••• ФІЗІОЛОГІЯ РОСЛИН ••• PLANT PHYSIOLOGY •••

UDC: 581.14:581.19:633.111.1

Вплив трофічного забезпечення на динаміку ростових процесів і вмісту вуглеводів у проростків озимої пшениці за яровизації

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Вивчали вплив контрастних умов трофічного забезпечення яровизації (верналізації) на ростову реакцію і динаміку вмісту різних фракцій розчинних вуглеводів в проростках двох сортів озимої пшениці Статна і Дорідна. В експериментах моделювали різні умови трофічного забезпечення яровизації шляхом додавання 3%-го розчину сахарози, а також ізолювання ендосперму – природного запасу вуглеводів і біологічно активних речовин. В ході проведених експериментів показано, що оптимальні умови трофічного забезпечення (варіант зернівки + вода) детермінують максимальний лінійний ріст і накопичення біомаси проростків протягом всього періоду яровизаційного впливу, надлишок екзогенних, цукрів (варіант зернівки + 3% сахароза) гальмує ростові процеси, дефіцит трофічних факторів (варіант ізольовані зародки + 3% сахароза) також гальмує ріст, а відсутність трофічного забезпечення (варіант ізольовані зародки + вода) повністю пригнічує ріст і накопичення біомаси проростками протягом 45-добового яровизаційного впливу. Встановлено, що динаміка зміни вмісту розчинних вуглеводів в проростках озимої пшениці також залежить від рівня трофічного забезпечення процесу яровизації і корелює зі змінами ростової реакції. Показано, що у всіх варіантах дослідів протягом усього періоду верналізації вміст олігоцукрів істотно перевищує вміст моноцукрів в проростках обох сортів. Оскільки моноцукри являються найбільш метаболічно активними вуглеводами, вірогідно, вони в максимальній кількості витрачаються на перших етапах яровизації (15–30 діб). Обговорюється, що різний рівень трофічного забезпечення може бути одним з вагомих чинників генетичної та/або епігенетичної регуляції процесу яровизації *Triticum aestivum* L. Зміни у метаболічних процесах, зокрема вуглеводному обміні, можуть впливати на зниження експресії генів *VRN*, які є мішенню епігенетичної регуляції, і в результаті цього на набуття здатності рослин пшениці м'якої переходити до колосіння. Припускається, що регуляторна роль вуглеводів в яровизаційному процесі може здійснюватися тільки при оптимальному рівні трофічного забезпечення.

Ключові слова*: Triticum aestivum L., яровизація, трофічне забезпечення, ростова реакція, розчинні вуглеводи.*

Effect of trophic support on the dynamics of growth processes and carbohydrate content of winter wheat sprouts under vernalization

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The influence of contrasting conditions of trophic support of vernalization on the growth reaction and dynamics of the content of various fractions of soluble carbohydrates of sprouts of two winter wheat varieties Statna and Doridna were studied. In experiments, the contrasting trophic conditions of vernalization were created by adding 3% sucrose solution, as well as isolation of endosperm, a natural reserve of carbohydrates and biologically active substances. It was shown that optimal conditions of trophic support (integral seeds + water) determined the maximum linear growth and accumulation of sprouts biomass during vernalization. The excess of exogenous sugars (integral seeds + 3% sucrose solution) inhibited growth processes. However, the deficit of trophic factors (isolated buds + 3% sucrose solution) also inhibited growth and the lack of trophic support (isolated buds + water) completely inhibited growth and accumulation of sprouts biomass during 45 days of vernalization. It was established that the dynamics of changes in soluble carbohydrates content in winter wheat sprouts also depended on the trophic support level of vernalization and correlated with changes of growth reaction. It was shown the oligosaccharide content was significantly higher than monosaccharide content of sprouts of all the variants of both varieties during the entire period of vernalization. In view of the fact that monosaccharides are the most metabolically active carbohydrates, they are probably spent as much as possible at the first stages of vernalization (15–30 days). It is discussed that different level of trophic support is able to be one of the important factors of genetic and/or epigenetic regulation of *Triticum aestivum* L. Thus, changes in metabolic processes, in particular carbohydrate metabolism, can effect on the reduction of *VRN* genes expression, which are the target of epigenetic regulation, and as a result, on the ability of soft wheat plants to flower. It is assumed that the regulatory role of carbohydrates in vernalization process can be realized only at the optimal level of trophic support.

Key words: *Triticum aestivum L.*, *vernalization, trophic support, growth reaction, soluble carbohydrates.*

DOI: 10.26565/2075-5457-2018-31-14

Влияние трофического обеспечения на динамику ростовых процессов и содержания углеводов в проростках озимой пшеницы при яровизации

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Изучали влияние контрастных условий трофического обеспечения яровизации (вернализации) на ростовую реакцию и динамику содержания различных фракций растворимых углеводов в проростках двух сортов озимой пшеницы Статна и Доридна. В экспериментах моделировали различные условия трофического обеспечения яровизации путем добавления 3%-го раствора сахарозы, а также изолирования эндосперма – природного запаса углеводов и биологически активных веществ. Было показано, что оптимальные условия трофического обеспечения (вариант зерновки + вода) детерминируют максимальный линейный рост и накопление биомассы проростков, избыток экзогенных сахаров (вариант зерновки + 3% сахароза) тормозит ростовые процессы, недостаток трофических факторов (вариант изолированные зародыши + 3% сахароза) также тормозит рост, а отсутствие трофического обеспечения (вариант изолированные зародыши + вода) полностью подавляет рост и накопление биомассы проростками в течении 45-суточного яровизационного воздействия. Установлено, что динамика изменения содержания растворимых углеводов в проростках озимой пшеницы также зависит от уровня трофического обеспечения процесса яровизации и коррелирует с изменениями ростовой реакции. Показано, что во всех вариантах в течение всего периода вернализации содержание олигосахаров существенно превышает содержание моносахаров в проростках обоих сортов. Поскольку моносахара являются наиболее метаболически активными углеводами, вероятно, они в максимальном количестве расходуются на первых этапах яровизации (15–30 суток). Обсуждается, что разный уровень трофического обеспечения может быть одним из весомых факторов генетической и/или эпигенетической регуляции процесса яровизации *Triticum aestivum* L. Изменения в метаболических процессах, в частности углеводном обмене, могут влиять на снижение экспрессии генов *VRN*, которые являются мишенью эпигенетической регуляции, и в результате этого на приобретение способности растений пшеницы мягкой переходить к колошению. Предполагается, что регуляторная роль углеводов в процессе яровизации может осуществляться только при оптимальном уровне трофического обеспечения.

Ключевые слова: *Triticum aestivum L., яровизация, трофическое обеспечение (факторы), ростовая реакция, растворимые углеводы.*

Introduction

One of the important and key stages of the development of winter wheat plants is the process of vernalization, which requires the complex of factors – temperature, water, oxygen and trophic support (Henderson et al., 2003). Vernalization has a metabolic nature, associated with physiological and biochemical processes occurring in a plant as an integral organism. Investigation of physiological processes during vernalization has led to the idea that a number of changes of plant metabolism occur. There is an accumulation of carbohydrates and soluble nitrogen-containing substances, increase of some enzyme activity and intensification of nucleic acids metabolism (Avksentieva, Zhmurko, 2011). A significant factor of the regulation of vernalization process is the genetic control. In wheat, the *VRN* genes system has been identified. It controls the need of vernalization and determines the type of plant development (spring or winter) (Dennis, Peacock, 2009). The *VRN* genes system includes several genes, among which the main ones are *Vrn 1*, *Vrn 2*, *Vrn 3* (Song et al., 2012; Sung, Amasino, 2005). These genes are one of the well-defined examples of epigenetic regulation, whose target in cereals is the *Vrn 2* gene (Shcherban, Salina, 2013). The expression of *Vrn 2* decreases under influence of a positive temperature due to the posttranscriptional mechanism (the processing of non-coding anti-sense RNA), which causes the modification of histone proteins and leads to an appropriate physiological response. Thus, plants can "memorize" the changes that occur in meristem cells caused by environmental conditions and stress. Those cells that get into germinal line are adaptive (Song et al., 2012; Sung, Amasino, 2005).

When passing through vernalization at sprouts stage, the need of metabolites is supported by the stock of plastic and biologically active substances (BAS) of an endosperm (Aoki et al., 2006). Carbohydrates play a central role in plant metabolism at the level of single cells and the whole organism. They are involved in reactions-responses to a number of stressors and act as signaling molecules that activate specific pathways of transduction of the stress or hormonal signal, resulting in important modifications of gene expression (Rosa et al., 2009; Baena et al., 2007; Baier et al., 2004). Sugars affect the expression of many genes involved in photosynthesis, glycolysis (Cho et al., 2006), nitric and sucrose metabolism, regulate the cell cycle (Riou-Khamlichi et al., 2000) and others. Sugar signaling can also intersect with other signaling pathways (O'Hara et al., 2013). In particular, reducing the trehalose-6-

phosphate synthase expression causes down-regulation of the *FT* gene (Flowering Locus T – MADS-box), which is responsible for a process of vernalization and very late flowering of *Arabidopsis thaliana* plants (Gol et al., 2017). In addition, the role of sugars in the transmission of a low-temperature signal has been confirmed and also as low molecular weight antioxidants (Rolland et al., 2002). It has been found that sugars can inhibit the mobilization of nutrients, thereby inhibit the development and growth in length of the plant aboveground part (Rolland et al., 2002). An exogenous sucrose can compensate the activity of regulators of shoots and roots meristem development (Eveland, Jackson, 2011). Sucrose is one of the main transport metabolites of a plant that supplies energy, plastic, signaling and other functions (Yuanyuan et al., 2009; Koch, 2004). Sucrose is the dominant transport form of sugars in the phloem, but it cannot directly be used for metabolic processes (Deryabin, Trunova, 2014). According to the literature, endogenous sucrose and glucose either act as substrates for cellular respiration or as osmolytes to support cellular homeostasis, whereas fructose is not associated with the osmolytic protection and synthesis of secondary metabolites (Rosa et al., 2009).

Thus, soluble carbohydrates play an important multifunctional role in the plant organism throughout the ontogenesis. In the period of vernalization, the long-term effect of positive temperatures, sugars can act as trophic substrates or transport forms of carbohydrates, or osmolytes – protectors from the low-temperature stress and signaling molecules that can indirectly regulate a plant development through the genes' expression or their epigenetic control.

The successful passing of vernalization process, probably, can be due to the optimal supply of trophic factors, which can determine the genetic and epigenetic control of vernalization gene expression.

Therefore, the aim of our work was to study the growth reactions and dynamics of the content of soluble carbohydrates of winter wheat sprouts under contrasting trophic conditions of vernalization.

Materials and methods

Seeds of two varieties of soft winter wheat *Triticum aestivum* L., Doridna and Statna (Plant Production Institute nd. a. V.Ya.Yuryev of NAAS) were used as a plant material. These varieties are of universal type of use, unpretentious to the cultivation conditions, tolerant to the main field diseases of winter wheat and have high winter resistance. Physiological and biochemical experiments were carried out at the Department of Plants and Microorganisms' Physiology and Biochemistry of V.N.Karazin Kharkiv National University during 2016–2017.

Since sugars as signaling molecules are involved in expression/repression of genes that determine plant development, we have used 3% sucrose solution in our experiments, simulating different levels of trophic support of vernalization. The vernalization of winter wheat sprouts with endosperm, which is a source of trophic and biologically active substances, causes the transition of plants to generative development. Such a variant of vernalization is optimal for the level of trophic support; its disorder can be excess, deficit or lack of trophic substances, in particular sugars. Based on the foregoing, the vernalization variants were grains + water (optimal trophic support), grains + 3% sucrose solution (excess of trophic support), isolated buds + water (without trophic support), 4) isolated buds + 3% sucrose solution (deficit of trophic support).

Wheat grains were sterilized by 5% sodium hypochlorite solution, sprouted in the dark at t=22±2ºC during two days. To simulate the contrasting conditions of trophic support, the endosperm was removed in some grains, leaving isolated buds. The vernalization was carried out in Petri dishes during 45 days at a fixed temperature +4ºC. Sampling (10 sprouts of each variant) was carried out at different stages – 15, 30 and 45 days – for biochemical and morphometric analysis. The total length of sprouts, the aboveground part and root, as well as total biomass, were determined.

A method, based on the reducing of potassium ferrocyanide in alkaline medium to ferrocyanide by reductive sugars, was used for a quantitative determination of soluble sugars content – monosaccharides, oligosaccharides and total soluble sugars in plant material. Ferrocyanide forms a steady blue color with sulfuric acid in the presence of gelatin. Based on the intensity of solution color, the amount of reducing sugars was determined by the photocolorimetric method (Yermakov et al., 1987).

Soluble sugars were determined in air-dried plant material, which was fixed by water vapor during 30 minutes at temperature 110ºC and drying during 1 hour at temperature 70ºC. Extracts of sugars were obtained by extraction with 80% ethyl alcohol. A supernatant was obtained for the analysis, after 10 minutes of centrifugation at 3000 rpm (Tymoshenko, Zhmurko, 2000; Yermakov et al., 1987). A similar method was used to determine the total soluble sugars, but with the prior hydrolysis of the extract by 5% HCl for 10 minutes. The content of oligosaccharides was calculated by the difference of content of total soluble sugars and monosaccharides. For the biochemical analysis and calibration graph, the analytical grade reagents were used.

In total, two biological and four analytical series of experiments were carried out. Statistical data processing was performed by Microsoft Excel 2010. The significance of differences between control and experimental variants was determined using Student's t-criterion, $P \leq 0.05$ (Atramentova, Utevskaya, 2008). The graphs show the mean values and their standard errors.

Results and discussion

Growth processes. It is known that plant growth mostly depends on the level of trophic substances support, in particular carbohydrates. Therefore, we have determined the dynamics of linear growth of sprouts under different conditions of trophic support during vernalization.

The results of experiments with Doridna sprouts are shown in Figure 1. They showed a gradual increase of a linear growth of the aboveground part and roots in variants grains + water and grains + 3% sucrose. However, in the variant of isolated buds + water, the growth processes did not occur during vernalization.

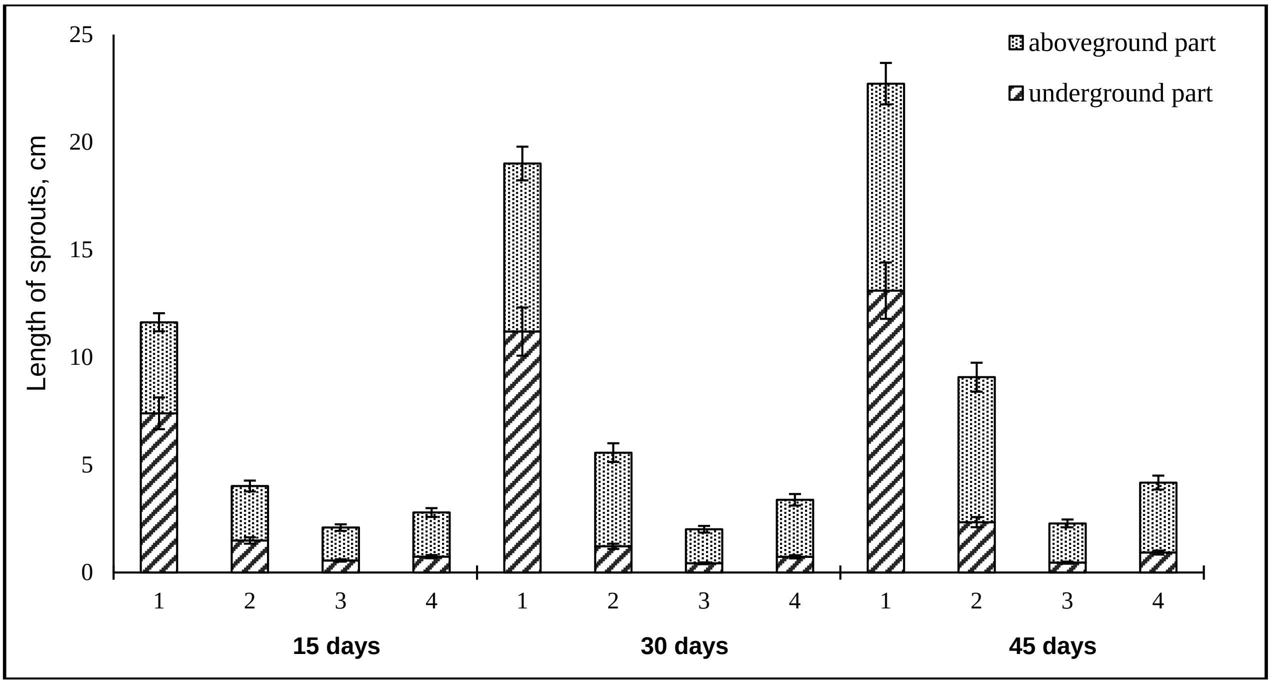

Fig. 1. Influence of contrasting conditions of trophic support on the growth reaction of winter wheat sprouts of the Doridna variety during vernalization: 1 – grains + water; 2 – grains + 3% sucrose solution; 3 – isolated buds + water; 4 – isolated buds + 3% sucrose solution

The sprouts of grains + water (optimal trophic support) were growing more intensively in about three-four times than grains + 3% sucrose (excessive trophic support) during all the period of vernalization on 15th, 30th and 45th days. The growth of sprouts of isolated buds + 3% sucrose (limited trophic support) was even slower and sprouts of isolated buds + water (lack of trophic support) were almost not growing. The results of determining the growth of Statna sprouts are shown in Figure 2. They were similar to those obtained in the experiment with Doridna. Thus, a linear growth of the aboveground part and roots was gradually intensifying in all variants of trophic support, excepting isolated buds + water. According to the intensity of sprouts growth, depending on the level of trophic support, variants were ranked as follows: grains + water > grains + sucrose > isolated buds + sucrose > isolated buds + water.

At all stages of exposure, on the 15, 30 and 45 days, in the variant of grain + water of both wheat varieties, the root system exaggerated the aboveground part of sprouts, unlike other variants (Fig. 1, 2). In particular, on the 15th day the underground part was twice as much as the aboveground, because the main role of roots of winter wheat, as well as other plants, is in absorbing water and nutrients from an environment and supplying other plant organs, especially in early stages of development (Man et al., 2016).

Thus, a linear growth of sprouts of both wheat varieties depends on the level of trophic support. Its excess (grains + sucrose), the deficit (isolated buds + sucrose), lack of (isolated buds + water) inhibit linear growth of sprouts, compared with optimal support (grains + water).

The integral indicator of the functioning of plant organism is biosynthetic processes, which are characterized by the biomass accumulation. Therefore, we have determined the dynamics of biomass of the wheat varieties sprouts during vernalization under different levels of trophic support. The results are shown in Figure 3. They have shown that biomass of Doridna sprouts has increased in all variants of trophic support, except the variant with its lack.

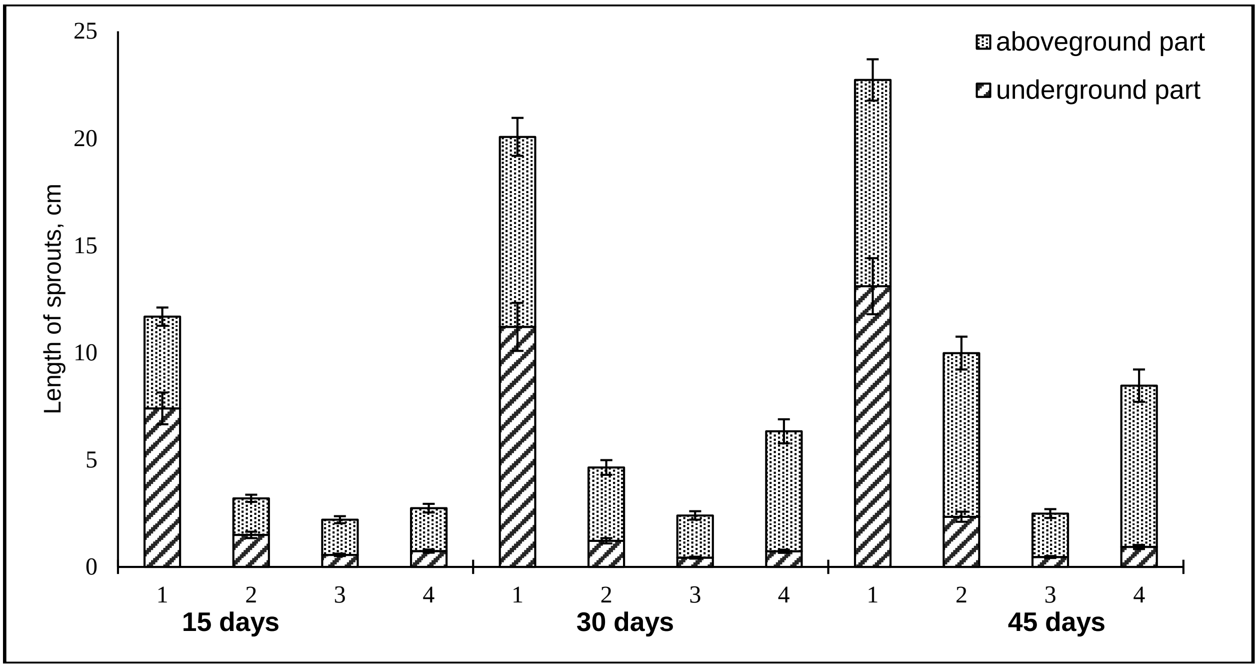

Fig. 2. Influence of contrasting conditions of trophic support on the growth of winter wheat sprouts of the Statna variety during vernalization: 1 – grains + water; 2 – grains + 3% sucrose solution; 3 – isolated buds + water; 4 – isolated buds + 3% sucrose solution

At the same time, the intensity of this process depended on the level of trophic support. Thus, the most intensive biomass accumulation occurred at the optimal level (grains + water). Excessive support (grains + sucrose) inhibited the formation of biomass in comparison with this process under optimal support. In this case, inhibition was shown largely in the variant of isolated buds + sucrose (Fig. 3).

The dynamics of the biomass formation of Statna sprouts was generally similar to this process in Doridna, but with some exceptions. The most intensive biomass was under optimal trophic support. Under its excess (grains + sucrose), the biomass of Statna sprouts has increased by the 30th day, but decreased by the 45th day. However, in this variant, the inhibition of the biomass accumulation has been occurring during vernalization, compared with the variant with optimal trophic support. The biomass of Statna sprouts under lack of trophic support has been increasing, but several times slower than under the optimal and excess ones. Under lack of support (buds + water), the biomass has not been changing during the entire period of vernalization (Fig. 3).

Thus, the determination of growth processes of two winter wheat varieties has shown their dependence on the trophic support during vernalization. Obtained results suggest that the trophic support of vernalization, along with biologically active substances and genetic factors, can be a significant factor in the regulation of winter wheat growth processes and development.

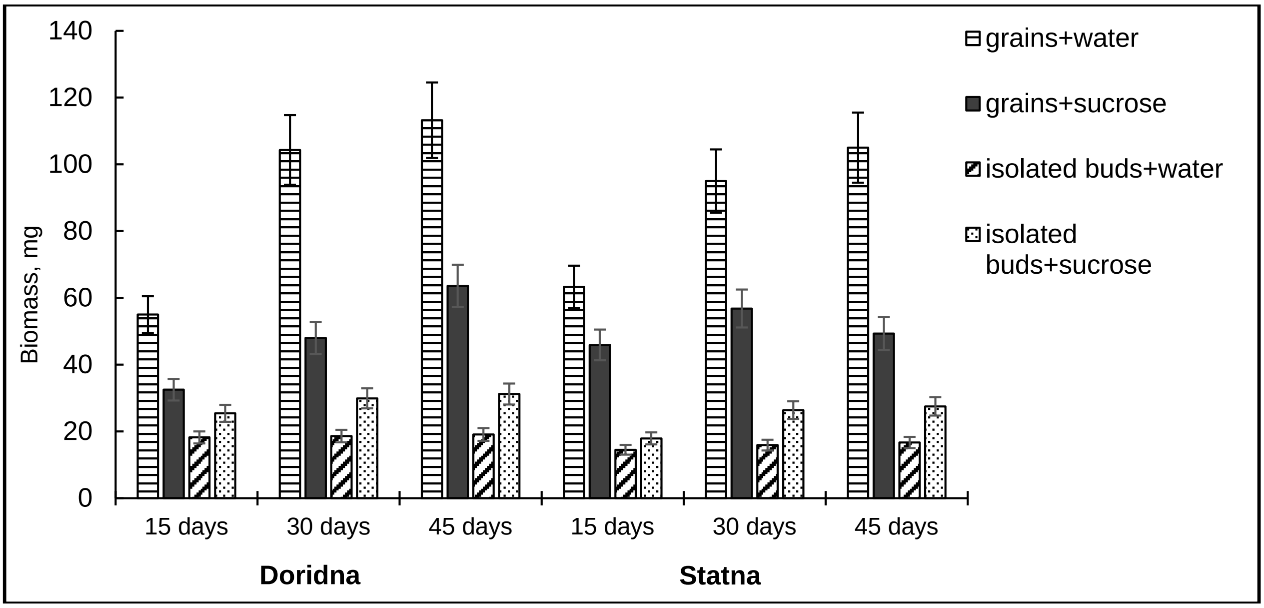

Fig. 3. Influence of contrasting conditions of trophic support on the biomass accumulation of sprouts of two winter wheat varieties during vernalization

The content of carbohydrates. The literature data presented in the review show that carbohydrates play a significant role as signaling molecules in the regulation of the plant growth and development, participating in the genes expression/repression. Their regulatory effect, probably, is realized when a certain optimal concentration is achieved in cell compartments, but cannot be realized when their content goes beyond the optimum, i.e. becomes excessive or insufficient. This fact can be confirmed by the fact that growth processes depend on the level of trophic support during vernalization.

In our model of the experiment, we assume that changes in the level of trophic support during the vernalization process can be achieved by changing the endogenous concentration of carbohydrates of sprouts. Therefore, we have determined the content of soluble carbohydrates of sprouts under different levels of trophic support.

The results of experiments with the Doridna variety are shown in Figure 4. They showed that the level of endogenous carbohydrates varies depending on the trophic support. The total content of carbohydrates (oligosaccharides + monosaccharides) was the highest in the variant of grains + water, a bit lower – in grains + sucrose, even lower – isolated buds + sucrose, the lowest – isolated germs + water. In this case, in all variants of the experiment, oligosaccharides content was substantially higher than monosaccharides. This fact, perhaps, is explained by the intensive involving of monosaccharides in metabolic processes.

The content of oligosaccharides in the first 15 days of vernalization was maximum in the sprouts of the grains + water, significantly lower in the grains + sucrose and isolated buds + water and minimum in the isolated buds + sucrose. During the next 15 days (at the 30th day) the content of oligosaccharides of sprouts of the grains + water and grains + sucrose significantly decreased. At the same time, in the isolated buds + water and isolated buds + sucrose there was a slight tendency to increase it. At the 45th day of vernalization, the content of oligosaccharides of the grains + water increased. In the grains + sucrose, their content increased. In the isolated buds + sucrose, it did not change, and in the case of isolated buds + water significantly decreased (Fig. 4). Consequently, the dynamics of oligosaccharides content depended on the level of trophic support of sucrose during vernalization.

As for the dynamics of the monosaccharides content during vernalization, it was another than that of the oligosaccharides. During 30 days of vernalization, in the sprouts of grains + water and grains + sucrose there was a tendency to monosaccharides decrease. During this period, changes of its content in the isolated buds + water were not detected. However, in the isolates buds + sucrose its content significantly decreased. At the 45th day of vernalization, the content of monosaccharides increased only in sprouts of the isolated embryos + sucrose, while in others decreased, compared with the 30th day (Fig. 4).

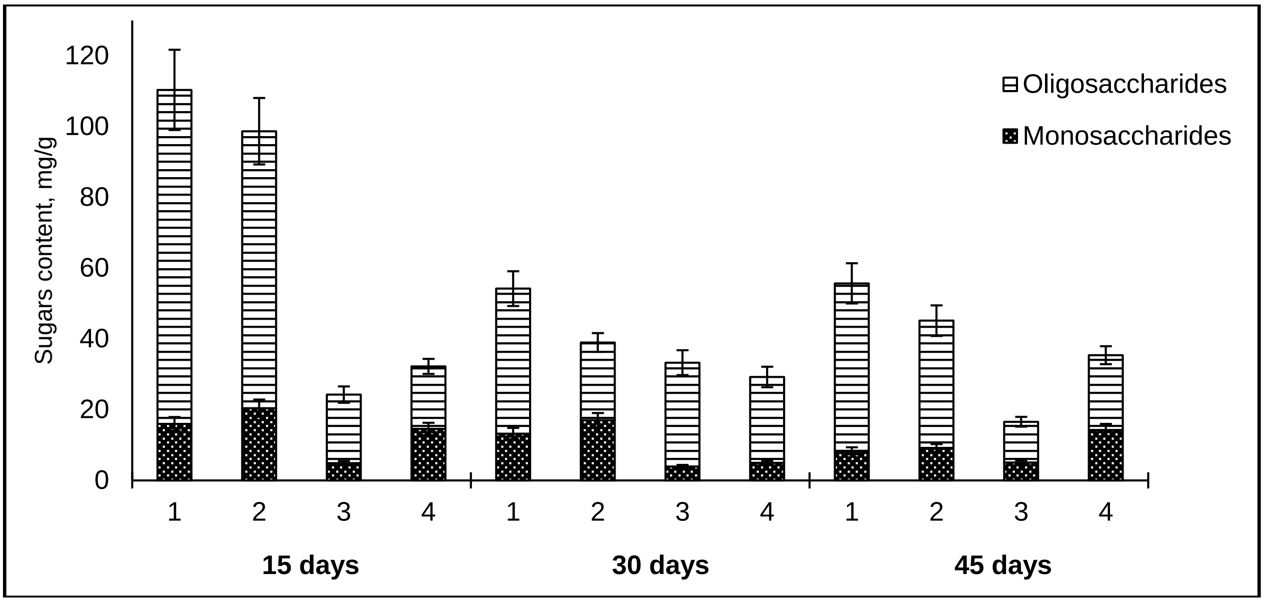

Fig. 4. Dynamics of soluble carbohydrates content of winter wheat sprouts of the Doridna variety under different conditions of trophic support during vernalization: 1 – grains + water; 2 – grains + 3% sucrose solution; 3 – isolated buds + water; 4 – isolated buds + 3% sucrose solution

The results of studying the dynamics of soluble carbohydrate content of the Statna sprouts are shown in Figure 5. They showed that the content of oligosaccharides was higher than the one of monosaccharides in most variants of the experiment, except isolated buds + sucrose on the 15th day of vernalization. The total sugars content was the highest in sprouts of grains + water and grains + sucrose; it was substantially lower in the isolated buds + sucrose and the minimum – in the isolated buds + water.

The content of oligosaccharides of the Statna sprouts at the 15th day was maximum in the grains + sucrose, much lower in the grains + water, while minimum and same in the isolated buds + water and isolated buds + sucrose. At the next 15 days of vernalization, the oligosaccharides content in the grains + water and grains + sucrose significantly decreased. At the same time, in the first it was more than in the second ones. The increase of the oligosaccharides content was identified in the isolated buds + water. This increase was higher in the isolated buds + sucrose than in the isolated buds + water. At the 45th day of vernalization, the content of oligosaccharides increased in all variants of trophic support, excepting the isolated buds + water, in which its content tended to decrease (Figure 5).

The dynamics of monosaccharides content was manifested in its decline from the 15th to the 30th day of vernalization in the sprouts of most variants, excepting the isolated buds + water. The content of grains + water and grains + sucrose kept on decreasing, while the isolated buds + sucrose conversely increased by the 45th day. The monosaccharides content in the isolated buds + water was the lowest compared with other variants and practically did not change during the entire period of vernalization. Comparing analysis of the dynamics of carbohydrate content of sprouts during vernalization, depending on the trophic support, showed significant differences between Doridna and Statna. Obtained results are likely related to genotypes and, probably, the intensity of the metabolic processes during the vernalization period.

Thus, the nature of change of the linear growth, biomass accumulation and content of endogenous sugars of sprouts of two winter wheat varieties during vernalization depended on the level of trophic support.

According to our data, the linear growth of sprouts and biosynthetic processes (accumulation of biomass) differed substantially from the variants of trophic support (in our case, sucrose), which can indicate the regulatory role of carbohydrates in this process. According to the literature, sugar can inhibit a linear growth and inhibit plant development (Rolland et al., 2002), which is exactly what we have set under excess of trophic supplies (grains + sucrose) compared with optimal trophic support (grains + water). The inhibition of growth under deficit (isolated buds + sucrose) of trophic support is probably related to a violation of the regulatory function of sugars. As a result, the minimum, created by the addition of sucrose solution, was used mainly as a plastic and energy material to ensure a minimum level of growth processes (Yuanyuan et al., 2009; Koch, 2004; Aoki et al., 2006). The signaling function of sugars presumably could not be fully performed (Rosa et al., 2009; Baena et al., 2007; Baier et al., 2004), as well as their participation in the expression and/or repression of genes (Cho et al., 2006; Riou-Khamlichi et al., 2000; Gol et al., 2017).

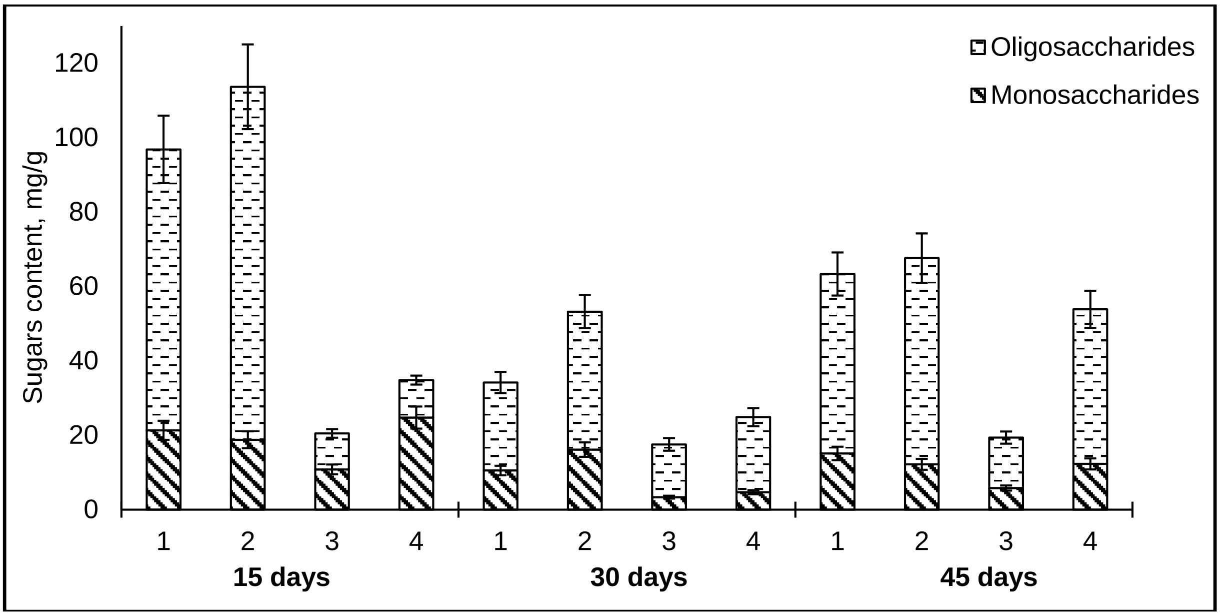

Fig. 5. Dynamics of the soluble carbohydrates content of winter wheat sprouts of the Statna variety under different conditions of trophic support during vernalization: 1 – grains + water; 2 – grains + 3% sucrose solution; 3 – isolated buds + water; 4 – isolated buds + 3% sucrose solution

The written, in our opinion, can explain the fact that we have established – almost complete lack of growth processes in the isolated buds + water. It is also possible that under changes of the level of trophic support (excess, deficit and lack) the hormonal regulation of growth processes during vernalization can be broken because sugar signaling overlaps with other signaling pathways, including hormonal (Rosa et al., 2009; O'Hara et al., 2013).

We have shown that the dynamics of the content of soluble carbohydrates (endogenous) during vernalization essentially depends on the level of trophic support (exogenous sucrose). It can also indicate the regulatory function of the trophic support in vernalization process.

According to data obtained, in the variants with optimal, excessive and insufficient support, the content of soluble carbohydrates of both varieties sprouts becomes higher on the 45th day of vernalization than at the 30th. However, under lack of trophic support, such an increase does not occur. It is known that 45 days of vernalization is sufficient for the transition of winter soft wheat to earing (Avksentieva, Zhmurko, 2011). This suggests that in the sprouts, metabolic processes, in particular, carbohydrate metabolism, are being activated at the end of vernalization, which is one of the important factors of reducing an expression of the *VRN 1* and *VRN 2* genes (Shcherban, Salina, 2013; Sung, Amasino, 2005; Song et al., 2012). Thus, wheat plants get the ability of transition to flowering. Consequently, according to our results, a different level of trophic support (in our experiments with sucrose) can be one of the important factors of genetic (and/or epigenetic) regulation of wheat vernalization. This condition can be confirmed by the data received earlier (Avksentieva, Shulik, 2017). It was shown that the vernalization of wheat sprouts, supplemented by sucrose solution, stimulated the cell division of root meristems, accelerated the pace of plant development. At the same time, these processes were significantly inhibited due to the lack of trophic support.

Since we have applied a model with different levels of trophic support and found dependence on it of growth processes, dynamics of carbohydrate content of sprouts of two winter wheat varieties, it can be assumed that the regulatory function of carbohydrates during vernalization is carried out under a certain level of their pool, which is optimal in plant cells.

The work was carried out within the frames of the state budget theme of the Department of Plant and Microorganism Physiology and Biochemistry of V.N.Karazin Kharkiv National University "Research of molecular and genetic, physiological and biochemical mechanisms of vernalization and photoperiodic control of plants' ontogenesis *in vivo* and *in vitro*" No. 0118U002104.

References

Aoki N., Scofield G.N., Wang X.-D. et al. Pathway of sugar transport in germinating wheat seeds // Plant Physiology. – 2006. – No. 141. – P. 1255–1263.
Atramentova L.A., Utevskaya O.M. Statistical methods in biology: a textbook. – Gorlovka: Likhtar, 2008. – 248p. (in Russian)
Avksentieva O.A., Zhmurko V.V. Physiology of flowering: tutorial. – Kharkiv: V.N.Karazin KhNU, 2011. – 130p. (in Russian)
Avksentieva O.A., Shulik V.V. Research of influence of contrasting trophic conditions of vernalization on the mitotic activity of meristems, growth and development of winter wheat // ScienceRise: Biological Science. – 2017. – Vol.2 (5). – P. 4–9. (in Ukrainian)
Baena G.E., Rolland F., Thevelein J.M., Sheen J. A central integrator of transcription network in plant stress and energy signaling // Nature. – 2007. – Vol.448 (7156). – P. 938–942.
Baier M., Hemman G., Holman R. et al. Characterization of mutants in *Arabidopsis* showing increased sugar-specific gene expression, growth, and developmental responses // Plant Physiology. – 2004. – Vol.134 (1). – P. 81–91.
Cho Y.H., Yoo S.D., Sheen J. Regulatory functions of nuclear hexokinase 1 complex in glucose signaling // Cell. – 2006. – Vol.127 (3). – P. 579–589.
Dennis E., Peacock W. Vernalization in cereals // Journal of Biology. – 2009. – Vol.8 (57). – P. 1–4.
Deryabin A.N., Trunova T.I. Morphological and biochemical characteristics of potato plants expressing the invertase gene *SUC2* from *Saccharomyces cerevisiae*, under cultivation *in vitro* // Tomsk State University Journal of Biology. – 2014. – Vol.4 (28). – P. 150–168. (in Russian)
Eveland A., Jackson D. Sugars, signalling, and plant development // Journal of Experimental Botany. – 2011. – Vol.63 (3). – P. 1–11.
Gol L., Tome T., Korff M. Floral transitions in wheat and barley: interactions between photoperiod, abiotic stresses, and nutrient status // Journal of Experimental Botany. – 2017. – Vol.68 (7). – P. 1–12.
Henderson I., Shindo C., Dean C. The need for winter in the switch to flowering // J. Annu. Rev. Genet. – 2003. – Vol.37. – P. 371–392.
Koch K. Sucrose metabolism: regulatory mechanisms and pivotal roles in sugar sensing and plant development // J. Current Opinion in Plant Biology. – 2004. – Vol.7. – P. 235–246.
Man J., Shi Y., Yu Zh., Zhang Y. Root growth, soil water variation, and grain yield response of winter wheat to supplemental irrigation // Plant Production Science. – 2016. – Vol.19 (2). – P. 193–205.
O'Hara L.E., Paul M.J., Wingler A. How do sugars regulate plant growth and development? New insight into the role of trehalose-6-phosphate // J. Molecular Plant. – 2013. – Vol.6 (2). – P. 261–274.
Riou-Khamlichi C., Menges M., Healy J., Murray J. Sugar control of the plant cell cycle: differential regulation of *Arabidopsis* D-type cyclin gene expression // J. Molecular Cell Biology. – 2000. – Vol.20. – P. 4513–4521.
Rolland F., Moore B., Sheen J. Sugar sensing and signaling in plants // J. Plant Cell. – 2002. – Vol.14. – P. 185–205.
Rosa M., Prado C., Podazza G. et al. Soluble sugars – metabolism, sensing and abiotic stress // Plant Signaling & Behavior. – 2009. – Vol.4 (5). – P. 388–393.
Shcherban A.S., Salina E.A. Epigenetic regulation of the expression of vernalization genes // J. Cytology. – 2013. – Vol.55 (4). – P. 234–237. (in Russian)
Song J., Angel A., Howard M., Dean C. Vernalization – a cold-induced epigenetic switch // Journal of Cell Science. – 2012. – Vol.125 (16). – P. 3723–3731.
Sung S., Amasino R. Remembering winter: toward a molecular understanding of vernalization // J. Annu. Rev. Plant Biol. – 2005. – Vol.56. – P. 491–508.
Tymoshenko V.F., Zhmurko V.V. Methods of analysis of carbohydrates: a guide to a large workshop for students at the Department of Plant Physiology and Biochemistry. – Kharkiv: KhNU, 2000. – 30p. (in Ukrainian)

Yermakov A.I., Arasimovich V.V., Yarosh N.P. et al. Methods of biochemical research of plants. – Leningrad: Agropromizdat. Leningrad Branch, 1987. – 430p. (in Russian)
Yuanyuan M., Yali Z., Jiang L., Hongbo S. Roles of plant soluble sugars and their responses to plant cold stress // African Journal of Biotechnology. – 2009. – Vol.8 (10). – P. 2004–2010.

Представлено: Н.І.Рябчун / **Presented by: N.I.Ryabchun**
Рецензент: Є.Е.Перський / Reviewer: Ye.E.Persky
Подано до редакції / *Received: 06.09.2018*

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