DRY MATTER AND NITROGEN ACCUMULATION BY STANDARD HEIGHT AND SEMI-DWARF BARLEY ISOTYPES[1]

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ABSTRACT- To assess nitrogen movement from the soil into the plant and within the plant, studies of dry matter and N accumulation are necessary. The objective of this experiment was to study the effect of 30, 60, 90 and 120 kg of N/ha on dry matter and N accumulation by four standard height-semi-dwarf normal mutant malting barley isotype pairs (Morex, Hazen, Norbert, Andre) and two check cultivars: Steptoe and Klages. Considerable differences among genotypes on dry matter accumulation until anthesis and dry matter lost during grain filling period were observed. Genotypic differences for pre-anthesis (range: 36.6 to 52.9 mg N/plant) and post-anthesis (range: -2.3 to 10.8 mg N/plant) N accumulation and in total N accumulation (range: 69 to 149.2 mg N/plant in 1987 and 41.3 to 56.5 mg N/ha in 1989) were observed. Within the isotype pairs, consistent differences were detected for post-anthesis and total N accumulation both favoring the standard isotypes. These differences were not affected by fertilizer N levels. Genotypic differences in N remobilization into the grain were also observed. Relationship between N and dry matter partitioning are discussed.

Index terms: *Hordeum vulgare*, nitrogen response, protein.

ACÚMULO DE MATÉRIA SECA E DE NITROGÊNIO POR GENÓTIPOS DE CEVADA COM ALTURA NORMAL E REDUZIDA

RESUMO- Para avaliar o movimento do nitrogênio do solo para a planta e dentro desta, estudos de acúmulo de matéria seca e de N são necessários. O objetivo deste trabalho foi o de estudar o efeito de 30, 60, 90 e 120 kg/ha de N no acúmulo de matéria seca e N em oito genótipos de cevada cervejeira (quatro com altura normal e quatro com altura reduzida, mutantes de cada um dos normais), e duas testemunhas. Verificou-se variabilidade entre os genótipos no acúmulo de matéria seca até a antese e na transferência desta para o grão. Foram observadas diferenças entre os genótipos no acúmulo de N até a antese (de 36,6 a 52,9 mg N/planta), após a antese (de -2,3 a 10,8 mg N/planta) e no total de N acumulado na planta (de 69 a 149,2 mg N/planta em 1987 e 41,3 a 56,5 mg N/planta em 1989). Diferenças consistentes foram observadas, entre os isótipos pares, no N acumulado após antese e no N total, ambos maiores nos isótipos de altura normal. Verificou-se, também, variabilidade entre os genótipos na remobilização do N para o grão. Discutem-se as relações entre distribuição de matéria seca e N na planta.

Termos para indexação: *Hordeum vulgare*, proteína, resposta ao nitrogênio.

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INTRODUCTION

Nitrogen is the most expensive fertilizer utilized on cereal crops and has significant impact on its cost production. A significant portion of the applied N may be lost by leaching and denitrification (Huber et al., 1977). Therefore, plant breeders are challenged to develop cultivars that have a better ability to absorb the N from the soil and partition most of the absorbed N to the grain. There are evidences for genetic control of some of the component traits that determine the nitrogen concentration in the grain (Cox et al., 1985; Nedel et al., 1997).

Some association between translocation of nitrogen and carbon compounds has been inferred by positive correlation between the proportion of total N in the grain and harvest index (Desai & Bhatia, 1978). To get an understanding of the assimilation and partitioning of N and C process in the context of plant growth and development, data on accumulation and partitioning of dry matter and nitrogen are necessary.

A negative correlation between grain yield and N in the grain has been reported in barley and wheat (Kramer, 1979). This negative correlation can be partly explained on bionergetic grounds. According to

Penning de Vries et al. (1974), 1 g of glucose produced by photosynthesis can be used by the crop to produce 0,83 g of carbohydrate or 0,40 g of protein. This would imply that the only way to increase protein without a decrease in yield, or vice versa, would be to increase photosynthetic capacity. This increase could be met by having a higher rate of photosynthesis per unit of leaf area, increasing leaf area or extending the period of photosynthetic activity, or by maximizing the mobilization of photosynthetic reserves into the grain (Bhatia & Rabson, 1976).

Grain yield and protein represents the end result of C and N metabolism. They are influenced by the sink size and by the ability to translocate assimilates from the site of synthesis, the source to the sink. It is generally accepted that current photosynthesis plays a dominating role in carbohydrate supply to the grain. Assimilation formed before anthesis contribute with less than 15 % to final grain weight under most non stress conditions (Austin et al., 1980). For N, however, it has been estimated that two thirds of the grain nitrogen is derived from nitrogen assimilated before anthesis and one-third from current assimilation (Cregan & Berkum, 1984). However this may vary greatly depending on soil moisture and N availability during the grain filling period.

The objective of this study was to determine the influence of soil N supply on the genotypic differences for nitrogen and dry matter accumulation using standard-height semi-dwarf normal mutant barley isotype pairs.

MATERIAL AND METHODS

Field experiments were conducted in 1987 and 1989 at the Spillman Agronomy Farm, near Pullman Washington on a Palouse silt loam soil (fine-silty, mixed mesic Pachic Ultic Haploxeroll). The two experimental crop years were preceeded by typical Palouse crops; peas (*Pisum sativum* L.) in 1986 and barley in 1988. The residual N to a depth of 0.9 m in the soil before planting was 19.5 and 9.3 mg N/kg in 1987 and 1989, respectively.

The design was a randomized complete block arranged in split-plots with four replications. The treatments were four N levels (30, 60, 90 and 120 kg N/ha) as main plots and ten spring barley genotypes as sub-plots. The barley genotypes included four standard height-semi-dwarf (SD) normal-mutant malting isotype pairs (Aydin, 1985; Ullrich & Aydin, 1988): Morex and Morex SD (6-row); Hazen and Hazen SD (6-row); Norbert and Norbert SD (2-row); Andre and Andre SD (2-row); and two check cultivars: Steptoe (6-row) as a yield check and Klages (2-row) as a malting quality check. Morex also served as a 6-row malting quality check. The genotypes description can be seen elsewhere (Nedel et al., 1993). The plot size was of 4 x 1.28 m and 4.8 x 1.28 m in 1987 and 1989, respectively.

Starter fertilizer was applied at 10 kg N ha^{-1}, 12.5 kg P ha^{-1} and 8.7 kg S ha^{-1} with the seed. The remaining N was placed 10 cm below the seed. Amonium nitrate was the N source. In 1989 an additional 45 kg P/ha, as triple superphosphate, and 20 kg S/ha, as $CaSO_4$ were broadcasted and incorporated into the soil prior to planting.

Plant samples were taken at Large's (1954) growth stages 10.4 (3/4 of the heads emerged) and at stage 11.3 (kernel dough). Ten plants were randomly harvested from within segments of the six internal rows of each plot where a uniform stand was observed. The plants harvested at stage 11.3 were divided into vegetative tissue (culm+leaves+chaff) and grain. Dry weight was obtained after drying for 72 hours at 55°C in a convection dryer. The vegetative samples were ground through a 1 mm sieve in a Wiley mill. The grain samples were ground through a 0.5 mm sieve in a Udy mill. Total N in the vegetative tissue and in the grain was determined by the micro-Kjeldahl method (Association of Official Agricultural Chemists, 1965). In the 1987 experiment, plants at anthesis were sampled on 30 cm length and the number of plants not counted. That's why results that envolved dry matter data at anthesis on its calculation are not presented.

From the parameters measured (dry weight and N concentration) the following variables were derived: 1) N yield in the shoot (leaf+culm+chaff) and grain (mg/pl) = (dry matter yield of component x % N in the tissue)/100; 2) total N yield at anthesis (mg/pl) = total shoot (leaf+culm+chaff) N yield at anthesis = pre-anthesis N accumulation; 3) total N yield at maturity (mg/pl) = shoot (leaf+culm+chaff) + grain N yield at maturity = Total N accumulation; 4) post-anthesis N accumulation (mg/pl) = total N accumulation - pre-anthesis N accumulation;5) N translocation (mg/pl) = pre-anthesis N accumulation- -shoot (leaf+culm+chaff) N yield at maturity.

Analyses of variance over years as well for individual years were conducted with MSTAT microcomputer statistical program (Michigan Statistic-C, 1989). As means comparisons of the various parameters of interest were between two means, either isotypes of a pair or overall standard vs semi-dwarf isotypes the independent t-test was used.

RESULTS AND DISCUSSION

Dry matter accumulation

Dry matter yields at maturity (stage 11.3) were considerably lower in 1989 than in 1987 (Table 1), probably the lower initial soil N level and lower rainfall in the 1989 experiment were factors that contributed

substantially to this difference. Grain yield and total biological yield of the standard isotypes Hazen, Norbert and Andre were greater than their derived semi-dwarf mutants (Table 1). The differences in vegetative dry weight could be due to the differences in plant height (Nedel et al., 1993) and in tillering capacity between each of the isotypes. Morex had significantly lower vegetative dry matter accumulation at anthesis and maturity than Morex SD in 1989. Morex SD was observed to have a thicker culm and a higher tillering capacity than Morex. Based on means over all standard and all semi-dwarf genotypes, the standard types had the higher dry matter accumulation for each variable at the two stages (Table 1). All genotypes showed a reduction in vegetative dry matter, from anthesis to maturity. Morex SD, Hazen, Norbert and Andre SD showed the highest reductions (31, 29, 28 and 35 %, respectively), indicating that these genotypes may have utilized more of the stem and leaf reserves formed prior to anthesis for filling the grain. Morex, Andre and Steptoe had substantially lower reductions (16, 16 and 10 % respectively) suggesting that they may have used assimilates primarily formed by photosynthesis during grain development. Genetic differences may account for differences in pre- and post-anthesis photosynthesis contributions to grain yield. Carbon partitioning can be influenced by environmental conditions as well (Evans & Wardlaw, 1976).

TABLE 1. Mean values for dry matter accumulation in vegetative tissue at anthesis and maturity, and grain and total biological yield by genotype averaged over N treatments.

Genotypes	Anthesis	Maturity					
	Veg. tissue	Veg.		Grain		Bio. yield	
	1989	1987	1989	1987	1989	1987	1989
	g/pl						
Morex	2.26**	3.36	1.89*	4.20	2.15	7.55	4.03
Morex SD	3.12	3.39	2.15	4.15	2.16	7.54	4.32
Hazen	2.97**	4.67**	2.11**	5.50**	2.32**	10.17**	4.42**
Hazen SD	2.41	2.86	1.88	3.19	1.64	6.05	3.52
Norbert	3.68**	4.33**	2.66*	4.04**	2.44**	8.37**	5.10**
Norbert SD	3.18	3.61	2.43	3.31	2.15	6.92	4.58
Andre	3.12**	2.86**	2.63**	3.09**	2.53**	5.95**	5.16**
Andre SD	2.61	2.07	1.69	2.32	2.05	4.39	3.75
Klages	3.53	3.69	2.77	3.50	2.40	7.19	5.17
Steptoe	2.12	3.58	1.90	4.99	2.59	8.56	4.49
Standard	3.00**	3.80**	2.32**	4.21**	2.35**	8.01**	4.67**
Semi-dwarf	2.83	2.98	2.04	3.24	2.00	6.23	4.04

*,** Significant difference between isotypes within a genotype according to t-test at P=0.05 and 0.01, respectively.

In 1987 the vegetative dry matter at maturity, grain yield and total biological yield did not show a significant response to N. However, there was a consistent tendency for the standard height isotypes to increase in dry weight (vegetative, grain yield, biological yield), while the semi-dwarfs had a slight decrease with increasing N fertilizer levels (Table 2). There were no differences in plant height in response to N for either standard height or semi-dwarf isotypes. However, there was a significant linear response to N fertilizer in the number of viable tillers at maturity for the standard isotypes (Nedel, 1990). This could partially explain the response tendency of dry matter accumulation in the vegetative tissue at maturity, grain yield and total biological yield of the standard isotypes. In 1989, standard and semi-dwarf isotypes showed significant responses to N in dry matter accumulation at anthesis and maturity, grain yield per plant and biological yield at maturity (Table 2). Grain yield per plant was strongly related to total N accumulation, in both years (1987 r= 0.95** and 1989 r= 0.84**).

TABLE 2. Mean values combined over standard and semi-dwarf genotypes for dry matter parameters under four N treatments[1].

Genotypes	1987				Sig.	1989				Sig.
	N_1	N_2	N_3	N_4		N_1	N_2	N_3	N_4	

Standard	-	-	-	-		2.5	2.8	3.1	3.3	LQ
Semi-dwarf	-	-	-	-		2.2	2.6	2.9	3.4	LQC
	Vegetative									
Standard	3.4	3.4	3.9	4.3	NS	1.8	2.2	2.5	2.5	LQ
Semi-dwarf	3.0	3.0	2.9	2.8	NS	1.6	1.8	2.2	2.4	LC
	Grain yield									
Standard	3.8	3.9	4.2	4.8	NS	1.8	2.3	2.6	2.5	LQC
Semi-dwarf	3.2	3.4	3.2	3.0	NS	1.6	1.8	2.2	2.2	LC
	Total									
Standard	7.2	7.4	8.1	9.2	NS	3.7	4.5	5.2	5.1	LQ
Semi-dwarf	6.3	6.4	6.2	5.8	NS	3.3	3.7	4.4	4.6	LC

[1] N_1, N_2, N_3 and N_4= 30, 60, 90 and 120 kg/ha of N, respectively; L = linear, Q = quadratic, C = cubic, NS = not significant.

N concentration, accumulation and translocation to the grain

Averaged over N treatments, there were relatively small differences between semi-dwarf and standard height isotypes in N concentration whether significant or not (Table 3). The differences were statistically significant in vegetative tissue at anthesis in 1989 (SD 16.4 vs Std. 15.4 g/kg) and in the grain in 1987 (SD 23.0 vs Std. 22.0 g/kg). Semi-dwarf and standard isotype responses were variable within isotype pairs, but most were significant and in all significant cases, except for the Morex pair, the N concentration was higher in the semi-dwarf than in the standard type in the vegetative tissue at anthesis. For N in the grain, only the Hazen pair consistently displayed a significant difference between isotypes, and the Hazen SD had a higher N concentration than standard Hazen.

TABLE 3. Mean values for N concentration and N assimilation in the vegetative tissue at anthesis and grain and total N assimilation by genotypes averaged over N treatments.

Genotypes	N				N						
	Anthesis		Grain		At anthesis	After anth		Grain		Total	
	1987	1989	1987	1989	1989	1987	1989	1987	1989	1987	1989
Morex	24.7**	17.0	21.2	17.3	38.6**	-	7.0**	89.3	37.4	113.0	45.6
Morex SD	23.0	16.0	21.1	16.9	50.9	-	-0.8	87.2	37.2	112.4	50.0
Hazen	24.6	15.5**	20.8**	16.8**	47.1	-	1.6	115.0**	39.5*	149.2**	48.7
Hazen SD	24.8	17.3	23.3	20.2	42.2	-	2.0	74.6	33.7	101.7	44.2
Norbert	20.7**	13.9**	23.7	18.0	51.6	-	3.9	96.8**	44.5*	122.1**	55.5
Norbert SD	21.9	16.0	23.9	17.7	52.2	-	-0.8	79.2	38.8	104.5	51.4
Andre	22.7**	15.2*	22.5**	17.3	47.9	-	8.6**	69.8**	44.7**	88.1**	56.5**
Andre SD	24.7	16.5	23.7	16.2	43.7	-	-2.3	54.9	33.9	69.0	41.3
Klages	20.3	14.7	21.8	17.3	52.9	-	1.5	76.8	42.0	100.6	54.5
Steptoe	22.1	17.1	18.0	14.6	36.6	-	10.8	90.3	38.4	115.1	47.4
Standard	23.2	15.4**	22.0**	17.4	46.3	-	5.3**	92.7**	41.5**	118.0**	51.6
Semi-dwarf	23.6	16.4	23.0	17.8	47.2	-	-0.5	74.0	35.9	96.9	46.7

*,** Significant difference between isotypes within a genotype according to t-test at P= 0.05 and 0.01, respectively.

Averaged over genotypes, a relatively small but consistent increase in the N concentration in the vegetative tissue at anthesis and in the grain in response to N fertilizer was observed in both years for both standard height and semi-dwarf genotypes with the magnitude of response being greater in 1989 (Table 4). For N concentration in the vegetative tissue at maturity the nitrogen x genotype interaction was significant in both years. Significant differences in N concentration in the vegetative tissue at maturity among N fertilizer levels occurred for all genotypes except Andre, Andre SD and Steptoe in 1987 and Morex, Norbert and Steptoe in 1989. Few semi-dwarf-standard isotype differences in N concentration in vegetative tissue at maturity occurred except for several N fertilizer levels in the Morex and Hazen pairs. In all cases the N concentration was higher in the semi-dwarf than in the standard isotype.

TABLE 4. Mean values combined over standard and semi-dwarf genotypes for N parameters measured for four N fertilizer treatments[1].

Genotypes	1987				Sig.	1989				Sig.
	N_1	N_2	N_3	N_4		N_1	N_2	N_3	N_4	
		N								
Standard	22.3	22.8	23.6	24.1	L	13.3	14.2	16.7	17.5	LC
Semi-dwarf	23.9	22.2	23.9	24.5	LQC	14.6	15.4	16.8	19.1	LQ
		N								
Standard	21.2	22.0	22.8	22.3	LQC	15.8	16.6	18.5	18.9	L
Semi-dwarf	22.5	22.7	23.6	23.4	LC	16.1	17.0	17.9	20.2	LQC
		N								
Standard	-	-	-	-		34.2	40.6	53.6	57.7	LQC
Semi-dwarf	-	-	-	-		33.5	40.7	49.0	65.8	LQ
		N								
Standard	81.9	86.4	95.5	106.9	L	30.2	38.7	49.3	47.8	LQC
Semi-dwarf	73.5	76.6	76.0	69.9	Q	27.2	31.3	39.4	45.7	L
		Total N								
Standard	101.7	108.5	124.3	137.7	LQ	37.0	47.6	61.3	60.5	LQ
Semi-dwarf	98.2	97.4	98.7	93.2	Q	34.4	40.4	51.0	61.1	LQ
		N								
Standard	-	-	-	-		2.8	7.0	8.7	2.7	Q
Semi-dwarf	-	-	-	-		0.8	-0.3	2.0	-4.6	LQC

[1] N_1, N_2, N_3, N_4 = 30, 60, 90 and 120 kg/ha of N, respectively; L= linear, Q= quadratic, C= cubic.

In 1989, at anthesis the Morex SD was the only semi-dwarf that showed significantly higher N accumulation than its standard height isotype (Table 3). However, no difference in the N concentration was observed between these two isotypes (Table 3), therefore, the biomass difference accounted for the N accumulation difference (Table 1). These results are supported by those obtained by Austin et al. (1980) and Dhugga & Waines (1989).

The standard height and semi-dwarf genotypes showed an increase in N accumulation at anthesis in 1989 with increasing levels of N fertilizer (Table 4). In both years there was a general increase in N accumulation in the grain and in the total N accumulation for the standard isotypes with increasing N fertilizer levels, while the semi-dwarf isotypes showed a similar response to N levels for these traits in 1989 only. This different response to N between the standard and semi-dwarf isotypes in 1987 for these two traits was probably due to a steady increase in the number of tillers in the standard isotypes with increasing N levels but not in the semi-dwarfs (Nedel, 1990). The rate of change in the grain yield per plant for every incremental change in pre-anthesis N accumulation differed significantly between the standard height and semi-dwarf isotypes (Table 5). The standard height isotypes decreased substantially from 0.033 g of grain yield per plant per mg of pre-anthesis N accumulated at 30 kg N/ha to 0.002 g at 120 kg N/ha. The semi-dwarfs had a more gradual decrease, from 0.030 g at 30 kg N/ha to 0.016 g to 120 kg N/ha. These results suggest that when the standard height isotypes reached a level of N accumulation in the vegetative tissue at anthesis between 40.6 and 53.6 mg/plant (Table 4), the grain yield no longer was dependent on N content in the vegetative tissue. Cox et al. (1985) reported a significant but low association (r= 0.27*) between these two traits in wheat at the lower N level and no correlation (r= -0.02) at the higher N levels. Paccaud et al. (1985) reported a significant but moderate association (r= 0.42*) between pre-anthesis N accumulation and grain yield.

TABLE 5. Regression analysis of grain yield (g/plant) on N assimilation prior to anthesis, combined over standard and semi-dwarf genotypes in 1989.

Genotypes	N level[1]	Regression of grain yield/plant			
		Intercept	Slope[2]	SE slope	r
		g/plant			
Standard	N_1	0.75	0.033**	0.005	0.85**
	N_2	1.53	0.019*	0.007	0.59*
	N_3	2.01	0.012	0.008	0.37
	N_4	2.43	0.002	0.009	0.07
	Combined	1.30	0.023**	0.003	0.69**
Semi-dwarf	N_1	0.67	0.030**	0.008	0.73**

N_2	0.79	0.026**	0.007	0.69**
N_3	0.97	0.025**	0.007	0.69**
N_4	1.22	0.016*	0.006	0.57*
Combined	1.06	0.020*	0.002	0.76**

[1] N_1, N_2, N_3 and N_4= 30, 60, 90 and 120 kg/ha of N, respectively.
[2] g/plant per mg N/plant uptake prior to anthesis.
*, ** Significant difference from 0 at P= 0.05 and 0.01, respectively; for N levels n= 16; for combined n= 64.

Both semi-dwarf and standard isotypes had a larger proportion of the variation in the total N accumulated by the plant explained by pre-anthesis N accumulation (Table 6). A tendency for the association to decrease between these two traits with increasing N fertilizer was observed in the standard genotypes (Table 7). Biological yield at anthesis also proved to be significantly correlated with pre-anthesis N accumulation (Table 6). Similar results were reported by Paccaud et al. (1985), Chand & Dev (1986) and Cox et al. (1986). The greater the N accumulated before anthesis, the greater the amount of N available for later translocation to the grain. This was indicated by the strong association (r= 0.98**) between pre-anthesis N accumulation and N remobilization (Table 6). A consistently significant association was observed between pre-anthesis N accumulation and N concentration in the grain for the standard isotypes across N fertilizer levels, while a moderate and variable association between these traits was observed for the semi-dwarf isotypes.

TABLE 6. Correlation of N assimilation prior to anthesis (mg/plant) with other traits combined over standard and semi-dwarf genotypes in 1989[1].

N assimilation prior to anthesis vs	St					Se				
	N_1	N_2	N_3	N_4	Combined	N_1	N_2	N_3	N_4	Combined
Total N assimilation (mg/plant)	0.91**	0.76**	0.65**	0.58*	0.84**	0.92**	0.73**	0.91**	0.72**	0.90**
N remobilization (mg/plant)	0.99**	0.97**	0.97**	0.96**	0.99**	0.99**	0.92**	0.93**	0.93**	0.98**
Biological yield at anthesis (g/plant)	0.87**	0.71**	0.88**	0.79**	0.82**	0.93**	0.76**	0.81**	0.83**	0.91**
N concentration in the grain (g/kg)	0.65**	0.73**	0.73**	0.55*	0.77**	0.54*	0.27	0.54*	0.28	0.62**

[1] N_1, N_2, N_3 and N_4= 30, 60, 90 and 120 kg/ha of N, respectively.
*, ** Significant at P= 0.05 and 0.01, respectively; for N levels n= 16; for combined n= 64.

There was an increase in N accumulation between anthesis and maturity by Morex, Hazen, Hazen SD, Norbert, Andre, Klages and Steptoe (Table 3), indicating that these genotypes continued to take up N from the soil, although translocation from roots may have also contributed.

Steptoe had the highest post-anthesis N accumulation with approximately 23%. Tillman et al. (1991) also observed that Steptoe had the highest post-anthesis N accumulation among the genotypes tested.

Morex SD, Norbert SD and Andre SD showed a net loss in above-ground N from the plant during grain filling.

Other studies have also reported negative values for some genotypes (Wetselaar & Farquhar, 1980; Dhugga & Waines, 1989; Tillman et al., 1991).

The standard isotypes showed a quadratic response to N fertilizer for nitrogen accumulation after anthesis and the semi-dwarfs a cubic response. Similar results were reported by Dhugga & Waines (1989) in wheat.

There was a significant association (r= 0.52**) between grain yield per plant and N accumulation during the grain filling period in the standard isotypes, indicating that the continuation of N uptake was important to achieve the yield obtained.

No association (r= 0.05) between these two traits was observed for the semi-dwarf isotypes. This difference in the association between these two traits in standard and semi-dwarf isotypes may be evidence for differences in the source-sink relationships between these genotypes, and may explain part of the genotypic variation for N uptake during grain filling.

There was a highly significant relationship between N uptake after anthesis and N concentration in the grain with 30 kg N/ha (r= 0.71**) and 60 kg N/ha (r= 0.64**) for the standard isotypes but not for the other two N fertilizer levels (Table 7). The relationship between these two traits in the semi-dwarf isotypes was moderate with the r value significant (0.66**) only at the 60 kg N/ha fertilizer level. Cox et al. (1986) did not find a correlation between post-anthesis N accumulation and N concentration in the grain in spring wheat.

TABLE 7. Correlation of N assimilation after anthesis (mg/plant) with other traits combined over standard and semi-dwarf genotypes in 1989[1].

N assimilation after anthesis vs	Standard					Semi-dwarf				
	N_1	N_2	N_3	N_4	Combined	N_1	N_2	N_3	N_4	Combined
Total N assimilation (mg/pl)	0.61*	0.72*	0.54*	0.42	0.46**	0.50*	0.58*	0.64**	0.35	0.13
N concentration in the grain (g/kg)	0.71**	0.64**	0.21	0.01	0.30*	0.41	0.66**	0.40	0.48	0.21
N remobilization (mg/pl)	0.11	-0.11	-0.48	-0.68**	-0.23	0.02	-0.43	-0.01	-0.62**	-0.45**

[1] N_1, N_2, N_3 and N_4= 30, 60, 90 and 120 kg/ha of N, respectively.

*, ** Significant at P= 0.05 and 0.01, respectively; for N levels n= 16; for combined n= 64.

However, Sanford & Mackown (1987) observed that post anthesis N uptake was associated with higher grain N concentration in winter wheat. An increase in the negative association between N uptake after anthesis and N remobilization for the standard isotypes was observed with increasing N fertilizer, r= 0.11 to -0.68** (Table 7). Similar results are reported by Pan et al. (1984) in corn. This trend was less consistent for the semi-dwarf isotypes. Since N accumulation is related to leaf activity (Marschner, 1986), and remobilization occurs through the degradation of proteins, this negative association could in part be related to this physiological process.

The genotype x N interaction was significant for N accumulation in the vegetative tissue at maturity in both years. In 1987 the standard isotypes Morex, Hazen and Norbert showed a significant linear response to increasing N fertilizer (Table 8). This linear increase in N accumulation in the vegetative tissue at maturity was mainly related to the vegetative tissue dry weight response to N (Table 2).

TABLE 8. Mean values for N assimilation in the vegetative tissue at maturity[1].

Genotypes	1987				Sig.	198				Sig.
	N_1	N_2	N_3	N_4		N_1	N_2	N_3	N_4	
Morex	18.7	21.9	23.4	30.4	L	5.8	7.8*	9.1**	9.9**	L
Morex SD	25.3	24.7	24.6	25.3	NS	7.9	11.2	16.6	15.1	LQ
Hazen	23.6	31.3	40.5**	41.0**	L	4.9	7.9	12.0	12.0*	L
Hazen SD	29.2	24.9	26.4	27.5	NS	6.8	9.2	9.9	16.1	L
Norbert	20.0*	20.0	29.3	31.5	L	9.0	9.9	12.4	12.7**	L
Norbert SD	28.6	19.6	26.6	25.9	NS	8.8	10.2	11.8	19.4	L
Andre	16.5	15.1	21.6*	19.8	NS	7.4	9.9	14.2**	15.8*	L
Andre SD	15.1	13.8	13.4	14.0	NS	5.3	5.7	7.7	10.8	L
Klages	24.0	19.1	24.0	27.8	NS	8.3	10.7	13.2	17.5	L
Steptoe	22.0	23.2	23.3	30.1	NS	6.5	7.1	11.8	10.4	L

[1] N_1, N_2, N_3 and N_4= 30, 60, 90 and 120 kg/ha of N, respectively; L= linear, q= Quadratic, NS= not significant.

*, ** Significant difference between isotypes within a genotype according to t-test at P= 0.05 and 0.01, respectively.

In 1989, all genotypes showed a significant linear response to N fertilization in N accumulation in the vegetative tissue at maturity (Table 8). Whereas the N accumulation response to increasing N fertilization tended to be positive and linear in all genotypes, a significant difference was detected in the linear trend within the Norbert and Andre isotype pairs indicating that the increase in N accumulation in the vegetative tissue at maturity by increasing N fertilizer was at a different rate for the two isotypes of each pair. This difference could account partially for the significance of the interaction.

In 1987 with the exception of the Morex isotype pair, there was a general tendency for the standard isotypes to have higher N accumulation in the vegetative tissue at maturity than their respective semi-dwarf isotypes (Table 8).

In 1989 there was a tendency for the reverse with the exception of the Andre isotype pair (Table 8). As the standard isotypes had higher vegetative dry weights at maturity compared with the semi-dwarfs (Table 1), these differences can be mainly attributed to the N concentration in the tissue. The higher N concentration in the vegetative tissue of the semi-dwarf mutants Morex SD, Hazen SD and Norbert SD in relation to their standard isotypes probably was due to their lower remobilization efficiency.

All standard height isotypes, except Morex, showed greater N accumulation in the grain than their respective semi-dwarf isotypes, and N accumulation in the grain was higher in the standard than in the semi-dwarf isotypes in both years (Table 3). This difference was mainly due to the higher grain yield of the standard isotypes (Table 1). N accumulation in the grain was affected significantly by N fertilization (Table 4). The response to N of the standard and semi-dwarf isotypes was different within years but inconsistent between years.

Total N accumulation was greater in the standard height isotypes Hazen, Norbert and Andre than for their derived semi-dwarf mutants in 1987 (Table 3).

Hazen was lower in N concentration in the grain than Hazen SD (Table 3) but higher in grain yield (Table 1).

Norbert and Andre had slight differences in N concentration in the grain in relation to their derived mutants but had significantly higher grain yield per plant, which accounted for the differences in the total N accumulation.

In 1989 only Andre had accumulated more N than its semi-dwarf isotype.

Total N accumulation was significantly higher in the standard than in the semi-dwarf isotypes in 1987 (Table 3).

Genotypic differences in total N accumulation have been reported for wheat and barley (Desai & Bhatia, 1978; Sanford & Mackown, 1987; Tillman et al., 1991).

CONCLUSIONS

1. Genotypic differences occur for the contribution of pre- and post-anthesis photosynthate to the grain, for pre- and post-anthesis and total N accumulation and N remobilization to the grain.

2. Pre-anthesis N accumulation influences the total N accumulation at maturity and the N remobilization in both standard height and semi-dwarf barleys.

3. Post-anthesis N accumulation influences the grain yield per plant of the standard height but not those of the semi-dwarf isotypes. In the standard isotypes 25 to 51 percent of the observed variation in the grain yield per plant is explained by the post-anthesis N accumulation.

4. Standard height isotypes have a higher total N accumulation at maturity than their derived semi-dwarfs.

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