



Studying the Genetic Gain of Traits Related to Remobilization and Photosynthesis in Bread Wheat Cultivars Released During Five Decades in Golestan Province of Iran

Hossein Avarsaji^a , Manoochehr Khodarahmi^{b*} , Marjan Diyanat^a , Islam Majidi Heravan^a ,
Habiballah Soughi^c 

^aDepartment of Horticultural Sciences and Agronomy, Science and Research Branch, Islamic Azad University, Tehran, IRAN

^bSeed and Plant Improvement Institute, Agricultural Research, Education and Extension Organization (AREEO), Karaj, IRAN

^cHorticulture Crops Research Department, Golestan Agricultural and Natural Resources Research and Education Center, AREEO, Gorgan, IRAN

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Corresponding Author: Manoochehr Khodarahmi, E-mail: khodarahmi_m@yahoo.com

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ABSTRACT

In order to determine the trend of breeding progress and the genetic gain in the Iran's Golestan province, twenty registered spring wheat cultivars, which had been widely cultivated from 1968 to 2018, were investigated. A randomized complete block design with three replications was conducted to study these cultivars in the research stations of Gorgan and Gonbad during three consecutive years (2015-2018). Different morphological characteristics, grain yield and yield components, and some important traits related to remobilization and photosynthesis were measured. Morphological traits including plant height, peduncle length, and spike length did not show any significant trend during the 50-year of breeding improvement in these regions; whereas significant increases were observed for grain yield, biological yield, harvest index, thousand kernel weight, and grain filling rate in the both areas. During the period

of breeding investigated, the total contribution of remobilization has decreased, in particular that from stem's, showed a significant decrease. In contrast, the amount, efficiency, and contribution of photosynthesis revealed to play a significant role in genetic improvement obtained for the cultivars' successful performances in the regions. Based on the results obtained from the study of different parts of the plants, in addition to being an important photosynthetic source for wheat, over the time, as compared to the other wheat organs, spike showed an increasing potential for the amount of remobilization. It is expected that genotypes selected for higher levels of remobilization abilities with increased photosynthesis, could result in breeding superior high-yielding cultivars in future of the national wheat programs.

Keywords: Genetic gain, Photosynthesis, Registered cultivars, Remobilization, Spring wheat

1. Introduction

Wheat (*Triticum aestivum* L.) with an annual production of more than 600 million tons across all the continents is the major crop cultivated worldwide (Goel et al. 2018). Wheat production has increased significantly from 222 million tons in 1961 until now (FAO 2021). However, there is still a long gap between the demand and the annual genetic gain of wheat. The average annual increase in wheat genetic gain has been reported to be 1%, while the demand for wheat has increased by 1.7% annually and will reach to one billion tons in 2050 (Tadesse et al. 2019).

The carbon required for grain filling in wheat comes from three sources: current assimilates, remobilization of assimilates stored in the stem and other parts of the plant before the anthesis stage, and remobilization of temporary assimilates stored in the stem after this stage (Bahrani et al. 2011). Photosynthesis is the most important source for providing photosynthetic assimilates needed for grain growth under favorable environmental conditions, but the contribution of remobilization of photosynthetic assimilates to the grain development of wheat increases under stress conditions (Mojtabaie Zamani et al. 2013; Ma et al. 2015).

According to the results of the study of Sun et al. (2021), by replacing cultivars improved between 1940 and 2010 in Shaanxi Province, China, the amount of dry matter mobilization from the stem has increased significantly under normal irrigation conditions. It was shown that, leaves and spikes were considered the most important photosynthetic resources in wheat, and the role of spike assimilates had been increased significantly during the years of wheat breeding under rainfed conditions. These researchers stated that the accumulation of assimilates in the stem and the photosynthesis of the spike, both caused the increase in the grain weight potential. In another study, it was reported that a higher yield can be due to a higher level of assimilation

during grain filling and remobilization of stored photosynthetic assimilates from stem and leaves to the sink (grain). Also, significant correlations between remobilization from spike and stem with grain yield were reported (Baral et al. 2020).

The warm and humid climate of northern Iran encompasses the provinces of Mazandaran, Guilan, Golestan and parts of Ardabil (Moghan). The Golestan province with about 350 000 hectares cultivation of wheat is the most important province in the northern region of Iran. This province with production of about one million ton per year (Agricultural Statistics Booklet 2021). However, in the current cropping season (2022-23) due to the occurrence of severe drought in this province, the production decreased greatly. Hence, limited number of cultivars have been released for this climate. In fact, only the investigated cultivars in this research have had the chance to perform under aforesaid stress conditions.

2. Material and Methods

In this study, 20 cultivars of wheat improved in the warm and humid climate of northern Iran between 1968 and 2018 were studied (Table 1). The cultivar, Ehsan, Tiregan and Merag were registered after the beginning of this study; which as promising breeding lines, were also investigated at the present study. The research was carried out with these cultivars using a randomized complete block design with three replications during the cropping years of 2015-2018 in the agricultural research stations of Gorgan (latitude, 36° 54' N and longitude, 54° 25' E) and Gonbad (latitude, 37° 16' N and longitude, 55° 12' E). The climate of Golestan province has several different types of sub-climates among which Gorgan's climate has been determined to reflect "Mediterranean climate" and "moderate semi-humid area"; Gonbad's climate has been classified as "cold Mediterranean" and "semi-dry area", based on the two different climatic classification methods "Köppen" and "Emberger", respectively. Meteorological statistics related to the rainfall and the average minimum and maximum temperatures in Gorgan and Gonbad during these three cropping years are presented in Table 2.

Table 1- Name of cultivar, pedigree and year of release of spring wheat cultivar released during 1968 to 2018 in the Gorgan and Gonbad in the northern climate of Iran

<i>Cultivar No.</i>	<i>Cultivar name</i>	<i>Year of release</i>	<i>Pedigree</i>
1	Inia	1968	LR64/SN64
2	Khazar1	1973	(P4160(F3)*Nr69)LR64
3	Moghan1	1974	LERMA-ROJO-64/NORIN-10-BREVOR//3*ANDES-ENANO
4	Moghan2	1976	Choti/Lerma, landrace from Indi
5	Alborz	1979	FRONTANA/MIDA//KENYA-117-A/3/2*COLLAFEN/4/SONORA-64/ KLEIN-RENDIDOR/3/CIANO-67//2*LERMA-ROJO-64/SONORA-64
6	Kaveh	1980	FORTUNA/PALOMA
7	Golestan	1986	ALONDRA "S"
8	Rasoul	1992	Veery"s"=KAVKAZ/(SIB)BUHO//KALYANSONA/BLUEBIRD
9	Tajan	1995	BOBWHITE/NEELKANT(CM67428-GM-LR-5M-3R-LB-Y)
10	Shiroudi	1997	NORD-DESPREZ/VG-9144//KALYANSONA/BLUEBIRD/3/YACO/4/VEERY-5
11	Milan	2001	BARKAT/90ZHONG87
12	Shanghai	2001	SHANGHI
13	Arta	2006	HD2206/Hork/Bul/6/CMH80A.253/2/M2A/CML//Ald*4/5/BH1146/H56.71// BH1146/3/CMH78.390/4/Seri 82/7/Hel/3*Cno79/7/2*Seri 82
14	Darya	2006	SHA4/CHIL
15	Moghan3	2006	LUNA/3/V763.23/V879.c8//PVN/4/PICUS/5/OPATA
16	Morvarid	2009	MILAN/(SHA7)SHANGHAI-7
17	Gonbad	2011	ATRAK/WANG-SHUI-BAI
18	Ehsan	2016	SABUF/7/ALTAR (224)//YACO/6/CROC_1/AE.SUARROSA (205)/5/BR12*3/4/IAS55*4/CI14123/3/IAS55*4/EG,AUS//IAS55*4/ALD 84/AE.SUARROSA
19	Tiregan	2017	PFAU/MILAN/5/CHEN/AEGILOPS (TAUS)//BCN/3/VEE#7/BOW/4/PASTOR SUARROSA
20	Merag	2018	PFAU/MILAN/3/SKAUZ/KS94U215//SKAUZ

Table 2- Meteorological statistics in Gorgan and Gonbad

	Year		2016				2017		
	Month	Dec	Jan	Feb	Mar	Apr	May	June	July
Gorgan	Total rainfall (mm)	26.2	2.5	79.5	18.5	40.4	37.1	2.2	5
	Ave. min. temp (°C)	1.7	2.5	1.6	4.5	8.5	14.3	18.4	22.5
	Ave. max. temp (°C)	13.1	13.5	10.7	16.6	19.6	26.3	31.9	34.4
	Year		2017				2018		
	Month	Dec	Jan	Feb	Mar	Apr	May	June	July
	Total rainfall (mm)	71.8	60	41.5	31.7	35.5	23.5	10.5	15
	Ave. min. temp (°C)	4.8	5.2	4.4	7.3	9.6	14.1	19.7	25.1
	Ave. max. temp (°C)	15.1	14	12.7	17.8	21.3	27.1	31.8	37.5
	Year		2018				2019		
	Month	Dec	Jan	Feb	Mar	Apr	May	June	July
	Total rainfall (mm)	48.8	126.3	127.3	121.4	69.8	41	3.0	24.7
	Ave. min. temp (°C)	7.2	3.6	4.2	5.6	10	13.6	19.8	23.9
Ave. max. temp (°C)	16.3	14.5	14.5	17.4	19.2	26.6	34.2	34.1	
Gonbad	Year		2016				2017		
	Month	Dec	Jan	Feb	Mar	Apr	May	June	July
	Total rainfall (mm)	37.5	9	94.6	35.6	37.2	30.4	0.3	7.1
	Ave. min. temp (°C)	1.4	2.5	1.8	4.7	8	14	18	22
	Ave. max. temp (°C)	15	14.3	7.6	11.7	21.5	28.8	35.5	37.7
	Year		2017				2018		
	Month	Dec	Jan	Feb	Mar	Apr	May	June	July
	Total rainfall (mm)	45.4	65.8	72.4	33.9	41.4	40.4	8.2	0.2
	Ave. min. temp (°C)	4.7	4.5	4.6	7.6	9.2	13.1	18.5	24.6
	Ave. max. temp (°C)	16.4	16.1	13.5	18	22	27.5	34.4	41.2
	Year		2018				2019		
	Month	Dec	Jan	Feb	Mar	Apr	May	June	July
Total rainfall (mm)	63.7	81.2	152.3	163.8	51.2	41.5	6.3	7.1	
Ave. min. temp (°C)	7.7	4.9	4.3	5.2	10.3	13.5	20.1	24.6	
Ave. max. temp (°C)	17	15.9	15.2	19.4	20.7	28.2	36.3	36.9	

Wheat cultivars were planted with a density of 350 grains per square meter in plots of 6.66 meters long, and 1.2 meters wide with 20 cm planting row spacing by a Wintersteiger planter on the November 22. The amount of chemical fertilizers used was determined based on the soil test (Table 3). Potash fertilizer (from the source of potassium sulfate at the rate of 100 kg/ha) and phosphate fertilizer (phosphate from the source of ammonium phosphate at the rate of 150 kg/ha) were added to the soil at the

time of cultivation, and nitrogen fertilizer (from the source of urea) was added twice (at the rate of 100 kg/ha at the time of cultivation, and at the rate of 100 kg/ha at the beginning of spring growth) were dispersed on to the soil. To manage broad- and narrow-leaf weeds, the herbicide Granstar (Tribenuron methyl DF 75%) at the rate of 20 grams per hectare (gr/ha), and the herbicide Puma Super (Fenoxaprop-p-ethyl) at the rate of 1.2 liters per hectare was used after the tillering and before stem elongation stage, respectively. In order to control rusts and other leaf spot diseases, the Folicur fungicide was sprayed once before spike swelling and then at the spike emergence stage, another same dose of this fungicide was applied. Also, to prevent and control Fusarium head blight at the flowering stage, Rex Duo fungicide was used.

Table 3- Soil characteristics of Gorgan and Gonbad farms (depth 0-30 cm)

Location	Texture	Specific gravity (g/cm ³)	Absorbable potassium (ppm)	Absorbable phosphorus (ppm)	Absorbable nitrogen (%)	Organic carbon (%)	pH	Electrical conductivity Ec*10 ³	Saturation (%)
Gorgan	Silty loam	1.3	296	13.7	0.13	1.3	7.1	1.1	43.6
Gonbad	Silty loam	1.3	700	14	0.14	1.4	7.6	3.8	52.1

During the growing season and after harvesting, various traits including the plant height (PLH), peduncle length (PDL), spike length (SPL), grain yield (YLD), biological yield (BYD), number of grains per spike (G/S), number of spikes per square meter (S/M²), thousand kernel weight (TKW), harvest index (HI) grain filling period (GFP) and grain filling rate (GFR) were measured. The harvest index was calculated by dividing the grain yield by the biological yield. The method of Cox et al. 1990 and Papakosta & Gayians 1991 was used to calculate the traits related to remobilization and photosynthesis. Data analysis was done after checking the assumption of homogeneity of experimental errors' variances using Bartlett's test. The data obtained through the combined analysis based on a randomized complete block design was then analyzed using the SAS software ver. 9.2. Linear regression analyses between the evaluated traits and the year of cultivar release were done using the software SPSS ver. 21 and the graphs were generated by an Excel software.

3. Results

The variance analysis of the studied traits revealed a significant difference among the cultivars improved during different years in terms of the most morphological, phenological and yield traits and yield components (Table 4). Also, there was a significant difference for the year of cultivars release in terms of the efficiency of remobilization from the spike and other leaves and the contribution of remobilization from other leaves, stem and total remobilization, at the probability level of one percent (P<0.01). For the trait remobilization from the other leaves, there was a significant difference at the probability level of five percent (P<0.05) (Table 5).

Table 4- Combined variance analysis of investigated traits based on the year of release in 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018

S.O.V	df	Mean Squares										
		PLH	PDL	SPL	YLD	BYD	G/S	S/M ²	TKW	HI	GFP	GFR
Year	2	392.41 ^{ns}	395.11 ^{ns}	5.89 ^{ns}	6.38 ^{ns}	67.19 ^{ns}	753.02 ^{ns}	69673.73 ^{ns}	390.52 ^{ns}	328.95 ^{ns}	1629.27 ^{ns}	0.85 ^{ns}
Region	1	2773.03 ^{ns}	71.97 ^{ns}	7.32 ^{ns}	33.94 ^{ns}	16.60 ^{ns}	30.51 ^{ns}	548109.85*	352.65 ^{ns}	647.08 ^{ns}	8623.13 ^{ns}	4.62 ^{ns}
Year Region ×	2	3254.27**	81.98 ^{ns}	11.56**	9.84**	60.46**	424.38**	8197.06 ^{ns}	44.27 ^{ns}	259.98**	299.71*	0.45**
(Year× Region) Rep	12	37.24	72.04	0.12	0.39	6.74	18.96	3362.35	17.17	13.64	5.74	0.01
Year of release	16	224.61**	44.17**	3.45**	10.42**	14.32**	154.65*	4057.27 ^{ns}	234.68**	203.62**	67.85**	0.18**
× Year of release Region	16	16.46 ^{ns}	14.18 ^{ns}	0.74 ^{ns}	1.21 ^{ns}	3.81 ^{ns}	37.57 ^{ns}	3273.28 ^{ns}	8.18 ^{ns}	39.43 ^{ns}	4.78 ^{ns}	0.01 ^{ns}
Year× Year of release	32	23.60 ^{ns}	10.025 ^{ns}	0.63 ^{ns}	0.34 ^{ns}	2.37 ^{ns}	66.93 ^{ns}	3462.74 ^{ns}	15.54 ^{ns}	27.51 ^{ns}	3.22 ^{ns}	0.02 ^{ns}
× Year of release Year× Region	32	44.61**	11.74 ^{ns}	0.78*	0.79**	2.78 ^{ns}	68.95**	2610.84 ^{ns}	13.76**	20.29 ^{ns}	6.69**	0.01**
Error	192	13.30	8.33	0.49	0.21	1.96	38.16	1847.04	5.38	14.20	2.93	0.006
CV (%)	-	3.64	7.95	7.32	10.83	10.84	16.02	11.11	5.90	13.44	4.53	7.08

* and ** significantly at 5 and 1 % probability levels, respectively; Plant height (PLH), Peduncle length (PDL), Spike length (SPL), Grain yield (YLD), Biological yield (BYD), Number of grains per spike (G/S), Number of spikes per square meter (S/M²), Thousand kernel weight (TKW), Harvest index (HI) Grain filling period (GFP) and Grain filling rate (GFR)

Table 5- Combined variance analysis of investigated traits related to the amount and efficiency remobilization of based on the year of release in 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018

S.O.V	df	Mean Squares									
		Amount of remobilization					Remobilization efficiency				
		Spike	Flag leaf	Other leaves	Stem	Total	Spike	Flag leaf	Other leaves	Stem	Total
Year	2	2.73	1.94 ^{ns}	56.32 ^{**}	0.04 ^{ns}	784.6 ^{ns}	39.97 ^{**}	0.54	0.013 ^{ns}	0.008 ^{ns}	7017.65 ^{ns}
Region	1	0.20	282.19	12932.11	15166.31	47.77	0.0043 ^{**}	0.123	0.034	0.001	0.830
Region × Year	2	28.46 ^{**}	1896.07 ^{**}	10218.47 ^{**}	3710.11 ^{**}	1421.2 ^{ns}	15.94 ^{**}	0.39	61.24 ^{**}	0.006	5761.07 ^{**}
Rep (Region × Year)	12	7.58	569.74	2134.59	6981.42	18492.91	0.0001	0.30	0.074	0.005	0.240
Year of release	16	21.72	223.96	807.69 [*]	5292.61	5227.18	0.0005 ^{**}	0.010	0.0149 ^{**}	0.005	0.023
Year of release × Region	16	2.76 ^{**}	217.04	1118.39 ^{**}	3617.69	6215.36	0.0003	0.013	0.018 ^{**}	0.0023	0.0337
Year of release × Year	32	23.04	267.10	312.71	2500.02 ^{ns}	5924.17 ^{ns}	0.0002	0.018	0.007	0.005	0.018
Year of release × Region × Year	32	17.45 ^{**}	384.98	179.76	3741.02 ^{ns}	6873.42 ^{ns}	0.0003	0.014	0.070 ^{**}	1.95 ^{**}	0.12 ^{**}
Error	192	4.68	206.99	378.73	5026.19	6535.84	0.0002	0.010	0.006	0.004	0.031
CV (%)	-	11.78	52.17	46.23	30.14	25.01	20.51	40	39.60	29.65	23.66

* and ** significantly at 5 and 1 % probability levels, respectively

Table (Continued) 5- Combined variance analysis of investigated traits related to contribution of remobilization based on the year of release in 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018

S.O.V	df	Mean Squares				
		Remobilization contributions				
		Spike	Flag leaf	Other leaves	Stem	Total
Year	2	0.77	1.91	0.74	1141.79	3847.16
Region	1	8.741	34.97	0.763	12161.34 ^{**}	11678.02 [*]
Region × Year	2	0.52	1.23	0.89	212.24	4547.04 [*]
Rep (Region × Year)	12	6.996	27.98	97.577	547.240	1131.53
Year of release	16	5.063	20.25	70.443 ^{**}	1222.67 ^{**}	1904.70 ^{**}
Year of release × Region	16	7.399	29.60	62.587 ^{**}	874.92 ^{**}	1648.23 ^{**}
Year of release × Year	32	0.30	0.64	0.12 ^{**}	267.04	1407.67 ^{**}
Year of release × Region × Year	32	10.46 ^{**}	15.49	17.15 ^{**}	219.74	622.01 ^{**}
Error	192	2.693	10.774	9.951	339.43	484.48
CV (%)	-	51.79	51.79	47.43	33.87	30.02

* and ** significantly at 5 and 1 % probability levels, respectively

There was a significant difference between the year of cultivar release in terms of all the traits related to the amount, efficiency and contribution of photosynthesis except for the amount of photosynthesis from other leaves (Table 6). The interaction effect of the region by year of release of the cultivar also for the traits of remobilization amount of spike and other leaves, remobilization efficiency from other leaves, contribution of remobilization from other leaves, stem and total remobilization, all traits related to photosynthesis except flag leaf photosynthesis efficiency and stem contribution of photosynthesis was significant at a probability level of one percentage. Linear regression graphs for the traits were drawn for each region separately where the interaction of

year of release was significant in the region. In contrast, for the traits where the interaction of year of release was not significant in the region, linear regression graphs were plotted using the average of data for the two regions (Table 7).

Table 6- Combined variance analysis of investigated traits related to the amount and efficiency of photosynthesis based on the year of release in 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018

S.O.V	df	Mean Squares									
		Amount of Photosynthesis					Photosynthesis efficiency				
		Spike	Flag leaf	Other leaves	Stem	Total	Spike	Flag leaf	Other leaves	Stem	Total
Year	1	241682.75**	225.33**	142459.52*	243.66**	35506.62**	48.91**	6.72	7.97 ^{ns}	0.09	8987.70**
Region	2	22031.87	2110.86	54321.19**	0.06 ^{ns}	1226.4 ^{ns}	0.170	95.43**	10.14	0.337**	194.616**
Region × Year	2	19352.21**	1473.57	2714.06	18.14**	4317.8	5.47**	9.81**	21.41**	0.035	54.18**
Rep(Region× Year)	12	2492.08	2837.93	3911.88	3.50	42394.75	0.462	1.94	0.557	0.005	5.946
Year of release	19	31115.44**	30549.95**	34413.72	29169.02**	473208.70	1.065**	3.43**	0.878**	0.023**	13.756**
Year of release× Region	19	13911.73**	15906.10**	15173.62**	13376.33*	214931.10**	0.577**	2.28	0.4596*	0.010	7.902**
Year of release× Year	38	1544.41**	1266.04	1921.86	0.07*	7467.65	0.51	1.54	0.21	1.18 ^{ns}	845.97**
Year of release× Region× Year	38	1170.66	2185.81 ^{ns}	2218.09	0.03	6490.34	0.47	0.97	0.65**	1.02**	3.37
Error	228	2514.97	2880.96	3163.28	7093.29	47293.98	0.161	1.50	0.182	0.007	3.103
CV (%)	-	11.23	12.27	13.30	35.67	14.09	20.97	27.47	21.24	39.58	20.47

* and ** significantly at 5 and 1 % probability levels, respectively

Table (Continued) 6- Combined variance analysis of investigated traits related to contribution of photosynthesis based on the year of release in 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018

S.O.V	df	Mean Squares				
		Photosynthesis contributions				
		Spike	Flag leaf	Other leaves	Stem	Total
Year	1	1.14	25.51	193.97	226.44	9807.36**
Region	2	8.74	34.98	122.68	5140.544**	4827.889
Region × Year	2	1.07	20.94	242.71**	279.71**	2647.01*
Rep (Region× Year)	12	6.996	27.97	97.573	135.331	859.264
Year of release	19	5.0635*	20.257*	70.429**	513.750*	840.726*
Year of release× Region	19	7.399**	29.605**	62.602**	332.700	725.734*
Year of release× Year	38	0.74	10.677	70.10**	411.24	1377.21**
Year of release× Region× Year	38	0.21	8.38	10.06	121.08	292.48 ^{ns}
Error	228	2.693	10.775	19.950	241.836	377.422
CV (%)	-	1.69	3.50	4.93	31.90	5.89

* and ** significantly at 5 and 1 % probability levels, respectively

Table 7– Mean of investigated traits based on the year of release in 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018

<i>Cultivar No.</i>	<i>Cultivar name</i>	<i>Year of release</i>	<i>Grain yield</i>	<i>Plant height</i>	<i>Thousand kernel weight</i>	<i>Biological yield</i>	<i>Harvest index</i>	<i>Spikes/M²</i>	<i>Peduncle length</i>	<i>Spike length</i>	<i>Grains/spike</i>	<i>Grain filling period</i>	<i>Grain filling rate</i>
Inia	1	1968	3.854	99.111	36.706	12.508	27.676	386.343	37.789	9.339	38.858	40.630	0.926
Khazar1	2	1973	3.918	98.667	35.672	12.021	27.333	375.130	34.011	9.782	37.072	40.333	0.912
Moghan1	3	1974	3.332	95.389	31.667	12.267	22.452	382.722	36.150	9.504	37.506	37.241	0.878
Moghan2	4	1976	3.989	96.778	35.278	12.545	27.570	411.398	35.868	9.814	42.422	35.389	1.021
Alborz	5	1979	3.710	100.444	41.894	13.023	26.435	393.426	37.078	10.611	36.692	40.519	1.066
Kaveh	6	1980	2.944	108.333	34.967	11.204	23.247	378.880	36.369	9.436	40.014	35.167	1.015
Golestan	7	1986	2.884	100.278	39.117	12.212	21.217	374.704	37.569	10.061	34.083	38.417	1.075
Rasoul	8	1992	4.580	99.222	41.306	12.981	30.334	396.444	35.724	9.806	37.700	37.083	1.144
Tajan	9	1995	4.995	95.389	39.939	12.458	31.991	374.944	36.231	9.725	39.519	38.630	1.055
Shiroudi	10	1997	4.717	96.389	41.867	12.416	29.990	373.870	34.503	9.483	38.083	40.065	1.070
Milan, Shanghai	11, 12	2001	4.863	98.694	42.444	12.961	31.009	387.368	34.540	9.047	34.950	37.833	1.151
Arta, Darya, Moghan3	13, 14, 15	2006	4.795	99.611	39.552	13.422	29.386	393.559	35.323	9.590	40.469	36.556	1.106
Morvarid	16	2009	5.186	102.111	39.222	13.596	32.808	387.370	39.579	8.972	42.511	37.417	1.067
Gonbad	17	2011	4.652	98.667	39.128	13.086	29.561	350.306	34.311	9.921	42.333	33.972	1.177
Ehsan	18	2016	4.510	105.389	45.344	14.395	25.885	392.769	36.213	10.043	34.625	36.778	1.267
Tiregan	19	2017	5.411	101.722	44.883	14.201	31.350	410.509	36.221	9.675	35.419	38.944	1.178
Merag	20	2018	4.752	104.556	38.850	14.567	28.330	401.750	38.963	8.828	43.028	37.528	1.057

Table (Continued) 7– Mean of investigated traits based on the year of release in 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018

<i>Cultivar No.</i>	<i>Cultivar name</i>	<i>Year of release</i>	<i>Spike dry matter remobilization</i>	<i>Flag leaf dry matter remobilization</i>	<i>Other leaves dry matter remobilization</i>	<i>Stem dry matter remobilization</i>	<i>Total dry matter remobilization</i>	<i>Spike dry matter remobilization efficiency</i>	<i>Flag leaf dry matter remobilization</i>	<i>Other leaves dry matter remobilization</i>	<i>Stem dry matter remobilization efficiency</i>	<i>Total dry matter remobilization efficiency</i>
Inia	1	1968	17.508	28.833	52.050	225.667	324.058	0.069	0.290	0.245	0.204	0.809
Khazar1	2	1973	17.717	17.167	32.167	260.000	327.050	0.078	0.209	0.172	0.227	0.686
Moghan1	3	1974	15.350	26.667	36.000	228.333	306.350	0.065	0.264	0.190	0.242	0.760
Moghan2	4	1976	17.017	21.167	64.333	218.333	320.850	0.070	0.219	0.300	0.198	0.788
Alborz	5	1979	16.567	27.000	47.833	250.000	341.400	0.075	0.301	0.241	0.237	0.855
Kaveh	6	1980	16.783	30.500	31.000	229.667	307.950	0.081	0.311	0.151	0.204	0.747
Golestan	7	1986	16.567	23.000	56.333	213.333	309.233	0.059	0.226	0.240	0.193	0.718
Rasoul	8	1992	18.608	25.667	58.333	285.000	387.608	0.084	0.236	0.256	0.266	0.843
Tajan	9	1995	17.608	24.833	51.667	254.333	348.442	0.078	0.266	0.230	0.227	0.801
Shiroudi	10	1997	19.817	32.867	42.333	210.000	305.017	0.090	0.313	0.223	0.197	0.823
Milan, Shanghai	11, 12	2001	17.017	25.417	38.833	260.000	341.267	0.078	0.248	0.191	0.249	0.766
Arta, Darya, Moghan3	13, 14, 15	2006	19.592	28.117	30.222	252.833	330.764	0.081	0.248	0.146	0.229	0.705
Morvarid	16	2009	19.100	32.667	33.833	188.167	273.767	0.095	0.298	0.159	0.164	0.716
Gonbad	17	2011	22.833	35.333	47.167	248.833	354.167	0.080	0.273	0.191	0.190	0.733
Ehsan	18	2016	19.667	26.500	38.383	235.000	319.550	0.072	0.201	0.161	0.211	0.644
Tiregan	19	2017	19.650	43.000	32.167	195.000	289.817	0.096	0.332	0.143	0.172	0.743
Merag	20	2018	19.833	21.167	49.833	183.333	274.167	0.078	0.205	0.217	0.172	0.673

Table (Continued) 7– Mean of investigated traits based on the year of release in 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018

<i>Cultivar No.</i>	<i>Cultivar name</i>	<i>Year of release</i>	<i>Contribution of spike dry matter remobilization</i>	<i>Contribution of flag leaf dry matter remobilization</i>	<i>Contribution of other leaves dry matter remobilization</i>	<i>Contribution of stem dry matter remobilization</i>	<i>Total contribution of dry matter remobilization</i>	<i>Spike photosynthesis</i>	<i>Flag leaf photosynthesis</i>	<i>Other leaves photosynthesis</i>	<i>Stem photosynthesis</i>	<i>Total photosynthesis</i>
Inia	1	1968	3.792	7.583	14.060	59.648	85.084	377.696	366.371	343.154	169.885	1257.106
Khazar1	2	1973	2.069	4.137	7.457	66.145	79.809	391.128	391.678	376.678	151.275	1310.758
Moghan1	3	1974	5.421	10.842	11.789	87.522	115.575	306.305	294.988	285.655	148.877	1035.825
Moghan2	4	1976	2.543	5.086	14.273	51.276	73.179	427.414	423.264	380.097	226.097	1456.872
Alborz	5	1979	3.176	6.352	10.686	60.045	80.258	404.782	394.348	373.515	171.348	1343.993
Kaveh	6	1980	4.426	8.852	8.287	68.565	90.129	355.933	342.216	341.716	180.550	1220.415
Golestan	7	1986	3.941	7.882	17.496	75.655	104.974	322.004	315.571	282.237	158.215	1078.027
Rasoul	8	1992	2.726	5.452	11.432	58.084	77.694	470.527	463.468	430.802	204.135	1568.931
Tajan	9	1995	2.334	4.667	10.020	47.782	64.802	520.319	513.094	486.261	283.594	1803.269
Shiroudi	10	1997	3.301	6.603	8.694	43.220	61.819	471.793	458.743	449.277	281.610	1661.424
Milan, Shanghai	11, 12	2001	2.568	5.136	7.604	51.829	67.137	490.789	482.389	468.973	247.806	1689.958
Arta, Darya, Moghan3	13, 14, 15	2006	2.914	5.829	6.146	51.749	66.638	472.791	464.266	462.160	239.549	1638.767
Morvarid	16	2009	3.062	6.124	6.476	34.591	50.253	522.883	509.316	508.150	353.816	1894.166
Gonbad	17	2011	3.723	7.446	9.794	51.658	72.621	455.102	442.602	430.769	229.102	1557.575
Ehsan	18	2016	2.723	5.446	8.124	52.698	68.991	468.206	461.373	449.490	252.873	1631.942
Tiregan	19	2017	4.108	8.216	6.144	34.686	53.154	534.943	511.593	522.427	359.593	1928.556
Merag	20	2018	2.152	4.303	9.954	37.208	53.617	499.877	498.544	469.877	336.377	1804.675

Table (Continued) 7– Mean of investigated traits based on the year of release in 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018

<i>Cultivar No.</i>	<i>Cultivar name</i>	<i>Year of release</i>	<i>Spike photosynthesis efficiency</i>	<i>Flag leaf photosynthesis efficiency</i>	<i>Other leaves photosynthesis efficiency</i>	<i>Stem photosynthesis efficiency</i>	<i>Total photosynthesis efficiency</i>	<i>Contribution of spike photosynthesis</i>	<i>Contribution of flag leaf photosynthesis</i>	<i>Contribution of other leaves photosynthesis</i>	<i>Contribution of stem photosynthesis</i>	<i>Spike photosynthesis efficiency</i>
Inia	1	1968	1.465	3.836	1.639	0.157	7.097	96.208	92.417	85.940	40.468	315.033
Khazar1	2	1973	1.707	4.854	1.993	0.133	8.688	97.931	95.863	92.543	34.685	321.022
Moghan1	3	1974	1.304	3.296	1.524	0.157	6.281	94.579	89.158	88.211	45.811	317.758
Moghan2	4	1976	1.774	4.627	1.796	0.221	8.418	97.457	94.914	85.727	48.724	326.821
Alborz	5	1979	1.814	4.607	1.846	0.163	8.430	96.824	93.648	89.314	39.955	319.742
Kaveh	6	1980	1.700	3.729	1.661	0.172	7.262	95.574	91.148	91.713	47.225	325.661
Golestan	7	1986	1.135	3.305	1.216	0.139	5.796	96.059	92.118	82.504	36.950	307.631
Rasoul	8	1992	2.103	4.623	1.872	0.196	8.794	97.274	94.548	88.568	41.916	322.306
Tajan	9	1995	2.304	5.763	2.488	0.259	10.814	97.666	95.333	89.980	52.218	335.198
Shiroudi	10	1997	2.131	4.723	2.445	0.268	9.568	96.699	93.397	91.306	56.780	338.181
Milan, Shanghai	11, 12	2001	2.217	5.085	2.331	0.240	9.874	97.432	94.864	92.396	48.171	332.863
Arta, Darya, Moghan3	13, 14, 15	2006	1.962	4.683	2.179	0.227	9.051	97.086	94.171	93.854	48.251	333.362
Morvarid	16	2009	2.610	4.782	2.463	0.316	10.171	96.938	93.876	93.524	65.409	349.747
Gonbad	17	2011	1.591	3.433	1.711	0.178	6.912	96.277	92.554	90.206	48.342	327.379
Ehsan	18	2016	1.690	3.563	1.930	0.234	7.418	97.277	94.554	91.876	47.302	331.009
Tiregan	19	2017	2.594	4.701	2.348	0.325	9.968	95.892	91.784	93.856	65.314	346.846
Merag	20	2018	2.029	5.232	2.029	0.312	9.603	97.848	95.697	90.046	62.792	346.383

Based on the results of linear regression analysis between grain yield and the year of cultivar release, grain yield had a significant and increasing trend during the cultivar improvement years in both Gorgan and Gonbad regions (Figure 1a). The average genetic improvement of cultivars from the year 1968 was estimated 30 kg/ha/yr for the grain yield ($R^2 = 0.56$, $P < 0.01$).

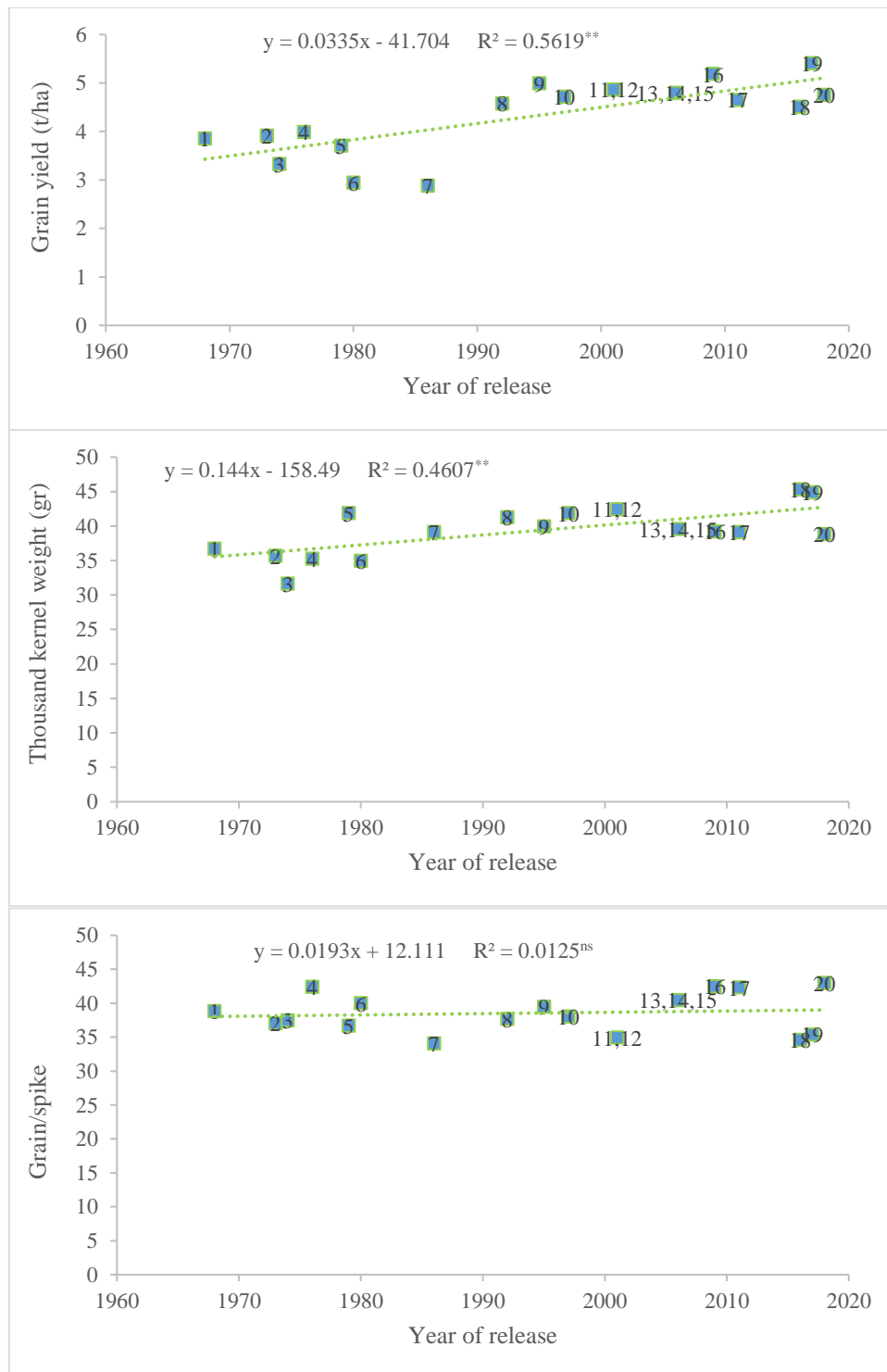


Figure 1- Liner regression equation between Grain yield (a), Thousand kernel weight (b) and Grain/spike (c) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

Based on the results of linear regression analysis, there was a significant relationship between the thousand kernel weight (TKW) and the year of cultivar release in the both regions (Figure 1b). The average genetic gain of TKW of cultivars from 1968

to 2018 in the two regions was 0.14 gr/yr ($R^2 = 0.46$, $P < 0.01$). There was a positive and significant correlation between TKW and YLD ($r = 0.596$, $P < 0.05$).

Although there was a significant difference in terms of the number of grains in the spike among the years of release of cultivars, it seems that during the wheat breeding program of the cultivars studied, the increase of the number of grains in none of the two regions of Gorgan and Gonbad was considered much because there was no significant trend during the years of their release. (Figure 1c). The correlation of this trait with grain yield was also not significant ($r = 0.261$ ns).

The trend of increasing the number of spikes per square meter, S/M^2 (with an average of 356.45) was not significant during the years of cultivar release in the two regions.

In this research, there was a no significant relationship between the spike/ m^2 and the year of cultivar release in the both regions (Figure 2a). The biological yield has increased and for this trait, a significant trend was observed during the years of cultivar release (Figure 2b). On average, the genetic gain from 1968 to 2018 for biological yield was estimated to be 42 kg/ha/yr ($R^2 = 0.65$, $P < 0.01$). The correlation of this trait with YLD was also positive and significant ($r = 0.933$, $P < 0.01$).

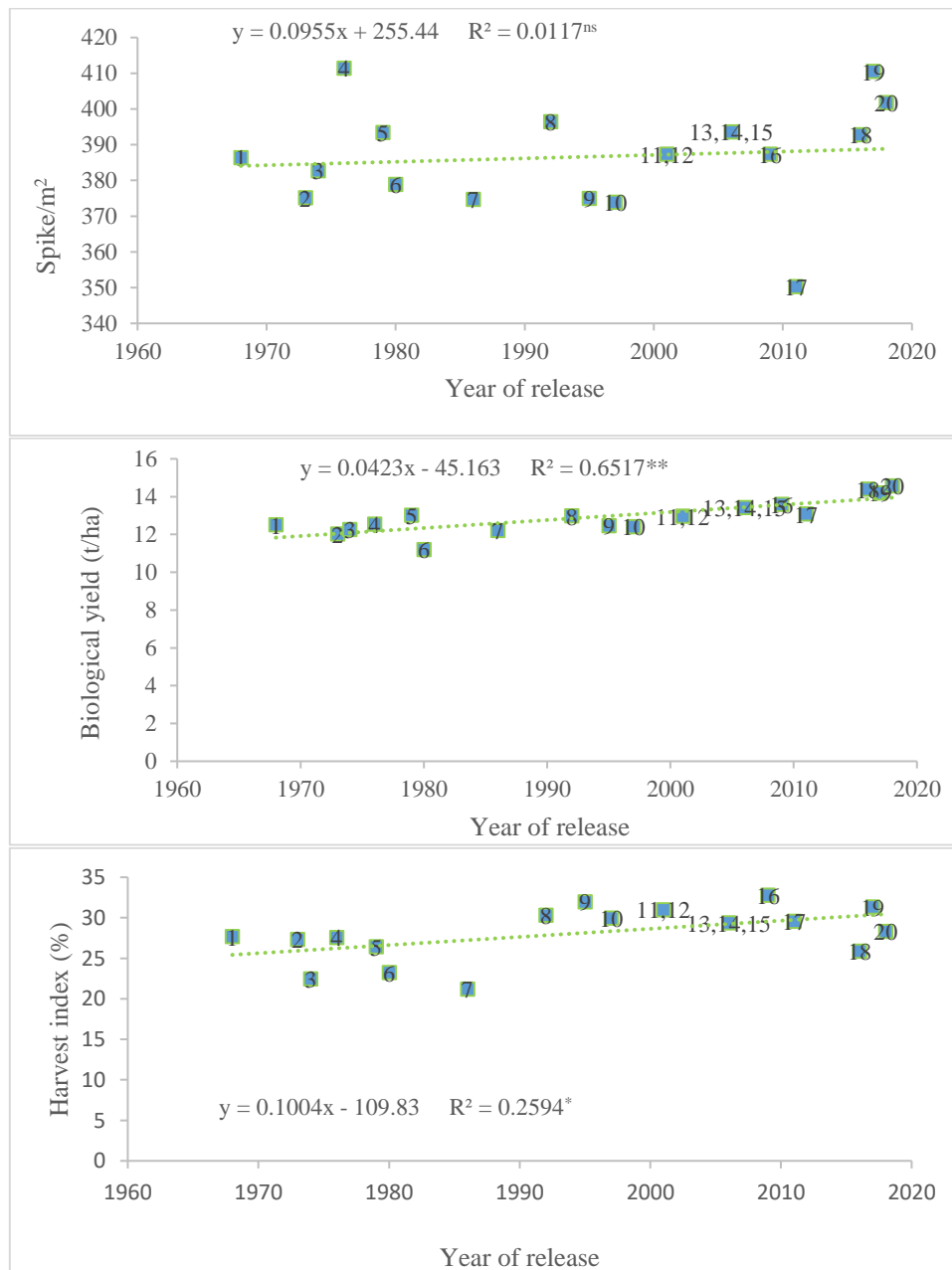


Figure 2- Liner regression equation between Spike/ m^2 (a), Biological yield (b) and Grain/spike (c) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

As shown in Figure 2c, based on the results of linear regression analysis, although to some extent, the harvest index has increased in both the regions, the increase of this trait during the period of cultivar release found to be significant ($P < 0.05$). The average genetic gain of harvest index of the cultivars investigated from 1968 to 2018 in the two regions of Gorgan was 0.1% per year ($R^2 = 0.25$, $P < 0.05$). A significant and positive correlation was observed between YLD and harvest index ($r = 0.941^{**}$).

Unlike the length of the grain filling period, which did not have a significant trend in any of the regions studied, the grain filling rate had significant increasing trend in the two regions (Figure 3a and 3b). The average genetic gain for grain filling rate from 1968 to 2017 in the two regions was 0.004 mg/day/yr ($R^2 = 0.62$, $P < 0.01$). The correlation of yield with grain filling rate was positive and significant ($r = 0.510^{**}$); where, the correlation of yield with the SFP was positive and non-significant ($r = 0.038$ ns).

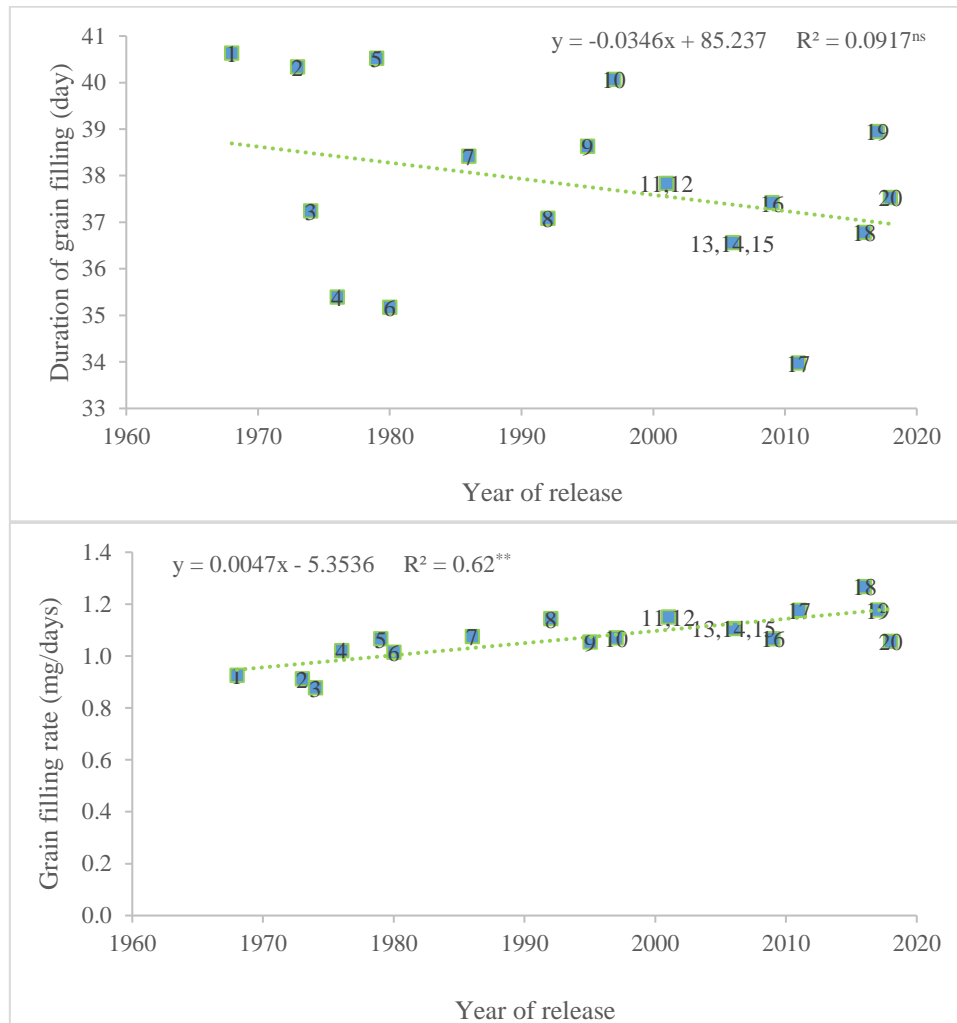


Figure 3- Liner regression equation between Duration of grain filling (a) and Grain filling rate (b) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

The results of analysis of variance showed a significant difference for plant height (PLH) in the years of release, but based on the results of linear regression analysis between the PLH and the year of release, the PLH even though not significantly, showed decreasing tend in the Gorgan region while to some extent increasing trend was observed in the Gonbad region as shown in Figure 4a. The correlation between the PLH (with an average of 101.80 cm for the all cultivars in both regions) and YLD was also negative and non-significant ($r = 0.164$ ns).

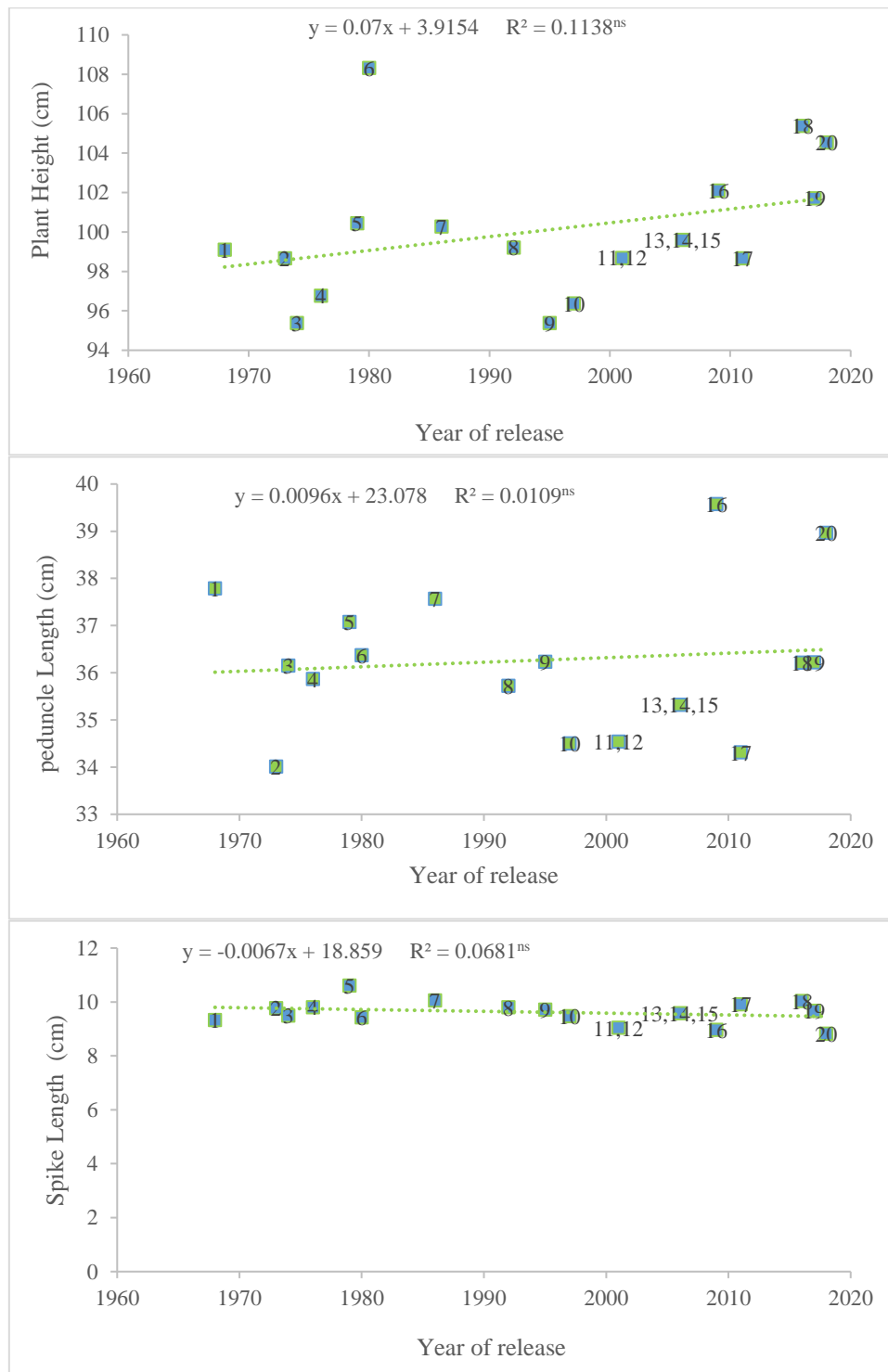


Figure 4- Liner regression equation between plant height (a), peduncle length (b) and spike length (c) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

Linear regression analysis of SPL and PDL with the year of cultivar release showed that during the years of cultivar improvement for these traits, PDL increased vs. SPL decreased. However, the changes were not statistically significant (Figure 4b and 4c). The correlation of these traits with the trait grain yield was also negative and non-significant. In this way, during the years of release, no attempt was made for selection to increase or decrease these traits.

Based on the results of the linear regression analysis of the amount of remobilization with the year of cultivar release, during the correction periods from 1968 to 2018, only the amount of remobilization from spike in both Gorgan and Gonbad regions has increased significantly, which means the selection was aimed at increasing the amount of remobilization from the spike. The amount of remobilization from the flag leaf also showed increasing but non-significant trend. On the other hand, the total amount

of remobilization showed increasing but non-significant trend, which may be due to the reduction of remobilization from other leaves of the plant and stem during the breeding years, although the trend of decreasing remobilization from other leaves (in both Gorgan and Gonbad regions) and the stem was also not significant (Figures 5 and 6).

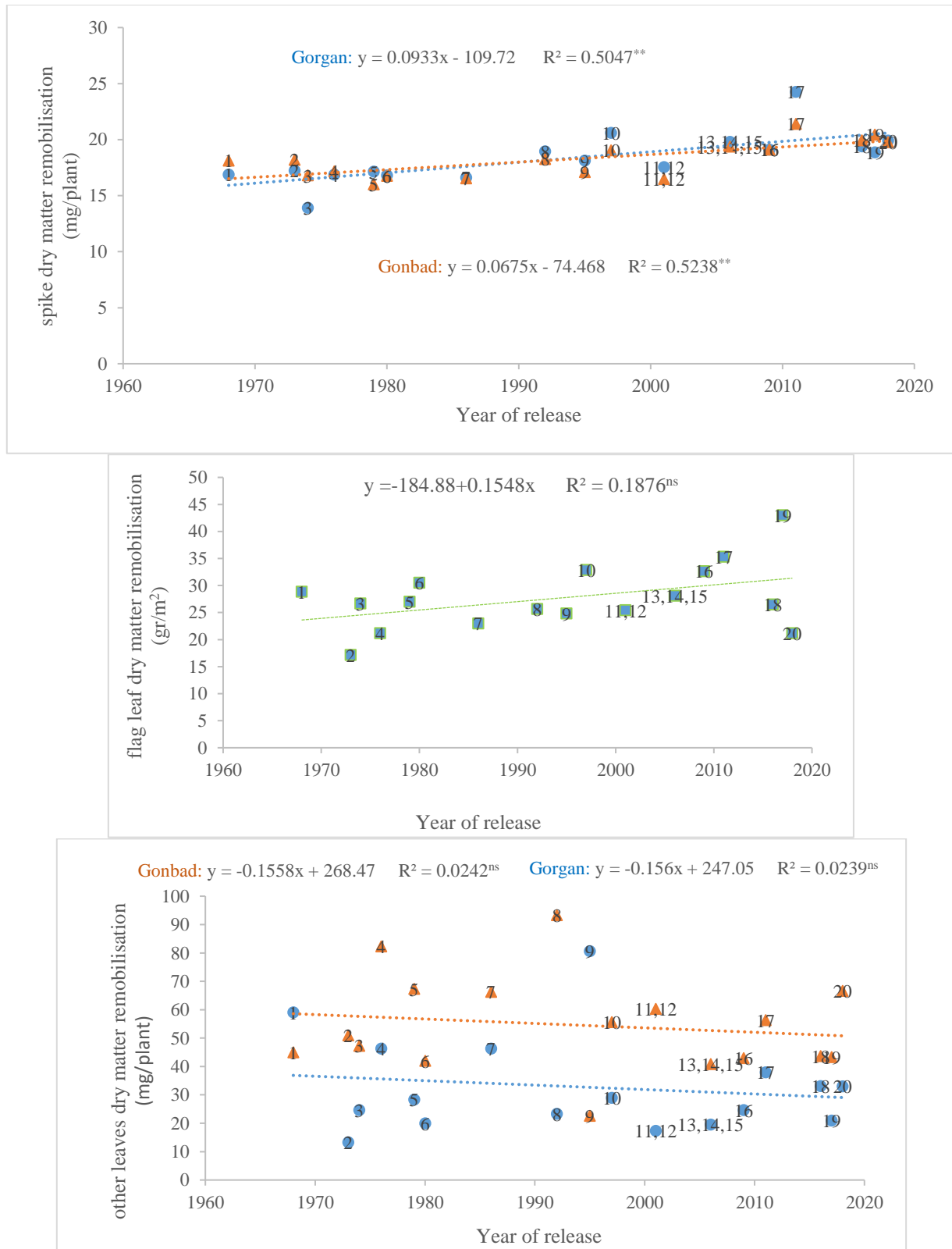


Figure 5- Liner regression equation between spike dry matter remobilization (a), flag leaf dry matter remobilization (b) and other leaves dry matter remobilization (c) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

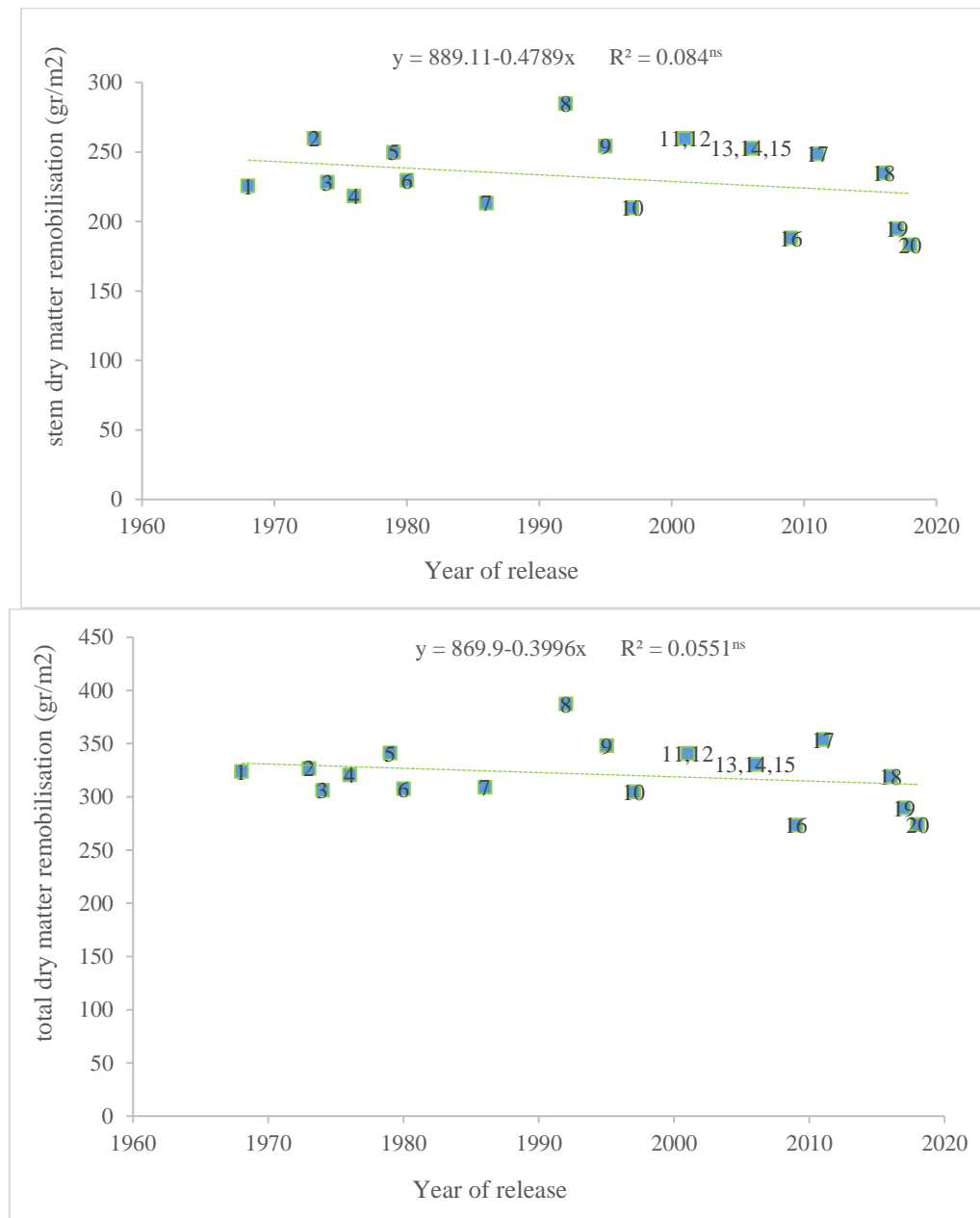


Figure 6- Linear regression equation between stem dry matter remobilization (a) and total dry matter remobilization (b) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

The average genetic gain values obtained for the trait of remobilization from spike for Gorgan and Gonbad regions were (0.093 gr/m²/yr; $R^2 = 0.51$, $P < 0.01$) and (0.067 gr/m²/yr; $R^2 = 0.52$, $P < 0.01$), respectively. The correlation of this trait with grain yield was also positive and significant ($r = 0.725$, $P < 0.05$).

Spike remobilization efficiency during the years of release of cultivars had a significant increasing trend at the five percent probability level, but total remobilization efficiency and flag leaf and stem remobilization efficiency did not show a significant trend in the years of cultivar release (Figures 7 and 8). Despite the decrease in the remobilization efficiency of other leaves in the Gorgan region, the trend of changes of this trait was not significant in both Gorgan and Gonbad regions. In this way, it can be stated that during the breeding activities to improve the yield of wheat in this region, selection was made to increase the efficiency of remobilization of spike, but no effort was made to change the remobilization efficiency of other parts of the wheat cultivars. Among different parts of a plant, only spike remobilization efficiency was increased, the correlation of spike remobilization efficiency with grain yield was also positive and significant ($r = 0.704$, $P < 0.05$), the correlation of total remobilization efficiency and other plant parts with yield was not significant. The percentage of genetic improvement for spike

remobilization efficiency trait was estimated to be 0.03 gr/gr per year during the 50 years of release of these cultivars ($R^2 = 0.28$, $P < 0.05$).

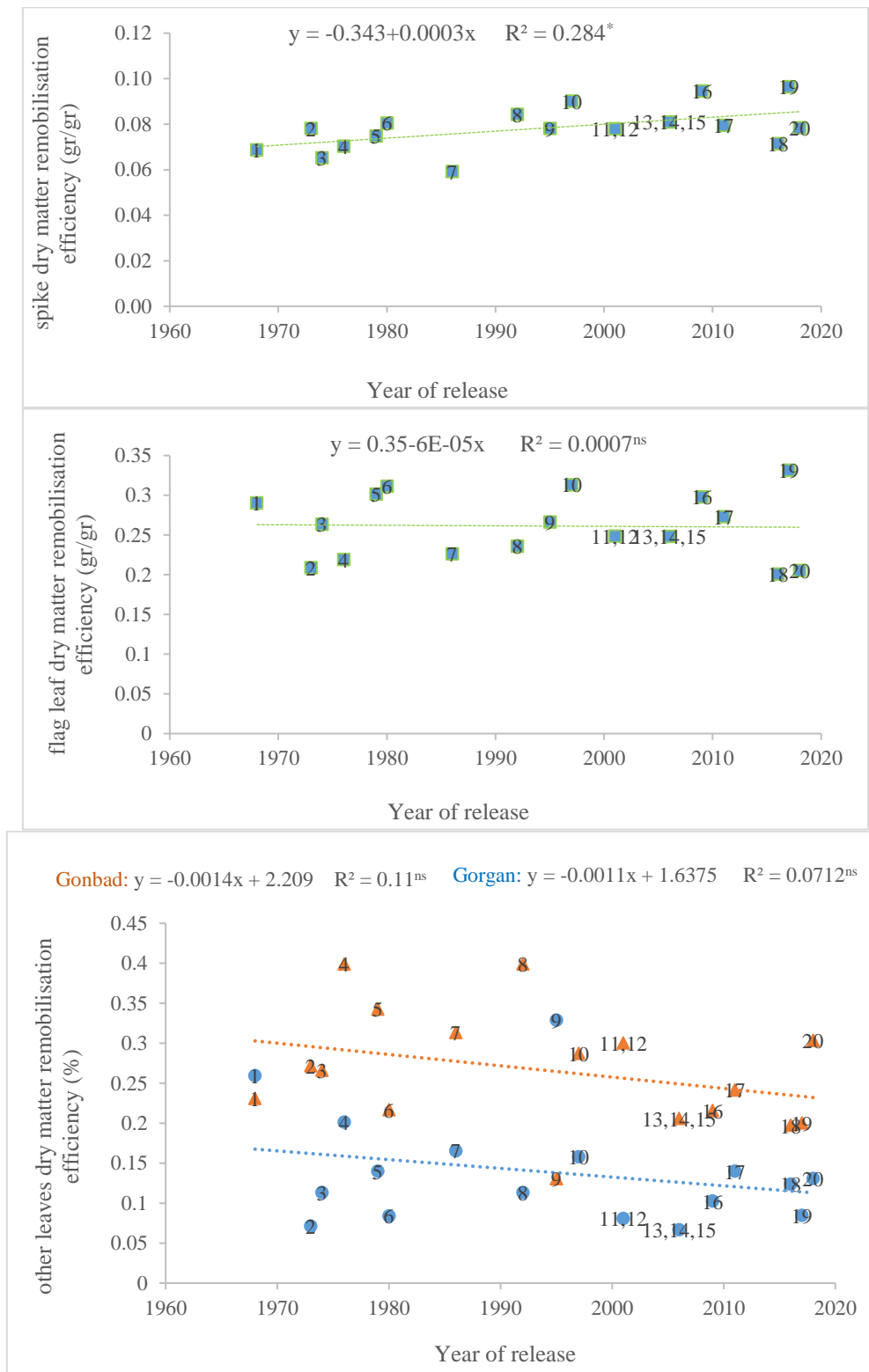


Figure 7- Liner regression equation between spike dry matter remobilization efficiency (a), flag leaf dry matter remobilization efficiency (b) and other leaves dry matter remobilization efficiency (c) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

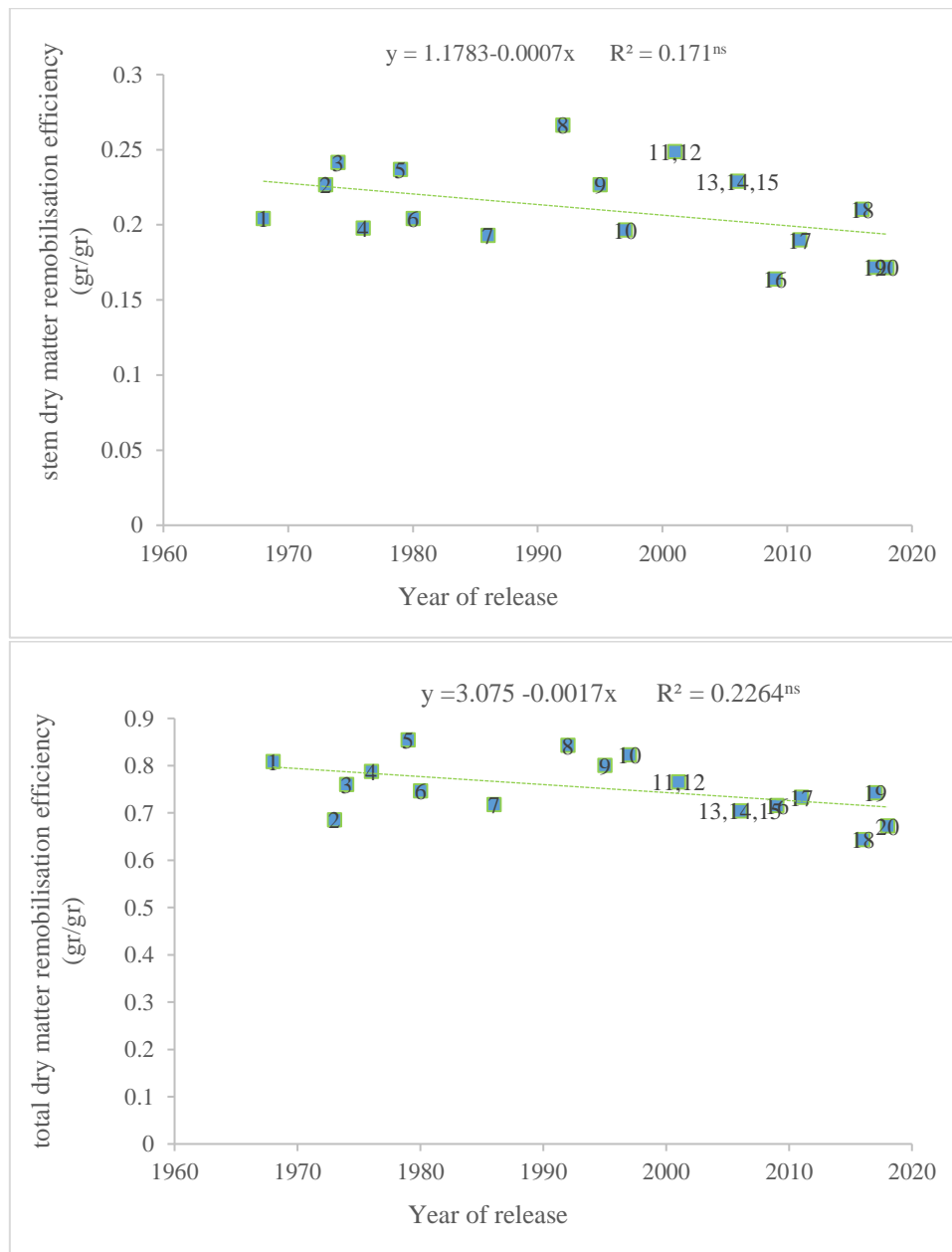


Figure 8- Linear regression equation between stem dry matter remobilization efficiency (a) and total dry matter remobilization efficiency (b) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

Based on the results of the analysis of the changes of remobilization during the years of cultivars improvement, the remobilization contributions of all parts of the plant and consequently the contribution of the total remobilization were decreased. However, this decrease was non-significant for the characteristics of the remobilization contribution of other leaves in the both regions, and significant for the total and stem remobilization contribution in both Gorgan and regions (Figures 9 and 10). The average reduction of stem and total remobilization contribution from 1968 to 2018 in the Gorgan region was $-0.853\%/yr$ ($R^2 = 0.36$, $P < 0.05$) and $-1.157\%/yr$ ($R^2 = 0.37$, $P < 0.01$) and in the Gonbad area, it was $-0.335\%/yr$ ($R^2 = 0.42$, $P < 0.01$) and $-0.314\%/yr$ ($R^2 = 0.31$, $P < 0.05$), respectively. It seems that with the decrease in the amount and efficiency of remobilization of other leaves of the plant except the flag leaf and stem, the contribution of these parts of the plant in remobilization had shown decreases during the breeding periods, and the selection to increase the amount and efficiency of remobilization of the spike had not been able to reduce the remobilization of the other parts. To compensate, the plant in this way, the amount, efficiency and contribution of total remobilization of the yield had been decreased during the cultivar breeding program. The correlation coefficient of the remobilization contribution of different plant parts and the total remobilization with grain yield was negative. This coefficient for the flag leaf remobilization contribution was $r = 0.595$, $P < 0.05$. The correlations for the remobilization contribution of other leaves ($r = -0.876$), stem ($r = -0.882$), and the contribution of total remobilization ($r = -0.928$) were all significant at the probability level of one percent.

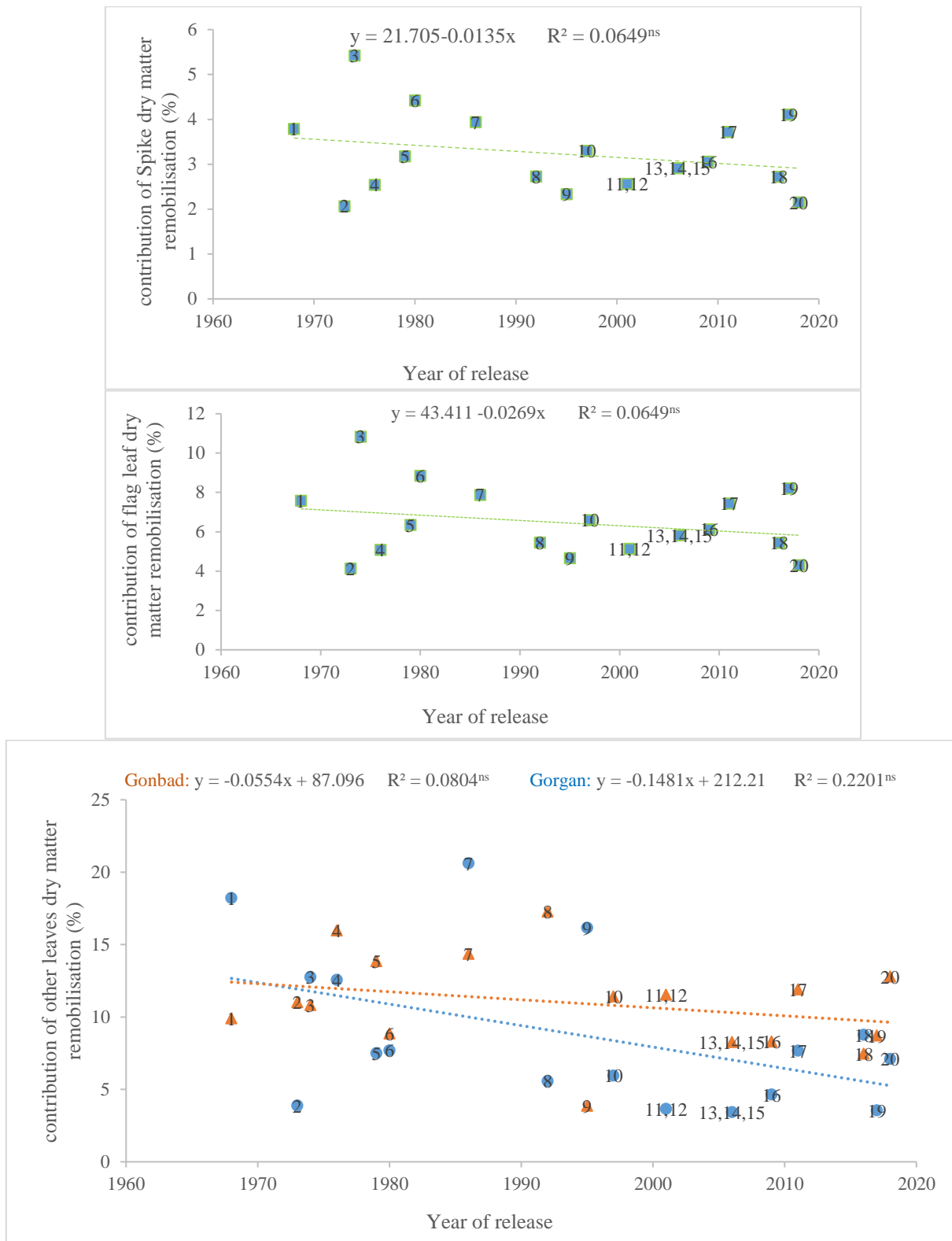


Figure 9- Liner regression equation between contribution of spike dry matter remobilization (a), contribution of flag leaf dry matter remobilization (b) and contribution of other leaves dry matter remobilization (c) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

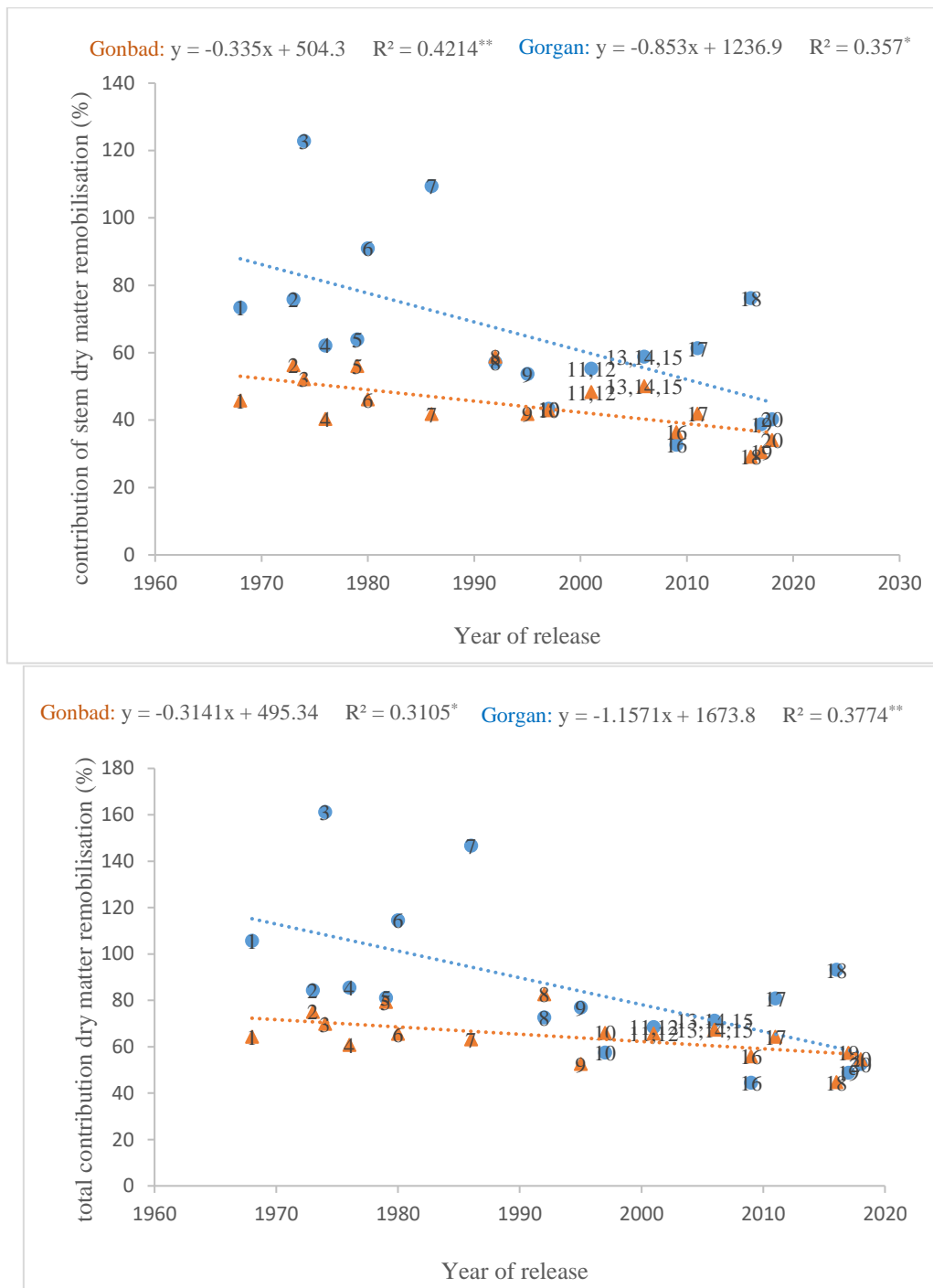


Figure 10- Liner regression equation between contribution of stem dry matter remobilization (a) and total contribution of dry matter remobilization (b) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

During the years of release of cultivars, the selections made for increasing the amount of photosynthesis from different parts of the plant and the overall increase of the amount of photosynthesis in wheat, so that these traits showed a significant increasing trend during the years of release of cultivars (Figures 11 and 12). The percentages of genetic gain for these traits in the Gorgan region 4.76 gr/m²/yr ($R^2 = 0.54$, $P < 0.01$), 4.86 ($R^2 = 0.54$, $P < 0.01$), 5.02 ($R^2 = 0.56$, $P < 0.01$), 3.89 ($R^2 = 0.45$, $P < 0.01$) and 18.53 ($R^2 = 0.54$, $P < 0.01$) and in the Gonbad area, 1.64 gr/m²/yr ($R^2 = 0.38$, $P < 0.01$), 1.38 ($R^2 = 0.26$, $P < 0.05$), 1.86 ($R^2 = 0.42$, $P < 0.01$), 2.72 ($R^2 = 0.54$, $P < 0.01$) and 7.61 ($R^2 = 0.47$, $P < 0.01$) were estimated. These traits showed a positive and highly significant correlation coefficient with YLD ($r = 0.928$, $r = 0.918$, $r = 0.931$, $r = 0.929$ and $r = 0.925$, respectively).

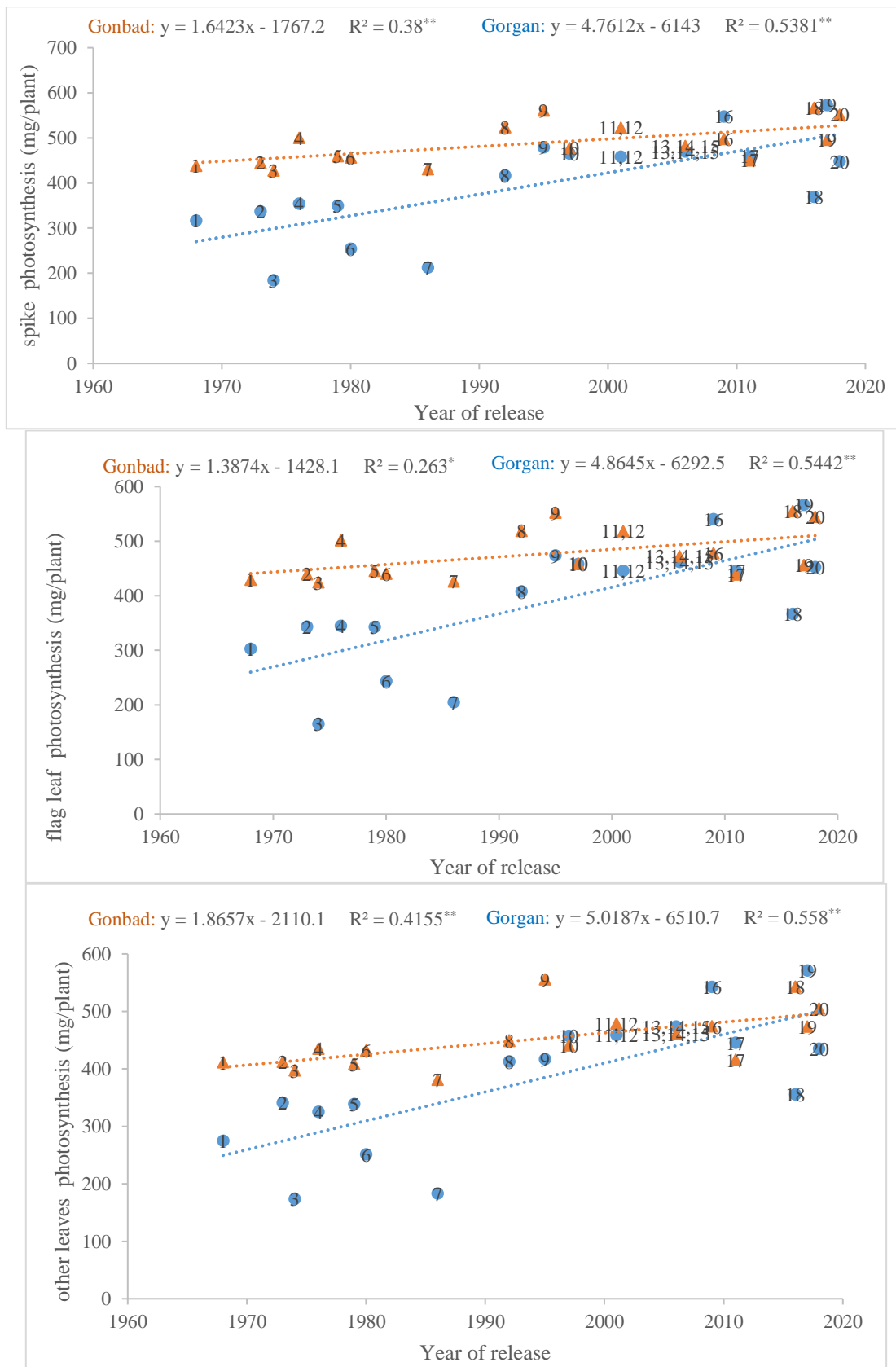


Figure 11- Liner regression equation between spike photosynthesis (a), flag leaf photosynthesis (b) and other leaves photosynthesis (c) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

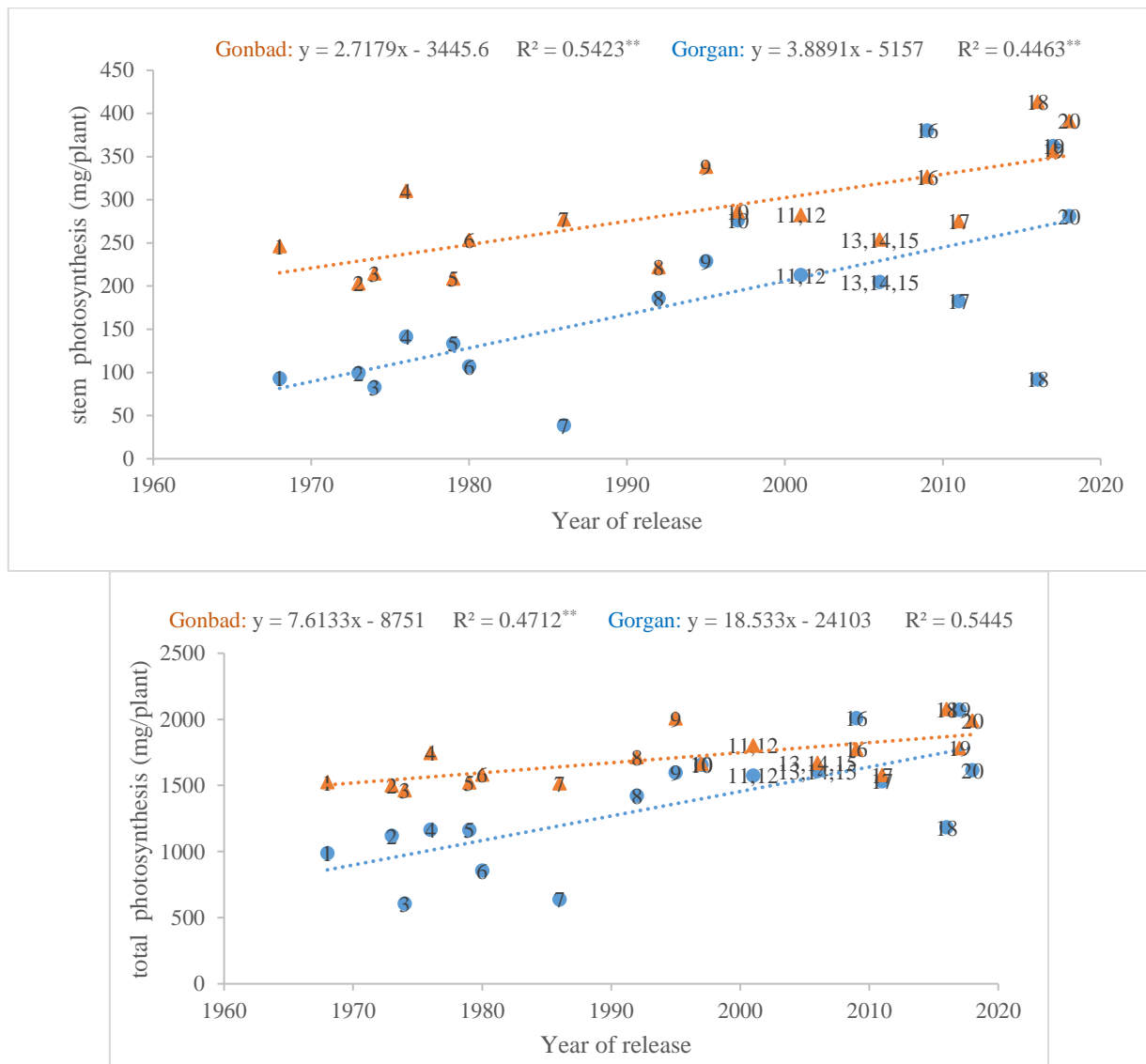


Figure 12- Liner regression equation between stem photosynthesis (a) and total photosynthesis (b) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

The photosynthesis efficiency of different parts of the plant and the total photosynthesis efficiency have also had increased during the years 1968 to 2018 in released wheat cultivars. However, as shown in the Figures 13 and 14, this trend was significant only for the total photosynthesis efficiency and those of spike and other leaves in the Gorgan region ($P < 0.05$) and for the photosynthetic efficiency of the stem in both the Gorgan and Gonbad regions ($P < 0.01$).

The genetic gain during the 50 years of breeding in the Gorgan region for the photosynthesis efficiency of spike and other leaves were 0.023 gr/gr/yr ($R^2 = 0.35$, $P < 0.05$) and 0.017 gr/gr/yr ($R^2 = 0.28$, $P < 0.05$), respectively. In this area, the genetic gain for total photosynthesis and for stem photosynthesis were estimated 0.075 gr/gr/yr ($R^2 = 0.31$, $P < 0.05$) and 0.003 gr/gr/yr ($R^2 = 0.40$, $P < 0.01$), respectively. The photosynthesis efficiency for stem was estimated 0.002 gr/gr/yr ($R^2 = 0.44$, $P < 0.05$) in the Gonbad area. However, the photosynthesis efficiency of spike ($r = 0.722$), flag leaf ($r = 0.540$), other leaves ($r = 0.784$), stem ($r = 0.786$) and total photosynthesis efficiency ($r = 0.718$) had a positive and significant correlation with grain yield.

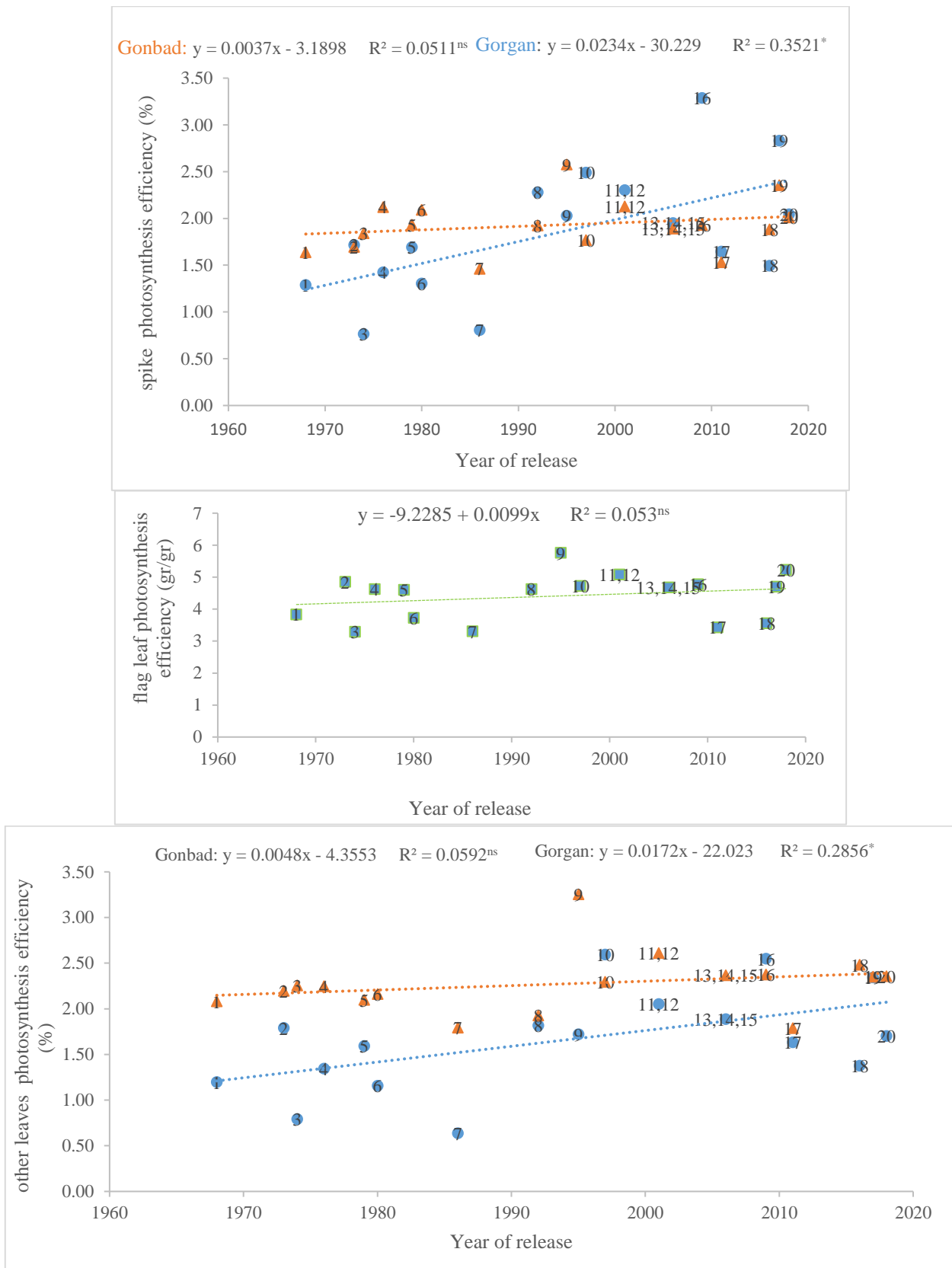


Figure 13- Linear regression equation between spike photosynthesis efficiency (a), flag leaf photosynthesis efficiency (b) and other leaves photosynthesis efficiency (c) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

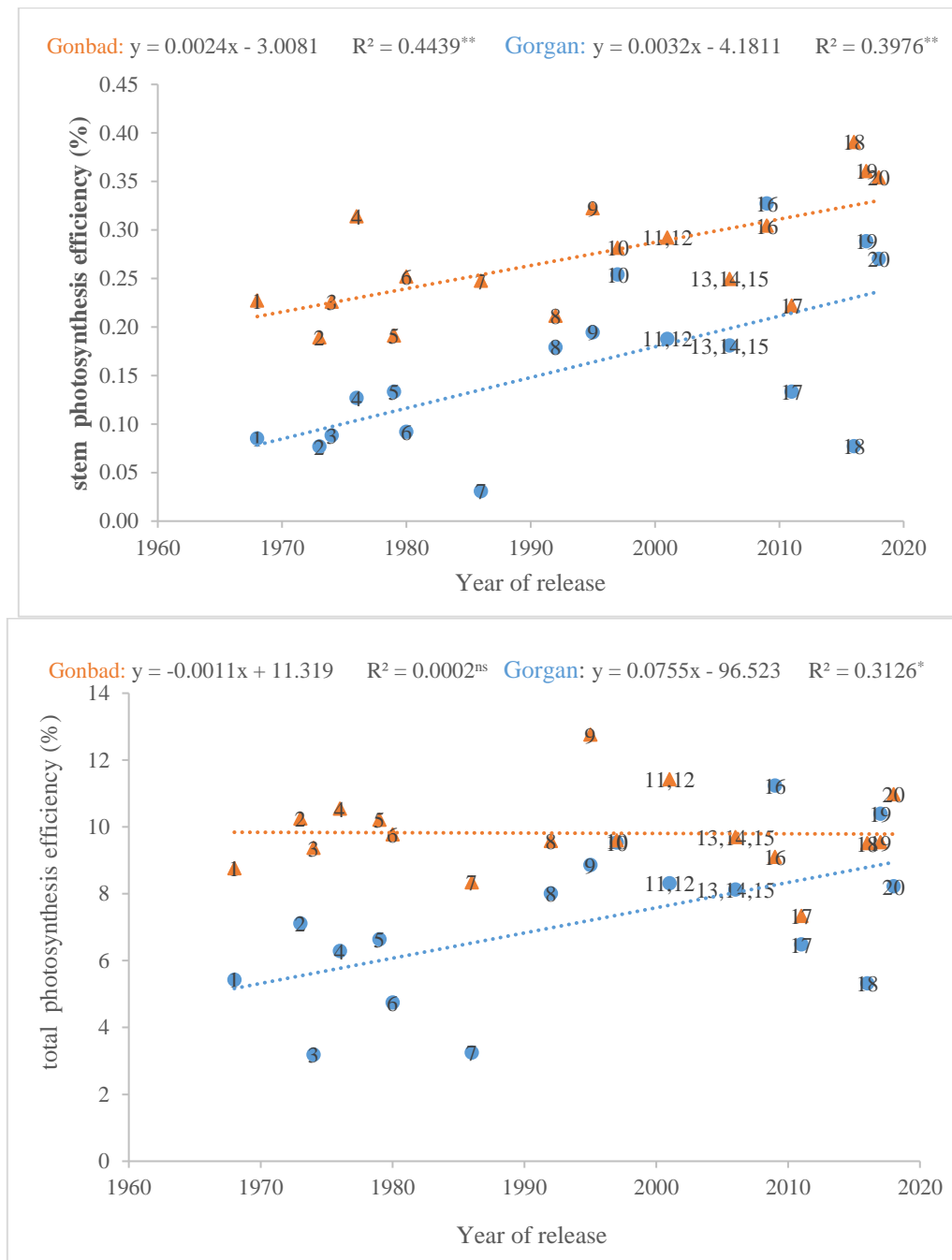


Figure 14- Liner regression equation between stem photosynthesis efficiency (a) and total photosynthesis efficiency (b) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

Considering the linear regression analysis, the contribution of photosynthesis of different parts of the plant and the contribution of total photosynthesis with the year of cultivar release were increased (Figures 15 and 16). In general, the photosynthesis had been increased in the cultivars released during recent years. The slope of the line regression of the photosynthesis, for spike and flag leaf in the Gorgan region, and for stems in the two regions showed increasing trends. The contribution of total photosynthesis was significant for Gonbad and Gorgan at the probability levels of five and one percent, respectively. The percentage of genetic gain in the Gorgan region for the contributions of the photosynthesis of the spike, the flag leaf, and the total photosynthesis were 0.052 ($R^2 = 0.26$, $P < 0.05$), 0.104 ($R^2 = 0.26$, $P < 0.05$), and 0.721 ($R^2 = 0.37$, $P < 0.01$). The percentage of genetic gain in the Gonbad region for the contribution of the total photosynthesis was 0.314 ($R^2 = 0.31$, $P < 0.05$) 0.383 ($R^2 = 0.50$, $P < 0.01$). These traits had positive and significant correlation coefficients with YLD ($r = 0.595$, $r = 0.687$ and $r = 0.800$, respectively).

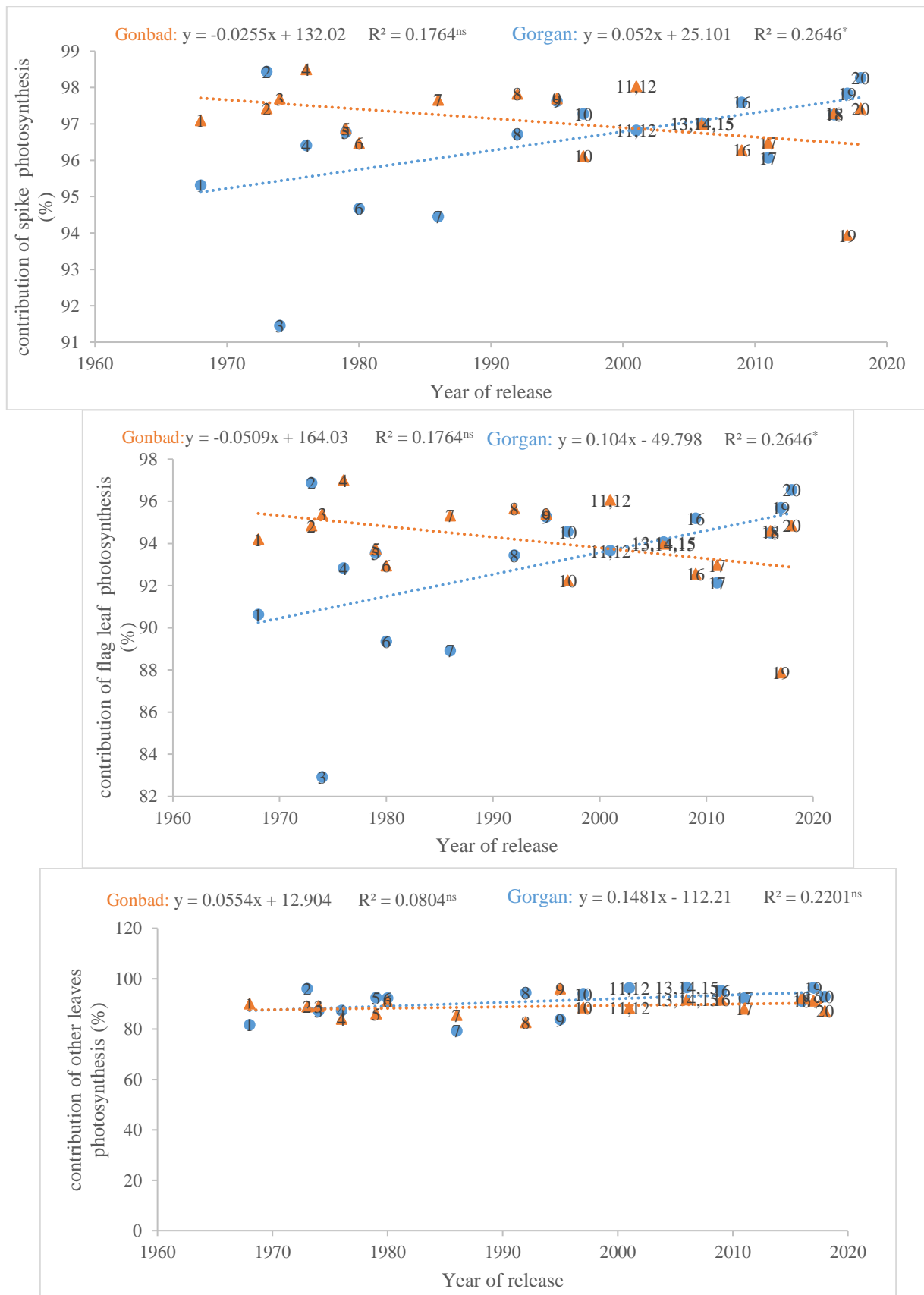


Figure 15- Liner regression equation between contribution of spike photosynthesis (a), contribution of flag leaf photosynthesis (b) and contribution of other leaves photosynthesis (c) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

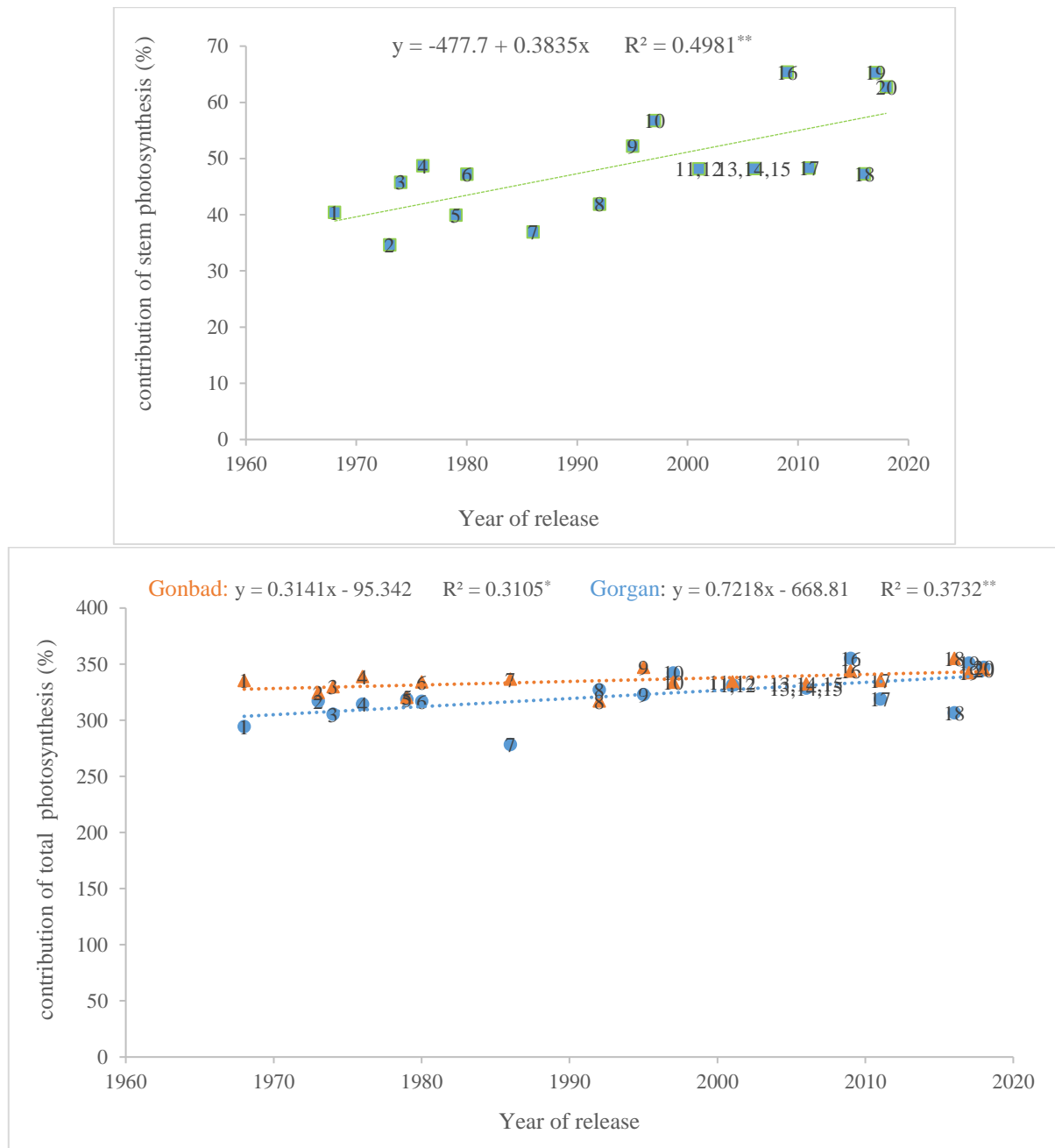


Figure 16- Liner regression equation between contribution of stem photosynthesis (a) and contribution of total photosynthesis (b) against the year of release of 20 historically most important wheat cultivars released in Gorgan and Gonbad in the north climate of Iran during 1968–2018; 1=Inia, 2=Khazar1, 3=Moghan1, 4=Moghan2, 5=Alborz, 6=Kaveh, 7=Golestan, 8=Rasoul, 9=Tajan, 10=Shiroudi, 11=Milan, 12=Shanghai, 13=Arta, 14=Darya, 15=Moghan3, 16=Morvarid, 17=Gonbad, 18=Ehsan, 19=Tiregan, 20=Merag

4. Discussion

In recent decades, the increase in wheat grain yield has decreased or even stopped. Meanwhile, increasing food production seems necessary due to the exponential growth of the population (Achilli et al. 2022). Awareness of the increase in the yield over the years due to the change of traits affecting it is necessary to understand the limiting factors of yield performance (Yadav et al. 2021). The source, sink and mobilization of assimilates are the three key factors that affect the formation of grain yield in wheat. The abundance of the source, the size of the sink and the unobstructed mobilization of assimilates increase the grain yield (Sun et al. 2021).

In this study, we investigated some morphological, phenological and physiological traits related to yield and its yield components in a set of cultivars released during the last 50 years in the warm and humid climate of northern Iran. For this purpose, field experiments were carried out in the Gorgan and Gonbad regions, the main wheat cultivation areas in the warm and humid northern climate of Iran. The results of our experiments showed that the morphological traits including PLH, PDL and

SPL did not show any significant changes during the years of cultivar release in the Gorgan and Gonbad regions. This is despite the fact that in a large number of previous studies, including those conducted in the temperate and cold climates of Iran, the results showed a decrease in the PLH of the new cultivars (Zand et al. 2002; Ant et al. 2013; Zarebayati et al. al., 2014; Alipour et al. 2019; Achilli et al. 2022; del Pozo et al. 2022; Yadav et al. 2021). The reason for not observing a significant trend in the trait of PLH in the northern climate may be the positive correlation of this trait with resistance to diseases such as FHB and foliar *Septoria*. The reason for this can be attributed to the proximity of the spikes of sensitive cultivars to the soil surface. Basically, genotypes with a PLH of less than 100 cm are closer to the plant remains on the soil surface, which increases the probability of contamination of the spikes and increases the sensitivity to the disease (Klar et al. 2007; Khodarahmi et al. 2023). It is likely that further PLH reduction in new cultivars will not occur in the future unless the correlation between PLH genes and *Fusarium* head blight resistance genes are broken by selection among numerous recombinant breeding lines made by the backcross method.

Rife et al. 2019 also reported a non-significant decreasing trend for the PLH of wheat cultivars released between 1992 and 2014 in the central plains.

The grain yield of cultivars released between 1968 and 2018 in the two regions of Gorgan and Gonbad showed a significant linear regression trend during the years of cultivar improvement and release. The yield increase of these cultivars was 30 kg/ha per year. The increase in biological yield, TKW and harvest index also had a significant linear trend in both regions, despite the increase in the S/M^2 and the number of grains per spike in both the regions, but none of these traits have had a significant progressive trend during the years of cultivar release. Increasing grain yield is the most important target of wheat breeding programs in the world, including Iran. The increase in annual bread wheat yield has been reported in many studies (Khodarahmi et al. 2023; Khan et al. 2022; Hanif et al. 2022; Yadav et al. 2021; Gerard et al. 2020; Rife et al. al. 2019). However, there is still a big gap between the demand and the annual genetic achievements of this crop in the world.

Grain yield in wheat is caused by the cumulative effects of its components, so identifying these components and their relationship with grain yield can be effective in selecting high-yielding cultivars (Tshikunde et al. 2019). The yield components in wheat include the number of grains per spike, the number of spikes per spike, the S/M^2 and TKW. Therefore, to increase grain yield, one or more of its components should be changed (Gibson & Paulsen 1999). Based on the results obtained in this study, there was a positive and significant correlation between YLD with the S/M^2 and TKW, which indicates the importance of selecting such traits for achieving genetic gain in grain yield during wheat breeding programs. Many other researchers have also reported an increase in yield and the yield components over the years of breeding wheat cultivars (Aisawi et al. 2015; Crespo-Herrera et al. 2018; Sadrjahani et al. 2017; Gerard et al. 2020; Yadav et al. 2021). It seems that the breeders in the Gorgan and Gonbad regions made their selection to increase the grain yield by increasing the TKW. The increase in TKW during a breeding process of cultivars had also been previously reported by Yao et al. (2019) and Yadav et al. (2021).

The number of grains per spike had an increasing but non-significant trend during the years of cultivar release. The correlation between this trait and YLD was positive and non-significant. Khodarahmi et al. (2023) and Alipour et al. (2019) also stated that the number of spike's grains did not have a significant change during the breeding programs, but the increase in the TKW had a significant trend in the breeding programs of the wheat cultivars in Iran, which may be due to a greater Farmers' tendency for choosing large grain wheats (with more TKW) for its better marketability.

The number of grains per spike is one of the traits affecting YLD (Esmailzadeh Moghadam et al. 2014; Khodarahmi & Vazan 2019; Qain et al. 2015; Tian et al. 2011; Philipp et al. 2018). Contrary to the results obtained in this study, Achilli et al. 2022 reported a significant increase in the number of grains per spike and no significant changes in TKW in the durum wheat cultivars released from 1934 to 2015.

The significant increasing trend of biological yield and harvest index in both the Gorgan and Gonbad regions can indicate the role of vegetative organs in increasing the photosynthesis or the remobilization of nutrients from these organs to the grain. The results obtained in this study are in accordance with the results obtained by Mróz et al. (2022), del Pozo et al. (2022), Hanif et al. (2021), Gao et al. (2017).

In wheat, an increase in a cultivar's yield depends on the increase in its biological yield while maintaining or improving its harvest index (Beche et al. 2014). Reynolds et al. (2011) and Blum (2016) believed that increasing biological performance in plants is the result of increasing the capacity or efficiency of photosynthesis. On the other hand, the yield of a crop is determined by the assimilates produced through photosynthesis in the grain filling stage, along with the mobilization of the assimilates from different parts of the plant before the flowering stage (Yang et al. 2022).

Contrary to the grain filling rate, which had a significant increase in both the Gorgan and Gonbad regions, the length of the grain filling period had a decreasing and non-significant trend, and the results obtained are in accordance with the results of Rahemi Karizaki et al. (2015). In contrast, Mróz et al. (2022) reported a significant increase in grain filling period in 20 wheat cultivars released since 1975 in Norway. The correlation between the SFP and yield was also non-significant ($r = 0.038$) and the correlation of grain filling rate with yield was positive and significant ($r = 0.510$). Attarbashi et al. (2001) also found a positive

and significant correlation between grain yield and grain filling rate and stated that the grain yield of wheat genotypes was not affected by the grain filling period.

In this study, when anthesis started from early to mid-April and grain filling took 6-7 weeks, the average temperature during grain filling was about 17-19 degrees Celsius. Milka et al. (2008) showed that each 1 °C increase in daily temperature above the optimum temperature for the grain filling, caused a decrease of approximately 2.8 mg in grain weight and 1.3 days during the grain filling period. Therefore, temperatures above the optimum range will eventually decrease the length of the grain filling period, despite the fact, high temperatures would increase the grain filling rate. In wheat, grain filling depends on three main sources: current assimilates produced by photosynthesis in leaves and stems, mobilization of stored carbohydrates and nitrogen-containing compounds in these organs and their subsequent remobilization to the spike and grains, and produced assimilates by the spike (Plaut et al. 2004; Kandić et al. 2023).

During the years of cultivars improvement, the contribution of remobilization decreased, which was significant for the total remobilization and that of and stem, but from the amount and efficiency of remobilization in the plant, the contribution of spike during the years of release of cultivars had a significant increasing trend. Under favorable conditions, remobilization can potentially contribute up to 20% of grain dry weight (Wardlaw & Willenbrink 2000). Although this ratio would increase significantly under drought conditions (Ehdaie et al. 2008).

For example, Zhang et al. (2011) showed that under water stress conditions, the contribution of spike and peduncle in grain weight was up to 73%. Sun et al. (2021) also reported an increase in remobilization from the spike during the breeding process of winter wheat cultivars from 1940 to 2010, but contrary to the results obtained in this study, these researchers stated that remobilization from the stem increased during the years of cultivar release which may be due to the reduction of the PLH in the cultivars investigated. One of the reasons for the decrease in the amount of stem remobilization in cultivars released in the northern climate of the country may be the lack of PLH reduction of cultivars in this region during the years of cultivar release, according to Austin et al. (1980) and Shearman et al. et al. (2005) carbohydrate remobilization from the stem of tall cultivars is less involved in the formation of grain yield as compared to the modern shorter cultivars with shorter stem height. Maydup et al. (2010) also stated that the contribution of stem in remobilization has decreased in modern cultivars.

The amount, efficiency and contribution of photosynthesis has been increasing during the years of cultivars improvement, and among the different parts of the plant, this increase has been significant for the spike and stem. Researchers believe that in C3 cereals, shoot (particularly the flag leaf) and the ear during grain filling play the main role as sources of assimilates (Sanchez-Bragado et al. 2014). Sun et al. (2021) also reported a significant increase in spike contribution in photosynthesis in eight winter wheat cultivars released between 1940 and 2010 in Shaanxi Province, China. The importance of participation of the green structure of wheat spikes in the filling of grains due to suitable light conditions for photosynthesis, a longer photosynthetic period after pollination compared to leaves and their availability to growing grains has been confirmed by many researchers (Maydupa et al. 2010).

Demotes-Mainard & Jeuffroy (2001) believe that wheat cultivars with larger and longer spikes have the ability to allocate more photosynthetic materials to grains as compared to those with smaller and shorter spikes. The contribution of spike photosynthesis in wheat varies from 10 to almost 80 percent of the materials absorbed in the grain depending on the cultivar and growing conditions (Maydup et al. 2010; Sanchez-Bragado et al. 2014; Rivera-Amado et al. 2020). Sanchez-Bragado et al. (2014) emphasized the increase of spike contribution in grain filling from 91 to 100% in native cultivars as compared to the increase from 49 to 82% in modern cultivars. According to the results of another research, under normal irrigation conditions, photosynthesis in spikes was much higher than one in flag leaves; whereas, photosynthesis in spikes decreased less than in one in flag leaves under water stress conditions (Abbad et al. 2004).

Based on the results of this study, the amount and contribution of photosynthesis of flag leaf had increased during the years of release of the cultivars in the Gorgan region. Sun et al. (2014) also reported an increase in flag leaf photosynthesis during the replacement of new breeding cultivars from 1940 to 2010 in Shaanxi Province, China.

5. Conclusions

The study of the genetic gain of the yield showed that the grain yield has increased from 3.854 t/ha in 1968 to 4.752 t/ha in 2018. The annual yield progress was estimated to be 30 kg/ha per year. It seems that the main reason for the genetic improvement in grain yield was the focus of the breeders on increasing the yield components, including the TKW and the S/M^2 , without a significant increase in the number of grains per spike. Plant morphological traits had no significant role in increasing YLD in the past 50 years.

During the years of cultivar improvement, while the amount, efficiency and contribution of the remobilization decreased which were in particular significant for the total's and stem's remobilization, the amount, efficiency and contribution of photosynthesis increased during these years. Based on the results obtained from studying different parts of the plant, spike proved to be an important photosynthetic source for wheat through which remobilization showed a significant increase over the time of

wheat improvement. Therefore, achieving a higher level of genetic improvement/gain in yield requires more efficiency enhancement in the national crop improvement programs through wider uses of genetic diversity to incorporate novel alleles expressing higher amounts of yield, taking into account a more efficient photosynthetic and remobilization from spike, as well as applying new breeding approaches such as speed breeding and genomic selection.

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