PHOTOSYNTHETIC CHARACTERISTICS OF SOUTHERN GREAT PLAINS HARD RED WINTER WHEAT CULTIVARS AND THEIR RESPONSE TO GRAZING STRESS

By

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LIST OF NOMENCLATURE

A	Photosynthetic Carbon Assimilation Rate, umol carbon m^{-2} s^{-1}
Chl a b^{-1}	Chlorophyll *a* to *b* Ratio
Chl_{tot}	Total Chlorophyll, g chlorophyll m^{-2}
E	Transpirational Water Loss, mmol water vapor m^{-2} s^{-1}
ETR	Electron Transport Rate, umol electrons m^{-2} s^{-1}
g_s	Stomatal Conductance to Water (unless noted otherwise), mol water vapor m^{-2} s^{-1}
HRW	Hard Red Winter Wheat
K	Water Use Efficiency Factor (WUE*VPD), expressed in relative units
LAI	Leaf Area Index, expressed as m^2 foliage (m^{-2} ground)
MTA	Mean Tilt Angle, expressed as degrees from the horizontal
NPQ*	Non-Photochemical Fluorescence Quenching Coefficient
PAR	Photosynthetically Active Radiation, umol photons m^{-2} s^{-1}
PSI, PSII	Photosystems one and two, respectively
q_N*	Non-Photochemical Fluorescence Quenching Coefficient
q_P	Photochemical Fluorescence Quenching Coefficient
RWC	Relative Water Content, %
VPD	Vapor Pressure Deficit, kPa
WUE	Water Use Efficiency, (umol CO_2 m^{-2} s^{-1}) (mol water vapor m^{-2} s^{-1})$^{-1}$

*Alternative methods of calculating the coefficient

INTRODUCTION

Winter Wheat Importance, History, and Evolutionary Aspects

Wheat has been a keystone crop for thousands of years and continues to top the list of dry matter food production the world over (Harlan, 1992). Wheat provides one-fifth of the world's total food calories, 60 to 80 % of the world's carbohydrates, and 14 to 18 % of the world's protein (Zohary and Hopf, 1993). *Triticum aestivum* (bread wheat) and *Triticum durum* (macaroni wheat) are the most widely grown wheat species today. *Triticum aestivum* is distinguished above *T. durum* due to its high-rising ability, a desired quality in bread baking. Currently, 90 % of the wheat grown is *T. aestivum* and it is gleaned from 500 million ha of land (Zohary and Hopf, 1993; Sauer, 1994).

Triticum aestivum is a self-pollinated, free-threshing plant from the *Gramineae* (grass) family (Sauer, 1994). This hexaploid species probably originated in the Caspian region and the area that is now Iran, through a cross of *Aegilops squarrosa* (a wild diploid wheat) and *T. turgidum* (emmer wheat) (Harlan, 1992; Zohary and Hopf, 1993; Sauer, 1994). This wheat soon became popular and spread through Asia and Europe and was brought to the United States with the colonists. In the state of Oklahoma, most of the cultivars grown today are descendents of Turkey Red, a hard red winter (HRW) wheat cultivar that was brought to Kansas by Crimean immigrants in the late nineteenth century (Sauer, 1994). Turkey is not grown by producers today, but it provided the germplasm to become the cornerstone of what is now the breadbasket of the world.

Triticum aestivum breeding programs have been established at many land grant institutions with the intention of improving cultivar yields for the state, nation, and world. During the first couple of decades of breeding, these programs produced new HRW wheat cultivars and distributed the new seed to producers in their state without regard for genetic diversity. Due to common ancestry from Turkey germplasm, the uniform varieties were more susceptible to disease and pests (Cox et al., 1986; Carver et al., 1989). As a result, it soon became necessary to direct breeding programs not only toward increasing yield, but also to disease and pest resistance. The development and proper use of herbicides and pesticides had an important impact on grain yields in conjunction with breeding efforts. Significant strides have been made toward increasing the number of cultivars available to producers. The International Maize and Wheat Improvement Center (CIMMYT) had more than 1.7 million wheat genotypes in its 1997 International Wheat Information System (IWIS).

With the introduction of genetically improved cultivars, prominent morphological characteristics have emerged. Cultivars have become shorter, moving from tall cultivars like Turkey to shorter-stature cultivars known as semidwarfs (Austin et al., 1980; Sauer, 1994). Khan and Tsunoda (1970) and Evans and Dunstone (1970) noticed larger leaves had emerged throughout the evolution of semidwarfs. In contrast, Austin et al. (1980) found no significant differences between old and modern leaf area indices (LAI) and mass, but noted lower stem weights had developed. It appears modern cultivars have shifted their emphasis from height to other important physical traits. Were these morphologic changes brought upon by physiologic alterations designed to bring about increased yields and disease resistance, or some other purpose? Cox and colleagues (1988) evaluated cultivars released from 1919 to 1987 and found a 0.6 % increase in yield per year (40.8 % total), and a little smaller increase per year in water stressed environments. Feyerherm et al. (1984) estimated HRW wheat yield increases ranged between 25 to 35 % from 1900 to 1970.

Most researchers in wheat evolution agree morphology has changed, resulting in increased yields with year of release, but they don't agree as to the cause. Feyerherm et al. (1984) argue that the large improvements in yield of HRW wheat are due primarily to genetically bred increases in stress resistance. An exception to this, however, is in areas where environmental conditions limit soil moisture and produce high temperatures during critical growth stages. These conditions have been improved in many areas by providing the most limited resource, water, to cropland through irrigation (Boyer, 1982). In addition, when genetic changes were made to improve the cultivars, if they weren't photosynthetic in nature, they increased water requirements in relation to dry matter increases (Austin et al., 1980).

Other authors agree yield increases are due to the shorter stature of the modern cultivars. This shorter stature allows them to be more efficient by reallocating energy otherwise used for height to increase tillering and thus dry matter production (Simpson, 1968; Austin et al., 1980; Sinha et al., 1981). The increased grain yield has been credited to variety improvement through increasing harvest index (ratio of grain yield to grain and straw yield) (Austin et al., 1980; Martin and Kiyomoto, 1985). The shorter cultivars also benefited because they have decreased lodging (Austin et al., 1980). According to Sinha et al. (1981), modern cultivars respond more to nitrogen fertilization than older varieties. Furthermore, A was shown to increase with nitrogen fertilization in dwarf wheat. This was possibly due to increased chlorophyll content, stomatal conductance (g_s) or ribulose-1,5-bisphosphate carboxylase (Rubisco) activity. Therefore, the photosynthetic carbon assimilation rate (A) not only provides assimilates for plant growth, but also affects water status and ultimately wheat yields. In conclusion, the importance of *T. aestivum* to nations around the world has directed the history and evolution of the species. Many improvement programs have striven and are continuing to strive to optimize the interactions between yield contributors of wheat: A, water status, nutrient status, morphological status (lodging), and other environmental and genetic factors.

Winter Wheat Importance and Impact on the southern Great Plains

Hard red winter wheat is widely grown throughout the southern Great Plains in states such as Kansas, Oklahoma, and Texas. In these states, many acres are planted in fall, grown throughout winter, and harvested in late spring. Many of the acres, however, are planted late summer, grown through fall, grazed in winter, and harvested late spring. This is a unique situation from which producers are able to achieve two crops: forage and grain. In 1998, Epplin et al. estimated that 66% of Oklahoma's wheat acres were grazed in this manner. With this dual-purpose practice, producers are given the opportunity to divide their risk. If stocker cattle are priced well and grain returns are low, then management can be shifted to utilize the wheat more for forage and vice versa.

Dual-purpose cropland continues to be a challenging management practice for producers in the southern Great Plains. It is imperative to carefully select planting dates and cultivars as well as optimum stocking rates and foraging timing. These added concerns make the dual-purpose management system more complicated than the normal rigors of a grain-only management system.

Dependent upon location and weather conditions, producers normally plant their HRW wheat in August or September for dual-purpose, and late September or October for grain-only systems (Winter and Thompson, 1987). Planting dates are crucial to either system; to have sufficient growth for winter foraging, the wheat must be planted early without compromising stress, pest and disease tolerance. For instance, for wheat planted in mid-August for a dual-purpose system, the cultivar seedling must be able to withstand water stress (Redmon et al., 1995), summer insect pressure, increased disease pressure, and a whole host of other stresses it may not have been genetically designed to resist.

Selecting the correct cultivar to maximize economic return for the dual-purpose management system also continues to challenge producers in the southern Great Plains. Genetically, cultivars have not been developed for this type of management. Breeders have selected and manipulated cultivars based on grain yield or stress resistance in a grain-only system, not on maximizing forage dry matter production and grain yield (Krenzer et al., 1992; Horn et al., 1995; Redmon et al., 1995; Krenzer et al., 1996). It is difficult, then, to select the best cultivar for both purposes. Only a few researchers have tried to analyze the fitness of grain-only cultivars for dual-purpose systems. Carver and colleagues evaluated twelve different cultivars (released from 1919 to 1997) near Marshall, Oklahoma in 1997 and found no increase in yield per year of release under the dual-purpose system (unpublished data). It has also been noted that grazed, tall cultivars suffer less lodging and are able to withstand greater leaf area removal than semidwarf cultivars (Redmon et al., 1995). Semidwarf, dual-purpose yields have surpassed grain-only yields only when grazing was terminated early in the season or poor soil fertility could not support a grain-only system (Pumphrey, 1970; Dunphy et al., 1982; Dunphy et al., 1984; Winter and Thompson, 1987; Redmon et al., 1995). Clearly, more research needs to be conducted to identify plant characteristics that maximize both grain and forage yields. This would enable breeders to begin selecting cultivars for this specific management system.

Foraging dates are crucial in determining dual-purpose success and failure. There must be adequate fall growth before stocking. The grazing start date, however, does not appear to be as imperative as the removal date. Dumphy et al. (1982, 1984) conducted studies in Texas and noted jointing as the critical stage for grazing termination. Jointing is the stage that is often referred to as 'internode elongation' and produces the stem that supports the grain head; this stage ends with the emergence of the flag leaf. They found forage removed after jointing caused significant decreases in yield. Winter and Thompson (1987) determined the variety TAM 105 could be grazed until the first of February before losing yield. In Oklahoma, the most definitive paper on this subject concluded that the most economically feasible time to terminate grazing HRW wheat is the first hollow stem stage (Redmon et al., 1996). This stage occurs before the wheat crown (growing point of the young seedling) emerges from the soil. The authors believe this is a superior method because it is more reliable than depending on calendar dates, which can vary from year to year due to weather or other dynamic factors. The method producers select to optimize forage and grain returns needs to depend on their ability to identify wheat growth stages as well as their yield goals and resources.

OBSERVATIONS

Past research is lacking on whether photosynthetic changes have occurred over the past decades of breeding HRW wheat cultivars important to the southern Great Plains. It is also unclear whether modern cultivar yields have increased due to better 'source' capacity and efficiency, superior 'sink' allocation, or some other mechanism. Photosynthetic organization and function ('source'), in particular, may be able to shed much light onto mechanistic reasons for increasing yields. The chief goals of researchers in this area are to make this primary function more efficient and maximal, while optimizing carbon allocation to economically important plant organs.

Photosynthesis, or in more measurable terms, carbon assimilation (A), is dependant on many factors. Maximal assimilation can be limited by photosynthetically active radiation (PAR), leaf area, stomatal density and g_s, chlorophyll concentrations and distribution, Rubisco activity, ribulose-1,5-bisphosphate (RuBP) regeneration and carbohydrate demand, to name a few (Dunstone et al., 1973; Shimshi and Ephrat, 1975; Farquhar et al., 1980; Sinha et al., 1981; Austin et al., 1982; Farquhar and Sharkey, 1982; Ellison et al., 1983; Rawson et al., 1983; Austin et al., 1984; Johnson et al., 1987). Photosynthesis and its components can be measured, quantified, and related to HRW wheat cultivars grwon over the past century in the southern Great Plains to identify significant differences and possible reasons for increases in yield.

The dual-purpose HRW wheat management system utilized in the southern Great Plains has been under-served by land-grant breeding programs (Krenzer et al., 1982; Redmon et al., 1995; Krenzer et al., 1996). Very few cultivars have previously been evaluated for superior forage and grain yield. Virtually no extensive studies have been conducted to quantify how basic 'source' differences impact both forage and grain yields (Pumphrey, 1970; Dunphy et al., 1982, Winter and Thompson, 1987; Krenzer et al., 1992; Horn et al., 1995; Redmon et al., 1995). These answers may be key in identifying characteristics that maximize wheat forage and grain yields so that breeders can begin selecting cultivars for both management systems in the southern Great Plains.

OBJECTIVES OF EXPERIMENTAL STUDY

1. Assess changes in A that may have occurred over the past decades of breeding HRW wheat cultivars important to the southern Great Plains.
2. Characterize and appraise dual-purpose production system effects on photosynthetic components of cultivars grown throughout the century.
3. Identify which photosynthetic components are significantly correlated with yield.
4. Conclude whether the gas exchange and chlorophyll fluorescence techniques employed in this study will be valuable tools for breeders to utilize in screening new cultivars for grain-only and dual-purpose systems.

MATERIALS AND METHODS

Plant Materials and Experimental Design

Twelve cultivars were selected according to their importance to the history of wheat breeding for the southern Great Plains and especially for Oklahoma. Table 1 indicates the release date for each cultivar as well as the breeder(s) credited with developing each cultivar, known disease resistance, and special characteristics.

The 1997-1998 and 1998-1999 experimental field site was located near Marshall, Oklahoma, which is situated in the north-central region of the state, in the heart of dual-purpose production acres. The soil mapping unit is kirkland silt loam (kb), with one to three % slopes. Characteristic of these soils, the upper profile is slightly acidic, with higher pH in the deeper subsoil region (Anonymous, 1960). For season 1997-1998, a soil sample was collected from throughout the site on August 27, 1997, the planting date of the dual-purpose plots. The soil pH was 5.2, with total available nitrogen at 27,776 kg km^{-2} (248 lbs ac^{-1}) (after anhydrous ammonia applied at 13,440 kg km^{-2} (120 lbs N ac^{-1})), and phosphorus and potassium were sufficient for our yield goals. In season 1998-1999, soil testing was done in July for the whole field. Soil pH was 4.7, leading to the decision to lime with two tons ECC (effective calcium carbonate) in July. Anhydrous ammonia was applied in August to bring the total available soil N to 20,832 kg km^{-2} (186 lbs ac^{-1}). Once again, phosphorus and potassium were sufficient for our yield goals. The previous cropping system on this land has been continuous wheat, a practice most producers in the region employ.

The dual-purpose plots were planted September 3, 1997 and September 28,1998, while the grain-only plots were planted on October 7, 1997 and October 16, 1998. Stocker cattle grazed the dual-purpose plots from October 28, 1997 to February 23, 1998 and November 17, 1998 to February 23, 1999.

Plots were arranged in two randomized complete block designs (RCBD) with five blocks for each treatment (grain only and dual-purpose). One block consisted of twelve plots (one of each cultivar) arranged at random. Plots had five rows each, were 1.2m wide and 3m long. Plots were treated with "Tilt" fungicide at a rate of 29.2 L km^{-2} (4 fl.

oz. per acre, at growth stage 8, when the flag leaf is emerging) in both years. "Baylaton" fungicide was also applied in 1997 at a rate of 14.6 L km^{-2} (2 fl. oz. per acre, at growth stage 10.6, when heading is taking place). These applications were designed to decrease disease interference. The blocks of wheat were separated by fill rows of a cultivar not included in the study. Plot rows were east-west facing in season 1997-1998, and north-south facing in season 1998-1999. Only mid-plot plants were included in the study to eliminate any edge effects. Yield data from each plot (reported in kg ha^{-1}) was collected by Dr. B. F. Carver's group and was used by permission. During the spring of 1999, plots were infected with soil borne mosaic and spindle streak mosaic viruses.

Evaluation of Plant Fitness in the Field

For the sake of convenience, relative water content, chlorophyll content, leaf area index, and mean tilt angle are pooled under the term fitness.

Relative Water Content

Relative water content (RWC) provides a baseline to evaluate the plant fitness under given environmental conditions. Sinclair and Ludlow (1985) argue physiological responses of plants are more highly correlated with RWC than with water potential. Measurements of RWC were conducted by clipping the last fully expanded leaf of one plant per plot at mid-day, tightly sealing it in a vial, and placing it on ice. This was completed for each plot, by sampling according to the randomization already present in each block. Once back in the lab, fresh weights (W_f) were measured and the vials partially filled with nanopure water. The turgid weights (W_t) were taken 24 hours later, followed by drying to constant weight in a 70°C oven to obtain dry weight (W_d).

Relative water content was calculated as: $RWC = 100 (W_f-W_d) (W_t-W_d)^{-1}$. Relative water content was evaluated only during spring and fall of 1998. These sampling periods were selected because meaningful differences between cultivars were anticipated only under conditions of moderate water stress and the only times where these conditions were present were during the spring and fall of 1998 (Oklahoma Mesonet Climatological Data).

Chlorophyll Content

Knowledge of chlorophyll content per unit leaf area (Chl_{tot}) is important in providing information about the light harvesting machinery prevalent in each cultivar. A cultivar's capacity to harvest light energy due to chlorophyll differences has been shown to impact A (Austin et al., 1982, Austin et al., 1983, Ellison et al., 1983). Chlorophyll content may also be an evolutionary important response to different types of stresses, perhaps even foraging stress. Chlorophyll content was determined by collecting a sample consisting of several fully expanded leaves from each plot. These samples were tightly sealed in vials and kept in an ice chest until back in the lab, where leaf areas were measured with a LI-3000 portable leaf area meter (LI-COR, Inc., Lincoln, NE). Total chlorophyll (Chl_{tot}) was extracted according to the procedure of Arnon (1949). The leaves were quantitatively homogenized in 80% acetone. The absorbencies of each sample was analyzed by a Spectronic 1201 spectrophotometer (Spectronic Instruments, Inc., Rochester, NY) using the multiple wavelength function set at these three points: 645 nm, 665 nm, and 720 nm. The first two wavelengths represent the absorption peaks of chlorophyll *b* and *a* in 80% acetone respectively. The 720nm wavelength is included to correct for possible light scattering by subtracting the value from the value at each of the other two wavelengths. The correction was always very small. In a perfect chlorophyll solution, the absorbance at 720nm should be zero because chlorophyll doesn't absorb this wavelength. Samples were collected and evaluated May and November, 1998 and also March and May, 1999. These dates were selected so that differences in dual-purpose production system effects could be noted (before foraging: November, 1998; after foraging: March, 1999) and so that A at the important flag leaf stage could be assessed (May, 1998 and 1999).

Growth Habit

Cultivars with different growth habits may have different photosynthetic responses to foraging. We anticipated that plots with low forage health and dry matter production would have low LAI, so we wanted to quantify these indices as well as the mean tilt angles (MTA) of leaves from the soil surface. Although an indirect method was employed in this study, these LAI measurements can be accurate, repeatable and reliable estimates. The LAI-2000 Plant Canopy Analyzer (LI-COR, Inc., Lincoln, NE) conveniently calculates LAI and MTA by measuring light transmittance through the leaf canopy. It is equipped with circular detectors which measure five distinct angles of light interception by the LAI-2050 optical sensor. To conduct plot LAI measurements, one above-canopy measurement was combined with three below-canopy measurements and repeated twice at different locations within each plot. The average LAI and MTA were calculated for each plot. Growth habit determinations were made during March and May of 1999 to quantify differences in spring growth, recovery after grazing, and differences in grain-filling characteristics of flag leaves.

Evaluation of Photosynthetic Characteristics

Gas Exchange Measurements.

Leaf CO_2 assimilation rate (A) was measured in 1998 using, the LI-6200 'closed system' and in 1999 using the LI-6400 'open system' (LI-COR, Inc., Lincoln, NE). The LI-6200 measures A by monitoring the length of time a leaf takes to draw down the CO_2 concentration in the air by a fixed amount. The LI-6400 mixes CO_2 into the air going into the chamber so that it is at a set CO_2 concentration, then measures the CO_2 concentration of air coming out of the chamber and calculates A from the difference in the two CO_2 concentrations and the air flow rate. Both of these systems were ideal for our measurements in the field because we were able to monitor leaf environmental characteristics such as PAR, relative humidity, and temperature. From this information, we were able to keep variability between plot measurements and days to a minimum. Along with A, other important factors were measured by the systems were stomatal conductance to water vapor (g_s), transpiration (E), and water use efficiency (WUE). The general equations used to calculate these parameters are given in appendix A.

All measurements were conducted at mid-day on the last fully expanded leaf between 1000 and 1500 μmol photons m^{-2} s^{-1}, which is at or above light saturation for wheat (Austin et al., 1984). The leaf was equilibrated in the chamber for about 60 seconds before sampling. When using the LI-6200, the draw down was set at seven uL CO_2 L^{-1} air while the LI-6400 took an instantaneous reading after a brief equilibration period. Between measurements, the chamber was shaded to minimize heating due to direct sunlight.

Fluorescence Measurements.

By studying fluorescence, the research was designed to try to visualize more details involved in the biochemistry of photosynthesis. We utilized fluorescence measurements as a method to assess the specific relationships between the two photosystems of the light reaction of photosynthesis and between the light reaction and dark reactions. At normal measurement temperatures, chlorophyll fluorescence is emitted by photosystem II (PSII) and almost exclusively reflects its status. Through several measured and derived parameters, however, fluorescence measurements can indicate conditions of both systems. When the PS II harvests light energy, the energy can be dissipated by several means: photosynthesis, heat, spillover to PSI, or fluorescence (Schreiber and Bilger, 1987; Bolhar-Nordenkampf and Oquist, 1993; Bjorkman and Demmig-Adams, 1995).

As an indicator of stress, PS II is ideal because it is one of the most susceptible processes. Bolhar-Nordenkampf and Oquist (1993) have found it useful for indicating stresses such as water limitations and temperature extremes. Karavaev et al. (1997) found positive correlations between the ratio of the fluorescence parameters $Fv\ Fm^{-1}$ to the rate of A per mg chlorophyll. Bjorkman and Adams (1995) found fluorescence to be a beneficial assay for stressed plants or plants with a lower photosynthetic capacity. Fluorescence has become an essential tool to many researchers interested in photosynthesis because these photosynthesis parameters currently can't be obtained in any other way *in vivo*.

Two major types of fluorescence tests can be referred to as dark-adapted measurements and modulated fluorescence kinetics measurements in the light (Schreiber et al., 1987). The parameters gained from the first test are Fo, Fm and Fv; and the ones gained from the second test are F, Fm', and Fo'. The term Fo refers to the minimum fluorescence emitted by chlorophyll in dark-adapted leaves with all PSII reaction centers open (Schreiber and Bilger, 1987; Krause and Weis, 1991). Fm reflects the maximal fluorescence value when all reaction centers are closed, as would be the case in a leaf exposed to a very bright light pulse (Schreiber and Bilger, 1987; Krause and Weis, 1991). F is the 'steady state' fluorescence from a sample that is being exposed to normal light as in the field, while Fm' is the maximal fluorescence produced when the illuminated sample is exposed to a bright saturating light pulse (Anonymous, 1993). The term Fo' should represent the same thing as Fo except some quenching of Fo might have developed in the light, such as from photoinhibition. For an example of these concepts and how key parameters are derived by pulse amplitude modulated chlorophyll fluorescence techniques, please refer to Appendix A.

In this study, a method similar to that of Rikika et al. (1997) was followed. The OS-500 Modulated Fluorometer (Opti-Sciences, Haverhill, MA) was fitted with a fiberoptic light guide and an open temperature/ PAR leaf clip that angles the face of the light pipe approximately 30 degrees relative to the plane of the leaf at a distance of 13 mm. To evaluate Fo and Fm, several fully expanded leaves were gathered from each plot early in the morning (before PS II was activated in the morning sun) and packed on ice in darkness. Once in the lab, dark-adapted fluorescence measurements were made. Leaves were placed into the PAR/ temperature clip and far-red light was applied for 10 s. Then a saturation pulse of PAR 8,630 umol $m^{-2} s^{-1}$ was used for 0.8 s. The modulation intensity was fixed at a PAR of 0.13 umol $m^{-2} s^{-1}$, while detector gain was at a setting of 60. The fluorescence measurements in the field were conducted at mid-day in full sunlight with the temperature/ PAR open clip in the same configuration as for the dark-adapted leaves. The protocol in the field was a 0.8 s saturation pulse, followed by darkening under a black cloth, 10 s far-red, and a Fo' measurement. In the dark-adapted test, the purpose of the far-red light was to drain Q_A of electrons to obtain a correct Fo. During the kinetic measurements in the field, pulses evaluated the quenching coefficients (discussed later) under conditions of normal A in the field. The far-red light was used to drain Q_A of electrons to allow measurement of Fo' (which should be the same as Fo unless photoinhibition has occurred).

The information gained from fluorescence doesn't end with measured values. Several important factors can be calculated. Fv is known as the variable fluorescence and is calculated as the difference between Fo and Fm. Two other important factors that were determined are q_P (the photochemical quenching coefficient) and q_N (the non-photochemical quenching coefficient). Photochemical quenching represents the oxidation state of the PS II electron acceptor (Q_A), while non-photochemical quenching is thought to consist of several components: the build-up of the proton gradient across the thylakoid membrane (qE), the 'state 1' to 'state 2' transition related to phosphorylation of some chlorophyll-protein complexes of the light harvesting antennae (qT), and photoinhibition of photosynthesis (qI) (Schreiber and Bilger, 1987; Krause and Weis, 1991). The calculations for each are as follows: $qP = (Fm'-F)\,(Fm'-Fo')^{-1}$, $q_N = (Fm-Fm')\,(Fm-Fo')^{-1}$. Additionally, the electron transport rate can be found by multiplying yield, $(Fm'-F)\,(Fm')^{-1}$, by 0.5 and 0.84 (Anonymous, 1993; Havaux et al., 1991). Because two photons are needed to move one electron through both photosystems, 0.5 is included, while 0.84 represents the typical percentage of PAR absorbed by photosynthetic pigments.

Statistical Analyses

The field and laboratory data collected spring 1998 and 1999 for each photosynthetic characteristic was compiled for each grazing treatment and an analysis of variance was performed in SAS (Statistical Analysis System, SAS Institute, Inc., Cary, NC) using the procedure 'Proc Mixed'. Dual-purpose blocks were analyzed separately from grain-only blocks. Blocks and year (1998 and 1999) were considered random effects while cultivar was the main effect in which this research was interested. November, 1998 and March, 1999 sampling dates were also analyzed (separately) for significant effects. Again, block was a random effect and cultivar was the main effect. Least significant difference (LSD) tests were conducted when significant main effects were found. In addition, simple linear regression/correlation using cultivar means was applied when cultivar effects were significant. In these comparisons, the oldest cultivar, Turkey, was omitted in the calculations due to high influence on the fitted line and difficulties in assigning a meaningful year of release.

RESULTS

The grain yield results, averaged over both 1998 and 1999, illustrate the expected and observed trends by producers and researchers alike. Figure 1 clearly demonstrates how breeding has remarkably increased this plant trait. This figure was produced from the means of each cultivar across both field seasons for each grazing treatment. Grain-only yields were significantly and positively correlated with year of release (r^2= 0.72, p=0.001). Dual-purpose managed grain yields were also significantly correlated with year of release (r^2=0.52, $p<0.05$). If the mean grain yields for each cultivar between the two grazing treatments is compared, every cultivar except 'Turkey' had higher grain yield in the grain-only environment than in the dual-purpose environment. It should also be recalled that the cattle were removed at the most desirable time, first hollow stem stage, and there was still a marked difference between grain yields under the two production systems.

GRAIN-ONLY RESULTS

Plant Fitness

There were no significant differences in plant fitness characteristics between cultivars in fall 1998. Significant differences were found between cultivars in both pre and postanthesis spring measurements as presented in Table 2. In March of 1999, significant differences were found in Chl_{tot} and LAI. As shown in Table 3, cultivars 'Triumph 64', '2163', and 'Karl 92' had the lowest Chl_{tot}, and 'TAM W-101' had the highest. Although the differences between cultivars were significant, there was no significant correlation found with either year of release or grain yield. Significant, positive relationships were found between postanthesis 1999 LAI and year of release (r^2=0.37, $p<0.05$) and is represented in Figure 2. Also noted in Figure 2, the same general trend was found in preanthesis 1999 measurements, but the trend was not found to be significant. Neither pre nor postanthesis LAI was found to be significantly related to grain yield.

Cultivar effects for postanthesis, combined spring 1998 and 1999 were significant ($p<0.05$) for Chl a b^{-1} ratio in the grain-only environment (Table 2). The LSD results are listed in Table 4. When tested for correlation, spring 1998 and 1999 Chl a b^{-1} ratios were not significantly correlated with year of release or grain yield. However, LSD results did not appear consistent for each year alone. This led to the reason for testing whether results were consistent over both virus and non-virus conditions. In order to do this, cultivar by year interaction was examined. It was found that differences between cultivars were significant in the spring of 1998, but not in 1999. Presumably, the virus effects did impact these measurements.

Photosynthetic Characteristics

Once again, there were no fall 1998 characteristics that distinguished significant differences among the twelve cultivars. In March of 1999, cultivars had significantly different g_s values (Table 2). 'Scout 66' had the lowest values while Triumph 64 and TAM 105 had the highest values (Table 3). March 1999 g_s was not significantly related to year of release or grain yield.

Several characteristics measured in both spring of 1998 and 1999 revealed cultivar effects. Significant gas exchange parameters listed in Table 2 are g_s, the water use efficiency factor (K), and A. Stomatal conductance to water uncovered highly significant differences between cultivars ($p<0.001$). When LSD results were analyzed (Table 4), it was discovered that the oldest cultivar Turkey had the lowest g_s values, and several of the more recent cultivars had the highest values. These results, however, did not seem to represent both season's data. Upon examination of each season separately, it was discovered that postanthesis g_s in 1998 were lower than in 1999. As discussed earlier, 1999 was a moist year, leading to the optimum conditions for virus effects. In 1998, there were significant differences between cultivars in g_s, but not in 1999. Water availability and possibly the presence of viruses may have contributed to these differences. Nevertheless, mean g_s over both seasons was significantly different between cultivars. Figure 3 demonstrates that postanthesis g_s is positively correlated with year of release (r^2=0.43, $p < 0.05$). The characteristic g_s was also correlated with an increase in grain yield at a p-value of 0.06.

K was calculated from the product of WUE and VPD, and it is a method used to 'normalize' WUE to account for differences in VPD (Condon et al., 1993). As shown in Table 4, Karl 92 had the lowest WUE and the oldest cultivar Turkey had the highest WUE. Represented in Figure 4, K proved to be negatively correlated (r^2=-0.46, $p<0.05$) with year of release, but not with grain yield. The difference revealed in A was due to Turkey having a lower mean value of A than the newer cultivars, excluding Scout 66 (Table 4). Consequently, A was not significantly correlated to either year of release or grain yield. The fluorescence characteristic, Fv Fm^{-1}, had significant cultivar effects as well (Table 2). Triumph 64 had the lowest Fv Fm^{-1} ratios but Karl 92 and Custer had the highest (Table 4). As a result, Fv Fm^{-1} was correlated with year of release (r^2=0.36, $p<0.05$) but did not prove to be correlated to grain yield.

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DUAL-PURPOSE RESULTS

Plant Fitness

Noted in Table 2, there was only one sampling period that resulted in differences between dual-purpose managed cultivars in plant fitness characteristics. In March of 1999, Chl_{tot} and Chl a b^{-1} ratios had significant cultivar effects. Table 3 reveals the least significant difference test details. One of the oldest cultivars had the lowest Chl_{tot} and one of the most recent cultivars had the highest values. As a result, Chl_{tot} was positively correlated with year of release (r^2=0.53, $p<0.05$) as shown in Figure 6. Chl_{tot} was also positively correlated with grain yield (r^2=0.40, $p<0.05$) as pictured in Figure 7. Chl a b^{-1} ratios were lowest in one of the newest cultivars and highest in the oldest cultivar (Table 3). The characteristic, Chl_{tot}, however, was not significantly correlated with either year of release or grain yield. Additionally, no dual-purpose, postanthesis (spring 1998 and 1999) plant fitness characteristics had significant cultivar effects.

Photosynthetic Characteristics

There were no significant differences in plant fitness characteristics between cultivars in fall 1998. In March of 1999, only q_N was significantly different between cultivars (Table 2) and the LSD results are listed in Table 3. Measured in March, 1999, q_N was not significantly correlated to year of release or grain yield.

Spring 1998 and 1999 measurements of flag leaves at anthesis brought to light two photosynthetic characteristics with significant cultivar effects: K and q_P (Table 2). Leaf WUE was lowest in 2163 (Table 4) and highest in Custer and 2174. In Figure 5, mean WUE under both grain-only and dual-purpose management is compared with year of release. Under the grain-only managed system, a negative correlation with year of

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release exists. In the dual-purpose system, on the other hand, WUE doesn't appear to have any systematic relationship with year of release or grain yield. The q_P, averaged over spring 1998 and 1999, was significantly different between cultivars as shown in Table 2. Vona had the lowest values, while Triumph 64 had the highest (Table 4). The characteristic q_P was not significantly related to year of release or grain yield.

DISCUSSION

During the spring of 1999, the experimental plots had both wheat soilborne mosaic and spindle streak mosaic virus (WSBMV and WSSMV, respectively) infestations. Both viruses are members of the potyvirus family, and it is thought that they are transmitted by the fungus *Polymyxa graminis* (Lommel et al., 1986; Cunfer et al., 1988; Rumjaun et al., 1996; Carroll et al., 1997). There is no treatment for these viruses, so the best way to combat them, if their presence is suspected, is to plant resistant wheat cultivars. The wet, cool spring conditions in 1999 were optimal for virus symptom development. Due to the nature of this study, however, this option was not viable and as a result many of the cultivars were affected. The infected plants were able to recover later in the spring, and symptoms began to decrease when the temperatures warmed, as reported previously (Bays et al., 1985; Lommel et al., 1986; Carroll et al., 1997). Little is known about how these viruses affect plant physiology, and photosynthesis specifically. Symptoms of these viruses include patches or spindle-shaped chlorosis development on the leaves. Thus, due to the presence of these viruses in 1999, the chlorophyll content data may not reflect normal, virus-free field conditions. Considering prior knowledge of

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these effects in 1999, cultivar by season interaction in this data was considered and discussed below.

GRAIN-ONLY

Plant Fitness

Significant differences were detected in preanthesis (March, 1999) Chl_{tot} and in postanthesis (spring 1998 and 1999) Chl a b^{-1} ratio. The differences found in Chl_{tot} content were that three cultivars, unrelated to year of release or grain yield, had lower values than the others, while TAM W-101 had higher values. Although there were significant cultivar effects, there simply was not a systematic relationship between cultivars and year of release or grain yield. It follows, then, that breeders do not appear to have indirectly selected for Chl_{tot}. Because Chl a b^{-1} ratios from postanthesis 1999 measurements did not appear different from each other, the cultivars were analyzed for season by cultivar interaction. Interaction was found and may be explained by the presence of viruses in 1999. In 1998, significant differences between cultivars were detected. In 1999, differences between cultivars were not evident, probably due to a leveling of differences between cultivars on account of the virus effects. Higher Chl a b^{-1} ratios result as the proportion of core and peripheral pigments change in order to optimize the light harvesting capacity relative to the capacity of photochemistry, i.e. to optimize the photosynthetic unit size (Demig-Adams and Adams, 1996). The highest postanthesis Chl a b^{-1} ratio in 1998 and in the combined analysis, was noted in the oldest cultivar, Turkey and a newer cultivar Karl 92, while 2163 had the lowest values. There was not a correlation between Chl a b^{-1} ratio and either year of release or grain yield. From these

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results, it can be concluded that breeders have not altered chlorophyll content or composition during selection of southern Great Plains HRW wheat cultivars for a grain-only production systtem. Therefore, as has been proposed earlier, there doesn't appear to be mechanistic differences between old and modern cultivars in either Chl_{tot} content or Chl a b^{-1} ratios (Sinha et al., 1981).

Postanthesis LAI appear to have increased in these cultivars over the past decades of breeding as depicted in Figure 2. In fact, the 1997 release, 2174, has a mean LAI that is a 33 % increase over one of the oldest releases in the study, Triumph 64. Although not significant, cultivars measured preanthesis appear to have the same general LAI trend, but lower overall values. TAM 105 had the lowest mean LAI measured both pre- and postanthesis, while 2174 and Karl 92 had consistently high mean values at both sampling times. It has been previously established that maximum photosynthetic tissue is needed at anthesis to achieve maximum yields in semidwarf cultivars (Dunphy et al., 1984; Redmon et al., 1995). In this regard, however, there was not a significant correlation between LAI and grain yield. It is an interesting finding that although not numerically significant from other cultivars, TAM 105 had the highest rates of A measured pre and postanthesis in 1999 (27.12 and 15.43 umol m^{-2} s^{-1}, respectively) as well as the lowest LAI. These findings would tend to confirm the negative relationship between A and leaf area found by others (Austin et al., 1982; Rawson et al., 1983; Bhagsari and Brown, 1986).

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Photosynthetic Characteristics

Stomatal conductance to water was found to be significantly different between cultivars in the combined, postanthesis spring 1998 and 1999 measurements. The LSD values listed in Table 3, however, did not appear to represent both seasons well. When compared, the values of g_s in 1998 were lower than in 1999. Significant differences between cultivars in g_s were only found in 1998. Thus water availability and virus effects may have contributed to this interaction. At the Marshall Mesonet weather station, rainfall from September 1997 to February 1998 was 11.98 inches and from March to May 1998 was 12.16 inches. Rainfall from Septemeber 1998 to February 1999 was 15.81 inches and March to May 1999 was 12.69 inches (Oklahoma Mesonet Climatological Data). It is likely that under more water-limited conditions, as in 1998, differences in g_s become evident, but under less water limitation, as in 1999, differences are not detected. Virus effects on g_s have not been amply studied to account for their contribution to this interaction. Because it is impossible to elucidate all potential season effects, or replicate them, conclusions must be based on both seasons' results.

Under the combined conditions of spring 1998 and 1999, flag leaf g_s appears to have increased with year of release as illustrated in Figure 3. Our results contrast with those of Sinha and others (1981) who found little difference in g_s between old and modern wheat cultivars. On the other hand, our results are consistent with the report of Fischer et al. (1998) who noted a 63% increase in g_s was correlated to a six-year yield progress in spring wheat. These researchers also concluded g_s should be further examined as an indirect yield selection criterion. An older paper of Shimshi and Ephrat (1975) also found a positive relationship between g_s and yield in spring wheat. Under the

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field conditions measured in this study, g_s was correlated with grain yield at a p-value of 0.06 (r^2=0.33). Therefore, breeders may have indirectly selected southern Great Plains HRW wheat cultivars for increased in g_s, which may have contributed to increased grain yields.

Stomatal conductance affects the supply of carbon dioxide to mesophyll cells, where it is fixed, and then ultimately used to make carbohydrates and other products. Stomatal conductance also controls the amount of water vapor lost from plants through E. Gas exchange factors dependant on g_s, A and WUE, also revealed insight into how breeders have indirectly manipulated HRW wheat cultivars these past four decades. Carbon assimilation rates did not appear to differ much between cultivars, except that the oldest cultivar in the study, Turkey, had the lowest value. This is interesting, due to the fact that nearly 50 % of the variability in A was accounted for by changes in g_s, which has significantly increased in cultivars grown throughout the past century. Turkey had the highest WUE, which decreased with year of release (Figure 4). It stands to reason that because the oldest cultivar, Turkey, has the lowest g_s value, the amount of carbon dioxide that can be fixed and the amount of water that can be lost is the smallest. In this way, Turkey may employ a 'conservative' approach while the more modern cultivars may be 'opportunistic' as described earlier (Siddique et al.,1990). Opportunistic cultivars have high g_s and thus high A when soil moisture is plentiful, but decrease g_s and A dramatically when soil moisture becomes limiting. Conservative cultivars have relatively low g_s and also A when soil moisture is high, and only gradually decrease g_s and A when moisture becomes limiting. Stomatal limitations to A and WUE have been found by many (Dunstone, et al., 1973; Planchon and Fesquet, 1982; Lal et al., 1996; Van Den

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Boogaard et al., 1997). Farquhar and Sharkey (1982) point out that the primary function of the stomata is in preventing severe water loss from the plant. Therefore, even though the stomatal limitation to CO_2 diffusion into the leaf is large, it still may only marginally limit A under some conditions. Our results indicate there may have been a stomatal limitation to A and WUE under the conditions of this experiment. A was positively associated with g_s ($p<0.001$) and K was negatively associated with g_s ($p<0.001$). We can not conclude g_s limitation absolutely, however, because A-C_i (CO_2 concentration in the internal air spaces of the leaf) curves were not conducted due to the large number of plots included in the study.

The conservative behavior of the older cultivars and the opportunistic behavior of the more modern cultivars may also relate to the increase in LAI with year of release. Leaf growth is more sensitive to stress than g_s or A (Farquhar and Sharkey, 1994). Therefore, a reason for the differences in LAI between the older and more modern cultivars may be due to their strategies. Older, conservative cultivars may compromise leaf area in order to maintain other leaf factors such as internal CO_2 and carbohydrate concentrations. Newer, opportunistic cultivars may be able to maintain higher LAI under more optimal conditions, and reduce it when under stress (i.e. the differences in LAI disappeared under the dual-purpose production system).

Chlorophyll fluorescence also appears to shine light onto differences between old and modern HRW wheat A. Postanthesis $Fv\ Fm^{-1}$ increased with year of release under the field conditions in this study. $Fv\ Fm^{-1}$ is thought to reflect the efficiency of excitation capture with all PSII reaction centers open (Genty et al., 1989; Krause and Weis, 1991; Farquhar and Sharkey, 1994). In other words, when PSII efficiencies are impacted by

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stresses, Fv Fm^{-1} decreases. In this research, though, the difference uncovered between the highest efficiency to lowest efficiency was only three %. Lu and Zhang (1998) make the point that Fv Fm^{-1} values decrease in senescing wheat leaves. Therefore, when measured postanthesis, these small differences may have appeared due to variation in senescence between the cultivars. Photosystem II efficiencies in using light were not significantly correlated with grain yield increases. These results indicate that breeders probably have not indirectly selected cultivars for any meaningful increase in efficiency of PSII excitation capture.

DUAL-PURPOSE

Plant Fitness

Preanthesis chlorophyll differences were detected in cultivars managed under the dual-purpose system, but not detected in postanthesis measurements. This difference in chlorophyll content may be explained as a consequence of postanthesis senescence. If the leaves had begun to senesce before the postanthesis samples were collected, chlorophyll may have started to break down and reduction in Chl a b^{-1} ratios may have occurred (Lu and Zhang, 1998). This may be quite likely in the postanthesis measurements, as has been suggested in several reports thus far. As discussed earlier, the presence of both WSBMV and WSSMV in the spring of 1999 may also have affected the thylakoid membranes, causing changes in chlorophyll content and composition. In the spring of 1998, under virus-free conditions, there were also significant chlorophyll effects detected. Of particular interest, preanthesis Chl_{tot} was found to increase with year of release and may also be responsible for about 40 % of the variability in dual-purpose

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managed grain yield. In fact, the highest Chl_{tot} found was in Custer and was a 60 % increase over the lowest Chl_{tot}.

The role of chlorophyll is to harvest light energy to be used in A. Chlorophyll a b^{-1} reflects the ratio of core to peripheral light-harvesting complexes (Demmig-Adams and Adams, 1996). In other words, if Chl a b^{-1} ratios are higher, there might be less emphasis on light collection due to high light pressure. Custer had both the highest mean Chl_{tot} and the lowest mean Chl a b^{-1} ratio suggesting much peripheral chlorophyll and a large photosynthetic unit size. Under dual-purpose management, this cultivar was focusing much of its preanthesis energy on light harvesting, resulting in high yield. Triumph 64 had the lowest Chl_{tot} content and one of the highest Chl a b^{-1} ratios suggesting little peripheral chlorophyll and a small photosynthetic unit size. At preanthesis, this cultivar may have been experiencing high light stress and was trying to focus on using the absorbed light energy in carbon assimilation (although not statistically significant, it did have one of the highest A values). This behavior might have been expressed in chlorophyll content and composition and resulted in lower grain yield. Even though differences were detected, Chl a b^{-1} ratios do not appear to have changed systematically in cultivars released each year and are not correlated with grain yield.

Photosynthetic Characteristics

There were a few pre and postanthesis cultivar effects under the dual-purpose management system. Two fluorescence parameters and one gas exchange parameter were found to differ between cultivars. Preanthesis q_N was found to differ between cultivars, but was not correlated to year of release or grain yield. The q_N is related to the

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fluorescence quenching that is non-photochemical in nature. When light is absorbed by chlorophyll, it can either be used for charge separation (q_P) or it can be given off as heat or fluorescence (Seaton and Walker, 1990; Bolhar-Nordenkampf and Oquist, 1993; Bjorkman and Demmig-Adams, 1995). When there are low-light conditions, most of the light energy is used in photochemistry (leading to high quantum yields) and very little is emitted as heat and fluorescence. Under high light conditions when PSII centers are closed, much of the absorbed light energy is emitted as heat, and there is an increase in the fluorescence intensity (Bolhar-Nordenkampf and Oquist, 1993). There are several components of q_N: the build-up of the proton gradient across the thylakoid membrane (qE), the 'state 1' to 'state 2' transition related to phosphorylation of LHCII (qT), and photoinhibition of photosynthesis (qI) (Krause and Weis, 1991). The method used to measure q_N in this study does not allow us to differentiate which components significantly differ between the cultivars. The results of the LSD test between cultivars for q_N did differentiate 2163 as having the lowest values and Vona having the highest. The q_N was also high in the cultivar Custer, which had high Chl_{tot} and low Chl a b^{-1} as discussed earlier. The cultivar 2163 had the lowest q_N values along with one of the highest Chl a b^{-1} and lowest Chl_{tot}. As mentioned previously, Custer appeared to be focusing much of its energy on light harvesting. It follows, that there was a mechanism observable by q_N, that was able to dissipate excessive radiation, if necessary. This was done in order to match ETR to other limiting components of photosynthesis (Farquhar and Sharkey, 1994). Havaux et al. (1991) stated that a possible function of non-photochemical energy dissipation is to avoid over-excitation of the reaction centers. This is accomplished by adjusting the photochemical reactions to better fit carbon metabolism needs. Custer may have displayed this process to match the greater light harvesting to its metabolic needs by maintaining high rates of q_N. In fact, q_N has been directly related to the amount of excess photon flux density (PFD) (Bjorkman and Demmig-Adams). Likewise, q_N has been found to tightly correlate with the formation of zeaxanthin, a carotenoid of the xanthophyll type. The xanthophyll cycle has been shown to be involved with protection under high light conditions (Shuangsong and Daquan, 1997). Many other authors have confirmed the xanthophyll cycle has a role in photoprotection and thermal dissipation of excess energy (i.e. Niyogi, 1999). Postanthesis q_N values were much higher and not significantly different, so they did not aid in elucidating the relationships behind preanthesis q_N values. They may have risen in value because temperatures and light intensities were greater under postanthesis conditions. In conclusion, even though it does not appear breeders have selected cultivars indirectly based on preanthesis q_N, the relationships between other measured parameters and cultivars explain many of the possible complex interactions behind photosynthesis and plant fitness.

Postanthesis K and q_P had significant cultivar effects under the dual-purpose management system, but were not significantly correlated with year of release or grain yield. These results differ from the grain-only management system in that K was negatively correlated with year of release. K was again correlated to and largely a function of postanthesis g_s. Under dual-purpose management, the newest cultivars had the highest WUE. This would appear to indicate that once again, modern cultivars are opportunistic: the two newest cultivars had the lowest WUE under the non-stressed, grain-only system and the highest WUE under the stressed, dual-purpose system. In this way, Custer emerges as a seemingly well-adjusted cultivar for these conditions. The cultivar is able to focus on light harvesting, utilize non-photochemical dissipation processes, and still maintain high WUE under foraging stress. Cultivar 2163 had high Chl a b^{-1}, low Chl_{tot}, low q_N, and low WUE.

The cultivars Custer and 2163 had relatively high q_P values, but Triumph 64 had the highest and Vona had the lowest. The q_P marks changes in the degree of openness of PSII reaction centers as compared to having all centers open as in the dark (no excitation pressure) (Havaux, Strasser, and Greppin, 1991). The q_P is a good estimate of PSII electron transport rate (ETR) (Schreiber and Bilger, 1987). Quantum yields (electrons per photon) are high under low light conditions and decrease at elevated PAR (Bolher-Nordenkampf and Oquist, 1993). Therefore, under postanthesis conditions, these three cultivars are able to maintain high quantum yields, while other cultivars (i.e. Vona) are not. Once again, although q_N, K and q_P were not correlated with year of release and grain yield, they do further explain how these vary in a logical way among cultivars.

CONCLUSIONS

Grain yields of southern Great Plains HRW wheat cultivars grown in a grain-only production system have significantly increased over the past decades of breeding. Although increases are present, the magnitude of the increases have not been as great under dual-purpose management.

The first objective of this study was to determine whether A of southern Great Plains cultivars (grain-only) have changed over the past four decades of breeding. We can not conclude that Chl_{tot} or Chl a b^{-1} ratios have changed due to breeding in these twelve cultivars under grain-only management. Postanthesis LAI has increased 33 % in the 1997 release over the 1964 release. This increase in LAI was not correlated with grain yield. Stomatal conductance appears to have increased with year of release under more water-limited conditions. At the same time, leaf WUE has decreased in these twelve cultivars grown throughout this century. Carbon assimilation rate was not correlated with year of release, but the oldest cultivar, Turkey, had a significantly lower A than the other cultivars. Lastly, it is possible that postanthesis maximum efficiency of excitation capture with all PSII reaction centers open ($Fv\ Fm^{-1}$) may have increased slightly with year of release. These differences were so small, however, that indicates breeders have not indirectly selected cultivars with meaningful increases in PSII excitation capture efficiency.

The second objective was to characterize and appraise dual-purpose production system effects on photosynthetic parameters of southern Great Plains cultivars grown throughout this past century. Under the conditions measured in this study, preanthesis Chl_{tot} seems to have increased in cultivars with year of release when managed for a dual-purpose system. Preanthesis Chl_{tot} was also correlated with increases in dual-purpose grain yields and may account for about 40 % of the variability. Significant differences were detected between dual-purpose cultivars, but were neither related to year of release nor grain yield. Overall, differences noted between cultivars in the grain-only system were reduced or nonexistent in the dual-purpose environment. The important trends due to breeding found under the grain-only system, namely the increases in leaf g_s and LAI and the decrease in leaf WUE, were not apparent under the dual-purpose system.

Identifying which photosynthetic components significantly correlate to grain yield was the third objective of this research. Under a grain-only management, g_s was correlated with grain yield at a p-value of 0.06. Due to the fact that g_s increased significantly with year of release, as did grain yields, this parameter should not be overlooked as an important grain yield component. Other researchers have found a similar relationship between g_s and grain yield (Shimshi and Ephrat, 1975; Fischer et al., 1981; Fischer et al., 1998). Under the conditions of this study, it was revealed that preanthesis Chl_{tot} was a considerable determinant of dual-purpose grain yield.

Finally, the last objective of this study was to determine whether the gas exchange and chlorophyll fluorescence techniques employed in this study would be valuable tools for breeders to utilize in screening new cultivars for grain-only and dual-purpose systems. Under the field conditions of this study, it does not appear these measurements explained yield increases adequately enough for breeders to utilize them for screening high-yielding cultivars. Under the conditions of studies done by others, the same techniques have proved useful. Therefore, these techniques should be further tested to determine whether they would be useful, rapid tools for southern Great Plains HRW wheat breeders. Obviously, if breeders were interested in achieving expression of certain characteristics like leaf WUE (which has been correlated to whole plant WUE), selecting premium cultivars with instruments should be quite useful.

The yield increases over the past decades of breeding southern Great Plains HRW wheat cultivars does not appear to be due to significant increases in photosynthesis, or its major parameters (i.e. g_s, WUE, Fv Fm^{-1}, etc.). Mann (1999) reported in Science that studies since the 1970s have failed to link grain yields to A and the reason might be due to high-yielding cultivars possessing more leaf area. Larger leaf area increases shading and thus lowers mean A. Nelson (1988) concluded that results from studies such as this have been disappointing due to high genotype by environment interaction and other non-photosynthetic characteristics that tend to over-shadow the yield vs. photosynthesis relationship. He concluded that genetic increases in leaf A are certainly possible, but that the genetic advantages come from improving the dark reactions during mid-day, high light conditions. These increases would need to be achieved by increasing protein synthesis or selecting cultivars for higher RuBP carboxylase, which has not been very promising. It has been shown that postanthesis A of wheat is affected by the source/sink ratio and depends on both cultivar and time after anthesis (Yin et al., 1998). This is perhaps the crux of this research, that 'source' may have been manipulated in cultivars the past four decades to optimize water availability conditions. Many researchers agree that with harvest indices nearing values as high as 50% and optimization of carbon partitioning ('sinks'), much of the future grain yield increases will need to come from maximizing A ('source') without raising water requirements (Nelson, 1988; Boote and Tollenaar, 1994; Sinclair, 1994; Malik and Wright, 1997; Mann, 1999).

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APPENDIX A

Gas Exchange Parameters Evaluated

$E = (e_i - e_a)\, r_t^{-1}$

$r_t = [(r_s\, r_c)\, (r_s + r_c)^{-1}] + r_a$

$A = (c_a - c_i)\, (1.6\, r_t)^{-1}$

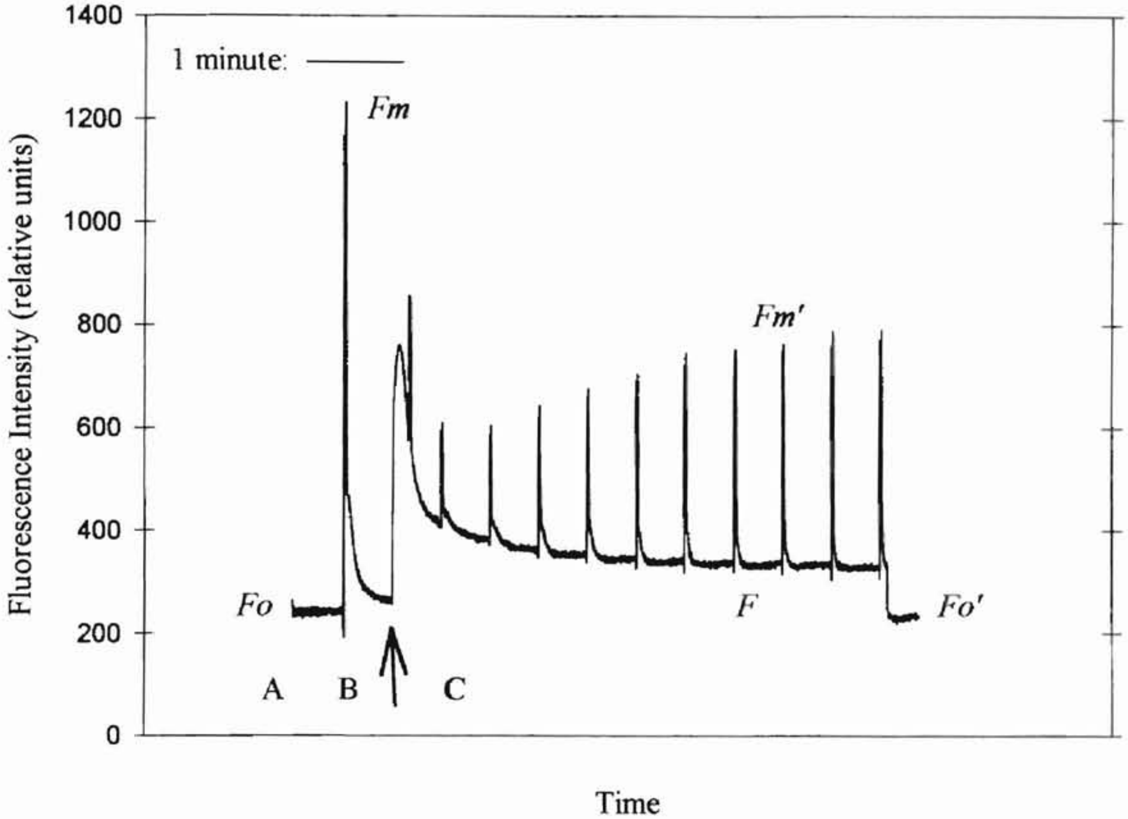
$WUE = A\, E^{-1}$

$K = WUE * VPD$

VPD = (saturated vapor pressure at sample air temp.)-(v. press. in sample cell)

E is the transpiration rate of a leaf in mmol $m^{-2}\ s^{-1}$. The terms e_i and e_a are the concentrations of water vapor in the leaf intercellular air space and in the air respectively. Total diffusive resistance to water vapor is r_t, r_s is the stomatal diffusive resistance to water vapor, r_c is the cuticular diffusive resistance to water vapor, and r_a is the boundary layer resistance to water vapor. A is carbon assimilation rate of a leaf in umol $m^{-2}\ s^{-1}$. The terms c_i and c_a are the concentrations of CO_2 in the leaf intercellular air space and in the air respectively. Also note, the diffusive resistance to CO_2 is calculated from the product of 1.6 and the diffusive resistance to H_2O vapor. K is a measure of WUE normalized to avoid differences due to different VPD (Condon et al., 1993).

Fluorescence Parameters Defined



A: Fluorescence level of dark-adaptated plant, with all PSII reaction centers 'open' (Q_A fully oxidized) (Fo)

B: Application of a saturating pulse, so that all reaction centers 'close' (Q_A fully reduced) (Fm)

Arrow: Point at which actinic light was turned on to drive photosynthesis

C: A series of saturating pulses were applied to determine changes in the quenching coefficients of the sample (F and Fm' are steady state and maximal fluorescence values just before and during these pulses)

Important Derived Equations (Anonymous, 1993; Van Kooten and Snel, 1990)

$Fv\ Fm^{-1}=(Fm-Fo)\ Fm^{-1}$, $Fv'\ (Fm')^{-1}=(Fm'-Fo')\ (Fm')^{-1}$, $Y=(Fm'-F)\ (Fm')^{-1}$, $ETR=Y*PAR*0.5*0.84$

$qP=(Fm'-F)\ (Fm'-Fo')^{-1}$, $qN=(Fm-Fm')\ (Fm-Fo')^{-1}$, $NPQ=(Fm-Fm')\ (Fm')^{-1}$

APPENDIX B

Table 1. *Triticum aestivum* cultivars utilized in experiments.

Cultivar	CI	Release Date	Breeder(s)	Disease Resistance	Other Traits	Reference
Turkey	CI1558	1919 *(1874)	Kansas Mennonites	Bunt	Late maturity, high lodging	Quisenberry & Reitz, 1974; Cox et al., 1988
Triumph 64	CI13679	1964	Joseph Danne	WSM, tan spot, powdery mildew	Early maturity, high lodging, high test weight	Schlehuber & Johnson, 1965; Bowden & Brooks, 1997; Krenzer et al., 1997a
Scout 66	CI13996	1967	Nebraska Agr. Exp. Sta., USDA-ARS	Stem rust	Late maturity, high lodging	Schmidt et al., 1971; Bowden & Brooks, 1997; Krenzer et al., 1997a
TAM W-101	CI15324	1971	Texas Agr. Exp. Sta., USDA-ARS	Bunt	Late maturity, water stress tolerant, good fall forage	Porter, 1974; Krenzer et al., 1997a
Vona	CI17441	1976	Colorado State U. Exp. Sta.	Stem rust	Early maturity	Welsh et al., 1978
TAM 105	CI17826	1979	Texas Agr. Exp. Sta., USDA-ARS	Some stem rust		Porter et al., 1980
Chisholm	PI486219	1983	OK Agr. Exp. Sta., USDA-ARS		Fair fall forage	Smith et al., 1985; Krenzer et al., 1997a
2157	PVP 8400027	1987	Pioneer Hi Bred Int'l.	Some leaf & stem rust, SBM	Hessian fly resistant	Annonymous, 1984

Cultivar	CI	Release Date	Breeder(s)	Disease Resistance	Other Traits	Reference
2163	PVP 890025	1989	Pioneer Hi Bred Int'l.	SBM, WSSM, powdery mildew, stem rust	Hessian fly resistant, good fall forage, low pH tolerant	Bowden & Brooks, 1997; Krenzer et al., 1997a
Karl 92	PI564245	1992	KS Agr. Exp. Sta., USDA-ARS	SBM, WSSM, powdery mildew	High test weight, good fall forage	Bowden & Brooks, 1997; Krenzer, et al., 1997a; Sears et al., 1997
Custer	N/A	1994	OK Agr. Exp. Sta.	Leaf & stem rust, tan spot, powdery mildew,	Good fall forage	Bowden & Brooks, 1997; Krenzer et al., 1997a; Anonymous, 1994
2174	N/A	1997	OK Agr. Exp. Sta.	SBM, WSSM, leaf rust, powdery mildew	Hessian fly resistant, good fall forage, some low pH tolerance	Bowden & Brooks, 1997; Krenzer et al., 1997a; Krenzer et al., 1997b

*1874 was the date Turkey was brought to Kansas, and 1919 is the date when producers actually began crude selection

Table 2. The cultivar effects found for major characteristics evaluated.

Sample Date	March 1999		Spring 1998 & 1999 Combined	
Treatment	Grain-only	Dual-purpose	Grain-only	Dual-purpose
A ($umol\ m^{-2}\ s^{-1}$)	ns	ns	$P < 0.05$	ns
g_s ($mol\ m^{-2}\ s^{-1}$)	$P < 0.05$	ns	$P < 0.001$	ns
K	ns	ns	$P < 0.05$	$P < 0.01$
$Fv\ Fm^{-1}$	ns	ns	$P < 0.01$	ns
$Fv'\ (Fm')^{-1}$	ns	ns	ns	ns
NPQ	ns	ns	ns	ns
q_P	ns	ns	ns	$P < 0.05$
q_N	ns	$P < 0.05$	ns	ns
$Chl\ a\ b^{-1}$	ns	$P < 0.05$	$P < 0.05$	ns
Chl_{tot} ($g\ m^{-2}$)	$P < 0.05$	$P < 0.05$	ns	ns
LAI (m^2 foliage (m^2 ground)$^{-1}$)	$P < 0.01$	ns	-	-
MTA (degrees from horizontal)	ns	ns	-	-

ns = not significant at $\alpha = 0.05$

\- = not measured, or not measured in both years

Table 3. Cultivar means and least significant difference values from preanthesis measurements in March, 1999.

	Grain-Only		Dual-Purpose		
Cultivar	Chl_{tot}	g_s	Chl_{tot}	Chl a b^{-1}	q_N
	g m^{-2}	mol m^{-2} s^{-1}	g m^{-2}		
Turkey	0.72	0.43	0.63	3.67	0.54
	ab	bcd	ab	e	bc
Triumph 64	0.66	0.51	0.61	3.40	0.41
	a	d	a	abcde	abc
Scout 66	0.73	0.30	0.72	3.25	0.52
	ab	a	abc	ab	bc
TAM W-101	0.90	0.44	0.78	3.53	0.39
	c	bcd	abcd	bcde	ab
Vona	0.76	0.45	0.72	3.33	0.60
	abc	bcd	abc	abcd	c
TAM 105	0.70	0.52	0.83	3.51	0.39
	ab	d	bcd	bcde	ab
Chisholm	0.77	0.40	0.79	3.59	0.56
	abc	abcd	abcd	de	bc
2157	0.77	0.46	0.80	3.29	0.49
	abc	cd	abcd	abc	bc
2163	0.65	0.43	0.67	3.58	0.24
	a	bcd	ab	cde	a
Karl 92	0.65	0.33	0.75	3.47	0.49
	a	ab	abcd	bcde	bc
Custer	0.83	0.41	0.98	3.15	0.54
	bc	abcd	d	a	bc
2174	0.79	0.36	0.91	3.49	0.37
	abc	abc	cd	bcde	ab

Cultivars with the same letter are not significantly different

Table 4. Cultivar means and least significant difference results from postanthesis measurements from combined spring 1998 and 1999.

Cultivar	Grain-Only					Dual-Purpose	
	Chl a b^{-1}	A	g_s	K	Fv Fm^{-1}	K	q_P
		umol m^{-2} s^{-1}	mol m^{-2} s^{-1}				
Turkey	3.98	9.7	0.15	64.9	0.827	65.7	1.16
	b	a	a	d	abcd	cd	ab
Triumph 64	3.81	13.1	0.24	60.8	0.817	59.5	2.40
	a	b	b	cd	a	abcd	c
Scout 66	3.83	12.6	0.27	53.6	0.822	55.2	1.56
	a	ab	bc	abc	abc	abc	ab
TAM W-101	3.84	13.8	0.29	51.6	0.830	56.0	1.68
	a	b	bc	abc	bcd	abc	abc
Vona	3.83	13.7	0.33	47.0	0.822	53.7	0.92
	a	b	c	ab	abc	abc	a
TAM 105	3.81	15.4	0.34	55.6	0.819	61.0	1.78
	a	b	c	bcd	ab	bcd	bc
Chisholm	3.84	13.4	0.30	49.6	0.830	59.3	1.47
	a	b	bc	ab	bcd	abcd	ab
2157	3.80	14.2	0.32	47.8	0.826	62.3	1.31
	a	b	c	ab	abc	bcd	ab
2163	3.78	14.2	0.30	52.2	0.827	50.4	1.67
	a	b	bc	abc	abcd	a	abc
Karl 92	3.88	13.1	0.31	44.4	0.832	53.4	1.13
	ab	b	bc	a	cd	ab	ab
Custer	3.79	14.6	0.33	49.7	0.838	68.6	1.78
	a	b	c	ab	d	d	bc
2174	3.79	14.8	0.31	47.8	0.826	67.3	0.95
	a	b	bc	ab	abc	d	ab

Cultivars with the same letter are not significantly different

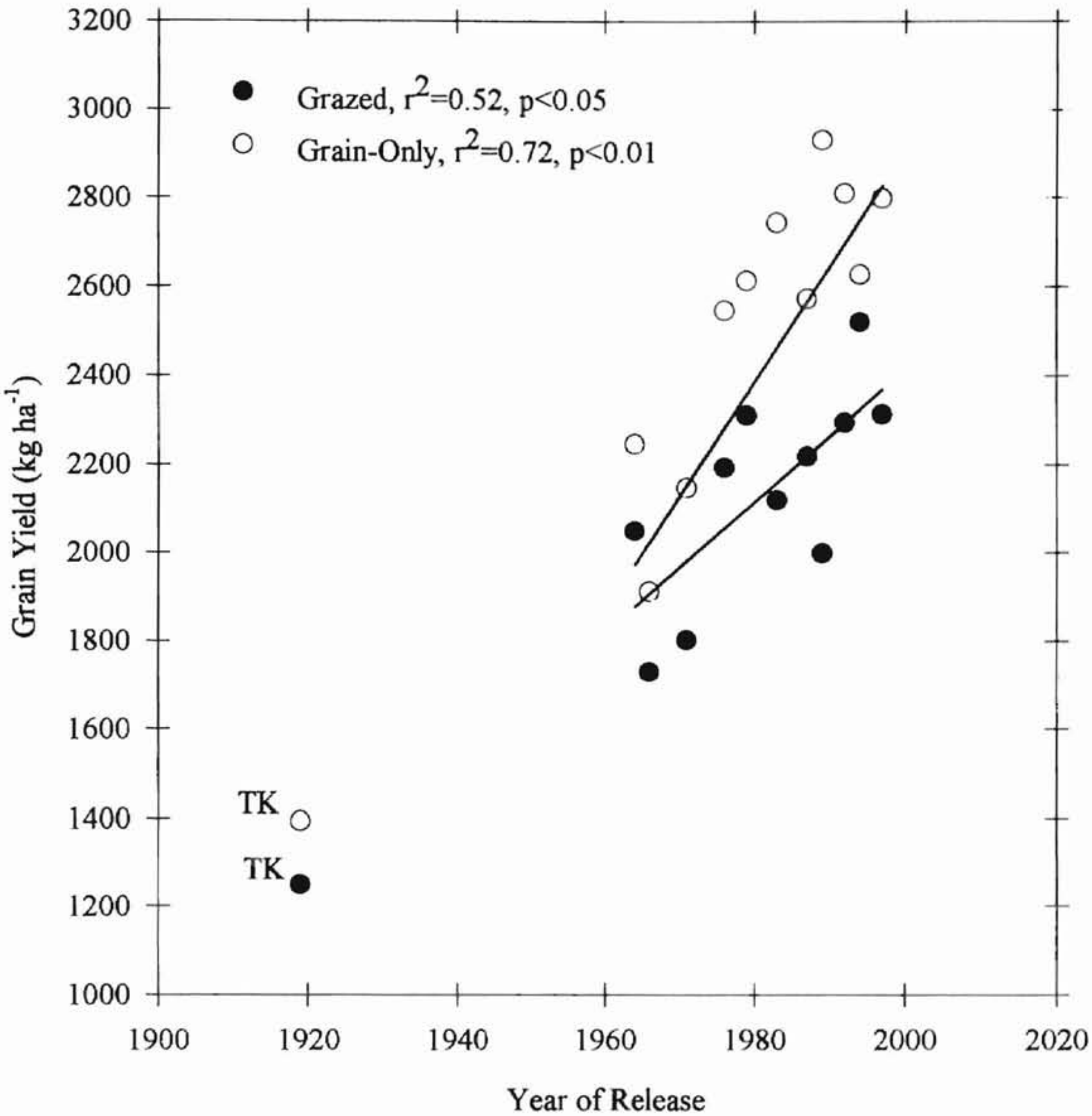


Figure 1. The relationship of mean grain yield to year of release for twelve southern Great Plains cultivars grown throughout this past century, evaluated near Marshall, Oklahoma in 1998-1999. 'TK' represents the cultivar Turkey and is not included in the trend lines.

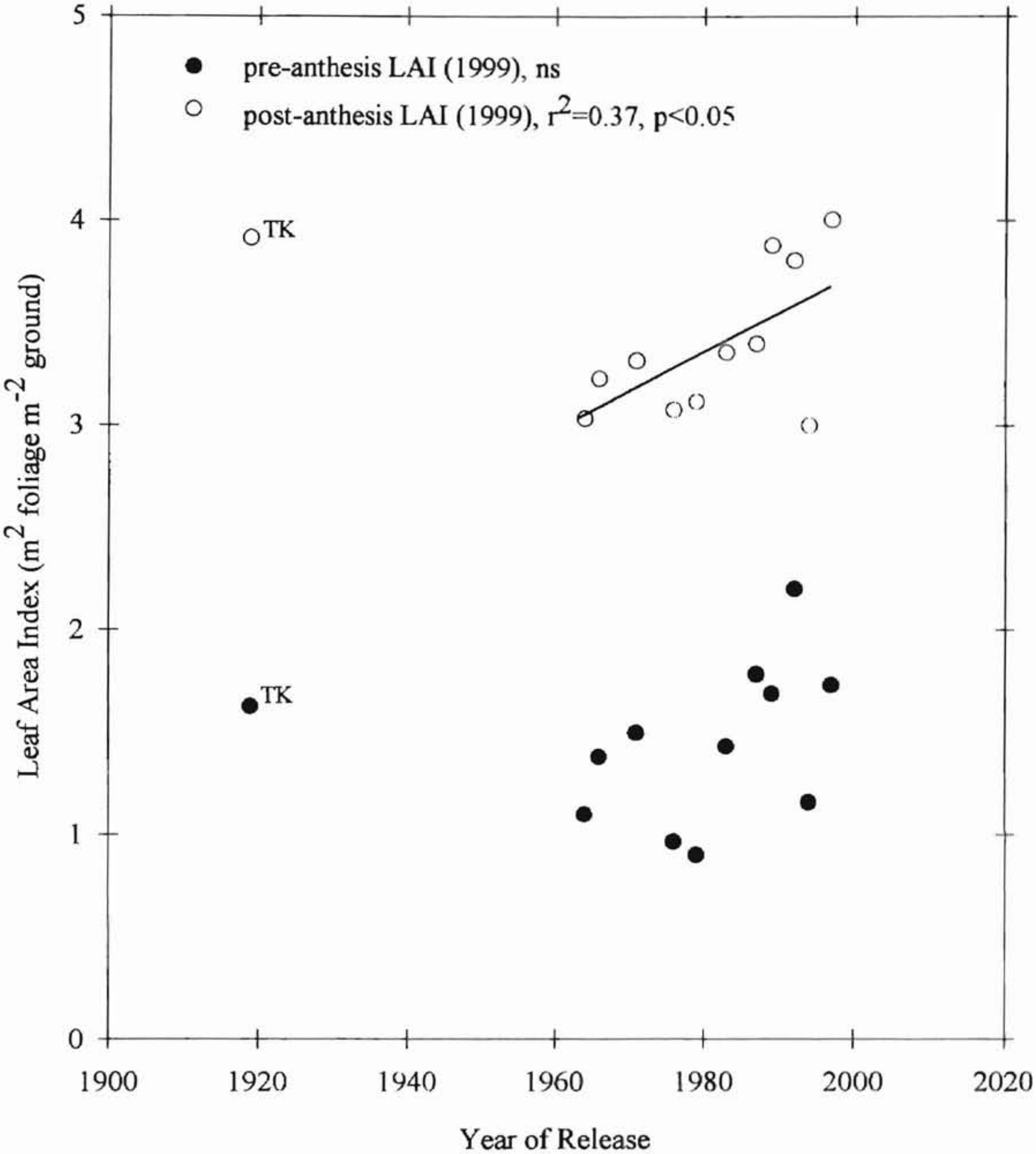


Figure 2. The relationships between pre and postanthesis mean LAI measured in 1999 and year of release for twelve southern Great Plains HRW wheat cultivars grown throughout this past century. 'TK' is the mean value for the cultivar 'Turkey' and is not included in the trend line.

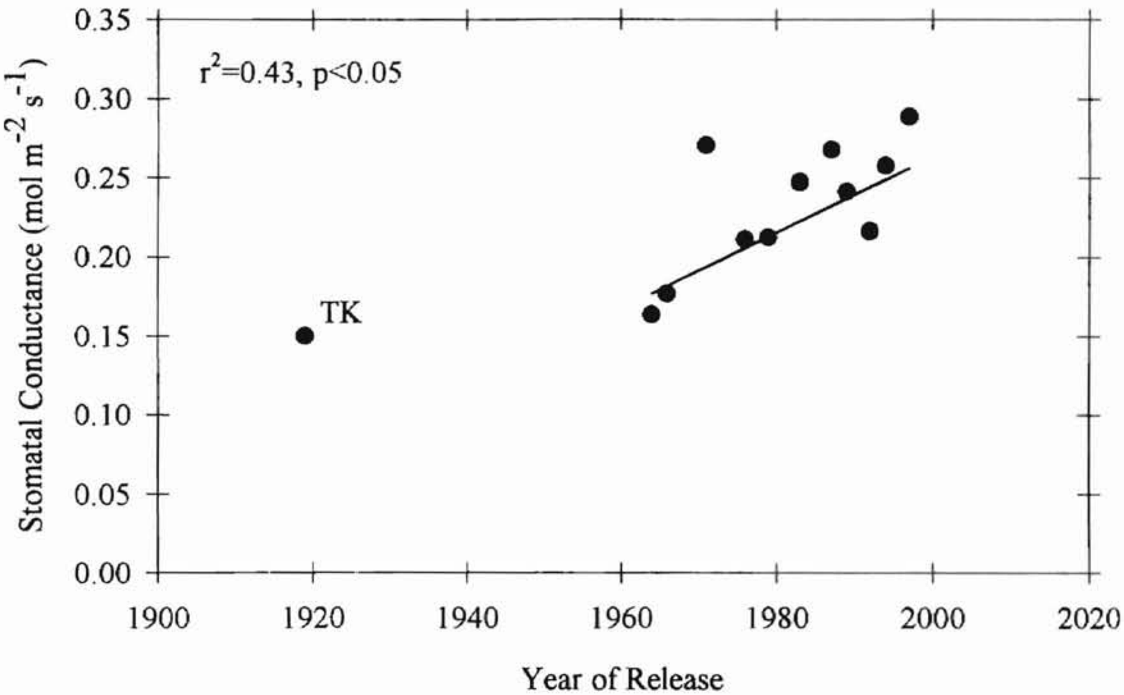


Figure 3. The relationship of mean leaf stomatal conductance measured in 1998-1999 to year of release for twelve southern Great Plains cultivars grown throughout this past century. 'TK' represents the cultivar 'Turkey' and is not included in the trend line.

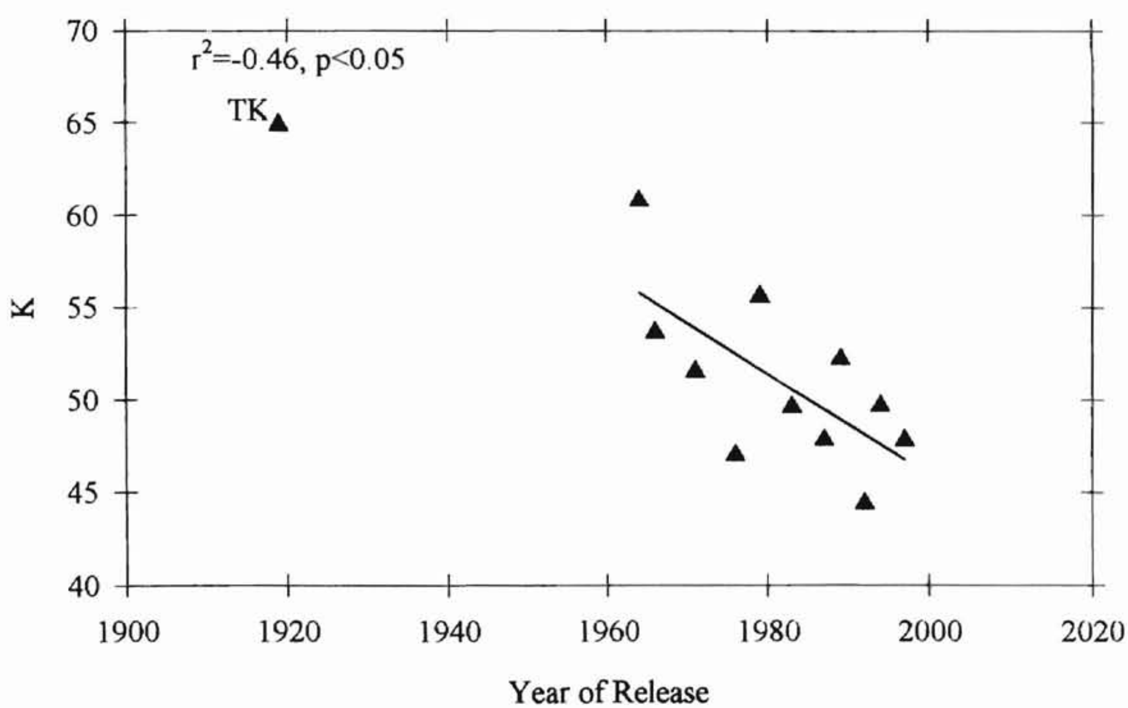


Figure 4. Progress in mean postanthesis K measured in 1998-1999 of twelve southern Great Plains wheat cultivars grown throughout this past century. 'TK' represents the cultivar 'Turkey' and is not included in the trend line.

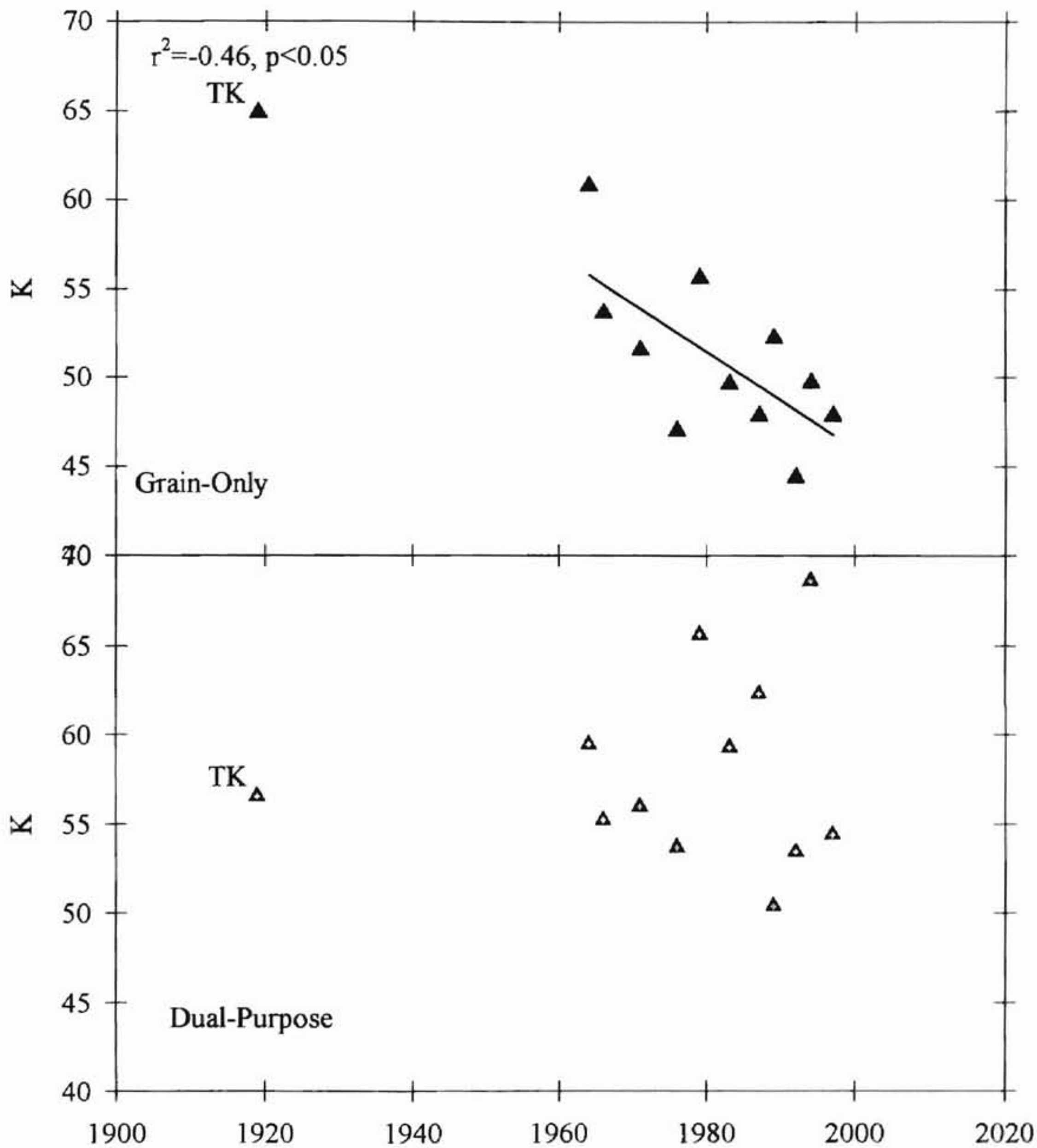


Figure 5. Leaf K of dual-purpose and grain-only plotsof flag leaves measured spring 1998 and 1999. 'TK' is the meanvalue of the cultivar 'Turkey' and is not included in the trend line.

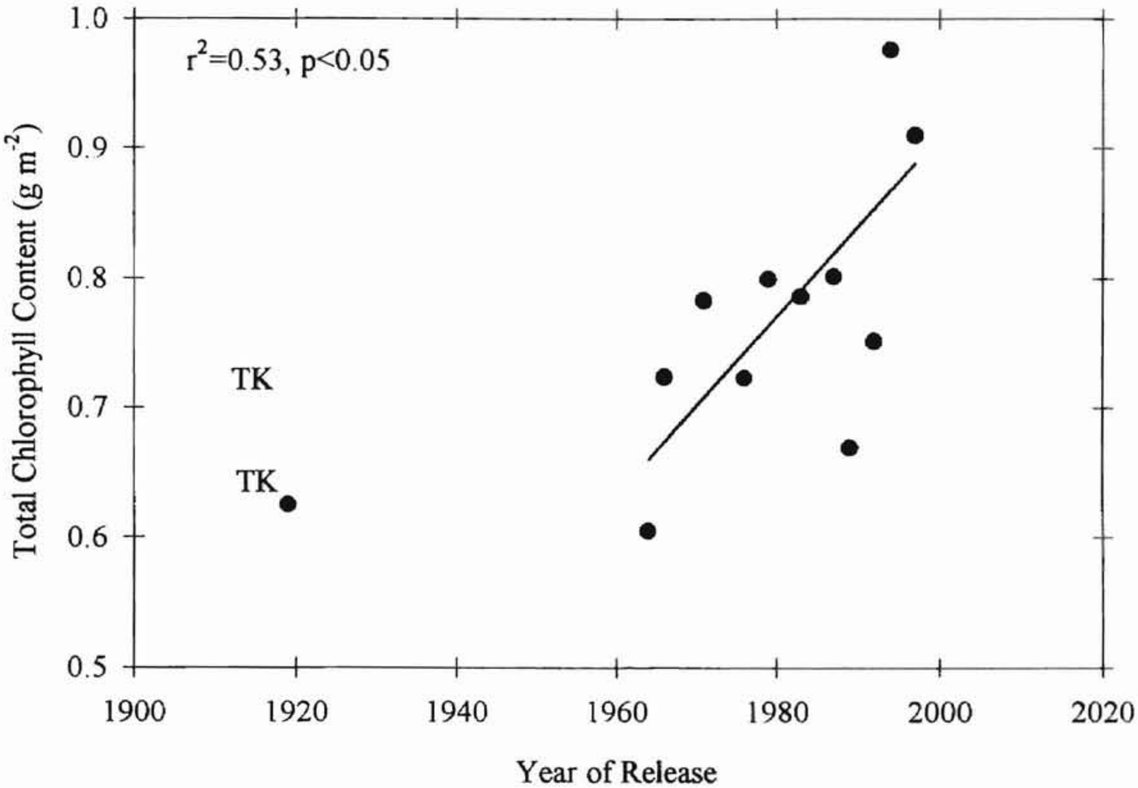


Figure 6. The progress of mean preanthesis total chlorophyll content measured in 1999 of twelve dual-purpose southern Great Plains wheat cultivars. 'TK' is the mean value of the cultivar 'Turkey' and is not included in the trend line.

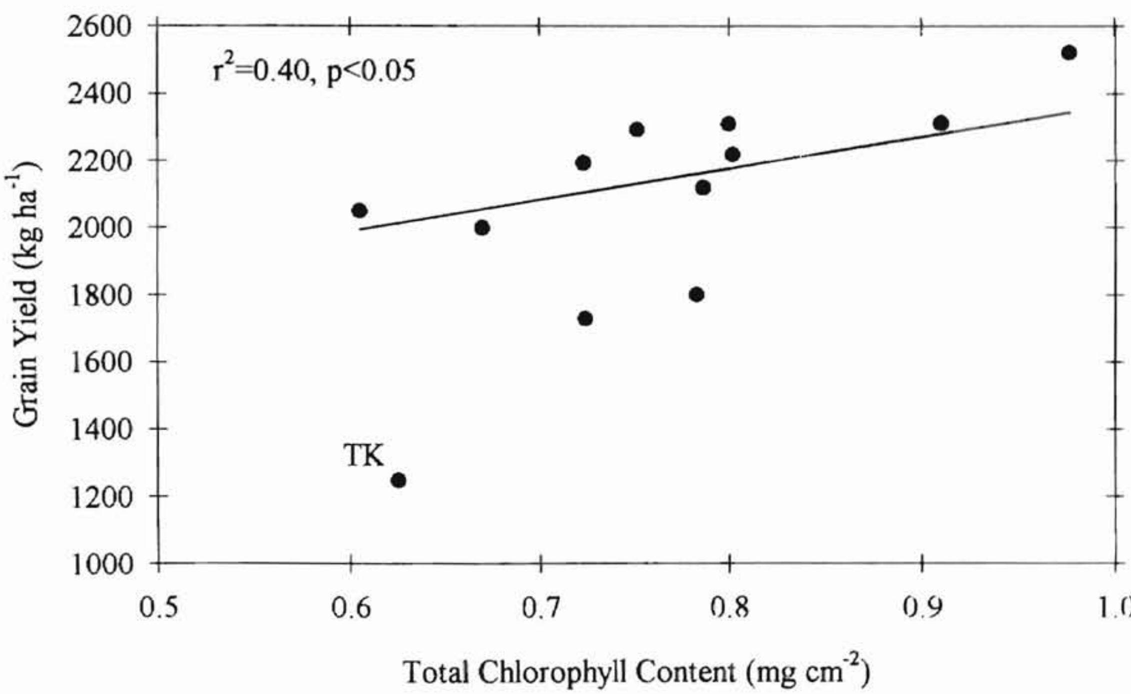


Figure 7. The relationship between mean preanthesis total chlorophyll content and grain yield of dual-purpose managed cultivars evaluated in 1999. 'TK' is the cultivar 'Turkey' and is not included in the solid trend line.

VITA

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