Effects of light intensity on nitrogen economy of spring barley (*Hordeum distichum* L.)

J. ELLEN & H. VAN OENE

Department of Field Crops and Grassland Science, Wageningen Agricultural University, Haarweg 333, 6709 RZ Wageningen, Netherlands

Received 20 December 1988; accepted 10 April 1989

Abstract

A pot experiment with spring barley, cv. Trumpf, was conducted in a phytotron. After spikelet initiation, three light intensities were applied: 6.50, 4.33 and 1.86 MJ m⁻². During the experiment, each pot (15 plants per pot) received 2016 mg N. The three light intensities hardly affected nutrogen uptake. For example, for the highest and lowest light levels the mean uptake was 102 and 114 mg N per plant on day 57, and 86 and 94 mg N per plant at the final harvest. Light intensity strongly increased DM yield per plant, and as a consequence raised the efficiency of nitrogen use at final harvest from 101 mg DM per mg N in the low light intensity to 175 mg DM per mg N in the high light intensity. Higher light intensity accelerated leaf senescence and shortened the photosynthetically active period by restricting the nitrogen concentration. The distribution of nitrogen over the various plant parts was slightly affected; the nitrogen harvest index was reduced at the lowest radiation. For grain yields with adequate N content, the supplied amount of nitrogen was probably too small.

Keywords: nitrogen uptake, nitrogen harvest index, dry matter production, radiation, spring barley

Introduction

The efficiency of nitrogen use as a ratio between dry matter yield and nitrogen yield, expressed as dry matter production per unit N, depends on supply of nitrogen and nitrogen recovery (Spiertz, 1980). The rate of leaf-photosynthesis largely depends on the nitrogen content in the leaves (Groot & Spiertz, 1989; Evans, 1983). For dry matter production the N content of the leaves need not be high, but the maintenance of a critical N content is important (Spiertz & Ellen, 1978).

A high level of solar radiation with ample supply of water and nitrogen results in high rates of crop photosynthesis and, as a consequence, high dry matter yields can be achieved (Spiertz & Allen, 1978). However, nitrogen yield and crop yield often differ between years, depending on growing conditions (Dilz et al., 1982).

In field experiments with spring barley, high dry matter production per unit N was found in a year with high, and a considerably lower dry matter production per unit N in a year with low radiation per unit ground area (J. Ellen, unpubl.).

J. ELLEN AND H. VAN OENE

In this paper the effects of different light intensities on N uptake, dry matter production and efficiency of N use of barley plants given equal applications of nitrogen will be presented and discussed.

Methods

The set-up of the experiment and the growing conditions were as described in an earlier publication (Ellen & van Oene, 1989). They will be summarized briefly here.

A pot experiment with spring barley, cv. Trumpf, was conducted in a phytotron. Three light intensities were applied: 6.50 (L1), 4.33 (L2) and 1.86 (L3) MJ m⁻² during 14 hours a day (these light quantities are synonymous with 129 (L1), 86 (L2) and 37 (L3) W m⁻², respectively (Ellen & van Oene, 1989)). From emergence (= day 0) until day 40, all plants were grown at the same light intensity of 6.50 MJ m^{-2} . On day 40 the different light intensities were established. The accumulated amounts of radiation during the total period of growth for L1, L2 and L3 were 936, 710 and 454 MJ m⁻², respectively.

Pots were filled with 5.25 kg clay soil and 20 seeds were sown per pot. Five days after emergence, the pots were thinned to 15 plants per pot. The pots were placed in saucers and the plants were watered daily. Water, and with that N, could not run to waste.

Mineral nutrients were supplied in three equal portions, dissolved in water, two days before emergence (GS 0) and on the 26th (GS 30) and 48th day (GS 35) after emergence (growth stages (GS) after Zadoks et al., 1974). The total nitrogen dressing was 2016 mg per pot (= 134 mg N per plant); this quantity was based on the expectation of about five shoots per plant with an average N uptake of about 17 mg per shoot. Too much N promotes secondary growth of tillers. The mineral nitrogen in the clay soil in the pots was not measured.

Before the different light intensities were applied, three pots were harvested per week. After day 40, two pots per treatment were harvested weekly. On day 144, by which time all plants were ripe for harvest, five pots per treatment were harvested as final harvest. The plants were dried and weighed per organ. Replications were pooled per plant organ for analysis of total nitrogen (N-Kjehldahl).

Results

The total N content in the leaves of the main stem and the total N yield and the N uptake at different light intensities are presented in Fig. 1 and Table 1. The effect of the second (day 26) and third (day 48) N application is clearly demonstrated in a rise of N content and N uptake. About two days after N application there was a strong increase of nitrogen in the plants (Fig. 1B). Before the third application the plants showed no visual and no real N deficit (Fig. 1A). It is not known why the amount of N in the plant fell from day 29 until day 43. The highest nitrogen amount was found on day 57 (Table 1) at the growth stages 41, 37 and 36 for L1, L2 and L3 plants, respectively. The differences in N yield among the light intensities were



Fig. 1. A. N content in the green leaves of the main stem (MS) until day 78 at 6.50 (L1), 4.33 (L2) and 1.86 (L3) MJ m⁻², respectively; day 144 is N content in dead leaves. B. Amounts of N (mg) in the aboveground parts of the plant and in the roots (mg per plant) during the pre-floral period of growth and at final harvest at L1, L2 and L3, respectively. Arrows show times of N applications after emergence.

Netherlands Journal of Agricultural Science 37 (1989)

J. ELLEN AND H. VAN OENE

Light intensity da		N amount (mg per plant)												
		total		roots		stems		green leaves		dead leaves		ears1		
	day	57	144	57	144	57	144	57	144	57	144	144		
L1		102	86	14	6	38	12	43	_	7	8	60		
L2		104	85	12	5	41	11	45	-	6	8	61		
L3		114	94	11	5	44	17	51	-	8	15	57		

Table 1. Distribution of nitrogen amount (in mg per plant) over various parts of the plant. Time of highest N uptake (day 57) and N uptake at final harvest (day 144) at 6.50 (L1), 4.33 (L2) and 1.86 (L3) MJ m^{-2} , respectively.

¹ Chaff plus kernels.

small, with N yield being somewhat larger in the lowest light intensity (Fig. 1). On day 57, about 80 % of the N supplied had been taken up by the crop at each light intensity. At final harvest (day 144), the proportions of the amount of nitrogen present on day 57 in L1, L2 and L3 plants were 84 %, 82 % and 82 %, respectively (some uptake of mineral nitrogen from the soil is possible).

Total dry matter production per plant, including roots, and grain production, was associated with differences in light intensities (Table 2). On day 144 the dry matter production calculated per mg N was 42 % higher in L1 than in L3 plants. So, substantially more dry matter per mg N was produced in L1 plants (Table 2).

The N content of the grains was low in all three light intensities (Table 2), especially in L1 and L2 plants.

The amount of N in the kernels, however, was about the same in all three light intensities: 55, 57 and 53 mg per plant for L1, L2 and L3 plants, respectively.

The nitrogen harvest index (NHI), calculated as the ratio of the amount of N in the grains and in the total above-ground parts of the plants at final harvest, was low. Less light (L3) resulted in a lower N harvest index (Table 2).

Dry matter production and number of days of green leaf area (LA) related to

Table 2. Dry matter (DM) yield (inclusive roots) and grain yield in g per plant, nitrogen yield (N)	in mg
per plant (inclusive roots), nitrogen use efficiency (inclusive roots), nitrogen content in the grains	s, and
nitrogen harvest index (exclusive roots) at 6.50 (L1), 4.33 (L2) and 1.86 (L3) MJ m ^{-2} .	

Light intensity		Total DM yield (g per plant)	Grain yield (g per plant)	Total N (mg per	l yield r plant)	N use o (mg D	efficiency M per mg N)	N content in the grains (%)	N harvest index
	day	144	144	57	144	57	144	144	144
L1		15.1	6.8	102	86	62	175	0.81	0.69
L2		12.6	6.0	104	85	45	149	0.95	0.71
L3		9.5	3.6	114	94	34	101	1.48	0.60

Netherlands Journal of Agricultural Science 37 (1989)

Light intensity		DM produc (mg per MJ	ction)	Grain production (mg per MJ)	Number of days of green leaf area	
	day	57	144	144		
L1		16.878	16.119	7.265	107	
L2		14.164	17.814	8.442	119	
L3		13.331	20.958	7.936	135	

Table 3. Dry matter (DM) and grain production in mg per MJ, related to 6.50 (L1), 4.33 (L2) and 1.86 (L3) MJ m⁻², respectively, and number of days of green leaf area.

light intensity are given in Table 3. More light resulted in dry matter production being higher on day 57. On day 144, more dry matter per MJ had been produced in L3, caused by more days of green leaf area and adaptation to changed light conditions by a lower specific leaf weight (Ellen & van Oene, 1989) between day 57 and day 144.

Discussion

In this experiment the uptake of nitrogen depended more on the physical limitations than on the physiological age of the plants. This is demonstrated in the equal N uptake at different growth stages (Fig. 1, Table 1). Obviously, production of carbohydrate, necessary for N uptake (Austin et al., 1977) need not to be high, because at low light level few carbohydrates were produced (Ellen & van Oene, 1989), whereas the differences in N uptake between light intensities and allocation to different plant parts were small. Only at low light intensity was somewhat more nitrogen taken up, especially in the leaves.

The decrease in the total amount of N in the plants between maximum uptake and maturity is an often reported phenomenon and many explanations for this loss are put forward (Wetselaar & Farquhar, 1980; Harper et al., 1987). In this experiment, loss of material by decomposition will probably mainly be responsible for the observed loss of N.

The low N contents of the kernels in this experiment combined with the low N harvest indices suggest that the supply of nitrogen for L1 and L2 plants was too small. This suggestion is supported by the high kernel yields (Ellen & van Oene, 1989) obtained under the favourable growing conditions in the phytotron.

The light use efficiency (dry matter production per MJ) was highest at lower light intensity, because the duration of the green leaf area was longer (Table 3).

The results show that light intensity affects the efficiency of nitrogen (Tables 2, 3). At final harvest, the efficiency of nitrogen, defined here as dry matter production per mg nitrogen taken up, was 42 % larger in L1 than in L3 plants. In a pot experiment with spring wheat, Spiertz (1974) also found a higher response in dry matter production at an increase of light intensity, with no differences in nitrogen application. De Vos (1977) found no differences in photosynthesis between winter wheat crops grown at two nitrogen applications during four weeks after anthesis.

J. ELLEN AND H. VAN OENE

Various authors (Groot & Spiertz, 1989; Evans, 1983) report a positive relationship between photosynthesis and leaf nitrogen content. Supply of nitrogen and carbohydrates to the grains are interrelated; during grain growth, nitrogen is withdrawn from the vegetative plant parts, resulting in a decline in leaf-photosynthesis. Plants at high light intensity with a small nitrogen supply have a short period of growth, but a high efficiency (Table 2). Evans (1983) found that a large reduction in nitrogen content per unit leaf area reduced assimilation rate much less, but senescence accelerated. Similar kinds of effects were found in this experiment. Under low light conditions, however, differences in photosynthetic rates caused by different leaf nitrogen contents are not found (Takano & Tsunoda, 1971). Leaf area values per plant were about the same till day 60; on day 78 they were 202, 252 and 301 cm² for L1, L2 and L3 plants, respectively (Ellen & van Oene, 1989). So, the lower efficiency of nitrogen at low light intensity is probably mainly attributable to relatively more N nitrate and less organic N in the plant than at higher light intensities (Felippe et al., 1975). The production of carbohydrates and with that the availability of reductant (NADH) for N assimilation by the nitrate reductase enzyme is too limited to enable more nitrogen to be incorporated into organic compounds (Nicholas et al., 1976; Aslam & Huffaker, 1984).

The highest nitrogen concentrations are found in the photosynthesizing and growing parts of the plant, for cereals this is in the upper leaves (Groot & Spiertz, 1989; Spiertz & Ellen, 1978). This inhomogeneous distribution of nitrogen over the canopy, with high concentrations in the upper leaves and lower concentrations in the lower layers, favours total assimilation. The allocation of nitrogen in a crop, therefore, is almost optimal.

Boosting production of a crop through nitrogen fertilization seems to depend more on a prolonged nitrogen supply (delaying senescence), on the condition that light intensity is high and plants can take up nitrogen, than on a high nitrogen level. An example of this is given by Morgan (1988) for spring wheat. Assimilation rate only increases slowly with leaf nitrogen content; therefore, high N fertilization, which increases leaf area and therefore shading, will offset this effect completely (Evans, 1983). In high-yielding crops, a continued N uptake is generally observed (Spiertz & Ellen, 1978). For high grain yields with adequate nitrogen concentrations, a prolonged nitrogen supply and uptake are required.

Acknowledgements

The authors would like to thank Dr J. H. J. Spiertz and Prof. P. C. Struik for their valuable comments on this manuscript.

References

Aslam, M. & R. C. Huffaker, 1984. Dependence of nitrate reduction on soluble carbohydrates in primary leaves of barley under aerobic conditions. *Plant Physiology* 75: 623-628.

Austin, R. B., M. A. Ford, J. A. Edrich & R. D. Blackwell, 1977. The nitrogen economy of winter wheat. Journal of Agricultural Science (Cambridge) 88: 159-167.

- Dilz, K., A. Darwinkel, R. Boon & L. J. M. Verstraeten, 1982. Intensive wheat production as related to nitrogen fertilization, crop production and soil nitrogen: experience in the Benelux. Proceedings of the Fertilizer Society, London, No 211, p. 93-147.
- Ellen, J. & H. van Oene, 1989. Effects of light intensity on yield components, carbohydrate economy and cell-wall constituents in spring barley (*Hordeum distichum L.*). Netherlands Journal of Agricultural Science 37: 000-000.
- Evans, J. R., 1983. Nitrogen and photosynthesis in the flag leaf of wheat (*Triticum aestivum* L.). Plant Physiology 72: 297-302.
- Felippe, G. N., J. E. Dale & Carol Mariott, 1975. The effects of irradiance on uptake and assimilation of nitrate by young barley seedlings. *Annals of Botany* 39: 43-55.
- Groot, J. J. R. & J. H. J. Spiertz, 1989. Photosynthesis and nitrogen translocation in cereals during grain filling and implications for crop yield. Proceedings International Congress of Plant Physiology, New Delhi (in press).
- Harper, L. A., R. R. Sharpe, G. W. Langdale & J. E. Giddens, 1987. Nitrogen cycling in a wheat crop: soil, plant, and aerial nitrogen transport. *Agronomy* 79: 965-973.
- Nicholas, J. C., J. E. Harper & R. H. Hageman, 1976. Nitrate reductase activity in soybeans (Glycine max (L.) Merr.). II. Energy limitations. Plant Physiology 58: 736-739.
- Morgan, J. A., 1988. Growth and canopy carbon dioxide exchange rate of spring wheat as affected by nitrogen status. Crop Science 28: 95-100.
- Spiertz, J. H. J., 1974. Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size. *Netherlands Journal of Agricultural Science* 22: 207-220.
- Spiertz, J. H. J. & J. Ellen, 1978. Effects of nitrogen on crop development and grain growth of winter wheat in relation to the carbohydrate and nitrogen economy of the wheat plant. *Netherlands Journal* of Agricultural Science 26: 233-249.
- Spiertz, J. H. J., 1980. Grain production of wheat in relation to nitrogen, weather and diseases. In: R. G. Hurd, P. V. Biscoe & C. Dennis (Eds), Opportunities for increasing crop yields, p. 97-113. Pitman Publishing Ltd, London.
- Takano, Y. & S Tsunoda, 1971. Curvilinear regression of the leaf photosynthetic rate on leaf nitrogen content among strains of *Oryza species*. Japanese Journal of Breeding 21: 69-76.
- Vos, N. M. de, 1977. Wheat. In: Th. Alberda (Ed), Crop photosynthesis: methods and compilation of the data obtained with mobile field equipment, p. 22-30. Agricultural Research Reports 865. Pudoc, Wageningen.
- Wetselaar, R. & D. D. Farquhar, 1980. Nitrogen losses from tops of plants. Advances in Agronomy 33: 263-302.
- Zadoks, J. C., T. T. Chang & C. F. Konzak, 1974. A decimal code for growth stages of cereals. Weed Research 14: 415-421.