Shoot Developmental Properties Associated with Grain Yield in Winter Wheat[1]

J. F. Shanahan, K. J. Donnelly, D. H. Smith, and D. E. Smika[2]

ABSTRACT

A large proportion of winter wheat (*Triticum aestivum* L.) tillers fail to produce grain-bearing spikes. Should tillers which fail to produce spikes be considered as lost photosynthate? Six selected winter wheat cultivars were grown under two nitrogen (N) fertilizer rates (0 and 70 kg N ha⁻¹) in a 3- year (1980–1982) field study on a Rago silt loam soil type (fine, montmorillonitic, Mesic Pachic Argiustolls) to evaluate the relationships among grain yield, shoot emergence, shoot survival, and yield components. Live emerged shoot number per unit area was determined at selected dates throughout the growing season. Final spike number per unit area, grain yield, and yield components were measured at physiological maturity. Grain yield was positively correlated with shoot survival in all three years but was not correlated with maximum live shoot number in any year. Maximum live shoot number was not correlated with kernel number of the spike-bearing shoots, and shoot survival was positively correlated with kernel number per spike in only 1 year of the study. Therefore, the production of spikeless shoots had little effect on the reproductive development of spike-bearing shoots. Maximum live shoot number was negatively correlated with shoot survival in 2 of the 3 years of the study. Shoot survival was positively correlated with spike number in all 3 years, and spike number was positively correlated with kernel number per unit area and grain yield in 3 of the 3 years. Thus, shoot survival was more important than the number of shoots initiated in establishing the critical yield components of spike number and kernel number per unit area.

***Additional index words:* *Triticum aestivum* L., Yield components, Shoot survival.**

HIGH tillering ability has generally been considered as a desirable trait for winter wheat (*Triticum aestivum* L.) production in the Great Plains region of the USA (Schmidt et al., 1978). Tillering allows the crop to adjust shoot number in response to poor stands and adverse environmental conditions such as injurious winter temperatures or drought, and to more favorable environmental conditions. However, a significant proportion of tillers which are initiated fail to produce grain-bearing spikes (Bremner, 1969; Austin and Jones, 1975; Evans et al., 1975). The degree of overproduction of tillers has often been up to two-thirds of the total tillers produced (Evans and Wardlaw, 1976). Should tillers or shoots which fail to produce spikes be considered as lost photosynthate?

Under most conditions, initiation and development of new tillers in cereals proceeds from shortly after seedling emergence through floral initiation (Rawson, 1971; Jewiss, 1972; Evans et al., 1975). Once rapid spike and stem development of the spike-bearing shoots begin, spike-bearing shoots appear to exert a distinct dominance over the spikeless tillers and tiller buds by suppressing their further development (Jewiss, 1972; Austin and Jones, 1975). Thus, senescence of late-emerging, spikeless tillers usually begins shortly after floral initiation (Rawson, 1971; Jewiss, 1972; Evans et al., 1975).

Several studies have addressed various factors responsible for the control of tillering. Most of these factors have been associated with control of the growth of tiller buds and emergence of tillers from the surrounding leaf sheath, rather than with control of the initiation of tiller buds (Evans et al., 1975). Factors suggested have included light (Friend, 1966; Evans et al., 1975), temperature (Friend, 1966; Rawson 1971; Smika, 1974), soil water (Black, 1970), plant density (Darwinkle, 1978), mineral nutrition (Bremner, 1969; Power and Alessi, 1978), plant hormones (Bunting and Drennan, 1966; Jewiss, 1972), and physical constraints (Williams and Langer, 1975). Interaction of these factors contributes to the complex nature of tillering that has been observed in many studies. Tiller or shoot senescence is determined by an equally complex interaction of many factors (Bunting and Drennan, 1966; Jewiss, 1972).

The question of whether spikeless tillers are beneficial or detrimental to grain production has not been fully answered. They may serve as sources of assimilate (Lupton and Pinthus, 1969) or as a reservoir for plant nutrients (Palfi and Dezsi, 1960). Alternatively, they may compete with the developing spike-bearing shoots for assimilate and/or nutrients during critical stages (Langer and Dougherty, 1976).

The objective of this study was to determine the interrelationships among maximum number of live shoots emerged, shoot survival, grain yield, and yield components of hard red winter wheat under field conditions of the Central Great Plains.

MATERIALS AND METHODS

Field experiments were conducted during the 1979–1980 (1980), 1980–1981 (1981), and 1981–1982 (1982) growing seasons at the Central Great Plains Research Station at Akron, CO. The plot sites had been in an alternate wheat-fallow rotation for the past 20 years and were considered generally typical of the Central Great Plains area. While the plot sites were not located on the same areas of the station, the soil type of each site was a Rago silt loam (fine, montmorillonitic, mesic Pachic Argiustolls).

Treatments consisted of factorial combinations of six winter wheat cultivars and two nitrogen (N) fertilizer application rates, 0 and 70 kg N ha⁻¹. The cultivars were 'Baca', 'Centurk 78', 'Nugaines', 'Trapper', 'Vona', and 'Wichita'. All cultivars except Nugaines (a soft white winter wheat) are of the hard red winter wheat market class. These

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[2] Assistant professor, former instructor (presently assistant professor, Dep. of Agronomy, Oklahoma State Univ., Stillwater, OK 74074), associate professor, Dep. of Agronomy, Colorado State Univ., Fort Collins, CO 80523, and soil scientist, USDA-ARS, Central Great Plains Res. Stn., Akron, CO 80720, respectively.

cultivars represent a range of phenotypic variation in maturity, height, adaptation, and yield potential. The experimental design was a randomized complete block with four replicates in 1980 and 1981. In 1982, the field design was changed to a split plot arrangement in a randomized complete block with N rates as the main plots and cultivars as the subplots to increase the precision of treatment comparisons between cultivars.

The plot dimensions were 1.8 × 9 m in 1980 and 5.4 × 9 m in 1981. In 1982, main plots were 21.6 × 15.2 m and subplots were 3.6 × 15.2 m. Row spacing was 30 cm in all years. Blocks were separated by a 1.8-m alley seeded with the cultivar Baca. The planting dates were 25 Sept. 1979, 18 Sept. 1980, and 15 Sept. 1981. Variation in seed size and germination (in petri dish at 25°C) among cultivars was used to adjust seeding rates for each cultivar so that uniform stands could be established. This planting density was approximately equal to the recommended seeding rate of 45 kg ha^{-1} for the region. A small-plot grain drill was used in seeding all plots.

In the fall of the growing season, shortly after stand establishment, representative soil samples were taken from one plot in each replication to a depth of 150 cm in 30-cm increments. The soil samples were air-dried and analyzed for nitrate N. Plots receiving the N fertilizer treatment were then top-dressed with ammonium nitrate (34-0-0) on 10 Oct. 1979, 3 Oct. 1980, and 13 Oct. 1981).

Three weeks after seeding, uniform 0.5-m sections of row within each plot were selected and marked with flags. Plants in each section were counted and thinned to a standard plant number (130 plants m^{-2}) that was considered to be the average emerged plant density for all cultivars.

All of the plants from a marked 0.5-m section of row within each treatment were harvested (by digging them up) at selected dates during the growing season. The samples were immediately refrigerated after each harvest, and counts were made later to determine plant and live shoot numbers.

Harvests were made at the end of fall growth, beginning of spring regrowth, and approximately every 2 weeks thereafter until maturity, and included a sampling at floral initiation and anthesis. The date of floral initiation for each treatment was determined by observing plants of each treatment for the appearance of double ridges (Bonnett, 1967) on the main shoot meristem. The main shoot was recognized by the presence of the subcrown internode attached to it. The date of anthesis for each treatment was visually estimated by noting when anther extrusion occurred on approximately 50% of the spikes of the plot. Physiological maturity was determined by plant senescence and total loss of green color from the spikes, including awns, outer glumes, and kernels. These indicators have proven to coincide closely with the date of maximum grain dry weight accumulation in hard red winter wheat in eastern Colorado (Donnelly, 1983).

At physiological maturity, grain yields were estimated from harvested areas of 0.61 m^{-2} in 1980 and 1.22 m^{-2} in 1981-1982. All grain weights were adjusted to oven-dry basis (100° C for 24 h). A final 0.5-m section was harvested for analysis of the yield components, spike number m^{-2}, kernel number per spike, and 1000 kernel weight (oven-dry). Kernel number m^{-2} was calculated from the product of spike number m^{-2} and kernel number per spike. Shoot survival was calculated by dividing spike number m^{2} by the maximum live shoot number m^{-2} during the growing season. Maximum live shoot number m^{-2} for each treatment was determined by comparison of shoot number across harvest dates within each growing season.

Table 1. Monthly summaries of average mean daily temperatures and total precipitation during the 1979-1980 (1980), 1980-1981 (1981), and 1981-1982 (1982) growing seasons at Akron, CO.

Month	Mean daily temperature			Precipitation		
	1980	1981	1982	1980	1981	1982
	°C			cm		
September†	18.5	17.3	17.8	1.8	3.2	0.4
October	11.6	10.1	9.9	1.3	0.8	2.6
November	−0.4	4.1	6.2	3.4	1.1	1.3
December	−0.4	2.4	0.4	1.7	0.1	0.1
January	−5.6	0.6	−3.5	1.5	0.5	0.4
February	−0.3	−0.3	−1.9	0.9	0.3	0.4
March	0.8	2.4	3.4	2.6	6.4	1.1
April	6.8	11.4	7.4	2.6	4.0	0.9
May	12.5	11.8	12.8	5.3	11.4	11.3
June	20.7	20.1	16.8	4.9	4.0	7.8
July‡	27.5	22.3	23.1	0.5	0.1	5.6
Total				26.5	31.9	31.9

† Mean daily temperatures were calculated from the date of seeding through the end of the month.
‡ Mean daily temperatures were calculated from the beginning of the month until the latest maturity date of all the treatments.

Analysis of variance was used to evaluate the effects of the treatments and their interaction on the response variables. Several methods of correlation and multiple regression analysis were considered to analyze the relationships among variables. However, Ledent and Moss (1979) have concluded that simple correlation analysis is as consistent as factor analysis or stepwise regression in ranking the association of morphological characters with yield. Therefore, the simpler method of linear correlation analysis was chosen to determine the interrelationships among response variables in this study. Treatment means were used as the input data for these analyses.

RESULTS AND DISCUSSION

The climatic conditions of the 1981 and 1982 growing seasons were quite different from those of the 1980 season. The fall and early winter of 1981 and 1982 were warmer than the same periods during the 1980 season (Table 1). Fall and winter plant development continued until 15 November, 30 November, and 15 December in the 1980, 1981, and 1982 growing seasons, respectively. Spring regrowth was initiated about 1 March all three years. Temperatures continued to be warmer during March and April of 1981 and 1982 than during these same months in 1980. The average date of floral initiation occurred on 27 Apr. 1980, 7 Apr. 1981, and 24 Mar. 1982. Thus, the warmer temperatures of 1981 and 1982 hastened plant development compared to that of the 1980 season. Temperatures during the remainder of the 1981 and 1982 growing seasons were equal to or less than those of the 1980 growing season. This reduced the rate of plant development during the latter part of 1981 and 1982, such that anthesis and physiological maturity occurred on nearly the same date all 3 years. Precipitation during the 1981 and 1982 seasons was greater than during the 1980 season. The precipitation in 1981 and 1982 was concentrated during the last four months of the season, whereas it was more evenly distributed throughout the 1980 growing season (Table 1).

Table 2. Grain yields and yield attributes of six winter wheat cultivars grown under two N fertilizer rates during the 1980, 1981, and 1982 growing seasons at Akron, CO.

Cultivar	N rate	Fall shoot no.			Maximum live shoot no.			Spike no.			Shoot survival†			Kernels per spike			Kernel no.			Kernel weight			Grain yield		
		1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982
	kg ha^{-1}	no. m^{-2}									%						no. × 10^{-3} m^{-2}			mg kernel^{-1}			kg ha^{-1}		
Baca		416	1001	2072	1527	1659	2512	644	701	806	42.2	42.3	32.1	19.9	19.3	18.6	12.8	13.5	15.0	23.8	30.5	28.8	3068	3849	4295
Centurk 78		407	945	2124	1562	1602	2517	618	652	902	39.6	40.1	36.1	26.0	24.6	19.5	16.1	16.0	17.6	19.9	27.8	24.5	3303	4330	4285
Nugaines		478	1095	2346	1834	1714	3056	507	611	721	27.7	35.7	23.5	26.9	25.9	17.8	13.6	15.8	12.8	20.1	26.2	25.0	2863	4048	3170
Trapper		–	823	2083	–	1586	2840	–	648	830	–	40.9	29.7	–	26.2	18.4	–	17.0	15.3	–	27.4	25.5	–	4466	3865
Vona		396	840	1964	1403	1548	2462	611	672	884	43.6	44.6	36.0	29.4	25.6	22.0	18.0	17.2	19.5	20.4	30.1	26.2	3664	4960	5070
Wichita		367	919	2059	1350	1565	2792	529	576	704	39.2	36.8	25.4	21.2	16.8	16.4	11.2	9.7	11.6	25.5	33.7	30.2	2879	2999	3475
$LSD_{0.05}$		42	83	217	315	NS	267	107	99	86	12.3	NS	4.0	2.9	3.1	1.1	1.5	1.5	1.3	2.0	1.7	1.2	383	441	368
	0	417	931	2095	1479	1521	2581	581	570	768	39.3	37.5	30.1	25.0	21.3	18.2	14.5	12.1	14.0	22.6	30.2	27.2	3310	3546	3770
	70	409	939	2121	1592	1690	2812	582	716	847	36.6	42.4	30.8	24.3	24.8	19.3	14.1	17.8	16.4	21.2	28.3	26.2	3001	4672	4283
	$LSD_{0.05}$	NS‡	NS	NS	NS	136	NS	NS	57	NS	NS	4.8	NS	NS	1.8	NS	NS	0.9	2.2	1.3	1.0	NS	242	255	NS
		413	935	2108	1536	1606	2697	582	643	808	38.0	40.0	30.5	24.7	23.1	18.8	14.3	15.0	15.2	21.9	29.3	26.7	3156	4109	4027

† Shoot survival = (spike no./maximum live shoot no.) × 100.
‡ NS = Not significant.

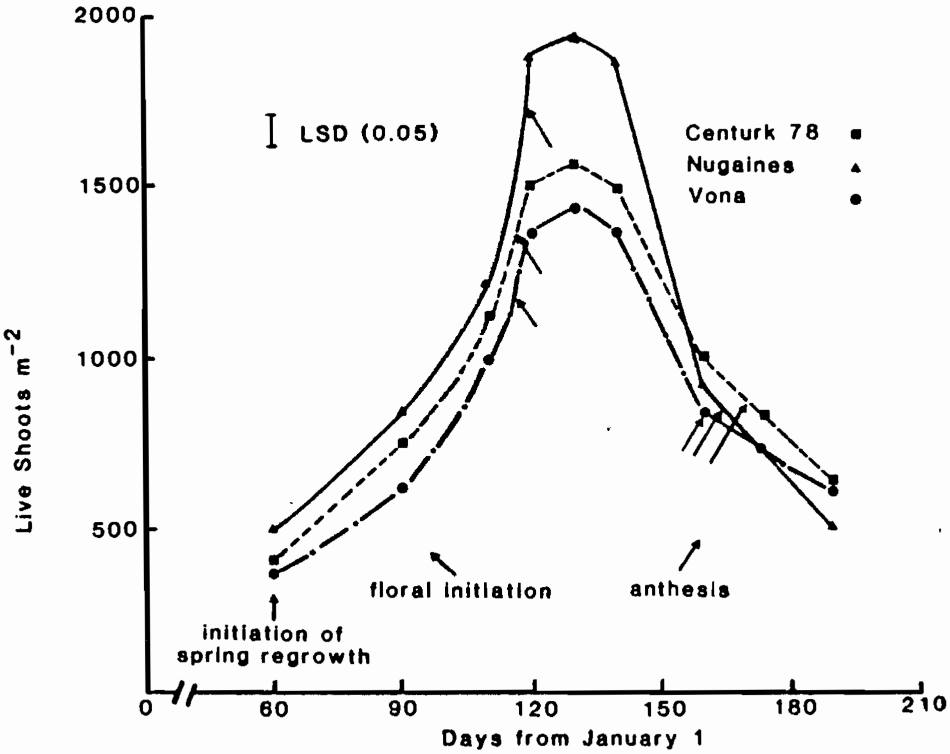

Fig. 1. Shoot number vs. time for three selected cultivars in the 1980 growing season. Shoot number existing at initiation of spring regrowth were developed during previous fall growth.

The pattern of development of shoot numbers over the 1980 growing season for three selected treatments (Fig. 1) was typical of the pattern of development of shoot number for the other treatments and years. The date on which maximum shoot number was attained was the same for all treatments and coincided closely with the date of floral initiation. Jewiss (1972) also noted that, in most cereals, development of maximum shoot number occurred very near to the time of floral initiation. Shoot senescence began soon after this developmental stage and was nearly completed by anthesis.

Treatment values for fall shoot number (shoot number present at the end of fall growth) and maximum live shoot number (the maximum number of shoots produced by each treatment for each growing season) are presented in Table 2 for the 1980, 1981, 1982 growing seasons. The cultivar Trapper was omitted from the analysis in 1980 because it did not produce an adequate plant population. Average fall shoot numbers differed significantly among all three years, with the smallest values observed in 1980 and the largest values in 1982. These differences were likely related to the temperatures and length of period for shoot development in the fall of each growing season. Smika (1974) reported that the optimum temperature for maximum tiller production in winter wheat was approximately 13 to 15° C. The average temperature for the period of seeding through December was 4.5, 6.7, and 7.3° C for 1980, 1981, and 1982 seasons, respectively.

Significant differences were found among cultivars in maximum live shoot number and shoot survival during 1980 and 1982 and in fall shoot number and

Table 3. Linear correlation coefficients among grain yield and various yield attributes during the 1980, 1981, and 1982 growing seasons at Akron, CO.

Yield attribute	Kernels spike^{-1}			Kernel weight			Max. shoot no. m^{-2}			Shoot survival			Spikes m^{-2}			Kernels m^{-2}		
	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982
Grain yield	0.59	0.86**	0.88**	−0.23	−0.61*	−0.19	−0.43	0.40	−0.49	0.64*	0.67*	0.83**	0.59	0.77**	0.84**	0.86**	0.97**	0.93**
Kernels m^{-2}	0.83**	0.89**	0.93**	−0.67*	−0.73**	−0.53	−0.07	0.51	−0.37	0.49	0.61*	0.83**	0.47	0.78**	0.93**			
Spikes m^{-2}	−0.08	0.41	0.72**	−0.04	0.45	−0.55	−0.38	0.60*	−0.33	0.79**	0.82**	0.86**						
Shoot survival	−0.11	0.21	0.69*	−0.18	−0.21	−0.32	−0.88**	0.04	−0.76**									
Max. shoot no. m^{-2}	0.25	0.35	−0.35	−0.53	−0.51	−0.21												
Kernel weight	−0.76*	−0.78**	−0.47															

*,** Significant at the 0.05 and 0.01 levels, respectively. Cultivar and nitrogen treatment means were used in the correlation analyses (n = 10 in 1980; n = 12 in 1981 and 1982).

spike number for all three years (Table 2). Although the difference among cultivars for shoot survival was not significant in 1981, the trend displayed by the cultivars was similar to that of 1980 and 1982. In general, these results indicate that production of shoots and spikes can be characterized within a range of two extremes. The cultivar Nugaines produced more fall and maximum live shoot numbers than Vona, while Vona maintained a higher percentage of surviving shoots than Nugaines. The remaining cultivars fell within this range of response.

Nitrogen fertilization had no effect on fall shoot number, maximum live shoot number, spike number, or shoot survival in 1980 and 1982 (Table 2). In 1981, N had no effect on fall shoot number (Table 2). However, the higher N level increased maximum live shoot number, shoot survival, and spike number in 1981. Therefore, the increased spike numbers produced by the high N rate were apparently a result of both more shoots initiated and increased survival of these shoots. Power and Alessi (1978) have emphasized the importance of available N on shoot survival. The difference in the N response between the three years was probably related to the high residual soil nitrate levels in 1980 (127 kg N ha^{-1}) and 1982 (92 kg N ha^{-1}) as compared to the low level in 1981 (58 kg N ha^{-1}). All cultivars responded similarly to N fertilizer for fall shoot number, maximum live shoot number, spike number, and shoot survival in all 3 years as indicated by the analysis of variance.

During all 3 years, cultivar differences were apparent for grain yield and all yield components (Table 2). The analysis of variance indicated that there was a variable response of the cultivars to applied N for kernel number per spike, kernel number per unit area, and grain yield only in 1981. Nugaines, Trapper, and Wichita exhibited no response to the high N rate for these attributes, while the remaining cultivars showed increases (data not shown). This contrasts with previous results (Holmes, 1973), which indicated that cultivars derived from Norin-10 showed a greater response to applied N for kernel number per spike than standard-height cultivars. Nugaines is a cultivar of Norin-10 parentage. However, Nugaines is a poorly adapted cultivar for this region, and may thus explain the conflicting results.

Grain yields and all yield components increased with nitrogen fertilization in 1981, while only kernel number increased in 1982. Grain yields were decreased with nitrogen fertilization in 1980. These results were again related to the differences in residual soil nitrate among the 3 years. The yield decline of 1980 associated with N application was related to a reduction in kernel size (Table 2). According to Boyer (1976), water stress during grain filling in corn reduces assimilate availability through lowered photosynthetic rates. The smaller kernel sizes of the high N treatments would tend to confirm the hypothesis that these treatments were subject to greater water stress during grain filling than the treatments receiving no N. Thus, while plant water stress was not directly monitored in this study, it may be speculated that increased water stress of the high N treatments was associated with the lower yields. Therefore, above optimal levels of soil N under limited water supply can lead to reduced grain yields, as has been observed by other researchers (Fischer and Kohn, 1966).

Kernel size values were considerably higher in 1981 and 1982 than in 1980 (Table 2), which apparently contributed to the higher grain yield of 1981 and 1982 as compared to 1980. These observations were likely due to the more favorable temperature and water conditions (Table 1) during the latter part of the 1981 and 1982 seasons compared to the 1980 season. High temperatures during the latter part of grain filling are detrimental to the development of high kernel weights (Sofield et al., 1977; Warrington et al., 1977; Wiegand and Cuellar, 1981). Average temperatures during July of 1980 were approximately 5° C higher than in July of 1981 and 1982 (Table 1).

Grain yield was positively correlated with shoot survival in all three years of the study (Table 3), while it was not correlated with maximum live shoot number in any year. Maximum live shoot number was negatively correlated with shoot survival in two of the three years. Frankel (1935) also noted that shoot survival and shoot density were negatively correlated. Under semi-arid conditions similar to the Great Plains, Fischer and Kohn (1966) reported that high shoot numbers during early vegetative growth led to lower shoot survival, increased water stress during grain filling, and reduced grain yields. It seems likely that treatments (i.e. cultivar Vona) in 1980 which produced higher shoot survival rates and fewer spikeless vegetative shoots were subjected to less water stress during grain filling, and consequently produced higher grain yields.

There was a positive correlation between grain yield and kernel number in all three years of the study, while kernel size was negatively correlated with grain yield in 1981 (Table 3), and was not linearly related to grain yield in the other two years, indicating that kernel number is more highly correlated with variation in grain yields within years than is kernel size. These results are similar to those of Fischer et al. (1977), Evans (1978), and Ellen and Spiertz (1980). In addition, Koomanoff (1981) found a positive correlation between kernel number and grain yield under similar conditions at the Akron station. Such consistent positive relationships between grain yield and kernel number suggest that grain yield in winter wheat is probably limited by a lack of sink strength during the grain filling period rather than source strength. If source strength was limiting, yield would more likely be related to kernel size.

Kernel number is the product of spike number and kernel number per spike. Kernel number per spike was positively correlated with kernel number in all three years, and spike number was positively correlated with kernel number in the 1981 and 1982 seasons (Table 3). Shoot survival was positively correlated with kernel number and spike number in 1981 and 1982. Thus, treatments which produced higher shoot survival values produced greater spike numbers, kernel numbers, and sink strength, resulting in higher grain yields.

Early crop growth factors during the spike development phase, such as shoot density and shoot survival, could conceivably affect the differentiation of spike components such as spikelet number per spike and kernel number per spikelet, which determine kernel number per spike. However, maximum shoot number at the time of floral initiation was not correlated with kernel number per spike in any year of the study (Table 3), while shoot survival was positively correlated with kernel number per spike only in 1982. Therefore, it appears that shoot density or shoot survival had little effect on the reproductive development of spike-bearing shoots. This is contrary to the results of Langer and Dougherty (1976).

Since maximum live shoot number was not negatively correlated with grain yield or yield components in this study, these data do not provide direct evidence that conclusively demonstrate that spikeless shoots were deleterious to grain yield. Nonetheless, the data of this study do support the hypothesis that shoot survival is more important than maximum live shoot number in establishing the critical yield component of spike number. Spike number in turn affects kernel number, which represents the sink capacity of the crop. In addition, shoot survival was negatively correlated with maximum shoot number in two of the 3 years of the study, providing indirect evidence that increased tillering increases intra-plant competition. Donald (1968) proposed the uniculm ideotype in cereals to overcome this tendency and make more efficient use of environmental resources. Evidence favoring this ideotype in barley was later provided by Donald (1979). Nonetheless, it would be interesting to compare low and high tillering type hard red winter wheats in similar genetic backgrounds at various seeding rates to determine the merit of the trait. Genetic variation for tillering and shoot survivial does appear to exist in the wheat germplasm (Atsmon and Jacobs, 1977; Austin et al., 1980).

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