An Analysis of Post-Anthesis Sink-Limited Winter Wheat Grain Yields Under Various Environments[1]

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ABSTRACT

Better understanding of the frequency of post-anthesis sink-limited winter wheat (*Triticum aestivum* L.) grain yields is needed in selecting genotypes with high yield potential and yield stability. Field studies were conducted at four locations (the major soil types were mesic, Aridic Paleustolls and mesic, Aridic Argiustolls) in eastern Colorado over the two cropping seasons of 1976-1977 (1977) and 1977-1978 (1978), using yield and yield component analysis, to determine the effect of sink limitations. Three hard red winter wheat cultivars were grown under four N fertilizer rates at each location to increase variation in grain yield and yield components. Variation was observed for grain yield and the yield components of spike no. (spike no. m^{-2}), kernel no. per spike, kernel no. (kernel no. m^{-2}), and kernel size (mg $kernel^{-1}$) across locations. Grain yield and yield component variation, due to cultivars or N treatments, were observed at six of the eight sites. Variation in grain yield within and across sites was more consistently correlated with kernel no. than kernel size. These results strongly suggest that wheat grain yields may be sink-limited during grain filling over a wide array of environments. Variation in kernel no. within locations was more consistently correlated with kernel no. per spike than spike number, while variation in kernel no. across locations was more highly associated with spike no. than kernel no. per spike. Thus, both yield components were important in establishing sink capacity under the variable environmental conditions of this study.

Additional index words: ***Triticum aestivum*** **L., Kernel number, Kernel size, Source-sink relationships.**

GRAIN yield of hard red winter wheat (*Triticum aestivum* L.) is a function of kernel no. (kernel no. per unit area) and kernel size. The number of potential kernel sites differentiated by a wheat crop depends upon developmental processes, such as tiller initiation, tiller abortion, and spike differentiation, that occur prior to anthesis (Willey and Holliday, 1971; Evans et al., 1975; Fischer, 1975). Kernel size is primarily determined during the grain-filling period (Sofield et al., 1977; Warrington et al., 1977), although it may be secondarily affected by kernel number (Fischer et al., 1977).

A large proportion of the grain carbohydrate is derived from CO_2 fixation during the grain-filling period (Evans et al., 1975). Therefore, maximum grain yield of the crop depends upon the capacity to produce (source strength) and utilize (sink strength) photosynthate during this period (Evans et al., 1975; Evans and Wardlaw, 1976). Fischer et al. (1977) have suggested that post-anthesis sink limited grain yields are distinguishable by a positive correlation between grain yield and kernel no. per unit area, while a lack of association between these two variables indicates source restricted grain yields. Other studies involving crop manipulation to alter the source-sink ratio during grain filling (Willey and Holliday, 1971; Fischer, 1975; Fischer and Laing, 1976; Fischer and HilleRisLambers, 1978) have indicated that sink-source relationships may be affected by environmental conditions.

Hard red winter wheat grown in the Great Plains area is subject to variable environmental conditions. It frequently encounters water and temperature stresses during grain filling. Knowledge of the effect of sink or source-limited grain yields would be useful in selecting genotypes with high yield potential and yield stability for this region.

The objective of this study was to determine the frequency of post-anthesis sink-limited grain yields. Association between grain yield, kernel no. per unit area, and other yield components were used as a means of determining sink limitations. Environmental, genotypic, and N fertilization effects were used to increase variation in grain yield and yield components.

MATERIALS AND METHODS

Four locations were used over the 2-year cropping periods of 1976 to 1977 (1977 season) and 1977 to 1978 (1978 season) to obtain eight nonirrigated sites in the principal winter wheat producing areas of eastern Colorado. The soil classification for each location is given in Table 1. All experimental sites had previously been in alternate wheat-fallow rotations.

Three hard red winter wheat cvs., Scout 66, Centurk, and Vona, were grown under four N fertilizer rates to increase grain yield and yield component variation. The four N rates were 0, 28, 56, and 84 kg ha^{-1}. The cultivars represent a range of phenotypic variation in a number of agronomic traits, including plant height and maturity. Scout 66 and Centurk are standard height cultivars, while Vona is a semidwarf, and Scout 66 and Vona are early maturity cultivars, whereas Centurk is a intermediate maturity cultivar.

The treatments were arranged in a randomized complete block design with four replicates. The plots were 15 m in length × 1.8 m in width, and they consisted of six 0.30-m spaced rows. A base seeding rate of 45 kg ha^{-1}, which is the recommended seeding rate for the area, was adjusted for variation in cultivar seed size so that equal seed numbers per unit area were sown for each cultivar. This seeding rate was approximately equal to 150 seeds m^{-2}. A small plot seeder was used to seed the plots. At the initiation of spring regrowth, plots receiving the N treatments were top dressed with ammonium nitrate. Prior to top dressing, soil samples were taken in 0.30-m increments to a depth of 1.20 m. The soil samples were air dried and analyzed for nitrate N. The amount of available nitrate N ranged from 19 to 88 kg ha^{-1} across the sites (Table 1). Thus, a range of N fertilizer responding sites was available for this experiment.

Immediately prior to harvest, spike no. m^{-2} was determined by averaging three counts of 1-m sections of row within each plot. The alleys between plots were then trimmed to assure equal plot length. The center four rows of each plot were then harvested for grain yield. Yields were not corrected for grain moisture content because harvesting occurred when grain moisture content was estimated to be 10% or less. A subsample of 1000 kernels from each treatment was used to determine kernel size (mg $kernel^{-1}$). Kernel no. (kernel no. m^{-2}) was calculated by dividing grain yield m^{-2} by kernel size. Kernel no. per spike was determined by dividing kernel no. by spike no.

An analysis of variance was performed on the data within

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each location and across sites to determine treatment and environmental effects on the variables. Several methods of correlation and multiple regression analysis were considered as a means of determining the relationship between grain yield and yield components. According to Ledent and Moss (1979), simple correlation analysis is as consistent as stepwise regression or factor analysis in ranking the association of various morphological yield components with grain yield. Therefore, the simpler method of linear correlation was used as the procedure for investigating the association between grain yield and yield components. The treatment means (n = 12) were used as the input data for within site analysis and the location means (n = 8) were used in the across location analysis.

Table 1. Soil classification and residual soil nitrate nitrogen (NO_3-N) at the experimental locations.

County and crop year	Soil series	Soil subgroup	NO_3-N (0–1.2 m)
			kg ha^{-1}
1977			
Adams	Weld	(fine, montmorillonitic, mesic Aridic Paleustolls)	56
Kit Carson	Keith	(fine, silty, mixed, mesic Aridic Argiustolls)	81
Lincoln	Weld	(fine, montmorillonitic, mesic Aridic Paleustolls)	81
Sedgwick	Julesburg	(coarse-loamy, mixed, mesic Aridic Argiustolls)	88
1978			
Adams	Weld	(fine, montmorillonitic, mesic Aridic Paleustolls)	19
Logan	Weld	(fine, montmorillonitic, mesic Aridic Paleustolls)	85
Sedgwick	Rago	(fine, montmorillonitic, mesic Pachic Argiustolls)	57
Washington	Platner	(fine, montmorillonitic, mesic Aridic Argiustolls)	86

RESULTS AND DISCUSSION

Plant diseases, lodging, or poor stands were not observed at any of the sites. Therefore, any yield variation observed in this study was primarily associated with treatment and environmental effects.

The combined analysis of variance over locations indicated that grain yields differed significantly (P≤0.01) across sites. Average grain yields ranged from 1690 kg ha^{-1} at the 1978 Adams location to 3250 kg ha^{-1} at the 1977 Kit Carson site (Tables 2 and 3). The analysis of variance within sites indicated that cultivars responded similarly to N fertilizer for grain yield at all the locations. Grain yield variation due to cultivars was obtained at two of the four sites in 1977 and at all the sites in 1978. Rankings of the cultivars for grain yield varied across locations (Tables 2 and 3). Grain yield responses to N fertilizer were noted at two and four locations in 1977 and 1978, respectively.

Table 2. Grain yield and yield components of three winter wheat cultivars grown under four N fertilizer rates at four locations in the 1977 growing season.

Location	Cultivar	Nitrogen fertilizer rate	Grain yield	Spike no.	Kernel no. per spike	Kernel no.	Kernel wt
County		kg ha^{-1}	kg ha^{-1}	no. m^{-2}		no. m^{-2}	mg kernel^{-1}
Adams	Scout 66		2 723ab*	458b	18.7a	8 555a	31.8c
	Centurk		2 912b	418a	25.0b	10 438b	27.8a
	Vona		2 682a	398a	23.6b	9 387ab	28.6b
		0	2 493a	404	20.9a	8 452a	29.3
		28	2 682	425	21.7ab	9 220ab	29.3
		56	2 966b	431	23.0bc	9 913b	29.9
		84	2 939b	420	24.2bc	10 165b	29.0
$\overline{X}$			2 722	425	22.4	9 460	29.4
CV (%)			9.7	12.0	12.0	9.5	3.0
Kit Carson	Scout 66		3 236	719b	15.4a	11 073a	29.3b
	Centurk		3 331	635ab	22.0b	13 970b	24.3a
	Vona		3 175	599a	22.0b	13 178b	24.6a
		0	3 162	585	20.9	12 227	27.0c
		28	3 270	658	19.4	12 765	26.2b
		56	3 317	672	19.4	13 037	26.0b
		84	3 243	689	19.4	13 367	25.1a
$\overline{X}$			3 247	651	19.8	12 740	26.1
CV (%)			15.4	20.0	12.0	11.8	3.0
Lincoln	Scout 66		2 493†	548b	14.5a	7 946a	31.5c
	Centurk		2 493	455a	20.5b	9 328b	26.9b
	Vona		2 648	481a	22.8c	10 967c	24.3a
		0	2 547	492ab	19.0ab	9 348ab	28.3
		28	2 757	495ab	20.8b	10 296b	27.7
		56	2 466	467a	20.3b	9 480ab	27.0
		84	2 412	528b	17.1a	9 029a	27.3
$\overline{X}$			2 545	495	19.3	9 414	27.6
CV (%)			17.2	11.0	15.0	12.3	5.0
Sedgwick	Scout 66		2 574ab	430	17.1	7 354	34.8c
	Centurk		2 466a	425	19.2	8 159	30.1a
	Vona		2 662b	446	19.1	8 517	31.2b
		0	2 284a	429	16.8a	7 205a	31.8a
		28	2 513b	416	18.9ab	7 865ab	31.9a
		56	2 696c	470	17.9a	8 419b	32.1ab
		84	2 770c	421	20.3b	8 551b	32.3b
$\overline{X}$			2 567	434	18.5	8 010	32.0
CV (%)			6.0	14.0	15.0	7.2	1.0

* Means followed by a common letter are not significantly different at 0.05 level. Duncan's Multiple Range Test was used on cultivar means and the LSD test was used on the N means.

† Means not followed by letters indicate that there was no significant treatment effect detected by the analysis of variance.

Variation ($P \leq 0.01$) among the sites was observed for all the yield components of spike no. (spike no. m^{-2}), kernel no. per spike, kernel no. (kernel no. m^{-2}), and kernel size (mg $kernel^{-1}$). At those sites where yield variation was detected, variability was also evident in at least three of the four yield components (Tables 2 and 3). The analysis of variance within sites indicated the cultivars also responded similarly to N for yield components. Spike no., kernel no. per spike, and kernel number responded positively to N fertilizer at five of the eight sites, while fertilizer N varied kernel size at six locations. Variation in yield components due to N fertilizer has been reported by many other workers (Barley and Naidu, 1964; Stickler and Pauli, 1964; Syme, 1967). Cultivar variation for spike no., kernel no. per spike, kernel no., and kernel size existed at five, seven, seven, and eight sites, respectively. The most pronounced differences among cultivars were evident for kernel number per spike and kernel size. Centurk and Vona produced more kernels per spike than Scout 66 at six and seven of the sites, respectively. Scout 66 produced the largest kernels at all of the sites. Cultivar differences were less consistent across locations for spike number and kernel number.

The relationships between grain yield and yield components are presented in Table 4. Since cultivar or N treatments did not vary grain yields at two of the 1977 sites, these sites were omitted from the within site correlation analysis. However, all eight sites were included in the across location analysis. Grain yield variation within sites was positively correlated with variation in kernel number at four of the six sites where yield variation was observed, while it was positively correlated with kernel size at only one location. The variation in grain yield across locations was also positively correlated with kernel no. Therefore, variation in kernel no., whether produced by environments, genotypes, or N fertilization was consistently associated with grain yields. These results, as Fischer et al. (1977) suggest, are indicative of limited sink capacity during the post-anthesis or grain-filling period.

Relationships between grain yield and kernel no. were not explored in recent winter wheat studies (Musick and Dusek, 1980; Keim and Kronstad, 1981; Wiegand et al., 1981). Based on the treatment means reported in these studies, our calculations using correlation analysis (Table 5) indicated that grain yields were more consistently correlated with kernel no. than kernel size. Thus, the results from these studies, which were conducted in Texas and Oregon (Table 5), are very similar to those of the present study. In addition, Fischer et al. (1977) and Ellen and Spiertz (1980) have

Table 3. Grain yield and yield components of three winter wheat cultivars grown under four N fertilizer rates at four locations in the 1978 growing season.

Location	Cultivar	Nitrogen fertilizer rate	Grain yield	Spike no.	Kernel no. per spike	Kernel no.	Kernel size
County		kg ha^{-1}	kg ha^{-1}	no. m^{-2}		no. m^{-2}	mg $kernel^{-1}$
Adams	Scout 66		1 588a†	437	14.0a	6 118a	31.4c
	Centurk		1 669a	461	16.7b	7 694b	26.3a
	Vona		1 824b	443	17.5b	7 743b	28.6b
		0	932a	332a	12.3a	4 086a	28.3a
		28	1 594b	411b	16.4b	6 733b	28.9b
		56	1 964c	462c	17.7c	8 169c	29.0b
		84	2 311d	545d	17.9c	9 753c	28.9b
$\bar{X}$			1 694	947	16.1	7 185	28.8
CV (%)			6.9	10.0	13.0	6.0	1.0
Logan	Scout 66		2 986b	569	18.4a	10 466a	33.1c
	Centurk		2 871a	570	22.6b	12 997b	25.6a
	Vona		3 047b	539	24.1b	12 982b	27.4b
		0	2 790a	508a	21.1	10 717a	30.5d
		28	3 020b	555b	21.8	12 089ab	29.1c
		56	3 020b	585b	21.5	12 586b	28.1b
		84	3 047b	587b	22.5	13 200b	27.2a
$\bar{X}$			2 968	559	21.7	12 148	28.7
CV (%)			6.0	8.0	10.0	7.5	2.0
Sedgwick	Scout 66		2 527b	538ab	18.1a	9 734a	30.3c
	Centurk		2 615b	563b	22.9c	12 880b	23.6a
	Vona		2 392a	524a	21.1b	11 048b	24.8b
		0	2 121a	458a	19.6a	8 971a	27.7c
		28	2 473b	476b	20.1a	9 575a	26.4b
		56	2 684c	557c	21.7b	12 088b	25.7b
		84	2 810d	604d	21.4b	12 917b	25.0a
$\bar{X}$			2 511	524	20.7	11 221	26.2
CV (%)			7.4	8.0	10.0	6.5	4.0
Washington	Scout 66		2 587b	538b	19.0a	10 220a	29.5c
	Centurk		2 256a	566c	19.2a	10 860a	24.1a
	Vona		2 554b	502a	22.8b	11 440b	25.7b
		0	2 466‡	514a	20.4	10 481	27.4c
		28	2 439	520a	20.5	10 649	26.7b
		56	2 527	550b	20.4	11 219	25.9a
		84	2 439	553b	20.0	11 049	25.7a
$\bar{X}$			2 466	535	20.3	10 840	26.4
CV (%)			7.9	7.0	11.0	8.2	2.0

* Means followed by a common letter are not significantly different at 0.05 level. Duncan's Multiple Range Test was used on cultivar means and the LSD test was used on the N means.

‡ Means not followed by letters indicate that there was no significant treatment effect detected by the analysis of variance.

Table 4. Linear correlation coefficients among grain yield and yield components.

Variables correlated	1977 Locations† Adams Co.	Sedgwick Co.	1978 Locations† Adams Co.	Washington Co.	Logan Co.	Sedgwick Co.	Across sites‡
Grain yield vs. spike no.	0.330	0.379	0.791**	−0.488	0.439	0.967**	0.656
Grain yield vs kernels spike⁻¹	0.506	0.529	0.946**	0.398	0.195	0.473	0.697
Grain yield vs kernel no.	0.862**	0.813*	0.974**	0.112	0.391	0.782**	0.802*
Grain yield vs kernel size	−0.159	0.182	0.027	0.686*	−0.013	−0.273	−0.196
Spike no. vs kernels spike⁻¹	−0.596*	−0.412	0.708**	−0.712**	−0.191	0.454	0.239
Spike no. vs kernel number	0.014	0.221	0.920**	−0.024	0.396	0.835**	0.891**
Spike no. vs kernel size	−0.519	0.227	0.017	−0.344	−0.230	−0.399	−0.747*
Kernels spike⁻¹ vs kernel no.	0.791**	0.796**	0.922**	0.717**	0.824**	0.867**	0.649
Kernels spike⁻¹ vs kernel size	−0.799*	−0.519	−0.317	−0.228	−0.823**	−0.936**	−0.197
Kernel no. vs kernel size	−0.632*	−0.412	−0.189	−0.644*	−0.916**	−0.791**	−0.657

*,** Significant at the 5 and 1% levels, respectively.
† Correlation coefficients were derived from use of cultivar and N fertilizer treatment averages (n = 12).
‡ Correlation coefficients were derived from use of site averages (n = 8).

Table 5. Relationship of kernel number per unit area and kernel size to grain yield computed from data taken from the literature.

Location	Treatments	Correlation of kernel no. vs grain yield	Correlation of kernel size vs grain yield	Literature source
Weslaco, Tex.	Cultivars and planting dates	0.881**	0.771**	Wiegand et al. (1981) 1977–1978 crop year, Table 5 (p. 35)
		0.873**	0.304	1978–1979 crop year, Table 5 (p. 35)
Bushland, Tex.	Cultivars, planting dates, and irrigation levels	0.772*	0.050	Musick and Dusek (1980) 1977–1978 crop year, Table 2 (p. 51)
Pendleton, Oreg.	Cultivars	0.889**	0.583*	Keim and Kronstad (1981) 1973–1974 crop year, Table 2 (p. 12)†

*,** Significant at the 5 and 1% levels, respectively.
† Data from Table 1 in this study was not included in the correlation analysis because values had been averaged over two locations, and there was no significant variation in grain yield among cultivars.

obtained similar results for spring wheat grown in central Mexico and winter wheat grown in the Netherlands, respectively. Similar relationships have also been reported for other cereals (Yoshida, 1972). Furthermore, Fischer (1980) has observed that the biggest effects of water stress on grain yields are usually associated with reductions in seed number rather than seed size. Thus, it would seem that there is overwhelming evidence to suggest that sink capacity is limiting during grain filling over a wide spectrum of environmental conditions. It may be that seed crops have sufficient photosynthetic capacity to fill more seeds than they form, as Fischer (1980) suggests.

Kernel size was negatively correlated with kernel no. per spike and kernel no. at three and four sites, respectively (Table 4). In addition, variation in kernel size across locations was negatively correlated with spike no. Such relationships reflect competition between developing kernels for limited assimilate availability, indicating a source restriction on grain yields (Fischer et al., 1977). Nevertheless, since kernel no. was more highly associated with grain yield than kernel size in this study, sink strength during grain filling was apparently more important than source strength in determining grain yields.

The components of kernel no., spike no. and kernel no. per spike, were associated with grain yield at only two and one of the sites, respectively (Table 4). However, variation in kernel no. per spike was highly associated with kernel no. at all sites. Spike number was associated with kernel no. at only two of the sites. Nonetheless, adjustment in spike number in response to environmental conditions was an important factor in determining kernel no., since variation in kernel no. across locations was positively correlated with spike no. Earlier studies (Willey and Holliday, 1971; Fischer, 1975) have shown that development of adequate spike no. and kernel no. are critical factors in determining grain yield.

Spike no. and potential kernel no. per spike are determined during the period prior to anthesis by such processes as tiller initiation, tiller abortion, differentiation of spikelet no. per spike, and floret development within the spikelets (Fischer et al., 1975). Therefore, this developmental phase is critical to establishment of adequate sink capacity for the grain-filling period. Investigation of factors that influence these developmental processes should have high priority in winter wheat improvement programs. Our results suggest that both genetic and cultural or environmental manipulation to improve sink capacity would result in higher grain yields.

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Bermudagrass, Tall Fescue, and Orchardgrass Pasture Combinations with Clover or N Fertilization for Grazing Steers. II. The Species Composition Index and Variability in Forage Growth and Consumption, and Animal Performance[1]

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ABSTRACT

Forage growth and consumption, animal gain, and beef production were estimated in a steer (*Bos* sp.) backgrounding experiment concurrently with several environmental, plant, and animal characteristics. This paper describes a technique that combines the dynamic changes in species composition in pastures over time into a Species Composition Index (SCI). This index can then be related to the effects of season, grazing periods, stocking rates, forage crude protein, precipitation, and air temperature on forage growth and consumption, and beef production. The SCI was compared to the traditional classification variable treatments to describe seven differently managed pasture combinations of different forage species. It was superior to treatments in explaining variability and appeared to be a sensitive tool for characterizing dynamically changing pasture compositions. It could be a useful and flexible tool in quantifying species cover in many other situations.

Additional index words: **Botanical composition, Concomitant variates, Average daily gain, Beef production, Clover-grass mixtures, *Cynodon dactylon* (L.) Pers., *Festuca arundinacea* Schreb., *Dactylis glomerata* L., *Trifolium repens* L.**

GRAZING experiments are difficult and expensive to conduct. Sufficient replication of experimental units (pastures) and numbers of sampling units (animals) to increase power of statistical tests (5) is often unaffordable. After considerable time and effort have been expended, the data obtained can often be reduced to one or two small tables. Even though this may be an outcome which is satisfactory for the practical utilization of the results by cattle (*Bos* sp.) producers, it often leads to frustration, because reasons for effects and consequences of interactions are not easy to explore or explain. The difficulties are aggravated by the inherent variability within such experiments—among animals, soil properties and topography, and pasture plants. It is often necessary that the results of treatment effects in a grazing study be considerably different in order for the results from statistical tests—rendered insensitive by the uncontrolled variability and insufficient replication—to be able to differentiate among treatments.

A pasture changes dynamically with time. Even when a pasture is comprised of a uniform stand of a single species or cultivar managed uniformly, the physiological status of the plant and nutritional value or acceptability of the forage to the grazing animal will change throughout the season. This problem is compounded when the pasture treatment in an experiment is designed to represent a mixture of two or more species which form a combination deemed desirable for the grazing animal. For example, pastures of two different treatments named X and Y might be represented as containing X_1 and Y_1 forage at the start of the grazing season. The symbols X and Y could represent two different species, or the same species subjected to different influences resulting in different growth or abundance. After some time (1 month, 1 week, 1 day) the quantities X and Y will have changed to X_2 and Y_2, where $X_1 \neq X_2 \neq Y_1 \neq Y_2$. At the end of the grazing season, there will be X_t and Y_t, where t is the last sampling. To represent each of the two vectors $[X_1, X_2, \ldots, X_t]$ and $[Y_1, Y_2, \ldots, Y_t]$ by treatment labels such as "fescue (*Festuca* sp.) + clover (*Trifolium* sp.)" or "orchardgrass (*Dactylis glomerata* L.) + clover" can be a misleading simplification; the combined effects of the factors affecting forage growth and consumption, and animal performance over time affect the two pastures differently.

Since different values of the classification variable treatments are deceptive for characterizing pasture conditions at different or even the same observation times, it can be argued instead that the treatments were applied in order to generate diverse forage conditions measured over time through observations of plant characteristics and animal performance.

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