Dry matter and nitrogen redistribution in autumn- and spring-sown wheats

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Abstract

Five cultivars of wheat were sown in May over two years and 4 cultivars in October of the first year. All cultivars were harvested at anthesis and maturity. In the first year, harvests were also taken at tillering and booting. Dry matter and nitrogen contents of plant components were measured on each occasion. Grain yields averaged 7.1 t/ha for the autumn sowings and 4.5 t/ha for the spring sowing. Grain nitrogen yields averaged 132 and 99 kg N/ha respectively. The proportion of grain growth from anthesis to maturity attributable to net redistribution of dry matter from leaves, stems and vegetative tillers ranged from 21% in the second autumn sowing to 50% in the first autumn sowing. The proportion of the net nitrogen increase in the grain from anthesis to maturity attributable to redistribution of nitrogen from leaves, stems, vegetative tillers and chaff averaged 95% for the autumn sowings and 81% for the spring sowing.

Additional key words: Triticum aestivum L., *yield components, growth stage.*

Introduction

Wheat crops have to be high yielding to be profitable, but also have to meet certain quality parameters to be acceptable to millers. In New Zealand, there has been a switch to spring-sown wheats to improve grain nitrogen levels to meet milling quality requirements, usually resulting in lower yields (Martin, 1987). This paper examines the dry matter accumulation, nitrogen uptake and dry matter and nitrogen redistribution in both autumn- and spring-sown wheat in an attempt to explain contrasting results between autumn and spring wheat crops.

Materials and Methods

Two trials have been fully described by Martin (1987), and a third by Martin *et al.* (1992). They were all carried out on a heavily-cropped Wakanui silt loam soil (New Zealand Soil Bureau, 1968) at the MAF Technology Research Farm, Lincoln, about 25 km south west of Christchurch. The first trial (Autumn 1) was sown on 6 May 1986, the second (Spring) on 3 October 1986, and the third (Autumn 2) on 5 June 1987. A split split plot design was used in Autumn 1 and Spring, with sowing date as main plot factors, cultivars as subplot factors, and nitrogen as subsubplot factors. In Autumn 2, a randomized block design was used with cultivars and nitrogen as treatments. In Autumn 1 and Autumn 2, analysis was restricted to the common cultivars: Batten, Kotare, Oroua, Rongotea and Tui. In Spring, the cultivars sown were Karamu, Oroua, Otane and Rongotea. The common nitrogen fertilizer treatments used for the 3 trials were either 50 kg nitrogen/ha at late tillering, 50 kg nitrogen/ha at late tillering plus 50 kg nitrogen/ha at booting, or 100 kg nitrogen/ha at late tillering. Nitrogen fertilizer was applied to Autumn 1 on 17 September and 31 October, to Spring on 17 November and 5 December, and to Autumn 2 on 21 September and 6 November.

In Autumn 1 and Spring, whole plants were sampled from two 0.25 m^2 quadrats in each plot at tillering and booting and total yield and nitrogen content were measured. At anthesis two 0.5 m^2 quadrats were sampled from all crops, and the plants divided into ears, leaves, stems and infertile tillers. Dry matter and nitrogen contents were determined on all these components. At final harvest of all crops, dry matter, yield and nitrogen content were determined for grain, chaff (non grain parts of the ear), leaves and stems from a subsample of a hand harvest sample taken from 3 m^2 in each plot.

Dry matters were determined by drying to constant weight at 85°C in a forced draught oven, and nitrogen contents were determined using the micro-Kjeldahl method.

The standard error of the grand mean was determined for each yield component at each harvest. Grand means between experiments were compared by dividing the difference between the grand means by the standard error of the difference between the 2 means, and using an appropriate T test calculated from the standard error of the mean and degrees of freedom for each trial.

Results

Differences between nitrogen treatments and cultivars were generally small and variable, and so only the grand means of the trials are presented in this paper.

Dry matter yield, nitrogen content and nitrogen yield data are presented in Table 1. The samples were quite variable at the tillering and booting stages, but Autumn 1 had more dry matter than Spring at both samplings, and there was no significant difference in nitrogen content. Nitrogen yield was significantly higher ($P<0.05$) in Autumn 1 at booting but not at tillering.

Dry matter yield at anthesis and maturity

Total and component dry matter yields at anthesis and maturity were generally highest in Autumn 1 and lowest in Spring; the differences between all 3 trials were significant ($P<0.05$), except for grain yield between Autumn 1 and Autumn 2 and for harvest index between Autumn 2 and Spring. For vegetative tillers at anthesis, Spring had significantly higher ($P<0.05$) dry matter than the two Autumn sowings.

At anthesis, Spring produced less than 40% and Autumn 2 only 62% of the total dry matter yield of Autumn 1. 17% of this dry matter was in the ear in Autumn 1, 20% in Autumn 2 and 25% in Spring. Most of the dry matter at anthesis was in the stem, 62% for Autumn 1, 56% for Autumn 2 and 49% for Spring. This declined to 34, 30 and 25% of the total by maturity for Autumn 1, Autumn 2 and Spring respectively. Leaf dry matter yield also declined from an average of 20% of the total dry matter at anthesis to around 7% at maturity.

At maturity, Spring produced 56% of the total dry matter yield, but 63% of the grain yield of the 2 autumn crops. Autumn 2 produced about the same grain yield as Autumn 1, but had 30% less non grain dry matter. Hence Spring and Autumn 2 had significantly higher harvest indices than Autumn 1. At maturity, chaff made up around 16% of the total dry matter in all 3 sowings.

Table 1. Dry matter yield (kg/ha), nitrogen content (%), and nitrogen yield of plants or plant components of autumn and spring sown wheat at 4 stages of growth. Standard errors of the grand mean in brackets. Data are means for cultivar and nitrogen treatments at 0% moisture.

	Yield (kg/ha)			Nitrogen content (%)			Nitrogen yield (kg/ha)		
	Autumn 1	Autumn 2	Spring	Autumn 1	Autumn 2	Spring	Autumn 1	Autumn 2	Spring
Tillering	440 (23)	-	320 (21)	3.80 (0.06)	-	3.99 (0.14)	16.1 (0.7)	-	12.8 (1.3)
Booting	3220 (124)	-	1410 (61)	1.94 (0.06)	-	2.70 (0.03)	62.3 (2.3)	-	38.1 (1.9)
Anthesis									
Ear	2280 (36)	1670 (19)	1330 (37)	1.69 (0.03)	2.02 (0.01)	1.86 (0.03)	38.6 (0.8)	33.7 (0.4)	24.5 (1.0)
Leaf	2750 (42)	1870 (24)	800 (28)	2.16 (0.03)	3.35 (0.03)	3.43 (0.04)	59.6 (1.4)	63.0 (1.1)	27.0 (1.2)
Stem	8480 (146)	4800 (58)	2640 (82)	0.60 (0.02)	1.09 (0.02)	1.24 (0.03)	51.0 (1.5)	51.9 (1.0)	32.3 (1.3)
Vegetative tillers	280 (26)	200 (20)	620 (46)	0.88 (0.04)	1.90 (0.05)	2.26 (0.05)	2.5 (0.3)	4.0 (0.5)	14.2 (1.2)
Total	13790 (240)	8540 (90)	5390 (171)	1.10 (0.06)	1.79 (0.02)	1.83 (0.03)	151.7 (3.7)	152.6 (2.3)	98.0 (4.3)
Maturity									
Grain	7130 (81)	7050 (72)	4490 (114)	1.76 (0.01)	1.97 (0.01)	2.22 (0.02)	125.0 (1.5)	138.8 (1.7)	99.2 (2.7)
Chaff	2430 (34)	2070 (45)	1640 (50)	0.38 (0.02)	0.37 (0.01)	0.42 (0.02)	9.3 (0.3)	7.6 (0.3)	6.8 (0.5)
Leaf	1920 (43)	780 (14)	460 (28)	0.56 (0.01)	0.92 (0.02)	1.00 (0.03)	10.7 (0.3)	7.1 (0.2)	4.7 (0.4)
Stem	5900 (74)	4250 (46)	2180 (64)	0.19 (0.01)	0.24 (0.01)	0.27 (0.01)	11.0 (0.4)	10.4 (0.2)	5.9 (0.3)
Total	17380 (169)	14150 (137)	8760 (227)	0.90 (0.0001)	1.16 (0.01)	1.33 (0.002)	156.1 (1.8)	163.9 (2.0)	116.6 (3.6)
Harvest Index	0.41 (0.003)	0.50 (0.003)	0.51 (0.004)				0.80 (0.43)	0.85 (0.27)	0.85 (0.50)

Nitrogen content and nitrogen yield at anthesis and maturity

Total and component nitrogen contents were generally highest in Spring and lowest in Autumn 1; the differences between all 3 trials were significant ($P<0.05$) at anthesis and maturity, except for leaf at anthesis between Spring and Autumn 2, and for chaff. However, at anthesis, Autumn 2 had significantly higher ($P<0.05$) ear nitrogen contents than Spring or Autumn 1.

Total and component nitrogen yields at anthesis and maturity were generally significantly lower ($P<0.05$) in Spring than in the autumn sowings, except for vegetative tillers at anthesis and for chaff and nitrogen harvest index at maturity. There was no significant difference between Autumn 1 and Autumn 2 in leaf, stem and total nitrogen yields at anthesis, and for stem nitrogen yield at maturity. The proportion of nitrogen in the ear increased from about 25% at anthesis to about 90% at maturity in all 3 crops. Leaf and stem nitrogen yield declined from around 30 to 40% each of the total at anthesis to around 11% combined at maturity in all 3 crops. Differences in nitrogen yields between crops were smaller than differences in dry matter yields, with Spring producing 64% of the total nitrogen yield of the 2 autumn crops at anthesis and 73% at maturity. Spring produced 79% of the grain nitrogen yield of Autumn 1, compared with 63% of the grain dry matter. At maturity, chaff made up 5% of the total nitrogen yields compared with 16% of the total dry matter yields in all 3 sowings.

Growth rates

Development time to anthesis and maturity were 35 days shorter for the June sown Autumn 2 compared to the May sown Autumn 1. The October sown Spring took only 40% of the time of Autumn 1 to reach anthesis, and less than half the time to reach maturity.

The rate of increase in dry matter yield was significantly higher ($P<0.05$) for Spring compared to Autumn 1 from sowing to late tillering (Table 2), but significantly lower ($P<0.05$) from late tillering to anthesis, and not significantly different from anthesis to maturity (taken as 700°C accumulated day degrees above a base temperature of 0°C). The overall rate of dry matter increase was therefore very similar between sowings. Autumn 2 had significantly higher rates of dry matter increase from anthesis to maturity and from sowing to maturity than the other 2 trials.

The rate of increase in nitrogen yields was significantly higher ($P<0.05$) in Spring compared with Autumn 1, except from booting to anthesis (Table 2). Autumn 2 had intermediate nitrogen yields, significantly different ($P<0.05$) to the other crops from sowing to maturity, but not between anthesis and maturity ($P<0.05$).

Redistribution of dry matter and nitrogen

Autumn 2 had a significantly greater increase in total dry matter from anthesis to maturity than the other 2 crops, but the increase in grain was not significantly different to Autumn 1 (Table 3). Table 3 assumes that all the losses in dry matter and nitrogen in the leaves and stems are redistributed to the ears, and that losses from the chaff go to the grain. Compared with Autumn 1, Autumn 2 had significantly more dry matter redistributed from the leaves but less from the stems and vegetative tillers; and less translocated to the grain but more to the chaff. The lower grain yield in Spring was mainly due to much less redistribution of dry matter out of the leaves and stems, especially compared to Autumn 1, although this was partially offset by higher redistribution from vegetative tillers.

If it is assumed that all the dry matter from the vegetative tillers was lost through respiration rather than redistributed to the grain, then the proportion of grain dry matter attributable to redistribution from the rest of the plant would be reduced by about 11% in Spring, but in Autumn 1 and Autumn 2, which had very few vegetative tillers, the proportion would be reduced by around 4%.

Table 2. Time between development stages (days) and rate of increase of dry matter and nitrogen yields (kg/ha/day) for autumn- and spring-sown wheat between these development stages.

	Days			Dry Matter			Nitrogen		
Stage	Autumn 1	Autumn 2	Spring	Autumn 1	Autumn 2	Spring	Autumn 1	Autumn 2	Spring
Sowing-late tillering	135	-	45	3.2 (0.2)	-	7.2 (0.5)	0.12 (0.01)	-	0.28 (0.03)
Late tillering-booting	40	-	18	69.7 (2.9)	-	60.5 (2.5)	0.87 (0.06)	-	1.35 (0.10)
Booting to anthesis	22	-	16	484.0 (11.7)	-	247.9 (12.2)	4.06 (0.23)	-	3.74 (0.35)
Anthesis to maturity	47	47	40	76.6 (5.9)	119.1 (2.3)	84.6 (7.0)	0.09 (0.11)	0.24 (0.05)	0.46 (0.13)
Sowing to maturity	244	209	119	71.2 (0.7)	67.7 (0.7)	73.6 (1.9)	0.64 (0.01)	0.78 (0.01)	0.98 (0.03)

Table 3. Change in weights (kg/ha) of dry matter and nitrogen from anthesis to maturity for autumn- and spring-sown wheat.

	Dry Matter			Nitrogen		
	Autumn 1	Autumn 2	Spring	Autumn 1	Autumn 2	Spring
Total	3590 (148)	5600 (107)	3370 (279)	4 (5.3)	11 (3.0)	19 (5.3)
Grain	7130 (81)	7050 (72)	4490 (114)	125 (1.5)	139 (1.7)	99 (2.7)
Chaff[a]	150 (45)	400 (46)	310 (64)	-29 (1.4)	-26 (0.5)	-17 (1.2)
Leaves	-830 (80)	-1100 (19)	-340 (46)	-50 (2.1)	-56 (1.0)	-22 (1.2)
Stem	-2570 (166)	-550 (49)	-460 (117)	-40 (1.5)	-41 (1.0)	-26 (1.2)
Vegetative tillers	-280 (26)	-200 (19)	-620 (46)	-3 (0.3)	-4 (0.5)	-14 (1.2)
Amount relocated to grain[b]	3550 (255)	1450 (88)	1110 (212)	121 (4.5)	128 (2.2)	79 (4.1)
Relocated as % of the increase in grain weight	50	21	25	97	92	81

[a] weight of chaff at maturity - weight of ear at anthesis. [b] assuming all weight loss relocated to grain.

There was no significant difference in total nitrogen uptake between anthesis and maturity between sowings (Table 3). Autumn 1 and Autumn 2 were not significantly different in amounts of nitrogen redistributed, except for grain nitrogen yield and amount redistributed from the leaves, and to the grain. Spring had a significantly lower amount of nitrogen redistributed from vegetative parts to the grain.

The proportion of the net nitrogen increase of the grain from anthesis to maturity attributable to redistribution (including redistribution from the chaff), was considerably higher than for dry matter. Neglecting the contribution from tillers has little effect in both autumn sowings, but reduced the redistribution from 81 to 68% for spring wheat.

Yield components

Compared to the 666 ears/m^2 in Autumn 1, ear populations were 18% lower in Autumn 2 and 34% lower in Spring (Table 4). However, grain numbers were 10% higher, significant ($P<0.05$) in the case of Autumn 2, but not Spring. Also, grain weights were about 5% higher ($P<0.05$) in both Autumn 2 and Spring.

Table 4. Yield components for autumn- and spring-sown wheat.

	Autumn 1	Autumn 2	Spring
Ears/m^2	666 (16)	564 (6)	373 (13)
Grains/ear	29.5 (0.7)	32.4 (0.3)	32.4 (1.3)
Grain weight (mg)	38.1 (0.2)	40.3 (0.2)	40.2 (0.2)

Discussion

The grain yields of the autumn-sown crops were more than 50% higher than that of the spring sowing, mainly because they had more ears resulting in 19,000 grains/m^2 compared with 12,000 for the spring crop. In contrast, Watson *et al.* (1963) found no difference in ear numbers between autumn- and spring-sown crops. The dry matter accumulation rate from sowing to maturity was very similar for all 3 sowings, so the greater yield of the 3 autumn-sown crops resulted from the longer growth period from sowing to anthesis, allowing the greater number of fertile tillers. The spring-sown crop, by contrast, had a greater weight of vegetative tillers at anthesis. The time from sowing to tillering was about 3 times as long in the autumn wheat, and allowed for more reproductive tillers to develop. Tiller production is related to thermal time, with earlier sowings producing more fertile tillers (Green *et al.*, 1981) and consequently higher leaf areas (Watson *et al.*, 1963).

One fifth to one half of the grain dry matter in the three sowings came from the net remobilization of reserves from other parts of the plant. These are similar to results from overseas studies reviewed by Evans *et al.* (1975), and underline the importance of post-anthesis photosynthesis to maximise grain filling. The second autumn-sown crop had low tiller numbers which would have reduced leaf area. The low tiller numbers, possibly because the long cropping history and very dry August and September, which would have restricted nitrogen availability and pre-anthesis uptake. The spring-sown crop was exposed to higher temperatures during grain filling, which increased the rate of grain filling but reduced the chronological duration of grain growth by 7 days and, therefore, reduced the opportunity to accumulate grain dry matter from current assimilation. Higher temperatures would also accelerate nitrogen transfer from leaves to grain and thus can lead to premature senescence of the leaves and early cessation of grain filling (Spiertz and de Vos, 1983). Therefore, it is essential to ensure that green leaf area is maintained as long as possible, through appropriate fungicide application and irrigation practices, especially in spring-sown crops.

Most of the cultivars in these trials usually tiller freely and so had high numbers of stems and ears per unit area. For the autumn sowings, this resulted in nearly 60% of the dry matter being in stem material at anthesis. Up to 30% of this was lost during grain filling. Rawson and Evans (1971) found that about two thirds of this loss was due to remobilization, with the rest due to respiration. The nitrogen content of the grain was lower in the autumn-sown wheats, as was the baking score (Martin, 1987). Even though a greater quantity of nitrogen was taken up by the grain in the autumn-sown crop, it was diluted by the much larger yield.

Spiertz and de Vos (1983) found a close relationship between ear number and nitrogen yield at anthesis, and this was apparent in these trials. Remobilization of nitrogen accounted for most of the nitrogen in the grain in these trials, which agreed with overseas studies (Austin *et al.*, 1977b). The sites had low fertility. Winter rainfall was above average for Autumn 1 and Spring (Martin, 1987), so it is likely that the soil reserves of available nitrogen were very low by the time the crops reached grain filling. In Autumn 2, a similar situation occurred, as low tiller numbers were indicative of low nitrogen levels after planting (Martin et al., 1992). Blackwell and Incoll (1981) found that as soil nitrogen status decreased, the nitrogen contribution from leaves to grain increased. Practically all this nitrogen comes from the top two leaves (Simpson *et al.*, 1983). As the amount of nitrogen translocated out of the leaves increases, the rate of photosynthesis by that leaf decreases (Gregory *et al.*, 1981), since 75% of the nitrogen in the leaf cells is in the chloroplasts (Stocking and Ongun, 1962).

The shorter duration from anthesis to maturity in the spring-sown crop will have curtailed nitrogen uptake. However, the shorter growth period was more than compensated for by a faster rate of nitrogen uptake by the grain, resulting in a higher final grain nitrogen content.

The nitrogen harvest indices in this trial are towards the high end of the range of data reported in the literature (Spiertz and de Vos, 1983). At anthesis, the proportion of dry matter (24%) and nitrogen (21%) in the ear was higher and in the stem (58% and 34% respectively) lower than that reported by Spiertz and de Vos (1983). This is probably a reflection of the semi dwarf wheats used in this study, which are characterised by relatively larger ears and shorter stems (Cross *et al.*, 1979).

The net contribution of dry matter relocated from stems and leaves in this study are higher than those reported in Europe (Spiertz and Vos, 1985). The contribution of relocated nitrogen to grain nitrogen is also at the higher end of European data (Spiertz and Vos, 1985). Nitrogen uptake from the soil can be markedly affected by soil moisture content (Gregory *et al.*, 1981). In these trials, the very wet conditions during winter could have led to nitrogen in the soil being depleted by leaching, resulting in greater remobilization of nitrogen from leaves and stems during grain filling. However, the relative levels of nitrogen in the plants at anthesis and maturity for all three sowings were similar to other work (Austin *et al.*, 1977b; Van Sanford and MacKown, 1987).

Assuming the nitrogen translocated to the grains is in the form of amino acids containing 16% nitrogen and the rest carbohydrate (Austin *et al.*, 1977b), then around 780 kg/ha of the dry matter translocated to the grains in the 2 autumn crops and 490 kg/ha in the spring-sown crop was associated directly with the nitrogen transfer. This was only 21% of the dry matter translocated in Autumn 1 but around half of the translocated dry matter in the other 2 crops. Similarly, amino acids or similar nitrogen compounds accounted for between 32% (Autumn 2) and 45% (Spring) of the losses in dry matter from the leaves in autumn- and spring-sown crops respectively — figures very similar to the 40% reported by Spiertz and Ellen (1978).

The calculated amounts of dry matter translocated were made by ignoring losses due to respiration. Austin *et al.* (1977a) have shown that such losses can be considerable, particularly from the stems. They found that, in some cultivars, little of the carbon fixed before anthesis found its way to the grain, but concluded that it would have been used to provide energy to relocate nitrogen and current photosynthate to the grain. Hence, the net relocation values given in this paper will still give relative differences between the trials. However, there can also be significant losses of nitrogen to the atmosphere during grain filling (Parton *et al.*, 1988). Also, this experiment only considered above-ground plant material. Remobilization of material to and from the roots, which can be substantial in some circumstances (Simpson et al., 1983), was not measured.

This study has shown that there are considerable differences in dry matter production, nitrogen uptake, and net redistribution of dry matter and nitrogen during grain filling both between autumn- and spring-sown wheat and between the same cultivars sown under the same nitrogen regime in different environments. More detailed studies are required to determine how these differences can be exploited to optimize the use of inputs such as nitrogen fertilizer.

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References

Austin, R.B., Edrich, J.A., Ford, M.A. and Blackwell, R.D. 1977a. The fate of the dry matter, carbohydrates and ^{14}C lost from the leaves and stems during grain filling. *Annals of Botany* ***41***, 1309-1321.

Austin, R.B., Edrich, J.A., Ford, M.A. and Blackwell, R.D. 1977b. The nitrogen economy of winter wheat. *Journal of Agricultural Science* ***88***, 159-167.

Blackwell, W.M. and Incoll, L.D. 1981. Nitrogen stress of winter wheat changed the determinants of yield and the distribution of nitrogen and total dry matter during grain filling. *Australian Journal of Plant Physiology* ***8***, 191-200.

Cross, R.J. and Haslemore, R.M. 1979. Nitrogen uptake and redistribution in Karamu and other spring wheats. *New Zealand Journal of Agricultural Research* ***22***, 547-552.

Evans, L.T., Wardlaw, I.F. and Fischer, R.A. 1975. Wheat. *In* Crop physiology: some case histories, (ed. L.T. Evans). pp. 101-149. C.U.P., Cambridge.

Green, C.F., Paulsen, G.A. and Ivins, J.D. 1985. Time of sowing and the development of winter wheat. *Journal of Agricultural Science* ***105***, 217-221.

Gregory, P.J., Marshall, B. and Biscoe, P.V. 1981. Nutrient relations of winter wheat. 3. Nitrogen uptake, photosynthesis of flag leaves and translocation of nitrogen to grain. *Journal of Agricultural Science* ***96***, 539-547.

Martin, R.J. 1987. The effect of time of nitrogen application on the yield and quality of contrasting cultivars of autumn sown wheat. *Proceedings Agronomy Society of New Zealand* ***17***, 103-8.

Martin, R.J., Sutton, K.H., Moyle, T., Hay, R.L. and Gillespie, R.N. 1992. The effect of nitrogen fertilizer on the yield and quality of six cultivars of autumn sown wheat. *New Zealand Journal of Crop and Horticultural Science* ***20***, in press

New Zealand Soil Bureau 1968. General survey of the soils of the South Island. New Zealand Soil Bureau Bulletin 27. 404 pp.

Parton, W.J., Morgan, J.A., Altenhofen, J.M. and Harper, L.A. 1988. Ammonia volatilization from spring plants. *Agronomy Journal* ***80***, 419-425.

Rawson, H.M. and Evans, L.T. 1971: The contribution of stem reserves to grain development in a range of wheat cultivars of different height. *Australian Journal of Agricultural Research* ***22***, 851-863.

Simpson, R.J., Lambers, H. and Dalling, M.J. 1983. Nitrogen redistribution during grain growth in wheat (*Triticum aestivum* L.). IV. Development of a quantitative model of the translocation of nitrogen to the grain. *Plant Physiology* ***71***, 7-14.

Spiertz, J.H.J. and Ellen, J. 1978. Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilisation of assimilates and nutrients. *Netherlands Journal of Agricultural Science* ***26***, 210-231.

Spiertz, J.H.J. and de Vos, N.M. 1983. Agronomical and physiological aspects of the role of nitrogen in yield formation of cereals. *Plant and Soil* ***75***, 379-391.

Spiertz, J.H.J., Vos, J. 1985. Grain growth of wheat and its limitations by carbohydrate and nitrogen supply. In Wheat Growth and Modelling, (eds. W. Day and R.K. Atkin). pp. 129-141. Plenum Press, New York.

Stocking, C.R. and Ongun, A. 1962. The intracellular distribution of some metallic elements in leaves. *American Journal of Botany* ***49***, 284-289.

van Sanford, D.A. and MacKown, C.T. 1987. Cultivar differences in nitrogen remobilisation during grain fill in soft red winter wheat. *Crop Science* ***27***, 295-300.

Watson, D.J., Thorne, G.N. and French, S.A.W. 1963. Analysis of growth and yield of winter and spring sown wheats. *Annals of Botany* ***27***, 1-22.