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JOURNAL OF PLANT NUTRITION, 15(2), 247-264 (1992)

DIURNAL UPTAKE OF NITRATE AND POTASSIUM DURING THE VEGETATIVE GROWTH OF TOMATO PLANTS

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ABSTRACT: Tomato plants (*Lycopersicon esculentum* Mill.) of the F_1 hybrid variety Turbo were grown in a NFT system for 22 days. On days 16 and 20-22 inclusive of the experiment, the diurnal variation in nitrate (NO_3), potassium (K), and water uptake rates were measured. Nitrate and K uptake rates were subject to large diurnal variation with maximum uptake rates occurring during the day period. Two peaks of diurnal uptake rates were identified, one large peak during the day period and a second much smaller one during the first 2-4 hours of the night. Under the conditions of the experiment, night nutrition made up 35 to 40% of the total daily uptake of K and NO_3. Water uptake rates followed a diurnal oscillation with a single peak pattern. Highest rates occurred at the middle of the photoperiod and lowest rates were measured at night. Over the entire day and night cycle there was no correlation between the rates of water and nutrient uptake. This may be of importance in the fertilization of hydroponically grown plants since in horticultural practice nutrients and water are supplied together in quantities large enough to meet plant water demand but not nutrient requirements.

INTRODUCTION

Current knowledge of diurnal variation in nutrient uptake by plants is still very sketchy. Studies on diurnal uptake of K and NO_3 have been made on monocotyledons (3,6,12,15,16,19) but are rare for dicotyledons in particular for tomato. Several authors have described a simple pattern of NO_3 and K uptake with highest uptake rates reached during the day period followed by a constant decline

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to minimum rates occurring during the night or early morning (3,6,9,15,20). A more complex rhythm with two peaks of uptake rates, one occurring during the day and another one during the night period has been reported for *Zea rmays* for K and NO_3 by Pan et al. (19) and for *Lolium rmultiflorum* for NO_3 by Hansen (12). For spinach grown under low light intensities and long night periods, Steingrover et al. (23) described maximum NO_3 uptake rates during the night period.

In horticultural practice where tomatoes are grown hydroponically, nutrient solution is supplied according to plant water demand. Computerized measurements of solar radiation and subsequent calculations of evapotranspiration monitor the rate of water and nutrient delivery. As a consequence of this system, nutrient supply is limited or completely absent during the night when water uptake and radiation are low. This regular practice can be questioned in view of the high nutrient uptake rates occurring during the night that have been described by the above authors. The lack of information about the short term nutritional needs of plants means that it is difficult to adjust nutrient supply to plant demand for hydroponically grown crops. Problems such as increased salinity (electro-conductivity) or drifts in composition of the nutrient solutions may thus occur especially when climatic conditions favour high plant water uptake.

This paper reports the results of an experiment to investigate diurnal uptake of nutrients by vegetative tomato plants in relation to plant water demand. Results are presented for the two ions taken up in largest quantities, K and NO_3 and which are essential for yield production in tomato.

MATERIAL AND METHODS

Growing Units: the NFT System: Plants were cultivated in growing units using a Nutrient Film Technique (NFT) system. Each growing unit consisted of 3 interconnecting sections, namely troughs, container and pump (Diagram 1). Details of these sections are as follows:

1. **Troughs:** a series of 2 troughs made out of PVC was positioned on a gentle slope (3-5%) so that the nutrient solution flowed under the influence of gravity.
2. **Container:** a plastic container holding 10 litres of nutrient solution was located beneath the troughs in order to collect the flowing nutrient solution.

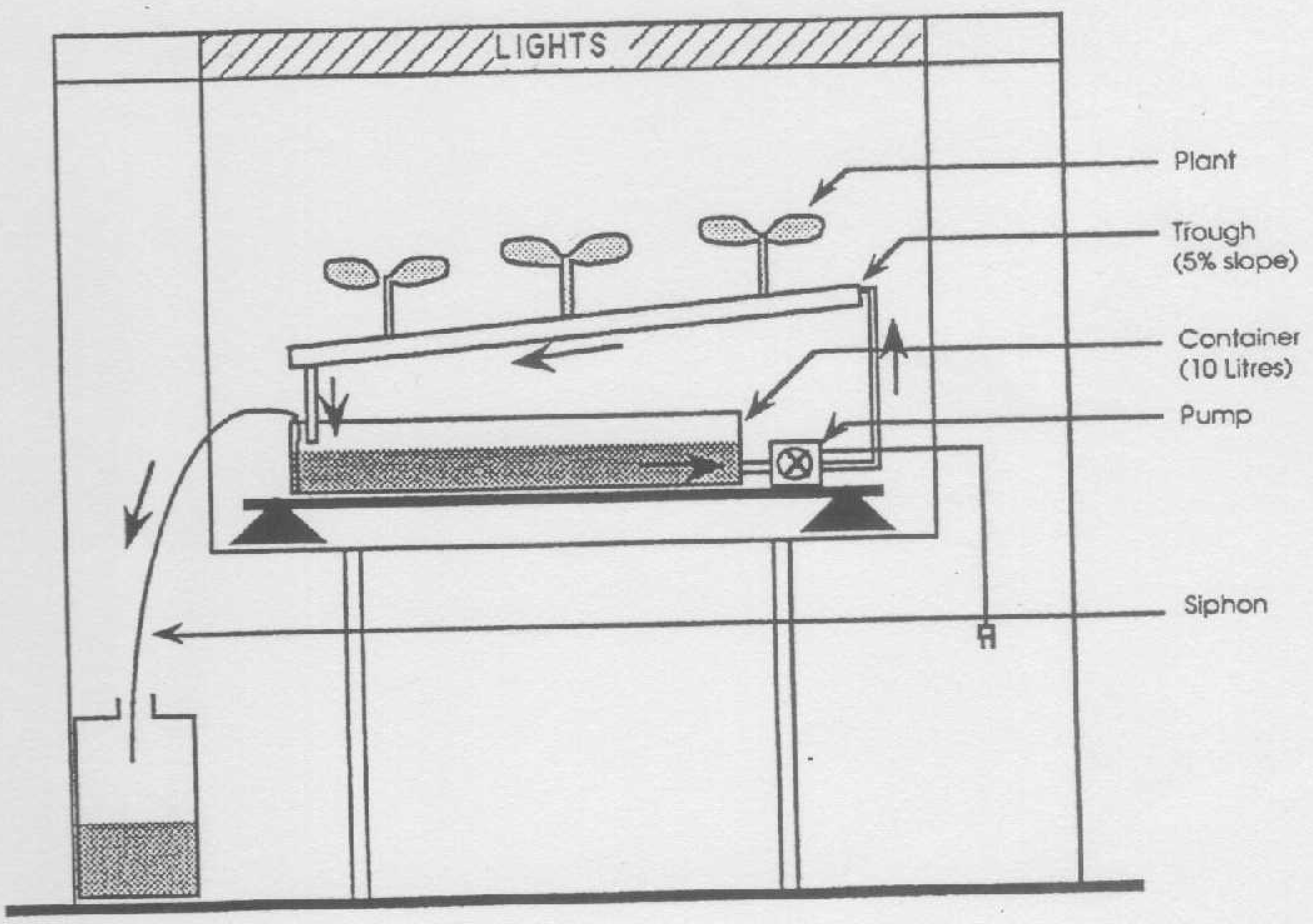

DIAGRAM 1. Schematic Representation of the Nutrient Film Technique (NFT) System.

3. **Pump:** a pump running continuously with a constant flow rate of 1 litre per minute raised the nutrient solution from the container to the head of each of the troughs. Since more than one trough was connected to the pump, a 3-way junction was used to distribute the solution to the troughs. Care was taken so that equal flow rates were obtained along each of the troughs.

The dimensions of the growth units used were calculated so as to fit in an O'Gorman controlled environment cabinet (21) with an internal growth cabinet of about 1.37 m x 1.37 m x 1.16 m high dimensions, allowing a 1.87 m^2 surface to grow the plants. Light levels were expected to lessen with ageing of the fluorescent tubes but were of the order of 620 $\mu E/m^2/s$ in the centre of the cabinet. Day and night periods were set to an equal length of time of 12 hours. Air temperature inside the cabinet was maintained constant at 25°C both day and night.

The choice of a size of volume (10 L) of nutrient solution was made for two reasons. In the first place, measurements of changes in a volume of this capacity could be made conveniently and accurately. Secondly this volume of nutrient solution was large enough to provide an adequate supply of nutrients between changes of solution. Nutrient uptake was monitored every 12 hours. Under conditions of rapid rates of nutrient depletion because of high plant demand, additional nutrient supplies were provided from a stock solution. This was achieved by means of a peristaltic pump set to an appropriate constant flow rate or by the use of a system the same as that used in hospitals for drop-feeding patients. When nutrient uptake rates were monitored every 2 hours, this additional supply of nutrients was done manually.

Each trough held 9 plants and 2 troughs were connected to the same pump via a 3-way junction, the third outlet pipe (return to the tank) being used to control the flow rate of the nutrient solution to 1 litre per trough per minute to ensure that the composition of the solution was not altered to any extent as it passed over the roots (1).

Plant Cultivation: Tomato plants (*Lycopersicon esculentum* Mill.) of the F_1 hybrid variety "Turbo" were grown from seed in a peat-perlite mixture and allowed to grow for 16 days in a greenhouse after germination. Seventy-two plants were then chosen and set up in a flowing nutrient system (time 0 of the experiment). Plants were selected by weight and ranged between 0.32 and 0.50 g. Four independent sets each of 18 plants were cultivated using the nutrient solution (see below). Plants were allowed an establishment period of 9 days during which the nutrient solutions were changed every two days. After that period, nutrient solutions were renewed twice daily. Nutrient uptake rates (K and NO_3-N) were monitored at the change of solutions every 12 hours at the end of each light and dark period throughout the rest of the experiment that lasted for 22 days. At the onset of day 16, however, K and NO_3-N uptake rates were measured every two hours over a 26 hour period ("short term measurements"). Observations were made on the 4 sets of plants to give 4 replicate measurements of diurnal variation of ion uptake rates by the plants. Similar measurements were again made at the onset of day 20 when, for two replicate sets of plants only, the uptake rates of the ions were measured every two hours throughout a period of 72 hours (from day 20 to 22, "long term measurements"). A summary of the plan of the experiment is given in Diagram 2.

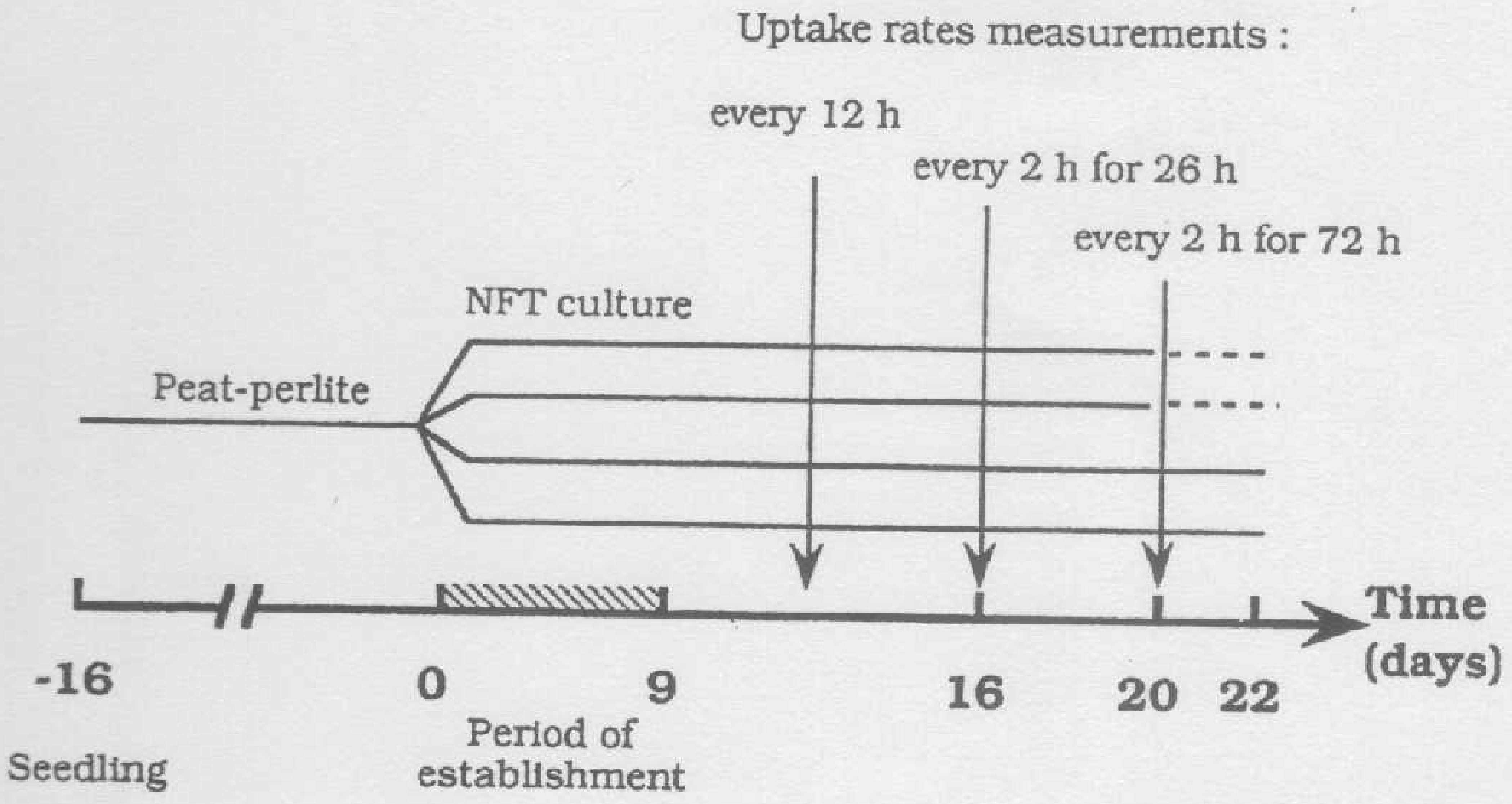

DIAGRAM 2. Summary of the Plan of the Experiment.

Nutrient Solution: Deionized water was used to make up the nutrient solution at the following concentrations: $Ca(NO_3)_2$, 2 mM; K_2SO_4, 0.5 mM; $Ca(H_2PO_4)_2$, 0.5 mM and $MgSO_4$, 1 mM. A full micronutrient solution provided: Fe-Na-EDTA, 50 µM; $MnSO_4$, 10 µM; H_3BO_3, 29.6 µM; $ZnSO_4$, 0.65 µM; $CuSO_4$, 0.95 µM; and Na_2MoO_4, 0.52 µM. The nutrient solution was prepared daily from individual stock solutions 1000 times [or 100 in the case of $Ca(H_2PO_4)_2$] concentrated. To control the pH of the nutrient solution to the required value (pH 5.5-6.0), a saturated freshly filtered solution of $Ca(OH)_2$ was added to the medium.

Sampling Procedure and Analytical Methods: In order to measure nutrient depletion, the following procedure was adopted: every two hours the pumps were stopped and the nutrient solution drained from the container into a second container by the means of a siphon (this step took about 5 minutes). The volume of solution was then measured by weighing using a 10 kg balance. An aliquot sample (20 mL) was taken for subsequent analysis and the remaining solution was poured back into the NFT container before switching on the pumps again. This procedure ensured that the plants remained undisturbed during the measurements.

In the aliquot sample, potassium concentration was determined by flame photometry and NO_3-N was measured by UV spectrophotometry (2) thus allowing the quantities of nutrient taken up by the plant between two successive measurements to be calculated and nutrient uptake rates established.

RESULTS

During the 9 day period of establishment after transplanting into the NFT system, extensive root development took place with uniform plant growth throughout the 4 populations of plants.

Short Term Measurements (26 hours): The rate of water uptake showed a diurnal rhythm (Fig. 1). During the light period, uptake rates gradually increased to maxima levels at the middle of the day (hours 4 to 8). Thereafter they declined slightly. With the onset of the dark period, uptake rates decreased sharply to lowest values at the middle of the night. These values were about 60% lower than the day maxima. The amplitude of variations in water uptake rates during the entire dark period was very limited. At the beginning of the following day period, uptake rates increased rapidly to a level similar to that measured 24 hours before. Similar values for diurnal variation in rates of water uptake were observed for the 4 sets of plants (see error bars). Of the daily water uptake, 32% was taken-up during the night (Table 1).

Diurnal variation in the uptake rates of K is shown in Figure 2. From the beginning of the day period, uptake rates increased two fold to reach maxima values towards the middle of the day after which they declined gradually until the end of the photoperiod. With the onset of the dark period, uptake rates of K increased significantly for the first 2 hours. A sharp decline was then measured for a further 4 hours when minima values were recorded. These were 70% lower than the day maxima. Uptake rates increased slightly at the end of the dark period to reach similar values as those measured 24 hours previously. From these measurements it was calculated that 63% of the K was taken up during the day and 37% at night (Table 1).

Nitrate uptake rates also followed a marked diurnal pattern (Fig. 2). As for potassium, two peaks of NO_3 uptake rates were measured which were concurrent with those of K. During the day, nitrate uptake rates increased by 50% to reach maxima values at the middle of the photoperiod after which they decreased until the end of the day. During the first hours of the night, NO_3-uptake rates increased

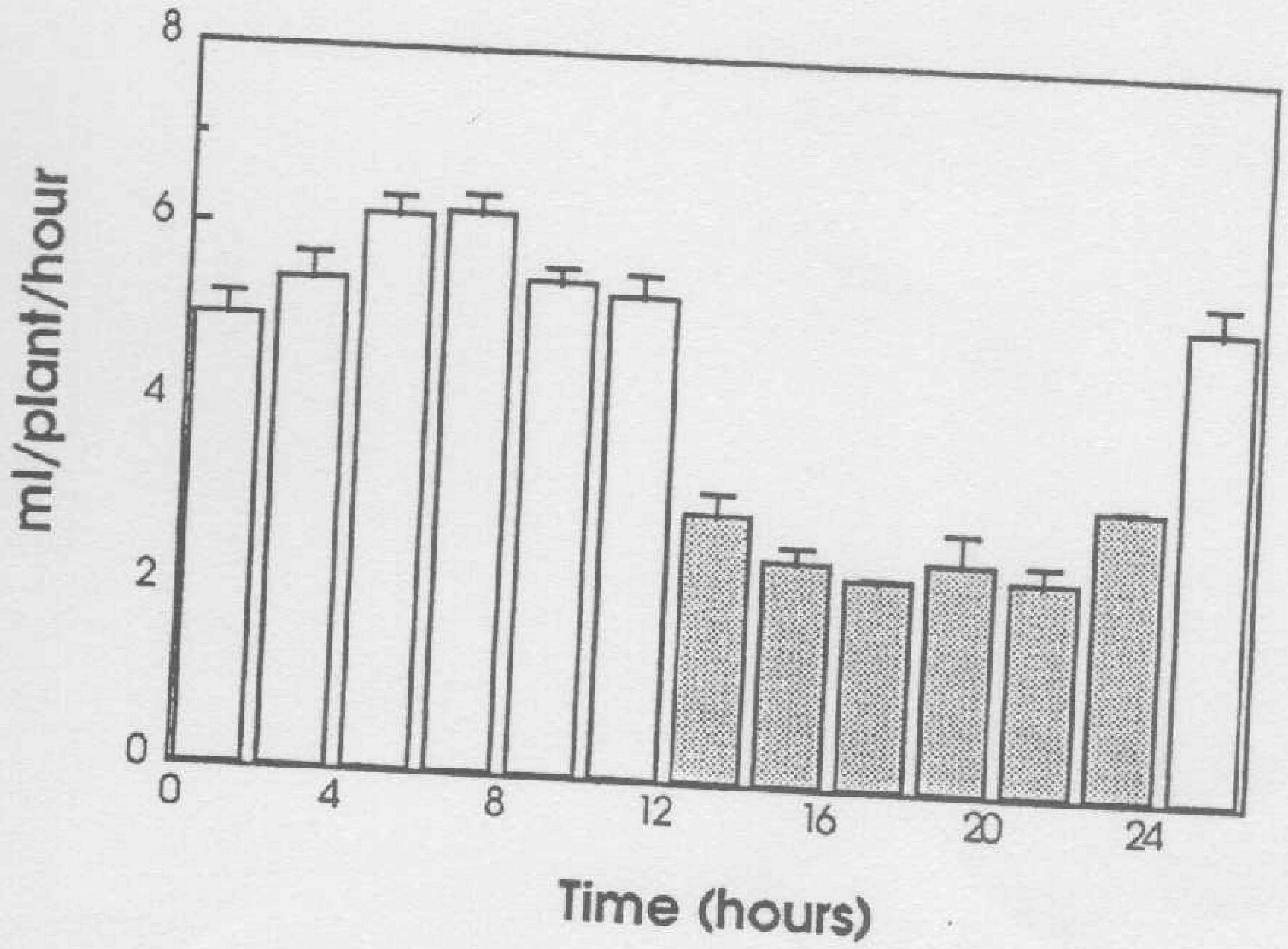

FIGURE 1. Diurnal Variation in the Rate of Uptake of Water During a Day/Night Cycle. The Values are Expressed as ml of Water Taken up per Plant per Hour. Bars are Standard Errors of Means (n=4 replicates). The Night Period is Indicated by the Shading.

TABLE 1. Water and Nutrient Uptakes (NO_3 and K) Over the 24 hours of Day 16 of the Experiment. Also Given is the Relative Contribution of Each Period to the Daily Uptake.

	Water uptake (ml. plant^{-1})	**NO_3 uptake**	**K uptake**	**NO_3 : K ratio**
		(mmol. plant $^{-1}$)		
Day period	67.1 (68%)	0.69 (59%)	0.41 (63%)	1.7
Night period	31.8 (32%)	0.48 (41%)	0.24 (37%)	2.0
Daily total	**98.9**	**1.17**	**0.65**	

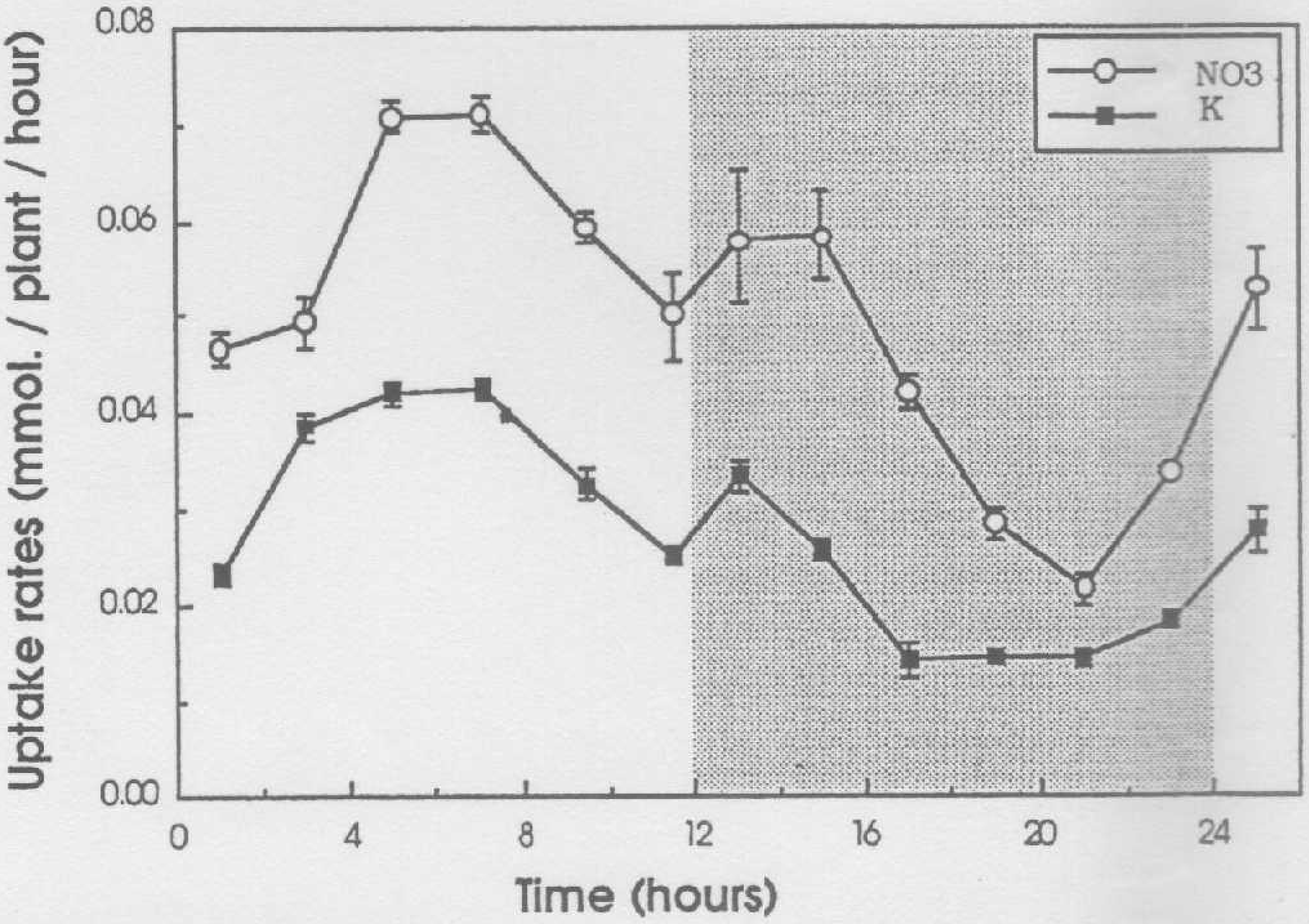

FIGURE 2. Uptake Rates of Potassium and Nitrate During a 26 Hour Period. Results are Expressed as mmol.plant^{-1}.hour^{-1}. Values are the Means of 4 Replicates. Error Bars are Associated With the Means When Greater than the Symbols. The Night Period is Indicated by the Shading.

slightly and then fell to minima levels which were 60 to 70 % lower than day maxima. With the onset of the light period NO_3-uptake rates reached values similar to those observed 24 hours previously. 59% of the NO_3 was taken up during the day and 41% during the night (Table 1). Over the 24 hour period, the uptake of NO_3 was considerably higher than that of K as expressed in terms of ion charge. The ratio of NO_3 to K taken up varied during the day and night cycle, being larger during the night period (Table l).

Long Term Measurements (72 hours): Water uptake showed regular diurnal variation over the 72 hour period (Fig. 3). Uptake rates were higher during the day than during the night. Water uptake increased rapidly when the lights were switched on with maxima uptake rates being reached at the middle of the photoperiod. Thereafter uptake rates declined. Uptake rates were lowest during the

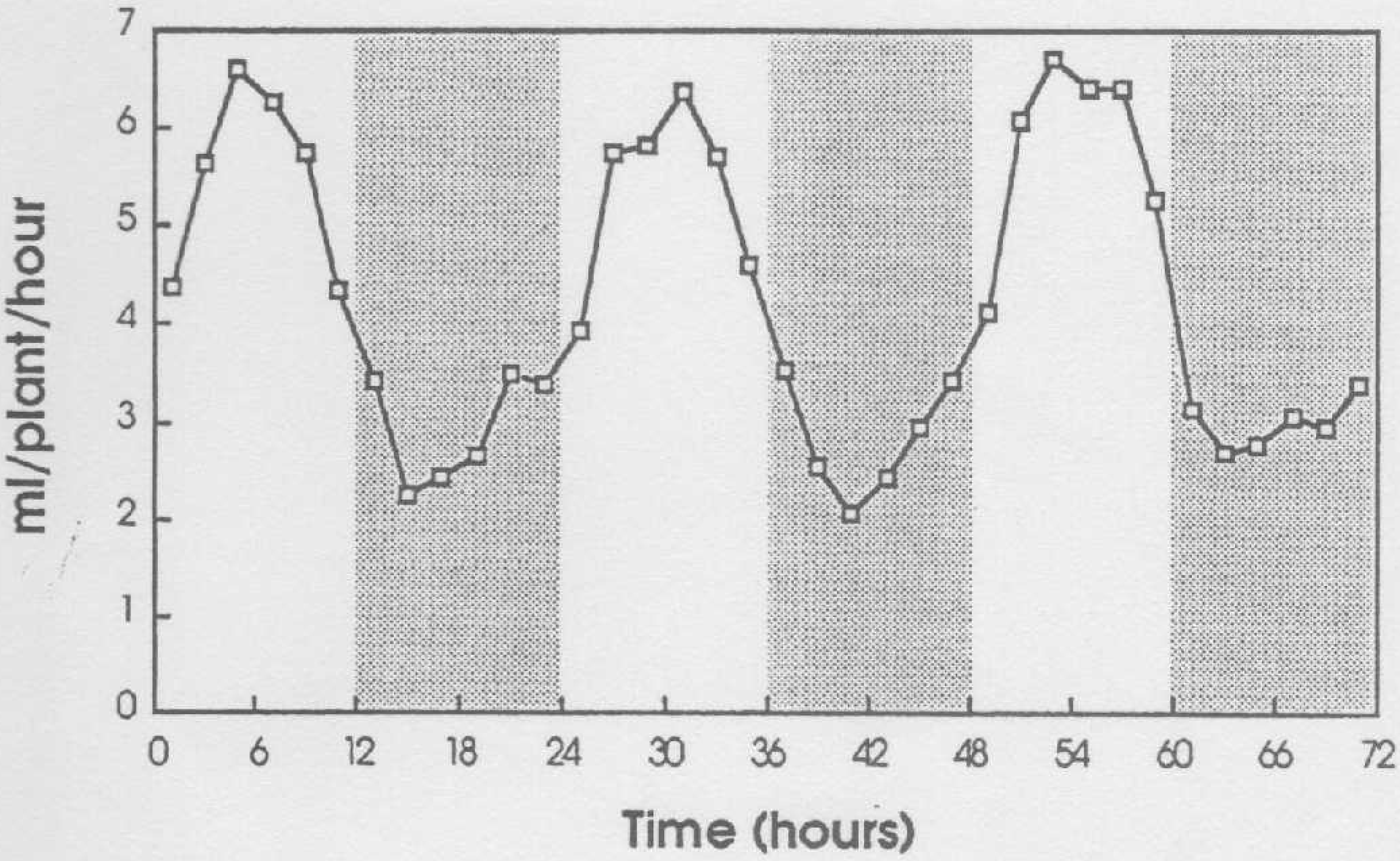

FIGURE 3. Diurnal Variations in Water Uptake Rates as Measured over 72 hours. The Night Periods are Indicated by the Shading. Results are the Mean Water Uptake Rates of Two Sets of Plants.

night period but started to increase before the onset of the light period. During the whole day and night cycle, a single peak of uptake was measured during the day period as was previously observed in Figure 1. This single peak pattern of water uptake was consistently reproduced every day during this series of measurements. Table 2 summarizes water uptake data collected over the 72 hour period. Plant water demand was about 2 fold higher during the day than during the night. Surprisingly plant water demand did not increase significantly over the three days of these observations even though the plants were growing rapidly.

Diurnal variation in potassium and nitrate uptake rates were calculated from the depletion curves obtained over the 72 hour period. In order to avoid a total nutrient depletion, additional supply of K_2SO_4 was made manually during the day periods (Fig. 4).

For K (Fig. 5), uptake rates were consistent with the dual peak pattern previously described. Uptake rates varied widely with time. A 2- to 2.4-fold increase occurred over the early part of the day to reach maxima levels at the

TABLE 2. Water Uptake Data for Days 20-22 of the Experiment. Also Given are the Relative Contribution of Each Period to the Daily Water Uptake.

	Day 20	**Day 21** (ml. plant^{-1})	**Day 22**
Day period	66.0 (65%)	64.6 (66%)	69.9 (66%)
Night period	35.3 (35%)	33.9 (34%)	35.9 (34%)
Daily total	**101.3**	**98.5**	**105.8**

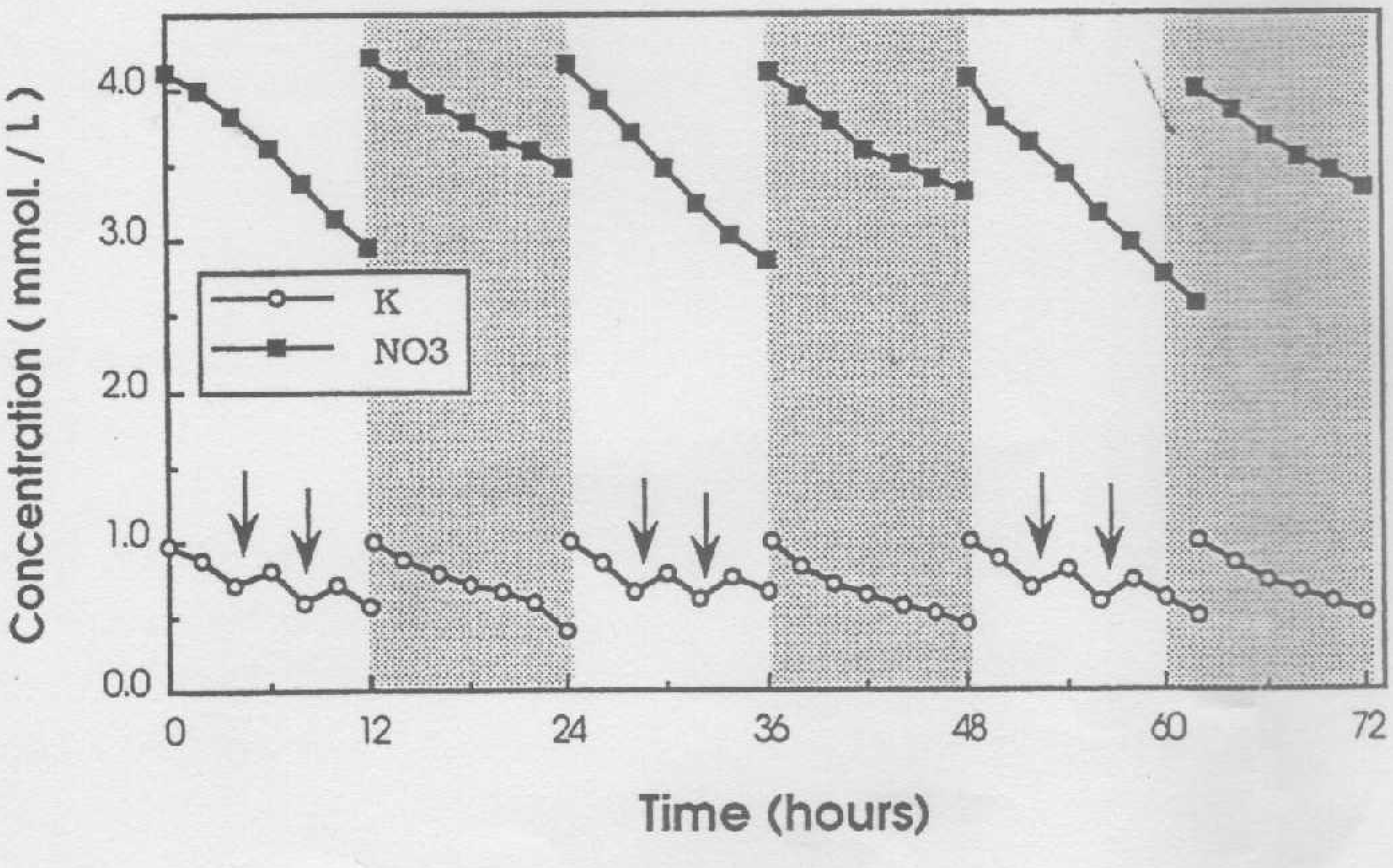

FIGURE 4. Average Changes in K and NO3 Concentrations (mM) in the Nutrient Solution over the 72 Hour Period of Measurement. The Arrows Indicate When Additional Supply of K_2SO_4 has been Made Manually in the Solution. The Nutrient Medium was Replenished Every 12 hours.

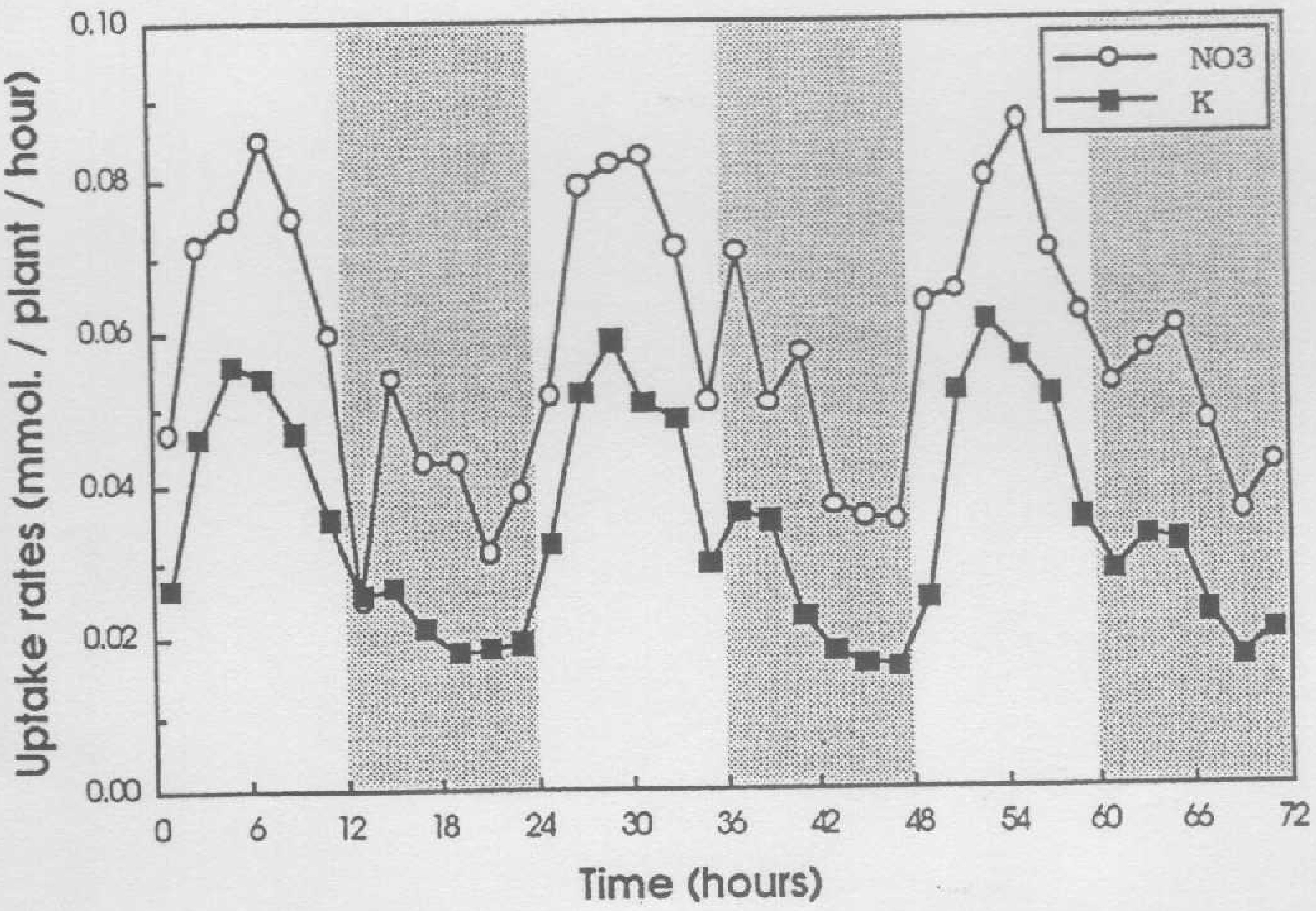

FIGURE 5. Uptake Rates of Nitrate and Potassium During a 72 hour Period. Results are Expressed as mmol. plant^{-1}hour^{-1}. Measurement Were Made Between Day 20 and 22. Each Point is the Mean Value From 2 Sets of Plants.

middle of the photoperiod. These high uptake rates were followed by a sharp decline until the end of the day period. A small increase then occurred again over a short period of time at the early part of the night period. Thereafter uptake rates declined to minima values which were about 30% of the day maxima. These rates remained low until the beginning of the next day period after which the cycle was repeated. In this series of measurements there was no clear increase in potassium uptake rates at the end of the night period before the lights came on, as described in Figure 2. The night potassium uptake consistently represented about 35% of the total daily uptake (Table 3). This value is similar to previous observations (Table 1).

The dual peak pattern of diurnal variation in NO_3-uptake rates was successfully measured over long periods of time (Fig. 5). Measurements, however, were not as regular as those for K. The low uptake rate value measured

TABLE 3. Daily Uptake of Potassium for Days 20-22. The Relative Contribution of Each Period to the Total Daily Uptake is Also Given.

	Day 20	**Day 21** (mmol. plant^{-1})	**Day 22**
Day period	0.53 (67%)	0.55 (65%)	0.56 (64%)
Night period	0.26 (33%)	0.29 (35%)	0.31 (36%)
Daily total	**0.79**	**0.84**	**0.87**

at time 13 hours may be accounted for by an experimental error in sampling. During the day period, uptake rates increased steadily to reach maxima values towards the middle of the photoperiod and then declined throughout the rest of the day. Following the onset of the dark period, NO_3-uptake rates rose sharply during the first 2-4 hours after which they declined again and became minima at the end of the night. These minima values were 60-65% lower than day maxima uptake rates. Results of uptake values over day and night periods are given in Table 4. From the table it can be seen that the night contribution to daily nitrate uptake was about 40%, this value being similar to that previously observed (Table 1).

The ratio between NO_3 and K uptake rates was not constant during the day and the night periods but tended to vary according to day and night oscillations, being higher at night as can be seen from Figure 6. This observation corroborates the findings presented in Table 1.

DISCUSSION

Diurnal variations in nutrient uptake rates were measured throughout day 16. These data clearly indicate that potassium and nitrate uptake rates varied widely with time and followed a complex rhythm. Under the conditions of the experiment two peaks of nutrient uptake were identified, one large peak of uptake occurring at the middle of the photoperiod and a second peak at the beginning of the night

TABLE 4. Daily Uptake of Nitrate During Days 20-22. Also Given is the Relative Contribution of Each Period to the Daily Nitrate Uptake.

	Day 20	**Day 21** (mmol. plant^{-1})	**Day 22**
Day period	0.83 (64%)	0.83 (59%)	0.86 (59%)
Night period	0.47 (36%)	0.57 (41%)	0.59 (41%)
Daily total	**1.30**	**1.40**	**1.45**

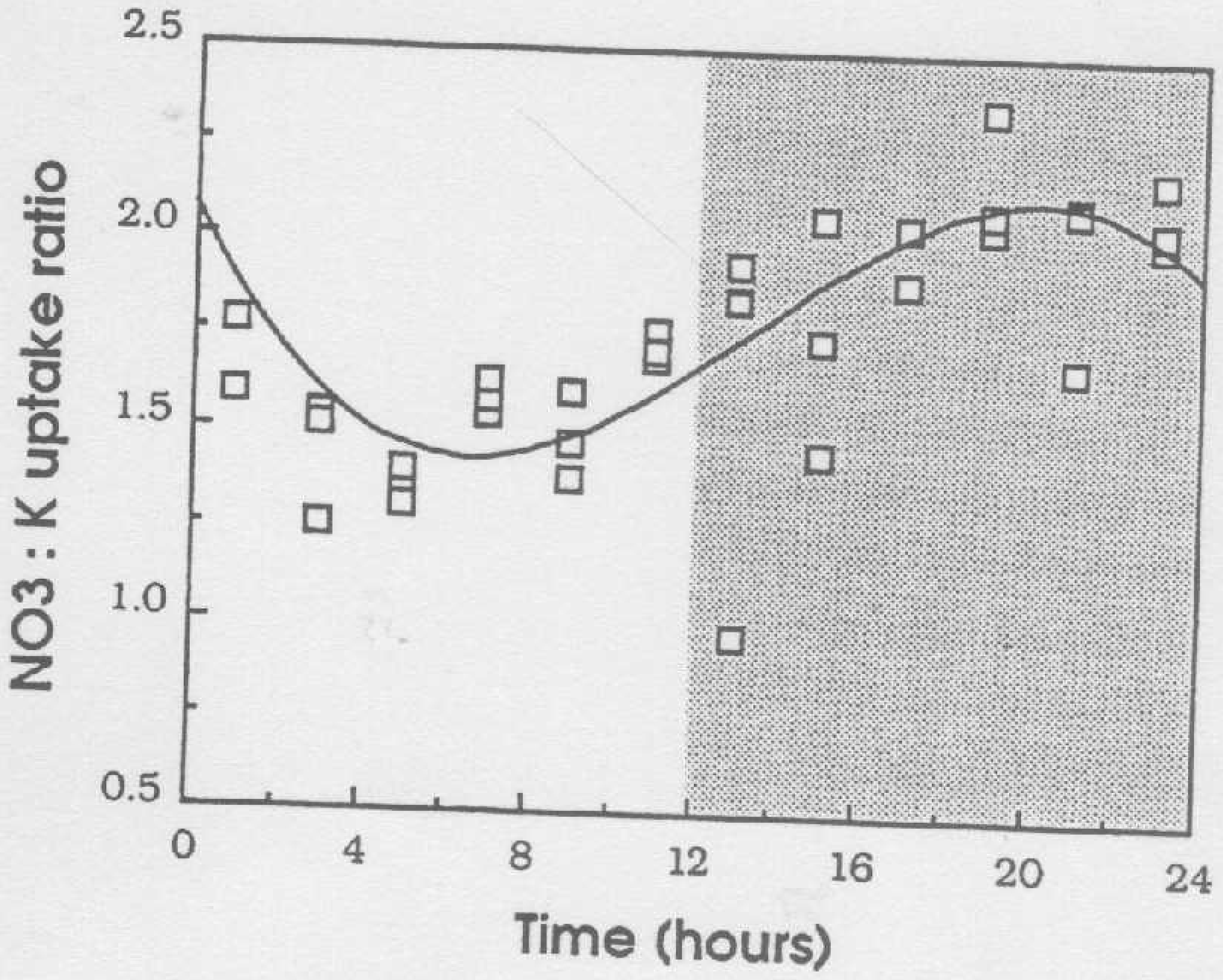

FIGURE 6. Day and Night Oscillations in the Ratio Between NO3 and K Uptake Rates. Values Plotted Here have been Obtained From the Three Days of Measurements.

period. These observations were initially made over a 26 hour period (Fig. 2) and were confirmed later over a much larger time span (*i.e.* 72 hours, Fig. 5). The diurnal oscillations in K and NO_3 uptake rates proved to be reproducible and were observed in other experiments (data not presented here). The importance of night nutrition can be seen from the data collected both over day 16 (Table 1) and days 20-22 (Tables 3 and 4) since between 35 to 40% of the daily NO_3 and K uptake took place during the night periods. The contribution of uptake at night to the total daily uptake seems to be fairly constant and was of the same magnitude in the early part of the experiment as in other of our experiments (data not shown). Such findings stress the fact that plants may have important nutritional needs during the dark periods and that this should be considered in the practice of fertilization of hydroponic cultures.

The reason for the diurnal variation in nutrient uptake is not clear. Rates of absorption of inorganic nutrients by roots of intact plants and in particular those of anions appear to be dependent upon a continuous supply of carbohydrates from the shoots (10) although the observed diurnal variations are not necessarily the direct consequence of variations in carbohydrates supply. Non-structural carbohydrates (mainly hexoses) [or eventually under particular conditions amino-acids, fatty acids and organic acids] are used for root respiration and degraded ultimately to form ATP as an energy source available for plant metabolism. It seems logical, therefore, to relate nutrient uptake to photosynthesis via the catabolic degradation of carbohydrates during root respiration. In experiments using *Zea mays* grown in water culture, Frossard (7) was able to demonstrate that photosynthesis is the driving force for the diurnal rhythm of root respiration. Unfortunately few authors have studied the two processes of root respiration and nutrient uptake simultaneously and there is a need for further investigation into the relationship between available carbohydrate sources in the roots and ion uptake, especially nitrate uptake.

It must be borne in mind that the energy cost of ion uptake is minute in comparison with that of other metabolic processes (4). Whether available energy is the limiting factor for ion acquisition by plants as described above, therefore, remains an open question. It has been established for some time that net NO_3 uptake is the result of rapid influx and efflux across the plasmamembrane (17), and Clarkson (5) has suggested that efflux could be the fine control for net NO_3 uptake. Scaife (22) proposed a pump/leak/buffer model which takes into account

NO_3 influx (pump), efflux (leak) and the rate of N removal from the plant NO_3 pool (buffer) to simulate diurnal variation in net NO_3 uptake rates. This model is based on the assumption that influx is constant throughout the day and night cycle while efflux varies according to the difference between internal and external NO_3 concentrations. The NO_3 pool of the plant is depleted for reduction and protein synthesis depending on the rate of photosynthesis and therefore the needs of the plant to maintain a high growth rate. Using this model, Scaife (22) was successful in simulating the diurnal variation in net NO_3-uptake rates of *Lolium perenne* as reported by Clement et at. (6), including the lag phase between maximum photosynthesis and maximum net NO_3-uptake rate.

Since photosynthesis is the most likely driving force for nutrient uptake, it offers an explanation for the single peak pattern of diurnal variation in nutrient uptake rates described by several authors (6,9,13,15,20). The existence of a more complex rhythm of nutrient uptake rates (dual peak pattern) described by other authors (12,19) and reported in this paper for tomato plants remains to be explained. For *Lolium multiforum*, Hansen (12) reported two peaks of nitrate uptake in phase with two diurnal peaks of root respiration. Supporting this finding, diurnal oscillations in root respiration following a dual peak pattern have been reported by several authors (8,11,14,16,18) and may account for the two peaks of nutrient uptake that we and others have observed (12,19). According to the findings of Pan et at. (19) the existence of a night peak of uptake is a genotypic property of the cultivar tested. This explanation may also account for the discrepancies in the patterns of diurnal ion uptake rates that have been reported in the literature.

The possibility that the night peak is of an artefactual nature should not be completely ruled out. Firstly, a single peak pattern of ion uptake has generally been observed with experiments conducted in greenhouses while dual peak uptake has been reported in growth chamber experiments in which the artificial light regime fails to simulate the natural diurnal variation in solar radiation. Secondly, results have been obtained from nutrient solution depletion studies (see Fig. 4) in which it is difficult to maintain a constant ionic environment at the root surface and nutrient depletion may become a limiting factor in ion uptake. For the tomato plants, in a parallel experiment which we conducted and in which nutrient solutions were completely renewed every two hours over 24 hours, only one peak of K- and NO_3-uptake rates could be identified (data not shown). Despite the absence of a night peak, however, the relative contribution of night nutrition to the total daily NO_3 and K uptake remained high (34 and 23%, respectively).

For both K and NO_3, marked day and night oscillation in uptake was observed. For K (Tables 1 and 3), day uptake was about two fold greater than night uptake but the contribution of the night to the daily potassium uptake was constant throughout the experiment at about 35%. In the nutrient medium the concentration of potassium was relatively low as compared to that of NO_3 (1 mM vs. 4 mM). As the experiment proceeded nutrient uptake increased. There was no evidence, however, that the plants were deprived of K since after day 14, an additional supply of K was made to the nutrient solution (Fig. 4). As for K, uptake of NO_3 during the day was larger than that during the night and the contribution of the night to the daily uptake was found constant at about 40% (Tables 1 and 4).

Plant water uptake may have been slightly overestimated during the experiment since no account was taken of possible water evaporation from the NFT system. Such a water loss would be expected to be relatively small, however, and the rate of loss more or less constant because of the stable climatic conditions in the growth room. It may be assumed therefore that the results were not affected by water evaporation, especially the relative proportion of day and night to daily water uptake. The day and night oscillations in water uptake with high uptake during the day and low at night (Fig. 1, Table 1) is not surprising since water uptake closely follows plant transpiration and thus stomatal movement which is directly dependent on light and dark regimes. Good positive correlations were found for the day periods between K- or NO_3-uptake rates and water uptake rates but interestingly there was no correlation between the same factors during the night periods. Several authors have reported that over the entire day and night cycle, nutrient uptake is not directly correlated with water uptake (9,12,16,19,24) and the results from this experiment support this idea. Since in horticultural practice, nutrient supply is monitored according to plant water demand, there is a need to investigate further the relationships between transpiration and nutrient uptake and the agricultural significance of the uptake of K and NO_3 at night which is independent of transpiration.

ACKNOWLEDGEMENTS

The authors wish to express their appreciations to Dr. G. A. Alloush and Mr. H.

Heuwinkel for their valuable help and stimulating discussions during the experimental work. The NFT system was prepared by Mr. S. Predine from INRA Antibes (France).

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