Cereal Research Communications
https://doi.org/10.1007/s42976-023-00451-w

ORIGINAL PAPER

Employing entire stem might underestimate the amount of carbohydrate remobilization in wheat

Mehdi Joudi[1] · **Mohammad Esmailpour**[2] · **Valiollah Mohammadi**[3] · **Ali Ahmadi**[3]

Received: 2 July 2023 / Accepted: 6 October 2023

Abstract
Stem reserve remobilization plays a prominent role in maintaining the stability of wheat grain yield. The present study aimed at comparing the amount of dry matter remobilization by employing both the entire stem and the separately weighted internodes in 18 wheat cultivars. To this end, the cultivars were examined under well-watered and terminal drought stress conditions at a Mediterranean climate during 2007–2009. They were also examined under well-watered condition in a subtropical climate during 2014–2015. Time-dependent changes in the weights of the entire stem as well as those of the internodes (peduncle, penultimate, and the lower internodes) were measured after anthesis. Results showed that the lower internodes remobilized their stored dry matter much earlier than the peduncle and penultimate. Moreover, in the majority of cultivars, the amount of entire stem dry matter remobilization was observed to be lower than that of the cumulative internode remobilization (i.e., sum of the remobilized dry matter from the individual internodes). This indicates that the employment of the entire stem for the calculation of the dry matter remobilization might underestimate this trait. Depending on the cultivars and the environmental conditions, the amount of underestimated remobilization was also found to range from 4 to 202 mg. Therefore, for the more precise measurement of the carbohydrate remobilization in wheat stems, the separate measurement of this trait in each internode is highly recommended.

Keywords Accumulation · Drought stress · Internodes and stem reserves · Remobilization · Water soluble carbohydrates · *Triticum aestivum* L.

Introduction

While wheat (*Triticum aestivum* L.) has been considered as the most important source of calories in various countries, drought stress is the primary barrier to its worldwide production. Moreover, as a result of the climate change, the production of wheat and, consequently, the global food security are expected to be more threatened by drought stress in the near future. This is particularly the case in drought-prone areas. Therefore, the investigation of the physiological mechanisms which improve the tolerance of wheat to variable environments paves the way for the sustainable production of this plant.

Under terminal drought stress, stem carbohydrate reserves become the major source of grain filling as leaf photosynthesis ceases (Zhang et al. 2015). These reserves are water-soluble carbohydrates (WSCs), mainly consisting of fructan and glucose, fructose, sucrose as well as various oligosaccharides (Joudi et al. 2012). While being temporarily accumulated in the wheat stem internodes, much of these

Communicated by Ildikó Karsai.

✉ Mehdi Joudi
mehdijoudi@gmail.com; joudi@uma.ac.ir

Mohammad Esmailpour
esmailpour@jahromu.ac.ir

Valiollah Mohammadi
vmohammadi@ut.ac.ir

Ali Ahmadi
ahmadia@ut.ac.ir

[1] Department of Plant Science and Medicinal Herbs, Meshgin–Shahr College of Agriculture, University of Mohaghegh Ardabili, Ardabil, Iran

[2] Department of Plant Production and Genetic, College of Agriculture, Jahrom University, PO BOX 74135-111, Jahrom, Iran

[3] Department of Agronomy and Plant Breeding, College of Agriculture, University of Tehran, Karaj, Iran

Published online: 31 October 2023

reserves are subsequently translocated toward the grains, depending on the environmental condition (Joudi and Van den Ende 2018). This is to say that, the more the severity of the condition is, the more contribution of stem WSCs in grain filling is expected. Researches have shown that reserve pools can potentially contribute to about 20% of the final grain weight and up to 50% of the grain yield under favorable conditions and under drought stress during the grain filling period, respectively (Hou et al. 2018 and the references therein). Accordingly, playing a crucial role in determining grain yield under both drought stress and non-stress conditions, the investigation and precise measurement of the stem reserves remobilization becomes of high significance.

Wheat stem is consisted of certain internodes known as the peduncle (the first internode below the spike), the penultimate (the one below the peduncle), and the lower internodes (Li et al. 2013). The net accumulation of the reserves mainly starts when the internodes reach their maximum lengths. Compared with the upper internodes, i.e., peduncle and penultimate, the lower ones chronologically arise earlier, which causes the accumulation of the reserves to take longer. In line with this, Ehdaie et al. (2006a) reported the highest amount of WSCs to be accumulated in the lower internodes (followed by the penultimate and the peduncle internodes) in both the drought stress and non-stress conditions. This is while, a number of studies found the carbohydrate to be mainly stored in the peduncle and the penultimate (Ma et al. 2014; Thapa et al. 2022).

While different cultivars greatly differ in their capacity for stem carbohydrates accumulation and remobilization, the influencing factors of such variations are not fully recognized. However, a number of factors have been stated for the variations in stem carbohydrate accumulation, including: (1) phenological events such as flowering time (Joudi and Van den Ende 2018), (2) physiological characteristics such as photosynthetic rate, sucrose loading and unloading in leaf and stem, as well as fructan synthesizing enzymes (Joudi et al. 2012 and the references therein), and (3) morphological traits such as the length, diameter, and solidness of the stem (Saint Pierre et al. 2010). In addition, the amount of remobilization among wheat population can be influenced by the amount of the accumulated reserves in the stem as well as the remobilization efficiency, which, in turn, depends on the strength of the sink (Thapa et al. 2022).

Carbohydrates accumulation and remobilization are also found to be greatly affected by environmental conditions. For example, Blum (1998) maintained that the rate of photoassimilation as well as the storage of assimilates reach their highest levels in an optimal condition. Therefore, compared with drought-stressed plants, well-watered and taller ones are found to store more carbohydrates in their stems (Davidson and Chevalier 1992). In another study, Plaut et al. (2004) demonstrated that, to increase stem cell water absorption, certain wheat cultivars used their stem carbohydrate reserves as an organic osmolyte, which, in turn, resulted in the reduction of their remobilization capacity. In contrast, Vosoghi Rad et al. (2022) showed the rate of assimilate remobilization to be significantly increased from the lower and the peduncle internodes in durum genotypes under terminal drought stress condition.

The amount of accumulation and remobilization of carbohydrates in wheat stem can be estimated either by monitoring the changes in stem dry weight (Ehdaie et al. 2006b; Ma et al. 2014; Thapa et al. 2022) or by measuring the stem WSCs content (Ehdaie et al. 2006a; Liu et al. 2020). As it is maintained by Ehdaie et al. (2008), the former is preferred as measuring the content of the stem WSCs is a time consuming and expensive task. This is also argued by Xue et al. (2009) who reported the measurement of the stem dry matter content as a rapid and low-cost selection tool for the genotypic ranking of WSCs concentrations among wheat cultivars.

The measurement of the accumulation and remobilization of the wheat stem dry matter can be performed via monitoring the maximum and minimum weights of the entire stem at post-anthesis and maturity stages, respectively (Al–Sheikh Ahmad et al. 2020; Yàñez et al. 2017; Yang et al. 2004, 2001). However, since the weight of the individual stem internodes changes independently over time, the maximum and minimum weights of the internodes at those stages have been employed for measuring these traits in some studies (Thapa et al. 2022; Ehdaie et al. 2006a,b). Nevertheless, to the best of the researchers' knowledge, the amount of the entire stem remobilization has not been compared with that of the cumulative internodes remobilization (sum of the remobilization of individual internodes) under different environmental conditions. So, the present study attempts to show that considering the weight of the entire stem might underestimate the amount of the accumulated and remobilized stem dry matter.

Materials and methods

Cultivars

The total number of 81 wheat cultivars was investigated at the Mediterranean climate of Iran, eighteen of which (also tested at subtropical region later) are analyzed here (Table 1). These cultivars with different origin could be cultivated under the given conditions (Joudi et al. 2014). There were differences among the evaluated cultivars with respect to their heights and relative maturity (Table 1). Moreover, according to the previous studies, no significant correlation was found between the phenological periods and the stem weight (Ehdaie et al. 2006b) or the stem WSC content

Table 1 Characteristics of the wheat cultivars grown at the subtropical region (Moghan site) of Iran during 2014–2015 growing season

Cultivars	Origin	Growth habit	Plant height	Relative maturity
Arta	Iran	Spring	Dwarf	Medium early
Azadi	Iran	Winter	Semi-dwarf	Medium late
Alvand	Iran	Facultative	Semi-dwarf	Medium early
Alamut	Iran	Winter	Semi-dwarf	Late
Bistoon	Iran	Winter	Semi-dwarf	Medium late
Pishtaz	Iran	Spring	Dwarf	Medium early
Yavarus	CIMMYT	Spring	Dwarf	Late
Rasul	CIMMYT	Spring	Semi-dwarf	Early
Sardari	Iran	Winter	Semi-dwarf	Late
Sumay3	China	–	Tall	Medium early
Shirudi	CIMMYT	Spring	Semi-dwarf	Medium late
Shiraz	Iran	Spring	Dwarf	Medium late
Gascogne	France	Winter	Dwarf	Late
Crossed Alborz	Iran	Spring	Dwarf	Early
Golestan	CIMMYT	Spring	Semi-dwarf	Medium early
Marun	Iran	Spring	Semi-dwarf	Early
Niknejhad	ICARDA	Spring	Dwarf	Early
Hamun	Iran	Spring	Dwarf	Medium early

(Ehdaie et al. 2006a), indicating the genotypic differences in the weight and in the WSC content of the stem not to be confounded by those in phenology (Ehdaie et al. 2008).

Sites of experiments

The experiments were carried out at Karaj and Moghan sites, with opposing environmental conditions. Karaj is located in the north central part of Iran (35°49'N, 51°0'E, and 1312 m asl), has a Mediterranean climate with cold winters, dry-warm springs, and summers, and the average annual precipitation of 243 mm. On the other hand, Moghan is located in the northwest of the country (39°36'N, 47°57'E, and 45 m asl), has a subtropical climate, with mild winters, humid-warm springs and summers, and the average annual precipitation of 271 mm. The monthly meteorological data collected during the experiments are provided in Supplemental Table S1.

Mediterranean climate experiments (Karaj site)

Experiments were conducted over crop seasons 2007–2008 and 2008–2009. In each season, two experiments were conducted simultaneously under well-watered (WW) and terminal drought stress (DS) conditions at the agriculture research farm of Tehran University. The 81 cultivars were sown on Nov 1–3, 2007, and on Nov 10–11, 2008. Seeding rate was adjusted by cultivar according to 1000 grain weight to achieve a target plant number of 300 m^{-2}. The experimental design was a simple lattice (9 × 9) with two replications. There were four rows in each plot in a north–south direction; rows were 4 m long with 0.2 m spacing. Fertilizer applied was 200 kg ha^{-1} of diammonium phosphate ($(NH_4)_2HPO_4$), and 100 kg ha^{-1} of urea ($CO\ (NH_2)_2$) before planting, and 50 kg ha^{-1} of urea top-dressed at jointing (Zadoks GS 31, Zadoks et al. 1974). Herbicides and insecticide were sprayed to prevent or control weeds and insects.

In the 2007–2008 and 2008–2009 seasons, WW and DS plants were irrigated five times from sowing to heading (when 50% of the plots had reached heading (Zadoks GS 55)). From this point, DS plants were no longer irrigated, whereas WW plots were irrigated a further three times in 2007–2008 and four times in 2008–2009 until maturity (Zadoks GS 94). Approximately, 55 mm of irrigation water was applied each time.

Subtropical climate experiment (Moghan region)

The experiment was carried out under WW condition during the 2014–2015 season at the agriculture research farm of Moghan College of Agriculture and Natural Resources, University of Mohaghegh Ardabili. The 18 wheat cultivars were sown on Nov 20, 2014, with the density of 300 plant per m^2. The randomized complete block design (RCBD) with three replications was used as the experimental design of the study. Four rows (with the length and space of 1 m and 0.2 m) were cultivated in each plot in the north–south direction. Fertilizer applications were as described above. Recommended practices were used for control of weeds and fungal diseases.

The plants were irrigated for five times from sowing to maturity, with approximately 55 mm of water at each irrigation. Compared with Karaj site, the less amount of water input used for the WW plants at Moghan can be argued to be due to the high level of relative humidity and the resultant low level of total evaporation of the site during the growing season (Supplemental Table S1).

Measured traits

In each plot, three main tillers were randomly harvested from the soil surface at anthesis (Ehdaie et al. 2006b). This was repeated at 7–days intervals after the anthesis and until the physiological maturity. The harvested main tillers were immediately dried in a forced-air dryer at 70 °C for 48 h. Then, each main tiller was divided into the spike and the entire stem. The entire stem was further divided into three segments, namely the peduncle, the penultimate, and the lower internodes. Leaf blades and sheaths were removed from the segments and then the weight of each segment was measured. The entire stem weight was calculated as the sum of its segments weight. Accordingly and based on the literature (Ma et al. 2014; Ehdaie et al. 2006b), the amount of remobilized dry matter was calculated as follows:

Dry matter remobilization of an entire stem = the maximum dry weight of the entire stem after anthesis minus the dry weight of the entire stem at maturity;

Dry matter remobilization of an individual internode (including peduncle, penultimate, or the lower internodes) = the maximum dry weight of the individual internode after anthesis minus the dry weight of the internode at maturity;

Cumulative remobilization of internodes = the dry matter remobilization of the peduncle plus the dry matter remobilization of the penultimate plus the dry matter remobilization of the lower internodes;

Remobilization efficiency of each internode segment was estimated using the proportion (%) of the mobilized dry matter relative to the maximum weight of that segment;

It was assumed in the equations that all of the dry matter lost from the stem or internodes was remobilized to the developing grains. Moreover, losses of dry matter due to plant respiration were not considered since the respiration is believed to largely rely on the current assimilation rather than the mobilized reserves (Ma et al. 2014).

Data analysis

Analyses of variance (ANOVA) were carried out using SAS statistical software (SAS Institute 1994). In the Mediterranean climate experiments (Karaj site), data from WW and DS conditions were analyzed separately in each growing season according to a lattice design. Subsequently, the adjusted means obtained for the 18 considered wheat cultivars from the first (replication 1) and the second year (replication 2) were combined based on the RCBD design (Joudi et al. 2014). Likewise, the data collected from the subtropical climate experiment (Moghan region) were analyzed based on the RCBD design. Means were also compared using the LSD test at 5% probability level.

Results

Dry matter accumulation

Mediterranean climate (Karaj site)–WW experiment

The maximum weight of the peduncle was attained at the 7th, 14th, and 21th days after anthesis (DAA) in 6, 9, and 3 cultivars, respectively. As can be seen in Table 2, the results ranged from 317 to 487 mg. Penultimate weight reached its peak at the 7th, 14th, and 21th DAA in 5, 9, and the remaining 4 cultivars, respectively. At the peak of the dry matter accumulation, the dry weight of the penultimate varied from 323 to 578 mg (Table 2).

Moreover, the lower internodes in 10 cultivars reached their maximum weight at anthesis, while post anthesis dry matter accumulation continued until the 7th and 14th DAA in 5 and 3 remaining cultivars, respectively (Table 2). At the maximal point, the mean dry weight of the lower internodes (623 mg) was found to be higher than those of the penultimate (414 mg) and peduncle (393 mg), suggesting more photo-assimilates being partitioned to the lower internodes (Table 2).

Also, the examined cultivars reached their maximum stem weight at different times. This is to say that, it was obtained at the 7th, 14th, and 21th DAA in 8, 7, and 3 cultivars, respectively. Accordingly, the maximum weight of the entire stem varied from 1143 mg in Arta to 1631 mg in Rasul (Table 2).

Mediterranean climate (Karaj site)–DS experiment

Among the examined cultivars, 6 reached their maximum peduncle weight at 7 days, 11 obtained it at 14 days, and 1 attained it at 21 DAA (Table 3). Moreover, at the point of maximal weight, the mean dry weight of peduncle under drought condition (366 mg) was 7% less than that of observed under WW condition (393 mg) (Tables 2 and 3).

Moreover, the accumulation of dry matter in the penultimate continued until 7, 14, and 21 DAA in 7, 10, and 1 cultivars/cultivar, respectively (Table 3). Drought, on average, decreased the maximum weight of penultimate by 11% (414 mg in WW condition vs. 370 mg in drought condition) (Table 2 and 3).

Furthermore, in the majority of the tested cultivars (11 cultivars), the dry weight of the lower internodes decreased after anthesis, indicating the maximum weight of the lower internodes in the cultivars to be achieved at anthesis or earlier (Table 3). When averaged among the drought stressed cultivars, the maximum weight of the lower internodes (553 mg) was observed to be higher than those of the penultimate (370 mg) and the peduncle (366 mg) (Table 3). Moreover, the imposed drought decreased the maximum weight of the lower internodes by 11%, on average, (623 mg in WW condition vs. 553 mg in DS condition) (Tables 2 and 3).

Compared with the WW condition, the duration of the dry matter accumulation was also shorter in the entire stem under DS (Tables 2 and 3). Averaged among cultivars, the maximum dry weight of the entire stem under drought condition (1248 mg) was found to be 10% less than that of under the irrigation one (1390 mg) (Tables 2 and 3).

Table 2 Means of the dry matter accumulation and remobilization (Rem.) in the different internodes as well as the entire stem of the wheat cultivars grown at the Mediterranean climate (Karaj site) of Iran under well-watered condition during 2007–2009 growing seasons. Cumulative remobilization (Cum. Rem.) is the sum of the internodes' remobilization. Remobilization efficiency (Rem. Eff.) was calculated as: (mobilized dry matter/maximum weight) × 100

Cultivars	Peduncle					Penultimate					Lower internodes					Entire stem				Cum. Rem. (mg)	Entire stem and Cum. Rem. Differences (mg)
	maximum weight (mg)	DAA*	weight at maturity (mg)	Rem. (mg)	Rem. Eff. (%)	maximum weight (mg)	DAA	weight at maturity (mg)	Rem. (mg)	Rem. Eff. (%)	maximum weight (mg)	DAA	weight at maturity (mg)	Rem. (mg)	Rem. Eff. (%)	maximum weight (mg)	DAA	weight at maturity (mg)	Rem. (mg)		
Arta	317	14	220	97	31	349	14	216	133	38	620	0	225	395	64	1143	14	661	482	624	− 142
Azadi	371	7	341	29	8	379	7	297	82	22	648	0	380	269	42	1357	7	1018	339	380	− 41
Alvand	412	21	330	82	20	424	21	289	135	32	630	0	384	246	39	1461	21	1003	458	462	− 4
Alamut	357	7	313	45	13	323	14	258	64	20	593	0	343	250	42	1216	7	914	302	359	− 57
Bistoon	354	21	269	85	24	412	21	308	104	25	804	14	462	343	43	1545	14	1038	507	532	− 25
Pishtaz	347	14	275	71	20	360	14	224	137	38	573	14	266	307	54	1280	14	765	515	515	0
Yavarus	487	7	359	128	26	360	7	232	128	36	584	7	297	286	49	1431	7	888	542	542	0
Rasul	439	21	345	94	21	437	21	339	98	22	780	0	464	316	41	1631	21	1147	484	508	− 25
Sardari	330	14	196	134	41	439	21	215	224	51	694	14	409	285	41	1423	21	820	603	644	− 41
Sumay3	426	14	346	80	19	466	14	332	134	29	645	0	479	166	26	1485	7	1157	328	381	− 52
Shirudi	384	14	332	52	14	414	14	320	94	23	660	0	408	252	38	1350	14	1061	289	397	− 108
Shiraz	371	14	281	90	24	339	14	227	112	33	503	0	309	194	39	1167	14	817	350	396	− 46
Gascogne	355	14	269	85	24	428	14	300	128	30	534	0	348	187	35	1266	14	917	349	400	− 50
C Alborz	442	14	407	35	8	452	14	333	119	26	579	7	278	301	52	1359	7	1017	342	455	− 113
Golestan	385	7	300	85	22	431	7	283	149	35	677	7	376	301	44	1493	7	958	534	534	0
Marun	409	7	340	69	17	578	7	404	173	30	630	7	321	309	49	1616	7	1065	551	551	0
Niknejhad	471	14	379	92	20	385	14	295	90	23	435	0	262	174	40	1275	14	935	340	356	− 16
Hamun	424	7	346	78	18	478	7	318	160	33	621	7	367	255	41	1523	7	1030	492	492	0
Mean	393		314	80	20	414		288	126	30	623		354	269	43	1390		956	434	474	
LSD	93		66	82	18	105		68	89	17	199		135	174	24	223		227	256	266	

*Days after anthesis on which the individual internode/entire stem attained its maximum weight

LSD least significant differences at 5% probability level

Table 3 Means of the dry matter accumulation and remobilization (Rem.) in the different internodes as well as the entire stem of the wheat cultivars grown at the Mediterranean climate (Karaj site) of Iran under drought stress condition during 2007–2009 growing seasons. Cumulative remobilization (Cum. Rem.) is the sum of the internodes' remobilization. Remobilization efficiency (Rem. Eff.) was calculated as: (mobilized dry matter/maximum weight) × 100

Cultivars	Peduncle					Penultimate					Lower internodes					Entire stem				Cum-Rem. (mg)	Entire stem and Cum. Rem. Differences (mg)
	maximum weight (mg)	DAA*	weight at maturity (mg)	Rem. (mg)	Rem. Eff. (%)	maximum weight (mg)	DAA	weight at maturity (mg)	Rem. (mg)	Rem. Eff. (%)	maximum weight (mg)	DAA	weight at maturity (mg)	Rem. (mg)	Rem. Eff. (%)	maximum weight (mg)	DAA	weight at maturity (mg)	Rem. (mg)		
Arta	286	14	243	43	15	322	14	216	107	33	456	0	250	206	45	1001	14	708	292	356	− 63
Azadi	323	21	265	58	18	315	21	237	78	25	478	7	300	178	37	1074	7	802	272	315	− 43
Alvand	410	14	326	84	20	381	14	286	95	25	580	0	312	268	46	1305	14	924	381	447	− 66
Alamut	336	7	270	66	20	308	7	240	68	22	473	7	299	174	37	1117	7	809	308	308	0
Bistoon	357	14	242	115	32	419	14	267	152	36	598	14	351	246	41	1374	14	860	514	513	0
Pishtaz	332	7	272	61	18	321	7	242	79	25	492	0	303	189	38	1111	7	817	294	329	− 35
Yavarus	467	7	344	123	26	352	7	249	102	29	620	0	304	316	51	1342	7	897	445	542	− 96
Rasul	459	14	342	117	25	507	14	328	179	35	780	0	422	358	46	1732	14	1092	640	654	− 14
Sardari	280	14	225	55	20	276	14	213	63	23	575	0	398	178	31	1055	7	835	220	296	− 76
Sumay3	391	7	303	88	23	400	7	302	98	25	645	0	460	185	29	1403	7	1065	338	371	− 33
Shirudi	348	7	276	72	21	353	7	262	90	25	582	7	412	170	29	1283	7	950	332	332	0
Shiraz	365	14	292	72	20	339	14	235	105	31	516	14	280	236	46	1219	14	807	412	412	0
Gascogne	325	7	272	53	16	387	7	267	119	31	549	0	236	313	57	1249	7	775	474	486	− 11
C Alborz	372	14	291	81	22	378	7	263	115	30	510	0	291	219	43	1243	7	845	398	416	− 18
Golestan	329	14	297	32	10	358	14	308	50	14	550	0	293	257	47	1126	0	898	228	339	− 111
Marun	391	14	250	141	36	456	14	273	184	40	570	7	268	302	53	1333	7	791	542	627	− 85
Niknejhad	492	14	333	159	32	389	14	261	129	33	463	0	236	227	49	1247	14	829	417	514	− 97
Hamun	329	14	291	37	11	405	14	295	110	27	510	14	289	221	43	1244	14	876	368	368	0
Mean	366		285	81	22	370		264	107	29	553		317	236	43	1248		866	382	424	
LSD	69		87	83	21	101		96	115	28	225		100	207	22	312		239	313	324	

*Days after anthesis on which the individual internode/entire stem attained its maximum weight

LSD least significant differences at 5% probability level

Subtropical climate (Moghan region)–WW experiment

As can be observed in Tables 2 and 4, the post-anthesis dry matter accumulation took longer in the subtropical region. This is to say that, in the majority of the tested cultivars (14 cultivars), the accumulation of the dry matter in the peduncle continued up to 21 DAA (Table 4), at the peak of which, the mean dry weight of the peduncle reached 423 mg, i.e., 30 mg more than that of observed in the Mediterranean climate under the WW condition (Tables 2 and 4).

Moreover, as can be seen in Table 4, the accumulation of the dry matter in the penultimate continued to the 7th, 14th, and 21st DAA in 1, 7, and 10 cultivar/cultivars, respectively. Accordingly, the mean dry weight of penultimate (462 mg) was found to be 10% more than that of observed in the Mediterranean climate under the WW condition (414 mg) at its maximal weight (Tables 2 and 4).

In addition, the duration of post-anthesis dry matter accumulation in the lower internodes was observed to be different among the cultivars (Table 4). To be more exact, the weight of the lower internodes reached its maximum by the 7th, 14th, and 21st DAA for 5, 6, and 7 cultivars, respectively, which was an indication of the longer duration of the dry matter accumulation in the lower internodes than that of the Mediterranean climate under WW condition (Tables 2 and 4). Overall, it can be argued that more dry weight was accumulated in the lower internodes of the examined cultivars than those studied at the Mediterranean climate under WW condition (Tables 2 and 4).

Furthermore, the longer post-anthesis dry matter accumulation period in the internodes was observed to result in greater total weight of the stem in the subtropical region. Averaged among cultivars, the maximum weight of the entire stem was found to be 1626 mg, i.e., 236 mg more than that of observed in the Mediterranean climate under WW condition (Table 2 and 4).

Dry matter remobilization and efficiency

Mediterranean climate (Karaj site)–WW experiment

In general, the mean of the remobilization was observed to be higher in the lower internodes (269 mg), followed by the penultimate (126 mg) and peduncle (80 mg). Similarly, the lower internodes had the highest mean of remobilization efficiency (43%), with the penultimate and peduncle coming next with mean remobilization efficiency of 30 and 20%, respectively. A significant correlation coefficient was also found between the dry matter remobilization and efficiency in the peduncle ($r=91$), penultimate ($r=0.86$), and lower internodes ($r=0.80$), indicating consistency between the amount and the efficiency of remobilization. As an example, the highest amount of remobilization from the peduncle and penultimate internodes and from the lower internodes were demonstrated by Sardari and Arta, respectively, which were also the best cultivars in terms of remobilization efficiency (Table 2).

Moreover, as can be seen in Table 2, while the dry matter remobilization of the entire stem ranged from 289 (Shirudi) to 603 mg (Sardari), that of the cumulative internodes remobilization differed from 356 (Niknejhad) to 644 mg (Sardari). Accordingly, the average remobilization of the entire stem and average of the cumulative internodes remobilization were 434 and 474 mg, respectively. Furthermore, as demonstrated in Table 2, the entire stem remobilization of 13 cultivars was found to be lesser than that of their cumulative internodes remobilization, which is an indication of the underestimation of the cultivars' entire stem remobilization. The highest and the lowest divergence between the entire stem and the cumulative internodes remobilization belonged to Arta (142 mg) and Alvand (4 mg), respectively. Yet, no such divergence was detected in the remaining five cultivars (Pishtaz, Yavarus, Golestan, Marun, and Hamun) (Table 2). Therefore, compared with the other examined cultivars, Sardari, Arta, Marun, Yavarus, and Golestan had the highest amount of cumulative remobilization (Table 2).

Mediterranean climate (Karaj site)–DS experiment

On average, while not changing the amount of remobilization in the peduncle (81 mg vs. 80 mg), drought was found to decrease that of the penultimate (107 mg vs. 126 mg) and the lower internodes (236 mg vs. 269 mg). Meanwhile, whereas drought stress increased the mean remobilization efficiency of the peduncle by 1.8%, that of the penultimate and the lower internodes were decreased by 1.5% and 0.5%, respectively. However, the cultivars responded differently to drought, when considering the amount of the mobilized dry matter as well as the efficiency of mobilization (Tables 2 and 3). To be more exact, in response to drought stress, the amount of remobilization was observed to be decreased in the internodes of all cultivars, except for 10 cultivars in their peduncle (Azadi, Alvand, Alamut, Bistoon, Rasul, Sumay3, Shirudi, Crossed Alborz, Marun, and Niknejhad), 5 in their penultimate (Alamut, Bistton, Rasul, Marun, and Niknejhad), and 7 in their lower internodes (Alvand, Yavarus, Rasul, Sumay3, Shiraz, Gascogne, and Niknejhad). As can be seen in Tables 2 and 3, Sardari, with generally the higher amount of remobilization under WW condition, was among those with the lowest amount under DS condition. Moreover, the remobilization amount of stem internodes was not reduced in Rasul and Niknejhad only. Such a mixed response to drought treatment was also observed for remobilization efficiency (Tables 2 and 3).

Moreover, whereas the highest entire stem remobilization was found in Rasul (640 mg), Marun (542 mg), and Bistoon

Table 4 Means of the dry matter accumulation and remobilization (Rem.) in the different internodes as well as the entire stem of the wheat cultivars grown at the subtropical climate (Moghan site) of Iran under well-watered condition during 2014–2015 growing seasons. Cumulative remobilization (Cum. Rem.) is the sum of the internodes' remobilization. Remobilization efficiency (Rem. Eff.) was calculated as: (mobilized dry matter/maximum weight) × 100

Cultivars	Peduncle					Penultimate					Lower internodes					Entire stem				Cum Rem. (mg)	Entire stem and Cum. Rem. Differences (mg)
	maximum weight (mg)	DAA*	weight at maturity (mg)	Rem. (mg)	Rem. Eff. (%)	maximum weight (mg)	DAA	weight at maturity (mg)	Rem. (mg)	Rem. Eff. (%)	maximum weight (mg)	DAA	weight at maturity (mg)	Rem. (mg)	Rem. Eff. (%)	maximum weight (mg)	DAA	weight at maturity (mg)	Rem. (mg)		
Arta	354	21	281	72	20	482	21	296	186	39	829	14	451	378	46	1642	21	1028	613	636	– 23
Azadi	392	21	253	139	35	400	14	227	173	43	740	7	410	330	45	1426	14	890	536	642	– 106
Alvand	462	14	297	165	36	526	14	284	242	46	1034	7	505	529	51	1942	7	1086	856	936	– 81
Alamut	398	21	265	133	33	445	21	252	193	43	751	21	445	306	41	1594	21	962	633	633	0
Bistoon	453	21	360	94	21	441	21	302	139	32	818	7	451	366	45	1510	21	1113	396	599	– 202
Pishtaz	397	21	272	126	32	422	14	228	193	46	692	14	380	313	45	1506	14	879	627	632	– 5
Yavarus	514	21	259	255	50	412	21	174	238	58	715	14	309	406	57	1620	21	743	877	899	– 22
Rasul	490	14	382	108	22	558	7	347	211	38	1052	7	623	429	41	2063	7	1352	710	748	– 38
Sardari	361	21	267	94	26	360	21	222	138	38	642	7	402	240	37	1268	21	891	377	472	– 95
Sumay3	425	21	253	172	40	416	14	251	165	40	696	21	364	332	48	1519	21	869	650	669	– 19
Shirudi	445	21	326	120	27	456	21	270	186	41	1036	14	524	511	49	1886	14	1120	766	817	– 51
Shiraz	455	21	310	145	32	466	21	244	221	47	638	21	317	321	50	1559	21	872	687	687	0
Gascogne	322	21	240	83	26	519	14	293	226	44	770	21	413	357	46	1565	21	946	619	665	– 46
C Alborz	394	14	278	116	29	414	14	264	149	36	818	14	402	416	51	1626	14	945	681	681	0
Golestan	411	21	307	104	25	462	21	266	196	42	841	21	539	302	36	1714	21	1112	602	602	0
Marun	362	14	318	45	12	521	14	278	243	47	690	14	361	329	48	1573	14	956	617	617	0
Niknejhad	595	21	359	236	40	569	21	249	320	56	609	21	316	293	48	1772	21	924	848	848	0
Hamun	390	21	273	117	30	454	21	250	204	45	632	21	304	328	52	1477	21	827	650	650	0
Mean	423		294	137	32	462		261	201	44	778		418	360	46	1626		973	652	699	
LSD	62		107	110	25	106		72	108	18	289		163	292	25	399		315	437	386	

*Days after anthesis on which the individual internode/entire stem attained its maximum weight

LSD least significant differences at 5% probability level

(514 mg), the lowest amount was observed in Sardari (220 mg), Golestan (228 mg), and Azadi (272 mg) (Table 3). In addition, the highest cumulative internodes remobilization was observed in Rasul (654 mg), Marun (627 mg), and Yavarus (542 mg), while the lowest was related to Sardari (296 mg), Alamut (308 mg), and Azadi (315 mg). Accordingly, it can be argued that the amount of dry matter remobilization and, thereby, the related ranking of the cultivars remarkably vary based on the consideration of either the entire stem or the cumulative internodes remobilization.

Also, the comparison of the amount of the entire stem and the cumulative internodes remobilization of each cultivar demonstrated the lesser amount of the former than (from 11 to 111 mg) the latter in thirteen cultivars. In the remaining five cultivars (Alamut, Bistoon, Shirudi, Shiraz, and Hamun), however, no differences were observed between the entire stem and the cumulative internodes remobilization (Table 3).

Subtropical climate (Moghan region)–WW experiment

Averaged among the cultivars, the dry matter remobilization was higher in the lower internodes (360 mg), followed by the penultimate (201 mg) and peduncle (137 mg). Similarly, the highest mean of remobilization efficiency was detected for the lower internodes (46%), which was followed by the penultimate (44%) and peduncle (32%) (Table 4). Moreover, the comparison of the WW experiments in Moghan (the subtropical region) and Karaj (the Mediterranean climate) revealed the former to have the higher mean of remobilization amount and efficiency (Tables 2 and 4).

Regardless of the cultivars, the entire stem remobilization was 652 mg on average, i.e., 47 mg less than that of observed in the cumulative internodes remobilization. Also, compared with the cumulative internodes remobilization, the entire stem remobilization was found to be lower in 11 cultivars. This is while, no differences were observed between the two methods in the remaining seven cultivars (Alamut, Shiraz, Crossed Alborz, Gholestan, Marun, Niknejhad, and Hamun) (Table 4). Under Moghan region, Alvand, Yavarus, Niknejhad, Shirudi, and Rasul had the highest cumulative internodes remobilization (Table 4), among which those of Yavarus and Rasul were also found to be higher under WW and DS conditions of Karaj (Tables 2, 3, and 4).

Discussion

Sucrose is mainly produced by leaves and such non-leaf organs as the stem, spike bracts, and awns. Accumulated in the form of WSCs, and especially as fructan, the main parts of the sucrose is transferred to the stem internodes near the anthesis stage (Zhang et al. 2015). The process is believed to sustain a sharp sucrose gradient between the photosynthetic organs and the stem. Consequently, the risk of sugar-mediated feedback inhibition of photosynthesis is reduced (Paul and Foyer 2001). In the later stages, the storage in the stem is broken down, i.e., the sucrose is resynthesized by sucrose phosphate synthase (SPS) and sucrose 6-phosphate phosphatase (SPP). Subsequently, it is translocated toward the developing grains. This contribution of the sucrose flux from the stem to the grain seems to be relatively more important for yield maximization under drought condition (Joudi et al. 2012).

As was observed in this study, the weights of the internodes were increased during the early stages of the grain growth, indicating the continuation of photo-assimilates accumulation in the stem even after anthesis. Moreover, the duration of dry matter accumulation in the upper internodes (peduncle and penultimate) were more than that of observed in the lower ones (Tables 2, 3, and 4). Previous reports maintained that the upper internodes, especially peduncle, elongated and developed mainly after anthesis. The rapid elongation of these internodes at the post-anthesis stages requires a large amount of carbon resources for structural component (Wakabayashi et al. 2022). By continuing photo-assimilates supply to this internode, surplus photo-assimilates are accumulated as storage carbohydrates. Interestingly, compared with the Mediterranean climate (Karaj site), dry matter accumulation of the internodes was observed to be higher in the subtropical condition (Moghan site) in the post-anthesis stage (Tables 2, 3, and 4). However, while not being fully understood, the reason can be attributed to the production of less tillers per main stem in such conditions.

The obtained results in this study also revealed the substantial genetic variations of the dry matter remobilization and efficiency from the internodes (Tables 2, 3 and 4). This is consistent with the findings of other studies (Ehdaie et al. 2006a, b; Vosoghi Rad et al. 2022), which, accordingly, corroborates the manipulation of this trait in wheat breeding programs. However, being more influenced by the environmental conditions (Tables 2, 3, and 4), the improvement of the traits is a challenging task.

Moreover, the remobilization amount and efficiency were found to be generally higher in the lower internodes, followed by penultimate and the peduncle, in all examined conditions (Tables 2, 3 and 4). According to Ehdaie et al. (2006b), the development of the lower internodes in wheat occurs in early spring when water supply and temperature are favorable for the growth of the plant. Accordingly, a large portion of the assimilates is accumulated in the lower internodes, which, in turn, could be a major source of the dry matter remobilization after anthesis.

On average, while the imposed drought stress under Mediterranean condition did not change the amount of dry matter remobilization in the peduncle, those of the penultimate and the lower internodes were decreased by 15% and 12%, respectively. Interestingly, compared with WW treatment, the maximum weight of the internodes was reduced by 7%, 11%, and 11% in the peduncle, penultimate, and lower internodes under the drought stress, respectively. As a results, whereas remobilization efficiency increased in the peduncle, it decreased in the penultimate and the lower internodes under DS, as compared with WW condition (Tables 2 and 3). The different response of the internodes to the drought treatment could be attributed to the differences in their growth stage as well as the initiation time of the terminal drought (Ehdaie et al. 2006b). As discussed by Ehdaie et al. (2006b), while terminal drought stress increased the dry matter remobilization from peduncle, those from the penultimate and the lower internodes were reported to be decreased. In their study, drought stress was also argued to improve remobilization efficiency in all internodes. Nevertheless, other findings demonstrated a significant increase in the rate and efficiency of assimilates remobilization from the stem internodes under drought stress (Ma et al. 2014; Vosoghi Rad et al. 2022). Hence, it can be argued that the remobilization amount and efficiency are differently influenced by the cultivar and the severity of the drought stress.

Based on the findings of the study, three scenarios are determined for the dry matter accumulation and remobilization in wheat stem internodes. In the first scenario, the accumulation of dry matter in all internodes is terminated at the same time. In other words, the remobilization of the stored materials from the internodes is initiated simultaneously. In this scenario, the amount of remobilization at the entire stem level will be the same as that of the cumulative remobilization of the internodes, which was observed in five cultivars under WW condition of Karaj, five under DS condition of Karaj, and seven in Moghan site (Tables 2, 3 and 4).

In the second scenario, the stem internodes do not attain their maximum weight simultaneously, i.e., it is obtained much earlier in the lower internodes than the upper ones (Ehdaie et al. 2006a, b). Based on this scenario, while the dry matter remobilization is triggered in the lower internodes, its accumulation could be continued in the upper parts. As long as the amount of remobilization from the lower internodes is less than that of dry matter accumulation in the upper sections, the entire stem weight would steadily continue to increase. Therefore, since the maximum weight of the entire stem is not yet attained, part (but not all) of dry matter remobilization from the lower internodes is not considered. It should be noted that the underestimation will only be taken place when the entire stem remobilization is considered. In other words, the employment of the cumulative internodes remobilization would abort this miscalculation. In line with this, this type of remobilization underestimating was observed in nine cultivars under WW condition of Karaj (Arta, Azadi, Alvand, Rasul, Sardari, Shirudi, Shiraz, Gascogne, and Niknejhad), in eight under DS condition of Karaj (Arta, Alvand, Pishtaz, Yavarus, Rasul, Sumay3, Gascogne, and Niknejhad), and in six in Moghan region (Arta, Bistoon, Yavarus, Sardari, Sumay3, and Gascogne) (Tables 2, 3, and 4).

In the third scenario, as described in the second one, stem segments do not obtain their maximum weight at the same time. Accordingly, both remobilization and accumulation may occur simultaneously within the lower and upper internodes of the stem, respectively; however, the amount of remobilization is more than that of accumulation. If the amount of remobilization from the stem internodes is higher than the dry matter accumulation, the maximum weight of the entire stem would decrease. It means that the maximum weight of the accumulating internodes will not be considered in the calculation of remobilization. Therefore, the amount of the calculated remobilization in the entire stem would be less than that of the cumulative internodes, which was observed in two cultivars (Bistoon and Crossed Alborz) under WW condition of Karaj, in three cultivars (Azadi, Golestan, and Marun) under DS condition of Karaj, and in four Cultivars (Alvand, Pishtaz, Rasul, and Shirudi) in Moghan region (Tables 2, 3 and 4).

Both the second and the third scenarios may inaccurately estimate the amount of the entire stem remobilization to be much less than that of the real values in a number of cultivars. On the one hand, part of the dry matter remobilization in those internodes, which reach their maximum weight prior to that of the entire stem would not be taken into account. Moreover, the accumulated dry matter would not be partly considered in the internodes gaining their maximum weight after that of the entire stem as well. Such problematic conditions were found in two cultivars (Alamut and Sumay3) under WW condition of Karaj, in two cultivars (Sardari and Crossed Alborz) under DS condition of Karaj, and in one cultivar (Azadi) in Moghan site (Tables 2, 3 and 4).

The accumulation and remobilization in the stem internodes have also been differently reported in other studies. For example, studying 11 diverse wheat cultivars under WW and terminal drought stress, Ehdaie et al. (2006a) reported an increase in the WSCs content of the peduncle and penultimate of the majority of the cultivars after anthesis, attaining their maximum content at 20 DAA. Moreover, the maximum WSCs content of the lower internodes was found to be generally attained at anthesis or up to 10 days afterwards. In addition, the rate of depletion of WSCs was reported to be faster in the lower internodes, compared with those in the peduncle and penultimate internodes, indicating the much faster remobilization of the stored WSCs in the lower than the upper internodes. Furthermore, each internode was suggested to accumulate and then to remobilize WSCs independently. In another study, working on a wheat cultivar under the combined waterlogging and shading stresses, Li et al.

(2013) reported the earlier commencement of the carbohydrate deposition process in the lower stem internodes. The amount of the remobilized dry matter was also found to be much more than those in the upper internodes. Yet, Zhang et al. (2015) reported that the fructan degradation process and activity of the related enzymes started earlier in wheat stem internodes under drought stress than non-stress condition. Since this was observed to be particularly the case in the lower parts of the stem and the sheath, it was argued that the stem segments responded differently to the imposed drought stress. Similar results have also been reported in the rice varieties (Wakabayashi et al. 2022).

However, the reasons behind the early initiation of carbohydrates remobilization from the lower internodes are unknown. In general, the internode elongation of wheat occurs sequentially from the lower to the upper nodal segments, making it possible for lower internodes to function as sinks and later on as the source organ much earlier than the upper internodes (Wakabayashi et al. 2022). During the early grain filling, if the current leaf photosynthesis is unable to thoroughly meet the sink/grain demand, part of the required photo-assimilates for the grain filling would be supplied by the dry matter remobilization from the lower internodes, which have already reached their maximum weight. In line with this, Liu et al. (2020) stated that WSCs concentration in the lower internodes were more susceptible to drought stress, which led them retain higher levels of WSCs to improve the plant's drought tolerance. As the grain continues to grow, the demand for photo-assimilates is increased much further. At the same time, the contribution of current photosynthesis in grain filling is gradually limited due to both the natural senescence of the leaves as well as the upcoming terminal drought and the heat stresses (Blum 1998). Consequently, along with the lower internodes, the upper ones (peduncle and penultimate) remobilize their stored carbohydrates to meet the sink (grains) demand.

Conclusion

The results obtained from various environmental conditions clearly revealed the possibility for the simultaneous occurrence of dry matter accumulation and remobilization in the stem internodes. Moreover, while the lower internodes were found to probably remobilize their stored carbohydrates, the upper ones could still accumulate the photo-assimilates. In addition, merely considering the changes in the entire stem weight might underestimate the amount of carbohydrate remobilization. Accordingly, depending on the cultivars and the environmental conditions, the amount of remobilized stem dry matter underestimated from 4 to 202 mg. Hence, in order for the more precise measurement of the carbohydrate remobilization in the wheat stem, the separate measurement of this trait in each internode is highly recommended. This is particularly crucial when different wheat cultivars are analyzed for their potential carbohydrates remobilization. This is also recommended to be considered in physiological and molecular studies focusing on carbohydrates remobilization of wheat stems.

The initiation of the earlier remobilization in the lower internodes also raises the question of whether the remobilized dry matters are temporarily and partly allocated to the upper internodes, or are directly transported to the spike and the developing grains. Compared with the upper internodes, the developing grains seem to be stronger sinks, and accordingly, to be most probably the final destination of the remobilized dry material from the lower internodes. However, this issue needs to be further investigated.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42976-023-00451-w.

Acknowledgements We gratefully acknowledge Morteza Kamrani, Asghar Ebadi, and Naser Sabaghnia for their helps and advices in data analysis.

Author contributions All authors contributed to the experiments performed at K site, where as M experiment carried out only by MJ. The first draft of the manuscript was prepared by MJ and improved by ME, VM, and AA. All authors read and approved the final manuscript.

Funding These works were funded by University of Mohaghegh Ardabili and University of Tehran.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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