

Growth, yield and composition of four winter cereals. II. Nitrogen and carbohydrate economy

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Abstract

A field experiment with three cultivars each of four winter cereals (wheat, rye, triticale and barley), sown at a seed rate for about 320 plants per m², was conducted in 1986 on a fertile clay soil. Nitrogen (N) fertilizer at a rate of 120 kg/ha for wheat and triticale and 60 kg/ha for rye and barley was split-dressed in two applications. N yield was highest in wheat (196 kg/ha) and lowest in rye (123 kg/ha). The amounts taken up were influenced by the rate of the N applications. The triticale cultivar Lasko and the barley cultivar Marinka had a higher N-uptake than the other triticale and barley cultivars. Nitrogen harvest index, i.e. the ratio of N in grains and N in above-ground dry matter at final harvest, was lowest in rye and highest in barley. N concentration in plant organs was higher in wheat and triticale than in rye and barley. This was probably caused by the difference in the level of N application. N use efficiency, expressed as grain dry matter production per kg N taken up, was 53 in wheat, 68 in rye, 50 in triticale and 61 in barley. In all species, the largest reserves of water-soluble carbohydrates (WSC) were found in the stems. Rye allocated more dry matter to stem growth before flowering than wheat, triticale and barley. Averaged over these cereals, 26% of WSC, produced before flowering, was used for redistribution and respiration during grain production.

Keywords: winter cereals, nitrogen uptake, nitrogen harvest index, water-soluble carbohydrates

Introduction

High-yielding cereal crops require an amount of nitrogen that usually is applied in more dressings. Applying all N in a single dose increases the risk of lodging (Mulder, 1955) and diseases (Darwinkel, 1980), resulting in lower yield per kg N taken up (Dilz et al., 1982). These risks can be reduced by splitting the N dressing, which also increases the N use efficiency, expressed as dry matter production per kg N taken up (Dilz et al., 1982). The yield response of cereals to N application can vary strongly (Graham et al., 1983; Mugwira & Bishnoi, 1980), because of variations in both uptake efficiency (kg N taken up per kg N applied) and utilization efficiency (kg grain per kg N taken up) and so can the N harvest index (NHI; Graham et al.,

1983). On fertile soils N application can be reduced because more (inorganic) N is available in the soil (Groot & Verberne, 1990; Widdowson et al., 1987).

Information about canopy structure and accumulation and reallocation of N and water-soluble carbohydrates (WSC) is important to understand yield potential and yield variability. The build-up of reserves and their availability for growth varies over the years (Austin et al., 1980) and among cultivars (Davidson & Chevalier, 1992; Ellen, 1990). The dynamics of WSC depend on the area index and duration of the green plant parts (Spiertz et al., 1971), light level (Ellen & Van Oene, 1989^a), pest and disease incidence (Darwinkel, 1980; Doodson et al., 1965; Ellen & Lange-rak, 1987; Spiertz, 1978), and N supply (Dilz et al., 1982; Spiertz & Ellen, 1978).

In a previous paper (Ellen, 1993) four winter cereals, wheat, rye, triticale and barley were compared with respect to biomass production, grain yield and canopy structure. In this paper uptake and use of nitrogen (N), and production and use of water-soluble carbohydrates (WSC) of these four cereals are compared.

Materials and Methods

The set-up of the experiment and the growing conditions were described earlier (Ellen, 1993), and are summarized here.

The experiment was conducted on a fertile clay soil in East Flevoland. Three cultivars of each species, as given in Table 1, were sown on 3 October 1985. The plants emerged on 18 October. Nitrogen (N) was split-dressed at a rate of 120 kg/ha for wheat and triticale and 60 kg/ha for rye and barley. The lower N application for the latter was chosen to reduce the risk of lodging. On 15 March 1986 the amount of inorganic N in the soil to 100 cm depth was measured as 60 kg/ha, and was the criterion in deciding on fertilizer application. During the growing season the N supply from the reserves of inorganic N can be quite large in this soil. Occurrence of diseases and pests was very low and was controlled with low dosages of pesticides. All crops grew healthy during the whole growing season.

Plots were periodically harvested (0.25 m²/plot) on 29/4, 13/5, 3/6, 30/6, 29/7 and 12/8, except for barley on the last date. Barley was combine-harvested on 1/8 and the other cereals on 14/8 (60 m² per plot). At each periodic harvest, total above-ground dry matter per plot was recorded and sub-samples were taken for chemical analysis. Plants were partitioned, dried per organ (70 °C) and ground for analysis of total N (N-Kjeldahl) and for water-soluble carbohydrates (for methods, see Spiertz, 1977).

Results

Data on crop growth and yield have been reported in a previous paper (Ellen, 1993).

N economy

N concentrations, N contents and N harvest index (NHI) at final harvest. The N concentrations, N contents and N harvest indices (NHI) at final harvest are given in Table 1. N concentrations in the straw were similar in all cereals (0.30%). N concen-

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Table 1. N-concentration (g/g $\times 100$) and N-uptake (kg/ha) in straw and grains and NHI (g/g $\times 100$) at final harvest.

Crop	Cultivar	N-concentration		N-yield			NHI ($\times 100$)
		Straw	Grains	Straw	Grains	Total	
Wheat	Arminda	0.31	1.94	29	170	198	85.6
	Obelisk	0.30	1.85	32	162	194	83.4
	Okapi	0.29	1.89	31	165	196	84.0
	Average	0.30	1.89	31	166	196	84.3
Rye	Admiraal	0.29	1.44	25	96	121	79.4
	Animo	0.31	1.45	26	96	122	78.4
	Dominant	0.28	1.52	24	101	126	80.5
	Average	0.29	1.47	25	98	123	79.4
Triticale	Bolero	0.29	1.86	31	145	176	82.3
	Lasko	0.28	2.17	27	182	209	87.1
	Salvo	0.30	1.91	29	161	190	84.6
	Average	0.29	1.98	29	163	192	84.7
Barley	Hasso	0.30	1.61	17	107	123	86.5
	Masto	0.34	1.62	17	108	125	86.3
	Marinka	0.29	1.73	20	113	134	84.7
	Average	0.31	1.65	18	109	127	85.8

trations in the grains, however, differed markedly. Wheat (1.89%) and triticale (1.98%) had the highest N concentrations and rye (1.47%) and barley (1.65%) the lowest. Among the cultivars of each species N concentrations in both grain and straw hardly varied, except in grains of Lasko (triticale) and Marinka (barley).

N content was highest in wheat (196 kg N/ha) and lowest in rye (123 kg N/ha). Inter-cultivar differences were small in wheat and rye, slightly greater in barley and substantial in triticale. Lasko (triticale) had the highest N content of all species.

N allocation over straw and grains (NHI) for rye was different from that of the other species, i.e. 79.4 versus 84.3, 84.7 and 85.8 for rye, wheat, triticale and barley, respectively. Lasko (triticale) had a higher, and Marinka (barley) a lower NHI than other cultivars of the same species; inter-cultivar differences for wheat and rye were not significant.

N-use efficiency

N-use efficiency, expressed as total above-ground dry matter production per kg N taken up, was 96 in wheat, 124 in rye, 96 in triticale and 98 in barley. Among cultivars of the same species, differences in N use-efficiency were less than 3 %, with the exception of the triticale cultivars; Lasko had on average a 4 % higher N use-efficiency than the two other cultivars. N-use efficiency, expressed as grain dry matter

production per kg N taken up, was 53 in wheat, 68 in rye, 50 in triticale and 61 in barley.

N concentration in leaves, stems, chaff, grains and roots. N concentration in the leaves of wheat and triticale was higher than in those of rye and barley (Fig. 1), because of different N applications. The concentration in the stems (first points in Fig. 1 refer to leaf sheaths) shows similar trends, but at a lower level. The stems had the lowest N concentrations of all plant parts. N concentration of chaff varied little among the cereals and, on average, was 0.15 % above that of the stems at final harvest. N concentration in the grains of wheat and triticale, averaged over the periodic harvests from 30/6 to 12/8, was 0.6 % higher than in those of rye and barley. In the course of grain filling the N concentration declined gradually as a result of dilution by increasing amounts of starch (Spiertz & Ellen, 1978). In the final phase of grain filling the N concentration slightly increased.

N concentration in the roots varied greatly among the cereals during the early phases of growth. Rye had the lowest root N concentration (0.78%) and triticale the highest (1.12%), averaged over the growing season. Root N concentration of wheat, triticale and barley decreased linearly during the beginning of the growing season until 3/6. Subsequently, root N concentration stabilized at a level of about 0.65%; only in triticale values of 0.75% were measured after 3/6.

N uptake and allocation

N contents in the above-ground parts of wheat (196 kg N/ha) and triticale (192 kg N/ha) were considerably higher than in those of rye (123 kg N/ha) and barley (127 kg N/ha). These differences showed up from the beginning of flowering (Fig. 2). The allocation of N over the various plant parts differed among the cereals. A large part of N taken up before growth stage 59 (Zadoks et al., 1974), was found in the leaves; it was highest in wheat (54 kg/ha; 43%), followed by triticale (49 kg/ha; 37%) and barley (41 kg/ha; 47%) and lowest in rye (31 kg/ha; 31%). The relative N contents in stems were quite similar in rye and triticale on the one hand and in wheat and barley on the other. The contents in chaff varied little among species. Averaged over the period 30/6 until final harvest (calculated as quantity per date, divided by number of measurements), 1.1 kg N/ha was measured in the chaff of wheat and triticale and 8 in that of rye and barley. At final harvest more than 80% of the N taken up was found in the grains, except in rye (Table 1).

N uptake just before flowering (GS 59) was 125 kg/ha in wheat, 100 in rye, 134 in triticale and 87 in barley. From that time till maturity N uptake per ha was 71 kg in wheat, 23 kg in rye, 58 kg in triticale and 40 kg in barley, corresponding to 36, 19, 30 and 31% of total above-ground N uptake, respectively.

After flowering, all cereals started to reallocate N from the leaves, stems and chaff to the grains.

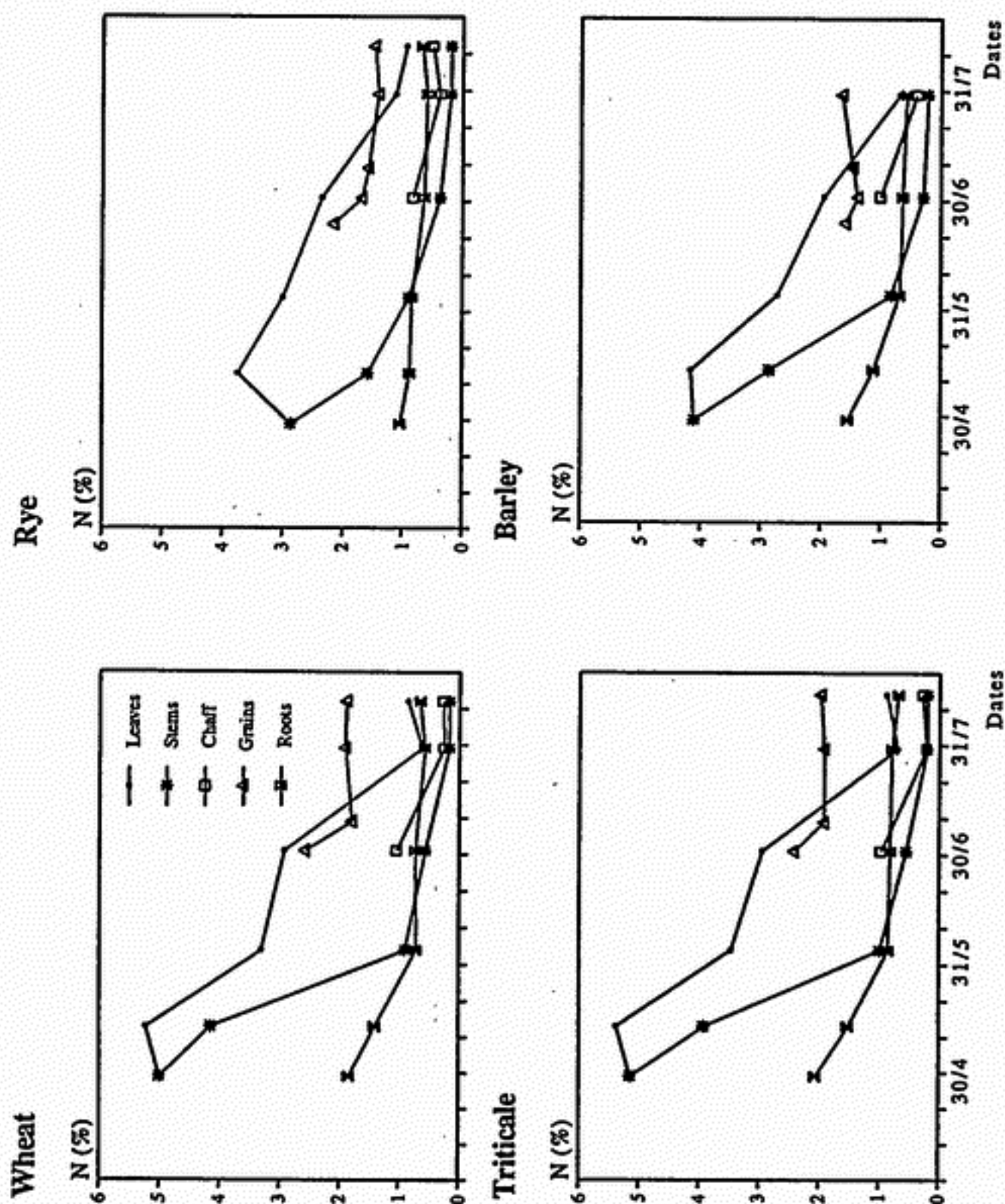
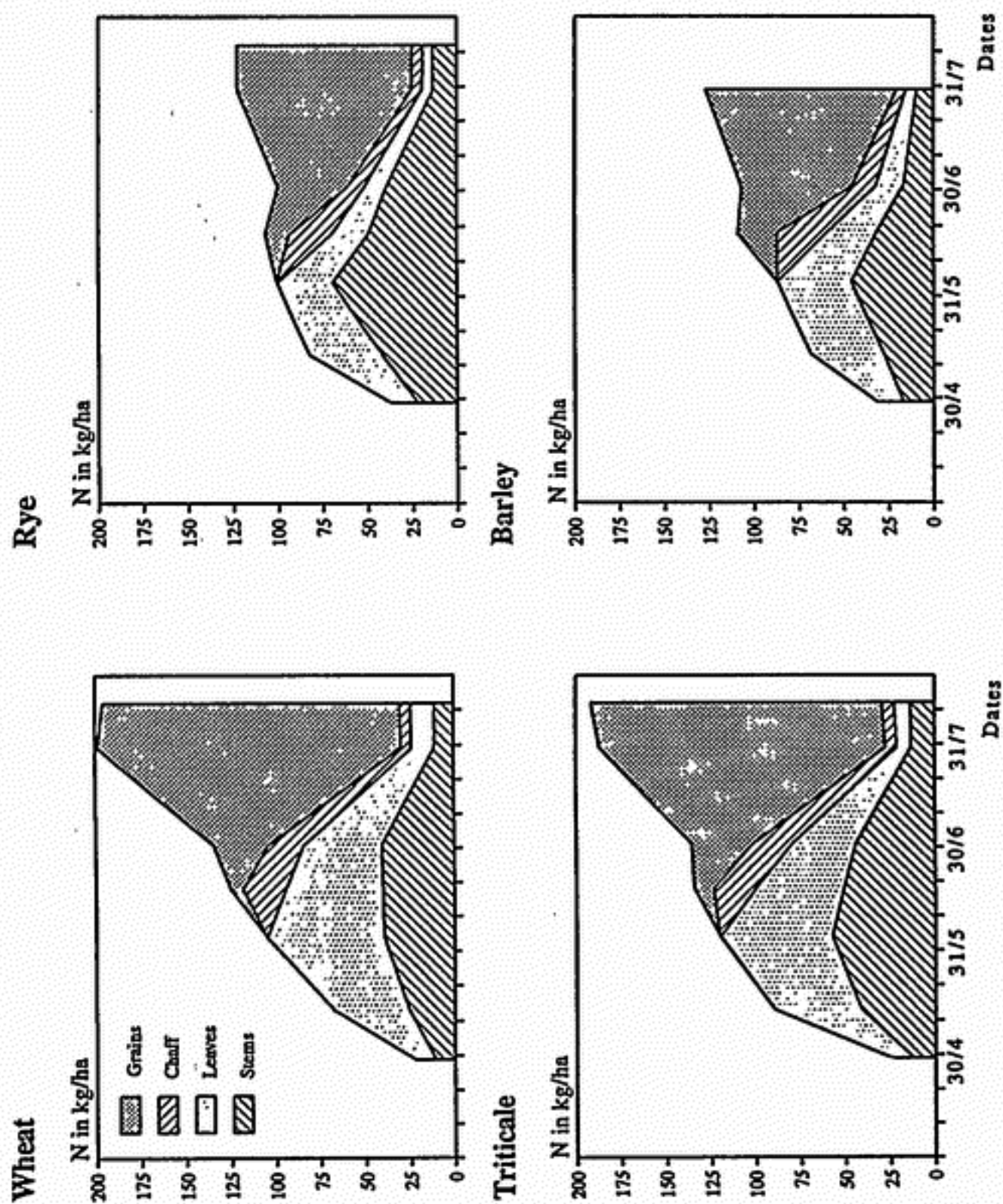
Fig. 1. N concentrations (g/g $\times 100$) in different plant parts.

Fig. 2. N (kg/ha) in different plant parts.



Water-soluble carbohydrates (WSC)

WSC concentration. The dynamics of WSC in the stems are particularly interesting because of their large absolute and relative changes (stems including leaf-sheaths). The highest WSC concentration in the stems of wheat (32%), barley (26%) and triticale (27%) was found on 3/6 and of rye (24%) on 30/6 (Fig. 3). The increase in WSC concentration started earliest in rye, which already had a WSC concentration (in leaves and stems) of 12% on 29/4, compared to only about 6% in the other species. Between 29/4 and 13/5 the increase in WSC concentration was largest in barley, followed by wheat and triticale. Date and value of the WSC peak cannot be read exactly from Fig. 3, because the sampling frequency was too low.

WSC concentration in leaves and roots was below 10% in all four cereals during the whole season, with small variations among cultivars. WSC concentration in the roots was initially lower than in the leaves, but that reversed later, except in barley, where the concentrations in the leaves exceeded those in the roots during the whole growing period, but for the final harvest date.

WSC concentration in chaff was highest in rye (21.3%) and lowest in triticale (8.2%) at the first measurement on 17/6. With increasing grain weight it decreased to 1% in all species at the last harvest date. The differences between cultivars were small.

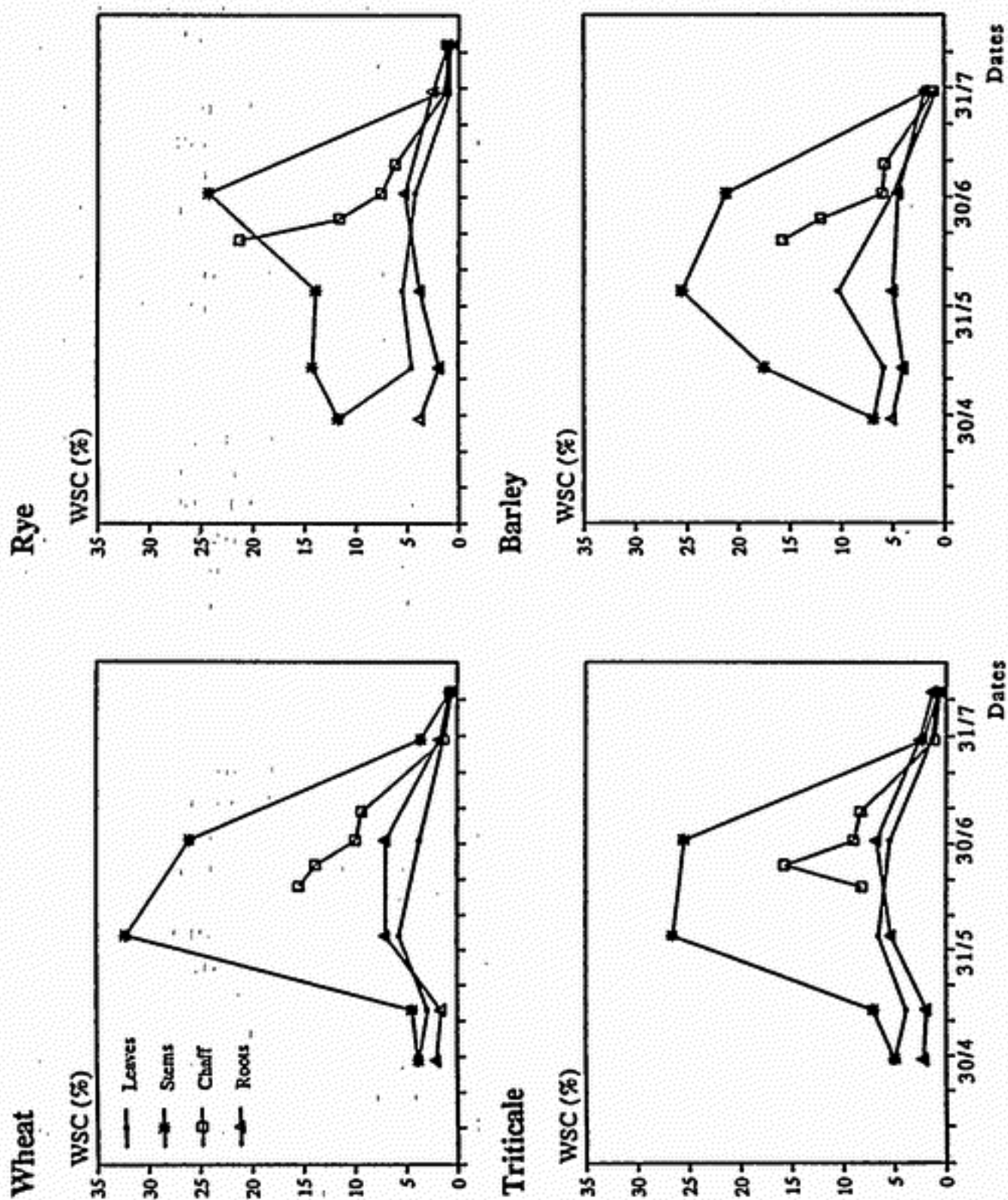
WSC content in stems. The highest WSC content in stems of wheat, rye and triticale was attained around 30/6, and in barley around 3/6 (Fig. 4). The total contents in kg/ha on those dates (leaves, stems and chaff) were 2180 (wheat), 2000 (rye), 2310 (triticale) and 1570 (barley), of which 85, 94, 88 and 90%, respectively, in the stems. From 30/6 onwards, total WSC content in all species sharply declined due to reallocation from these plant parts to the grains. At final harvest differences among the species were insignificant; average WSC content was 76 kg/ha.

Discussion

Differences in N economy among the species were small in relative sense, but the absolute differences were considerable (Figs. 1 and 2; Table 1). Of course, the differences in N application rate played an important role, as witnessed by the N concentrations, the N yields and the N allocation to the various plant parts. Total N uptake at first sampling date was similar in wheat and triticale (23 kg/ha) on the one hand and in rye (37 kg/ha) and barley (32 kg/ha) on the other. Until flowering, the rate of N uptake was highest in wheat and triticale and somewhat lower for rye, followed by barley. After flowering it was appreciable in wheat and triticale, and low in rye and barley (Fig. 2). The lower total N uptake in rye at maturity cannot solely be attributed to lower N supply as the availability of N from natural sources may be assumed equal for all crops. Two explanations are possible:

- at flowering all available N was exhausted (Fig. 2) and dry matter production per kg N taken up was high; limited N availability under favourable weather conditions usually results in high N use efficiency (Ellen, 1993; Spiertz & Ellen, 1978);

Fig. 3. WSC concentrations ($\text{g/g} \times 100$) in different plant parts.



- the high dry matter production above ground suggests a high root production (Barracough, 1984). This also leads to high rates of sloughing off. Under low N supply, microbial decomposition of this root material may lead to immobilization of available N.

Graham et al. (1983) concluded that triticale did not differ from the traditional cereals in N requirements for potential yield. However, they found at equal N applications to all cereals concentrations in grains of triticale that were similar to those of rye on the one hand, and also similar, but lower concentrations in wheat and barley on the other. Grain yield of rye was, however, on average 37% lower, hence the dilution effect was much smaller in their experiment. Our conclusion is that for high yielding crops not only the level of N uptake, but much more the N-use efficiency, expressed in dry grain production per kg N taken up, is important. For instance, the level of grain yields in winter wheat, as found by Spiertz & Ellen (1978) with higher top dressings than in this experiment, was lower. N-use efficiency (grain production per kg N taken up) in wheat under comparable weather conditions was in their experiment approximately 20% lower. For baking or brewing quality, there are different criteria, because higher or lower protein concentrations are, beside cultivar characteristic, dependent on availability of N. Experiments at CIMMYT in Mexico, cited by Ford et al. (1984), showed differences in N response among triticale cultivars. The cultivar Lasko also showed a deviating N economy, with a 13% higher N concentration in the grains and higher NHI than the other two cultivars (Table 1). The cause of the differences between Lasko on the one hand and Bolero and Salvo on the other is not clear.

Rye and barley showed similar N yields, in accordance with the similar N-applications. The N concentration in rye grains and straw, however, was lower because of its higher total dry matter production (Ellen, 1993). The N concentration in the various plant parts was mostly lower in rye and barley than in wheat and triticale (Fig. 1), parallel to total N-uptake.

During the linear phase of grain filling the N concentration in the grains decreases because of the relatively higher rate of carbohydrate accumulation (Fig. 1; Ellen, 1987; Spiertz & Ellen, 1978). At final harvest, concentrations in vegetative plant parts were practically similar in all species, but substantially different in the grains. In the final phase of grain filling N concentration slightly increased, probably due to respiration of carbohydrates in the grains and/or accelerated translocation of N from senescing plant parts, as suggested by Van Keulen & Seligman (1987).

The initially low N concentration in the roots of rye could be related to the fast early development of this crop, resulting in an N demand of the above-ground parts exceeding uptake, which may have been restricted by low soil temperature.

Rye deviated from the other species in having at flowering a higher proportion of N stored in stems and less in leaves (Fig. 2). This is related to a high stem/leaf ratio. The ratio of stem weight to leaf weight on 30/6 was, on average, 93% in rye, compared to 83 in wheat, 87 in triticale and 88 in barley.

The very high N harvest indices (Table 1) may partly be explained by the favourable health status of the cereals, ensuring unimpaired translocation of N (Gliemerth & Kübler, 1977). N uptake continued almost till the end of grain filling, probably as

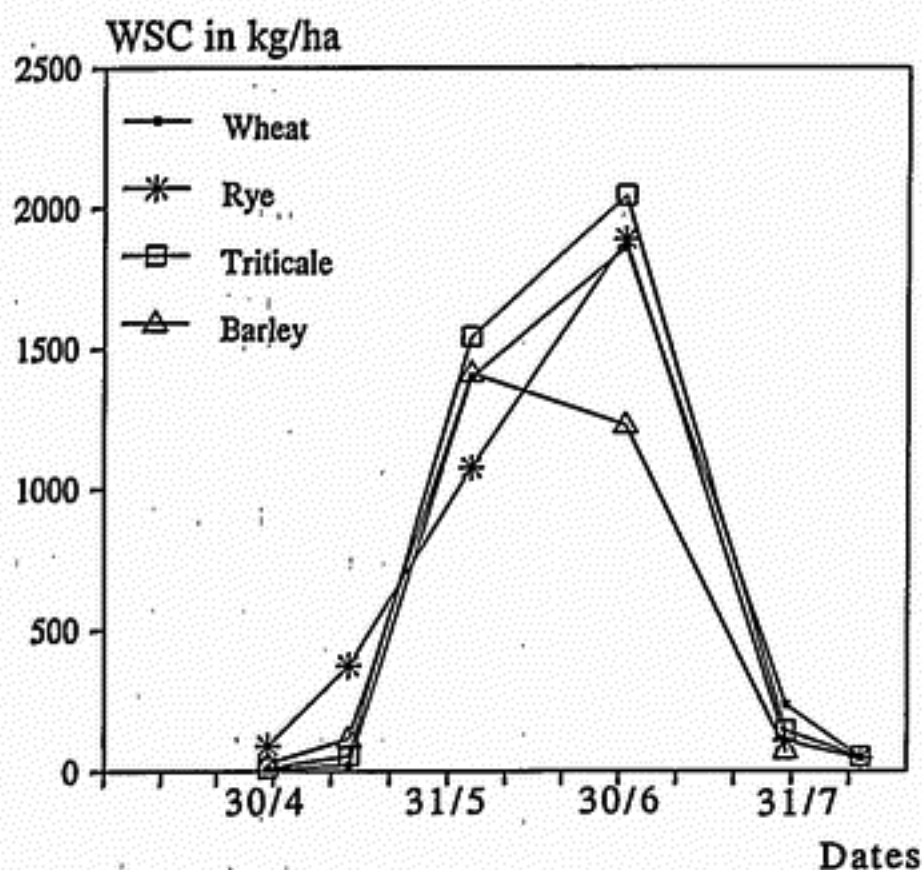


Fig. 4. WSC (kg/ha) in stems.

a result of photosynthetic activity of the upper stem parts (Spiertz et al., 1971). The high grain yields (Ellen, 1993), also observed by Spiertz & Ellen (1978), may be associated with this phenomenon, as in a year with high radiation levels during ear development and grain filling and negligible effects of diseases and pests. High light intensity also resulted in the highest N use efficiency (Ellen & Van Oene, 1989^b). Graham et al. (1983) showed that the response of rye to N was very small, as a result of relatively high natural soil fertility and favourable weather conditions, leading to some lodging. N applications exceeding 35 kg/ha did not result in higher dry matter and grain production in their experiment. N concentrations in the grains were highest in rye and increased from 2.50 at 35 to 2.66% at 140 kg N/ha; that in the straw from 0.73 to 1.05%. This demonstrates that in their experiment N was not the limiting factor for dry matter and grain production. Calculated from their experiment, N-utilization for grain production, expressed as NHI, was lowest for rye as it was in our experiment (Table 1). Again, in our experiment soil fertility and weather conditions were favourable, as can be concluded from N yields and grain yields (Table 1; Ellen, 1993).

The low WSC concentration in the stems of rye until 3/6 (Fig. 3) may be the result of the demand for assimilates by the growing stem (Ellen, 1990). Figure 4 shows that the initial increase in WSC in rye was higher than in the other crops, because of phenological development. Between 29/4 and 13/5 the increase in WSC in rye exceeded that in the other species. This is probably related to the faster development and earlier maximum leaf size. From 13/5 until 3/6 dry matter accumulation was similar for

all crops (Ellen, 1993), not only suggesting a comparable assimilate production, but also that large amounts of WSC were consumed for stem growth (Fig. 4). This growth also suggests competition between stem, leaf and ear growth. Stem growth in rye apparently had higher priority than in the other species, causing a slower increase in WSC surplus until the start of linear grain filling (Fig. 4). In this way, plant structure of rye differs from the other cereals. The pattern of WSC accumulation was similar, but the highest level distinctly lower in barley. Grain filling in barley accelerated more than in the other species. This is also expressed in an earlier decrease in WSC in the stems (Fig. 4).

The photosynthetic capacity in rye was lower than that in the other species, due to the earlier development and small leaf area. At nearly the same time this was followed by stem and ear growth, leading to competition for photosynthates. Photosynthate supply from other sources, especially the peduncle, which is an important photosynthetically active source for WSC production, may partly alleviate this constraint (Spiertz et al., 1971). Also barley was early in growth and plant development, but had more leaves for photosynthate production. Nevertheless, compared to the other cereals, grain growth in rye seemed to be more dependent on WSC stored before flowering.

On 30/6, when grain filling had started in all cereals (Ellen, 1993), 89% of the total WSC reserves, averaged over all species, was found in the stems. Remobilization of WSC started in all species parallelly in various organs (Fig. 3), shortly after beginning of grain growth and removal was practically complete; the reserve concentrations in vegetative plant parts at maturity were, averaged over all species, 1%. On the basis of the data of 30/6, the apparent contribution of WSC reserves to grain yield was calculated as 25% in wheat, 30 in rye, 28 in triticale and 24 in barley. This corresponds to respectively 2190, 1990, 2300 and 1590 kg dm per ha. Weather conditions (Austin et al., 1980), damage by diseases (Spiertz, 1978), cultivar characteristics (Ellen, 1990) and N applications (Ellen, 1991; Spiertz & Ellen, 1978) influence this relative contribution to grain yield.

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