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Title: Effect of Nitrogen Fertilizer and Irrigation on Acacia senegal Seedling Biomass and Photosynthesis

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Seedlings of Acacia senegal were grown in a glass greenhouse to study the effect of nitrogen and irrigation regimes on dry matter production and allocation to different plant organs, net photosynthesis per unit leaf area, and nitrogen content in the different plant organs. Ammonium nitrate (NH_4NO_3) was used in this study, as the source of inorganic nitrogen.

The nitrogen treatment consisted of four levels: 0, 30, 100, and 200 ppm of N which were added with the irrigation solution. Irrigation treatment consisted of irrigation every two, five or ten days.

Nitrogen fertilization, irrigation regimes, and their interaction significantly affect the total stem, root, and leaf dry weight. However, low and moderate levels of N with irrigation every two days, resulted in higher total plant dry weight.

Contrary to the initial hypothesis of the study, net photosynthesis showed no significant differences among the N treatments, but a decrease occurred after the fifth day since irrigation; this was also followed by a low net CO_2 uptake. Stomatal conductance was affected significantly by the N and irrigation treatments.

Total N content in the whole seedlings, stems, roots, and leaves was found to be high at low to moderate application of N, with irrigation every two days, while percent N in these parts showed a marked increase with increasing the N added. Moreover, percent N in roots showed the highest increase compared to percent N in stems and leaves.

Effect of Nitrogen Fertilizer and Irrigation on *Acacia senegal* Seedling Biomass and Photosynthesis

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INTRODUCTION

General Introduction

Acacia senegal (L.) Willd, is a small tree or bush, which is usually 6 meters, sometimes up to 12 meters high, with a flat and spreading or rounded crown. Most of the time it is abundant in dry, thorn scrub areas (Sahni, 1968). *A. senegal* is found in a belt 30 kilometers wide along the southern frontier of the Sahara desert from Mauritania to Sudan, Ethiopia and Somalia, and it also grows in East Africa as far as Mozambique, the Transvaal, and Natal; along the southern coast of Arabia and Iran, and in Pakistan and western India (National Academy of Sciences, 1979).

It is found in areas which are too dry for general agriculture and livestock. In Sudan, *A. senegal*, which is the main producer of gum arabic, has two main areas of distribution. The first one is on stabilized sands with rainfall of 280 mm or higher, mostly concentrated between 280-450 mm; the second area is on dark, cracking clays with rainfall of 500 mm (Sahni, 1968). *A. senegal* starts producing leaves just before the rains; most trees shed their leaves

irregularly in November or December. In any given area some trees retain their leaves longer than those in moist areas. The rainy season begins in June and ends toward mid-October. Flowering and seed production occur from December to April, after the rains stop. Average January maximum and minimum temperatures within A. senegal distribution in the Sudan, range between 31° and 13° C (January and December are the coolest months), while average maximium and minimum temperature for May ranges from 39° to 24° C (March, April and May are the hottest months) (El Hadi, 1984). The temperature decrease after June is associated with the beginning of the rainy season, and it continues to decrease until it reaches a minimum in January. Then it starts to increase again until May.

Natural regeneration of this species has many problems. The mortality of germinating seeds in the field can reach 84% (Seif, Eldin and Obeid, 1973). Also, the seedlings which survive face a long dry season (October-May) after a very short growing season, resulting in high mortality rates. El Hadi (1984) estimated that the survival of trees grown from seeds rarely exceeds 10 percent. All of these factors lead to a density of the gum trees which is below the desired optimal levels. Artificial regeneration of seedlings in the nursery using seeds treated to break their dormancy gives a first year survival rate of 85 percent. Nursery establishment is expensive but produces healthy seedlings which survive better, resulting in better stands and compensating for the added expense.

Benefits of A. senegal include the following :

1. Production of gum arabic, the third most important commercial commodity in the Sudan.
2. Improvement of soil fertility. Jewill and Manton (1954), quoted from Booth (1966), found soil nitrogen content to increase after cultivation for 30 years under Acacia, compared with a soil of similar mechanical composition which had been under cropping for 30 years. This is due to nitrogen fixation by the symbiotic relationship of this species with strains of bacteria from the genus Rhizobium.
3. Controlling soil erosion, with it is massive long root system.
4. Leaves and buds have high nutritive value as fodder for browsing animals.

Considering the importance of A. senegal and the potential benefits of artificial regeneration for this species in terms of higher survival and growth rate in the field, the objective of this study was to evaluate the effect of nitrogen fertilization and different irrigation regimes at on the following:

1. Nitrogen uptake.
2. Photosynthesis per unit leaf area and for the whole plant.
3. The growth and pattern of development.

Nitrogen Nutrition

The forms of N compounds available to plants are of great importance. The initial concept was that N is utilized by plants as ammonia, which evolves from organic matter during plant decomposition. In 1846 Salm Horstmar prepared a standard solution for sand cultures using sodium nitrate instead of NH_4NO_3, and subsequently discovered that plants may feed exclusively on nitrate, thereby surviving without ammonium (quoted from Prianishnikov, 1951). We now know that N compounds are available to plants from the most oxidized to the most reduced forms. Even free N can not be excluded entirely because some species can fix atmospheric nitrogen. The question of which one is better or more efficient seems to vary between species according to their evolution and the presence and location of the enzymes responsible for N metabolism. Beevers and Hageman (1980) stated that ammonium is oxidized to nitrate by soil organisms when soil is well-aerated, moist and above 7^{o}-10^{o} C. This could explain the inability of higher plants to tolerate high quantities of ammonium, since they evolved under conditions of ammonium N limitation such that there was little selection pressure to evolve such regulation. While most plants can utilize effectively either ammonium or nitrate ions, nitrate is considered to be the preferred form. However, Gamborg and Shyluk (1970) proposed that the most suitable inorganic N source for growing plant cells is a mixture of ammonium and nitrate. Also Mohanty and Fletcher (1976) found that ammonium when applied with

nitrate resulted in a twofold increase in growth and nitrate reductase activity of Paul's Scarlet rose suspension culture. Pate (1980) found no ammonium in the xylem stream leaving the roots and going to the stem. This may indicate that nitrate is the major source of inorganic N available to the leaves of most land plants. Nitrate is reduced by nitrate reductase to the ammonium form which requires carbohydrate oxidation.

Ammonium and ammonia are toxic to plant tissues and cannot be accumulated to any appreciable extent without damage to the plant (Hageman, 1980). Beevers and Hageman (1980) proposed that ammonium is detoxified in the roots by conversion to amino acids or amides. However, Miflin and Lea (1976) pointed out that the ammonium ion, regardless of origin, must be combined with a carbohydrate skeleton to produce amino acids. Thus the ammonium and nitrate assimilation requires directly, or indirectly, a substantial amount of energy from carbohydrate reserves.

Stewart and Larher (1980) stated that amino acids and other soluble nitrogenous compounds play essential roles in plant metabolism, being the primary products of inorganic N assimilation, and precursors of proteins and nucleic acids. Ingestad (1982) pointed out that with increasing N application rate, or with increased internal concentration, growth will increase in a linear manner until it reaches a saturation point where growth will be reduced. This can be explained by the above-mentioned points, that at a certain point the N assimilated will be more than needed for the metabolic process,

and it will be stored in amino acids, or protein forms which consume more of the photosynthate (maintenance respiration).

Nitrogen Nutrition and Photosynthesis

Photosynthesis in green plants is a process which utilizes the light energy to produce carbohydrates from carbon dioxide (CO_2) and water (H_2O). The rate of CO_2 fixation often is referred to as gross photosynthesis. Net photosynthesis usually is defined empirically as the measured rate of net flux of CO_2 into a leaf. The difference between gross and net photosynthesis is the loss of CO_2 during dark respiration and photo respiration in case of C_3 plants. Photosynthesis or CO_2 fixation can be viewed as a function of a series of diffusion resistances in stomates and chloroplasts, in which N compounds (mainly proteins) play a major role .

A. The Chloroplast Level:

The process which occurs in the chloroplast consists of two sets of reactions, light and dark. The light reactions are initiated by light absorption via specialized pigments in the chloroplast. These pigments, which are complexed with proteins, are chlorophyll a and/or b, and the carotenoids. Light energy is absorbed by chlorophyll and electrons are transferred from H_2O via photoelectron transport chain to reduce nicotinamide adenine dinucleotide phosphate (NADP) to NADPH producing adenosine triphosphate (ATP). The photosystems and the

electron transport chains are composed mainly of soluble and insoluble proteins. The next steps are the dark reactions in which the ATP and NADPH are used in the conversion of CO_2 to carbohydrates (Calvin cycle). The principal rate-limiting dark reaction of photosynthesis is catalyzed by the enzyme ribulose 1-5 biphosphate carboxylase oxygenase (Rubisco). This enzyme comprises a substantial fraction of the total leaf protein (Mooney and Gulmon 1979), together with the photoelectron transport chains which are mainly proteins.

Therefore, N nutrition influences the amount of chlorophyll, the electron transport chain, and the amount and activity of Rubisco.

B. Stomatal Level:

Stomata have dual functions: the regulation of transpiration, while permitting CO_2 to diffuse into the leaf to maintain photosynthesis (Rasche, 1975; Farquhar and Sharkey 1982). To facilitate this function it responds to vapor pressure deficit, CO_2 concentration and other environmental conditions. It is also well documented that there is a linear relationship between stomatal conductance and the CO_2 assimilation rate. This was observed with Oryza sativa, Zea mays, rice, and Eucalyptus (Wong, Cowan and Farquhar 1979).

Wong, Cowan and Farquhar (1979), and Von Caemmerer and Farquhar (1981) reported that with decreasing levels of N nutrition, stomatal conductance decreases.

It is evident that N has a great impact on the net assimilation

at the chloroplast level and the stomatal level. This relationship can be extended to include whole plant leaves and total plant productivity.

Recent research with agricultural crops indicates that there is often a good correlation between leaf N content and net photosynthesis rates. This was observed in rice by Yoshida and Coronel (1976), soybeans by Buttery et al. (1981), wheat by Migus and Hunt (1980), peas by DeJong and Phillips (1981), peaches by DeJong(1982). This relation was also observed in Eucalyptus by Mooney et al. (1978).

Nitrogen and Forest Nurseries

The primary purpose of forest nurseries is to produce trees to form new forests. Therefore, maintaining adequate fertility in the nursery soil is important to assure production of high-quality planting stock (Van den Driessche, 1984). Nitrogen commonly is applied to increase seedling size and its effect has been studied with several species. Switzer and Nelson (1963) found that N application led to an increase in dry weight, and that the growth response to nursery treatment is related to seedling size and N status. They did not find any correlation of N status with seedling survival rate of pine.

Van den Driessche (1977) working with lodgepole pine, observed that the size and dry weight of shoot and root attained in one or two years increased linearly with the amount of N fertilizer applied. The

root to shoot ratio decreased with increase in N application, but the decrease in root to shoot ratio was progressively less as the N application increased. The same pattern also was observed by Van den Driessche (1982) with Douglas-fir.

Irrigation

Through the course of evolution, and by the driving force of natural selection, water has played a central role in determining the species distribution. The responses and adaptations of species to water status are critical factors determining their success in any environmental habitat. Arid zone plants have developed a special mechanism for drought resistance and higher water use efficiency.

Plant growth usually is determined by the interaction of the environment and physiological processes within the plants. Since water availability is a dominant factor of the physical environment, water is considered an important factor in shaping the growth pattern. Water balance is of great importance when it limits the growth rate of plants. This may be when an excess of soil water blocks root aeration, hence reducing roots functioning and leading to a change in the pattern of photosynthate allocation. Shortage of water causes a reduction in photosynthesis and transpiration, and possibly also a change in the distribution of new biomass. Mild water stress promotes growth of root systems relative to the shoots (Hsiao et al., 1976).

Thus, successful nursery irrigation systems should address the

plant environment interactions and the differing species capacities to grow according to different irrigation frequencies and intensities. The function of irrigation should be to promote plant growth with a desirable root :shoot ratio for better performance of the seedlings after outplanting.

Objectives

It is evident that fertilizers, especially N, have a great impact on plant growth in terms of their size and pattern of development. Also, as reported earlier, Ingestad (1982), indicated that the growth rates of plants will increase with increasing fertilizer concentration until a saturation point is reached. Further application will lead to reduction in growth. Hence, identification of growth of shoots (tops and leaves) and roots in response to fertilization and irrigation is critical for nursery cultural practices. Such information will have a substantial impact on decisions concerning the amount of fertilizer to be applied and irrigation frequencies. This can be used to produce seedlings which have optimal dimensions and ratios of tops, roots, and leaves. Moreover, this can reduce the cost from using unnecessary fertilizers. The first objective of this study is to characterize and evaluate the effect of frequent application of different levels of ammonium (NH_4NO_3) and irrigation frequencies on:

1. Weight of whole plant- total, root, top and leaf biomass of young A. senegal seedlings, and the biomass

ratios of these organs.

2. Stomatal behavior - diffusive conductance and its effect on net CO_2 assimilation.

The second objective of this study depends on the assumption that net photosynthesis can be considered as an overall indicator of the physiological responses associated with fertilization and plant water relations. I hypothesized that the photosynthetic efficiency per unit leaf area, and/or the whole plant is a function of NH_4NO_3 applied and the N content in the leaves.

MATERIAL AND METHODS

Greenhouse Culture

A greenhouse experiment was conducted from June to October, 1983, at the Forest Research Laboratory glass greenhouse K at Oregon State University. The temperature and light were controlled by automatic timers in the greenhouse. A light timer was programmed to provide 12 hours of 17,000 Lux supplemented light . Average day and night temperatures were 27^{o} and 18^{o} C respectively.

Forest soil was brought from a coastal forest area near Burnt Woods, Oregon, and mixed with sand and perlite in a proportion of 80, 16, and 4, respectively. Sand and perlite were added to facilitate the removal of roots at the end of the experiment. Nitrogen, carbon content, and the C:N ratio were 0.14 %, 3.52 %, and 25:1, respectively in the soil mixture. Containers composed of long glass tubes placed on small plastic dishes were filled with 2 kg of the soil mixture. The tubes, which were 40 cm long, 9 cm in diameter, and open at each end, were wrapped with dark polyethylene sheets to provide a dark environment for the roots.

Seeds of *A. senegal* were collected in January 1982, by the Medani Forest Research Station, Sudan. Seeds were non-endospermic, hard, light to dark brown in color, and their average weight was 0.1 g/seed. The external dormancy resulting from the hard seed coat was broken by soaking the seeds in 5% sulfuric acid for 10 min, and then washing

thoroughly with water. Four seeds were planted in each container.

Seed germination began after 2 days, and containers were thinned to leave 2 seedlings in each of the two-hundred forty containers, which were assigned randomly among four ammonium nitrate levels, having N concentrations 0, 30, 100, and 200 ppm with irrigation twice a week. This is equivalent to addition of 0, 0.006, 0.02, 0.04 g of NH_4NO_3 per kg of soil. Other nutrients, macro and micro were added in a sufficient amount once a week with the irrigation solution to maintain a balanced nutrient solution. Forms and concentrations of the nutrients are shown in Table 1.

Inoculation of the seedlings was tried with different Rhizobium strains from mesquite, ground peas, and a culture of Rhiziobium assumed to be from Acacia senegal . No nodules were observed and, using the acetylene reduction assay, no N fixation was detected. This may indicate a specific Rhizobium-Acacia host relationship.

Irrigation was with 150 ml of nutrient solution for each container (container volume = 2.5 liter), applied 3 times a week. One month after germination, 3 watering regimes were adopted for each NH_4NO_3 treatment. These were irrigation every 2, 5, or 10 days. Correction of NH_4NO_3 and other nutrients was made so that the 5 and 10 day watering regimes received the equivalent amount of NH_4NO_3 and other nutrients each 5 or 10 days according to the watering regime . Thus, the experimental design was a factorial with 4 levels of ammonium nitrate and 3 watering frequencies with 40 replications.

Net Photosynthesis

Net photosynthesis in this context refers to the net CO_2 flow between the leaves and atmosphere produced through photosynthesis. Measurements were started at 10:30 a.m. on a single leaf from each replication in the upper one-third of the canopy. Measurements were done on the same plants for 3 cycles, each of 10 days in a different leaf.

Gas sample collection usually took 2 hours. Net photosynthesis of single leaves was measured using a portable Plexiglas chamber, built in the Forest Research Laboratory Workshop. The chamber is similar to that described by Ehleringer and Cook (1980).

A hand-held Plexiglas hinged box leaf chamber with volume equal to 0.163 liter was fitted with a fan (fan volume = 0.7×10^{-3} liter). The jaws of the chamber were sealed with foam rubber gaskets. A nylon web (volume = 1.7×10^{-4} liter) was used to keep the leaf surface flat inside the chamber. The chamber was equipped with 2 syringe ports,each fitted with a rubber serum stopper to facilitate sampling. Measurements began by enclosing a leaf in the chamber, with the fan running and within a few seconds withdrawing a 1 ml gas sample with a 1 ml plastic syringe. Another sample of the same size was collected after 45 seconds. Syringes were inserted into a silicon rubber piece immediately after their withdrawal. Upon completion of all measurements the samples were transported to the laboratory for CO_2 analysis.

Photosynthetic photon flux density was measured using a LiCor Model 185B Quantum radiometer photometer.

Gas Chromatographic Analysis

A 5830A gas chromatograph manufactured by Hewlett-Packard was used for gas analysis. This machine was equipped with a thermal conductivity detector (TCD), and automatic integrator. Two columns were fitted in the machine, together with a precolumn containing $CaCl_2$ which functions to remove water vapor.

The first column was 2 m long, 5.4 mm diameter copper column packed with Poropack Q (50-80 mesh). The second column was 2 m long, 6.4 mm diameter copper column packed with Poropack R (80-100 mesh). Both columns were conditioned after they were packed. The gas chromatograph was set to the following operating conditions: oven, injection, and TCD temperatures at 50, 150 and 250^{o} C respectively. Helium was used as a carrier gas with a flow rate of 45 ml per minute in both columns. The gas chromatograph was set at the above conditions 3-4 hours before actual analysis of gas samples in order to reach equilibrium. The injection septum was changed after every 30 injections.

Two peaks were observed after 0.13 and 0.37 minutes from sample injection, the second one being the CO_2 peak. Construction of standard curves was accomplished by regressing the area (in chart units) of the CO_2 peak, obtained from the integrator, against known

CO_2 concentration. R^2 values ranged between 0.997-0.999.

The gas samples were injected, and the difference in the concentration between the first and second samples on the same leaf (C) multiplied by the chamber volume (V) was assumed to be the amount of net CO_2 fixed by that leaf in 45 seconds.

The net photosynthesis (P) in mg of CO_2 per hour per dm^2 was calculated according to the following formula:

$$P = \frac{C \times 60 \times 60 \times V \times 100}{LA \times T}$$

where:

C= The concentration difference between the first and second sample in mg of CO_2.

V = The chamber volume (162 cm^2)

LA= Projected leaf area measured by LiCor area meter in cm^2.

T = Time between the first and second sample (45 seconds).

Stomatal Conductance

Diffusive stomatal conductance was measured with a LiCor Model LT 1600 steady state porometer. Measurements were done on the same leaves that were sampled for net photosynthesis. Four replications were assigned randomly for net photosynthesis and stomatal conductance measurements at 3 months from germination.

Biomass

Seedlings were harvested after 4 months. Fresh and dry weights of tops, leaves and roots of each seedling were determined.

Nutrient Analyses

Total nitrogen content for leaves, roots and tops was determined using a semi-micro Kjeldahl digest.

Total soil C and N were measured for the initial soil mixture in each treatment using a micro-Kjeldahl digest for N and a LEICO 12 Carbon analyzer for C.

Data Analysis

Subprograms of the statistical package for the social sciences (SPSS) were used to analyze the data. The subprogram MANOVA was used for the analysis of variance, means and standard error computations, while the subprogram ONE-WAY was used for multiple comparisons. Comparisons of stomatal conductance means for days since irrigation was based on the protected LSD criterion, while Tukey's range was used for the other comparisons.

RESULTS

A summary of the results, with emphasis on the main points, will be presented in this section. The following abbreviations will be used throughout the coming sections: N_0, N_{30}, N_{100}, N_{200} will represent 0, 30, 100, and 200 ppm of N treatments, respectively. I_2, I_5, and I_{10} will be equal to irrigation every two days, five days, and ten days, respectively. Significant differences will always refer to $P < 0.05$.

Growth

Analysis of variance (Anova) showed that ammonium nitrate, irrigation frequency, and their interaction had significant effects on the pattern and magnitude of dry matter allocation to leaves, roots, stems and total biomass of A. senegal seedlings (Table II).

Four months after germination, significantly higher total dry weights were obtained under $N_{100}I_2$ and $N_{30}I_2$ (Fig. 1, Table IX). They were almost twice the mean of all the other treatments. Moreover, these data suggest that there is no evidence that NH_4NO_3 had any pronounced effect within and among the I_5 and I_{10} irrigation treatments. Also, stem dry weights were found to have a similar pattern to that observed with total biomass (Fig. 2, Table IX). $N_{100}I_2$ and $N_{30}I_2$ yielded significantly higher dry matter, with 100% increase

over the mean of all the other treatments, which were not significantly different from each other. The root dry weight data showed a similar pattern, but roots were less affected by water stress. As indicated in Fig. 3, $N_{30}I_2$ increased the root weight by 50% compared to the other treatments, while the stems and total biomass increased by 100%. Leaf weights of $N_{100}I_2$ and $N_{30}I_2$ showed the highest increases, which were 3-fold times the means of all the other treatments. Moreover, this is the only case in which $N_{100}I_5$ was significantly higher than $N_{100}I_{10}$ (Fig. 4, Table IX).

Significant effects also were observed on efficiency (dry matter production per unit N applied) of total biomass production and on production efficiency of stems; significant effects were found for roots and leaves by NH_4NO_3, and irrigation. The interaction between NH_4NO_3 and irrigation was not found to be significantly different except for the roots (Table III a,b,c,d).

The N production efficiency of total plant biomass data clearly demonstrated that low levels of N expressed significantly higher efficiency (Fig. 6). Within N_{100} all the irrigation treatments were different, while within N_{30} only I_2 and I_{10} were significantly different. The same results and patterns were observed with the stem data (Fig. 7). Roots showed the highest N efficiency compared to total biomass, stems, and leaves. Also $N_{30}I_2$ had the highest root N efficiency (Fig 8). However, in no case did irrigation treatment show significant differences within N_{30} and N_{100}. Likewise, higher N production efficiency was obtained at low levels of N and irrigation

every two days. The treatment means of leaf N efficiency also showed significantly higher results with increasing irrigation frequency at any one level of N applied (Fig. 9).

Root:shoot ratios were found to be high under water stress conditions (Fig. 5, Table X). I_{10} was significantly higher than I_5 at any N level (Fig. 5, Table X). $N_{30}I_2$ and $N_{100}I_2$ showed the lowest root:shoot ratios, which also were significantly lower than N_0I_2. Leaf:root and leaf:stem ratios (Table X), were highest with irrigation every two days. Moreover, the specific leaf area (leaf area per weight in cm^2 $gram^{-1}$) showed that only irrigation and the interaction between irrigation and N had a significant effect (Table VII). The interaction is clear in Fig. 11, where only $N_{30}I_5$ was higher than $N_{30}I_5$ and $N_{30}I_{10}$.

Nitrogen Content

Total N content in the whole seedlings, stems, roots, and leaves, was found to be greatly affected by the quantity of N applied, irrigation frequency, and N-irrigation interaction (Table IV). Furthermore, it was evident from the comparisons of the means, that low to moderate levels of N combined with frequent irrigation resulted in higher total N content in the whole plant (Fig. 11, Table XI). This was true likewise for total N in the leaves, stems and roots (Figs. 12, 13 and 14, Table XI).

Analysis of variance of the N percentage in different plant

tissues (Tables V, XII) showed the following: stems and roots were affected significantly by the N treatments, irrigation treatments, and their interaction. However, only the irrigation treatments were found not to have a significant effect on the percentage of leaf N. Furthermore, leaves, stems and roots showed a marked increase in N percentage, with increasing the amount of N applied (Figs. 14, 15 and 16, Table XII). The magnitude of the increase varied between roots, stems and leaves. Roots (Fig. 15) showed a two-fold increase when $N_{200}I_2$, $N_{200}I_5$, and $N_{200}I_{100}$, were compared with N_0 treatments. Stems (Fig. 14) showed a 1.7-fold increase, and in the leaves, a slight but significantly higher percent was obtained (Fig. 16).

Net Photosynthesis and Stomatal Conductance

Contrary to my hypothesis, the response of net photosynthesis to N treatment was not found to be significant The analysis of variance showed $P = 0.86$ (Table VII). Irrigation treatment, as well as irrigation by N interaction term were never statistically significant.

The days elapsed since the last irrigation were found to have a significant effect on net CO_2 uptake (Table VIIB). There also was a general trend in the levels of N treatment towards maintaining a high constant level for the first four days (mean = 19 $mgCO_2\ dm^{-2}h^{-1}$). A decrease occurred after the fifth day, followed by a low net CO_2 uptake for the rest of the 10-day cycle (Fig. 20). A clearer representation of this trend is shown in Fig. 21, in which the

weighted means of the N treatment were plotted against days since irrigation.

Days since irrigation were found to have a significant effect on stomatal opening and closure (Table VIII). But unlike photosynthesis, stomatal conductance showed a significant response to N treatment (Table VIII).

Stomatal conductance means for each N level following days since irrigation (Fig. 18) clearly demonstrates that stomatal conductance increased with increasing N level. However, within each N level a trend similar to photosynthesis response was observed. The conductance decreased after the fifth day, and maintained a low level for the rest of the ten day period. The drop was proportionally less in the case of N_{200} and N_{100} compared to N_{30} and N_0. Figure 19 showed the general trend of the weighted means of N treatment within each day.

DISCUSSION

Growth

In this experiment, as shown earlier, ammonium nitrate and irrigation had a marked effect on total dry mass and its distribution among the different plant organs (Table IX, Figs. 1, 2, 3 and 4). The significance of the interaction terms shows that, with irrigation every two days, and with low to moderate levels of N , higher total dry weight results.

The rate at which seedlings accumulate dry mass is conditioned by the gross rate of C fixation and the rate at which CO_2 is released in respiration. This means that the dry mass increase results from the excess of photosynthesis over respiration and the lost tissues and organs (leaf abscission, root turnover, and bark). Furthermore, respiration in turn can be partitioned into maintenance respiration (that required to support existing structural and life processes), and growth respiration (that needed to support the creation of new living structures).

Ting (1982) emphasized that the growth and development of a flowering plant is a complex phenomenon, which results partly from its genetic predetermination and partly from its environment. Thus, the surrounding environment has a great impact on the different physiological processes within the plant and is the driving force for

natural selection and appearance of adapted species in different habitats.

The concept of a limiting factor, in which the response to a factor in an amount less or more than optimum will be accompanied by a response, would be useful in explaining these results. The N effect was found to be limited by the availability of moisture. However when N is considered as the variable in the every-two-days-irrigation regime, the dry mass data were found to be in agreement with that reported by Ingestad (1982). He showed that the relative increase in external N resulted in a higher growth rate of birch and alder seedlings until it reached an optimum level; further addition caused no increase and then a reduction or lethal effect was observed after the supra optimum conditions (after nutrient requirement was saturated).

A possible explanation for this depressive effect is that mentioned earlier by Beevers and Hageman (1980). They discussed the energetics of ammonium incorporation into carbohydrate skeletons to produce amino acids. Ammonium is generated inside the plant tissues by direct uptake of ammonium or reduction of nitrate by the activity of nitrate reductase enzyme. Since free ammonia is considered to be toxic (Beevers and Hageman 1980), it has to be converted to amino acids, regardless of its origin. The excess generation and storage of amino acids and proteins will increase maintenance respiration.

The percentage of N found in the different tissues of A. senegal may support this suggestion. As shown in Figs. 14, 15 and 16, higher

percentages of N in the leaves, stems and roots were associated with increasing the amount of N added. By increasing the internal N per unit weight beyond a certain level we may limit growth by consuming photosynthate, and also may have a repressive action at the gene level.

The balance between the shoot and root (or their relative growth rates) is important in understanding the mechanism by which seedlings adapt to their habitat, and in explaining variation in dry matter production.

The data presented in Figs. 2, 3, 4, and 5, and Tables IX and X, clearly demonstrated that a large proportion of the photosynthate was allocated to the roots under all the treatments. The variation observed within the root:shoot ratio data is due to the treatments.

Levitt (1980), indicated that the developmental pattern which included relatively greater allocation to roots during their early growth stages would presumably indicate adaptive advantage and tend to increase their survival ability. However, A. senegal evolved under conditions where moisture is one of the main limiting factors. This indicates the necessity for increasing the absorption surface and long-reaching roots for water microsites. In this study, water availability was found to be the principal factor for increasing or reducing the root:shoot ratio. There also is a tendency, although not significant, for lower root:shoot ratios under optimum N conditions (Fig. 5).

The shoot data (stems and leaves) are in agreement with what was

observed by Ledig et al. (1970). The leaves and stems were greatly affected by stress conditions. The leaf data (Fig. 4), indicate that leaf ontogeny is highly controlled by the level of N under the different irrigation regimes. The drop in leaf dry weight under water stress conditions could be explained by leaf abscission and reduced growth. Further, the specific leaf area (Fig. 11) is almost constant except within N_{30} where lack of moisture tends to reduce the transpiring surface in order to conserve water.

The N-use efficiency, which is defined in this text as the production of dry matter per unit of N added, showed a sharp decline with increasing nitrogen above 30 ppm, and irrigation interval greater than every two days (Figs. 6, 7 and 8). These results are supported by the biomass data discussed earlier. Brown (1978) speculated about the reduced N use (biomass production per unit of N in the plant), within the Leguminosae family. He pointed out the possibility that the symbiotic relationship with Rhizobium bacteria decreased the need for more efficient utilization of N.

Nitrogen Content

Ting (1982) reported that the storage proteins found in roots serve primarily as storage for N and C which were consumed during the stages of growth and regrowth.

In this study, root N content per unit dry weight showed the highest proportional increase compared to stems and leaves with

increasing N level from 0 ppm to 200 ppm (Table XII). Further root:shoot ratio was shown to be high (Fig. 5) to begin with and especially under water stress conditions. This may be evidence that A. senegal roots serve as a principal storage organ for protein. However, it would be an adaptive feature to use roots as a N storage organ, since the natural distribution of A. senegal is in an arid zone, where it sheds leaves after the rainy season.

The comparison between the total N content in the whole seedlings, stems, roots and leaves (Table XI) shows significantly higher total N content under low to moderate levels of N only with irrigation every two days. This may reflect an effect of water stress on N uptake over and above the effect of water and N stress on growth.

Net Photosynthesis and Stomatal Conductance

In this study the net photosynthetic capacity of A. senegal seedling leaves expressed on a leaf area basis was not affected by N treatment (Table VII). Although the % N in N_{200} leaves was significantly higher than in those of N_0 (Fig. 16), there is no evidence of higher net photosynthesis rates.

Thus, the nature of the relationship between leaf N per unit weight, or level of nitrogen added, and net leaf CO_2 assimilation is in contrast to the earlier stated hypothesis. These results differ from those reported for the following species: Pisum sativum (DeJong and Phillips, 1981), wheat (Migus and Hunt, 1980), Eucalyptus (Mooney

et al., 1979), rice (Yoshida and Coronel, 1976), and peach (DeJong, 1982).

If the primary role of plants is to convert CO_2 into organic form through photosynthesis, then leaf N content, and/or soil N can be viewed as a primary cost in construction and maintenance of the photosynthetic apparatus. This appears likely since the ribulose bisphosphate carboxylase oxygenase, makes up a substantial fraction of the total leaf protein (Mooney and Gulmon, 1979). Also, as mentioned previously N is a limiting factor for plant growth and its assimilation requires substantial amounts of energy. In addition to that, plant maintenance respiration has been directly correlated with tissue N level (Irving and Silsbury, 1981), which represents additional cost. Therefore, if we consider N as a limited expensive variable, it is logical to expect that CO_2 assimilation will have a positive linear correlation with N, in order to have high N use efficiency.

A plant which supports symbiotic N fixation has additional physiological capabilities. On one hand, this species, under natural conditions, evolved to allocate photosynthate to the symbiotic relationship with the Rhizobium bacteria, which adds more to the N cost, and on the other hand is less dependent upon availability of inorganic N. Leguminous species may have developed the bacterial symbiotic relationship through the course of evolution, due to conditions of N limitation. Having more available N endows these plants with more resources, to synthesize N compounds which help the

plant defend against insects and other animals and also against disease.

In line with this, Brown (1978) stated that:

> in the large Leguminosae family, no C_4 species has been identified, although members of this family are adapted to diverse climates. It is possible that the symbiotic relationship with Rhizobium bacteria, common to legumes, alleviated the need for more efficient utilization of nitrogen by these species and reduced the evolutionary pressure for acquisition of C_4 characteristics.

Thus, the data obtained here can indicate that, when leaf N is plentiful, part of it will serve as storage protein. Further, beyond a certain leaf N content per unit leaf weight, chloroplast (internal, mesophyll) resistance and stomatal resistance will decrease just enough to allow more gross photosynthesis to take care of the increase in maintenance respiration. Thus, net photosynthesis will not be affected.

The net photosynthesis, however, of the whole plant is higher under $N_{30}I_2$ and $N_{100}I_2$ compared to other treatments. This is true because their leaf dry weight is significantly higher than with the other treatments (Fig. 4). Moreover, the specific leaf area is not different except in $N_{30}I_2$, which was higher only when compared to $N_{30}I_5$ and $N_{30}I_{10}$ (Fig. 11). Thus the total leaf area of $N_{30}I_2$ and $N_{100}I_2$ is higher than with the other treatments.

The outcome of the stomatal conductance data is in agreement with that reported by Wong et al (1979) and Von Caemmerer and Farquhar (1981). There is a tendency for a higher stomatal conductance with increasing N applied, although only N_0 and N_{200} were consistently different through the ten day cycle (Fig. 18). At the same time, seedlings under N_{200} showed a significantly higher percent of leaf N compared to N_{30}. The observed stomatal conductance increase, without similar increase in net photosynthesis, may support the logic that actually there is an increase in gross photosynthesis, but this is leveled out due to an increase in maintenance respiration.

Stomatal conductance and net photosynthesis projected similar trends with regard to days since irrigation (Figs. 18 and 20). Although no measurement of water potential was done, these data suggest that there is a drop in stomatal conductance when leaf water potential reached a critical initial level.

At this point stomata may serve as a first line of defense for reduction of water loss, and consequently, their closure will impose limitations on net CO_2 assimilation. Further moisture stress caused leaf abscission and/or reduction in leaf growth (Fig. 4). This may be considered as a second line of defense to reduce water loss. Leaf abscission in response to moisture stress has been shown by Sahni (1968).

CONCLUSIONS

The principal objectives of this study were to assess the effect of different levels of N and irrigation frequencies on (1) total dry matter production and its relative distribution between the stem, leaf and root; and (2) stomatal conductance. An additional hypothesis was that net photosynthetic efficiency per unit leaf area is a function of the external N concentration and/or the internal percent of N per unit leaf weight. The following conclusions were reached:

(1) Irrigation frequency and N treatment were found to have a highly significant effect on total dry weight and its distribution among the root and shoot systems.

(2) Addition of a low level of N accompanied by frequent irrigation resulted in production of high total dry weight in both shoot and root. However, the shoot system showed a progressively higher increase. Furthermore, high N levels and less frequent irrigation resulted in lower dry weight, while the root system was less affected.

(3) Stomatal conductance was significantly higher with higher levels of N. A decline was observed after the fifth day since irrigation.

(4) Net photosynthesis per unit leaf area was not found to be affected by N treatment. However, a decrease started after the fifth day following irrigation.

The results obtained from this study can be considered as initial steps for further research to determine the optimum nutrient requirements of A. senegal seedlings in the nursery, using low to moderate levels of N. Also, performance of the seedlings after out-planting in the field will help in to determine the nutrient regime used for propagation. Studies of nitrogen fixation using the right Rhizobium strain in terms of the amount fixed in relation to:

1. Soil water potential.
2. Soil and external environment temperature.

will also aid in determinig the optimum nutrient requirement.

The next areas which need study will be:

1. Plant-soil water relations.
2. Vegetative propagation as a mean for improving A. senegal stands.

Table 1

Nutrient Levels Applied with Weekly Irrigation

A. Macronutrients:

Compound	Molarity	g/kg of soil
K_2SO_4	0.00158	0.020
$MgSO_4.7H_2O$	0.00200	0.037
$KHPO_4$	0.00100	0.010
$CaSO_4.2H_2O$	0.00600	0.077
$CaCl_2$	0.00050	0.004

B. Micronutrients:

Compound	Stock Solution (ppm)	ml/kg of soil
H_2BO_3	250	0.032
$MnSO_4.4H_2O$	250	0.032
$ZnSO_4.7H_2O$	50	0.006
$CuSO_4.5H_2O$	20	0.003
$NaMo.2H_2O$	10	0.001
$CoCl_2$	360	0.003
FeDDHA	1000	0.150

Table II.

Analysis of Variance of Total Biomass, Stem, Root and Leaf Dry Weight with Respect to Ammonium Nitrate and Irrigation Frequency.

A: Total Biomass

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	12.6455	< 0.001
Irrigation treatment	2	27.2302	< 0.001
Nitrogen x Irrigation	6	4.3583	< 0.001
Error	318	0.5467	

B. Stem Weight

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	1.0860	< 0.001
Irrigation treatment	2	2.3480	< 0.001
Nitrogen x Irrigation	6	0.4751	< 0.001
Error	318	0.0482	

Table II (cont.)

C. Root Weight

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	1.6838	< 0.001
Irrigation treatment	2	6.8623	< 0.001
Nitrogen x Irrigation	6	0.2476	< 0.14
Error	318	0.1518	

D. Leaf Weight

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	0.8573	< 0.001
Irrigation treatment	2	3.4345	< 0.001
Nitrogen x Irrigation	6	0.3602	< 0.001
Error	318	0.0284	

Table III.

Analysis of Variance of Production Efficiency with Nitrogen and Irrigation Treatments

A. Total Biomass Nitrogen Efficiency

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	4931.6329	< 0.001
Irrigation	2	441.9217	< 0.001
Nitrogen x Irrigation	6	270.7989	< 0.001
Error	318	9.7089	

B. Stem Nitrogen Efficiency

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	351.2842	< 0.001
Irrigation treatment	2	43.8608	< 0.001
Nitrogen x Irrigation	6	28.6792	< 0.001
Error	318	0.9052	

Table III(cont.)

C. Root Nitrogen Efficiency

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	1473.3679	< 0.001
Irrigation treatment	2	62.2724	< 0.001
Nitrogen x Irrigation	6	42.5971	< 0.001
Error	318	3.4923	

D. Leaf Nitrogen Efficiency

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	172.0443	< 0.001
Irrigation treatment	2	42.4724	< 0.001
Nitrogen x Irrigation	6	21.2726	< 0.001
Error	318	0.5139	

Table IV.

Analysis of Variance of Total Nitrogen Content in Whole Seedlings, in Stems, in Roots and in Leaves as a Response to Nitrogen and Irrigation treatments

A. Whole Seedlings

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	0.00303	< 0.001
Irrigation treatment	2	0.00317	< 0.001
Nitrogen x Irrigation	6	0.00042	< 0.001
Error	64	0.00001	

B. Stems

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	0.00053	< 0.001
Irrigation treatments	2	0.00146	< 0.001
Nitrogen x Irrigation	6	0.00021	< 0.001
Error	64	0.0000017	

Table IV (cont.)

C. Roots

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	0.00017	< 0.001
Irrigation treatment	2	0.00006	< 0.001
Nitrogen x Irrigation	6	0.00002	< 0.001
Error	64	0.0000017	

D. Leaves

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	0.00043	< 0.001
Irrigation treatment	2	0.00011	< 0.001
Nitrogen x Irrigation	6	0.00004	< 0.001
Error	64	0.00006	

Table V.

Analysis of Variance of Percent Nitrogen in Stems, Roots, and Leaves.

A. Percent Nitrogen in Stems

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	4.985	< 0.001
Irrigation treatment	2	1.515	< 0.001
Nitrogen x Irrigation	6	0.3382	< 0.001
Error	64	0.07578	

B. Percent Nitrogen in Roots

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	5.3750	< 0.001
Irrigation treatment	2	0.3727	< 0.001
Nitrogen x Irrigation	6	0.3257	< 0.005
Error	64	0.0613	

Table V (cont.)

C. Percent Nitrogen in Leaves

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	5.6007	< 0.001
Irrigation treatment	2	0.0673	0.604
Nitrogen x Irrigation	6	0.3086	0.043
Error	64	0.1324	

Table VI.

Analysis of Variance of Specific Leaf Area
with Respect to Nitrogen and
Irrigation Treatments

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	899.63	0.66
Irrigation treatment	2	6423.10	0.025
Nitrogen x Irrigation	6	3810.30	0.043
Error	132	1701.33	

Table VII.

Analysis of Variance for Photosynthesis with Respect to Irrigation and Nitrogen Treatments.

A. Days of measurements

Source of variation	df	Mean square	Significance of F
		Main unit	
Nitrogen	3	243.28	0.86
Irrigation	2	2046.30	0.13
Nitrogen x Irrigation	6	1184.77	0.13
Nitrogen x Irrigation x Replication	36	94.91	
		Subunit	
Days	9	1515.18	0.08
Nitrogen x Days	27	877.43	0.47
Irrigation x Days	18	1030.67	0.28
Nitrogen x Irrigation x Days	54	861.62	0.51
Error	324	879.18	

Table VII (cont.)

B. Days since irrigation

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	16.233	0.86
Days since irrigation	9	321.904	0.0001
Days x Nitrogen	27	36.103	0.988
Error	440	75.102	

Table VIII.

Analysis of Variance for Stomatal Conductance with Respect to Nitrogen and Irrigation Treatments.

Source of variation	df	Mean square	Significance of F
Nitrogen treatment	3	0.06281	0.0006
Days since irrigation	9	0.40697	0.0001
Days x Nitrogen	27	0.00668	.993
Error	440		

Table IX

Treatment Means for Total Dry Weight, Leaf Dry Weight, Stem Dry Weight, and Root Dry Weight.

Tukey's range for multiple comparisons is given. Means with the same letters are not significantly different at $P < 0.05$.

Treatment	Total Dry Weight (grams)	Leaf Dry Weight (grams)	Stem Dry Weight (grams)	Root Dry Weight (grams)
N_0I_2	1.88^{b}	$0.34^{b,c,d}$	$0.47^{a,b}$	$1.08^{b,c}$
N_0I_5	$1.78^{a,b}$	$0.25^{a,b,c,d}$	$0.46^{a,b}$	$1.07^{b,c}$
N_0I_{10}	$1.51^{a,b}$	0.17^{a}	$0.38^{a,b}$	$0.96^{a,b}$
$N_{30}I_2$	3.29^{c}	0.71^{e}	0.94^{c}	1.65^{d}
$N_{30}I_5$	1.90^{b}	$0.32^{a,b,c,d}$	$0.48^{a,b}$	$1.11^{b,c}$
$N_{30}I_{10}$	$1.62^{a,b}$	$0.23^{a,b,c}$	$0.39^{a,b}$	$0.99^{a,b,c}$
$N_{100}I_2$	2.93^{c}	0.75^{e}	0.81^{c}	$1.37^{c,d}$
$N_{100}I_5$	2.05^{b}	$0.38^{c,d}$	0.54^{b}	$1.13^{b,c}$
$N_{100}I_{10}$	$1.45^{a,b}$	0.17^{a}	$0.40^{a,b}$	$0.88^{a,b}$
$N_{200}I_2$	$1.68^{a,b}$	0.39^{d}	$0.44^{a,b}$	$0.84^{a,b}$
$N_{200}I_5$	$1.63^{a,b}$	$0.27^{a,b,c,d}$	$0.46^{a,b}$	$0.95^{a,b}$
$N_{200}I_{10}$	1.09^{a}	$0.21^{a.b}$	0.27^{a}	0.61^{a}

Table X.

Treatment Means for Root:Shoot (stem & leaves) Ratio, Leaf:Stem Ratio, and Root:Leaf Ratio on a Dry Weight Basis

Tukey's range for multiple comparisons is given. Means with the same letters are not significantly different at $P < 0.05$.

Treatment	Root:Shoot Ratio	Leaf:Stem Ratio	Root:Leaf Ratio
N_0I_2	$1.378^{c,d}$	$0.770^{b,c,d}$	$3.753^{b,c}$
N_0I_5	$1.526^{d,e}$	$0.579^{a,b}$	$4.817^{c,d}$
N_0I_{10}	1.755^{e}	0.518^{a}	5.935^{d}
$N_{30}I_2$	$1.025^{a,b}$	$0.802^{b,c,d}$	$2.470^{a,b}$
$N_{30}I_5$	$1.423^{d,e}$	$0.693^{a,b,c,d}$	$4.022^{b,c,d}$
$N_{30}I_{10}$	$1.603^{d,e}$	$0.620^{a,b,c}$	$5.019^{c,d}$
$N_{100}I_2$	0.885^{a}	0.945^{d}	1.863^{a}
$N_{100}I_5$	$1.288^{b,c,d}$	$0.762^{a,b,c,d}$	$3.503^{a,b,c}$
$N_{100}I_{10}$	$1.576^{d,e}$	0.497^{a}	6.073^{d}
$N_{200}I_2$	$1.073^{a,b,c}$	0.927^{d}	$2.306^{a,b}$
$N_{200}I_5$	$1.336^{b,c,d}$	$0.610^{a,b,c}$	$4.460^{c,d}$
$N_{200}I_{10}$	$1.400^{c,d,e}$	$0.882^{c,d}$	$3.922^{b,c,d}$

Table XI

Treatment Means for Total Nitrogen in the Whole Plant, in Leaves, in Stems, and in Roots.

Tukey's range for multiple comparisons is given. Means with the same letters are not significantly different at $P < 0.05$.

Treatment	Total Nitrogen in the Whole Plant (grams)	Total Nitrogen in the Leaves (grams)	Total Nitrogen in the Stems (grams)	Total Nitrogen in the Roots (grams)
N_0I_2	$0.028^{a,b}$	$0.011^{c,d}$	0.005^{a}	0.012^{a}
N_0I_5	$0.027^{a,b}$	$0.009^{b,c}$	0.005^{a}	0.012^{a}
N_0I_{10}	0.025^{a}	0.006^{a}	$0.007^{a,b}$	0.012^{a}
$N_{30}I_2$	0.059^{e}	0.029^{f}	0.012^{d}	$0.018^{c,d}$
$N_{30}I_5$	$0.033^{b,c}$	$0.012^{c,d}$	$0.008^{b,c}$	$0.013^{a,b}$
$N_{30}I_{10}$	$0.032^{a,b,c}$	$0.009^{b,c}$	$0.0075^{a,b}$	$0.015^{a,b,c}$
$N_{100}I_2$	0.075^{g}	0.035^{g}	0.016^{e}	0.025^{e}
$N_{100}I_5$	$0.053^{e,f}$	0.017^{e}	0.011^{d}	0.026^{e}
$N_{100}I_{10}$	$0.038^{c,d}$	$0.007^{a,b}$	0.011^{d}	$0.019^{c,d}$
$N_{200}I_2$	0.050^{e}	0.018^{e}	$0.0106^{c,d}$	$0.022^{d,e}$
$N_{200}I_5$	0.042^{d}	0.013^{d}	0.0109^{d}	$0.018^{b,c,d}$
$N_{200}I_{10}$	$0.030^{a,b}$	0.010^{c}	$0.006^{a,b}$	$0.014^{a,b}$

Table XII

Treatment Means for Percent Nitrogen on a Dry Weight Basis for Stems, Roots, and Leaves.

Tukey's range for multiple comparisons is given. Means with the same letters are not significantly different at $P < 0.05$.

Treatment	Percent Nitrogen in Stems	Percent Nitrogen in Roots	Percent Nitrogen in Leaves
N_0I_2	1.134^{a}	1.074^{a}	3.227^{a}
N_0I_5	1.147^{a}	1.136^{a}	$3.729^{a,b}$
N_0I_{10}	$1.703^{b,c}$	1.283^{a}	$3.493^{a,b}$
$N_{30}I_2$	$1.241^{a,b}$	1.117^{a}	$4.113^{b,c,d,e}$
$N_{30}I_5$	$1.698^{b,c}$	1.205^{a}	$3.807^{a,b,c}$
$N_{30}I_{10}$	$1.920^{c,d}$	$1.510^{a,b}$	$3.972^{b,c,d}$
$N_{100}I_2$	$1.963^{c,d}$	$1.810^{b,c}$	$4.613^{d,e}$
$N_{100}I_5$	$2.032^{c,d}$	$1.902^{b,c}$	$4.487^{c,d,e}$
$N_{100}I_{10}$	2.782^{e}	$2.186^{c,d}$	$4.188^{b,c,d,e}$
$N_{200}I_2$	$2.404^{d,e}$	2.583^{d}	$4.526^{d,e}$
$N_{200}I_5$	$2.363^{d,e}$	$1.870^{b,c}$	4.777^{e}
$N_{200}I_{10}$	$2.035^{d,e}$	$2.210^{c,d}$	4.759^{e}

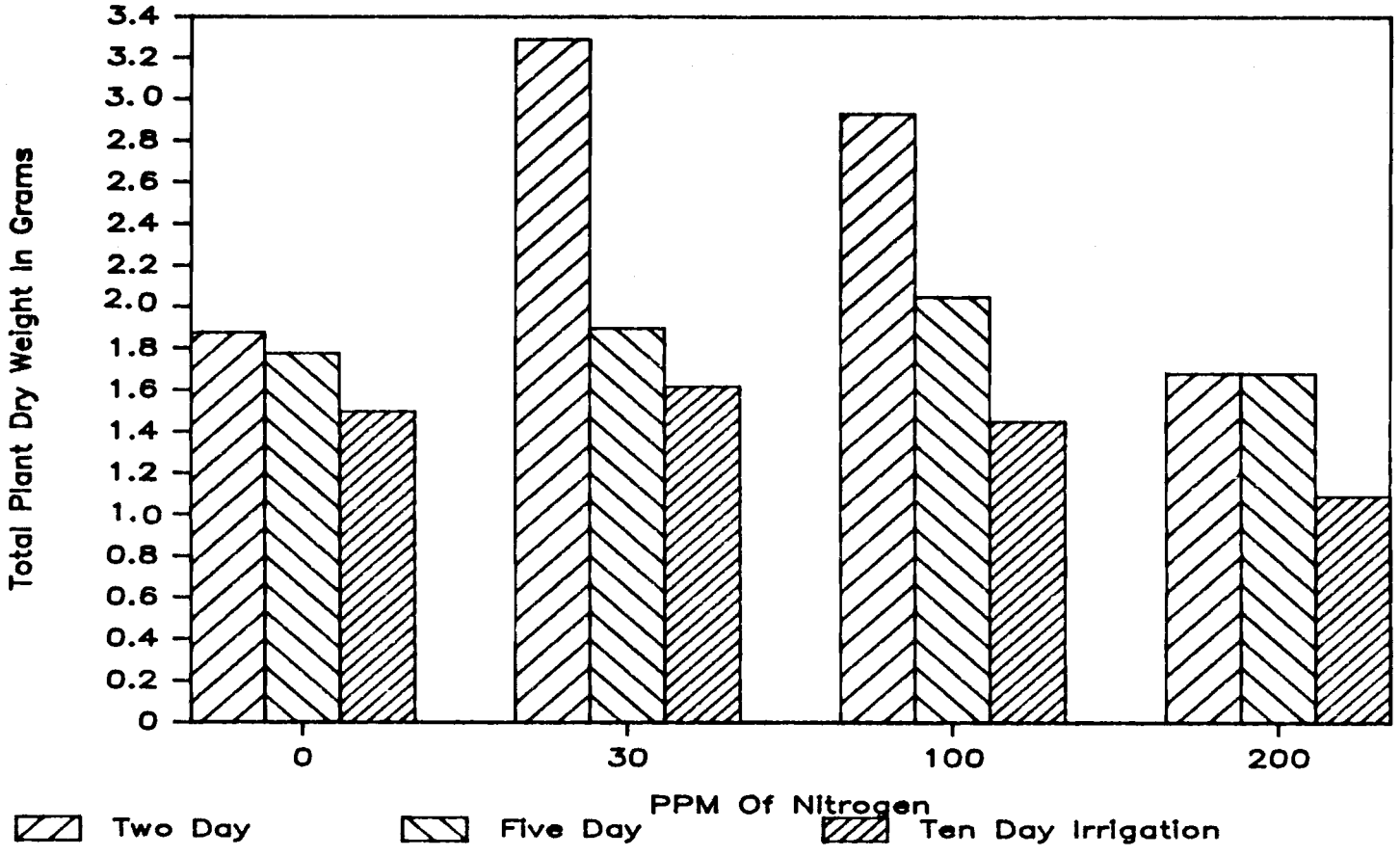

Figure 1. Histograms showing the mean values of total plant dry weight in grams of the watering regimes within each nitrogen level.

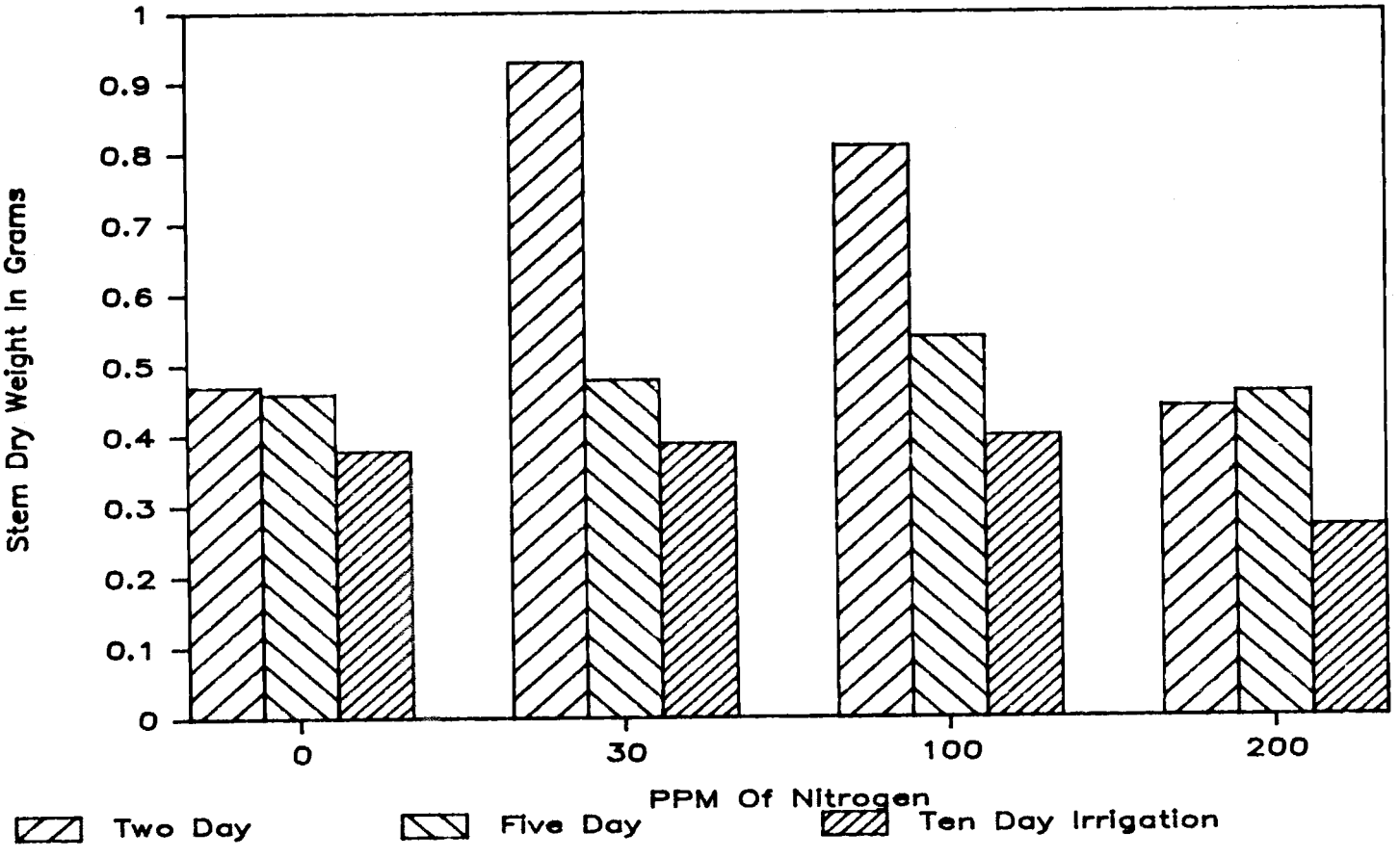

Figure 2. Histograms showing the mean values of stem dry weight in grams of the watering regimes within each nitrogen level.

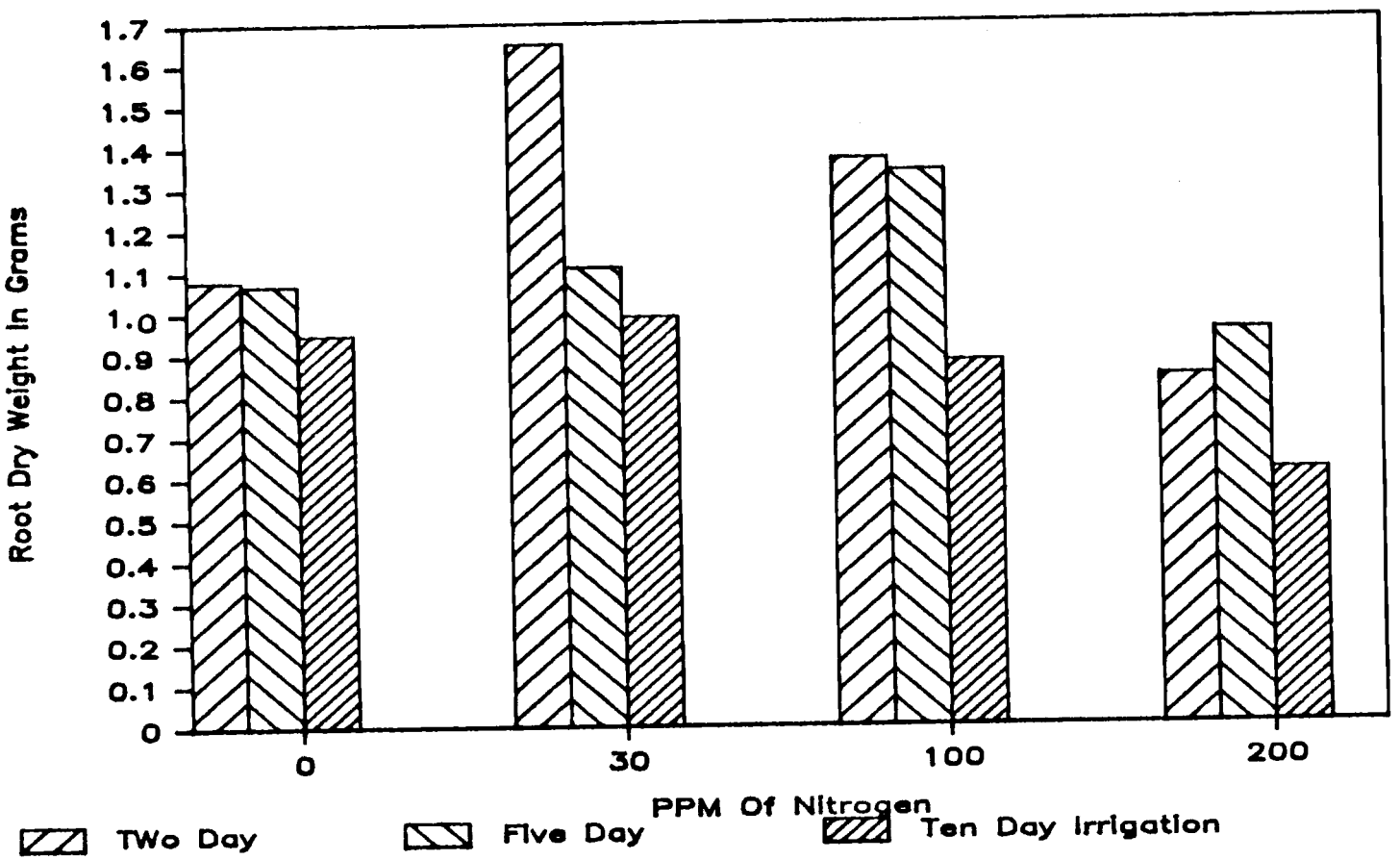

Figure 3. Histograms showing the mean values of root dry weight in grams for the watering regimes within each nitrogen level.

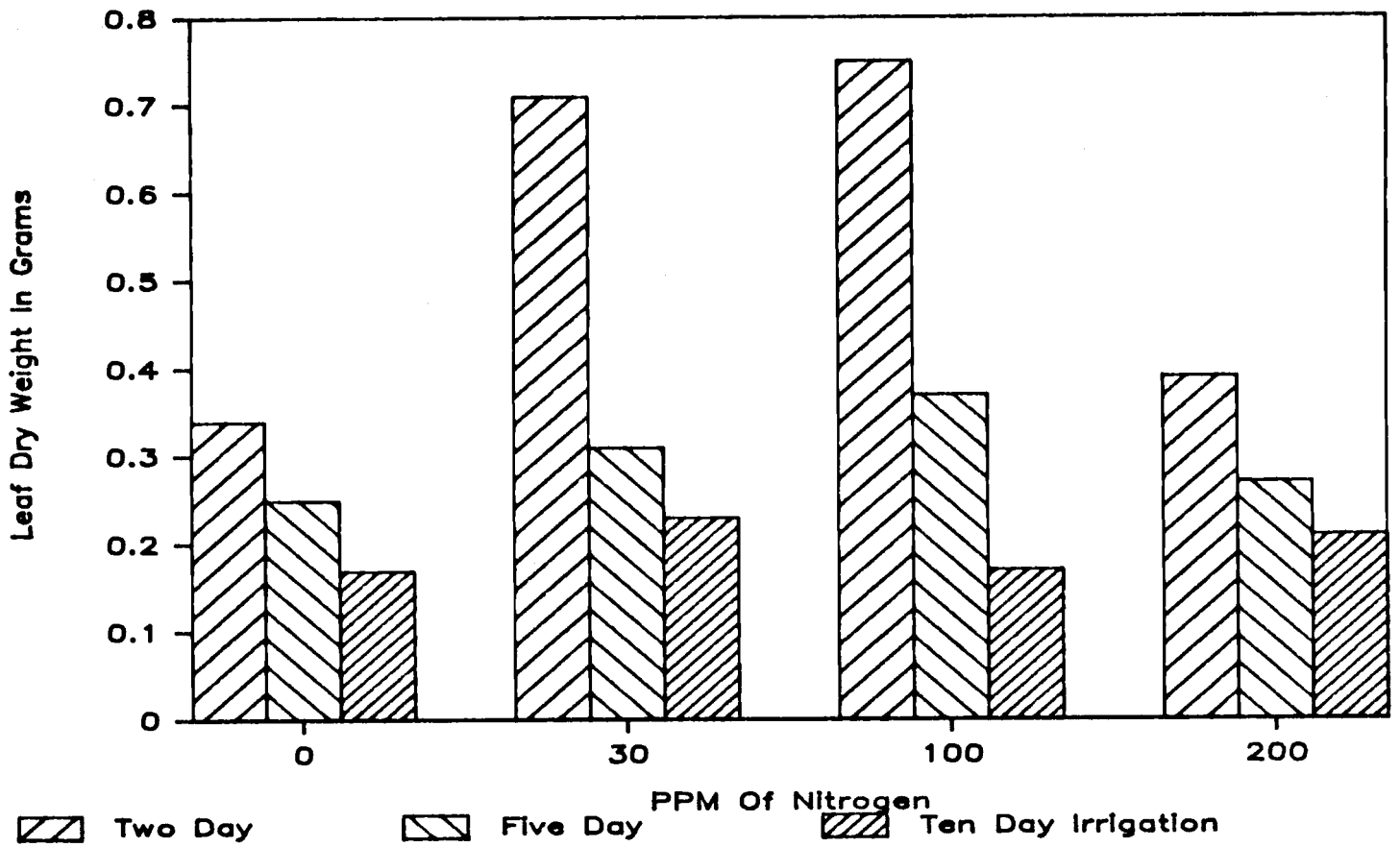

Figure 4. Histograms showing the mean values of leaf dry weight in grams for the watering regimes within each nitrogen level.

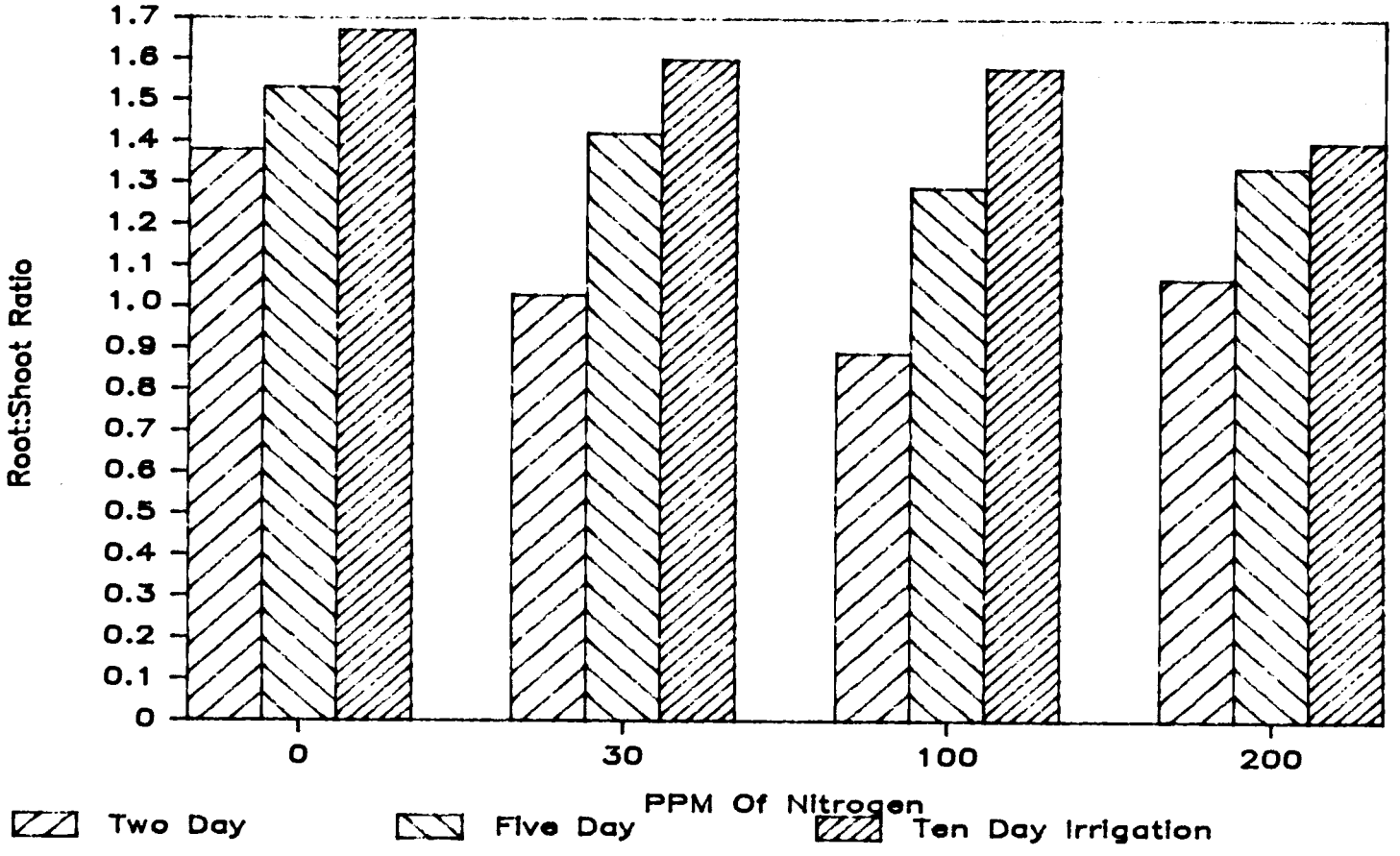

Figure 5. Mean values of root:shoot (leaves + stem) ratio of the watering regimes within each nitrogen level.

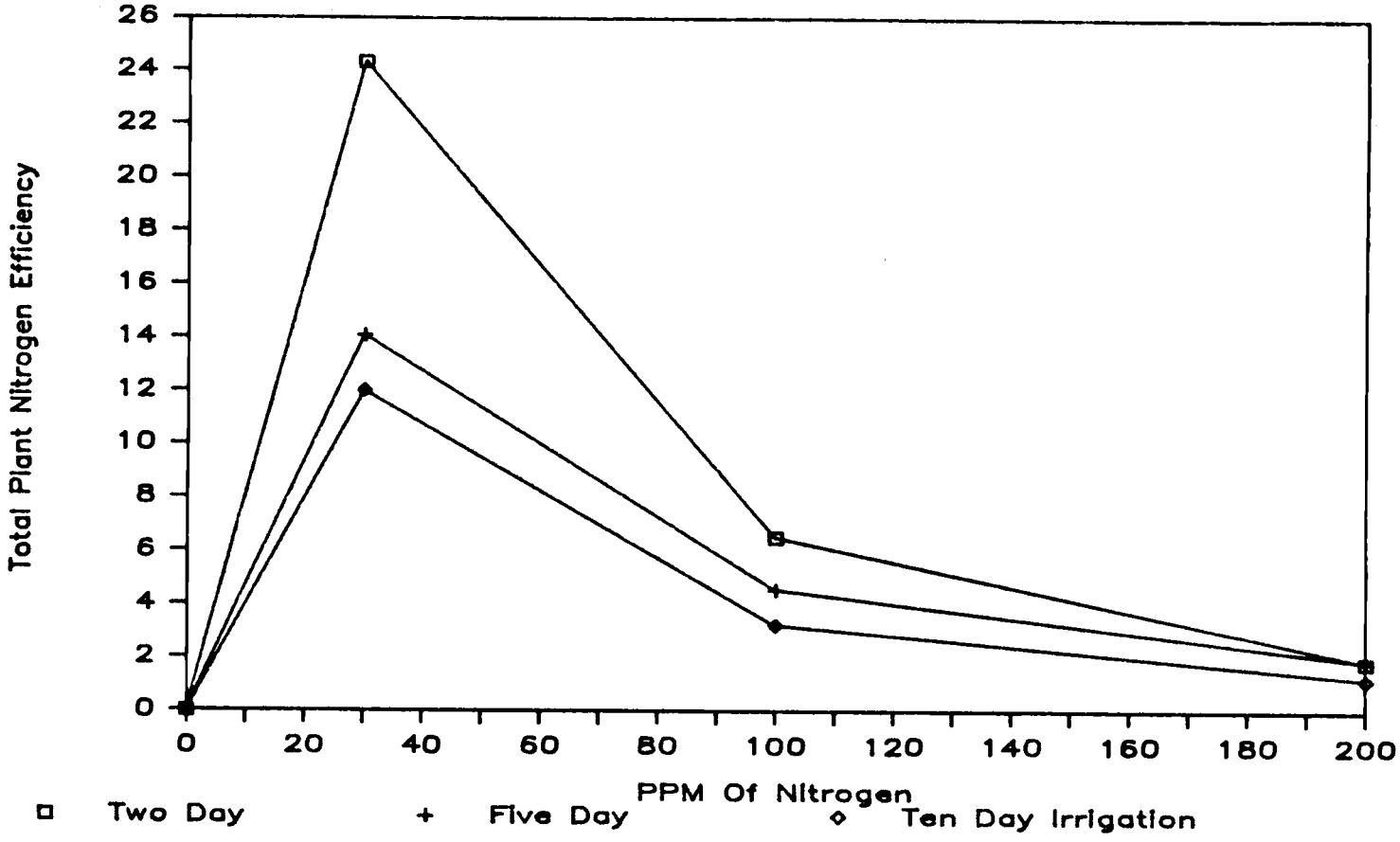

Figure 6. Mean values of nitrogen efficiency of total plant dry weight at four nitrogen levels within each watering regime.

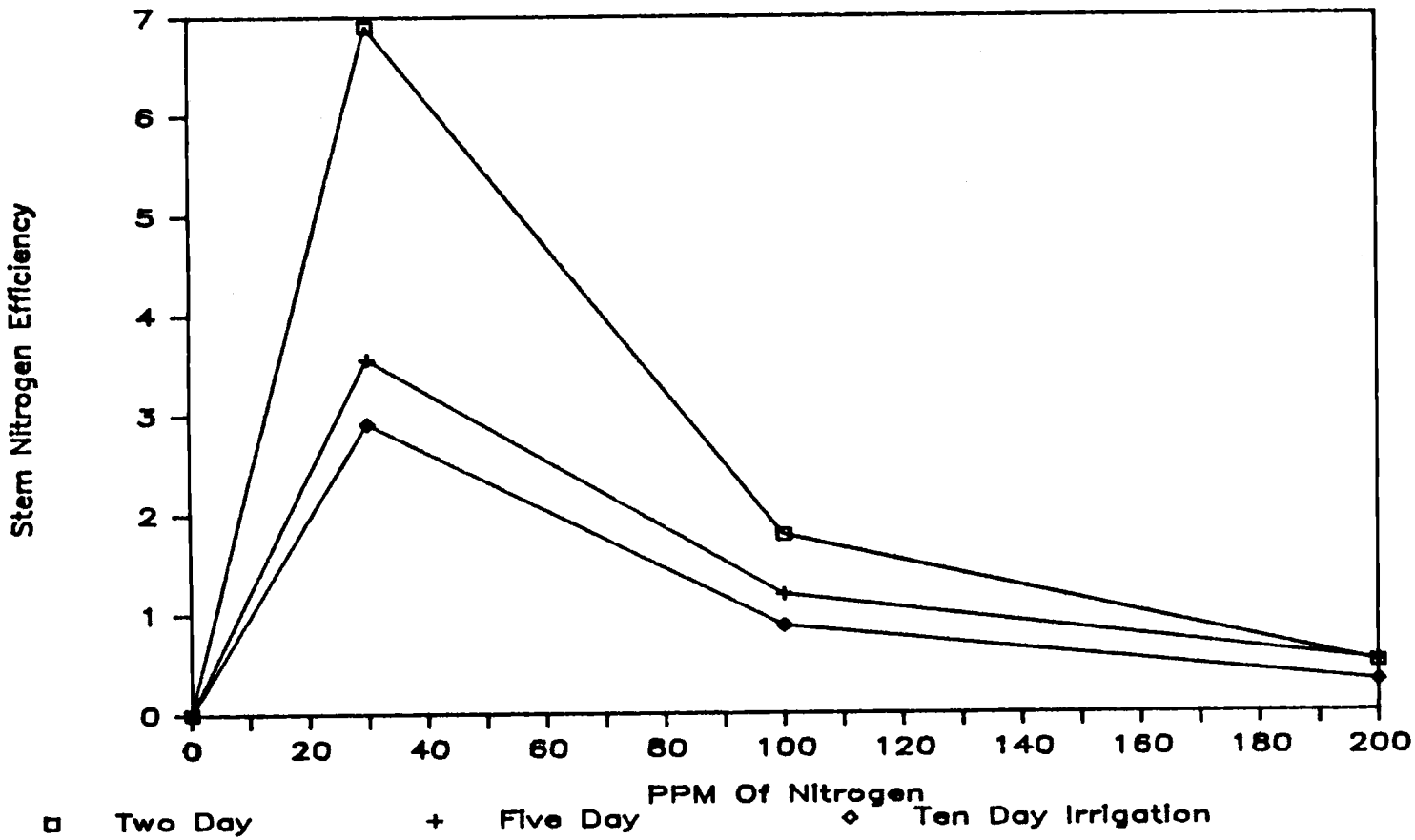

Figure 7. Mean values of nitrogen efficiency of stem dry weight at four nitrogen levels within each watering regime.

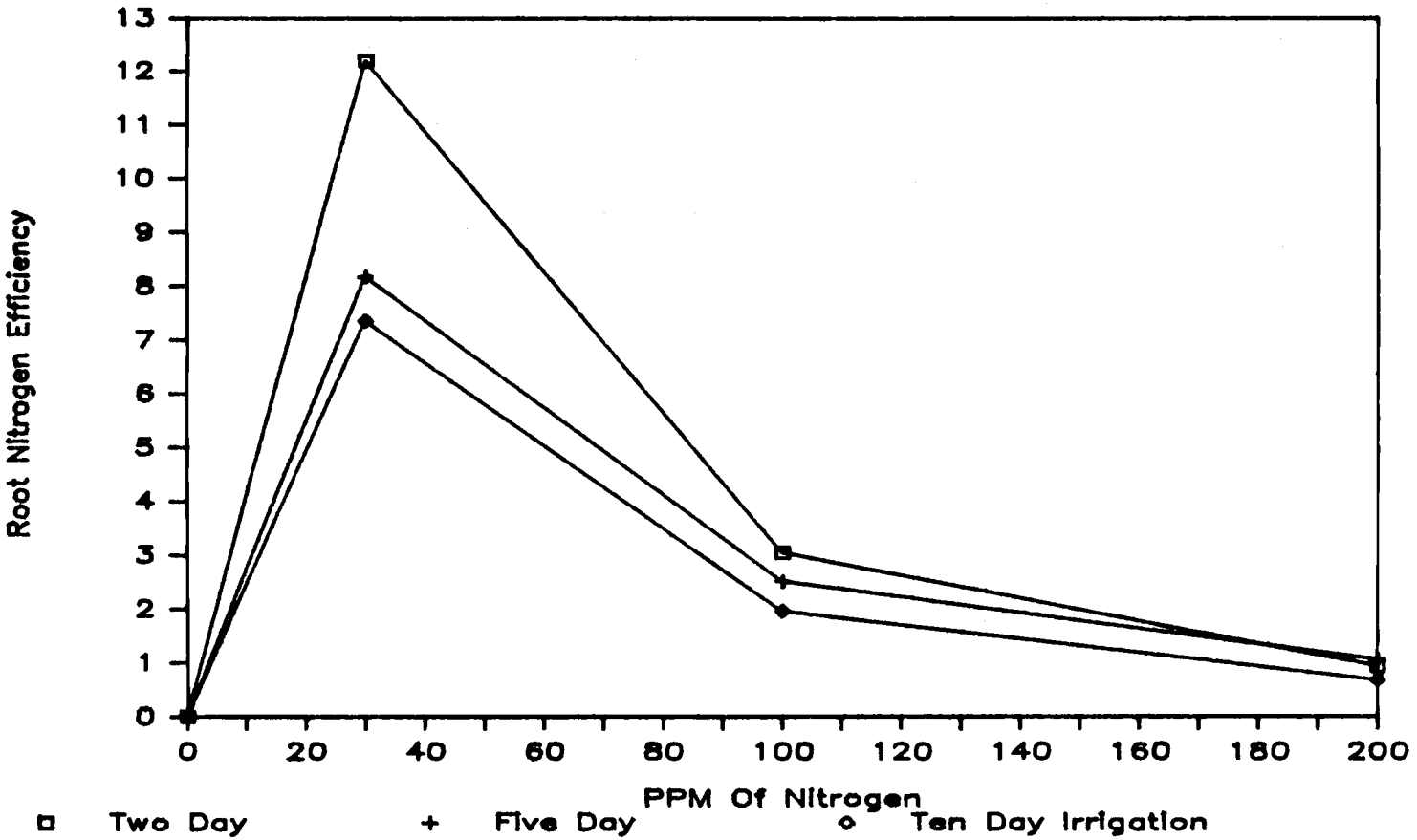

Figure 8. Mean values of nitrogen efficiency of root dry weight at four nitrogen levels within each watering regime.

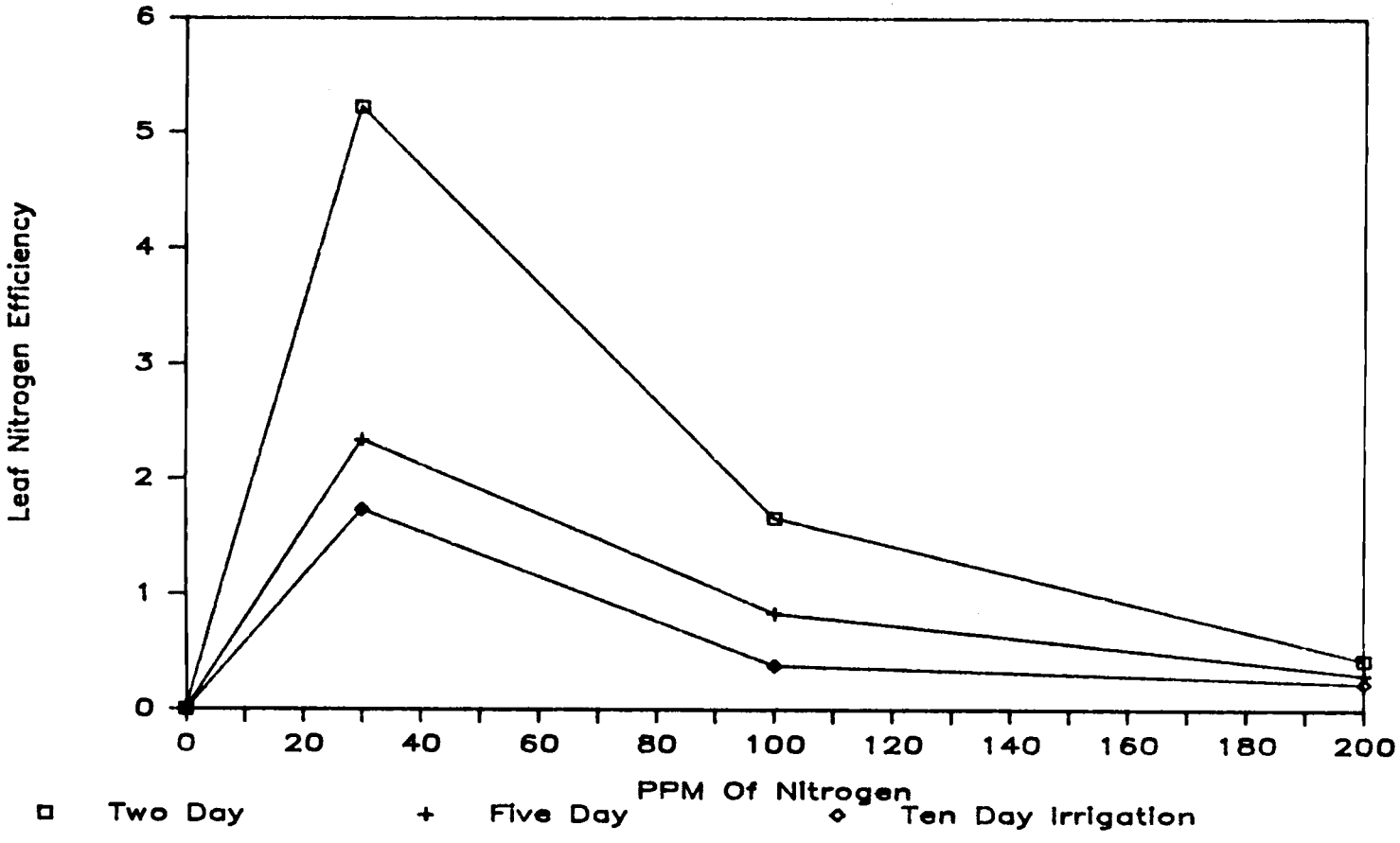

Figure 9. Mean values of nitrogen efficiency of leaf dry weight at four nitrogen levels within each watering regime.

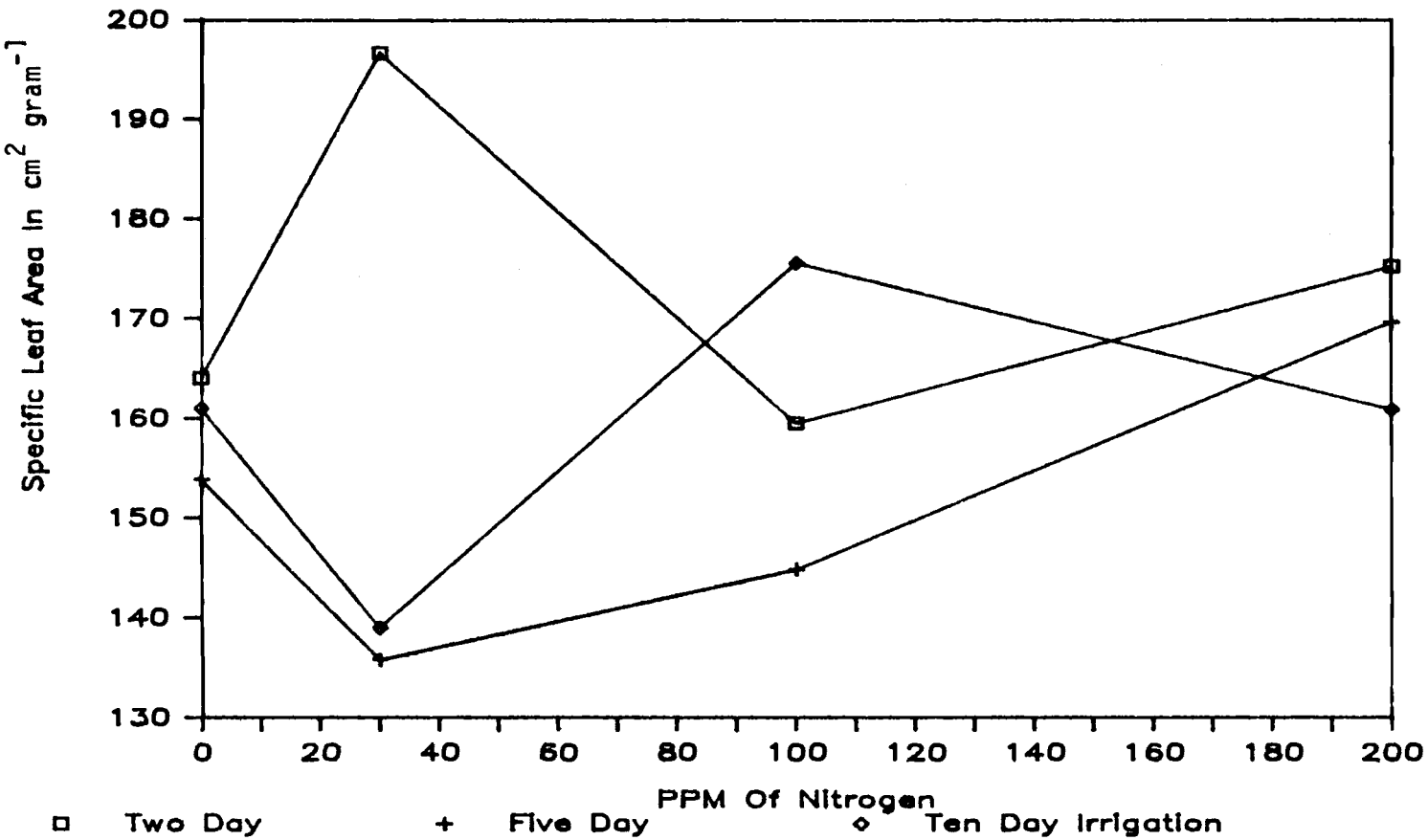

Figure 10. Mean values of specific leaf area in cm^2 $gram^{-1}$ at four different nitrogen levels within each watering regime.

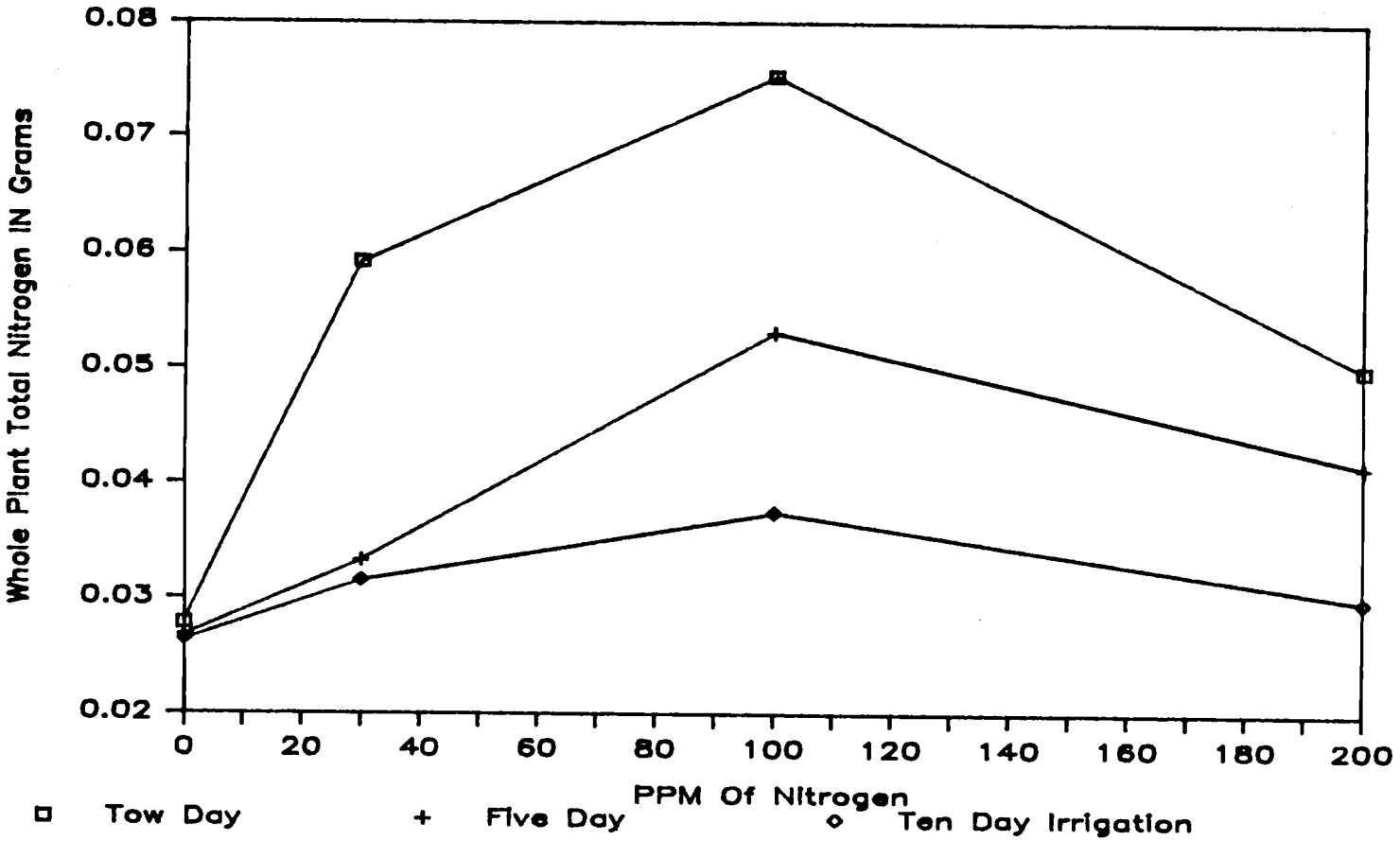

Figure 11. Mean values of whole plant total nitrogen at four of the nitrogen treatment levels within each watering regime.

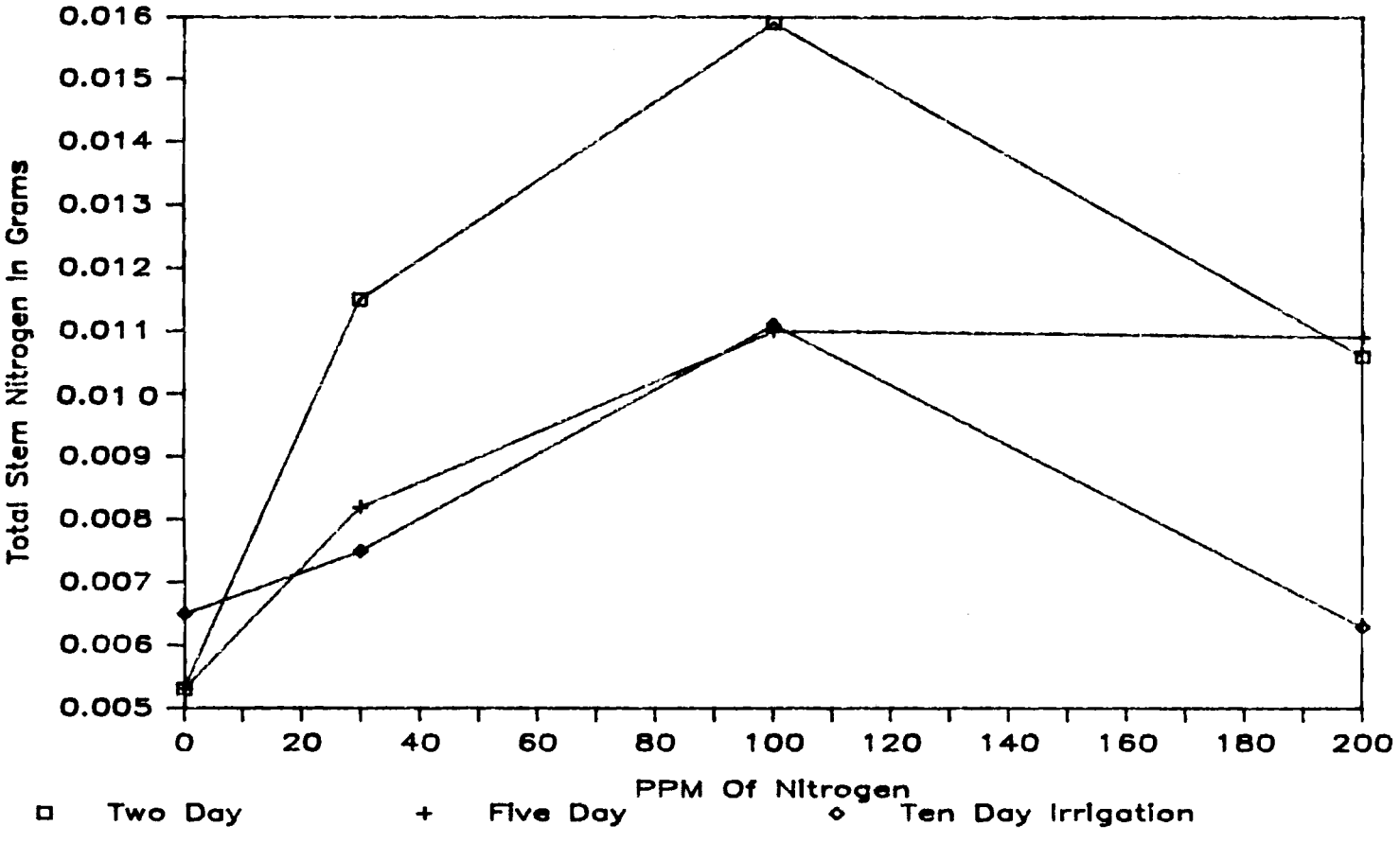

Figure 12. Mean values of stem total nitrogen at four nitrogen treatment levels within each watering regime.

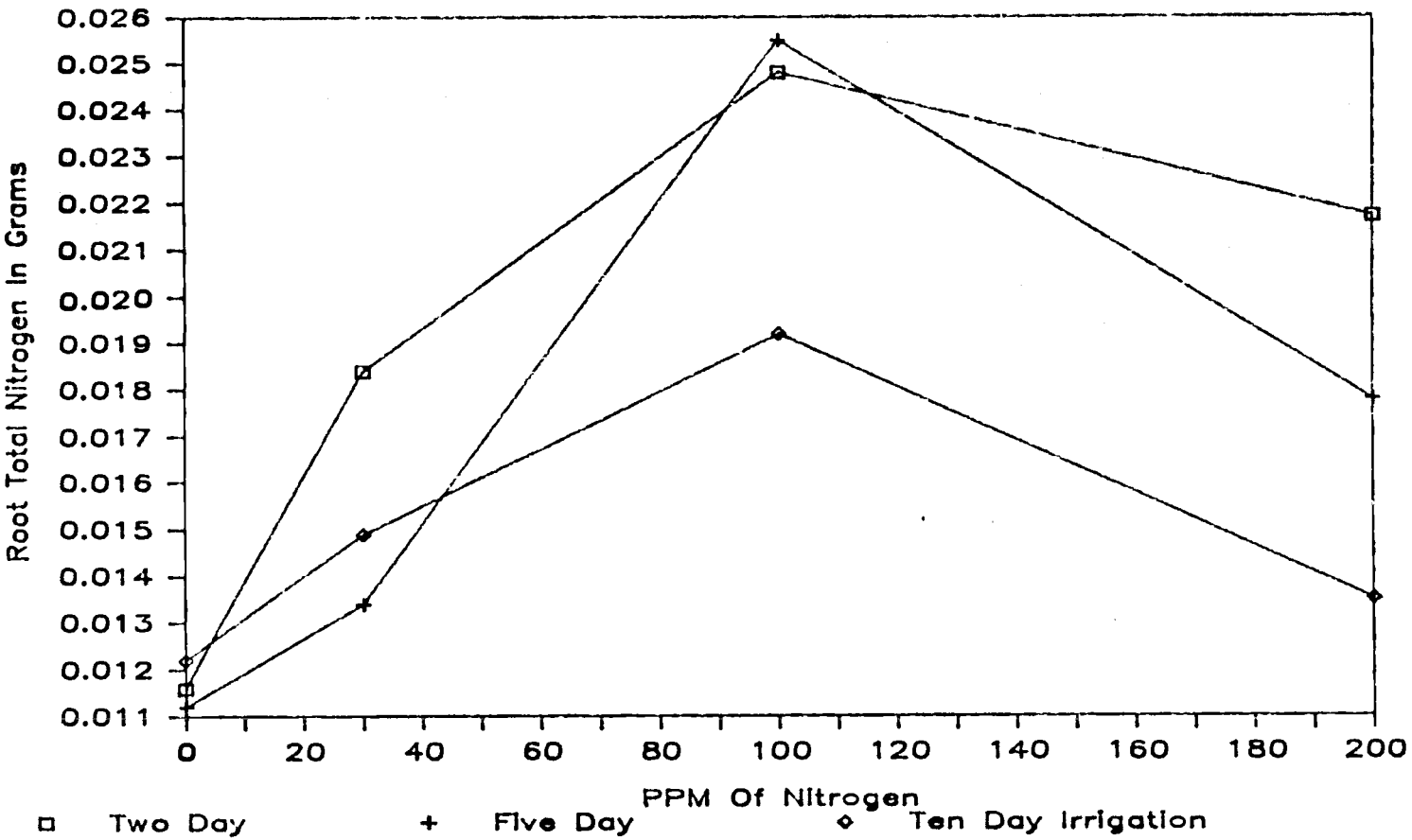

Figure 13. Mean values of root total nitrogen at four nitrogen treatment levels within each watering regime.

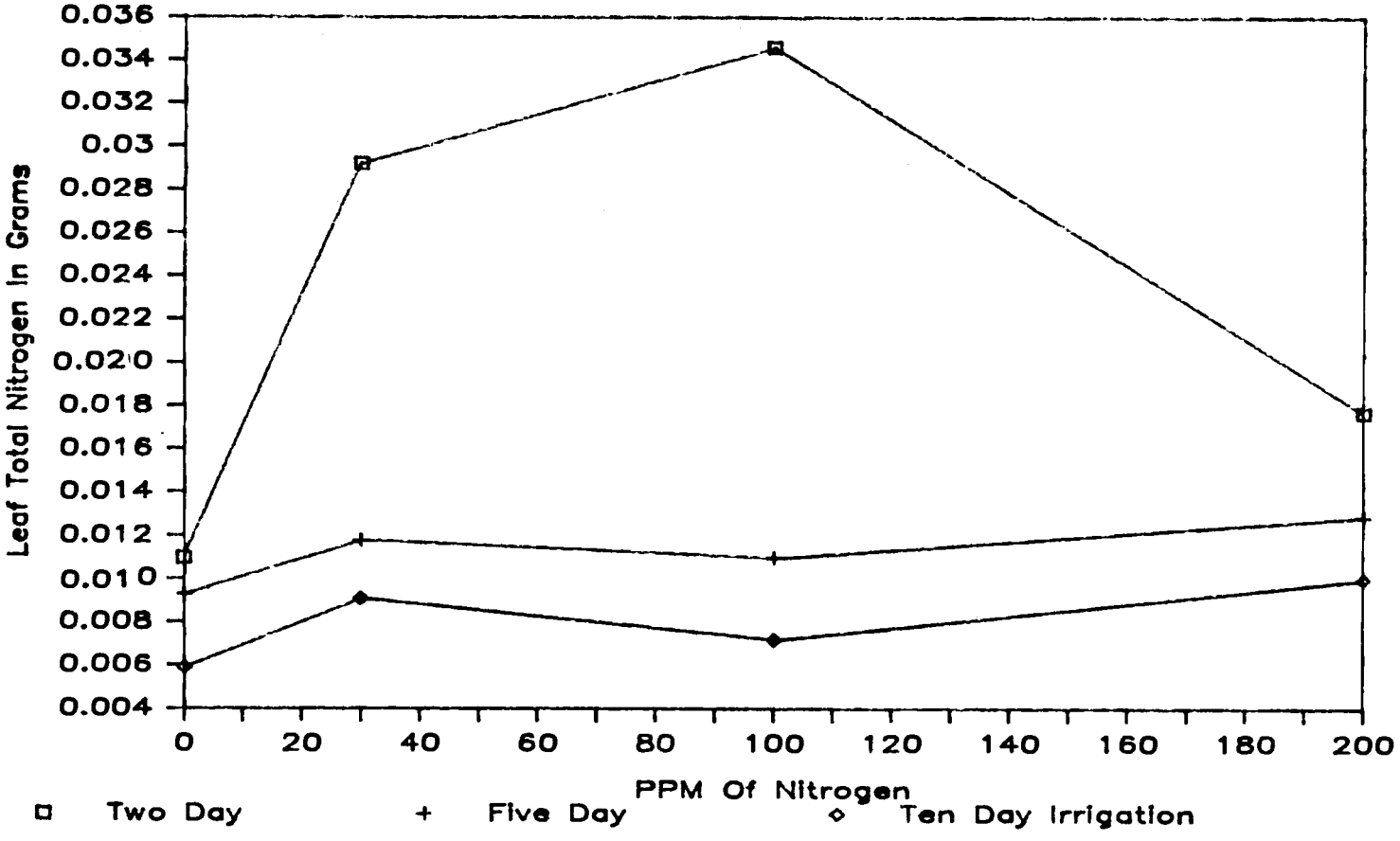

Figure 14. Mean values of total leaf nitrogen content at four nitrogen treatment levels within each watering regime.

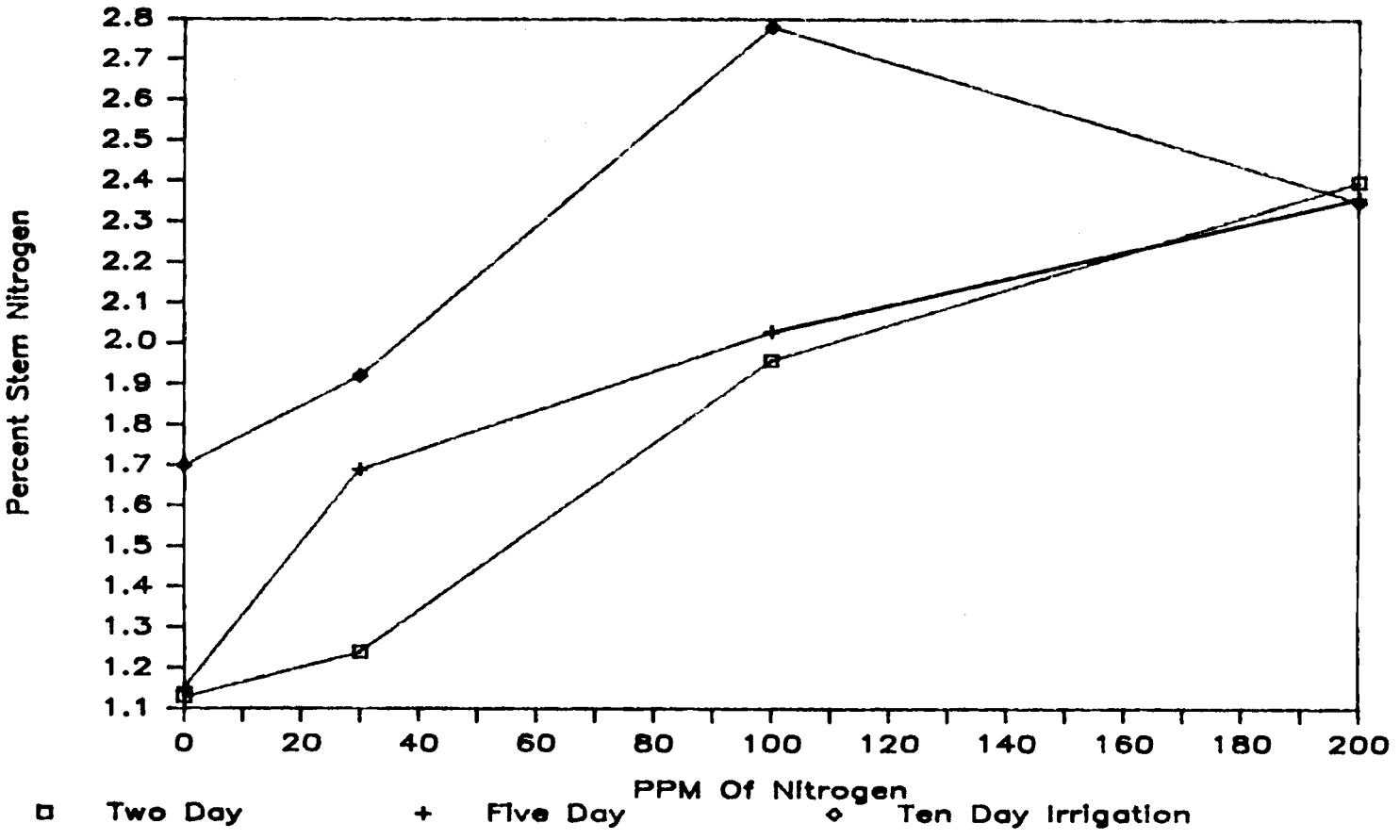

Figure 15. Percent stem nitrogen at four nitrogen treatment levels within each watering regime.

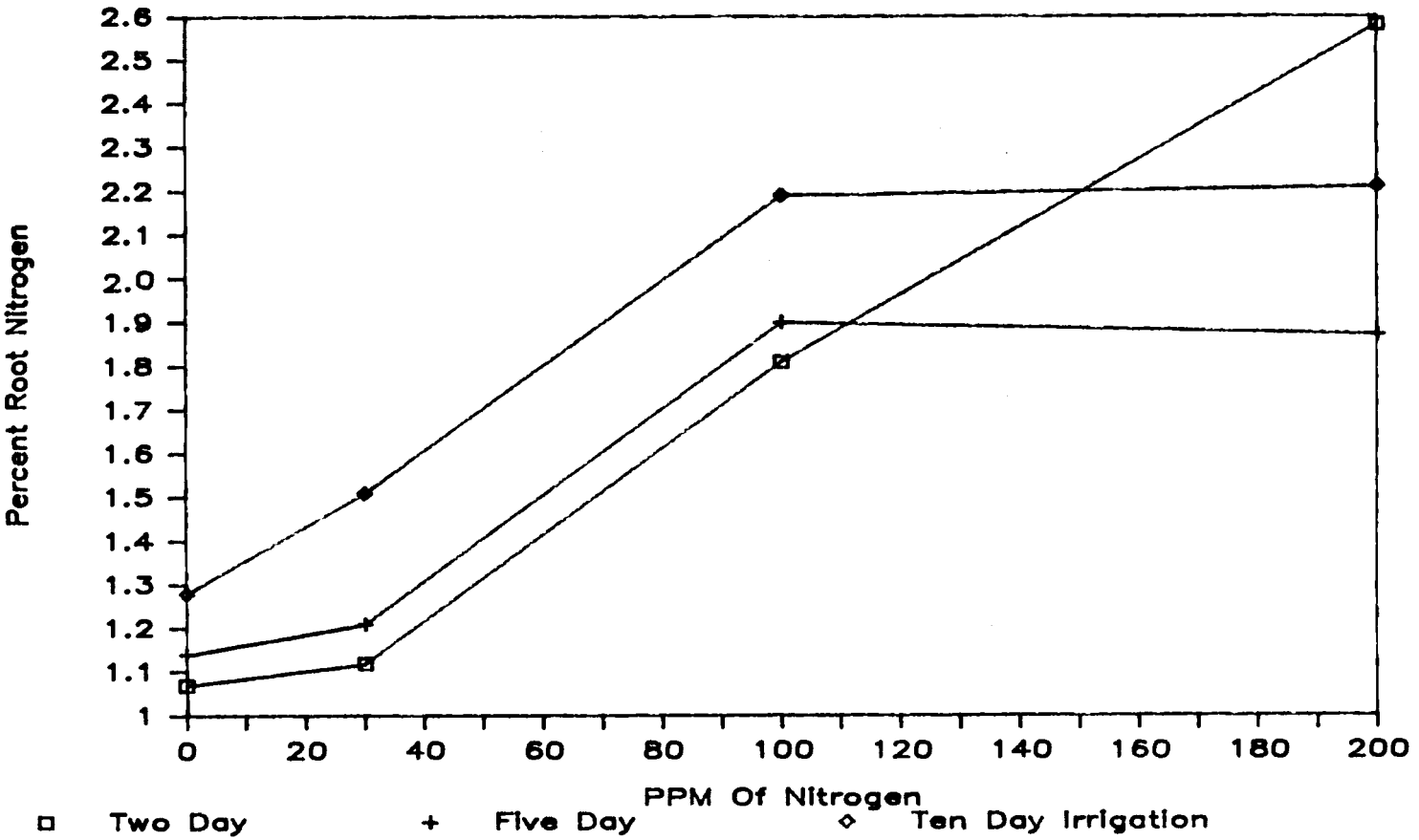

Figure 16. Percent root nitrogen at four nitrogen treatment levels within each watering regime.

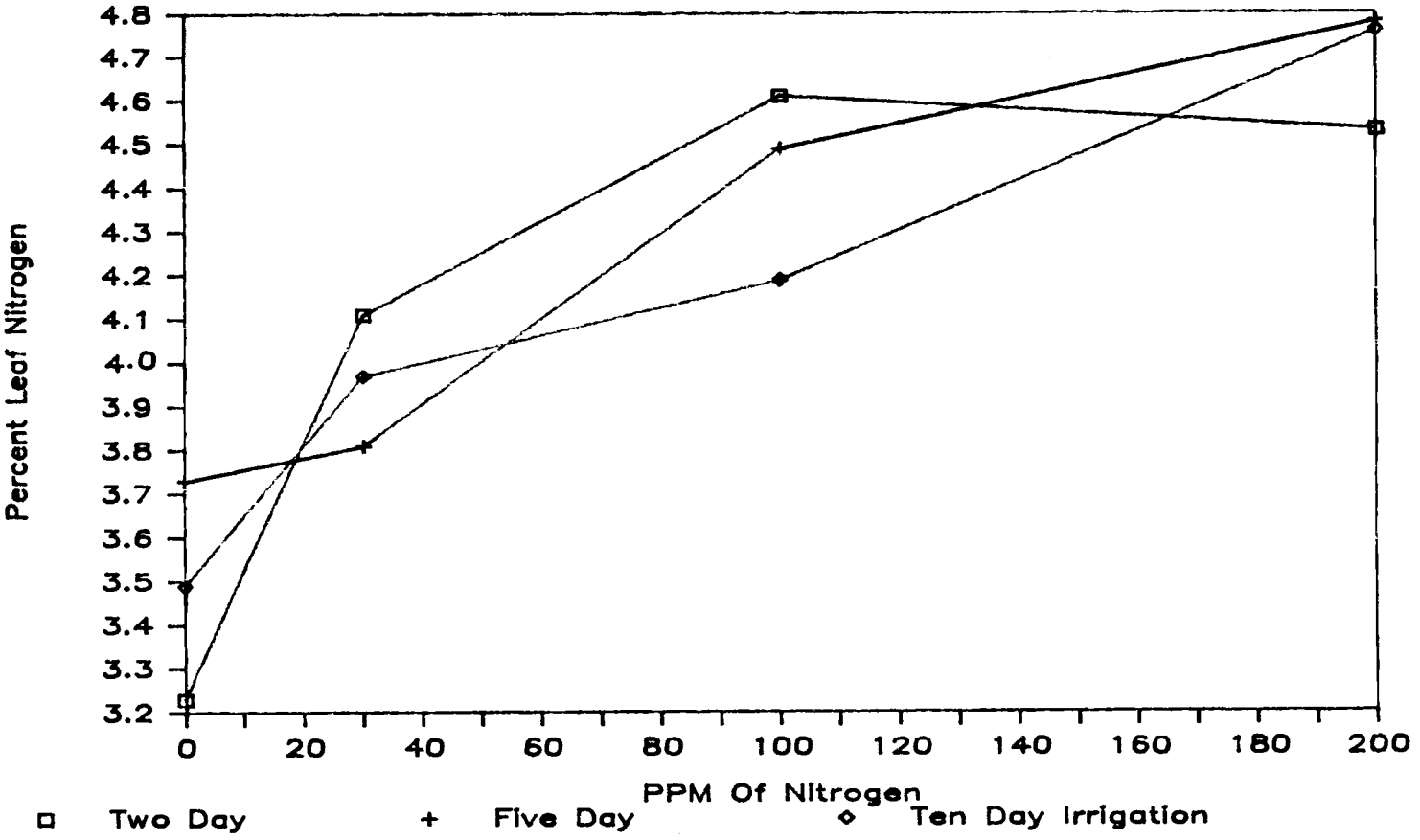

Figure 17. Percent leaf nitrogen at four nitrogen treatment levels within each watering regime.

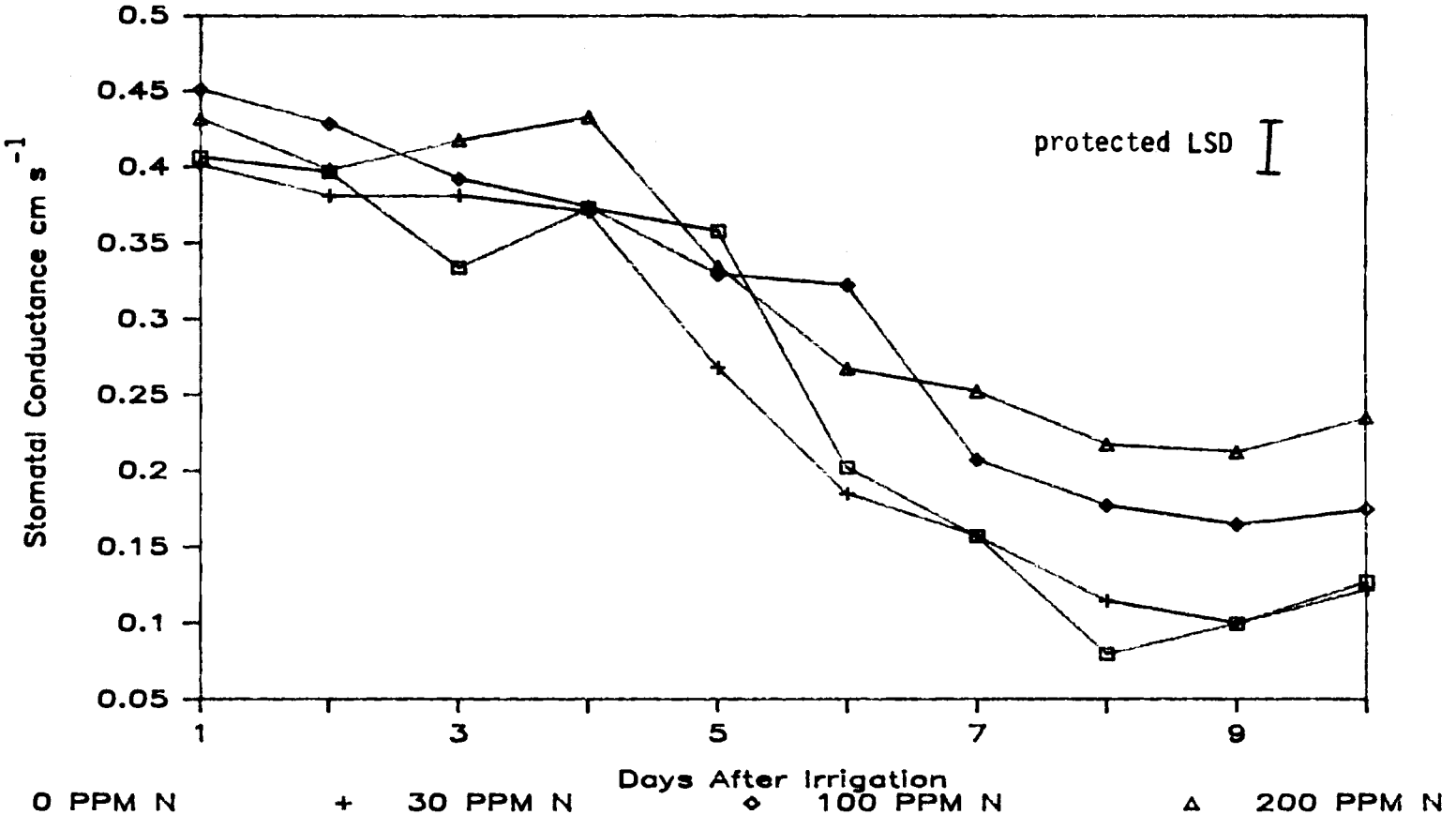

Figure 18. Mean values of stomatal conductance at four nitrogen levels after 1-10 days since irrigation.

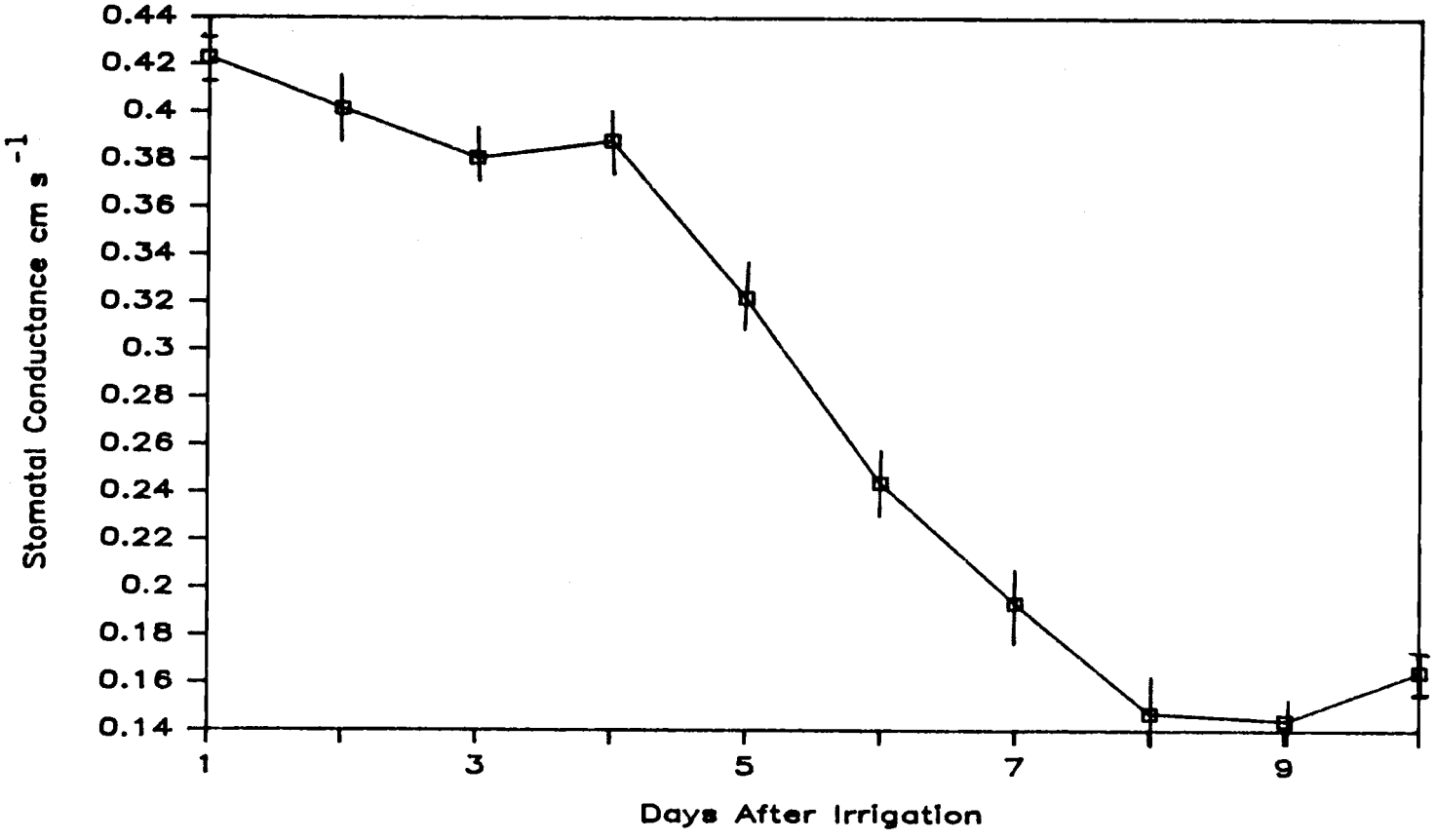

Figure 19. Weighted means of stomatal conductance of all four nitrogen treatment levels after 1-10 days since irrigation.

Vertical bars represent standard errors.

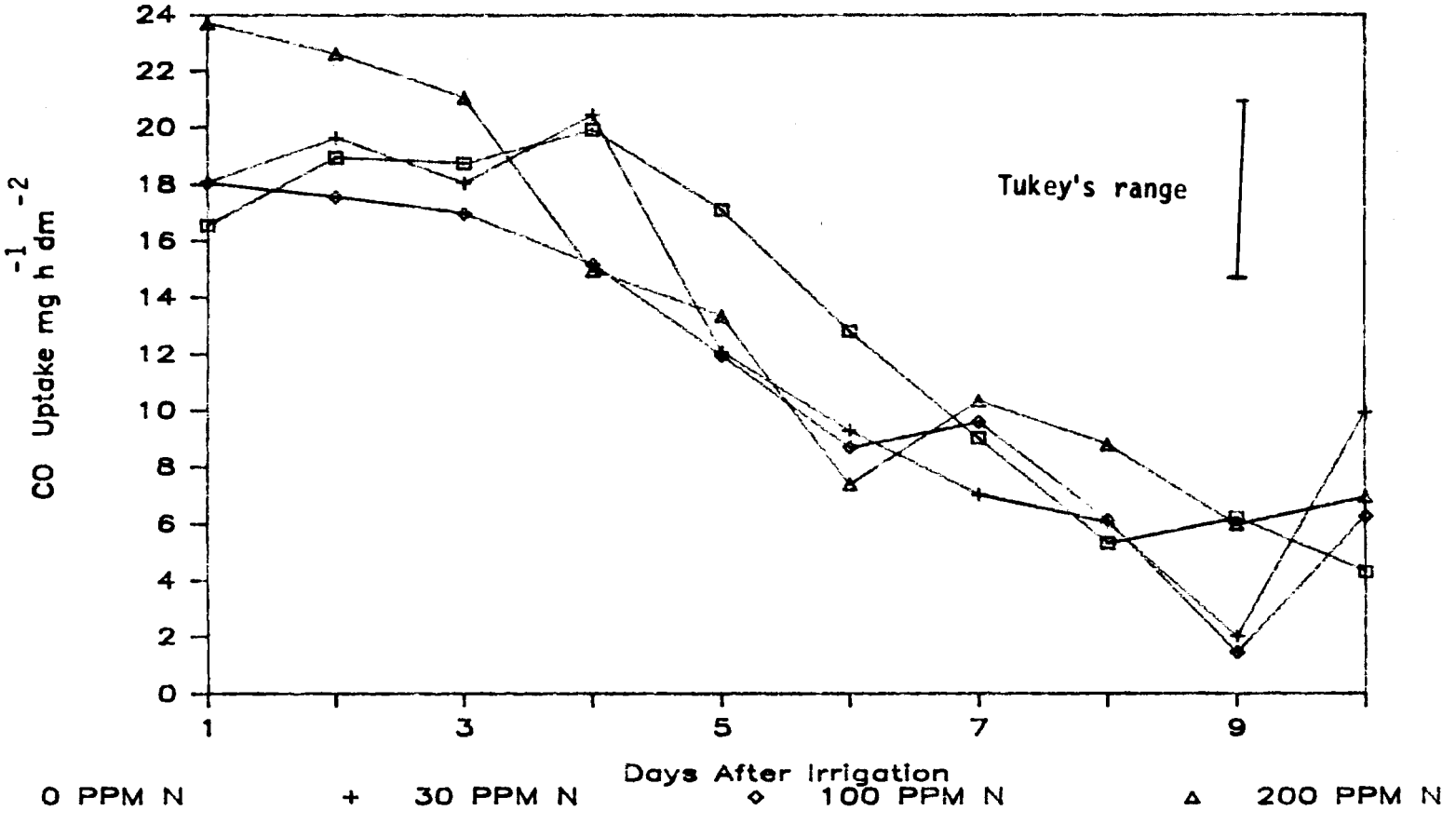

Figure 20. Mean values of net CO_2 assimilation in mg of CO_2 h^{-1} d m^{-2} leaf area at four nitrogen levels after 1-10 days since irrigation.

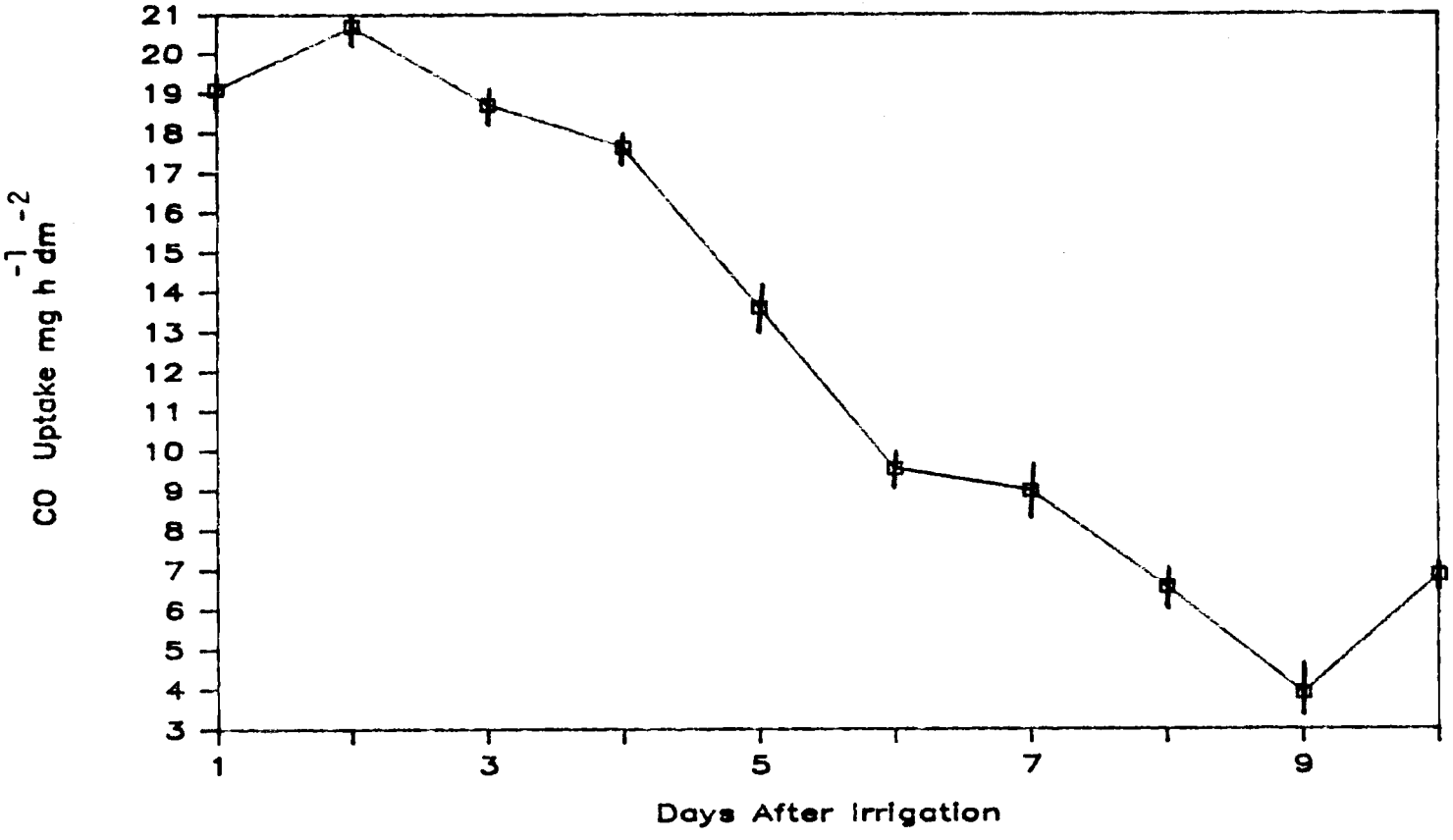

Figure 21. Weighted means of net CO_2 fixed in mg h^{-1} d m^{-2} leaf area all four nitrogen levels after 1-10 days since irrigation.

Vertical bars represent standard errors.

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