), tomato (Pill and Lambeth, 1977), sugarbeet (Stuart and Haddock, 1968), and rough lemon seedlings (Wander and Sites, 1956).

All of the foregoing symptoms are manifestations of impaired physiological processes. One of the major effect of NH_4^+ is on photophosphorylation (Haynes and Goh, 1978). Ammonium acts as a ferryboat-type uncoupler, inhibiting ATP formation in both chloroplasts and mitochondria but permitting electron flow (Puritch and Barker, 1967; Salisbury and Ross, 1978). This limits photosynthesis and, thereby, the carbohydrate pool. Mengel and Kirkby (1987) indicate NH_4^+ toxicity results mainly from NH_3 (aqueous) at low concentrations. Ammonia particularly affects root growth. The toxic effects of NH_4^+ resulting from NH_3 are more likely to occur at higher values of pH. Bennett (1974) suggested that NH_3 can be toxic because it can traverse cell

membranes. Heber et al. (1974) showed that the outer chloroplast membrane was impermeable to NH_4^+ but allowed the diffusion of NH_3. Gibbs and Calo (1959) reported NH_3 in uncoupling photophosphorylation at the thylakoid membrane of the chloroplast, Vines and Weddings (1960) showed respiration inhibited by NH_3. Toxic effects of NH_4^+ to plant growth also result directly from NH_4^+ particularly in very acidic media (Mengel and Kirkby, 1987). Both shoot and root growth are affected (Maynard and Barker, 1969) in this case.

Plants which complex NH_4^+ into organic N in the roots have a greater range of tolerance to NH_4^+ nutrition than those which translocate NH_4^+ freely to the shoots (Maynard and Barker, 1969).

The NH_4^+:NO_3^- ratio in the medium governs NH_4^+ acquisition and plant growth response (Mills et al., 1976). Ammonium concentrations high enough to induce toxicity symptoms can be maintained without adverse effects when NO_3^- supplies part of the N form (McElhannon and Mills, 1978).

Kirkby (1969) noted that NH_4^+ toxicity could be induced by poor aeration of the growing medium. Hewitt (1970) found that poor media aeration was tolerated more under conditions of NO_3^- nutrition. Roots, although injured by NH_4^+ toxicity, are apparently able to tolerate NH_4^+ as long as an abundant supply of carbohydrate is available (Reisenauer, 1978).

2.1.4.5: NO_3^- Toxicity

Plants can tolerate high tissue levels of NO_3^- (Maynard and Barker, 1971). Excessive NO_3^- can be toxic, but the mechanism of toxicity is unknown. Whiptail of cauliflower, a manifestation of Mo deficiency, is due to the accumulations of NO_3^- in the leaf margins (Candella et al., 1957). Reddy and Menary (1990) observed NO_3^- toxicity in *Boronia megastigma* when they were fed with NO_3^- greater than 25 mM per plant. Nitrate accumulated in plant tissue inhibiting NRA at high NO_3^-. These authors concluded that the low NRA is a genetic adaptation to the low NO_3^- availability in the native soils of the boronia plant.

2.2: Effects of Salt Stress on Plant Growth

It has been known for a long time that an excessive amount of salt in the root environment reduces the growth of plants and results in low crop yield. At present, several comprehensive reviews on physiology of plant response to salt stress are available (Bernstein and Hayward, 1958; O'Leary, 1971; Maas and Nieman, 1978; Rains, 1979; Greenway and Munns, 1980).

2.2.1: Salt Tolerance of Plant Species

The response to salinity differs greatly among various plant species. The salt tolerance list published by the U.S. Salinity Laboratory represents the relative tolerance of crop plants grown under recommended practices for the southwestern United States (Richards, 1954). Based on extensive review of existing data, Maas and Hoffman (1977)

further developed the salt tolerance evaluation table, which furnished a guide to relate tolerance among various crop plants. Such differences in salt tolerance have been established between closely related species (Greenway, 1973). Among the gramineae family, particularly barley and wheat, a significant difference in salt tolerance has been recognized by many investigators. Barley has been consistently reported to be more tolerant than wheat to salinity (Eaton, 1942; Ayers, Brown and Wadleigh, 1952; Ballantyne, 1962; Bower and Tamimi, 1979; Greenway, 1973; Bernstein, Francois and Clark, 1974; Pessarakli et al., 1981) and to alkalinity (Pearson and Bernstein, 1959).

Eaton (1942) reported a decrement in dry weight of Baart wheat by salinity of 50 to 100 meq/liter, and that plants in 200 meq/liter made little growth. Hira and Singh (1973) observed a significant decrease in grain and straw yield of wheat at an EC of 12 mmhos/cm. Hummadi (1977) showed that the grain and straw production of dwarf Mexican wheat 'Sonora 64' decreased linearly with increasing soil salinity and a 50 % decrement in grain yield at EC 8.5 mmhos/cm. With the same wheat cultivar, Jadav et al. (1976) observed a 50 % grain yield decrement associated with a substrate osmotic pressure of about 4 bars in sand culture. Ballantyne (1962) also observed that yields of wheat and barley on saline soils in Canada, were reduced to 50 % by EC of 6.5 and 8.0 mmhos/cm, respectively.

Barakat, Fakhry and Khalil (1970) reported somewhat different results with Egyptian wheat as soil containing 3000 ppm of salts in the saturation extract gave the same grain yield as that containing 200 ppm salts, and raising the salinity up to 6000 ppm (about 9 dS/m) decreased the yield by only 6 %. Comparing other observations,

these authors considered that wheat is more tolerant to salinity under certain soil conditions. Aceves-N et al. (1975) also considered that the wheat cultivar ' India 66' has high salt tolerance because the soil osmotic pressure associated with a 50 % grain yield decrement was 7.3 bars with NaCl; twice the previously reported limit for wheat.

Most reports are in agreement with the reputation of barley as a very salt tolerant species. According to Greenway (1962), the growth of barley was not appreciably affected by NaCl as high as 100 meq/liter. At the low nutrient level, however, the growth was substantially reduced by salinity, and this finding suggests that the salt tolerance of plant species is only a relative concept and that other experimental conditions should be clearly defined to determine the tolerance. Bernstein et al. (1974), confirmed that a 9 bars salinity level allowed significant barley yields but almost completely depressed the wheat yield.

It is generally thought that the differences in capacity of osmotic adjustment and resistance to specific ion toxicity are responsible for difference in salt tolerance (Bernstein and Hayward, 1958; Greenway, 1973). Greenway (1965) suggested that salt tolerance would depend on resistance to high internal ion concentrations as well as rapid osmotic adjustment.

2.2.2: Varietal Difference in Salt Tolerance

Although salt tolerance is usually reported as a single value for a crop, several examples of varietal differences have been recognized (Greenway, 1973). Ayers et al. (1952) tested the salt tolerance of four cultivars of barley and two cultivars of wheat on

artificially salinized field plots ranging from 400 to 20,400 ppm salt, and found that barley was more salt tolerant than wheat, and that there was a marked difference in the salt tolerance among the cultivars of these crops. A highly tolerant barley cultivar, California Mariout, could produce grain satisfactorily even though irrigated over most of the growth cycle with water containing 20,400 ppm salt, providing that the salinity level in the soil was relatively low during the seedling stage. Suhayda et al.(1992) compared the growth and ion relations of the commercial cultivar Harrington with foxtail barley under saline conditions. These authors reported reduction in leaf area, shoot growth, root growth and the root- shoot ratio of Harrington seedlings relative to foxtail barley. They also observed that H. jubatum seedlings accumulated less Na from the medium than Harrington and preferentially compartmentalized Na in root rather than shoot tissue. Gong et al.(1990) compared two barley cultivars, Jian No.4 and Yang Cao, under saline conditions. They observed inhibition of plant growth in both cultivars and Cl absorption and Na contents in plants were increased. Torres et al. (1974) observed that the relative grain yields among Mexican wheat cultivars, under a given NaCl stress were positively correlated with the length of the maturity period.

2.2.3: Factors Influencing Salt Tolerance

Salt tolerance is influenced by various factors, including climate, soil fertility and growth stage of plant. Magistad et al. (1943) suggested that climatic conditions often influence plant response to salinity and many crops appear less salt tolerant when grown in a hot, dry climate than in a cool, humid one.

Soil fertility interacts with salinity to affect the apparent tolerance of many crops. Particularly, the interaction with N-fertilization is of importance and will be mentioned in a later section. Concerning K interaction, Greenway (1963) showed that NaCl treatment increased the Cl and Na content and decreased the K content of barley. These changes in ion contents were usually most pronounced at the lowest nutrient concentrations, and he concluded that salinity reduces plant growth with low nutrients.

Sarin and Narayanan (1968) reported that wheat cultivars exhibited variable salt 'suspectivity to inhibited germination. Salinities of EC 2 to 16 mmohs/cm reduced germination both by causing a delay in germination and lowering the final population of germinated seeds. However, Mexican wheat has been reported to show tolerance to salt stress, germinating freely in the presence of 16 to 20 atm of osmotic pressure (Torres, Bingham and Oertli, 1974). Donovan (1968) found that barley was tolerant to high levels of salinity during seed germination, while there was a delay in emergence under highly saline conditions.

2.2.4: Physiology of Salt Tolerance

The growth of most plants except for halophytes is retarded by salt stress. The mechanism of growth depression has been studied from various aspects; morphology, physiology and enzymatic biochemistry. The mechanisms by which salts affect growth are still not completely understood, but the salinity effects on plant growth could be summarized into three major aspects; osmotic effect, specific ion effect, and nutritional imbalance.

At first, salinity effects on plant growth were thought to be primarily due to the low water potentials of the root environment. In general, salinity and drought would have an essentially similar action. Therefore, Wadleigh and Ayers (1945) calculated total moisture stress as the sum of osmotic pressure and moisture tension, and suggested that plant growth depression could be expressed as a function of total soil moisture stress regardless of whether the stress arises from salinity or moisture tension. Gauch and Wadleigh (1944) observed the growth reduction of field crops due to high osmotic pressure of the root media which impairs the root ability to absorb water. This was called physiological drought.

However, it has been found when plants are subject to gradually increasing salinity, the osmotic pressure of the plant cells also increases proportionally (Bernstein, 1961; Slatyer, 1961). This increasing osmotic pressure, i.e., lowering osmotic potential, in plant cells to cope with the decreasing total potential of the root media is called osmotic adjustment. If the turgor pressure of the plant cells remain constant, there would be a corresponding adjustment of the plant, and the water potential gradient from plant to the solution would be maintained within limits (Bernstein, 1963). On the basis of osmotic adjustment of plants, the "physiological drought" concept has been eliminated as the cause of growth inhibition under stress. Bernstein and Hayward (1958) suggested that both osmotic and specific toxic effect of ions may play an important role.

Salt may exert detrimental effects on plant growth through the toxicity of one or more specific ions. Toxicity of Cl (Richard, 1954) and SO_4 have been reported for many plant species (Eaton, 1942; Sarin, 1961). An accumulation of toxic ions is thought to

result in disturbed ion uptake. Aceves-N et al. (1975) reported that excess Ca in plant tissues stimulated an accumulation of Cl more than did Na, and this additional Cl specific ion effect could contribute to the yield decrement of wheat.

A number of investigators demonstrated that nutrient uptake by certain plant species is curtailed by salinization. Gauch and Eaton (1942) reported that the addition of both Cl and SO_4 salts reduced K and Ca, and had little effect on total-N, P and Mg by barley plants. In particular, N uptake is important as has been reported by many investigators. Greenway (1963) showed the inhibition of K uptake by salinity. Hassan et al. (1970) reported a significant decrease in P, K, Ca, Fe and Cu uptake by barley and corn plants under artificially adjusted salinity with Na_2SO_4, $MgSO_4$ and $CaCl_2$. Conversely, Na and Mn uptake were increased by salinity. Torres and Bingham (1973) suggested that the growth retardation associated with excessive NaCl is due partly to a Cl induced NO_3 deficiency. In addition, SO_4-induced Ca deficiency has been commonly observed. Thus, salinity occasionally induces nutritional imbalances or deficiencies that causes the decreased growth or plant injury not attributed to osmotic effect alone.

Osmotic adjustment has been known as a means by which plants adapt to salinity as well as to water limiting conditions. It has been suggested that plants which can adapt to saline environments are those which undergo osmotic adjustment (O'Leary, 1971; Greenway, 1973). However, the growth of plant is reduced even under full osmotic adjustment. Explanation for growth reduction, as summarized by Hsiao et al. (1976), may lie partly in toxicity of the ions taken up in large amounts in achieving the adjustment, or may lie simply in ionic imbalance (Bernstein, 1963). Another reason may

be the energy expended in accumulation of organic solutes or ion uptake to maintain turgor (Slatyer, 1961). Greenway (1973) summarized the interaction between osmotic and specific ion effects and described that if osmotic adjustment occurs, considerable amounts of metabolic product would be required, particularly in the case of sugars. He estimated that at external concentrations of 100 meq/liter NaCl, the cell sap would have to accumulate about 30 g/liter of hexose sugars or 60 g/liter of disaccharides. On the other hand, he continued, osmotic adjustment might also be induced by salt uptake into the cells, and this would avoid a considerable drain on the available C and energy supply of plants; however, salt uptake induced the danger of toxicities.

O'Leary (1971) reviewed data from various sources and proposed a unified theory to explain the growth inhibition due to salinity. The basis of his theory was based on the reductions of root permeability to water flow and of hormone (cytokinin) delivery from roots to leaves by salinity.

2.3: Effects of Salt Stress on Nitrogen Uptake by Plants

2.3.1: Nitrogen Uptake and Contents in Plants

The effects of salt stress on N nutrition in plants has been studied for various kinds of plants using different methods such as kind of salts, culture methods, and etc. The results are still controversial.

For barley and wheat, different results have been reported. Gauch and Eaton (1942) reported that sodium salt substrate (NaCl and Na_2SO_4) had either little or no effect on total-N concentration in barley plants. However, several investigators have reported

a decrease in N content in plants caused by salt stress. Using a sand culture technique with saline nutrient solution ranging from control to 6,000 ppm of NaCl and $CaCl_2$ mixture. Heikal (1977) observed that total-N content on a dry weight basis of wheat leaves and radish leaves was decreased by salinity, whereas that of sunflower leaves was increased. Torres and Bingham (1973) grew Mexican wheat to full maturity in sand culture with variable levels of substrate NO_3 and NaCl. These workers found that increased salinity enhanced the uptake of Na, Cl, Ca and P. On the other hand, leaf concentrations of NO_3, total-N, K, and Mg decreased with salinization at early spike emergence stage. Hummadi (1977) also found a decrease in total-N and NO_3 uptake with increasing soil salinity in Mexican wheat, 'Sonora 64'. Using wheat seedlings, Sarin (1961) observed a decline in total-N % in $NaSO_4$ treatment, and Bhardwaj and Rao (1962) showed similar results in 0.2 % Na_2CO_3 treatment. Meyer and Gingerich (1966) also observed a decrease in N % in shoots and roots of wheat seedlings with increasing stress up to 9 bars of osmotic pressure.

In contrast, some authors have reported an increase in N content in plants growing in saline substrate. Lal and Singh (1973) studied the effect of different qualities of irrigation water and fertilizer upon nutrient uptake by wheat plants in a field experiment, and reported that an increase in the EC_e and SAR of water decreased the total uptake of N, P, K and Cl as well as the grain and straw yield. At the same time, these authors observed an increase in N and Na content (%) of grain and straw with increasing salinity and alkalinity levels. Abrol (1968) found somewhat different results in that the N content in wheat plants increased with increasing ESP under standard

fertilization, but not in the high N treatment. Helal and Mengel (1979) investigated the influence of NaCl salinity and KCl addition on uptake and turnover of labelled-N ($^{15}NH_4{}^{15}NO_3$) in a solution culture experiment with 31 day old barley plants, and found that total ^{15}N content of roots decreased with increasing NaCl salinity, while that of the shoot increased. Bernstein et al. (1974) reported that leaf N concentration increased with increasing salinity at all N fertilization levels so that salinity did not aggravate N deficiency. Jadav et al. (1976) grew Mexican wheat 'Sonora 64' in sand culture and investigated the salinity effects on N use of the plants. These authors concluded that salinity reduced total-N uptake, but the depressed dry weights resulted in higher N concentration in the straw.

To explain these different results, Frota and Tucker (1978b), who observed in red kidney beans that dry matter production and total-N per plant decreased as the percent N increased in the stressed plants, concluded that these different results were probably due to a dilution effect or concentration effect depending on the relative severity of salt effect on growths or N uptake. Furthermore, Pessarakli (1981) confirmed the dilution effect for N content of cotton plants.

2.3.2: Salinity-Fertility Interaction

During reclamation of saline soils, effects of fertilization on crop yield have been studied by many investigators. The beneficial effect of fertilization on moderately saline soils or with saline water has been generally indicated. Studying the effects of various salt-fertilizer combinations on the growth and composition of barley, Dregene and

Mojallali (1968) found that application of N, P and K fertilizers reduced the adverse effect of low to moderate levels of soil salinity on yields. Luken (1962) observed an increase in yield of wheat grown on a saline soil under dryland conditions with high application rates of N and P fertilizers. At high salinity levels (EC = 24 mmohs/cm), he found no yield increase due to P additions. Similarly, Lal and Singh (1973) observed a beneficial effect of increased fertilization level on nutrient uptake and grain and straw yield of wheat grown with high levels of EC(3.45 mmhos/cm) and SAR (16.73). Abrol (1968) found a considerable increase in the dry matter production and N content of wheat plant grown at a high level of Na, with a medium level of P and high level of N fertilizers. Finally, Bernstein et al.(1974), who investigated the interaction of salinity and nutrition for barley, wheat, corn and six vegetable crops in large outdoor sand culture, found that yield of the crops tested increased with N and P fertilization when salinity was not a dominant limiting factor. When salinity severely limited crop growth, the fertilizers were relatively ineffective in increasing yield.

2.3.3: Effects of Salt Stress on Nitrogen Metabolism in Plants

2.3.3.1: Protein synthesis

The specific conditions prevailing in saline media markedly influence plant metabolism, especially N metabolism. It is generally observed that there is a tendency for amino acids and amides to accumulate in salt stressed plants, due to inhibited protein synthesis (Strogonov, 1962; Udovanko, Sinelnikova and Khazova, 1971; Frota and Tucker, 1978a). Strogonov (1962) emphasized that disturbed protein synthesis in plants

is associated with the accumulation of toxic diamines, intermediaries of N metabolism, in plant cells subjected to salinity. Pessarakli (1981) and Udovenko et al. (1971) reported that under saline conditions an accumulation of ammonium in wheat, buckwheat, bean and pea plants occurred and they also mentioned an inhibition of nitrate reduction and ammonium incorporation into amino acids. Later the authors found that in barley, wheat, pea and bean plants, the non-protein-N fraction increased under salt stress, whereas the protein-N fraction changed irregularly, and concluded that the quality of changes in N metabolism in plants with different salt tolerance is identical; however, the quantity of changes is dependant on the level of salt tolerance of plants. Therefore, lower salt tolerance is associated with more pronounced metabolic changes of N in the plant.

Several investigators confirmed a decrease in protein content of wheat plants under stress. Sarin (1961) and Bhardwaj and Rao (1962) observed disturbed protein synthesis in wheat seedlings due to Na_2SO_4 and Na_2CO_3 salinity. Stutte and Todd (1969) and Todd and Yoo (1964) found a reduction in protein content in wheat leaves by increasing water stress. Hsiao (1973) suggested that a decrease in protein content by water stress may reflect either a retardation of protein synthesis or an acceleration of degradation.

Frota and Tucker (1978a) noted that the incorporation of ^{15}N into protein synthesis was inhibited by salt and water stress regardless of the N sources; NO_3 or NH_4. The inhibition was more severe under salt stress compared to water stress. Helal and Mengel (1979) also reported that salinization impaired growth and incorporation of labelled N into the protein fraction after their solution culture experiment with barley plants. And,

these authors supported the point of view that impairment of protein metabolism is an important aspect of salt stress. Furthermore, they suggested that it is probably induced by the disturbance of the K/Na balance of the plant tissues under saline conditions, so that K addition enhances N uptake and incorporation into protein and reduces the accumulation of inorganic N and finally improved the growth of salinized plants.

Since the formation of m-RNA ribosome complexes are essential for protein synthesis, reduction in polyribosome percentages in the plant tissue was thought to be indicative of reduced protein synthesis. Therefore, polyribosome level under salt or water stress have been examined for various kinds of plants.

For barley and wheat, Rhodes and Matsuda (1976) detected the rapid changes in polyribosome levels in shoots following a short duration of salt or water stress, and suggested that growth rate reductions might be directly proportional to reduction in polyribosome level during the stress. Meanwhile, Itai, Richmond and Vaadia (1968) advocated a key role for cytokinin in modulating protein synthesis during salt and water stress.

Bernstein (1963) suggested the possibility that increased osmotic pressure of the cell or increased concentrations of specific ions may alter the activity of some enzymes. Changes in enzyme activities caused by water stress were reviewed by Todd (1972), and he concluded that severe stress or desiccation generally lowers enzyme levels, and nitrate reductase is one of the enzymes which appears to be reduced most readily by stress. Special attention has been given to nitrate reductase activity because this enzyme plays a key role in N metabolism. Many studies have shown that there is an inhibition of

nitrate reductase activity under water stress. Huffaker et al. (1970) observed decreased activities of both nitrate and nitrite reductase in barley seedlings subjected to water stress. In addition, Plaut (1973) observed a significant decrease in nitrate reductase activity of wheat seedlings when relative water content was reduced by 7 % only, and he concluded that water and salt stress inhibit N metabolism in the seedlings by affecting the nitrate reductase activity (Plaut, 1974).

CHAPTER 3

MATERIAL AND METHODS

The experiments in this study were conducted in a walk-in growth chamber (Percival Model NC 255 A Boone, Iowa).

Barley (*Hordeum vulgare L. cv. Arivat*) plants were used to study the N uptake rate under different NH_4^+-N: NO_3^--N ratios and salinity stress. Barley was selected for this study primarily because it is salt tolerant and a major grain crop grown on both saline and non-saline soils throughout the world. Secondly, it has been studied extensively by many investigators to determine the optimum nitrogen rate under both saline and non-saline conditions (Dregene and Mojallali, 1958; Lukin, 1962; Lal and Singh, 1973; and Bernstein et al., 1974).

Solution culture was chosen because it enables the investigator to control precisely the composition of the solution surrounding the roots. As pointed out by Epstein (1972), soils are not amenable to close experimental control because they are complex and heterogenous media. Moreover, due to the difficulty of maintaining specific N ratios in soils, plants were grown hydroponically. This need arises because microorganisms readily convert NH_4^+ to NO_3^- (nitrification) in moist, warm, well aerated soils, making it difficult or impossible to maintain all or a large part of N as NH_4^+. Therefore, the use of a solution culture is an important experimental approach for investigation of NH_4^+-NO_3^- nutrition.

3.1: Environmental Conditions

Light in the growth chamber was provided by a combination of 12 incandescent 100-watt tungsten bulbs and 28 cool white 229 cm fluorescent bulbs. The light intensity at the upper plant leaves was approximately 75 W/m^2. The chamber was programmed to cycle 14 hours light and 10 hours dark with a gradual change between light and dark periods. All lights were on from 0600 to 2000 hours. The air temperature was maintained at 22 ± 2 ^0C during the light period and 20 ± 2 ^0C during the dark period. There was a time lag of about 30 minutes to reach full light intensity and a one hour delay in reaching the dark period air temperature. The relative humidity of the air in the chamber was about 50 % and 60 % during the light and dark period, respectively. The air inside the growth chamber was circulated continuously by five fans mounted on the walls of the chamber. The aeration of the nutrient solutions was provided by a rubber tube from an air line through a short section of glass tubing immersed in the nutrient solutions.

3.2: Preparation of Plants for Experiment

Barley (*Hordeum vulgare L. cv. Arivat*) plants were used in this study. Seeds of barley were rapidly washed with 5 % (v/v) clorox containing 5.25 percent hypochlorite (the Clorox Company, Oakland, California) and rinsed many times with water after elimination of small and broken seeds. Eight seeds were then arranged in a row, between folded, sterilized germination paper (Kimberly-Clark Corporation, Neenah, Wisconsin). The germination papers were soaked with water, covered by a plastic wrap, rolled up and placed upright in 600 ml beaker containing 150 ml water. About 400 seeds were prepared

for germination this way for each experiment. The beakers were placed in an incubator (Environator Corporation, West Napa, California). The seeds were kept in the dark at 22 ± 2 ^{0}C and periodically necessary amounts of water were added to the beakers to compensate for loss by evaporation. The wraps were checked every other day. Poorly germinated or contaminated seeds were eliminated. One week after the start of incubation, the beakers were uncovered, since about 90 % of seeds emerged the first leaf from coleoptile out of the towel. The beakers were transferred to the growth chamber where the young seedlings were given seven days of light, temperature, and relative humidity as mentioned above.

Most of the barley seedlings reached the second leaf emergence stage after two weeks from the start of incubation. Two uniform seedlings were transplanted to each polyethylene container containing 1.5 liters of modified Hoagland-Arnon solution with the addition of micro-nutrient solution (Table 3.2) and 0.5 % Fe solution (solution b) (Hoagland and Arnon, 1950). The containers were covered to avoid evaporation. The cover contained two holes fitted with plastic foam to hold the plants. All solutions contained 100 ppm N but five different NH_4^+/NO_3^- ratios (Table 3.1). All other nutrients in each of the experimental solutions, except SO_4, were brought to the same level by adding various salts. The pH of the solution was monitored and adjusted to approximately 6.0 by adding 0.5 N NaOH.

Afterwards, the plants were grown under controlled environmental conditions, and levels of the culture solution in pots were maintained at 1.5 liters by adding water throughout the growing period. The nutrient solution was constantly aerated during the

Table 3.1: Amounts of various salts added to make the described NH_4^+/NO_3^- ratio (mL/L).

Molar con.	Salt	0/100	25/75	50/50	75/25	100/0
0.5	K_2SO_4	0.43	3.64	2.21	4.00	4.00
0.5	$(NH_4)_2SO_4$	0.00	1.79	3.57	5.36	7.14
1.0	KH_2PO_4	1.00	1.00	1.00	1.00	1.00
1.0	KNO_3	3.57	0.36	1.79	0.00	0.00
1.0	$Ca(NO_3)_2$	1.79	2.50	0.89	0.89	0.00
1.0	$MgSO_4$	2.00	2.00	2.00	2.00	2.00
0.01	$CaSO_4$	71.00	0.00	161.00	161.00	250.00

Table 3.1 a : Composition of micro-nutrient solution

Substance	gram dissolved in a liter of H_2O
H_3BO_3	2.86
$MnCl_2.4H_2O$	1.81
$ZnSO_4.7H_2O$	0.22
$CuSO_4.5H_2O$	0.08
$H_2MoO_4.H_2O$	0.02

Solution b :

0.5 % Fe solution was prepared by dissolving 3.625 g of Fe EDOHA in deionized water and make up to one liter. One ml of the diluted solution was added to each liter of nutrient solution so as to 1 ppm in the nutrient solution.

Table 3.2: Nutrient composition of N-free nutrient solution.

Substance	ml in a liter of nutrient solution	
	Full strength	1/10 strength
0.5 M K_2SO_4	5	0.5
1.0 M $MgSO_4$	2	0.2
0.05 M $Ca(H_2PO_4)_2.H_2O$	10	1.0
0.01 M $CaSO_4.2H_2O$	200	20
Solution a	1	1.0
Solution b	1	1.0

Table 3.3: ^{15}N application

Treatment	Period (HOURS)		Dose
	EXP #2	EXP #3	(mL/pot)
C1	6	6	5
C2	12	12	10
C3	24	18	20

experiment with a regulated flow of cleaned air. The nutrient solution was changed at 15 days intervals.

3.3: Experimental Procedures

3.3.1: Experiment 1

The first experiment was conducted to study the nitrogen uptake at five different NH_4^+/NO_3^- ratios (100/0, 75/25, 50/50, 25/75 and 0/100) and three different NaCl salinity levels (0, 6, and 12 bars) at the late stem extension growth stage (30 days after transplanting). The plants were grown in modified Hoagland-Arnon solutions, and the salt stress levels were achieved by adding NaCl to the culture solution.

Salt stress treatments were started by adding NaCl to the nutrient solution two weeks after transplanting. Sodium chloride was chosen for this work because it contains the most common ions, Na^+ and Cl^-, found in saline soils (Mulwani and Pollard, 1939). For each bar of stress, 24 mmol/L of NaCl were added to the culture solution. The salt stress was gradually increased. The salinity level was increased by two bars every second day. Measured electrical conductivities of solution at 25 ^{0}C were 1.83, 13.95, 26.78 dS/m for 0, 6, 12 bars treatment, respectively. The treatments were factorial combinations of 3 salinity levels, 5 NH_4^+/NO_3^- ratios and 3 replications. All experimental units (solution containers) had two plants. Units were placed randomly within replications on the growth chamber benches in a Randomized Complete Block Design (RCBD). No ^{15}N was applied in this experiment.

After harvesting, plants were immediately separated into roots and shoots. The plant parts were weighed (fresh weight) after rinsing the roots in deionized water. The plant samples were weighed (dry weight) after 48 hours in oven at 60 ^{0}C. The dried plant samples were ground to pass a 40-mesh screen in a Wiley mill for analyses of total-N and nitrate. The solution samples were taken from the pots after every 15 days throughout the growth and the solution samples were analyzed for NH_4^+ and NO_3^- to estimate the N uptake plants indirectly. Plant samples were analyzed for NO_3^- and total N. Ammonium and NO_3^- were determined using the steam distillation method (Keeney and Nelson, 1982). Total N was determined using micro-Kjeldahl digestion and steam distillation method (Bremner and Mulvaney, 1982). The plant samples were extracted using 1 M KCl solution and nitrate was determined using the steam distillation method.

3.3.2: Experiment 2

The second experiment was conducted to study the dry mattern nitrogen accumulation and nitrogen uptake at five different NH_4^+/NO_3^- ratios (100/0, 75/25, 50/50, 25/75 and 0/100) and two different NaCl salinity levels (0 and 8 bars) at late stem extension growth stage (30 days after transplanting). The second experiment was similar to experiment 1 except 0, and 8 bars salinity levels and ^{15}N was applied. The salinity levels were changed based on the results obtained from experiment 1. The treatments were 2 salinity levels , 5 NH_4^+/NO_3^- ratios, 3 replications and 3 time periods. Experimental units were placed randomly within replications on the growth chamber

benches in a Randomized Complete Block Design (RCBD). The duration of this study was 31 days. Measured electrical conductivities of solution at 25 ^{0}C were 1.83 and 16.83 dS/m for 0 and 8 bars treatment, respectively.

For the short term N uptake experiments, NH_4^+-labelled ^{15}N-enriched sources [$(^{15}NH_4)_2SO_4$ and $^{15}NH_4NO_3$] and a NO_3^--labelled ^{15}N-enriched source [$K^{15}NO_3$] were added to the 1/10 th strength N-free nutrient solution after the plants had grown under salt stress conditions for two weeks. The plants were N-starved for three days in a N-free culture solution prior to addition of ^{15}N. The composition of the nutrient solution is given in Table 3.2. The atom percent of ^{15}N in the source was 99.9.

Meanwhile, a series of containers holding 1.5 liters of 1/10 strength N-free culture solution plus 0 and 192 mmol/L NaCl for control and 8 bars of osmotic pressure, respectively, were prepared. A specific amount of NH_4^+-labelled ^{15}N or NO_3^--labelled ^{15}N solution, containing one mg ^{15}N per mL, was added to the culture solution in proportion to the designated uptake period, to get the desired levels of ^{15}N concentration (Table.3.3).

At 9:00 am, plants were transferred to the prepared ^{15}N-enriched culture solution of corresponding salinity level. Six hours later (3:00 pm), the first set of plants (6 hours ^{15}N uptake) were harvested. The second set of plants (12 hours ^{15}N uptake) were harvested at 9:00 pm., while the final harvest was 24 hours after the start of the ^{15}N uptake experiment (9:00 am in the next day).

Solution samples were taken at 0, 6, 12, 18 and 24 hours after ^{15}N application, to measure the short term N uptake rate from solution over time periods. The volume of the culture solution in each pot was maintained at the initial volume by adding deionized

water before the solution samples were taken. Total-N (Kjeldahl-N) (Bremner and Mulvaney, 1982) and ^{15}N contents of plant tissue were determined at three time intervals; 6, 12, and 24 hours after ^{15}N treatment using destructive sampling. Nitrogen isotope ratio for NH_4^+, NO_3^- and total N was determined using an isotope-ratio mass spectrometer.

3.3.3: Experiment 3

This experiment was similar to the second experiment except the duration of the study and the time intervals. Experiment 3 was conducted for 45 days and ^{15}N content of plant tissue were determined at three time intervals; 6, 12, and 18 hours after ^{15}N treatment. The solution samples were taken at 0, 6, 12, 15 and 18 hours after ^{15}N application to measure the uptake rate from solution over time periods.

3.4: Statistical Analysis

Data were analyzed using SAS statistical program (SAS Institute Inc., Cary, NC) in the GLM (General Linear Model Procedures) mode. The means were compared by the Fisher's protected "Least Significant Difference" test. The 5 % level of significance was used in all comparisons.

CHAPTER 4

RESULTS AND DISCUSSION

4.1: Dry Matter Production

The effects of different NH_4^+ to NO_3^- ratios and NaCl salinity on the dry matter production of barley plants are shown in Tables 4.1, 4.2 and 4.3. In all the three experiments, the plants receiving mixed N nutrition produced significantly ($P<0.05$) higher root and shoot dry matter yield as compared to the plants grown in ammonium or nitrate alone. The plants grown in 50 % NH_4^+ and 25 % NH_4^+ produced the highest yield among all the treatments in all three experiments. In experiments 2 and 3, barley plants produced significantly ($P<0.05$) lower root and shoot dry matter yield when grown in 100 % ammonium as compared to the plants grown in 100 % nitrate.

The dry matter yield indicated that growth of barley plants was inhibited by high NH_4^+-N concentration when supplied with little or no NO_3^--N (75 % and 100% NH_4^+). This detrimental effect of high NH_4^+ was more acute when no NO_3^--N was supplied. Ideally, NH_4^+ should be the best source of N, for it should be used more efficiently in the plants than would NO_3^- (Barker and Mills, 1980). However, when sufficient N is supplied to meet the goals of production and N is supplied only in the NH_4^+ form, the toxic accumulation of uncomplexed NH_4^+ overrides the potential benefit, for much of the energy production of the plants must go into carbon skeletons for the incorporation of NH_4^+ and its detoxification. This process diverts energy and carbohydrates away from

Table 4.1: Effect of different NH_4^+ to NO_3^- ratios and salinity on dry matter production and N uptake of barley plants (Experiment 1).

NH_4^+ † (%)	Salinity	Dry Matter ‡			N Uptake ‡		
		Root	Shoot	Total	NH_4^+-N	NO_3^--N	Total N
	(bars)	g/pot			mg/pot		
100	0	0.56	1.67	2.23	115	0	115
	6	0.39	1.05	1.44	68	0	68
	12	0.39	0.93	1.32	66	0	66
75	0	0.98	2.80	3.78	125	57	182
	6	1.11	2.32	3.43	115	43	158
	12	1.14	2.30	3.44	118	39	157
50	0	1.19	2.67	3.86	93	87	180
	6	1.07	2.13	3.20	95	48	143
	12	0.77	1.50	2.27	87	34	121
25	0	1.20	2.63	3.83	55	119	174
	6	0.54	1.15	1.69	46	51	97
	12	0.85	1.67	2.52	53	53	106
0	0	0.53	1.30	1.83	0	92	92
	6	0.38	0.81	1.19	0	45	45
	12	0.37	0.63	1.00	0	45	45
$LSD_{(0.05)}$		0.34	0.56	0.82	18	18	22
Salinity		*	**	**	*	**	**
N		**	**	**	**	**	**
Salinity*N		NS	NS	*	NS	**	*

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

† Values denote the percentage of nitrogen as NH_4^+-N in the nutrient solution.

‡ Each value for dry matter and N uptake is the mean for three replications and three harvest times.

Table 4.2: Effect of different NH_4^+ to NO_3^- ratios and salinity on dry matter production and N uptake of barley plants (Experiment 2).

NH_4^+ † (%)	Salinity	Dry Matter ‡			N Uptake ‡		
		Root	Shoot	Total	NH_4^+-N	NO_3^--N	Total N
	(bars)	g/pot			mg/pot		
100	0	0.70	2.11	2.81	129	0	129
	8	0.52	1.58	2.10	99	0	99
75	0	0.93	3.82	4.75	156	46	202
	8	0.84	2.48	3.32	87	37	124
50	0	1.54	4.12	5.66	111	96	207
	8	0.67	2.14	2.81	68	47	115
25	0	1.65	4.12	5.77	50	133	183
	8	0.72	2.21	2.93	38	77	115
0	0	0.91	2.60	3.51	0	132	132
	8	0.47	1.31	1.78	0	70	70
$LSD_{(0.05)}$		0.27	0.53	0.77	13	17	21
Salinity		**	**	**	**	**	**
N		**	**	**	**	**	**
Salinity*N		**	*	**	**	**	*

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.
† Values denote the percentage of nitrogen as NH_4^+-N in the nutrient solution.
‡ Each value for dry matter and N uptake is the mean for three replications and three harvest times.

Table 4.3: Effect of different NH_4^+ to NO_3^- ratios and salinity on dry matter production and N uptake of barley plants (Experiment 3).

NH_4^+ † (%)	Salinity	Dry Matter ‡			N Uptake ‡		
		Root	Shoot	Total	NH_4^+-N	NO_3^--N	Total N
	(bars)	g/pot			mg/pot		
100	0	1.06	3.79	4.85	224	0	224
	8	0.66	3.18	3.84	163	0	163
75	0	2.45	6.71	9.16	231	92	323
	8	1.05	4.19	5.24	161	58	219
50	0	4.46	10.20	14.66	164	164	328
	8	1.39	4.86	6.25	158	117	275
25	0	3.96	9.90	13.86	88	232	320
	8	1.32	4.75	6.07	83	168	251
0	0	2.55	6.98	9.53	0	295	295
	8	0.69	2.25	2.94	0	128	128
$LSD_{(0.05)}$		0.52	0.96	1.40	10	13	14
Salinity		**	**	**	**	**	**
N		**	**	**	**	**	**
Salinity*N		**	**	**	**	**	**

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

† Values denote the percentage of nitrogen as NH_4^+-N in the nutrient solution.

‡ Each value for dry matter and N uptake is the mean for three replications and three harvest times.

growth. The toxicity of high NH_4^+ concentration to plants has been reported previously by Nittler and Kenny (1976) in perennial rye grass (*Lolium perenne L*).

These results are in agreement with the results reported by Gamborg and Shyluk (1970), Green et al. (1973), Joiner and Knoop (1969), Cox and Reisenauer (1973), Domska (1974) and Van Den Driessche (1971). Cox and Reisenauer (1973) found that in wheat, the growth rate and yield of plants grown where ammonium had been added to a root media already containing adequate nitrate (200 uM) exceeded those of plants grown in nitrate or ammonium alone. It was suggested that the yield and growth enhancement were due to the reduced energy requirement resulting from using ammonium instead of nitrate in protein synthesis, and from increased photosynthetic capacity. Several possible reasons have been reported for increased dry matter yield due to mixed N nutrition by research workers. Weissman (1964) reported maximum amino acid accumulation when both ammonium and nitrate were supplied and the presence of ammonium and nitrate in roots could stimulate formation of glutamic acid, which plays a central role in the synthesis of amino acids. Enhanced rate of amino acid transport to leaves may permit the establishment of higher protein levels (Olsen, 1986; and Weissman, 1964).

Dry matter production was negatively correlated with the level of salinity (Tables 4.1, 4.2 and 4.3). Higher dry matter yield was produced when plants were grown in mixed ammonium and nitrate nutrition and salinity stress as compared to ammonium or nitrate alone under salinity stress. This trend was evident in all the three experiments. In experiment 1, plants grown in 75 % NH_4^+ at 6 and 12 bars salinity stress gave

significantly higher dry matter yield. The same trend was found in experiment 2, where the salinity level was 8 bars. In experiment 3, the plants grown in 50 % NH_4^+ at 8 bars salinity level gave significantly higher yield. The better dry matter yield of plants grown in 50 % NH_4^+ in experiment 3 might be due to highest N uptake at later growth stages as compared to experiments 1 and 2. These results support the findings of Michael et al. (1970) and Uesato (1974). These workers concluded that the optimum NH_4^+/NO_3^- ratio may change with the age of the plant. This may explain the difference between experiments 1 and 2, with plants grown for 30 days after transplanting, and experiment 3, with plants grown for 45 days after transplanting.

Salinity and mixed N nutrition interaction for dry matter yield was found significant ($p<0.05$) in experiments 2 and 3. Salinity significantly reduced grain yield, but at each salinity level a significant increase was induced by mixed ammonium-nitrate nutrition in comparison to nitrate alone (Tables 4.2 and 4.3). Results regarding the effects of salinity and N source on yields are in good agreement with those obtained by Shaviv et al. (1990) and Ben-Hayyim and Goffer (1988). Studying the effects of various salt fertilizer combinations on the growth and composition of barley, Gregene and Mojallali (1968) found that application of N, P, and K reduced the effects of low to moderate levels of salinity on yield. Bernstein et al., (1974) who investigated the interaction of salinity and nutrition of barley, wheat, corn and six vegetable crops in a large outdoor sand culture, found that yield of the crops tested increased with N and P fertilization when salinity was not a dominant limiting factor. It seems that plants grown

in mixed NH_4^+ and NO_3^- nutrition under salinity stress received more balanced nutrition as compared to the plants grown in either NH_4^+ or NO_3^- alone under identical salt stress.

Salt tolerance for cereal crops, is generally compared with a 50% decrease in grain yield at maturity. Therefore, the present results could not be referred directly to the crop salt tolerance. Within a species, it would be possible to estimate grain yield from N content in leaves before maturity by referring to the correlation reported by Torres and Bingham (1973), Jadav et al. (1976) and Hummadi (1977) for Mexican wheat. However, it is apparently impossible to apply the relationship to barley. Barakat et al. (1970) noted that high salt stress depressed vegetative growth of wheat much more than grain yield, so that prediction of salt tolerance from vegetative growth may be misleading.

4.2: Nitrogen Uptake

The N uptake by barley plants during all the experiments were calculated from the NH_4^+-N and NO_3^--N loss from the nutrient solution. Tables 4.1, 4.2 and 4.3 show NH_4^+, NO_3^- and cumulative N uptake by barley plants. The highest ammonium uptake was observed in the 75 % NH_4^+ treatment plants. The highest nitrate uptake was observed in the 25, and 0 % NH_4^+ treatments in experiments 1, and 2, and in the 0 % NH_4^+ treatments in experiment 3. The highest cumulative N uptake was found in the 50 % NH_4^+ treatment in all three experiments.

In all the experiments, the plants receiving mixed N nutrition showed significantly ($P < 0.05$) higher NH_4^+, NO_3^- and cumulative N uptake as compared to plants grown in either ammonium or nitrate. The results are in agreement with Gentry et al. (1989) and Cox and Reisenauer (1973). They also reported higher N uptake by wheat plants grown in mixed N nutrition. These findings suggest that the additional production of dry matter resulting from mixed N nutrition may be related to enhanced N uptake.

The total N uptake per pot followed a pattern of decreasing N uptake with increasing salinity levels similar to the effects on dry matter production. Decreased NH_4^+ and NO_3^- uptake by plants was observed under NaCl salinity conditions. The cumulative N uptake by barley plants under saline conditions, grown either in NH_4^+ or NO_3^- alone, was significantly ($P < 0.05$) lower as compared to plants grown in mixed N nutrition. It seems that mixed N nutrition is advantageous when compared to NH_4^+ or NO_3^- nutrition even under saline conditions.

The significant decrease in uptake of both NH_4^+ and NO_3^- by barley plants under salt stress is in agreement with the work of Kretschmer et al.(1953), Lunin and Gallatin (1965), Mattas and Pauli (1965), Wilson et al. (1970), Udovenko et al.(1971), Frota and Tucker (1978 a) and Lal and Singh (1973). However, Hernado et al.(1967) found that N uptake by tomato plants was not influenced by the level of NaCl in the root zone; but their conclusions were based on nitrogen concentration in plants rather than total N uptake. The low uptake of N under saline conditions might be related to a number of factors such as high uptake of Cl^- (Jadav, 1969), or a high uptake of Na which in turn might suppress the absorption of NH_4^+ (Palfi, 1965). Torres and Bingham (1973) also

reported that growth retardation associated with excessive NaCl is due to in part to a Cl^- induced NO_3^- deficiency. Thus salinity, occasionally induces nutritional imbalances or deficiencies.

The salinity x N interaction effect was found significant ($P<0.05$) for nitrogen uptake in all the three experiments. The salinity fertility interaction was more evident where mixed N nutrition was applied and this trend was observed in all the experiments. There was significantly higher N uptake in plants grown in mixed N nutrition as compared to plants grown with ammonium or nitrate alone under the same salinity levels. Shaviv et al. (1990) found that the advantage of mixed N nutrition was not due to nitrate-chloride antagonism. They concluded that sodium concentration in plant tissues increased with salinity, but was reduced by increasing proportion of ammonium in the medium. This effect may be attributed to competition between ammonium and sodium for root uptake sites.

4.3: Nitrate Contents

Tables 4.4, 4.5 and 4.6 show root and shoot NO_3^- contents (mg/g). It is evident from the data that significantly higher root NO_3^- contents were found in treatments where all N was supplied in NO_3^- form. This trend was observed in all the experiments. This indicates that NO_3^- assimilation in plant roots grown in 100 % NO_3^- was significantly lower as compared to mixed N nutrition and comparatively more accumulation was

Table 4.4: Effect of different NH_4^+ to NO_3^- ratios and salinity on NO_3^- -N, total N and water uptake of barley plants (Experiment 1).

NH_4^+ † (%)	Salinity	NO_3^--N content ‡		Total N ‡		Water Uptake ‡
		Root	Shoot	Root	Shoot	
	(bars)	------ mg/g --------		-------- mg/pot------		mL/pot
100	0	0.15	0.23	26.41	85.65	933
	6	0.30	0.12	14.94	45.82	935
	12	0.18	0.15	14.35	37.68	773
75	0	2.99	3.01	36.88	131.30	1376
	6	5.06	0.84	39.74	106.29	1276
	12	4.46	0.65	42.87	97.90	1085
50	0	4.47	5.13	40.28	124.82	1478
	6	7.19	1.31	41.52	92.67	1163
	12	5.66	1.65	29.60	59.26	951
25	0	6.39	5.21	42.80	115.25	1445
	6	5.64	1.23	20.15	46.22	898
	12	8.50	1.31	30.41	64.75	1100
0	0	11.70	5.84	24.83	57.91	976
	6	11.98	2.27	14.22	31.07	835
	12	11.40	2.71	13.35	21.40	778
LSD(0.05)		3.10	2.09	5.64	7.51	226
Salinity		NS	**	*	**	**
N		**	**	NS	*	**
Salinity*N		NS	NS	NS	NS	**

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

† Values denote the percentage of nitrogen as NH_4^+-N in the nutrient solution.

‡ Each value for NO_3^--N, total N, and water uptake is the mean for three replications and three harvest times.

Table 4.5: Effect of different NH_4^+ to NO_3^- ratios and salinity on NO_3^- -N, total N and water uptake of barley plants (Experiment 2).

NH_4^+ † (%)	Salinity	NO_3^--N content ‡		Total N ‡		Water Uptake‡
		Root	Shoot	Root	Shoot	
	(bars)	------ mg/g --------		-------- mg/pot-----		mL/pot
100	0	0.12	0.11	24.81	99.41	882
	8	0.12	0.10	18.04	72.28	420
75	0	2.53	1.51	27.56	160.87	1462
	8	16.19	0.80	26.77	90.24	682
50	0	12.07	2.32	40.60	159.13	2184
	8	18.84	0.81	21.50	83.54	636
25	0	14.52	3.70	36.00	145.97	2359
	8	28.77	1.37	22.17	81.99	601
0	0	34.65	5.78	25.76	95.68	1583
	8	38.14	1.87	14.96	50.12	536
$LSD_{(0.05)}$		4.69	0.50	3.52	4.87	164
Salinity		**	**	*	**	**
N		**	**	**	NS	**
Salinity*N		**	**	*	NS	**

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

† Values denote the percentage of nitrogen as NH_4^+-N in the nutrient solution.

‡ Each value for NO_3^--N, total N, and water uptake is the mean for three replications and three harvest times.

Table 4.6: Effect of different NH_4^+ to NO_3^- ratios and salinity on NO_3^- -N, total N and water uptake of barley plants (Experiment 3).

NH_4^+ † (%)	Salinity	NO_3^--N content ‡		Total N ‡		Water Uptake‡
		Root	Shoot	Root	Shoot	
	(bars)	------ mg/g --------		-------- mg/pot-----		mL/pot
100	0	0.13	0.57	41.63	184.09	1675
	8	0.10	0.29	20.77	130.02	787
75	0	0.67	2.40	81.46	251.19	2432
	8	0.88	0.89	29.11	144.69	1366
50	0	0.70	1.82	87.03	271.75	3598
	8	4.05	1.20	28.89	171.60	1118
25	0	1.63	3.24	75.06	257.25	4553
	8	9.19	1.74	38.42	179.29	1297
0	0	2.35	2.84	62.18	209.20	3708
	8	8.85	2.29	20.65	76.14	960
$LSD_{(0.05)}$		0.52	0.28	3.46	4.51	325
Salinity		**	**	NS	*	**
N		**	**	**	**	**
Salinity*N		**	**	**	**	**

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.
† Values denote the percentage of nitrogen as NH_4^+-N in the nutrient solution.
‡ Each value for NO_3^--N, total N, and water uptake is the mean for three replications and three harvest times.

taking place. But in the case of experiment 3, overall root NO_3^- concentrations were low compared to root NO_3^- concentrations in experiments 1 and 2. As already mentioned, NO_3^- uptake from solution was similar in 25 % NH_4^+ and 0 % NH_4^+ in all the experiments.

These results are in agreement with those of Lewis and Chadwick (1983), Lewis et al. (1982) and Murphy and Lewis (1987). Lewis and Chadwick (1983) reported that the shoot is the main organ of NO_3^- assimilation and that root is the major organ for ammonium assimilation. When both were fed to the plants, combined shoot and root assimilation of NO_3^- was observed. The root NO_3^- contents of 100 % nitrate fed plants in all the experiments support this hypothesis. They also found that in xylem sap 66 % of the ^{15}N supply to the shoot was in the form of NO_3^- where plants received all NO_3^-. This demonstrated that the NO_3^- supply largely bypassed the storage pool of the root. It is loaded directly into the xylem. They also noted that in nitrate+ammonium fed plants, the nitrate content of the xylem sap was considerably lower than that of nitrate fed plants. They also mentioned that the highest rate of incorporation of ^{15}N into organic N was exhibited by the mixed N fed plants, followed by NH_4-fed plants, and then NO_3^--fed plants.

Tables 4.4, 4.5 and 4.6 show that root NO_3^- concentrations in salinity treatments were significantly ($P < 0.05$) higher in all the experiments. This occurred despite the fact that NaCl salinity decreased N uptake. The shoot NO_3^- concentrations of plants grown in saline treatments were significantly lower when compared to the plants grown in non-

saline treatments. This shows that salinity caused NO_3^- accumulation in plant roots and reduced nitrate assimilation.

The most probable reason for the accumulation of NO_3^- and lower organic N synthesis in the NO_3^- treated plants is a limitation in nitrate reductase activity (Hageman and Flesher, 1960). Another possibility is that discussed by Hay, Earley and De Turk (1953) who found that a high salt content in the tissue for prolonged periods could lead to reduced nitrate reductase activity. Bernstein (1963) also mentioned the possibility that increased osmotic pressure of the cell or increased concentration of specific ions may alter the activity of some enzymes. Water uptake was significantly ($P < 0.05$) reduced in the salinity treatments. This trend was noted in all the experiments. Huffaker et al. (1970) observed decreased activities of both NO_3^- and nitrate reductase activity (NRA) in barley seedlings subjected to water stress. Plaut (1974) also reported that salt stress inhibits N metabolism in the wheat seedlings by affecting the nitrate reductase activity.

The salinity x N interaction was significant ($P < 0.01$) in experiments 2 and 3. Root nitrate concentrations were found significantly higher at 8 bar salinity level in spite of lower nitrate uptake. As pointed out by many investigators, this accumulation of nitrate in saline conditions was due to inhibition of nitrate reductase activity in treatments where 0 and 25 % NH_4^+ was applied.

4.4: Total N Content of Plants

Tables 4.4, 4.5 and 4.6 show the effects of different NH_4^+/NO_3^- ratios and salinity levels on total N contents in root and shoot samples of barley plants. Both root

and shoot N concentration were significantly ($P < 0.05$) higher in plants grown with 100 % NH_4^+ as compared to all the other NH_4^+/NO_3^- ratios in all the three experiments. This indicates the greater effectiveness of NH_4^+-N in increasing N concentration in plant shoots while decreasing plant growth due to its toxicity. The relationship between N-form, N concentration in plant tissues, and plant growth were explained by Schrader et al. (1972). These authors concluded that the higher N concentration in plants grown with NH_4^+-N suggested that NH_4^+ was detoxified in the roots through direct incorporation into organic-N form while NO_3^- was transported to the leaves for enzymatic reduction by nitrate reductase. It is evident from the root, shoot, and total N data that total N contents of plants with mixed N nutrition were significantly higher than either ammonium or nitrate fed plants (Tables 4.4, 4.5 and 4.6). This trend was generally observed in all the experiments. The plants grown in 50 % NH_4^+ contained significantly higher N concentrations in experiment 2 and 3. However, N contents were found similar in plants grown with 75, 50 and 25 % NH_4^+.

These results are in agreement with those of Lewis and Chadwick (1983), Heberer and Below (1989), Lewis et al. (1981), Weissman (1951) and Cox and Reisenauer (1973). The results of these experiments supports the findings of Cox and Reisenauer (1973) in that the plant receiving the mixed nitrate-ammonium N supply showed fastest N assimilation into the organic form and also produced the largest plants. The increased N assimilation of the mixed N fed plants over ammonium fed plants can be ascribed to the nitrate assimilatory contribution to the shoots augmenting the major ammonium assimilatory contribution of the roots. The presence of nitrate in the feeding medium

must also stimulate growth in some other ways, however, to produce larger, more robust plants of mixed N nutrition. Even though the medium around the roots of the plants was vigorously aerated, this stimulation could be in the form of an additional oxidizing source allowing increased root respiration (Lea, 1979) and consequent improvement in the absorption of other nutrients.

Generally, total N contents in roots and shoots based upon mg/pot were significantly higher under non-saline conditions in all the treatments and in all the experiments (Tables 4.4, 4.5 and 4.6). The beneficial effects of fertilization in moderately saline conditions was generally indicated. While studying the effects of various salt fertilizer combinations on the growth and composition of barley, Gregene and Mojallali (1968) found that application of N, P and K fertilizer reduced the adverse effects of low to moderate levels of salinity.

Several investigators have reported a decrease in N content in plants caused by salt stress. Heikal (1977) reported that total N contents of wheat leaves and radish leaves were decreased by salinity. Torres and Bingham (1973) grew Mexican wheat to full maturity in sand culture with variable levels of substrate NO_3^- and NaCl. They found that increased salinity enhanced the uptake of Na, Cl, Ca, and P. However, leaf nitrate concentration, total N, K, and Mg were decreased with salinization. Hummadi (1977) also found a decrease in total N and NO_3^- uptake with increasing soil salinity in Mexican wheat, 'Sonora 64'. Meyer and Gingrich (1966) also observed a decrease in N % in shoots and roots of wheat seedlings with increasing stress up to 9 bars of osmotic

pressure. Helal and Mengel (1979) concluded that total ^{15}N contents of roots decreased with increasing NaCl salinity in 31 day old barley plants.

In contrast, some authors reported an increase in N content in plants growing in saline substrates. Abrol (1968) found that the N concentration in wheat plants increased with increasing ESP under standard fertilization, but this increase did not occur in high N treatments.

To explain these different results, Frota and Tucker (1978b), observed in red kidney beans that dry matter production and total N per plant decreased as the N concentration increased in the stressed plants, and concluded that these different results were probably due to a dilution or concentration effects depending upon the relative severity of salt effect on growth or N uptake. Furthermore, Pessarakali (1981) confirmed the dilution effect of N concentration in cotton crop.

4.5: Water Uptake

The water uptake by plants were determined during the study period. The values recorded in the Tables 4.4, 4.5 and 4.6 are considered to be the water loss through transpiration by barley plants. The water uptake by barley plants under different NH_4^+/NO_3^- ratios and NaCl salinity levels is shown in Table 4.4, 4.5 and 4.6.

The plants grown with mixed N nutrition in experiment 1, consumed significantly ($P<0.05$) higher amounts of water as compared to the plants grown in either NH_4^+ or NO_3^- alone.

In experiment 2, the plants grown in 50 and 25 % NH_4^+ utilized significantly ($P < 0.05$) higher amounts of water as compared to the plants in all the other treatments. The plants grown with 100 % NH_4^+ utilized the least amount of water and there was a statistically non-significant difference in water uptake by the plants grown in 75 and 0 % NH_4^+ treatments.

Plants were grown for 45 days after transplanting in experiment 3. The plants grown with 25 % NH_4^+ absorbed the highest amount of water while the plants grown in 50 and 0 % NH_4^+ absorbed similar amounts of water. In all the three experiments, the plants grown with 100 % NH_4^+-N utilized the least amount of water and the plants grown with 25 % NH_4^+ consumed the highest amount. It can be implied that when ammonium-N was the dominant form it affected water uptake significantly due to inhibition of respiration and decreased root cell permeability (Vines and Wedding, 1960). However, when nitrate was the dominant-N form plants consumed significantly higher amounts of water, higher N uptake and higher dry matter production than dominant ammonium-N form. Viets et al. (1946) reported that ammonium nutrition alone leads to insufficient water uptake due to decreased solute concentration in the vacuoles. Polizotto et al. (1975) found that NH_4^+ treatment inhibited water uptake and also produced lower Ca and Mg concentrations in potato.

The 8 bar treatment significantly decreased the water uptake in all the NH_4^+/NO_3^- ratios as compared to the control in experiments 2 and 3. Total water uptake per pot decreased significantly with increasing salinity.

The effect of salt stress on transpiration rate has been studied for several plant species. The reported results are consistent in the point that transpiration rate or water absorption is reduced by salinity. Frota and Tucker (1978 b) also observed a reduction of water absorption by both salt and water stress treatments in kidney beans. For wheat, Aceves-N et al. (1975) observed a reduction in transpiration by salinity in the root medium. Hira and Singh (1973) reported that the transpiration rate per unit leaf area significantly decreased at the salinity level of 12 mmhos/cm in the soil. They generally agreed that the root permeability, expressed as hydraulic conductivity of the root system, was decreased significantly under stress. This may be another explanation for the reduction in water uptake rate and may contribute to a similar reduction in nutrient uptake, resulting in retarded plant growth and decreased dry matter yield under salt stress. The salinity x N interaction effect was found highly significant ($P < 0.01$) on water uptake. Salinity generally inhibited the water uptake due to decrease in cell permeability. This effect was more severe when NH_4^+ was the dominant N-form. The higher water uptake was observed in mixed N nutrition under saline conditions.

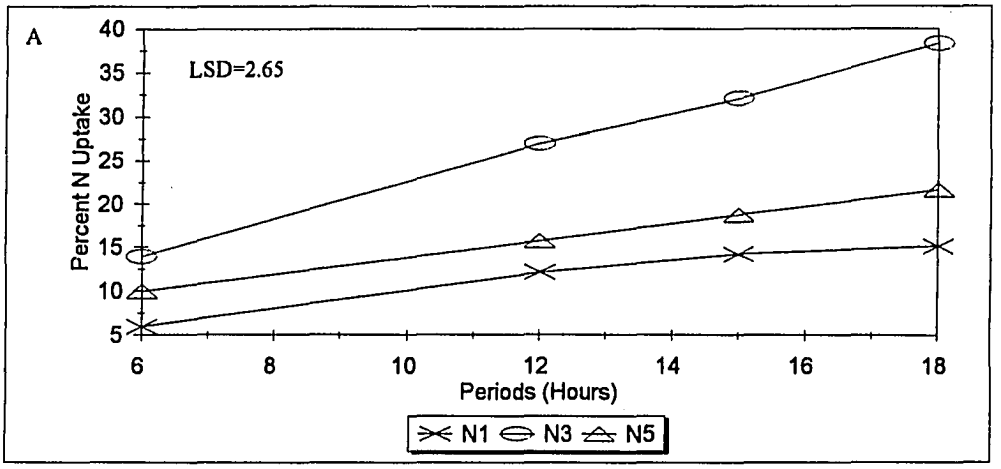
4.6: Apparent Uptake by N Solution Loss

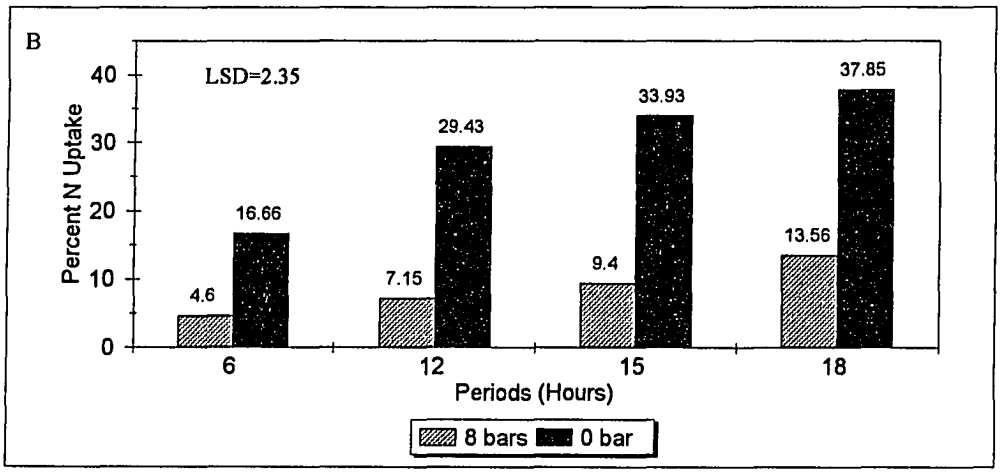
Cumulative N uptake was studied by analysis of solution samples taken from 100, 50, and 0 % NH_4^+ treatments after 6, 12, 15, and 18 hour intervals from the solution, and the results are illustrated in Fig. 4.1. The cumulative curve showed nearly linear uptake during the 6, 12, 15, and 18 hours period. After 12 hours, the slope of curve

slightly declined in the 100 % NH_4^+ treatment (Fig. 4.1 A). This decline is considered to be the effect of darkness in the growth chamber on ammonium uptake.

The N uptake percentage was significantly ($P<0.01$) affected by NH_4^+ to NO_3^- ratios. It was highest in the 50 % NH_4^+ treatment followed by the 0 % NH_4^+ treatment and the 100 % NH_4^+ treatment (Table 4.1 C). Lewis and Chadwick (1983) reported that ^{15}N uptake by 20-day old barley plants was highest in mixed-N-fed plants. They reported more NH_4^+ uptake than NO_3^- uptake. This study indicated more NO_3^- uptake than NH_4^+ uptake by 45 days old barley plants. The reason might be due to the difference in the age of the plants. Studies with some species have indicated that young plants absorb NH_4^+ more readily than NO_3^-. However, as the plant ages the converse is true (Hewitt, 1966 and Michael et al. 1970). The possible explanation for this is the change in carbohydrate contents of roots on ageing.

The N uptake percentage was also significantly affected ($P<0.01$) by salinity levels (Fig.4.1 C). The high level of salinity caused substantial reduction in N uptake percentage in all the treatments but N uptake percentages were comparatively less affected in the 50 % NH_4^+ treatment at the same salinity levels. The N uptake percentage was significantly different over time. The highest uptake was found after 18 hours in the 50 % NH_4^+ treatment.





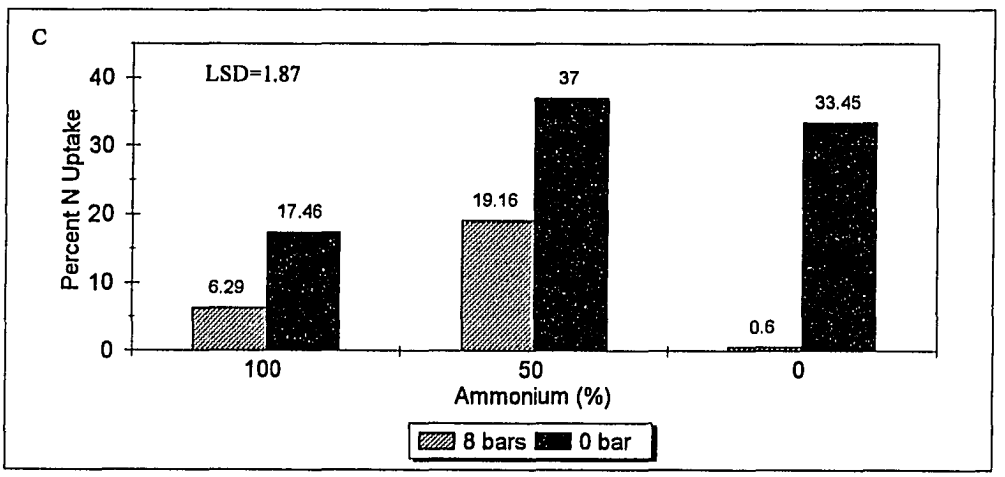


Fig. 4.1: Effect of ammonium to nitrate ratios and salinity levels on N-15 uptake
(A) Ammonium(%) and period interaction (B) period and salinity interaction
(C) Ammonium (%) and salinity interaction

4.7: ^{15}N Content in Plants

The ^{15}N content of barley plants and the distribution of the absorbed ^{15}N in the shoots and roots were examined by analysis of the plant material. Tables 4.7 show the ^{15}N content of roots and shoots. It is very important to note that 100 and 0 % treatments were labelled with 100 % $^{15}NH_4^+$ and 100 % $^{15}NO_3^-$, respectively. The 75 % NH_4^+ treatment was labelled with 75 % $^{15}NH_4^+$. The 50 and 25 % NH_4^+ treatments were labelled by 50 % $^{15}NO_3^-$. For comparison, only percent ^{15}N recovery will be reported.

It is evident from Table 4.7 that ^{15}N recovery in the 75, 50, 25, and 0 % NH_4^+ treatments were statistically similar. Labelled nitrate recovery was highest in the 50 % NH_4^+ treatment but nothing can be said about NH_4^+ uptake in this treatment because only the NO_3^- source was labelled. Nitrogen-15 recovery was significantly higher in the 0 % NH_4^+ treatment compared to the 100 % NH_4^+ treatment.

Both $^{15}NH_4^+$ and $^{15}NO_3^-$ uptake were drastically reduced by salinity in all the treatments. The plants fed with $^{15}NO_3^-$ source inhibited nitrate uptake more severally under saline conditions than the $^{15}NH_4^+$ fed plants under similar conditions. The reason might be the NO_3^- and Cl^- antagonostic effects and Cl^- has more affinity for water than NO_3^-. In 50 % NH_4^+ treatment, $^{15}NO_3^-$ recovery due to salinity was significantly less affected. Reduction in ^{15}N uptake pattern followed the same reduction pattern as total N and dry matter yield under stress conditions. This is an indication that the absorbed ^{15}N was incorporated into proteins and contributed to plant growth and development as reflected in dry matter production. Substantial difference between ^{15}N uptake by different

Table 4.7: Effect of different NH_4^+ to NO_3^- ratios and salinity on ^{15}N contents of root and shoot (Experiment 3).

NH4† %	Salt bars	Period (hours)	^{15}N Contents‡			^{15}N Recovery‡		
			Root	Shoot	Total	Root	Shoot	Total
			mg/pot			%		
100	0	6	1.17	1.70	2.87	6	9	15
		12	2.33	2.47	4.80	12	12	24
		18	2.35	3.00	5.35	12	15	27
	8	6	0.49	0.35	0.85	2	2	4
		12	0.45	0.35	0.80	2	2	4
		18	1.57	1.33	2.90	8	8	16
75	0	6	1.70	1.41	3.11	11	10	21
		12	2.93	2.52	5.45	20	17	37
		18	5.04	3.40	8.44	34	23	57
	8	6	0.98	0.82	1.80	7	5	12
		12	0.19	0.77	0.96	1	5	6
		18	1.22	0.81	2.01	8	5	13
50	0	6	1.11	1.02	2.13	11	10	21
		12	2.20	2.16	4.36	22	22	44
		18	3.12	3.26	6.38	31	31	62
	8	6	0.86	0.52	1.38	8	5	13
		12	0.89	0.67	1.56	9	9	18
		18	1.56	1.34	2.90	15	13	28
25	0	6	1.16	0.69	1.85	12	7	19
		12	2.34	1.39	3.73	23	14	37
		18	4.15	3.30	7.45	41	33	74

(Cont.....)

Table 4.7: Effects of different NH_4^+ to NO_3^- ratios and salinity on ^{15}N contents of root and shoot (Experiment 3) (Cont.....)

NH4† %	Salinity bars	Period (hours)	^{15}N Contents‡ Root	Shoot	Total	^{15}N Recovery ‡ Root	Shoot	Total
			---------- mg/pot----------			----------%----------		
25	8	6	0.21	0.05	0.26	2.1	0.5	2.6
		12	0.09	0.06	0.15	1	0.6	1.6
		18	0.17	0.08	0.25	1.7	0.8	2.5
0	0	6	1.98	1.39	3.37	10	7	17
		12	4.42	2.48	6.90	22	34	56
		18	8.50	6.88	15.3	42	34.4	76.5
	8	6	0.09	0.02	0.12	0.51	0.1	0.61
		12	0.08	0.02	0.1	0.51	0.1	0.61
		18	0.06	0.06	0.12	0.51	0.1	0.61
LSD (0.05)			1.44	1.62	2.62	12	12	18.5
NH4 %			**	**	**	**	**	**
Salinity levels			**	**	**	**	**	**
Period			**	**	**	**	*	**
NH4 %*Salinity			**	**	**	**	NS	**
NH4 %*Period			**	*	**	*	NS	*
Salinity*Period			**	**	**	*	NS	NS
NH4 %*Salinity*Period			**	**	**	NS	NS	NS

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.
† Values denote the salinity levels (bars) in the nutrient solution.
‡ Each value for ^{15}N contents and % N recovery is the mean for three replications.

to NO_3^- ratios at each salinity levels implies a significant interaction effect between NH_4^+ to NO_3^- ratios and salinity levels at each harvest for each plant part. Significant increase in ^{15}N uptake percent by these plants under high salinity levels are in agreement with experimental data obtained with red kidney beans (Frota and Tucker, 1978; Saad, 1979), cotton (Pessarakli and Tucker, 1988) and tomato (Pessarakli and Tucker, 1988).

CHAPTER 5

SUMMARY AND CONCLUSIONS

The effects of salinity and five different ammonium to nitrate ratios on dry matter production, N uptake, nitrate contents, total Kjeldahl-N contents of plants, water uptake, and uptake of $^{15}NH_4$ or $^{15}NO_3$ were studied at the late stem extension stage of barley. The following is the summary of findings.

The plants receiving mixed N-nutrition produced significantly ($P<0.05$) higher root and shoot dry matter yields as compared to plants grown in ammonium or nitrate alone. The plants grown in 50/50 and 25/75 NH_4^+/NO_3^- ratios produced the highest yield among all the NH_4^+/NO_3^- ratios. The dry matter yield of barley was inhibited by high NH_4^+-N concentration when no NO_3^- was supplied.

The dry matter production was negatively correlated with the levels of salinity. Higher dry matter yields were produced when plants were grown in mixed N-nutrition under salinity stress as compared to ammonium and nitrate alone under identical saline conditions. Salinity and N-nutrition effects were found significant.

The plants receiving mixed N nutrition showed significantly higher ammonium, nitrate and cumulative N uptake as compared to plants grown in either ammonium or nitrate alone. The cumulative N uptake was higher in case of 50/50 and 25/75 NH_4^+/NO_3^- ratios.

The total N uptake followed a pattern of decreasing N uptake with increasing salinity levels similar to the effects on dry matter production. The inhibition of uptake

was either due to the depressed cumulative N uptake itself or to the reduced dry matter production.

Highest root NO_3^- contents were found in the 0 % NH_4^+ treatment. Nitrate assimilation in plant roots grown in 100 % NO_3^- was significantly lower as compared to plant roots fed with mixed N nutrition, while nitrate uptake was similar in 25 % NH_4^+ and 0 % NH_4^+. Root NO_3^- concentration in salinity treatments were significantly ($P<0.05$) higher in all experiments. This occurred despite the fact that the NaCl salinity effect decreased the N uptake. The shoot NO_3^- concentrations of plants grown in saline conditions were significantly lower when compared to the plants grown in non saline conditions. This shows that NaCl caused NO_3^- accumulation in plant roots and reduced nitrate assimilation.

Both root and shoot N concentrations were significantly higher ($P<0.05$) in plants grown with 100 % NH_4^+ as compared to all the other NH_4^+/NO_3^- ratios. This indicates the greater effectiveness of NH_4^+-N in increasing N concentration in plant shoots while decreasing plant growth due to its toxicity. It is evident from the root, shoot and total N data that total N contents of plants with mixed N nutrition were significantly higher than either ammonium or nitrate fed plants. The plants grown in 50 % NH_4^+ contained significantly higher N contents.

Root N concentrations in plants grown with 50 % NH_4^+ were statistically similar both under saline and non-saline conditions but N concentration was significantly lower as compared to plants grown in all other treatments. Root N concentrations in plants fed with 100 % NH_4^+ and 75 % NH_4^+ were significantly higher in non-saline conditions

as compared to saline conditions. On the other hand, root N concentration was significantly higher under saline conditions where plants were fed with 25 % NH_4^+ and 0 % NH_4^+ ratios. This shows that when NH_4^+-N form was dominant, salt depressed the N uptake and where NO_3^--N was dominant, salinity affected the N uptake and also caused nitrate accumulation. Generally, total N contents in roots and shoots based upon mg/pot were significantly higher under non- saline conditions. The beneficial effects of fertilization in moderately saline conditions was generally indicated. Nitrogen contents were significantly higher in 50 % NH_4^+ under non saline conditions but N concentration was lower than all other ratios.

The plants grown with 100 % NH_4^+ utilized the least amount of water and the plants grown with 25 % NH_4^+ utilized the highest amount. Salinity treatment significantly decreased the water uptake in all the ammonium to nitrate ratios. The reduction in water uptake may contribute to similar reduction in nutrient uptake rate, resulting in retarded plant growth and decreased dry matter production under salt stress.

APPENDIX 1

EXPERIMENTAL DATA

Experiment 1
DATA
APPENDIX

OBS	REP	NLEV	SALT	STEM	ROOT	NH_4	NO_3	STOTN	TRTNO3
				dry weight		uptake from solution			
				----g-----		------ mg/pot------			mg/g
1	1	1	1	1.42	0.5	102.4	0.00	102.42	0.8
2	1	1	2	0.77	0.4	54.6	0.00	54.62	0.2
3	1	1	3	0.86	0.3	53.9	0.00	53.91	0.7
4	1	2	1	2.46	1.0	121.5	51.46	172.99	17.5
5	1	2	2	2.22	1.1	115.0	34.29	149.27	42.4
6	1	2	3	1.66	1.0	89.7	32.53	122.25	36.6
7	1	3	1	2.28	0.9	83.1	82.68	165.80	72.4
8	1	3	2	1.95	0.9	88.2	40.84	129.00	54.4
9	1	3	3	0.89	0.5	91.8	24.34	116.14	22.0
10	1	4	1	1.94	0.7	54.2	115.60	169.80	77.1
11	1	4	2	1.31	0.6	49.9	35.59	85.57	33.1
12	1	4	3	1.69	0.6	54.9	44.83	99.79	54.3
13	1	5	1	1.19	0.6	0.00	91.95	91.95	67.1
14	1	5	2	1.04	0.4	0.00	30.54	30.54	38.0
15	1	5	3	0.67	0.4	0.00	45.66	45.66	38.3
16	2	1	1	1.70	0.6	124.83	0.00	124.83	1.2
17	2	1	2	0.92	0.4	60.90	0.00	60.90	2.2
18	2	1	3	0.94	0.5	68.51	0.00	68.51	0.1
19	2	2	1	2.45	0.9	118.17	55.55	173.72	30.3
20	2	2	2	1.80	0.8	91.96	46.43	138.39	54.8
21	2	2	3	2.34	1.2	142.74	28.83	171.57	69.6
22	2	3	1	2.39	1.5	95.80	87.40	183.20	41.4
23	2	3	2	2.34	1.3	99.74	54.49	154.23	94.1
24	2	3	3	1.75	0.9	85.11	37.75	122.86	57.8
25	2	4	1	3.10	1.8	56.33	121.08	177.41	58.6
26	2	4	2	0.93	0.4	43.53	31.51	75.04	26.6
27	2	4	3	1.24	0.8	51.60	34.39	85.99	49.9
28	2	5	1	1.40	0.5	0.00	91.50	91.50	59.9
29	2	5	2	0.59	0.3	0.00	38.27	38.27	38.7
30	2	5	3	0.52	0.2	0.00	34.56	34.56	29.3
31	3	1	1	1.90	0.6	116.28	0.00	116.28	0.5
32	3	1	2	1.46	0.5	87.66	0.00	87.66	1.2
33	3	1	3	1.00	0.4	74.76	0.00	74.76	1.1
34	3	2	1	3.49	1.0	135.18	62.59	197.77	39.8
35	3	2	2	2.95	1.4	137.28	47.46	184.74	68.5
36	3	2	3	2.89	1.3	122.54	56.86	179.40	49.0
37	3	3	1	3.35	1.2	99.33	91.81	191.14	31.3
38	3	3	2	2.10	1.0	96.42	47.94	144.36	84.5
39	3	3	3	1.86	0.9	83.57	38.58	122.15	56.5
40	3	4	1	2.86	1.1	52.92	120.00	172.92	56.8
41	3	4	2	1.20	0.6	44.16	86.55	130.71	30.5
42	3	4	3	2.08	1.1	53.48	80.04	133.52	120.9
43	3	5	1	1.32	0.5	0.00	93.49	93.49	61.1
44	3	5	2	0.80	0.4	0.00	66.30	66.30	57.1
45	3	5	3	0.71	0.5	0.00	55.63	55.63	56.9

Experiment 1
DATA

OBS	$RTNO_3$	$TLFNO_3$	$LFNO_3$	Root N	Stem N	Water use	TOT N
		----leaf NO_3---					
	mg/g	mg/pot	mg/g	---mg/pot---		mL/pot	mg/pot
1	1.7	4.82	3.40	45.2	56.5	960	101.7
2	0.6	1.48	1.49	38.9	40.5	1135	79.4
3	2.5	1.31	1.52	34.5	36.0	795	70.5
4	17.7	94.66	38.48	42.1	53.0	1675	95.1
5	38.8	14.28	6.80	34.4	43.5	1410	77.9
6	38.1	11.73	7.07	36.2	42.1	1080	78.3
7	79.5	179.85	75.88	42.5	55.3	1620	97.8
8	57.8	19.64	10.07	38.0	43.1	1290	81.1
9	44.9	20.20	12.24	36.5	36.7	1040	73.2
10	107.0	170.24	69.48	43.0	48.5	1225	91.5
11	51.7	16.63	12.69	37.1	41.0	945	78.1
12	83.6	22.91	13.55	33.6	36.2	1245	69.8
13	113.8	84.32	70.86	46.6	45.5	1115	92.1
14	86.4	8.53	8.21	34.8	43.9	1065	78.7
15	93.4	13.58	18.11	33.6	29.3	1090	62.9
16	1.9	3.82	2.25	45.4	54.1	885	99.5
17	5.9	0.75	0.81	36.1	41.9	800	78.0
18	0.3	129.22	1.37	38.2	40.3	690	78.5
19	32.2	88.00	33.98	38.9	51.3	1195	90.2
20	64.5	21.24	11.42	36.8	49.1	1190	85.9
21	56.6	12.91	5.51	37.9	42.7	1200	80.6
22	28.0	96.91	28.58	30.1	42.4	1485	72.5
23	73.5	31.20	13.33	36.6	40.8	1160	77.4
24	60.9	31.81	18.18	37.7	40.2	945	77.9
25	32.8	83.48	23.51	30.1	39.2	1730	69.3
26	62.0	11.48	12.35	38.2	40.9	905	79.1
27	61.7	11.86	9.57	34.2	39.4	1035	73.6
28	117.6	107.28	73.48	46.6	48.0	1050	94.6
29	143.4	20.19	34.22	33.9	33.7	770	67.6
30	127.5	21.82	41.97	33.4	38.6	585	72.0
31	0.8	2.64	1.39	50.7	44.6	955	95.3
32	2.5	1.95	1.33	38.0	46.4	870	84.4
33	2.6	1.80	1.80	37.8	44.2	835	82.0
34	39.0	63.04	18.06	32.4	39.5	1260	71.9
35	48.6	21.78	7.16	35.8	45.4	1230	81.2
36	39.2	20.62	7.13	37.6	42.8	975	80.4
37	26.5	170.50	49.42	31.9	43.9	1330	75.8
38	84.4	33.67	16.03	42.0	46.9	1040	88.9
39	64.2	35.68	19.18	39.9	40.2	870	80.1
40	52.1	181.45	63.43	39.7	45.6	1380	85.3
41	55.4	14.09	11.74	36.9	39.1	845	76.0
42	109.9	34.10	16.39	37.9	40.5	1020	78.4
43	119.8	41.04	31.09	45.6	39.7	765	85.3
44	129.6	20.54	25.67	41.4	34.6	670	76.0
45	121.0	15.17	21.37	39.6	34.5	660	74.1

Experiment 2

DATA

OBS	REP	NLEV	SALT	PERIOD	STEM	ROOT	NO_3	NH_4
				hours	dry weight -----g-----		uptake from solut. ----- mg/pot------	
1	1	1	0	6	2.53	0.82	0.00	130.60
2	1	1	0	12	2.44	0.84	0.00	149.00
3	1	1	0	24	1.87	0.60	0.00	119.20
4	1	1	1	6	1.45	0.39	0.00	90.66
5	1	1	1	12	1.28	0.42	0.00	89.78
6	1	1	1	24	1.52	0.41	0.00	80.84
7	1	2	0	6	2.61	0.43	45.84	106.00
8	1	2	0	12	3.53	0.96	44.55	151.60
9	1	2	0	24	4.38	1.15	48.43	176.60
10	1	2	1	6	2.11	0.73	36.55	70.62
11	1	2	1	12	2.18	1.33	48.73	83.79
12	1	2	1	24	2.06	0.71	36.00	76.25
13	1	3	0	6	3.76	1.30	92.17	102.30
14	1	3	0	12	3.18	1.16	81.65	92.89
15	1	3	0	24	3.72	1.53	98.06	120.80
16	1	3	1	6	2.45	0.64	39.96	92.03
17	1	3	1	12	2.11	0.61	26.77	84.11
18	1	3	1	24	1.71	0.57	28.83	54.95
19	1	4	0	6	3.90	1.51	130.30	55.63
20	1	4	0	12	3.93	1.45	134.30	57.20
21	1	4	0	24	3.07	0.95	130.70	47.30
22	1	4	1	6	1.32	0.41	36.22	34.11
23	1	4	1	12	2.62	0.93	140.30	37.48
24	1	4	1	24	2.53	0.84	93.56	40.31
25	1	5	0	6	3.46	1.19	137.50	0.00
26	1	5	0	12	2.43	0.80	101.40	0.00
27	1	5	0	24	2.27	0.73	96.27	0.00
28	1	5	1	6	1.03	0.33	51.02	0.00
29	1	5	1	12	1.04	0.38	54.72	0.00
30	1	5	1	24	0.94	0.35	56.06	0.00
31	2	1	0	6	2.37	0.68	0.00	130.30
32	2	1	0	12	2.00	0.72	0.00	137.80
33	2	1	0	24	2.10	0.71	0.00	123.00
34	2	1	1	6	1.57	0.78	0.00	98.32
35	2	1	1	12	1.54	0.51	0.00	102.90
36	2	1	1	24	1.76	0.65	0.00	112.80
37	2	2	0	6	3.69	0.89	48.12	133.60
38	2	2	0	12	4.19	1.02	44.76	156.30
39	2	2	0	24	4.27	1.23	49.45	166.10
40	2	2	1	6	4.31	1.33	51.22	146.90
41	2	2	1	12	1.43	0.43	26.28	71.76
42	2	2	1	24	2.90	0.94	36.83	109.80
43	2	3	0	6	4.06	1.42	85.37	114.10
44	2	3	0	12	4.53	1.55	110.10	116.40
45	2	3	0	24	3.98	1.63	95.01	112.00
46	2	3	1	6	2.69	0.79	60.36	65.25
47	2	3	1	12	1.71	0.56	24.66	73.28
48	2	3	1	24	1.00	0.33	45.79	50.24
49	2	4	0	6	3.58	1.29	146.00	50.52
50	2	4	0	12	3.50	1.18	131.00	50.92
51	2	4	0	24	5.51	2.84	141.30	52.51
52	2	4	1	6	1.82	0.66	56.24	40.85

OBS	REP	NLEV	SALT	PERIOD	STEM	ROOT	NO_3	NH_4
				hours	dry weight ----g-----		uptake from solut. ------ mg/pot------	
53	2	4	1	12	3.12	0.99	90.47	43.14
54	2	4	1	24	2.09	0.67	66.03	36.00
55	2	5	0	6	2.47	0.88	136.90	0.00
56	2	5	0	12	3.92	1.55	195.30	0.00
57	2	5	0	24	2.66	0.81	147.70	0.00
58	2	5	1	6	1.69	0.62	98.65	0.00
59	2	5	1	12	1.45	0.56	82.65	0.00
60	2	5	1	24	1.54	0.53	74.55	0.00
61	3	1	0	6	1.79	0.57	0.00	117.80
62	3	1	0	12	1.88	0.48	0.00	118.60
63	3	1	0	24	2.03	0.86	0.00	138.00
64	3	1	1	6	1.69	0.48	0.00	107.30
65	3	1	1	12	1.92	0.64	0.00	127.40
66	3	1	1	24	1.50	0.44	0.00	79.82
67	3	2	0	6	3.63	0.80	45.29	169.80
68	3	2	0	12	3.72	0.86	46.44	165.00
69	3	2	0	24	4.35	1.03	48.07	175.90
70	3	2	1	6	2.62	0.77	36.57	87.12
71	3	2	1	12	2.53	0.72	37.39	72.71
72	3	2	1	24	2.13	0.65	29.44	60.12
73	3	3	0	6	4.04	1.19	97.11	102.90
74	3	3	0	12	4.76	1.88	105.30	120.70
75	3	3	0	24	5.07	2.19	102.70	118.40
76	3	3	1	6	2.27	0.90	62.38	76.69
77	3	3	1	12	2.47	0.73	67.93	59.27
78	3	3	1	24	2.85	0.91	68.55	52.02
79	3	4	0	6	3.85	1.53	115.40	38.16
80	3	4	0	12	4.41	1.87	147.20	55.35
81	3	4	0	24	5.37	2.25	122.60	44.79
82	3	4	1	6	2.11	0.65	78.57	36.01
83	3	4	1	12	1.82	0.61	62.85	36.94
84	3	4	1	24	2.44	0.70	71.03	39.78
85	3	5	0	6	1.71	0.56	92.75	0.00
86	3	5	0	12	1.72	0.64	110.60	0.00
87	3	5	0	24	2.78	1.04	170.70	0.00
88	3	5	1	6	1.48	0.53	65.27	0.00
89	3	5	1	12	1.51	0.48	79.86	0.00
90	3	5	1	24	1.11	0.44	64.58	0.00

OBS	N uptake mg/pot	leaf NO_3 mg/g	Root NO_3 mg/g	Leaf N total mg/pot	Root N total mg/pot	Total N mg/pot	WATUSE mL/pot
1	130.60	0.11	0.12	42.15	28.54	70.70	930
2	149.00	0.10	0.15	46.33	35.93	82.26	1005
3	119.20	0.15	0.10	46.77	42.40	89.18	960
4	90.66	0.04	0.14	49.35	32.56	81.61	545
5	89.78	0.04	0.15	38.20	34.15	72.36	555
6	80.84	0.03	0.15	49.45	33.53	82.93	380
7	151.80	1.00	2.70	39.21	30.48	69.70	1470
8	196.20	1.25	2.35	42.06	27.25	69.32	1565
9	225.00	1.30	3.35	42.02	33.72	75.74	1790
10	107.20	0.80	24.00	39.82	31.90	71.72	955
11	132.50	0.60	16.75	41.62	29.13	71.10	915
12	112.30	0.65	17.40	43.33	29.12	72.46	610
13	194.50	2.20	10.05	41.06	26.47	67.53	1960
14	174.50	2.55	9.75	40.83	29.63	70.47	1835
15	218.80	2.20	9.50	41.24	25.65	66.89	2795
16	132.00	0.90	19.00	42.74	32.41	75.16	715
17	110.90	0.70	21.50	38.38	30.40	68.79	620
18	83.78	0.60	20.70	33.85	27.05	60.90	670
19	185.90	2.00	11.15	35.98	22.75	58.73	2200
20	191.50	2.10	11.65	37.67	26.27	63.94	1775
21	178.00	2.35	12.65	45.63	31.62	77.26	2520
22	70.33	1.30	37.10	40.86	32.66	73.52	580
23	177.70	1.15	39.20	40.42	33.48	73.91	625
24	133.90	1.50	34.60	39.40	28.91	68.32	715
25	137.50	4.20	39.60	28.12	24.80	52.92	2030
26	101.40	4.90	44.00	27.26	33.16	60.42	1630
27	96.27	5.35	46.15	27.95	33.54	61.49	1525
28	51.02	2.05	39.35	35.95	36.74	72.69	470
29	54.72	1.75	42.25	38.35	34.70	73.05	615
30	56.06	1.95	41.35	37.84	32.52	70.36	495
31	130.30	0.10	0.10	44.15	32.36	76.52	1105
32	137.80	0.10	0.12	53.08	39.01	92.09	805
33	123.00	0.10	0.14	43.92	37.64	81.57	840
34	98.32	0.04	0.13	42.11	32.32	74.89	405
35	102.90	0.04	0.10	46.73	27.66	74.39	455
36	112.80	0.50	0.12	49.01	31.68	80.70	415
37	181.70	1.75	2.25	42.17	28.55	70.72	1270
38	201.00	1.70	2.30	39.65	27.54	67.19	1270
39	215.60	1.70	2.30	41.51	27.86	69.37	1870
40	198.10	0.95	18.15	37.76	23.66	61.42	560
41	98.04	0.80	16.65	39.96	33.41	73.37	610
42	146.60	1.05	17.20	38.55	30.18	68.74	670
43	199.40	2.20	13.85	38.96	25.42	64.39	1930
44	226.40	2.30	12.60	37.29	32.25	69.55	2090
45	207.10	2.30	10.45	40.85	24.46	65.31	2545
46	125.60	0.80	12.30	32.61	26.76	59.37	550
47	97.94	0.75	12.20	44.97	28.67	73.65	470
48	96.03	0.70	12.35	38.46	23.80	62.23	545
49	196.50	5.55	20.10	40.46	27.79	68.25	2030
50	181.90	4.90	18.55	40.76	28.95	69.72	2370
51	193.80	4.50	17.75	28.94	19.16	48.11	2815
52	97.09	1.60	28.10	41.20	29.96	71.16	715

OBS	N uptake mg/pot	leaf NO_3 mg/g	Root NO_3 mg/g	Leaf N total mg/pot	Root N total mg/pot	Total N mg/pot	WATUSE mL/pot
53	133.60	1.35	27.15	34.11	26.90	61.01	505
54	102.00	1.40	30.30	34.93	28.03	62.97	485
55	136.90	7.00	33.75	41.07	28.49	69.57	1390
56	195.30	6.35	42.75	39.39	27.49	66.88	1530
57	147.70	6.15	37.90	42.38	33.17	75.56	1945
58	98.65	1.75	39.00	40.43	32.92	73.36	570
59	82.65	1.70	43.45	38.82	33.62	72.45	595
60	74.55	1.55	41.80	35.77	34.14	69.92	465
61	117.80	0.10	0.10	52.76	38.96	91.72	715
62	118.60	0.13	0.10	48.03	36.01	84.04	670
63	138.00	0.13	0.10	48.89	32.87	81.77	915
64	107.30	0.04	0.10	48.20	33.02	81.22	320
65	127.40	0.06	0.10	46.57	32.57	79.15	365
66	79.82	0.04	0.10	40.16	28.60	68.77	345
67	215.10	1.65	1.90	46.64	29.58	76.22	1325
68	211.40	1.70	2.60	46.68	30.77	77.46	1175
69	223.90	1.55	3.00	43.01	31.26	74.27	1430
70	123.70	0.80	12.10	33.72	31.01	64.74	585
71	110.10	0.75	12.25	26.25	31.00	57.26	700
72	89.56	0.80	11.20	28.83	31.03	59.86	535
73	200.10	2.50	14.05	40.24	27.74	67.98	2060
74	226.00	2.40	12.65	36.96	24.67	61.64	1965
75	221.10	2.20	15.75	32.78	23.74	56.52	2480
76	139.10	0.95	24.20	46.55	33.62	80.17	600
77	127.20	0.90	22.45	35.33	34.90	70.23	780
78	120.60	0.95	24.85	29.28	29.78	59.07	780
79	153.60	3.75	12.30	30.12	23.62	53.83	1915
80	202.50	4.05	13.35	35.66	23.57	59.23	2265
81	167.40	4.10	13.25	30.72	28.83	59.55	3345
82	114.60	1.35	21.50	41.33	32.35	73.68	605
83	99.79	1.30	20.45	36.63	34.11	70.75	520
84	110.80	1.35	20.60	28.71	34.76	63.48	660
85	92.75	6.25	21.20	35.74	31.43	67.18	1365
86	110.60	6.75	23.60	45.36	35.13	80.49	1355
87	170.70	5.10	22.90	45.44	31.87	77.31	1480
88	65.27	1.80	31.15	39.21	56.03	95.25	445
89	79.86	2.05	32.05	39.71	28.09	67.81	755
90	64.58	2.20	32.90	36.87	31.06	67.94	420

Experiment 3
DATA

OBS	REP	NLEV	SALT	PERIOD	STEM	ROOT	NO_3	NH_4	Total N
				hours	dry weight		uptake from solution.		
					----g-----		-- mg/pot---		mg/pot
1	1	1	0	6	4.11	0.90	0.00	235.48	235.48
2	1	1	0	12	3.11	0.94	0.00	205.89	205.89
3	1	1	0	18	3.82	0.96	0.00	218.90	218.90
4	1	1	1	6	3.28	0.65	0.00	166.65	166.65
5	1	1	1	12	3.14	0.65	0.00	156.07	156.07
6	1	1	1	18	3.63	0.81	0.00	176.43	176.43
7	1	2	0	6	7.41	2.85	92.38	237.49	329.88
8	1	2	0	12	5.43	1.47	86.98	199.36	286.35
9	1	2	0	18	6.26	2.47	90.43	235.59	326.02
10	1	2	1	6	4.19	1.13	59.41	163.21	222.63
11	1	2	1	12	3.25	1.10	52.38	189.07	241.45
12	1	2	1	18	4.09	1.04	56.95	153.06	210.01
13	1	3	0	6	10.90	5.16	166.66	167.19	333.85
14	1	3	0	12	9.23	3.87	164.52	166.41	330.93
15	1	3	0	18	8.67	3.44	164.88	164.05	328.93
16	1	3	1	6	5.89	2.01	90.76	164.31	255.07
17	1	3	1	12	4.02	0.97	101.52	150.51	252.03
18	1	3	1	18	5.88	1.36	132.28	164.89	297.18
19	1	4	0	6	12.30	4.89	238.86	84.34	323.20
20	1	4	0	12	7.68	2.61	216.00	86.05	302.05
21	1	4	0	18	8.59	2.71	237.12	88.11	325.23
22	1	4	1	6	4.84	1.51	155.91	83.74	239.65
23	1	4	1	12	2.17	0.66	150.76	69.45	220.21
24	1	4	1	18	4.73	1.32	157.72	86.47	244.20
25	1	5	0	6	5.62	2.25	300.06	0.00	300.06
26	1	5	0	12	6.99	2.29	253.98	0.00	253.98
27	1	5	0	6	7.21	3.24	322.93	0.00	322.93
28	1	5	1	12	1.64	0.62	120.10	0.00	120.10
29	1	5	1	18	2.00	0.56	137.58	0.00	137.58
30	1	5	1	6	2.44	0.70	121.68	0.00	121.68
31	2	1	0	12	3.52	1.02	0.00	220.30	220.30
32	2	1	0	18	3.94	1.15	0.00	230.10	230.10
33	2	1	0	6	4.00	1.16	0.00	213.34	213.34
34	2	1	1	12	2.92	0.62	0.00	157.75	157.75
35	2	1	1	18	2.99	0.65	0.00	177.94	177.94
36	2	1	1	6	3.04	0.69	0.00	163.60	163.60
37	2	2	0	12	6.60	1.79	93.70	240.48	334.18
38	2	2	0	18	8.01	3.25	91.48	238.21	329.70
39	2	2	0	6	6.43	2.22	92.76	231.60	324.36
40	2	2	1	12	4.47	0.96	62.20	162.40	224.00
41	2	2	1	18	4.27	1.06	63.46	163.45	226.92
42	2	2	1	12	4.38	1.04	63.10	149.71	212.82
43	2	3	0	6	10.60	5.77	164.19	164.20	328.39
44	2	3	0	12	9.97	4.06	165.67	162.48	328.15
45	2	3	0	18	10.10	3.24	162.07	162.89	324.96
46	2	3	1	6	2.48	0.73	165.60	109.81	275.41
47	2	3	1	12	5.70	1.83	127.77	164.35	292.12
48	2	3	1	18	3.94	1.46	148.30	167.61	315.91
49	2	4	0	6	8.30	3.48	235.44	85.84	321.28
50	2	4	0	12	11.00	5.14	226.93	90.84	317.77
51	2	4	0	18	9.84	4.17	233.76	87.00	320.76
52	2	4	1	6	5.13	1.52	167.31	91.02	258.33

OBS	REP	NLEV	SALT	PERIOD	STEM	ROOT	NO_3	NH_4	Total N
				hours	dry weight		uptake from solution		
					---g---		-- mg/pot---		mg/pot
53	2	4	1	12	5.25	1.44	177.01	94.19	271.20
54	2	4	1	18	4.80	1.39	159.90	87.63	247.53
55	2	5	0	6	6.95	2.58	286.50	0.00	286.50
56	2	5	0	12	4.40	1.22	302.88	0.00	302.88
57	2	5	0	18	8.62	3.35	289.35	0.00	289.35
58	2	5	1	6	1.82	0.60	103.45	0.00	103.45
59	2	5	1	12	2.01	0.58	143.83	0.00	143.83
60	2	5	1	18	2.66	0.85	134.86	0.00	134.86
61	3	1	0	6	3.83	1.05	0.00	236.34	236.34
62	3	1	0	12	4.09	1.04	0.00	234.12	234.12
63	3	1	0	18	3.73	1.23	0.00	224.66	224.66
64	3	1	1	6	3.29	0.62	0.00	161.74	161.74
65	3	1	1	12	3.32	0.63	0.00	164.63	164.63
66	3	1	1	18	3.05	0.66	0.00	146.47	146.47
67	3	2	0	6	6.45	1.91	91.82	224.52	316.34
68	3	2	0	12	7.46	3.74	94.90	236.49	331.39
69	3	2	0	18	6.34	2.35	96.27	233.50	329.77
70	3	2	1	6	4.60	1.09	58.63	159.47	218.10
71	3	2	1	12	3.93	0.88	53.91	150.07	203.98
72	3	2	1	18	4.56	1.14	55.80	158.58	214.38
73	3	3	0	6	10.70	4.72	162.84	163.53	326.37
74	3	3	0	12	11.80	5.00	164.37	162.69	327.06
75	3	3	0	18	10.30	4.91	163.99	166.30	330.30
76	3	3	1	6	5.20	1.40	95.79	166.47	262.26
77	3	3	1	12	5.59	1.34	105.51	166.41	271.92
78	3	3	1	18	5.06	1.38	90.43	166.84	257.28
79	3	4	0	6	10.60	4.73	222.45	87.31	309.76
80	3	4	0	12	10.60	3.97	240.37	88.15	328.53
81	3	4	0	18	10.20	3.97	240.31	89.83	330.15
82	3	4	1	6	5.25	1.49	183.40	88.47	271.87
83	3	4	1	12	6.50	1.40	181.80	52.83	234.63
84	3	4	1	18	4.06	1.17	180.06	89.20	269.26
85	3	5	0	6	6.06	1.77	294.17	0.00	294.17
86	3	5	0	12	9.96	3.88	318.27	0.00	318.27
87	3	5	0	18	7.05	2.38	283.42	0.00	283.42
88	3	5	1	6	1.79	0.53	89.17	0.00	89.17
89	3	5	1	12	3.29	0.95	172.65	0.00	172.65
90	3	5	1	18	2.60	0.82	124.87	0.00	124.87

OBS	TILL	Root NO3	Leaf NO3	N leaf Total	N root Total	N Total	Water use
		mg/g	mg/g	mg/pot	mg/pot	mg/pot	mL/pot
1	29	0.15	0.61	49.25	32.76	82.01	1870
2	27	0.12	0.55	49.72	35.39	85.12	1465
3	27	0.08	0.55	51.56	39.02	90.59	1785
4	28	0.00	0.30	42.44	32.64	75.08	670
5	21	0.02	0.27	43.67	32.41	76.08	755
6	16	0.08	0.29	41.25	31.94	73.20	740
7	61	0.75	2.51	36.78	30.66	67.44	2260
8	31	0.74	2.28	44.86	32.59	77.45	2825
9	47	0.74	2.49	40.37	33.81	74.19	2465
10	28	0.92	0.82	40.43	30.99	71.42	1520
11	17	1.09	0.83	31.81	20.70	52.51	1815
12	23	1.05	0.79	32.45	27.81	60.26	1580
13	66	0.87	1.93	24.48	16.82	41.31	3790
14	57	0.90	1.78	30.43	22.86	53.29	3670
15	62	0.90	1.67	33.10	24.31	57.42	3405
16	46	3.91	1.03	34.42	16.38	50.80	1300
17	25	3.27	1.14	34.86	13.23	48.10	485
18	36	3.95	1.08	27.37	13.87	41.25	1135
19	52	1.63	3.30	23.78	13.75	37.53	4950
20	40	1.58	3.02	32.48	21.02	53.51	4030
21	46	1.88	3.15	34.36	22.08	56.44	4255
22	31	8.64	1.40	42.54	27.89	70.44	1325
23	16	7.72	1.59	34.89	19.00	53.90	990
24	29	7.65	1.64	37.56	24.91	62.48	1405
25	28	1.55	2.11	20.95	21.08	42.04	2650
26	38	1.54	2.66	21.80	24.30	46.11	4820
27	46	2.04	2.24	30.86	21.59	52.46	3720
28	13	9.33	1.85	32.99	31.74	64.74	1045
29	11	8.36	2.51	35.06	28.40	63.47	925
30	16	8.49	2.15	32.31	25.84	58.15	870
31	28	0.11	0.61	50.41	41.64	92.05	1545
32	27	0.08	0.47	46.71	38.78	85.49	1700
33	30	0.05	0.51	47.48	38.26	85.74	1965
34	22	0.05	0.31	44.98	31.52	76.51	775
35	32	0.05	0.29	41.72	32.33	74.06	960
36	16	0.09	0.28	38.62	32.54	71.16	985
37	47	0.73	1.98	44.14	35.76	79.91	2205
38	44	0.77	2.03	23.87	27.28	51.16	2560
39	38	0.71	2.40	32.43	35.20	67.63	3170
40	31	0.76	0.87	40.80	27.95	68.75	1160
41	27	1.10	0.87	43.96	25.31	69.27	1199
42	24	0.97	1.02	34.06	25.23	59.30	1605
43	57	0.77	1.89	26.87	15.33	42.20	3260
44	46	0.81	1.89	28.66	26.04	54.71	3700
45	56	0.83	1.80	23.81	15.69	39.50	3775
46	16	4.45	1.61	43.11	24.94	68.05	1075
47	38	4.91	1.12	38.17	16.28	54.45	1225
48	47	4.93	1.38	40.45	13.75	54.20	1000
49	54	1.66	2.90	21.98	17.35	39.33	4475
50	42	1.59	3.56	22.98	18.11	41.09	5000
51	55	1.56	3.93	26.60	22.19	48.80	4415
52	41	10.25	2.32	38.47	33.96	72.43	1405

OBS	TILL	Root NO3	Leaf NO3	N leaf Total	N root Total	N Total	Water use
		mg/g	mg/g	mg/pot	mg/pot	mg/pot	mL/pot
53	31	7.85	1.85	40.55	26.28	66.83	1150
54	23	9.05	1.85	39.55	26.05	65.60	1440
55	42	1.91	3.73	30.04	22.53	52.58	3710
56	27	2.34	4.12	41.01	29.00	70.01	3385
57	50	3.08	3.12	30.30	22.20	52.51	3450
58	13	8.95	2.12	34.14	30.07	64.21	900
59	15	8.76	3.43	34.17	25.82	60.00	680
60	17	8.62	2.37	32.45	30.67	63.12	1315
61	29	0.21	0.56	52.26	40.58	92.84	1670
62	30	0.18	0.63	44.27	40.74	85.01	1600
63	33	0.13	0.65	45.62	44.84	90.47	1480
64	19	0.23	0.31	36.21	31.29	67.50	635
65	24	0.22	0.29	37.58	32.13	69.72	775
66	15	0.14	0.27	41.54	24.46	66.01	790
67	50	0.32	2.67	38.49	38.40	76.89	1900
68	41	0.40	2.89	37.61	33.07	70.68	2200
69	37	0.81	2.40	42.86	36.78	79.65	2310
70	39	0.71	0.95	33.19	32.00	65.19	1155
71	34	0.71	0.96	31.79	29.48	61.28	870
72	27	0.60	0.98	37.49	30.32	67.81	1395
73	59	0.28	1.79	23.98	17.06	41.04	825
74	54	0.32	1.86	23.37	18.16	41.53	3305
75	51	0.56	1.78	26.22	21.98	48.20	3660
76	38	3.85	1.10	41.74	30.93	72.67	1080
77	30	3.55	1.07	31.86	29.63	61.49	1450
78	36	3.66	1.30	32.86	29.32	62.18	1320
79	55	1.72	2.90	21.98	18.15	40.14	4010
80	37	1.45	3.29	25.62	18.65	44.28	4435
81	47	1.53	3.17	27.36	22.09	49.45	5415
82	35	11.38	1.65	40.24	36.08	76.33	1215
83	22	10.99	1.69	35.16	29.17	64.34	1505
84	26	9.17	1.71	29.45	32.48	61.93	1245
85	35	2.75	2.62	39.29	30.67	69.96	4075
86	53	2.72	2.61	26.05	23.10	49.15	3630
87	53	3.23	2.34	34.32	31.37	65.70	3940
88	12	8.58	1.92	32.51	28.76	61.28	900
89	22	10.00	2.17	37.65	32.99	70.64	920
90	15	8.51	2.08	31.91	29.92	61.84	1090

APPENDIX
Schedule of Experiment #1.

Day	Operation
0	*Seed germination started by planting seeds in brown paper towel and covered.
7	*The towels were uncovered in order to expose young seedlings to light.
15	*Seedlings were transplanted into 1.5 liter polyethylene pots with full strength modified Hoagland solution.
	*First solution sampling.
21	*Second solution sampling.
30	*Third solution sampling.
	*New Hoagland solution after third sampling.
	*First two bars salt treatment was started by addition of 48 meq NaCl/liter.
	*Salt stress was increased gradually by addition of 2 bars every other day until reaching desired salinity levels in the treatments.
36	*Fourth solution sampling.
45	*Plant harvesting.
	*Fifth solution sampling.

Schedule of Experiment #2.

Day	Operation
0	*Seed germination started by planting seeds in brown paper towel and covered.
7	*The towels were uncovered in order to expose young seedlings to light.
15	*Seedlings were transplanted into 1.5 liter polyethylene pots with full strength modified Hoagland solution.
	*First solution sampling.
30	*Third solution sampling.
	*New Hoagland solution after third sampling.
	*First two bars salt treatment was started by addition of 48 meq NaCl/liter.
	*Salt stress was increased gradually by addition of 2 bars every other day until reaching desired salinity levels in the treatments.
42	*The plants were transferred into N-lacking culture solution containing the specified amounts of salt levels.

Schedule of Experiment #2.- - - Continued

45	*The plants were transferred into 1/10 th strength N-lacking culture solution treated by ^{15}N and NaCl. (9:00 am).*Six hours later (3:00 pm), the first set of plants were harvested for 6 hours ^{15}N uptake. Twelve hours from the initial time (9:00 pm), the second set of plants were harvested for 12 hours ^{15}N uptake.
46	*At 3:00 am, the third set of plants were harvested for 18 hour ^{15}N uptake. *At 9:00 am, the fourth set of plants were harvested for 24 hour ^{15}N uptake.

Schedule of Experiment # 3.

Day	Operation
0	*Seed germination started by planting seeds in brown paper towel and covered.
7	*The towels were uncovered in order to expose young seedlings to light.
15	*Seedlings were transplanted into 1.5 liter polyethylene pots with full strength modified Hoagland solution.
	*First solution sampling.
30	*Third solution sampling.
	*New Hoagland solution after third sampling.
	*First two bars salt treatment was started by addition of 48 meq NaCl/liter.
	*Salt stress was increased gradually by addition of 2 bars every other day until reaching desired salinity levels in the treatments.
45	*Fourth solution sampling.
	*New Hoagland solution after fourth sampling

Schedule of Experiment # 3.- - - Continued

57	*The plants were transferred into N-lacking culture solution containing the specified amounts of salt levels.
59	*The plants were transferred into 1/10 th strength N-lacking culture solution treated by ^{15}N and NaCl. (9:00 am).
	*Six hours later (3:00 pm), the first set of plants were harvested for 6 hours ^{15}N uptake. Twelve hours from the initial time (9:00 pm), the second set of plants were harvested for 12 hours ^{15}N uptake.
60	*At 12:00 am, the third set of plants were harvested for 15 hour ^{15}N uptake.
	*At 3:00 am, the fourth set of plants were harvested for 18 hour ^{15}N uptake.

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