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Photosynthetic Capacity, Leaf Size and Plant Height in Wheat (Triticum aestivum L.)

Deborah L. Bishop
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PHOTOSYNTHETIC CAPACITY, LEAF SIZE AND PLANT HEIGHT
IN WHEAT (Triticum aestivum L.)

by

Deborah Lyn Bishop

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE
in

Plant Science
(Crop Physiology)

Approved:

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1991
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Deborah Lyn Bishop
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ABSTRACT

Photosynthetic Capacity, Leaf Size and Plant Height in Wheat (*Triticum aestivum* L.)

by

Deborah L. Bishop, Master of Science
Utah State University, 1991

Major Professor: Dr. Bruce Bugbee
Department: Plants, Soils and Biometeorology

Plant breeders often examine leaf size, plant height and photosynthetic capacity in an effort to increase wheat yield. This study was concerned with the relationship between these parameters in dwarf and semidwarf wheat cultivars (*Triticum aestivum* L.) with a wide range in flag leaf size. Photosynthetic capacity was measured at anthesis using photosynthesis versus intercellular CO$_2$ response curves to determine maximum photosynthetic rate and ribulose-1,5-bisphosphate carboxylase efficiency. Leaf area, chlorophyll concentration, stomatal density, interveinal distance and dry mass partitioning were also examined. Smaller flag leaves had greater carboxylation efficiency and closer vein spacing. Dwarf wheat had higher chlorophyll concentrations and maximum photosynthetic rates at anthesis than the taller semi-dwarfs. Dwarf cultivars had lower photosynthetic rates before anthesis, suggesting preanthesis feedback inhibition of photosynthesis, possibly due to a smaller sink capacity of its stem. (78 pages)
INTRODUCTION

Through the years, crop physiologists have cooperated with plant breeders/geneticists to examine the various physiological, anatomical and biochemical traits that may increase wheat yield. Higher wheat yields have been achieved by substantial increases in the harvest index, as more assimilate from the primary source (flag leaf) was allocated to the primary sink (grain) (Hay and Walker, 1989). Dwarfing genes in wheat, introduced for lodging resistance, decreased culm height and were associated with a reduction in leaf size. Both leaf size and plant height have been linked to photosynthetic capacity in wheat. Morgan et al. (1990) found that the reduction in leaf size associated with dwarfing genes concentrated leaf photosynthetic machinery (i.e., higher: mesophyll cell number, stomatal density, chlorophyll concentration and ribulose-1,5-bisphosphate carboxylase (RuBPc) per unit LA) and increased photosynthetic capacity. LeCain et al. 1989 attributed the increased leaf photosynthesis, RuBPc efficiency and photosynthetic capacity to the increase in RuBPc per unit leaf area, and all of these traits were associated with shorter stature wheat.

Herzog (1986) suggested that the photosynthetic capacity of a wheat stand during anthesis and maturity was a combination of source size and activity, which could be described by the following parameters: photosynthetic rate, RuBPc activity, chlorophyll concentration and flag leaf area.

Our NASA-funded project is concerned with growing wheat in the controlled, volume-limited environments of space. Because efficient use of
space and high yields are critical, we are interested in full dwarf wheats (less than 45 cm tall) with high photosynthetic potential. This study examined the relationship of leaf size to plant height and photosynthetic capacity of the flag leaf. The results may be useful in selection of wheat cultivars with high photosynthetic potential and in developing guidelines for genetic selection.
Leaf size appears to be associated with important physiological and anatomical parameters in wheat (*Triticum aestivum* L.). This study examined the relationship between leaf size (length, width and area) and flag leaf photosynthetic capacity in dwarf and semi-dwarf wheat cultivars with a wide range in flag leaf size. Photosynthetic capacity was evaluated at anthesis using physiological parameters (maximum net photosynthetic rate and ribulose-1,5-bisphosphate carboxylase efficiency) and anatomical parameters (chlorophyll concentration, stomatal density, interveinal distance and specific leaf weight). Plants were grown with supplemental CO$_2$ (370 µmol mol$^{-1}$), high light (1000 µmol m$^{-2}$ s$^{-1}$), 22/15°C day/night temperatures, ample nutrients and water. Photosynthesis was measured in the laboratory with a closed gas exchange system under a constant light level (2000 µmol m$^{-2}$ s$^{-1}$) and elevated carbon dioxide (1000 µmol mol$^{-1}$). Flag leaf size was not related to maximum photosynthetic rate, but smaller leaves had a higher ribulose-1,5-bisphosphate carboxylase efficiency as determined by the initial slope of photosynthesis versus intercellular CO$_2$ response curves. There were no significant relationships between flag leaf size and chlorophyll concentration, stomatal density and specific leaf weight, but small leaves had closer interveinal distances.
INTRODUCTION

The substantial increase in yield that accompanied the domestication and breeding of wheat has been coupled with a seemingly anomalous progressive reduction in the rate of photosynthesis per unit leaf area (Austin et al., 1982; Rawson et al., 1983). This evolutionary decrease in photosynthesis may be related to an increase in flag leaf area because leaf area (LA) may vary inversely with CO$_2$ exchange per unit leaf area (CER$_{LA}$, a measure of net photosynthetic rate).

Apparently leaf and grain size increased as ploidy increased from the primitive diploid, *Triticum aegilops*, to the modern hexaploid wheat species; these changes were also associated with a decrease in CER$_{LA}$. The advanced wheats more than compensated for their lower rates of photosynthesis by an increase in overall leaf area (Evans and Dunstone, 1970). The early diploid and tetraploid progenitors had smaller, narrower leaves that were thicker and hairier than leaves of modern-day hexaploid wheats. Furthermore, wild and cultivated wheats differed anatomically. The smaller-leaf diploids and tetraploids contained higher concentrations of chlorophyll and nitrogen (Evans and Dunstone, 1970). These factors indicate that increases in photosynthesis may be due to increased absorption of photosynthetically active radiation and/or increased ribulose-1,5-bisphosphate carboxylation capacity, as approximately 50% of nitrogen in leaf protein occurs as ribulose-1,5-bisphosphate (RuBP). Other anatomical characters thought to contribute to
higher net photosynthetic rates of early wheats are greater stomatal densities, smaller mesophyll cell size and smaller interveinal distances (LeCain et al., 1989; Morgan et al., 1990).

There is no clear relationship between flag leaf photosynthesis per unit leaf area and grain yield, which may reflect the negative correlation between photosynthesis and leaf size (Herzog, 1986). However, the following leaf anatomical factors, chlorophyll concentration, stomatal density, interveinal distance and specific leaf weight, may be associated with leaf size and may affect photosynthesis. Net photosynthetic rate and ribulose-1,5-bisphosphate carboxylase concentration, chlorophyll concentration and flag leaf area have been used to assess photosynthetic capacity (Herzog, 1986). Small leaves appeared to be more photosynthetically efficient, and have higher CER rates as well as higher RuBPc efficiency (Morgan et al., 1990). LeCain et al. (1989) also found leaf size was negatively correlated with CER LA in isolines of wheat. However, CER LA was also found to be inversely related to leaf size in willow (Patton and Jones, 1989), small-leafed barley, rice and perennial ryegrass (Bhagsari and Brown, 1986).

Leaf size may be related to RuBPc efficiency per unit LA. The diploid wheats T. boeoticum and T. monococcum, which had the smallest leaf areas, contained the highest amounts of RuBPc, whereas the hexaploid wheats T. spelta and T. aestivum, which had the largest leaf areas, contained the least RuBPc. Higher CER LA in wheat with smaller leaves may be due to smaller
mesophyll cells and higher RuBPc concentrations (Lieckfeldt, 1989). Flag leaf anatomical parameters that may affect photosynthetic capacity are chlorophyll concentration, stomatal density, interveinal distance and specific leaf weight. Chlorophyll concentration may directly influence flag leaf photosynthesis. Small-leaf wheat often has a higher chlorophyll concentration than the large-leaf cultivars, which may reflect the fact that the number of chloroplasts per cell does not increase in proportion to leaf and cell size (Planchon, 1979). Stomatal density, which may influence CO$_2$ diffusion to the intercellular spaces, has also been reduced in modern cultivars; stomatal density was greatest in the small-leafed diploids and least in the larger-leafed hexaploid wheats (Singh and Tsunoda, 1978). A shorter interveinal distance (a higher vein density per leaf area) may result in a shorter, more direct path for the translocation of assimilates from the chloroplasts to the veins (Austin et al., 1982) and may thus increase CER$_{LA}$. Specific leaf weight (SLW), defined as dry weight per unit area of leaf and a direct measure of leaf thickness, may also be important. SLW was higher in small-leaf wheat cultivars (Bhagsari and Brown, 1986). It was positively correlated with CER$_{LA}$ in hexaploid *Triticum* wheat species (Dunstone and Evans, 1974) and in soybean leaves because thicker leaves contain more chlorophyll (Dornhoff and Shibles, 1976).

An understanding of the relationship between LA and CER$_{LA}$ may help in selecting crops for high CER, and may provide an avenue to improve yield. Because small leaves tend to have higher net photosynthetic rates per unit leaf
area (Austin et al., 1982; Bagasari and Brown, 1986; LeCain et al., 1989; Morgan et al., 1990), wheat cultivars with small leaves may be more efficient in a canopy environment, provided that the plant density is high enough to intercept available radiation. Berdahl et al. (1972) reported higher grain yields from wheat with smaller erect leaves, which they attributed to reduced competition for light and found this theory consistent with models that predict better penetration of light into a plant canopy with small leaves, thus increasing total photosynthetic activity. Studies of single leaf photosynthesis have generally involved the uppermost flag leaf, which contributes the most photosynthate (64%) to the developing grain in comparison with the subtending leaves (Rawson et al., 1983), and measurements are generally taken at anthesis when flag leaf photosynthesis is at its maximum (Austin et al., 1982; Aslam and Hunt, 1978; Evans et al., 1975). Genetic factors and environmental conditions (e.g., CO₂ levels, nutrient levels and temperature) directly affect leaf photosynthesis and leaf anatomy and must be considered.

Much controversy exists concerning the relationship between flag leaf size and photosynthetic capacity. Previous studies, which have confirmed significant inverse relationships between leaf size and factors affecting photosynthetic capacity, have differed in methodology, yet have attempted to generalize these relationships for wheat. Some studies have measured maximum CER LA at ambient CO₂ (340 µmol mol⁻¹) conditions on the fully expanded flag leaf using diverse wheat genotypes (Austin et al., 1982). While
others have taken maximum CER_{LA} measurements on the youngest, fully expanded leaf, during the tillering stage, using genetically similar semi-dwarf and tall isolines of wheat (LeCain et al., 1989; Morgan et al., 1990).

This study examined the relationship between leaf size and photosynthetic capacity of the flag leaf, as described by maximum CER_{LA}, RuBPc efficiency, chlorophyll concentration and leaf area, as well as related morphological (SLW) and anatomical (stomatal density and interveinal distance) parameters.
MATERIALS AND METHODS

Plant Culture

Two dwarf (Super Dwarf, BB-19) and three semi-dwarf (Veery-10, Yecora rojo, IBWSN 199) wheat cultivars representing a range of leaf sizes were selected. Plants were grown in a controlled environment with ample water and nutrients, high light (1000 \(\mu\text{mol m}^{-2} \text{s}^{-1}\)), 16 hr photoperiod, 22/15°C day/night temperatures, slightly enriched CO\(_2\) levels (370 \(\mu\text{mol mol}^{-1}\)), and 50% relative humidity during the day. Three seeds were planted in 12 cm x 12 cm x 12 cm plastic pots (6 pots per cultivar), in a 1:1:1 mixture of peat, vermiculite and perlite. Plants were thinned to one plant per pot after seedling establishment. Pots were arranged in a randomized block design to eliminate the variability due to environmental gradients and spaced 2.5 cm apart in each block to minimize shading. Plants were watered twice daily with a 20-5-30 nutrient solution (Peter’s Manual, 1989) using drip irrigation. Light was provided by high-pressure sodium lamps. Flag leaves of each cultivar were positioned at the same distance from the light source throughout the growth period to minimize any variability due to cultivar height differences and provide a uniform light environment. Carbon dioxide was elevated to 370 \(\mu\text{mol mol}^{-1}\).

Photosynthesis and chlorophyll were measured on the fully expanded flag leaf (Haun Stage 7) of the primary head at anthesis (Appendix E), while stomatal density, interveinal distance and specific leaf weight were determined on the fully expanded flag leaves at the termination of each trial. Three
replicate trials were performed and six flag leaves per cultivar were measured for each trial.

**Flag Leaf Size**

Flag leaf areas were measured with a Leaf Area Meter (LI-COR, model 3000) by destructive harvest at the termination of the study. Leaf length and width were measured to an accuracy of 0.1 mm using a caliper.

**Maximum CO₂ Exchange Measurements**

CO₂ exchange rate versus intercellular CO₂ (Ci) response curves were measured in the laboratory with a closed gas exchange system (LI-COR, model 6200). Maximum CER₇₆ for flag leaves was determined at a Ci of 650 µmol mol⁻¹, the concentration that CER₇₆ initially leveled off for all cultivars. The initial slope of the response curve relating CER₇₆ to Ci (50-150 µmol mol⁻¹) was used as an estimate of RuBPc efficiency. (A typical curve is shown in Appendix B; von Caemmerer and Farquhar, 1981.) CER₇₆ and Ci response curves were measured at a starting CO₂ concentration of 1000 µmol mol⁻¹ CO₂ and continued until the CO₂ compensation point was reached using continuous draw-down by the leaf. The system was modified so that CO₂ concentration remained constant between measurements in the open mode and was measured in the closed mode. System and chamber leak rates were measured at frequent intervals and subtracted from the CO₂ exchange rate (McDermitt et al., 1989).
PPF was supplied by a high-pressure sodium lamp positioned above a 4-cm-deep water bath. The leaf chamber of the gas exchange system was mounted on a tripod and positioned below the water bath to receive light levels of 2000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). The water bath filtered out most of the longwave radiation, thus reducing the heat load and making it possible to maintain leaf temperatures at 25\(^\circ\)C. A fan positioned above the leaf chamber helped cool the surrounding air. Two small fans inside the chamber kept CO\(_2\) levels uniform. CO\(_2\)-containing gas from compressed gas cylinders was humidified to 70% by bubbling through 1000 ml Erlenmeyer flasks prior to entry into the chamber. The first flask contained 450 ml of water and the second flask was empty. Maintaining relative humidity at 70% during measurements helped to ensure uniform stomatal conductance across the leaf (McDermitt et al., 1989). Chamber temperature and relative humidity were allowed to equilibrate prior to measurement.

**Chlorophyll Concentration**

A Minolta Chlorophyll Meter (SPAD-502) was used to determine the amount of chlorophyll in flag leaves. Chlorophyll concentration was measured in SPAD units and converted to mg m\(^{-2}\) using an extinction coefficient for chlorophyll (Porra et al., 1989) and the regression equation developed for wheat by Monje and Bugbee (1991).
Stomatal Density

To make stomatal epidermal peels, a drop of acetone was applied to a 1 cm² midsection of the flag leaf, a plastic slide was placed over the treated area, and uniform pressure was applied. Removal of the epidermal layer with the slide provided a permanent record of stomatal distribution, which was uniform across the flag leaf, and thus the epidermal peel from the midsection was representative of the entire width of the flag leaf. Stomatal impressions of both abaxial and adaxial leaf surfaces were counted under a Leitz microscope (100X magnification), and stomatal densities were calculated.

Interveinal Distance

Interveinal distance was measured under a Leitz microscope (100X magnification). The number of veins across the entire width of the flag leaf was determined from epidermal peels (procedure described above for stomatal density counts) stained with safranin, for viewing vascular tissue. Results were compared with a clearing method, in which sodium hydroxide and commercial bleach were used to oxidize and remove chlorophyll from leaves before staining with safranin. Both methods gave similar results.

Specific Leaf Weight

Flag leaves were destructively harvested two weeks post anthesis prior to senescence. Leaf area was determined and individual leaves were dried at 70°C for 48 hrs. Dry mass was measured to an accuracy of 0.1 mg using a
Sartorius mechanical balance. Dry mass per unit leaf area (SLW) was calculated.

**Statistical Analysis**

Linear regression analysis was used to determine the closeness of the relationships ($r^2$), significance of relationship (p-value) and the magnitude of slope between leaf size (length, width and area), the physiological factors (maximum net photosynthetic rate and RuBPc efficiency) and the anatomical factors (chlorophyll concentration, stomatal density, interveinal distance and SLW).
RESULTS

Flag leaf area is influenced by both genetic and environmental components. In the four trials, flag leaf area varied within and between cultivars (Fig. 1). The fact that flag leaf area for each cultivar remained within discrete ranges, as indicated by standard error bars, indicated that genetic control was also a factor. We studied cultivars with a wide range in leaf size and plant height with the following four combinations: semi-dwarf (IBWSN 199) and dwarf (BB-19) cultivars with large leaves and semi-dwarf (Veery-10, Yecora rojo) and dwarf (Super Dwarf) cultivars with small leaves. Trial 2 was eliminated from results and replaced with trial 4 due to the limited range in flag leaf area within and between cultivars, possibly from higher air temperatures during the trial.

Flag Leaf Size and Photosynthesis

Maximum flag leaf CER_{LA} determined at a Ci of 650 µmol mol^{-1}, the maximum Ci achieved by all cultivars, was not related to flag leaf size (area, length or width) in any of the three trials (Fig. 2,3,4).

Flag Leaf Size and RuBPc Efficiency

Regression analysis confirmed that there was a significant negative relationship between RuBP carboxylation efficiency and leaf size (area $r^2=.54$; $p \leq .0002$, length $r^2=.51$; $p \leq .0001$, and width $r^2=.59$; $p \leq .0000$) in all trials (Fig. 2,3,4). Individual regression lines for each trial are shown in Appendix F.
Flag Leaf Size and Anatomy

Flag leaf size was positively related to interveinal distance in all three trials: area ($r^2 = .55; p \leq .0001$), length ($r^2 = .48; p \leq .0000$), and width ($r^2 = .35; p \leq .0002$), but flag leaf size was not correlated with chlorophyll concentration, stomatal density or specific leaf weight (Fig. 5,6,7). Individual regression lines for each trial are shown in Appendix F.
DISCUSSION

Leaf size was associated with photosynthetic capacity: smaller leaves had greater carboxylation efficiency and less distance between veins. Our results were consistent with those of Morgan et al. (1990), who found that smaller wheat leaves had higher RuBPc concentrations and suggested smaller leaves may have a higher RuBPc efficiency. These results are similar to those reported by Austin et al. (1982), who also found that narrower leaves had smaller interveinal distances.

Although others have reported that CER of the flag leaf was negatively correlated with leaf size (area, length or width) and with related parameters of chlorophyll concentration, stomatal density, and specific leaf weight (LeCain et al., 1989), we found no relationship between flag leaf size and maximum CERILA, or the related parameters of chlorophyll concentration, stomatal density and specific leaf weight. These differences may reflect the fact that we examined wheat cultivars at anthesis with a wide range in leaf size, while other studies examined isolines of wheat during the tillering stage (LeCain et al., 1989; Morgan et al., 1990). They suggested that the variability associated with the use of genetically diverse wheat may confound the relationship between leaf size and gas exchange; therefore, isolines have been used in the past to minimize this problem. Hobbs (1988) associated genetic variability in CER with chlorophyll content, specific leaf weight and leaf size. The phenotypic plasticity of wheat leaves to their environment can result in as much as a 100-
fold variation in CER_{LA} (Pearcy et al., 1987). However, we found variability in flag leaf size of cultivars grown under strictly controlled environments (Fig. 2) was considerably less than in outdoor-grown wheat.

Although there was no effect of leaf size on maximum CER_{LA} at high CO_{2} (1000 \mu mol m^{-2} s^{-1}), our findings supported those of LeCain et al. (1989) and Morgan et al. (1990), who found smaller leaves had a higher CER_{LA} under ambient CO_{2} conditions. These finding have significant implications for field production.

Smaller leaves may have a higher CER_{LA}, but carbon assimilation may be greater in genotypes with a high leaf area index (Gent and Kiyomoto, 1985). To further elucidate how the results of single leaf studies relate to the plant and canopy, future research should examine the relationship between flag leaf photosynthesis and carbon partitioning to the grain.
REFERENCES


Fig. 1. Mean flag leaf area for dwarf (Super Dwarf and BB-19) and semi-dwarf (Veery-10, Yecora rojo and IBWSN-199) wheat cultivars over four trials. Standard error bars are shown on the left of graph.
Fig. 2. Flag leaf area and its correlation with maximum CO₂ exchange rate and RuBP carboxylation efficiency at anthesis for three trials (● Trial 1, Δ Trial 3, ▲ Trial 4). The units for carboxylation efficiency were obtained from the initial slope of the CER_{LA} versus Ci response curve (μmol m⁻² s⁻¹/μmol mol⁻¹ = mol m⁻² s⁻¹).
Fig. 3. Flag leaf length and its correlation with maximum CO$_2$ exchange rate and RuBP carboxylation efficiency at anthesis for three trials ( ● Trial 1, △ Trial 3, ▲ Trial 4). The units for carboxylation efficiency were obtained from the initial slope of the CER$_{LA}$ versus Ci response curve ($\mu$mol m$^{-2}$s$^{-1}$/µmol mol$^{-1}$ = mol m$^{-2}$s$^{-1}$).
Fig. 4. Flag leaf width and its correlation with maximum CO$_2$ exchange rate and RuBP carboxylation efficiency at anthesis for three trials (• Trial 1, △ Trial 3, ▲ Trial 4). The units for carboxylation efficiency were obtained from the initial slope of the CER$_{LA}$ versus Ci response curve (μmol m$^{-2}$ s$^{-1}$/μmol mol$^{-1}$ = mol m$^{-2}$ s$^{-1}$).
Fig. 5. Flag leaf area and its correlation with leaf anatomy (chlorophyll concentration, stomatal density, specific leaf weight and interveinal distance) for three trials (o Trial 1, △ Trial 3, △ Trial 4).
Fig. 6. Flag leaf length and its correlation with leaf anatomy (chlorophyll concentration, stomatal density, specific leaf weight and interveinal distance) for three trials (● Trial 1, △ Trial 3, ▲ Trial 4).
Fig. 7. Flag leaf width and its correlation with leaf anatomy (chlorophyll concentration, stomatal density, specific leaf weight and interveinal distance) for three trials (  ● Trial 1, △ Trial 3, ▲ Trial 4).
SOURCE AND SINK CAPACITY IN DWARF AND SEMI-DWARF WHEAT

ABSTRACT

Plant height may affect sink size, which may influence photosynthetic capacity. This study examined the relationship between photosynthetic capacity and the activities of source and sink in dwarf and semi-dwarf wheat (*Triticum aestivum* L.). We assessed this relationship by measuring the following parameters: maximum photosynthetic rate, ribulose-1,5-bisphosphate carboxylase (RuBPc) efficiency, chlorophyll concentration, leaf area and dry mass partitioning of carbohydrates. Plants were grown under controlled environmental conditions: slightly enriched CO$_2$ (370 µmol mol$^{-1}$), high light (1000 µmol m$^{-2}$ s$^{-1}$), 50% relative humidity, 22/15°C day/night temperatures, ample nutrients and water. Photosynthetic capacity was determined at anthesis using photosynthesis versus internal CO$_2$ concentration curves measured under high light (2000 µmol m$^{-2}$ s$^{-1}$), and high initial CO$_2$ concentration (1000 µmol mol$^{-1}$). Dwarf wheat cultivars had higher maximum photosynthetic rates and more chlorophyll per unit leaf area than the taller semi-dwarfs. Ear removal at anthesis in dwarf wheat decreased maximum photosynthesis by 40%, whereas the effect of ear removal in semi-dwarfs was less than 5%. We speculate that the ear at anthesis is a critically important sink for dwarf wheats, while semi-dwarfs transport assimilate to other significant sinks (i.e., stems).
INTRODUCTION

Dwarfing genes such as Rht1 and Rht2, which have been used to reduce plant height (Allan, 1989), have been responsible for substantial increases in harvest index (50%) and lodging resistance, thus contributing to marked increases in modern wheat yields (Gent and Kiyomoto, 1985). Higher grain yields and harvest indices of the shorter modern varieties have been attributed to reduced competition between the developing ear and stem; a reduction in height was accompanied by a reduction in stem weight per unit area (Hay and Walker, 1989; Kulshrestha and Tsunoda, 1981). Studying photosynthetic capacity of wheat in relation to plant height could identify mechanisms to further increase the harvest index and elucidate limitations to grain yield.

Several mechanisms control grain yield. Grain yield in wheat may be limited by the assimilate supply to the growing grains (source) and the capacity of the grain to accumulate assimilate (sink) (Evans et al., 1970). Grain size, grain number and sink strength are genetically influenced (Fischer and HilleRisLambers, 1978; Thornley, 1979; Walpole and Morgan, 1970). Increased photosynthetic capacity was correlated with increased kernel weight and grains/m² (Fischer, 1975).

Past research concerning transfer of assimilate in wheat found that mostly sucrose was transported (Herzog, 1986). Wheat leaves accumulated much less starch (Hay and Walker, 1989) than sucrose, with a sucrose/starch ratio of five (Bell and Incoll, 1982). The characteristics of assimilate movement
between source and sink agreed with Munch's pressure flow hypothesis, which states that translocation depended on the source:sink concentration gradient and in turn affects the rate of photosynthesis and the velocity at which assimilates were translocated (Herzog, 1982; Wardlaw and Moncur, 1976). LeCain et al. (1989) found that dwarfing genes were associated with smaller interveinal distances, which positioned cells closer to veins. Dwarf wheat may thus transport assimilate more efficiently. Carbohydrate deposition was determined in part by proximity to the source, and remobilization depended on the relationship between photosynthetic capacity and grain demand (Herzog, 1986). Walpole and Morgan (1970) suggested that proximity to assimilate supply (source) as well as the physiological activity of sinks (Herzog, 1986) affected carbohydrate deposition in the grain (sink), i.e., the upper nodes and internodes were preferentially supplied with carbohydrates because they were closer to the source (Herzog, 1986).

Source limitation of photosynthate may be more important than sink limitation particularly at grain filling (Fischer, 1975; Herzog, 1986; Martinez-Carrasco and Thorne, 1979), although sink limitation may be the predominant influence later during grain-filling when the demands of competing sinks have lessened (Hay and Walker, 1989). The flag leaf is a reliable predictor of source capacity (Evans et al., 1970), because the main source for carbon used in grain filling in modern wheats is produced by current flag leaf photosynthesis (Austin and Edrich, 1975). Herzog (1986) stated that photosynthetic capacity of a
wheat stand from anthesis to maturity was a combination of source size and activity, which was adequately described by the following flag leaf parameters: photosynthetic rate, RuBPC efficiency, chlorophyll concentration and leaf area. He used chlorophyll concentration and RuBPC activity to assess source capacity of the flag leaf (chlorophyll content roughly paralleled photosynthetic rate) and considered RuBPC, which generally constitutes about 50% of the total soluble protein found in leaves, to be rate limiting in photosynthesis.

Pyke and Leech (1985) found that the flag leaves of semi-dwarf genotypes of modern hexaploid wheat, which tended to have smaller leaves, contained more RuBPC per unit area than the flag leaves of tall genotypes, which suggested that dwarf lines had greater photosynthetic carboxylation capacity. von Caemmerer and Farquhar (1981) reported that the concentration of RuBPC may limit CERLA at low Ci and therefore RuBPC efficiency may be predicted from the initial slope of photosynthetic rate versus internal CO₂ concentration. Dwarfing genes were also found associated with higher maximum CERLA and chlorophyll concentrations (Morgan et al., 1990; Kulshretha and Tsunoda, 1981).

Dwarf cultivars may partition carbohydrate differently than semi-dwarfs. Dry matter accumulation in cereal grains occurs in a sigmoidal pattern with three distinguishable growth phases: the initial lag phase, the linear phase, and the maturation phase (Herzog, 1986). Source and sink activities were at their maximum during the linear phase and grain growth appeared to be limited.
most by the capacity of the grains to absorb sucrose and synthesize starch (Herzog, 1982). Prior to anthesis, surplus carbohydrate was deposited mainly in the stems; carbohydrates were then relocated to the ear shortly before and after anthesis (Fischer and HilleRisLambers, 1978). During grain filling, stems lost 30% or more of their dry weight to the head as carbohydrates (Austin et al. 1977). Conversely, Herzog (1986) reported that stem reserves were generally not mobilized unless a wheat plant was under stress. In wheat, the stems contributed 2.7 to 12.2% (in periods of stress) of carbohydrate to the grain yield (Austin et al., 1980). Sofield et al. (1977) reported that current photosynthetic rates did not limit grain yield as supply of photosynthate was adequate at all stages of development due to mobilization from other parts of the plant (lower internodes). Under adverse conditions at grain filling, taller wheats may have a competitive advantage because assimilate stored in stems acted as a buffer when current photosynthesis was not adequate; the stems of taller wheat at anthesis contained a higher proportion of flag leaf assimilates than did the stems of dwarf cultivars (Rawson and Evans, 1971). The role of assimilate partitioning of dry mass in cultivars of differing heights is still not clear. Gent and Kiyomoto (1985) found that total biomass at maturity was similar in dwarf and semi-dwarf cultivars, which suggests that there may be no difference in carbohydrate storage capacity, although shorter cultivars had higher stem respiration rate per unit dry weight (Pyke and Leech, 1985; Rawson and Evans, 1971).
Past researchers have attempted to determine the sink strength of the ear by measuring the effects of ear removal on flag leaf photosynthesis at anthesis. Wardlaw and Moncur (1976) suggested that the ear controls the supply of assimilate, which was consistent with the findings of Hay and Walker (1989), who found that the plant at anthesis directed more assimilates to the ear from sinks in the subtending leaves and lower parts, thus competing with alternative sinks in roots and young tillers. Also assimilate movement in the peduncle was reduced immediately after grain was removed from the ear (Wardlaw and Moncur, 1976). Austin and Edrich (1975) found that more of the assimilated carbon remained in the flag leaves of de-eared plants and that appreciable portions of $^{14}$C were transferred to the young tillers and roots. No assimilated carbon was transferred to these organs when the primary ear was present. Wardlaw and Moncur (1976) found that assimilate movement in the peduncle decreased immediately after grains were removed from the ear. In contrast, Austin and Edrich (1975) found ear removal during anthesis reduced flag leaf photosynthesis by less than 10% and that ear removal did not affect subtending leaves. However, others reported a 40% reduction in CER$_{LA}$ following removal of the wheat ear, an effect that was partially reversed by shading of the lower leaves (Hay and Walker, 1989). Radley (1978) reported that culms of degrained plants contained as much as 77% more sucrose than culms of intact plants five weeks after anthesis.

Sink activity and capacity are also affected by exogenous factors
(temperature, light, water and nutrients, particularly N) and endogenous factors (phytohormones, i.e., cytokinins) (Herzog, 1986). Borojevic and Williams (1982) studied genotype x environment interactions and found that environmental factors had greater effects on source capacity than on sink capacity. Our ability to raise wheat under strictly controlled conditions enabled us to minimize these environmental effects.

Past research concerning the relationship of plant height and photosynthetic capacity has been inconclusive and contradictory. Kulshrestha and Tsunoda (1981) reported that dwarfing genes (semi-dwarfs) increased CER_{LA}, but other studies found no difference between plant height and flag leaf photosynthesis (Austin et al., 1977; Gent and Kiyomoto, 1985; Rawson and Evans, 1971). While some studies report that a substantial portion of assimilates were allocated from the stem to the grain (Austin et al., 1977), others suggest that stem reserves were mobilized only during severe stress (Herzog, 1986). Another major controversy over the effects of source and sink concerns the effect of ear removal. Some authors reported a substantial reduction (40%) in flag leaf photosynthesis with ear removal (Hay and Walker, 1989) while others reported little or no effect (Austin and Edrich, 1975). The primary objective of our research was to examine the influence of plant height on the ratio of source to sink capacity at anthesis in dwarf and semi-dwarf wheat. Photosynthetic rate versus intercellular CO$_2$ response curves were used to more fully understand the relation of plant height to photosynthetic capacity.
MATERIALS AND METHODS

Plant Culture

Five cultivars of dwarf (Super Dwarf, BB-19) and semi-dwarf (Veery-10, Yecora rojo, IBWSN 199) were selected. Plants were grown in a strictly controlled environment with ample water and nutrients, high light (1000 µmol m$^{-2}$ s$^{-1}$), 16 hr photoperiod, 22/15°C day/night temperatures, slightly enriched CO$_2$ levels (370 µmol mol$^{-1}$), and 50% relative humidity. Three seeds were planted in 12 cm x 12 cm x 12 cm plastic pots (6 pots per cultivar), in a 1:1:1 mixture of peat, vermiculite and perlite. Plants were then thinned to one plant per pot after seedling establishment. Pots were arranged in a randomized block design to eliminate variability due to environmental gradients and spaced 2.5 cm apart in each block to minimize shading. Plants were watered twice daily with 20-5-30 nutrient solution (Peter's Reference Manual, 1989) using drip irrigation. Light (1000 µmol m$^{-2}$ s$^{-1}$) was provided by high pressure sodium lamps. Flag leaves of each cultivar were positioned at the same distance from light source throughout the growth period to minimize any variability due to cultivar height differences and provide a uniform light environment. Supplemental CO$_2$ (370 µmol mol$^{-1}$) was provided by compressed gas cylinders and was distributed by circulating fans.
Determination of Source Capacity

Maximum Photosynthesis and RuBPC efficiency

Maximum $CER_{LA}$ and RuBPC efficiency were measured with a closed gas exchange system (LI-6200, model 6200) using $CER_{LA}$ versus $Ci$ response curves on the fully expanded flag leaf (Haun Stage 7) of the primary head at anthesis (Appendix E). Maximum $CER_{LA}$ was measured at $Ci$ 650 µmol mol$^{-1}$, the highest $Ci$ concentration obtained by all five cultivars studied and RuBPC efficiency was estimated from the initial slope of the curve (50-150 µmol mol$^{-1}$) where $CER$ is limited by regeneration of RuBP (von Caemmerer and Farquhar, 1981) (Appendix B). Three replicate trials were performed and $CER$ versus $Ci$ response curves were measured on four flag leaves per cultivar for each trial by $CO_2$ depletion over a 45 min. sampling interval. Measurements were taken with an initial $CO_2$ concentration of 1000 µmol mol$^{-1}$ until the $CO_2$ compensation point was reached. Flag leaves were equilibrated for 1 hr in a 1 L leaf cuvette under high light (2000 µmol m$^{-2}$ s$^{-1}$) provided by a high pressure sodium lamp positioned above a 4-cm-deep water bath, which filtered out longwave radiation, thereby reducing the heat load on the leaf. Leaf temperature was maintained at 25°C. A circulating fan positioned above the leaf cuvette cooled the surrounding air, while the two small fans inside the cuvette reduced leaf boundary layer and kept $CO_2$ levels uniform. High relative humidity (RH) during $CER_{LA}$ versus $Ci$ curve measurement ensured uniform stomatal conductance across the leaf (McDermitt et al., 1989), RH was
maintained at 70% relative humidity by bubbling CO\textsubscript{2} from compressed gas cylinders through a water bath prior to entry into the cuvette. Measurements were taken at the same time interval (mid morning until mid afternoon) to avoid any possible interaction with circadian rhythms involved in the cycling of photosynthesis, transpiration and stomatal oscillations. Pallas (1973) found no diurnal endogenous changes in photosynthesis or transpiration in monocot grasses.

*Flag Leaf Area and Chlorophyll*

Flag leaf area was measured in cm\textsuperscript{2} with a leaf area meter (LI-COR, model 3000) by destructive harvest at the termination of anthesis.

A Minolta Chlorophyll Meter (SPAD-502) was used to determine the amount of chlorophyll in flag leaves. Chlorophyll concentration was measured in SPAD units and converted to mg m\textsuperscript{-2} using extinction coefficient for chlorophyll (Porra et al., 1989) and the regression equation developed for wheat by Monje and Bugbee (1991).

*Determination of Sink Capacity*

*Sink Strength*

Four plants per cultivar were de-eared at anthesis in order to examine the effects of sink limitation. Three replicate trials were performed and CER\textsubscript{LA} versus Ci response curves were developed for both de-eared and control plants using the conditions described above to measure maximum photosynthesis and
RuB Pc efficiency. CER_LA versus Ci response curves were measured immediately and six hours following ear removal to determine if there had been any initial hormonal shock effect (Herzog, 1986).

**Partitioning of Dry Mass**

Ratios of dry mass of sources (leaves) and sinks (sheaths, stems and heads) expressed as a percentage of the total dry mass of the primary tiller were determined 5 days after anthesis. Six plants of each cultivar were placed in the dark for 48 hrs in order to deplete nonstructural carbohydrates. Plants were then destructively sectioned into stems, leaves, head and placed in the drying oven at 70°C for 48 hrs. Dry mass was measured in grams using an electronic balance.

**Statistical Analysis**

Linear regression analysis was used to determine the closeness of the fit ($r^2$) and significance of relationship (p-value) between plant height and related parameters for photosynthetic capacity: maximum photosynthetic rate, RuB Pc efficiency, chlorophyll concentration and dry mass partitioning. Differences in dry mass partitioning for the five cultivars studied were observed using statistical analysis, ANOVA, completely randomized design. LSD was determined using the Student-Newman-Keuls Test at a $p \leq .05$ level of significance.
RESULTS

Plant Height and Source Capacity

*Maximum Photosynthesis and RuBPC Efficiency*

CER\textsubscript{LA} versus intercellular CO\textsubscript{2} (Ci) curves (Appendix B), which were used to assess photosynthetic potential (maximum CER\textsubscript{LA} RuBPC efficiency) at preanthesis and anthesis, revealed differences in the dwarf and semi-dwarf wheat cultivars. The dwarfs had lower saturated CER\textsubscript{LA} at preanthesis and experienced a substantial increase in CER\textsubscript{LA} at anthesis, whereas the CER\textsubscript{LA} versus Ci curves for the semi-dwarf were similar at preanthesis and anthesis (Fig. 8). The percentage increase in maximum CER\textsubscript{LA} from preanthesis to anthesis was substantially greater (42%) in dwarf cultivars than in semi-dwarfs, which had no increase (Fig. 9).

There was a significant negative correlation between plant height and CER\textsubscript{LA} in all three trials ($r^2 = .33$, $p \leq .0000$). Maximum CER\textsubscript{LA} (650 $\mu$mol mol\textsuperscript{-1}) was higher in dwarf cultivars than in semi-dwarf wheat (Fig. 10). Plant height was weakly related to RuBPC efficiency ($r^2 = .15$, $p \leq .0487$) (Fig. 10). The initial slopes of CER\textsubscript{LA} versus Ci response curves were similar in all cultivars studied.

*Chlorophyll Concentration and Flag Leaf Area*

Plant height was related to chlorophyll concentration and over three trials studied; shorter cultivars had significantly higher chlorophyll
concentrations ($r^2 = .83, p \leq .0000$) (Fig. 11). We found a weak positive correlation between plant height and flag leaf area ($r^2 = .18, p \leq .0112$) (Fig. 11).

**Plant Height and Sink Capacity**

*Ear Detachment at Anthesis*

We compared sink strength of the ear in the dwarf and semi-dwarf cultivars by direct manipulation of sink strength via ear removal at anthesis (representative data, Fig. 12). $CER_{LA}$ versus $Ci$ curves revealed dramatic differences in the effects of ear removal between dwarf and semi-dwarf cultivars. Ear removal reduced maximum flag leaf photosynthesis by an average of 40% in dwarf wheats, and less than 5% for the semi-dwarfs, although ear removal had little or no effect on $CER_{LA}$ at lower levels of $Ci$ (50-150 µmol mol$^{-1}$) as the initial slopes with and without the ear were similar for dwarf and semi-dwarf cultivars. The percentage decrease in maximum $CER_{LA}$ in dwarf and semi-dwarf cultivars differed slightly when compared with maximum $CER_{LA}$ measurements taken on flag leaf of same plant 24 hours earlier or with leaf of control plant (Figures 13,14; derived from Figure 12).

*Dry Mass Partitioning*

Plant height was positively related to stem mass ($r^2 = .34, p \leq .0000$) over the five cultivars studied (Fig. 15), suggesting that taller cultivars allocated more carbohydrate to the stem. Plant height was not related to ear mass or the combined mass of potential sinks (stem, sheath and ear). Under uniform light,
plant height was positively related to tiller number \( (r^2=.49, p \leq .0000) \). There were significant differences in dry mass partitioning post anthesis between the five cultivars, based on total dry mass (stems, leaves, sheaths and ear) of the primary tiller (Table 1), although dwarf and semi-dwarf cultivars partitioned similar amounts of dry mass to leaves, sheaths, stems and ears.
DISCUSSION

At anthesis, dwarf wheat exhibited a higher maximum CER_{LA} and chlorophyll concentrations than the taller semi-dwarfs. There was a weak relationship between plant height and flag leaf area (Fig. 11). Contrary to the findings of this study, LeCain et al. (1989) found that a reduction in plant height was accompanied by a reduction in leaf size, which concentrated photosynthetic machinery, i.e., chlorophyll. In all trials, the CO_2-saturated rate of photosynthesis in dwarf cultivars was reduced at preanthesis, although the initial slopes were similar from preanthesis to anthesis. Hay and Walker (1989) attributed this to feedback inhibition of photosynthesis, which often occurs in conditions favoring high CER_{LA} (i.e. saturating light, elevated CO_2) and results when insufficient demand for assimilate by the ear causes carbohydrate to accumulate in the flag leaf. The accumulation of carbohydrates is accompanied by the impairment of RuBP regeneration in the Calvin cycle (Sage, 1990). This feedback inhibition of photosynthesis at preanthesis in dwarf cultivars, which was characterized by a depression in flag leaf photosynthesis, was alleviated at anthesis, as the sink strength of the head increased during grain filling.

The effects of ear removal from dwarf and semi-dwarf cultivars indicated that sink strength at anthesis was greater in dwarf wheats as shown in a substantial increase (42%) in maximum CER_{LA} at anthesis. Based on these maximum CO_2 exchange rates (at Ci of 650 µmol mol^{-1}), we found that sink strength of the ear is an important determinant in the transport of assimilates
in dwarf but not in semi-dwarf wheat. Our results suggest that the taller semi-dwarfs translocate assimilate to other major sinks (i.e., stems, tillers) in addition to the ear during grain filling, whereas the ear at anthesis may be the single most important sink in dwarf wheats.

Rawson and Evans (1971) hypothesized that dwarf wheat had less buffering capacity in the stem and thus less assimilate to allocate to the head in times of stress. In this study, however, there were no significant differences in dry matter partitioning (expressed on a percentage basis) for dwarf and semi-dwarf cultivars (Table 1), even though taller cultivars had a greater stem mass and greater tillering capacity (Fig. 15). Our results also conflict with those of Austin et al. (1980) who found tall genotypes partitioned 30% more dry mass to stems than double dwarf genotypes. However, Rawson and Evans (1971) found that the specific respiration rate in the stem was inversely proportional to stem height (dwarf cultivars produced substantially more CO$_2$ per gram of stem than the taller cultivars), yet they found virtually no difference in stem weight between tall and semi-dwarf cultivars. In contrast, other studies found that taller wheat cultivars had greater total losses of CO$_2$ from stems following anthesis and lower grain yields than dwarf cultivars, which had lower shoot respiration rates (Rawson and Evans, 1971).

Dwarf cultivars may have a higher single-leaf CER$_{LA}$, but this does not necessarily result in higher canopy photosynthesis (Morgan et al., 1990). The ultimate goal of our research is to understand the relationship between single-
leaf and canopy CER, and how this affects yield. To date, no net differences in canopy CER have been observed between plants of differing heights at anthesis (Kiyomoto and Gent, 1989).
REFERENCES


Fig. 8. Representative curves of CO₂ exchange rate versus intercellular CO₂ for dwarf (BB-19) and semi-dwarf (IBWSN-199) cultivars at 5-d preanthesis and anthesis.
Fig. 9. Percentage increase in maximum CO₂ exchange rate (Ci=650 µmol mol⁻¹) from 5-d preanthesis to anthesis for dwarf (Super dwarf, 24-27 cm; BB-19, 35-45 cm) and semi-dwarf (Veery-10, 45-50 cm; Yecora Rojo, 59-61 cm; IBWSN-199, 78-85 cm) cultivars over three trials.
Fig. 10. Plant height and its correlation with maximum CO$_2$ exchange rate (Ci=650 µmol mol$^{-1}$ and RuBP carboxylation efficiency of the flag leaf at anthesis for three trials (○ Trial 1, Δ Trial 3, ▲ Trial 4). The units for carboxylation efficiency were obtained from the initial slope of the CER$_{LA}$ versus Ci response curve (µmol m$^{-2}$ s$^{-1}$/µmol mol$^{-1}$ = mol m$^{-2}$ s$^{-1}$).
Fig. 11. Plant height and its correlation with chlorophyll concentration and flag leaf area at anthesis for three trials (● Trial 1, △ Trial 3, ▲ Trial 4).
Fig. 12. Representative curves of the effect of ear removal on CO$_2$ exchange rate at anthesis for dwarf (BB-19) and semi-dwarf (IBWSN-199) wheat cultivars.
Fig. 13. Percentage decrease in maximum CO$_2$ exchange rate (Ci=650 µmol mol$^{-1}$) with ear removal at anthesis compared with the same leaf 24 h earlier for dwarf (Super dwarf, 24-27 cm; BB-19, 35-45 cm and semi-dwarf (Veery-10, 45-50 cm; Yecora Rojo, 59-61 cm; IBWSN-199, 78-85 cm) cultivars in three trials.
Fig. 14. Percentage decrease in maximum CO$_2$ exchange rate (Ci=650 µmol mol$^{-1}$) with ear removal at anthesis compared with the control plant with an ear for dwarf (Super dwarf, 24-27 cm; BB-19, 35-45 cm) and semi-dwarf (Veery-10, 45-50 cm; Yecora Rojo 59-61 cm; IBWSN-199, 78-85 cm) cultivars in three trials.
Fig. 15. Plant height and its relationship to dry mass partitioning expressed per the primary tiller (stem mass, ear mass, and stem+sheath+ear mass) and tiller number per plant for dwarf and semi-dwarf cultivars.
Table 1. Ratio of the dry mass of sources (leaves) and sinks (sheaths, stems and heads) expressed as a percentage of the total dry mass of the primary tiller 5-d after anthesis. Data are the mean (six plants each) of 2 dwarf (Super Dwarf and BB-19) and 3 semi-dwarf (Veery-10, Yecora Rojo and IBWSN-199) cultivars.

<table>
<thead>
<tr>
<th>Cultivars</th>
<th>Flag Leaf/All Leaves</th>
<th>Flag Leaf/Total</th>
<th>Leaves/Total</th>
<th>Sheaths/Total</th>
<th>Stems/Total</th>
<th>Ear/Total</th>
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<tr>
<td>SP. DWF.</td>
<td>17%</td>
<td>3.2%</td>
<td>12%</td>
<td>5.4%</td>
<td>30%</td>
<td>52%</td>
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<tr>
<td>BB-19</td>
<td>26%</td>
<td>7.4%</td>
<td>20%</td>
<td>8.8%</td>
<td>42%</td>
<td>29%</td>
</tr>
<tr>
<td>V-10</td>
<td>21%</td>
<td>4.0%</td>
<td>11%</td>
<td>6.6%</td>
<td>37%</td>
<td>46%</td>
</tr>
<tr>
<td>YRO</td>
<td>19%</td>
<td>2.5%</td>
<td>10%</td>
<td>3.4%</td>
<td>51%</td>
<td>35%</td>
</tr>
<tr>
<td>IB-199</td>
<td>24%</td>
<td>5.7%</td>
<td>17%</td>
<td>7.9%</td>
<td>42%</td>
<td>34%</td>
</tr>
<tr>
<td>LSD</td>
<td>4.5%</td>
<td>14%</td>
<td>2.0%</td>
<td>2.0%</td>
<td>7.2%</td>
<td>6.0%</td>
</tr>
<tr>
<td>p≤.05</td>
<td>.0008**</td>
<td>.2603 ns</td>
<td>.0000***</td>
<td>.0025**</td>
<td>.0001**</td>
<td>.0000***</td>
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</table>
CONCLUSIONS

Smaller flag leaves had a higher RuBP carboxylase efficiency, but did not have higher maximum rates of photosynthesis. Smaller leaves also had closer vein distances, which may mean a shorter, more direct, pathway for the translocation of assimilates out of the leaf. Flag leaf size was not related to chlorophyll concentration, stomatal density or specific leaf weight.

Plant height was associated with flag leaf photosynthetic capacity. Dwarf wheat cultivars had higher maximum photosynthetic rates and more chlorophyll per unit flag leaf area than the taller semi-dwarfs. Dwarf wheats displayed a lower maximum flag leaf photosynthetic rate at preanthesis followed by a substantial (40%) increase in maximum photosynthesis at anthesis, suggesting feedback inhibition of photosynthesis at preanthesis. This increase did not occur in the semi-dwarfs. Ear removal at anthesis in dwarf wheat decreased maximum photosynthesis by approximately 40%, while the effect of ear removal in semi-dwarf wheats was less than 5%. Although no consistent differences were found in dry mass partitioning between dwarf and semi-dwarfs, the data suggest that the ear at anthesis is a critically important sink for dwarf wheats, while semi-dwarfs transport assimilate to other significant sinks (i.e., stems).
APPENDICES
### APPENDIX A

Table 2. Nutrient Formula for Peters Professional Fertilizer (20-5-30)

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Nutrient Levels (ppm) at 100 ppm Nitrogen</th>
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<tr>
<td>Ca</td>
<td>0.480</td>
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<tr>
<td>Mg</td>
<td>0.250</td>
</tr>
<tr>
<td>Na</td>
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<td>S</td>
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<tr>
<td>B</td>
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<tr>
<td>Cl</td>
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</tr>
<tr>
<td>Cu</td>
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</tr>
<tr>
<td>Fe</td>
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<tr>
<td>Mn</td>
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</tr>
<tr>
<td>Mo</td>
<td>0.005</td>
</tr>
<tr>
<td>Zn</td>
<td>0.013</td>
</tr>
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Fig. 16. Representative CO₂ exchange rate versus intercellular CO₂ response curve used to estimate maximum CER₂₄ and RuBPc efficiency. Replicate curves measured on same leaf.
Table 3. Symbols, Parameters and Units Used in Analyzing Data with the Portable Photosynthesis System LI-6200 Primer (Version 2.01)

**Measured Parameters**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Parameter</th>
<th>Units</th>
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<tr>
<td>P</td>
<td>barometric pressure</td>
<td>mb</td>
</tr>
<tr>
<td>V</td>
<td>volume</td>
<td>cm³</td>
</tr>
<tr>
<td>A</td>
<td>leaf area within chamber</td>
<td>cm²</td>
</tr>
<tr>
<td>BC</td>
<td>boundary layer conductance of one side of the leaf</td>
<td>mol m⁻² s⁻¹</td>
</tr>
<tr>
<td>STMRAT</td>
<td>an estimate of the ratio of stomatal resistances of one side of the leaf to the other</td>
<td></td>
</tr>
<tr>
<td>Fx</td>
<td>maximum flow rate that can be achieved through the desiccant</td>
<td>µmol s⁻¹</td>
</tr>
<tr>
<td>TIME</td>
<td>the number of seconds since the start time</td>
<td>s</td>
</tr>
<tr>
<td>PAR</td>
<td>the quantum sensor reading</td>
<td>µmol m² s⁻¹</td>
</tr>
<tr>
<td>TAIR</td>
<td>air temperature in the leaf chamber</td>
<td>°C</td>
</tr>
<tr>
<td>TLEAF</td>
<td>leaf temperature</td>
<td>°C</td>
</tr>
<tr>
<td>CO₂</td>
<td>CO₂ concentration</td>
<td>µmol mol⁻¹</td>
</tr>
<tr>
<td>FLOW</td>
<td>flow rate through the desiccant</td>
<td>µmol m² s⁻¹</td>
</tr>
<tr>
<td>RH</td>
<td>relative humidity</td>
<td>%</td>
</tr>
<tr>
<td>EAIR</td>
<td>vapor pressure of the air in the leaf chamber</td>
<td>mb</td>
</tr>
<tr>
<td>DE/DT</td>
<td>the difference in vapor pressure between the last two samples</td>
<td></td>
</tr>
<tr>
<td>DC/DT</td>
<td>the difference in CO₂ concentration between the last two samples</td>
<td></td>
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</tbody>
</table>

**Calculated Parameters**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Parameter</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>PHOTO</td>
<td>net photosynthesis</td>
<td>µmol m² s⁻¹</td>
</tr>
<tr>
<td>CMOL</td>
<td>stomatal conductance</td>
<td>mol m² s⁻¹</td>
</tr>
<tr>
<td>CINT</td>
<td>intercellular CO₂ concentration</td>
<td>µmol mol⁻¹</td>
</tr>
<tr>
<td>RS</td>
<td>stomatal resistance</td>
<td>s cm⁻¹</td>
</tr>
<tr>
<td>CS</td>
<td>stomatal conductance</td>
<td>cm s⁻¹</td>
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</table>

**Additional Parameters**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Parameter</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vt</td>
<td>total volume of system</td>
<td>cm³</td>
</tr>
<tr>
<td>Vg</td>
<td>IRGA volume including hoses to chamber</td>
<td>cm³</td>
</tr>
<tr>
<td>Kabs</td>
<td>water absorption factor</td>
<td></td>
</tr>
</tbody>
</table>
The derivations for transpiration, photosynthesis, intercellular CO₂ and the leak rate constant equations are based on an analysis of the mass balance of water and CO₂ in the LI-6200 system.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>T&lt;sub&gt;a&lt;/sub&gt;</td>
<td>°C</td>
<td>Chamber air temperature</td>
</tr>
<tr>
<td>F&lt;sub&gt;d&lt;/sub&gt;</td>
<td>µmol s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Flow through desiccant</td>
</tr>
<tr>
<td>e</td>
<td>mb</td>
<td>Vapor pressure of air</td>
</tr>
<tr>
<td>δe/δt</td>
<td>mb s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Rate of change of e</td>
</tr>
<tr>
<td>E</td>
<td>mol m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Transpiration rate</td>
</tr>
<tr>
<td>P</td>
<td>mb</td>
<td>Atmospheric pressure</td>
</tr>
<tr>
<td>S</td>
<td>cm&lt;sup&gt;2&lt;/sup&gt;</td>
<td>Leaf area</td>
</tr>
<tr>
<td>V&lt;sub&gt;t&lt;/sub&gt;</td>
<td>cm&lt;sup&gt;3&lt;/sup&gt;</td>
<td>Total volume</td>
</tr>
<tr>
<td>F&lt;sub&gt;x&lt;/sub&gt;</td>
<td>µmol s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Maximum flow rate</td>
</tr>
<tr>
<td>V&lt;sub&gt;g&lt;/sub&gt;</td>
<td>cm&lt;sup&gt;3&lt;/sup&gt;</td>
<td>IRGA volume</td>
</tr>
<tr>
<td>K&lt;sub&gt;abs&lt;/sub&gt;</td>
<td></td>
<td>Absorption coefficient</td>
</tr>
<tr>
<td>T&lt;sub&gt;l&lt;/sub&gt;</td>
<td>°C</td>
<td>Leaf temperature</td>
</tr>
<tr>
<td>g&lt;sub&gt;sw&lt;/sub&gt;</td>
<td>mol m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Stomatal conductance, water</td>
</tr>
<tr>
<td>e&lt;sub&gt;s&lt;/sub&gt;()</td>
<td>mb</td>
<td>Sat. vapor pressure function</td>
</tr>
<tr>
<td>g&lt;sub&gt;bwo&lt;/sub&gt;</td>
<td>mol m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>One-sided boundary layer cond.</td>
</tr>
<tr>
<td>K</td>
<td></td>
<td>Stomatal ratio</td>
</tr>
<tr>
<td>C</td>
<td>µl l&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>CO₂ concentration</td>
</tr>
<tr>
<td>δC/δt</td>
<td>µl l&lt;sup&gt;-1&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Rate of CO₂ change</td>
</tr>
<tr>
<td>A</td>
<td>µmol m&lt;sup&gt;-2&lt;/sup&gt; s&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Photosynthetic rate of leaf</td>
</tr>
</tbody>
</table>
Transpiration

\[
E = \frac{E_d\epsilon + \left[ \frac{K_{abs}}{100P} \right] [V_1 - E_d V_x]}{8.314 (T_a + 273) F_x} \frac{\delta x}{\delta t}
\]

Photosynthesis

\[
A = \frac{E_d C}{100 S P} - \frac{P G V_t}{8.314 (T_a + 273) S} \frac{\delta C}{\delta t} - C E G
\]

Intercellular CO₂

\[
C_i = \frac{[g_{ic} - \bar{E}] C_a - A}{2} = \frac{[g_{ic} + \bar{E}]}{2}
\]

Leak Corrections

The chamber leak rate time constant \( \Gamma \) has been shown to be independent of CO₂ gradient \( (C_a - C_c) \). Leaks can be modeled by:

\[
\frac{\delta C}{\delta t|\text{leak}} = \frac{C_a - C_c}{\Gamma}
\]

\[
\Gamma = \frac{C_a - C_c}{\delta C/\delta t}
\]
APPENDIX E

Fig. 17. Mean maximum CO₂ exchange rate per unit leaf area versus time for six dwarf (Super Dwarf) and six semi-dwarf (Veery-10) plants, expressed 5 days pre and post anthesis.
Individual Regression Line for Flag Leaf Area and its Correlation with CERLA and RuBP carboxylation Efficiency.

Fig. 18. Flag leaf area and its correlation with maximum CO₂ exchange rate and RuBP carboxylation efficiency at anthesis for three trials (● Trial 1, △ Trial 3, ▲ Trial 4). The units for carboxylation efficiency were obtained from the initial slope of the CER_{LA} versus Ci response curve (μmol m⁻² s⁻¹/μmol mol⁻¹ = mol m⁻² s⁻¹).
Fig. 19. Flag leaf length and its correlation with maximum CO₂ exchange rate and RuBP carboxylation efficiency at anthesis for three trials (● Trial 1, Δ Trial 3, ▲ Trial 4). The units for carboxylation efficiency were obtained from the initial slope of the CER₅ₐ versus Ci response curve (µmol m⁻² s⁻¹/µmol mol⁻¹ = mol m⁻² s⁻¹).
Fig. 20. Flag leaf width and its correlation with maximum CO$_2$ exchange rate and RuBP carboxylation efficiency at anthesis for three trials (○ Trial 1, Δ Trial 3, Δ Trial 4). The units for carboxylation efficiency were obtained from the initial slope of the CER$_{LA}$ versus Ci response curve ($\mu$mol m$^{-2}$ s$^{-1}$/µmol mol$^{-1}$ = mol m$^{-2}$ s$^{-1}$).
Fig. 21. Flag leaf area and its correlation with leaf anatomy (chlorophyll concentration, stomatal density, specific leaf weight and interveinal distance) for three trials (● Trial 1, Δ Trial 3, ▲ Trial 4).
Fig. 22. Flag leaf length and its correlation with leaf anatomy (chlorophyll concentration, stomatal density, specific leaf weight and interveinal distance) for three trials (● Trial 1, Δ Trial 3, ▲ Trial 4).
Fig. 23. Flag leaf width and its correlation with leaf anatomy (chlorophyll concentration, stomatal density, specific leaf weight and interveinal distance) for three trials ( • Trial 1, Δ Trial 3, ▲ Trial 4).