Photosynthetic Capacity and Dry Mass Partitioning in Dwarf and Semi-dwarf Wheat (*Triticum aestivum* L.)

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Summary

Efficient use of space and high yields are critical for long-term food production aboard the International Space Station. The selection of a full dwarf wheat (less than 30 cm tall) with high photosynthetic and yield potential is a necessary prerequisite for growing wheat in the controlled, volume-limited environments available aboard long-term spaceflight missions. This study evaluated the photosynthetic capacity and carbon partitioning of a full-dwarf wheat cultivar, Super Dwarf, which is routinely used in spaceflight studies aboard U.S. space shuttle and NASA/Mir missions and made comparisons with other dwarf and semi-dwarf wheat cultivars utilized in other ground-based studies in plant space biology. Photosynthetic capacity of the flag leaf in two dwarf (Super Dwarf, BB-19), and three semi-dwarf (Veery-10, Yecora Rojo, IBWSN 199) wheat cultivars (*Triticum aestivum* L.) was assessed by measuring: net maximum photosynthetic rate, RuBP carboxylation efficiency, chlorophyll concentration and flag leaf area. Dry mass partitioning of carbohydrates to the leaves, sheaths, stems and ear was also assessed. Plants were grown under controlled environmental conditions in three replicate studies: slightly enriched CO_2 (370 µmol mol^{-1}), high photosynthetic photon flux (1000 µmol m^{-2} s^{-1}; 58 mol m^{-2} d^{-1}) for a 16 h photoperiod, 22/15 °C day/night temperatures, ample nutrients and water provided by one-half strength Hoagland's nutrient solution (Hoagland and Arnon, 1950). Photosynthetic capacity of the flag leaf was determined at anthesis using net CO_2 exchange rate versus internal CO_2 concentration curves measured under saturating light (2000 µmol m^{-2} s^{-1}) and CO_2 (1000 µmol mol^{-1}). Dwarf wheat cultivars had greater photosynthetic capacities than the taller semi-dwarfs, they averaged 20 % higher maximum net photosynthetic rates compared to the taller semi-dwarfs, but these higher rates occurred only at anthesis, had slightly greater carboxylation efficiencies and significantly increased chlorophyll concentrations per unit leaf area. The reduced-height wheat had significantly less dry mass fraction in the stem but greater dry mass partitioned to the ear than the taller semi-dwarfs (Yecora rojo, IBWSN-199). Studies with detached heads confirm that the head is a significant sink in the shorter wheat cultivars.

Key words: Photosynthetic capacity, dry mass partitioning, source, sink, wheat Triticum aestivum (L.), dwarf and semi-dwarf cultivars.

Abbreviations: CER_{LA} = CO_2 exchange rate per unit leaf area; Ci = intercellular CO_2 concentration; RuBPc = ribulose-1,5-bisphosphate carboylase; rubisco = ribulose-1,5-bisphosphate carboylase; PPF = photosynthetic photon flux.

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Introduction

Several studies indicate that dwarf wheat cultivars have higher maximum CO_2 exchange rates (CER_{LA}, a measure of net photosynthetic rate) and chlorophyll concentrations than tall cultivars (Morgan et al., 1990; Kulshrestha and Tsunoda, 1981). Plant height, which in some cases is associated with sink size, may influence photosynthetic capacity (Bonnett and Incoll, 1993 a; Ehdaie and Waines, 1994; Gent, 1995; Wardlaw, 1990). Dwarfing genes such as Rht1 and Rht2 derived from ‹Norin 10›, which have been used to reduce plant height (Allen, 1989) have substantially increased harvest index and lodging resistance, thus increasing wheat yields (Gent and Kiyomoto, 1985; Gent, 1995). Higher grain yields and harvest indices of the shorter modern cultivars reduce competition between the developing ear and stem because a reduction in height is accompanied by a reduction in stem mass (Rawson and Evans, 1971).

Studying the relationship between photosynthetic capacity, stem mass and plant height could further identify mechanisms to increase harvest index and elucidate limitations to grain yield. Grain size, number and sink strength are partially under genetic control (Fischer and HillieRisLambers, 1978; Thornley, 1979; Walpole and Morgan, 1970). Grain yield may be limited either by the supply of assimilate (source) or by the accumulation of assimilate (sink) (Evans et al., 1970; Suwignyo et al., 1995; Wardlaw, 1990). Source limitation of photosynthate may be more important during early grain-filling while sink limitation may be more important during late grain-filling, when there is less demand from competing sinks (Fischer, 1975; Herzog, 1986; Martinez-Carrasco and Thorne, 1979).

The flag leaf is a reliable predictor of source capacity; current flag leaf photosynthesis is the main source of carbon for grain filling (Austin and Edrich, 1975; Evans et al., 1970). From anthesis to maturity, photosynthetic capacity depends on source size and activity, which can be described by the following flag leaf parameters: CO_2 exchange rate, RuBP carboxylation efficiency, chlorophyll concentration and leaf area (Herzog, 1986). The flag leaves of semi-dwarf genotypes, tend to have smaller leaves and contain more rubisco per unit area than do the flag leaves of tall genotypes (Pyke and Leech, 1985), perhaps due to greater photosynthetic carboxylation capacity. RuBPc efficiency involves rubisco, an enzyme that generally constitutes about 50 % of the total soluble protein in leaves and may limit photosynthesis (Van Oosten et al., 1995) and could be increased in dwarf lines.

Dwarf cultivars partition carbohydrate differently from semi-dwarfs. Gent (1995) proposed that a reduction in wheat stem height may reduce light interception and therefore result in associated decreases in canopy photosynthesis and biomass accumulation. He reported 20 % increases in light interception, biomass and canopy photosynthesis in tall as compared to semi-dwarf isolines of wheat early in development. After spike emergence there were no apparent differences in canopy light interception and photosynthesis among the height classes (Gent, 1995; Kiyomoto and Gent, 1989). Other studies report higher net photosynthesis per unit leaf area for dwarf wheat compared to taller isolines (Kulshrestha and Tsunoda, 1981; Morgan et al., 1990); however, in unre-lated genotypes, dwarf wheat was reported to have lower single-leaf photosynthetic rates than the taller cultivars (Rawson and Evans, 1971). In addition, unrelated wheat cultivars with greater numbers of dwarfing genes were reported to have higher respiration rates per unit biomass than taller genotypes (Rawson and Evans, 1971; Gent and Kiyomoto, 1985). Both studies were designed to examine the parameters of net CO_2 exchange rate and dry mass partitioning in relation to genetic variation among cultivars of varying heights.

Many studies have examined the various components of reserve mobilization and its relation to net CER and to enzymes associated with photosynthetic capacity (Austin et al., 1977; Brown and Huber, 1987; Fischer and HillieRisLambers, 1978; Gent and Kiyomoto, 1985; Gent, 1995; Huber, 1983; Kulshrestha and Tsunoda, 1981; Rawson and Evans, 1971). The carbon exchange rate (CER) of the flag leaf is influenced by: the export capacity of the leaf, the number, size and demand of competing sinks and source proximity to the primary sink (Wardlaw, 1990), all of which may affect the accumulation of dry matter, net photosynthesis and the transfer of assimilates to the growing ear. According to LeCain et al. (1989), dwarfing genes are associated with smaller interveinal distances, which may position cells closer to veins and facilitate the translocation of assimilate to the ear and possibly enhance flag leaf photosynthesis. De-earing plants soon after anthesis, thereby manipulating the balance between the sinks and sources can be used to ascertain the relationship between sources and sinks and further discern if the amount of assimilate stored in the stem influences that balance (Bonnett and Incoll, 1993).

Prior to anthesis, surplus carbohydrate is deposited mainly in the stems and is relocated to the ear shortly before and after anthesis (Fischer and HillieRisLambers, 1978). Austin et al. (1977) and Rawson and Evans (1971) demonstrated that during grain filling, stems can lose as much as 30 % of their dry mass to the head as carbohydrates. Stem reserves have been found to make an increased contribution to the final grain mass, approximately 50 % when the plant was under stress (Austin et al., 1980; Herzog, 1986). Under adverse conditions at grain filling, taller wheat may have a competitive advantage because assimilate stored in stems can act as a buffer if current photosynthesis is not adequate. However under non-stress conditions at anthesis, the stems of taller wheat may also contain a higher proportion of flag leaf assimilates than do the stems of dwarf cultivars. Rawson and Evans (1971) did not detect any differences between tall and dwarf cultivars in the utilization of stem reserves. The present research examined differences in dry mass partitioning between full-dwarf and semi-dwarf cultivars and may help resolve whether reserves are important in relation to dry mass partitioning to the ear and overall yield differences between cultivars of varying heights.

There are conflicting reports concerning the relationship between plant height and photosynthetic capacity. While certain studies have indicated that dwarfing genes (semi-dwarfs) increase CER_{LA} (Kulshrestha and Tsunoda,1981; Morgan et al., 1990), others found either no difference between plant height and flag leaf photosynthesis (Gent and Kiyomoto, 1985; Rawson and Evans, 1971), or varying differences in canopy photosynthesis between tall and dwarf isolines before

and after spike emergence (Gent, 1995). The main objectives of this research were to establish if a relationship exists between plant height and photosynthetic capacity of the flag leaf at anthesis in full-dwarf and semi-dwarf wheat and to relate changes to the sink capacity of the ear and dry matter accumulation in the plant.

Materials and Methods

Plant Growth Conditions

Two dwarf: Super Dwarf, BB-19, (25 and 35 cm in mean height respectively) and three semi-dwarf: Veery-10, Yecora Rojo, IBWSN 199 (45, 68 and 85 cm in mean height respectively) wheat cultivars representing a range of plant height that are routinely used in spaceflight and related ground based research were selected. The dwarf wheat cultivars were selected for their exceptionally reduced height and capacity for high yields in optimal environments. Plants were grown in a controlled environment providing high photosynthetic photon flux (PPF = $1000 \mu mol\,m^{-2}\,s^{-1}$; $57.6\,mol\,m^{-2}\,d^{-1}$), 16 h photoperiod provided by high pressure sodium lamps, 22/15 °C day/ night temperatures, slightly enriched CO_2 levels ($370 \mu mol\,mol^{-1}$), and approximately 50 % relative humidity during the day/night. Nutrients were supplied by one-half strength Hoagland's solution (Hoagland and Arnon, 1950). Three seeds were planted in $12\,cm \times 12\,cm \times 12\,cm$ plastic pots (six 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 arranged in a randomized block design were spaced 8.0 cm apart in each block to minimize shading. Plants were automatically watered twice daily with a complete nutrient solution including 5 mmol L^{-1} nitrate and 5 mmol L^{-1} ammonium. Flag leaves of each cultivar were positioned at the same distance from the light source throughout the growth period to provide a uniform light environment. Supplemental CO_2 provided by compressed gas cylinders was distributed by circulating fans.

Maximum Photosynthesis and RuBPc Efficiency

Source activity was assessed as suggested by Christ (1989) by measuring the photosynthetic activity of single leaves using a time course of single leaf photosynthesis. Net CO_2 exchange rate versus intercellular CO_2 (C_i) response curves were measured on the midsection of the flag leaf under saturating PPF ($2000 \mu mol\,m^{-2}\,s^{-1}$) using an open gas exchange system (LI-COR, model 6200). Plant height for each cultivar was determined at anthesis. Three consecutive trials were performed and six replicate flag leaves were measured per cultivar. Two replicate curves were then taken on the same leaf (Fig. 1). Maximum CER_{LA} for flag leaves was determined at a Ci of $650 \mu mol\,mol^{-1}$, the concentration that CER_{LA} initially saturated for all cultivars. The initial slope of the response curve relating CER_{LA} to Ci (from $50-150 \mu mol\,mol^{-1}$) was used as an estimate of RuBPc efficiency (von Caemmerer and Farquhar, 1981). CER_{LA} and C_i response curves were measured at a starting CO_2 concentration of $1000 \mu mol\,mol^{-1}$ and continued until the CO_2 compensation point was reached using continuous draw-down by the leaf. The LI-COR system was modified to keep CO_2 concentration constant in the open mode, allowing the flag leaf to acclimate for 30 min before measurements were taken in the closed mode. This acclimation step was performed as suggested by Sage et al. (1988), who confirmed that activation of rubisco was shown to decline for 30 min following the transfer of the plant to an elevated CO_2 environment. System and chamber leak rates were measured at frequent intervals and were used to make small corrections in CO_2 exchange rates (McDermitt et al., 1989).

PPF was supplied by a high-pressure sodium lamp positioned above a 4-cm-deep circulating water bath, which filtered out most of the longwave radiation (Bubenheim et al., 1988), thus reducing the heat load on the leaf. The water bath and a fan positioned above the leaf chamber maintained leaf temperature at 25 °C. Compressed air with a CO_2 concentration of $1000 \mu mol\,mol^{-1}$ was humidified to 70 % by bubbling through water in Erlenmeyer flasks prior to entry into the chamber. Chamber temperature and relative humidity were allowed to equilibrate prior to measurement. Measurements were taken at the same time interval (mid morning until mid afternoon) to minimize possible diurnal effects, though, the wheat cultivars selected for this study did not differ significantly in rates of light saturated photosynthesis thoughout the day (data not shown). Furthermore, continuous measurements of canopy photosynthesis of wheat at anthesis grown under similar environmental conditions indicated that photosynthesis was constant during the photoperiod in steady-state conditions (Bugbee, 1992; Bugbee and Monje, 1992; Wheeler et al., 1993).

Flag Leaf Area and Chlorophyll

Flag leaf areas were measured using a leaf area meter (LI-COR, model 3000). A chlorophyll meter (Minolta, model SPAD-502) was used to determine the chlorophyll concentration in the flag leaf of each cultivar (six measurements per flag leaf). 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 (1992). Flag leaf areas and chlorophyll concentrations were averaged for six plants per cultivar in each of the three trials and compared to measurements of plant height at anthesis.

Maximum Photosynthesis and Sink Capacity of the Ear

Four plants per cultivar were de-eared at anthesis in order to access the balance between the sources and sinks and the effects of de-earing on sink limitation (Bonnett and Incoll, 1993). Three consecutive trials were conducted. CER_{LA} versus Ci response curves were developed for both de-eared and control plants under the conditions described above to measure maximum photosynthesis and RuBPc efficiency. CER_{LA} versus Ci response curves were measured immediately and 24 h following ear removal to eliminate any initial shock effects due to ear detachment (Herzog, 1986).

Dry Mass Partitioning

Ratios of dry mass of sources (flag leaf, all leaves) and sinks (sheaths, stems and heads) expressed as a percentage of the total dry mass of the primary tiller were determined 5 d after anthesis. Directly following measurements for maximum photosynthesis, plants were destructively sectioned into stems, leaves and heads and dried at 70 °C for 48 h. Dry mass was determined for six replicate plants per cultivar for all three trials.

Statistical Analysis

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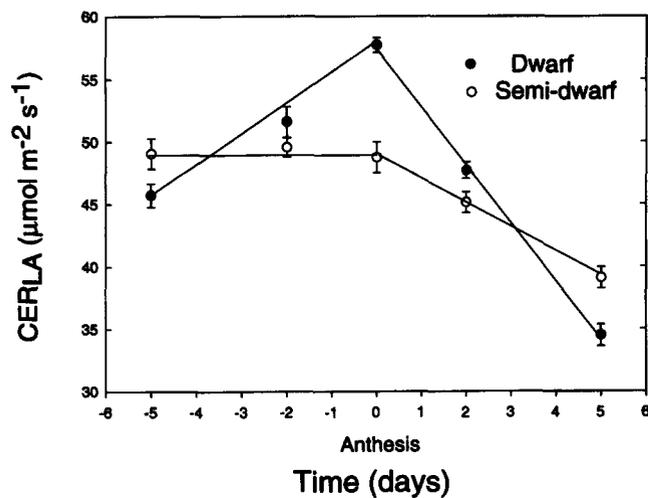
Results

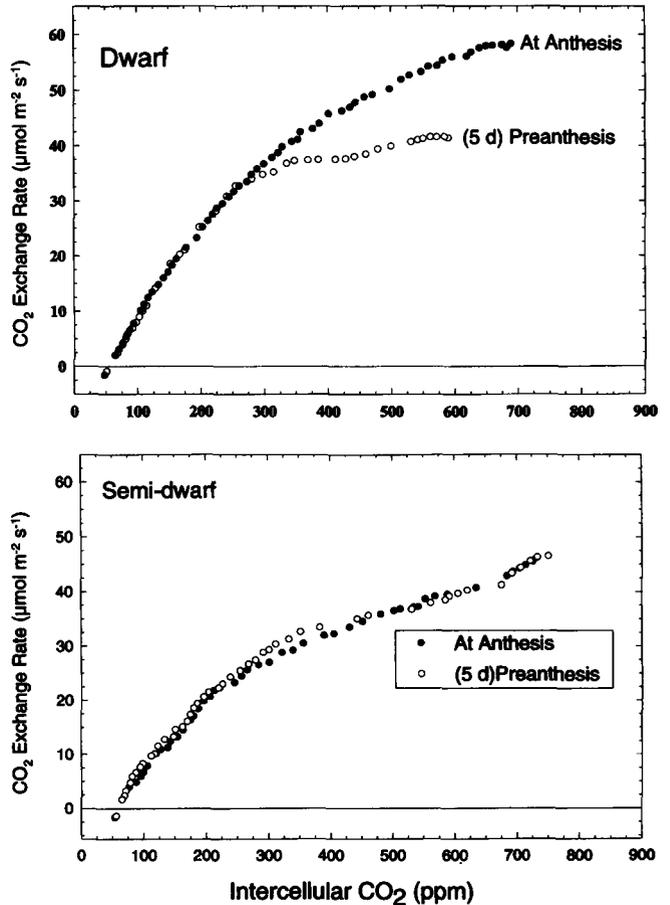### Maximum Photosynthesis and RUBPc Efficiency

CER_{LA} versus intercellular CO_2 (C_i) curves were used to assess photosynthetic potential (maximum CER_{LA}, RUBPc efficiency (Fig. 1). In the dwarfs, saturated CER_{LA} was lower prior to anthesis, increased significantly at anthesis and then decreased dramatically 5 d post anthesis, while the CER_{LA} for the semi-dwarf cultivars was relatively stable from 5 d preanthesis to anthesis with a similar sharp decline 5 d post anthesis (Fig. 2). Dwarf cultivars had a 14 % increase in maximum
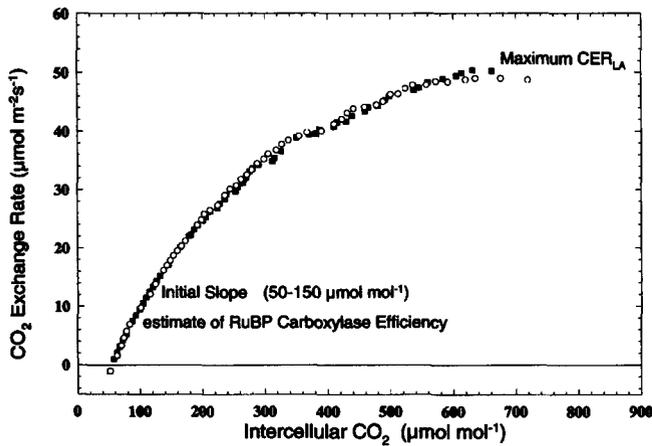
Fig. 1: Representative net CO_2 exchange rate versus intercellular CO_2 response curve measured on wheat, cv. Super Dwarf and used to estimate maximum CER_{LA} and RuBPc efficiency. Replicate curves were measured on same flag leaf at a saturating PPF ($2000 \, \mu mol \, m^{-2} s^{-1}$) and CO_2 concentration ($1000 \, \mu mol \, mol^{-1}$) after a 30 min. acclimation period between each curve.

Fig. 3: Representative net CO_2 exchange rate versus intercellular CO_2 curves at 5 d preanthesis and anthesis for dwarf (BB-19) and semi-dwarf (IBWSN-199) cultivars at 5 d preanthesis and anthesis.

Fig. 2: Net CO_2 exchange rate for dwarf and semi-dwarf wheat cultivars for 10 d around anthesis. Standard error bars represented on graph. Data represent pooled mean net CO_2 exchange rates for dwarf cultivars (Super Dwarf, BB-19) and semi-dwarf cultivars (Veery 10, Yecora Rojo, IBWSN-199).

photosythesis over semi-dwarfs at anthesis. CER_{LA} from preanthesis to anthesis increased by 20 % in dwarf cultivars, whereas semi-dwarfs showed no increase (Fig. 3). The dwarf cultivars on average had a larger percent increase in maximum CER_{LA} at anthesis compared to the semi-dwarfs for three consecutive trials ($r^2 = 0.55$) (Fig. 4).

There was a significant negative correlation between plant height and CER_{LA} at anthesis in all three trials ($r^2 = 0.33$, $p \leq 0.001$). Maximum CER_{LA} measured at a constant intercellular CO_2 concentration for all the cultivars ($C_i = 650 \, \mu mol \, mol^{-1}$) was higher in dwarf than in semi-dwarf cultivars at anthesis (Fig. 5). Plant height was only weakly related to RuBPc efficiency ($r^2 = 0.15$, $p \leq 0.0487$) (Fig. 5).

Chlorophyll Concentration and Flag Leaf Area

Chlorophyll concentration was significantly higher in the shorter cultivars ($r^2 = 0.83$, $p \leq 0.001$) (Fig. 6). There was only a weak positive correlation between plant height and flag leaf area ($r^2 = 0.18$, $p \leq 0.0112$) (Fig. 6).
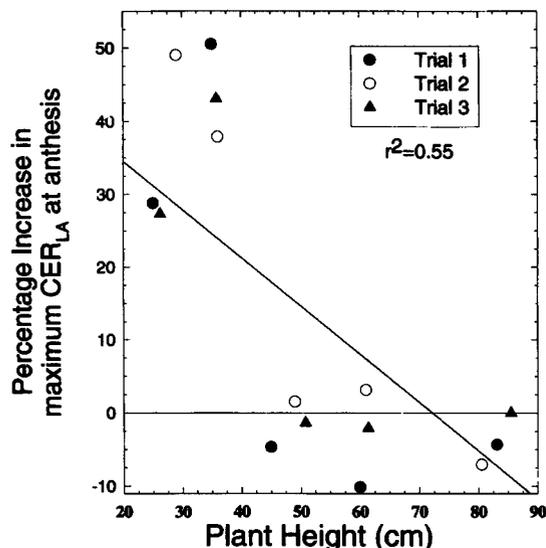
Fig. 4: Percent increase in maximum CO_2 exchange rate (Ci = 650 μmol mol⁻¹) from 5 d preanthesis to anthesis for dwarf (Super Dwarf, 25–27 cm; BB-19, 35–45 cm) and semi-dwarf (Veery-10, 45–50 cm; Yecora Rojo, 59–70 cm; IBWSN-199, 75–85 cm) cultivars over three trials.
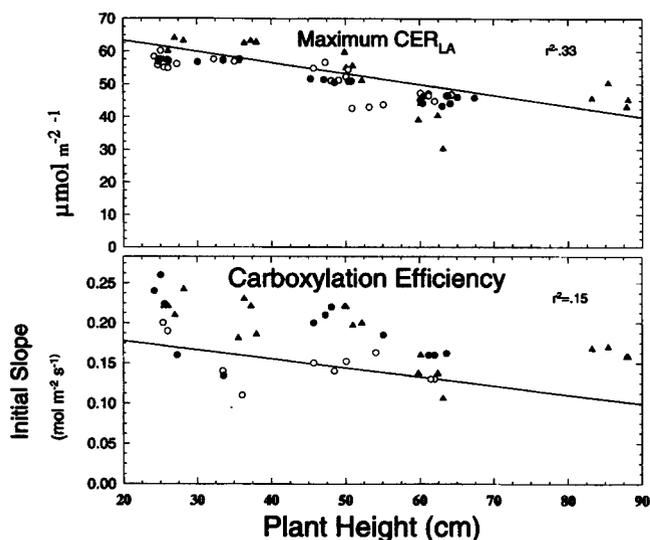
Fig. 5: Plant height and its correlation with maximum CO_2 exchange rate (Ci = 650 μmol mol⁻¹) and RuBP carboxylation efficiency of the flag leaf at anthesis for three trials (● Trial 1, ○ Trial 2, ▲ Trial 3). The fitted slope of the CER_{LA} versus Ci response curve is shown.

Maximum Photosynthesis and Sink Capacity of the Ear

Ear removal reduced maximum flag leaf photosynthesis, which was estimated at a saturating intercellular CO_2 concentration of 650 ppm by 40 % in dwarf wheat with no significant reduction in semi-dwarfs (Fig. 7). The percent decrease in maximum CER_{LA} was inversely related to plant height when compared with maximum CER_{LA} measurements

taken on the flag leaf of the control plant with the ear intact ($r^2 = 0.80$) (Fig. 8). CER_{LA} versus Ci curves were not significantly different when measured on the plants at 24 h post ear removal and compared to the controls at 24 h post anthesis. Flag-leaf photosynthesis in semi-dwarf cultivars was found to be slightly reduced in CER measurements at 24 h post anthesis in plants with and without the ear when compared to the photosynthetic rates at anthesis.

Dry Mass Partitioning

Plant height was positively related to stem mass ($p \leq 0.001$/ Table 1), suggesting that taller cultivars may have more carbohydrate storage capacity in the stem. At anthesis, the five cultivars differed significantly in their partitioning of dry mass (stems, leaves, sheaths and ear) of the primary tiller (Table 1). Relative stem mass was significantly greater for semi-dwarf compared to full-dwarf wheats and were on average 0.90 grams/primary culm for semi-dwarf versus 0.65 grams/primary culm for dwarf wheat. Relative ear mass was only slightly greater in the shorter cultivars (Super Dwarf, BB-19 and Veery-10), which averaged 2.1 grams/ear versus 1.8 grams/ ear in the taller semi-dwarfs. The shorter cultivars partitioned on average 10 % more assimilate to the ear than did the taller semi-dwarfs, which partitioned 13 % more assimilates to the stems.

Discussion

Although there are a number of studies that try to correlate photosynthetic rates between isolines of wheat varying in height (Gent, 1995; LeCain et al., 1989; Morgan et al.,
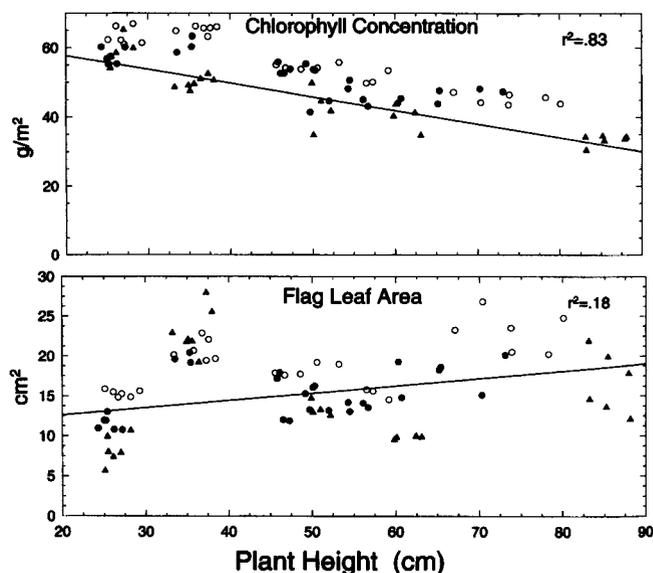
Fig. 6: Plant height and its correlation with chlorophyll concentration and flag-leaf area at anthesis for three trials (● Trial 1, ○ Trial 2, ▲ Trial 3).

1990), not many have correlated any differences to the partitioning of carbon. This study was performed to examine the relationships between net CO_2 exchange rate and dry matter accumulation in dwarf and semi-dwarf wheat. Our study examined CER_{LA} at saturating levels of Ci using an initial CO_2 concentration of 1000 µmol mol^{-1} in wheat cultivars of varying heights. At anthesis, maximum CER_{LA}, chlorophyll concentration and RuBPc efficiency were higher in dwarf wheat compared to the taller semi-dwarfs. These differences were not related to flag leaf area. LeCain et al. (1989) and Morgan et al. (1990) found that a reduction in plant height was accompanied by a reduction in leaf size, which concentrated the photosynthetic machinery, i.e. chlorophyll, rubisco, etc.

End-product regulation or feedback inhibition of photosynthesis at preanthesis may be the cause of the minor depression in flag leaf photosynthesis seen in the dwarf cultivars, which was alleviated as the sink strength of the head increased at anthesis. The lower CER_{LA} rates in dwarf cultivars may be attributed to feedback inhibition of photosynthesis, which often occurs when conditions favor high CER_{LA} (i.e.
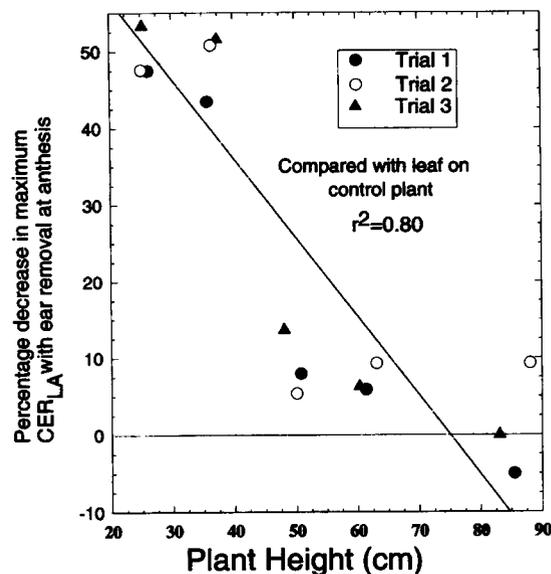
Fig. 8: Percent decrease in maximum CO_2 exchange rate (Ci = 650 µmol mol^{-1}) taken 24 h after ear removal at anthesis compared with the control plant for dwarf (Super Dwarf, 24–27 cm; BB-19, 35–45 cm) and semi-dwarf (Veery-10, 45–50 cm; Yecora Rojo, 59–70 cm; IBWSN-199, 78–85 cm) cultivars in three trials.

Table 1: Ratio of the dry mass of sources (leaves) and sinks (sheaths, stems and ears) 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 semidwarf (Veery-10, Yecora Rojo and IBWSN-199) cultivars. Measurements were taken on the primary tiller only.

Cultivar	Flag leaf: Total	Leaves: Total	Sheath: Total	Stem: Total	Ear: Total
Super Dwarf	3.2 a	12 c	5.4 c	30 cd	52 a
BB-19	7.4 a	20 a	8.8 a	29 d	42 b
Veery-10	4.0 a	11 c	6.6 bc	37 bc	46 ab
Yecora rojo	2.5 a	10 c	3.4 d	51 a	35 c
IBWSN-199	5.7 a	17 b	7.9 ab	42 b	34 c
LSD [%]	14	2.0	2.0	7.2	6.0
p ≤0.05	0.260	0.001	0.003	0.001	0.001
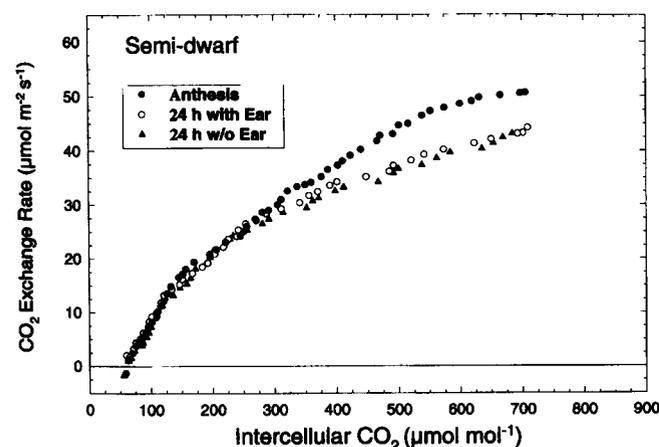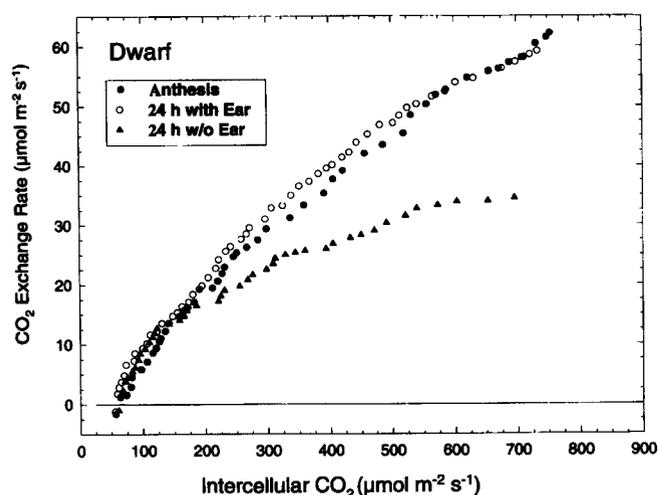
Fig. 7: Representative curves of the effect of ear removal on CO_2 exchange rate for dwarf (BB-19) and semi-dwarf (IBWSN-199) wheat. Curves were taken at anthesis and 24 h following ear removal.

saturating light, elevated CO_2) when insufficient demand for assimilate by the ear causes carbohydrate to accumulate in the flag leaf and resultant impairment of the regeneration of RuBP in the Calvin cycle (Sage, 1990). Another plausible explanation for the lack of feedback inhibition in the de-eared semi-dwarfs is that stem elongation may still be taking place in the semi-dwarfs until at least anthesis, thus providing another sink for assimilates. In all trials, the CO_2-saturated photosynthetic rate was lower in dwarf cultivars at preanthesis than at anthesis. No differences between preanthesis and anthesis CO_2-saturated photosynthesis were found for the semi-dwarf cultivars and RuBPc efficiency of the dwarf wheat at anthesis was only slightly greater between cultivars of varying height classes.

Assimilate is temporarily stored in the stems of cereals as both pre- and post-anthesis mobilization occurs in response to the demand of assimilate from the ear during grain filling (Bonnet and Incoll, 1993). At anthesis, sink strength was greater in dwarf wheat as indicated by the substantial increase (42 %) in maximum CER_{LA} at anthesis (Fig. 4). Removal of sinks was used to study end product regulation on carbon exchange rate. Ear detachment in dwarf cultivars resulted in the removal of a predominant sink, which resulted in decreases in CER_{LA} at anthesis and may in turn may be associated with sink-limiting conditions. No decrease in CER_{LA} with ear removal was apparent for semi-dwarf wheat. The taller semi-dwarfs can apparently translocate assimilate to other major sinks (i.e. stems, tillers, roots) in addition to the ear during grain filling, whereas the ear at anthesis appears to be the single most important sink in the dwarf wheat. The intercellular concentrations of CO_2 (Ci) decreased in both dwarfs after ear removal (Figs. 7, 8). Suwignyo et al. (1995) also reports that manipulation of the sink and source influenced the carbon exchange rate in intact leaves. They further confirmed that the CER of a source leaf is heavily influenced by the demand of the sinks and associated with the accumulation of dry mass. Factors responsible for the control of carbon partitioning may differ between dwarf and semi-dwarf wheat and it may be possible that dwarf wheat is more sensitive to sink-controlled photosynthesis. Our findings also conform to the model developed by Charmont (1993), which predicts that down-regulation of photosynthesis and associated reductions in rubisco are less likely to occur in plants that have the ability to adapt their sink capacity to increased source capacity. The lack of change in CER_{LA} with ear removal in semi-dwarf wheat may be due to their increased sink capacity because of a greater number of alternative sinks available.

Herzog (1986) hypothesized that dwarf wheat had less buffering capacity in the stem due to less dry mass and thus had less assimilate to allocate to the head in times of stress. The dwarf cultivars in this study had a significantly smaller dry mass fraction in the stem (Table 1). Our results support those of Austin et al. (1980), who found tall barley genotypes partitioned 30 % more dry mass to stems than did semi-dwarf genotypes. We found significant differences in how dwarf and semi-dwarf cultivars partitioned dry mass (Table 1). The shorter cultivars partitioned more dry mass to the ear, whereas the taller wheat partitioned the majority of their assimilates to the stem.

The higher CER_{LA} of dwarf cultivars observed in this study may not necessarily result in higher canopy photosynthesis (Gent, 1995; Morgan et al., 1990), possibly because these higher rates were limited to the window of anthesis. The reduced-height wheat had significantly less dry mass fraction in the stem, which may be related to the greater dry mass partitioned to the ear in the dwarfs compared to the taller semi-dwarfs.

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