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RATE AND DURATION OF SPIKELET INITIATION IN TEN WINTER WHEAT CULTIVARS

by

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B.S., Kansas State University, 1981

A MASTER'S THESIS

submitted in partial fulfillmet of the requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1983

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ACKNOWLEDGMENTS

I would like to express sincere appreciation to the following people whose assistance made this research possible: Rollin Sears for his suggestions, guidance, and advise. Drs. Kanemasu and Paulsen for serving on my advisory committee. My co-workers and friends, especially Arron Guenzi and Gary Day for their help in the analysis of the data and discussion of the problem. My parents, Morris and Louise Grotheer, for their assistance and constant support. And finally to my husband, Michael, for his tremendous help and patience. Thank you.

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LITERATURE REVIEW

Yield in wheat can be broken down into four components, tiller number, spikelet number, floret number, and grain weight. These components combine and compensate for each other during the life cycle of wheat to provide for a high or low yield.

The life cycle of wheat is divided into the vegetative and the reproductive stages of growth. The formation of double ridges (DR) marks the shift from vegetative growth to reproductive growth. During vegetative growth the leaf ridge is dominant and leaf primordia are initiated. During reproductive growth the spikelet ridge is dominant and spikelet primordia are initiated. Spikelets continue to be initiated acropetally until the terminal spikelet (TS) is initiated (Bonnett, 1966).

The rate and duration of spikelet initiation determine the final spikelet number. Duration is the length of time, in days, from DR formation to TS formation. Rate is computed as the final spikelet number divided by the duration and is expressed in spikelets/day. At the point of TS formation maximum potential spikelet number is fixed. Whingwiri and Stern (1982) suggested that potential floret number is also fixed at this point. They proposed that florets initiated after TS formation fail to form grain. They hypothesized that the vascular system between the rachis and the floret developed as the floret was initiated. After TS formation the vascular development was inhibited and further florets failed to form grain. Up to 72% of the florets initiated did not contribute to yield. If potential floret number and spikelet number are both determined

during the duration of spikelet initiation, then this period is especially critical to yield potential.

Both rate and duration of spikelet initiation are sensitive to environmental conditions, therefore, spikelet number is sensitive to the environment also. Temperature, soil fertility, photoperiod, light intensity, and water availability are all environmental conditions influencing spikelet initiation and spikelet number in wheat.

Temperature not only affects the rates and durations of developmental stages but also their relative occurrences. Friend et al. (1963) and Halse and Weir (1974) noted that floral initiation, or DR formation, was delayed by low temperatures and hastened by high temperatures. Friend et al. proposed two theories to explain this effect: 1.) Increased temperatures cause an increased rate of production of flowering inducing substances, or 2.) Increased temperatures cause an increase in the sensitivity of the meristematic cells to a given level of flowering inducing substances. Friend (1965) also showed that increased temperature from 10 to 30C increased the rate of apex elongation and resulted in earlier anthesis in 'Marquis' wheat.

Wall and Cartwright (1974) working with 14 spring wheats of differing origin concluded there are three effects of temperature: 1.) Temperature affects the rate of extension growth, 2.) Warm temperatures decrease leaf and spikelet number, and 3.) Venalization at cooler temperatures decreases the number of vegetative nodes and the number of spikelets. Although they concluded that the cooler temperature treatment increased the

number of spikelet primordia, Wall and Cartwright (1974) cautioned that effects of varying temperature on spikelet number are confounded with unrelated effects on the rate of extension growth.

The inverse relationship between rate and duration of spikelet formation as affected by temperature was demonstrated by Rahman and Wilson (1978). Increased temperatures up to 23/16C day/night temperature resulted in a increased rate and a decreased duration of spikelet initiation. A further increase in temperature caused a variable response. Spikelet number was decreased at the high temperature treatment. There was enough variation in genotypic response amoung the six cultivars tested, however, to conclude that rate and duration are seperate factors determining spikelet number.

Halse and Weir (1974) also noted variation amoung the five cultivars they examined in response to temperature effect on spikelet number. Their initial study (1970) showed little temperature effect but the temperature ranges evaluated were not wide enough. After a second test, their overall conclusion was the same. Duration was inversely related to temperature and rate was positively related to temperature. Friend (1965) observed varying temperature effects under different light intensities. With high light intensities, 25 to 30C was optimum for a high rate of spikelet initiation. At low light intensities 15 to 20C was optimum for a high rate of spikelet initiation. Duration was lengthened by low temperatures resulting in an increased spikelet number. Friend suggested that under the low temperature treatment there was more advanced

spike development, or more floret differentiation, before TS formation. There also must have been a longer apex with more ridges at the time of DR formation. Friend concluded that the low temperature treatment retarded the rate of morphological development of the spike more than the rate of growth of the whole plant and prolonged the duration of spike development resulting in large spikes at anthesis. No final yield data were collected to determine if the increase in spike size resulted in an increased grain yield.

Rawson (1970) and Warrington et al. (1977) observed similar effects of temperature on the rate and duration of spikelet initiation. Both noted higher rates at the high temperature treatments and increased durations at the low temperature treatments, and pointed out the importance of the vegetative stage of growth to spikelet number. The longer the length of time from seeding to DR formation and from DR formation to TS formation, the more spikelets/spike. Rawson stated that an increase in spikelet number, and therefore spikelets/spike, can only be obtained through an extension of the growing period.

Nutrient supply, especially N supply, also affects yield component development. Deficiency of N may result in decreased grain yields in wheat due to a decrease in tiller number and number of grains set/spike. Whingwiri and Kemp (1980) used four N treatments of 0N, 3kg N, 10kg N, and 30kg N and showed that increasing N resulted in an increase in tiller number, dry matter, grain yield, and plant size. Spikelet number also increased with increasing N due to an increase in the rate of

spikelet primordium production. The most marked increase was between 0kg N to 10kg N. With high N treatment duration of spikelet primordia production decreased but this effect was less than the rate effect. They concluded that N supply affected grain yield/ear most by influencing the ability of florets to set grain rather than by actually varying the spikelet number. The best grain yield did not occur at the maximum N treatment, rather at the 10kg N treatment. Mutual shading of shoots or perhaps poorer N nutrition of the tillers due to N application technique were possible explanations.

Single (1964) conducted a similar study using hydroponics to demonstrate the effect of N supply on yield component development. N levels were 0, 2, 8, and 56 ppm N. Single also observed an increase in spikelet number and fertility with increasing N supply. He noted that increasing the N supply prior to flag leaf appearance resulted in an increase in the proportion of fertile florets. He concluded that any serious nutrient deficiency just prior to spike initiation would result in a reduced spikelet number. An ample nutrient supply at this stage would result in formation of extra nodes on the rachis and an increase in potential spikelets.

Langer and Liew (1973) conducted a study to detemine at which stage is N supply most critical to spikelet number and grain production. They concluded that spikelet number increased only when high N was applied at the DR stage. Highest grain production occured when high N was supplied between TS and head emergence.

Holmes (1973) worked with two very different phenotypes and

noted differences in inflorescence development resulting from different N and P treatments. Using 'Pitic' and 'Marquis', Holmes generalized that treatments which increased the rate of apex development also decreased leaf, spikelet, and grain numbers, and decreased the duration of primordium production. An increased rate occured under low nutrient conditions.

Rahman and Wilson (1977b) noted an effect of P supply on spikelet development. P supplied at sowing increased spikelet number/ear, rate of spikelet initiation, and apex length of all seven cultivars tested. P supply had no effect on duration of the vegetative, spikelet, or elongation stages or on leaf number. They related the effect of P on the rate of spikelet initiation to the effect of P on cell division and cytokinin activity. P is known to increase the rate of cell division and the increased rate of spikelet initiation may reflect this. P may also affect cytokinin activity and its function in spikelet development.

Daylength and light intensity are two other factors affecting spikelet number in wheat. An inverse relationship was demonstrated between rate and duration of spikelet initiation. Rahman and Wilson (1977a) evaluated eight wheats for factors related to photoperiod that affect spikelet number. As photoperiod decreased from 24hr to 8hr, rate of spikelet initiation decreased and duration increased. Rahman and Wilson also observed that by changing the photoperiod at floral initiation, spikelet number could be altered. An increased spikelet number was associated with an increased duration of vegetative and spikelet initiation phases, so that with a low

photoperiod spikelet number was high. They concluded that the main factors determining spikelet number were the rate and duration of the spikelet initiation stage.

A high spikelet number as a result of decreased daylength is well documented (Halse and Weir, 1970; Rawson, 1971; Holmes, 1973; and Wall and Cartwright, 1974). Amoung the seven diverse wheats evaluated by Rawson (1971) it was determined that up to 30 spikelets/spike could be produced under low photoperiod conditions. Halse and Weir (1970) noted that floral initiation occured earlier and development was accelerated under long day conditions. Wall and Cartwright (1974) noted that delayed heading accompanied the high spikelet number under short day conditions.

The response to photoperiod varied between the cultivars tested in all cases. Holmes (1973) noted a greater response in rate of development in the standard height cultivar 'Marquis' compared to the response to photoperiod in the semidwarf 'Pitic'.

Both the duration of light and its intensity effect spike development. Friend (1963) observed that with increased light intensity from 200 to 2500 ft-c floral initiation occured earlier. High light intensities increased leaf number and spikelet number in 'Marquis' wheat. This was probably due to an increased rate of development under high light intensity conditions.

Rahman et al. (1977) observed spikelet production under a high light intensity and under a low light intensity and noted that under a low intensity duration of vegetative, spikelet, and

ear elongation phases were lengthened. Spikelet number, leaf number, and rate of spikelet initiation decreased under the low light intensity treatment.

The effect on yield of poor water availability depends on the stage of development when the stress is applied. Fischer (1973) observed that stress from lack of water at all stages of growth reduced yield by reducing the photosynthetic area relative to the area existing at the time the stress was applied. Langer and Ampong (1970) stressed plants for water at the DR stage and noted a decrease in spikelet number. Spikelet number was only affected by drought conditions at the DR stage. Similarly, Day and Intalap (1970) applied water stress to spring wheat at jointing, flowering, and the dough stage. The jointing stage, which roughly corresponds to TS, appeared to be a critical stage in regard to water stress. They noted several results of water stress at jointing: early flowering, shorter plants, increased lodging, lower grain yield, lower grain volumn-weight, fewer tillers, and fewer seeds/head.

The genetic factors determining spikelet number and the rate and duration of spikelet initiation are not clearly understood. It is fairly well established that rate and duration of spikelet initiation are independant characteristics and are under seperate genetic control. Chapman and McNeal (1971) studied the genetics of spikelet number in parental, F1, F2, and single back crosses in a spring wheat cross, 'Henry' X 'Lemhi 53'. They suggested that additive gene action had the greatest effect on spikelet number. Halloran (1974) worked with 'Chinese Spring' and 'Hope' and their 21 chromosome substitution

lines and estimated that a minimum of six chromosomes determined spikelet number. The four chromosomes 1B, 5D, 2D, and 3D caused an increase in spikelet number while 2B and 6B caused a reduction in spikelet number compared to normal Chinese Spring. Halloran suggested that genes that are specifically effective in changing spikelet number could be incorporated by breeding. He did not determine which factor was controlled, rate or duration of spikelet initiation.

Rahman et al. compared an adapted cultivar to a land race cultivar under two photoperiods. Under the 24hr photoperiod treatment spikelet number appeared to be a quantitative trait with high spikelet number being dominant and controlled by a single gene. Under the 12hr photoperiod treatment low spikelet number was dominant and appeared to be governed by a single gene. Rahman et al. suggested this gene likely governed differences in photoperiodic sensitivity and masked the action of any gene for spikelet number. They recommended that further studies be conducted under conditions that minimize differences in rate and duration of spikelet initiation between parents or conduct the test under any environment but use parents having similar developmental patterns.

This early study showed some indication that rate was a heritable trait and likely a dominant characteristic. This indication led to another study using only land races. Rahman et al. (1978) conluded that spikelet number was under simple genetic control with high spikelet number being dominant. They suggested that the gene determining spikelet number does so by determining the rate of spikelet initiation. Their final

conclusion was that differences in spikelet number not due to environmental effects are due to a major gene with possible modifiers and that this gene likely controls the rate of spikelet initiation.

Although there is little plant breeders can do to change the environment under which plant breeding is performed, it is useful to vary environmental conditions to understand how such things as rate and duration of spikelet initiation are related and what plants are capable of producing. Research has shown that rate and duration of spikelet initiation are inversely related and combine to initiate either few or many spikelets. There is enough exception to this relationship, however, to conclude that rate and duration are independant factors determining spikelet number and could perhaps be manipulated by plant breeders through use of the major gene determing rate of spikelet initiation

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INTRODUCTION

Spikelet number, floret number, tiller number, and grain weight are the four components that contribute to yield in winter wheat (Triticum aestivum L.). Potential spikelet number and potential floret number are two yield components that are determined in a matter of a few weeks in the early spring in Kansas (17). The duration and rate of spikelet initiation determine the final spikelet number (10). Duration is the time from double ridge (DR) formation to terminal spikelet (TS) formation. Rate of spikelet initiation is computed as the final spikelet number divided by its duration, and is expressed in spikelets/day. If both potential floret number and spikelet number are determined during the duration of spikelet initiation, then this period is especially critical to yield potential.

Rate and duration of spikelet initiation are both sensitive to environmental conditions. Controlled environment studies have shown a general inverse relationship between rate and duration of spikelet initiation (12, 13, 14). Temperature, photoperiod, light intensity, soil moisture, and soil fertility are all environmental factors affecting spikelet initiation. Rate and duration are inversely affected by temperature. Rahman and Wilson (13) showed that increased temperatures increased rate but decreased the duration of spikelet initiation. The reverse occured under low temperature treatments, rate was reduced and duration was increased. When they decreased photoperiod from 24hr to 8hr, duration of spikelet initiation

lengthened but the rate decreased (12). An increase in spikelet number was associated with the increased duration caused by the low photoperiod. Low light intensities encouraged a longer duration of spikelet initiation and a decreased rate and spikelet number (14). Langer and Ampong (9) imposed water stress to plants at the DR stage and observed a decrease in final spikelet number. Day and Intalap (4) noted that water stress at the jointing stage resulted in earlier flowering, shorter plants, increased lodging, lower grain yield, fewer tillers, and fewer seeds/head. Soil fertility, particularly nitrogen supply, affected the rate of spikelet initiation. Whingwiri and Kemp (16) observed that rate and spikelet number increased with increasing nitrogen, but nitrogen treatment had almost no effect on the duration of spikelet initiation.

Rate of floret initiation may influence the eventual number of seeds/spikelet. Whingwiri and Stern (17) recently concluded that florets initiated after TS formation fail to form grain implying that TS formation marked the determination of both potential spikelet number and potential floret number.

In a comparitive study between 'Norin 10' and Norin-10 derived short-statured wheats, Fisher (6) noted marked differences in spikelet initiation and development. He observed greater spikelet initiation and more fertile florets in the short wheats. In a similar study, Brooking and Kirby (1) did not observe consistent differences in shoot apex morphogenesis and credited the high yield potential of the dwarf types to assimilate partitioning during development.

In studies to understand the genetic mechanisms of spikelet

initiation Rahman and Wilson (11) concluded that the rate and duration of spikelet initiation are independant characteristics and are under seperate genetic control. Chapman and McNeal (2) concluded that spikelet number was under quantitative genetic control and exhibited incomplete dominance. Halloran, (7) working with 'Chinese Spring' and 'Hope', suggested that six major genes and a number of minor genes influenced spikelet number. More recently, Rahman et al. (10) concluded that a major gene with possible modifiers controlled the rate of spikelet initiation.

The objective of this study was to determine genotypic differences in rate and duration of spikelet initiation in ten winter wheat cultivars. The ten cultivars represented varying phenotypes and yield potentials. We were interested in making three comparisons regarding these cultivars. We compared rate and duration of spikelet initiation amoung: 1) benchmark cultivars which represented significant steps towards higher yields and dominated Kansas acreage, 2) semidwarf and standard height wheats, and 3) semidwarf cultivars and hybrid wheats. In each comparison we examined trends in spikelet initiation, measured as either duration or rate, that may have accompanied yield improvements of these distinct ideotypes over time.

MATERIALS AND METHODS

Ten cultivars of winter wheat (Table 1) varying in phenotype were planted at a rate of 45kg/ha. Two planting dates with four replications each were evaluated. The first date was planted 10 Oct. 1981 and the second date planted 28 Oct. 1981. Plots were 5.5m long and 0.5m wide, containing three rows 17.5cm apart. The plots were located on the North Agronomy Farm Manhattan, Kansas on a Smolan silt loam. 70 lb nitrogen and 30lb phosphorous were applied preplant and incorporated.

Duration of spikelet initiation is the time, in days, from double ridge (DR) formation to terminal spikelet (TS) formation. To determine the duration of spikelet initiation, two plants/plot were sampled two to three times weekly beginning 23 Mar. 1982. The main culm of the plants was dissected under a dissecting microscope to determine the stage of growth and estimate the date of DR formation followed by TS formation. The estimates from the four plots of each cultivar were averaged to obtain the average duration for a given cultivar. Stages of growth were estimated with the aid of the Kirby and Appleyard guide (8).

At harvest, ten plants were pulled at random from each plot and total number of spikelets/spike were counted. Rate of spikelet initiation was computed as total spikelet number divided by duration and was recorded as spikelets/day. Plant height, tiller number, days to anthesis, accumulated temperature during spikelet initiation, and accumulated temperature from TS to anthesis were also recorded. Thermal units were calculated

by summing the positive mean daily temperatures, assuming a base temperature of 0C. Mean daily temperatures were considered as the mean of the maximum and minimum daily temperature and added for the period of time between DR formation and TS formation and between TS formation and anthesis. Gravimetric soil moisture saples were taken 2 Apr. 1982, 21 Apr. 1982, and 2 June 1982 at 15cm intervals to a depth of 180cm. Percentage soil moisture by weight was calculated. Air temperature was measured 6km from the plots at the Weather Data Library, Cardwell Hall on the Kansas State University campus. Conditions were nearly optimum during spikelet initiation. Temperatures were cool and moisture was available.

Samples not dissected daily were preserved in a 6:3:1 v/v solution of ethanol, glacial acetic acid, and chloroform (3). Samples can be stored for approxiamately six months in the refrigerator. This method bleached the samples making them unsuitable for photographing, however, stage of spikelet initiation could still be determined.

The experimental design was a randomized, complete block. Analysis of variance, Fischer's L.S.D. and Duncan's multiple range tests were used to determine significant differences. Regression analysis was used to evaluate the correlations of interest.

A preliminary floret study was also initiated using 'Newton' and 'Scout' to determine the shortfall of floret production (17). Fall-sown plants were transplanted from the field to the growth chamber on 29 Jan. 1982. The plants were acclimated at 15C and 11hr day length for three weeks, then

grown under a 17/12C day/night temperature regime and a 16hr photoperiod. Three plants were sampled twice a week up to the boot stage. Floret primordia were counted. At maturity, final grain number/spikelet was determined so that percent shortfall could be calculated.

%Shortfall = [1 - (grains formed/florets initiated)] x 100

RESULTS AND DISCUSSION

Genotypic differences were observed for both rate and duration of spikelet initiation. Differences in duration of spikelet initiation were significant at both planting dates. Differences in rate were significant in the first planting date and the combined analysis (Table 2). The late sowing had a decreasing effect on duration of spikelet initiation. Duration decreased from an average of 18.2 days in planting date 1 to 16.8 days in planting date 2. Durations of developmental stages typically decrease with late sowing (15). This may be attributed to higher temperatures in the later spring and/or daylength. Soil moisture measurements indicated that the soil profile was above 50% available soil moisture from planting to anthesis, therefore, soil moisture was not a limiting factor for either planting date.

Another way to consider duration of spikelet formation is in terms of accumulated temperature. Gallagher (5) plotted the life cycle of barley in terms of primordial number and thermal units rather than time to remove any distorting influence of variation in temperature experienced in the field. In this way, mean daily temperatures above an appropriate base (0C for temperate cereals) are accumulated for a given period of growth. Duration of spikelet initiation and accumulated thermal units were positively correlated with R-square values of 0.94 and 0.60 for planting dates 1 and 2 respectively (Table 3). Duration in days and thermal units were both negatively correlated with rate and positively correlated with date of flowering and spikelet

number. The ranking of the cultivars for accumulated thermal units was fairly consistent with the ranking for duration in days and was also consistent between planting dates.

To compensate for decreased durations of developmental stages, resulting from delayed planting, rates typically increase. In this study, rate increased from an average of 0.97 spikelets/day in planting date 1 to 1.09 spikelets/day in date 2. The result was an increase in final spikelet number from an average of 17.49 spikelets/spike in planting date 1 to 18.04 spikelets/spike in date 2. This increase in spikelet number did not necessarily increase yield, however, due to a decrease in tiller number in the second planting date. Delayed planting also delayed the onset of spikelet initiation by about ten days. The average DR initiaion date was 30 March in planting date 1 and 9 April in planting date 2.

Rate of spikelet initiation may also be considered in terms of thermal units by expressing in spikelets/degree (Table 2). This may be a more consistent measure because it excludes some of the variation due to temperature fluctuations. The ranking of the cultivars was fairly consistent with the ranking for rate in spikelets/day. In the remainder of the discussion, rate and duration will be discussed in terms of spikelets/day and days respectively.

Accumulated thermal units between TS and anthesis was not correlated with duration of spikelet initiation or accumulated thermal units from DR to TS, nor was it correlated with spikelet number or rate of spikelet initiation. It was, however, positively correlated with date of flowering.

Amoung the three comparisons an inverse relationship between rate and duration of spikelet initiation was observed. The first comparison was amoung benchmark cutivars. The cultivars 'Turkey', 'Pawnee', 'Scout', and 'Newton' are considered benchmark cultivars because they were significant steps towards higher yields in Kansas and were well represented in hectares planted. Turkey had the longest duration, the slowest rate of spikelet initiation of all the cultivars examined, and the highest thermal unit requirement for both TS and anthesis (Table 2). The magnitude of decrease in the duration of spikelet initation for benchmark cultivars was 3.8 days in planting date 1 and 4.3 days in planting date 2. The reverse occured for rate of spikelet initiation. Pawnee, Scout, and Newton all had increased rates, when compared to Turkey, with Newton having the greatest rate. The magnitude of increase in rate of spikelet initiation was 0.17 spikelets/day in planting date 1 and was not significant in planting date 2. The observed trend when comparing Turkey, Pawnee, and Scout was a shift towards a decreased duration, an increased rate of spikelet initiation, and a lower thermal requirement for initiation of TS. As wheat breeders have selected for superior plant types and higher yields they may have simultaneously selected for shorter durations and higher rates of spikelet initation. The release of Newton in 1977 reversed the selection of shorter duration and lower thermal requirements for TS, however, the breeder was able to attain an increase in rate of spikelet initiation. This may be attributed to the dwarfing genes in Newton. The characteristic of a high rate and a long

duration should favor spike development. Accordingly, Newton had a higher average final spikelet number of 19.23 spikelets/spike compared to 16.85 spikelets/spike formed on Scout (Table 2).

The second comparison of interest was between semidwarf and standard height cultivars. The cultivars used for this comparison were semidwarfs 'Vona', Newton, and 'Hawk' and the standard height cultivars 'Larned' and Scout. Comparisons between semidwarf and standard height cultivars demonstrated differences in duration but not in rate of spikelet initiation (Table 2). The semidwarfs had longer durations than the standard height wheats. On the average, duration of spikelet initiation was about 2.2 days longer in the semidwarfs. Differences in rate of spikelet initiation between the semidwarfs and the standard height types were not significant, although all five of these cultivars were ranked high to medium for rate amoung the ten cultivars tested. The semidwarfs consistently initiated more spikelets/spike than their taller counterparts. The end result was an increased final spikelet number in the semidwarfs. The magnitude of increase was an average of 2.2 additional spikelets/spike on the semidwarfs. This increase could be attributed to the longer duration of spikelet initation observed in the semidwarfs.

In a comparative study between short-statured wheats with 'Norin 10' in their ancestry and standard height wheats, Fisher (6) also noted that more spikelets were initiated in the short wheats. He observed more fertile florets/spikelet in the short wheats due to a strong apical dominance within the individual

spikelets. In a study making similar comparisons, Brooking and Kirby (1) found no consistent difference in spikelet and floret primordium initiation between standard height and short-statured wheats. They did, however, note an increased fertile floret number in the short wheats. They credited this to assimilate partitioning during development that favored the formation of fertile florets at anthesis.

The third comparison of interest was between semidwarf pure lines and hybrids. Three hybrids, 'HW1010', 'Bounty 100', and 'DK104A' were compared with Vona, Newton, and Hawk. Vona, Newton, and Hawk had significantly longer durations than either Bounty 100 or DK104A (Table 2). HW1010 was not significantly different in duration than the pure lines. The average difference in duration between the pure lines and the hybrids was 2.1 days. DK104A had the shortest duration of spikelet initiation but the fastest rate at 1.14 spikelets/day (Table 2). This was the only cultivar that could be distinguished, in terms of rate, from the others. Newton and Hawk initiated more spikelets than the two hybrids DK104A and Bounty 100. Since both DK104A and Bounty 100 contain Triticum timopheevi L. cytoplasm their observed differences from HW1010 or the three pure lines may indicate that the cytoplasm could influence both rate and duration of spikelet initiation.

A strict inverse relationship between rate and duration of spikelet initiation has been reported suggesting that spikelet number is the heritable character with rate and duration being the consequences. This inverse relationship has been demonstrated by varying environmental conditions (12, 13, 14).

In this study rate and duration were inversely correlated with R-square values of 0.74 and 0.66 for planting dates 1 and 2 resectively (Table 3). However, results presented here also show enough deviation from this relationship to conclude it is not invariable. The hybrid vs. pure line comparison shows some of the deviation from the overall inverse relationship between rate and duration of spikelet initiation. The pure lines were ranked higher than the hybrids for duration of spikelet initiation but were not consistently ranked lower for rate, as the inverse relationship would imply. Rather, in the combined analysis, both Newton and Hawk had rates comparable to DK104A, the highest ranking line evaluated. So Newton and Hawk had both a long duration and a high rate, and were consistently ranked high for final spikelet number. The combination of a long duration and a high rate favored spike development of Hawk and Newton.

Because there are four yield components in wheat, an increased final spikelet number does not necessarily mean an increased yield. Whingwiri and Stern (17) have suggested, however, that the duration of spikelet initiation is especially critical because both of the yield components spikelet/spike and potential florets/spike are fixed during the duration of spikelet initiation. Whingwiri and Stern studied floret survival in wheat and concluded that florets initiated after the formation of TS fail to form grain. They postulated that the vascular system between the floret and the rachis developed as the floret was initiated. After TS formation the vascular development was inihibited and further florets failed to form

grain. It was observed that on each spikelet, the first two florets were initiated before the TS and about 97% of them formed grain. The fourth floret rarely formed grain and was typically initiated after the TS. The third floret was intermediate. On the average they observed a shortfall of 72%, i.e. 72% of the florets initiated did not produce grain.

Results from our floret study were consistent in demonstrating the inefficiency of floret production. It was clear that many more florets were initiated than would form grain. As many as 11 florets were initiated in spikelets of Newton. Up to 68% of the florets initiated in Newton failed to form grain (Table 4). In Scout the shortfall was 78%. These results support those of Whingwiri and Stern. They stated that if tiller number, spikelets/spike, and florets/spikelet are all fixed by TS formation on the main tiller then the scope for increasing yield may be limited to increasing the rate of floret initiation, which did not seem hopeful. They observed little change in rate of floret initiation regardless of treatment or rate of spikelet initiation. Their research, however, involved only one cultivar. Because our results showed genotypic variation for both rate and duration of spikelet initiation, then we would expect differences in rate of floret initiation also. Therefore, the scope for increasing yield through rate of floret intiation may not be as narrow as Whingwiri and Stern suggested. The cultivars Newton and Hawk are known to produce up to five kernels/spikelet under favorable conditions, implying a high rate of floret initiation. These cultivars also had high rates of spikelet initiation.

Final spikelet number is a consequence of rate and duration of spikelet initiation. Rahman and Wilson (11) increased rate of spikelet initiation by supplementing P to P deficient plants without effecting duration. Rate and duration were shown to be independant characteristics and assumed to be under seperate genetic control. Rahman et al. (10) later concluded that differences in final spikelet number not due to differences in response to light and temperature were due to the action of a major gene with possible modifiers. This gene likely controlled the rate of spikelet initiation.

In summary, we concluded that genotypic differences for both rate and duration of spikelet initiation were present in the ten cultivars tested. With yield improvements, benchmark cultivars have progressed towards a shorter duration and a faster rate of spikelet initiation. Semidwarf wheats had a longer duration than the standard height wheats and maintained a high rate. Hybrids had a short duration and a fast rate of spikelet initiation. Overall, rate and duration were inversely correlated.

In the hopes of increasing potential grain sites, perhaps breeders could use this variation in rate and duration of spikelet initiation to their advantage. If the duration of spikelet initiation is extended towards anthesis there may be a problem with late flowering and high temperatures as duration and flowering date were positively correlated. If spikelet initiation were to begin earlier there may be damage from cold temperatures after breaking of winter dormancy in winter wheat, and perhaps a decreased leaf number in spring wheat (5).

Selection for a high rate of spikelet initiation and floret initiation may result in an increased number of potential grain sites.

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Table 1. Cultivars planted, their date of release, average height, and flowering date.

Cultivars	Date Released	Height cm	Date of Flowering*
@Turkey	1873	115a	152a
@Pawnee	1943	102b	144c
@Scout	1963	102b	144c
Larned	1976	96c	144c
Vona	1976	68g	141e
Hawk	1981	77e	144c
@Newton	1977	81d	145b
#HW1010	exp.	70g	141e
#Bounty 100	1982	73f	142d
#DK104A	exp.	73f	141e
L.S.D. 0.05		<3	<1

*Days after 1 Jan.
@Considered benchmark types representing significant steps towards higher yields and dominating Kansas acreage.
#Hybrid wheats.

Table 2. Duration, rate, average final spikelet number and accumulated thermal units (C) from DR to TS and from TS to anthesis for planting dates 1 and 2 and the combined analysis.

	DURATION IN DAYS		
Cultivars	Date 1	Date 2	Combined
Turkey	21.5a	18.8a	20.1a
Pawnee	20.3ab	18.5a	19.4ab
Vona	19.3bc	17.8ab	18.4bc
Newton	19.0bc	17.5ab	18.3bc
Hawk	18.8bc	17.5ab	18.1bc
HW1010	18.8bc	16.5abc	17.6cd
Scout	17.8cd	14.5c	16.1de
Bounty 100	16.3de	15.0c	15.6e
Larned	15.5e	16.5abc	16.0e
DK104A	15.3e	15.5bc	15.4e
L.S.D. 0.05	2.0	2.4	1.5

RATE SPIKELETS/DAY

Cultivar	Date 1	Date 2	Combined
DK104A	1.14a	1.11	1.13a
Larned	1.05ab	1.05	1.05ab
Newton	0.99bc	1.13	1.06ab
Hawk	0.99bc	1.10	1.04ab
Bounty 100	0.98bc	1.07	1.03ab
HW1010	0.96bc	1.13	1.05ab
Vona	0.93bcd	1.05	1.00b
Scout	0.93bcd	1.19	1.06ab
Pawnee	0.91cd	1.06	0.98bc
Turkey	0.82d	0.97	0.89c
L.S.D. 0.05	0.12	NS	0.11

RATE SPIKELETS/DEGREE

Cultivar	Date 1	Date 2	Combined
DK104A	0.103a	0.092a	0.097a
Larned	0.094ab	0.073de	0.084bc
Bounty 100	0.087bc	0.087abc	0.087b
Hawk	0.083bcd	0.078bcd	0.081bc
Scout	0.083bcd	0.079bcd	0.081bc
HW1010	0.082bcd	0.089ab	0.086b
Newton	0.082bcd	0.076cde	0.079bc
Vona	0.079bcd	0.087abc	0.083bc
Pawnee	0.076cd	0.075de	0.076cd
Turkey	0.071d	0.065e	0.068d
L.S.D 0.05	0.015	0.011	0.010

SPIKELET NO.

Cultivar	Date 1	Date 2	Combined
Newton	18.65a	19.80a	19.23a
Hawk	18.46ab	18.88bc	18.67bc
Pawnee	18.23abc	19.50ab	18.86ab
HW1010	18.05abcd	18.23c	18.14cd
Vona	17.88bcd	18.53c	18.20cd
Turkey	17.63cd	18.08cd	17.85de
DK104A	17.43d	17.25de	17.34ef
Scout	16.53e	17.18e	16.85fg
Larned	16.08e	16.95e	16.51gh
Bounty 100	15.98e	16.00f	15.99h
L.S.D 0.05	0.73	0.83	0.54

ACCUMULATED THERMAL UNITS DR TO TS

Cultivar	Date 1	Date 2	Combined
Turkey	248.8a	277.6a	263.2a
Pawnee	242.4a	260.1ab	251.3ab
Newton	227.9ab	258.6ab	243.2ab
Vona	227.4ab	214.8def	221.1cd
Hawk	222.4ab	244.2bc	233.3bc
HW1010	220.1ab	207.6efg	213.8cd
Scout	209.5bc	217.9cde	213.8cd
Bounty 100	186.2cd	184.6g	185.4e
Larned	177.7d	235.8bcd	206.7d
DK104A	170.5d	187.7fg	179.1e
p<0.01			

ACCUMULATED THERMAL UNITS TS TO ANTHESIS

Cultivar	Date 1	Date 2	Combined
Turkey	626.3a	687.6a	656.9a
Scout	590.8ab	592.7bc	591.7bc
Larned	590.4ab	591.9bc	591.2bc
DK104A	586.8ab	577.9c	582.4bcd
Bounty 100	579.9b	610.9b	595.4b
Newton	571.6b	575.2c	573.4bcd
Pawnee	563.4bc	560.6c	562.0de
Hawk	549.6bcd	579.7bc	564.6de
HW1010	527.6cd	559.4c	543.5e
Vona	514.6d	565.3c	539.9e
p<0.01			

Table 3. R-square values for correlations between flowering date (F), duration (DU), rate (R), spikelet number (SP), and accumulated thermal units (TU) for planting dates 1 and 2.

	R-SQUARE	
F*DU	+0.29**	+0.14**
F*R	-0.22**	-0.10*
DU*R	-0.73**	-0.65**
SP*R	NS	NS
SP*DU	+0.22**	+0.18**
TU*DU	+0.94**	+0.60**
TU*SP	+0.21**	+0.24**
TU*R	-0.72**	-0.28**
TU*F	+0.22**	+0.51**

*P<0.05
**P<0.01

Table 4. Grains formed, florets initiated and % shortfall values for Newton and Scout.

	GRAINS FORMED	FLORETS INITIATED	% SHORTFALL
Newton	2.75a	8.55a	67.84
Scout	1.64b	7.53b	78.22
L.S.D 0.05	0.74	1.00	

APPENDIX

Dates of initiation of DR and TS for planting dates 1 and 2.

Cultivar	Date 1 DR	Date 1 TS	Date 2 DR	Date 2 TS
DK104A	3/30	4/14	4/6	4/21
Hawk	3/31	4/19	4/9	4/27
Bounty 100	3/30	4/15	4/6	4/21
Vona	3/30	4/18	4/6	4/23
Newton	3/30	4/18	4/11	4/28
Pawnee	3/29	4/18	4/9	4/27
Turkey	3/31	4/22	4/12	4/31
HW1010	3/29	4/17	4/6	4/23
Larned	3/31	4/15	4/9	4/26
Scout	3/29	4/16	4/12	4/26
Mean	3/30	4/17	4/9	4/25

Moisture at 15cm increments to 180cm at three dates during the 1982 growing season.

Depth (cm)	gm/gm 2 April	21 April	2 June
15	12.93	8.49	15.54
30	16.85	15.36	16.32
45	15.93	15.49	13.99
60	14.17	17.27	17.85
75	17.52	18.20	16.75
90	16.79	17.16	15.17
105	16.05	14.34	15.31
120	17.56	17.63	15.23
135	16.21	15.66	15.22
150	15.36	16.07	14.45
165	14.03	13.74	13.95
180	15.10	15.26	15.04

Maximum and minimum temperatures (C) for the growing season 10 Oct. 1981 through 10 July 1982.

	Oct		Nov		Dec	
day	max	min	max	min	max	min
1			15.00	9.44	4.44	0.00
2			13.33	7.22	8.89	-1.67
3			15.56	7.22	10.56	-1.67
4			12.22	8.33	8.89	-1.11
5			15.56	5.56	10.56	-2.78
6			15.56	-2.22	16.11	1.67
7			19.44	0.00	17.78	5.56
8			16.67	5.00	10.56	-3.33
9			7.78	-3.33	6.67	-2.22
10	18.33	7.22	15.00	-3.89	2.22	-2.78
11	18.33	7.78	16.11	-1.11	3.89	1.11
12	18.33	13.89	20.00	1.67	3.89	1.67
13	20.56	17.78	19.44	1.67	4.44	0.56
14	20.56	13.33	18.33	7.78	2.78	-1.67
15	17.22	9.44	20.00	10.00	2.22	-2.22
16	16.67	8.89	20.00	3.89	-1.11	-8.33
17	20.00	12.22	23.33	7.20	-8.33	-16.67
18	12.78	6.11	18.88	9.44	-9.44	-17.78
19	22.78	0.00	9.44	-1.11	-5.00	-17.78
20	23.33	11.67	3.89	-3.89	2.78	-11.11
21	16.67	6.67	10.56	-5.56	2.78	1.11
22	10.56	1.67	17.22	-3.33	2.78	0.56
23	7.22	-3.33	15.00	6.11	5.00	-7.22
24	11.11	1.11	12.78	0.00	7.22	-7.78
25	11.11	5.56	19.44	5.00	7.22	-3.89
26	15.56	0.00	10.00	3.33	3.33	-6.67
27	21.67	5.56	5.00	-6.67	2.22	-8.33
28	21.67	10.56	6.11	-1.11	0.00	-8.89
29	25.00	10.00	9.44	-3.33	4.44	-11.67
30	18.33	13.89	7.78	3.89	10.56	-7.22
31	15.56	12.22			6.67	-6.67

	Jan		Feb		Mar	
day	max	min	max	min	max	min
1	-2.22	-10.00	3.33	-7.22	20.56	-3.89
2	6.11	-4.44	0.00	-7.78	15.56	1.67
3	-3.33	-9.44	-7.78	-18.33	1.67	-2.22
4	2.78	-15.00	-13.89	-20.00	1.67	-5.56
5	6.11	-9.44	-12.78	-18.33	-2.22	-6.11
6	-6.67	-15.00	-4.44	-23.33	6.11	-12.22
7	-5.56	-17.22	2.22	-15.00	3.89	-10.00
8	5.00	-10.55	-6.11	-10.00	8.89	-3.89
9	-1.67	-15.00	-9.44	-19.44	10.56	-7.78
10	-11.11	-26.11	-4.44	-18.89	26.11	-3.89
11	-5.56	-21.11	0.00	-17.78	19.44	0.56
12	-7.22	-11.11	1.67	-6.11	22.78	2.78
13	-7.78	-21.11	3.88	-12.22	17.78	-1.67
14	8.33	-14.44	6.67	-1.11	10.56	5.00
15	5.56	-8.33	7.22	2.22	15.00	5.00
16	-8.33	-20.00	5.00	2.22	18.89	7.22
17	-0.56	-16.67	3.89	1.11	23.89	3.89
18	8.89	-8.33	12.78	1.11	11.67	7.78
19	7.22	-8.33	18.89	-1.11	23.89	8.33
20	-1.11	-5.56	18.89	3.33	14.44	2.22
21	-2.78	-7.22	21.11	-1.11	8.89	-3.89
22	5.00	-9.44	25.56	-1.11	12.78	-5.00
23	-6.67	-15.00	17.78	1.11	13.89	1.67
24	-0.56	-14.44	6.67	0.00	13.89	-0.56
25	5.56	-7.78	2.22	-5.00	8.33	-0.56
26	11.67	-8.89	3.89	-7.78	12.22	-6.11
27	11.67	4.44	11.11	-7.78	11.11	0.00
28	6.11	-6.11	13.33	-3.89	12.22	1.67
29	9.44	1.11			15.56	5.00
30	3.33	-3.33			20.00	10.00
31	-2.78	-11.67			20.00	1.67

	Apr		May		June	
day	max	min	max	min	max	min
1	26.67	1.11	20.56	11.67	20.56	5.00
2	27.22	6.67	23.33	12.78	18.33	12.22
3	15.00	0.00	28.33	15.56	17.78	12.22
4	11.11	-0.56	30.56	18.33	21.11	12.78
5	7.78	-0.56	26.11	15.56	23.33	12.22
6	5.56	-7.22	15.00	6.67	31.11	20.00
7	6.11	0.00	23.33	5.56	28.33	12.22
8	9.44	-0.56	27.78	13.33	32.22	19.44
9	13.89	-5.56	28.33	16.67	28.33	17.22
10	15.56	1.67	17.22	17.78	24.44	8.33
11	22.78	4.44	28.89	15.00	21.67	14.44
12	29.44	11.11	22.78	15.00	25.56	13.89
13	23.89	8.33	23.33	16.67	26.67	15.00
14	30.56	11.67	22.22	13.33	30.00	17.78
15	30.56	17.78	24.44	11.11	27.78	17.22
16	26.67	10.00	23.33	15.56	24.44	12.78
17	17.22	2.78	23.89	15.00	28.89	13.33
18	23.33	1.11	27.78	12.78	24.44	12.22
19	20.00	10.56	28.33	17.22	25.56	12.78
20	13.33	0.00	26.11	16.11	29.44	16.11
21	16.11	-2.22	23.33	12.78	30.00	14.44
22	17.22	0.00	20.56	11.67	27.78	13.89
23	21.67	1.67	24.44	11.67	26.67	16.68
24	22.22	10.56	21.67	15.56	29.44	17.78
25	17.22	8.89	23.33	16.67	26.67	19.44
26	21.11	7.22	21.11	11.67	28.33	17.22
27	15.56	5.56	26.67	10.00	25.56	19.44
28	10.56	6.11	27.22	17.78	30.56	18.89
29	13.33	6.67	26.67	16.11	34.44	19.44
30	17.22	10.56	26.11	15.00	29.44	21.67
31			22.22	13.33		

	July	
day	max	min
1	26.11	20.00
2	33.89	20.56
3	36.67	21.67
4	35.56	23.89
5	33.33	24.44
6	32.22	21.67
7	30.56	15.00
8	31.11	17.22
9	30.00	21.11
10	28.33	35.56

RATE AND DURAION OF SPIKELET INITIATION IN TEN WINTER WHEAT CULTIVARS

by

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B.S., Kansas State University, 1981

AN ABSTRACT OF A MASTER'S THESIS

Submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

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1983

Abstract

Yield potential is determined early in the life cycle of winter wheat. Number of spikelets/spike and florets/spikelet are determined in a matter of a few weeks in the early spring. To determine differences amoung cultivars for rate and duration of spikelet initiation, ten cultivars varying in phenotype were planted at two planting dates with four replications each. Plants were sampled and dissected two to three times weekly in the spring to estimate the duration and rate of the spikelet initiation stage. Duration is the length of time, in days, from double ridge formation to terminal spikelet formation. At harvest, total numbers of spikelets/spike were counted. Rate of spikelet initiation was computed as total spikelet number divided by duration. Comparisons of interest included differences between benchmark cultivars, semidwarf vs. standard height wheats, and semidwarf pure lines vs. hybrids. Overall differences between cultivars for duration of spikelet initiation were significant. Values ranged from 15.3 days for the hybrid 'DK104A' to 21.5 days for 'Turkey'. Rate of spikelet initiation was also significantly different between cultivars. Rate ranged from 1.14 spikelets/day in DK104A to 0.82 spikelets/day in Turkey. The overall trend was towards a faster rate as duration decreased. To estimate the magnitude and efficiency of floret production, florets initiated and average grain number/spikelet were counted in two of the cultivars. Percent shortfall was 68% in 'Newton' and 78% in 'Scout', i.e. 68% and 78% of the florets initiated in Newton and Scout

respectively did not contribute to final yield. These results suggest the possibility of improving wheat spike types and yield through manipulation of the spikelet initiation stage.