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SOLAR RADIATION USE EFFICIENCY AND THE AMOUNT OF WATER-SOLUBLE CARBOHYDRATES IN THE STEM AS FACTORS IN IMPROVING WHEAT YIELDS

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In current conditions, characterized by a decrease in the precipitation amount in spring and summer, its uneven amounts with the increased frequency and duration of periods of high temperatures, stable production of wheat grain requires the investigation of the possibilities of improving its yield. The search for the traits, related to high yields, resistance, and adaptivity to stresses in wheat genotypes is the object of many studies. The aim of this review is to analyze two promising traits which can potentially be improved. One of the main factors for wheat yield growth is known to be the absorption of photosynthetically active radiation by crops of wheat. It has now approached the maximum possible level, so a promising way for further breeding is to enhance its use efficiency. In this regard, the review discusses the current state of research on the efficiency of photosynthetically active radiation use by this important food crop. Based on literature data and the results of our own research in Ukraine and taking into account that genetic variations in the values of radiation use efficiency can differ by a factor of 2–3, the role of genotypic characteristics of wheat varieties as an important resource for enhancing radiation use efficiency is analyzed. The relationships between radiation use efficiency and plant dry matter formation for different genotypes and under different growing conditions are considered. It is shown that the main factor that affects enhancing solar radiation use efficiency is the increase in plant dry matter formation. Given the complexity of determining the efficiency of radiation use, the biomass of winter wheat plants in the early stages of spring vegetation is also discussed as a sign of a variety with a higher efficiency of converting light energy into biomass. It is substantiated that the effect of this trait on yield may be associated with a better supply of assimilates, which will further contribute to the formation of a well-grained spike. Another important trait in enhancing the grain productivity of wheat is the content or amount of water-soluble carbohydrates deposited in the stem. The ability to accumulate reserve assimilates in the stems before intensive grain filling is often considered a sign of drought tolerance of the variety, since the level of moisture supply significantly affects the accumulation of water-soluble carbohydrates in the stem. Moreover, there are evidences of a positive effect of increased amounts of water-soluble carbohydrates in the stem on yield, regardless of water supply conditions. Therefore, this review discusses the role of both growing conditions and genotype for the accumulation and remobilization of reserve assimilates from the stem or its individual internodes to grain filling. Based on the literature data on the increase in the amount of water-soluble carbohydrates in the stem of wheat varieties with different breeding periods and on the genetic yield increase in them, it has been substantiated that the content of water-soluble carbohydrates in the stem can be a potential trait related to yield. One of the factors influencing the increase in the content of water-soluble carbohydrates in the stem on the yield is the depositary role of the stem as an intermediate reserve for further remobilization of accumulated assimilates. Although the positive effect of water-soluble carbohydrates in the wheat stem in compensating for grain yield has been proven mainly under water stress, the sufficient genetic diversity of their content, as well as the medium and high heritability under different conditions indicate the prospects for further research into this trait in increasing wheat yield.

Key words: *Triticum aestivum* L., varieties, productivity, efficiency of radiation conversion into biomass, stem-deposited carbohydrates.

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INTRODUCTION

Food shortage is one of the main global challenges. The current demand for staple foods is already outpacing the growth of crop yields, particularly cereals, and indicates a potential food shortage by the middle of the twenty-first century (Long et al., 2015; Molotoks et al., 2021; van Dijk et al., 2021). The aggravation of the food shortage problem in recent times is caused by climatic factors, in particular, droughts, high temperatures, and heavy rainfall (Neupane et al., 2022). The situation in Ukraine can serve as an example, where almost all crop fields are located in risky farming zones, i.e. areas with a natural precipitation deficit, where there is a constant risk of crop loss in dry years. This is confirmed by the data on average annual precipitation in Ukraine: over the thirty years (from 1961 to 1990), it was 578 mm, while the indicator of sustainable agriculture is 700 mm or more (Adamenko, 2019). The main factor, reducing the yield of crops, is the lack of soil moisture during the growing season (April–October). Climatological data confirm that Ukraine has seen a slight increase in precipitation in winter and a significant decrease in summer in recent years (Adamenko, 2019). For example, from 2014 to–2018, in 10 regions of Ukraine, the precipitation amount was 7–12% lower than norm, and in 2015, in the western and central regions, it was almost three times less than norm. In addition, the nature of precipitation is changing: the number of ineffective heavy downpours is increasing, which often causes more harm than good after long dry periods.

According to climatologists, the decrease in the number of days with precipitation and the increase in the duration of the rainless period, which occur against the background of a raise in air temperature, indicate an increase in the aridity of the climate in Ukraine (Shevchenko and Balabukh, 2024). In particular, in 2021, the Zaporizhia region experienced almost 90 days without precipitation, and then a third of the annual norm fell in 1.5 days. The intensity of precipitation is also increasing. Thus, in June 2021, a three-month norm of precipitation fell on Ai-Petri in a day. Such precipitation is of no benefit to plants and, in addition, significantly increases the risk of soil erosion, causing floods and inundation (Shevchenko and Balabukh, 2024)

It is believed that there is a high probability that global warming will lead to a deterioration in climatic conditions on 2 million hectares of land in Ukraine in 10 years. The intense warming of recent decades has led to changes in the structure of agricultural production, the area under crops, and their yields. The Steppe zone, which accounts for 46% of cereal crops, currently accounts for only 35% of total grain production, compared to 45% in 1990. The average grain yields in this zone, despite a 21% increase nationwide, decreased from 3.58 tons/ha in 1990 to 3.22 tons/ha in 2013–2017 (Ivaniuta et al., 2020).

Furthermore, a number of socio-economic factors also affect food security. For instance, from 2000 to 2021, the global share of arable lands decreased by 86 million ha (Statistical Yearbook, World Food and Agriculture, 2023, p. 38). Moreover, in a number of countries, there is a tendency to reduce nitrogen fertilizer application rates, both in terms of their cost and environmental considerations (Brisson et al., 2010; Lesk et al., 2016). Meeting food demand is also becoming more difficult due to increased competition for alternative land use, depletion of natural resources, and deteriorating soil quality (Yadav et al., 2017).

Based on what has been stated above, the search for new effective ways to identify opportunities to increase the yield of crops, including wheat (*Triticum aestivum* L.), remains relevant. Wheat, one of the most important food crops, plays a crucial role in global food security and agri-food systems worldwide (Acevedo et al., 2018). In 2023, the area under its cultivation was more than 215 million hectares, with a global production of about 800 million tons of grain (Statistical Yearbook, World Food and Agriculture, 2023, p. 14). According to the, for Ukraine the total area under spring wheat in 2025 will be 222.7 thousand hectares (https://www.rada.gov.ua/news/news_kom/258168.html), and under winter wheat, about 4.35 million hectares (https://www.rada.gov.ua/news/news_kom/255439.html).

Wheat provides about 20% of the total calories and proteins contained in food worldwide (Lobell and Gourdji, 2012; Shiferaw et al., 2013). Its value is associated with the high nutritional value of the grain, which has a higher protein content than rice, corn, or other staple cereals (Khan and Zeb, 2007; Morgun and Rybalka, 2017). Moreover, wheat proteins contain essential amino acids (Shaheen et al., 2016). The unique properties of gluten allow for the use of wheat to produce bread, other bakery products, noodles and pasta, and a number of functional ingredients (Morgun and Rybalka, 2017). The importance of growing winter wheat is also conditioned by the possibility of optimizing organizational and economic farming: sowing wheat in autumn reduces the workload on farms during spring sowing, and its earlier maturation compared to spring wheat reduces it during harvest.

ENHANCING RADIATION USE EFFICIENCY

The potential yield of crops depends on the following main components: the amount of solar radiation reaching the upper boundary of the crop (1), its absorption by plants (2), the efficiency of converting solar radiation into biomass (3), and the harvest index (4). The first component of the classical, so-called Monteith equation depends mainly on the location of crop cultivation, i.e., it is determined by geographic latitude. Moreover, the amount of total radiation in a particular geographical area depends on atmospheric transparency and cloud cover, as well as the season and time of day (Monteith, 1977).

The second (2) and last (4) components of the equation, unlike the first, can be influenced by humans through breeding or changes in cultivation technologies. For example, during the Green Revolution, the yield potential of wheat was increased mainly through the use of genotypes with raise in the partitioning of the above-ground biomass towards spikes and grains. However, since the early 1990s, there has been no systematic progress in the value of the wheat harvest index from the threshold values of 0.50–0.62 (Sinclair, 1998; Slafer et al., 2023). Various approaches have been applied to increase the absorption of photosynthetically active radiation (PAR) by crops: via accelerating the formation of an optimal leaf index at the beginning of the growing season, extending the life span of leaves during the grain filling period by the agricultural technology, the use of varieties with the stay-green trait or late-ripening varieties (Richards, 2000; Xu et al., 2024). As a result, the absorption of PAR by crops of modern varieties has also already approached the maximum possible values (Zhu et al., 2010; Murchie et al., 2023). The leaf index of modern high-yielding varieties has reached the values of 3.5–4.5 m^2 of leaves per 1 m^2 of soil. The portion of PAR absorbed by crops with a leaf index of more than 4 is more than 90% (Bégué, 1993). However, exceeding such values may not lead to further yield growth (Rahman et al., 2014), mainly because of the deterioration of solar energy use due to intershading of leaves and increased respiration costs. Thus, crop absorption of PAR and the harvest index have undergone positive changes, but further improvement is unlikely.

These limitations to enhacement in PAR absorption emphasize the importance of PAR use efficiency as a factor that can still be used to improve wheat yields. The radiation use efficiency (RUE) is defined as the ratio between the dry matter produced during a certain period and the absorbed photosynthetically active radiation during the same period. For instance, Murchie E.H. et al. (2009) believed that the best, and perhaps the only, way to promote yield growth is to increase the efficiency of PAR conversion into biomass. Possible ways to increase the productivity of crops, including wheat, by increasing the PAR use efficiency are widely discussed in the modern literature, where aspects such as canopy structure, efficiency in chloroplasts, photosynthetic ability distribution, stomatal behaviour and transpiration/respiration are considered (Furbank et al., 2019; Xin and Tao, 2019; Morales et al., 2020; Cho et al., 2022; Burgess et al., 2023; Murchie et al., 2023).

The genotypic characteristics of varieties can be an important resource for increasing the efficiency of PAR use (Pradhan et al., 2018; Gerard et al., 2024; Wang et al., 2024). According to the literature, the genetic variations in RUE can be significant, differing by a factor of 2–3. For example, for 12 varieties of spring wheat, the minimum RUE values for the period from 40 days after germination to the initiation of booting were 1.63 and 2.20 g MJ^{-1} (under two cultivation technologies), and the maximum values were 2.67 and 3.20, from the initiation of booting to the appearance of inflorescences, respectively — 2.47 and 2.32, and 3.59 and 3.27 g MJ^{-1} (Moroyoqui-Parra et al., 2024). Similarly, the results of a two-year study of 150 elite spring wheat genotypes showed a wide range of changes in RUE: from 1.47 to 3.43 for the period from sowing closure to heading and from 0.96 to 2.96 for the period of 7 days after anthesis and up to physiological maturity (Molero et al., 2019).

The significant role of genotype in increasing RUE is emphasized by the fact that other possibilities to reach this goal are considered exhausted. For example, the evaluation of the effect of tillage (conventional or with vetch used as green manure) and two doses of nitrogen fertilizers showed that neither the tillage system nor the significant difference in nitrogen application affected radiation use efficiency: its value for all variants of the experiment ranged within 0.91–1.20 g MJ^{-1}. However, after a dose of 90 kg N ha^{-1}, a significant (approximately 2-fold compared to the control) increase in the aboveground biomass of winter wheat crops was observed (Kandel et al., 2019). Therefore, it is believed that even a small increase in RUE can have a significant impact on biomass and, in turn, on yield, provided that the economic value of the crop is maintained at a constant level (Molero et al., 2019).

According to the literature, RUE has a positive correlation with plant dry matter production (Awal et al., 2017; Tao et al., 2018; Molero et al., 2019; Priadkina et al., 2020; Moroyoqui-Parra et al., 2024). Thus, the production of more dry matter is considered to be one of the features of wheat varieties with increased solar radiation use efficiency. In particular, it has been shown that the RUE for certain periods of vegetation positively correlates with the formation of plant dry matter. Thus, according to the results of field experiments with eight varieties of English breeding, which differed in terms of breeding time and height, it was shown that the values of RUE for the period from the phase of stem elongation to flowering (GS 31-61) and total biomass per unit of sowing in the varieties, bred in the 1990s, were higher than in those of the late 1970s – early 1980s (Shearman et al., 2005). The authors also noted the presence of genetic differences between varieties in terms of RUE: significant genetic differences in the RUE value were observed not only for the varieties differing in height and architectonics (tall and semi-dwarf) but also among semi-dwarf varieties. Moreover, the growth of aboveground biomass per unit area of sowing and the radiation use efficiency during the vegetative period of plant development (0.012 g MJ^{-1} per year) was accompanied by an annual genetic increase in grain yield (0.12 mg ha^{-1} per year). Therefore, the selection aimed at increasing wheat productivity by selecting the best genotypes contributed, among other things, to the selection of varieties with increased RUE (Gerard et al., 2024).

The comparative analysis of five spring wheat varieties of the Bangladesh Agricultural Research Institute (BARI), which differed in phenological development, morphological and economic traits, enabled identification of varieties that accumulated more total dry matter and had a higher average RUE during the growing season (Awal et al., 2017). For example, wheat variety BARI-23 had a dry matter mass per unit area of about 1,000 g m^{-2} at 102 days after sowing, while BARI-27 had about 800 g m^{-2}. The average RUE of the former variety for this period was also significantly higher than that of the latter, 0.91 and 0.68 g MJ^{-1}, respectively (Awal et al., 2017). These authors also noted that for all five varieties studied, the seasonal change in the RUE was irregular. Variety BARI-23 and variety BARI-25 demonstrated the best performance indices, while variety BARI-27 showed low productivity.

Wheat varieties of Ukrainian breeding, which differ in total dry matter per unit area of sowing in certain periods of vegetation, also have differences in terms of RUE. In particular, in experiments with three modern varieties of winter wheat, the effect of the variety and foliar treatment of plants with a complex of microelements and its mixture with carbamide on the leaf index of crops, dry matter accumulation and the photosynthetically active radiation use efficiency by crops was analyzed. It was found that the dry matter weight of Astarta variety at the flowering, milk, and milk-wax ripeness phases was higher than that of Malynivka and Smuhlianka varieties both in the control variant and under the influence of both treatments (Priadkina et al., 2019). The Astarta variety in all variants was also characterized by higher efficiency of photosynthetically active radiation use by crops during the flowering — milk ripeness period (0.58 in the control variant and 0.85–0.91 g MJ^{-1} under the treatment) than in the corresponding variants for the varieties Malynivka and Smuhlianka (0.30–0.33 in the control and 0.49–0.56 in the experimental variants). During the period of milk and milk-wax ripeness, the efficiency of photosynthetically active radiation use by crops of this variety exceeded the corresponding values of the last two varieties only when plants were treated with a microelement complex chelated by carboxylic acid. It is interesting to note that, according to our data, at the later stages of ontogeny, the more productive Astarta variety (with yields, depending on the treatments, of 8.42–9.29 tons/ha) had both higher biomass and RUE for the period preceding harvest than Smuhlianka (7.21–7.82 tons/ha) (Priadkina et al., 2019). According to Awal M.A. et al., BARI-23 variety, with a yield of 2.6 t/ha, had higher biomass at the end of the growing season than BARI-27 variety with a yield of 1.6 t/ha, while RUE at the later stages of ontogeny, on the contrary, was higher in the less productive BARI-27 variety than in the more productive BARI-23 (Awal et al., 2017).

The analysis of changes in RUE and plant dry matter formation over 4 periods of spring and summer vegetation of five modern varieties (years of breeding — 2017–2018) and the well-known winter wheat variety Smuhlianka of earlier selection (2004) also showed the unidirectional nature of their changes (Priadkina et al., 2020). From the spikelet emergence phase (GS 55) to the milky-wax ripeness phase (GS 80), the dry matter mass formed by plants growing per 1 sq.m. of soil of the varieties Hospodarka, Kyivska 17 and Pochayna in 2018 was, on average, 1.44–1.67, and in 2019 — 1.22–1.51 times higher than that of the varieties Krasnopilka, Smuhlianka and Poradnytsia. Similarly, the RUE values for these periods in the first group of varieties were higher than in the second one: during the period heading – flowering in 2018, the average value for the first three varieties was 2.37 g, in 2019 — 2.95, while in the last three varieties, respectively, 1.51 and 2.23 g MJ^{-1}. This pattern was maintained during the flowering period – milky-wax ripeness, respectively, 1.86 and 2.03 and 1.00–1.11 g MJ^{-1} (Priadkina et al., 2020). The first three varieties also had higher grain yields in both years: 8.60–8.72 (in 2018) and 9.15–9.78 tons/ha (in 2019), while in varieties Krasnopilka, Smuhlianka and Poradnytsia it fluctuated within 7.12–7.85 and 7.88–8.48 tons/ha, respectively.

Many recent studies have also found a positive correlation between the value of RUE for certain periods and crop biomass. For example, a significant correlation was found between RUE for the period before grain filling (from 40 days after germination to 7 days after flowering) and biomass of twelve spring wheat varieties, with the closeness of this relationship depending on the type of plant location on the soil (Moroyoqui-Parra et al., 2024). When plants were grown on raised beds (with row spacing of 0.24 and 0.56 m), the correlation coefficient between RUE values during this period and the biomass at the flowering phase was 0.72, and at the physiological ripeness phase 0.86; when grown on a flat surface (with row spacing of 0.20 m), it was not significant. A direct correlation of RUE values for the period of seven days after flowering and before physiological maturity with final biomass ($r = 0.83$) was established in a two-year experiment with 150 elite spring wheat genotypes (Molero et al., 2019). Similar results were obtained in a large-scale study with 209 typical Chinese varieties of different breeding periods (from 1944 to 2018) in four locations: the correlation coefficient reached 0.85 (Li et al., 2022). All of this confirms that an increase in the aboveground biomass due to increased RUE will contribute to higher yield.

The increase in grain productivity of wheat varieties characterized by higher solar radiation use efficiency may be due to an increase in biomass at the early stages of ontogeny, as well as the formation of more grains. This may be due to the fact that they can contain a larger number of grains. In particular, a number of researchers have found a positive correlation between pre-flowering RUE and the number of wheat grains per unit area (Tao et al., 2018; Molero et al., 2019; Moroyoqui-Parra et al., 2024). We have also found that the efficiency of PAR use by crops in the period from heading to milky-wax ripeness was higher in varieties with higher biomass in the early stages of the spring growing season (Pryadkina et al., 2017). This may be due to the fact that in the early stages of organogenesis (at the beginning of the stem elongation) spikelets primordia are formed, i.e. the number of spikelets in the spike is determined (Zadoks et al., 1974). The rapid growth of the assimilation surface in the early stages of ontogeny, due to the increase in light absorption by crops, contributes to the formation of more assimilates that can be used for further growth. This assumption, in particular, can be confirmed by the increase in grain yield of spring wheat, which, during the period from the end of tillering to the beginning of the stem elongation phase, was grown under increased CO_2 concentration, i.e., artificially created conditions for increased assimilates formation (Fischer and Aguilar, 1976). Therefore, plants, forming more biomass in the early stages and having a better supply of assimilates, can form more grains.

STEM STORAGE CARBOHYDRATES

Another factor in increasing yields is the formation of a fund of storage assimilates (carbohydrates) (Li et al., 2015; Liu et al., 2020; Ntawuguranayo et al., 2024). The availability of a fund of storage assimilates, namely carbohydrates and nitrogen-containing compounds that can accumulate in the stems before (and during) anthesis — is considered one of the reserves for increasing yields. Most literature data demonstrate that under stressful conditions during grain filling, the use of water-soluble carbohydrates accumulated before flowering can partially compensate for the decrease in the formation of photoassimilates caused by the inhibition of photosynthesis (Kiriziy et al., 2014; Li et al., 2015; Ovenden et al., 2017; Liu et al., 2020). There is also evidence that even under conditions of moderate drought, grain filling in wheat depends more on stored non-structural carbohydrates than on current photosynthesis (Ehdaie et al., 2006; Slewinski et al., 2012). According to the data of Thapa S.I. et al. (2021), obtained regarding eight wheat varieties, the contribution of dry matter, re-mobilized from the stem into grain, did not depend on the water supply conditions: both in a rather wet year, and in a dry year, its share in grain fluctuated within close margins, 39–58% and 37–63%, respectively. The authors noted a higher contribution of the genotype than that of cultivation conditions.

Significant genotypic differences in the amount of water-soluble carbohydrates (WSC) in stems and leaf sheaths during flowering in English-bred varieties, obtained from 1972 to 1995, were shown by Shearman V.J. et al. (2005). In varieties of earlier breeding, their number was lower, with an average increase of 4.6 g m^{-2} annually. Similarly, a significant difference in the content of water-soluble carbohydrates in the stems at certain dates of vegetation was found in 26 varieties of winter wheat of Chinese selection, which had a significant difference in over the period of breeding (from 1950 to 2012). The minimum content of water-soluble carbohydrates at the flowering stage was 4.6 mg/g, the maximum — 16.7 mg/g, on the 10^{th} and 20^{th} day after this phase, the limits of their changes ranged from 8.5 to 18.1 and from 5.5 to 14.3 mg/g, respectively (Gao et al., 2017). The genetic yield increase of the group of varieties studied was 57.5 kg ha^{-1} per year. The authors believed that one of the determining factors of yield is the content of water-soluble carbohydrates on the 10^{th} day after flowering and propose to use this indicator as a breeding trait to increase the genetic potential of wheat grain productivity (Gao et al., 2017).

The level of moisture availability significantly affects the accumulation of water-soluble carbohydrates in the stem. Under optimal soil moisturization, a significant part of the WSC is deposited in the stem after the beginning of flowering, and their maximal accumulation is observed on days 14–17 (Tarasiuk and Stasik, 2022) and even day 21 (Liu et al., 2020) after flowering. Drought can significantly reduce the duration of WSC accumulation up to 7 days after the beginning of flowering in drought-sensitive varieties and 14 days in drought-resistant varieties (Tarasiuk and Stasik, 2022; Liu et al., 2020). It was recently shown that, under severe heat stress, the maximum WSC accumulation can be reached much earlier (Ntawuguranayo et al., 2024).

It is interesting to note that in our studies in Ukraine, varieties differed significantly in the level of maximal accumulation of water-soluble carbohydrates in the stem, 1.3 times under optimal conditions and 1.5 times under drought, but the efficiency of remobilization of the stem-deposited WSC was high and close (84–96%) in all studied varieties, regardless of moisture conditions (Morgun et al., 2024). Therefore, the differences between winter wheat varieties in terms of depositing capacity are determined mainly by the level of WSC accumulation and it cannot be significantly improved by increasing the efficiency of remobilization. Similarly, high and close values of WSC remobilization efficiency (81–96% under well-watered and 91–97% under drought conditions) were observed in a pot experiment with eight Bangladeshi wheat varieties (Islam et al., 2021). In earlier field experiments by Ehdaie B. et al. (2006) with ten diverse bread and durum wheat varieties, generally high values of WSC remobilization efficiency under well-watered conditions were found for the lower internodes (an average of 84%, more than 76% for nine varieties, and 57% for the remaining one), slightly lower for the penultimate internode (an average of 77%, more than 79% for seven varieties, and 39–69% for the remaining three), and moderate to low for the peduncle (an average of 64%, more than 70% for five varieties, and 19–64% for the remaining five). The lower internodes, penultimate internode and peduncle contibuted on average 51, 30 and 19% of the stem mobilized WSC, respectively. Drought improved the mobilization efficiency by 33% in the peduncle, 17% in the penultimate internode, and 11% in the lower internodes. The amount of WSC mobilized was highly correlated with the maximum accumulated WSC, with correlation coefficients ranging from 0.89 to 0.99, depending on the internode and irrigation regime.

It is worth noting that wheat varieties may differ in the content and amount of water-soluble carbohydrates in individual internodes, as mentioned above. In a field experiment with six bread winter wheat varieties, we have shown that, during the flowering stage, the amount of water-soluble carbohydrates of the upper internodes ranged from 17–19 mg (in Krasnopilka and Poradnytsia varieties) to 23–30 mg (in Kyivska-17, Horodnytsia, Pochayna, and Smuhlianka varieties) (Morgun et al., 2022). In the milk ripeness stage, the higher-yielding varieties Kyivska-17 and Horodnytsia (8.16 and 6.87 tons/ha) were characterized by the highest amount of carbohydrates in the 2nd internode — 168.4 and 202.9 mg, while in the other four varieties (with yields from 5.30 to 6.06 tons/ha) it was lower: from 101.9 to 126.0 mg. It was found that the depositing capacity of the 2nd and 3rd internodes of the stem of the main shoot from above had a significant effect on the grain productivity of the six studied varieties of bread winter wheat (Morgun et al., 2022).

The higher amounts of WSC in the penultimate and lower internodes and their larger contribution to the total remobilized WSC have been demonstrated in numerous studies (Khoshro et al., 2014; Li et al., 2015; Zhang et al., 2015; Hou et al., 2018). In contrast, Liu et al. (2020) reported a greater contribution to overall WSC accumulation and remobilization from the upper (peduncle) internode. A significant positive correlation between WSC accumulation and peduncle length under various experimental conditions were reported in recent study (Ntawuguranayo et al., 2024).

According to Li et al. (2015), based on the analysis of 262 winter wheat varieties and lines from different countries, under conditions of sufficient water supply, the amount of water-soluble carbohydrates from internodes located below the upper one during flowering and milk ripeness had a significant positive correlation with the weight of 1,000 grains under drought conditions. These authors also noted that although varieties have been randomly selected for their WSC content over the past fifty years of wheat breeding, the average number of favorable WSC alleles increased from 1.13 in the period before 1960 to 4.41 in the period after 2000. The varieties with a larger pool of metabolites, in addition to assimilates produced during current photosynthesis, can use a pool of reserve assimilates (carbohydrates) for grain filling.

In conclusion, some studies confirm that varieties with a higher content or amount of WSC in the stem are characterized by higher yields not only under water stress. In other experiments, only a slight or a growing conditions dependent relationship between these indicators was found. Thus, the difficulty in improving such a trait as the content of WSC is the significant influence of the growing conditions, the stage of plant development, and the organ (whole stem, individual internodes, or leaf sheaths). For example, the analysis of the WSC content in the stems on the 15th day after flowering of 301 soft wheat genotypes under different growing conditions (irrigation, precipitation, and drought) showed that their accumulation is either a moderate or low heritable trait, which depends more on environmental influences than on genotypic characteristics (Gaur et al., 2022a). On the other hand, sufficient genetic diversity in terms of WSC content in stems and its remobilization into grain in different wheat germplasm is accompanied by medium to high heritability of this trait under different experimental conditions (Li et al., 2015; Ovenden et al., 2017; Liu et al., 2020; Gaur et al., 2022b). Therefore, further efforts to study the physiological, genetic, and molecular aspects of WSC accumulation and remobilization in stem will contribute to a better understanding of the role of this trait in increasing wheat yield (Gaur et al., 2022b).

CONCLUSIONS

To summarize, the search for new traits associated with wheat yield improvement continues to be relevant. The traits discussed in this review are among those that can still be an important resource for increasing wheat yields. In particular, the significant (2–3 times) difference between varieties in radiation use efficiency, as well as the positive correlation between the value of RUE for certain periods and biomass and yield, found for many varieties and under different growing conditions. They confirm the importance of this indicator for breeding (Murchi et al., 2023; Gerard et al., 2024; Wang et al., 2024). The main factor influencing the increase in the solar radiation use efficiency is the increase in the formation of plant dry matter. However, due to the complexity of determining such an indicator as RUE (in particular, the need for daily measurement of PAR), a related trait can be used in breeding programs — the biomass of winter wheat plants in the early stages of spring vegetation. The influence of this indicator on yield is related to the fact that due to faster formation of the assimilation surface and increased light absorption by crops, plants with higher biomass in the early stages of ontogeny can form more grains due to a better supply of assimilates. This, in turn, can further contribute to the formation of a well-grained spikelet (Murchie et al., 2023; Slafer et al., 2023).

The second important trait associated with an increase in grain productivity is the content or amount of water-soluble carbohydrates in the whole stem or its individual segments, 10–15 days after flowering. The ability to accumulate assimilates in the stem during the vegetative and early reproductive periods can make a significant contribution to grain filling. The remobilization of assimilates, deposited in the stem, may promote higher yields (Slewinski et al., 2012; Slafer et al., 2023).

WSC content has not yet been widely used as a direct breeding criterion, possibly due to the complexity of WSC phenotyping and environmental variability (Ovenden et al., 2017). The maximum accumulation (the peak) depends on environmental conditions, where under severe abiotic stress, the peak of WSC accumulation may be reached earlier (Liu et al., 2020; Tarasiuk and Stasik, 2022; Ntawuguranayo et al., 2024). Further studies on the physiological, genetic, and molecular aspects of reserve WSC accumulation and remobilization in the stem will contribute to a better understanding of its role in increasing wheat productivity and to the development of reliable indicators (proxies) of high WSC yield contribution under various environmental conditions.

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Adherence to ethical principles: this article does not contain any studies involving humans and animals as study objects.

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ЕФЕКТИВНІСТЬ ВИКОРИСТАННЯ СОНЯЧНОЇ РАДІАЦІЇ ТА КІЛЬКІСТЬ ВОДОРОЗЧИННИХ ВУГЛЕВОДІВ У СТЕБЛІ ЯК ФАКТОРІВ ЗБІЛЬШЕННЯ ВРОЖАЙНОСТІ ПШЕНИЦІ

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Для сталого виробництва зерна пшениці в сучасних умовах зміни клімату, які характеризуються зменшенням кількості опадів навесні та влітку, нерівномірності їх випадіння зі збільшенням частоти й тривалості періодів високих температур, актуальними є дослідження можливостей збільшення її врожайності. Пошук ознак, пов’язаних із високою врожайністю, стійкістю та адаптивністю до дії стресів у генотипів пшениці є об’єктом багатьох досліджень. **Метою** цього огляду є аналіз двох перспективних ознак, які потенційно можна покращити. Відомо, що одним із основних факторів зростання врожайності пшениці наприкінці минулого століття було поглинання фотосинтетично активної радіації посівами пшениці. Зараз воно наблизилося до максимально можливого рівня, тому перспективним способом його вдосконалення для подальшої селекції є підвищення ефективності його використання. У зв’язку з цим в огляді розглядається сучасний стан досліджень ефективності використання фотосинтетично активної радіації цієї важливої продовольчою культурою. На основі літературних даних і результатів власних досліджень в Україні, а також враховуючи, що генетичні варіації у значеннях ефективності використання радіації можуть відрізнятися у 2–3 рази, аналізується роль генотипних особливостей сортів пшениці як важливого ресурсу для підвищення ефективності використання радіації. Розглянуто взаємозв'язки між ефективністю використання радіації з формуванням сухої речовини рослин для різних генотипів і за різних умов вирощування. Показано, що основним фактором, якій впливає на підвищення ефективності використання сонячної радіації, є збільшення утворення сухої речовини рослин. З огляду на складність визначення ефективності використання радіації, також обговорюється маса сухої речовини рослин озимої пшениці на ранніх стадіях весняної вегетації як ознака сорту з вищою ефективністю перетворення світлової енергії в біомасу. Обгрунтовано, що вплив цього показника на врожайність може бути пов'язаний із кращим забезпеченням асимілятами, що надалі сприятиме формуванню добре озерненого колоса. Ще однією важливою ознакою для збільшення зернової продуктивності пшениці є вміст або кількість водорозчинних вуглеводів у стеблі. Здатність накопичувати резервні асиміляти у стеблах до початку інтенсивного наливу зерна частіше розглядають як ознаку посухостійкості сорта, оскільки рівень вологозабезпеченості істотно впливає на накопичення водорозчинних вуглеводів в стеблі. Більш того, є свідчення щодо позитивного впливу підвищеної кількості водорозчинних вуглеводів стебла на врожайність незалежно від умов водозабезпечення. Тому в цьому огляді обговорюється роль як умов вирощування, так і генотипу на накопичення і ремобілізацію запасних асимілятів зі стебла або його окремих міжвузлів на наливання зерна. Базуючись на літературних даних щодо збільшення кількості водорозчинних вуглеводів у стеблі сортів пшениці із різним періодом селекції та на генетичному прирості врожаю у них, обґрунтовано, що вміст водорозчинних вуглеводів стебла може бути потенційною ознакою пов'язаною з врожайністю. Одним із факторів впливу підвищення вмісту водорозчинних вуглеводів стебла на врожайність може бути депонувальна роль стебла як проміжного резерву для подальшої ремобілізації накопичених асимілятів. Хоча позитивний внесок водорозчинних вуглеводів в стеблі пшениці у компенсацію врожаю зерна доведений переважно за дії водного стресу, достатня генетична різноманітність їх вмісту та середня і висока успадковуваність за різних умов, засвідчують перспективність подальших досліджень цієї ознаки у збільшенні врожайності пшениці.

Ключові слова: пшениця (*Triticum aestivum* L.), сорта, продуктивність, ефективність перетворення сонячної радіації в біомасу, депоновані у стеблі вуглеводи.