

Effects of nitrogen on leaf growth of temperate cereals: A review

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Abstract

Under agricultural conditions where soil moisture is adequate, low nitrogen (N) availability is usually the main soil factor limiting the growth and yield of temperate cereals. As the response to additional N is generally substantial, the strategic application of fertilizer N is an important management tool used to increase yields. Nitrogen availability can affect photosynthetic rate per unit leaf area but often the main reason for the large effect of additional N on crop growth is that it increases leaf area per plant and consequently increases leaf area index (leaf area per unit land area): this results in increased crop photosynthesis. This paper reviews recent work on the influence of N on leaf growth of temperate cereals from seed germination through to maturity. New data are presented in order to provide greater understanding of the mechanism of the nitrate effects on 1) mobilization of seed reserves; 2) partitioning of dry matter to leaf, stem and root and 3) expansion of leaves. The effects of additional N on leaf and plant growth are discussed in relation to crop growth in terms of canopy development and grain yield. Areas where further research is required are highlighted.

Additional key words: seed reserve mobilization, nitrate, dry matter partitioning, leaf expansion, cell size, canopy development, grain yield.

Introduction

Under agricultural conditions where soil moisture is adequate, low nitrogen (N) availability is usually the main soil factor limiting the growth and yield of temperate cereals. As the response to additional N is generally substantial, the strategic application of fertilizer N is frequently an important management tool used to increase yields. In New Zealand, barley (*Hordeum vulgare* L.) is the most important cereal in terms of area sown (96,000 ha) and tonnage harvested (435,000 T) (Department of Statistics, 1991). Second to barley is wheat (*Triticum aestivum* L.) which is grown on approximately 40,000 ha with 188,000 T being harvested. Recommended N fertilizer rates for cereal crops in New Zealand depend on the species sown, the N status of the soil and the end use of the crop. Usually, 50 kg N ha⁻¹ applied at sowing is recommended for malting barleys, while up to 100 kg N ha⁻¹, applied at sowing and anthesis, is recommended for high protein bread wheats (Montgomery, 1986a,b). N fertilizer can be added in a range of forms such as urea, calcium ammonium nitrate, ammonium sulphate or a mixture like 'calurea' (calcium nitrate plus urea). However, under temperate agricultural

conditions, rates of nitrification are usually rapid and nitrate (NO₃⁻) is likely to be the dominant form of N available to, and taken up by, temperate cereals in most soils (Haynes *et al.*, 1986). Overall N fertilizer usage in New Zealand is low compared to that in Western Europe, but it has increased steadily over the past decade with nearly 46,000 T being applied in 1991 (FAO, 1992).

Plant dry matter usually contains 1 - 6% N, depending on species, age, plant organ and environmental conditions (Haynes *et al.*, 1986; Mengel and Kirkby, 1987). N is a constituent of many cellular components such as nucleic acids, chlorophyll, proteins, enzymes, cell membranes and cell walls which are vital to the function and growth of plants. Therefore the rate and/or extent of processes that utilise these compounds will be affected by plant N status. Such processes include photosynthesis. Additional N can increase the rate of photosynthesis per unit leaf area by, for example, increasing the concentrations of photosynthetic pigments and enzymes (Lawlor *et al.*, 1987). However, the major influence of additional N on crop growth under agricultural conditions appears to be due to increased total leaf area (Andrews *et al.*, 1991b and references therein). This paper reviews recent work on the

influence of N on leaf growth of temperate cereals. New data are presented to provide greater understanding of the mechanism of the NO_3^- effect on 1) mobilization of seed reserves; 2) partitioning of dry matter to leaf, stem and root and 3) expansion of leaves. The effects of additional N on leaf and plant growth are discussed in relation to crop growth in terms of canopy development and grain yield. Areas where further research is required are highlighted.

Materials and Methods

The new data on the effects of N availability on dry matter partitioning, plant leaf area development, canopy development and crop growth presented in this review were obtained in experiments carried out recently by the authors.

i) Partitioning of dry matter (experiment 1)

Seeds of barley (cv. Triumph; mean weight - 45 mg), obtained from the Canterbury Malting Company, Christchurch, New Zealand, were germinated on paper towels moistened with distilled water. After 4 d, seedlings with a coleoptile length of approximately 10 mm were transferred to 80 mm diameter, 180 mm tall pots (one per pot) containing a vermiculite/perlite (1:1 v/v) mixture soaked in basal nutrient solution (Andrews, Love and Sprent, 1989) containing the appropriate N concentration. There were 9 rates of N (0, 0.5, 1, 2, 3, 4, 5, 6 or 10 mol m^{-3}) supplied as either NO_3^- (KNO_3) or ammonium (NH_4^+)(NH_4SO_4). In all treatments, potassium was maintained at 13.6 mol m^{-3} using potassium sulphate where appropriate. Pots were flushed every 3 d with the appropriate nutrient solution. Plants were grown under controlled environment conditions with a photoperiod of 14 h, a light level of approximately 400 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and day/night temperatures of $20/15 \pm 2^\circ\text{C}$. Plants were harvested 30 d after sowing (DAS) and separated into leaf, stem and root. Total leaf area was measured using a LI-COR model 3100 area analyser (LI-COR, Lincoln, NE, U.S.A) and the plant parts dried separately for dry weight (d.wt) determination. Reduced-N content of the plant parts was determined using Kjeldahl digestion and a "Kjeltec Autosampler System 1035 analyser" (Tecator; Höganäs, Sweden).

ii) Leaf area development (experiments 2a and 2b)

The same lot of barley seed and environmental conditions as in experiment 1 were used in experiments 2a and 2b. In experiment 2a, 7 rates (0, 0.5, 1, 2, 4, 6 and 10 mol m^{-3}) of NO_3^- or NH_4^+ were used. The lengths

of individual main stem leaves 2 - 4 were measured daily until full extension was reached. Leaf length was taken as the leaf tip to point of leaf emergence from the coleoptile for leaf 2 and leaf tip to where the leaf subtended the leaf sheath for leaves 3 and 4. Leaves were considered fully extended when three successive measurements were identical. Plants were harvested 30 DAS and the final area of individual leaves determined. Leaf extension over time was analysed using variates derived from a generalised logistic curve, as described by Andrews *et al.* (1991b). In a similar experiment (experiment 2b) epidermal impressions using nail varnish were taken from three positions on leaf 3 of plants supplied 0.5 and 5 mol m^{-3} NO_3^- . Impressions were mounted on a glass slide and average cell size (non-veinal cells only) determined using a microscope. By compensating for the area estimated to be taken up by veins, cell number was calculated as leaf area divided by average cell area.

iii) Canopy development (experiment 3)

In a field experiment, wheat (cv. Otane) and barley (cv. Triumph) were sown into a conventionally cultivated weed free seed bed. The experiment was sited near Lincoln, New Zealand on a Templeton silt loam. Over the course of the experiment (September 1991 to February 1992) solar radiation receipts and temperatures were close to the long term average but it was slightly wetter than normal. N (0, 100 and 200 kg ha^{-1}) was applied as urea at sowing. The extent of the canopy was measured at approximately 1 week intervals until anthesis using a LI-COR 2100 canopy analyser. Final dry matter and grain yield were determined by hand-harvesting all plants from a 1 m^2 quadrat. Prior to threshing, a subsample (approximately 10% by weight) was kept to evaluate components of yield. N content of the grain was determined as in experiment 1.

Seed Reserve Mobilization and Leaf Growth

The growth of cereal seedlings depends on seed N content (specifically endosperm N) and external N supply. Increased seed N content often results in greater seedling growth. For wheat seedlings 21 DAS, total plant d.wt and area of main stem leaves 1 - 3 were greater for high N seed than for low N seed (Lowe and Ries, 1972, 1973). Also, for barley harvested 6 DAS, seedlings from high N seed had greater reserve mobilization, total plant d.wt, area of leaf 1, leaf protein concentration and photosynthetic rate (Metvier and Dale, 1977a,b; Rahman and Goodman, 1983). Additional NO_3^-

had little effect on seedlings from high N seed, but increased the growth rate of seedlings from low N seed and, if applied early (2 DAS), resulted in similar growth rates for the two seed lines. It was proposed that additional NO_3^- resulted in increased levels of organic N which compensated in some way (probably via photosynthesis) for low levels of endogenous N in low N seed (Metivier and Dale, 1977b). However, more recently, additional NO_3^- has been shown to increase the rate of mobilization of seed reserves in a range of temperate cereals grown in darkness or prior to emergence from the substrate (Nátr, 1988; Andrews *et al.*, 1991a,c). The magnitude of the response of leaf 1 to NO_3^- in above-ground studies was similar to that of seedlings prior to emergence and it was proposed that the major part of the response to NO_3^- in emerged seedlings was due to enhanced reserve mobilization (Andrews *et al.*, 1991a).

Recent work has examined the mechanism of the NO_3^- effect on endosperm mobilization in barley (Lieffering *et al.*, 1992). Prior to emergence, additional N as NO_3^- , but not NH_4^+ , resulted in an increase in reserve mobilization rate (Table 1). Total N in the seedlings for both N forms was similar, and as NH_4^+ -N constituted only a small proportion (<0.2%) of total N in seedlings supplied NH_4^+ , then N assimilation was as great with NH_4^+ as with NO_3^- (Table 1). The N-containing products of NO_3^- and NH_4^+ assimilation are likely to be similar (Layzell, 1990). Thus, although NO_3^- effects on barley seedlings appear to be related to the amount of NO_3^- taken up, they do not appear to be related to products of NO_3^- assimilation (Table 1, Andrews *et al.*, 1991a,c). Seedling water content increased with NO_3^- but not with NH_4^+ (Table 1). Also, NO_3^- accumulated to levels in the shoot and root that would contribute substantially to the osmotic potential of the tissues. Therefore, the NO_3^- effect on mobilization of seed reserves could be related to increased water uptake due

to NO_3^- accumulation.

Chloride (Cl^-) is an ion which is readily taken up by plants but which is not assimilated and can result in substantial increases in percentage water in the shoot and root (Clarkson and Hanson, 1980; Andrews *et al.*, 1989). Addition of 5 mol m^{-3} Cl^- to barley seedlings prior to emergence increased both reserve mobilization and seedling water content (Table 2). This is strong evidence to support the proposal that the NO_3^- effects on seed reserves are osmotic. It was proposed that NO_3^- caused increased water uptake by seedlings which resulted in increased water entering the caryopsis and hence a greater rate of reserve mobilization (Lieffering *et al.*, 1992). If NO_3^- accumulates in the endosperm reserves then this would have a more direct effect on water uptake by the caryopsis. It is possible that increased water uptake could influence mobilization of endosperm seed reserves by stimulating the enzyme α -amylase, the activity of which appears to be the main factor governing

Table 2. Effects of 5 mol m^{-3} applied nitrate (NO_3^-) or chloride (Cl^-) on shoot (S) and root (R) fresh weight (f.wt) and dry weight (d.wt), caryopsis (C) d.wt and shoot to root d.wt ratio (S:R) of barley (*Hordeum vulgare* L. cv. Triumph) prior to emergence from the substrate.

Applied treatment	F.wt (mg)		D.wt (mg)			S:R
	S	R	S	C	R	
Nil	105.6	121.5	9.98	17.57	6.41	1.55
NO_3^-	148.5	127.5	12.67	14.37	6.34	1.99
Cl^-	139.5	128.9	11.93	15.36	6.24	1.91
s.e.m.	4.8	4.5	0.52	0.25	0.20	0.07

Table 1. Effects of 5 mol m^{-3} applied nitrate (NO_3^-) or ammonium (NH_4^+) on shoot (S) and root (R) fresh weight (f.wt) and d.wt, caryopsis (C) d.wt, shoot to root d.wt ratio (S:R) and total nitrogen (N), NO_3^- -N and NH_4^+ -N content of barley (*Hordeum vulgare* L. cv. Triumph) prior to emergence from the substrate.

Applied N	F.wt (mg)		D.wt (mg)			S:R	N ($\mu\text{g seedling}^{-1}$)		
	S	R	S	C	R		Total N	NO_3^- -N	NH_4^+ -N
Nil	94.4	97.6	8.67	14.06	6.38	1.36	610.5	5.1	0.5
NH_4^+	99.1	90.3	8.36	14.51	6.02	1.39	920.2	4.6	1.4
NO_3^-	138.5	107.8	10.31	12.46	6.33	1.63	976.9	185.2	0.7
s.e.m.	4.3	5.2	0.37	0.41	0.14	0.06	15.4	10.2	0.5

starch breakdown and which is sensitive to seed water potentials (Jones, 1969; Jones and Armstrong, 1971; Wilson, 1971). Increased reserve mobilization and greater early growth of seedlings with high N seed may also be due to increased water uptake. The rate and degree of imbibition, the physical process of water absorption by the seed, are closely related to the colloidal properties of the seed (Cardwell, 1984). Proteins are the dominant form of seed N and represent the major colloidal constituent of seeds (Arnott and Jones, 1971). For wheat and barley seeds, rates of water uptake increased as a result of higher seed N (Lopez and Grabe, 1971). Also, α -amylase activity has been found to be higher in wheat seedlings grown from high %N seed (Ching and Rynd, 1978). Further work needs to be carried out to determine the relationships between seed N content, NO_3^- uptake, water uptake, α -amylase activity and reserve mobilization.

Partitioning of Dry Matter to Leaves

Nitrogen availability can affect the partitioning of dry matter to the leaf, stem and root of temperate cereals from the seedling stage through to maturity (Table 1; Hocking and Meyer, 1991; Andrews *et al.*, 1992). Usually shoot to root d.wt ratio (S:R) increases with increased N supply regardless of form supplied or of its effects on growth (Andrews, 1992 and references therein) although during seedling development this need not be the case (Tables 1,2). At this stage, plant (shoot+root) d.wt, in comparison with plant N, shows a better correlation with S:R. Leaf weight ratio (LWR; leaf d.wt as a fraction of total plant d.wt) appears to increase with NO_3^- supply over the range in which total plant d.wt increases, then either changes little or increases further with increasing NO_3^- supply thereafter (Hocking and Meyer, 1991; Andrews *et al.*, 1992). Little information is available with regard to N effects on LWR through the different stages of plant development. For the five main temperate cereals, in the vegetative phase, LWR increased from around 0.3 to 0.4 with increased NO_3^- supply from 0.5 to 5 mol m^{-3} , the range normally found in agricultural soils (Andrews *et al.*, 1992). In a separate study, using reproductive wheat plants, LWR increased from around 0.2 to 0.3 with increased NO_3^- concentration from 0.5 to 12 mol m^{-3} (Hocking and Meyer, 1991). The mechanism of the N effect on dry matter partitioning is not known. For a range of species supplied NO_3^- , S:R was positively correlated with tissue N content (eg. Hirose, 1986; Ingestad and Agren, 1991; Boot *et al.*, 1992). Several reports indicate that for a similar total plant d.wt, S:R is greater with NH_4^+ than with NO_3^- as an

N supply (Andrews, 1992;1993). Experiment 1 compared the effects of NO_3^- and NH_4^+ on S:R, LWR and tissue reduced-N content of barley in the vegetative phase. Total plant d.wt increased with applied NO_3^- or NH_4^+ concentration over the range 0 - 6 mol m^{-3} , then changed little with increasing N supply thereafter (Fig. 1a). Leaf area increased with applied N over the range 0 - 10 mol m^{-3} (Fig. 1b). At higher external N concentrations both d.wt and total leaf area were greater for plants supplied NO_3^- . Shoot to root ratio and LWR increased with increasing total plant d.wt up to 6 mol m^{-3} applied N (Figs. 1c,d) but for any given d.wt both parameters were greater for plants supplied NH_4^+ , as has been found previously (Cox and Reisenhauer, 1973; Timpo and Neyra, 1983; Bowman and Paul, 1988; Troelstra *et al.*, 1992). However, for a given plant d.wt, tissue reduced-N content was greater with NH_4^+ than with NO_3^- and if S:R and LWR are plotted against plant reduced-N content, then there are no significant differences between the two forms of N (Figs. 1e,f).

Andrews (1992) proposed that the NO_3^- effect on S:R can be explained by the effect of increased NO_3^- assimilation and protein synthesis on photosynthesis, and hence growth, and by competition between the NO_3^- assimilation/protein synthesis processes and growth for energy derived from photosynthesis. It was argued that increased NO_3^- assimilation/protein synthesis results in an increased proportion of energy from photosynthesis being utilised in processing N at the expense of growth, and that this is reflected in a higher tissue reduced-N content. Over part of the external NO_3^- concentration range 0.1 to 20 mol m^{-3} , the effect of increased NO_3^- assimilation/protein synthesis on photosynthesis is so great that increased photosynthate is available for growth. It was proposed that the increase in shoot d.wt relative to root d.wt over this range is due to proximity of the shoot to the carbon (C) source and increased N availability for growth. As NO_3^- assimilation/protein synthesis increases, N use efficiency decreases. When NO_3^- assimilation/protein synthesis increases to a point where photosynthate available for dry matter production decreases, S:R will still increase as the shoot will realise a greater proportion of its growth potential due to its proximity to the source of C and the availability of reduced N for growth.

There are reports in the literature that dry matter production per unit N is greater for NO_3^- than for NH_4^+ (Cox and Reisenhauer, 1973; Bowman and Paul, 1988; Troelstra *et al.*, 1992). This was found to be the case in experiment 1 (Fig. 2a). It was also found that leaf area per unit leaf N was greater for plants supplied NO_3^- (Fig. 2b). This effect does not appear to have been reported

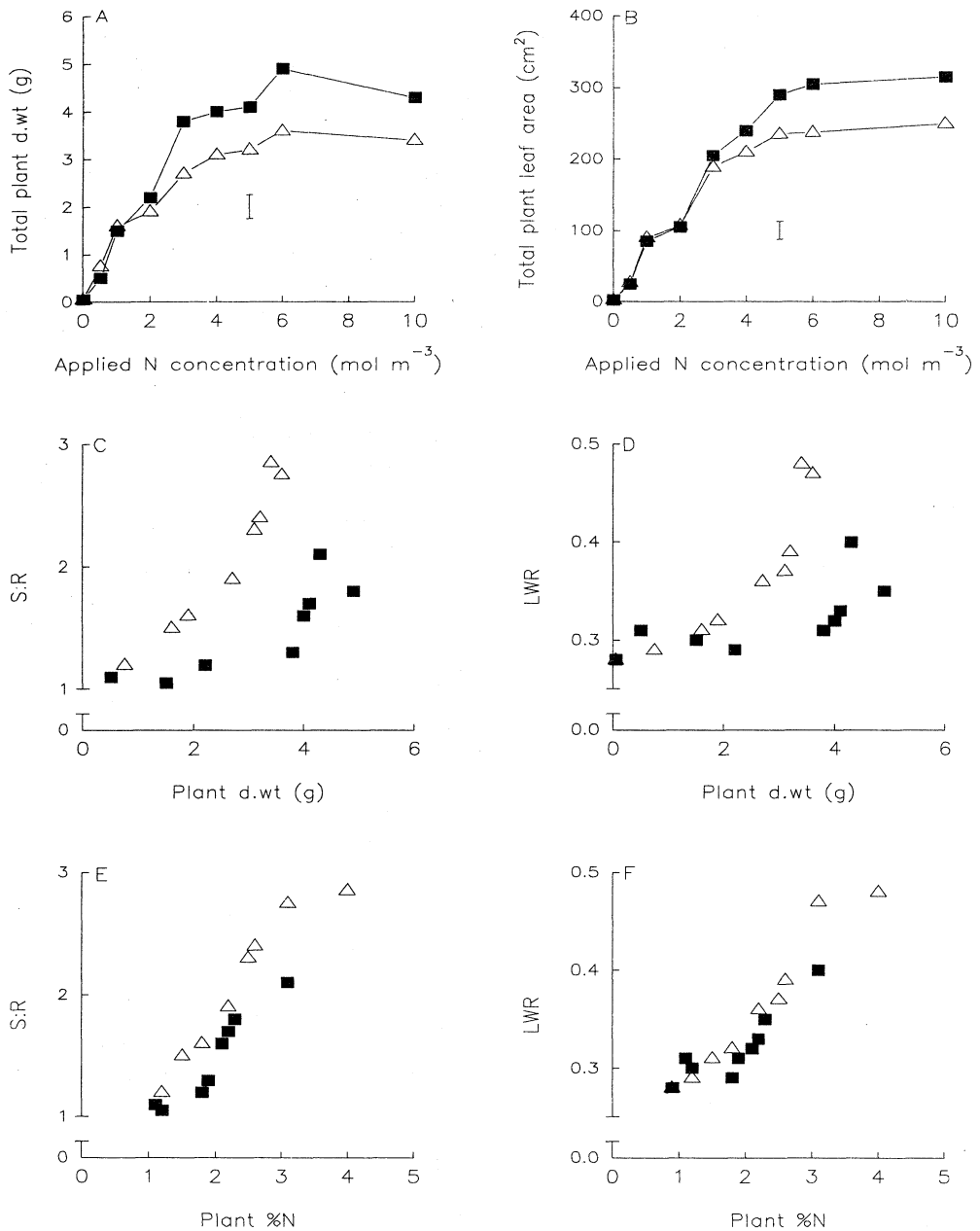


Figure 1. The effects of different concentrations of applied nitrate (■) or ammonium (Δ) on total plant dry weight (d.w.t)(A) and leaf area (B) and the relationships between shoot to root d.w.t ratio (S:R) and plant d.w.t (C), leaf weight ratio (LWR) and plant d.w.t (D), S:R and plant %N (E) and LWR and plant %N (F) for the two N forms. Error bars indicate LSD_{0.05}.

before. Possible reasons for greater efficiency in leaf area production with NO_3^- in comparison with NH_4^+ are discussed below.

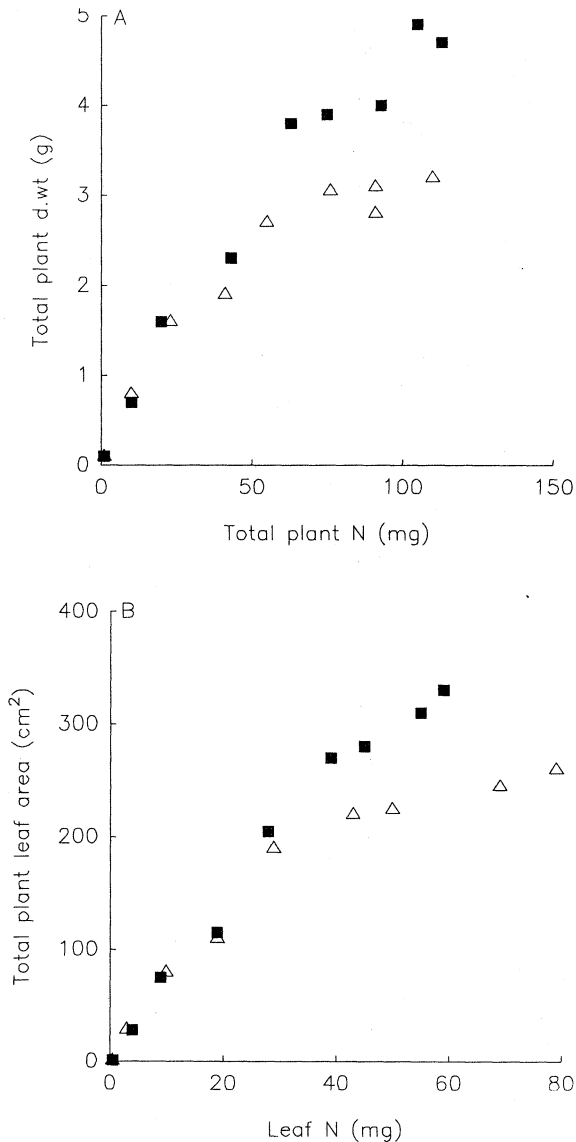


Figure 2. The relationships between total plant dry weight (d.w.t) and total plant N (A) and total plant leaf area and leaf N (B) of barley supplied various concentrations of nitrate (■) or ammonium (Δ).

Leaf Area Development

Nitrogen availability strongly influences the growth characteristics of leaves of the five main temperate cereals (Andrews *et al.*, 1991b). Specifically, additional N as NO_3^- over the range 0.1 - 5 mol m⁻³ caused a decrease in duration of extension growth but increased maximum and mean extension rate and final length of main stem leaves 2 - 4. In general, the greater part of these responses occurred with increased applied NO_3^- from 0.1 - 1.0 mol m⁻³. The magnitude of the response to NO_3^- was considerable and increased with increased leaf number 1 - 4. For example, increased applied NO_3^- from 0.1 to 1.0 mol m⁻³ caused a two to threefold increase in maximum and mean extension rates and at least a twofold increase in final length of leaf 3 of all cereals. Nitrate also had effects on area of leaves 1 - 4 of all cereals. As with final length, final area increased substantially with increased applied NO_3^- from 0.1 - 1.0 mol m⁻³. In contrast to leaf length, leaf area for all species increased substantially with increased applied NO_3^- from 1.0 - 5.0 mol m⁻³. These data emphasise that even in cases where rate of leaf extension and final leaf length are unaffected by NO_3^- supply, leaf area can be affected greatly.

Increased individual leaf area with additional N must be due to increased cell size, increased cell number and/or changes in leaf architecture. The main effect of additional N has usually been attributed to increased total cell number, although cell size has also been found to increase (Humphries and Wheeler, 1963; Dale, 1972; Dale and Milthorpe, 1983; Hay and Walker, 1989). We have found that NH_4^+ is similar to NO_3^- with respect to its effects on duration of growth, extension rate, and final length and area of main stem leaves 2 - 5 of barley (experiment 2a - data for leaf 4 are shown in Fig. 3). The major part of the response occurred over the range 0 - 2 mol m⁻³. In experiment 2b, individual area of leaf 3 was twice as great at 5.0 mol m⁻³ NO_3^- compared to 0.5 mol m⁻³ (Table 3). Increased leaf area with additional NO_3^- was associated with an increase in both epidermal

Figure 3. (opposite) The effects of different concentrations of applied nitrate (■) or ammonium (Δ) on the duration of growth (A), mean extension rate (B) and final leaf area (C) of leaf 4 of barley (*Hordeum vulgare* L. cv. Triumph). Error bars indicate LSD_{0.05}.

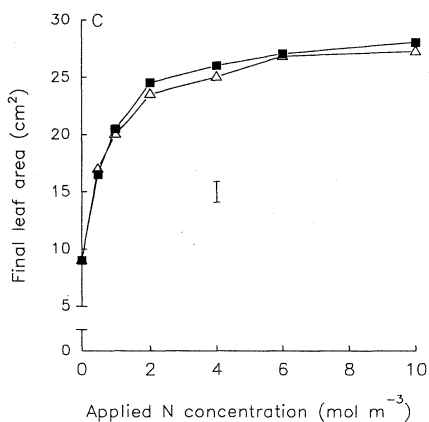
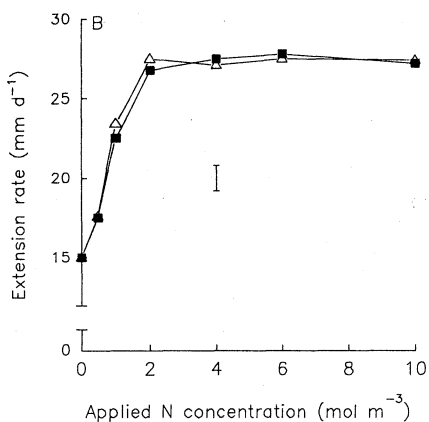
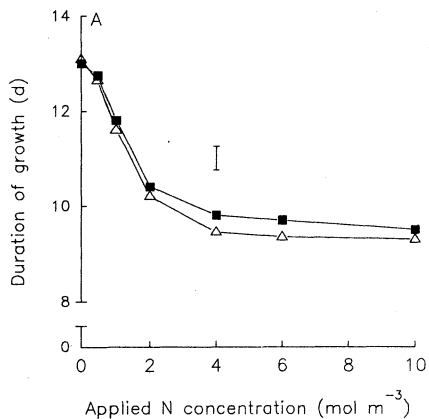


Table 3. The effects of 0.5 or 5.0 mol m⁻³ nitrate (NO₃) on area, non-veinal epidermal cell number and cell area (see text) of leaf 3 of barley (*Hordeum vulgare* L. cv. Triumph).

Applied NO ₃ ⁻ (mol m ⁻³)	Leaf area (cm ²)	Cell number (x10 ⁷ leaf ⁻¹)	Cell area (x10 ⁻⁷ cm ²)
0.5	5.63	1.07	2.34
5.0	12.70	1.42	4.00
s.e.m.	0.28	0.04	0.06

cell number and size. However, for this leaf at least, increased leaf area with additional NO₃⁻ was due more to increased cell size than to increased cell number.

Cell expansion requires the influx of water into the cell. This occurs in part as a result of the lowering of the cell water potential through the accumulation of solutes. Final cell size is determined by the availability of solutes and water, the extensibility of the existing cell wall and the availability of C for new cell wall material. The most common solute in plant cells appears to be sucrose, produced by photosynthesis (Morgan, 1984). Nitrogen availability strongly influences photosynthetic rate, hence greater cell size with additional NO₃⁻ could be due to increased C assimilation resulting in greater sucrose availability for osmoticum and cell wall production. Greater leaf area per unit N with NO₃⁻ compared to NH₄⁺ (Fig. 2) could be due to increased levels of osmoticum and hence differences in cell size. In this case differences in site and pathway of NO₃⁻ and NH₄⁺ assimilation may be important. In plants, NH₄⁺-N is converted into amino acid-N primarily in the root; if NH₄⁺ is transported to the shoot it can be toxic (Mehrer and Mohr, 1989). In contrast, at high external NO₃⁻ concentrations, a substantial, if not major, proportion of NO₃⁻ assimilation in cereals occurs in the shoot (Andrews *et al.*, 1992). Nitrate can accumulate to substantial levels in cereal leaves (Andrews *et al.*, 1992) and together with counter ions such as potassium, can contribute to the osmotic potential of the cell (Blom-Zandstra and Lampe, 1985; Steingrover *et al.*, 1986). In addition, the assimilation of NO₃⁻ leads to the generation of hydroxyl ions. Hydroxyl ions are neutralized by organic acids which are also osmotically active (Raven, 1985). Hence, at higher external N concentrations, increased leaf area per unit N with NO₃⁻ compared to NH₄⁺ could at least in part be due to increased cell size caused by greater levels of osmoticum. Further work is required to determine the nature and concentration of solutes in the leaves of plants

supplied different levels of NO_3^- and NH_4^+ to assess the importance of site of NO_3^- assimilation in determining leaf area.

At the plant level, additional N can increase total plant leaf area in cereals by increasing leaf number. Under field conditions, additional N does not normally have a strong effect on rate of development of the main stem (Langer and Liew, 1973) and increased leaf number with additional N is likely to be due to increased tiller production and/or more leaves per tiller. The capacity to produce tillers varies considerably in temperate cereals. For example, unculm barleys have little capacity for tiller production while some cultivars of rye can have over 20 tillers. Tillering capacity appears to be an important factor determining the ability of cereals to respond to N and hence, to some extent determines the overall growth potential of the plant (Andrews *et al.*, 1992). Most commercial cultivars have some tillering capacity and an increase in leaf number via increased tiller number is likely to contribute to increased plant leaf area with additional N. For example, it has been shown that additional N at sowing can result in a 40%

increase in tiller number of Otane wheat by the 5th leaf stage under conditions where the rate of development of the main stem is unaffected by additional N (Andrews *et al.*, 1990).

Canopy Development

At the crop level, individual plants form a canopy. The extent of canopy development is usually quantified in terms of the leaf area index (LAI, leaf area per unit ground area). LAI determines the fraction of available photosynthetically active radiation intercepted by the canopy and hence crop dry matter production (Hay and Walker, 1989). For cereals, crop dry matter production is usually positively correlated with grain yield (Biscoe and Gallagher, 1977).

The effects of additional N on individual leaf and total plant leaf area are reflected at the crop level by increases in rate of canopy development, maximum LAI

Table 4. The effects of 0, 100 or 200 kg ha⁻¹ N applied at sowing to spring barley (*Hordeum vulgare* L. cv. Triumph) and wheat (*Triticum aestivum* L. cv. Otane) grown at Lincoln, Canterbury. Mean canopy growth rate (MGR), maximum canopy leaf area index (MAXLAI) attained and final quadrat grain yield are presented.

Applied N (kg ha ⁻¹)	Barley	Wheat
MGR (LAI d⁻¹)		
0	0.077	0.037
100	0.121	0.040
200	0.128	0.046
s.e.m.	0.007	0.002
MAXLAI		
0	4.4	3.2
100	5.5	3.8
200	6.0	4.0
s.e.m.	0.25	0.15
Grain yield (T ha⁻¹) (quadrat)		
0	6.70	5.80
100	7.67	6.55
200	7.86	6.64
s.e.m.	0.15	0.10

Table 5. Effects of N application at sowing on seed head number, grains per head, individual grain weight and grain %N of spring sown barley (*Hordeum vulgare* L. cv. Triumph) and wheat (*Triticum aestivum* L. cv. Otane).

Applied N (kg ha ⁻¹)	Barley	Wheat
Head number (m⁻²)		
0	821	427
100	1028	493
200	1049	483
s.e.m.	13.8	12.1
Grains per head		
0	25.0	35.1
100	27.5	37.5
200	27.2	38.6
s.e.m.	0.41	0.74
Individual grain weight (mg)		
0	51.0	53.4
100	46.1	51.9
200	44.7	51.7
s.e.m.	1.4	1.09
Grain %N		
0	1.52	2.06
100	1.93	2.33
200	2.21	2.38
s.e.m.	0.12	0.09

achieved and final grain yield (experiment 3 - Table 4). Often, the component of yield most affected by additional N is head number, which usually reflects an increase in the tiller number (Table 5, Hay and Walker, 1989; Wibberley, 1989). Nitrogen availability can also affect grain quality. In experiment 3, N applied at sowing increased the grain N content of both species (Table 5). For wheat, high grain N content is desirable as it increases baking quality while for barley low grain N results in better malting characteristics (Wibberley, 1989).

Conclusions

This paper reviews the effects of N on leaf growth of temperate cereals. It is concluded that:

- 1) Nitrogen availability affects leaf growth from the seedling stage to maturity.
- 2) Increased rate of mobilization of seed reserves with additional NO_3^- is related to increased water uptake.
- 3) An important factor determining partitioning of dry matter to leaf, stem and root is plant N content.
- 4) Increased individual leaf area with additional N is due to greater cell number and greater cell size.
- 5) For most cultivars, increased leaf number due to increased tillering is likely to contribute substantially to increased leaf area with additional N.

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