

# Mixed Nitrogen Nutrition and Productivity of Wheat Grown in Hydroponics

J. A. HEBERER and F. E. BELOW\*

Department of Agronomy, University of Illinois, 1102 South Goodwin Ave., Urbana, IL 61801, USA

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## ABSTRACT

The objective of this study was to study the effects of nitrogen (N) supplied as either mixtures of  $\text{NO}_3$  and  $\text{NH}_4$  or as all  $\text{NO}_3$  on the final yield of spring wheat. Two separate greenhouse experiments evaluated the durum spring wheat (*Triticum durum* L.) cultivar 'Inbar' in 1986, and the hard red spring wheat (*Triticum aestivum* L.) cultivar 'Len' in 1987. Nitrogen treatments consisted of all  $\text{NO}_3$  or mixtures (75/25 or 50/50) of  $\text{NO}_3$  and  $\text{NH}_4$ . At maturity, plants were harvested, separated into leaves, stems, roots, and grain, and each part analysed for dry matter and chemical composition.

Compared to plants receiving only  $\text{NO}_3$  as the source of N, mixed N nutrition resulted in greater accumulation of whole plant reduced-N (49 to 108% more), phosphorus (38 to 69% more), and potassium (25% more) for both cultivars. In all cases, plants produced higher grain yields (28% for Len to 78% for Inbar) when grown with mixed N nutrition than with only  $\text{NO}_3$ . The yield increase was not associated with heavier grains or more grains per ear, but rather with an increase in the number of ear-bearing tillers per plant. For both cultivars, the higher yields with mixed N resulted from the production of more total biomass (36 to 76%) as the partitioning of dry matter between plant parts was not altered by N treatment. Under the hydroponic conditions of this experiment, the utilization of both  $\text{NO}_3$  and  $\text{NH}_4$  resulted in greater growth, nutrient absorption, and yield than  $\text{NO}_3$  alone, which was primarily associated with an enhancement in tiller development.

Key words: *Triticum aestivum* L., *Triticum durum* L., spring wheat, hydroponics, ammonium nutrition, nitrate nutrition, tillering, yield components, partitioning.

## INTRODUCTION

Nitrogen is unique among the essential mineral elements in that plants can utilize it in both anionic ( $\text{NO}_3$ ) or cationic ( $\text{NH}_4$ ) forms. Although most crop species can grow on either form, it has been well-documented that supplying plants with mixtures of  $\text{NO}_3$  and  $\text{NH}_4$  often results in better vegetative growth and enhanced nutrient accumulation than either form separately (Haynes and Goh, 1978; Hageman, 1984). Due to the difficulty in maintaining specific N ratios in soils much of this evidence has been obtained by growing plants hydroponically. This necessity arises because in warm, well-aerated soils microorganisms readily convert  $\text{NH}_4$  to  $\text{NO}_3$  (nitrification) making all, or high,  $\text{NH}_4$  systems nearly impossible to achieve. However, the use of ammoniacal fertilizers along with nitrification inhibitors may result in more of a mixed N (i.e. both  $\text{NO}_3$  and  $\text{NH}_4$ ) diet than is normally available to plant roots. Therefore,

hydroponic experiments comparing all  $\text{NO}_3$  nutrition to mixed N (up to 50%  $\text{NH}_4$ ) may have some validity with regard to possible production conditions.

For young wheat (*Triticum aestivum* L.) plants grown in solution culture, Weissman (1951) reported that d. wt, total protein content, and protein concentration were all higher in leaves of plants grown on  $\text{NH}_4$  plus  $\text{NO}_3$  than on either form alone. Similarly, Cox and Reisenauer (1973) observed a 74% increase in vegetative d. wt of 16-d-old wheat plants when  $\text{NH}_4$  was supplied as 17% of the total N, as compared to plants grown with only  $\text{NO}_3$ . Comparing various  $\text{NO}_3/\text{NH}_4$  ratios to all  $\text{NO}_3$ , Gashaw and Mugwira (1981) reported that 31-d-old wheat, rye (*Secale cereale* L.), and triticale (*Triticosecale*, Wittmack) plants were all heavier when grown with N mixtures containing 25 or 50%  $\text{NH}_4$  than when grown with 100%  $\text{NO}_3$ .

Although results of these studies indicate that vegetative growth of wheat is enhanced when both  $\text{NO}_3$  and  $\text{NH}_4$  are present, the effects of such

\* For correspondence.

treatments on final productivity are less certain as in none of the above examples were the plants grown to maturity. Therefore, the objective of this study was to compare the effect of mixtures of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  to solely  $\text{NO}_3^-$  on grain yield and yield components, and on the final accumulation and partitioning of biomass, reduced N, phosphorus, and potassium for hydroponically grown wheat.

## MATERIALS AND METHODS

### Cultural Procedures

Experiments were conducted in the greenhouse in the winter of 1986 and 1987 to test the effects of form and ratio of N on two species of spring wheat. In 1986, durum spring wheat plants (*Triticum durum* cv. Inbar) were grown to maturity in solution culture hydroponics. In 1987, a hard red spring wheat variety (cv. Len) was grown to maturity under similar conditions. Seed was sown on 11 January and 23 January in 1986 and 1987, respectively. Natural lighting was supplemented with metal halide lamps (approx.  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  between 400 and 700 nm wavelength at the canopy surface) to provide 14 h of illumination. Greenhouse temperatures were maintained at  $24^\circ\text{C}$  during the photoperiod and  $18^\circ\text{C}$  during the dark. Under these conditions, colour and morphological development of hydroponically-grown plants were similar to field-grown plants. In 1986, the N treatments consisted of three ratios of  $\text{NO}_3^-$ -N to  $\text{NH}_4^+$ -N: 100/0, 75/25, and 50/50. In 1987, only the 100/0 and 50/50 treatments were tested. In both years, treatments were arranged in a randomized complete block design with five hydroponic vessels for each treatment.

Vessels were 7 litre polyethylene pots painted black and covered with aluminum foil and arranged so that each occupied  $0.212 \text{ m}^2$  of bench. The concentration of nutrients of full strength solution for each of the treatment solutions are shown in Table 1. In these solutions, S, K, Ca, and Mg were all allowed to vary (largest fluctuation in S) in order to achieve the best possible balance between the ion concentrations. This problem results from the difference in charges of the  $\text{NO}_3^-$  and  $\text{NH}_4^+$  ions, and from limitations in the number of mineral salt combinations that are suitable for preparing nutrient solutions. Iron was added daily as ferrous sulphate to maintain the Fe level at  $105 \mu\text{M}$  ( $1.5 \text{ ml pot}^{-1}$  of  $0.03 \text{ M FeSO}_4$ ) (Hageman *et al.*, 1961). A full complement of micronutrients (Cu, Zn, B, and Mo) was included at concentrations according to Hoagland and Arnon (1950), except for Mn which was four times higher.

For aeration and pH control of the solution an ion exchange column was added to each culture

TABLE 1. The concentration of macronutrient ions (mM) in the nutrient solutions used to evaluate the effect of mixtures of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  vs.  $\text{NO}_3^-$  alone on the growth of spring wheat under hydroponic conditions

Element	$\text{NO}_3^-$ -N/ $\text{NH}_4^+$ -N (ratio)		
	100/0	75/25	50/50
N ( $\text{NO}_3^-$ )	8.86	6.71	4.43
N ( $\text{NH}_4^+$ )	0	2.21	4.43
P	0.97	0.97	0.97
K	4.09	3.58	3.07
Mg	1.97	1.81	1.64
Ca	2.99	2.50	2.00
S	2.09	2.93	4.74

vessel that continuously recirculated the solution. This column was loaded with 75 ml of the appropriate (approx. 3:1) mixture of  $\text{H}^+$  and  $\text{Ca}^{2+}$  forms of Amberlite IRC 50 cation exchange resin to maintain a pH of  $5.5 \pm 0.5$  (Harper and Nicholas, 1976). When the solution pH deviated more than 0.5 unit from 5.5 the exchange column was replaced.

Six seeds per vessel were germinated directly into one-quarter strength treatment solution (Table 1) by the use of a 'collar-seed-wick' assemblage inserted into holes (1.5 cm) on the perimeter of the culture vessel lid. The collar-wick system involved inclosing the seed within a collar (a 3 cm section of plastic tubing cut lengthwise and filled with vermiculite) which was connected to a wick made of 8 cm of cotton string inserted in the overlap of the collar. The wick wetted the vermiculite which supplied the imbibing seed with water. The moisture level of the seed was controlled by adjusting the solution level in the culture vessel. This technique allowed for undisturbed growth of the newly emergent radicle and resulted in excellent seedling uniformity.

Five days after emergence (DAE), when the majority of radicles had penetrated the solution surface, the wicks between the collar and the solution were removed. The solution level was adjusted so that roots were sufficiently submerged to absorb water, while maintaining the proper moisture status of the seed crown. Two days later the plants were thinned to four uniform plants per pot, giving a stand density equivalent to 125 plants  $\text{m}^{-2}$ . Following germination on 25% of full strength solution, the nutrient ion concentration was increased according to the following schedule: 50% at 25 DAE, 60% at 30 DAE, 70% at 40 DAE, 85% at 45 DAE, and 100% at 50 DAE.

TABLE 2. The effect of mixtures of  $\text{NO}_3$  and  $\text{NH}_4$  vs.  $\text{NO}_3$  alone on grain yield and yield components for two cultivars of spring wheat grown in hydroponics

Cultivar	$\text{NO}_3\text{-N}/\text{NH}_4\text{-N}$ (ratio)	Grain yield ( $\text{g m}^{-2}$ )	Grain weight (mg)	Grain no. spike <sup>-1</sup>	Ear no. $\text{m}^{-2}$
Inbar	100/0	386	49	28	283
	75/25	688	52	30	434
	50/50	646	51	29	434
	LSD	47	NS	NS	40
Len	100/0	494	40	31	396
	50/50	631	40	28	566
	LSD	60	NS	NS	70

LSD, least significant difference at  $P < 0.05$ ; NS, not significant.

Between intervals, the concentrations of  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$  in solution were monitored and the complete nutrient solution changed when the concentration of either ion fell below one-half of its initial level.

#### Sampling and Analysis

Physiological maturity (estimated visually by complete loss of green colour from glumes) occurred at 134 and 111 DAE for plants in 1986 and 1987, respectively. At physiological maturity, plants were harvested, divided into leaves, stems, roots, and heads and each part dried to constant weight at 80 °C in a forced-draft oven (Heberer, Below and Hageman, 1985). Dried heads were threshed, the chaff discarded, and the grain re-dried as above. Dried samples were weighed, mechanically ground to pass a 2 mm screen and used for chemical analysis. For each plant fraction, tissue was analysed for total N,  $\text{NO}_3\text{-N}$ , phosphorus, and potassium as described previously (Heberer *et al.*, 1985). Reduced N was determined by subtracting the  $\text{NO}_3\text{-N}$  concentration from the total-N concentration. Whole plant constituents were obtained by summing the values for the plant parts. Data from each experiment were analysed separately by analysis of variance procedures and the least significant difference ( $P \leq 0.05$ ) was calculated for parameters exhibiting a significant N form effect.

#### RESULTS

For hydroponically-grown plants of both cultivars, N mixtures resulted in significantly higher grain yield compared to plants grown with all  $\text{NO}_3$  (Table 2). For both cultivars, the increase in grain yield was primarily the result of an increased number of ear bearing tillers, as N treatment had no significant effect on grain number per ear or

individual grain weight for either cultivar (Table 2). When grown with mixed N, Inbar plants produced 53% more (both treatments), and Len plants 43% more tillers than  $\text{NO}_3$  grown plants. This difference in tillering was evident as early as 20 DAE and was markedly noticeable by 30 DAE (Fig. 1).

Plants receiving an equal mixture of  $\text{NO}_3$  and  $\text{NH}_4$  produced 36% (Len) to 76% (Inbar) more whole plant dry matter by physiological maturity than  $\text{NO}_3$  grown plants (Table 3). Compared to  $\text{NO}_3$  grown plants, mixed N nutrition increased whole plant reduced N content of Inbar plants by 100 (50/50 treatment) to 108% (75/25 treatment) and phosphorus content by 69% (Table 3). For Len plants, the mixed N treatment increased whole plant reduced N, phosphorus, and potassium contents by 49, 38, and 25%, respectively.

The various N treatments had no effect on the final distribution of dry matter among the various plant parts for either cultivar (Table 4). Because Inbar plants produced substantial amounts of barren vegetation (6 to 9% of the total dry matter), the partitioning of dry matter to the grain was less than for Len plants. The accumulation of total plant reduced N differed in response to N treatment and the distribution of this N to the various plant parts was also altered (Table 4). With Inbar, growth on N mixtures resulted in increased partitioning of reduced N to the leaves (100 to 160%) and stems (66%), decreased (10%) allocation to the grain, and had no effect on partitioning to the roots. For Len plants, only the reduced N accumulated in the stems increased as a function of mixed N (50%), while the N partitioned to the grain decreased (9%). Barren culms produced by Inbar plants contained from 15 to 19% of the whole plant reduced N at maturity and may have acted as an alternate sink for N that was not needed to support grain development. In contrast,

TABLE 3. The effect of mixtures of  $\text{NO}_3$  and  $\text{NH}_4$  vs.  $\text{NO}_3$  alone on accumulation of whole plant dry matter, reduced N, phosphorus, and potassium at physiological maturity for two cultivars of spring wheat grown in hydroponics

Cultivar	$\text{NO}_3\text{-N}/\text{NH}_4\text{-N}$ (ratio)	Dry† matter ( $\text{g m}^{-2}$ )	Reduced N ( $\text{g m}^{-2}$ )	Phosphorus ( $\text{g m}^{-2}$ )	Potassium ( $\text{g m}^{-2}$ )
Inbar	100/0	899	22.1	6.5	—
	75/25	1611	46.0	11.1	—
	50/50	1585	44.4	11.0	—
	LSD	130	3.9	0.6	—
Len	100/0	1240	25.9	7.3	31.9
	50/50	1683	38.6	10.1	39.9
	LSD	150	3.8	0.7	6.4

LSD, least significant difference at  $P < 0.05$ .

† Includes chaff for dry matter only.



100/0

75/25

50/50

FIG. 1. Tillering response of the durum spring wheat cultivar 'Inbar' at 30 d after emergence when grown in hydroponics with N as only  $\text{NO}_3$  (100/0) or as mixtures (75/25 and 50/50) of  $\text{NO}_3$  and  $\text{NH}_4$ .

for Len plants, which did not produce barren vegetation, the roots appeared to act as the storage reservoir for excess reduced N as they contained 24% (compared to approx. 6% for Inbar) of the whole plant reduced N at maturity (Table 4).

The distribution of whole plant phosphorus among the various plant parts was also altered by N treatment, with both cultivars exhibiting similar responses (Table 4). Compared to  $\text{NO}_3$  grown plants, growth on mixed N resulted in decreased phosphorus (37%) allocation to the roots, greater

(33 to 58%) partitioning to the leaves, and had no effect on partitioning to the stems or grain. Similar to the distribution of reduced N, Len plants partitioned substantially more of their whole plant phosphorus to the roots than did Inbar (approx. three times more) which appeared to be related to the production of barren culms by Inbar plants.

Growth on N mixtures resulted in an alteration in partitioning of potassium between leaves and stems (more in leaves and less in stems) but had no effect on potassium partitioning to roots or grain

TABLE 4. The effect of mixtures of  $\text{NO}_3$  and  $\text{NH}_4$  vs.  $\text{NO}_3$  alone on partitioning of dry matter, reduced N, phosphorus, and potassium among plant parts at physiological maturity for two cultivars of spring wheat grown in hydroponics

Cultivar	$\text{NO}_3\text{-N}/\text{NH}_4\text{-N}$ (ratio)	Plant part†				
		Leaves	Stems	Roots	Grain	Barren culms
Dry Matter (% of total)						
Inbar	100/0	9	20	7	43	9
	75/25	12	20	5	43	9
	50/50	13	20	8	41	6
	LSD	NS	NS	NS	NS	NS
Len	100/0	10	23	10	40	—
	50/50	11	23	11	39	—
	LSD	NS	NS	NS	NS	—
Reduced N (% of total)						
Inbar	100/0	5	6	7	62	19
	75/25	10	10	5	56	19
	50/50	13	10	6	56	15
	LSD	4	3	NS	5	NS
Len	100/0	10	8	24	58	—
	50/50	11	12	24	53	—
	LSD	NS	3	NS	4	—
Phosphorus (% of total)						
Inbar	100/0	18	24	11	33	14
	75/25	24	23	8	33	12
	50/50	27	24	8	31	10
	LSD	4	NS	3	NS	NS
Len	100/0	12	19	30	39	—
	50/50	19	22	22	37	—
	LSD	5	NS	6	NS	—
Potassium (% of total)						
Len	100/0	14	60	17	9	—
	50/50	20	54	17	9	—
	LSD	4	5	NS	NS	—

LSD, least significant difference at  $P < 0.05$ ; NS, not significant.

† Percentage of dry matter present in chaff not shown.

(Table 4). Unlike reduced N and phosphorus, the majority of whole plant potassium was partitioned to the stems and the smallest proportion was partitioned to the grain.

#### DISCUSSION

Although mixed N nutrition resulted in higher grain yields and more total biomass than  $\text{NO}_3$  grown plants, the magnitude of these increases differed between the two wheat species. For the durum spring wheat cultivar Inbar, grain yield was increased 67% (50/50) to 78% (75/25) by the  $\text{NO}_3/\text{NH}_4$  treatments, while for the hard red spring wheat cultivar Len, the 50/50 mixture increased yield by only 36% (Table 2). Similarly, mixed N nutrition increased total biomass pro-

duction of Inbar by 78% (average of both treatments) compared to 36% for Len (Table 3). This difference between the cultivars in response to mixed N nutrition appears to be associated with variation in their ability to utilize  $\text{NO}_3$ , because Len produced 27% more grain yield and 36% more total biomass than Inbar when grown with only  $\text{NO}_3$ . In contrast, grain yield and biomass production of both cultivars was similar when grown with mixed N (Tables 2 and 3).

For both cultivars, the N treatments did not alter the partitioning of dry matter among the various plant parts (Table 4) which indicates that the additional biomass resulting from mixed N nutrition (Table 3) was wholly responsible for the increase in grain yields (Table 2). In addition, the higher grain yield of both cultivars with mixed N

s not due to heavier grains or more grains per ear, but rather was the result of an increase in the number of ear bearing tillers per plant (Table 2). Similar mixed-N induced increases in vegetative tillering, and grain yield, have been reported for rice (*Oryza sativa* L.) grown in solution culture (Lori *et al.*, 1985) and spring wheat grown in soil (Bock, 1987; Leyshon, Campbell, and Warder, 1980). Because the tillering difference in our study is visually, and markedly, apparent by 30 DAE (Fig. 1) this observation suggests that the yield enhancing effect of mixed N nutrition may occur early in the plant's life cycle.

Although the physiological basis for the increased tillering with mixed N nutrition is not entirely clear, additional N accumulation may be at least partially responsible. Under field conditions, N availability is known to be related to an enhancement in tiller development and survival (Power and Alessi 1978; Roy and Gallagher, 1984; Hertz and DeVos, 1983). In hydroponics, growth of mixed N increased the whole plant reduced N content (49% for Len up to 109% for Inbar) and concentration (9% for Len up to 16% for Inbar) of both cultivars compared to all  $\text{NO}_3$  plants (Table 3). These increases are similar to those previously reported for vegetative wheat plants (Cox and Reisenauer, 1973; Gashaw and Mugwira, 1981; Weissman, 1951) and suggests that when grown with only  $\text{NO}_3$  wheat may be unable to acquire sufficient N for maximum tiller development and yield.

Alternatively, because  $\text{NO}_3$  requires reduction, while  $\text{NH}_4$  can be assimilated directly, a potential energy savings could be realized by plants obtaining a large portion of their total N as  $\text{NH}_4$  (Salsac *et al.*, 1987). In addition, because the  $\text{NH}_4$  ion must be assimilated in the root, while  $\text{NO}_3$  can be assimilated in either the root or the shoot (Haynes and Goh, 1978; Hageman, 1984), an alteration in vegetative assimilate partitioning may also be responsible for the differences in growth. Thus, the mixed N induced increase in tillering and yield may be only indirectly related to enhanced N accumulation.

Some support for this view is apparent in our data, where, for both cultivars, the proportional increases in tiller number and yield resulting from mixed N nutrition were lower than the corresponding increases in N accumulation (Tables 2 and 3). In addition, compared to  $\text{NO}_3$  grown plants, both cultivars partitioned a greater proportion of their accumulated N to vegetative plant parts and a lesser proportion to the grain when grown with mixed N (Table 4). This data indicates that plants exposed to a continuous supply of  $\text{NH}_4$  along with  $\text{NO}_3$  can accumulate more N than is

needed to achieve maximum yields. However, because  $\text{NH}_4$  was still available after completion of tillering we do not know if it resulted in additional N accumulation which was not coupled to tiller development. If this suggestion is true it raises the possibility that  $\text{NH}_4$  may not need to be available for the wheat plant's entire life cycle in order to increase growth and yield.

Although mixed N nutrition increased the total accumulation of phosphorus for both cultivars, and potassium for Len, we do not believe these increases are directly responsible for the improved growth and yield. This conclusion is based on the finding that the overall concentrations of these constituents were similar to, or lower than, those in  $\text{NO}_3$  grown plants (Table 3). Furthermore, while mixed N nutrition did alter the distribution of phosphorus and potassium between the vegetative plant parts, it did not influence the proportion present in the grain (Table 4).

For Inbar plants, the lack of significant difference between the 75/25 and the 50/50  $\text{NO}_3/\text{NH}_4$  treatments for any of the parameters measured suggests that the absolute ratio of  $\text{NO}_3$  to  $\text{NH}_4$  is not as important as is the availability of some  $\text{NH}_4$ . This finding has important implications for using mixed N nutrition to improve wheat productivity as specific  $\text{NO}_3/\text{NH}_4$  ratios would be much more difficult to obtain in the field. However, under the hydroponic conditions of this experiment, each of the N forms was freely available throughout the plant's life cycle. Because this situation is difficult to achieve in soils, much additional research is needed before the potential improvements in wheat yields from mixed N nutrition can be readily attained under production conditions.

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#### LITERATURE CITED

- BOCK, B. R., 1987. Increases in maximum yield of spring wheat by maintaining relatively high ammonium/nitrate ratios in soil. *Journal of Fertilizer Issues* 4, 68-72.
- COX, W. J. and REISENAUER, H. M., 1973. Growth and ion uptake by wheat seedlings supplied nitrogen as

- nitrate, or ammonium, or both. *Plant and Soil* **38**, 363–80.
- GASHAW, L. and MUGWIRA, L. M., 1981. Ammonium-N and nitrate-N effects on growth and mineral composition of triticale, wheat, and rye. *Agronomy Journal* **73**, 47–51.
- HAGEMAN, R. H., 1984. Ammonium versus nitrate nutrition of higher plants, pp. 67–85. In *Nitrogen in Crop Production*, ed. R. D. Hauck, 804 pp. American Society of Agronomy, Madison, WI.
- FLESHER, D., WABOL, J. J. and STORCK, D. H., 1961. An improved nutrient culture technique for growing corn under greenhouse conditions. *Agronomy Journal* **53**, 175–80.
- HARPER, J. E. and NICHOLAS, J. C., 1976. Control of nutrient solution pH with an ion-exchange system: effect on soybean nodulation. *Physiologia Plantarum* **38**, 24–8.
- HAYNES, R. J. and GOH, K. M., 1978. Ammonium and nitrate nutrition of plants. *Biological Reviews* **53**, 465–510.
- HEBERER, J. A., BELOW, F. E. and HAGEMAN, R. H., 1985. Drying method effect on leaf chemical constituents of four crop species. *Crop Science* **25**, 1117–9.
- HOAGLAND, D. R. and ARNON, D. I., 1950. The water culture method for growing plants without soil. *California Agriculture Experiment Station Circular* **347**.
- LEYSHON, A. J., CAMPBELL, C. A. and WARDER, F. G., 1980. Comparison of the effect of  $\text{NO}_3^-$  and  $\text{NH}_4^+$ -N on growth, yield, and yield components of Manitou spring wheat and Conquest barley. *Canadian Journal of Plant Science* **60**, 1063–70.
- MORI, S., UCHINO, H., SAGO, F., SUZUKI, S. and NISHIKAWA, A., 1985. Alleviation effect of arginine on artificially reduced grain yield of  $\text{NH}_4^+$ - or  $\text{NO}_3^-$ -fed rice. *Soil Science and Plant Nutrition* **31**, 55–67.
- POWER, J. F. and ALESSI, J., 1978. Tiller development and yield of standard and semidwarf spring wheat varieties as affected by nitrogen fertilizer. *Journal of Agricultural Science, Cambridge* **90**, 97–108.
- ROY, S. K. and GALLAGHER, J. N., 1984. Production and survival of wheat tillers in relation to plant growth and development, pp. 59–67. In *Wheat Growth and Modelling*, eds W. Day and R. K. Atkin, 407 pp. NATO ASI Series, Volume 86, Plenum Publishing Corporation, New York and London.
- SALSAC, L., CHAILLOU, S., MOROT-GAUDRY, J. F., LE-SAINT, C. and JOLIVET, E., 1987. Nitrate and ammonium nutrition in plants. *Plant Physiology and Biochemistry* **25**, 805–12.
- SPIERTZ, J. H. J. and DEVOS, N. M., 1983. Agronomical and physiological aspects of the role of nitrogen in yield formation of cereals. *Plant and Soil* **75**, 379–91.
- WEISSMAN, G. S. 1951. Nitrogen metabolism of wheat seedlings as influenced by the ammonium:nitrate ratio and the hydrogen ion concentration. *American Journal of Botany* **38**, 162–74.