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THESIS

EFFECTS OF IRRIGATION SCHEDULING ON SPRING WHEAT CULTIVARS

Submitted by
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ON SPRING WHEAT CULTIVARS

This thesis is approved as a creditable and independant investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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CHAPTER I

INTRODUCTION

Wheat is grown on more hectares in South Dakota than any other crop. Cold temperatures leave winter wheat susceptible to freeze injury in much of the state's wheat belt so over half of the wheat hectares are planted to spring wheat. As irrigated hectares have increased in the state, interest has risen in the production of spring wheat under irrigation as an alternative to or in rotation with corn and other crops.

Little information is available on irrigation practices in spring wheat production in South Dakota. Irrigation studies have been done in the state as early as 1949 but results have been inconsistant. Recent irrigated yield trials at Redfield and Gettysberg, South Dakota indicate that improved grain yields can be achieved with irrigation but improvement depends on many factors. In 1984, 25 cultivars were grown in these irrigated trials. At Redfield, little yield improvement was seen over dryland yields. Improvement at Gettysberg was greater (83).

Grain yields obtained under irrigation are disappointingly low when compared to the apparent yield potential of these cultivars. The average yield of the top nine cultivars grown under irrigation at Gettysberg was 4.37 Mg/ha while the same nine cultivars averaged 6.34 Mg/ha at Fargo, North Dakota under dryland conditions during the same year.

Of course, many factors contribute to these yield differences including effects of the preceding crop, diseases, temperature and photoperiod, even if we assume that irrigation eliminates the effects of water stress. If proper irrigation scheduling is not utilized however, avoidable yield losses due to water stress could be a factor. Therefore, this study was initiated at Redfield, South Dakota with the objective of determining an irrigation schedule that would optimize the grain yield of adapted cultivars and aid in determining genetic yield potential when water is not a limiting factor.

CHAPTER II

LITERATURE REVIEW

Function of Water

Water in the plant serves four general functions. It is the major constituent of physiologically active tissue. Photosynthesis and hydrolic processes such as starch digestion use water as a chemical reagent. It is used as a solvent in which salts, sugars and other solutes move from cell to cell and organ to organ and finally it maintains turgidity in plant cells.

Stress

When environmental conditions alter the wheat plant's ability to develop or function optimally it undergoes stress. The main environmental factors affecting plant growth are temperature and moisture. Both factors can have direct and indirect effects on optimal plant function that are at times interrelated. The ultimate result of stress will depend on the intensity and duration of the stress, stage of development of the plant, and the plant's genetic capacity to physiologically respond to suboptimal conditions.

Temperature Effects

Temperatures above an optimum have the general effect of increasing the wheat plant's rate of development through it's stages of growth (10,27). Campbell et al

(15) found that increasing temperatures from 21 to 27 degrees celsius in the growth chamber decreased total leaf area, vegetative dry matter and grain dry matter. High temperatures have been found to be the main factor controlling grain yield (60,12). Because less vegetative matter is produced under high temperatures, total moisture use is reduced (14).

Johnson et al (44) saw a strong influence of high temperatures on apparent photosynthesis, evapotranspiration, and leaf area index. Temperature is thus able to alter the source through reducing leaf area and photosynthetic rates and the sink by influencing spikelet number, kernel number and kernel weight (12).

Moisture Effects

The water status of a plant depends on it's association with both the atmosphere and the soil (51). Moisture is absorbed from the soil by the plant roots. This absorption is controlled by the extent and efficiency of the root system, soil aeration, soil temperature, soil solution concentration, free energy status of the soil moisture and the rate of water loss in the above ground plant parts. The rate of water loss or transpiration depends upon leaf area and structure, the extent of stomatal opening and environmental factors that affect the magnitude of the vapor pressure gradient from leaf to air (51). Because of resistance in the shoot and root, there is a tendency for water absorption to lag behind transpiration. This lag can result in stress during sunny days even in well watered conditions (51).

Soil Moisture

Since wheat plants absorb their water from the soil, soil moisture content will to some extent determine eventual grain yields. Lehane et al (54), in looking at past climatic and yield data determined that five inches of available water are needed before a wheat crop in Saskatchewan will produce any grain. Then, for each additional inch of water, yield increases by 3.5 to 4.0 bushels per acre. Other factors, however, were found to alter this relationship. Kramer (51) showed growth and yields of wheat were not always correlated closely with soil moisture. Drought can cause more severe and prolonged stress in plants but water deficits caused by excessive water loss are more common. Because they are controlled by different sets of factors, absorption and transpiration do not stay precisely in step (31). Therefore, studies done on the effects of soil moisture on wheat grain yields may not indicate directly how water stress is effecting grain yields. A study by Lehane and Staple (54) showed soil type influenced the effect of stress. In loam soil, early stress resulted in lower yields than in clay soil. Growth chamber studies relating soil moisture to wheat grain yields may not be indicative of field conditions. In the field soil-plant resistances may be smaller due to larger soil volume (31).

Evapotranspiration

Evapotranspiration (ET) is the amount of water a crop is using through evaporation and transporation. Seasonal total evapotranspiration is related linearily to grain yield in wheat (77,38) and is dependent at any given period on soil type, soil moisture levels, plant growth stage, plant genotype and atmospheric conditions (27,45,25,38). Several studies have utilized the relationship of evapotranspiration to yield in determining optimum irrigation scheduling. Hang and Singh (38,77) used a line source to irrigate wheat daily on both a coarse and medium textured soil. They found that they optimized maximum yield per unit of water applied when they irrigated at a rate of 40% of the evapotranspiration. Evapotranspiration was calculated from pan evaporation assuming .95 * pan evaporation is equal to ET. Singh (77) measured ET in a wheat crop and calculated two yield reduction equations; one assuming equal sensitivity to ET deficits (ETD) at every growth stage and a second assuming different sensitivities. From these equations they hoped to optimize water use efficiency (yield/ET) by scheduling ETD's at growth stages that showed quantitatively less sensitivity.

Models describing the ET process in wheat have been developed by Denmead and Miller, and Rasmussen and Hanks (24,64).

Plant Water Status

Evapotranspiration deficits occur when water lost through stomates exceeds water absorbed by the roots. In wheat, even moderate crop transpiration rates require the maintenance of rather steep gradients in water potential from the soil to the top leaves (24). Therefore, the plant's water status will directly effect transpiration and grain yield.

Plant water status can be measured in several ways. Fischer et al (34) measured the leaf water potential, osmotic potential, leaf permeability and leaf turgor potential in wheat to determine the effect of drought on the plant's water status. They found that drought reduced leaf permeability, leaf water potential and osmotic potential and that these effects were cultivar dependent. Plant water status and its eventual correlation to grain yield under drought conditions is apparently effected by environment and genotype. Studies using different cultivars in different environments often produce conflicting results.

Xylem pressure potential was measured by Sojka et al (79) to find a method for screening for drought resistance. Jones (46) in England found the use of leaf water potential and leaf conductance as impractical for selection criteria for drought resistance cultivars since ranking changed and correlations were not highly significant. Sojka et al (80) in Mexico, however, found high correlation between a cultivar's seasonal plant water status and its yield by relating yields of 14 cultivars to their xylem pressure potential and adaxial leaf diffusion resistance. By measuring water status twice a day (daybreak and midday) he determined diurnal recovery is important to a cultivar's ability to yield in drought conditions. Cultivars with xylem pressure potentials that were not able to recover to zero overnight suffered greater grain yield losses.

Water status of the wheat plant changes diurnally and with age. Jones, Sojka, Fischer and Maurer, and Sanchez and Horton (46,79,33,34) found that leaf water potential fell with the age of the tissue even under irrigated conditions. With continuing drought, Knovalov (50) found leaf water status to be more sensitive than moisture levels in the developing grain.

Osmotic adjustment, the accumulation of solutes in plant tissue in response to dehydration, is a mechanism the wheat plant can use to maintain turgor pressure at a lower water potential than in unadjusted plants (80,34). Physiological processes such as cell elongation and stomatal opening are dependent on positive turgor. Johnson et al

(43) found that wheat cultivars differing in drought resistance show different abilities to adjust osmotically. Fisher and Sanchez (34) saw that changes in leaf turgor pressure declined at less than half the rate of leaf water potential. By accumulating solute such as amino acids or potassium, turgidity and ultimately essential physiological processes can be maintained.

Stomates

The opening and closing of a plant's stomates will control both its loss of water through transpiration and assimilation of carbon dioxide through photosynthesis. Stomatal control depends upon the relative turgidity of the stomate's two guard cells. Stomatal sensitivity to the plant's water status depends upon genotype, age and preconditioning. In wheat and other crops, critical leaf water potential for stomatal closure depends on the conditions under which the plants were grown (74). Wheat plants growing in drier environments may osmotically adjust the turgor in their guard cells and maintain open stomates at lower leaf water potentials (34). Jones (46), however, found no evidence in his study in England that stomatal behavior adapted to previous drought stress. Conflicts between studies may be due to cultivar differences and levels of stress imposed in a particular environment. Frank et al (36) found stomatal closure to be affected by both leaf position and age. Wheat plants under water stress conditions recovered (stomatal opening) more rapidly at earlier stages of growth. Fischer (31) found stomatal closure to be less sensitive to plant water stress in older plants. Stomates of wheat leaves were most open just before anthesis in Jones' (46) study. He felt that cultivars with more sensitive stomates might be more adapted to short periods of severe stress while less responsive stomates might do better where the plant grows mainly on stored water.

In a field study, Shimshi and Ephrat (73) observed differences in stomatal aperture as they related to short term photosynthesis, short term transpiration, long term water consumption and grain yield. They found a high correlation of stomatal aperture to transpiration, photosynthesis and grain yield and a low correlation to long term water consumption. They likewise found large differences in stomatal aperature among cultivars. These differences may be partially due to abscissic acid levels in the stomate since one cultivar with closed stomates had twice the abscissic acid level of a larger aperatured cultivar. Transpiration rates were more directly related to stomate diameter than photosynthetic rates indicating other resistances besides carbon dioxide diffusion into the stomatal cavity are involved with photosynthesis.

Conditioning

The response of wheat genotypes to water deficits or stress conditions can be variable depending on the environment they are grown in. Conditioning can occur if the plants undergo stress at a young age. Todd and Webster (87) found that conditioned plants are less photosynthetically sensitive to loss of turgidity after a period of drought. Simmelsgaard (74) observed that wheat plants grown under moderate stress conditions seemed to adapt themselves so that their stomates remain open over a wider range of root water potentials through osmoregulation of the leaf. Wheat plants grown in a medium with a higher water potential are not able to osmoregulate to the same extent. Singh (77) found wheat stressed slightly in the vegetative stage is tolerant of stress in booting-heading. Young tissues suffered the greatest reduction in growth rate in a study by Campbell and Davidson (10), but because protein hydrolysis is not active, growth recovered if stress was removed. Older wheat leaf tissue senesced rapidly and probably failed to recover.

Therefore, the time of the stress period can make a significant difference in the plant's response. Simmelgaard (74) felt that a considerable part of the decrease in growth rate of wheat under water stress (in terms of dry matter accumulation) may be caused by wilting of leaves grown before the stress period. The leaves wilted because they are not able to adapt to the stress signals.

Drought Resistance Mechanisms

The effect that water stress has on the water status of wheat can be altered by drought resistance mechanisms. Basically all mechanisms fall into one of three categories. Avoidance mechanisms help maintain a high tissue water status under drought stress conditions. Plants with tolerance mechanisms are able to produce despite high internal water stress. Other cultivars escape water stress through early maturity and complete their life cycle before the onset of stress conditions (49).

As mentioned before, wheat cultivars of certain genotypes grown under dry conditions are able to avoid the effects of water stress and maintain turgidity through osmoregulation. Kaul (47) looked at differences in suction forces in wheat cultivars adapted to a dryland prairie environment using a thermocouple psychrometer. He reasoned that high suction force parallels high osmotic stress and found that it appeared to be the major factor in determining relative drought resistance. Cultivars showed small differences in suction forces but the difference could, he felt, account for the lower vegetative mass, degrees of water stress and use of stored water associated with drought resistant cultivars. Johnson et al (43) looked for differences in osmotic adjustment between a drought resistant and drought susceptable cultivar. Although the growth of the resistant cultivar was less than the susceptable cultivar it did have a somewhat greater osmotic adjustment. Cultivars examined in studies by Konovalov (50) and Sojka et al (80) utilized several mechanisms to resist drought. Some cultivars avoided water stress with waxy cuticles on leaf and stem surfaces, leaf curling and higher diffusion resistance on abaxial surfaces. Maturation was increased and vegetative mass suffered less water loss in others. Sojka et al (80) found low correlations of height to drought tolerance in 12 bread wheat cultivars. Fischer and Maurer (33) however found that tall bread wheats tended to show less drought susceptability than semidwarf cultivars by implementing both avoidance and tolerance mechanisms. Their lower yield potential though gives them an advantage in only severe stress conditions. Keim et al (49) found that some wheat cultivars showed tolerance to drought by maintaining a high number of productive tillers despire high internal water stress. Other cultivars avoided drought effects and maintained higher yields by depending on kernel weight rather than kernel or tiller number. Fischer et al (35) found widely adapted genotypes for dryland conditions to be intermediate in their characteristics. Drought resistance can therefore be expressed in a variety of ways and highly adapted high yielding cultivars are likely to have the genes for several resistant mechanisms.

Critical Growth Stages

Wheat, being a determinant plant, undergoes different stages of development during its life cycle. Some studies support the contention that wheat has one or several critical stages of growth (22,3,66,91). The organ growing most rapidly at the time of stress is the one most effected and grain yield will be reduced most by stress at the critical stage. Other studies contend however that it is the intensity and duration of a water deficit in the wheat plant and not the growth stage at which the stress occurs that will determine the effect on yield (77,17).

Possibly the reason for this conflict in ideas is related to the diversity of environments that wheat is grown in. In some environments the water status of the plant at a particular stage may be the most critical factor controlling grain yield. In other environments or growing seasons other factors such as temperature, wind, humidity or disease may confound the influence of moisture stress and no critical period will be evident through growth analysis studies.

Physiology of Yield

The economic importance of bread wheat is based on its ability to produce high quality grain. The production of grain by the wheat plant involves a complicated series of interrelated processes. Some processes involve the assembly of a source where through photosynthesis, carbon dioxide is assimilated into sugars. Other processes construct the plant's grain sink. The source and sink interact as assimilate is translocated to the grains via a biofeedback mechanism (88,65).

Consequently, the yield of grain produced by a wheat plant depends on the size and interaction of the source and sink.

Sink Size

The assembly of the wheat plant's sink is an ongoing process that begins relatively early in the plant's life cycle. Sink size is determined by both genetic control and the availability of structural carbohydrates from the source. Grain yield will eventually be a function of the number of grains per plant and grain weight. The number of grains is a product of spikes per plant, spikelets per spike, and fertile florets per spikelet. Source-sink interaction occurs immediately in the wheat plant's development since head primordia, the root system and leaf development will all demand structural carbohydrates.

Root System

Crapo et al (20) found that the wheat plant responds to limited photosynthate by restricting root growth. Under high light intensity and adequate available moisture, root growth utilizes a large proportion of the chemical energy translocated to the root. When wheat plants are shaded, the carbohydrate supply to root decreases and the proportion of energy diverted to growth declines in favor of metabolic processes more critical to the survival of the organ and plant. Potassium uptake and respiration in the root will continue while root growth is slowed or stopped. These results imply that maintenance of existing root tissue and functions has priority over the production of new tissue. This study indicates that in water stress conditions, root growth can be limited due to limited photosynthate. Results of a study by Campbell and Read (15) indicate similar priorities in wheat plants under water stress. When moisture stress was increased and light intensity decreased, root growth was depressed more than shoot growth. Root dry matter was more sensitive to moisture differences than stem dry matter. In another study by Campbell et al (10) however, early moisture stress tended to decrease stem and leaf weight in proportion to roots. He felt this could indicate greater translocation of assimilates to roots due to moisture stress.

In a field study, Connor (18) found that the wheat cultivar grown allocated more of its resources to root growth in response to sustained soil moisture stress. He felt this indicates that wheat plants have evolved through the selection for short-term solutions based upon maximizing immediate growth. Since wheat evolved in mixed species communities, this may have been a competitive advantage.

So do wheat plants respond to water stress by promoting more growth in search of water or repressing growth to conserve resources? Drought resistant cultivars have been noted to have large root systems (21). Other researchers feel that cultivars are more efficient users of soil moisture if their early root growth is restricted and they utilize stored soil moisture later in development during the grain fill period. Apparently drought resistance can be expressed in cultivars that utilize either response. The success of the cultivar in producing high grain yield depends on whether it responds correctly to the environmental conditions it encountered.

Tillering

The extent of tiller initiation in wheat and other small grains can have large effects on eventual grain yields (58,49,3,70,18). The ability to maintain a high number of tillers to maturity is important in determining yield differences under drought stress in cultivars and high tiller numbers can compensate for poor germination or thin stands in a wheat crop (49,56). Sensitivity of individual tillers in a plant to soil moisture or water stress varies. Main tillers showed a greater sensitivity to water stress than smaller secondary tillers, probably due to smaller stem size.

Stress level and timing effects tillering differentially. Wheat plants in low water stress treatments in a study by Campbell and Read (15) had more tillers than plants grown under high stress. Robins and Domingo (66), however, found severe moisture stress increased tillering in wheat plants primarily due to a second growth of tillers following heading. Short periods of stress increased tillering in a study by Aspinall (3) while continued stress cycles suppressed tillering. In the same study early stress had little effect on early tiller development but reduced kernel number in the late tillers. When plants were stressed after anthesis tillering was suppressed. Tillering was the only growth stage, however, that showed no sensitivity to moisture stress in studies by Campbell et al (14,10).

Wheat plants show conditioning to stress if the stress period occurs at tillering. Campbell and Davidson (12) found yields of plants stressed from tillering on were generally greater than yields of plants stressed from the boot stage on. Unproductive tiller number increased the later the initiation of a single stress period in a study by Aspinall (3).

Obviously the tillering response of wheat to moisture stress varies in different studies. Again most of the difference can be contributed to when the stress was applied, the severity of the stress and the cultivar's genetic capacity to interact. In general, tillering appears to be a major factor determining yield and initially establishes the crops maximum sink size. Reduction in this sink size by sensitivity to stress can be compensated for though by development of other sink factors in later stages.

Jointing-Boot Stage

Wheat plants in the jointing stage are building their sink capacity through the development of spike primordia. Spike size in terms of spikelet number and florets per spikelet is determined at this stage of growth and can be sensitive to moisture stres (12,84,28). Fischer (31) found that spike size was unaffected by stress early or late in the jointing stage. Oosterhuis and Cartwright (59) showed, however, that water stress just before spike initiation reduced the final number of fertile florets per spike by forming fewer spikelet primordia. Death of florets and entire spikelets at the terminal and basal end of the spike occurred when stress was applied during late internode elongation. The glumes, lemma and palea for the spikelets and florets were initiated but as a sink they showed low priority. Basal spikelets were also a lower priority sink in a study by Stockman et al. (85). Restricting carbohydrate supply by shading reduced competant floret number and eventually kernels per spike. The treatment's effect was greater in basal than in distal or especially central spikelets. Apparently there is a high demand for assimilate at this growth stage. Grains per spike were reduced in plants undergoing water stress at or before heading in a study by Fischer (31) due to the interruption of carbohydrate supply. Rapid elongation of the spike, anthers and carpels as well as meiosis in the pollen mother cell occur at this time. Wheat plants will often produce abnormal anthers and normal female parts when stressed during this period, rendering them male sterile. Pollen sterility was found to be the cause of water stress induced depression of seed set by Saini, Aspinal and Bingham (68,6). Pollen cells developing under stressed conditions failed to accumulate materials in their cytoplasm, had thin pollen walls, and were inviable upon release from the tetrads. Cross pollination with unstressed plants in this study confirmed male sterility and female fertility (68).

Water stress treatments at jointing did not result in the desication of male tissue but rather leaf tissue. It appears that the water stress effect on the generative tissue was an indirect result of lowering the water status elsewhere in the plant (68).

Individual florets within a spikelet show differential sensitivity to stress at the jointing stage. Tertiary florets showed a random response to water stress treatments in Saini's (68) study while florets most likely to develop grains in normal situations were most consistantly effected by the water stress. This is possibly due to asynchrony in meiotic events among florets in the same spikelet. Florets developing earlier or later than the application of stress may escape detrimental effects on microsporgenesis.

Heading-Anthesis

The events of heading and anthesis are genetically controlled and environmentally influenced in wheat cultivars. Both temperature and water stress can either advance or delay these events depending on the level of stress intensity (6). Angus et al (1), Jones (46) and Meyer et al (56) found that severe water stress delayed development on wheat while mild stress hastened development. The mechanisms responsible for the delay of development involve the cessation of all cell division and shoot apex development. Hastened development might be due to associated leaf temperature increases that promote the chemical processes involved. Modification of the normal sequence of development so that fewer cell divisions are required before anthesis may be another way the plant is adapting to water stress (1). Davidson and Birch (21) found in a greenhouse study that wheat plants tended to have two broad categories of shoots. Major or primary, generally the first four tillers in the plant, were very tolerant of water stress up to anthesis. Younger minor shoots produce grain in direct proportion to water supply so were more sensitive to water stress.

Water stress between heading and anthesis reduces grain yield in wheat by lowering the number of grains per spike. Stress after anthesis has little effect on grain number (3). Spratt and Gasser (84) found that water stress at heading had little effect on yields of leaves, stems, and chaff but decreased grain yields so gave smaller grain to straw ratios. Drought during anthesis reduced grain yields 45-59% in a study by Campbell and Davidson (13).

Stockman et al (85) found plasticity in wheat floret number associated with non-meiotic factors. Assimilate supply available to florets at anthesis determined their survival. Increasing irradiance increased grain number per plant but not grain yield in proportion. Apparently assimilate available after the initiation of grain development limited yields.

Sugar levels are an important factor in the determination of grain set at least until several days after anthesis. Waters et al (93) concluded this by detaching wheat spikes and placing them in culture at different levels of sucrose and abscissic acid. The ears were detached prior to ear emergence to correspond with pollen mother cell meiosis. Higher sucrose levels induced higher grain numbers per ear. Abscissic acid indirectly decreased kernel number by decreasing sucrose levels in the developing florets and spikelets. The wheat plant's sensitivity to sucrose levels was greater during meiotic events than after anthesis. When drought stress occurs, abscissic acid accumulates in wheat plants and may be responsible for reducing grain number following water deficits by affecting pollen fertility.

Grain Filling

Water stress during the grain filling period can lower kernel weight and subsequently grain yields (22,12). This can be done via two methods. The stress can shorten the grain filling period and it can slow the rate of assimilate production and translocation to the developing grain.

Duration and rate of grain growth in wheat can vary substantially depending on cultivar and environmental conditions (78). Evidence indicates that the rate of filling is controlled genetically and the duration of filling is environmentally controlled, temperature being a major factor (78,94). The early part of grain development was more sensitive than later periods in a study by Simmons et al (75). They altered assimilate supply by defoliation and sink size by grain removal and found the treatments effected grain weight and growth rate when done early. Growth rates of grains have been found to be dependent upon floret position within the ear, central spikelets being effected less by stress (78,7).

The storage capacity of the grain is determined by endosperm cell number and cell volume. The duration of the cell production phase tends to be constant while the rate of cell production varies with water stress (7). Wardlaw (91) found an initial increase in grain size due to stress conditions associated with a greater rate of endosperm cell division. Assimilate concentrations did not appear to be limiting cell division in developing grain in a study by Singh and Jenner (76). Brooks et al (8) found endosperm cell number was unaffected by water deficit. Initially grain dry matter was unaffected by water deficit but grain filling terminated earlier. It appears that endosperm cell volume has a more significant effect on grain weight than cell number. Brocklehurst et al (7) found shrivelled grain resulted from failure of endosperm cells to fill completely. This was characterized by a reduction in the number of "B" type starch granules.

Once endosperm cells are produced, actual filling of the cells with protein and starch storage reserves begins. Filling proceeds through the translocation of both stored and currently assimilated products. Campbell et al

(13), Kaul (48), and Konovalov (50) found grain filling to be directly related to photosynthetic activity in the upper plant parts. Decreased photosynthesis and increased respiration during drought are the main factors contributing to grain yield loss (50). Under moderate stress, lower leaves will contribute current assimilate to grain filling but severe stress limits their contribution (48). Stockman et al (85) and Sofield et al (78) found that when assimilate is limited during grain filling, distal and basal florets are affected more. Water soluble carbohydrate increased in developing grains with additional light, response being quite rapid to the added assimilate supply. Extra assimilate contributed to greater floret survival as more florets formed eventually filled (85). Control of the filling process appears to be at the spike level since environmental conditions altering photosynthesis and thus assimilate supply effected growth rate per ear not growth rate per grain (85).

With increasing water stress the percent protein in the grain tends to increase. One reason for this could be the reduction in carbohydrate production under water stress in relation to protein levels. Water status in the grain could also be changing, altering metabolic reactions such as starch synthesis (8). Konovalov (50) found mobile "N" compounds produced by proteolysis may be immediately assimilated by the grain during drought. In his study levels of nitrogen changed relatively more than levels of carbon during drought. Possibly due to a greater carbohydrate respiration and intensified proteolysis. High temperatures associated with drought stress could directly effect synthetic processes in the grain (78). Brooks et al (8) found that the supply of sucrose was not the limiting factor in the eventual cessation of cereal grain starch synthesis. Cessation was associated with a loss of the capacity of the endosperm to convert sucrose to starch. Protein synthesis and starch synthesis in the developing grain may have different susceptibilities to whatever physiological changes occur in the grain due to water deficit.

Water stress has more effect on leaf and stem tissue during the grain filling period than on the actual developing grain. Aspinal (3) found that as grain growth proceeds, grain becomes progressively less sensitive to drought. Single short periods of water stress had little effect on grain growth and only long periods deterred growth. Water stress caused wilting and senescence in leaf and stem tissue in studies by Wardlaw (91,90) but had little effect on the water status of developing grains. Short periods of stress at grain fill in fact induced more rapid development in wheat plants in a study by Knovalov (50). The more susceptible vegetative part responded to the water stress by increasing respiration and metabolism and translocating faster to the grain. Photosynthesis was depressed to a greater extent in leaf and stem tissue than in the spike when stressed by water deficits in a study by Wardlaw (91). Fischer (31) found that water stress did not alter the capacity of the grains to grow given a certain assimilate supply or the capacity of green tissue to photosynthesize give a certain rate of withdraw. It appears that water stress does not directly damage the ovum or the conductive tissue feeding it. It's effect seems to be more involved with the source factors and control of translocation.

Photosynthesis

Grain yield differences between some cultivars are due to sink size rather than photosynthetic capacity (6). Some studies though attribute yield differences to assimilate availability. Lupton (55) felt that cultivar differences in grain yield in his study were determined chiefly by differences in the rate of photosynthesis or in translocation pattern rather than by differences in the capacity of the developing grain as a sink for carbohydrate. Dedio et al (23) used a differential respirometer to measure flag leaf photosynthesis after heading in four cultivars of wheat. There were no differences among the cultivars in photosynthetic rates when grown under non-stressed conditions. Under water stress, cultivar differences in photosynthetic rates were apparent. Some studies have shown a lack of relationship between photosynthesis and grain yield but many of these are based on instantaneous measurements of carbon dioxide exchange at standardized conditions, not season long photosynthesis in the field. Zeliltch (97) felt that the plant's source and sink are connected by feedback like effects on photosynthesis. Photosynthetic and storage capacities are closely balanced and grain yield will depend on the interaction.

Water stress will directly influence the photosynthetic area of a wheat crop, and the plant shows sensitivity to stress at every stage of growth (31). Meyer and Green (56) found that wheat leaf growth showed a rapid response to water deficit. The major factor effecting photosynthetic area in Fischer's (31) study was the early senescence of green parts during the stress period. Early water stress of the plants however seemed to delay leaf senescence through conditioning. In a growth chamber study, wheat plants grown at a lower temperature produced a larger leaf surface area (14). In the field, temperature as well as water stress could influence photosynthetic area. The timing of water stress appears to influence the ability of the wheat plant to respond in terms of its photosynthetic area. Campbell and Davidson (10) found that wheat plants stressed early had a reduced leaf size but recovered when stress was removed. When the plants were stressed later their photosynthetic area could not recover.

Glaucous wheat cultivars are able to yield more grain than non-glaucous cultivars when near isogenic lines were compared due to a longer maintenance of leaf area by delayed senscence (42).

Photosynthetic rates vary with tissue age, temperature, water status and genotype. Flag leaves tend to show the highest rates of photosynthesis during the grain filling period and consequently contribute more to grain filling (62). As leaves age, photosynthesis shows a general decline (16,95). The flag leaf showed a greater sensitivity to water stress than other plant parts in several studies. Frank et al (36) found that stress developed more rapidly in the flag leaf at heading than in the fifth leaf at tillering. Leaf water potential in the flag leaf showed a less rapid decrease than photosynthetic rate. Apparently water stress has its most direct effect on photosynthetic rates and less effect on growth and translocation at grain filling. Evans et al (30) found that drought reduced photosynthetic rate of both the flag leaf and penultimate leaf much more than it affected yield. Wardlaw (89) felt that reduction of flag leaf photosynthesis was a direct effect on the flag leaf itself. The water stress caused a delay and reduction of sugar transfer from the assimilating tissue to the conducting tissue and did not affect translocation in the conducting tissue. Because grain yield in stressed wheat plants was not depressed to the same extent that photosynthesis was, Wardlaw (30) felt stored assimilate or reserve photosynthetic capacity is utilized in the stressed plants.

Stress not only reduces photosynthetic rate but it also limits assimilate supply by raising respiration. Twenty percent of the total carbon assimilated can be lost through respiration (16). Johnson et al (44) found that increasing temperature likely increases photorespiration and mitocondrial respiration. The latter may represent an increasingly greater proportion of total respiration during grain development as protein and carbohydrate is translocated. The grain itself contributed 66% of the total ear respiration 15 days after anthesis in a study by Carr and Wardlaw (16).

Stomatal sensitivity to water stress will greatly influence assimilation rates. Under water stress conditions, the soil moisture content is less than the turgor loss point in the guard cells and the wheat plant virtually ceases to assimilate carbon dioxide because the stomates will close (25). Wheat plants growing under water stress in a study by Frank et al (36) underwent larger changes in stomatal resistance in relation to photosynthesis. When stressed plants were rewatered, photosynthesis rapidly recovered but never reached control or prestress levels. Apparently other factors besides stomatal closure were affecting photosynthesis. Possibly damage to the photochemical system (36). Abscissic acid levels increased in stressed plants and tend to induce stomatal closure (93).

Some studies indicate that spike or ear photosynthesis can contribute to grain yield differences. Awned cultivars are noted to have a higher rate or spike photosynthesis than awnless cultivars (16,30). Since the spike is less sensitive to dessication than leaf tissue, awned cultivars are considered to be superior in certain climates more susceptible to drought. Evans et al (30) found drought reduced yields 20% in awnless and only 11% in awned cultivars.

Translocation

Both the pattern and the rate of translocation in wheat are affected by water stress. Asana et al (2) found that water stressed plants translocated at the same rate (as indicated by 1000 kernel weight) as non-stressed plants for up to three weeks. After that long of a stress period, leaf and stem senescence increased and translocation to the grain was reduced. Changes in weight ratios of different plant organs under water stress in several studies have been due to a modification of translocation (90). These studies indicate that water stress reduces photosynthesis in the leaves so more photosynthate is translocated to the spike from the lower leaves. When the level of stress effects growth, translocation is affected. When growth is eliminated, translocation is insensitive to stress (90). Wardlaw (88) found that by removing two thirds of the developing kernels from the spike, translocation downward in the plant increased and roots and crowns showed a faster accumulation of labeled carbon (Carbon 14). Movement up the stem slowed to one-third of the velocity of control plants and retention of the Carbon 14 increased in the translocating tissue. Less total labeled carbon went to the spike. In the leaf tissue, Carbon 14 translocation rate in both the blade and the sheath was not altered by sink size reduction. Translocation rate was not changed by water stress in a study by Wardlaw (89). Several days of leaf wilting failed to slow grain growth in the wheat plants but a change in assimilate distribution was seen in the lower parts of the grain. There was also a greater retention of assimilate in the wilted leaves and a prolonging of movement of assimilates out of the leaf. Wardlaw (89) felt water stress may interfere with the phloem loading process. Loading of assimilates is against a concentration gradient and therefore requires energy. Water stress could therefore uncouple respiration and phosphorylation. There would be a greater reduction in the transfer of assimilates to the conducting tissue than in photosynthesis and the result would be the observed accumulation of sugar in the leaf. Under water stress, there is a slower rate of movement from leaf to stem and a slower rate of allocation to the spike. Yet the actual velocity of assimilate movement in the translocatory tissue is not directly affected by water stress.

As mentioned previously, wheat plants under water stress are able to alter their pattern of translocation and this apparently enables them to compensate to a degree for lower availability of flag leaf assimilates. Under non-stressed conditions, upward movement of assimilate occurs almost entirely from the top two internodes during grain filling (92). Flag leaves are more sensitive to water stress than other plant parts so stressed plants will rely to a greater extent on assimilate from other organs (30,10). Little carbon fixed before anthesis finds its way to the grain under normal growing conditions while carbon assimilated during grain filling contributes to a much greater extent. Austin et al (4) found only 7% of early labeled assimilate contributed to grain yield while 40% of the Carbon 14 assimilated later in the plant's development was translocated to the grain. The plant's top internode serves as a channel for translocation, the lower internodes as storage for sugars (92). Lal et al (53) found that under water stress there is a greater utilization of both stored carbohydrates and photosynthate from lower leaves. Dry weight of the top internode was much less sensitive to water stress than the next internode below in a study by

Wardlaw (91). The contribution of pre-anthesis stored assimilate depends on water stress. Bidinger et al (5) found 12% of the pre-anthesis label was translocated to the grain in irrigated wheat while dryland wheat utilized 27%. Grain yield superiority of the drought resistant cultivar Pitic 62 over Gabo in a study by Davidson and Birch (21) was attributed to an ability to utilize stored assimilates since both cultivars had similar dry matter production levels after anthesis. Stressed plants in this study produced more grain than dry matter after anthesis. Austin et al (4) saw minor translocation differences in genotypes and felt loss of material from the stems may be a reflection of the balance between the demands exerted by the grain sink and the supply from the source. Some stem weight loss in this study was attributed to wasteful, uncoupled respiration or respiration to drive synthetic reactions in other parts of the plant. Stored assimilates, however, do appear to be able to buffer grain yield against environmental stress (5).

Nitrogen Translocation

Nitrogen does not follow the same patterns of translocation to the grain under water stress as carbohydrates. Therefore, higher protein percentage in the grain is seen under water stressed conditions and an inverse relationship often exists between protein and yield

(12, 11, 15). Spratt and Gasser (84) found that drought during stem extension or heading almost stopped nitrogen uptake but not dry matter production. Under adequate moisture conditions, 80% of the total nitrogen is taken up early and stored by the plant while total dry matter accumulation reaches only 50% at the boot stage. Under drought stress the difference between percent of nitrogen taken up and percent of dry matter produced was reduced (84). Campbell and Davidson (12) found the nitrogen levels in the soil had the most direct influence on grain protein percentage while moisture and temperature influenced protein percentage indirectly through yield. Under high moisture stress however, fertilizer nitrogen had no effect on protein concentration in a study by Campbell and Davidson (13). The sequence of flow of nitrogen assimilates in wheat is to the roots and leaves until flag leaf emergence. Then nitrogen levels decrease there rapidly and flow is to the stem. From anthesis to maturity nitrogen is lost in the stems and is translocated to the spike (10). Lal et al (53) found that rapid accumulation of nitrogen in the grain was accompanied by a decrease in culm, leaf, flag leaf and spike chaff nitrogen indicating translocation. High yielding cultivars will translocate 70% of their total plant nitrogen to the grain under irrigation and 60% under dryland conditions (53). Therefore it appears that protein percentage is higher in the grain of water stressed wheat plants because nitrogen translocation is effected less by the stress than carbohydrate translocation.

Yield Components and Yield

The grain yield of wheat will depend on the interaction of sink and source factors. Water stress early in the plant's development can reduce yield potential while stress late in development prevents potential from being realized (56). Many studies have examined the effects of water stress on yield by analyzing yield differences as they arise through effects on different components (58,49,46,11). Different studies show different components to be most affected by water stress and consequently most influential on grain yield (49,46,58). These studies indicate that stress occurred at a critical period in development for the plant and the component affected was probably developing most rapidly at the time of the stress period. Many studies show that one component's influence on grain yield is reduced by negative indirect effects of one or more yield components due to compensation (49). Jones (46) found that drought's main effect was a reduction in tiller number but grain yield was compensated for by increasing the number of grains per spike. Bingham (6) felt that one could determine whether or not a yield component was responsible for grain yield differences or just a product of yield differences if the component and environment (stress treatment) have the same cultivar by treatment interaction. Other studies have used multiple regression models to explain yield differences through components in combinations (35,11). Often these multiple regression models will explain more of the yield differences than single component models indicating compensation and the lack of one critical growth stage. Shanahan et al (72) felt that sink limited grain yields would show a high correlation between yield components and yield. Source limited grain yields should have low correlations between componants and yield. In his study the relative importance of source and sink varied with year and location, therefore, the timing and intensity of environmental stresses determined how important a particular component of yield was.

Breeding

Selecting for drought resistance characteristics in wheat is apparently difficult because high grain yield in wheat can be achieved in many different ways. Lines can be selected that are better at retranslocating stored assimilates during grain filling or producing assimilates during grain fill. Maximum yield potential varieties would be able to do both (4). Some research indicates yield increases through breeding have mainly come through increasing the harvest index (81). Roy and Murty (67) found that several traits including synchronous tillering, seedling vigor, coloeptiller length and days to heading showed stability over environments and indicated adaptation to a stress environment. Fischer and Wood (35) examined the performance of a diverse cross section of bread wheat cultivars under drought and non-drought conditions. The study showed some positive correlations and prediction equations but ranking of cultivars changed with a change in drought intensity. Laing and Fischer (52) looked at the adaptability to semidwarf and tall cultivars of wheat grown over 44 locations that varied in rainfall. Norin-10 semidwarfs outyielded old tall cultivars in all but the driest environments. They suggested combining the drought resistance of old tall cultivars with the high yield potential of the semidwarfs. Dry matter accumulation and loss patterns in a range of wheat genotypes of varying drought resistance were determined in a study by Clark and Townley-Smith (17) and related to drought resistance and yield. They found a lack of relationship between specific morphological traits and drought resistance and felt growth analysis was of little direct use in a drought resistance breeding program in a variable environment. Aspinall et al (3) argued that stress conditions are impossible to duplicate in an uncontrolled environment either in time of stress or with plants with different histories of stress. Apparently environmental variability from year to year prevents the feasibility of selecting for drought resistance based on specific criteria. Stable performance in grain yield over several years in a stress environment is probably the result of the utilization of many adaptive measures.

Applications

Studies of water stress effects on wheat grain yield can indicate inherent weaknesses in production practices and the plants genetic capacity to respond to the stress. Therefore results from these studies can have practical implications in determining seeding rates, fertility levels and irrigation schedules as well as selection criteria in breeding programs.

Types of Studies

Many approaches have been used to determine the effect of water stress on grain yield in wheat. Some studies examine plants grown under controlled environments in either the greenhouse or growth chamber. Others look at field grown plants. The level of stress applied to plants can be determined by several methods. Many studies take direct measurements of water status in the plant parts. Others determine stress levels by soil moisture content, amount of water applied or osmotic potential of growth media when plants are grown in water only. Response of the wheat plant to the stress can be measured as the plants are growing by radioactive labeling, at particular stages of growth by dry matter weight of different parts, or at maturity by measuring grain yield and yield components.

Inferences made regarding plant response to water stress in a particular study will be valid only to a certain extent. Plant response in the greenhouse or growth chamber may not be indicitive of response in the field. One time measurements of water status or photosynthesis can show large variences depending on plant genotype, plant growth stage and climatic conditions. Season long measurements depend on the overall conditions of a particular growing season. Therefore results from all studies should be interpreted with caution. At best, general tendencies may only be indicated and significant changes in any one factor controlling plant response (stress level, stress timing, accompanying temperature or irradiance) can change these tendencies.

Irrigation Scheduling

Utilizing proper irrigation scheduling to maximize grain yields and optimize water use efficiency has been attempted in several studies. Criteria for scheduling irrigation vary, and similar results can be obtained using different criteria (57). The success of a particular schedule in maximizing yield depends on the soil type, climatic conditions, plant conditioning, genotype and method of water application.

Many irrigation schedules are based on the premise that water deficits in the plant should be avoided during critical stages of growth. The critical stage can vary so in order to utilize schedules based on this, the critical stage must first be identified. Day and Intalap (22) withheld irrigation water at one of three stages of development in wheat and found stress at all three stages reduced yield. Stress at jointing however reduced yield to a greater extent than stress at heading or dough stages. Robins and Domingo (66) found that in Prosser, Washington, nonstressed wheat yields reached 90 bushels per acre. Grain yield reductions were greatest when stress was imposed during or after heading. They found no benefit in irrigating spring wheat prior to boot stage unless stress was indicated by curling or wilting of the leaves. In a study by Lehane and Staple (54) early water stress had no effect on grain yields while late stress on loam soil reduced yields. The yield reduction was less with late stress on clay soil. Wheat plants in a study by Fischer (31) appeared to have a critical period 15 days before anthesis.

Other irrigation schedules are determined by rate and accumulation of evapotranspiration deficit. A study by Angus and Moncur (1) used five rates of water application ranging from 11% more than ET to 23% less than evapotranspiration. Total amounts of water applied were 485 to 688 mm in five to seven applications and grain yields were proportional to water use. They determined that even slight deficits at jointing should be avoided and irrigations should be scheduled to replace evapotranspiration. Misra and Pant (57) looked at several criteria in scheduling irrigations in spring wheat. Irrigation treatments were applied depending on either plant physiological stage, soil moisture levels, evapotranspiration levels or plant water status. When scheduling was based on physiological stage, four or six treatments were applied. Fifty percent available soil moisture or .05 atm. of soil moisture tension were the soil moisture levels at which irrigation was scheduled while ET criteria level was 90% of ET loss. Four levels of leaf water potential were used for plant water status criteria. Seven centimeters of water was applied at each treatment. The success of the schedules in terms of grain yield produced varied in the two years of the study. Generally, schedules based on growth stages, soil moisture and 3 bar or 6 bar leaf water potentials were equally effective and superior to schedules based on higher leaf water potentials or pan evaporation.

Determining optimum irrigation schedules and optimum irrigation rates has been integrated effectively in studies with the application of water using a line source. A pattern of application which is uniform along the length of the study area and continuously but uniformly variable across the study area can be produced with a line source (40). Using a line source allows for more variables or treatment levels in a study and since incremental changes from treatment to treatment are small there is no need for a buffer area between plots. Wind or application of water at uneven frequencies to plots however can limit the system's effectiveness (40).

Hang and Miller (38,39) used a line source to apply various amounts of water and scheduled applications based on evapotranspiration. At the line source the water applied was 1.00 times ET on loam soil and 1.15 times ET on sandy soil. Water was applied every morning to avoid wind. Adjacent treatments in the study were not significantly different in terms of grain yield produced but soil type influenced response to water applied. Maximum yields on sandy soil were 7.0 Mg per ha and 6.2 Mg per ha on loam soil. The water holding capacity of the loam soil buffered wheat against ET deficits and grain yield failed to increase past 40% of ET. Higher applications of water on loam soil tended to reduce yields due to lodging and poorer soil aeration. Soil differences therefore greatly influence rates and schedules.

Irrigation can likewise be influenced by the rate of development of water stress. Meyer and Green (56) found that treatments with less time to adapt to an increasing water deficit were not able to compensate by adjusting yield components as effectively as well adapted dryland plots. Dryland plots produced only 9000 grains per square meter compared to 12,000 grains per square meter in well watered plots. Grain filling however was more effective in the drier plots so yield differences were reduced. Miles (personal communication) recommends withholding irrigation of winter wheat in Colorado during the vegetative stages to prevent the wheat plant from becoming "lazy" and developing a shallow root system. Highest grain yields were seen in a study by Campbell (9) when plants were grown under dry conditions to flag leaf emergence then wet conditions thereafter. Conditioning of the plants to water stress was also seen by Singh (77). Using three levels of water and scheduling at three physiological stages; vegetative, booting/heading and flowering to grain development. He found that conditioning plants with 15% moisture stress left them less sensitive to water stress at the boot stage. They felt best results could be obtained when water deficits are spread out over the early stages of plant development.

Irrigation scheduling can thus be effected by several factors and maximum yields can be obtained through a variety of schedules.

Determining an irrigation schedule to maximize grain yields appears to be a complex problem. Because of interactions with other environmental factors and the ability of the adapted wheat plant to compensate, soil moisture levels determined by irrigation will probably not show a consistent effect on grain yield. Studying the variability created by soil moisture differences should, however, give both the irrigator and the breeder indications of the relative importance of soil moisture availability and plant response to irrigated conditions.

CHAPTER III

MATERIALS AND METHODS

Site Description

The study site was established at the James Valley Research Center in central Spink County. This area is representative of spring wheat production areas of northeastern South Dakota. Average yearly precipitation at the site is 473 mm, but is extremely variable (82). Seventy-eight percent of the annual precipitation falls in the form of thundershowers during the growing season (82). Temperatures vary widely at the study site on both a daily and seasonal basis. Highs can be over 40°C during the growing season and lows of 0°C can occur after May 14th on an average of once every two growing seasons. The study was conducted on a Beotia Silt loam, a fine-silty, mixed Pachicudic Haploboroll. Typically these soils have dark gray silt loam A horizons, grayish brown silt loam B2 horizons and pale yellow silt loam C horizons. In cultivated fields they have slopes less than 1%.

Cultivars

Two cultivars were used in the study; Butte, a tall early heading cultivar and Len which is a semidwarf and medium late type. Both cultivars are well adapted to South Dakota growing conditions, have stable and high grain yield potential and are two of the most widely grown cultivars in the state. The cultivars were planted in 6.1 m strips with a John Deere double disc drill. Each strip extended the length of the study area and was replicated five times by alternating Len and Butte. In 1983 the strips were adjacent and in 1984 a 1.53 meter winter wheat border separated the cultivar strips.

Treatments

Water treatments were established using three line sources within the study area. The line sources applied a continuous gradient of water that decreased with distance from the line. One line source established a gradient throughout the growing season; a second line source established a gradient from emergence to heading and the third established a gradient from heading to maturity. Sprinkler heads with both spreader and distance nozzles were used to produce the continuous water gradient. The three line sources were placed perpendicular to the replicated cultivar strips. In 1983 the lines were 12.2 m apart and 15.25 m apart in 1984. Line diameter was 101.6 mm for the main line and 76.2 mm for the three lateral lines. Twenty-five mm diameter risers .915 m tall were spaced at 6.1 m intervals on each of the laterals. Rainbird sprinkler heads were used and set on a full circle revolution. Water was pumped at a pressure of 345 kPa through the line. A spring wheat border of 20 meters surrounded the study to reduce any border effect. Maximum application distance under calm conditions was approximately 18.3 meters from each sprinkler head. Since riser spacing was at 6.1 meters along each line source, water application was triple overlapped along each line. Spacing between line sources was 12.2 and 15.25 meters in 1983 and 1984 respectively so in both years plots between the lines received water from both sources. The full season line was always run simultaneously with either the early season or the late season line. Therefore, plots in the study area received one of a possible four types of water treatments as follows (Table A-7):

1. Plots to the south of the early season line received a gradient of water to heading, then were uniformly dry except for rainfall. (Treatments 1-6)
2. Plots between the early and full season lines received water from both lines to heading. Water received from one line was the inverse of the amount received from the other so water application between the lines was uniform. (Treatments 7-10)
3. Plots between the full season and the late season line received a uniform amount of water after heading in the same manner as described in (2). Prior to heading these plots received

a gradient of water from the full season line. (Treatments 11-15)

4. Plots to the north of the late season line received a gradient of water after heading and were uniformly dry prior to heading except for rainfall. (Treatments 16-21)

Irrigation treatments were applied in an effort to maintain soil moisture gradients. Tensiometers were placed next to the line source at 15.2, 30.4, and 60.8 cm depths. When soil moisture tensions reached .035 kPa at 30.4 cm, soil moisture was assumed to be below field capacity and water was supplied to bring soil moisture levels up to field capacity at the line. Most applications were at night or in the evening to avoid wind. Applications were avoided at anthesis to reduce the infection level of Fusarium species.

Planting and Cultural Practices

Planting dates were April 22, 1983 and April 17, 1984. Field preparation prior to planting consisted of field cultivating and discing. No fall tillage was done in either year. The previous crop in both years was sunflowers. Seeding rate for each cultivar was 100.8 kg per ha and at planting soil moisture was good. Soil tests were taken to determine the soil nitrate level from 0 to 60 cm. Fertilizer was applied to bring the total nitrogen level to 268.8 kg per ha for a yield goal of 6.72 Mg per ha.

Phosphorus and potassium tested adequate for this yield goal. In 1983 212 kg per ha of 46-0-0 granular urea was double spread dry while 28% liquid Urea-Ammonium Nitrate was sprayed in 1984. Diammonium Phosphate 18-46-0 was applied at 90 kg per ha as a starter in both years.

Weed control in both years was excellent. Triflurilin at a .84 kg per ha rate was applied and incorporated post-plant for control of grassy weeds while Bronate (Bromoxynil plus MCPA) at a 1.2 L per ha rate was sprayed at the five leaf stage to control broad leaf weeds and volunteer sunflowers.

In 1984 plots were treated with Mancozeb at grain fill to prevent septoria and pyrenophora infestation of the flag leaf. Army worms were noted in the plots in 1984 but levels of infestation were not high enough to significantly decrease yield.

Measurements and Procedures

Soil moisture readings were taken with a neutron probe. Access tubes were placed 3.05 m apart in two transects perpendicular to the three line sources. The transects covered the width of the study area so that the moisture gradients established by the line sources could be measured. Readings were taken from 15.2 cm to 122 cm at 15.2 cm intervals. Moisture levels were measured in this way twice weekly throughout the growing season.

Neutron probe counts were converted to water content on a volume basis by the formula: Water content (204.8*mm/ha*m)= (.00073* Count-2) * .06 or water content (204.8*mm/ha*m)= (.0019* Count-2) * .06, depending on the probe used. Moisture differences across the gradients were small at 91.5 to 122 cm so only the total moisture in the top 91.5 cm was used in the analysis.

Twenty-one and 23 access tubes per transect were used in 1983 and 1984 respectively. Plots 3.05 by 6.10 m were established in the study area. The plots consisted of 1.523 m on both sides of the access tube location while width of the drill strip determined plot length.

Growth stage readings and tiller counts were taken each week in the plots. Yield components were determined prior to harvest by the following methods. All readings were taken in two replications.

Grains per spike and spikelets per spike were determined by randomly selecting ten spikes per plot. An average of the ten spikes was used to represent individual plots.

Productive and nonproductive spikes per square meter were determined by randomly sampling a one meter length of row in each plot. This number was multiplied by 6.5, the number of rows per meter.

Thousand grain weight was determined by counting 1000 grains of a random sample from each plot on a seed counter and weighing on an electronic balance.

Plots were harvested using a Hege single plot combine and grain from each plot was weighed electronically to determine yield.

A Technicon infro-alyzer 300 was used to analyze grain protein percentage in each plot. Random samples were ground with a Udy cyclone sample mill into flour in preparation for protein analysis. Accuracy of this method was checked by comparing standards to Kjeldahl analysis and no significant differences were found.

Harvest dates were August 8 in 1983 and August 10 in 1984.

Statistical Analysis

Because the irrigation treatments were applied systematically with the three line sources, an analysis of varience procedure cannot be used to analyze treatment, replication and cultivar effects or their interactions. Significant differences between irrigation treatments cannot be determined. Instead regression and multiple regression using the SAS Leaps procedure was utilized to determine the relationships between evapotranspiration (ET) at each treatment and the development of grain yield and yield components. Then the interaction of these yield components in the determination of eventual yield was analyzed with path coefficients to separate the direct and indirect effects. Path coefficient analysis was performed according to the method of Dewey and Lu (26).

Soil moisture and rain gauge readings from the two transects were averaged in all regressions. Grain yield, thousand grain weight and protein percentage were analyzed in five replications while spikelets per spike, grains per spike and spikes per square meter were analyzed with two replications.

Evapotranspiration at each treatment for each growth stage was calculated by determining soil moisture differences between growth stages from the neutron probe readings and subtracting this from the water applied to each plot by irrigation and rainfall during that stage of growth.

CHAPTER IV

RESULTS

Temperature and Precipitation

Temperature and precipitation data are listed on Table 1. Average daily minimum and maximum temperatures along with monthly means are included for both years of the study. These are compared to long term (70 year) averages at the study site.

Temperatures were cooler than average in April, May and June of both years. July temperatures were warmer than average in 1983 and cooler than average in 1984. August temperatures were above average in both years and warmest in 1983.

Precipitation was above average in June, July and August in both years and in April of 1984. May of both years and April of 1983 were drier than normal. In general the rainfall events were effective and not in heavy thundershowers. Therefore there was little runoff.

Soil Moisture Gradients

The soil moisture levels for each treatment at every growth stage are listed on Tables 2 and 3. As mentioned previously, the line sources were run simultaneously and spaced close enough to allow for overlap in the plots between the lines. Establishment of either uniform

Table 1. Climatic data for the study site at Redfield, South Dakota

TEMPERATURE (°C)

Month	1983			1984			LONG TERM		
	Average Daily Max.	Average Daily Min.	Average Monthly Mean	Average Daily Max.	Average Daily Min.	Average Monthly Mean	Average Daily Max.	Average Daily Min.	Average Monthly Mean
April	11.0	- .7	5.2	12.9	1.8	7.4	15.0	0.3	7.6
May	19.6	4.3	12.0	19.2	4.9	12.1	21.6	6.7	14.1
June	24.5	12.1	18.3	25.2	13.0	19.1	26.7	12.4	19.6
July	31.0	17.2	24.1	29.4	15.1	22.2	31.0	15.1	23.1
August	33.7	17.2	25.4	30.6	14.7	22.7	30.0	14.0	22.0

PRECIPITATION (mm)

Month	1983		1984	
	Precipitation	Departure From Normal	Precipitation	Departure From Normal
April	18.54	- 33.53	60.54	+ 8.38
May	52.32	- 22.35	59.18	- 15.49
June	125.73	+ 32.26	152.40	+ 58.93
July	71.88	+ 8.89	67.31	+ 4.32
August	92.20	+ 42.16	119.63	+ 69.60
SEASONAL TOTAL	360.67	+ 27.43	459.06	+125.84

Table 2. Soil moistures (mm in top .92 meter profile) at each stage of growth for each treatment in 1983.

GROWTH STAGES

Treat-ment	Till.	Boot	Head.	Anth.	Milk	Dough	Ripe
1	249.6	246.7	248.2	242.0	239.2	241.6	207.4
2	252.4	246.2	243.6	241.6	237.2	237.9	205.7
3	253.8	253.1	250.7	246.5	243.5	242.9	210.9
4	259.2	257.1	255.5	249.1	244.1	245.7	205.0
5	269.9	266.9	265.5	256.3	255.7	255.9	228.4
6	260.5	259.2	255.7	250.8	244.9	245.8	208.6
7	276.1	262.0	259.9	253.0	248.9	249.0	223.1
8	261.4	265.0	260.1	254.0	247.8	248.9	241.9
9	266.9	268.7	266.1	260.1	257.6	259.5	262.5
10	272.0	282.7	281.1	274.4	273.7	270.4	286.1
11	267.3	278.7	274.9	265.7	265.6	264.4	273.9
12	267.0	271.8	268.5	263.3	260.1	260.1	277.8
13	262.9	268.7	266.8	260.6	258.8	258.9	272.2
14	271.4	274.1	272.0	266.0	264.2	264.8	281.0
15	269.3	271.0	269.7	262.0	265.6	264.7	278.0
16	267.9	260.8	258.5	254.6	253.6	253.7	246.7
17	280.4	276.7	277.2	270.0	272.4	269.8	256.8
18	271.7	265.9	264.7	258.3	257.9	259.7	236.0
19	279.9	275.7	274.5	268.9	266.7	267.5	230.0
20	274.4	271.8	270.3	263.5	263.2	265.3	234.0
21	277.8	270.2	271.3	268.6	265.1	269.2	230.8

Table 3. Soil moistures (mm in top .92 meter profile) at each stage of growth for each treatment in 1984.

	GROWTH STAGES						
Treatment	Till.	Boot	Head.	Anth.	Milk	Dough	Ripe
1	290.5	294.0	292.5	285.6	261.4	267.6	267.8
2	288.6	288.0	292.8	285.3	273.0	274.3	277.0
3	287.7	298.1	299.3	284.4	266.1	263.1	278.9
4	283.2	293.8	288.8	282.2	271.6	266.5	277.9
5	279.9	291.6	284.2	278.4	269.2	264.0	270.3
6	275.2	287.9	285.8	277.6	274.3	264.7	277.2
7	279.6	293.6	288.4	284.6	280.4	274.8	284.2
8	295.2	295.8	290.4	287.8	285.6	280.8	278.7
9	288.9	299.2	294.1	292.5	294.3	285.0	292.3
10	298.6	306.6	300.8	300.1	268.7	292.6	303.3
11	292.5	299.3	294.2	294.5	287.5	285.4	291.0
12	299.0	295.0	298.3	298.2	290.2	288.8	295.8
13	300.6	305.1	301.3	297.4	293.3	291.0	308.5
14	301.4	307.7	303.0	297.4	292.6	288.3	305.3
15	305.9	310.1	306.3	301.1	294.7	287.3	295.0
16	304.8	306.9	302.1	296.5	287.8	282.8	289.4
17	296.7	305.2	297.1	290.8	280.6	274.6	289.0
18	305.2	307.5	303.1	304.4	287.8	282.8	290.9
19	291.8	302.0	296.2	288.3	286.7	270.3	276.7
20	290.1	296.3	290.3	281.1	286.4	261.9	271.4
21	286.9	298.0	293.0	285.2	285.2	264.8	265.0
22	293.9	314.7	296.2	294.5	285.8	278.9	290.6
23	296.6	308.3	292.5	297.8	287.1	283.6	296.5

soil moisture levels or a continuous gradient of soil moisture depends upon a lack of interference from both rainfall and winds. Unfortunately, both environmental factors influenced the establishment of the soil moisture treatments in both years.

In 1983 line sources were placed at treatments 7 and 11 prior to heading and at treatments 11 and 15 after heading.

In 1984 line sources were placed at treatments 7 and 12 prior to heading and at treatments 12 and 17 after heading.

In both years treatment number increased from south to north so that treatment 1 was always at the south end of the study area. Interference from the prevailing southerly winds caused the water treatments to be skewed to the north. Treatments at the south end of the study area tended to be drier throughout the growing season in both 1983 and 1984. Treatments next to and directly north of the full season lines tended to have a relatively greater amount of soil moisture throughout the growing season. Other treatments had an intermediate amount of soil moisture that varied with wind and rain effects.

Levels of soil moisture did not vary greatly from stage to stage. Generally levels were somewhat lower at the ripe stage in 1983.

Therefore, the soil moisture differences in the study in both 1983 and 1984 are less systematic than intended. A continuous gradient of applied water was not always achieved. The soil moisture differences established did however create variability in grain yield and yield component development.

Evapotranspiration levels for each treatment at each growth stage along with total ET at each treatment are listed on Tables 4 and 5 for 1983 and 1984 respectively. Evapotranspiration was determined by subtracting the differences in soil moisture between successive growth stages from the amount of water applied to each treatment through both irrigation and rainfall. It was assumed that no significant runoff or gravitational loss of water occurred.

Evapotranspiration levels varied more between growth stages than the soil moisture levels. At the same time the soil moisture levels did not vary in the same manner as the ET levels in a particular growth stage. At the early growth stage ET increased with rainfalll and irrigation since much of the soil surface was not covered by the crop canopy and evaporation was responsible for much of the water use (ET). Later differences in ET are likely due to plant water use (transpiration) since the canopy was nearly completely covering the soil surface.

Rate of Development

The irrigation treatments affected the rate of

Table 4. Evapotranspiration (mm per .92m profile) at each growth stage for each treatment in 1983.

Treat-ment	Tiller-ing	Joint	Boot	Head-ing	Anthe-sis	Milk	Dough	Ripe	Total
1	5.84	47.24	5.08	24.13	6.60	44.95	14.98	97.53	246.38
2	6.60	53.84	2.79	26.92	4.57	45.46	14.98	100.83	256.03
3	7.62	49.53	3.04	26.67	6.35	46.22	16.51	102.36	258.31
4	6.85	46.73	5.84	26.67	5.84	46.99	16.51	113.03	268.47
5	8.38	48.26	6.60	27.68	9.14	44.70	16.51	111.25	272.54
6	6.09	49.53	5.08	28.19	5.84	47.49	16.25	127.76	286.25
7	21.59	50.03	5.33	26.41	6.85	46.48	15.74	140.97	313.43
8	13.20	46.99	5.08	27.17	8.12	45.97	15.74	135.89	298.19
9	22.35	50.54	3.04	28.19	6.35	45.72	15.74	147.06	319.02
10	31.49	51.56	2.28	33.27	5.84	36.06	18.28	137.92	316.73
11	24.13	52.57	5.08	28.44	14.98	36.06	17.01	146.55	324.86
12	44.95	36.32	7.36	27.17	5.33	46.73	16.00	142.24	326.13
13	48.00	42.41	4.06	27.43	5.84	45.97	14.73	94.99	283.46
14	49.02	46.99	3.81	27.43	3.30	46.73	15.49	98.80	291.59
15	34.03	45.97	5.08	26.16	8.89	39.87	16.00	87.88	263.90
16	35.05	53.34	2.79	27.43	4.31	38.10	15.74	93.72	270.51
17	35.30	49.78	4.31	25.40	6.60	42.16	16.76	93.47	273.81
18	18.03	51.81	3.55	25.65	6.85	42.41	17.78	103.37	269.49
19	18.28	52.83	7.87	20.82	6.60	50.03	14.98	101.60	273.05
20	7.36	47.75	3.81	24.89	5.58	49.53	13.71	102.87	255.52
21	9.14	47.75	4.82	21.59	4.57	44.70	12.95	106.17	251.71

Table 5. Evapotranspiration (mm per .92m profile) at each growth stage for each treatment in 1984.

Treatment	Tillering	Joint	Boot	Heading	Anthesis	Milk	Dough	Ripe	Total
1	22.09	45.21	51.81	53.08	19.30	41.65	38.86	30.98	303.02
2	25.14	45.46	54.61	53.84	14.22	34.79	49.78	22.35	300.22
3	29.21	39.37	45.72	45.72	23.36	36.32	44.70	21.84	286.25
4	26.41	46.48	40.64	48.51	34.29	34.54	55.62	29.71	316.23
5	26.41	43.68	51.05	75.69	1.52	30.48	50.29	9.39	288.54
6	23.87	45.46	45.72	47.75	32.25	29.71	53.34	4.31	282.44
7	23.62	44.45	48.26	47.49	39.37	35.30	51.05	-10.66	278.89
8	17.52	49.78	46.99	51.30	36.32	36.57	56.64	-10.16	284.98
9	21.84	44.79	46.73	50.03	38.86	42.16	53.34	- 1.77	296.16
10	22.86	44.45	45.46	53.34	36.57	48.26	53.84	10.41	315.21
11	25.90	44.19	51.56	55.11	47.75	67.31	63.75	29.21	384.81
12	26.41	43.94	57.91	52.83	39.11	71.62	63.75	28.19	383.79
13	25.14	43.94	56.13	57.65	41.40	71.12	57.81	26.41	379.73
14	23.87	44.45	53.59	61.21	25.14	66.29	44.70	32.78	352.04
15	24.63	43.18	56.13	46.48	18.79	66.80	46.22	43.68	345.94
16	25.40	46.99	54.10	48.00	13.71	68.58	40.89	61.72	359.41
17	27.17	41.91	54.61	50.03	5.84	68.07	41.40	55.88	344.93
18	24.89	43.18	56.13	47.24	2.79	66.80	40.64	57.91	339.59
19	23.11	42.92	51.81	54.86	6.60	48.76	60.96	41.65	330.70
20	22.86	44.45	52.07	53.84	7.87	43.18	75.69	32.76	332.74
21	23.87	41.65	52.32	50.29	6.60	36.06	62.48	29.71	303.02
22	22.60	43.43	44.70	55.62	3.81	34.03	49.53	19.30	273.05
23	21.84	41.40	53.08	61.21	0.76	36.83	53.59	25.90	294.64

development of both cultivars. Heading was delayed as increasing amounts of water were applied through irrigation in both years. Sampling was done on a weekly basis, therefore the extent of the effect can only be estimated. For both cultivars a delay of three days in heading occurred when comparing the extremes. This increased rate of development was carried into grain filling although the extent of the delay was reduced as the crop matured and was not existant at maturity. The difference in rate of development was even more apparent between cultivars. Heading in Len was three to five days later than Butte across treatments.

The ultimate effect of delaying development by irrigation is that the time from initial grain development to physiological maturity occurs during a period of warmer temperatures and higher stress. This generally produces a negative effect on yield.

Ranges and Means

Means and ranges of yield and yield components for both cultivars over both years are listed on Tables 6 and 7. Average yields in 1984 were approximately 2 Mg/ha greater than in 1983 for both cultivars. Spikes per square meter, thousand grain weight, and spikelets per spike were greater in 1984 while grains per spike were greater in 1983 for both Len and Butte.

Table 6. Ranges and means for yield and yield components for 1983.

BUTTE

Variable	Mean	Std. Dev.	Minimum	Maximum	Range
Yield (Mg/ha)	3.02	.35	2.47	3.68	1.21
1000 Grain Wt. (g)	25.13	1.17	23.06	26.94	3.88
Grams/Spike	29.29	1.59	25.80	32.65	6.85
Spikelets/Spike	15.61	-	14.65	16.35	1.70
Spikes/Square Meter	609.44	79.11	484.25	793.00	308.75

LEN

Variable	Mean	Std. Dev.	Minimum	Maximum	Range
Yield (Mg/ha)	2.80	.24	2.37	3.23	.86
1000 Grain Wt. (g)	26.03	.71	24.62	27.22	.26
Grains/Spike	26.39	1.70	22.85	28.95	.61
Spikelets/Spike	15.50	-	14.70	16.25	1.55
Spikes/Square Meter	635.77	56.42	526.50	734.50	208.00

Table 7. Ranges and means for yield and yield components for 1984.

BUTTE

Variable	Mean	Std. Dev.	Minimum	Maximum	Range
Yield (Mg/ha)	5.13	.18	4.82	5.54	.821
1000 Grain Wt. (g)	28.55	.61	27.28	29.64	2.36
Grains/Spike	28.85	1.89	25.30	32.55	7.25
Spikelets/Spike	15.86	-	15.20	16.50	1.30
Spikes/Square Meter	677.10	67.99	447.25	832.00	354.25

LEN

Variable	Mean	Std. Dev.	Minimum	Maximum	Range
Yield (Mg/ha)	4.63	.22	4.02	4.91	.89
1000 Grain Wt. (g)	27.06	.62	25.46	28.08	2.62
Grains/Spike	26.11	2.03	21.70	31.25	9.55
Spikelets/Spike	16.53	-	15.75	17.45	1.70
Spikes/Square Meter	651.30	50.25	539.50	724.75	185.25

Variability (in terms of standard deviations) was less in 1984 than in 1983 for all components except grains per spike for both cultivars.

Butte outyielded Len in both years of the study but did not always have greater yield component development. In 1983 Butte had a greater average number of grains per spike but a lower average thousand grain weight and number of spikes per square meter. Butte generally showed more variability than Len in its components indicating more responsiveness to the irrigation treatments in 1983.

In 1984 Butte showed greater development of all components except spikelets per spike. Variability in this year of the study was similar between cultivars.

Protein Percentage

Measurements of percent protein content are listed on Appendix Tables A1-A4. Generally there was very little variation in protein percent between treatments in a given year. All treatments for both cultivars were within a range of about 1.5% in 1983 and 1% in 1984 for both Len and Butte. An inverse relationship between yield and protein percent was expressed. Yields in 1984 were higher while protein was lower. In 1983 yields were lower and percent protein greater. Protein levels were relatively high indicating adequate nitrogen fertility in both years.

Extreme Comparisons

Grain yield and corresponding yield components for the highest and lowest yielding treatments are shown in Tables 8 and 9. These Tables indicate which yield components contributed to the yield differences seen in the study. In 1983 (Table 8) thousand grain weight for Butte and thousand grain weight and grains per spike for Len are greater in the higher yielding plots. Spikes per square meter however tend to be less in the higher yielding plots. Yield component differences between the highest and lowest yielding plots in 1984 are small, making trends difficult to see from comparisons.

Tables 10 and 11 compare the soil moisture present at each stage of growth for the highest and lowest yielding treatments. Treatment 20 was the highest yielding treatment for Butte and the second highest yielding for Len in 1983 (Table 10). Treatment 1 was the highest yielding Len and second highest Butte treatment. Soil moistures in these two treatments are compared to soil moistures in treatment 9 at each stage of growth. Treatment 9 was the lowest yielding treatment in 1983 for both cultivars. Comparisons for 1984 treatments (Table 11) are between 23 and 1 (Butte high yield to low yield), 14 and 1 (Butte high yield to low yield), and 23 and 14 (Len high yield to low yield).

The soil moisture comparisons for 1983 show that

Table 8. Yield extremes with associated yield components for 1983.

BUTTE
TREATMENT NUMBER

	20	21	1	9	8	7
Yield (Mg/ha)	3.68	3.31	3.59	2.47	2.65	2.49
1000 Grain Wt. (g)	26.63	26.94	25.30	23.98	24.18	24.16
Spikes/Square Meter	627.25	552.50	484.25	711.75	653.25	546.00
Spikelets/Spike	15.85	15.85	15.55	15.55	16.35	15.85
Grains/Spike	30.45	29.75	28.65	29.45	30.50	29.65

LEN
TREATMENT NUMBER

	20	21	1	9	8	7
Yield (Mg/ha)	3.19	3.13	3.23	2.37	2.37	2.55
1000 Grain Wt. (g)	26.44	26.31	26.64	24.98	25.20	24.62
Spikes/Square Meter	526.50	598.00	633.75	734.50	715.00	650.00
Spikelets/Spike	14.70	15.85	15.80	16.15	14.90	15.05
Grains/Spike	27.20	26.30	26.35	24.05	24.95	25.95

Table 9. Yield extremes with associated yield components for 1984.

BUTTE
TREATMENT NUMBER

	14	23	20	1	3	12
Yield (Mg/ha)	5.54	5.47	5.31	4.82	4.83	4.95
1000 Grain Wt. (g)	28.38	28.42	28.40	29.14	29.38	28.78
Spikes/Square Meter	672.75	659.75	663.00	617.50	741.00	637.00
Spikelets/Spike	15.63	15.75	15.83	16.00	16.20	15.70
Grains/Spike	31.15	29.50	30.60	29.55	31.45	32.60

LEN
TREATMENT NUMBER

	23	16	9	2	15	14
Yield (Mg/ha)	4.91	4.87	4.88	4.18	4.37	4.02
1000 Grain Wt. (g)	26.20	27.46	26.90	26.72	28.08	27.22
Spikes/Square Meter	646.75	565.50	630.60	581.75	640.25	640.25
Spikelets/Spike	16.45	16.70	16.65	16.20	17.30	16.65
Grains/Spike	28.30	27.20	27.45	25.85	31.25	24.40

Table 10. Comparisons of soil moistures (mm. in .92m profile) at each growth stage for high and low yielding treatments in 1983.

Growth Stage	Treatment 20	Treatment 1	Treatment 9	20-9	1-9
Tillering	273.3	243.6	262.6	+ 10.7	- 19.1
Late Tillering	265.9	237.7	260.6	+ 5.3	- 22.9
Jointing	276.4	248.7	268.2	+ 8.1	- 19.6
Boot	272.5	243.6	265.2	+ 7.3	- 21.6
Heading	272.5	244.3	261.9	+ 10.7	- 12.5
Anthesis	267.0	237.7	255.5	+ 10.7	- 17.5
Milk	259.1	234.4	251.5	+ 7.6	- 17.0
Dough	267.0	236.0	252.2	+ 14.7	- 16.3
Ripe	238.3	205.0	253.0	- 14.7	- 48.0

Treatment 20 - Highest yielding Butte 2nd highest Len.
Treatment 1 - Highest yielding Len 2nd highest Butte.
Treatment 9 - Lowest yielding Len and Butte.

Table 11. Comparisons of soil moistures (mm in .92 m profile) at each growth stage for high and low yielding treatments in 1984.

Stage	23	14	1	23-1	14-1	23-14
Tillering	294.6	297.2	280.7	+ 13.9	+ 16.5	- 2.60
Late Tillering	296.9	301.5	283.2	+ 13.7	+ 18.3	- 4.60
Jointing	292.4	291.8	274.6	+ 17.8	+ 17.2	+ .60
Boot	305.3	304.3	288.8	+ 16.5	+ 15.5	+ 1.00
Heading	295.1	299.2	291.8	+ 3.30	+ 7.4	- 4.10
Anthesis	294.4	294.4	277.9	+ 16.5	+ 16.5	0.00
Milk	288.5	288.5	258.6	+ 29.9	+ 29.9	0.00
Dough	280.7	283.7	258.1	+ 22.6	+ 25.6	- 3.00
Ripe	287.0	318.8	254.5	+ 32.5	+ 64.3	-31.80

Treatment 23 - High yielding Len and Butte.
Treatment 14 - High yielding Butte low yielding Len.
Treatment 1 - Low yielding Butte.

the highest yielding treatment for Butte had more soil moisture than the lowest yielding treatment at every growth stage except for ripe. Len, on the other hand, had less soil moisture in the higher yielding treatment at every growth stage. This trend was repeated in 1984. Higher yielding treatments for Butte had more moisture than lower yielding treatments at all stages of growth. Soil moisture differences between high and low yielding treatments were smaller for Len in 1984. There was more soil moisture in the highest yielding treatment in only the jointing and boot stage.

Simple Correlations

Correlations of evapotranspiration (ET) at a single growth stage to yield components are found on Tables 12-15 for each cultivar and each year.

In general, both yield and yield components were negatively correlated with ET for both cultivars in both years.

A significant negative correlation (.05) of grain yield with ET at dough and highly significant (.01) negative correlations of yield with ET at heading and ripe were found in 1983 for both cultivars. In 1984, the only significant correlation of yield with ET at a single growth stage was the positive correlation at heading for Butte.

For Butte in 1983, spikes per square meter,

Table 12. Butte 1983 correlation coefficients for evapotranspiration at a single growth stage with yield and yield components.

Stage of Growth	Yield	Spikes/ Square Meter	Spikelets/ Spike	Grains/ Spike	1000 Grain Wt.
Tillering	- .11	- .23	- .29	- .03	- .04
Jointing	.01	.34	.01	- .05	.14
Boot	.11	- .24	- .27	- .05	.08
Heading	- .69**	.33	.12	- .25	- .75**
Anthesis	- .20	- .08	.01	.02	- .25
Milk	.22	.05	.10	.17	.17
Dough	- .50*	.26	- .12	- .16	- .46*
Ripe	- .64**	.37	.20	- .05	- .73**
Total ET	- .64**	--	--	--	--

* .05 Level of significance.
** .01 Level of significance.

Table 13. Len 1983 correlation coefficients for evapotranspiration at a single growth stage with yield and yield components.

Stage of Growth	Yield	Spikes/ Square Meter	Spikelets/ Spike	Grains/ Spike	1000 Grain Wt.
Tillering	.00	.14	- .17	.17	- .27
Jointing	- .10	- .15	.03	- .07	.17
Boot	.01	.14	.02	.08	- .06
Heading	- .53*	.23	- .10	- .53*	- .22
Anthesis	- .22	.37	- .13	- .16	- .33
Milk	.02	- .20	.08	.14	.17
Dough	- .44*	.24	- .05	- .30	- .20
Ripe	- .55**	.49*	.00	- .73**	- .64**
Total ET	- .54**	--	--	--	--

* .05 Level of significance.
** .01 Level of significance.

Table 14. Butte 1984 correlation coefficients for evapotranspiration at a single stage of growth with yield and yield components.

Stage of Growth	Yield	Spikes/ Square Meter	Spikelets/ Spike	Grains/ Spike	1000 Grain Wt.
Tillering	- .26	.11	.27	- .03	.17
Jointing	.13	.26	- .11	- .01	- .08
Boot	.17	- .44*	.36	.17	- .30
Heading	.45*	.00	- .41*	.00	- .35
Anthesis	- .26	.24	- .32	- .05	- .07
Milk	.12	- .30	.60**	.28	- .38
Dough	.11	- .13	.05	.11	- .25
Ripe	.10	- .35	.66**	.14	- .07
Total	.12	--	--	--	--

* .05 Level of significance.
** .01 Level of significance.

Table 15. Len 1984 correlations for evapotranspiration at a single growth stage with yield and yield components.

Stage of Growth	Yield	Spikes/ Square Meter	Spikelets/ Spike	Grains/ Spike	1000 Grain Wt.
Tillering	- .36	- .08	.16	.07	.09
Jointing	.08	.01	- .33	- .40*	- .22
Boot	- .18	- .29	.63**	.22	- .61**
Heading	- .02	- .01	- .08	- .29	- .32
Anthesis	- .10	.09	- .21	- .46*	- .04
Milk	- .26	- .21	.62**	.14	.61**
Dough	.22	.34	.24	- .29	- .24
Ripe	- .18	- .17	.57**	.130	.42*
Total	- .24	--	--	--	--

* .05 Level of significance.
** .01 Level of significance.

spikelets per spike and grains per spike had no significant correlations with ET at any stage of growth. Len, on the other hand, had a significant positive correlation of spikes per square meter with ET at ripe and a significant negative correlation of grains per spike with ET at heading. Statistically ET at ripe for Len is highly negative correlated to grains per spike, although grain number has been determined before this stage of growth. Thousand grain weight shows highly significant negative correlations with ET at heading and ripe stages in Butte and a significant negative correlation at dough. Thousand grain weight has a highly significant negative correlation with ET at ripe for Len.

In 1984, Butte shows a significant negative correlation with spikes per square meter and ET at boot. Since spikelets per spike are determined prior to heading, significant correlations to ET at later stages of growth will not be considered.

Len is more closely correlated to ET than Butte in 1984. Spikelets per spike and thousand grain weight were highly significantly correlated with ET at boot. At jointing and anthesis, ET had a significant negative correlation with grains per spike. Thousand grain weight is positively correlated with ET at the milk (highly significant) and ripe (significant) stages.

Correlations for grain yield with total seasonal ET are also listed on Tables 12-15. The only significant correlations are in 1983 with both Len and Butte. The correlations are highly negatively significant for both cultivars. Yields tended to decrease as total seasonal water use increased.

Multiple Regressions

Multiple regressions were utilized to determine the closest linear association of ET to grain yield and yield components. The results are listed in Tables 16-19. The SAS procedure Leaps was used and the multiple regression model giving the highest coefficient of determination with the fewest appropriate independent variables was selected as the best model.

The multiple regression models for ET versus grain yield in 1983 had highly significant coefficients of determination (R^2) for both Len and Butte. The four variable model for Butte (Table 16) utilized ET at the later stages of growth while the five variable model for Len (Table 17) used both early and later stages. In both models, ET had negative effects on yield as they had in the correlations.

The same trend was seen in the multiple regression model for ET at growth stages and thousand grain weight for each cultivar. Again the models were highly significant, utilized ET at four later stages for Butte and five stages

Table 16. Best multiple regression model for ET at growth stages versus yield and yield components for Butte in 1983.

GRAIN YIELD	= 6.87 - 1.78H - 1.03D - .34M - .17R	R^2 = .62 r = .79**
THOUSAND GRAIN WEIGHT	= 40.77 - 8.40H - 1.99A - 2.26M - .53R	R^2 = .79 r - .89**
GRAINS PER SPIKE	= 43.19 - 2.61J - 11.61B - 7.5H + 4.02A	R^2 = .15 r - .39
SPIKELETS PER SPIKE	= 16.48 - .23T - .35J	R^2 = .10 r - .10
SPIKES PER SQUARE METER	= 85.90 + 2.85T + 36.57A	R^2 = .18 R = .42

* .05 Level of significance.
** .01 Level of significance.

T - ET at tillering.
J - ET at jointing.
B - ET at boot.
H - ET at healing.

A - ET at anthesis.
M - ET at milk.
D - ET at dough.
R - ET at ripe.

Table 17. Best multiple regression model for ET at growth stages versus yield and yield components for Len in 1983.

GRAIN YIELD	$= 7.27 - (.53J) - (1.25B) - (1.83H) - (.59M) - (.06R)$	$R^2 = .55$ r = .74**
THOUSAND GRAIN WEIGHT	$= 28.46 - (.33T) - (1.61H) - (1.91A) - (.91M) - (.42R)$	$R^2 - .56$ r = .75**
GRAINS PER SPIKE	$= 36.83 + 1.04T - 10.83H$	$R^2 = .40$ r = .63**
SPIKELETS PER SPIKE	$= 16.13 - .15T - .21J - .49B$	$R^2 = .04$ r - .20
SPIKES PER SQUARE METER	$= 11.66 - 5.48T + 18.07J + 49.86H$	$R^2 = .28$ R = .53

* .05 Level of significance.
** .01 Level of significance.

T - ET at tillering.
J - ET at jointing.
B - ET at boot.
H - ET at healing.

A - ET at anthesis.
M - ET at milk.
D - ET at dough.
R - ET at ripe.

Table 18. Best multiple regression model for ET at growth stages versus yield and yield components for Butte in 1984.

GRAIN YIELD	$= 5.59 - .69T - .28B + .31H - .09A + .15M$	$R^2 = .40$ $r = .63$*
THOUSAND GRAIN WEIGHT	$= 30.48 + 1.74T - .87H - .37D - .52M$	$R^2 = .43$ $r = .66$*
GRAINS PER SPIKE	$= 32.83 - 3.07B - 1.52A + 1.10D + 2.74M - 1.16R$	$R^2 = .17$ $r = .41$
SPIKELETS PER SPIKE	$= 15.79 - .43H + .24D + .14M + .22R$	$R^2 = .65$ $r = .80$**
SPIKES PER SQUARE METER	$= 32.85 + 42.92T + 46.39J - 25.03B$	$R^2 = .33$ $r = .57$*

* .05 Level of significance.
** .01 Level of significance.

T - ET at tillering.
J - ET at jointing.
B - ET at boot.
H - ET at healing.
A - ET at anthesis.
M - ET at milk.
D - ET at dough.
R - ET at ripe.

Table 19. Best multiple regression model for ET at growth stages versus yield and yield components for Len in 1984.

GRAIN YIELD	$= 5.52 - .71T - .21B - .07A + .13D$	$R^2 = .21$ r = .46
THOUSAND GRAIN WEIGHT	$= 26.19 + 1.41B - 1.18H - .42A + .68M - .42R$	$R^2 = .61$ r = .78**
GRAINS PER SPIKE	$= 39.81 - 4.83H - 3.73A + 2.27M - 2.03R$	$R^2 = .51$ r = .71**
SPIKELETS PER SPIKE	$= 15.5 - 1.05J + 1.4B$	$R^2 = .43$ r = .66**
SPIKES PER SQUARE METER	$= 108.8 - 11.62B + 7.09D$	$R^2 = .19$ r = .43

* .05 Level of significance.
** .01 Level of significance.

T - ET at tillering.
J - ET at jointing.
B - ET at boot.
H - ET at healing.
A - ET at anthesis.
M - ET at milk.
D - ET at dough.
R - ET at ripe.

for Len, and showed a negative correlation between ET and thousand grain weight.

Grains per spike were highly significantly correlated with ET at tillering (positive effect) and heading (negative effect) in a two variable model with Len. Butte had no significant model in 1983 for grains per spike. Both spikelets per spike and spikes per square meter failed to show significant correlations with ET in multiple regression models with each cultivar in 1983.

Multiple regression indicates a different response to ET in the two cultivars in 1984. Only Butte had a significant model for grain yield and this model used ET at early growth stages instead of later stages as in 1983. Thousand grain weight, spikes per square meter and spikelets per spike per square meter likewise had significant multiple regression models with Butte.

Len in 1984 had only the yield components of thousand grain weight, grains per spike and spikelets per spike significantly correlated with ET using multiple regression. The thousand grain weight model uses ET at five growth stages. Evapotranspiration at four stages is used in the grains per spike model while spikelets per spike are determined best by ET at jointing and boot.

As with the simple correlations, most variables in the multiple regression models had a negative effect on yield and the components of yield.

Tillering Pattern

The association of productive tillering at each stage of growth with ET was determined by regressing spikes per square meter on ET at growth stages with both simple and multiple regression. Results of the simple correlations for both cultivars in both years are presented in Tables 20-23. The best multiple regression models are in Tables 24-27.

In 1983, Butte had significant positive correlations of spikes per square meter at heading, anthesis and milk with ET at heading. Spikes per square meter at ripe showed a significant negative correlation with ET at jointing (Table 20).

For Len in 1983 (Table 21), spikes per square meter at heading, milk, dough and ripe were highly significantly correlated with ET at heading and spikes per square meter at anthesis were significantly correlated with ET at anthesis. All of these correlations were positive. Spikes per square meter at the boot stage had a significant negative correlation with ET at tillering. Spikes per square meter at dough likewise showed significant positive correlations with ET at anthesis and at dough. Spikes per square meter at ripe were significantly and highly significantly correlated with ET at anthesis and ripe respectively. These correlations were again positive.

In 1984 fewer tiller counts were made during the

Table 20. Correlation coefficient for productive spikes per square meter at growth stages vs ET at growth stages for Butte in 1983.

Growth Stage	Boot	Heading	Anthesis	Milk	Dough	Ripe
Tillering	-.34	-.05	.12	-.22	-.07	.17
Jointing	.14	-.06	.24	.22	.28	-.46*
Boot	-.18	-.04	-.19	.02	.04	.34
Heading	-	.50*	.51*	.54*	.07	-.26
Anthesis	-	-	.34	.40	.09	.00
Milk	-	-	-	-.16	-.10	.38
Dough	-	-	-	-	.03	-.25
Ripe	-	-	-	-	-	.13

* .05 Level of significance.
** .01 Level of significance.

Table 21. Correlation coefficient for productive spikes per square meter at growth stages vs ET at growth stages for Len in 1983.

Growth Stage	Boot	Heading	Anthesis	Milk	Dough	Ripe
Tillering	-.46*	.03	-.14	-.02	-.14	.13
Jointing	.20	.04	.03	-.02	.06	-.03
Boot	.09	.12	-.27	.07	-.11	-0-
Heading	-	.77**	.49*	.63**	.61**	.60**
Anthesis	-	-	.12	.40	.47*	.54*
Milk	-	-	-	-.16	-.35	-.38
Dough	-	-	-	-	.50*	.38
Ripe	-	-	-	-	-	.78**

* .05 Level of significance.
** .01 Level of significance.

Table 22. Correlation coefficients for productive spikes per square meter at growth stages vs ET at growth stages for Butte in 1984.

PRODUCTIVE SPIKES PER SQUARE METER

Growth Stage	Tillering	Heading	Milk
Tillering	.07	.12	-.04
Jointing	-.03	.29	.24
Boot	-	-.13	.22
Heading	-	.10	-.05
Anthesis	-	-	.28
Milk	-	-	.08

Table 23. Correlation coefficients for productive spikes per square meter at growth stages vs ET at growth stages for Len in 1984.

PRODUCTIVE SPIKES PER SQUARE METER

Growth Stage	Tillering	Heading	Milk
Tillering	.22	.19	.17
Jointing	.19	-.28	-.20
Boot	-	-.21	-.02
Heading	-	.12	.19
Anthesis	-	-	-.18
Milk	-	-	-.48*

* .05 Level of significance
** .01 Level of significance

Table 24. Best multiple regression model for spikes per square meter vs ET for Butte in 1983.

Spikes per Square Meter	Best R^2 Model	
Boot =	15.22 -18.22T[1] +114.00H	R^2 = .36 r = .60*
Heading =	-62.33 - 8.84T +92.79B +150.10H	R^2 = .34 r = .58*
Anthesis =	- 3.39 - 6.73T +86.15H + 39.87A	R^2 = .40 r = .63*
Milk =	-166.90 -10.94T +37.78J +173.5B +172.9H	R^2 = .62 r = .79**
Dough =	- 19.82 +46.71 +104.0B + 68.2H - 97.34D	R^2 = .19 r = .44
Ripe =	126.7 + 8.33T - 33.82J - 66.59B - 69.98H +45.49A + 38.06M + 5.96R	R^2 = .43 r = .66*

* .05 Level of significance

** .01 Level of significance

[1] Symbols T, J, B, H, A, M, D, R stand for ET at tillering, jointing, boot, heading, anthesis, milk, dough and ripe respectively.

Table 25. Best multiple regression model for spikes per square meter vs ET for Len in 1983.

Tiller per Meter at	Best R^2 Model				
Boot =	-36.26	-32.64T[1]	+175.10H		R^2 = .52 r = .72**
Heading =	-152.4	- 9.42T	+118.8B	+229.0H	R^2 = .70 r = .84**
Anthesis =	12.90	- 8.65T	+95.87H		R^2 = .32 r = .57*
Milk =	-135.60 + 37.14M	+59.08B	+140.00H	+ 65.02A	R^2 = .64 r = .80**
Dough =	33.81	- 4.73	+ 61.21	+ 35.47	R^2 = .61 r = .78**
Ripe =	43.27 + 6.60R	+45.60H	+ 41.13A	- 42.12D	R^2 = .78 r = .88**

* .05 Level of significance
** .01 Level of significance

[1] Symbols T, J, B, H, A, M, D & R stand for ET at tillering, jointing, boot, heading, anthesis, milk, dough and ripe.

Table 26. Best multiple regression models for spikes per square meter vs ET for Butte in 1984.

Spikes per square meter at:		Best Multiple Regression Model:	
Tillering	=	129.1 + 13.36T[1]	R^2 = .004 r = .06
Heading	=	− 9.21 + 36.16T + 39.59J + 10.84H + 7.88A	R^2 = .34 r = .58
Milk	=	− 31.11 + 28.18J + 48.23B + 5.75D − 8.59M	R^2 = .31 r = .56

* .05 Level of significance
** .01 Level of significance

[1] Symbols T, J, B, H, A, M, D & R stand for ET at tillering, jointing, boot, heading, anthesis, milk, dough and ripe respectively.

Table 27. Best multiple regression models for spikes per square meter vs ET for Len in 1984.

Spikes per square meter at:		Best Multiple Regression Model:
Tillering	=	96 + 82.25T[1] + 88.74J R^2 = .17 r = .41
Heading	=	169.7 + 41.16T - 34.69B - 12.98A R^2 = .31 r = .56*
Milk	=	- 8.61 + 48.90T + 50.55B + 4.51A - 22.25M R^2 = .57 r = .75**

* .05 Level of significance
** .01 Level of significance

[1] Symbols T, J, B, H, A, M, D & R stand for ET at tillering, jointing, boot, heading, anthesis, milk, dough and ripe respectively.

growing season (Tables 22-23). The only significant correlations between ET and tillering were with spikes per square meter at heading and ET at anthesis for Butte (positive association) and spikes per square meter at milk with ET at milk for Len (negative association).

Multiple regression models for Butte (Table 20) in 1983 were significant for spikes per square meter at boot, heading and anthesis while highly significant for spikes per square meter at milk. Evapotranspiration at tillering has a negative effect in all four of these models and ET at heading has a positive effect.

Multiple regression models for Len (Table 25) are highly significant for spikes per square meter at every stage of growth except anthesis where the two variable model there is significant at the .05 level. In every model ET at heading is used and has as a positive effect on spike number. Evapotranspiration at tillering again has a negative effect on spike number when used in these models.

Butte in 1984 showed no significant response to ET according to the multiple regression models (Table 26). Len, however, was responsive to ET differences in 1984 (Table 27). The four variable model of ET versus spikes per square meter at milk was significant at the .01 level and the three variable model for spikes per square meter at heading was significant at the .05 level. In both models, ET at tillering has a positive effect on tillering.

Nonproductive Tillering

Counts of nonproductive spikes were taken prior to harvest along with counts of productive spikes. Correlations of nonproductive spikes per square meter with ET at separate growth stages are listed on Tables 28 and 29. In 1983 spikes per square meter for Butte were more closely correlated with ET than spikes per square meter for Len (Table 28). At heading and anthesis ET is significantly correlated to nonproductive spike number and ET at the ripe stage and total ET are highly significantly correlated to nonproductive tillers. Nonproductive spikes per square meter for Len are significantly correlated with ET only at the ripe stage and this correlation is negative.

Nonproductive tillering in 1984 (Table 29) shows no significant correlation with ET at any growth stage or with total ET.

Multiple regression models of ET versus nonproductive spikes per square meter are on Tables 30 and 31. In both years for both cultivars these models explain more of the variability in nonproductive spike number than simple regression does. Significant models are found only with Butte in 1983 (Table 30). In that model ET at anthesis and ripe have a positive effect on nonproductive tillering while ET at jointing has a negative effect.

Table 28. Correlation of nonproductive spikes per square meter with ET in 1983.

ET at	Butte	Len
Tillering	< .30	.07
Jointing	- .35	< .07
Boot	.30	< .07
Heading	.49*	- .34
Anthesis	.52*	< .07
Milk	< .30	- .24
Dough	< .30	- .11
Ripe	.74**	- .47*
Total ET	.75**	- .40

* .05 level of significance
** .01 level of significance

Table 29. Correlation of nonproductive spikes per square meter with ET in 1984.

ET at	Butte	Len
Tillering	< .05	.12
Jointing	< .05	- .11
Boot	.05	.22
Heading	- .25	- .24
Anthesis	- .18	< .11
Milk	.19	< .11
Dough	- .31	< .11
Ripe	.29	.20
Total ET	< .05	.13

* .05 level of significance
** .01 level of significance

Table 30. Best multiple regression models for nonproductive spikes per square meter vs ET in 1983.

Butte
Non-Productive Spikes per Square Meter = 12.41 - 12.47J[1] + 20.82A + 3.93R R^2 = .76 r = .87*

Len
Non-Productive Spikes per Square Meter = 48.67 - 13.61H - 9.77M - 1.18R R^2 = .42 r = .65

* .05 Level of significance
** .01 Level of significance

[1] Symbols J, H, A, M, R stand for ET at jointing, heading, anthesis, milk and ripe respectively.

Table 31. Best multiple regression models for nonproductive tillers vs ET in 1984.

Butte
Non-Productive Tillers $= 16.96 - 2.5H^1 - 2.2D = .86R$
$R^2 = .18$ $r = .42$

Len
Non-Productive Tillers $= -14.60 + 13.99B + 5.53A - 7.98M + 15.63R$
$R^2 = .41$ $r = .64$

* .05 Level of significance

** .01 Level of significance

[1] Symbols H, D, R, B, A, M stand for ET at heading, dough, ripe, boot, anthesis, and milk respectively.

Correlations of Yield Components and Path Coefficient Analysis

The relationships between yield and yield components were analyzed for each cultivar and each year. Phenotypic correlation coefficients were calculated for every possible combination between grain yield, thousand grain weight, spikes per square meter and grains per spike. These correlations for both log transformed and nontransformed data are listed on Tables 32 and 33. Logarithimacally transformed data produced nearly identical correlations to non-transformed data. Path coefficient analysis thus was performed using correlations from non-transformed data according to the method of Dewey and Lu (26) in order to determine the direct and indirect effects of the yield components on yield. In Tables 34-37 these correlations are explained in terms of direct and indirect effects.

In 1983 high correlations were found between thousand grain weight and grain yield for Len and Butte. Both of these correlations were highly significant and positive. Other significant correlations in 1983 were thousand grain weight with grains per spike in both Len and Butte (positive), spikes per square meter with yield (negative), and grains per spike with yield (positive). The latter two were in Len only.

In 1984 there were few correlations between yield

Table 32. Correlations of yield and yield components on all combinations for transformed and non-transformed data in 1983.

BUTTE

	CORRELATIONS	
	Non-Transformed	Transformed
ThGW[1] vs Yield	.76*	.76**
ThGW vs Spikes	- .26	- .28
ThGW vs Grains	.45*	.50*
Spikes vs Yield	- .31	- .30
Spikes vs Grains	.14	.11
Grains vs Yield	.19	.25

LEN

	CORRELATIONS	
	Non-Transformed	Transformed
ThGW vs Yield	.63**	.65**
ThGW vs Spikes	- .32	- .33
ThGW vs Grains	.50*	.51*
Spikes vs Yield	- .43*	- .44*
Spikes vs Grains	- .16	- .12
Grains vs Yield	.50*	.53*

[1] ThGW = Thousand Grain Weight
* .05 Level of Significance
** .01 Level of Significance

Table 33. Correlations of yield and yield components on all combinations for transformed and non-transformed data in 1984.

BUTTE

	CORRELATIONS	
	Non-Transformed	Transformed
ThGW[1] vs Yield	- .52*	- .51*
ThGW vs Spikes	.36	.34
ThGW vs Grains	- .34	- .28
Spikes vs Yield	- .16	- .14
Spikes vs Grains	- .48*	- .42*
Grains vs Yield	.12	.11

LEN

	CORRELATIONS	
	Non-Transformed	Transformed
ThGW vs Yield	- .05	- .06
ThGW vs Spikes	- .21	- .26
ThGW vs Grains	.36	.36
Spikes vs Yield	.01	.01
Spikes vs Grains	- .34	- .40
Grains vs Yield	.19	.18

[1] ThGW = Thousand Grain Weight

* .05 Level of Significance

Table 34. Direct and indirect effects contributing to correlations of yield components with yield for Butte in 1983.

Thousand Grain Weight with Grain Yield	
r = .76	
Direct effect	.81
Indirect effect via spikes	.03
Indirect effect via grains	- .08
	.76
Spikes Per Square Meter with Grain Yield	
r = - .31	
Direct effect	- .07
Indirect effect via grains	- .02
Indirect effect via ThGW[1]	- .22
	.31
Grains Per Spike with Grain Yield	
r = .19	
Direct effect	- .16
Indirect effect via ThGW	.36
Indirect effect via spike	- .01
	.19

[1] ThGW = Thousand Grain Weight

Table 35. Direct and indirect effects contributing to correlations of yield components with yield for Len in 1983.

Thousand Grain Weight with Grain Yield	
r = .63	
Direct effect	.43
Indirect effect via spikes	.08
Indirect effect via grains	.12
	.63
Spikes Per Square Meter with Grain Yield	
r = - .43	
Direct effect	- .25
Indirect effect via grains	- .09
Indirect effect via ThGW[1]	- .09
	- .43
Grains Per Spike with Grain Yield	
r = .50	
Direct effect	.25
Indirect effect via ThGW	.16
Indirect effect via spike	.09
	.50

[1] ThGW - Thousand Grain Weight

Table 36. Direct and indirect effects contributing to correlations of yield components with yield for Butte in 1984.

Thousand Grain Weight with Grain Yield

r = -.52	
Direct effect	- .54
Indirect effect via spikes	.002
Indirect effect via grains	.02
	- .52

Spikes Per Square Meter with Grain Yield

r = -.16	
Direct effect	.006
Indirect effect via grains	.03
Indirect effect via ThGW[1]	- .19
	- .16

Grains Per Spike with Grain Yield

r = .12	
Direct effect	- .06
Indirect effect via ThGW	.18
Indirect effect via spike	.002
	.12

[1] ThGW = Thousand Grain Weight

Table 37. Direct and indirect effects contributing to correlations of yield components with yield for Len in 1984.

Thousand Grain Weight with Grain Yield	
r = -.05	
Direct effect	- .13
Indirect effect via spikes	- .01
Indirect effect via grains	.09
	-.05
Spikes Per Square Meter with Grain Yield	
r = .01	
Direct effect	.07
Indirect effect via grains	- .09
Indirect effect via ThGW[1]	.03
	.01
Grains Per Spike with Grain Yield	
r = .19	
Direct effect	.26
Indirect effect via ThGW	- .05
Indirect effect via spike	- .02
	.19

[1] ThGW = Thousand Grain Weight

and yield components that were significant. Only the negative correlations of thousand grain weight with yield and spikes per square meter with grains per spike were significant for Butte while Len in 1984 had no significant correlations between any of its yield components and yield.

The largest direct effect for Butte in 1983 and 1984 and Len in 1983 was the effect of thousand grain weight on grain yield (Tables 34-37). In 1983 the effect was positive for both cultivars but in 1984 the effect was negative. In all three cases the direct effect was largely responsible for the significant correlation between thousand grain weight and yield.

Spikes per square meter were negatively correlated to grain yield in both years except with Len in 1984 where the correlation is essentially zero. In 1983 this negative correlation is due to the combined negative direct effect and indirect effects. In 1984 the negative correlation is due to the negative indirect effect via grain weight.

Grains per spike were positively correlated with grain yield in both years with both cultivars. With Len in both years the positive correlation is due to the direct effect while with Butte the indirect effect via thousand grain weight contributes most to the positive correlation. In 1984 the positive indirect effect is a product of the negative correlation between grain number and grain weight and the direct effect of grain weight on grain yield. Grain weight increases as fewer grains per spike are produced but the net effect is a reduction in yield. In 1983 the positive indirect effect is a product of the positive effect of grain weight on yield and the positive correlation of grain weight and grain number. The higher yielding plots not only had more grains per spike but the grains actually filled more.

CHAPTER V

DISCUSSION

Weather

Results of any study are biased by the influence of the particular environmental conditions that existed during each growing season. This study was no exception. The two growing seasons were different from each other and somewhat atypical of average growing seasons for the region.

Average daily maximum, daily minimum and monthly mean temperatures varied between years but were comparable to the long term averages (Table 1). Temperature effects were not evaluated in this study but were probably more favorable in 1984 when yields were greater.

Rainfall, on the other hand, was not typical of the long term averages. Both years had total rainfall above the long term average. Rainfall in 1983 was 27.43 mm above the normal while 1984 rainfall was 125.74 mm above average. The two years varied in the distribution of their above average precipitations. Below average rainfall in April and May in 1983 would tend to emphasize the importance of the early developmental processes while above average rainfall in June, July and August in 1983 would diminish the effect of moisture on later developmental processes. The rainfall pattern was different in 1984. Only May precipitation was below normal but soil moisture differences were diminished by above average rains in April. Later season rainfall was even greater than that in 1983. Therefore the influence of soil moisture differences on the development of the cultivars should be even less pronounced in 1984.

Soil Moisture Gradients

Tables 2-5 list the soil moisture and ET gradients established at each stage of growth during both years of the study. As mentioned previously the gradients have been altered by both prevailing winds and above average rainfall. Soil type has been shown to effect soil moisture gradient establishment and plant response to soil moisture in several studies (39,38,54). Finer textured clay soils will diminish water stress because of their water holding capacity. Sandy soils will tend to hold less water and soil moisture stress can be more apparent. This study was done on a silt loam soil and from the soil moisture gradients it appears that soil moistures tended to be maintained through the growing season. High soil moisture treatments tended to remain high through the growing season and low moisture treatments remained low.

Rate of Development

Several studies show that severe water and temperature stress delays the rate of development in wheat plants while mild stress hastens development (10,27,6,1, 56,46). In this study, levels of water stress were not severe so treatments receiving more irrigation developed at a slower rate than the less watered treatments. This was especially true of the later heading cultivar Len. Since this delay would tend to push heading and grain filling back into the hotter days of July, the mildly stressed treatments may actually be at an advantage. However, the effect of the treatment on rate of development was less than the cultivar effect with Butte being earlier than Len.

Ranges and Means

The differences between the two growing seasons are evident when examining means and ranges for yield and yield components (Tables 6-7). Nineteen eighty four was a more favorable year for the expression of grain yield potential than 1983. The lowest yielding treatment in 1984 yielded more than the highest yielding treatment in 1983 for both Butte and Len. The only yield component to follow this trend was thousand grain weight for Butte. All other yield components have ranges of variability that overlap between years. This indicates that the development of individual components of yield in response to the irrigation treatments will not in themselves determine the eventual grain yield response. Rather the interaction of the yield components determines yield and this interaction is apparently different in the two seasons. This interaction will be addressed further when the path coefficient analysis is discussed.

Tables 6 and 7 indicate that the irrigation treatments created more variability in yield and yield component development in 1983. Standard deviations for all factors except grains per spike are greater in 1983. This is to be expected since greater rainfaill in 1984 reduced treatment differences.

Extreme Comparisons

By examining the yield extremes and the soil moistures associated with the high and low yielding treatments (Tables 8-11), a general response of grain yield to the irrigation treatments can be seen. The response however is unclear.

Butte yields more than Len in both years of the study (Tables 8-9). The cultivars seem to achieve higher yield in similar ways. In 1983 both Butte and Len produced heavier grains and fewer spikes per square meter in their high yielding treatments when compared to the low yielding treatments. Len also produces more grains per spike in the high yielding treatment. In 1984 yield differences were not as large between high and low treatments. With extreme comparisons it is difficult to see which yield components contributed to the yield differences. Since grain yield for both cultivars was greater in 1984 and thus closer to its genetic potential, there may be more subtle interaction between components determining eventual yield.

Soil moisture differences between high and low yielding treatments indicate that Butte and Len can both achieve high yields in different ways. In 1983 treatment 9 was the lowest yielding for both Len and Butte while treatments 20 and 1 were either the highest or second highest yielding (Table 8). Comparing soil moistures in treatments 20 and 9 (Table 10) indicates that increased yield comes from an increase in soil moisture while comparing treatments 1 and 9 indicates the opposite relationship. Apparently higher yields can be achieved in several ways.

In 1984 the response to soil moisture was again unclear. Treatment 14 was the highest yielding for Butte and the lowest yielding for Len (Table 9). With Butte the highest yielding treatment had more soil moisture than the lowest yielding treatment throughout the growing season. With Len the opposite is true (Table 11).

Of course, examining the extremes will not indicate overall realtionships or statistically significant correlations. It can, however, point to associations that regression analysis can further explain.

Regression Analysis

Regression of evapotranspiration at particular growth stages on grain yield and yield components indicates the response of those parameters to the irrigation treatments. Correlation coefficients for each cultivar in each year are on Tables 12-15. Because of the excessive rainfall and reduced treatment effects in 1984 yield and yield components are not as closely correlated to ET as they are in 1983.

Both yields and total ET levels tended to be greater in 1984. This indicates that the wheat crop was able to utilize more water in the more favorable year. This relationship has been found in other studies with wheat and with other crops. Evapotranspiration and yield within a given year, however, have the opposite relationship.

In 1983 ET at heading and grain filling (dough and ripe) were those stages most closely correlated to grain yield in both Len and Butte (Tables 12-13). All of the significant correlations were negative. During those three periods of development, grain yield decreased as evapotranspiration increased. This same relationship was found with yield and total ET. Studies by Miller and Hang (38) and Singh et al (76) have found a positive correlation between ET and grain yield on both a seasonal and a growth stage basis. Reasons for the opposite relationship in this study are likely due to the fact that ET is influenced not only by the availability of water (soil moisture) but also by temperature. The later stages of development of spring wheat in South Dakota tend to coincide with periods of high temperatures and hot dry winds. From July 14 to July 28 in

1983 high temperatures ranged from 27.2 to 36.1 degrees celsius and lows from 13.3 to 22.8 degrees celsius at the study site. All plots in the study encountered similar temperatures yet the plots closest to the full and early season line sources suffered the largest yield reductions. Plots closest to these line sources responded to the early season moisture by producing more tillers and consequently had more leaf area per plant by the grain filling period. This larger leaf canopy left these plots more susceptible to evapotranspiration deficit. Plots further away from the early and full season line developed fewer tillers so on a plant basis underwent less stress during the later stages of grain filling.

Since increasing tillers and leaf area per plant leaves the wheat plant more susceptible to stress at grain filling, thousand grain weight should be the component of yield most effected by these conditions. Correlations indicate that this is in fact the case. Correlations are negative and significant for Butte at heading, dough, and ripe and negative and significant at ripe for Len. Other studies indicate that stress at grain filling can lower grain weight and subsequently grain yield by reducing both the rate of translocation to the grain and the period of grain filling (12,22,78,24). Temperature was found to be a major factor determining the duration of grain filling. Konovalov (56), Wardlaw (90, 91), and Aspinall et al (3) found that leaf tissue was more sensitive to stress at the grain filling period than the developing grains. Stress at grain filling seems to be involved with source factors and the control of tranlocation as well as the utilization of stored assimilate (53,21,5).

The two cultivars differed somewhat in their response to the environment in 1983. Len had a significant negative correlation for ET at heading with grains per spike. Butte too had a negative correlation for grains per spike with ET at heading but the correlation was not significant. This genetic difference in response is probably due to Len's later heading date. Butte underwent heading and anthesis from June 17 to June 21. During that period high temperatures at the study site ranged from 20.6 to 25.6 degrees Celcius. Len underwent heading and anthesis from June 21 to June 25 which coincided with a period of higher temperatures (highs from 28.4 to 32.8 degrees Celcius). Several studies support this association of temperature and water stress to a reduction in grain number (6,1,56,46,3,84).

Therefore, plots in this study that used less soil moisture through evapotranspiration at heading and grain fill yielded more for two main reasons.

1. With fewer tillers per plant they consequently had less leaf canopy per plant to transpire. Soil moisture was depleted to a

lesser extent leaving more for grain filling processes.

2. Plants in the lower yielding plots had built a potentially larger sink by producing more secondary tillers but because of the temperature stress encountered during heading and grain filling, this potential sink was not developed. The increase in secondary tillers, in fact, was probably detrimental to eventual yield. More tillers and a larger leaf canopy per plant increases susceptibility to stress. This stress shortens the time of grain filling and interferes with translocation of assimilate out of the leaf tissue. The plant was not able to transport sufficient water. Therefore fewer grains develop and grains that develop are lighter.

In this study evapotranspiration appears to be more a measure of temperature stress than water stress.

Multiple Regression

Multiple regression indicates that the development of grain yield in 1983 was different in the two cultivars used in the study (Tables 16-19). Len and Butte both had models showing highly significant R^2 for yield versus ET. The four variable model for Butte utilized the later stages of growth. Evapotranspiration at each growth stage was negatively correlated to yield.

The model for Len in 1983 utilizes ET at both late and early growth stages. This indicates that the components that develop earlier in the growing season, grains per spike and spikes per square meter, contribute more to yield of Len than to the yield of Butte.

Since four and five variables are used in the regression models that give the highest R^2 there is apparently no single critical stage of growth for the two cultivars in 1983. Other studies support these findings and indicate that yield in wheat is a result of the development and interaction of several processes (77,17). Intensity and duration of a stress period are probably more critical to the eventual yield produced than is the developmental stage at which the stress occurs.

The absence of a critical growth stage for wheat in South Dakota is emphasized by multiple regression models from 1984 (Tables 18-19). Only Butte had a significant multiple regression model in 1984 and this five variable model utilized earlier stages of growth than the 1983 multiple regression model. The environmental differences between years resulted in a different response in the same genotype.

Multiple regressions for the association of yield components to ET are also on Table 16-19. These multiple regression models explain more of the variability in yield components than the simple regression models. This again indicates that development of the components of yield does not depend on the conditions at one critical stage but rather the unique set of conditions encountered by the wheat plant during a particular growing season. Therefore, some components have significant models in only one season, some in both and some in neither.

Tiller Development

Productive spikes per square meter at harvest have a low correlation with ET at most stages of growth. Tiller development during the growing season, however, was responsive to ET. Tables 20-23 show the correlations of spikes per square meter at each stage of growth with ET. Tillering in Butte and Len was responsive to the soil moisture differences established in 1983 but only to a small degree in 1984. This is seen in the simple correlations as well as the multiple regression models (Tables 24-27).

In 1983, spikes per square meter in both cultivars were responsive to moisture use at heading. Butte showed no response to moisture use in the later stages while Len did show significant and highly significant response to ET at anthesis, dough and ripe stages. All tillers counted were productive tillers.

This again points to the lateness of Len as a reason for yield reduction. Butte invests less assimilate into producing secondary tillers. Len, however, tillers more if soil moisture is available (significant positive correlations to ET). Butte determines its final number of productive tillers before the later stages of growth. Len develops at a slower rate and fails to differentiate between productive and nonproductive tillers until later when temperature stress is greater.

Moisture use at heading seemed to have the major impact on the tillering of both cultivars used in this study. After heading Len and Butte vary in their response to the environment.

Multiple regressions (Tables 24-27) indicate that the productive tiller number is a result of moisture conditions at several growth stages. The best multiple regression models in 1983 showed significant correlations to spikes per square meter at all growth stages for Len and all but dough and ripe for Butte. The correlations are greater than the simple regression correlation coefficients. Therefore final tiller number was determined earlier in Butte than in Len but both cultivars respond to the moisture present at several stages of growth and not one critical stage.

Soil moisture differences in 1984 were so small as to not significantly effect tillering except at grain filling for Len (Tables 22-23).

Nonproductive Tillering

Correlations of non-productive tillers per square meter at harvest with ET at growth stages are listed on Tables 28 and 29. These correlations emphasize the relationships indicated by the productive tiller with ET correlations. Non-productive tillers for Butte in 1983 (Table 28) were significantly correlated with ET at heading and anthesis and highly significantly correlated with ET at ripe and total ET. Len had significant correlation with ET only at ripe and the correlation there is negative.

These correlations again indicate that ET has a detrimental effect on grain yield by increasing the number of non-productive tillers per plant. Butte was more responsive to total ET and to ET at earlier stages of development emphasizing its earlier response to the environment in comparison to Len. Both cultivars had similar percentages of non-productive tillers (Appendix Tables 1-4) but by differentiating between productive and non-productive at an earlier stage of development, Butte was able to mature tillers more synchronously and waste less assimilate and water on grains that would not eventually be filled.

Yield Component Correlations and Path Coefficient Analysis

Grain yield in wheat is the result of the development and interaction of spike number, grains per spike and weight per grain. Correlations of these components to yield and to each other are on Tables 32 and 33 for both logarithmically transformed and nontransformed data. These correlations indicate the mutual association between yield and yield components.

Path coefficient analysis is the separation of the correlation of yield and yield components into direct and indirect effects. A path coefficient is a standardized partial regression coefficient and measures the direct effect of a yield component on grain yield. The effect is measured in standard deviation units and is thus directly comparable to other path coefficients.

Components of grain yield in wheat are interrelated and their relationship varies with both genotype and environment. Therefore path coefficient analysis is a useful means to estimate the independent contribution of each component to yield. It provides an explanation for differences in the relationship between cultivars and between environments. Without a means of separating these correlations into direct and indirect effects the relative importance of the relationship can be confusing.

Phenotypic correlations indicate that yield component compensation varies with both genotype and environment. Significant correlations are similar for Len and Butte in 1983 between thousand grain weight and yield and thousand grain weight and grains per spike. Len, however, had significant correlations between grains per spike and yield and spikes per square meter and yield. The latter was a negative correlation. This indicates that grains per spike and spikes per square meter are more related to eventual grain yield in Len than they are in Butte.

In 1984 correlations changed dramatically. Len had no significant correlations while correlations for Butte changed sign and magnitude. Thousand grain weight had a significant but negative correlation to grain yield in this environment instead of the positive correlation to yield it had in 1983. Spikes per square meter and grains per spike were likewise significantly negatively correlated.

The means by which genotype and environment change these correlations can be explained with the path coefficient analysis.

Thousand grain weight's significant correlations to yield with Len and Butte in 1983 and Butte in 1984 are due to relatively large direct effects in all three situations (Tables 34-36). In 1983 the direct effect is positive. With other variables held constant, increasing thousand grain weight increases yield. The environment in 1984, however, created a different relationship since the direct effect is negative.

Why did increasing thousand grain weight decrease yield in 1984? From the path coefficient analysis we can see it is because of the relationship of the other two components to grain weight (Table 36). Spikes per square meter are negatively correlated to grain yield because of a negative indirect effect through grain weight. Grains per spike are positively correlated to yield due to the indirect effect via thousand grain weight. Therefore, higher yielding plots of Butte in 1984 had fewer tillers and fewer but heavier grains.

In 1983 the relationship between yield components in Butte changed. Thousand grain weight is again the component with the highest correlation to grain yield but in 1983 yield increases as grain weight increases. Spikes per square meter are negatively correlated to grain weight. Grains per spike had a negative direct effect of grain yield. Because of a larger positive indirect effect through thousand grain weight however, they are positively correlated to grain yield. In 1983, therefore, higher yielding plots of Butte had fewer tillers but more and heavier grains.

Thousand grain weight was again positively correlated to grain yield with Len in 1984. The path analysis reveals the correlation is due to a positive direct effect as well as positive indirect effects through spikes per square meter and grains per spike. Spikes per square meter are negatively correlated to yield because the direct and indirect effects are all negative. Grains per spike are positively correlated to grain yield due to positive direct and indirect effects. Higher yielding plots of Len responded to the irrigation much the same way Butte did in

1983. High yield came from fewer tillers, more grains per spike and heavier grains. The main difference between the two cultivars in 1983 was that the direct effect of grains per spike is negative in Butte and positive in Len. The net result is that grain number contributes more to yield in Len in 1983.

Len in 1984 has a similar direct effect of grain per spike on grain yield. Indirect effects are small giving grain number per spike a positive correlation with grain yield (Table 37). Correlations of the other two yield components to grain yield are very small. This is because direct and indirect effects are small and tend to cancel. The only component that seemed to vary its response to the irrigation for Len in 1984 was grains per spike. The small yield differences observed are thus due to variation in that component. Compensation between the others is minimal.

The component of yield that consistently has a negative correlation with grain yield in this study is spike per square meter (tillering). Path coefficient analysis show that the negative correlation can be attributed to the direct effect with Len in 1983, and to the indirect effect via thousand grain weight with Butte in both years. Tillering therefore appears to be detrimental to maximum grain yield under irrigation.

This negative effect appears at first to be contradictory since tiller production is the initial step in determining yield potential. The answer lies in the fact that grain number is negatively associated with tiller number and grain number is the only component positively correlated to yield for both cultivars in both years. High yielding plots tended to always have more grains per spike but fewer spikes per square meter. In South Dakota stress from heading to maturity appears to prevent the development of secondary tillers. The yield potential created by high tillering is difficult to maintain because of this temperature stress.

Thousand grain weight varied with environment. In 1983 plots with more grains per spike had heavier grains; the opposite was true in 1984. This difference is probably associated with the yield level differences seen between 1984 and 1983. The yield levels were higher for both cultivars in 1984 so all components may have been closer to their genetic maximum. Consequently there was more competition for assimilates between grains at grain fill in 1984. Grain weights were higher in 1984 but either competition for assimilate or an inadequate grain filling period caused compensation between grain number and grain weight.

Regression analysis indicated that stress at heading and grain filling in 1983 was detrimental to the development of grain number, grain weight and grain yield for both cultivars. This is supported by the path analysis.

Plots that developed more tillers underwent more stress (higher ET), had more floret abortion per spike (fewer grains per spike) and were more susceptible to stress at grain fill. Again the development of yield potential through tillering does not seem to be a favorable trait in South Dakota's climate.

This is evident when looking at the differences between the two cultivars used. Butte consistantly produces fewer spikes per square meter and more grains per spike than Len and heads three or four days earlier. This is advantageous in South Dakota because of the tendancy for hot dry weather in July. Butte is able to out-yield Len because it invests less photosynthate during the vegetative stage into the production of tillers and the assembly of a larger source. Then it develops at a faster rate than Len so is able to produce more grains and fill them before later season temperature stress reduces yield.

Yield Potential

The maximum grain yield potential of both cultivars was not approached in the two years of this study. Even in 1984 maximum yield of Butte and Len were far below yields these genotypes achieve in other environments. Both cultivars have reached yield of over 6.72 Mg/ha in Fargo, North Dakota. Maximum yields in this study were 5.54 Mg/ha.

In order to reach this higher yield level the wheat plants would theoretically need to produce approximately 580 to 650 spikes per square meter, 35 to 40 grains per spike and have a thousand grain weight around 30 grams. The tillering and thousand grain weights are within the ranges seen in this study (Table 11). Grains per spike, however, were lower than this theoretical level. If both cultivars were able to produce 2.5 grains per spikelet this level could be reached. Basal and terminal spikelets failed to develop fertile florets on many of the spikes in this study. Other studies contribute this failure to develop to both temperature and water stress during spike primordia development (85,59,68). Floret abortion and pollen sterility at anthesis due to high temperature has been documented in other studies (6,1,56,46). It appears that grain development is restricted in South Dakota for two reasons. Development is hastened by temperatures above an optimum. This allows less time for floret development. Secondly, leaf tissue is sensitive to temperature and water stress and since there is a high demand for assimilate during both primordia and grain development, only the strongest sinks will be translocated to. Therefore we found the negative correlations of yield and grain number to ET at heading and then later at grain filling. Basil and terminal spikelets fail to develop while central spikelets abort some of their fertile florets. Consequently, fewer grains per spike develop.

Without the capacity to maximize grains per spike, the genetic yield potential of wheat cultivars will be difficult to achieve in South Dakota. The limitations imposed by water stress can in theory be eliminated by proper irrigation scheduling. This study indicates, however, that temperature stress is reducing yield potential even in well watered conditions. In a study on winter wheat in Washington state by Johnson, Witters and Ciha (44), warmer temperatures were found to increase ET and reduce photosynthesis. This indicated that photosynthetic reduction was not due to stomate closure but rather a temperature sensitivity in the photosynthetic process. They found water use efficiency (as measured by the ratio or photosynthesis to ET) to be greatest during cooler, cloudy days. These researchers felt early maturing cultivars that avoid a high late season heat load would have an increased water use efficiency.

In South Dakota, selecting for earliness in spring wheat cultivars should have the same benefit. Late season temperature stress appears to be a major source of yield reduction even under irrigation or during wetter growing seasons.

A second factor that a breeder could select against to increase yields is the tendancy to produce late secondary tillers. When tillering is not synchronized in a plant, the plant will have to allocate its assimilate between sinks that are at different stages of development. The temperature stress later in the growing season will be especially detrimental to the later maturing tillers. If at the vegetative stage the wheat plant allocates more assimilate to primordia development and less to tillering, the wasted production of late tillers can be avoided.

Many studies have shown the futility of selecting for an increase in the development of a particular yield component because yield component compensation will tend to alter its contribution to yield in a given environment (57). Unproductive tillering however is a wasteful utilization of resources for a plant and in fact leaves the plant with a larger, more stress susceptible canopy. Consequently tillering in a wheat cultivar should be synchronized so that all spikes are matured as early as possible.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The above average rainfalls during the 1983 and 1984 growing seasons diminished the effect of the irrigation treatments applied in this study. Therefore the influence of water stress on spring wheat development could not be studied as effectively as desired. This study does indicate, however, that temperature stress can diminish grain yields in adapted cultivars even during wet years or with irrigation.

Regression analysis shows that the development of grain yield, thousand grain weight and grains per spike are negatively correlated with ET. Evapotranspiration is highest in the plots that had more early season soil moisture and consequently produced more tillers. Therefore in 1983 the high temperatures encountered by Len at heading and both cultivars at grain filling diminished the development of grains per spike, thousand grain weight and grain yield. High tillering creates a larger canopy and the sensitivity of leaf tissue to temperature stress results in the negative correlations seen in 1983. Because of small soil moisture differences among treatments in 1984, very few significant correlations to evapotranspiration were observed.

Multiple regression of evapotranspiration at growth stages on grain yield and yield components indicates that no single stage of growth is critical to spring wheat development. Most significant models used four or five variables indicating that yield and yield component development was the result of conditions throughout the stages of plant development.

Tiller development during the growing season was significantly correlated to ET with both simple and multiple regression models. This indicates that tillering was responsive to soil moisture differences established by the irrigation treatments. Correlations are positive so unlike the other yield components, tillering increases with increasing moisture use (Tables 20-27). Other factors though besides soil moisture must influence the maintenance of productive tillers since the final tiller counts do not show these same significant positive correlations to ET (Tables 12-21). Non-productive tillers are positively correlated with ET at some stages with Butte and negatively correlated with ET for Len only at the ripe stage (Tables 28-31). The two cultivars used in this study thus behave differently in terms of tiller production and tiller maintenance. Butte tillers less in response to the early season water and is more responsive to water or temperature stress at an earlier stage of development than Len. Len is less responsive to ET differences that develop by mid-season and consequently attempts to carry more secondary productive tillers into the high temperature stress period of late July. Therefore Butte is more adapted to the type of environmental stresses encountered in South Dakota in terms of its pattern of tillering and tiller maintenance.

Path coefficient analysis shows the interactions between yield components that create the yield differences observed. They indicate that the two cultivars interacted differently in each year and differently from one another.

Both cultivars in both years have a positive correlation between grains per spike and grain yield. With Len in both years, path analysis indicates this is due to a positive direct effect while the direct effect in Butte in both years is negative. The positive indirect effect through thousand grain weight overrides the negative direct effect in Butte.

Thousand grain weight strongly influenced grain yield in both cultivars in 1983 and Butte in 1984. The correlations are mainly due to direct effects. In 1983, though, the direct effects are positive while in 1984 they are negative. Path analysis reveals that the negative direct effect in 1984 is the result of the negative correlation between grains per spike and grain weight.

Spikes per square meter showed a negative correlation to grain yield. With Butte the negative indirect effect via thousand grain weight was largely responsible while Len in 1983 had a large negative direct effect.

Butte's yield superiority to Len in both years was probably due to its earliness and ability to synchronize tiller development. Even though the change in environment from 1983 to 1984 altered the contribution of grain weight to grain yield, this cultivar was still able to out-yield Len. Apparently a higher yielding genotype should be able to reach high yield by several paths.

Earliness is a drought escape mechanism Butte utilizes to yield well despite water and temperature stress. Selection for earliness by the breeder will probably be an effective means of avoiding the yield losses that result from late season temperature stress.

Selection against genotypes that produce late secondary tillers should also be a means of avoiding late season heat stress in cultivars. Plants that produce fewer more synchronous tillers would be able to produce more grains per spike and fill those grains more effectively.

Finally, a breeder might be able to increase yield in South Dakota's environment by selecting for head types with more florets per spikelet or spikelets per spike. Path analysis emphasizes the importance of grain number to grain yield. If a genotype can produce more grains per spike during the relatively short period of head development, this would be advantageous.

Even when adequate soil moisture is available to the wheat plant, high temperatures can create deficiencies in the plant's water status. Therefore the elimination of all water stress induced yield losses may not be possible even with irrigation. In South Dakota, temperatures may even be high enough to directly restrict translocation, slow phloem loading or inhibit the photosynthetic process. Still, proper irrigation scheduling to avoid longer term water shortages should be an effective means of stabilizing grain yield in an environment as variable as South Dakota's. Scheduling applications and determining rates will depend upon factors such as soil type and environmental conditions of that season. Therefore a proper schedule will change with years and with locations. Temperature stress probably lowers the yield potential for adapted cultivars, however, and spring wheat producers should consider this restriction when estimating the potential economic benefits of investing in irrigation.

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LIST OF APPENDICES TABLES

Table A-1. Yield, yield components and protein at each treatment for Butte in 1983.

Treat-ment	YLD (Mg/ha)	1000 Grain Wt. (g)	Percent Protein	Grains Per Spike	Productive Spikes Per Sq. Meter	Non-Prod. Spikes Per Sq. Meter
1	3.58	25.30	15.24	31.50	484.25	58.50
2	3.12	24.88	15.76	32.85	793.00	52.00
3	2.89	23.98	16.26	30.75	575.25	45.50
4	2.75	25.50	16.26	35.60	705.25	78.00
5	2.69	24.52	16.42	29.65	581.75	123.50
6	2.89	24.01	16.36	30.55	617.50	58.50
7	2.49	24.16	17.08	32.85	546.00	104.00
8	2.65	24.18	16.26	33.65	653.25	113.75
9	2.46	23.97	16.82	32.00	711.75	120.25
10	2.50	23.06	16.64	27.90	718.25	81.25
11	2.93	24.13	15.90	33.70	627.25	133.25
12	3.04	23.86	15.92	31.50	594.75	139.75
13	3.08	25.06	15.66	32.15	516.75	74.75
14	3.00	25.67	15.66	33.70	607.75	55.25
15	2.94	25.79	15.44	31.15	490.75	81.25
16	3.25	26.19	15.40	32.15	516.75	61.75
17	3.16	26.27	15.40	33.85	637.00	39.00
18	3.33	26.81	15.52	34.45	617.50	35.75
19	3.54	26.73	15.58	30.95	624.00	35.75
20	3.68	26.62	15.50	33.10	627.25	45.5
21	3.31	26.94	15.34	32.60	552.50	35.75

Table A-2. Yield, yield components and protein at each treatment for Len in 1983.

Treatment	YLD (Mg/ha)	1000 Grain Wt. (g)	Percent Protein	Grains Per Spike	Productive Spikes Per Sq. Meter	Non-Prod. Spikes Per Sq. Meter
1	3.22	26.63	15.74	28.75	633.75	94.25
2	2.80	27.21	15.62	30.00	650.00	74.75
3	2.81	26.92	16.04	28.95	598.00	68.25
4	2.74	26.19	16.20	31.55	640.25	65.00
5	2.47	25.59	16.40	27.25	676.00	94.25
6	2.63	26.14	16.84	25.45	568.75	48.75
7	2.55	24.62	16.36	28.40	650.00	65.00
8	2.36	25.20	16.58	27.45	715.00	87.75
9	2.36	24.98	16.76	26.80	734.50	68.25
10	2.60	25.02	16.34	25.15	572.00	45.50
11	2.91	25.60	16.10	27.85	711.75	68.25
12	2.88	26.17	16.08	28.50	718.25	81.25
13	2.80	25.18	15.90	30.45	614.25	52.00
14	2.92	26.18	16.02	30.65	627.25	81.25
15	2.85	25.78	15.84	30.55	637.00	107.25
16	2.88	26.72	16.00	30.55	656.50	123.50
17	2.84	26.59	15.94	31.25	575.25	91.00
18	2.91	26.53	15.94	29.70	672.75	100.75
19	2.87	26.57	15.86	30.05	575.25	68.25
20	3.19	26.44	15.54	30.00	526.50	78.00
21	3.13	26.31	15.44	28.85	598.00	87.75

Table A-3. Yield, yield components and protein at each treatment for Butte in 1984.

Treat-ment	YLD (Mg/ha)	1000 Grain Wt. (g)	Percent Protein	Grains Per Spike	Productive Spikes Per Sq. Meter	Non-Prod. Spikes Per Sq. Meter
1	4.81	29.14	15.10	29.55	617.50	19.50
2	5.03	29.60	15.22	32.15	744.25	48.75
3	4.83	29.38	14.88	31.45	741.00	29.25
4	5.11	29.16	15.08	29.45	718.25	81.25
5	5.28	27.86	14.86	30.85	737.75	32.50
6	5.02	28.58	14.78	28.25	832.00	61.75
7	4.97	29.64	14.88	29.35	718.25	65.00
8	5.20	27.96	15.44	33.00	702.00	39.00
9	5.16	28.00	15.05	32.50	650.00	71.50
10	5.06	28.90	15.12	32.70	721.50	26.00
11	5.09	27.98	14.94	33.45	718.25	26.00
12	4.95	28.78	15.30	32.60	637.00	26.00
13	5.10	27.28	14.96	33.20	614.25	42.25
14	5.53	28.38	15.12	31.15	672.75	87.75
15	5.26	27.78	15.00	32.80	620.75	74.75
16	5.30	28.36	14.88	33.70	659.75	55.25
17	5.08	28.32	14.58	30.60	627.25	68.25
18	5.02	29.02	14.84	31.60	711.75	100.75
19	4.99	28.62	15.30	30.60	656.50	55.25
20	5.31	28.40	15.22	30.60	663.00	48.75
21	5.16	28.22	14.94	35.40	477.75	35.75
22	5.14	28.90	14.56	35.25	672.75	45.50
23	5.47	28.42	15.54	29.50	659.75	58.50

Table A-4. Yield, yield components and protein at each treatment for Len in 1984.

Treat-ment	YLD (Mg/ha)	1000 Grain Wt. (g)	Percent Protein	Grains Per Spike	Productive Spikes Per Sq. Meter	Non-Prod. Spikes Per Sq. Meter
1	4.78	27.70	15.38	28.15	633.75	104.00
2	4.17	26.72	14.72	29.30	581.75	81.25
3	4.43	27.00	14.96	27.70	676.00	74.75
4	4.52	25.46	15.10	26.40	727.50	78.00
5	4.70	26.20	14.94	26.85	640.25	19.50
6	4.67	27.06	14.88	27.95	724.75	22.75
7	4.84	27.18	15.12	29.95	627.25	55.25
8	4.69	26.62	15.04	25.15	695.50	45.50
9	4.87	26.90	15.00	29.95	630.50	26.00
10	4.67	27.00	15.04	30.20	539.50	35.75
11	4.51	26.78	15.74	25.80	636.50	32.50
12	4.60	27.58	15.06	27.80	695.50	58.50
13	4.58	27.52	15.06	27.00	676.00	84.50
14	4.02	27.22	15.42	26.45	640.25	58.50
15	4.37	28.08	14.74	33.95	640.25	65.00
16	4.86	27.46	15.16	29.65	565.50	48.75
17	4.64	27.92	14.96	30.10	594.75	48.75
18	4.53	27.30	15.08	30.60	656.60	48.75
19	4.76	27.90	15.04	29.10	718.25	58.50
20	4.84	26.78	15.36	29.35	663.00	68.25
21	4.65	27.20	15.36	29.55	630.50	81.25
22	4.64	26.60	15.02	30.60	724.75	45.50
23	4.91	26.20	14.96	31.40	646.75	45.50

Table A-5. Water applied (mm) with irrigation at each growth stage for each treatment in 1983.

	GROWTH STAGE							
Treat-ment	Tiller-ing	Jointing	Boot	Head-ing	Anthe-sis	Milk	Dough	Ripe
1	-	-	-	-	-	-	-	20.3
2	-	-	-	-	-	-	-	22.9
3	-	-	-	-	-	-	-	24.1
4	-	-	-	-	-	-	-	33.0
5	-	-	-	-	-	-	-	33.0
6	-	-	-	-	-	-	-	53.3
7	7.7	-	-	-	-	-	-	71.1
8	7.7	-	-	-	-	-	-	90.2
9	20.3	-	-	-	-	-	-	101.6
10	33.0	-	-	-	-	-	-	106.7
11	33.0	-	-	-	-	-	-	111.8
12	43.2	-	-	-	-	-	-	115.6
13	43.2	-	-	-	-	-	-	68.6
14	43.2	-	-	-	-	-	-	73.7
15	27.9	-	-	-	-	-	-	57.2
16	27.9	-	-	-	-	-	-	45.7
17	27.9	-	-	-	-	-	-	33.0
18	10.2	-	-	-	-	-	-	31.8
19	10.2	-	-	-	-	-	-	24.1
20	-	-	-	-	-	-	-	27.9
21	-	-	-	-	-	-	-	22.9

Table A-6. Water applied (mm) with irrigation at each growth stage for each treatment in 1984.

GROWTH STAGE

Treatment	Tillering	Jointing	Boot	Heading	Anthesis	Milk	Dough	Ripe
1	-	-	-	30.5	5.3	-	20.8	-
2	-	-	-	30.5	2.5	-	21.8	-
3	-	-	-	20.3	8.9	-	21.3	-
4	-	-	-	24.1	17.8	-	30.7	-
5	-	-	-	22.9	21.1	-	27.2	-
6	-	-	-	21.6	30.5	-	30.7	-
7	-	-	-	19.1	35.1	-	36.8	-
8	-	-	-	19.1	35.8	7.6	37.6	7.6
9	-	-	-	19.1	37.3	12.7	33.5	12.7
10	-	-	-	19.1	35.1	20.3	33.0	20.3
11	-	-	-	22.9	48.5	35.6	43.2	33.0
12	-	-	-	25.4	39.4	40.6	44.5	43.2
13	-	-	-	30.5	34.8	43.2	36.3	40.6
14	-	-	-	21.6	20.3	38.1	22.1	40.6
15	-	-	-	17.8	12.7	38.1	20.8	38.1
16	-	-	-	17.8	8.1	38.1	17.0	38.1
17	-	-	-	17.8	-	35.6	16.5	40.6
18	-	-	-	17.8	-	30.5	15.7	43.2
19	-	-	-	22.9	-	20.3	30.7	22.9
20	-	-	-	22.9	-	17.8	40.9	17.8
21	-	-	-	19.1	-	8.9	30.7	12.7
22	-	-	-	17.8	-	2.5	25.4	7.6
23	-	-	-	25.4	-	5.3	31.2	5.1

Table A-7. Establishment of water gradients using three line sources.