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Dynamics of Structural Dry Matter, Water Soluble Carbohydrates and Leaf Senescence Mediate the Response of Winter Wheat Yield to Soil Cover and Water Availability

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Abstract: Plastic film mulching often increases the yield of winter wheat in the Loess Plateau of China, but the physiological mechanisms are unclear, especially in response to the interaction between mulch and water supply. In this study, we investigated the interactive effects of initial soil water (dry, moderate, and wet), soil cover (plastic mulch, bare soil), and seasonal conditions on the dynamics of dry matter partitioning, water-soluble carbohydrates (WSC), and flag leaf senescence, and their relations with yield and its components. Plastic mulch increased dry matter accumulation at anthesis and maturity relative to bare soil, with no interaction with season or initial soil water. Allocation of dry matter to leaf, stem, and spike did not change with soil cover. Compared with bare soil, mulch increased WSC accumulation by 14% at anthesis and its translocation by 16%. Soil cover did not influence the senescence of flag leaf after anthesis as indicated by similar dynamics of the C:N ratio. Grain yield was higher under plastic mulch than bare soil in two out of three seasons, and was associated with a higher translocation amount of WSC and post-anthesis dry matter that linked grain weight, grain number, and harvest index.

Keywords: plastic film mulch; dry matter; anthesis; phenology; flag leaf; C:N of flag leaf

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1. Introduction

Wheat is one of the main food crops in the world, and more than 60% of wheat is rainfed [1,2]. Seasonal water shortage, large variations in inter- and intra-annual precipitation, and excessive evaporation are major constraints to rainfed wheat production in arid and semiarid areas [1,3,4]. Mulches including straw [5,6], sand or gravel [7], and plastic film [6,8,9] have been extensively tested to increase precipitation utilization efficiency. Plastic mulch reduces soil evaporation, increases soil temperature and root and shoot growth, and increases winter wheat yield and water use efficiency compared to bare ground in the Loess Plateau [10,11]. In contrast, plastic mulch, shortens the leaf life span, the duration of grain filling, and the yield of spring wheat when encountering severe drought and high soil temperature after anthesis [12,13]. Thus, soil cover and seasonal conditions interactively impact crop performance.

Labile carbohydrates, operationally defined as water-soluble carbohydrates (WSC), are stored in the shoot of cereal crops, and can buffer grain growth but involve tradeoffs with both root growth and grain set, resulting in neutral, negative, and occasionally positive correlations with wheat grain yield [14–16]. Straw mulching combined with subsoiling or with no-tillage increased wheat dry matter accumulation and the amount of WSC translocated to grain relative to conventional tillage [1,17] and plastic mulch increased the

WSC content of late-sown wheat at overwinter stage [18]. Conservation tillage and/or its combination with subsoiling increased chlorophyll content in wheat flag leaf, enhanced the photosynthetic rate, and post-anthesis dry matter accumulation by 4–5% relative to conventional practices [19,20].

In drylands, wheat yield relies on both seasonal precipitation and the water stored in the soil during fallow [6,21,22]. However, it is not clear how plastic mulch and water stored before sowing interactively influence the dynamics of dry matter partitioning, WSC, and leaf senescence, and their links to yield in winter wheat. This study hypothesized that improved hydrothermal conditions of rainfed wheat under mulch could (i) increase the accumulation of both structural dry matter and WSC at anthesis, (ii) delay flag leaf senescence, (iii) increase post-anthesis dry matter, and (iv) favor WSC translocation. In this context, we investigate the interaction of stored water before sowing, growing season conditions, and mulch on pre-and post-anthesis dry matter, WSC accumulation and translocation, flag leaf senescence after anthesis, and their association with wheat yield.

2. Materials and Methods

2.1. Site and Crop Husbandry

The field experiment was conducted from September 2017 to June 2021 at a site (34°72′ N, 108°17′ E, 995 m a.s.l.) in Yujiagong Village, Yongshou County of Shaanxi Province in the Loess Plateau China as described by Zhang et al. [11]. The soil is a Cambisol [23]. Soil properties (0–0.2 m) before experiment establishment in 2017 were 16.6 g kg^{-1} of soil organic carbon content, 0.93 g kg^{-1} of total nitrogen, 21.2 mg kg^{-1} of available phosphorus, 165 mg kg^{-1} of available potassium, and pH of 8.6. The annual average temperature is 10.8 °C and the frost-free period is 210 days. The average annual precipitation is 574 mm, which primarily falls between July and September. Owing to severe frost damage in Spring, 2018, data from the 2017 to 2018 season were excluded from the analysis. The actual precipitation in the wheat growing period was 130 mm (52% before anthesis, 42% after anthesis) in 2018–2019, 193 mm (68%, 32%) in 2019–2020, and 266 mm (82%, 18%) in 2020–2021. According to the classification of precipitation [24], the first growing period was dry, the second was normal, and the third was wet. The water table is below 30 m and, thus, groundwater is unavailable for crops.

Wheat (cv Tongmai 6, a common local variety) was sown manually between 29 September and 1 October, and harvested on 7 July 2019, 13 July 2020, and 22 June 2021. The seeding rate was 270 seeds m^{-2} with a row space of 0.2 m in controls and 0.3 m in plots with plastic mulch. Crops were fertilized with urea (135 kg N ha^{-1}) and superphosphates (39 kg P ha^{-1}) before sowing each season. Diseases, pests, and weeds were controlled using local practices.

2.2. Treatments and Experimental Design

The experiment was a factorial with three initial soil water (SW) levels (wet, moderate, and dry), two soil covers, plastic film mulch (FM, clear plastic film, thickness = 0.008 mm), and bare ground (CK), and three seasons. The treatments were established in a randomized block design with four replicates. The FM was set up by machinery with a furrow of 0.30 m width and ridge of 0.15 m height, then manually covered plastic film on the ridges. Each plot was 5.7 m long × 5.5 m wide, including 28 rows for CK and 20 rows for FM. The soil water treatments were set according to Dang et al. [25], who classified available soil water in 0–2 m profile into three categories, i.e., dry, below 200 mm, moderate, between 200 and 250 mm, and wet, above 250 mm. To generate the dry treatment, we grew beans or maize during fallow (middle June to early September). The moderate treatment was a traditional bare fallow, and the wet treatment was generated with groundwater irrigation before sowing in each season except for the last season. High rainfall during fallow in 2020–2021, i.e., 435 mm, precluded the establishment of the dry treatment; hence, only two treatments were compared: moderate and wet.

2.3. Sampling and Measurements

Shoot biomass at anthesis was measured in 0.1–0.2 m^2 samples and plants were separated into leaf, stem, and ear. At maturity, grain yield, shoot biomass, ear number, grains per ear, and grain weight were measured, and harvest index and grain number per unit area were calculated. The estimation of both yield and shoot biomass was based on a sample of 4–6 m^2 per plot, ear population was based on 1–2 m^2, and grains per ear were randomly counted on ten ears per plot. Harvest index was calculated as grain yield divided by shoot biomass. Additionally, subsamples (0.1–0.2 m^2) were taken, and plants were separated into leaf, stem, grain, rachis, and glume. Water soluble carbohydrates were measured with the anthrone method in stem and spike at anthesis, and stem and rachis + glume at maturity [1].

In each plot, 150 to 200 plants with the same flowering date were tagged, and ten flag leaves were randomly sampled from tagged plants at 5- or 7-day intervals from anthesis to maturity. The samples were dried at 75 °C, then the dried samples were pulverized for the determination of total nitrogen and organic carbon, and to calculate C:N. Total nitrogen was determined by a high-resolution automatic analyzer (AA3, SEAL Company, Germany) following digestion with H_2SO_4-H_2O_2, and organic carbon content was determined by potassium dichromate ($K_2Cr_2O_7$) oxidation at 170–180 °C, followed by titration with 0.1 mol L^{-1} ferrous sulfate; soil available phosphorus was determined by the Olsen (sodium bicarbonate) method, available potassium was extracted with 1 mol L^{-1} ammonium acetate (pH = 7.0) and measured with a flame photometer, soil pH was determined with a pH electrode at a soil-to-water ratio of 1:1 [26].

2.4. Calculations and Statistical Analyses

$$\text{Pre-anthesis dry matter (kg ha}^{-1}) = \text{leaf + stem + ear dry matter at anthesis (kg ha}^{-1}) \tag{1}$$

$$\text{Post-anthesis dry matter (kg ha}^{-1}) = \text{shoot dry matter at maturity (kg ha}^{-1}) - \text{pre-anthesis dry matter (kg ha}^{-1}) \tag{2}$$

WSC content and its translocation (amount and ratio) were calculated as follows [27]:

$$\text{WSC content (kg ha}^{-1}) = \text{WSC concentration (\%)} \times \text{organ biomass (kg ha}^{-1})/100 \tag{3}$$

$$\text{apparent WSC translocation (kg ha}^{-1}) = \text{WSC content at anthesis (kg ha}^{-1}) - \text{WSC content at maturity (kg ha}^{-1}) \tag{4}$$

$$\text{apparent WSC translocation ratio (\%)} = \text{WSC translocation (kg ha}^{-1})/\text{WSC content at anthesis (kg ha}^{-1}) \times 100 \tag{5}$$

This calculation over-estimates translocation, as respiration is assumed to be negligible, hence the term "apparent" [1].

$$\text{Structural dry matter (kg ha}^{-1}) = \text{Shoot biomass (kg ha}^{-1}) - \text{WSC content (kg ha}^{-1}) \tag{6}$$

An exponential function was used to describe the dynamics of the flag leaf C:N ratio after anthesis

$$\mathrm{y} = a\mathrm{e}^{b\mathrm{x}} \tag{7}$$

where y is the C:N ratio, x is days after anthesis, *a* is the C:N ratio at anthesis, and *b* is the rate of change in the C:N ratio after anthesis.

Following the method used in the study of Hu et al. [1], traits were compared in scatter plots of FM vs. CK, and linear regressions were fitted to quantify departures from y = x representing no difference between treatments; Model II, reduced major axis regression was used to account for error in both x and y [28]. Structural equation modeling (SEM) was conducted in Amos Graphics to analyze the relationships between yield and other crop traits to demonstrate the physiological link for yield formation.

Two-way ANOVA was used to assess the response of crop traits to soil cover, initial soil water, and their interactions each year. The statistical analyses were performed with SPSS 18.0 software.

3. Results

3.1. Wheat Pre-Anthesis and Post-Anthesis Dry Matter, Grain Yield, and Yield Components

Table 1 showed pre-anthesis dry matter, post-anthesis dry matter, yield, and its components. Pre-anthesis dry matter varied from 868 to 14,887 kg ha^{-1} and was affected by initial soil water, and mulch in 2018–2019 and 2020–2021 and their interaction in 2018–2019 (Table 1). Mulch increased pre-anthesis dry matter with wet and moderate initial soil water in 2018–2019 and with moderate soil water in 2019–2020. Post-anthesis dry matter varied from 370 to 7012 kg ha^{-1} in response to initial soil water, and mulch in 2018–2019 and 2020–2021, but was only affected by initial soil water in 2019–2020 (Table 1). Mulch increased post-anthesis dry matter compared to the control at all three levels of initial soil water in 2018–2019, and with moderate soil water in 2019–2020 and 2020–2021. Shoot biomass at maturity varied from 906 to 18571 kg ha^{-1} and was affected by initial soil water, mulch in three seasons, and their interaction in 2018–2019 and 2019–2020 (Table 1). Mulch increased shoot biomass at maturity compared to the control at all three levels of initial soil water in 2018–2019, and at moderate soil water in 2019–2020.

Table 1. Pre-anthesis dry matter (Pre-DM), post-anthesis dry matter (Post-DM), shoot biomass at maturity, grain yield, and yield components in a factorial study combining initial soil water (wet, moderate, dry), and mulch (CK, bare ground control; FM, plastic film mulching), and three growing seasons. Mean and standard errors of four replicates are presented for 2018–2019 and 2019–2020. In 2020–2021, high rainfall during fallow precluded the dry treatment, and results are for moderate (n = 4) and wet (n = 8) treatments only. p is from the ANOVA testing effect of water (W), mulch (M), and their interactions.

Season	Water	Mulch	Pre-DM	Post-DM	Shoot Biomass at Maturity	Grain Yield	Harvest Index	Grain Number	Grain Weight
			kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}		m^{-2}	mg
2018–2019	wet	CK	3013 ± 57	1158 ± 15	4117 ± 61	1675 ± 41	0.41 ± 0.004	4306 ± 249	40 ± 0.8
		FM	5279 ± 276	2276 ± 125	7287 ± 370	3130 ± 173	0.43 ± 0.010	8734 ± 151	43 ± 1.0
	moderate	CK	2216 ± 116	776 ± 51	2862 ± 151	1135 ± 67	0.40 ± 0.007	5591 ± 454	43 ± 1.3
		FM	4373 ± 347	1894 ± 140	6336 ± 243	2971 ± 121	0.47 ± 0.007	7351 ± 384	44 ± 0.5
	dry	CK	868 ± 16	370 ± 115	906 ± 24	234 ± 6	0.26 ± 0.012	2855 ± 479	26 ± 1.0
		FM	913 ± 21	1329 ± 158	2256 ± 15	730 ± 33	0.32 ± 0.015	3068 ± 440	27 ± 1.3
p									
	Water (W)		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Mulch (M)		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.099
	W × M		<0.001	0.781	0.005	0.003	0.111	0.001	0.572
2019–2020	wet	CK	12,549 ± 522	6202 ± 364	17,312 ± 331	7768 ± 193	0.45 ± 0.004	18,252 ± 409	40 ± 0.2
		FM	12,571 ± 498	5975 ± 308	16,994 ± 743	7604 ± 197	0.43 ± 0.001	17,982 ± 476	41 ± 0.4
	moderate	CK	11,194 ± 163	4665 ± 70	13,644 ± 97	5983 ± 10	0.44 ± 0.003	14,495 ± 1175	39 ± 0.6
		FM	12,401 ± 199	5945 ± 163	16,323 ± 213	7230 ± 170	0.44 ± 0.005	17,108 ± 1225	39 ± 0.2
	dry	CK	11,304 ± 1026	4500 ± 585	10,806 ± 276	4490 ± 147	0.42 ± 0.004	12,927 ± 1769	41 ± 0.7
		FM	10,599 ± 591	4088 ± 248	12,951 ± 820	5613 ± 219	0.41 ± 0.004	11,801 ± 966	41 ± 0.3
p									
	Water (W)		0.079	0.001	<0.001	<0.001	0.001	0.001	<0.001
	Mulch (M)		0.751	0.503	0.004	0.001	0.195	0.702	0.855
	W × M		0.369	0.079	0.032	0.004	0.082	0.331	0.646
2020–2021	wet	CK	13,747 ± 425	5948 ± 446	16,744 ± 661	7665 ± 415	0.45 ± 0.017	21,640 ± 996	47 ± 0.4
		FM	14,887 ± 461	7012 ± 289	18,571 ± 561	8733 ± 271	0.47 ± 0.007	21,961 ± 1177	47 ± 0.4
	moderate	CK	12,709 ± 647	5159 ± 234	15,153 ± 694	7267 ± 48	0.47 ± 0.015	12,918 ± 677	48 ± 0.6
		FM	13,494 ± 307	5840 ± 81	16,410 ± 329	7545 ± 185	0.46 ± 0.003	14,786 ± 1498	49 ± 0.2
p									
	Water (W)		0.012	0.004	0.003	0.126	0.711	<0.001	0.734
	Mulch (M)		0.041	0.010	0.012	0.999	0.750	0.313	0.833
	W × M		0.693	0.529	0.616	0.987	0.424	0.473	0.471

To clarify the differences between pre- and post-anthesis dry matter accumulation, shoot biomass at maturity, and proportions of dry matter partitioning in different organs between FM and CK, and their interactions with the environment, plotting the above traits in three tested seasons with FM against CK showed that mulch increased pre- and post-anthesis dry matter, and shoot biomass at maturity, but had no obvious effects on dry matter distribution in various organs (Figures 1 and 2). Moreover, the effects of mulch on those traits had no interaction with the environment.

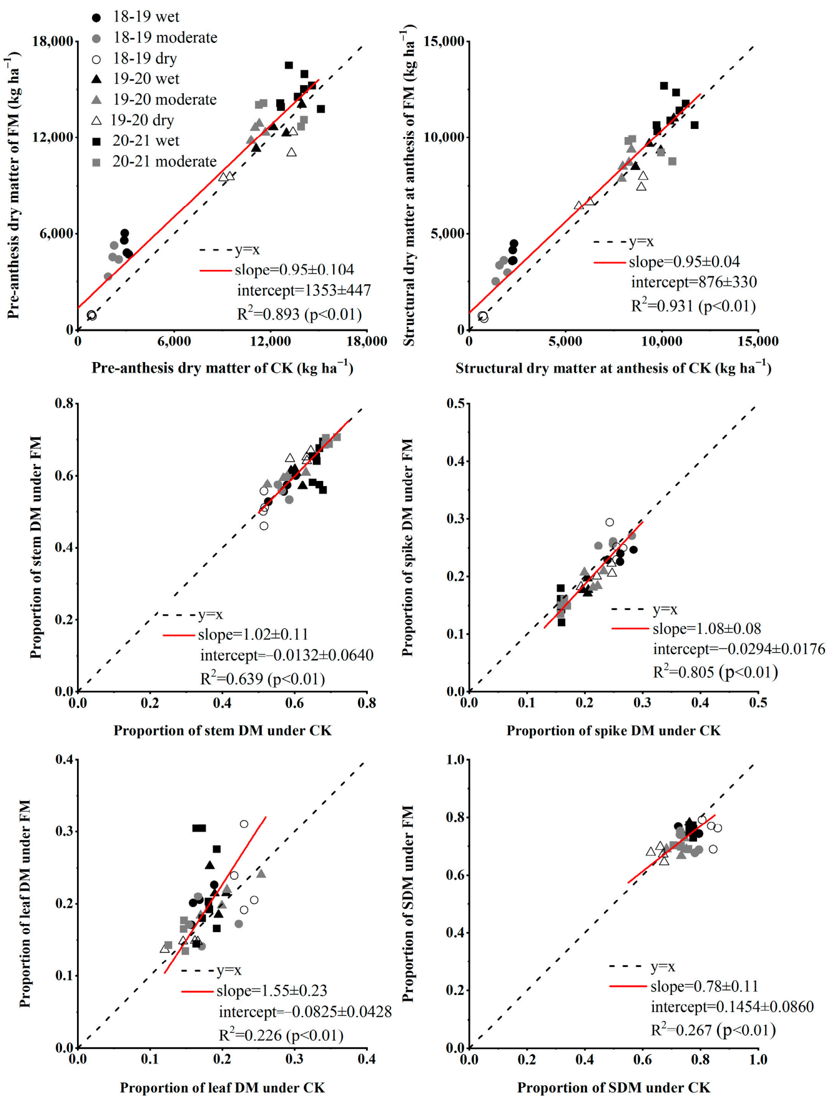

Figure 1. Comparison of pre-anthesis dry matter, structural dry matter, and proportion of various organ's dry matter (leaf DM, stem DM, ear DM, structural DM) to above-ground dry matter (AGDM) at anthesis between plastic film mulching (FM) and bare ground (CK) wheat crops. Data including all treatments and seasons. Red solid line and equation is Model II regression accounting for error in both x and y. Standard error of slope and intercept is presented.

Grain yield varied from 234 to 8733 kg ha^{-1} and was affected by initial soil water, mulch, and their interaction in 2018–2019 and 2019–2020 (Table 1). Mulch increased grain yield when compared to the control at all levels of initial soil water in 2018–2019, as well as at the moderate and dry treatments in 2019–2020. The Harvest index ranged from 0.26 to 0.47 and was affected by initial soil water in 2018–2019 and 2019–2020, and mulch in 2018–2019 (Table 1). Compared to the control, mulch increased the harvest index at the moderate and dry treatments in 2018–2019; however, decreased the harvest index at the wet treatments in 2019–2020. Grain number and grain weight varied with initial soil water in all three seasons. Mulch and its interaction with initial soil water impacted the grain number in 2018–2019 (Table 1).

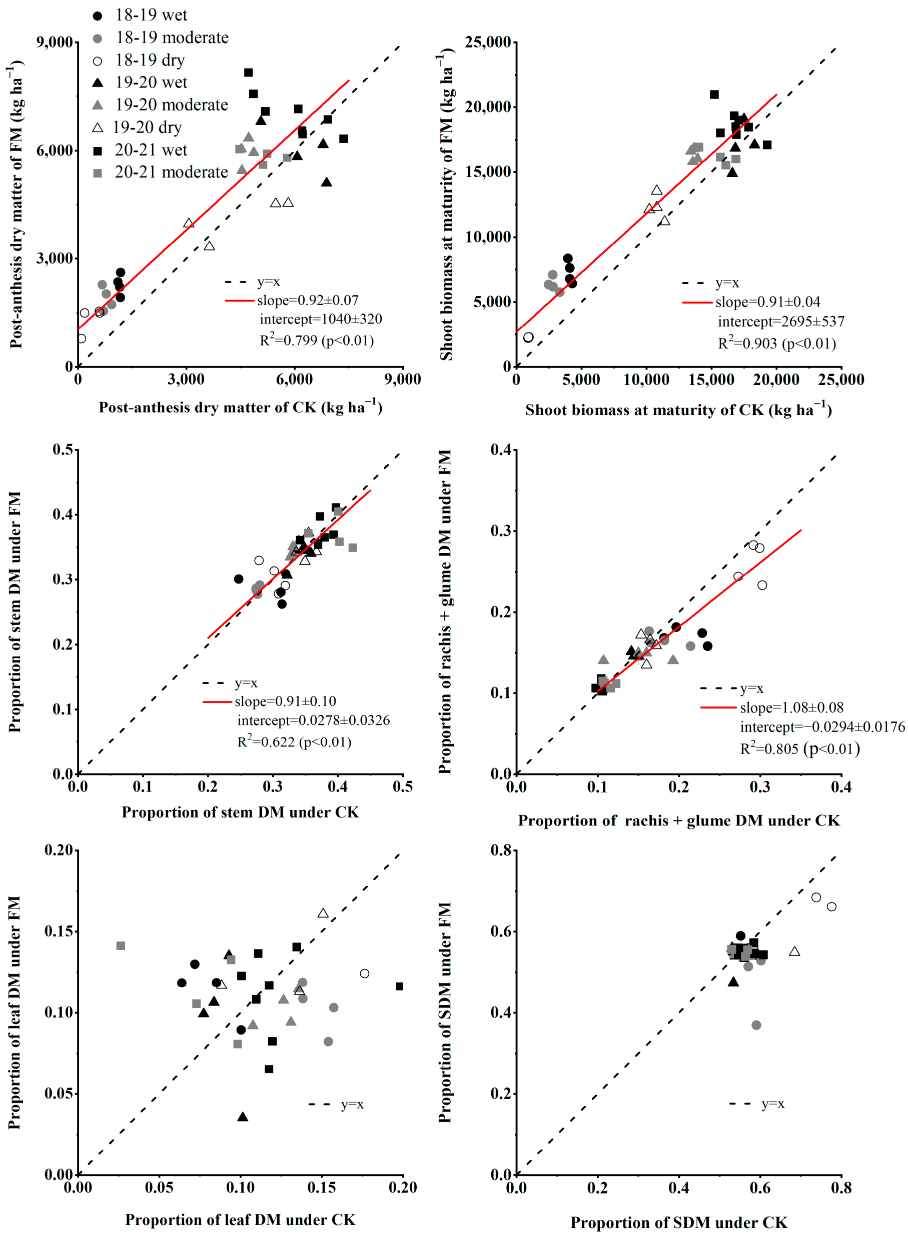

Figure 2. Comparison of post-anthesis dry matter, shoot biomass at maturity, and proportion of various organ's dry matter (leaf DM, stem DM, ear DM, rachis and glume DM, structural DM) to above-ground dry matter (AGDM) at maturity between plastic film mulching (FM) and bare ground (CK) wheat crops. Data including all treatments and seasons. Red solid line and equation is Model II regression accounting for error in both x and y. Standard error of slope and intercept is presented.

3.2. Structural Dry Matter, and Water Soluble Carbohydrates Accumulation and Translocation

Structural dry matter at anthesis ranged from 689 to 11,336 kg ha^{-1} (Table 2). Initial soil water affected structural dry matter in three seasons, while mulch only impacted SDM in 2018–2019. Across seasons, mulch increased SDM by 7.9%, without obvious interaction with the environment (Figure 1).

Table 2. Structural dry matter at anthesis (SDM), water-soluble carbohydrates (WSC) content at anthesis and maturity, and apparent translocation (amount and ratio) in a factorial study combined initial soil water (wet, moderate, dry) with mulch (CK, bare ground control; FM, plastic film mulching). Mean and standard errors of four replicates are presented for 2018–2019 and 2019–2020. In 2020–2021, high rainfall during fallow precluded the dry treatment, and results are for moderate (*n* = 4) and wet (*n* = 8) treatments only. p is from the ANOVA testing effect of water (W), mulch (M), and their interactions.

Season	Water	Mulch	SDM	WSC			
				Anthesis	Maturity	Translocation Amount	Translocation Ratio
			kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	%
2018–2019	wet	CK	2282 ± 19	700 ± 59	96 ± 6	604 ± 55	86 ± 1
		FM	3958 ± 218	1236 ± 87	128 ± 4	1109 ± 85	90 ± 1
	moderate	CK	1686 ± 131	506 ± 22	56 ± 9	450 ± 24	89 ± 2
		FM	3107 ± 118	1204 ± 143	122 ± 17	1082 ± 129	90 ± 1
	dry	CK	727 ± 22	129 ± 7	51 ± 7	78 ± 8	60 ± 5
		FM	689 ± 35	207 ± 14	61 ± 9	146 ± 14	71 ± 4
p							
	Water (W)		<0.001	<0.001	<0.001	<0.001	<0.001
	Mulch (M)		<0.001	<0.001	<0.001	<0.001	0.067
	W × M		<0.001	0.148	<0.001	0.478	0.603
2019–2020	wet	CK	9630 ± 425	2773 ± 148	776 ± 68	1997 ± 131	72 ± 2
		FM	9616 ± 524	2736 ± 34	851 ± 86	1886 ± 83	69 ± 3
	moderate	CK	8149 ± 123	2905 ± 196	971 ± 86	1934 ± 215	66 ± 4
		FM	8606 ± 307	3586 ± 96	921 ± 94	2665 ± 91	74 ± 2
	dry	CK	7475 ± 877	3727 ± 261	1101 ± 129	2626 ± 267	70 ± 4
		FM	7119 ± 351	3356 ± 284	821 ± 85	2535 ± 276	75 ± 3
p							
	Water (W)		0.001	0.008	0.001	0.035	0.751
	Mulch (M)		0.980	0.548	0.840	0.349	0.259
	W × M		0.639	0.080	0.698	0.129	0.313
2020–2021	wet	CK	10,290 ± 352	3019 ± 99	648 ± 38	2371 ± 83	79 ± 1
		FM	11,336 ± 431	3289 ± 135	830 ± 93	2459 ± 154	75 ± 3
	moderate	CK	9305 ± 559	3295 ± 214	730 ± 91	2565 ± 131	78 ± 2
		FM	9424 ± 271	3903 ± 74	869 ± 81	3034 ± 141	78 ± 2
p							
	Water (W)		<0.001	0.002	0.413	0.005	0.518
	Mulch (M)		0.231	0.003	0.039	0.033	0.250
	W × M		0.380	0.198	0.767	0.132	0.368

WSC content at anthesis varied with mulch in 2018–2019 and 2020–2021, and with initial soil water in all three seasons, from 129 to 3903 kg ha^{-1} (Table 2). Mulch increased WSC content at anthesis compared with bare ground at all three levels of initial soil water in 2018–2019, and in the moderate treatment in 2019–2020, and 2020–2021. WSC content at maturity varied from 51 to 1101 kg ha^{-1} in response to initial soil water in 2018–2019 and 2019–2020, mulch in 2018–2019 and 2020–2021, and their interaction in 2018–2019 (Table 2). For example, mulch increased WSC content at maturity at the wet and moderate treatments in 2018–2019, but not with dry soil in 2018–2019, and at all the two or three levels of initial soil water in the other two seasons.

WSC translocation amount varied from 78 to 3034 kg ha^{-1} in response to initial soil water in three seasons, and it varied with mulch in 2018–2019 and 2020–2021. Mulch increased WSC translocation amount at all levels of initial soil water in 2018–2019, and in the moderate treatment in 2019–2020, and at all levels of initial soil water in 2020–2021.

WSC translocation ratio varied from 60 to 90% and was only affected by initial soil water in 2018–2019.

Across seasons, plotting WSC accumulation and translocation with FM against CK showed that mulch increased both WSC content at anthesis and WSC translocation amount by 13.6% and 15.9%, on average (Figure 3). However, the WSC content at maturity and WSC translocation ratio did not vary with ground cover (Figure 3).

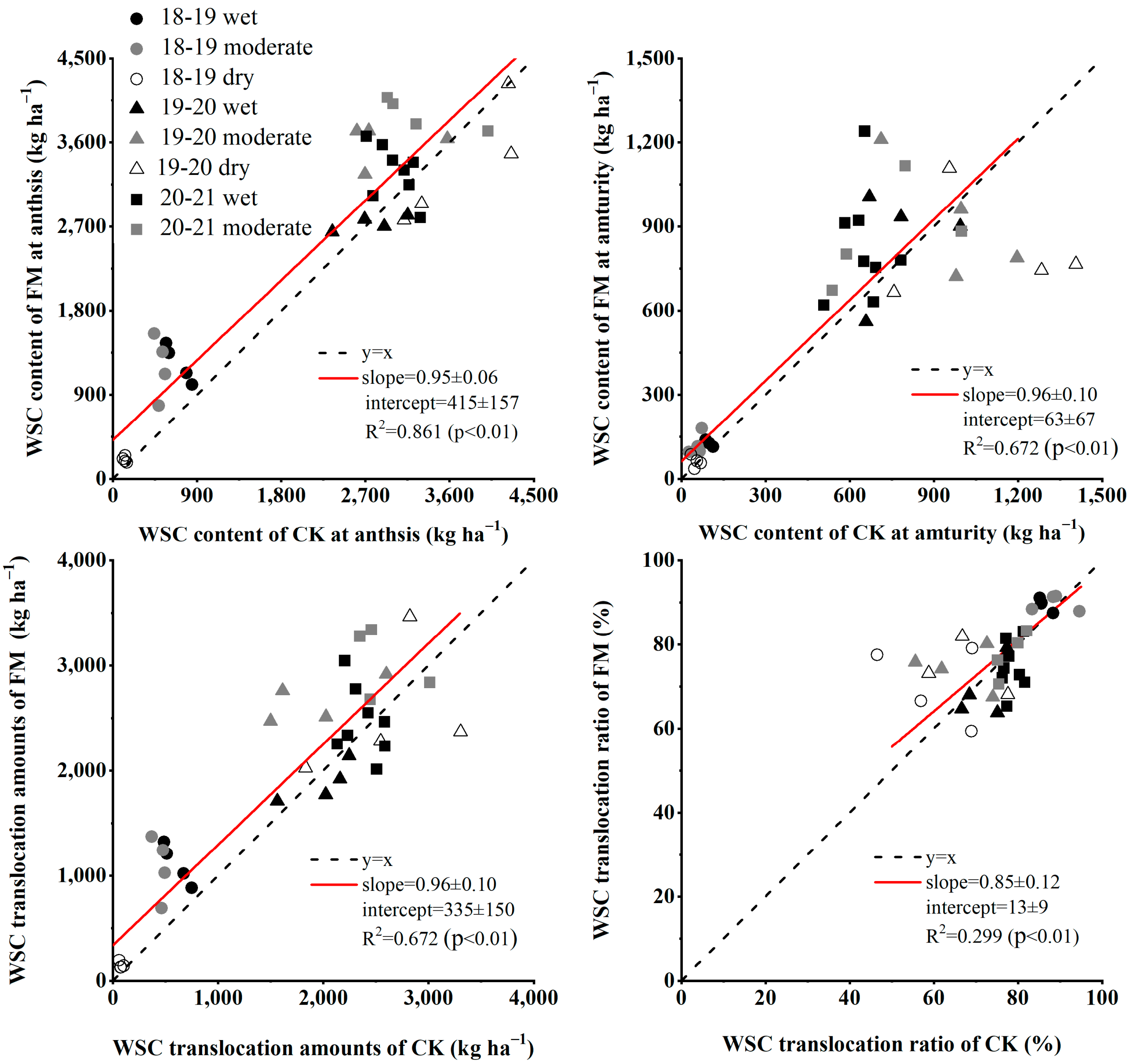

Figure 3. Comparison of water-soluble carbohydrates (WSC) between plastic film mulching (FM) and bare ground control (CK) wheat crops. WSC content at anthesis and maturity, apparent translocation amount, and ratio. Data including all treatments and seasons. Red solid line and equation is Model II regression accounting for error in both x and y. Standard error of slope and intercept is presented.

3.3. Dynamics of the C:N of Flag Leaf after Anthesis

An exponential function (Equation (7)) described the change in the C:N of flag leaf after anthesis (Figure 4). Parameter *a*, representing C:N at anthesis, varied from 2.83 to 13.25, and *b*, representing the change rate of C:N, varied from 0.037 to 0.062 d^{-1} (Table 3). Parameter *a* decreased with an increase in initial soil water, and the opposite was true for b. Both parameters were similar for mulch and control treatments.

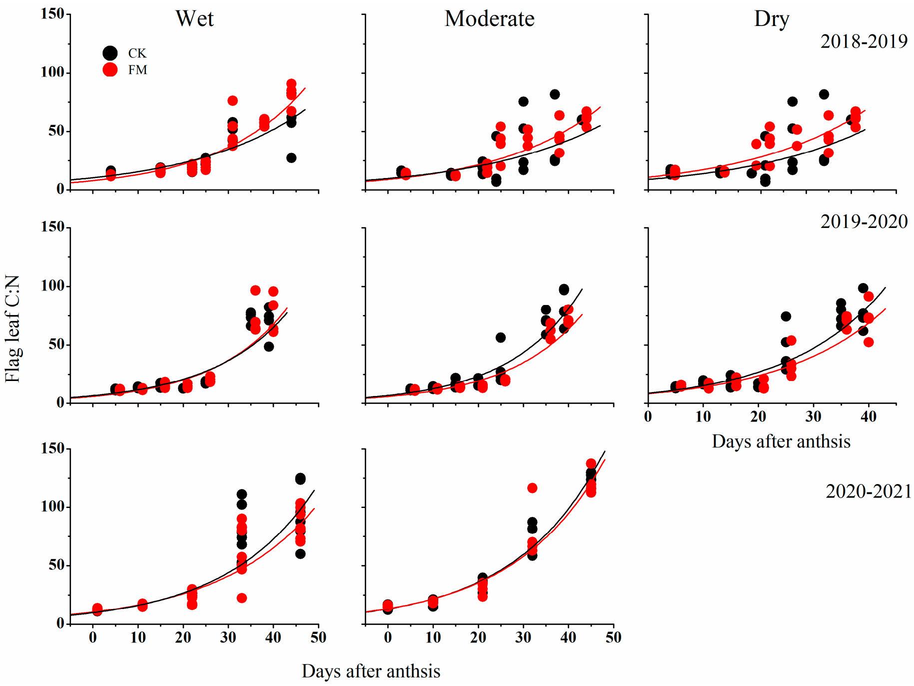

Figure 4. Change in C:N of flag leaf after anthesis of wheat grown under two in a factorial with two soil covers (plastic film mulching, FM, bare ground control, CK) and three levels of initial soil water (wet, moderate, dry) in three seasons.

Table 3. Coefficients of exponential equation (y = $ae^{(bx)}$) that described the change in flag leaf C:N ratio after anthesis under plastic film mulching (FM) and bare ground control (CK) at different initial soil water levels (wet, moderate, dry). In 2020–2021, high rainfall during fallow precluded the dry treatment, and results are for moderate (n = 4) and wet (n = 8) treatments only.

Season	Water	Mulch	a	b (d^{-1})	R^2	N
2018–2019	wet	CK	10.37	0.040	0.75	28
		FM	7.87	0.051	0.86	28
	moderate	CK	9.72	0.037	0.46	28
		FM	8.98	0.044	0.76	28
	dry	CK	10.67	0.036	0.46	28
		FM	13.13	0.038	0.75	28
2019–2020	wet	CK	6.55	0.057	0.80	28
		FM	5.90	0.061	0.86	28
	moderate	CK	6.73	0.062	0.88	28
		FM	5.83	0.057	0.88	28
	dry	CK	8.57	0.057	0.81	28
		FM	8.13	0.053	0.80	28
2020–2021	wet	CK	9.77	0.050	0.87	40
		FM	10.38	0.046	0.87	40
	moderate	CK	13.11	0.051	0.96	20
		FM	13.25	0.049	0.93	20
2018–2019			10.12 ± 0.73	0.041 ± 0.017		
2019–2020			6.96 ± 0.47	0.058 ± 0.024		
2020–2021			11.63 ± 0.74	0.049 ± 0.020		
	wet		8.47 ± 0.81	0.051 ± 0.021		
	moderate		9.59 ± 1.27	0.050 ± 0.021		
	dry		10.13 ± 0.93	0.046 ± 0.019		
		CK	9.44 ± 0.76	0.049 ± 0.017		
		FM	9.18 ± 1.02	0.050 ± 0.018		

R^2 is the coefficient of determination for $y = ae^{(bx)}$ models. N is the number of observations used to fit the equation.

3.4. Associations between Traits

Figure 5 showed the structural equation modeling for the relationships between yield and other crop traits. High WSC content at anthesis favored the amount of WSC translocation and was associated with a high rate of change in the C:N of flag leaf. Higher translocation amount of WSC increased grain weight, then improved harvest index and grain yield. Increased C:N of flag leaf at anthesis was also related to a higher amount of WSC translocation, while the rate of change rate in the C:N of flag leaf was decreased; however, the higher rate of change rate in the C:N of flag leaf favored a higher harvest index. High structural dry matter at anthesis was associated with more accumulation of dry matter after anthesis, which was linked to grains number, harvest index, and yield.

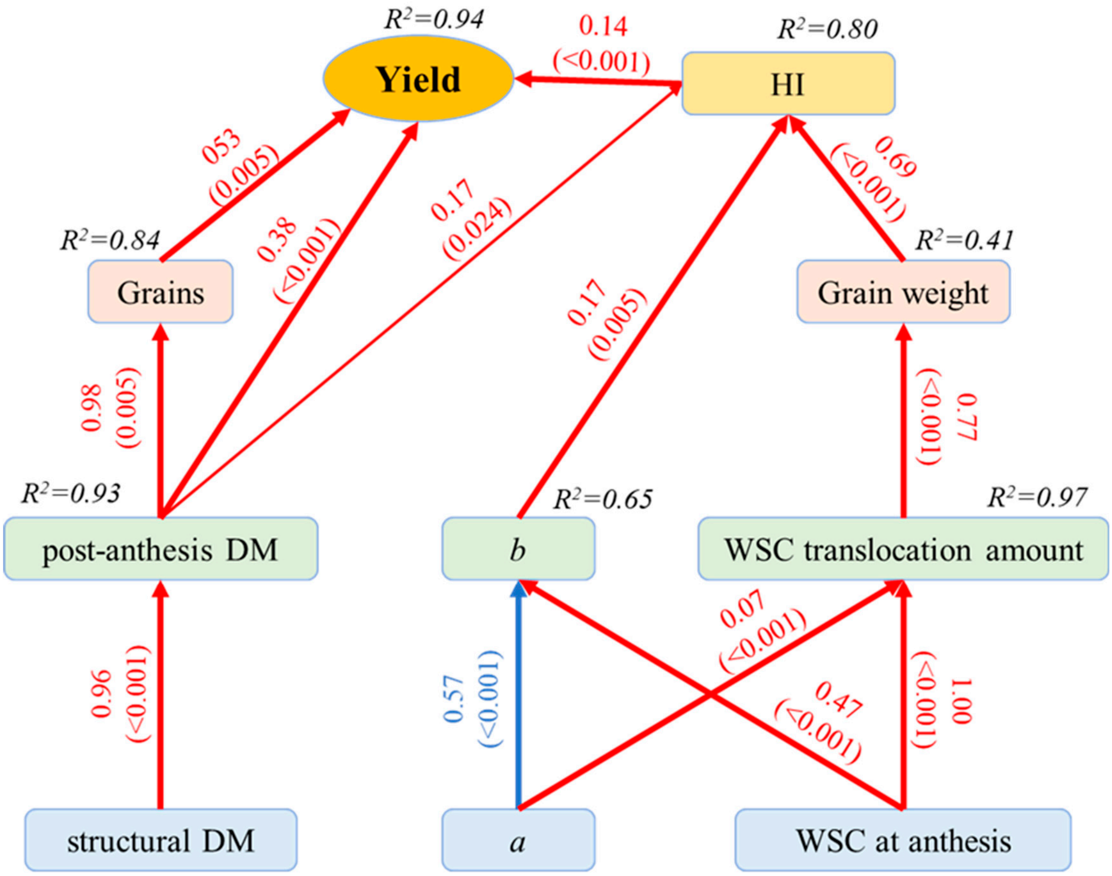

Figure 5. Structural equation modeling showing the relationship between yield and its components grain weight, grain number, harvest index (HI) and structural dry matter (DM) at anthesis, water-soluble carbohydrates content at anthesis (WSC at anthesis), coefficients of the exponential equation describing the dynamics of the flag leaf C:N ratio after anthesis (a, b), apparent translocation amount of WSC (WSC translocation amount), and post-anthesis dry matter (DM). Numbers next to arrows are the standardized coefficient and p in parentheses. The goodness of fit was 0.90. Blue arrows denote negative correlations and red arrows denote positive correlations. The thickness of the arrow indicates the significance of the relationship.

4. Discussion

Wheat yield depends on the amount and partitioning of dry matter before and after anthesis. Here, we found that plastic mulch increased dry matter accumulation but did not change the distribution of dry matter before and after anthesis, and dry matter partitioning between organs, as found by others [29,30].

Mulch increased pre-anthesis dry matter under tested conditions (Figure 1), in agreement with previous studies [31,32]. The reason is that mulch improves soil temperature [8,11] and reduces soil water loss [33,34], which benefits seedling emergence and tillering, and rapid growth after regreening [35]. The increment of pre-anthesis dry matter under mulch was more in WSC content and less in SDM, and subsequently, WSC translocation was greater relative to bare ground (Table 2, Figure 3). Straw mulching combined with subsoiling or no-tillage increased WSC translocation by 9% or 8% over conventional practice, which was ascribed to increased water supply [17]. We also observed that post-anthesis evapotranspiration was generally higher under mulch than under bare ground [11]. A higher WSC translocation amount was ascribed to more grains under FM than bare soil, which served a larger size of the sink for converting the available source of WSC [36]. It was also closely correlated with grain weight and harvest index (Figure 5). However, the WSC translocation ratio did not vary with soil cover (Table 2, Figure 3), which might be related to the similar senescence of flag leaf as indicated by the rate of change in C:N (*b*) (Table 3, Figure 4). Our results suggest wheat breeding programs may target to maximize stem reserve accumulation and mobilization in terminal stressful environments.

The photosynthetic assimilation of the flag leaf after anthesis is one of the important sources for filling wheat grain. Mulch increased post-anthesis dry matter under both dry and wet conditions (Figure 2), which was associated with higher grain number and harvest index and thus higher yield (Figure 5). Previous studies have reported that mulch increased dry matter accumulation after anthesis in both rain-fed and irrigated wheat [31,32]. This may be related to a slightly lower C:N ratio of flag leaf at anthesis (*a*) under mulch relative to bare ground (Table 3), which is linked to a higher assimilation rate [37]. Additionally, mulch increased wheat leaf area, favoring photosynthetic assimilation [38], and thus increased dry matter accumulation after anthesis. However, for spring wheat, plastic mulch did not affect dry matter accumulation after anthesis under severe drought [39]. Water use after anthesis correlated with dry matter accumulation after anthesis [40]. We found that mulch increased water use after anthesis, which was related to deeper roots being able to use soil moisture stored in deep soil layers typical of this environment [11]. However, the contribution of dry matter accumulation after anthesis to wheat yield was independent of ground cover. The coordination of WSC translocation and post-anthesis dry matter accumulation warrants further research.

In conclusion, mulch increased dry matter accumulation before and after anthesis and WSC accumulation and translocation—traits that contributed to yield under a wide range of environmental conditions. These results might provide a valuable reference for future wheat breeding programs.

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