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Effects of Timing and Defoliation Intensity on Growth, Yield and Gas Exchange Rate of Wheat Grown under Well-Watered and Drought Conditions

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Abstract: The aim of this research was to determine the effects of timing and intensity of source reduction on grain yield of wheat under well-watered and drought stress conditions. A field experiment was conducted at the research farm of the Agriculture College, University of Tehran, Karaj, in 2003-2004. Drought stress was imposed when plants were at the second node stage by withholding watering and plants were re-irrigated when they showed signs of wilting or leaf rolling, particularly during the morning. Various intensities of leaf defoliation were performed at three growth stages: booting, anthesis and 20 days after anthesis. Flag leaf gas exchange parameters as well as chlorophyll content measurements were made 20 days after defoliation at each growth stage. Generally leaf removal appeared to stimulate an increase of net photosynthesis rate (p_n) and stomatal conductance (g_s) of the remaining flag leaf. With leaf removal, stability of the flag leaf chlorophyll content tended to increase. Neither grain yield, nor protein content were affected by defoliation. Interestingly, even removal of all leaves at anthesis stage did not reduce grain yield and grain protein significantly. Increased remobilization of stored photoassimilate, decreased maintenance respiration by source reduction and therefore enhanced photoassimilate partitioning toward grain and spike photosynthesis might be responsible for sustain grain growth in this condition.

Key words: Defoliation, drought stress, photosynthesis, source and sink relationship, wheat

INTRODUCTION

Limited rainfall and drought stress occur frequently during the grain filling stage of wheat in many wheat growing areas. The problem is particularly serious in arid and semi-arid areas, where many developing and under developed countries happen to fall. In these regions during the drought period water potential in the rhizosphere becomes sufficiently negative and reduces water availability to suboptimal levels for plant growth.

Wheat is an important cereal crop and serves as a stable food in many countries. Growth of wheat kernels is reduced depending upon the degree of water stress and on the rate of stress development, thereby limiting final grain yield (Plaut *et al.*, 2004). Wheat yield and water use efficiency have been greatly improved by increase of Harvest Index (HI) through the introduction of dwarf/semi-dwarf cultivars. However, recent analysis suggests that improving these traits by genetic improvement might have dropped over the last decade (Zhu *et al.*, 2004). Therefore, the study of traits contributing to enhance drought tolerance seems a good approach to improve crop yield in drought conditions.

Water from growing season precipitation is rapidly lost from the rooting zone by transpiration or soil evaporation depending, in part, on the size of the precipitation event and structural and physiological characteristics of the vegetation (Yepez *et al.*, 2005). Water lost from the canopy surface is determined by rate of transpiration (Schreiber, 2001). Varieties with low transpiration rates can conserve higher relative water content in water-deficient conditions (Sanchez *et al.*, 2001). Therefore removal of transpiring leaves which are less effective in grain filling could be one way to decrease water loss by plant and increase Water Use Efficiency (WUE). However, it is not clear if this manipulation allows plants to be more productive under drought conditions.

Manipulation of the source:sink ratio in wheat by artificial reduction in grain number per inflorescence or defoliation has been trailed in several experiments to provide clear evidence that plants experience periods during the growing cycle when yield is mainly limited by the source strength, the sink capacity, or co-limited by both (Borras *et al.*, 2004). Some authors concluded that final grain weight was somewhat limited by the ability of the source to provide assimilation during grain filling

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(Cruz-Aguado *et al.*, 1999). In contrast, data from other experiments have indicated that wheat yield is sink-limited during grain filling (Savin and Slafer, 1991; Slafer and Savin, 1994). Borras *et al.* (2004) reviewed the literature on the magnitude of the seed weight response as a function of the assimilate availability during the seed filling period in order to test quantitatively whether source or sink limitation in seed growth was predominant in wheat. They reported that growth of wheat seeds is apparently more sink-than source-limited under most conditions.

It seems that source:sink manipulation could regulate plant physiological traits such as net photosynthesis rate (P_n), water use efficiency and leaf chlorophyll content of winter wheat, however, the direction and magnitude of the regulation varies with time and cultivar. Zhu *et al.* (2004) in Australia revealed that an early-sown late maturity wheat responded to defoliation at late tillering with an increased grain yield (by 7.3%) through an increase of harvest index (by 10.7%) and grain water use efficiency (WUE by 22%) compared to the control, but defoliation at booting stage had negative effects on almost all components. These treatments also enhanced stomatal conductance and photosynthetic capacity of remaining leaves at anthesis. Both defoliation treatments of a crop sown two months later resulted in yield reduction. In a study in which two winter wheat cultivars were subjected tomanipulaiton of source-sink balance during anthesis, Yin *et al.* (1998) also found that at the initial grain filling stage the large grain cultivar was sensitive to source reduction leading to an increase of net photosynthesis rate by 10%; however, little effect of source reduction was observed in small grain cultivar. In this regard, Zhenline *et al.* (1998) reported that the effect of source:sink manipulation on p_n was related to the occurrence of plant senescence at the time of late grain filling. Source reduction altered the senescence and reduced the p_n, meanwhile, sinks reduction delayed senescence and increased the p_n.

From the discussion it appears that in species such as wheat sink limitation is predominant. Therefore source reduction may have no significant effect on grain yield. On the other hand, leaf removal could increase WUE by reducing transpiration and enhancing net photosynthesis, stomatal conductance and Relative Water Content (RWC) of remaining leaves particularly under semi-arid condition. The aim of this research, therefore, was to determine the effect of timing and intensity of source reduction on grain yield of wheat under well-watered and drought stress conditions. It was hypothesized that by reducing transpiring demand during the vegetative period, more water would be available for grain filling in the event that terminal drought occurred.

MATERIALS AND METHODS

Two experiments were conducted simultaneously under well-watered and drought stress conditions at the research farm of Tehran University, Karaj (35° 55' N, 50° 54' E and 1312 m asl) during the 2003-2004 growing season. The soil type of experimental site was clay loam with a clay type of montmorillonite, pH of 7.8 and EC = 0.44 dS m^{-1}. Annals mean precipitation is 345 mm, with only about 50% falling during the wheat growth period (From November to July).

The winter wheat cultivar, Ghods, with high yielding potential was selected. Seeds were planted on 15 November 2003 at a planting density of 90 kg ha^{-1} (300 seeds m^{-2}). The experimental design was a Randomized Complete Block Design with 3 replications. Plot size was 1 m wide and 1 m long with 0.2 m between-row spacing. There were four rows in each plot in an E-W direction. Fertilizer was applied at 200 kg ha^{-1} ammonium phosphate and 100 kg ha^{-1} urea before planting and 50 kg ha^{-1} Urea was side-dressed at the jointing stage in the spring.

Drought stress was started at 164 Day After Sowing (DAS). Control plants were given four irrigations (at 3, 164, 177 and 189 DAS) and droughted plants received three irrigations (at 3, 182 and 189 DAS) from the date of sowing to maturity. At the time of droughted plants re-irrigation (182 DAS), soil water potential reached 17 bars (derived from the relationship between soil water content: soil water potential) at a depth of 35 cm. Defoliation treatments were imposed at booting, anthesis and 20 days after anthesis as shown in Table 1.

Physiological measurements: Flag leaf RWC, chlorophyll content as well as gas exchange measurements were made 20 days after each defoliation treatment. Because of early leaf senescence in droughted plants, these characters were not measured for D6, D7 and D8 treatments.

Table 1: Details of defoliation treatments and treatment code. Defoliation treatments run at three growth stages: Booting (D1 and D2), anthesis (D3, D4 and D5) and 20 days after anthesis (D6, D7 and D8)

Control (plants untouched)	D0
Booting	
All leaves removed except the flag leaf	D1
All leaves removed except the flag leaf and penultimate leaf	D2
Anthesis	
All leaves removed	D3
All leaves removed except the flag leaf	D4
All leaves removed except the flag leaf and penultimate leaf	D5
20 days After anthesis	
All leaves removed	D6
All leaves removed except the flag leaf	D7
All leaves removed except the flag leaf and penultimate leaf	D8

For RWC measurements immediately after cutting at the base of lamina, leaves were sealed within plastic bags and quickly transferred to the laboratory. Fresh weights were determined within 1 h after excision. Turgid weights were obtained after soaking leaves in distilled water in the tubes for 5-7 h at room temperature (about 20°C) and under the low light condition of the laboratory. After soaking, leaves were quickly and carefully blotted dry with tissue paper to determine turgid weight. Dry weights were obtained after oven drying the leaf samples for 70°C. RWC was calculated from the equation of Schonfeld *et al.* (1988).

$$RWC\,(\%) = \frac{Fresh\;weight - Dry\;weight}{Turgid\,weight - Dry\,weight} \times 100$$

The Minolta SPAD-502 chlorophyll meter was used to acquire a rapid estimate of flag leaf chlorophyll content. Ten measurements were taken per plot. The results were then averaged, resulting in a single value to represent each plot.

Gas exchange measurements were taken on fully expanded flag leaves. Net photosynthesis rate (p_n) and stomatal conductance (g_s) were measured for three leaves in each plot using a portable photosynthesis system (IRGA model LCA4, ADC, Hoddeson, UK). Data were collected between 9:00 to 11:00 h from healthy plants near the center of each plot. Gas exchange measurements were taken under constant leaf temperature (usually 30±1°C) and photosynthetic photon flux density (PPFD, 1300 μmol m^{-2} sec^{-1}).

Grain yield and grain protein content: At maturity, a central 0.25 m^2 of each plot was harvested. Each sample was oven-dried at 80°C and the grain weight for the each treatment was computed. Grain protein content was determined using a Grain Analyzer (Zeltex ZX-800).

Data analysis: All data were analyzed with analysis of variance using a Proc GLM procedure of SAS (SAS Institute, 1994). Analyses were conducted separately for each growing conditions. Mean separation was obtained using a Duncan's New Multiple Range Test at the 0.05 probability level.

RESULTS

RWC and chlorophyll content: As expected, drought stress caused a significant reduction in flag leaf RWC. However as shown in Fig. 1, defoliated plant showed less reduction in RWC under drought stress condition compared to nondefoliated plants experiencing a similar level of drought stress, albeit not significantly.
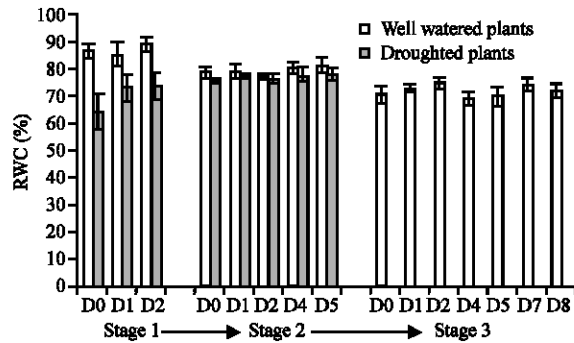

Fig. 1: RWC (%) for defoliated plants at three growth stages (stage 1:20 days after booting; stage 2:20 days after anthesis; stage 3:40 days after anthesis) in well watered and drought stress conditions. Values shown are Mean±SE of three replications

Flag leaf chlorophyll content declined during the second half of the grain filling period (after stage 2) and the rate of senescence was greater in the droughted plants when compared to well-watered plants. In droughted and irrigated conditions, leaf senescence progressed from the bottom to the top and the defoliation treatments influenced flag leaf chlorophyll content. Under the well-watered condition, generally, the chlorophyll content of the flag leaf was increased by defoliation treatments at all three stages of measurements, the amount of average increase was more evident at latter stages, i.e., flag leaf chlorophyll content (across all different defoliation treatments) at stage 1, 2 and 3 were 2.8, 5.34 and 18% more than nondefoliated treatment respectively (Fig. 2). Under drought stress the flag leaf chlorophyll content also tended to increase after defoliation (Fig. 2).

Photosynthesis, WUE and stomatal conductance: Drought stress imposed in the present work affected the p_n rate; as seen in Fig. 2, in response to drought stress this parameter significantly decreased. In non-defoliated plants p_n declined by about 55 and 38% in response to drought stress at stage 1 and 2, respectively. This result is in agreement with previous studies showing that p_n decreases as drought stress occurs. However the negative effects of drought stress on p_n were alleviated in plants defoliated at anthesis. Thus defoliation modified the response of net photosynthesis to drought stress.

Generally leaf removal appeared to stimulate the increase of p_n in the both drought stress and well-watered conditions (Fig. 2). Differences for p_n between defoliation treatments and their respected control plants were more

Table 2: Grain yield, seed dry weight and grain protein content of defoliated plants in well-watered and droughted plants

	Irrigated plants			Droughted plants		
Treatments	Grain protein content (%)	Seed dry weight (g)	Grain yield (0.25 g m^{-2})	Grain protein content (%)	Seed dry weight (g)	Grain yield (0.25 g m^{-2})
D0	11.40[a]	40.36[ab]	154.3[ab]	11.47[abc]	30.82[ab]	126.8[a]
D1	11.27[a]	40.09[b]	167.7[ab]	11.07[bc]	31.45[a]	116.5[a]
D2	10.97[a]	41.02[ab]	178.0[a]	11.07[bc]	30.27[ab]	126.8[a]
D3	11.43[a]	39.64[b]	149.0[b]	10.60[c]	29.02[b]	123.7[a]
D4	11.17[a]	42.15[a]	159.7[ab]	11.43[abc]	29.99[ab]	128.3[a]
D5	11.63[a]	41.53[ab]	143.4[b]	11.27[abc]	31.85[a]	127.4[a]
D6	11.07[a]	41.60[ab]	156.1[ab]	12.13[c]	29.61[ab]	114.7[a]
D7	11.47[a]	40.78[ab]	158.0[ab]	11.70[b]	31.49[a]	115.9[a]
D8	11.33[a]	39.60[b]	166.6[ab]	11.97[a]	31.18[ab]	127.8[a]

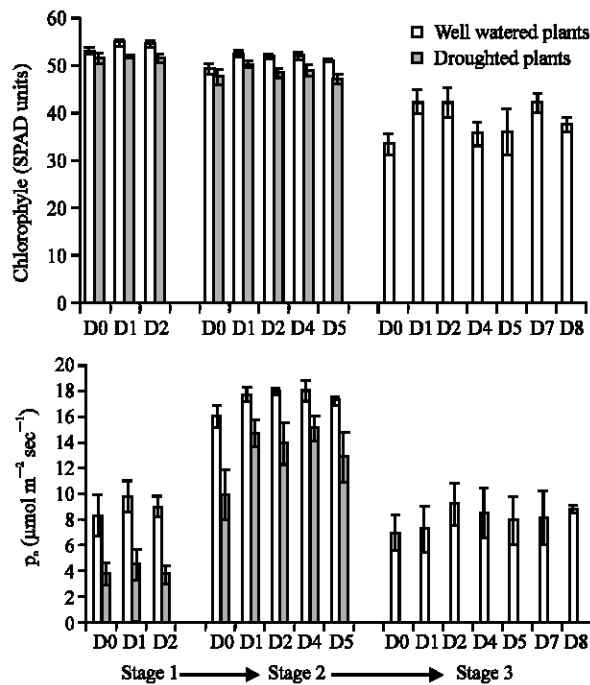Mean values with different letter(s) are significantly different at p = 0.05

Fig. 2: Flag leaf chlorophyll content and net photosynthesis rate (p_n) for defoliated plants at three growth stages (stage 1: 20 days after booting; stage 2: 20 days after anthesis; stage 3: 40 days after anthesis) in well watered and drought stress conditions. Values shown are Mean±SE of three replications

evident at later stages of measurements. Under the well-watered condition, for example, p_n for D0, D1 and D2 was 8.27, 9.76 and 8.94 μmol m^{-2} sec^{-1} at stage 1 (20 days after booting) and 16, 17.7 and 17.9 μmol m^{-2} sec^{-1} at stage 2 (20 days after anthesis). Thus we can conclude that the experimentally-induced change in source size (i.e., assimilate demand) does not bring about an immediate change in the net photosynthesis rate.
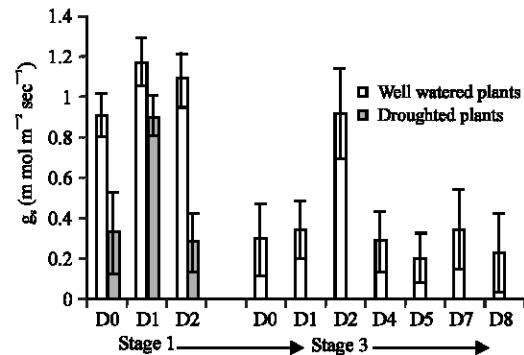

Fig. 3: Stomatal conductance (mmol m^{-2} sec^{-1}) for defoliated plants at two growth stages (stage 1:20 days after booting; stage 3:40 days after anthesis) in well watered and drought stress conditions. Values shown are Mean±SE of three replications. Stomatal conductance was not measured at stage 2 (20 days after anthesis)

The water use efficiency, ratio of photosynthesis to transpiration rates, for both droughted and control conditions was similar to that observed in net photosynthesis rate in which stressed and unstressed defoliated plants appeared to have slightly higher WUE than control plants (Data not shown).

Water stress significantly decreased stomatal conductance which indicated that drought-induced inhibition of p_n could be primarily due to stomatal closure (Fig. 3). Irrespective of the presence or absence of drought stress, defoliated plants showed a higher g_s rate (not significant). This was accompanied by a similar increase in intercellular CO_2 concentration (c_i) during the measurement time (data not shown).

Grain yield, seed dry weight and grain protein content: Grain yield and seed dry weight were affected by drought stress in nondefoliated plants. These traits in droughted plants were 18 and 24% less than those of well-watered plants, respectively (Table 2).

Generally defoliation had no appreciable effect on grain yield and related components in either doughted or control conditions. Interestingly grain yield and seed dry weight in all leaf removal treatments (D3 and D6) did not decrease significantly relative to nondefoliated plants (Table 2). Hence it appears that in this cultivar grain weight and ultimately grain yield was not restricted by the availability of assimilate during the effective period of grain filling.

Grain protein content in the droughted and well-watered plants is shown in Table 2. As observed for grain yield, grain protein content at maturity in both droughted and well-watered plants was not significantly influenced by source reduction. Grain protein content even in the most extreme defoliation treatment (removal of all leaves in D3 and D6) did not decreased significantly in either drought or well-watered treatment when compared to the control plants.

DISCUSSION

Plant water status was evaluated by the determination of relative water content in remaining flag leaf. On average the amount of RWC in defoliated plants under drought condition increased by about 13 and 4% at stage 1 and 2, respectively (Fig. 1), although those changes were not statically significant. Possible explanation to no significant effects of leaf removal on flag leaf RWC is that, while reducing transpiration, the defoliation inevitably increased bare soil evaporation as soil was exposed following defoliation. It seems that through defoliation accompanied with other crop management e.g., increase plant density it may be possible to optimize use of soil water in water deficit conditions.

Leaf chlorophyll content is an indicator of the photosynthetic activity and its stability for the continuation of assimilate biosynthesis. Results of this study revealed that flag leaf chlorophyll content was slightly high in defoliated plants (Fig. 2), indicating that the imposed defoliation treatment has a positive effect on chlorophyll content on the remaining flag leaf. In contrast to our results, Zhenlin *et al.* (1998) reported that partial defoliation of two wheat cultivars caused the concentration of the chlorophyll in remaining leaves to drop sharply, which indicated accelerated senescence. Rajcan and Tollenaar (1999) asserted that one of the important factors regulating leaf senescence at the whole plant level is the source-sink relationship. These authors described two types of premature leaf senescence that can occurred in maize during grain filling due to an imbalance of assimilate supply and demand: (i) senescence due to small source:sink (i.e., assimilate

starvation) and (ii) senescence due to large source:sink (i.e., excessive assimilate accumulation). Present results showed that grain of the cultivar Ghods normally grows under a saturation level of assimilate availability that maximizes their final weight. Therefore, it can be hypothesized that defoliation effects a balanced relationship between assimilate supply and demand, leading to chlorophyll stability.

Net photosynthesis and stomatal conductance was enhanced by defoliation in the current study (Fig. 2 and 3). This is consistent with result of Zhu *et al.* (2004) who found defoliation of wheat at the mid tillering stage slightly increased the p_n and g_s in the remaining leaves. That stomatal conductance followed a similar trend as p_n (Fig. 2 and 3) indicates that changes in p_n could be primarily attributed to stomatal responses and effects of defoliation and water stress on p_n were mediated via changes in stomatal conductance. The association between p_n and g_s has been reported by others (Flexas and Medrano, 2002; Lawlor, 2002). It is reported that at all stages of crop growth, the demand for photosynthetic assimilate has a pronounced effect on the photosynthesis rate: i.e., there are feedback effects of sink demand on source activity (Azcon-Bieto, 1983). Atsmon *et al.* (1986) found that partial defoliation of wheat led to an increase in flag leaf p_n, whereas, removal of the basal grains of the ear lowered it at all measurement times beyond two weeks after anthesis. Therefore it can be concluded that the slight increase of p_n and g_s after defoliation can be attributed, in part, to feedback effects of the sink on the source during grain filling.

Data obtained in this study showed that grain weight was insensitive to defoliation in cultivar Ghods. This indicates that grain weight in this cultivar is not restricted by the availability of assimilate. We hypothesis that the following factors may contribute to this:

Role of reserves: Wheat, like most other plants, has the ability to buffer any imbalance between source and sink capacity by storing carbohydrate during periods of excess production and mobilization these reserves when the demands of growth exceed the supply of carbohydrate available through current photosynthesis (Evans and Wardlaw, 1996). Differences in the efficiency of remobilization of assimilate temporarily stored in the stem for seed production may be an important aspect determining seed dry weight responses when assimilate availability is reduced. The efficiency of wheat in remobilization pre-flowering stored assimilates and using them for seed growth was calculated to be around 0.68-0.78 g of seed g^{-1} of stored assimilates (Borras *et al.*, 2004). Thus may explain why seed yield in wheat appears to be insensitive to reduction in current assimilate production during seed filling.

Sink limitation: Limitations to crop yields are frequently sought in either photosynthesis-the source of assimilate-or in the sink-the site of assimilate utilization (Egli and Bruening, 2001). Many articles have reported yield responses of major crops to source-sink manipulation during the seed filling period. However analysis of this system does not always clearly identify the yield limiting process. For example, the conclusion of sink-limited yield based on seed dry weight response may be incorrect, because photosynthetic activity of the source organs has a pronounced effect on subsequent demand by the sink organs., i.e., source effects on sink demand. On the other hand, remobilization of the stored carbohydrate may minimize the source limitation.

In the current study, seed dry weight even in the most extreme condition (removal of all leaves at anthesis stage) was not decreased significantly in either drought or well-watered conditions when compared to the non-defoliated plants. Removal of all leaves at anthesis decreased the source effect on subsequent demand by the sink organs. On the other hand, full defoliation at this stage when canopy photosynthesis is close to its peak and the maximum rate of storage occurs, minimizes the support of remobilization toward grain. Therefore it can be concluded that seed growth of cultivar Ghods is more sink than source limited.

Ear photosynthesis: Photosynthesis by the ear itself during the early stage of grain growth may be as important a source as that by the flag leaf, especially in awned cultivars (Evans and Wardlaw, 1996). Some authors (Evans and Rawson, 1970; Richards, 1996) reported that the photosynthesis of the spike and the flag leaf blade alone could meet the requirements of the grains at all times during grain filling. It suggested that photosynthesis of spike and peduncle do fulfill a major part of the requirements of grains in defoliated plants.

Respiration: As we know, respiration is about divided between growth and maintenance (Gent, 1994). Carbon lost through maintenance respiration become more important in older crops as plant size increases and the relative growth rate slows. Maintenance respiration is affected by plant dry weight as well as temperature (Penning de Vries, 1975). Thus it is assumed that defoliation and therefore decrease of plant dry weight may lead to a fall of the maintenance respiration fraction and allow more grain growth from a given amount of carbon assimilates.

Grain nitrogen is derived from N uptake and N mobilized from vegetative organs. Rossato *et al.* (2001) reported that during flowering and grain filling, the capacity for N uptake significantly declines. Consequently most N used for grain filling is derivesdfrom mobilization of stored N in vegetative tissues. Thus it seems that source limitation by leaf removal induced a decrease in total N per grain. However, result showed that grain protein content was not decreased significantly in either drought or well-watered conditions when compared to the control plants. The explanation for these observations is probably that N reserves in stem and spike could meet the N demand of grain during the effective grain filling period. Furthermore, many studies have documented a positive effect of defoliation on N remobilization when compared with non-defoliated plants. For example *Trifoliom repense* remobilized a greater percentage of available N after defoliation, suggesting that the depletion of stored N was faster in such plants (Corre *et al.*, 1996). Also Thornton and Millard (1996) reported that the relative remobilization of N to growing leaves was greater in *Loliom perenne* after a single defoliation than in non-defoliated plants. In addition, when evaluating the importance of defoliation on wheat, defoliated plants showed a greater reduction of N reserves compared with control plants (Zhenlin *et al.*, 1998). Therefore it can be concluded, after defoliation N was remobilized from remaining tissues to provide the N required for grain filling. This allowed the plants to compensate grain N demand.

In conclusion, results suggest that cultivar Ghods does not show a consistent trend toward a reduction in grain weight if the availability of assimilate is reduced. Important implications for breeders may be derived from the present study and direct genetic modification of leaf area may result in enhanced yields when water is limited. Although the most appropriate way of modifying leaf area will depend on the climate of particular region and the constraints on the crop, there is considerable scope for genetic modification. Selection for low leaf area early in the life of the plant could delay the attainment of full ground cover and hence reduce early water use. These strategies would be useful in regions where total rainfall is low and does not readily support the plant growth.

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