Preharvest Sprouting and Post-anthesis Development of Hard Winter Wheat as Affected by Nitrogen Nutrition

by

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PART I
PREHARVEST SPROUTING OF HARD WINTER WHEAT AS AFFECTED BY NITROGEN NUTRITION

INTRODUCTION

Preharvest sprouting seriously reduces agronomic, milling, and baking qualities of hard wheat (Triticum aestivum L.) grain. Sprouting of grain decreases its test weight and increases the activity of hydrolytic enzymes, most notably a-amylase (EC 3.2.1.1) (Swanson, 1946; Perten, 1964; Greenaway, 1969; Bhatt et al., 1981). Resistance of mature grain to preharvest sprouting depends primarily on the level and duration of dormancy. Although dormancy is genetically controlled, its level and duration are affected by many environmental factors (Belderok, 1968; Lalluka, 1976; Mac Key, 1976; Olsson and Mattsson, 1976; Svensson, 1976; Nielsen et al., 1984).

Agronomic factors that affect preharvest sprouting of wheat have not been investigated thoroughly. In particular, effects of plant nitrogen nutrition and grain nitrogen concentration on preharvest sprouting are not well understood. Belderok (1968) reviewed early work on the subject and concluded that nitrogen fertilization had no significant effect on dormancy in wheat. More recently, Huang and Varriano-Marston (1980) reported highly significant linear correlations of grain protein concentration with visible sprouting damage, a-amylase activity, specific a-amylase activity, and falling number. Tanner (1978) also found that heavy, late side-dressings of nitrogenous fertilizer increased the frequency of vivipary in maize (Zea mays L.).

Bhatt et al. (1981), on the other hand, found no significant differences in a-amylase activity and falling number attributable to nitrogen fertilization of wheat. Reasons for a significant interaction between falling number and nitrogen fertilization for two sprouting-resistant genotypes in their study were not elucidated.

Nitrogen fertilization induced relatively small differences in wheat grain protein in the above studies (Bhatt et al., 1981; Huang and Varriano-Marston, 1980) and any association between nitrogen nutrition and sprouting response was not resolved. To date, no study has clearly determined the effect of plant nitrogen nutrition and subsequent grain nitrogen concentration on dormancy in temperate cereals. The present study utilizes techniques adapted from Henson and Waines (1983) to induce marked differences in grain nitrogen concentration in five wheat genotypes differing in susceptibility to preharvest sprouting (McCrate et al., 1981). The level of dormancy 15 days after physiological maturity is examined to assess effects of nitrogen nutrition and genotype on sprouting susceptibility and the relationship to grain nitrogen concentration.

MATERIALS AND METHODS

Grain color, height class, and preharvest sprouting characteristics (McCrate et al., 1981) of the five hard winter wheat (*Triticum aestivum* L.) genotypes in the study are summarized in Table 1. Treatments consisted of the five genotypes, low and high nitrogen regimes, and simulated rain vs.

no rain. The study was conducted in a glasshouse under natural lighting (ca. 950 $uE \cdot m^{-2} \cdot s^{-1}$ at solar noon) extended to 16 hr by incandescent lighting (ca. 10 $uE \cdot m^{-2} \cdot s^{-1}$). Temperature was 29 C day and 21 C night.

Vernalized seedlings were transplanted to plastic containers (four plants per container) holding ca. 7.5 kg of steam-sterilized sand. The sand was saturated with distilled water and then irrigated with 300 ml of nutrient solution containing 5 $mmol \cdot L^{-1}$ KNO_3, 5 $mmol \cdot L^{-1}$ $Ca(NO_3)_2 \cdot 4H_2O$, 2 $mmol \cdot L^{-1}$ $MgSO_4 \cdot 7H_2O$, 0.5 $mmol \cdot L^{-1}$ KH_2PO_4, 50 $umol \cdot L^{-1}$ KCl, 25 $umol \cdot L^{-1}$ H_3BO_3, 5 $umol \cdot L^{-1}$ $MnSO_4 \cdot H_2O$, 2 $umol \cdot L^{-1}$ $ZnSO_4 \cdot 7H_2O$, 0.5 $umol \cdot L^{-1}$ $CuSO_4 \cdot 5H_2O$, and 15 $nmol \cdot L^{-1}$ $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$. Iron was supplied as 43 $umol \cdot L^{-1}$ $FeSO_4 \cdot 7H_2O$ with 53 $umol \cdot L^{-1}$ tartartic acid. Containers were arranged in a randomized complete block design with three replications.

Plants were grown to the early boot stage (Feekes scale 9; Large, 1954) with weekly irrigations of ca. 600 ml nutrient solution per container. Supplemental irrigations with distilled water maintained an adequate water supply. A nitrogen deprivation treatment (low N) was initiated at Feekes scale 9 by leaching nutrients from the containers with distilled water until the leachate contained minimal ($A < 0.01$) nitrate according to the N-1 napthylethylene diamine di-HCl color reaction (Woolley et al., 1960). Leaching was accomplished in less than four hours. The sand then was irrigated with nutrient solution containing KCl and $CaCl_2 \cdot 2H_2O$ instead of KNO_3 and $Ca(NO_3)_2 \cdot 4H_2O$, respectively. The standard nutrient solution was continued in the other containers for a high nitrogen treatment.

Individual spikes were tagged one day after first anther extrusion. Since nitrogen fertility affects maturation and senescence (Lamb, 1967; Langer and Liew, 1973), the date when kernels in the center of spikes lost chlorophyll from the pigment strand was noted as an indicator of physiological maturity (Hanft and Wych, 1982). Fifteen days after physiological maturity, when grain moisture was ca. 140 g·kg dry wt^{-1}, spikes were harvested, placed in plastic bags, and held at -20 C to arrest after-ripening (Mares, 1983).

Simulated rain treatment was imposed by placing harvested spikes upright on styrofoam boards and applying 50 mm "rain" during a 2-hr period (McCrate et al., 1981). Spikes then were maintained in the rain simulator at 100% relative humidity for 5 d. After the rain treatment, spikes were dried in a forced-air oven at 40 C for 4 d and individually hand-threshed. The number of nonsprouted and sprouted kernels in each spike was determined; kernels were considered sprouted if the pericarp above the embryo was ruptured.

Spikes that were not treated in the rain simulator were individually hand-threshed and dried at 40 C for 4 d. The total number of kernels, kernels exhibiting yellowberry, and grain dry weight were recorded on a per spike basis. Grain from both treatments was ground in a Udy Cyclone mill to pass a 1-mm screen. The flour was used for duplicate nitrogen determinations by the standard microkjeldahl method and for a-amylase determinations by a modified method of Mathewson and Pomeranz (1979). The modifications included using 200 mg of flour, Cibacron-Blue amylose tablets (D&S Instrument, Ltd., Pullman,

WA), and incubating the reaction mixture at 50 C for 5 min. Absorbance was measured at 620 nm. Milli-Dextrinizing Units (mDU) per tube were calculated from a standard curve prepared with a standard barley malt (sample 84-A, Malt Analysis Check Service, Fargo, ND).

Data were analyzed by SAS Analysis of Variance and MANOVA procedures (SAS Institute Inc., 1982). Correlations were generated by pooling within-cell correlations to avoid errors in simple linear correlations due to uniform response by treatment. Analysis indicated a very low probability ($P > 0.5$) that treatment location (blocking) had any effect, so data were pooled across replications and analyzed as a completely randomized design (Carmer et al., 1969). Pooling of data across replications did not change any conclusions at the alpha = 0.05 level. Mean square errors (MSE) are given for tabular data as a measure of experimental precision.

RESULTS

High plant nitrogen nutrition treatment (high N regime) significantly increased grain yield of only two genotypes over the low N regime (Table 2). Grain nitrogen concentration, however, was increased 2-fold or more in all genotypes by the high N regime as compared to the low N regime. Under the low nitrogen regime, 'Lancota' grain contained significantly lower nitrogen concentration than the other genotypes, which did not differ at the $P \leq 0.05$ level. Under the high N regime, grain nitrogen concentration was higher in Lancota than in 'Parker 76'

and 'Newton'. Newton grain had lower N concentration than both tall genotypes and its white-grain sibling, 'KS75216'. Grain from none of the genotypes exhibited yellowberry under the high N regime, whereas, 53.2% to 96.8% of the kernels exhibited yellowberry under the low N treatment. The five genotypes were equally susceptible to yellowberry.

Visible preharvest sprouting after simulated rain (Table 3) differed among the five genotypes as observed in other studies (Bhatt et al., 1981; McCrate et al., 1981). High plant nitrogen nutrition significantly increased the incidence of preharvest sprouting of the semidwarf genotypes Newton and KS75216. No sprouting occurred in the two very resistant genotypes, Clark's Cream and Lancota, under either nitrogen regime. Sprouting of Parker 76 grain was high under both regimes and was not significantly affected by N nutrition. The correlation between grain nitrogen concentration and percentage of visible preharvest sprouting ($r = 0.62$) was highly significant.

a-Amylase activity in the dry grain did not differ among genotypes and was not correlated with grain N concentration (Table 4). Simulated rain prompted marked differences among genotypes, however. It increased a-amylase activity in Newton grain from high N plants and in KS75216 and Parker 76 grain from both low and high N plants.

High grain N concentration increased the level of a-amylase activity after simulated rain treatment of Newton, KS75216 and Parker 76 (Table 4). The correlation between a-amylase activity and grain nitrogen concentration for these three genotypes after

simulated rain was highly significant (r = 0.78). Across all genotypes, a-amylase activity was highly correlated with percentage visible sprouting (r = 0.91) (Table 3).

DISCUSSION

Preharvest sprouting of wheat is dependent on genotype (Belderok, 1968; Bhatt et al., 1981; Bingham and Whitmore, 1966; McCrate et al., 1981) and environmental conditions such as moisture and temperature (Lalluka, 1976; Nielsen et al., 1984; Olsson and Mattsson, 1976). The marked effect of nitrogen nutrition on rain-induced sprouting and a-amylase activity of susceptible genotypes but not of resistant genotypes is consistant with these interactions.

Low levels of basal a-amylase, the activity in sound unsprouted mature grain, were similar to those in field studies (Bhatt et al., 1981; McCrate et al., 1981). Basal a-amylase activity was not affected by nitrogen nutrition and did not differ among genotypes. It is genetically independent of activity in sprouted grain and cannot be used as a predictor of sprouting resistance (Bingham and Whitmore, 1966). Indeed, basal a-amylase expressed as activity·mg nitrogen^{-1} (specific activity) instead of as activity·g dry weight^{-1} was over 2-fold higher in low-nitrogen grain than in high-nitrogen grain. These data indicate that basal a-amylase activity is genetically determined and independent of plant nitrogen nutrition and grain nitrogen concentration.

Simulated rain induced the marked genotypic differences in

preharvest sprouting observed in other studies (Bhatt et al., 1981; McCrate et al., 1981) and allowed expression of the effects of nitrogen nutrition. Use of nutrient solution culture (Henson and Waines, 1983; Langer and Liew, 1973) also caused much greater differences in grain nitrogen concentration than previously obtained in field studies (Bhatt et al., 1981; Huang and Varriano-Marston, 1980). The results showed that high grain nitrogen concentration increases sprouting percentage, a-amylase activity·g dry weight^{-1}, or both, but only in genotypes that have moderate or low resistance to sprouting. The strong dormancy in Clark's Cream and Lancota (McCrate et al., 1981) is not altered by nitrogen nutrition.

Increased sprouting and/or a-amylase activity of the susceptible genotypes KS75216 and Parker 76 can be attributed only indirectly to effects of high nitrogen concentration. Neither a-amylase specific activity, per cent sprouting·mg nitrogen^{-1}, nor a-amylase activity·per cent sprouting^{-1} were stimulated by high levels of nitrogen. The effect may be related, however, to the rapid germination of high-protein seeds and prompt seedling emergence observed in other studies (Torres and Paulsen, 1982).

The highly significant correlations between preharvest sprouting percentage and grain nitrogen concentration do not contradict results of Huang and Varriano-Marston (1980). They found a significant negative correlation between grain protein concentration and preharvest sprouting by calculating simple linear corrlelations across all genotypes. Their results imply a relationship between intrinsic grain protein potential of the

genotypes and preharvest sprouting, not an effect of grain N concentration within genotype on sprouting. The high correlation between percentage preharvest sprouting and a-amylase activity on both a dry weight and a nitrogen basis is in accordance with other reports (Bhatt et al., 1981; Gordon et al., 1977; Huang and Varriano-Marston, 1980; McCrate et al., 1981).

We concluded that nutrient solution culture induces marked differences in grain nitrogen concentration in wheat. High levels of nitrogen fertilization increase rain-induced preharvest spouting in genotypes with moderate or low levels of resistance. However, genotypes with strong resistance and all genotypes in areas where conditions are not conducive to preharvest sprouting can be fertilized safely without increasing the risk of preharvest sprouting.

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Table 1. Grain color, height class, and preharvest sprouting susceptibility of five hard winter wheat genotypes under study.

Genotype	Grain color	Height class	Srouting character +
Lancota	Red	Tall	Very resistant
Newton	Red	Semidwarf	Resistant
Parker 76	Red	Tall	Susceptible
Clark's Cream	White	Tall	Very resistant
KS75216	White	Semidwarf	Susceptible

+ After McCrate et al.,1981.

Table 2. Yield, nitrogen concentration, and percentage yellowberry of grain of five hard winter wheat genotypes as affected by nitrogen regime.

	Grain yield		Nitrogen concentration		Yellowberry	
	Nitrogen regime					
Genotype	Low	High	Low	High	Low	High
	--g·plant^{-1}--		-g N·kg grain^{-1}-		-----%-----	
Lancota	1.51	1.58	14.5	36.3	96.8	0
Clark's Cream	1.23	1.55	16.0	35.3	82.6	0
Newton	1.10	1.93	16.1	33.2	53.2	0
KS75216	1.21	2.01	16.3	35.6	68.0	0
Parker 76	1.51	1.48	17.3	34.4	89.6	0
LSD (0.05)	NS	NS	1.5	1.5	NS	NS
LSD (0.05)	0.49		1.5		28.6	
MSE	0.086		1.6		292.8	

Table 3. Percentage and radians (transformed percentage) of preharvest sprouting of grain of five hard winter wheat genotypes grown under two nitrogen regimes and exposed to simulated rain.

Genotype	Nitrogen regime: Low		Nitrogen regime: High	
	--%--	Angle +	--%--	Angle
Clark's Cream	0.0	0.0	0.0	0.0
Lancota	0.0	0.0	0.0	0.0
Newton	0.0	0.0	21.1	0.46
KS75216	25.7	0.53	53.0	0.82
Parker 76	42.5	0.71	55.9	0.84
LSD (0.05) *		0.14		
MSE		0.0072		

+ Angle=Arc Sin$\sqrt{\text{proportion}}$ in radians.
* Angle transformed data and LSD should be used for all pair-wise comparisons.

Table 4. a-Amylase activity of grain of five hard winter wheat genotypes grown under two nitrogen regimes with and without simulated rain after harvest.

	Rain treatment			
	Control (no rain)		50 mm rain	
	Nitrogen regime			
Genotype	Low	High	Low	High
	mDU·g dry wt^{-1}			
Clark's Cream	19	15	21	28
Lancota	25	24	37	55
Newton	19	27	595	1 496
KS75216	19	24	2 119	3 233
Parker 76	37	27	2 361	3 367
LSD (0.05)			875	
MSE			275 939	

PART II
POST-ANTHESIS DEVELOPMENT OF HARD WINTER WHEAT AS AFFECTED BY NITROGEN NUTRITION

INTRODUCTION

Wheat (*Triticum aestivum* L.) grain yield and nitrogen concentration are usually inversely related (Langer and Liew, 1973; McNeal and Davis, 1954; Stuber et al., 1962; Grant and McCalla, 1949; Schlehuber and Tucker, 1959). Most wheat grain nitrogen comes from remobilization of vegetative nitrogen (Carpenter et al., 1952; Dalling et al., 1976; McNeal et al., 1968; Pearman et al., 1977; Rao et al., 1977). Remobilization of vegetative nitrogen for grain development, however, accelerates senescence and reduces photosynthetic activity of leaves (Evans, 1983; Sinclair and de Witt, 1975). The duration of photosynthetic area after anthesis and grain yield are highly positively correlated (Simpson, 1968).

Post-anthesis nitrogen nutrition should be an important determinate of grain yield in wheat, but experimental evidence is contradictory. Nitrogen fertilization at late developmental stages may increase grain yield (Finney et al., 1957; Hucklesby et al., 1971; Spiertz and van de Haar, 1978; Spiertz and Ellen, 1978) or have no effect (McNeal et al., 1963; Langer and Liew, 1973; Miezan et al., 1977; Robinson et al., 1979; Henson and Waines, 1983).

Grain yield was increased consistantly by nitrogen application prior to anthesis of wheat (Finney et al., 1957; Hucklesby et al., 1971) and occasionally by nitrogen application

at anthesis or later (Finney et al., 1957). Spiertz and Ellen (1978) and Spiertz and van de Haar (1978) reported nitrogen applied at the boot stage increased grain yield, single kernel weight, grain growth rate, and harvest index. Most of the increase in yield was attributed to more kernels per spike, and high grain yield was associated with high grain nitrogen concentration (Spiertz and Ellen, 1978).

Other studies show little response to late application of nitrogen. Grain yield was not affected when nitrogen was applied at the boot stage (Robinson et al., 1979) or just prior to anthesis of wheat (McNeal et al., 1963; Miezan, et al., 1977) in the field. Langer and Liew (1973) and Henson and Waines (1983) used solution cultures to induce differential nitrogen levels at specific developmental stages. Level of nitrogen nutrition after spike emergence had no effect on grain yield and yield components of main culms of wheat, but high N increased leaf area duration (Langer and Liew, 1973). Since only main culms were allowed to develop, compensatory effects of tillering could not be ascertained. In studies by Henson and Waines (1983), nitrogen deprivation at the boot stage of wheat had no effect on grain yield per plant or harvest index.

The present study was initiated to reconcile the different findings on importance of nitrogen nutrition of wheat during grain development and to understand the inverse relationship between wheat grain yield and nitrogen concentration. Studies were conducted under controlled conditions with nutrient solution culture to develop marked differences in nitrogen nutrition in five genotypes.

MATERIALS AND METHODS

Three standard height hard winter wheat (Triticum aestivum L.) genotypes ('Clark's Cream', 'Lancota', and 'Parker 76'), two semidwarf genotypes ('Newton' and 'KS75216'), three post-anthesis harvest dates, and two nitrogen nutrition regimes were experimental main effects. The experiment was conducted in a glasshouse as a randomized complete block design with three replications.

Seedlings were vernalized for 40 d at 5 C at the 2- to 3-leaf stage and transplanted into plastic containers (four plants per container) holding ca. 7.5 kg of steam-sterilized sand. Glasshouse conditions and nutrient regimes were identical to those reported previously (Morris and Paulsen, 1984). Plants were grown to the early boot stage (Feekes scale 9; Large, 1954) with weekly irrigations of ca. 600 ml nutrient solution containing 5 mmol·L^{-1} KNO_3 and 5 mmol·L^{-1} $Ca(NO_3)_2 \cdot 4H_2O$. At Feekes stage 9, a nitrogen deprivation treatment (low N) was initiated by leaching nutrients from the containers with distilled water and subsequently using nutrient solution containing KCl and $CaCl_2 \cdot 2H_2O$ instead of KNO_3 and $Ca(NO_3)_2 \cdot 4H_2O$, respectively. The standard nutrient solution was continued in the other containers for a high nitrogen treatment.

Spikes were harvested 10, 20, or 40 days after first anther extrusion. Kernels were removed by hand and counted on all dates and were visually examined for yellowberry at the 40-day harvest. Vegetation samples, consisting of the aerial portion of plants minus the grain, were collected when spikes were harvested.

Grain and vegetation were dried in a forced air oven at 65 C for 72 hr and dry weights were recorded. Dried samples were ground in a Udy Cyclone mill to pass a 1-mm screen and the meal was used for duplicate nitrogen determinations by the standard microkjeldahl method.

Mean grain growth rates ($\overline{GGR}$) per plant and per kernel were calculated according to Radford (1967) for each harvest. Data were analyzed by SAS Analysis of Variance and MANOVA procedures (SAS Institute Inc., 1982). Correlations are pooled within-class correlations to avoid errors in simple linear correlations due to uniform treatment response. For tabular data, mean square errors (MSE) are given as a measure of the experimental precision and LSD (least significant difference) at the $P \leq 0.05$ level is used for pair-wise comparisons.

RESULTS

Plants grown with high N nutrition produced significantly more biological yield than plants grown with low N nutrition averaged over all genotypes at the 20- and 40-day harvests, but not at the 10-day harvest (Table 1). Biological yield of individual genotypes differed between low and high N regimes in only a few instances, however. The tall genotypes Clark's Cream and Lancota produced the highest biological yields, whereas the tall genotype Parker 76 was not significantly different from the two semidwarf genotypes (means over harvest dates and N regimes).

Biological N yield increased under the high N regime but not under the low N regime as harvest date progressed (Table 1).

Averaged over genotypes, plants grown under the high N regime contained more biological N than plants grown under the low N regime at all three harvest dates. Genotype ranking for total N yield paralleled that for total dry matter yield, but differences were smaller.

Mean grain yield per plant was significantly higher from the high N than from the low N regime at all but the first sampling date. Means across all genotypes and all harvest dates were 1.15 and 1.46 $g \cdot plant^{-1}$ for low and high N regimes, respectively (Table 1). Genotypes did not differ in grain yield averaged over harvest dates and N regimes. Mean grain yields of tall and semidwarf genotypes were nearly identical under high N nutrition, whereas grain yield of tall genotypes was higher (alpha $\leq$ 0.10) under low N nutrition. Grain yield was highly significantly correlated with spikes per plant, kernels per plant, kernels per spike, and kernel weight (r = 0.47, 0.87, 0.66, and 0.52, respectively).

The number of spikes per plant (Table 2) was the yield component affected most by high N plant nutrition. Plants grown with high N nutrition produced 27% more spikes than plants grown with low N nutrition (2.15 and 2.73 spikes per plant, respectively), averaged across genotypes and harvest dates. No trend in yield components due to height class was evident.

Mean grain growth rates per plant and per kernel were favored by high N plant nutrition (Table 2). High N nutrition increased mean grain growth rates per plant most during the first 10 days of grain development, and increased mean grain growth per kernel during the first 20 days after anthesis averaged over

genotypes. Mean grain growth rate per plant and per kernel were highest during the first 20 days after anthesis (79.9 mg·plant^{-1}·day^{-1} and 283 ug·kernel^{-1}·day^{-1}, respectively). Mean grain growth rates decreased dramatically during late grain filling. Mean grain growth rate per plant was significantly positively correlated with kernels per plant, grain yield per plant, kernel weight, and vegetation dry weight per plant (r = 0.90, 0.92, 0.43, and 0.69, respectively). Mean grain growth rate per kernel was significantly positively correlated with grain yield per plant, grain yield per spike, and kernel weight (r = 0.42, 0.64, 0.90, respectively).

Grain N concentration over all genotypes grown under low N nutrition remained nearly constant during development. Means were 17.97, 17.29 and 18.68 g N·kg dry weight^{-1} for the 10-, 20- and 40-day harvests, respectively (Table 3). Mean grain N concentration did not differ among the three harvest dates. Grain N concentration of plants grown with high N nutrition increased significantly from 10 to 40 days after anthesis, but not during the 10- to 20-day period (25.36, 26.55 and 31.55 g N·kg dry weight^{-1} for the 10-, 20- and 40-day harvests, respectively).

High nitrogen nutrition highly significantly increased vegetation N concentration. Means across genotypes and harvest dates were 5.4 and 10.0 g N·kg dry weight^{-1} for the low and high N regimes, respectively (Table 4). At the low N level, mean vegetation N concentration across all genotypes decreased as grain filling progressed (7.25, 4.70 and 4.18 g N·kg dry weight^{-1}

for 10-, 20- and 40-day harvests, respectively). Vegetation N concentration of genotypes was similar when averaged across all harvest dates and N regimes. Semidwarf genotypes had significantly higher vegetation N concentration than tall genotypes under the low N nutrition regime, however. Means across harvest dates were 5.9 and 5.0 g N·kg dry weight^{-1} for semidwarf and tall genotypes, respectively. Under high N nutrition, vegetation N concentration did not differ between the two height classes (9.9 and 10.1 g N·kg dry weight^{-1} for semidwarf and tall genotypes, respectively). High N nutrition nearly stopped net loss of vegetative N during grain development. The slight decrease in vegetation N concentration across all genotypes from 10 to 40 days after anthesis was, however, significant (10.82 and 9.52 g N·kg dry weight^{-1} for 10- and 40-day harvests, respectively).

Total vegetation N content was highest at the 10-day harvest and decreased thereafter under the low N regime (Table 5). Under the high N regime, vegetative N remained constant even though the amount of total grain N increased dramatically. Under both N regimes, total grain N increased approximately 3-fold from the 10- to 40-day harvests with the largest increase occurring between 10 and 20 days after anthesis. High N plant nutrition, however, stimulated over twice as much grain and vegetation N yield than low N nutrition across genotypes.

Harvest index did not differ significantly among genotypes and was not affected by N nutrition (data not shown). Semidwarf genotypes had no significant advantage over tall genotypes for harvest index or nitrogen harvest index. However, nitrogen

harvest index was positively significantly affected by N nutrition. As grain filling progressed, nitrogen harvest index increased significantly at each harvest date.

DISCUSSION

The results show that nitrogen nutrition during late developmental stages of wheat is an important determinate of plant productivity. High N plant nutrition during grain development greatly favored grain and vegetation N concentrations, mean grain growth rates, and grain yield. Since sink (grain) demand for N is preferentially met by root uptake (Neales et al., 1963), N fertilization reduces net remobilization of vegetative N, thereby increasing and prolonging the viability of leaves (Evans, 1983; Sinclair and de Witt, 1975).

The number of kernels per plant was the single most important determinate of grain yield per plant (r^2 = 0.76) in this study. Spiertz and Ellen (1978) and Spiertz and van de Haar (1978) found that the number of kernels per area was the primary determinate of grain yield of wheat under constant seeding rates in the field. However, they found that kernels per spike increased relatively more than number of spikes due to N fertilization at the early boot stage.

Kernel density was not the only yield component increased by high N nutrition, however. Results indicated that high N nutrition also increased the rate of grain growth per plant and per kernel. Spiertz and Ellen (1978) and Spiertz and van de Haar (1978) also found that N fertilization increased grain growth

rate per m^2, which was associated with the number of kernels per m^2. It is clear, however, that N also promotes growth of individual kernels.

Tall genotypes may have a protein concentration advantage over semidwarf genotypes because the proportionately larger amount of vegetation of the former acts as a reservoir of N for the grain (Kramer, 1979). Our results also suggest that tall genotypes tend to have superior grain yields under low N nutrition, probably for the same reason. Grain N concentration was similar for all genotypes, but total grain N content (N concentration x grain wt) was higher in two tall genotypes than in the semidwarf genotypes. Additional studies are necessary to confirm this apparent superiority of tall genotypes under low N nutrition. On the other hand, no advantage due to height class was apparent under high N nutrition.

The two nitrogen nutrition regimes induced marked differences in the post-anthesis nitrogen economy of wheat plants. High N nutrition supplied relatively large amounts of N to the grain without a net loss of N from vegetation. The nearly constant vegetation N concentration may indicate that an upper limit of grain N concentration established under high N nutrition is approximately maintained during grain development. Plants grown under the low N nutrition regime, however, remobilized vegetative N.

High N nutrition late in development stimulates N uptake by grain (Finney et al., 1957; Spiertz and van de Haar, 1978). Results showed that high N increased N import by grain relative

to carbohydrate so that grain N concentration increased over time in all but one instance (Table 3). Under low N nutrition, however, N import to the grain paralleled carbohydrate import and grain N concentration remained fairly constant.

Our results and those of Spiertz and Ellen (1978) indicate that wheat grain yield and protein concentration can be increased simultaneously by properly timing N application. Previous studies (Langer and Liew, 1973; McNeal and Davis, 1954; Grant and McCalla, 1949; Schlehuber and Tucker, 1959) reported grain yield and protein concentration are inversely related. In most of these studies, however, high grain yield and low protein concentration were associated with early application of N. Langer and Liew (1973) also found that high N nutrition from double ridge to floral initiation growth stages produced high grain yield with low grain N concentration. On the other hand, high N nutrition from ear emergence to maturity produced 54% less grain yield, but 32% higher grain N concentration. In our studies, high N supplied throughout plant development gave high grain yield and high grain N concentration. This may have occurred because we induced a greater range of N levels than normally occur under field conditions and other resources, particularly moisture and temperature, were favorable for growth.

We concluded that ample levels of N during late developmental stages are necessary for maximum yields of high-protein grain. Kernel numbers, kernel growth rate, and N content are all favored by high levels of N during grain development. Application of these results to field conditions is uncertain; similar benefits would be expected, however, if soil N is low and other

resources for growth are high. Multiple split-applications of N fertilizer might be used to achieve high N plant nutrition during grain development.

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Table 1. Biological dry matter and nitrogen yields of aerial plant parts, and mean grain yields of five hard winter wheat genotypes grown under two nitrogen regimes.

	Days after anthesis					
	10		20		40	
	Nitrogen regime					
Genotype	Low	High	Low	High	Low	High
	Biological dry matter yield					
	$g \cdot plant^{-1}$					
KS75216	3.03	4.88	3.76	4.74	3.97	4.86
Clark's Cream	5.42	4.56	5.50	5.78	5.49	6.63
Parker 76	3.40	2.95	4.49	5.11	3.84	4.76
Lancota	4.34	4.53	5.86	6.46	5.05	6.88
Newton	3.03	3.39	3.49	5.66	3.62	5.81
LSD (0.05)	1.58					
MSE	1.18					
	Biological nitrogen yield					
	$mg \cdot plant^{-1}$					
KS75216	33	70	35	74	38	91
Clark's Cream	43	62	45	97	48	105
Parker 76	34	37	38	76	33	80
Lancota	30	64	45	93	45	116
Newton	28	40	29	84	33	92
LSD (0.05)	30					
MSE	347					
	Grain Yield					
	$g \cdot plant^{-1}$					
MEAN	0.59	0.70	1.39	1.80	1.48	1.89
LSD (0.05)	0.34					
MSE	0.22					

Table 2. Numbers of spikes per plant ($SPK \cdot PL^{-1}$), kernel weights (K-WT), mean grain growth rates per plant ($\overline{GGR} \cdot PL^{-1}$), and mean grain growth rates per kernel ($\overline{GGR} \cdot K^{-1}$) of five hard winter wheat genotypes grown under two nitrogen regimes.

	$SPK \cdot PL^{-1}$		K-WT +	$\overline{GGR} \cdot PL^{-1}$		$\overline{GGR} \cdot K^{-1}$	
	Nitrogen regime						
Genotype	Low	High	combined *	Low	High	Low	High
	$plant^{-1}$		$mg \cdot kernel^{-1}$	$mg \cdot plant^{-1} \cdot d^{-1}$		$ug \cdot kernel^{-1} \cdot d^{-1}$	
Newton	1.94	2.53	22.9	46.0	70.6	207	237
Lancota	2.19	3.17	25.3	59.8	67.7	239	218
Clark's Cream	2.19	2.67	28.2	67.4	77.3	237	264
KS75216	2.22	2.97	21.2	52.3	74.0	226	248
Parker 76	2.19	2.36	24.7	50.2	56.0	222	230
LSD (0.05)	0.47		4.0	18.7		28	
MSE	0.25		10.7	394.6		862	

+ Kernel weights from mature grain only.
* Kernel weights not significantly different for nitrogen regimes.

Table 3. Grain nitrogen concentrations at three sampling dates of five hard winter wheat genotypes grown under two nitrogen regimes.

	Days after anthesis					
	10		20		40	
	Nitrogen regime					
Genotype	Low	High	Low	High	Low	High
	g N·kg dry wt^{-1}					
KS75216	21.47	28.10	18.32	26.85	20.88	35.30
Clark's Cream	18.58	24.85	16.77	29.67	18.65	30.03
Parker 76	18.00	23.52	18.38	25.18	18.97	31.62
Lancota	15.53	26.02	15.88	26.62	17.40	32.08
Newton	16.25	24.32	17.08	24.42	17.50	28.73
LSD (0.05)	3.51					
MSE	4.62					

Table 4. Vegetation nitrogen concentrations at three sampling dates of five hard winter wheat genotypes grown under two nitrogen regimes.

	Days after anthesis					
	10		20		40	
	Nitrogen regime					
Genotype	Low	High	Low	High	Low	High
	g N·kg dry wt^{-1}					
KS75216	8.20	11.05	4.95	8.80	4.33	11.95
Clark's Cream	6.32	11.20	4.53	10.92	4.18	7.87
Parker 76	8.25	10.25	4.13	9.87	3.72	9.40
Lancota	5.60	12.38	4.78	9.57	3.75	9.62
Newton	7.87	9.22	5.13	9.55	4.90	8.80
LSD (0.05)	2.33					
MSE	2.03					

Table 5. Total grain and vegetation N contents per plant of five hard winter wheat genotypes grown under two nitrogen regimes.

Days after anthesis	Total Vegetation N		Total grain N	
	Nitrogen regime			
	Low	High	Low	High
	mg·plant^{-1}			
10	22	37	11	18
20	15	37	23	48
40	12	37	27	60
LSD (0.05)	6		9	
MSE	63.9		168	

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Craig F. Morris
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Preharvest Sprouting and Post-anthesis Development of Hard Winter Wheat as Affected by Nitrogen Nutrition

by

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Preharvest sprouting seriously reduces quality of hard winter wheat (Triticum aestivum L.) grain. Nitrogen fertilization is used to increase grain yield and protein content, but its effect on preharvest sprouting is unclear. Also, grain yield and protein concentration are usually inversely related. Most wheat grain nitrogen comes from remobilization of vegetative nitrogen. Remobilization, however, accelerates senescence and reduces photosynthetic activity of leaves. Therefore, post-anthesis nitrogen nutrition should be an important determinate of grain yield of wheat. Research was conducted to determine the effect of nitrogen nutrition on preharvest sprouting (Part I), to reconcile different findings on importance of nitrogen nutrition of wheat during grain development and to understand the inverse grain yield/nitrogen concentration relationship (Part II). Five wheat genotypes differing in susceptibility to preharvest sprouting were grown in sand with nutrient solution in a glasshouse. Differential nitrogen regimes were imposed by leaching nutrients from one set of plants at Feekes scale 9. Complete nutrient solution or solution devoid of N were used until plants were mature for high and low N regimes, respectively.

In Part I, grain dormancy was assessed 15 d after physiological maturity by treating spikes with simulated rain. Grain from control (no simulated rain) spikes had no preharvest sprouting and low similar a-amylase activity in all genotypes. Simulated rain did not cause preharvest sprouting or increase a-amylase activity in highly resistant genotypes 'Clark's Cream'

and 'Lancota', but increased preharvest sprouting and a-amylase activity in susceptible genotypes 'KS75216' and 'Parker 76'. High N fertility increased absolute a-amylase activity but not specific a-amylase activity (activity·protein^{-1}).

In Part II, plants were harvested 10, 20, or 40 days after anthesis and analyzed for grain and vegetation yields, yield components and grain and vegetation N concentrations. High N nutrition increased mean biological dry matter yield and grain yield 20 and 40 days after anthesis. Grain yield was significantly correlated with number of spikes per plant, kernels per plant, kernels per spike, and kernel weight. Spikes per plant was the yield component most increased by high N nutrition. Also, mean grain growth rates per plant and per kernel were favored by high N nutrition. Grain N concentration under low N nutrition remained fairly constant, but increased under the high N regime over time. High N nutrition increased vegetation N concentration and biological N yields. Under high N nutrition, vegetation N content remained fairly constant, but decreased under low N nutrition as grain filling progressed.

We concluded that high levels of nitrogen fertilization increase rain-induced preharvest sprouting in genotypes with moderate or low levels of resistance. However, genotypes with strong resistance and all genotypes in areas where conditions are not conducive to preharvest sprouting can be safely fertilized without increasing the risk of preharvest sprouting. Ample levels of N during late developmental stages are necessary for maximum yield of high-protein grain. Kernel numbers, kernel growth rate, and N content are all favored by high levels of N

during grain development. Applications of these results to field conditions is uncertatin; similar benefits would be expected, however, if soil N is low and other resources for growth are high. Multiple split-applications of N fertilizer might be used to achieve high N plant nutrition during grain development.