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Winter wheat flag leave morphometric traits under drought

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Abstract

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Comprehensive studies of winter wheat plants genetic variability at morphological, physiological, genetic, cellular and molecular levels under unfavorable conditions are relevant to prevent the negative impact of climate change yields. In two-year field experiments studied flag leaf morphometric and pigments traits of 6 modern varieties of winter wheat under natural drought during the periods of reproductive organs formation as well as grain filling. Under drought high-productive winter wheat varieties are characterized by high flag leaf dry weight at anthesis and a lower ratio of carotenoids to chlorophyll at milk ripeness it was found. A positive relationship between the grain productivity of the main shoot ear of winter wheat, as well as yield and flag leaf dry weight at anthesis was established. Based on the literature data, the presence of quantitative traits loci in wheat chromosomes that affect drought tolerance through the regulation of flag leaf assimilation apparatus traits was analyzed. The higher yields of varieties with the best features of the assimilation apparatus of the flag leaf under natural drought in both years of research it has been suggested that genes that control drought tolerance may be linked to genes that affect on the assimilation apparatus characteristics.

Keywords: soft winter wheat (*Triticum aestivum* L.); drought tolerance; leaf dry weight; yield

Introduction

Wheat, which is a strategic grain crop in the world with sown areas of more than 200 million hectares (Rauf et al., 2015), is a drought-sensitive plant. Drought is considered to be the main factor in the annual variability of wheat yield, which is about 40% in the main zones of its cultivation worldwide (Zampieri, 2017). A middling appraisal yield losses in agricultural crops due to drought stress in foremost wheat-producing countries range from 10 to 50% (Zulkiffal et al., 2021). Improving the drought tolerance of this crop remains an urgent task today in Ukraine, where almost all sown areas of cultivated plants are at constant risk of crop loss in dry years (https://mepr.gov.ua...2020). Analytical analysis of the effects of climate change has shown a high probability that global climate change will worsen the conditions for agricultural crops in Ukraine on 2 million hectares of land (Ivanyuta, 2020). Drought, depending on duration and severity of stress, as well as the phenological stages, causes negative effect on wheat grain productivity (Farooq et al., 2014). So, post-anthesis mild drought decreased wheat yield by 1–30%, while a prolonged mild drought during the anthesis and filling stages reduced grain yields by 58–92% (Zhang et al., 2018). Drought during grain filling primarily reduces grain weight, as well as the speed, duration and quality of grain filling, which ultimately leads to significant crop losses.

The drought negative effects on wheat during the vegetative phase limited carbohydrate synthesis for cell division and expansion via stomatal closure and partial inhibition of photosynthesis (Zhang et al., 2018). And during reproductive period it is associated with flag leaf senescence speed-up, reduced carbon assimilation, impaired photosynthetic metabolism and damage to the structure of the photosynthetic apparatus and cellular structures by reactive oxygen species (Golldack et al., 2011; Stasik et al., 2020). All this leads to limited grain filling, unbalanced production of growth hormones, as well as changes in the activity of enzymes involved in carbon metabolism, both in organs-donor of metabolite and acceptors ones (Abid et al., 2018).

Tissue dehydration, which occurs during drought, also changes plant physiological and biochemical processes, affects on the growth processes, anatomy and morphology (Elbar et al., 2019; Kappor et al., 2020). In particular, it affects on morphological and physiological characteristics of leaves assimilation apparatus, which plays an important role in the efficiency of photosynthesis (Morgun et al., 2019). Morphological changes can contribute to the water use efficiency and ensure optimal carbon metabolism to increase plant tolerance to drought. Therefore, the research of the adaptive capacity of these traits will help to understand the mechanisms of drought adaptation. In addition, although many drought-resistant chromosomes are already known (Edae et al., 2014; Gahlaut et al., 2017; Ballesta et al., 2020; Rabby et al., 2021), the important question remains whether these chromosomes and genomic regions in them are connected with morphological and biochemical features of the leaf assimilation apparatus. Detection of morphometric and critical physiological markers of drought tolerance will accelerate a breeding and their further researches by molecular genetic methods.

Since the flag leaf serves as an essential source of assimilates during grain filling, believe that their high-throughput phenotyping is crucial to determine their physiological and genetic basis of yield formation and drought adaptation (Siddiqui et al., 2021). Due to this the aim of the study was to comparative analyses of the morphometric traits of the flag leaf under the drought for an identify markers related to its tolerance to water insuffisance, to further elucidate the mechanisms underlying the drought resistance of winter wheat.

Materials and Methods

Experiment was conducted in 2019/2020 and 2020/2021 growing seasons at the experimental field of the Institute of Plant Physiology and Genetics of National Academy of Science of Ukraine (Kyiv region) under natural moisture conditions. The soil was light-gray, podzolized, light-loamy.

The plant material were 6 medium-early varieties of soft winter wheat (*Triticum aestivum* L.): Kyivska 17, Horodnytsia, Pochaina, Poradnytsia, Krasnopilka and Smuhlianka. The field designs were randomized complete blocks with three replications. Each plot was 6.7 m long with 10 rows spaced 15 cm, the area of each block was 10 m^2. During the growing season, 145 kg of nitrogen and 90 kg of phosphorus and potassium per hectare ($N_{145}P_{90}K_{90}$) were added. The seed rate, agrotechnics and canopy management are generally accepted for this culture in the forest-steppe agro-climatic zone (Morgun et al., 2015).

The period of winter wheat vegetation in 2019-2020 was characterized by a significant (by 1.1-5.5°C) increase in average daily air temperature compared to the long-term climatic norm, except for May, when it was lower than the norm by 3.1^{0}C. In February, April and May in 2021, on the contrary, air temperature was lower by 1.1-2.2°C, but in another month it exceeded the climatic norm. In both researched years, during the period of reproductive organs formation, the air temperature was lower (by 1.1 and 3.1°C in 2020 and 2021, respectively) than the climatic norm, and during grain-filling period, conversely, was higher than norm (by 1.4 and 3.3°C). In addition, the period of autumn vegetation and spring regrowth in 2020 was characterized by less than normal rainfall, while in May it was more than twice as high. Conditions for the spring-summer growing season of wheat in 2021 were more favorable.

The level of territory moisture supply was assessed by Selyaninov's hydrothermal coefficient (HTC): HTC= $(\Sigma R \times 10)/\Sigma t$, where ΣR and Σt – accordingly sum of precipitations and temperatures in the period, when the temperature has not been lower than 10°C (Selyaninov, 1928). The period of reproductive organs formation in 2020 was characterized by arid conditions (HTC in June was 0.78), and of grain filling – very arid (0.64), in 2021 these two periods, respectively, were very arid (0.38) and arid (0.83). In both years, excessive moisture was noted in May, but during periods of reproductive organs formation and grain filling were observed arid conditions. HTC in June and July was below 1, which corresponds to satisfactory moisture supply (Figure 1).

Determination of morphometric and pigments parameters was performed on main shoots, which were cut on ground level, biochemical – in the average samples formed from these shoots. The number of main shoots at anthesis and milk ripeness was 10, at full ripeness – 20. At the crop maturity, 20 winter wheat plants were harvested manually at the ground level from each plot. Weight of grain per plant, number of grains in an ear, 1000 grains weight were determined separately on the main and side shoots. These plants were separated into leaves, stems and sheaths, spike axis and glumes, and grains

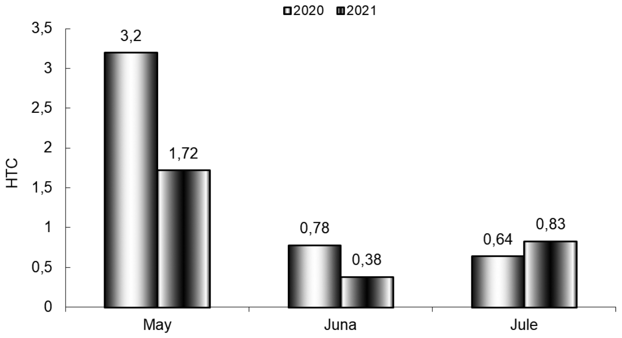

Fig. 1. Selyaninov's hydrothermal coefficient during periods of reproductive organs formation and grain filling in 2020 and 2021

To determine the dry weight of individual plant organs, the fixation was performed at a temperature of 105°C for 3 hours and then dried to constant weight at a temperature of 65°C. The leaves area was counted upon by their length and width with a koefficient of 0.75. Specific leaf weight (SLW) calculated dividing the dry weight of leaves by their surface area. Leaf angle is defined as the inclination between the midrib of the leaf blade and the vertical stem of a plant (Shiman, 1967). Grown stages (GS) were identified on the basis of external morphological characteristics of formed organs every 3-4 days (Zadoks et al., 1974).

The chlorophyll *a* and *b*, as well as total carotenoids content were extracted from the leaf disks using non-maceration method with dimethyl sulfoxide by the method of A.P. Wellburn (Wellburn, 1994). The recalculation of the pigment content per g of fresh weight was performed taking into account all dilutions and the leaves weight. Every sample for determine the pigments content was averaged from the leaves of 5 plants. The pigments content was determined at 3 replicates.

The data were statistically analyzed using "Microsoft Excel" according to generally accepted methods of variation statistics (Dospekhov, 1973) and criterion of reliable differences of Tukey's test for average values. The results are expressed as means and standard error (m ± SE). Significant differences between the data were determined by LSD ($p \leq 0.05$) and are represented at figures and tables with different letters.

Results

Under the conditions of natural drought, the highest yields in both years were winter wheat varieties Kyivska-17 and Horodnytsia (Figure 2a). The grain productivity of the ear of main shoot of these two varieties was also higher than others, with the exception of variety Pochaina in 2021 (Figure 2b).

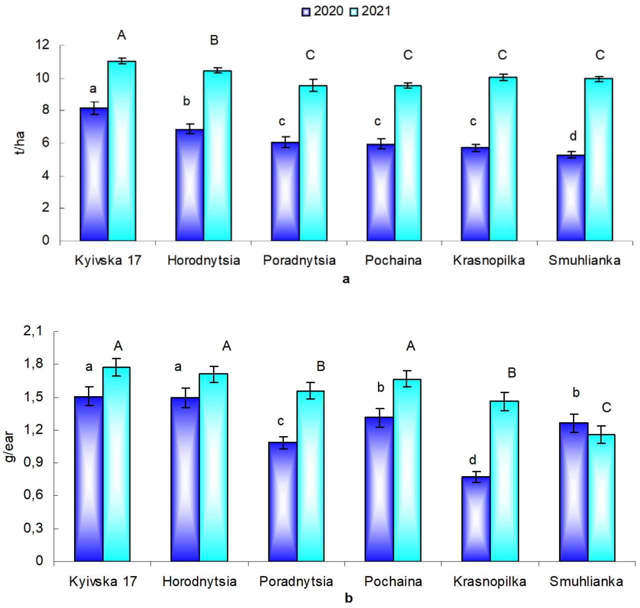

Fig. 2. Yield, t/ha, (a) and grain productivity of main shoot ear, g, (b) of winter wheat varieties in years with drought stress during both periods of grain formation and filling

Note: meanings denoted by the same Latin letters (lowercase – 2020, uppercase – 2021), differ insignificantly at $p \leq 0.05$

Analysis of the variability of the assimilation surface was performed on some traits during the reproductive stages of wheat varieties: flag leaf angle, area, dry weight, as well as specific leaf weight.

A characteristic feature of 6 winter wheat varieties is the erect upper leaves: the angle of inclination of the flag and sub-flag leaves to the stem at anthesis (GS 65) and milk ripeness (GS 75) did not exceed 45°. The erect position of leaves on the stem at milk ripeness contributes to better illumination of the stem, which also has photosynthetic ability. Wheat varieties with erect leaves have a superior net carbon fixation capacity due to greater absorption of light energy by the elements of the crop. This assumption is confirmed by the results of mathematical modeling, which showed that carbon uptake by plants in crops with erect upper leaves is significantly higher than with horizontal, both under conditions of perpendicular incidence of sunlight on a clear day and when the sun's angles decrease (Long et al., 2006). Therefore, equal position of upper leaves suggest that all varieties differed insignificantly in radiation regime within crops and in the access of carbon dioxide.

The highest total chlorophyll content (Chl a+b) in the average sample of green leaves at anthesis in both years was varieties Kyivska 17 and Pochaina, the lowest – varieties Krasnopilka and Poradnytsia (Table 1). At milk ripeness the highest chlorophyll content in 2020 remains in the leaves of variety with the highest yield (Kyivska 17) and – with the lowest yield (Poradnytsia), in 2021 – in the varieties Kyivska 17 and Pochaina. Thus, of the whole group of varieties, the highest content of photosynthetic pigments in both years was observed in Kyivska 17. This variety, together with Horodnytsia, also had a lower ratio of carotenoids to chlorophyll at milk ripening (Table 1).

Increased of carotenoid content is associated with plant aging or exposure to unfavorable factors (Vermaas, 1993). Therefore, a decrease of chlorophyll content against the background of an increase of carotenoids content (i.e., an increase in their ratio) may indicate unfavorable conditions or the prevalence of aging. A smaller value of this ratio, than in other varieties, at milk ripeness was noted in the variety Kyivska 17 in both years and in the variety Horodnitsia in 2021. Thus, the best functional state of the pigment apparatus of varieties Kyivska 17 and Horodnytsia at later stages of ontogenesis can be considered as one of the traits of the adaptive potential of their assimilation apparatus under drought.

The highest flag leaf area at anthesis in both years had varieties Kyivska 17 (respectively, 33.5±1.7 and 43.3±1.9 cm^2 in 2020 and 2021) and Horodnytsia (30.8±1.6 and 36.7±1.8 cm^2), the smallest – variety Smuhlianka (24.2±1.1 and 25.6±1.2 cm^2). At milk ripeness its larger area was retained by variety Kyivska 17 (35.4±1.7 and 37.2±1.2 cm^2) and the lowest values were observed in the Krasnopilka variety (17.1±2.0 and 26.2± 0.8 cm^2). In both years the main shoot leaves area at

Table 1. The content (mg/g of fresh weight) and the ratio of photosynthetic pigments in flag leaves at anthesis and milk ripeness

Variety	Pigments content, mg/g of fresh weight		Ratio	
	Chlorophyll Chl (a+b)	Carotenoid (Car)	Chl a/b	Car/Chl (a+b)
	Anthesis, 2020			
Kyivska 17	3.43±0.10a	0.51±0.02a	1.82±0.02a	0.15±0.01a
Horodnytsia	2.82±0.01b	0.45±0.01b	1.77±0.01b	0.16±0.01a
Smuhlianka	2.85±0.11b	0.46±0.01b	1.80±0.02a	0.16±0.01a
Pochaina	3.24±0.16a	0.50±0.02a	1.75±0.03b	0.16±0.01a
Krasnopilka	2.66±0.11b	0.40±0.01c	1.76±0.02b	0.15±0.01a
Poradnytsia	2.68±0.15b	0.48±0.01a	1.84±0.04a	0.18±0.01ab
	Milk ripeness, 2020			
Kyivska 17	3.30±0.10a	0.47±0.01a	1.78±0.05a	0.14±0.01a
Horodnytsia	2.87±0.04b	0.48±0.01a	2.03±0.02b	0.17±0.01b
Smuhlianka	2.86±0.09b	0.46±0.01a	1.87±0.03c	0.16±0.01b
Pochaina	2.55±0.05c	0.39±0.01b	1.81±0.02a	0.16±0.01b
Krasnopilka	2.39±0.03d	0.40±0.01b	1.92±0.05c	0.17±0.01b
Poradnytsia	3.03±0.04e	0.47±0.01a	1.84±0.01cd	0.17±0.01b
	Anthesis, 2021			
Kyivska 17	3.19±0.11a	0.53±0.01a	3.10±0.07a	0.17±0.01a
Horodnytsia	2.90±0.07b	0.49±0.02b	3.12±0.04a	0.17±0.01a
Smuhlianka	2.83±0.09b	0.52±0.01a	3.23±0.07b	0.18±0.01a
Pochaina	3.24±0.06a	0.60±0.01c	3.10±0.05a	0.18±0.01a
Krasnopilka	2.76±0.06bc	0.55±0.02a	3.33±0.01c	0.20±0.01b
Poradnytsia	2.77±0.05bc	0.52±0.01a	3.19±0.06b	0.19±0.01ab
	Milk ripeness, 2021			
Kyivska 17	2.89±0.10a	0.54±0.01a	3.20±0.01a	0.19±0.01a
Horodnytsia	2.54±0.09b	0.48±0.02b	3.39±0.11b	0.19±0.01a
Smuhlianka	2.33±0.09c	0.50±0.01c	3.41±0.05b	0.21±0.01ab
Pochaina	2.77±0.14b	0.56±0.03a	3.33±0.05bc	0.20±0.01ab
Krasnopilka	2.22±0.07c	0.48±0.02b	3.41±0.03b	0.22±0.01b
Poradnytsia	2.41±0.08bc	0.53±0.02a	3.35±0.05bc	0.22±0.01b

Note: here and in table 2 meanings denoted by the same Latin letters differ insignificantly at $p \leq 0.05$.

anthesis in more productive varieties Kyivska 17 (respectively, 91.7±4.8 and 135.8±5.0 cm^2 in 2020 and 2021) and Horodnytsia (81.5±2.8 and 103.7± 4.1cm^2) was higher than in other varieties, too. Besides, in the variety Kyivska 17 it exceeded the value in other varieties and at milk ripeness. A similar pattern was found for dry weight of the flag leaf and all leaves of the main shoot (Table 2): high-yielding varieties had higher than less-yielding, dry weight of leaves in both years.

Wherein SLW of flag leaves at anthesis in year with drought during grain filling (HTC = 0.38, 2021) of high-productive varieties ranged within their values in year with less severe drought (HTC = 0.78, 2020): respectively 5.4-5.6 and 5.4-5.8 mg/cm^2, while in less-productive ones differed significantly: respectively, 5.9-6.1 and 4.8-5.2 mg/cm^2. At milk ripeness, regardless of the degree of drought, high-yielding varieties exceeded less-productive ones. The difference between different yield varieties by SLW of flag leaves was more significant in the later stages of ontogenesis. Thus, the comparative analysis of the two-year datas of specific flag leaf weight showed that in more productive varieties it exceeded the value of less productive at milk ripeness.

The main marker of wheat's tolerance to drought is considered its yield, however, since high-yielding varieties also differed in greater ear grain weight of the main shoot (Figure 2), we analyzed the relationship between morphometric parameters with both indicators.

Ear grain productivity of the main shoot at anthesis by 85-70% was determined by flag leaf dry weight, at milk ripeness – 70-82% (Figure 3a). The influence of the flag leaf area on grain productivity of the main shoot ear was slightly smaller – respectively, the coefficients of determination of this relationship were 68 and 59% at anthesis and 63 and 41% at milk ripeness (Figure 3b). The influence of SLW on the grain productivity of the main shoot ear at first stage varied significantly over the years of research: in 2020 the coefficient of determination reached 91%, and in 2021 was

Table 2. Dry weight of individual leaves and main shoot ones, mg, of six winter wheat varieties

Сорт	N of leaf (from top)				Main shoot
	1 (flag)	2	3	4	
	Anthesis, 2020				
Kyivska 17	181±13a	138±6a	98±6a	13±9a	430±24a
Horodnytsia	179±13a	129±9a	96±6a	10±7a	414±24a
Smuhlianka	120±6b	104±4b	69±11b	9±8a	302±17b
Pochaina	155±9c	103±4b	76±6b	16±9a	350±10c
Krasnopilka	118±7b	121±7a	89±4a	18±8a	345±11c
Poradnytsia	130±5b	103±4b	74±10b	29±12b	337±24c
	Milk ripeness, 2020				
Kyivska 17	202±12a	108±13a	-	-	311±17a
Horodnytsia	138±9b	79±8b	31±10a	-	247±13b
Smuhlianka	126±6b	63±10b	7±5b	-	197±11c
Pochaina	145±8b	62±14b	26±11a	-	233±14b
Krasnopilka	84±11c	42±10c	19±6a	-	145±19d
Poradnytsia	86±5c	72±5b	-	-	158±7d
	Anthesis, 2021				
Kyivska 17	240±11a	173±6a	134±4a	58±16a	605±18a
Horodnytsia	195±7b	126±4b	100±5b	15±10b	437±19b
Smuhlianka	137±8c	112±6c	91±5b	32±13c	372±19c
Pochaina	181±12b	131±5b	100±7b	56±16a	468±15b
Krasnopilka	180±6b	99±4ad	82±5c	52±12a	414±19b
Poradnytsia	158±8d	168±7a	114±7bd	72±13a	511±19d
	Milk ripeness, 2021				
Kyivska 17	207±8a	179±5a	129±7a	25±13a	540±23a
Horodnytsia	182±7b	98±6b	47±14b	16±11a	343±24b
Smuhlianka	133±6c	125±8c	71±13c		329±22b
Pochaina	190±12b	142±9d	98±13c		430±19c
Krasnopilka	140±6c	114±4c	86±6c	12±8a	351±14b
Poradnytsia	183±10b	162±8a	104±13c		449±19c

insignificant, at milk ripeness – was close to both years 69 and 64% (Figure 3c).

The coefficient of determination of the relationship between yield and dry weight of flag leaf at anthesis was close in both years (74% in 2020 and 69% in 2021). While at milk ripeness it differed significantly, respectively – 60 and 8% (Figure 4a). The flag leaf area at anthesis determined the yield by 94 and 74%, respectively, in 2020 and 2021, at milk ripeness – by 49 and 5% (Figure 4b). The influence of the specific leaf weight on the yield in both phases was low (Figure 4c).

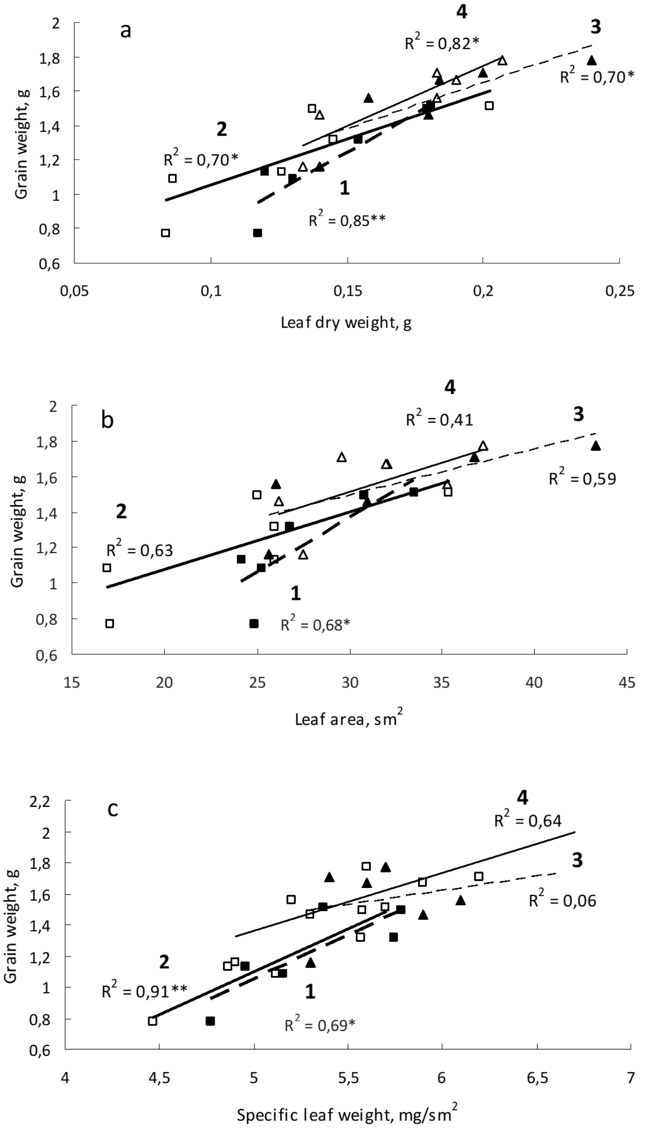

Fig. 3. Linear correlation between grain weight of main shoot ear of winter wheat grown under natural drought and traits related to flag leaf morphology of main shoots at anthesis (lines 1 (■), 3 (▲)– respectively, 2020 and 2021) and milk ripeness (2 (□) and 4(Δ)): a – dry weight, b – area, c – specific leaf weight

Note: *, ** – correlation coefficient is significant at p ≤0.05 and 0.001, respectively

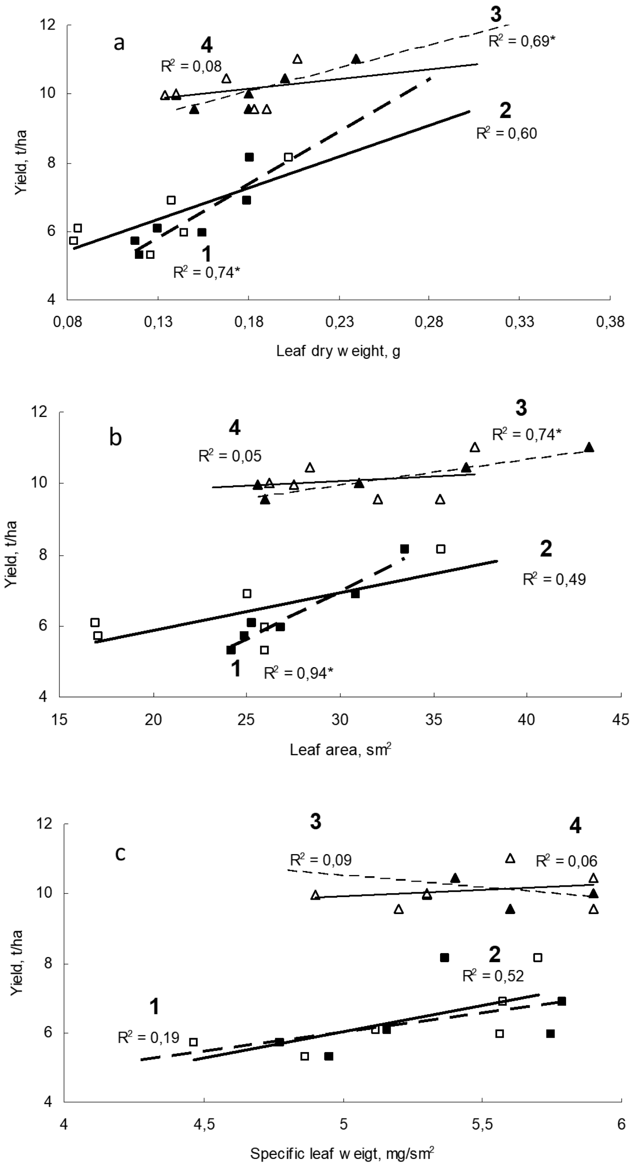

Fig. 4. Linear correlation between yield of winter wheat grown under natural drought and traits related to flag leaf morphology of main shoots at anthesis (lines 1, 3 – respectively, 2020 and 2021) and milk ripeness (2 and 4): a – dry weight, b – area, c – specific leaf weight

Note: *, ** – correlation coefficient is significant at p ≤0.05 and 0.001, respectively

According to the correlation analysis, in both years the dependence of grain weight of main shoot ear was significant and positive with flag leaf dry weight at anthesis (r = 0.92±0.19 and 0.84±0.28) and at milk ripeness (r = 0.84±0.28 and 0.90±0.21). The flag leaf dry weight at first stage (r = 0.86±0.26 and 0.83±0.28) and its area (r = 0.97±0.13 and 0.86±0.28) were closely correlated with the winter wheat yield.

Thus, in years with drought conditions during the period of grain formation and filling, both the ear grain weight of the main shoot and the yield were closely related to flag leaf dry weight at anthesis. The posistive correlation of this trait under such conditions indicates that the flag leaf dry weight at this stage can serve as a morphometric marker of a tolerance of winter wheat to drought.

Discussion

A positive correlation was found between various traits related to flag leaf morphology with ear grain weight or yield (Johnson et al., 1990; Quarrie et al., 2006; Isidro et al., 2012; Al-Tahir, 2014; Rahal-Bouziane et al., 2018). In particular, the analysis of the dependence between the length and area of the flag leaf of 120 recombinant inbred lines (F8), obtained by crossing two varieties of wheat with high yields (Q9086) and high drought resistance (Longjian 19), and ear weight, as well as yield showed close relationship between them (Yang et al., 2016).

We found that the high-yielding varieties had a higher dry weight of the flag leaf at anthesis. On the one hand, this contradicts the idea that a smaller flag leaf by limiting water loss (due to transpiration) under drought conditions can contribute to better drought tolerance. However, on the other hand, its larger size allows the synthesis of more assimilates that can be used for the growth of other organs, including roots, the growth of which can contribute to better use of water from the soil. In particular, it has been shown that even a 5% increase in the distribution of assimilates between root and shoot in favor of the root led to a 50% increase in aboveground biomass of winter cereals on the 100th day of growth (Richards, 1987).

In addition, a significant part of modern wheat varieties has wheat-rye translocation (1BL.1RS or 1AL.1RS). The contribution of the rye genome can also contribute to greater drought tolerance, in particular by preserving the area of leaves and the content of photosynthetic pigments in them. Thus, we have previously established that in the winter wheat variety Favoritka, which contains wheat-rye translocation 1BL.1RS, under conditions of soil drought during the period of earing – anthesis, the total chlorophyll content decreased by 25% compared to the variant with sufficient water supply, while Myronivska 808 without such translocation decreased more – by 35% (Morgun et al., 2016). The chlorophyll *b* content was significantly reduced in the variety without translocation. Thus, the pigment apparatus of winter wheat containing wheat-rye translocation did not undergo significant structural changes, while in the variety without translocation there was a decrease in the number of light-harvesting complexes relative to the reaction centers of photosystems in thylakoid membranes. Better ecological plasticity of winter wheat varieties with wheat-rye translocations is also associated with their remontancy (Morgun, 2016).

Higher drought tolerance of wheat varieties with wheat-rye translocation is confirmed by their higher yields. In particular, it was found that under conditions of limited water supply (one watering per vegetation) the lines of durum wheat of the cultivar Seri M82 with translocation of the T1BL.1RS chromosome had a higher yield (2.9 t/ha), than isogenic lines 1B (2.6 t/ha), while under optimal conditions (five irrigations) they did not differ significantly (7.5 and 7.6 t/ha) (Villareal et al., 1998). In six-year experiments, it was found that Ukrainian winter wheat varieties with translations 1AL.1RS and 1BL.1RS were on 0.87-0.95 t/ha higher than varieties without translocations (Morgun, 2016). At the same time, the influence of translocation on grain yield depends on both environmental conditions and genetic characteristics (Peake et al., 2011).

In addition, the influence of flag leaf traits on wheat grain productivity may be related to the functional activity of its photosynthetic apparatus. Thus, it was found that differences in the photosynthesis rate among different genotypes of C_3 plants are associated with their biochemical traits of leaves, as well as morphological and anatomical structure (Sharkey, 1985). The positive effect of leaf blade enlargement may be due to the increase of chloroplasts number per unit area of leaf and photosynthetic enzymes, including Rubisco Lambers et al. (2008), von Caemmerer & Farquhar (1981) and Poorter et al. (2009). Which, in turn, can affect their photosynthetic activity. In particular, the increase in grain productivity of the whole plant (30-40% compared to wild type) in transgenic wheat lines of generation T4 with increased levels and activity of the Calvin-Benson cycle enzyme sedoheptulose-1,7-bisphosphatase (SBPase), is associated with increased leaves photosynthic capacity (Driever et al., 2017).

Thus, both own and literature data show that the best adaptive capacity of the assimilation apparatus of winter wheat plants, which increases their yield under drought, is related to their morphological changes, as well as optimal carbon metabolism and effective functional activity of the photosynthetic apparatus.

Detection of morphometric and physiologic markers of drought tolerance is important to accelerate the wheat breeding, as stable quantitative trait locus (QTL) mapping is considered one of the promising ways to improve wheat resistance to this stress. A number of chromosomes and genomic regions in them are already known to be associated with drought tolerance. Edae and co-authors consider the most important chromosomes 1B, 4AL, 5B, 6B, 7A and 7B (Edae et al., 2014). The key role of chromosome 4A in drought tolerance has been established by studying the drought resistance of 382 varieties and promising lines of the Institute of Agriculture of Chile and Uruguay and the International Center for Wheat and Corn Improvement (CIMMYT) (Ballesta et al., 2020). Specific genomic regions of chromosomes 5A and 7A are also considered important for improving wheat tolerance to drought (Gahlaut et al., 2017). Six drought-related QTLs were identified on chromosome 7B, 2B and 2D (Rabby et al., 2021) by analyzing quantitative trait locus of spring wheat inbred lines derived from a cross between drought-resistant Reeder and high-yielding Albany. Twenty stable QTL morphological traits potentially useful for genetic improvement of wheat drought resistance have been identified on different chromosomes (Yang et al., 2016).

There is also a lot of data in the literature on chromosomes associated with markers of wheat flag leaf assimilation apparatus. Thus, QTL related to flag leaf size (length, width and area) was found in spring wheat chromosomes 1B, 2B, 2D, 3A, 3B, 3D, 5B, 6A and 6B, together with QTL of 1000 grain weight, grain weight and grain filling period (Edae et al., 2014). Two specific intervals of the marker Xwmc694-Xwmc156 on chromosome 1B and Xbarc1072-Xwmc272 on chromosome 2B were identified, which are re-

Table 3. Some chromosomes that control drought resistance of spring and winter wheat and flag leaf assimilation apparatus traits (in parentheses – literature source)

Chromosomes, associated with drought resistance*	Flag leaf traits		
	morphological	pigment	photosynthetic apparatus activity
1B	Length, width, area (Edae et al., 2014)	Chlorophyll content (Peleg et al., 2009)	Minimum fluorescence yield of PS II (Ilyas et al., 2014)
	Length, width, area & angle (Yang et al., 2016)		
	Width & angle (Liu et al., 2018)		
2B	Length, width, area (Edae et al., 2014)	Rate of senescence (Verma et al., 2004)	Maximum quantum yield of PS II (Li et al., 2014; Siddiqui et al., 2021)
	Length, width, area & angle (Yang et al., 2016)	Chlorophyll content (Peleg et al., 2009, Bhusal et al., 2018)	
	Length & width (Liu et al., 2018)	Chlorophyll and carotenoids content (Li et al., 2014)	
	Fresh biomasse (Siddiqui et al., 2021)		
4A	Fresh biomasse (Siddiqui et al., 2021)	Chlorophyll content (Zhang etal. 2009)	
5A	Length, area (Liu et al., 2018)	Chlorophyll content (Peleg et al., 2009; Puttamadanayaka et al., 2021)	Maximum quantum yield of PS II (Czyczylo-Mysza et al., 2011)
	Fresh weight (Verma et al., 2021)	Chlorophyll and carotenoids content (Li et al., 2014)	
5B	Width (Isidro et al., 2012)	Chlorophyll content (Peleg et al., 2009, Bhusal et al., 2018; Puttamadanayaka et al., 2021)	Maximum quantum yield of PS II (Fv/Fm) (Li et al., 2014)
	Length, width, area (Edae et al., 2014)	Chlorophyll and carotenoids content (Li et al., 2014)	
6B	Length, width, area (Edae et al., 2014)	Chlorophyll content (Li et al., 2014)	
	Area (Puttamadanayaka et al., 2021)	Greenness index (Siddiqui et al., 2021)	
	Angle (Liu et al., 2018)		

*Note** – according to literature data

lated to the length, width, area and angle of the flag leaf (Yang et al., 2016). The presence of four marker intervals on chromosome 5B (Isidro et al., 2012) related to the width of the flag leaf has been confirmed. Analysis of the intergeneric population of recombinant inbred crossbreeding lines of drought-resistant wheat varieties C306 and HUW206 showed that QTL, which controls the potential quantum efficiency of photosystem II (QFv/Fm.ksu-3B) and chlorophyll content (QChl) under local conditions chromosome 3B in the marker range Xbarc68– Xbarc101 and explain 35–40% of phenotypic variations for each trait (Kumar et al., 2012). It was also found that QTLs associated with photosynthesis are located on chromosomes 5D, 6D, 7D, with indicators of photosynthetic activity – on 4A and 2D (Kulkarni et al., 2017).

Analysis of the literature shows that some chromosomes that contain drought-resistant QTL also have quantitative trait locus that affect the morphological, biochemical characteristics of wheat flag leaf and indicators of functional activity of its photosynthetic apparatus (Table 3).

The location of QTL on the same chromosomes associated with drought tolerance and photosynthetic apparatus of the wheat flag leaf may indicate that genes, controlling drought tolerance may be linked to genes that control traits of the assimilation apparatus and can be jointly inherited. QTLs with a pleiotropic effect or multiple linkages are considered potential target regions for mapping and selection using markers in wheat breeding programs (Liu et al., 2018).

Conclusions

Our results show that all researched varieties of winter wheat were characterized by erect upper leaves. This contributed to the same radiation regime within their crops and access of carbon dioxide to plants, but did not affect the adaptation of varieties to drought.

Analysis of the ratio carotenoids/chlorophyll at milk ripeness revealed that under drought during the grain filling period, the most productive varieties of winter wheat have a better functional state of the pigment apparatus at late stages of ontogenesis. A positive relationship between the grain productivity of the main shoot ear of winter wheat, as well as yield and flag leaf dry weight at anthesis was established. Thus, flag leaf dry weight at anthesis could be used as selection criteria in winter wheat breeding for drought tolerance. Detection of morphological and physiological traits associated with winter drought tolerance of wheat may be the basis for further study by molecular genetic methods and accelerate the selection process. This study also showed the presence of links between drought tolerance loci and flag leaf photosynthetic components. What can be used to increase the yield of winter wheat and sustainability to water-deficit stress.

Based on the literature, it has been suggested that drought tolerance genes may be linked to genes that affect the assimilation apparatus and may be co-inherited. This assumption is confirmed by the higher yields of varieties with the best traits of flag leaf assimilation apparatus under natural drought, in both years of research.

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