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The Effect of Water Stress on Remobilization of Pre-anthesis Stored Assimilates to Grains in Wheat

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Abstract
Five bread wheat (*Triticum aestivum* L.) cultivars including Kavir, Pishtaz, Niknejad, Omid and Roshan were evaluated in a split plot experiment based on randomized complete block design with three replications. Water stress and well-watered conditions were assigned to the main plots and varieties to the subplots. Water stress was imposed by withholding irrigation at the booting stage. During a period of 45 days, which spanned before and after anthesis, plants were sampled and changes in dry matter of peduncle and penultimate internodes were assessed. An increase in grain weight was accompanied with a decrease in peduncle and penultimate internodes dry matter, which could be attributed to the remobilization of stored assimilates to grains. Remobilization of stored assimilates was relatively higher under water-stress condition as compared with the well-watered environment. Under water stress condition, tall cultivars remobilized more assimilates than the dwarf genotypes. In the well-watered plots, remobilization percentage from peduncle was more than penultimate internodes in tall varieties as compared with the dwarf varieties. On the other hand, under water stress condition, more assimilates were remobilized from penultimate than the peduncle in dwarf varieties as compared to the tall genotypes. In the dwarf genotypes assimilates remobilization was reduced under water stress conditions while it was increased in the tall cultivars.

Keywords: Assimilate, Drought, Remobilization, Wheat

Introduction
Different physiological processes are involved in grain development and yield of wheat crop under water stress condition (Austin 1989, Richards 1996). Current photosynthesis, remobilization of assimilates stored in the vegetative organs and cell division are among the most important factors (Rawson and Hoestra 1969, Austin *et al*. 1977, Nicolas *et al.* 1985, Austin 1989, Davidson and Chevalier 1992). Sufficient amount of light, water and nutrient elements in the growing media are also

necessary for physiological processes to take place at optimum level (Levitt 1983). To reduce the detrimental effect of drought on yield, many plants including cereals store carbohydrates in the vegetative organs such as stems and leaves before reproductive stage and then remobilize them into the grains (Nicolas *et al*. 1985, Kobata *et al.* 1992, Kobata *et al.* 1994, Ehdaie and Waines 1996, Richards 1996). This feature has been proposed as a selection criterion for selecting more stable genotypes in terms of grain yield particularly under water stress condition (Blum *et al*. 1991, Regan 1993, Ehdaie and Waines 1996, Nicolas 1996). This may cause both biological and grain yield to increase under such a stressful condition.

Wheat is the most important crop plant grown in the semi-arid regions of Iran in which usually experiences water stress during grain filling period. Under such conditions, normal grains could be obtained if pre-anthesis stored carbohydrates in the stem can be remobilized efficiently (Blum *et al*. 1983a, Blum *et al*. 1983b, Ehdaie and Waines 1996). Pre-anthesis assimilates were shown to provide up to 27% of the final grain yield (Bedinger *et al*. 1977) and even more under dry environmental conditions (Pheloung and Siddique 1991). In wheat, genotypic variation has been found for translocation efficiency (Blum *et al.* 1991, Regan *et al.* 1993, Ehdaie and Waines 1996) though environmental conditions significantly affect genotypes ability to remobilize the stored assimilates.

Application of a chemical desiccant at post-anthesis stage can stop current photosynthesis. Therefore, tolerance to drought stress, in terms of translocation-based grain filling can be evaluated by comparison of cultivars without active leaves but with carbohydrate stores in their stems (Regan *et al.* 1993). In wheat, selecting such plants with large grains led to the improvement of grain weight (Regan *et al*. 1993).

There are few reports regarding the role of pre-anthesis stored assimilates on grain filling of wheat under water stress condition (Shakiba *et al.* 1996). This study was, then, performed to investigate the effect of water stress on remobilization of assimilates from main stem internodes to the grains in tall and dwarf varieties of wheat. For this purpose, several bread wheat cultivars, recommended for planting in dryland conditions of the central and southern part of Iran, were used in the experiment.

Materials and Methods

This experiment was conducted in the research field of Faculty of Agriculture, Kerman University with an average annual precipitation of 143.2 mm in 2004- 2005. Seeds of five bread wheat cultivars including three dwarf (Kavir, Pishtaz, Niknejad) and two tall (Omid and Roshan) genotypes which were recommended for planting in warm dryland conditions of central and southern parts of Iran, were sown in 5×2 square meter experimental plots. Two groups of such plots were considered as main plots and randomly assigned to two different water supplying regimes. During the period from seeding to the beginning of stem elongation, all plots were normally irrigated and thereafter well-watered plots were continued to be irrigated whereas the water stressed plots not irrigated to provide water stress development in plants. Well-watered plots were irrigated at booting, flowering and grain filling stages. Plots were replicated three times, based on a randomized complete block design, each with a different randomly arrangement of sub-plots (five wheat cultivars). During a period of 45 days before and after anthesis, plants was sampled and divided into peduncle and penultimate internodes, ears and grains. These parts were then oven dried at 75°C for 72 hrs and weighted. Samplings were done at ear emergence, 50% flowering, early grain filling (milky stage), mid grain filling (dough stage) and physiological maturity. Each time six plants per plot were sampled. Dry matter changes of these parts-expressed as the sample means-before and after anthesis were then calculated. Positive differences between dry matter at two successive stages were attributed to the storage of assimilates and negative values to remobilization to the grains. Remobilization percentage (*R%*) was calculated using the following equation:

$$R\% = \frac{d_1 - d_2}{d_1} \times 100$$

In which, d_1 is the internode dry weight at the stage with highest value and d_2 is its dry weight at physiological maturity.

In order to determine the stress level imposed to the plants during the growth period right after the last irrigation in water stressed plots, segments of flag leaves were taken from both well-watered and water-stressed plants at flowering, milky and soft dough stages. All samples in a day were taken within one hour at 11:00-12:00 AM local time. Immediately after cutting, fresh leaf weight was measured (*FW*). Then, leaf samples were immediately saturated to full turgidity on the lower shelf of a lab refrigerator (about 8-10^{o}C) in darkness over a wet sponge for 4 hrs and again were weighted (*SW*). Finally, samples were oven dried at 80^{o}C for 24 hrs and weighted (*DW*). Leaf relative water content (*RWC*) was, then, calculated using the following equation:

$$\mathrm{RWC} = \frac{\mathrm{FW} - \mathrm{DW}}{\mathrm{SW} - \mathrm{DW}} \times 100$$

Data were subjected to analysis of variance. Mean values were compared using Duncan's multiple range test.

Results and Discussion

a) Leaf RWC: At all three sampling stages, well-watered plants had higher *RWC* than water-stressed plants. Under both well-watered and water-stressed conditions, *RWC* was higher in the first than the second and third sampling stages Results also showed that at all stages Roshan and Omid (tall varieties) had the highest *RWC* as compared to the dwarf genotypes. Generally, Roshan indicated the highest *RWC* at all sampling stages under well-watered and Omid under water stress condition (Table 1). Several mechanisms has been proposed to be responsible for higher *RWC* under such conditions such as partially opened stomata, smaller leaf area, leaf rolling and osmotic adjustment (Jones & Lezenby 1988, Saneoka, 1996), enhancement of senescence in extra leaves, leaf orientation on stem and leaf angel to stem (Humphreys 1981, Levitt 1983, Austin 1989).

b) Grain dry weight: During the sampling period, grain dry weight was increased up to maturity under both well-watered and water stressed conditions. However, almost in all cultivars grain dry weight was higher in well-watered as compared to the water-stressed condition. On the other hand, grain weight tended to increase more sharply under water stress condition particularly at later growth stages, as shown in Figure 1. This may be due to higher rates of assimilate remobilization from internodes to the grains under stress condition.

Table 1. Relative water content rates (%) of flag leaf at flowering, milky and soft dough sampling stages

	Well-watered					Water-stressed				
Stage	Roshan	Pishtaz	Kavir	Omid	Niknejad	Roshan	Pishtaz	Kavir	Omid	Niknejad
Flowering	97.4[a]	95.9[ab]	94.7[bc]	93.0[cd]	92.0[d]	89.9[e]	86.6[f]	82.7[g]	88.8[e]	84.2[g]
Milky	96.6[a]	96.0[a]	92.0[b]	93.1[b]	90.3[b]	83.1[d]	71.3[f]	68.6[c]	78.3[e]	71.0[f]
Soft dough	92.3[a]	91.0[ab]	89.0[b]	89.3[ab]	88.5[b]	78.6[c]	66.6[e]	63.6[f]	75[d]	67.3[e]

Differences between mean values within each sampling stage which are followed by the same letter are not significantly different at 5% level of probability.

c) Peduncle dry weight: Significant differences were found for peduncle dry weight under both well-watered and water-stressed conditions (Table 2). In all varieties, peduncle dry weight increased up to a maximum value and then decreased up to physiological maturity (Figures 1 & 2). In all varieties the increase in peduncle dry weight continued until the middle of the grain filling stage under well-watered condition, except Omid that had the highest dry weight in the early grain filling; thereafter dry weight decreased until physiological maturity (Figure 2). In both environments, dry weight of all varieties was then started to decrease until plants reached physiological maturity. The rate of decrease was more in water-stressed as compared with the well-watered condition. This may be the result of the adverse effect of water stress on photosynthesis, less amount of stored assimilates in stem or beginning of remobilization from peduncle to grains. Under water stress condition, Omid and Pishtaz at the flowering, Roshan and Kavir at the early grain filling and Niknejad at the middle of grain filling stages had the highest dry weight (Figure 1). Under well-watered condition due to higher amounts of stored assimilates, plants continued to store assimilates in peduncle for a longer

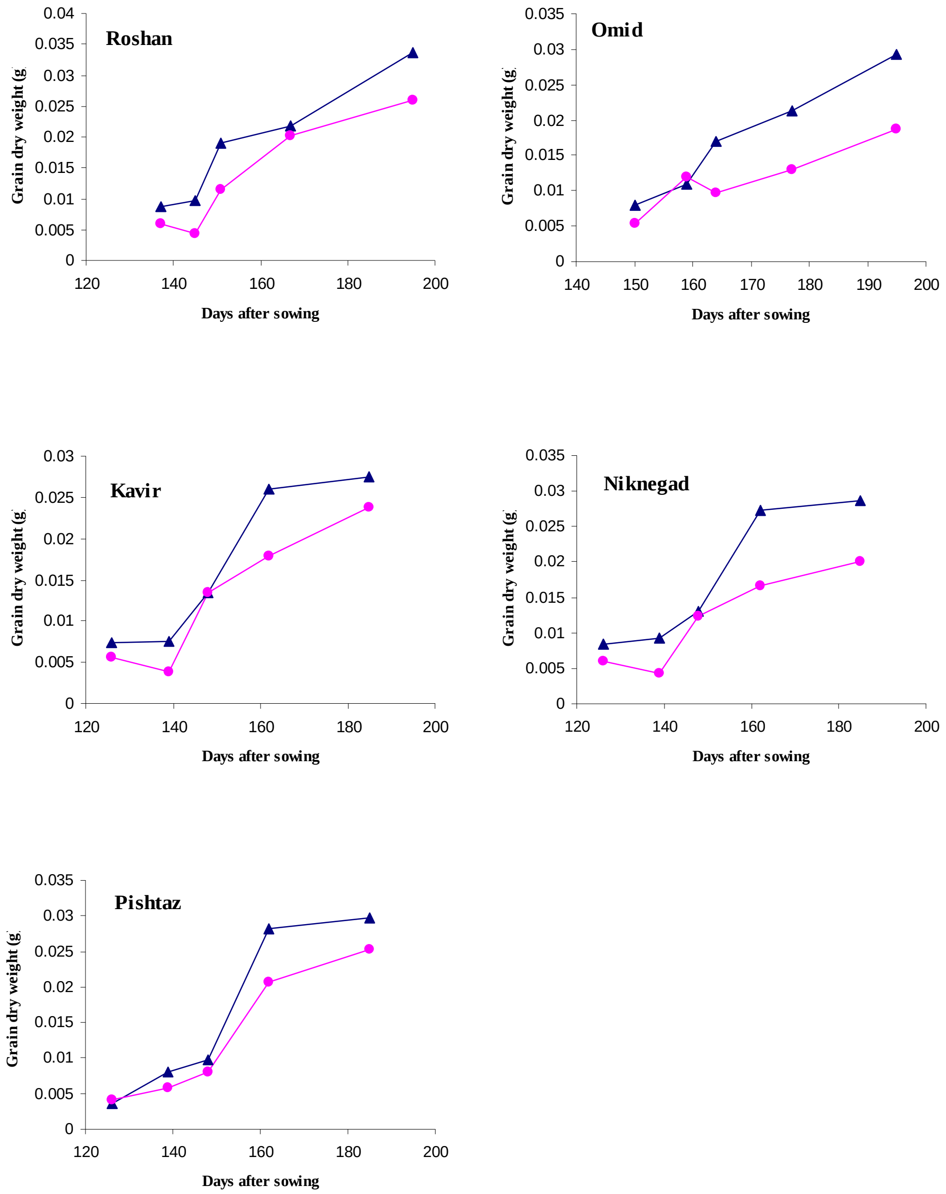


Figure 1. Time course of wheat cultivars grain dry weight change at different growth stages under well watered (triangles) and water-stressed (circles) conditions

period of time as compared with the water stress condition. Decrease in dry matter was started earlier in water-stressed plants due to more sink demand for assimilates and carbohydrates (Shakiba *et al.* 1996).

d) Penultimate internode dry weight: Effects of water condition, variety, and their interaction were significant on remobilization percentage of dry matter in the penultimate internode (Table 2). All varieties reached the highest value of penultimate dry weight during grain filling stage (Figures 3 & 4). In the well-watered condition, penultimate internode dry weight of all varieties

Table 2. Effects of water stress condition and variety on peduncle and penultimate internode dry weight during pre-and post-anthesis growth stages of wheat

SV	df	Ear emergence		Flowering		50% flowering		Mid grain filling		Maturity	
		Peduncle	penultimate	Peduncle	penultimate	Peduncle	penultimate	Peduncle	penultimate	Peduncle	penultimate
Water Stress	1	ns	*	**	*	**	ns	**	**	**	**
Variety	4	ns	**	ns	**	**	*	*	*	*	**
Interaction	4	ns	ns	ns	ns	**	ns	ns	*	**	**

* and **: Significant at 5% and 1% probability levels, respectively. ns: Non-significant

was more than the water-stressed condition. Under water stress treatment, Roshan at the flowering and other varieties at the early grain filling stages had the highest penultimate dry weight and thereafter, started to decrease until physiological maturity (Figure 4). Under well-watered condition, Omid at the flowering and other varieties at the mid-grain filling stages had the highest penultimate internode dry weight and thereafter decreased in all varieties until physiological maturity (Figure 3). Under well-watered condition, plants were expected to continue to store assimilates in the penultimate internode for a longer period of time than water-stressed condition, which may be due to higher levels of relative water content. In the water stressed plants, the penultimate dry weight decreased which could be due to lower rates of hotosynthesis and higher rate of respiration and sinks demand for assimilates (Shakiba *et al.* 1996).

e) Peduncle remobilization percentage *(R%)*: Results showed that after reaching to its maximum dry matter, peduncle dry weight started to decline from grain filling to physiological maturity indicating that assimilates move to the grains. Effects of water stress, variety and water stress × variety interaction on the percent of remobilized assimilates were significant (Table 3). Roshan and Pishtaz, with 36.9% and 25.4%, showed the highest and lowest remobilization, respectively. The difference between water-stressed and well-

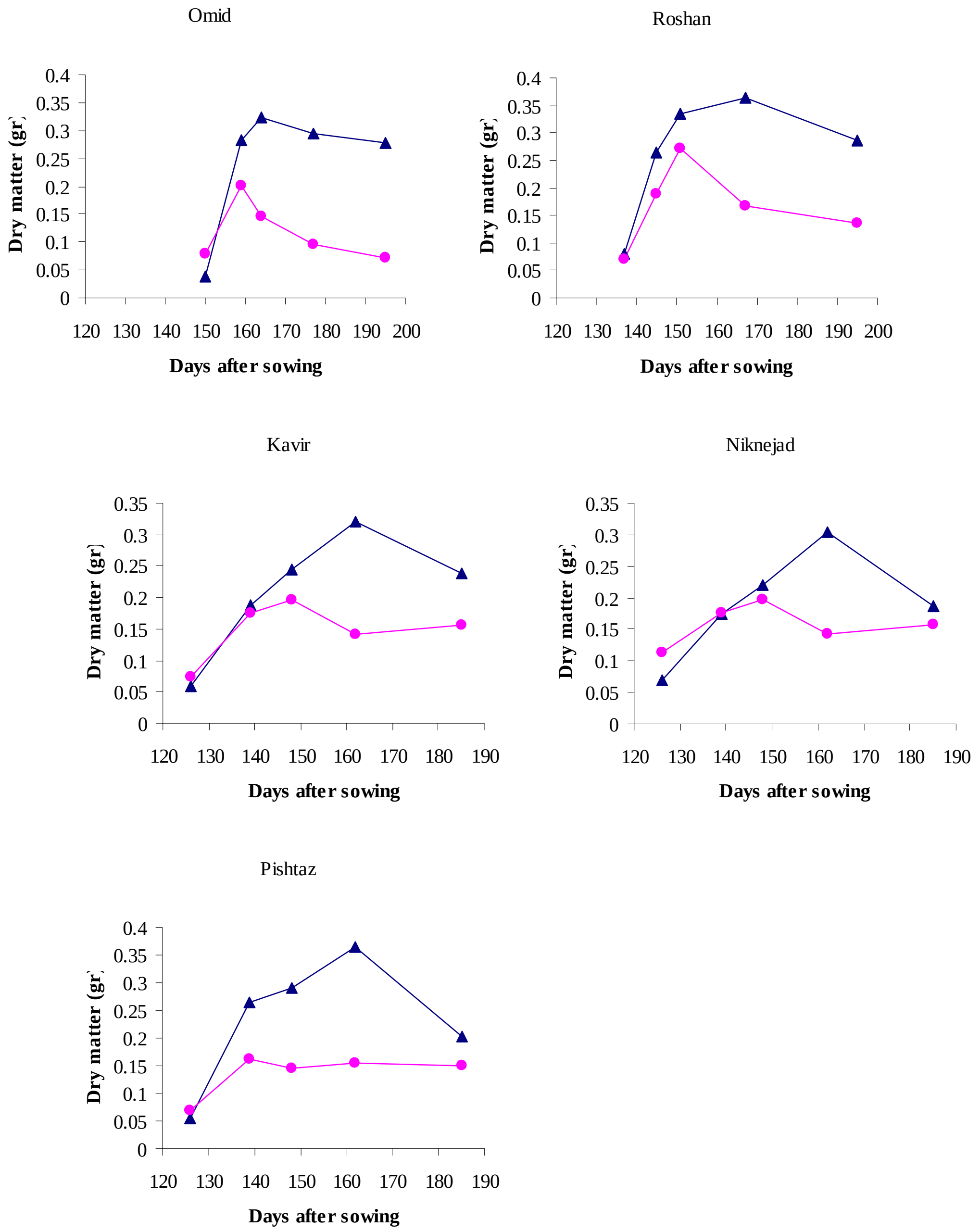


Figure 2. Time course of wheat cultivars peduncle dry weight change at different growth stages under well-watered (triangles) and warter stress (circles) conditions

watered conditions for the percentage of assimilates remobilization was also significant (data not shown). Mean values for water-stressed and well-watered conditions were 28.4% and 33.3%, respectively (Figure 4). It has been reported that contribution of the pre-anthesis assimilates of stem to grain was greater under drought (46.6%) than well-watered (29.5%) field conditions (Pheloung and Siddique 1991). In the well-watered plants, assimilate remobilization ranged from 13.8% in Omid to 44.4% in Niknejad (Figure 4). On the other hand, under water stress condition assimilate remobilization was lowest in Niknejad (8.57%) and highest in Roshan (52.68%) and Omid (50.40%) (Figure 4). Under the well-watered condition, tall varieties (Omid and Roshan) had the lowest *R%* from peduncle to the grains while dwarf genotypes, particularly Niknejad, indicated the highest value. In the water stress condition, tall varieties showed the highest *R%* (Figure 4) and, generally, it was two to three times more than the *R%* observed in the plants under well-watered condition. *R%* declined in the dwarf varieties under the water stress condition. Obviously, photo-assimilates have to move in a longer distance in the tall varieties. This in turn may increase the hydraulic resistance of the phloem against the movement of photo-assimilates (Setter 1993). Therefore, increasing the hydraulic resistance may not be considered as the cause of decreased *R*% in the dwarf cultivars unless the increasing resistance is caused by reducing the diameter of the phloem elements (O'Brien *et al.* 1985). On the other hand, slower rate of photo-assimilate remobilization as a result of lower capacity of the dwarf varieties to store photo-assimilates produced before anthesis and lower sink demand for assimilates due to smaller grains and slower rate of endosperm cell division (Ober *et al*. 1991, Setter & Flannigan 2001) may also be considered as the cause of lower R%. Significant water stress × variety interaction indicated that *R%* in different varieties were different in well-watered and water stress conditions. It has been shown that, at first, assimilates mobilize from fully expanded leaves to enhance developing organs and this mobilization takes place separately in each stem and tiller (Rawson & Hoestera 1964). Leaf assimilates are then temporarily stored in the peduncle and penultimate internodes. Assimilates from flag leaf were shown to be used as the main source for remobilization to the grains (Rawson & Hoestera 1964). More partitioning of the flag leaf assimilates has been observed in tall varieties and at the beginning of enhanced kernel growth (Madore and Waines 1996) and a decline of dry weight was observed that is due to the movement of dry matter or respiration (Rawson & Evans 1971). Internode weight at anthesis and post-anthesis was higher in tall varieties as compared with semi dwarf genotypes (Nicolas *et al.* 1985, Madore and Waines 1996). In our experiment, tall varieties also showed higher peduncle biomass and more remobilization from this organ. Other researchers also reported the same results in wheat (Phelonge and Siddique 1991, Madore and Waines 1996, Ehdaei and Waines 1996). Austin *et al.* (1977) showed that remobilization of stored assimilates to grains was higher in tall varieties in which stem and leaf dry weight decreasd rapidly after anthesis, so higher remobilization in the tall varieties was expected to be due to faster remobilization of assimilates to grains. Among the dwarf varieties, Kavir had the highest *R%* (40.9%) and Omid and Roshan had the lowest value in the well-watered than water stressed treatments (Figure 4).

Remobilization in the tall varieties was two or three times higher in the water stress condition as compared with the well-watered condition. A decline was observed in the dwarf varieties. Among dwarf varieties, the highest *R%* was observed in Kavir and Niknejad under water stress and well-watered conditions, respectively. Rawson and Evans (1971) reported the higher possibility of lower storage and susceptibility to environmental stresses in modern dwarf varieties.

Table 3. Effects of water stress condition and variety on peduncle and penultimate internode remobilization percentage

SV	df	Remobilization percentage	
		peduncle	penultimate
Water stress	1	*	**
Variety	4	*	ns
Interaction	4	**	**

* and **: Significant at 5% and 1% probability levels, respectively. ns: Non-significant

f) Penultimate internode remobilization percentage *(R%)*: Data analysis showed that withholding irrigation caused significant decrease in penultimate dry matter in all varieties. Water stress and water stress × variety interaction were significant for the percent of remobilized assimilates (Table 3). Considering penultimate internode, Kavir and Omid, with 47.9% and 39.1%, showed the highest and the lowest remobilization percentage, respectively. Under well-watered and water-stressed conditions mean *R%* were 39.4% and 50.4%, respectively. Under the well-watered condition *R%* from penultimate internode ranged from 53.5% in Niknejad to 16.5% in Omid (Figure 5). In the water-stressed plants, however, it ranged from 61.7% in Omid to 39.3% in Pishtaz (Figure 5). In Omid, Roshan and Kavir, *R%* from penultimate in the water-stressed condition was more than the well-watered condition. However, it was lower in Pishtaz and Niknejad. Omid and

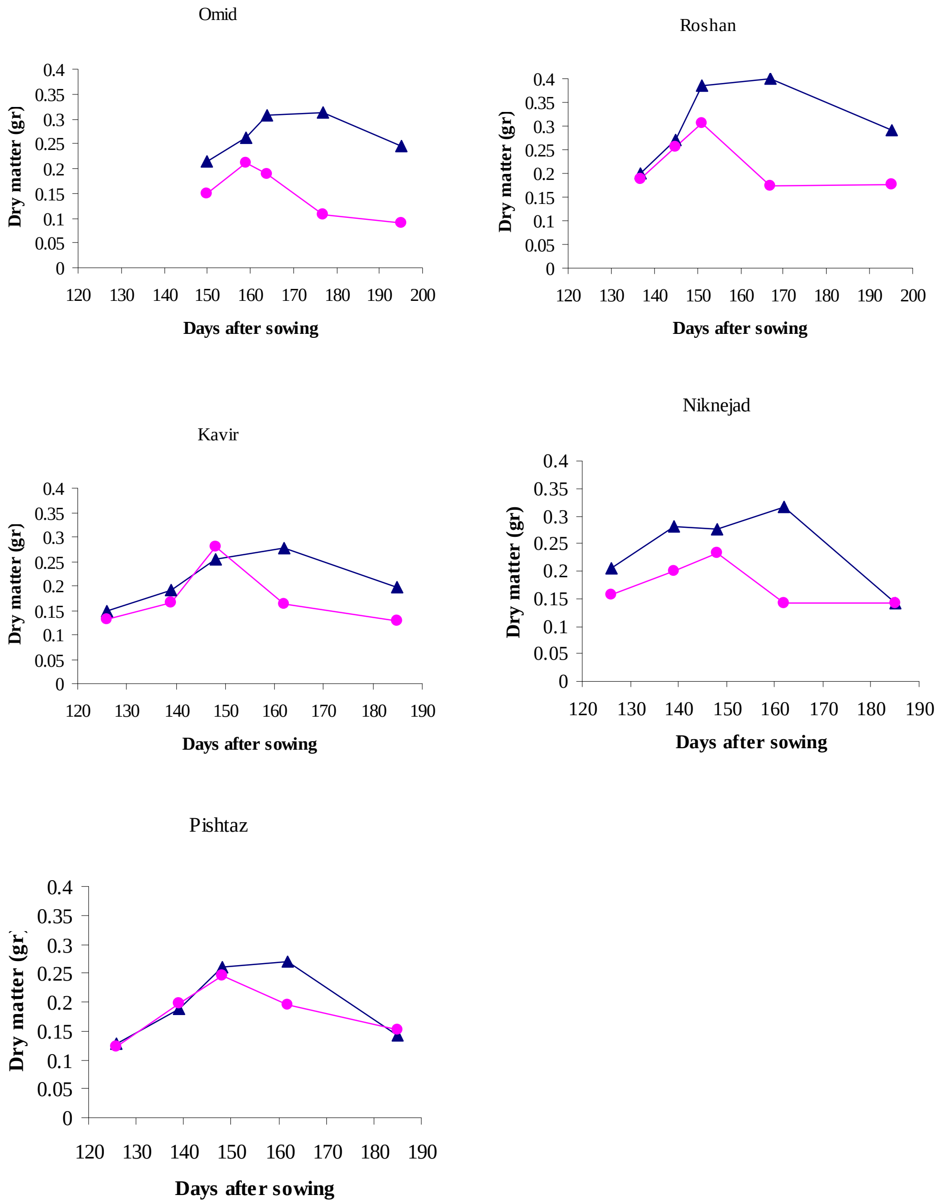
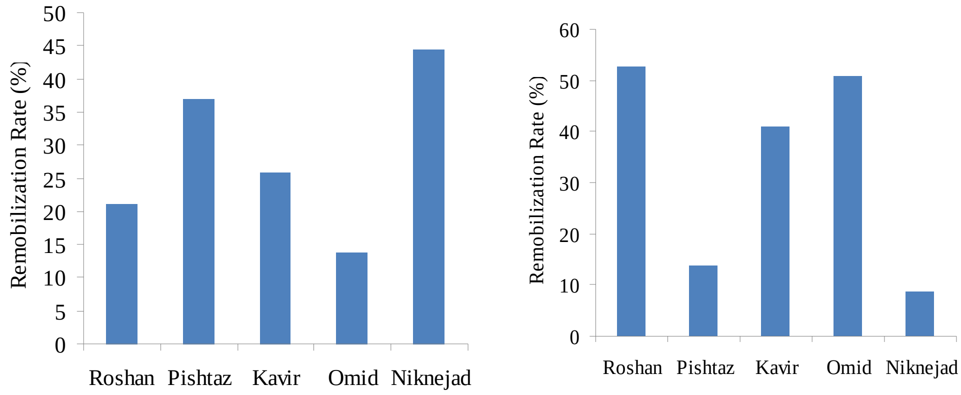
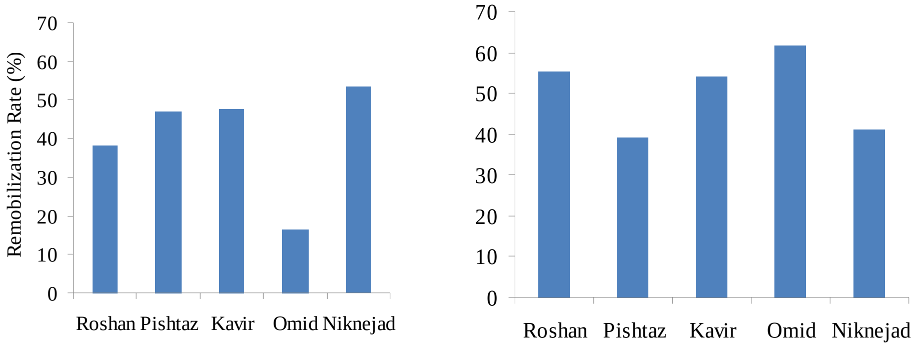


Figure 3. Time course of wheat cultivars penultimate internode dry weight change at different growth stages under well watered (triangles) and water-stressed (circles) conditions



FigureFigureure 4. Stored assimilates remobilization (%) from peduncle to grains in wheat cultivars grown under well-watered (left) and water-stressed (right) conditions

Roshan (tall varieties) had the highest *R%* in the water-stressed environment. Omid and Roshan, with 61.7% and 55.5%, had the highest *R%* under water-stressed condition. *R%* increased to more than three folds in Omid. In tall varieties, *R%* from peduncle and penultimate internodes were higher. Madore and Waines (1996) also reported the same results. In the case of Omid and Roshan, remobilization rate under well-watered condition decreased to less than 50% of the water stress condition. In the water-stressed condition, *R%* decreased in the dwarf varieties but increased in the tall genotypes. In the dwarf varieties, *R%* from penultimate was more than peduncle under both conditions. The same results were observed in the tall varieties although the differences between the two sources were low. Nicolas *et al.* (1985) found that sources were low. Nicolas *et al.* (1985) found that sources were low. Nicolas *et al.* (1985) found that three days before flowering,assimilates start to accumulate in the penultimate internode and reach their maximum values nine days after anthesis. At this period source of assimilates precedes sink demand. Davidson and Chevaliar (1992) concluded that among internodes, penultimate was the strongest internode to reserve assimilates, coming from leaf blades, and later remobilization of them to the ear. Mador and Waines (1996) reported that mean *R%* from the penultimate internode was more than peduncle showing its higher contribution to grain filling. As the photosynthetic machinery of plants is working at its highest capacity, the penultimate internode



FigureFigureure 5. Stored assimilates remobilization (%) from penultimate internode to grains in wheat cultivars grown under well-watered (left) and water-stressed (right) conditions

dry weight, after full elongation, starts to increase indicating the availability of assimilates needed for both plant structure and reservation in stem tissues. Remobilization of stored dry matter from the second internode to the top of the stem and ear then makes the internodes dry weight to decrease. Respiration is also responsible for stem dry matter decrease particularly because air and plant canopy temperature begin to increase later in the growing season, which coincides with the grain filling stage (Rawson & Evans 1971, Austin 1977, Austin 1989, Phelonge & Siddique 1991, Davidson & Chevaliar 1992). Current leaf photosynthesis can not compensate for such high levels of respiration particularly under stress condition (Phelonge & Siddique 1991). Under such conditions, remarkable amounts of dry matter are expected to come from pre-anthesis storages to fill the grains (Gent 1994). Varieties showed a faster decrease in internode dry weight under water stress condition. Both peduncle and penultimate internodes had a role in remobilization. Higher *R%* of the tall varieties as compared with the dwarf genotypes could be due to higher levels of water status which is reflected in the higher flag leaf *RWC*, higher photosynthetic activity and efficiency of remobilization from both internodes (Rawson & Evans, 1971, Madore and Waines 1996). Although remobilization was observed under both growing conditions but it was more under the water stress than the well-watered condition.

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