

RATE AND DURATION OF SPIKELET INITIATION, THEIR
INHERITANCE AND RELATIONSHIPS TO YIELD COMPONENTS
IN WHEAT

by

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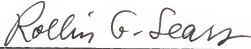
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LITERATURE REVIEW

Final grain yield in wheat (*Triticum aestivum* L. em. Thell) is the end product of the interaction of a large number of physiological and biochemical processes in the plant (Rahman et al., 1977). It can be expressed in terms of its four described components; Total yield = (spikes/unit area) x (spikelets/spike) x (kernels/spikelet) x (kernel weight). Obviously, the number of spikelets per spike is one of the major attributes to the final grain yield. Rawson (1970) found that the number of spikelets per spike, which is closely related to kernel number, was determined by the duration of the period from floral initiation to terminal spikelet formation. Rahman et al. (1977) concluded that the variation in spikelet number is due to major genes which affect the rate of spikelet initiation. These results indicated that the rate and duration of spikelet initiation between double ridge and terminal spikelet stage are the primary determinants to spikelet number. Therefore, a concentrated study on the inheritance of rate and duration of spikelet initiation and their relationships to yield and yield components should provide the possibility of improving yield through genetic manipulation, and at the very least provide further information to better understand yield component compensation.

This review begins by briefly describing the development of different stages of the wheat spike and its yield components; the effects of environmental factors on them and the inheritance of

these traits and the relationships that exist among these traits.

I. DEVELOPMENT OF THE WHEAT SPIKE

The life cycle of the wheat plant can be divided into two stages: vegetative and reproductive. In the mature grain, an embryo plant is present. Its shoot apex has three to four leaf primordia and a tiller bud is present in the axil of the coleoptile tiller and the axil of leaf (Kirby, 1981). Between seed germination and double ridge, the leaf ridge is dominant and leaf primordia are initiated. At late vegetative stage, the smooth round meristematic dome of the shoot apex becomes more cylindrical and the leaf primordia can be seen under a light microscope. Once the apex changes from vegetative to reproductive, no more leaf primordia are produced (Bonnett, 1966).

During spike development, the spikelet ridge is dominant and spikelet primordia are initiated. Baker and Gallagher (1983) found that double ridges appeared when very nearly 50% of the final number of spikelets are present. At double ridge stage, the primordia which will differentiate to become spikelet are visible. The upper, larger ridge is the primordium which will develop into the spikelet, and the lower, less prominent ridge is a leaf primordium which is suppressed after the double stage except at the base of the spike where it forms the collar, a structure visible at harvest. Spikelets continue to be initiated acropetally until the terminal spikelet is initiated (Bonnett, 1966). Klepper et al (1983) presented a numerical staging scheme

for measuring the progression of wheat spike development in which they described spike development in 7 stages. They reported that stage 2, the occurrence of the double ridge stage, and stage 7, terminal spikelet formation, are clearly measured by this system. Since double ridge stage indicates that leaf initiation has ceased and terminal spikelet formation sets the limit on spikelet number, precisely measuring these two stages will be useful in predicting yield.

Soon after spikelet primordia formation, florets develop with each spikelet acropetally and alternately from an indeterminate meristem, and it is concomitant with spike and stem extension. Baker and Gallagher (1983) reported that floret initiation was completed at about the time that the flag leaf appeared. At boot stage, the final number of florets will be determined and individual floret parts become well defined with pistal, style and anthers. In each spikelet, six to eight florets are often initiated, but only three or less of these usually bear grain, and the basal spikelets of field grown wheat commonly fail to develop any competent florets at all (Mastsuda et al, unpublished). Whingwiri and Stern (1982) studied floret survival in wheat and observed that the terminal spikelet stage is critical to the shortfall of a given cultivar. They found that the first two florets of each spikelet were initiated before terminal spikelet formation and about 97% of them formed grain. Florets formed after terminal spikelet stage rarely formed grain thus creating a shortfall in grain numbers 'vs' floret number which reaches as high as 75% in some cultivars. Similar results were

reported by Peterman et al.(1985), that increased floret numbers prior to terminal spikelet formation would result in lower shortfall.

II. EFFECTS OF ENVIRONMENTAL FACTORS ON SPIKELET INITIATION AND OTHER YIELD COMPONENTS

(A). Rate and Duration of Spikelet Initiation

Rate and duration of spikelet initiation are two important determinates of the number of spikelets per spike. Rawson (1971) concluded that large numbers of spikelets were achieved by long duration and high rate of spikelet initiation which were strongly dependent on environmental factors. He found that at a 15 °C day/ 10 °C night temperature regime, duration of spikelet initiation increased as the photoperiod decreased from 16 to 14, 12, 10 and 8 hours. Similar conclusions have been made by Rahman and Wilson (1977) that the duration of spikelet phase increased as the photoperiod decreased from 24 to 8 hours, but rate was decreased. They reported that responses to varying photoperiod for these parameters were similar in different cultivars but the magnitude of the responses differed. Oosterhuis and Cartwright (1983) examined effects of photoperiod on spike development of semi-dwarf spring wheat. They found that decreasing photoperiod from 16 to 8 hours prolonged duration of spikelet initiation. Rate of spikelet initiation was greater at a high temperature (30 °C) than at a low temperature (10 °C). Low spikelet numbers at high temperature were due to a shorter duration of spikelet initiation

(Friend et al.,1963; Friend,1965). Similar results for various temperatures imposed during spike development were obtained by Rawson (1970), Halse and Weir (1974), and Warrington et al. (1977). Rahman and Wilson (1978) found that a rise in temperature from 10-15 to 23-26 °C increased the rate of spikelet initiation, but that duration decreased.

The effect of light intensity on rate and duration of spikelet initiation has been studied by a few workers, but the reported results are conflicting. An increase in light intensity between 2153 and 2691 lux resulted in an increased rate of spikelet initiation (Friend et al., 1963). Rahman et al. (1977) concluded that at low light intensities, the duration of spikelet initiation was longer, but the number of spikelets was smaller than at higher light intensities, because the rate of spikelet initiation was decreased. Fried (1965), however, reported that plants with fewer spikelets under low light intensities was due to a shorter duration of spikelet development. The inverse relationship between rate and duration of spikelet initiation with highly significant R-square values has been reported by Peterman et al (1985).

(B). Number of Spikelets Per Spike

Rawson (1970), and Cackett and Wall (1971) have shown that the number of kernels per spikelet is relatively consistent over a range of climatic conditions and yield levels, therefore, spikelet number may be the most important determinant of kernel number per spike. One way in which wheat yield can be modified by

climatic adaptation is through the influence of various environmental factors on the number of spikelets per spike as this affects grain number (Pinthus, 1967). Photoperiod, temperature, including vernalization responses, and their interaction with genotype are the most important factors in the control of spikelet number (Friend, 1965; Halse and Weir, 1970; 1974; Rawson, 1970; 1971; Wall and Cartwright, 1974; Rahman and Wilson, 1977; Oosterhuis and Cartwright, 1983).

Reports vary as to the effects of temperature on spikelet numbers per spike. Halse and Weir (1970) failed to obtain any effect on spikelet number by growing plants under two temperatures (12/7 and 18/13 °C). However, using a wider range of temperatures (10/15 -- 26/21 °C), Halse and Weir (1974) found that the spikelet number was lower at the two extremes (10/5 and 26/21 °C) and higher at the three intermediate temperatures (14/9, 18/13 and 22/17 °C). These results suggest the optimum, minimum and maximum temperatures for wheat spike development, recognizing differences between genotypes in temperature response. Wall and Cartwright (1974) shown that the early cultivars and vernalized late cultivars had fewer spikelets at high temperature treatment (25/20 °C), while unvernallized late cultivars tended to have more spikelets, indicating that vernalization shortened duration of spikelet initiation, resulting in fewer spikelets per spike.

The period of growth during which spikelet number is determined is one of the more sensitive growth phases. So, spikelet number may also be varied by light intensity (Friend,1965; Rawson

1970 and Rahman et al, 1977), and by the level of nitrogen nutrition (Single, 1964; Whingwiri and Kemp, 1980). Whingwiri and Kemp (1980) found that spikelet number tends to increase with increasing nitrogen supply and this increase in spikelet number was attributed to an increased rate of spikelet initiation without apparent effect on duration.

(C). Kernel Number Per Spike

There have been several studies on effects of environmental factors on potential kernel number per spike. Fischer and Maurer (1976) found that in spring wheat, kernel number was the yield component most affected by temperature modifications. As mean temperature during jointing (a period of active floret development) was increased from an average of 14.1 to 21.2 °C, kernel number per spikelet declined from 2.0 to 1.6 , significantly reducing yield. The period from double ridge stage through anthesis was shortened by increased temperature, apparently resulting in decreased kernel number per spike (Rawson and Bagga, 1979). Warrington et al. (1977) concluded that when the period of spike development is hastened by high temperature, the growth of the late forming florets is apparently cut short, often resulting in reductions of competent florets and subsequently potential kernel number per spike. Similar results were reported by Fischer and Maurer (1976) that shorter development periods resulted in a reduction in competent florets and subsequent kernels per spike. High positive correlations between leaf area and grain yield has been reported by Warrington et al. (1977)

and Rawson and Bagga (1979).

The number of kernels per spike in wheat can be reduced by reducing number of spikelets per spike and number of kernels per spikelet under water stress. Langer and Ampong (1970) grew single wheat plants in greenhouse pots and imposed water deficits at various growth stages; they found that spikelets per spike were reduced only when plants were stressed near the double ridge stage, when spikelet primordia were forming. They also observed fewer kernels per spike resulted when water stress was imposed from spikelet formation to anthesis. In growth chambers, Fischer (1973) stressed wheat plants for periods of 1 to 4 days at various times 3 weeks either side of heading. He found a moderate stress 5-15 days before heading had a major effect on yield components, apparently impairing floret development, and sharply reducing kernels per spikelet. Wardlaw (1971) and Evans et al (1972) have shown that water deficits just after anthesis caused a reduction in kernels per spike. In their studies, pollination and/or fertilization was apparently impaired, leading to fewer kernels per spikelet. However, Fischer (1973) reported that water stress sensitivity of grain yield per spike was decreased after head emergence. To investigate the effect of water stress on plant development, Oosterhuis and Cartwright (1983) employed six water stress treatments on a semidwarf spring wheat cultivar Devul. The treatments consisted of a well-watered control (T₀), and five periods of soil water stress (T₁ through T₅) each of 1-week duration, imposed at different development stages between planting and spike emergence. They found water stress resulted in

a decrease in kernel number in all treatments, particularly in T1 (late vegetative transition phase) and T5 (boot stage) where kernel number was reduced 27.5% in T1 and 29.9% in T5 compared to the control.

(D). Kernel Weight.

Kernel weight in wheat is strongly influenced by temperature and water availability during the grain filling period. The most commonly observed response to high temperature during kernel filling is a reduction in kernel weight (Spiertz,1974; Fischer and Maurer, 1976; Bagga and Rawson, 1977; Warrington et al, 1977; Kolderup, 1979). Wiegand and Cuellar (1981) estimated that the influence of temperature during kernel development in the field was strong enough to affect grain yield 20 to 25%. They found the kernel filling period was shortened an average of 3.1 days/degree C increase in temperature, with kernel weight decreasing about 2.8 mg per kernel per degree C increase above about 15 C. Spiertz (1977) reported that the initial kernel growth rate was generally stimulated with temperature increasing, but this partial compensation was not great enough to offset the kernel weight reduction associated with shorter grain filling period. Spiertz (1977) applied temperature treatments to wheat plants after anthesis and found that as temperature increased from 10 to 25°C, senescence and respiration rates were promoted, apparently resulting in a shortage of carbohydrate, causing decreased kernel weight. Asana and Williams (1965) reported that the reduction in kernel weight was mainly due to higher grain respiration rate

with increasing temperature, because senescence was hastened only slightly and potential assimilate supply was not greatly reduced comparing 31 °C with 25 °C treatments.

Kernel weight also can be reduced by post anthesis water stress (Davidson and Birch, 1978; Sionit et al., 1980). This can result from either reduced assimilate translocation to developing kernels and / or reduced photosynthetic production. Bidinger et al (1977) used ^{14}C labelling and changes in above ground dry weight to assess the contribution of postanthesis assimilate to grain yield in irrigated and droughted wheat in the field. The relative contribution of pre-anthesis assimilate rose from 13% under irrigation to 27% under drought. But the absolute contribution of pre-anthesis assimilate to kernel weight, as a proportion of total above ground dry weight, was only 8.5 and 11.5 percent in the irrigated and drought treatments, respectively.

Under water deficits, stomatal closure obviously reduces photosynthesis by restricting CO_2 uptake (Johnson et al., 1981). In addition, stomatal closure can cause an increase in leaf temperature which could promote senescence of the remaining photosynthetic tissue (Spirtz, 1977). As the senescence rate increases, both leaf duration and grain yield can be reduced. Fischer and Kohn (1966) reported grain yield was highly correlated with leaf duration ($r = 0.97$). The effect of water stress is not only important during the post-anthesis period but also pre-anthesis. Hsiao (1973) reported that leaf expansion is very sensitive to water deficits, so water stress could lower

potential leaf area indices before anthesis, potentially reducing photosynthesis before and after anthesis.

III. INHERITANCE OF RATE AND DURATION OF SPIKELET INITIATION AND YIELD COMPONENTS

(A). Rate and Duration of Spikelet Initiation

The rate and duration of spikelet initiation, which determine spikelet number (Rahman et al, 1977), are not only influenced by environmental factors (Friend, 1965; Rawson, 1970; Rahman and Wilson, 1978), but also controlled by specific genotype (Halloran, 1974; Rahman et al, 1977; 1978). Peterman et al (1985) observed the rate and duration of spikelet initiation in ten winter wheat cultivars and concluded that overall genetic differences between cultivars for rate and duration of spikelet initiation was significant, which suggested that those two characters are heritable. Halloran (1974) reported that the expression of spikelet number per spike was dependent on genes which differentially influenced the rate of spikelet initiation or which independently extended, or shortened, the time of duration for spikelet initiation. Rahman (1977) reported that spikelet number in a wheat was affected by rate of spikelet initiation which was a heritable trait with partial dominance for high rate. In the following study, Rahman et al (1978) chose two spring wheats 8-23 (P1) and 8-27 (P2) as parents, in which the mean rate of spikelet initiation was significantly greater in P2 than in P1. They found that the means of the F1, F2 and backcross F1

populations were intermediate between the parental means but nearer to the higher parental mean, indicating partial dominance gene(s). The conclusion drawn from the evidence was that the difference in spikelet number was due to the action of a major gene with possible modifiers which acts by controlling the rate of spikelet initiation. They proposed that it should be possible to develop cultivars with high spikelet number per spike by increasing the rate of spikelet initiation.

(B). Spikelet Number Per Spike

There are numerous publications dealing with the inheritance of spikelets per spike in wheat, but the results reported are often conflicting. Pugsley (1965) studied the inheritance of photoperiod response in spring wheat and observed a close association between earliness and low spikelet number which was thought to be governed by a single gene. However, he concluded from observations on spikelet number in other crosses that additional genes might be involved. Chapman and McNeal (1971) concluded from a cross of Henry/Lemhi 53 that spikelet number was under quantitative genetic control and exhibited incomplete dominance. Ketata et al.(1976a) conducted two experiments at two locations in which the same 10 cultivars were crossed with 2 testers in both experiments except tester lines differed between experiments. They found additive gene action was predominant in both experiments, suggesting that improvement of this trait can be achieved through standard selection protocol. Similar results were reported by Ketata (1976b). Rahman (1977) studied the

genetic control of spikelet number of hexaploid wheat in controlled environmental cabinets and found that the high spikelet number appeared to be partially dominant, and the estimates of genetic effects suggested both additive and dominance effects contributed significantly to genetic variation. Gupta and Ahmad (1982) have shown that the high genetic gain (10.44 and 9.08%) and high heritability (46.91 and 40.44%) were observed for spikelet number per spike in both F1 and F2 generations. This was attributed to a greater contribution of additive genetic variation and a marginal role of non-additive variation in controlling the inheritance of this character.

Halloran (1974) estimated the number of genes controlling spikelet number by using two cultivars Chinese Spring and Hope, and the 21 chromosome substitution lines of Hope in Chinese Spring. He reported that the minimal estimate of the number of genes determining spikelet number is six; Four, located on chromosomes 1B, 2D, 3D and 5D respectively, which increased spikelet number, and two, located at chromosomes 2B and 6B which reduced spikelet number.

(C). Kernel Number Per Spikelet

Heritability estimates of yield and yield components indicate that certain components of grain yield in wheat are more heritable than yield per-se (Ketata et al, 1976 and Johnson et al 1966). Ketata et al. (1976b) reported that additive and dominance effects were the major contributors to inheritance of kernels per spikelet, and heritability estimates for kernels per spikelet

(0.28 \pm 0.18) was higher than that for total grain yield (0.16 \pm 0.19). Relatively high heritability estimates for kernels per spikelet of wheat in both the broad and narrow senses were also reported by Sayed (1978). Intermediate broad and low narrow sense heritability estimates for kernel number per spikelet were reported by Ibrahim et al.(1983), suggesting large environmental effects.

Kernels per spikelet can be affected by fertility which means the union of a male and a female gametes to form a zygote. Halloran (1974) found the genetic control for the fertility between two cultivars, Chinese Spring and Hope, appeared to relatively simple. The magnitude of the influence of chromosomes 5A, 7B and 2D, which increased fertility of Chinese Spring, were of minor effect, while chromosome 7A and 6B, which reduced fertility of Chinese Spring, was a major effect. He concluded that the action of both chromosome 7A and 6B which substantially reduced fertility in a Chinese Spring background was quite possibly due to the action of discrete fertility-controlling genes. Sears (1954) previously had made similar observations about the influence of these two chromosomes on fertility.

Considering the heritable nature of the kernels per spikelet, a closer examination and knowledge of the specific genetic control of this character may provide further avenues for yield improvement by increasing kernel number per spikelet or decreasing shortfall.

IV. INTERRELATIONSHIP AMONG YIELD AND YIELD COMPONENTS

It is well known that the inheritance of final grain yield in wheat is very complex being determined by both 1) interaction between genotype and environmental factors, and 2) interaction among yield components within a given genotype. Therefore, the relationship between grain yield and yield components and interactions among yield components have been subjected to intensive study in the past years. Gupta and Ahmad (1982) reported that high heritability values were found for spikelet number per spike and 100-kernel weight in both F₁ and F₂ generations and these two traits are highly correlated to grain yield per plant in both generations. Low heritability estimates were reported for spikelet number and kernel number per spike by Ketata et al (1976b). Conflicting results reported in previous studies may be due to the differences in genetic background and combining ability of parents used. Rawson (1970) reported that a close correlation between spikelet number and grain yield was found for several cultivars, but not for others.

In the study of heterosis and combining ability for yield components of wheat, Bhatt (1971) has shown the degree of expression, in descending order, was kernel weight, number of kernels per spike, grain yield per plant and number of spikelets per spike. For a given cross, only some of the yield components are important for expression of yield heterosis. This is because each component competes for the same total amount of metabolic

substrate produced by the plant, and conditions which favor the development of one component could have an adverse effect on other components (Kronsted and Foote, 1964; Bhatt, 1971). This agrees with the observation that the parent which is a good combiner for grain yield is also a good combiner for at least one of the yield components. Combining ability for grain yield seems to be influenced by the combining ability for its components (Singh and Gupta, 1969). Therefore, compromises for the desired levels of each component may have to be made in order to obtain maximum grain yield. Ahmad et al (1979) and Gill et al (1972) reported that there was a close relationship between the best specific combiners and hybrids exhibiting the best heterotic response over the best parent for spikelets per spike, kernel per spike, kernel weight and grain yield per spike. The specific combining ability (SCA) effects of F₁'s were related to the general combining ability (GCA) effects of their parents. Superior combinations involved at least one parent with high GCA (Singh and Gupta, 1969; Gyawali et al, 1968). By comparing the ratio between variances of GCA and SCA, Bhatt (1971) found that the variances of GCA were larger than those of SCA for yield and yield components, which suggested that the major portion of the genetic variance in the base population was additive in nature. Similar results have been found by Knott (1965), Brown et al (1966) and Gyawali et al (1968). The preponderance of additive genetic variance for these traits indicates that the parents of a given combination can be selected on the basis of their GCA.

SUMMARY

Final grain yield per spike in wheat is determined by the contribution of each yield component, which is affected by both genetic and environmental factors. Some reports indicate that spikelet number is related to the rate of spikelet initiation and duration from double ridge stage to terminal spikelet formation, which are influenced by temperature, photoperiod and light intensity. Other studies show that different wheat cultivars often show different degrees of response to imposed environmental conditions, which indicates that genetic variability exists for improving both rate and duration of spikelet initiation to maximize spikelets per spike and kernels per spikelet.

Kernels per spikelet are often reduced by 1) reducing competent florets per spikelet as high temperature shortens floret developmental period, and 2) impairing fertilization processes when heat and water stress occur during or just after anthesis. However, differences in shortfall among cultivars under similar environmental conditions indicate that it is possible to select low shortfall cultivars by plant breeding.

Because the inheritance of total grain yield is more complex than that of individual yield components and grain yield is correlated to yield components, visual selection for specific yield components is more efficient than selection on total grain yield per-se. In addition, results of combining ability analysis show that the contribution of a given yield component to final

grain yield varies from one genotype to another and high heterosis hybrids often are made from parents with high general combining ability for at least one or two of the yield components. Therefore, general combining ability could be used as a parental selection criterion in a wheat breeding program.

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CHAPTER I

THE RATE AND DURATION OF SPIKELET INITIATION AND THEIR RELATIONSHIPS TO YIELD COMPONENTS IN WHEAT

ABSTRACT

Inheritance of rate and duration of spikelet initiation and their relationships to yield components in wheat (*Triticum aestivum* L.) were studied in two experiments, involving both field and growth chambers. Rate and duration were estimated by dissecting the main culm of sampled plants at double ridge and terminal spikelet stages. At maturity, kernels/spike and kernel weight/spike were measured.

Rate and duration of spikelet initiation were measured in days (DU) and accumulated thermal units (TU). High positive correlations between DU and TU, and between rate spikelets/day and rate spikelets/degree suggested that either of these methods can be used to evaluate spikelet initiation characters.

Significant difference in rate and duration of spikelet initiation among parents and F₁'s indicated that these two traits are heritable. Results indicated that high rate was controlled by dominant genes and the inheritance of duration of spikelet initiation is additive.

Spikelets/spike was correlated with kernels/spike and kernel weight/spike, so that improvement in grain yield can be achieved by increasing spikelets/spike. Variance analysis of combining ability showed that the major portion of genetic variation for spikelets/spike was due to additive gene effects, suggesting that selection for spikelets/spike would be effective.

INTRODUCTION

The number of spikelets per spike in wheat (*Tricum aestivum* L.) is largely determined by the rate and duration of spikelet initiation from the double ridge (DR) stage through terminal spikelet (TS) formation (Halloran, 1974, Rahman and Wilson, 1977, Rahman et al., 1978 and Peterman et al., 1985). The duration of spikelet initiation is the period of time, in days, between DR and TS, and the rate is the ratio between total spikelets initiated and duration, expressed as spikelets/day (Peterman et al., 1985). Previous studies show that both rate and duration are not only heritable traits, but also are influenced by environmental factors, such as temperature and day length.

Reports vary as to the effects of temperature on changes in the spike development and subsequent spikelet number per spike. Warrington et al. (1977) found a small effect on spikelet number per spike when plants were grown at three temperatures (25/20, 20/15, 15/10°C). Using a wider temperature range (10/5-26/21°C), Halse and Weir (1974) found that spikelet number was lower at the two extremes (10/5 and 26/21 °C) and higher at the intermediate temperatures (14/9, 18/13 and 22/17 °C). High temperatures which reduced spikelet number were attributed to shortening the duration of spikelet initiation, and low temperature decreased the rate of spikelet initiation. Rahman and Wilson (1978) reported that the rate of spikelet initiation increased, but duration decreased as temperature increased from 16/9 to 23/16°C,

resulting in fewer spikelets per spike.

The variation in response to temperature treatments among cultivars indicates that the sensitivity to temperature which in turn affects spike development may be controlled by genetic factors (Wall and Cartwright, 1974). Halloran (1974) postulated that the expression of spikelet number per spike was dependent on genes which differentially influenced the rate of spikelet initiation or which somewhat independently extended, or shortened, the time of duration for spikelet initiation. Rahman et al. (1978) concluded that spikelet number per spike was under simple genetic control with dominance for high spikelet number, which suggested that the gene determining spikelet number does so by determining the rate of spikelet initiation.

From the view point of wheat improvement, combining ability for economic traits may be regarded as an important criterion to choose parents for crossing (Kronsted and Foote, 1964, Brown et al., 1966, Verma and Luthra, 1983). Singh and Gupta (1969) found that high heterosis at least involved one parent with high general combining ability (GCA) for grain yield, and the parents, which were high combiners for grain yield, were also high combiners for at least two of the yield components. Therefore, the understanding of fundamental genetic morphogenesis, its relation to yield and yield components, and combining ability of economic traits of cultivars should facilitate indentifying parents which might yield superior F₁ hybrids, or breeding populations.

The objectives of this study are to (1) determine difference

in rate and duration of spikelet initiation between genotypes, (2) describe the effects of rate and duration on yield components, and (3) evaluate parents used through combining ability analysis.

MATERIALS AND METHODS

The parents and F1's of a three-parent diallel cross, excluding reciprocals, were evaluated in 1983 and 1984. Parents were selected based upon their reported genetic differences in rate and duration; 'Pawnee', long duration and slow rate, 'Larned', short duration and fast rate, and 'Newton', intermediate for both traits (Peterman et al, 1985). Three experiments were conducted, two in a growth chamber (GC83 and GC84) and one field experiment grown at Manhattan, KS., 1984.

For each growth chamber study, sixty seeds of each F1 and parent were vernalized at 5°C for 8 weeks and then transplanted to the growth chamber. The daylength was extended from 12 to 18 hours by increasing daylength one hour every three days by incandescent and fluorescent lights (5,000 lux). Temperature was maintained at 15/10 °C, day/night. A completely randomized design with 16 pots of each genotype and two plants per 9.5 cm² pot was utilized. Plants were grown in a 1:1:1 mixture of sand, clay loam and peat moss, and were supplied with a nutrient solution once a month and watered as needed.

Two plants of each genotype were sampled three times weekly and the main culm of the plants dissected under a dissecting microscope to determine the stage of growth and estimate the date of double ridge (DR) stage followed by terminal spikelet (TS) formation. Additionally, five plants of each genotype were sampled at DR and TS respectively to generate mean values for

both growth stages. The main culm of each sampled plant was dissected under a light microscope and the number of spikelets per spike was counted at TS. Samples not dissected daily were preserved in a 6:3:1 v/v solution of ethanol, glacial acetic acid, and chloroform (Peterman et al, 1985). All procedures to determine developmental stage followed the Cereal Development Guide (Kirby and Appleyard, 1981).

At harvest, five plants of each genotype were randomly sampled and kernels per spike and kernel weight per spike were measured.

Parents and their Fl's were also planted at the North Agronomy Farm, Manhattan, Kansas in a randomized complete block with four replications. Each plot was 1.0 M long, containing 3 rows 30 cm apart, with 4 cm between plants. Procedures for sampling and dissecting were identical as used in the growth chamber studies. At maturity, five individual plants of each genotype were harvested from each replication and number of kernels and kernel weight of the main spike were recorded.

Air temperature was measured 6 km from the field plots at the standard weather shelter and archived at the Weather Data Library, Cardwell Hall on the Kansas State University campus. The maximum and minimum positive daily temperatures were recorded for the period of time between DR and TS formation. Accumulated thermal units (TU) were calculated as:

$$TU (^{\circ}C) = \left(\frac{\text{Max.} - \text{Min.}}{2} - 0^{\circ}C \right)$$

in which $0^{\circ}C$ is usually considered the base temperature for

wheat (Baker, 1982).

The duration and rate of spikelet initiation was computed for each experiment;

Duration = days between DR and TS

$$\text{Rate} = \frac{\text{Total spikelets initiated}}{\text{Duration (days)}}$$

The analysis of the data for combining ability and estimates of combining ability effects followed the technique of Griffing (1956) for Model I, Method 2.

RESULTS

Rate and Duration of Spikelet Initiation

Mean rate (spikelets/day) and duration (days) of spikelet initiation for parents and their F1's for both growth chamber and field experiments is shown in Table 1. Bartlett's Homogeneity of variance test was not significant which allowed pooling of the G83 and G84 data.

Larned had the highest rate, and the shortest duration, Pawnee the slowest rate and longest duration and Newton was intermediate for duration and was similar to Pawnee in rate. These agree with rankings made by Peterman et al (1985). The range in duration was comparable for field and growth chamber studies. Rates of spikelet initiation tended to be faster in the growth chamber experiments. Although changes in relative rank for both rate and duration did occur between studies, they were small and only included changes among intermediate types. From these data, it appears that genotypes can be accurately assessed for their rate and duration of spikelet initiation by utilizing growth chambers.

The length of duration for F1's approached the mid-parent value for Newton/Pawnee and Newton/Larned, and equaled the mid-parent value for Pawnee/Larned. Rate of spikelet initiation in every case, except one in the field study, approached the high parent value. The Pawnee/Larned cross grown in the field had rate

value similar to Pawnee. This exception was probably caused by chlorosis and poor vigor observed in this cross.

Accumulated thermal units (TU) for rate and duration of spikelet initiation for both field and growth chamber experiments can be found in Table 2. Ranking for both parents and F1's for rate and duration is identical if one utilizes days (table 1) or accumulated heat units (Table 2). Correlations between TU and duration was 0.92 for field data and 1.00 for growth chamber data, and correlation between rate spikelets/day and rate spikelets/ $^{\circ}\text{C}$ day was 0.67 for field and 0.70 for growth chamber experiments, all highly significant (Table 3). These results suggested that predicting either rate or duration by utilizing accumulated heat units appears feasible. The correlations of spikelets per spike with duration and with accumulated thermal units (TU) are shown in Figure 1 and Figure 2 respectively. A general trend indicates that the number of spikelets per spike increased as either DU or TU increased regardless of the genetic background between cultivars. For a given genotype, the responses in spikelets per spike to both TU and DU were identical, even though the magnitude of response was different between field and growth chamber experiments. This may allow an early season estimate of both spikelets/spike and kernels/spikelet provided individual genotype responses are known.

Interrelationships Among Duration, Rate and Yield Components

Significant differences among parents and F1's for spikelets/

spike, kernels/spike and kernel weight/spike were observed (Table 4). In general, kernels/spike and kernel weight per spike increased as the spikelets per spike increased with exception of Pawnee. Pawnee had high spikelet number per spike but low kernel number and kernel weight per spike.

Correlation coefficients among rate and duration of spikelet initiation, spikelets/spike, kernels/spike and kernel weight/spike are found in Table 5. Number of spikelets per spike were positively correlated to the duration, kernels per spike and kernel weight per spike, and kernels per spike was positively correlated to rate of spikelet initiation, which suggested that kernel number per spike can be increased by increasing both rate and duration of spikelet initiation. However, negative correlations between rate and duration were observed in both field and growth chamber experiments (Table 5), which indicated that it may be difficult to improve these two traits simultaneously.

Combining Ability

The variance analysis of combining ability revealed that variance due to general combining ability (GCA) was highly significant for all characters. Specific combining ability (SCA) was highly significant for all traits except duration (0.05) and spikelets/spike (NS), Table 6. The ratio of GCA/SCA variances, an indicator of gene action (Verma and Luthra, 1983) revealed that the variances of GCA were larger than those of SCA for duration of spikelet initiation, spikelets/spike and kernels/spike, and

smaller for rate of spikelet initiation and kernel weight/spike. Estimates of GCA effects of the parents are presented in Table 7. Newton was a better combiner for all five traits while Larned was poor with negative GCA effects except for rate of spikelet initiation. Pawnee combined well for high spikelet number and long duration but was poor for rate of spikelet initiation, kernels/spike and kernel weight/spike.

DISCUSSION

Differences in rate and duration of spikelet initiation among parents and Fls (Table 1) indicated that these two traits are heritable. Rahman and Wilson (1977a) reported that the rate and duration of spikelet initiation were independent characters, presumably under separate genetic control. Similar conclusions were made by Halloran and Pennell (1982) and Peterman et al (1985). Data presented here suggests that duration of spikelet initiation for Fl's was close to mid-parent values which suggested that duration is controlled by additive genes. Rate of spikelet initiation of each Fl was equal or close to their high parents, indicating that the inheritance of rate of spikelet initiation is dominant.

Using accumulated thermal units ($^{\circ}\text{C}$) to measure wheat spikelet initiation instead of rate and duration in days could a more consistent measure because it excludes some of the variation due to temperature fluctuation (Peterman et al. 1985). High correlation of DU to TU and that of rate spikelets/day to rate spikelets/ $^{\circ}\text{C}$ day (Table 3) suggested that using either thermal units in degree C or time period in days to evaluate rate and duration of spikelet initiation can give reliable results. Positive correlation between DU and TU was also reported by Peterman et al (1985).

Kernels per spike by definition is confounded by measurements of spikelets per spike and kernels per spikelet. Rawson (1970)

and Cackett and Wall (1971) have reported that number of kernels per spikelet is relatively constant over a range of climatic conditions and yield levels. Our data showed significant correlation between spikelets/spike and kernels/spike (Table 5), which confirms the hypothesis proposed by Wall and Cartwright (1974) that the number of spikelets may be an important determinant of kernel number per spike.

Reports on how spikelet number per spike are affected by rate and duration of spikelet initiation are conflicting. Rahman et al. (1977a) found that the variation in spikelet number was closely associated with duration of spikelet initiation, but they reported in 1978 that spikelets per spike was determined by the rate. Results from our experiments (Table 5) indicate that both rate and duration of spikelet initiation were correlated to spikelets per spike. This finding agrees with the conclusion of Rahman and Wilson (1977b) and Rahman et al (1977b) that the main factors determining spikelet number are rate and duration of spikelet initiation.

Results from combining ability analysis showed that the variances of GCA were larger than those of SCA for duration of spikelet initiation, spikelets/spike and kernels/spike, which suggests that the major portion of the genetic variance in these three traits was additive in nature. The preponderance of additive genetic variance for these traits indicated that the parents involved in these crosses can be selected on the basis of their GCA effects. The findings that performance of F₁'s for these three traits were equal or close to their mid-parent

values confirmed that additive genetic variance was the most predominant portion of the genetic variance for the traits considered. Similar conclusions have been reached by measuring spikelets/spike and kernels/spike (Singh and Gupta, 1969; Bhatt, 1971; Gill et al, 1972; Ketata et al, 1976b; and Verma and Luthra, 1983). Both GCA and SCA variances were highly significant for rate of spikelet initiation and kernel weight per spike. The ratio of GCA/SCA variances indicated that the variances for GCA were smaller than those of SCA for these two traits, which indicated that a large part of the total genetic variation observed for rate of spikelet initiation and kernel weight per spike was associated with genes which were dominant in their effects.

The apparent trend over the past 50 years of crop improvement in the Great Plains has been to shorten duration and increase rate (Peterman et al., 1985). Present semidwarf cultivars deviate from this pattern by maintaining a fast rate and longer duration resulting in greater numbers of spikelets/spike. This progress within pure lines should continue given the additive genetic nature of duration. Hybrid wheat should be able to utilize the dominant gene action governing rate to further increase kernels/spikelet. Strategies to optimize heterosis would be to select lines with long durations and intermediate rates hybridized with lines with high rates.

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TABLES

Table 1. The mean duration (days) and rate (spikelets/day) of spikelet initiation for parents and Fl's from growth chambers (GC) and field experiments (FE), conducted at Manhattan, KS, 1984.

Genotype	Duration (days)		Rate (spikelets/day)	
	FE	GC	FE	GC
Newton	17.75	17.10	0.83	0.96
Pawnee	18.75	17.20	0.82	0.92
Larned	14.85	13.00	0.86	1.07
Newton/Pawnee	17.95	16.50	0.83	0.98
Newton/Larned	15.95	14.50	0.85	1.05
Pawnee/Larned	16.80	15.70	0.82	1.04
LSD _{0.05}	0.45	0.76	0.02	0.04

Table 2. Accumulated thermal units ($^{\circ}$ C) from double ridge (DR) to terminal spikelet (TS) and the rate of spikelet formation (spikelets/degree day) for both field (FE) and growth chamber (GC) experiments.

Genotype	Accumulated thermal units (DR to TS)			Rate (spikelets/degree day)		
	FE	GC	1983*	FE	GC	1983*
Newton	221.1	213.8	228	0.088	0.098	0.082
Pawnee	233.6	215.0	242	0.085	0.095	0.076
Larned	181.6	162.5	178	0.090	0.109	0.094
Newton/Pawnee	226.4	206.3		0.086	0.098	
Newton/Larned	193.2	181.3		0.092	0.109	
Pawnee/Larned	213.6	196.3		0.084	0.099	
LSD _{0.05}	5.9	9.5	31.9	0.003	0.006	0.015

* data from Peterman et al, 1985.

Table 3. Correlation coefficients among duration (DU), accumulated thermal units (TU), rate spikelets/day and rate spikelets/degree day for both field (FE) and growth chamber (GC) experiments.

		DU (days)	TU (°C)	Rate (spikelets/°C day)
Rate (spikelets/day)	FE	-0.52**	-0.46**	0.67**
	GC	-0.37**	-0.37**	0.70**
DU (days)	FE		0.92**	-0.47**
	GC		1.00**	-0.61**
TU (°C)	FE			-0.68**
	GC			-0.61**

** means significant at 1% level.

Table 4. Mean spikelets/spike, kernels/spike and kernel weight/spike (g) for parents and Fl's from growth chamber (GC) and field experiments (FE).

Population	Spikelets/spike		Kernels/spike		Kernel Wt./spike	
	FE	GC	FE	GC	FE	GC
Newton	19.35	21.00	63.70	51.79	1.47	1.81
Pawnee	19.75	20.04	45.77	39.58	1.37	1.25
Larned	16.30	18.00	49.09	45.78	1.44	1.58
Newton/Pawnee	19.40	20.50	51.61	47.97	1.56	1.74
Newton/Larned	17.70	19.70	56.50	49.96	1.56	1.78
Pawnee/Larned	17.95	19.40	41.88	41.08	1.14	1.45
LSD _{0.05}	0.40	0.58	5.68	3.73	0.19	0.11

Table 5. Correlation coefficients among rate (spikelets/day), duration (days DR to TS), SP/S (spikelets/spike), KN/S (Kernel number/spike) and KW/S (kernel weight/spike) for growth chamber (GC) and field experiments (FE).

		Rate	Duration	KN/S	KW/S
SP/S	FE	-0.062	0.809**	0.212	0.004
	GC	0.269*	0.610**	0.363**	0.455**
Rate	FE		-0.515**	0.266**	0.088
	GC		-0.365**	0.235	0.428**
Duration	FE			-0.075	-0.002
	GC			0.010	-0.075
KN/S	FE				0.653**
	GC				0.903**

*, ** mean significant at 5% and 1% level, respectively.

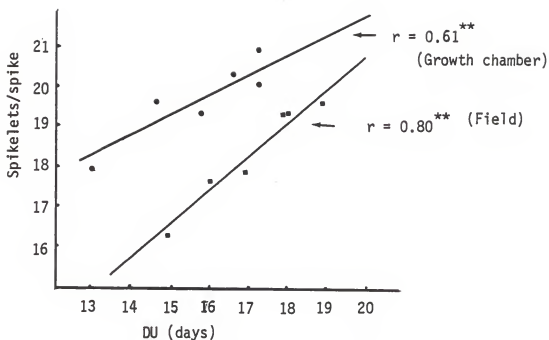


Figure 1. Correlation between spikelets/spike and duration for both field and growth chamber experiments.

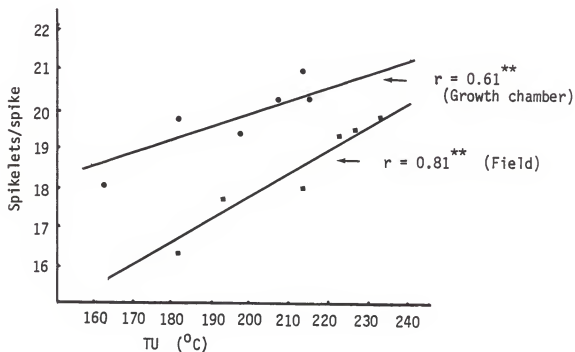


Figure 2. Correlation between spikelets/spike and accumulated thermal units (TU, °C) for both field and growth chamber experiments.

Table 6. Mean squares for combining ability analysis based on model I for rate (spikelets/day), duration (DR to TS), spikelets/spike (SP/S), kernels/spike (KN/S) and kernel weight/spike (KW/S) from field experiment.

Source	DF	Mean Squares				
		Rate	Duration	SP/S	KN/S	KW/S
G C A	2	0.0006**	5.0820**	4.4021**	280.06**	0.0219**
S C A	3	0.0023**	0.0427*	0.0076	25.13**	0.0262**
Error	96	0.0001	0.0146	0.0219	0.82	0.0011
GCA/SCA		0.26	119.01	579.22	11.44	0.84

*, ** mean significant at 5% and 1% level, respectively.

Table 7. General combining ability effects for rate (spikelets/day), duration (DR TO TS), spikelets/spike (SP/S), kernels/spike (KN/S) and kernel weight/spike (KW/S) of a three-parent winter wheat diallel cross.

Trait	Newton	Pawnee	Larned	S.E. (gi-gj)
Rate	0.0021	-0.0122	0.0101	0.0005
Duration	0.273	0.843	-1.116	0.1167
SP/S	0.433	0.643	-1.076	0.175
KN/S	5.964	-4.134	-1.830	0.3263
KW/S	0.0750	-0.0504	-0.0246	0.0084

CHAPTER II

FLORET DEVELOPMENT AND ITS RELATIONSHIP TO KERNELS PER SPIKE IN WHEAT

ABSTRACT

Two winter wheat (*Triticum aestivum* L.) cultivars , 'Newton' and 'Stephens' and their hybrid were used to study shortfall and to examine the influence of rate and duration of spikelet initiation on the shortfall, kernels per spike and kernel weight.

Two identical experiments were conducted, both under greenhouse conditions. Rate and duration of spikelet initiation (in days) and florets per spike initiated at terminal spikelet (TS) formation were measured. At maturity total number of florets initiated, kernels per spike and single kernel weight were measured.

Shortfall ranged from 64.51% for Stephens, 66.85% for Newton and 66.21% for their hybrid. Florets formed after TS did not form grain emphasizing the importance of this stage in regard to kernel formation. Rate and duration were not correlated with shortfall. Both traits influence floret number prior to TS, but subsequent floret initiation after TS varied with each genotype.

Potential fertile florets and kernels per spike can be increased by increasing the rate of spikelet initiation or the duration of spikelet initiation prior to TS. Stephens maintains a high kernel number per spike by having a long duration. Newton maintains high kernel number by having intermediate values for both rate and duration. Kernel per spike in the hybrid was not significantly different from either parent despite having a fast rate and long duration combined.

Shortfall as a measurement is helpful in understanding grain formation in wheat. As a selectable trait, kernels per spike will still be more valuable to the plant breeder.

INTRODUCTION

Kernels per spike represent one of the three yield components of wheat, and the actual number of kernels formed per spike is a heritable trait and can be controlled by plant breeders (Ketata et al, 1976b and Ibrahim et al, 1983). Kirby (1974) reported that a maximum of nine florets per spikelet can be formed in all spikelets but some of the late-formed florets died, leaving two to four potentially fertile florets. Whingwiri and Stern (1982) reported that florets initiated before terminal spikelet formation developed into grain but the florets initiated after terminal spikelet formation did not, which suggested that terminal spikelet stage may be a critical phase in regulating maximum number of kernels per spike. They described this phenomena as shortfall which denotes the proportion of florets which fail to develop into grain. The number of kernels per spike is strongly influenced by environmental factors which affect either or both rate and duration of spikelet initiation (Bremner and Davidson, 1978, Ibrahim et al., 1983).

Whingwiri and Stern (1982) reported that the number of kernels per spikelet was increased by adding nitrogen which hastened the initiation of florets but did not affect the number of florets initiated. This indicated that the rate of floret initiation could be an important factor affecting floret survival, which directly determines kernels per spike. Water availability also is important for floret survival. Oosterhuis and Cartwright (1983)

applied water stress at five different development stages between planting and spike emergence. They found that both the double ridge and boot stages were sensitive to water stress which adversely affected floret survival. Water stress at double ridge resulted in a shortened duration of spikelet initiation, which caused fewer florets initiated before terminal spikelet formation. At boot stage, water stress caused death of florets, resulting in fewer kernels per spike. The magnitude of response of floret survival to environmental factors varies between cultivars, which suggests that genetic difference in floret survival exists among wheat cultivars. Peterman et al. (1985) investigated the floret initiation and shortfall of cultivars 'Newton' and 'Scout', they found that the shortfall of Newton was lower than that of Scout which indicated that genetic variation in shortfall exists between these two varieties. Previous studies dealing with the inheritance of kernels per spike have suggested that epistasis (Ibrahim et al., 1983) and as well as dominance and additive genetic variation (Ketata et al., 1976a) influence final kernel number per spike.

This study was initiated to study the relationship between shortfall and final number of kernels per spike. Furthermore it was of interest to describe the relationship between rate, duration of spikelet initiation and shortfall as they influence kernels per spike in divergent parents and their F₁.

MATERIALS AND METHODS

Two parents 'Newton' 'Stephens' and their F1 were utilized. Two identical experiments were conducted in the green house in the spring of 1983 and 1984. A randomize complete block with three replications were used. Parents and their F1 were grown in one gallon pots with 4 plants/pot. Extra plants were grown to determine the approximate developmental stages of double ridge (DR) and terminal spikelet (TS) formation, prior to sampling within the experiment. Three plants of each genotype were sampled from each replication at DR and TS and the main culm was dissected under a dissecting microscope to estimate the rate and duration of spikelet initiation. The estimated number of spikelets per spike and the number of florets per spike were recorded at TS.

Three plants were harvested from each replication at maturity and kernels per spike and single kernel weight were measured from the main spike.

The duration and rate of spikelet initiation and shortfall were computed as follows:

Duration = days between DR and TS

Rate =
$$\frac{\text{spikelets initiated}}{\text{duration}}$$

Shortfall % =
$$\left(1 - \frac{\text{kernels per spike}}{\text{florets per spike formed}}\right) \times 100$$

RESULTS AND DISCUSSION

The means for rate and duration of spikelet initiation, spikelets per spike, florets per spike, shortfall and single kernel weight for each parent and their hybrid are found in Table 1. Newton and Stephens are varieties recognized for their large spikes. In this study both genotypes and their hybrid produced equivalent numbers of spikelets per spike. Significant differences were observed for rate and duration, florets and kernels per spike, kernel weight and shortfall. Newton maintained a faster rate of spikelet initiation. The rate of the hybrid was similar to Newton indicating that dominant or partially dominant gene action controls rate. This was confirmed in experiment 1. Stephens has a significantly longer duration than Newton and the hybrid was intermediate, but greater than the theoretical mid-parent value. In the previous study, duration appears to be controlled by additive genes (experiment 1). In this experiment the duration of the hybrid indicates the involvement of dominant gene action as well.

Shortfall is a measurement describing the actual number of kernels developed per spikelet versus the potential number that could be formed. Genotypes with greater numbers of seeds/spikelet have lower shortfall values. Stephens has a low shortfall and produces more seeds per spike than Newton. The hybrid's shortfall was similar to Newton. Shortfall as defined by Whingwiri and Stern (1982) will be most affected by rate and duration of

spikelet initiation. Optimum rates and durations should result in greater numbers of florets developed prior to TS which would result in lower shortfalls. In this experiment the hybrid had a fast rate, equivalent to Newton and a intermediate duration, which should have increased kernels per spike and lowered shortfall. The shortfall value was similar to Newton and significantly greater than Stephens. Additional genetic or environmental factors appear to influence the expression of shortfall besides rate and duration.

Rate and duration were both correlated with spikelets/spike in this study. Duration, however, was much more influential on the final number of kernels per spike, and kernel weight. In the field studies conducted in experiment #1, rate had a more significant impact on final kernel number. Under stress conditions, rate may contribute more significantly to floret formation than duration. The breeding of Great Plains wheats has resulted in shorter duration and faster rate (Peterman et al, 1985). Stephens, a high yielding soft white winter wheat cultivar from Oregon, however maintains a long duration to obtain both high spikelet and kernel numbers. Favorable growing conditions, especially during the spikelet initiation stages may enhance selection of genotypes with longer durations. Under Great Plains environments, characterized by frequent heat and drought stresses, a fast rate has resulted in lower shortfall values, and increased kernels per spike.

Kernel weight was negatively correlated with rate and positively correlated with duration. Rapid rate may allow for

more florets per spike prior to TS, however, these florets would be smaller in size (ie. lemma and palea). Grafius (1976) has demonstrated that the size of the floret is one of the primary limiting factors for kernel size in barley. Longer duration should allow a proportionately longer growth period for establishment of a larger lemma and palea meristem resulting in larger florets and subsequently larger kernels.

Final number of kernels per spike and their kernel weight are two of the most influential yield components in wheat. Plant breeders are systematically improving both traits by visual selection. Previous studies have indicated both traits to be intermediate in heritability and influenced by both additive and dominant gene action. Rate and duration of spikelet initiation directly influence kernels per spike and are correlated with kernel weight. Rate is at least partially controlled by dominant gene action and duration behaves in an additive manner. Strong selection for kernels per spike may result in increases in rate or duration or both. Under stress environments, faster rate would appear to influence final kernel number. In optimum environments longer durations may be more desirable than faster rates. Simultaneous, divergent selection for kernels/spike should develop different gene pools for increased number of kernels per spike.

Shortfall as a measurement for selection is difficult to measure and primarily describes kernels per spike. Decreasing shortfall values, ultimately changes either or both rate and duration and is manifested in increased kernels per spike. The

interactions of these traits, however, should aid the plant breeder in understanding the effects of visual plant selection for kernels per spike and kernel weight.

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TABLES

Table 1. The rate (spikelets/day), duration (days) of spikelet initiation, spikelets per spike (SP/S), florets per spike (FL/S), Kernels per spike (KN/S), shortfall (SF) and single kernel weight (Wt/K) of two winter wheats and their Fl grown in the greenhouse.

Population	Rate	duration	SP/S	FL/S	KN/S	SF(%)	Wt/K(mg)
Newton (NWT)	0.88a*	18.06b	20.9a	66.6c	52.9c	66.9a	36.2b
Stephens (SPN)	0.83b	19.61a	21.3a	69.6a	57.3a	64.5b	41.0ab
Fl 'NWT/SPN'	0.86a	19.28ab	21.3a	68.5b	54.6b	66.2a	42.3a

*, within columns followed by the same letter are not significantly difference at the 5% level according to Duncan's Multiple Range Test.

Table 2. The correlation coefficients among the rate (spikelets/day), duration (days) of spikelet initiation, spikelets per spike (SP/S), florets per spike (FL/S), kernels per spike (KN/S), shortfall (SF) and single kernel weight (Wt/K).

Traits	Duration	SP/S	FL/S	KN/S	SF(%)	Wt/K(mg)
Rate	-0.28*	0.52**	0.10	0.09	-0.13	-0.39**
Duration		0.59**	0.43**	0.38**	-0.13	0.29*
SP/S			0.52**	0.51**	-0.33**	-0.10
FL/S				0.80**	0.23	0.18
KN/S					-0.55**	0.03
SF(%)						0.19

*, ** mean significant at 5% and 1% levels, respectively.

RATE AND DURATION OF SPIKELET INITIATION, THEIR
INHERITANCE AND RELATIONSHIPS TO YIELD COMPONENTS
IN WHEAT

by

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ABSTRACT

Yield potential is determined early in the life cycle of wheat cultivars. This is particularly true for the period of spikelet initiation where the number of spikelets and potential florets are determined. To determine the relationship between spikelet initiation and final grain yield per spike, the rate and duration of spikelet initiation and their inheritance were studied using three cultivars, Newton, Pawnee, Larned and their F1's in experiment 1 and 2.

The rate and duration of spikelet initiation was estimated by both time period in days and accumulated thermal units (C). Significant difference in rate and duration of spikelet initiation among parents and F1's indicated that these two traits are heritable. Results indicated that rate of spikelet initiation was dominant and duration was additive gene action. Correlation coefficients for spikelets/spike with rate and duration of spikelet initiation indicated that the number of spikelets/spike can be increased by improving either rate or duration of spikelet initiation.

Genetic variation for spikelets/spike was due to additive gene effects, which suggested that selection for high spikelets/spike should be effective. High positive correlations between spikelets/spike, kernels/spike and kernel weight/spike indicated that improvement in grain yield can be achieved by increasing number of spikelets/spike.

To determine the differences between genotypes for kernel numbers per spikelet the rate and duration of spikelet initiation was measured as it influences shortfall. Shortfall is defined as $1 - (\text{kernels/spike} / \text{florets per spike formed}) \times 100$. Shortfall ranged from 64.1% for Stephens, 66.85% for Newton and 66.21% for their hybrid. Florets formed after the terminal spikelet stage did not form grain, emphasizing the importance of this stage in regard to kernel formation. Rate and duration were not correlated with shortfall. Both traits influence floret number prior to terminal spikelet, but subsequent floret initiation after terminal spikelet varied with each genotype. Shortfall as a measurement is helpful in understanding grain formation in wheat, but kernels per spike will still be a more valuable trait to select in the plant breeding program.