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ORIGINAL ARTICLE

Features of leaf photosynthetic apparatus of sugar beet under retardants treatment

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We studied the influence of antigibberellin compounds with different mechanisms of action-Paclobutrazole (0.05%) and Dextrel (0.3%) on the formation of leaf surface, structure of photosynthetic apparatus and features of leaf functioning under retardants artificial growth control on sugar beet plants. We found that retardants treatment slowed the growth of total leaf surface of sugar beet. At the same time, application of Paclobutrazole (0.05%) caused a greater retardation effect on plant growth. The number of dead leaves of treated plants during vegetation season was unchanged compared to control. We established that decrease in the leaf area was accompanied by their thickening due to increase in the size of palisade and spongy parenchyma cells, decrease in the size of epidermal cells and increase in the number of stomatas per unit leaf area. Stomatal index which characterizes the ratio of number of stomata form to the total number of epidermal cells on the same leaf area was identical for all experimental variants, notably, the ratio of stomata and other epidermal cells not changed under retardants application. The rate of photosynthesis of retardants-treated leaves was lower than in a control, and the proportion of respiratory processes in their carbon dioxide gas exchange was greater. Dextrel and Paclobutrazole differently influenced on the ratio of leaf and mesophilic resistances of CO_2 diffusion and concentration of carbon dioxide in intercellular spaces, that indicates about different regulation of assimilation apparatus activity with their participation. Retardants are a powerful means to regulate the assimilation apparatus activity, one of the donor-acceptor system component, and can be used for the targeted regulation of plastic substances redistribution in sugar beet.

Keywords: Retardants; mesostructural organization; photosynthesis; dark and photorespiration; sugar beet (*Beta vulgaris* L.)

Introduction

According to modern concepts, the higher plants represent a single donor-acceptor system (“source-sink”), whose functioning is determined by the genetic development program. There are three zones of assimilates acceptance: growth zones, nutrient uptake zones and active metabolism zones (Kiriziy et al., 2014). Formation of economic harvest is determined by the strategy of assimilate redistribution between these basic acceptors. The development of donor-acceptor ("source-sink") systems of plant opens the prospects of artificially redistributing of assimilates flows from vegetative growth processes to the fruits formation and growth needs, and therefore, it is a potential factor in increasing the agricultural crops productivity (Bonelli et al., 2016; Dewi and Darussalam, 2018; Kumar et al., 2012; Rogach et al., 2016; Kuryata and Khodanitska, 2018; Yu et al., 2015; Shevchuk, 2018).

Phytohormonal growth regulators or their antagonists affect to enhance the attracting activity of acceptor zones, which results in intensification of carbon dioxide fixation during photosynthesis, increased photosynthetic productivity and redistribution of assimilates from leaves to growth or storage zones (Cai et al., 2014; Mohammad and Mohammad, 2013; Ljung et al. 2015; Zheng et al., 2012).

Synthetic growth inhibitors - retardants - received the greatest value in agricultural practice among the numerous plant growth regulators. Despite the fact that these substances have different chemical nature, they all exhibit antigibberellin action and are united by their ability to inhibit plant growth (Pobudkiewicz, 2014; Koutroubas and Damalas, 2016).

Retardants due to the regulation of growth processes, insertion in metabolic processes, can improve the water regime, increase plant resistance to unfavorable environmental factors, in particular extreme temperatures, increase drought and high-temperature strength, frost, phytopathogenic microorganisms and pests resistance (Ullah et al., 2018; Farooq et al., 2012; Dwivedi et al., 2017; Upreti and Sharma, 2016; Zhao et al., 2017).

It is highly effective to use retardants in cereals, which increased their resistance to lodging (Kamran et al., 2018; Vashchenko et al., 2014; Kamran et al., 2018). Application of retardants, ethyleneproducer and their derivatives leads to an increase in the productivity of oilseed (Kuryata et al., 2017; Kuryata and Polyvanyi, 2018; Kuryata and Khodanitska, 2018; Poprotska and Kuryata, 2017); legumes (Han et al., 2017; Kuryata and Golunova, 2018), vegetable crops (Rademacher, 2015; Kuryata and Kravets 2018). Broadly used retardants in floriculture to shorten shoots of ornamental plants and increase the number of vegetative propagation organs (Wu et al., 2018).

It is known that productivity of sugar beet in many respects depends on the rate of formation and functional activity of the first and second decimal leaves. At the same time, the plants of this culture have a high leaf-forming potential, in some cases in the first year of life on the plant can be formed 40-90 leaves with a total area of 3 to 6 thousand cm^2. In addition, the fourth and subsequent dozens leaves often not complete their development as a result of low night temperatures. Since the leave a significant period of time stays as an acceptor of assimilates, until 50-60% of the maximum length, an additional powerful attractive zone is created. The enhancement of leaf surface indexes above 3.5 not bring any benefit, since the leaves obscure each other and compete with root in assimilates. It is shown that the removal of apices and part of late leaf not affect the productivity of plants (Kiriziy et al., 2014). Since it is not practical to limit the growth of excess leaves by surgical means, it is necessary to search for other, more effective means of leaf growth inhibition processes. In this case, the issue of this study was to find out the effect of retardant Paclobutrazole and Dextrel on the leaf surface formation, structure of photosynthetic apparatus and features of leaf functioning under artificial regulating growth retardants application on sugar beet plants.

Methods

Sugar beet plants of hybrid Roberta were grown in vegetative vessels with 32 kg of soil capacity with the addition of nutritional mixture VNIS. The lower irrigation was applied, soil moisture content during the vegetation maintained at 60 % of the total moisture content.

The experiment was carried out with the application of triazole derivative Paclobutrazole (P 333) -4,4-Dimethyl-2- (1,2,4-triazolyl-1) -1 (4-chlorophenyl) pentane-3 derivative of 1,2,4-triazole, which is synthesized by «ACI» (United Kingdom) (Soumya et al., 2017) and ethylenereleasing compound Dextrel D-(+)-threo-1-(p-nitrophenol)-1,3-dixispropylammonium, 2-chloroethyl-phosphonic acid, which is synthesized at the Institute of Organic Chemistry of the National Academy of Sciences of Ukraine.

The treatment was applied with aqueous solution of Paclobutrazole (0.05%) and Dextrel (0.3%) at the period of 14-16 leaves formation.

Mesostructural characteristics of leaves was determined at a fixed material. For preservation was used a mixture of equal parts of ethanol, glycerol and water with addition of 1 % formalin. It was used as maceration agent 5 % solution of acetic acid in 2 mol/l hydrochloric acid. For analysis, it was selected the middle-layer leaves of the shoots, which completely ended their growth, after 30 days drugs-treated plants.

Determination of epidermal cells size was carried out by the maceration of partial leaf tissue method. The estimation of epidermal cells area was performed by using a microscope and ocular micrometer MOB-1-15x, counted the number of cells in the tissue per unit vision area, followed by the calculation of one cell and its volume.

The pigments content was determined in the fresh material by spectrophotometric method on the spectrophotometer SF-18. It was determined the total leaf surface area, number of leaves and number of dead leaves during the vegetation once every 10 days. Intensity of carbon dioxide gas exchange was measured on non-separated middle-layer leaves from the plant which completely ended their growth under controlled conditions on installation mounted of infrared optical-acoustic gas analyzer GIAM-5M. A part of the leave to the right of central vein was placed in a thermostable leave chamber (25 °C) in the 3 × 7 cm size. The leave was lit by a KG-2000 incandescent lamp through a water filter. The intensity of lighting is 400 W/m2. It was blown through the chamber a purified atmospheric air with a natural concentration of CO_2. The air humidity after camera was measured by a thermoelectric microscope. It was calculated the parameters of carbon dioxide gas exchange and transpiration. Sampling for analysis was carried out with five analytical replication of the research (AOAS, 2010).

The statistical processing of results was carried out using the statistical software Statistica 6.0. The reliability of obtained results between control and experiment varient was assessed with the use of Student's t-test. Tables and figures show mean values for the years of research and their standard errors.

Results

It was found that the growth of total leaf surface of experimental hybrid Roberta plants inhibited under redardants application (Table 1). At the same time, a more growth-inhibiting effect was found under 0.05% Paclobutrazole interaction. In treated plant, number of leaves that died during the period of vegetation was unchanged compared to control. The obtained results suggest that Paclobutrazole treatment caused formation of rooting habitus of experimental plants (Figure 1).

Table 1. Area of leaf surface and number of leaves under retardants treatment on sugar beet Roberta.

Measurements	Area of leaf surface at the end of vegetation, cm^2	Number of leaves formed during vegetation	Area of dead leaves during vegetation, cm^2	Number of dead leaves during vegetation
Control	1751 ± 74	48.1 ± 1.82	1335 ± 81	12.0 ± 0.52
0.3% Dextrel	1498 ± 50*	50.0 ± 1.63	1254 ± 75	12.1 ± 0.62
0.05% Paclobutrazole	1290 ± 43*	49.3 ± 1.61	1495 ± 95	11.0 ± 0.53

Note: * - difference is significant at p<0.05.

It is known that the character of photosynthetic process, energy and substrate support of morphogenesis is largely determined by the anatomical and morphological features of leaf.
The analysis of mesostructural organization of sugar beet leaf treated by retardants indicate significant anatomical changes. In particular, decrease in the leaf area of treated plants was accompanied by thickening of lamina, and this thickening was achieved due to increased volume of palisade and linear dimensions of spongy parenchyma of leave with increment of chlorophyll content in tissues (Table 2). Similar changes were observed in Solanum melongena plants under application of Esphon, Tebuconazol and Chlormequat chloride (Kuryata et al., 2016), as well as Solanum tuberosum plants under Tebuconazol and Chlormequat chloride (Rogach et al., 2016).
The volume of spongy cells parenchyma wasn’t count, due to the fact that the cells are in the wrong shape. Reduction of leaf area of experimental plants was accompanied by an increase in size of main leaf cells weight, the results indicate that retardants caused a decrease in the meristematic activity of marginal meristems.
At the same time, it is drawn attention to the fact that experimental plants were characterized an increase in the number of stomata per unit area of leaf and an increase in the area of a stoma. An increase in the number and area of stomatas was also observed in potato plants under the influence of Tebuconazole and Chlormequat chloride (Rogach et al., 2016). It should be noted that an increase in the number of stomata per unit area of epidermis correlated with the decrease in the size of main epidermal cells.

Figure 1. Application of retardants on rooting habitus formation of sugar beet Roberta.

The calculation of stomatal index, which characterizes the ratio of number of stomata form to the total number of epidermal cells on the same leaf area, indicates that for all variants of experiment it was the same, the ratio of stomata and other cells of epidermis under retardants not changed (Table 2).

Table 2. Leaf mesostructural organization of sugar beet Roberta under retardants treatment.

Measurement	**Control**	**0.3% Dextrel**	**0.05% Paclobutrazole**
Thickness of leave. μm	169.0 ± 2.12	254.2 ± 4.06*	221.3 ± 6.14*
Partial volume tissue on leaf cross section. % :			
epidermis	22.5 ± 0.92	19.3 ± 0.71*	14.4 ± 1.80*
chlorenchyma	77.5 ± 2.14	80.7 ± 1.42	85.6 ± 2.43*
Volume of palisade parenchyma. μm^3	6069 ± 137	6884 ± 280*	7840 ± 207*
Length of spongy cells. μm	26.9 ± 0.50	28.1 ± 0.42	27.3 ± 0.70
Width of spongy cells. μm	23.6 ± 0.50	24.7 ± 0.84	22.5 ± 0.43
Number of stomatas on 1 mm^2 of the abaxial leaf surface	350.1 ± 3.02	400.0 ± 5.11*	400.2 ± 5.04*
Area of a stoma. μm 2	267.1 ± 6.02	333.1 ± 3.11*	280.2 ± 7.05
Area of an epidermal cell. μm 2	505.0 ± 5.02	434.3 ± 4.11*	415.2 ± 5.07*
Stomatal index	0.15	0.15	0.15
Total chlorophyll content (a+b). % per leaf fresh matter weight	0.52 ± 0.014	0.58 ± 0.011*	0.63 ± 0.010*

Note: * - difference is significant at $p<0.05$.

It was visually marked the reduction of intercellular space in chlorenchyma leaves of experimental plants. It is known that the growth of epidermal cells with normal development of leave lasts longer than the growth of chlorenchyma cells. Consequantly, intercellularities are formed and the distance between formed chlorenchyma cells increased. Accordinly, it was noted a pattern, in our opinion, that indicates an earlier termination of epidermal cells growth under the influence of retardants.

The photosynthesis and breathing are an important element in the production process of plants. The intensity of photosynthesis and respiration of plants depends on age, growth rate, weight ratio of individual organs and is closely related to other processes that occur in the plant and environmental factors. It is known that breathing processes are a powerful metabolic acceptor of assimilates, the total respiratory rate can range from 10 to 80 % of carbon absorbed by photosynthesis. At the same time, the literature data indicates that influence of retardants on plants respiration and photosynthesis is fragmentary in nature. Thus, Uniconazole treatment increased the chlorophyll content of Landoltia punctata leaves and the net photosynthesis ratio by regulating the basic enzymes that involved in the biosynthesis of endogenous hormone and chlorophyll (Liu et al., 2015), and application of Chlorcholinchloride on Phaseolus vulgaris L. plants resulted in increased tolerance of photosystem II (Kreslavskii et al., 2011). Limited data on the action of plant growth inhibitors on ratio of respiration and photosynthesis significantly reduces the possibility to analyze the influence of this group of growth regulators on the donor-acceptor system formation and determines the need for in-depth study of the issue.

Therefore, it is advisable to analyze the relationship between the processes of respiration and photosynthesis, value of photorespiration in the overall balance of carbon metabolism for retardants application on sugar beet plants. Consequantly, the evidence from this study suggest a variety of retardants Paclobutrazole and Dextrel treatment on photosynthesis and gas exchange of sugar beet plants in order to optimize the crop production process.

The growth function of plant depends not only on the structure and power of photosynthetic apparatus, but is an integral manifestation of physiological processes, among which an important place belongs to the ratio of respiration and photosynthesis in the ontogenesis of individual organs and a whole plant.

It was found that surgically removed of lamina part (acceptor) on sugar beet plants decrease in the rate of photosynthesis with simultaneous intensification of dark respiration (Kiriziy et al., 2014).

The issues of photosynthetic maintenance of plant morphogenesis during the changes in donor-acceptor relations in plants are adequately covered, however, respiratory features, the role of plant photorespiration and magnitude of respiratory costs compared to gross-photosynthesis during transition to other donor-acceptor relations in general, and under the influence of retardants, in particular, it was not clarified.

Table 3. Rate of photosynthesis, dark and photorespiration of leaf under retardants application on sugar beet Roberta.

Measurement	**Control**	**0.3% Dextrel**	**0.05% Paclobutrazole**
Carbon dioxide gas exchange of leaf. mg $CO_2/(dm^2 \cdot h)$: Apparent photosynthesis P	21.5 ± 0.02	19.9 ± 0.02*	18.2 ± 0.04*
Photorespiration Rp	6.5 ± 0.03	6.1 ± 0.03*	6.0 ± 0.03*
Dark respiration Rd	3.5 ± 0.03	3.8 ± 0.09*	3.5 ± 0.03
Rp/P	0.30 ± 0.004	0.32 ± 0.003*	0.33 ± 0.003*
Rd/P	0.16 ± 0.002	0.20 ± 0.003*	0.19 ± 0.003
Diffusion resistance. s/cm	3.76 ± 0.009	4.05 ± 0.005*	3.68 ± 0.002*
leaf r_l			
mesophyll r_m	6.14 ± 0.05	7.11 ± 0.05*	8.13 ± 0.02*

The results of the study suggest that application of retardants caused changes in gas exchange of the plant. In treated plants, mesophilic resistance of leaves (rm) increased (Table 3), that was accompanied by decrease in the rate of photosynthesis, despite increase in the chlorophyll content in leaf tissues (Table 3).

Discussion

Retardants Dextrel and Paklobutrazole significantly influenced on the morphogenesis of sugar beet plants hybrid Roberta. The formation of total leaf surface reduced under compounds treatment. Paclobutrazole interaction caused the most-clear growth-inhibiting effect on plants. Application of this compounds formed the rosette habitus of plants.

Number of dead leaves during vegetation of retardant-treated sugar beet plants was unchanged. Assimilating surface area of treated plants was reduced with simultaneous thickening of lamina due to increased volume of palisade and linear dimensions of spongy parenchyma of leave.

The interaction of retardants led to increase the number of stomata per unit leaf area and increase area of a stoma. The increase in the number of stomata per unit epidermal area correlated with reduction of the main epidermal cells size. So, retardants contribute to an earlier termination of epidermal cells growth.

It was established that stomatal index, which characterizes the ratio of number of stomata form to the total number of epidermal cells on the same leaf area, wasn’t change under Dextrel and Paclobutrazole treatment.

Application of retardants led to reduce the intercellular space in chlorenchyma of sugar beet leaves. It is known that mesophyllic resistance depends on the volume of intercellular spaces, size of free mesophyll cell surface, physicochemical conditions of carbon dioxide exchange from cell surface to chloroplast and activity of ribulose bisphosphate-carboxylase. The results of the study of mesostructural organization of sugar beet leaf indicate that one of the reasons for increase in mesophyllic resistance under retardants treatment is the thickening of leave and reduction of intercellular spaces due to an earlier termination of epidermal cells growth.

It was found that an increase in costs on photorespiration and dark respiration of leaves, which were fully formed after the treatment of retardants with different mechanisms of action - Paclobutrazole and Dextrel is an important fact to understand the functioning of donor-acceptor system of plants.

The factors that limit donor function of leave after retardant interaction are a decrease in leaf surface area due to a reduction in proliferative activity of meristem, an increase in mesophyllic resistance of CO_2 diffusion, an inhibition of the rate of assimilates utilization in growth processes in the leave, and their outflow to the upper tier leaves, that are consumers. All this leads to decrease intensity of CO_2 assimilation and increase the share of respiratory costs on carbon dioxide gas exchange, which is a sign of the presence of unused assimilates excess in leave.

It should be noted that the experimental compounds have a different effect on the components of diffuse resistance. The leaf rl and mesophyllic rm resistance of Dextrel-treated plants simultaneously increased, whereas Paclobutrazole treatment had practically no effect on rl with substantial growth of rm. It can be concluded that effect of Paclobutrazole on photosynthetic apparatus is not limited to inhibit the photosynthesis by excess assimilates (in this case, the effect that occurs by Dextrel application is more likely to be expected), and compound may be involved in the regulation of photosynthetic processes.

Conclusions

Plant growth retardants-Dextrel and Paclobutrazole-affect the anatomical and physiological parameters of photosynthetic apparatus of sugar beet, which results in a decrease of leaf surface area, apparent photosynthesis and an increase in the share of respiratory costs on carbon dioxide gas balance.

Retardants are a powerful regulators of assimilative activity, one of the components of plant donor-acceptor system and can be used for the targeted regulation of plastic substances redistribution in sugar beet.

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