

ASSIMILATION AND PARTITIONING OF CARBOHYDRATES AND NITROGEN
AND EFFECT OF MANAGEMENT PRACTICES ON ISOGENIC TALL,
SEMIDWARF, AND DOUBLEDWARF WHEAT LINES

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TABLE OF CONTENTS

	Page
PART I: Assimilation and Partitioning of Carbohydrates and Nitrogen in Isogenic Tall, Semidwarf, and Doubledwarf Winter Wheat	1
Materials and Methods	3
Results	5
Discussion	13
References	15
PART II: Response of Yield Attributes of Isogenic Tall, Semidwarf, and Doubledwarf Winter Wheat lines to Nitrogen Fertilizer and Seeding Rate	17
Materials and Methods	18
Results	20
Discussion	28
References	31
ACKNOWLEDGMENTS	33
APPENDIX	34

LIST OF TABLES

Table		Page
I-1	Dry matter partitioning of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines under controlled environmental conditions	6
I-2	Yield components of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines under controlled environmental conditions	7
I-3	Distribution of carbohydrate fractions and nitrogen in plant parts of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat under controlled environmental conditions	8
I-4	Ribulose biphosphate carboxylase activity (RuBPCA) and nitrate reductase activity (NRA) in leaf blades of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines under controlled environmental conditions	10
I-5	Leaf area index (LAI), net assimilation rate (NAR), crop growth rate (CGR), and relative growth rate (RGR) of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines under field conditions	11
I-6	Dry matter partitioning and yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines under field conditions	12
II-1	Response of yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines to nitrogen fertilizer at two Kansas locations	21
II-2	Response of yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines to seeding rate at two Kansas conditions . .	22
II-3	Simple correlations of grain yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines with nitrogen fertilizer at two Kansas locations	23

Table		Page
II-4	Simple correlations of grain yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines with seeding rate at two Kansas locations	25
II-5	Simple correlations among grain yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines at Manhattan, Kansas, during 1981	26
II-6	Simple correlations among grain yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines at Hutchinson, Kansas, during 1981	27

PART I

ASSIMILATION AND PARTITIONING OF CARBOHYDRATES AND NITROGEN IN ISOGENIC TALL, SEMIDWARF AND DOUBLEDWARF HARD WINTER WHEAT

The most frequently noted advantage of semidwarf wheats is their harvest index (McNeal et al., 1972; Spiertz and van de Haar, 1978; Thorne, Welbank, and Blackwood, 1969; Walcott and Laing, 1976). Few studies, however, explored the physiological basis for the advantageous harvest index of semidwarf wheats. Semidwarf wheats allocated more photosynthate to production of large spikes, probably because carbohydrate requirement of the stem is less than in tall wheats (Syme, 1969). A similar situation may exist for nitrogen; however, much wheat grain nitrogen is translocated from the vegetation (Halloran, 1981).

Semidwarf cultivars may have a large grain to leaf ratio because a high proportion of the photosynthate produced after flowering was moved to the grain (Thorne et al., 1969), although their leaf area was no greater than that of tall cultivars (Makunga et al., 1978). Spikes of semidwarf cultivars also may be a better sink for photosynthates than spikes of tall cultivars and hence able to accumulate more of the carbohydrate produced by the plants, a usual result of more grains per spike (McNeal et al., 1972).

Water soluble carbohydrates also reached higher concentrations in stems of semidwarf wheats than tall wheats (Spiertz and van de Haar, 1978). There is little evidence, however, of cultivar differences in translocation pattern, apart from an indication that the second leaves contribute more to grain yield in semidwarf

wheats than in tall wheats (Lupton, 1972). When different leaves were supplied with ^{14}C , the proportion of label in the spike was greatest for semidwarf wheats and least for tall wheats (Makunga et al., 1978). However, Lupton (1972) found the translocation pattern was similar in tall and semidwarf lines; distribution of photosynthate (Makunga et al., 1978) and absorption of $^{14}\text{CO}_2$ by either of the top two leaves and the photosynthetic rate (Pearman, Thomas and Thorne, 1978) also did not differ.

Nitrate reduction in the leaves and the ability to translocate reduced N from foliage to grain are important determinants of grain protein content. Near-isogenic semidwarf and tall lines of hard red spring and durum wheats had similar seasonal average nitrate reductase activities (Deckard et al., 1977). Semidwarf lines accumulated significantly less reduced N per tiller than tall lines, however, and percent N in stems was lower in dwarf lines than in tall lines of both hard red spring wheats and durum wheat during grain filling (Ford and Thorne, 1975).

Rate of photosynthesis depends on carboxylase activity among other factors. RuBPC activity was significantly higher at anthesis than at other stages of growth in wheat genotypes (Murthy and Singh, 1979).

The present studies were initiated to determine the pattern of assimilation and partitioning of photosynthate and nitrogen—factors that together comprise harvest index—in isogenic tall, semidwarf and doubledwarf hard red winter wheats. Investigations were conducted under controlled environmental conditions as well as a range of field treatments used for growing wheat.

MATERIALS AND METHODS

Two experiments were conducted under controlled environmental conditions. Isogenic tall and semidwarf and doubledwarf (Norin 10/5*Pawnee) 'Pawnee' winter wheat (Triticum aestivum L.) lines developed by E. G. Heyne (personal communication) and completely randomized design with three replications were used for both studies. Plants were grown in Hoagland nutrient solutions (Hoagland and Arnon, 1950) in 2-liter opaque containers. Six 7-week-old seedlings vernalized at 3°C were transplanted to each container and grown in an environmental chamber at 27°C during daytime and 17°C during night. Light intensity was 30,000 Lux at plant height during a 14-hour photoperiod. All solutions were renewed weekly and supplemented FeSO_4 solution was added semiweekly.

Plant growth stages were defined according to Waldren and Flowerday (1979). Plants were randomly sampled at four growth stages, jointing, anthesis, soft dough, and maturity. At each stage, plants were separated into leaf blades, sheaths, stems, roots, spikes, and grains as those parts developed. Nitrate reductase activity was determined by the procedure of Heuer and Plaut (1978) and ribulose biphosphate carboxylase activity was determined by the procedure of Norton, Welch and Hartman (1975). The balance of the samples was dried at 70°C for 72 hours, weighed, and ground to pass a 20-mesh screen. Total nitrogen content of the samples was determined by microkjedahl (A.O.A.C., 1950) and available carbohydrate fractions were determined by the procedure of Okajima and Smith (1964).

A field study comparing the three lines was conducted at the

Agronomy Research Farm, Manhattan, Kansas, during the 1980-1981 crop year. The soil type was silt clay loam, pH 6.3, containing 5.9 ppm available NH_4^+ -N and 19.0 ppm available NO_3^- -N. The three isogenic Pawnee wheat lines were seeded at the rate of 60 kg/ha in plots 1.2 m wide by 10 m long containing 6 rows 20 cm apart in a randomized complete block design with four replications. Nitrogen fertilizer at the rate of 45 kg/ha as ammonium nitrate was top-dressed during early spring.

Growth analysis was performed on the three lines during reproductive growth. Two 25-cm-long sections of plants were cut at ground level from two center rows of each plot 25 April, 10 May, 19 May, 26 May, 1 June, and 6 June. At each date, plants were separated into leaves, stems, and spikes as those parts developed. The samples were dried at approximately 60 C for 5 days for leaf, stem, spike, and total dry matter determinations. Growth analysis formulae given by Hunt (1978) were used to calculate leaf area index (LAI), net assimilation rate (NAR), crop growth rate (CGR), and relative growth rate (RGR). An area of 10.9 m² in each plot was harvested by a plot combine at maturity. Moisture content of the grain was determined with an electronic moisture meter. Grain yield and test weight were adjusted to 14 % moisture content.

RESULTS

Distribution of dry matter among plants parts of isogenic tall, semidwarf and doubledwarf winter wheat lines decreased in leaves and stems and increased in spikes as plants developed (Table 1). The major differences among the lines were in the portion of dry matter contained in the leaf blades, which was higher in one or both of the dwarf lines than in the tall line at anthesis and soft dough growth stages.

Yield components of the isogenic lines are shown in Table 2. The tall and semidwarf lines had significantly more total dry matter, higher kernel number, and greater grain yield than the doubledwarf line. Spike number and weight were highest for the semidwarf line and lowest for the doubledwarf line. The 1000-kernel weight of the tall line exceeded that of the semidwarf line but not the doubledwarf line. Harvest index was 0.34 for the tall line, 0.42 for the semidwarf line, and 0.31 for the doubledwarf line. Partial floret sterility observed in the doubledwarf wheat probably caused the lower kernel number and low grain yield of that line.

The content of sugars (sucrose and reducing sugars) changed more in the stems and roots than in the leaves as the plants developed (Table 3). Sugar contents were highest at jointing and were lowest at maturity in stems and at soft dough in roots. Fructosan contents in sheaths, stems, and roots increased from the soft dough stage to maturity. Few differences occurred among the three lines at any growth stage. Nitrogen contents significantly decreased in leaf blades, stems, and roots as plants developed to

Table 1. Dry matter partitioning of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines under controlled environmental conditions.

Growth stage	Isogenic line	Plant parts					Total dry matter g/plant
		Blades	Sheaths	Stems	Roots	Spikes	
		----- % of total dry matter -----					
Jointing	TL	38.7a*	—	45.5a	15.8ab	—	2.41ef
	SD	41.9a	—	44.3ab	13.8ab	—	2.78ef
	DD	41.5a	—	43.4abc	15.1ab	—	2.14f
Anthesis	TL	20.5cd	14.6a	35.5abcde	9.3ab	20.1c	10.5bcd
	SD	24.7b	12.7a	31.5abcde	10.2ab	20.9c	8.1d
	DD	31.3a	13.4a	25.1cde	11.1ab	19.1c	6.9de
Soft dough	TL	14.7d	10.8a	26.3bcde	12.8ab	35.4b	20.90a
	SD	14.8d	10.0a	26.0bcde	16.0ab	32.2b	21.86a
	DD	20.7cd	9.2a	21.5de	13.0ab	35.6b	14.66b
Maturity	TL	—	9.2a	24.5cde	9.7ab	56.6a	14.43b
	SD	—	8.5a	20.7de	11.0ab	59.8a	13.15cb
	DD	—	10.3a	17.1e	9.5ab	63.1a	9.52cd
Mean	TL	24.6**	11.5	33.0	11.9	37.4	12.05
	SD	27.1	10.4	30.6	12.8	38.0	11.47
	DD	31.2	11.0	29.3	12.2	39.3	8.30

* Column values for isogenic lines with the same letter are not significantly different at 5% level.

** means followed by same line are not significantly different at the Duncan 5% level.

TL-tall; SD-semidwarf; DD-doubledwarf line.

Table 2. Yield components of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines under controlled environments.

Yield component	Isogenic line		
	Tall	Semidwarf	Doubledwarf
Grain yield g/plant	4.08a*	4.84a	2.56b
Total dry matter g/plant	14.43a	13.15a	9.52b
Spike number no./plant	7.5b	9.5a	7.2b
Spike weight g/plant	8.85b	9.54a	6.46c
Kernel number no./spike	17.7a	19.3a	10.7b
Kernel weight g/1000	31.3a	29.9b	30.3ab

* Row values for isogenic lines with the same letter are not significantly different at the Duncan 5% level.

Table 3. Distribution of carbohydrate fractions and nitrogen in plant parts of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat under controlled environmental conditions.

Growth stage	Sugar				Fructosan				Nitrogen				
	Line	Blades	Sheaths	Stems	Roots	Blades	Sheaths	Stems	Roots	Blades	Sheaths	Stems	Roots
	%												
Jointing	TL	15.3ab*	—	21.4ab	12.5ab	5.1b	—	4.7b	6.3cde	4.3b	—	2.8b	4.3ab
	SD	19.7a	—	16.4ab	14.7a	5.9ab	—	4.9b	7.2bcd	4.4ab	—	2.9b	3.9abcd
	DD	15.0ab	—	15.3abc	15.7a	6.6ab	—	6.0b	8.7abc	4.8a	—	3.9a	4.5a
Anthesis	TL	7.2bc	9.0ab	14.9abc	10.6abc	4.9b	4.1b	5.4b	4.1e	3.4de	1.6bcd	1.5de	3.2de
	SD	6.9c	9.3ab	17.0ab	10.7abc	4.5b	4.9b	4.4b	4.9de	3.8cd	2.0b	2.0c	3.0e
	DD	7.2bc	9.3ab	15.9ab	11.5ab	4.9b	4.1b	5.0b	6.4cde	4.2bc	2.6a	2.6b	4.1abc
Soft dough	TL	9.7ab	7.2ab	11.5bcd	5.1d	6.5ab	6.4ab	6.0ab	8.7abc	2.5fg	1.1e	1.0fg	2.8e
	SD	6.9c	7.2ab	13.1abc	5.1d	6.5ab	5.3b	4.9b	9.1abc	2.4gh	1.2de	1.3ef	2.8e
	DD	8.5bc	9.3ab	11.5bcd	5.1d	7.9a	6.4ab	6.4ab	9.4ab	3.0ef	2.0b	1.9cd	3.7abcd
Maturity	TL	—	6.5b	5.1d	7.2bcd	—	9.5a	6.4ab	11.1a	—	1.3cde	1.0g	2.8e
	SD	—	11.5ab	7.2cd	5.9cd	—	9.1a	8.7a	11.2a	—	1.5cde	1.4ef	3.3cde
	DD	—	14.5a	7.2cd	7.2bcd	—	6.4ab	6.4ab	11.1a	—	1.7bc	1.6cd	3.6bcd
Mean	TL	11.4**	7.5	13.2	8.9	6.3	6.7	5.6	7.6	3.4	1.3	1.6	3.3
	SD	12.4	9.3	13.4	9.1	6.3	6.4	5.7	8.1	3.5	1.6	1.9	3.3
	DD	11.6	11.0	12.5	9.9	7.5	5.7	5.6	8.5	4.0	2.1	2.5	4.0

* Column values for isogenic lines with the same latter are not significantly different at 5% level.

** Means followed by same line are not significantly different at the Duncan 5% level.

TL-tall; SD-semidwarf; DD-doubledwarf line.

the soft dough stage and then stayed nearly constant until maturity. The content of nitrogen in all plant parts frequently varied directly with the complement of dwarfing genes, being lowest in the tall line and highest in the doubledwarf line.

Ribulose biphosphate carboxylase activity increased from jointing to anthesis and then declined as plants developed and did not differ among the three lines (Table 4). Nitrate reductase activity significantly decreased in all three lines as the plants matured and also did not differ among the isogenic lines.

LAI decreased consistently from pre-heading to hard dough stage and NAR was highest from 19 May to 26 May (time interval 3) for all lines (Table 5). CGR was highest for the tall line and lowest for the doubledwarf line from 26 May to 1 June (time interval 4), however, no differences in LAI, NAR, CGR and RGR were observed among the three lines.

Dry matter partitioning of isogenic wheat lines in the field decreased in leaves and stems and increased in spikes as plants developed (Table 6). A significantly higher proportion of total dry matter was contained in the spikes of the doubledwarf line than the tall line at anthesis; at the soft dough stage, spikes were proportionally heaviest in the doubledwarf line and lightest in the tall line. Differences among the lines diminished by the hard dough stage, however. The tall and semidwarf lines had significantly higher grain yield, test weight, total dry matter, spike number, and 1000-kernel weight than the doubledwarf line. The semidwarf and doubledwarf lines, however, had significantly higher kernel number than the tall line. Harvest index was higher

Table 4. Ribulose biphosphate carboxylase activity (RuBPCA) and nitrate reductase activity (NRA) in leaf blades of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines under controlled environmental conditions.

Growth stage	Isogenic line	RuBPC	NR
		$\mu\text{mol}\text{CO}_2, \text{gfw}^{-1}, \text{min}^{-1}$	$\mu\text{mol}\text{NO}_2, \text{gfw}^{-1}, \text{hr}^{-1}$
Jointing	TL	131b*	.5.7a
	SD	124b	5.9a
	DD	138b	5.4a
Anthesis	TL	250a	2.8b
	SD	243a	2.8b
	DD	152a	3.5b
Soft dough	TL	91b	0.9c
	SD	80b	0.9c
	DD	114b	1.3c
Mean	TL	157.3**	3.1
	SD	149.0	3.2
	DD	134.7	3.4

* Column values for isogenic lines with the same letter are not significantly different at 5% level.

** Means followed by same line are not significantly different at the Duncan 5% level.

TL-tall; SD-semidwarf; DD-doubledwarf line.

Table 5. Leaf area index (LAI), net assimilation rate (NAR), crop growth rate (CGR), and relative growth rate (RGR) of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines under field conditions.

Time interval	LAI			NAR			CGR			RGR		
	TL	SD	DD	TL	SD	DD	TL	SD	DD	TL	SD	DD
	---cm ² cm ² ---			-mg dm ⁻² day ⁻¹ -			-- mg day ⁻¹ -			--mg g ⁻¹ day ⁻¹ -		
1**	2.6a*	2.27a	2.85a	6a	8a	6a	24a	32a	22a	17a	23a	19a
2	1.5a	1.6a	1.2a	8a	7a	6a	16a	16a	10a	10a	10a	7a
3	0.9a	0.9a	0.6a	26a	24a	28a	34a	30a	32a	19a	16a	20a
4	0.4a	0.4a	0.3a	—	—	—	32a	22ab	14b	16a	10a	8a
Mean	1.4a	1.3a	1.2a	13a	13a	13a	27a	25a	20a	16a	15a	14a

* Row values for isogenic lines with the same letter are not significant at the Duncan 5% level.

** Time interval;

1=25 April(pre-heading) to 10 May (anthesis);

2=10 May to 19 May;

3=19 May to 26 May;

4=26 May to 1 June;

for the doubledwarf line (0.58) than for the two other lines (0.54).

DISCUSSION

Grain yield of the isogenic wheat lines depended on a complex of many plant attributes, some of which were mutually exclusive. The three major attributes appeared to be amount of dry matter accumulated, distribution of the dry matter among plant parts, and the carbohydrate and nitrogen economy of the plants. Yield differential among the lines was almost entirely due to the carbohydrate economy and only slightly to capacity to take up nitrogen from the soil, differences that were also associated with high yield potential of new cultivars (Bingham, 1976).

The high yield capacity of dwarf cultivars partly derived from the pattern of carbohydrate distribution before heading when competition for carbohydrates between developing spikes and extending stems was most intense (Syme, 1969; Walcott and Laing, 1976). The tall wheat line had greater biological yield (total dry matter) than the dwarf lines and had a greater proportion of its total dry matter in sheaths and stems; however, the dwarf lines had a greater proportion of assimilates in leaves, roots and spikes. Thus, assimilates were used more for structural sheath and stem materials in the tall line and more for the developing spikes in the dwarf lines. Spikes were better sinks for photosynthates in the dwarf lines than in the tall line and, hence, the former were able to develop greater number of grains per spike (McNeal et al., 1972). That pattern of dry matter distribution also largely

contributed to the increased harvest index of the dwarf lines (McNeal et al., 1972; Spiertz and van de Haar, 1978; Thorne et al., 1969; Walcott and Laing, 1976).

The balance between production of assimilates by the plant and their utilization by the grain may be reflected by the accumulation of reserve substances, mainly carbohydrates, in the stems. Large differences in contents of nonstructural carbohydrates after anthesis indicated the loss of carbohydrates from the vegetative plant part was caused by increased utilization of assimilates for grain growth and possibly for respiration. The higher proportion of total dry matter in stems of the tall line was not caused by high content of carbohydrate fractions.

Most of the grain protein in wheat was derived from remobilization of nitrogen from the vegetative plant parts (Halloran, 1981). The efficiency of translocation of nitrogen from the vegetative parts to the developing grains was lower for the dwarf lines than for the tall line. That may cause the dwarf lines to have lower grain protein content. Similar activities of RuBPC and NR in leaf blades showed that those enzymes were not responsible for differential yields among the three lines in this experiment. The pattern of assimilation and partitioning of photosynthate and nitrogen lead to the conclusion that the carbohydrate and nitrogen supply to the grains was not yield-limiting and grain yield depended mainly on number of grains per spike and the number of spikes per unit area.

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PART II

RESPONSE OF YIELD ATTRIBUTES OF ISOGENIC TALL, SEMIDWARF, AND DOUBLEDWARF WINTER WHEAT LINES TO NITROGEN FERTILIZER AND SEEDING RATE

Grain yield of wheat is a function of many attributes. Three of the most important yield components are number of spikes per unit area, number of kernels per spike, and weight of kernels (Schlehuber and Tucker, 1967). Those determinants of yield are affected by both genetic factors (Syme, 1969; Walcott and Laing, 1976; Spiertz and van de Haar, 1978) and agronomic practices (Osman and Mahmoud, 1981; Watson, Thorne, and French, 1963; Vogel and Allan, and Peterson, 1963; Faris and De Pauw, 1981).

The yield superiority of dwarf wheats over tall wheats was attributed to several advantages of the former: reduced competition between stem and grain for post-anthesis assimilates (Syme, 1969; Walcott et al., 1976), greater capacity to vary grain number (Spiertz and van de Haar, 1978), and more efficient production of grain per unit leaf area (Thorne, Welbank, and Blackwood, 1969). Those advantages usually were manifested as a higher harvest index for dwarf wheats than for tall wheats (Kim and Paulsen, 1982; Thorne et al., 1969; Walcott and Liang, 1976).

Agronomic inputs usually cause greater responses in dwarf wheats than in tall wheats. Semidwarf wheat cultivars, for instance, were more capable than tall wheats of economically responding to large amounts of nitrogen fertilizer (Osman and Mahmoud, 1981; Watson et al., 1963; Vogel and Allan, 1963). Similarly, The optimum seeding rate for maximum yield was higher for semidwarf wheats

than for tall wheats (Thorne and Blacklock, 1971; Faris and De Pauw, 1981). Reason for the greater responsiveness of dwarf wheats to agronomic inputs, however, were usually not the same as the reasons given for their yield superiority over tall wheats. High yield of dwarf wheats with high nitrogen fertilizer rates and seeding rates, for instance, were often associated with lodging resistance (Borojevic, 1968; Pinthus, 1973).

We investigated whether the attributes that gave dwarf wheats their yield superiority over tall wheats were also those that gave them their greater responsiveness to agronomic inputs. Iso-genic tall, semidwarf, and doubledwarf lines were used to minimize genetic differences other than those associated with height.

MATERIALS AND METHODS

Three isogenic tall and semidwarf and doubledwarf (Norin 10/5*Pawnee) ' Pawnee ' winter wheat (Triticum aestivum L.) lines were used for the studies at the Agronomy experiment fields at Hutchinson and at Manhattan, Kansas, during the 1980-1981 crop year. The soil types were clay loam, pH 6.4, containing 7.4ppm NH_4^+ - N and 13.8 ppm NO_3^- - N at Hutchinson and silt clay loam, pH 6. containing 5.9 ppm NH_4^+ - N and 19.0 ppm NO_3^- - N at Manhattan.

The experiments were planted in a split-split -plot design with three nitrogen fertilizer rates as main plots, three seeding rates as sub plots, and the three isogenic lines as sub-sub-plots in four replications. The three genotypes were seeded at 30, 60, and 90 kg per ha at Hutchinson October 11 and at Manhattan October

4, 1980. Nitrogen fertilizer at rates of 0, 45, and 90 kg per ha as ammonium nitrate was topdressed during early spring. Each sub-sub-plot was 1.2 m wide and contained 6 rows spaced 20 cm apart; sub-sub-plot length was 7.5 m at Hutchinson and 10 m at Manhattan.

Plant height was determined from four measurements taken randomly in each sub-sub-plot near maturity. The final spike number and kernels per spike were measured at maturity on plants from 0.2 m² soil area. Total and fertile spikelets were counted from 10 spikes per plot at maturity. Kernel weight was determined directly from threshed spike samples after oven drying the grain at 65 C. Areas of 8 m² and 10.9 m² in each sub-sub-plot were harvested by plot combine at maturity at Hutchinson and Manhattan, respectively.

Moisture content of grain was determined with an electronic moisture meter and grain yield and test weight were adjusted to 14 % moisture. Samples for 1000-kernel weight were dried at 65 C for 3 days and then were counted and weighed. Protein content of grain was determined by infra-red reflectance and expressed on a 14 % moisture basis.

RESULTS

Grain yields of the three lines differed only at the high nitrogen fertilizer rates and high seeding rates, where yields of the tall line or semidwarf line or both exceeded yields of the doubledwarf line (Tables 1 and 2). Low yields of the double-dwarf line were associated with low grain test weight, low threshing rate, and low 1000-kernel weight; however, kernel number per spike and fertile spikelet ratio were higher in the double-dwarf line than in the other lines. Harvest index was higher for the dwarf lines than for the tall line and, whereas plant height was decreased proportionally to the dwarfing gene complement, spike length was not affected. Grain protein content of the three lines was also similar at similar nitrogen fertilizer rates.

Nitrogen fertilizer increased kernel number per spike, fertile spikelet ratio, and harvest index of the semidwarf line and decreased grain test weight of all lines at Manhattan (Table 1). Fertile spikelet ratios of tall and semidwarf lines were positively associated with nitrogen rate, but test weight and threshing rate of doubledwarf line and 1000-kernel weight of the semidwarf line were negatively associated with nitrogen rate at Manhattan (Table 3). Kernels per spike in the tall line and spike length of the semidwarf line were positively correlated with nitrogen fertilizer rate at Hutchinson.

High seeding rates increased grain yields of the doubledwarf line at both locations and the tall line at Hutchinson, but had no effect on the semidwarf line at both locations (Table 2). They also increased grain test weight of the doubledwarf line at both

Table 1. Response of yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines to nitrogen fertilizer at two Kansas locations.

Iso- genic gen line	Nitro- Grain Test		Spike		Kernel		Kernel Spike-		Fertile		Thre-		Protein		Harvest		Plant		Spike	
	kg/ha	kg/ha	kg/hl	no/m ²	g/1000	---no/spike---	number	ratio	spikelet	shing	rate	index	height	length	cm	cm	cm	cm	cm	cm
Manhattan																				
TL	0	2565a	70.4a	750abc	32ab	14bc	16.6a	69d	71ab	71ab	11.1ab	35c	84a	6.7a						
	45	2548a	69.8ab	830a	30c	14bc	16.4a	71cd	73ab	73ab	12.1a	37c	82a	6.9a						
	90	2406abc	69.4b	805abc	31bc	14bc	16.8a	72cd	70bc	70bc	10.7d	36c	82a	7.0a						
SD	0	2510ab	70.6a	730abc	33a	14bc	16.5a	74bc	75a	75a	11.2bcd	38bc	74b	6.6a						
	45	2328abc	69.8b	785abc	31bc	15abc	16.8a	78a	75a	75a	11.9ab	40ab	72b	6.8a						
	90	2536a	69.7b	815ab	31bc	16a	16.5a	79a	75a	75a	10.8	41a	75b	7.0a						
DD	0	2382abc	67.2c	700c	27d	15abc	16.3a	76ab	74ab	74ab	11.1cd	41a	49c	6.3a						
	45	2240bc	66.0d	745abc	26de	16a	16.5a	79a	64d	64d	11.6abc	41a	48c	7.0a						
	90	2200c	64.4e	710bc	25e	17a	16.3a	78a	66cd	66cd	11.0d	40ab	48c	6.6a						
Hutchinson																				
TL	0	3284bc	77.1a	635a	33a	17c	—	—	—	—	11.3b	39d	87a	7.0bc						
	45	3355b	76.5ab	550ab	32a	19b	—	—	—	—	12.5ab	39d	88a	7.2bc						
	90	3455ab	76.6ab	575ab	32a	19b	—	—	—	—	12.1ab	39d	87a	7.1bc						
SD	0	3507ab	76.0bc	615ab	34a	18bc	—	—	—	—	12.0ab	41cd	78b	6.7c						
	45	3245bc	75.6c	575ab	34a	19b	—	—	—	—	12.4ab	41cd	77b	7.2bc						
	90	3708a	76.0bc	580ab	33a	20ab	—	—	—	—	11.7ab	42bc	77b	7.4ab						
DD	0	3175bc	73.8d	550ab	30b	23a	—	—	—	—	11.7ab	46a	54d	7.2bc						
	45	2958c	73.5d	510b	30b	24a	—	—	—	—	12.7a	42bc	59c	7.6a						
	90	2943c	72.7e	500b	28c	23a	—	—	—	—	11.9ab	44b	52d	7.1bc						

Column values for each nitrogen level with the same letter are not significantly different at the Duncan 5% level.

TL-tall; SD-semidwarf; DD-doubledwarf line.

Table 2. Response of yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines to seeding rate at two Kansas locations.

Iso- genic line	See- ding	Grain yield kg/ha	Test weight kg/hl	Spike number no/m ²	Kernel weight g/1000	Manhattan			Hutchinson			Harvest index	Plant height cm	Spike length cm
						number	ratio	%	number	ratio	%			
TL	30	2501a	70.4a	765abc	32a	15bcd	17.3ab	71b	72ab	11.5a	37bc	83a	7.2a	
	60	2494a	70.0ab	790ab	31ab	14de	16.7bcd	71b	72ab	11.2a	35d	83a	6.9a	
	90	2525a	69.3b	830a	30b	12f	15.8e	70b	70bc	11.3a	36cd	81ab	6.6a	
SD	30	2561a	69.2b	770abc	32a	17a	17.4a	79a	73ab	11.4a	40ab	80bc	7.3a	
	60	2372a	70.4a	775abc	32a	15bcd	16.4cde	76a	77a	11.0a	40ab	73cd	6.6a	
	90	2441a	70.6a	780abc	31ab	13ef	16.0de	75a	75a	11.4a	39ab	71d	6.5a	
DD	30	2033b	65.1d	695bc	26c	17a	16.9abc	79a	65d	11.6a	40a	50e	6.7a	
	60	2341a	66.1c	670c	25c	16abc	16.3cde	77a	66cd	11.0a	41a	50e	6.7a	
	90	2448a	66.5c	790ab	26c	14de	15.8e	78a	73ab	11.3a	41a	45e	6.5a	
TL	30	2990c	76.4ab	520b	33a	20b	—	—	—	11.8ab	39cd	87a	7.3ab	
	60	3654a	76.7ab	580ab	33a	18cd	—	—	—	11.7ab	39cd	87a	7.2b	
	90	3450ab	77.0a	660a	32ab	16d	—	—	—	12.3ab	38d	88a	6.9b	
SD	30	3360ab	75.7c	525b	34a	22b	—	—	—	12.0ab	43b	78b	7.4ab	
	60	3387ab	75.9c	595ab	34a	18c	—	—	—	11.8ab	41bc	78b	7.1b	
	90	3713a	76.1bc	645a	33a	16d	—	—	—	12.4ab	40cd	76b	6.8b	
DD	30	2489d	71.9e	500b	27d	26a	—	—	—	12.9a	41c	56c	7.8a	
	60	3124bc	73.9d	505b	29c	22b	—	—	—	11.4b	45a	55c	7.0b	
	90	3462ab	74.2d	555ab	31b	22b	—	—	—	12.0ab	46a	54c	7.2ab	

Column values for each seeding rate with the same letter are not significantly different at the Duncan 5% level.

TL-tall; SD-semidwarf; DD-doubledwarf line.

Table 3. Simple correlations of grain yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines with nitrogen fertilizer at two Kansas locations.

Iso- genic line	Grain yield	Test weight	Spike per m ²	1000 kernel weight	Kernel per spike	Spikelet Fertile Thre-		Protein Harvest	Plant height	Spike length
						per spike	ratio rate			
----- r -----										
Manhattan										
TL	-0.2032	-0.3261	0.1550	-0.2982	0.1068	0.0562	0.3346 [*]	-0.0984	-0.1159	0.0817 -0.1257 0.2038
SD	0.0281	-0.2485	0.2982	-0.4224 [*]	0.3077	0.0001	0.4312 ^{**}	-0.0431	-0.1442	0.3847 [*] 0.0376 0.2516
DD	-0.2674	-0.5300 ^{**}	0.0288	-0.3265	0.2429	0.0001	0.1739	-0.3423 [*]	-0.0548	-0.1353 -0.0246 0.1330
Hutchinson										
TL	0.1451	-0.2073	-0.1939	0.0051	0.3417 [*]	—	—	—	0.1944	0.1071 -0.0101 0.0780
SD	0.1949	0.0216	-0.1959	-0.1982	0.2235	—	—	—	-0.0841	0.2127 -0.1074 0.4033 [*]
DD	-0.1701	-0.3123	-0.1681	-0.2537	-0.0113	—	—	—	0.0439	-0.1899 -0.0781 -0.0465

*,** significant; highly significant at p.05 and p.01 level, respectively.
TL-tall; SD-semidwarf; DD-doubledwarf line.

locations; at Manhattan, test weight decreased in the tall line and increased in the semidwarf line as seeding rate increased. Threshing rate of the doubledwarf line also increased as seeding rate increased. Number of kernels and spikelets per spike, however, decreased in all lines as the seeding rate increased. Effects of seeding rate on other plant traits were small.

Grain yield of all lines at Hutchinson and of the doubledwarf line at Manhattan were positively associated with seeding rate (Table 4). Spike number of the doubledwarf line at Hutchinson were also positively associated with seeding rate. Kernels per spike and spikelets per spike, on other hand, were negatively associated with seeding rate in all lines as was spike length of the tall and semidwarf lines. Other traits were not consistently related to seeding rate.

Grain yields were positively associated with test weight and spike number per unit area of all lines and with 1000-kernel weight of tall and doubledwarf lines at either or both locations (Tables 5 and 6). Traits that were negatively associated with yield were only observed in the doubledwarf line and included spikelet number per spike at Manhattan and kernel number and spike length at Hutchinson. Test weights were positively associated with kernel number and spikelet number of the tall line and with 1000-kernel weight of all lines at Manhattan. They were negatively correlated, however, with kernel number and fertile spikelet ratio of the semidwarf line at Manhattan and with kernel number of both dwarf lines at either or both locations.

Harvest indices were positively associated with kernel number

Table 4. Simple correlations of grain yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines with seeding rate at two Kansas locations.

Iso- genic line	Grain yield	Test weight	Spike per m ²	1000 kernel weight	kernel per spike	kernel per spike	per spike	Fertile ratio	Thre- shing rate	Protein percent	Harvest index	Plant height	Spike length
----- r -----													
Manhattan													
TL	0.0300	-0.3845*	0.1695	-0.3586*	-0.6761**	-0.5340**	-0.0239	-0.2415	-0.0527	-0.2451	-0.1158	-0.4650**	
SD	-0.1304	0.4018*	0.1397	-0.1320	-0.6422**	-0.6082**	-0.3216	0.2230	0.0029	-0.0869	-0.3493*	-0.5142**	
DD	0.6134**	0.2569	0.3452*	0.0556	-0.4859**	-0.7144**	-0.0828	0.3622*	-0.1404	0.0312	-0.3747*	-0.0919	
Hutchinson													
TL	0.3885*	0.2500	0.4442**	-0.4115*	-0.7455**	—	—	—	—	0.1391	-0.2786	0.0194	-0.3640*
SD	0.3426*	0.2805	0.3776*	-0.1724	-0.7152**	—	—	—	—	0.1274	-0.4405**	-0.2049	-0.3440*
DD	0.7152**	0.6245**	0.1983	0.4953**	-0.6343**	—	—	—	—	-0.1884	0.4222*	-0.1625	-0.2874

*, **, Significant at 5%, and 1% level, respectively.

TL-tall; SD-semidwarf; DD-doubledwarf line.

Table 5. Simple correlations among grain yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines at Manhattan, Kansas, during 1981.

Iso- genic line	Test weight	Harvest index	Spike no.	Kernel per spike	1000 kernel weight	Spikelet per spike	Fertile spikelet ratio	Spike length
	TWT	HI	SPKN	KNLN	KWT	SPKLN	FTLR	SPKL
----- r -----								
<u>TALL</u>								
YLD	0.5343**	-0.0046	0.3706*	0.2116	0.4062*	0.1757	0.1039	0.0934
TWT		0.1736	0.2336	0.3931*	0.5511**	0.4481**	0.1920	0.1426
HI			-0.2723	0.4516**	0.3729*	0.1824	-0.0955	0.3910*
SPKN				-0.1288	-0.0491	0.1894	0.1663	0.0314
KNLN					0.5126**	0.3610*	0.1302	0.6280**
KWT						0.1856	-0.0327	0.4330**
SPKLN							0.1084	0.4182*
FTLR								-0.0137
<u>SEMI DWARF</u>								
YLD	0.0387	0.0218	0.1668	0.1900	-0.0487	0.1644	0.3959*	0.1193
TWT		-0.0792	-0.1121	-0.3568*	0.3619*	-0.1417	-0.3444*	-0.2511
HI			-0.1166	0.5772**	0.0399	-0.0272	0.2714	0.0915
SPKN				-0.0011	-0.0502	0.3399*	0.2371	0.0661
KNLN					0.0288	0.3466*	0.3309*	0.3166
KWT						-0.0292	-0.2789	-0.1083
SPKLN							-0.0105	0.2059
FTLR								0.3176
<u>DOUBLEDWARF</u>								
YLD	0.3597*	0.1656	0.3451*	-0.3041	0.4154*	-0.4327**	-0.0743	0.0033
TWT		0.2363	0.0277	-0.2019	0.3905*	0.1115	-0.0358	-0.2463
HI			0.1120	0.1416	0.5516**	0.1104	0.0577	0.2540
SPKN				-0.3099	0.2499	-0.2447	0.3681*	0.1186
KNLN					-0.1498	0.3802*	-0.0771	0.1506
KWT						0.0996	0.1013	0.0127
SPKLN							0.0270	0.2082
FTLR								0.4087*

*, **, Significant at p_{.05} and p_{.01} level, respectively.

YLD-yield.

Table 6. Simple correlations among grain yield attributes of isogenic tall, semidwarf, and doubledwarf Pawnee winter wheat lines at Hutchinson, Kansas, during 1981.

Iso- genic line	Test weight	Harvest index	Spike no.	Kernel per spike	1000 kernel weight	Spike length
	TWT	HI	SPKN	KNLN	KWT	SPKL
----- r -----						
<u>TALL</u>						
YLD	0.2525	0.2763	0.3066	-0.2137	0.0333	-0.0258
TWT		0.2485	0.2832	-0.2437	0.1226	-0.3407*
HI			0.0373	0.3854*	0.3552*	-0.0415
SPKN				-0.4725**	-0.4065*	-0.2120
KNLN					0.1617	0.3038
KWT						0.0675
<u>SEMIDWARF</u>						
YLD	0.4076*	0.1271	0.3711*	-0.1943	-0.2852	0.0562
TWT		0.0039	0.3639*	-0.3299*	0.0359	-0.0220
HI			-0.0314	0.4552**	0.1682	0.3184
SPKN				-0.4364**	-0.2016	-0.1915
KNLN					-0.0847	0.3476*
KWT						0.0194
<u>DOUBLEDWARF</u>						
YLD	0.6696**	0.5465**	0.0168	-0.5441**	0.5035**	-0.3575*
TWT		0.4527**	0.1214	-0.6128**	0.5033**	-0.2223
HI			-0.1128	0.5794**	0.1392	-0.4032*
SPKN				-0.2589	0.3784*	-0.0041
KNLN					-0.3667*	0.5455**
KWT						-0.0152

*, **, Significant at p.05 and p.01 level, respectively.
YLD-yield.

per spike of tall and semidwarf lines at both locations, and with 1000-kernel weight of all lines at either or both locations. Harvest index of the tall line was also positively associated with spike length at Manhattan, but that of the doubledwarf line was negatively associated with spike length at Hutchinson.

DISCUSSION

Grain yields of the three Pawnee genotypes varied in the different environments. Yield attributes of the genotypes, however, differently responded to nitrogen level and seeding rate and varied in relative importance among the lines themselves.

There was no evidence that dwarf lines required more nitrogen or responded better to nitrogen fertilizer than tall lines (Thorne et al., 1971). The small response probably occurred because available soil nitrogen content was high. That result disagreed with other reports that short cultivars responded more than tall cultivars to nitrogen fertilizer (Osman and Mahmoud, 1981; Watson et al., 1963; Vogel et al., 1963). However, grain yield of the semidwarf line was favored at high nitrogen fertilizer by better response of yield attributes, fertile spikelet ratio, spike length, harvest index, and kernel number per spike. Fertile spikelet ratio of the genotypes favorably responded to nitrogen fertilizer, probably because it influenced rate of spikelet production (Single, 1964; Whingwiri and Kemp, 1980). However, other yield attributes of the genotypes—test weight, 1000-kernel weight and threshing rate—generally unfavorably responded to nitrogen fertilizer and thus,

grain yields of the three lines were not affected by nitrogen fertilizer in this experiment.

Grain yield was more responsive to seeding rate in the doubledwarf line than in the other lines. Moreover, test weight and spike number per unit area of one or both dwarf lines were also usually more responsive to seeding rate than those of the tall line (Faris and De Pauw, 1981; Thorne and Blacklock, 1971). That response appeared to be conditioned by morphophysiological characteristics (Pendleton and Dungan, 1960; Briggs, 1975). Grain yields of dwarf lines were positively associated with seeding rate as were test weights and spike numbers per unit area of one or both dwarf lines. However, kernels and spikelets per spike were significantly negatively associated with seeding rate, as generally were spike length of tall and semidwarf lines. Those effects may be due to the result of interplant or intraplant competition that restricted the nutrition, moisture, and solar radiation at high seeding rate (Darwinkel, 1978).

Grain yield of each genotype highly depended on the its predominant yield attributes. Grain yield mainly depended upon test weight and spike number per unit area. Test weight depended on kernel number and 1000-kernel weight. Kernel number highly depended on spikelet number and spike length. Whingwiri and Kemp (1980) reported that kernels per spike depended more on the number of fertile spikelets per spike and the number of grains per fertile spikelet than on total spikelet numbers. Harvest index was highly associated with kernel number per spike and 1000-kernel weight. Any gain in single yield attributes that was offset by a decrease in one or both of the other components would produce no gain in total yield.

However, an advance in one component with others remaining constant would produce an equal advance in total yield. Response of yield attributes to agronomic inputs lead to the conclusion that dwarf lines neither require more nitrogen or respond better to nitrogen than do tall lines. The greater response to seeding rate by dwarf lines than by tall line in this experiment, however, suggested that the former required more plants per unit soil to achieve its optimum leaf area index.

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APPENDIX

Table A1. Analysis of variance for grain and yield attributes for nitrogen fertilizer and seeding rate at Manhattan in 1981.

Source of variation	d.f.	Grain yield	Test weight	Grain protein	Harvest index	Spike number	Kernel number	Kernel weight	Spikelet number	Fertile ratio	Threshing rate	Plant height	Spike length
Nitrogen	2	287585.6	43.1**	22.4	0.002	2812.9	32.02	60.8*	0.4	258.7**	208.6*	50.2	0.3
Error N	6	671226.7	10.3	62.3	0.009	4833.0	26.3	23.7	3.05	62.8	58.8	524.9	2.6
Seeding	2	209023.7	7.2	3.9	0.002	2307.0	206.8*	9.6	34.8**	52.9	129.2	301.4**	2.3
N x S	4	177375.5	3.8	2.9	0.007	676.2	25.03	10.7	1.3	55.9	161.7	150.9*	5.5
Error S	18	624408.9	32.8	9.9	0.01	10095.9	65.9	65.8	14.6	314.1	873.1	293.3	2.6
Line	2	1083724.9	398.9**	0.02	0.04*	4657.5*	70.3**	744.6*	1.7	1054.8**	889.1**	22705.1**	9.0
N x L	4	420735.8	15.9**	1.1	0.004	1005.8	11.4	2.2	1.7	35.5	448.1**	48.4	1.0
S x L	4	1135988.6*	25.8**	0.8	0.003	2731.0	9.9	24.9	1.3	48.03	389.8*	84.4	1.0
N x S x L	8	439137.1	19.5*	3.1	0.005	4223.9	11.7	22.4	4.68	119.8	172.8	94.9	3.6
Error L	54	5500752.4	58.1	35.4	0.049	30604.5	197.3	144.3	32.7	970.5	1432.7	1983.1	37.6

*, ** significant at the .05 and .01 levels, respectively

Table A2. Analysis of variance for grain and yield attributes for nitrogen fertilizer and seeding rate at Hutchinson in 1981.

Source of variation	d.f.	Grain yield	Test weight	Grain protein	Harvest index	Spike number	Kernel number	Kernel weight	Plant height	Spike length
Nitrogen	2	648719.1	5.75	14.3	0.001	16798.9	12.9	97.4	135.0	3.33*
Error N	6	1212778.1	7.68	102.5	0.01	6009.1	23.09	260.0	183.5	0.7
Seeding	2	6876149.9**	23.3**	8.4	0.002	3692.4	417.4**	28.6	49.1	5.6**
N x S	4	158226.03	8.5*	2.3	0.002	8152.1	11.1	199.3	23.9	0.9
Error S	18	2534514.3	7.5	36.2	0.02	27584.7	52.2	746.6	273.9	7.6
Line	2	4115544.8**	222.5**	0.5	0.05**	651.6	602.7**	129.9	19610.4**	1.4
N x L	4	1224845.3	6.3	4.3	0.009*	4807.6	23.6	289.5	167.2	2.9
S x L	4	2680626.8**	17.2**	9.8	0.019**	8252.6	16.7	41.5	44.3	1.1
N x S x L	8	523859.8	5.2	4.1	0.992	18892.3	6.6	413.7	218.3	2.6
Error L	54	8298733.04	42.6	86.6	0.037	88134.0	233.0	2474.6	1434.4	21.98

*, ** significant at the .05 and .01 levels, respectively

ASSIMILATION AND PARTITIONING OF CARBOHYDRATES AND NITROGEN
AND EFFECT OF MANAGEMENT PRACTICES ON ISOGENIC TALL,
SEMIDWARF, AND DOUBLEDWARF WHEAT LINES

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Dwarf wheat (Triticum aestivum L.) cultivars predominate in many wheat-producing areas of the world. Their yield superiority is usually attributed to higher harvest index compared to conventional tall cultivars, but the physiological basis for the favorable harvest index is not clear. Present studies determined patterns of assimilation and partitioning of photosynthate and nitrogen in different wheat plant types and investigated whether attributes that give dwarf wheats their yield superiority over tall wheats are also those that make them more responsive to agronomic inputs. Isogenic tall, semidwarf (rht_1 or rht_2), and doubledwarf ($rht_1 + rht_2$) 'Pawnee' hard red winter wheat lines were grown under controlled environmental conditions as well as field conditions. Plants were sampled at jointing, anthesis, soft dough, and maturity growth stages and separated into plant parts as they developed. Nitrate reductase (NR) and ribulose biphosphate carboxylase (RuBPC) activities, growth analysis, dry matter partitioning, yield components, and distribution of carbohydrate fractions and total nitrogen contents in plant parts were determined. RuBPC and NR activities differed among growth stages but not among isogenic lines. The portion of dry matter contained in the leaf blades was higher in one or both dwarf lines under growth chamber conditions and in the spike of the doubledwarf line than in the tall line under field conditions at anthesis and soft dough growth stages. LAI, NAR, CGR, and RGR also differed among growth stages but not among lines. The tall and semidwarf lines had significantly higher grain yield, test weight, total dry matter, spike number, and 1000-kernel weight than the doubledwarf line under either or both experimental conditions. The dwarf lines, however, had significantly

higher kernel number per spike and higher harvest index than the tall line under one or both experimental conditions. Few differences in carbohydrate fractions occurred among the three lines; nitrogen contents, however, were lowest in the tall line and highest in the doubledwarf line under controlled conditions. The three genotypes were planted in a split-split-plot design with nitrogen fertilizer rates of 0, 45, and 90 kg/ha as main plots and seeding rates of 30, 60, and 90 kg/ha as sub-plots in four replications at Hutchinson and Manhattan, Kansas during 1980-1981. There was no evidence that dwarf lines responded better than the tall line to nitrogen fertilizer, however, fertile spikelet ratio, spike length, harvest index, and kernel number per spike of the semidwarf line were favored at high nitrogen rates. Grain yield was more responsive to seeding rate in the doubledwarf line than in the other lines. Moreover, test weight and spike number per unit area were more responsive to seeding rate in one or both dwarf lines than in the tall line. Grain yield of each genotype highly depended on the predominant yield attributes - test weight and spike number per unit area. Carbohydrate and nitrogen supplies to the grains were not yield-limiting; however, the dwarf lines required more plants per unit soil to achieve their optimum leaf area index.