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Remobilization of Dry Matter in Wheat: Effects of Nitrogen Application and Post-Anthesis Water Deficit During Grain Filling

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Abstract. Pre-anthesis stored dry matter in wheat (Triticum aestivum L.) is important in a Mediterranean climate because grain filling greatly depends on the remobilization of pre-anthesis assimilates.A water deficit at the post-anthesis stage may increase the dry matter stored before anthesis.This field study assessed the effects of post-anthesis water deficit and the application of nitrogen (N) fertilizer on three wheat cultivars. Data collected over 2 years showed that, in wheat with a post-anthesis water deficit (WD), dry matter remobilization efficiency reached its maximum (29%) at 80 kg N ha^{-1}, but further additions of N decreased it. The contribution of remobilized dry matter to a grain ranged from 7% to 23% of the grain's dry weight and, in WD grain, was 78% more than that of well-watered (WW) grain. Grain from plots on which fertilizer had been applied had a lower proportion of remobilized dry matter than did grain from unfertilized plots. For grain from adequately fertilized treatments, limited irrigation was associated with reduced dry matter remobilization. The amount of non-structural carbohydrates (NSC) remaining in parts of the plant was much greater in the WW than in the WD treatments. The 160 kg N ha^{-1} treatment also left more NSC unused than did the no N treatment. The active grain-filling period was shortened substantially by a water deficit, but this was countered by the application of 160 kg N ha^{-1}. Grain-filling rates for all cultivars or all N treatments were increased by inducing a water deficit. For WD grains, kernel weight was reduced when fertilizer application rates were 0,80 kg N ha^{-1}, but increased when rates were 160 kg N ha^{-1}, unlike WW grain exposed to similar fertilizer regimes. The grain yield of WD wheat was reduced by 25%, and that of grain receiving no fertilizer was 15% lower than that receiving 80 kg N ha^{-1}. Among three wheat cultivars, cv. Chamran produced the highest grain yield (19% higher than that of either cv. Shiraz or cv. Marvdasht). It was concluded that the stored carbohydrate had provided an important buffer against water stress during grain filling, in terms of yield.

Keywords: Grain filling rate, grain filling period, grain yield, kernel weight, non-structural carbohydrate residue.

1. Introduction

During spring, in the Mediterranean climate of southern Iran, decreased rainfall and increased evaporation and temperature coincide with the grain-filling stage of wheat (Fathi 2005). Consequently, wheat crops often experience a water deficit during grain filling, which limits subsequent grain yield (Spiertz et al. 2006; Barnabas et al. 2008). The carbon (C) necessary for grain filling in wheat comes from three sources: current assimilation, remobilisation of pre-anthesis assimilates stored in the stem and other parts of the plant and retranslocation of assimilates stored temporarily in the stem after anthesis. To understand the reduction in grain yield arising from post-anthesis water deficits, it is necessary to identify which of these sources of C is limiting the grain-filling process (Ercoli et al. 2008). Post-anthesis water deficits are known to reduce C assimilation and hence the availability of current assimilates for grain filling, but they are not considered to affect the translocation of C to the grain (Ercoli et al. 2006). A water deficit during grain filling increases the proportion of stored assimilates relative to current assimilates in the grain (Yang et al. 2000), but whether this reflects a larger actual mobilisation of stored assimilates rather than simply a reduction in current

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assimilation is not known (Fan et al. 2005). In Iran, nitrogen (N) application results in an undesired delayed senescence, leading to a low kernel weight. Low grain weight can also occur, in northern Iran, when the hot and dry winds typical of the end of the growing season coincide with delayed senescence: such winds dehydrate the wheat rapidly. Early senescence induced by water stress may increase the rate of grain filling and improve kernel weight in this case. The objectives of this study were to assess (i) the effect of a post-anthesis water deficit on the remobilisation dry matter stored in various plant tissues and its contribution to grain yield during the grain-filling period and (ii) the interacting effects of N fertilisation and post-anthesis water deficit on dry matter remobilisation in three wheat cultivars.

2. Materials and Methods

The study was conducted at Shiraz Agricultural Research Station in Iran (52°36'E, 29°33'N) for two years (2006-2008). The experiment was established in a randomized complete block design with a split-split plot arrangement with four replications. Main plots consisted of irrigation treatments, which were WW (well watered) and WD (Post anthesis water deficit) (65% FC). Sub-plots consisted of fertilizer treatment, which were N1=0, N2=80, and N3=160 kg ha^{-1} of nitrogen and sub-sub plots consisted of three cultivars, i.e. Shiraz, Marvdasht, and Chamran. These cultivars were chosen as representative samples of winter wheat cultivars widely grown in the south of Iran that differs in anthesis dates. Plots were sown on 11 November 2007 and on 14 November 2008 with a cone seeder, and were 8 m long and 1.5 m wide, with 6 rows 0.2 m apart. The gypsum blocks used in the experiment are made by Delmhorst Instrument Co. Twenty main stems that headed on the same day were tagged for each treatment. As the tagged main stems of each cultivar reached anthesis, 10 plants in each plot were removed and main stems were divided into spike, flag leaf blade, lower leaves, and stem. At maturity, 10 additional tagged plants were removed and the main stems were subdivided in the same way as at anthesis. Samples were dried to constant weight at 70°C, weighed, and ground to pass a 0.4-mm mesh. Average kernel weight was determined by weighing 250 kernels randomly taken from the bulk grain sample in each plot. The grain filling process was fitted to the Richard (1959) growth equation as described by: $W = A/(1+Be^{-kt})^{1\backslash W}$ (Zhu et al. 1988), where W is kernel weight (mg), A is final grain weight, t is time after anthesis (d), and B, k, and N are coefficients determined by regression. The active grain-filling period was defined as that when W was from 5% (t1) to 95% (t2) of A. The average grain-filling rate during this period was calculated from t1 to t2. Fifteen to 20 plants were sampled from each treatment at 6-day intervals from anthesis to maturity for the measurement of non-structural carbohydrates (NSC) in the stem, flag leaf and other leaves. The method for extraction of NSC was modified according to the method by Yoshida et al. (1976). The four central rows (of 6 rows) of each plot were harvested for assessment of grain yield (kg ha^{-1}). Various parameters for dry matter, within different parts of the wheat plant, were calculated as follows (Papakosta & Gagianas 1991): Apparent dry matter remobilisation (mg $plant^{-1}$) = Dry matter at anthesis [Spike + flag leaf + stem + lower leaves] – dry matter at maturity. Apparent dry matter remobilisation efficiency (%) = (dry matter remobilisation / dry matter at anthesis) ×100. Contribution of apparent dry mater remobilisation to grain (%) = (Dry matter remobilisation / grain yield) × 100. Data were analysed by analyses of variance using the general linear model (GLM) procedure provided by SAS (2001). Combined analysis of variance between years assumed that replications were random, and that irrigation, N fertiliser and cultivars were fixed. When significant differences were found (P = 0.05), the Duncan's multiple range test (DMRT) was carried out.

3. Results and Discussion

3.1. Dry matter remobilisation

The apparent percentages of remobilised reserves, and their contribution to the grain weight, were significantly higher in grain exposed to the WD treatment (Table 1a and 1b). Dry matter remobilisation in all parts of the plant was increased by 14–42% under the WD regime compared with the WW one. At maturity, 173 mg $plant^{-1}$ of the spike dry weight had been remobilised to the grains under the WD treatment, a 20% increase over spike dry weight of WW plants (Table 1a). For the flag leaves and stem, a dry weight of 9 and 277 mg $plant^{-1}$, respectively, were remobilised under the WD regime, which were 14% and 42% above those of corresponding WW treatments (Table 1a). Table 1b shows that NSC were substantially reduced after water the deficit was imposed, with the reduction being greater under the 0-and 80-kg ha^{-1} N regimes than under the 160-kg N ha^{-1} one. The amount of NSC remaining in parts of the plant was much greater under the WW treatment than under the WD treatment (Table 1b). The 160-kg ha^{-1} treatment also left more NSC unused than did the 0-N treatment. Acreche & Slafer (2009) and Alvaro et al. (2007) demonstrated that stomata begin to close 5 days after anthesis, when Ψleaf fell to –1.5 MPa.

3.2. Dry matter remobilisation efficiency

Water deficit markedly affected the dry matter remobilisation efficiency, causing it to increase by 29% (Table 1b). With the WD treatment, dry matter remobilisation efficiency increased with the application of 80 kg N ha^{-1} but decreased with further addition of N (Table 2). It appears that the amount of retained dry matter depends on the cultivars and prevailing growth conditions, although genetic variability in dry matter remobilisation has been reported (Reynolds & Trethowan 2007; Saint Pierre et al. 2008).

3.3. Contribution of dry matter to the grain

The contribution of dry matter remobilisation to the grain ranged from 7% to 23% of grain dry weight (Tables 1a, 1b) and differed among cultivars. Similar values were reported for barley (*Hordeum vulgare* L.) by Krček et al. (2008), who concluded that pre-anthesis storage of carbohydrates is very important for grain yields. Contribution of dry matter remobilisation to the grain under WD was 78% more than that of under WW conditions (Table 1b). In the Mediterranean climate, rising temperatures and declining soil moisture prevailing at the post-anthesis period limit net assimilation rates; therefore, the contribution of post-anthesis dry matter to the grain is greater. In this study, well-fertilised plants showed a lower contribution of stored dry matter to grain than did unfertilised plants (Table 1b).

3.4. Kernel weight

In the 0- and 80-kg N ha^{-1} treatments, kernel weight under the WD regime was less than that of plants under the WW regime, indicating that the decrease in photosynthesis could not be compensated for by an increased remobilisation of carbon reserves (Table 2). When a high amount of N was applied, kernel weight was increased under the water deficit. The obvious explanation for such a result is that, when N was heavily used, delayed senescence led to a slow grain filling, and a poor remobilisation and partitioning of assimilates into the grain. For the high N application rate, the gain from accelerated grain filling and increased remobilisation of pre-anthesis assimilates outweighed the loss of reduced photosynthesis and early senescence as a result of water stress.

3.5. Grain yield

Water deficit markedly affected grain yield (Tables 1b, 2), causing a reduction of 25%. The reduction resulted from a decrease in grain size, but not in grain number. Grain yield increased in response to the applied N, with the grain yield of the plants that did not receive N being 15% lower than those receiving 80 kg N ha^{-1} (Table 1b). Average winter wheat yields were 5135 and 5832 kg grain ha^{-1} for the 0- and 80-kg N ha^{-1} treatments, respectively (Table 1b). Grain yield was reduced by water deficit under 80 kg N compared to 0 kg N ha^{-1},but increased under 160 kg N ha^{-1} when compared with respective WW treatments (Table 2). For the WD treatment, water became more limiting than fertility, and there was no yield response to the applied N. The N response data may be used in determining N fertiliser rates for specific yield goals. Water deficit at the grain-filling period induces early senescence, reduces photosynthesis and shortens the grain filling period (Inoue et al. 2004; Waines 2006). Such responses would result in the reduction of kernel weight, straw yield and grain yield (Alvaro et al. 2007; Karam et al. 2009).

Table 1a. Mean values of dry matter remobilisation (DMR) and DMR efficiency (DMRE) of spike, flag leaf, stem and lower leaf of three wheat cultivars under three N application and two water regimes in 2006–2008.

Treatments	DMR of spike (mg plant^{-1})	DMR of flag leaf (mg plant^{-1})	DMR of stem (mg plant^{-1})	DMR of lower leaves (mg plant^{-1})	DMRE of spike (%)	DMRE of flag leaf (%)	DMRE of stem (%)	DMRE of lower leaves (%)
Irrigation†(I)								
WW	139	4	186	30	22.57	20.57	13.91	19.322
WD	173	9	277	39	27.09	26.49	18.21	22.99
LSD (0.05)	19	0.9	21	5	3.2	3.2	1.6	2.1
Nitrogen (N) kg ha^{-1}								
0	143	2.6	212	33	28.13	23.60	14.80	20.51
80	146	16	227	49	24.18	23.94	16.97	23.59
160	190	16	271	37	22.01	23.04	16.42	19.36
LSD (0.05)	21	1.1	20	5.1	2.8	3.1	1.4	2
Cultivar (C)								
Shiraz	158	16	269	34	22.03	26.38	16.48	19.58
Marvdasht	173	18	200	43	24.26	23.92	13.52	21.78
Chamran	153	1.5	241	37	28.20	20.29	18.18	22.10
LSD (0.05)	21	1.3	19	4.6	2.6	3.1	1.1	1.9

†: WW = well-watered treatment and WD = post-anthesis water deficit.

Table 1b. Total dry matter remobilisation (DMR) and DMR efficiency (DMRE), and mean values of contribution of dry matter to grain, active grain-filling period, grain-filling rate, NSC† residue, kernel weight, grain yield and harvest index, of three wheat cultivars under three N application and two water regimes in 2006-2008.

Treatments	Total DMR (mg plant^{-1})	Total DMRE (%)	Contribution of DMR to grain (%)	Active grain-filling period (days)	Grain filling-rate (mg day^{-1})	NSC residue (mg g^{-1} DW)	Kernel weight (g)	Grain yield (kg ha^{-1})
Irrigation (I)‡								
WW	377	17.01	7.88	37	0.8	232	33.78	5897
WD	513	22.01	14.54	25	1.9	120	27.57	4410
LSD (0.05)	35	0.9	1.7	4.8	0.2	19	4.7	1177
Nitrogen (N) kg ha^{-1}								
0	427	19.96	14.35	29	1.9	67	31.08	5135
80	448	20.51	10.86	35	1.6	188	35.94	5832
160	459	18.06	8.42	41	1.1	222	36.02	5823
LSD (0.05)	37	1	1.8	4.9	0.3	22	4.9	1185
Cultivar (C)								
Shiraz	482	19.05	13.77	42	0.7	219	30.83	4799
Marvdasht	427	18.18	14.69	38	1.3	162	27.49	4908
Chamran	525	21.30	9.17	27	1.8	113	33.72	5853
LSD (0.05)	37	1	1.8	5	0.2	23	4.7	1298

†: Non-structural carbohydrates. ‡: WW = well-watered treatment and WD = post-anthesis water deficit.

Table 2. Mean values of dry matter remobilisation (DMR) and DMR efficiency (DMRE) of spike, flag leaf, stem and lower leaf; contribution of dry matter to grain, active grain-filling period, grain-filling rate, NSC† residue, kernel weight, grain yield and harvest index, as affected by N application and irrigation regime in 2006–2008.

Treatments		DMR of spike (mg plant^{-1})	DMR of flag leaf (mg plant^{-1})	DMR of stem (mg plant^{-1})	DMR of lower leaves (mg plant^{-1})	DMRE of spike (%)	DMRE of flag leaf (%)	DMRE of stem (%)	DMRE of lower leaves (%)
Irrigation ‡	Nitrogen (kg ha^{-1})								
WW	0	147	1.1	234	19	23.95	20.71	14.77	15.60
	80	139	13	135	58	21.70	19.36	9.78	25.75
	160	146	13	204	27	22.05	21.63	9.78	16.60
WD	0	149	5	307	47	24.38	26.48	19.16	25.42
	80	240	18	288	41	34.92	28.51	19.80	21.42
	160	145	20	250	47	21.96	24.45	15.65	22.12
	LSD (0.05)	22	1.6	27	4.6	2.9	2.8	1.8	2.6
		Total DMR (mg plant^{-1})	Total DMRE (%)	Contribution of DMR to grain (%)	Active grain-filling period (d)	Grain-filling rate (mg day^{-1})	NSC residue (mg g^{-1} DW)	Kernel weight (g)	Grain yield (kg ha^{-1})
WW	0		18.10	8.16	29	1.7	106	35.13	5931
	80	401	16.33	8.05	38	1.2	232	33.56	5884
	160	338	16.58	7.42	41	0.9	263	32.66	5873
WD	0	391	21.80	13.55	19	1.4	73	29.02	4337
	80	462	24.68	18.63	30	0.9	184	26.30	4320
	160	495	19.53	11.42	33	0.8	203	27.38	4572
		581							
	LSD (0.05)		2.5	1.4	3.1	0.2	25	2.9	1201

†: Non-structural carbohydrates. ‡: WW = well watered treatment and WD = post-anthesis water deficit.
*,** Significant at 0.05 and 0.01 probability levels, respectively. NS = non-significant at *P* > 0.05.

4. Conclusion

This study has demonstrated that the grain-filling rate of wheat, while affected by water deficit, is maintained above what is expected from post-anthesis dry matter accumulation because remobilisation of assimilates to the grain continued despite a reduction in C assimilation. Stems were more important than the other parts of the plant in the remobilisation of dry matter to the grain during the grain-filling period. The excessive use of N in Iran results in unfavourably delayed senescence. Early senescence induced by water stress could increase the rate of grain filling and improve kernel weight in this case.

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