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STUDY OF PHOTOSYNTHETIC GAS EXCHANGE PARAMETERS AND RELATIVE WATER CONTENT OF FLAG LEAF IN SOFT WHEAT GENOTYPES UNDER DIFFERENT WATER SUPPLY CONDITIONS

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ИЗУЧЕНИЕ ПАРАМЕТРОВ ФОТОСИНТЕТИЧЕСКОГО ГАЗООБМЕНА И ОТНОСИТЕЛЬНОГО СОДЕРЖАНИЯ ВОДЫ ФЛАГОВОГО ЛИСТА ГЕНОТИПОВ МЯГКОЙ ПШЕНИЦЫ ПРИ РАЗЛИЧНЫХ УСЛОВИЯХ ВОДООБЕСПЕЧЕННОСТИ

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Abstract. The results of the study of the relative water content (RWC) and photosynthetic gas exchange parameters of the flag leaves in 21 soft wheat genotypes under rainfed conditions of Mountain Shirvan have been presented in the paper. The research was performed with drought-exposed and irrigated variants during the grain filling phase. RWC of the flag leaves of Vostorg, Murov 2, Tale 38, and Gyrmyzy gul 1 genotypes was higher both under drought and irrigated conditions. There was a positive correlation between RWC and earing time, and a negative correlation between RWC and plant height. The average difference in RWC between irrigated and drought-exposed variants for all genotypes was 10.1%. In 12thIWWYT no. 9 and 12thIWWYT no. 20 lines, this difference was high (26.5 and 19.6%), while in Gyzyl bughda, Murov 2, and Ferrigineum 2/19 genotypes, it was low (3.5, 3.6, and 2.9%). The highest values of the rate of photosynthesis were observed in the drought-exposed genotypes Sheki 1, Aran, Tale 38, and Zirva 85 (14.2, 14.8, 14.1, and 14.3 μmol CO_2 m^{-2} s^{-1}), and in the irrigated genotypes Aran, Vostorg, and 12thIWWYT no. 9 (24.9, 23.4, and 24.0 μmol CO_2 m^{-2} s^{-1}). Stomatal conductance (0.115, 0.120, 0.130, 0.164 mol H_2O m^{-2} s^{-1}), the concentration of CO_2 in intercellular spaces (146.3, 156, 5, 181.7, and 213.7 μmol CO_2mol^{-1}) and the transpiration rate (3.32, 3.58, 4.13 and 4.44 mmol H_2O m^{-2} s^{-1}) were higher in the Sheki 1, Aran, Tale 38, and Zirva 85 varieties, which manifest higher photosynthetic rate under drought conditions than other genotypes. A significant positive correlation of RWC with the rate of photosynthesis, the stomatal conductance, the concentration of CO_2 in intercellular spaces, and the rate of transpiration was found under drought stress conditions.

Аннотация. В статье представлены результаты изучения показателей относительного содержания воды (ОСВ) и параметров фотосинтетического газообмена флаговых листьев у 21 генотипа мягкой пшеницы в условиях богарного земледелия Горного Ширвана. Исследования проводились на засушливых и орошаемых вариантах в фазу налива зерна. ОСВ флаговых листьев генотипов Восторг, Муров 2, Тале 38 и Гырмызы гул 1 выше как в засушливых, так и в орошаемых условиях. Выявлена положительная корреляция между ОСВ и временем колошения и отрицательная корреляция между ОСВ и высотой растения. Средняя разница в ОСВ между орошаемым и засушливым вариантами для всех генотипов составила 10,1%. У линий 12thIWWYT №9 и 12thIWWYT №20 эта разница была высокой (26,5 и 19,6%), а у генотипов Гызыл бугда, Муров 2 и Ferrigineum 2/19 — низкой (3,5, 3,6 и 2,9%). Наиболее высокие значения скорости фотосинтеза отмечены у засухоустойчивых генотипов Шеки 1, Аран, Тале 38 и Зирва 85 (14,2, 14,8, 14,1 и 14,3 мкмоль CO_2 м$^{-2}$ с$^{-1}$), а на орошаемых генотипы Аран, Восторг и 12thIWWYT №9 (24,9, 23,4 и 24,0 мкмоль CO_2 м$^{-2}$ с$^{-1}$). Устьичная проводимость (0,115, 0,120, 0,130, 0,164 моль H_2O м$^{-2}$ с$^{-1}$), концентрация CO_2 в межклетниках (146,3, 156, 5, 181,7 и 213,7 мкмоль CO_2 моль$^{-1}$) и скорость транспирации (3,32, 3,58, 4,13 и 4,44 ммоль H_2O м$^{-2}$ с$^{-1}$) были выше у сортов Шеки 1, Аран, Тале 38 и Зирва 85, проявляющих более высокую скорость фотосинтеза в условиях засухи, чем другие генотипы. В условиях засухи обнаружена достоверная положительная корреляционная связь ОСВ со скоростью фотосинтеза, устьичной проводимостью, концентрацией CO_2 в межклетниках и скоростью транспирации.

Keywords: flag leaf, soft wheat, drought stress, relative water content.

Ключевые слова: флаговый лист, мягкая пшеница, стресс вызванный засухой, относительное содержание воды.

Introduction

Being the main food of people, wheat is the most cultivated plant in the world, including our country. Due to the absence of the possibility to expand the cultivated areas, the most effective way to meet the growing demand of the population in modern times, is to increase the harvest from a single area. Increasing the productivity of wheat can be realized by the development of varieties that are resistant to diseases and pests, have high stability, and are suitable for the ecological conditions of each region. The productivity of agricultural crops is limited by a number of abiotic factors and among them, drought is considered to be at the top. One of the complex measures envisaged to protect field plants from drought is the creation of drought-tolerant varieties [3]. Plants are considered drought-tolerant if they can adapt to the effects of drought during their ontogenesis without a severe loss for themselves and their generations. Establishing the mechanism of drought tolerance in plants is a very complex and time-consuming process. Therefore, it is important to study the morphological and physiological characteristics of plants under different growing conditions. Photosynthesis is one of the main physiological processes in the formation of plant productivity, and more than 90% of dry biomass is formed at the expense of organic matter formed during this process [3, 14, 17]. Drought strongly affects the gas exchange parameters of cultivated plants, detains the growth of leaves, disrupts the photosynthetic mechanism, accelerates the oxidation of chloroplast lipids, and causes changes in the structure of pigments and proteins [6, 15]. The intensity of photosynthesis depends not only on the species of plants but also on the influence of external environmental factors. Lack of water primarily leads to a decrease in stomatal conductance and plants try to maintain the water regime by decreasing transpiration. As a result, the amount of carbon dioxide absorbed by the leaves also decreases [1, 10]. The most effective way to limit water loss is to decrease stomatal conductance by closing the stomata to a certain extent, as a result of which the amount of carbon dioxide entering the leaves and its concentration in intercellular spaces decrease [12]. Water scarcity ultimately leads to disruption of gas exchange during the photosynthesis process and a decrease in productivity. Thus, the photosynthesis process plays an important role in the formation of plant productivity, and the rate of this process strongly depends on the water supply of plants. Therefore, the study of the relative water content of leaves and photosynthetic gas exchange parameters under water deficiency and normal water supply conditions is of both scientific and practical importance.

Materials and Methods

The research was conducted at the Gobustan Regional Experimental Station (GRES) of the Research Institute of Crop Husbandry. The experimental site is located at an altitude of 800.0 m above sea level and has a light chestnut soil type. According to the average multi-year data, the atmospheric precipitation amount in the region is 350.0-400.0 mm (data from Gobustan Hydrometeorological Station). The objects of the research were 12 varieties and 9 lines of soft wheat differing in morphophysiological characteristics. Planting was conducted in 3 repetitions in the form of randomly placed blocks using experimental beds of 1.0 m^2 and the sowing rate was 450 seeds per 1 m^2. To make a difference in water supply, late drought conditions were created artificially in early May by covering one block with a transparent polyethylene material, while the second block was irrigated.

Parameters of photosynthetic gas exchange such as photosynthesis rate — P_n, stomatal conductance — g_s, concentration of carbon dioxide (CO_2) in intercellular spaces — C_i, and transpiration rate — T_r were measured using a Portable Photosynthesis System LI-COR 6400 XT (LI-Cor Biosciences, Lincoln, USA) equipped with a 6 cm^2 leaf chamber (Long, Bernacchi, 2003). In this system, the rate of photosynthesis ($\mu molCO_2\ m^{-2}s^{-1}$) and transpiration ($mmol\ H_2O\ m^{-2}s^{-1}$) is calculated based on the difference in concentrations of CO_2 and water vapor in the air flow entering and leaving the chamber. Gas exchange parameters were recorded 45 seconds after the leaf was placed in the chamber. Measurements were conducted in 5-7 repetitions. Relative water content (RWC) was determined in fully mature flag leaves. For this, the samples were taken at the hottest time of the day (between 14^{00} and 15^{00}). The collected leaf samples were placed in plastic bags and brought to the laboratory, the bottom and tip parts were cut, the remaining part was weighed on an analytical scale and the fresh weight was determined (FW) [2]. Then, the leaf samples were placed in numbered test bottles containing distilled water and refrigerated at 4°C for one day until saturation. After a day, the leaves were completely dried with filter paper, weighed again, and the turgid weight (TW) was determined. Then, numbered tags were attached to the leaves and dried in a thermostat until constant weight at 85°C, and dry weight (DW) was determined. Based on the determined weights, the relative water content of the leaves was calculated as a percentage according to the following equation [9]: $RWC\ (\%) = [(FW-DW) / (TW-DW)] \times 100$, where FW — fresh weight, TW — turgid weight, DW — dry weight.

The results were analyzed in JMP 5.0.1 statistical software package.

Results and Discussion

Leaf relative water content (RWC) is a measure of plant water status and is used as an important indicator of drought tolerance and reflects metabolic activity in tissues [7]. A decrease in relative water content in response to drought stress was observed in various plant species [16]). Under drought stress, the water balance of plants is disturbed, and as a result, the relative water content (RWC) and water potential (Ψ) of leaves decrease [8]. Due to its connection to drought tolerance, leaf RWC can be considered a better indicator of water stress than other morphophysiological and biochemical parameters of plants [11]. In several studies, it was noted that the difference in RWC of durum wheat genotypes under water stress conditions was related to their ability to absorb more water from the soil and control its loss through stomata [5]. At the same time, under conditions of water shortage, the genotypes maintain a high level of RWC, as a result of the deeper penetration of the root system, more water can be absorbed, and it may be due to the limitation of water loss through the synthesis of osmotic active substances in the leaves [4].

A long period of vegetation of the wheat plant occurs throughout the spring and early summer. The intensity of the morphophysiological processes taking place in the plant during this period plays an important role in the formation of productivity. Under rainfed conditions, which are not provided with moisture, precipitation is not stable in the spring-summer period and drought stress is experienced from time to time. Leaf RWC, which expresses the share of the water from the total content, is an indicator of the difference between water assimilated from the soil and evaporated by genotypes simultaneously. The relative water content of flag leaves of 21 soft wheat genotypes was determined under drought stress and irrigated conditions in Mountain Shirvan, where moisture is not stable. Determinations were performed in the hottest period of the day between 14^{00} and 15^{00} during the grain filling phase and the results are shown in Figure 1.

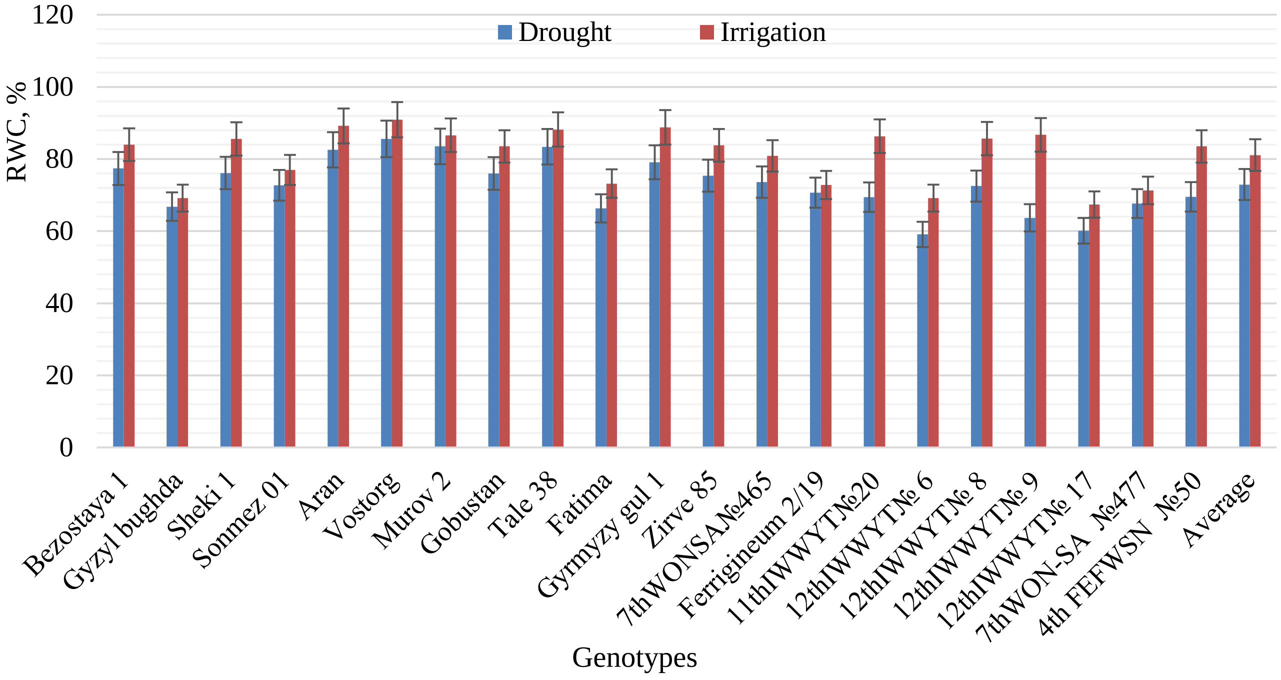

Figure 1. Relative water content in flag leaves of the studied genotypes

As seen in Figure 1, the average values of the relative water content of the flag leaf in the studied genotypes were 72.9% and 81.1% under drought stress and irrigated conditions, respectively. In the drought variant, the variation between genotypes was 26.5% (59.1-85.6%), and in the irrigated variant, it was smaller and amounted to 23.5% (67.4-90.9%). High values of the parameter were found in Vostorg, Murov 2, Tale 38, Gyrmyzy gul 1, and Aran genotypes in both drought-exposed and irrigated variants. Although the Sheki 1 variety showed high results in the irrigated variant, its relative water content in the drought-exposed variant was at the average level. In the irrigated variants, a larger number of genotypes showed high results. The smallest values of RWC were detected for the genotypes 12thIWWYT no. 6, 12thIWWYT no. 17, 12thIWWYT no. 9, Fatima, Gyzyl bughda, 7thWON-SA no. 477, and Ferrigineum 2/19 under both drought and normal conditions. Genotypes with higher RWC were found to be late earing while those with a lower RWC were mostly early earing. The flag leaves of the late-earing varieties were younger on the day of the experiment, which we believe can explain the above fact. It should be noted that the RWC of early-earing varieties such as Murov 2, Gobustan, Zirva 85, and 7thWON-SA no. 465 are at the upper or middle level. This can indicate that the tolerance of these varieties against dehydration was higher on that day. The correlation between the RWC values of the genotypes and the earing time was examined, and significant correlations were observed with r=0.51* in drought-exposed and r=0.54* in irrigated variants (Figure 2).

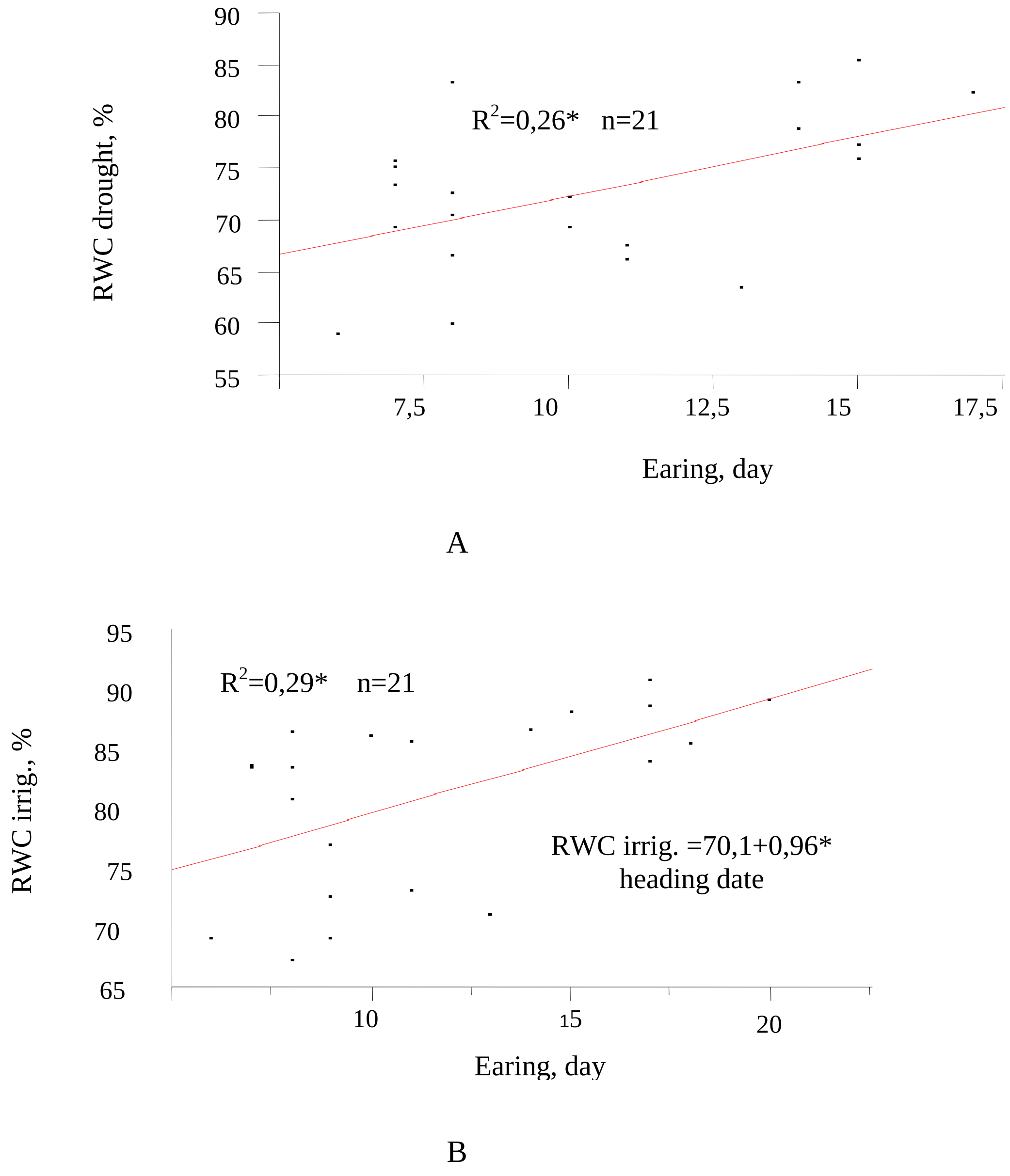

Figure 2. Correlation between relative water content and earing time. Note: A — drought, B — irrigation

Although a positive correlation between RWC and earing time was expected in the drought-exposed variants, this relationship was also detected in the irrigated variant. We believe this correlation is due to the genotypic difference in the water retention capacity of the flag leaves of the genotypes. The relationship between the relative water content of the flag leaf and the plant height of the investigated genotypes was examined. A negative correlation equal to $r=-0.53^*$ and $r=-0.46^*$ was observed in drought-exposed and irrigated variants, respectively. Thus, the height of the plant plays a limiting role in the transfer of water absorbed from the soil to the upper parts of the plant. It can be concluded that although plant height plays a certain role in plant tolerance to drought conditions, it also creates an obstacle in the transfer of water absorbed from the soil to the upper parts of the plant.

According to the average values, there was a 10.1% difference between the RWC values determined in the irrigated and drought variants of the genotypes. This difference was the highest in the 12thIWWYT no. 9 and 11thIWWYT no. 20 lines, being 26.5 and 19.6%, respectively, and in the Gyzyl bughda, Murov 2, and Ferrigineum 2/19 genotypes, these values were low and amounted to 3.5, 3.6, and 2.9%, respectively. The big difference between the lines 12thIWWYT no. 9 and 11thIWWYT no. 20 is due to small RWC values in the drought-exposed variants. A small difference was observed between Gyzyl bughda and Ferrigineum 2/19, because RWC values were small in both variants, and in Murov 2, they were big in both variants. Therefore, when studying the difference in the values of this parameter between the irrigated and drought-exposed variants, it is also necessary to pay attention to its absolute values. From this point of view, the small difference between the genotypes Gyzyl bughda and Ferrigineum 2/19 does not indicate that they absorb water at a high level and that their leaves have a high-water retention capacity. In Murov 2, the small difference is accompanied by a high absolute value of RWC, so it can be an indicator of good absorption and retention of water even in the drought-exposed variants. In the 12thIWWYT no. 9 and 11thIWWYT no. 20 lines, the low values of RWC in the drought-exposed variants can be considered as the result of the greater effect of water deficiency.

Table 1 presents the results of measuring photosynthetic gas exchange parameters. The variance analysis showed significant differences at the 0.01 level of significance between the studied genotypes in all measurements for the values of photosynthetic gas exchange parameters. Based on the least significant difference (LSD), distinction groups were found, in which genotypes a, b, c, etc. were located in groups and differences between genotypes were visible. The highest values of the rate of photosynthesis in the drought-exposed variants were 14.2, 14.8, 14.1, and 14.3 μmol CO_2 $m^{-2}s^{-1}$, respectively, in the Sheki 1, Aran, Tale 38, and Zirva 85 varieties. In the irrigated variant, the highest values of this parameter were observed in the Aran, Vostorg, and 12thIWWYT no. 9 genotypes (24.9, 23.4, and 24.0 μmol CO_2 m^{-2} s^{-1}). It should be noted that in the genotypes Sheki 1, Aran, Tale 38, and Zirva 85, the photosynthetic rate of which was high in the drought-exposed variants, stomatal conductance (0.115, 0.120, 0.130, 0.164 mol H_2O m^{-2} s^{-1}), the concentration of CO_2 in intercellular spaces (146, 3, 156.5, 181.7 and 213.7 μmol CO_2 mol^{-1}) and the rate of transpiration (3.32, 3.58, 4.13 and 4.44 mmol H_2O m^{-2} s^{-1}) were higher compared to other genotypes. In the drought-exposed variants of the genotypes Gobustan, 7thWON-SA no. 465, 12thIWWYT no. 8, and 12thIWWYT no. 17, low values were found for the parameters such as the rate of photosynthesis (8.7, 9.1, 7.4, and 8.3 μmol CO_2 m^{-2} s^{-1}) stomatal conductance (0.040, 0.049, 0.044, and 0.047 mol H_2O m^{-2} s^{-1}), CO_2 concentration in intercellular spaces (70.17, 91.7, 96.02, and 97.35 μmol CO_2 mol^{1}), and the rate of transpiration (1.43, 1.54, 1.43, and 1.33 mmol H_2O m^{-2} s^{-1}). In the irrigated variants, the lowest values of those parameters were observed in Sheki 1, Gobustan, and 12thIWWYT no. 8 genotypes. It should be noted that the genotypes with high values of T_r also have high stomatal conductance, while the genotypes with low T_r values have low stomatal conductance. This shows that the rate of transpiration is mainly regulated by stomatal conductance.

Table 1

PHOTOSYNTHETIC GAS EXCHANGE PARAMETERS
OF FLAG LEAVES IN STUDIED GENOTYPES

Genotypes	P_n $\mu molCO_2m^{-2}s^{-1}$		g_s $molH_2Om^{-2}s^{-1}$		C_i $\mu molCO_2mol^{-1}$		T_r $mmolH_2Om^{-2}s^{-1}$	
	drought	*irrigation*	*drought*	*irrigation*	*drought*	*irrigation*	*drought*	*irrigation*
Bezostaya 1	13.6 b-f	15.7 l	0.093 d.e	0.269 e.f	117.3 e	259.5 b	2.95 e	5.53 g-i
Gyzyl bughda	13.6 c-f	18.9 g-i	0.098 d	0.228 g.h	122.8 e	211.3 f.g	2.93 e	5.46 h-j
Sheki 1	14.2 a-c	18.5 h.i	0.115 c	0.18 k	146.3 c.d	188.8 j.k	3.32 d	4.85 k.l
Sonmez 01	11.1 h.i	19.5 f.g	0.055 i.j	0.217 h.i	91.39 g.h	196.8 i-k	2.01 g.h	5.26 i-k
Aran	14.8 a	24.9 a	0.12 c	0.35 c	156.5 c.d	220.3 e.f	3.58 c	6.81 b.c
Vostorg	13.2 e.f	23.4 b	0.09 e.f	0.462 a	157.8 c	256.7 b	2.81 e.f	7.96 a
Murov 2	13.4d-f	19.4 g.h	0.09 d.e	0.265 e.f	115.5 e.f	224.8 d.e	2.89 e	5.84 e-h
Gobustan	8.7 m	16.3 k.l	0.04 l	0.2 i-k	70.17 i	221.2 e.f	1.43 i	4.78 l
Tale 38	14.1 a-d	20.8 c.d	0.13 b	0.3 d	181.7 b	229.0 d.e	4.13 b	6.28 d.e
Fatima	11.9 g	18.9 g-i	0.08 f.g	0.212 h-j	125.7 e	199.5 h-j	2.57 f	5.8 f.g.h
Gyrmyzy gul 1	13.1 e.f	19.8 d-g	0.112 c	0.348 c	171.8 b	273.8 a	3.65 c	6.09 e.f
Zirva 85	14.3 a.b	18.0 i.j	0.164 a	0.264 f	213.7 a	235.3 c.d	4.44 a	6.72 c.d
7thWON-SA no. 465	9.1 l m	21.4 c	0.049 j-l	0.308 d	91.7 g.h	228.8 d.e	1.54 i	6.73 c.d
Ferrigineum 2/19	11.8 g.h	19.6 e-g	0.071 g.h	0.286 d.e	117.3 e	229.5 d.e	2.26 g	6.06 e.f
11thIWWYT no. 20	12.9 f	20.6 c-e	0.095 d.e	0.218 h.i	143.3 d	185.8 k	3.04 e	5.93 e-g
12thIWWYT no. 6	9.4 k.l	21.3 c	0.062 h.i	0.232 g.h	122.2 e	191.8 j.k	2.00 h	5.54 g-i
12thIWWYT no. 8	7.4 n	16.5 k.l	0.044 k.l	0.248 f.g	96.02 g	241.7 c	1.43 i	5.03 j-l
12thIWWYT no. 9	13.8 b-e	24.0 a.b	0.086 e.f	0.417 b	99.22 g	241.5 c	2.55 f	7.27 b
12thIWWYT no. 17	8.3 m	20.4 c-f	0.047 j-l	0.204 i.j	97.35 g	186.5 k	1.33 i	4.74 l
7thWON-SA no. 477	9.8 j.k	17.2 j.k	0.053 i.j	0.195 j.k	103.5 f.g	208.8 g.h	1.48 i	4.73 l
4thFEFWSN no. 50	10.5 i.j	16.1 l	0.053 i-k	0.179 k	81.72 h.i	203.3 g-i	1.89 h	4.66 l
Average	*11.9*	*19.6*	*0.083*	*0.266*	*124.9*	*220.7*	*2.58*	*5.81*
LSD	*0.77***	*1.0***	*0.0093***	*0.0222***	*13.44***	*11.3***	*0.26***	*0.48***
CV %	*5.7*	*4.5*	*9.9*	*7.2*	*9.4*	*4.5*	*8.7*	*7.1*

Note: **correlation is significant at 0.01 significance level

The study of photosynthetic gas exchange parameters, especially the relationship between the rate of photosynthesis and other morphophysiological characteristics of genotypes, is of both theoretical and practical importance. Table 2 shows the correlations between photosynthetic gas exchange parameters and relative water content (RWC), which determines daytime water status in the flag leaves of genotypes and earing time. As seen in the table, the highest correlation was observed between photosynthetic gas exchange parameters and the relative water content of the leaves.

Thus, under drought conditions, RWC has a significant positive correlation with the rate of photosynthesis, stomatal conductance, the concentration of CO_2 in intercellular spaces, and the rate of transpiration. In the irrigated variants, significant correlations with other parameters were noted, except for the rate of photosynthesis. It suggests that the significant correlation between the relative water content of the leaf and the photosynthetic gas exchange parameters is a result of the regulation of stomatal conductance by RWC, which determines the leaf water status. The absence of a correlation between the rate of photosynthesis and RWC in the irrigated variants is probably due to the fact that contrary to the drought conditions, in this case, the rate of photosynthesis is more dependent on other morphophysiological characteristics of the genotypes.

Table 2

CORRELATION BETWEEN PHOTOSYNTHETIC GAS EXCHANGE PARAMETERS
AND SOME MORPHOPHYSIOLOGICAL CHARACTERISTICS

	Drought				*Irrigation*			
Parameters	P_n	g_s	C_i	T_r	P_n	g_s	C_i	T_r
RWC	0.49^{*}	0.47^{*}	0.45^{*}	0.53^{*}	ÖD	0.53^{*}	0.51^{*}	0.47^{*}
Earing time	0.59^{**}	0.47^{*}	0.43^{*}	0.50^{*}	ÖD	0.50^{*}	ÖD	ÖD

Note: **correlation is significant at 0.01 significance level, *correlation is significant at 0.05 significance level

Conclusions

Under rainfed conditions, the relative water content and photosynthetic gas exchange parameters of the flag leaf of winter bread wheat depended on the water supply. Genotypic differences in the value of the studied parameters were observed. A positive correlation was observed between RWC and earing time, and a negative correlation was found between RWC and plant height. The average difference in RWC between irrigated and drought-exposed variants was 10.1% for all genotypes. A significant positive correlation was found between RWC and the rate of photosynthesis, stomatal conductance, concentration of CO_2 in intercellular spaces, and the rate of transpiration under drought stress conditions. It was concluded that the relative water content and photosynthetic gas exchange parameters of the flag leaf can be applied in the selection process of winter bread wheat.

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