

Dry Matter and Nitrogen Remobilization of Two Wheat Genotypes under Post - anthesis Water Stress Conditions

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ABSTRACT

Current assimilation, as a source of carbon for grain filling in cereals, may be limited for normal grain filling under Mediterranean climate. In such conditions reserves accumulated before anthesis play an important role in grain growth, but the extent of their contribution depends on prevailing environmental conditions. The experiment described here was carried out to determine the effects of different levels of water stress on dry matter and nitrogen accumulation and their remobilization from the shoot to the grain. The pot experiment was conducted in the glasshouse using two wheat cultivars (Sun 92A and Vasco) differing in yield and protein content. The plants were subjected to water stress at 10 days after anthesis (daa). The following treatments were established: not watered (severe stress), medium stress (-2 Mpa water potential of the Flag leaf), mild stress (-1 Mpa water optional of the Flag leaf), divided root and control. Results indicated that the dry matter and N content of vegetative organs and its concentration were greater at 24 daa than at maturity under all conditions. Water stress during the post anthesis period was unfavorable to a high assimilation rate, so yield was determined to a great extent by the availability of water and the behavior of the cultivars related to shoot reserve remobilization during the grain filling period.

Keywords: Dry matter, Remobilization, Water stress, Wheat (*Triticum aestivum* L.).

INTRODUCTION

In the Mediterranean climate, wheat grain filling period is subjected to several physical and biotic stresses. Current assimilation, as a source of carbon for grain filling, may be limited for normal grain filling under this climate (Blum, 1998). Reserves accumulated before anthesis play an important role in grain growth, but the extent of their contribution depends on prevailing environmental conditions. This is particularly important for wheat growing under Mediterranean environmental conditions because of hot and dry weather and low photosynthesis after anthesis. Under optimal growing conditions with regard to temperature, water regime (David-

son and Chealier, 1992) and mineral nutrition (Papkosta and Gagiana, 1991) carbon assimilation rates are high and a proportion of the assimilates is allocated to storage. Stem reserve remobilization is affected by water stress during grain filling, even the rate of development of water stress may affect shoot reserve remobilization (Palta *et al.* 1994)

The calculated proportion of yield provided by translocation of pre-anthesis assimilates for wheat is estimated at between 7% and 57% (Austin *et al.* 1977; Bidinger *et al.* 1977; Gallagher *et al.* 1975, 1976). Genetic variability in dry matter remobilization has been reported (Davidson and Birch 1978) and the extent of this remobilization is subject to genotype x year interaction (Wych

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et al. 1982). According to Palta *et al.* (1994), total grain carbon with a rapid water deficit was reduced by 24 % relative to the slow rate. Recently, Blum (1998) has reported that the relative contribution of stem reserves to total grain mass per ear or to grain yield were estimated at between 6% and 100% depending on experimental conditions and cultivars used.

Previous studies have indicated that grain nitrogen in wheat primarily originates as a result of translocation from vegetative parts after anthesis (Simmons and Moss, 1978). Pheloung and Siddique (1991) found that the higher yielding cultivars had less reserve storage and suffered greater reductions in grain yield under drought stress during grain filling, compared with the potentially lower yielding cultivar. Bhatia and Rabson (1976) have reported that the grain protein concentration might be improved by selecting genotypes that translocate a higher percentage of nitrogen from vegetative organs to the grain.

Field evaluation of growth and yield during or following stress is difficult because the stress cannot be controlled. This is particularly true where different genotypes are being compared since they are usually at different stages of development at any one time and therefore comparisons at the later stages are not meaningful. It is also difficult to ensure similar stresses for genotypes with different growth habits. Although environmental conditions in the glasshouse and growth room are unlike those in the field in same respects, at least the level of water stress can be controlled, and the other difficulties avoided (Tahmasebi Sarvestani, 1995). The purposes of this experiment were fourfold:

- (1) To determine the effects of different levels of water stress on the accumulation of dry matter and nitrogen in the wheat grain during grain filling.
- (2) To identify the effects of different levels of water stress on the remobilization of dry matter and nitrogen from different parts of the shoot, possibly to the grain.
- (3) To examine the effects of drought in

the upper section of the root while the lower section was watered, on accumulation of dry matter and nitrogen in the grain and remobilization of them from different parts of the shoot during grain filling.

MATERIAL AND METHODS

The experiment was conducted in pots in the glasshouse using two wheat genotypes (Sun 92A and Vasco) differing in yield and protein content. These genotypes were chosen because they had been used in the studies of Stoddard and Marshall (1990). Plants were grown in pots 20 cm deep containing recycled soil (3 kg) and adequate nutrients. Ten seeds were sown per pot and seedlings thinned to six plants per pot after emergence and plants were restricted to a single culm by removing all tillers as they emerged. A randomized complete design with three replications was used. Calculated parameters and standard statistical procedures were used for the analysis of variance. Plants were grown with the natural photoperiod for Adelaide (Australia) in the months of January to May at a controlled temperature ($25 \pm 2^\circ\text{C}$ during the day and $16 \pm 2^\circ\text{C}$ at night). All pots were watered and maintained at approximate field capacity until 10 days after anthesis by weighing the pots two times per week and adding water to make up for the loss in weight. A pressure bomb was used to estimate the water potential of the plant. The flag leaf to be measured was excised from the plant at the junction of the lamina and sheath with a sharp blade and was immediately inserted through a slit in a rubber stopper and placed in the pressure bomb which was sited close to the plants. The leaf blade extended about 2 cm through the rubber stopper. Pressure was then applied slowly from a compressed-air cylinder until the xylem sap was just visible on the cut surface of the leaf. The sap on the cut end was observed with a $10 \times$ magnification hand lens. The pressure reading was recorded and expressed as the flag leaf water potential. All pots were watered under the same water re-

gime (around field capacity) until the start of grain filling (ten days after anthesis).

Water treatments were imposed from ten days after anthesis (daa) by withholding water and monitoring the water potential of the flag leaf of the plants. The following treatments were established:

1) Control: pots were watered throughout the experiment.

2) Mild stress: water was withheld from day 10 after anthesis but pots were rewatered when the water potential of the flag leaf fell to -1 Mpa. This cycle was repeated until maturity.

3) Medium stress: water was withheld at day 10 after anthesis and pots were rewatered when the water potential of the flag leaf fell to -2 Mpa. This cycle was repeated until maturity.

4) Divided root: plants were grown in pots with a hydrophobic barrier (2-3 cm gravel) which divided the root system horizontally; the lower section was watered but the upper part was not watered from day 10 after anthesis.

5) Severe stress (no watering): Water was withheld completely from 10 daa.

At day 24 after anthesis (around middle of grain filling) and at maturity, three pots from each treatment were harvested and the above ground parts separated into chaff, flag leaf, other leaves, internodes, peduncle and grain. These were dried at 85° C for 48 hours and weighed. Nitrogen concentration was determined by the standard macro-Kjeldahl procedure. The various attributes relating to dry matter and nitrogen movement in the shoot were evaluated as follows:

- 1) Dry matter remobilization (mg per shoot) = (dry matter at day 24 after anthesis in the organ) - (dry matter at maturity in the same organ).
- 2) Dry matter remobilization efficiency (%) = [(Dry matter remobilized) / (dry matter at day 24)] x 100.
- 3) Contribution of reserves of assimilate to grain (%) = (Dry matter remobilized / grain dry matter accumulation between day 24 and maturity) x 100.

4) Harvest index (HI) = Grain yield per shoot / total aboveground biomass per shoot.

5) Nitrogen remobilization (mg per shoot) = N content at day 24 after anthesis - N content at maturity.

6) Nitrogen remobilization efficiency (%) = (N remobilization / N content at day 24 after anthesis) x 100.

7) Nitrogen decrement (-) or increment (+) (mg per shoot) = N content at day 24 - N content at maturity.

8) Contribution of vegetative nitrogen to grain (%) = (nitrogen remobilized / grain nitrogen accumulation between day 24 and maturity) x 100.

9) Nitrogen harvest index (NHI) = Grain N (mg per shoot) / total N content of above ground parts (mg per shoot).

RESULTS

Flag Leaf Water Relations

Water potential (total) of the flag leaf of Sun 92A (Figure 1) which was similar to the Vasco cultivar declined slowly from day 12 followed by a rapid decrease from day 18 in severe stress (non-watered) conditions. On day 21, water potential in the medium stress treatment increased because the plants were rewatered. Under non-watered conditions, the water potential of both genotypes declined throughout the experiment until 31 days after the withholding of water. After this time, the flag leaf under this treatment was completely senescent. It was assumed that, under the divided root treatment, water relations were the same as the control conditions.

Yield

The effects of water stress treatments on the grain weight are presented in Table 1. There were significant interactions ($P < 0.05$) between water stress treatments and cultivars. Grain yield was significantly higher in

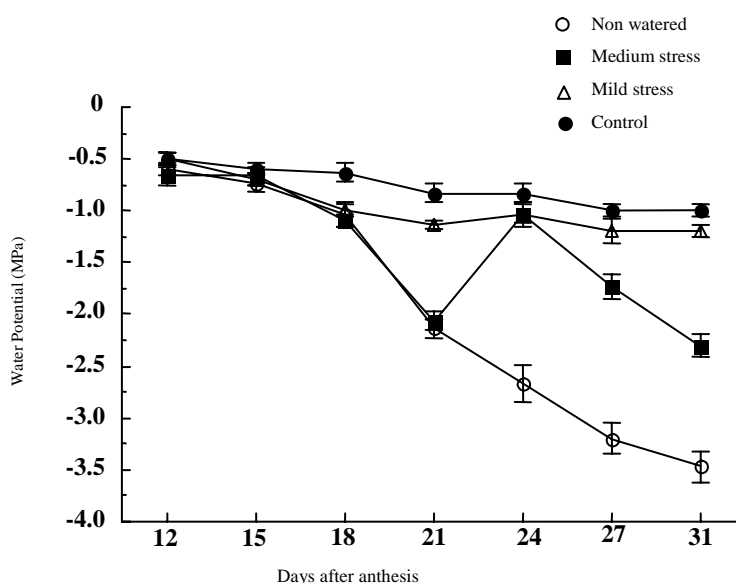


Figure 1. The water relations of the flag leaf of Sun 92A cultivar under different levels of water stress between days 10 and 31 after anthesis.

Vasco than in Sun 92A in all except the non-watered treatment at day 24 (Table 1). Water stress significantly decreased dry matter content in the grain of both cultivars at day 24 and at maturity under most conditions. In general, the extent of the reduction was related to the level of stress. Grain dry weight in Sun 92A cultivar under the divided root system did not differ from control while it was different in Vasco (Table 1).

Grain Nitrogen Accumulation

The interaction between water stress treat-

ment and cultivar on nitrogen accumulation in the grain is presented in Table 2. At 24 days after anthesis, N accumulation in the grain of cultivars under both control and medium water stress was similar (Table 2). At maturity, however, significantly more nitrogen was accumulated in the grain of Vasco (medium protein concentration) than in Sun 92A (high protein concentration) under all except the most severe stress treatment. The pattern of N accumulation between day 24 and maturity was generally similar to grain dry matter accumulation in both cultivars.

Since cultivars varied for grain yield and

Table 1. Grain dry matter accumulation (mg per shoot) as affected by different treatments of water stress in two cultivars of wheat during grain filling.

Treatment	Day 24		Maturity	
	Sun 92A	Vasco	Sun 92A	Vasco
Control	415 b	704 b	1130 a	1827 a
Divided root	471 b	935 a	1124 a	1648 b
Mild stress	620 a	761 b	1062 a	1555 bc
Medium stress	412 b	577 c	715 b	1404 c
Severe stress	404b	312d	480c	636d

Means followed by the same letter in each column are not significantly different at 5% level using LSD test.

Table 2. Grain nitrogen accumulation (mg per shoot) as affected by different treatments of water stress in two cultivars of wheat during grainfilling.

Treatments	Day 24		Maturity	
	Sun 92A	Vasco	Sun 92A	Vasco
Control	14b	15b	35a	44a
Divided root	14 b	22 a	37 a	43 a
Mild stress	19 a	17 b	37 a	43 a
Medium stress	13b	15b	29b	39b
Severe stress	16 a	10 c	21 c	22 c

Means followed by the same letter in each column are not significantly different at 5% level using LSD test.

nitrogen, the effects of water stress on yield and grain nitrogen content, expressed as a percentage of controls are shown in Table 3. Grain yield per shoot was more sensitive to water stress than grain nitrogen. Under non-watered conditions, grain yield reductions in Sun 92A and Vasco were 58% and 66% respectively, while the corresponding values in nitrogen were 40% and 50% respectively (Table 3). At maturity, grain produced under water stress had a significantly higher percentage of nitrogen than under conditions of adequate water in both cultivars (Table 4). The NHI was also significantly higher under control and divided root treatments than water stress conditions in both cultivars (Table 4).

Dry Matter Remobilization

Dry matter was remobilized from different parts of the shoot (except chaff) between day 24 and maturity (Table 5). Dry matter remobilization from different parts of the shoot

in all treatments showed differences between two cultivars. The remobilization of DM in the control treatment was higher than that in the stress treatment. The divided root treatment remobilized more DM than stress treatment and less than control.

Nitrogen Remobilization

Nitrogen remobilization from different parts of the shoot between the two harvests was different between cultivars and also between water stress treatments (Table 6). More nitrogen was remobilized from the shoot of Vasco than from Sun 92A. Remobilization of N was higher in the control than other treatments during grain filling period. Although only part of the root system in the divided root treatment was stressed, it appeared to reduce the remobilization of N from the shoot.

Table 3. Grain nitrogen content and yield as a percentage of control at maturity.

Treatments	Grain Nitrogen		Grain Yield	
	Sun 92A	Vasco	Sun 92A	Vasco
	Percent			
Control	100	100	100	100
Divided root	106	96	99	76
Mild stress	105	96	93	85
Medium stress	83	89	45	71
Severe stress	60	50	42	34



Table 4. Summary of grain physiological parameters under well watered, divided root and stress (means of 3 treatments) conditions in two wheat cultivars at maturity.

Parameter	Control		Divided root		Stress	
	Sun 92A	Vasco	Sun 92A	Vasco	Sun 92A	Vasco
DM (mg per shoot)	1130	1827	1124	1648	752	1198
N (mg per shoot)	35	44	37	43	29	34
Grain N (%)	3.1	2.4	3.4	2.6	4.0	3.0
NHI (%)	77	76	76	73	66	63
HI (%)	56	51	55	49	45	41

Table 5. Dry matter increment (+) and remobilization (-) from vegetative parts in two wheat cultivars under control, divided root and stress (average of three water stress treatments) conditions between day 24 and maturity.

	Control		Divided root		Stress		Control		Divided root		Stress	
	V1 ^a	V2 ^b	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
Increment (+) and remobilization (-) (mg per shoot)							Apparent remobilization efficiency (%)					
Grain	+715	+1123	+563	+713	+273	+649	-	-	-	-	-	-
Internodes	-82	-106	-73	-51	-33	-13	20	22	10	23	36	12
Peduncle	-32	-67	-15	-58	-34	-24	20	22	30	13	10	4
Flag leaf	-39	-50	-66	-28	-10	+5	33	17	22	14	5	0
Other leaves	-73	-93	-52	-72	-17	-9	-16	-16	-33	-20	-34	-12
Chaff	+39	+73	+77	+87	+70	+46	-	-	-	-	-	-

^aV1= Sun 92A ^bV2= Vasco

DISCUSSION

Severe and medium water stress imposed on the plants affected the accumulation of nitrogen and dry matter in the grain of both cultivars at maturity (Tables 1, 2). Brooks *et al.* (1982) have found that protein, as a percentage of grain dry matter, increases with drought. Results from this study also showed an increase of grain nitrogen percentage

(N%) and a decrease of dry matter under water stress conditions during grain filling (Table 4). The grain N yield (mg per shoot) was lower under water stress than in non-stressed conditions while the nitrogen percentage was higher, indicating that the higher percentage N of grains was probably due to the small size of the grain under stress.

Comparatively speaking, stress decreased

Table 6. Grain nitrogen increment (+) and vegetative parts remobilization (-) in two wheat cultivars under stress (average of three water stress treatments), divided root and control between day 24 and maturity. V1=Sun 92A; V2=Vasco.

	Control		Divided root		Stress		Control		Divided root		Stress	
	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
Increment (+) and remobilization (-) (mg per shoot)							Apparent remobilization efficiency (%)					
Grain	+21	+29	+24	+20	+13	+21	-	-	-	-	-	-
Internodes	-1.5	-2.7	-2.2	-2.7	-0.9	-1.6	71	62	78	67	47	42
Peduncle	-1	-1	-1.1	-1.2	-1.0	-0.7	50	43	50	40	50	22
Flag leaf	-4.9	-5.8	-4.5	-5.5	-3.0	-2.3	74	81	71	80	39	40
Other leaves	-6.2	-10.1	-5.9	-6.2	-2.7	-3.7	73	73	70	61	32	30
Chaff	-1.7	-1.9	+1.2	0	+0.8	+0.3	24	23	-	-	-	-

dry matter accumulation more than N accumulation in the grain under severe water stress (Table 3) indicating differences in the relative sensitivity of the two processes to water stress. Grain dry weight is an expression rate of dry matter accumulation and grain growth duration (Brocklehurst, 1978). Water stress in this experiment reduced grain dry weight in both cultivars probably by reducing the rate of DM accumulation in the grain.

HI is the end product of the interaction between genetic, environmental and agronomic factors, and is highly influenced by environment (Siddique *et al.* 1989a). Results of the present study showed that HI reached the highest value under non-water stressed conditions and was lowest in water stress (means of three treatments, Table 4). The highest HI found in the literature was 60% for early-planted spring wheat cultivar "Twin" in Utah (Hanks and Sorensen 1984), while the lowest values of slightly less than 20% were found for wheat growing under major water deficit in southern Iran (Poostchi *et al.* 1972), and for wheat growing under severe stress after anthesis in Australia (Pastoral 1977). NHI also reached its highest value (77% in Sun 92A) under control conditions and its lowest value (63%) in Vasco under the stress conditions (Table 4).

In this experiment it was also assumed that the loss of DM and N between day 24 and maturity is an estimate of the actual amount remobilized. However, as leaves and other organs are still producing DM between day 24 and maturity, the estimate of the amount remobilized or contributed to the grain may be an under estimate of the actual amount.

These results suggested that the high protein cultivar was not more efficient at remobilizing N from the vegetative tissue into the developing grain than the medium protein cultivar. Mikesell and Paulsen (1971), however, have noted that high protein cultivars have a greater proportion of their shoot N in the grain at maturity than low protein cultivars. In both cultivars leaves remobilized far more N than any other organ and N was apparently not remobilized from the chaff in

either cultivar under stress. It appears, therefore, that the amount of nitrogen remobilized depends on cultivar and prevailing growth conditions, and upon the part of the shoot under consideration.

By maturity, the N content in vegetative parts declined considerably more than did the dry matter. Non-stressed plants remobilized more N than did stressed plants. This result confirms that water stress is an important factor affecting the accumulation of dry matter and nitrogen in the grain and also in the remobilization of dry matter and nitrogen from the shoot during grain filling. Water stress reduced the fraction of the N content of the shoot remobilized (Table 6) in both cultivars, and had the greater effects on the leaves which made the largest contribution to grain N.

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انتقال مجدد ماده خشك و نیتروژن دو رقم گندم در شرایط تنش رطوبت بعد از گلدهی

ذ. طهماسبی سروستانی، سی. اف. جنر و گ. مک دونالد

چکیده

در شرایط آب و هوای مدیترانه‌ای در غلات امکان محدودیت اسیمیلاتهای جاری به عنوان منبع کربن در مرحله پرشدن وجود دارد. در چنین شرایطی ذخایر تجمع یافته قبل از گلدهی نقش بسیار مهمی در رشد دانه دارند، اما سهم مشارکت این ذخایر مرتبط با شرایط محیطی است. به منظور تعیین اثرات تیمارهای مختلف تنش رطوبتی بر تجمع ماده خشك و نیتروژن در دانه و نیز انتقال مجدد آنها از اندام های هوایی به دانه این آزمایش به اجراء در آمد. آزمایش گلدانی در شرایط گلخانه با استفاده از دو رقم گندم (Sun 92A, Vasco) که دارای عملکرد دانه و پروتئین متفاوت بودند انجام گرفت. گیاهان در مرحله ۱۰ روز بعد از گلدهی تحت تأثیر تنش رطوبت قرار گرفتند. در این آزمایش تیمارهای تنش رطوبتی شامل قطع آب (تنش شدید)، تنش رطوبتی متوسط (۲- مگاپاسکال پتانسل آب برگ پرچم)، تنش رطوبتی ملایم (۱- مگاپاسکال پتانسل آب برگ پرچم)، تقسیم ریشه (تنش رطوبتی در بخش بالای ریشه) و شاهد اعمال گردید. نتایج نشان داد تجمع ماده خشك و نیتروژن در اندام های رویشی در مرحله ۲۴ روز پس از گلدهی بیشتر از مرحله رسیدگی تحت همه شرایط بود. تنش رطوبتی در مرحله بعد از گلدهی اثری نامناسب بر میزان جذب اسیمیلاتها داشت و بنابراین میزان محصول وابستگی نسبتاً زیادی به میزان دسترسی به رطوبت و رفتار ژنوتیپ ها از نظر انتقال مجدد ذخایر موجود در اندامهای هوایی در مرحله پرشدن دانه داشت.