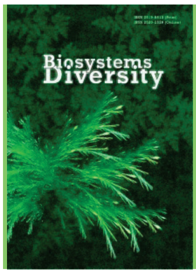

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Depositing capacity of winter wheat stem segments under natural drought during grain filling in Ukrainian forest steppe conditions

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Drought is a major abiotic factor adversely affecting wheat productivity. Water deficit reduces significantly photosynthesis and hence the remobilization of stored assimilate reserves from the stem becomes important sources for grain filling. We assessed the ability of different stem internodes and leaf sheaths to deposit and remobilize reserve assimilates as well as their role in grain yield formation in 6 winter wheat varieties under drought conditions during the period of grain filling. The dry weight and content of water-soluble carbohydrates in the dry matter of stem internodes and leaf sheaths of the main shoot was determined at anthesis, the beginning of milk ripeness and full grain ripeness. The total amount of water-soluble carbohydrates in stem segments was calculated as the product of their specific content in the dry matter of the stem segment and its mass. The amount of remobilized dry matter and water-soluble carbohydrates for each segment was estimated as the difference between the appropriate values at anthesis or milk ripeness and full ripeness. The maximum accumulation of water-soluble carbohydrates in the stem was reached at early milk ripeness. The most productive varieties Kyivska 17 and Horodnytsia had the largest amount of remobilized water-soluble carbohydrates in all internodes. Depositing capacity of the second and third (counting from the top) internodes was higher compared to others and has a significant effect on the grain productivity of wheat varieties studied. Despite significant variability and strong genotype x year interaction of the relationships between depositing capacity traits of different stem segments and grain productivity, mainly tight correlations were found for dry matter and total water-soluble carbohydrates accumulation and remobilization in second and third internodes with yield and grain weight per spike. The obtained data suggests that the remobilization of deposited water-soluble carbohydrates is an important factor contributing to the filling of winter wheat grain in arid conditions and more detailed studies of relationships of depositing capacity of individual stem segments with yield can be useful for development of breeding tools for further genetic yield improvement.

Keywords: *Triticum aestivum* L.; culm reserves; water-soluble carbohydrates; internodes; yield; arid conditions.

Introduction

Wheat, which occupies more than 200 million hectares in the world, is considered as one of staple grain crops (Rauf et al., 2015; Bondarenko & Nazarenko, 2020; Nazarenko, 2020). Within the period 2016–2020, on average 753–763 million tons of wheat grain was produced annually in the world (Food Outlook – Biannual Report on Global Food Markets. Food Outlook, Rome). The benefits of wheat are brought about by its nutritional value and many other factors. In particular, the use of winter wheat reduces the intensity of farming work both during spring sowing period and during harvest due to its earlier, compared to spring wheat, ripening. Wheat plays an important role in the field crop rotation as a precursor to several other crops (Onopriienko et al., 2020; Miroshnychenko et al., 2021). The unique properties of gluten allow wheat to be used to make bread, bakery and pasta. In addition, wheat grain is an important constituent of Ukraine's export earnings. According to the Ministry of Economy, wheat exports in 2021 increased about 1.5 times compared to 2015 and reached 20.5 million tons (Cheremisina, 2021). Exports of cereals, a third part of which were wheat, accounted for 19.2% of Ukraine's total export earnings.

However, the problem of providing humanity with wheat grain has been exacerbated in recent years by adverse climate change. Drought is one of the most important causes of wheat yield loss (Lesk et al., 2016; Matiu et al., 2017; Leng & Hall, 2019; Masliev et al., 2020). This problem is especially relevant for Ukraine, as almost all cultivation areas are in the zone of risky agriculture under a constant risk of crop loss in dry years (Ivanyuta et al., 2020). The frequency of droughts in the country has almost doubled in the last 20 years. There is a high probability that global warming will lead to worsening climate conditions on 2 million hectares of land in 10 years. At the same time, the average grain yield in the Steppe zone, where almost half of cereal crop areas are concentrated, is declining already now despite its growth nationwide. Thus, the average yield of grain crops for the last five years in the Forest-Steppe and Polissya increased by 46–61% compared to 1990 but decreased by 10% in the Steppe (Ivanyuta et al., 2020).

All of the above testifies to the relevance of research on ways to improve wheat tolerance to drought. It is known that drought is particularly harmful to the photosynthetic apparatus: the canopy leaf area, the pigment content, as well as the CO_2 assimilation rate are reduced (Kiriziy et al., 2014). All this leads to a decrease in the amount of assimilates formed during photosynthesis. If the drought occurs during the grain filling period, the deficit of photoassimilates, used for this process, can be compensated to some extent by the remobilization of nutrients deposited in other organs. In particular, the grain filling under drought can occur by consuming water-soluble (non-structural) carbohydrates and other substances, mainly nitrogen-containing compounds capable of remobilization into grains (Ruuska et al., 2006; Pierre et al., 2010; Li et al., 2015; Morgun et al., 2019). It is believed that even in conditions of moderate drought, the grain filling in wheat may depend more on non-structural carbohydrates reserved in the stem than on current photosynthesis (Ehdaie et al., 2006a; Slewinski, 2012). Depending of the genotype, the content of water-soluble carbohydrates (WSC) in the stem can be 20–40% of dry matter (Ehdaie et al., 2008; Zhang et al., 2015).

Many studies have confirmed a positive relationship between the amount of WSC deposited in the stem and grain productivity in plants affected by drought during the reproductive period (Dong et al., 2009; Dreccer et al., 2009; Li et al., 2015; Zhang et al., 2015). It is shown that the share of assimilates remobilized from stem in the final grain yield varies from 20% to 40% under well-watered conditions (Dreccer et al., 2009) and can be more than 70% under drought at the period of grain filling (Ehdaie et al., 2006a; Islam et al., 2021). The increased contribution of deposited assimilates in the formation of grain yield under water-limited condition during grain filling resulted from the inhibition of current photosynthesis.

In recent years, the accumulation of WSC in different segments of the stem (internodes and leaf sheaths) and their role in the process of grain filling have been intensively studied. In particular, significant differences between the upper (peduncle), penultimate and lower internodes were found in the amount of remobilized dry matter (Ehdaie et al., 2006a) and WSC (Ehdaie et al., 2006b) in10 varieties of spring wheat. In some stem internodes of two drought-resistant wheat varieties and their double haploid lines, significant fluctuations in content of fructan (10–60%), the main component of water-soluble carbohydrates of wheat stem, were found (Zhang et al., 2015). It was also observed that the WSC remobilization in lower internodes was higher than in upper ones (Liu et al., 2020).

Studies conducted under different weather conditions revealed a high degree of inheritance of genotypic differences in the WSC content in the stems of wheat (Ruuska et al., 2006). At the same time, the relationship between the storage capacity of the stem and the yield of wheat varieties largely depends on the climatic conditions of the region where the experiments were conducted (Ovenden et al., 2017) and possibility of its use as selection criteria for breeding remains unclear (del Pozo et al., 2016; Sadras et al., 2020). Bearing in mind a usage in breeding practice it is also important to define a most appropriate period of plant ontogenesis (growth stage) when characteristics of stem depositing ability should be evaluated to procure the most representative correlation with grain yield. This necessitates further research on the depositing function of the stem and its role in the production process of wheat for a particular region. However, the studies of the role of different shoot segments in the storage of reserve assimilates and they remobilization during grain filling in winter wheat varieties of Ukrainian selection are scarce.

In this work, we studied the depositing capacity characteristics for different internodes and leaf sheaths of the main shoot and their relationship with grain productivity in winter wheat varieties under arid conditions during the period of grain filling. Elucidation of genotypic characteristics and the role of different internodes of the stem in the deposition and remobilization of reserve assimilates in wheat varieties are important for further genetic yield improvement.

Materials and methods

Six varieties of winter wheat (*Triticum aestivum* L.) were used in this study. Five of them (Kyivska 17, Horodnytsia, Pochayna, Poradnytsia and Krasnopilka) are modern varieties included to the State Register of Plant Varieties Suitable for Distribution in Ukraine in 2017–2018 and an earlier variety Smuhlianka included to the Register in 2003. Field experiments were conducted during the growing seasons of 2019/2020 and 2020/2021 under the conditions of natural rainfall moisture supply at the experimental field of the Institute of Plant Physiology and Genetics of National Academy of Science of Ukraine.

The experimental field has light-grey podzolic light-loamy soil with 1.6% of humus, 0.05% of inorganic nitrogen, 0.04% of mobile phosphorus and 1.3% of exchangeable potassium. Seeds were sown at density 5.70 million seeds per 1 ha in plots 1.5 m x 6.7 m = 10 m^2. Three replicates were applied for each variety. Before sowing and during the growing season, 145 kg of nitrogen (N) and 90 kg of phosphorus (P_2O_5) and potassium (K_2O) were applied per 1 ha. Other field management followed generally accepted local practices for this culture (Morgun et al., 2014).

Meteorological conditions during the experiment differed in some features compared to long-term averages (Table 1). In general, the conditions of spring vegetation of winter wheat in 2020 were worse than in 2021, especially in May when the processes of formation of generative organs are underway. Thus, the average monthly air temperature for May of the first of these years was 3.1 ℃ lower than the climatological normal (CN); some days, the difference was 5–8 ℃. In the second year, the deviation of the average monthly temperature from the CN for May was slightly smaller (1.4 ℃). Furthermore, there was a double excess of precipitation in this month of 2020, while in 2021, it was close to normal.

Table 1
Deviation of meteorological parameters from the climatological normal (CN) and Selyaninov's hydrothermal coefficient (HTC) during the spring-summer vegetation period in 2020 and 2021

Month	Deviation from the CN of average monthly air temperature, ℃		Monthly precipitation, % of climatic norm		Selyaninov's hydrothermal coefficient	
	2020	2021	2020	2021	2020	2021
April	+0.6	–0.2	86	110	–[#]	–
May	–3.1*	–1.4*	214*	119*	3.03	1.72
June	+3.1*	+1.8	62*	33*	0.78	0.38
July	+1.4	+3.3*	67	92	0.64	0.83

Note: [#] – hydrothermal coefficient is calculated for conditions when the air temperature is above 10 ℃; * – the biggest difference (up and down) with the average long-term value for each year.

The temperature regime of summer vegetation was characterized by exceeding the CN in both years. In 2020, a significant excess over the CN was observed from June 6 to July 7 during the period of grain formation and filling. Overall, the average daily air temperature for the period anthesis – milk ripeness exceeded the normal by 5.7 °C, and its maximum values during this period ranged from 26.1 to 33.3 °C. The effect of elevated temperatures in June and July 2020 and in June 2021 was exacerbated by the lack of precipitation. Deficit of soil water moisture for some periods of wheat reproductive development was evidenced by Selyaninov's hydrothermal coefficient (HTC) calculated using the standard formula (Tkachenko, 2015). The level of soil moisture supply in May was excessive – 1.72–3.20 (the normal HTC value equal 1), while in June and July, the meteorological conditions were arid, which did not contribute to the optimal development of wheat crops and grain filling. In general, weather conditions in 2020 were less favourable for the growth and development of wheat, as confirmed by lower than in 2021 yields of the studied varieties (Fig. 1).

The determination of morphometric parameters was carried out using the main shoot of 20 plants, biochemical indices were measured using the composite samples formed from these shoots. Three analytical replicates were taken. Each main shoot was divided into (counting from the top) 1st (peduncle), 2nd (penultimate), 3rd and combined 4th and 5th (lower) internodes and combined sample of leaf sheaths. To determine the dry weight of some plant organs, the samples were fixed in an oven at 105 °C for one hour and then dried to constant weight at 65 °C.

The content of WSC in the dry matter of stem internodes and leaf sheaths of the main shoot was determined at anthesis (GS 65), at the beginning of milk ripeness (GS 73) and full maturity (GS 99). WSC were extracted from 0.5 g of air-dried and ground sample using boiling distiled water. WSC content was quantified by the method of Ermakov et al. (1972). The total amount of water-soluble carbohydrates in stem segments was calculated as the product of their specific content in the dry matter of the stem segment and its mass. The amount of remobilized WSC for each segment was estimated as the difference between the values of total amount at anthesis or milk ripeness and full ripeness. The magnitude of remobilized assimilates was quantified as the difference between dry weight at anthesis or milk ripeness and full ripeness.

Phenological observations of the stages of plant development were carried out by the external morphological changes of the formed organs every 3–4 days (Zadoks et al., 1974). Indices of the structure of grain productivity were determined on 20 main shoots of winter wheat plants in the phase of full ripeness of grain. Yield was determined by direct harvesting method in three replications of each variety. The accounting area of each of replicates was 10 m^2.

The data were statistically analyzed using ANOVA and criterion of significant differences of Tukey's test for average values. The results are expressed as mean and standard error (x ± SE). Differences between the data were considered significant at $P < 0.05$.

Results

Analysis of grain yield data of the studied winter wheat varieties showed that the varieties more productive under natural drought during the grain filling period were Kyivska 17 (respectively, 8.16 ± 0.39 and

11.04 ± 0.15 t/ha in 2020 and 2021) and Horodnytsia (6.87 ± 0.28 and 10.46 ± 0.17 t/ha, Fig. 1). Yields of the four other varieties ranged from 5.30 to 6.06 t/ha in 2020 and from 9.54 to 10.46 in 2021.

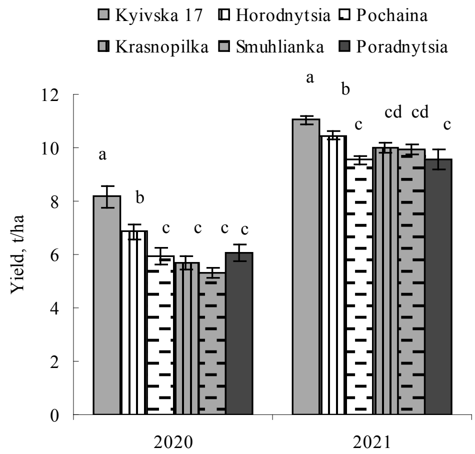

Fig. 1. Grain yield, t/ha, of winter wheat varieties in years with drought at the period of grain filling: x ± SE, n = 3; values, designated by the same letters, are statistically insignificant at P < 0.05 for each year; the vertical bars represent SE

As the weather conditions in 2020 were less favourable for the formation of the winter wheat yield, which led to more significant inter-varietal differences, the results of the 2019/2020 experiment will be presented in more detail below. Only the most important data will be displayed for the 2020/2021 growing season.

In 2020, variety Kyivska 17 stood out by the highest dry weight of the 1st, 2nd and 3rd top internodes at anthesis, while varieties Pochaina and Poradnytsia had the smallest dry weight of the 1st and 2nd internodes, and the 3rd – also Krasnopilka (Fig. 2a). The dry weight of combined 4th and 5th internodes at this stage did not differ significantly in the varieties studied. At early milk stage, the dry weight of 1-3 top internodes increased in comparison with the anthesis by an average of 27-71 mg, but dry weight of lower internodes decreased in all varieties except Kyivska 17 and Smuhlianka (Fig. 2b). At this stage, the dry weight of the 1st (peduncle) internode in more and less yielding varieties fluctuated within close limits; significantly lower values were recorded for the variety Poradnytsia. The dry weight of the 2nd (penultimate) and 3rd internodes in the most productive variety Kyivska 17 exceeded the values of other varieties. At the same time, the dry weight of lower internodes was the highest in the high-yielding variety Kyivska 17 and in the relatively less yielding in Smuhlianka variety (Fig. 2b). In general, the peduncle internode had the lowest dry weight at both anthesis and early milk stage, lower internodes had the highest dry weight at anthesis and the 2nd internode showed maximal dry matter accumulation at early milk stage.

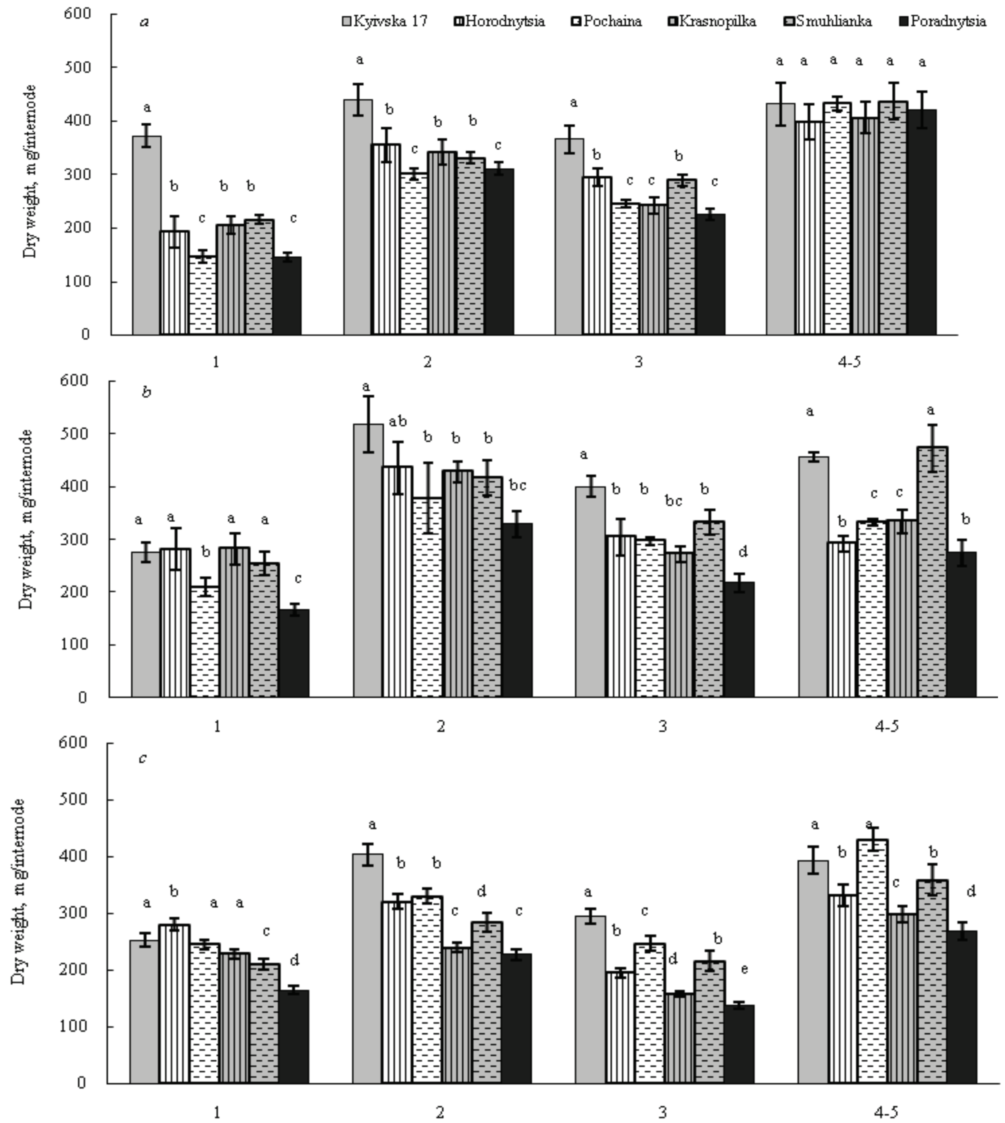

Fig. 2. Dry weight (mg/internode) of different internodes of the main shoot of winter wheat varieties at anthesis (*a*), early milk stage (*b*) and full (*c*) ripeness: x ± SE, n = 20; here and in Figures 3 and 4: values, designated by the same letters, are statistically insignificant at P < 0.05 for each internode; *1* – peduncle, *2* – penultimate, *3* – 3rd internode from top, 4–5 – 4–5th internodes from top

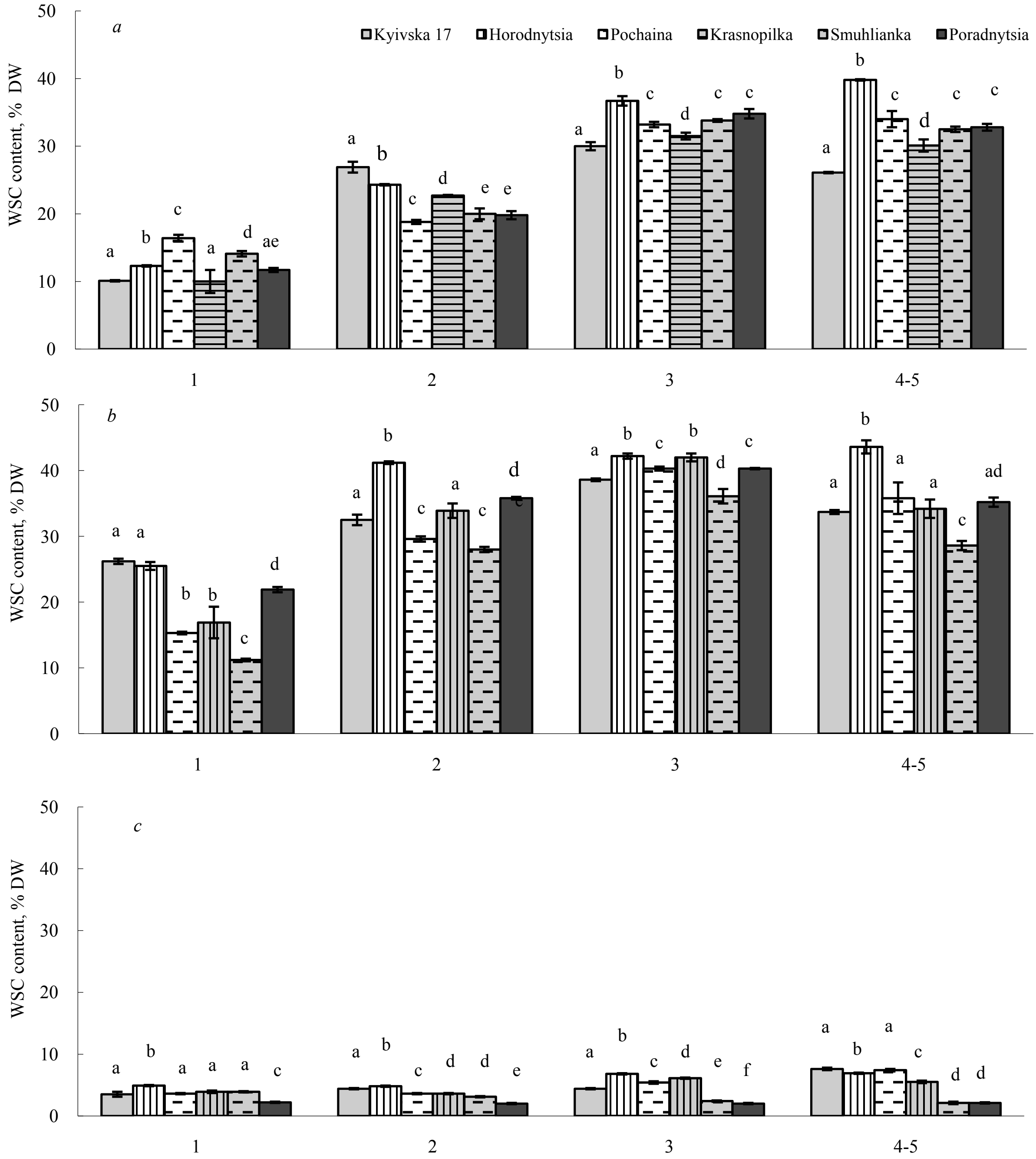

Fig. 3. Specific content of water soluble carbohydrates (% of DW) of different internodes of the main shoot of winter wheat varieties at anthesis (*a*), early milk stage (*b*) and full (*c*) ripeness: x ± SE, n = 20

At full maturity, the content of water-soluble carbohydrates decreased several times, reaching values in the range of 2.1–7.6% (Fig. 3c). The varieties Poradnytsia and Smuhlianka had the lowest values. In general, the highest values of WSC specific content were observed at early milk ripeness, and the lowest at full ripeness.

The total amount of water-soluble carbohydrates in segments of the shoot was determined by weight of segment and specific carbohydrate content. The amount of WSC at anthesis in the peduncle was 2–5 times less than in other stem internodes (Fig. 4a). The highest values were found in lower internodes. At milk ripeness, WSC total amount in all varieties, on average, doubled in the first and second internodes, rose by 28.0% in third internode and remained at about the same level in lower internodes as compared to anthesis (Fig. 4b). Varieties Kyivska 17 and Horodnytsia at this stage stood out by the high amount of carbohydrates in all internodes, especially a significant advantage was recorded for the second internode. Varieties Poradnytsia and Krasnopilka had the lowest values of WSC total amount in internodes below peduncle corresponding to low specific content. In contrast, variety Smuhlianka with lowest WSC specific content in these internodes had middle values of WSC total amount due to higher biomass weight. At full maturity, the WSC total amount in stem internodes decreased dramatically comprising from 4.1% to 18.0% of its value at early milk stage (Fig. 4c). At that, WSC total amount in more productive varieties exceeded its level in less productive ones.

It should be noted that the maximum accumulation of the total amount of water-soluble carbohydrates in all stem internodes, except the lowest, in the wheat varieties studied was observed at early milk ripeness (GS 73). Fall in the total amount of carbohydrates to the stage of full maturity reflects their remobilization and use, mainly for grain filling (Slewinski, 2012). In the varieties Poradnytsia, Smuhlianka and Pochaina, the maximum levels of accumulation of the WSC total amount in 4–5 internodes were found at anthesis, which indicates an earlier onset of remobilization of carbohydrates from the lower internodes in these varieties.

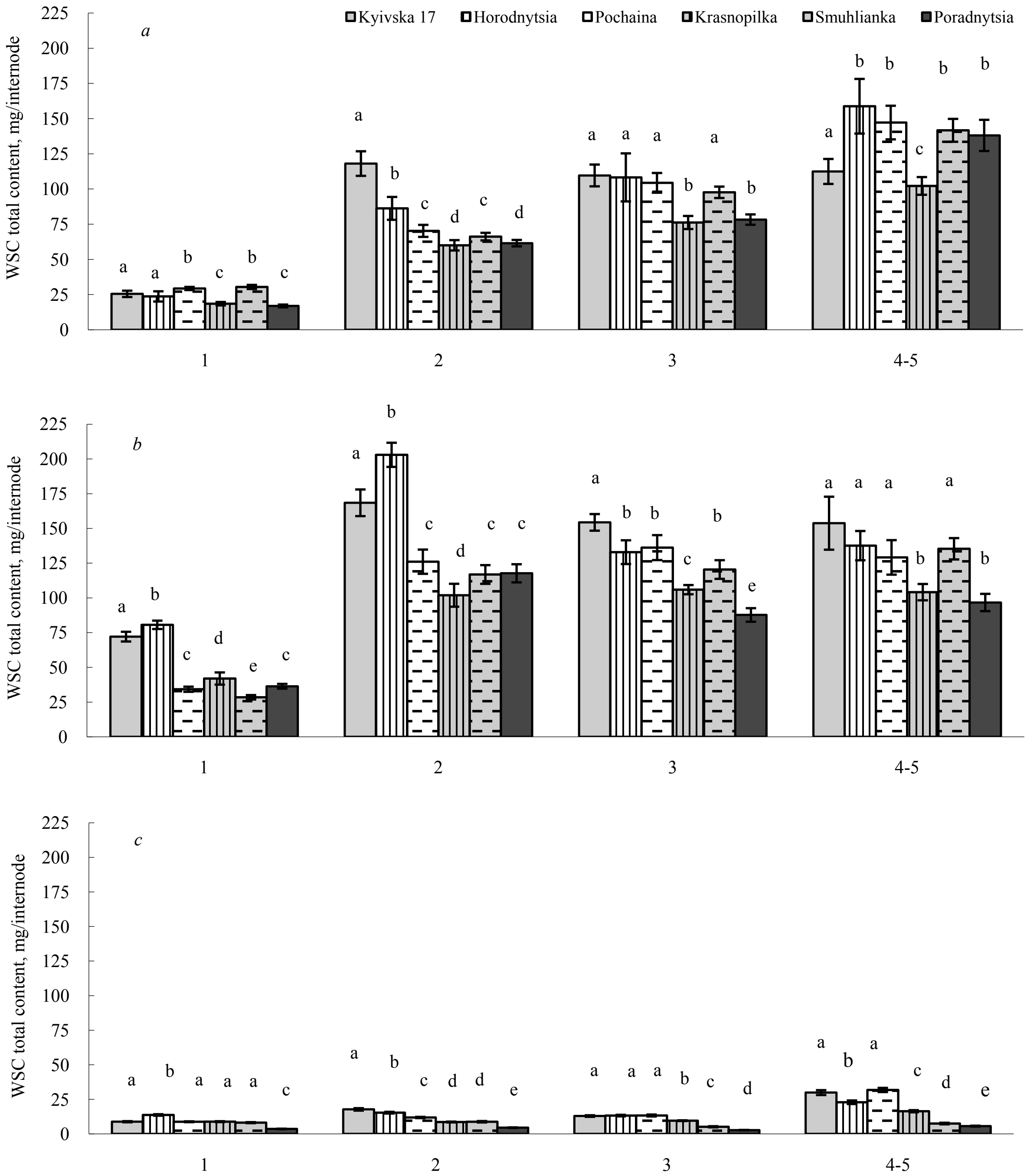

Fig. 4. Total content of water soluble carbohydrates (mg/internode) in different internodes of the main shoot of winter wheat varieties at anthesis (*a*), early milk stage (*b*) and full (*c*) ripeness: x ± SE, n = 20

The dry weight of the sheaths of all leaves at anthesis was almost equal to the dry weight of individual internodes; it ranged from 542 to 596 mg in varieties Kyivska 17, Horodnytsia, Krasnopilka, and Smuhlianka and was lower, 427 and 495 mg, in varieties Pochaina and Poradnytsia, respectively (Fig. 5a). At early milk ripeness, it remained at a high level in the first two varieties and Smuhlianka, but decreased in the others, especially in the varieties Krasnopilka and Poradnytsia. At full maturity, the dry weight of the sheaths decreased compared to maximal values at anthesis, however, it is worth noting that this decrease was smaller than the decline in the stem internodes' weight. More productive varieties, in general, had higher dry weight of leaf sheaths than less productive varieties in all studied development stages. Variety Poradnytsia had the lowest weight of dry matter of sheaths.

Variety Horodnytsia had the highest specific content of water-soluble carbohydrates in leaf sheaths in all studied stages. It had 1.3–2.2 times and 1.1–3.2 times higher WSC content than other varieties at anthesis and early milk stage, respectively (Fig. 5b). Interestingly, variety Poradnytsia also had the high WSC content in the sheaths in all studied phases.

It is worth mentioning that the specific content of WSC in the leaf sheaths was generally 2–3 times lower than in stem internodes. In contrast to the stem, the maximum values of dry weight, the WSC specific content and total amount in the leaf sheaths were recorded at anthesis, not at milk ripeness, and the decrease in carbohydrate levels at the end of the growing season was also weaker than in internodes in almost all varieties. The different dynamics of ontogenetic changes in the level of WSC in the leaf sheaths and stem internodes, apparently to some extent, reflects the different functional role of carbohydrates in these organs. If the accumulation of water-soluble carbohydrates in the stems is mainly related to the temporary storage and use for grain filling, in metabolically more active leaf sheaths, the osmoprotective, regulatory and signaling functions of water-soluble carbohydrates may be more important (Saddhe et al., 2021). The total amount of water-soluble carbohydrates in the sheaths of Horodnytsia was higher than in other varieties at anthesis and at milk ripeness and exceeded its value in other varieties by 1.2–3.7 times (Fig. 5c).

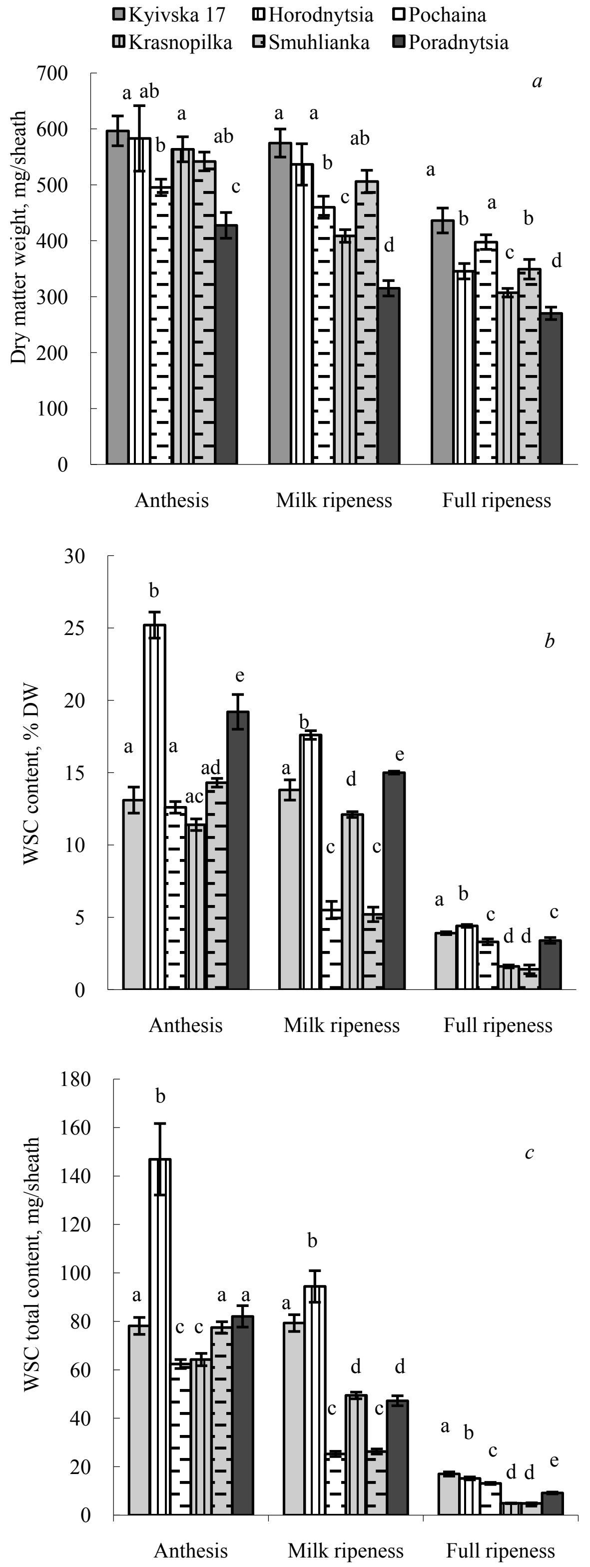

Fig. 5. Dry matter weight (*a*), specific content of water soluble carbohydrates (*b*) and total content of water soluble carbohydrates (*c*) in all leaf sheaths of the main shoot of winter wheat varieties: x ± SE, n = 20; values, designated by the same letters, are statistically insignificant at $P < 0.05$

However, even in this variety, the maximum accumulation of carbohydrates in all leaf sheaths was much smaller than in the second internode of the stem. In most of the studied varieties, the maximum values of the WSC total amount in all leaf sheaths were almost twice less than the maximum values for any stem internodes except the peduncle. During the period of anthesis – full maturity, the total amount of WSC in the sheaths decreased in all varieties by 4.6–15.9 times.

To estimate the amount of assimilates deposited and remobilized for grain filling in individual segments of the stem, the difference between the dry weight for the periods from anthesis to full ripeness and from milk to full ripeness was calculated (Fig. 6), likewise the difference between WSC total amount in these periods was quantified for deposited water-soluble carbohydrates (Fig. 7). It was found that dry weight of the 1st internode at full ripeness significantly decreased compared to anthesis in variety Kyivska 17, practically did not change in Smuhlianka while in other varieties it increased (Fig. 6a). In all lower internodes of all varieties, the dry weight during this period decreased. Thus, a clear pattern of these changes among more and less productive varieties was not revealed. Slightly larger values of weight difference were observed in less productive varieties for 4–5 internodes.

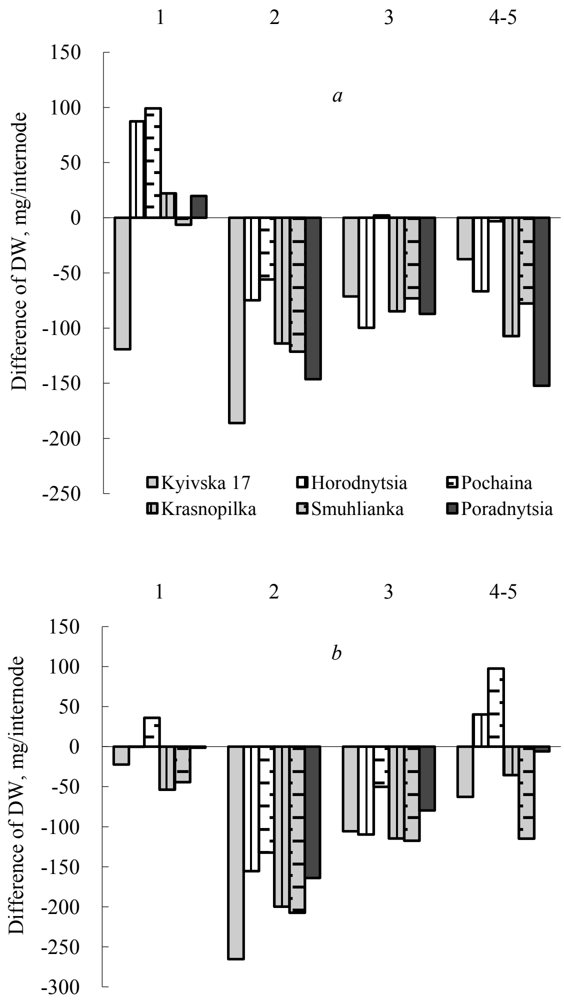

Fig. 6. The difference between the dry weight of internodes at full ripeness and anthesis (*a*) and full and early milk ripeness (*b*); here and in Figure 7: *1*, *2*, *3* and *4–5* – internodes number counting from the top

For the period from early milk to full ripeness, the dry weight of the first internode changed less significantly (Fig. 6b). Changes in the weight of 4–5 internodes were also less pronounced and definite. At the same time, the weight of the second and third internodes during this period decreased significantly in all varieties, reflecting a significant magnitude of assimilates remobilization. High level of biomass remobilization in the second and third internodes was observed both in the high-yielding variety Kyivska 17 and in the less productive variety Krasnopilka and Smuhlianka.

In contrast to the dry weight, the total amount of water-soluble carbohydrates in stem internodes decreased in all varieties for both periods of measurements, reflecting a significant level of remobilization (Fig. 7). The decrease in total amount for the period from anthesis to full maturity in the second internode of the three more productive varieties was stronger than that of three less productive varieties (Fig. 7a). In the third internode, the number of remobilized WSC in the most productive varieties and in the Smuhlianka variety was higher than in the Krasnopilka and Poradnytsia. The largest values of the difference in the total amount of water-soluble carbohydrates for period anthesis – full maturity were recorded for the lower internodes.

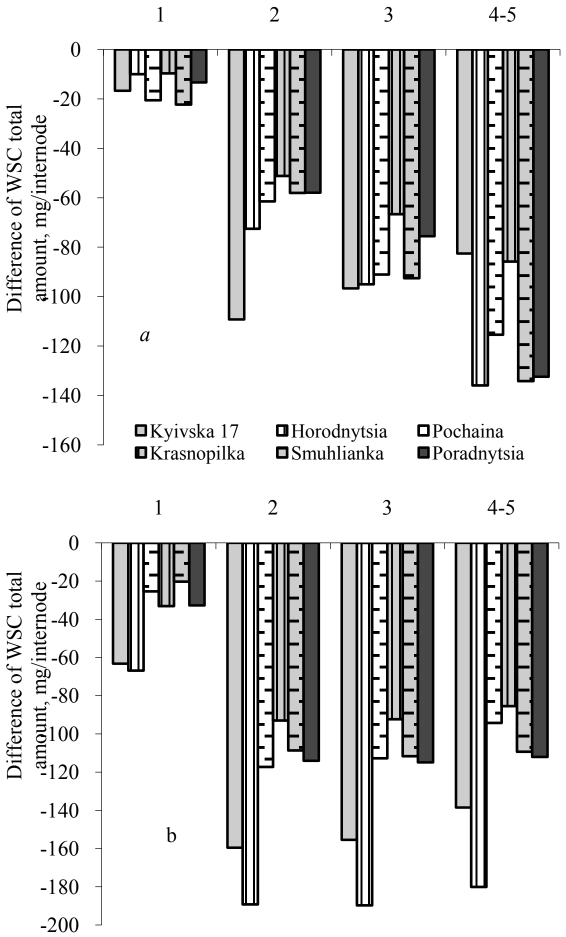

Fig. 7. The difference between the total amount of water-soluble carbohydrates of internodes at full ripeness and anthesis (*a*) and at full and early milk ripeness (*b*)

The values of the difference in the total amount of WSC for the period from early milk to full maturity, in general, were larger than for the period from anthesis to full maturity, and therefore more accurately reflect the storage capacity of stem internodes and the amount of remobilized carbohydrates (Fig. 7b). Higher values for the period from anthesis to full maturity were found only for 4–5 internodes in varieties Pochaina, Smuglyanka and Poradnytsia. In the two most productive varieties Kyivska 17 and Horodnytsia, the amount of remobilized carbohydrates was higher than in other varieties in all internodes.

Different internodes had different contributions to the overall remobilization of water-soluble carbohydrates. The smallest share (5.8–12.2%) was noted for the first internode. The values for the second and third internodes were almost the same and varied between 30.1% and 33.5%, which were slightly higher than for the lower internodes (26.8–31.2%).

At full ripeness, the dry weight of the sheaths of all leaves, as well as the total amount of water-soluble carbohydrates was less than the corresponding values at anthesis and early milk stage in all varieties studied (Fig. 8). Both the more productive variety Horodnytsia and the less productive variety Krasnopilka showed a significant decrease in the dry weight of sheaths during the anthesis period and full maturity. For period early milk – full maturity, a large reduction of dry weight of leaf sheaths was observed in two contrasting by productivity varieties: Horodnytsia and Smuhlianka.

The total amount of water-soluble carbohydrates in the sheaths of all leaves decreased most in the high-yielding variety Horodnytsia for both studied periods, however, for other varieties a certain pattern of this decrease between more and less productive varieties was not observed.

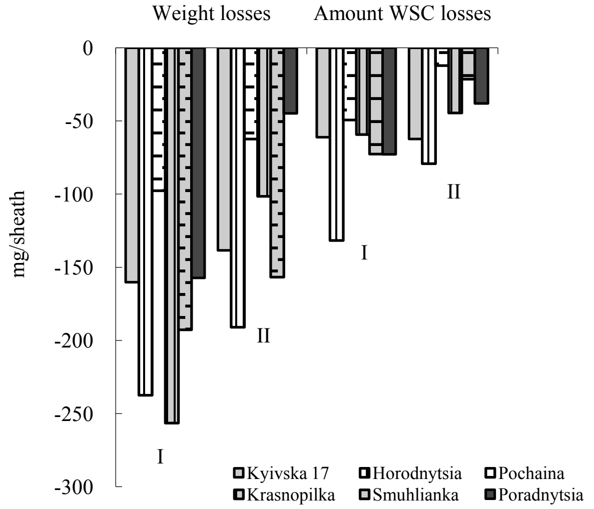

Fig. 8. Magnitude of decrease in the dry weight and the total amount of water-soluble carbohydrates in leaf sheaths (mg) for periods anthesis – full ripeness (I) and early milk – full ripeness (II)

Correlation analysis revealed significant variability and different nature of the relationships between traits of the depositing capacity of different stem internodes and leaf sheaths of the main shoot and grain productivity (Table 2). Mainly strong positive correlations of grain weight per ear and grain yield per hectare in both years of research were observed with dry weight and total amount of water-soluble carbohydrates in some segments of the shoot. Correlations between specific water-soluble carbohydrate content and grain productivity were usually weaker and more variable depending on the year of the study. However, in both years there was a high positive correlation between yield and the specific content of water-soluble carbohydrates in the upper internode at early milk ripeness.

At the same time, it should be noted that the characteristics of stem storage capacity were, for the most part, more closely associated with the grain yield per unit land area than with the grain weight of main shoot ear. Importantly, the values of the correlation coefficients with grain productivity were higher for the total amount of WSC at early milk ripeness compared to the data taken at anthesis.

The grain weight per ear most closely correlated with dry weight of the second and third internodes at anthesis and the second internode at early milk, as well as with the total amount of WSC in the lower (4–5) internodes at early milk stage. At the same time, the grain yield per hectare was more strongly and steady correlated with specific content of WSC in the first internode at early milk ripeness and the total amount of WSC in the third internode at anthesis and in the first, second, third internodes and sheath at early milk ripeness.

High positive correlation was found between ear grain weight and amount of remobilized water-soluble carbohydrates, calculated as the difference between their total amount in shoot segments at early milk and full ripeness, which indicates on the importance of the contribution of deposited carbohydrates in the formation of grain productivity (Table 3). The correlations for the remobilization characteristics calculated by the difference between the carbohydrate content at anthesis and the full ripeness were, in general, slightly lower. The difference in dry weight of shoot segments calculated for the respective growth stages correlated with the grain productivity much more weakly than the difference in the total content of water-soluble carbohydrates. The correlations of differences in dry weight of stem segments were also higher for yield per unit of soil area than for grain weight per ear.

Table 2
Coefficients of Pearson's correlation for characteristics of biomass and water-soluble carbohydrates accumulation in the segments of the main shoot with the grain weight per ear and grain yield of winter wheat varieties in 2020 and 2021

Traits	Growth stage	Stem segment	Correlation coefficients with grain yield		yield	
			2020	2021	2020	2021
Dry weight	anthesis	1st internode	0.462	0.425	0.579	0.556
		2nd internode	0.894*	0.561	0.783	0.342
		3rd internode	0.783	0.777	0.688	0.571
		4–5th internodes	0.635	0.751	0.196	0.039
		leaf sheaths	0.324	0.964	0.485	0.028
	early milk ripeness	1st internode	0.488	0.289	0.430	0.868*
		2nd internode	0.945*	0.557	0.715	0.604
		3rd internode	0.721	0.441	0.573	0.679
		4–5th internodes	0.359	0.189	0.216	0.014
		leaf sheaths	0.698	0.110	0.565	0.841*
WSC specific content	anthesis	1st internode	0.204	0.056	0.465	0.606
		2nd internode	0.433	0.291	–0.853*	0.823*
		3rd internode	0.160	0.365	0.328	0.621
		4–5th internodes	0.211	0.079	0.303	0.140
		leaf sheaths	0.426	0.161	0.171	0.316
	early milk ripeness	1st internode	0.566	0.408	0.860*	0.856*
		2nd internode	0.221	0.097	0.369	0.561
		3rd internode	–0.111	0.645	0.104	0.744
		4–5th internodes	0.436	0.584	0.365	0.409
		leaf sheaths	0.221	0.422	0.572	0.857*
Amount of WSC	anthesis	1st internode	0.476	0.467	0.035	0.249
		2nd internode	0.783	0.449	0.951*	0.668
		3rd internode	0.915*	0.484	0.572	0.903*
		4–5th internodes	0.489	0.749	0.186	0.041
		leaf sheaths	0.529	0.271	0.321	0.361
	early milk ripeness	1st internode	0.670	0.369	0.840*	0.861*
		2nd internode	0.850*	0.430	0.730	0.706
		3rd internode	0.770	0.554	0.660	0.759
		4–5th internodes	0.800	0.772	0.610	0.414
		leaf sheaths	0.540	0.291	0.780	0.888*

Note: * – values are significant at $P < 0.05$.

Table 3
Coefficients of Pearson's correlation of the amount of assimilates, remobilized for the specific growth period, with the weight of grain per ear and the yield of winter wheat varieties in 2020 and 2021

Traits	Remobilization characteristics	Stem segment	Period: anthesis – full ripeness		early milk – full ripeness	
			2020	2021	2020	2021
Grain weight per ear	difference in WSC total amount	1st internode	0.225	0.159	0.672	0.309
		2nd internode	0.752	0.363	0.863*	0.388
		3rd internode	0.923*	0.394	0.841*	0.508
		4–5th internodes	0.165	0.709	0.763	0.771
		leaf sheaths	0.406	0.081	0.415	0.217
	difference in dry weight	1st internode	0.129	0.002	0.546	–0.075
		2nd internode	0.028	–0.008	0.066	–0.017
		3rd internode	0.151	0.202	0.165	–0.500
		4–5th internodes	0.611	–0.002	0.273	–0.701
		leaf sheaths	–0.373	0.453	0.431	–0.461
Yield	difference in WSC total amount	1st internode	0.209	0.337	0.872*	0.883*
		2nd internode	0.954	0.630	0.754	0.742
		3rd internode	0.495	0.926*	0.716	0.800
		4–5th internodes	0.432	–0.085	0.628	0.397
		leaf sheaths	0.498	0.263	0.481	0.897*
	difference in dry weight	1st internode	0.550	0.675	0.552	0.936*
		2nd internode	0.486	0.318	0.513	0.678
		3rd internode	0.166	0.651	0.104	0.560
		4–5th internodes	0.339	–0.875*	0.046	–0.742
		leaf sheaths	0.342	–0.083	0.517	0.599

Note: * – values are significant at $P < 0.05$.

Among individual stem segments, stably high positive correlation with yield was found for the amount of remobilized water-soluble carbohydrates in the second and third internodes, using the measurements taken at both anthesis and early milk ripeness. Besides that, high values of correlation coefficients for yield were observed with the difference in dry weight for both growth periods studied and the difference in WSC total amount at early milk ripeness in the first internode, while for grain weight per ear strong correlation was found with the amount of remobilized water-soluble carbohydrates in second, third and lower internodes.

Discussion

The possibility of increasing wheat productivity is associated with a rise in the deposition of reserve assimilates (carbohydrates and nitrogen-containing compounds) that accumulate in the stems before and some time after anthesis (Álvaro et al., 2008; Gao et al., 2017; Liu et al., 2020). Drought conditions during grain filling can significantly inhibit photosynthesis, therefore, remobilization of carbon stored in the stem can partially compensate the loss of current assimilates and, thus, contribute to increased yields under such conditions (Kiriziy et al., 2014).

In particular, it was found that the difference between the maximum of stem dry weight at anthesis or at the onset of grain filling and its value at full ripeness, as well as the contribution of assimilates accumulated in the stem before the anthesis in grain filling in modern varieties (released by 2000–2010) is higher than in old ones (1940–1950) (Sun et al., 2021). It is also shown that contribution of remobilized dry matter of the stem in the period from anthesis to full maturity to the grain filling under drought was higher (54.4%) than under irrigation (38.5%) (Thapa et al., 2021). At the same time, significant genotypic differences in the contribution of the assimilates remobilized from the stem to the grains under different conditions of water supply were revealed. Thus, in field experiments it was shown that this contribution in 11 wheat cultivars varied from 19.1% to 53.6% under irrigation and from 36.6% to 65.4% under drought conditions (Ehdai et al., 2008).

The results obtained in our work show that, in general, the maximum accumulation of dry biomass and water-soluble carbohydrates' content in the main shoot stem was reached at early milk ripeness, although there are some differences between varieties and different segments of the stem. Thus, the greatest accumulation of biomass in the lower internodes (4th and 5th from the top) was observed at anthesis, after that at early milk ripeness, the dry weight of these internodes decreased in most of the studied varieties. It can be assumed that this decrease is related to the use of assimilates stored in the lower internodes for the growth of lateral shoots, while assimilates deposited in the upper internodes are remobilized mainly for grain filling.

The question on the contribution of different internodes to wheat grain filling in drought conditions is still debatable. Thus, it was found that the differences between the maximum and minimum dry weight of the upper internode in 10 varieties of bread wheat and one of durum wheat ranged from 5 to 198 mg under normal water supply and from 81 to 151 mg under drought conditions, while these amounted, respectively, 97 to 317 and 65 to 226 mg for the penultimate internode and 199 to 487 and 196 to 451 mg for the lower (3rd and 4th from the top) internodes (Ehdai et al., 2006). On average, the remobilization of dry matter was higher under drought conditions than under irrigation by 18% in the upper internode, by 21% in the penultimate internode for all genotypes, whereas in the lower internodes, it greatly varied depending on genotypes: for some the values under drought were higher than at watering, for others they were close under both conditions of water supply.

It was also found that losses of dry matter on average for 11 genotypes of Azerbaijani and Iranian wheat for the period from anthesis to full ripeness from the upper, penultimate and lower internodes under drought conditions were greater (76.9, 182.3 and 208.6 mg, respectively) than under sufficient water supply (51.2, 106.8 and 100 mg, respectively) (Pireivatlou & Aliyev, 2008). It is worth noting, the loss of dry matter from the upper internode under drought was two – three times less than from the penultimate and lower ones. Similarly, a larger increase in the efficiency of dry matter remobilization under severe water stress was shown for the lower internodes (137% compared to control) than for the upper ones (33%) in two varieties of spring wheat (Ma et al., 2014). It was suggested that gradients of water-soluble carbohydrates created along the stem are larger under drought conditions and since the efficiency of their remobilization in the lower internodes is higher than in the upper, this is likely to contribute to the flow of carbon from the stem to the grain being formed (Liu et al., 2020).

Lower water-soluble carbohydrates content in the upper internode (about 45%) and leaf sheaths (about 40%) compared to the penultimate internode and lower part of stem (about 50%) was found in plants of two haploid lines obtained by crossing two wheat varieties with different drought-adaptation strategies: preferably maintaining the grain weight or number of grains (Zhang et al., 2015). In the line DH 307 with higher weight of 1000 grains, the content of water-soluble carbohydrates at 20 days after anthesis was significantly reduced by drought in the penultimate internode, lower parts of stem, and sheaths, while in DH 338 with more grain number, the drought effects were small.

Nevertheless, a study with 36 wheat genotypes with different stem solidness showed a close positive correlation (r = 0.56) of the total amount of water-soluble carbohydrates in the upper internode and grain productivity under conditions of water deficiency (Pierre et al., 2010).

In general, the role of assimilates deposited in the stem for wheat yield formation increases significantly under drought conditions. This is related to the disruption of the photosynthetic processes caused by drought, thus there may not be enough photoassimilates for the respiration and grain filling (Kiriziy et al., 2014; Sadras et al., 2020). Moreover, additional assimilates are needed for the functioning of protective mechanisms under adverse conditions (McDowell, 2011).

The results of our study show that the depositing capacity of the second and third internodes had a major impact on the grain productivity of the varieties studied. It is established that the largest part of reserve water-soluble carbohydrates was deposited and remobilized for grain filling in these segments. The importance of their role is evidenced by the tight correlations between indices of grain yield and the amount of water-soluble carbohydrates accumulated prior to grain filling and remobilized in these internodes (Tables 2 and 3). High values of the coefficient of correlation with grain productivity were also noted for the some features of depositing capacity of the peduncle (first internode), however the total amount of water-soluble carbohydrates deposited in this internode was about twice less than in the second or third internodes. In other studies it was shown that new high-yielding variety Podilska Niva surpassed significantly the varieties of the earlier selection Yednist and Zbruch by stem storage capacity (Zborivska et al., 2021). In this case, stored carbohydrates in Podilska Niva accumulated mainly in the lower internodes of the stem, while in Yednist and Zbruch varieties – in the upper ones.

The stem depositing capacity may also be assessed by the difference between the mass of dry matter at anthesis/early milk ripeness and at full ripeness (Ehdai et al., 2006a; Ma et al., 2014; Thapa et al., 2021). In our experiments, the difference in dry weight of the single segments of stem and leaf sheaths during the periods anthesis – full ripeness and milk – full ripeness correlated much worse with grain productivity than the difference in total water-soluble carbohydrates. According to the data of other studies, the main contribution to yield under drought conditions is due to the biomass remobilization from the middle part of the stem (Thapa et al., 2021). We showed a greater loss of the dry matter (both absolute – by weight and relative – in percent) during grain development in the third internode compared with the second, fouth or first internodes.

Conclusion

The results of our study show that the accumulation of dry matter and total amount of water-soluble carbohydrates as well as their specific content in the 2–5th (counting from the top) internodes of the stem at anthesis and milk ripeness were greater than the corresponding values for first internode and leaf sheaths. The second and third internodes had the highest depositing capacity. The most productive newest varieties Kyivska 17 and Horodnytsia differed from other varieties by the largest accumulation of the total amount of water-soluble carbohydrates in the first and second internodes. At the same time, the remobilization of water-soluble carbohydrates (reduction of their total amount during the period from milk to full ripeness) in these varieties was more significant than in other varieties for all segments of the shoot. The close positive correlation between the grain yield of winter wheat varieties and traits of the depositing capacity of the stem suggests that the remobilization of deposited water-soluble carbohydrates is an important factor contributing to grain filling in winter wheat under drought. Assessment of the relationships of these traits for individual segments of the stem with yield can be useful for breeding for productivity in arid conditions.

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