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Features of morphogenesis, accumulation and redistribution of assimilate and nitrogen containing compounds in tomatoes under retardants treatment

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We studied the influence of ethylene product Esphon® and triazole derivative Folicur® on the morphogenesis and productivity of tomatoes. The obtained results explained the significant role of morphological and mesostructural components of "source-sink" relation system of tomatoes in the formation of crop productivity. We established that the Folicur application resulted in more significant anatomical and morphological changes in the formation of leaf apparatus in comparison with the ethylene producer: the measurement of number, weight, area of leaf surface, and leaf index were higher in this variant of experiment. We also noted the appropriate changes in the mesostructure measurement of leaves: thickness of leave – main photosynthetic tissue of chlorenchyma, assimilatory cells size of palisade and spongy parenchyma. Analysis of depositing possibilities of plants vegetative organs at the fruitification stage indicates the importance of temporary postponement of nonstructural carbohydrates and nitrogen containing compounds in them followed by reutilization for carpogenesis needs. Application of Folicur resulted on the formation of a more powerful donor sphere and in the early fruit growth and formation stages are postponed more carbohydrates in vegetative organs of tomato plants compared to control. The content of sugars and starch in the roots, stems and leaves of plants under Folicur treatment was highest in all organs of the plant throughout the fruitification phase compared to control and variant with Esphon application. Our results also testify to the possibilities of nitrogen compounds remobilize from vegetative organs to carpogenesis needs. After Folicur treatment, the most intense decrease in the content of nitrogen containing compounds was observed during the transition from the fruit formation stage to green fruits stage in roots and stem of plant during the period of the most intense tomatoes growth. We concluded that a significant increase the yield of tomato crop was caused by the more powerful donor sphere formation and reutilization of assimilates and nitrogen containing compounds after Folicur application.
Key words: "source-sink" relation; retardants; morphogenesis; productivity; tomato (*Lygopersicon esculentum* L.).

Introduction

The determination of mechanisms formation and donor-acceptor ("source-sink" relation) system functioning is the highest level in the hierarchy processes for the operation of a plant as a whole system, that opens possibilities for assimilates redistribution between plant organs in ontogenesis, and therefore – optimization of the agricultural crops production process (Kiriziy et al., 2014; Yu et al., 2015). The concept of "source-sink" relation system is used as for analyzing the reserve substances redistribution between plant organs during the period of seeds, tubers, rhizomes germination (heterotrophic growth phase) (Poprotska, 2014, Poprotska and Kuryata, 2016; Kuryata et al., 2017), and for analyzing the relationships between growth processes and photosynthesis in autotrophic phase development at the different vegetation stages (Liu et al., 2014; Yu et al., 2015; Bonelli et al., 2016). In this case, photosynthesis processes represent as the main donor, and growth processes - as an acceptor of assimilates. The regulation of these relations can be realized with the participation of various regulatory mechanisms (Kumar et al., 2012; Pobudkiewicz, 2014; Rogach et al., 2016).

Donor and acceptor spheres of plants are connected by a system of direct and inverse connection (hormonal, trophic), which provides reciprocal correction of growth processes and photosynthesis. Synthetic growth regulators application can artificially change the morphogenesis, activity of growth and photosynthetic processes, regulate plant loading with fruits and seeds (Kasem and Abd El-Baset, 2015; Carvalho et al., 2016; Koutroubas and Damalas, 2016). In essence, the utilization of such drugs makes it possible to artificially simulate a different degree of stress "source-sink" relation system in the plant and find out, through which morphological, anatomical and physiological changes occur assimilates redistribution between plant organs (Yan et al., 2013; Yan et al., 2015; Wang et al., 2016).
It is also known that the storage substances of a different type play a role of buffer between photosynthesis as a "source" of assimilates and growth of structural matter of vegetative, storage and reproductive organs, and as a "sink" of assimilates, which defines to some extent the independence of growth processes from photosynthesis (Kiriziy et al., 2014). But it is not well established the intermediate assimilates depositing and elements of mineral nutrition in the vegetative organs as an additional reserve that used for carpogenesis processes (fruits and seeds formation).
One of the most common groups of synthetic plant growth regulators is retardants – antigibberellin drugs that either inhibit the gibberellin synthesis or block formation of the hormone-receptor complex, that preventing the growth-stimulating effect of phytohormone (Kuryata, 2009; Sang-Kuk and Hak-Yoon, 2014). The application of the first group retardants triazole derivatives (Panyapruek et al., 2016; Sousa Lima et al., 2016), are more widely used to regulate the growth and crop productivity, while the application of ethylene producers remains not adequately explored for growth process regulation. It is known that the application of retardants leads to delay the linear growth, with often increasing crop yields (Souza et al., 2010; Matysiak and Kaczmarek, 2013; Pavlista, 2013; Matsoukis et al., 2015). In this case, the influence of retardants with different mechanism action on the morphological and physiological features of source-sink relation functioning is insufficiently studied. In this regard, the objective of this study was investigating the features of morphogenesis, formation of a photosynthetic apparatus, accumulation and redistribution of nonstructural carbohydrates and nitrogen containing compounds in tomato plants under Folicur and Esphon antigibberellin retardants treatment.

Methods

The experiment was conducted using triazole derivative Folicur and ethylene producer Esphon. The active compound of commercial drug Folicur is tebuconazole ($C_{16}H_{22}ClN_3O$)-(RS)-1r-chlorophenyl-4,4-dimethyl-3-(1H-1,2,4-triazol-1-yl-methyl) pentan-3-yl. The manufacturer is Bayer Crop Science AG (Germany). Esphon – 65 % solution of dichlorethyl phosphonic acid (2-CEPA, $C_2H_6ClO_3P$). Manufacturer of LLC "Agrosintez" (Russia).
A field-based micro-trial setup was established at a specialized farm FG "Solskyi" in Vinnitsa region from 2015 to 2017 on the high yield and ultra precocious deterministic hybrid of Dutch selection tomatoes Solerosso. The experiment followed a randomized block design (10 m^2) with five replications. The treatment was applied via foliar spraying OP-2 with aqueous solution of 0.025 % Folicur and 0.05 % Esphon (per active compound) once at the time of initiation of budding to complete wetting of leaves. Control plants were treated with water.
Phytometric measurements (plant height, leaf area, weight of dry and fresh matter of organs and full plants, area of leaf surface) were determined on 20 plants at the green ripeness stage at the fruitification phase. At the same phase, the leaf index (LI) was defined as the area of all leaves per unit soil surface.
The weight of dry matter of plants organs was determined by the liquid nitrogen fixation, dismembered, kept in a drying-oven for one hour at 105 ° C, then for 4 hours at 85 ° C and dried in air to an air-dry state.
Mesostructural organization of leaves during the field-based micro-trial setup was studied at the end of the vegetative season at a fixed material of the middle-layer leaves of the shoots, which completely ended their growth. For preservation was used a mixture of equal parts of ethanol, glycerol and water (1:1:1) with addition of 1 % formalin. Measurement of cells sizes was performed by using a microscope "Mikmed-1" and ocular micrometer MOB-1-15x. Determination of individual cells size of chlorenchyma was carried out after the maceration of leaf tissues with a 5% solution of acetic acid in 2 mol/L hydrochloric acid. At the beginning of fruitification phase (three weeks after treatment), in the stages of green and brown tomatoes ripeness, it was determined the total of sugars and starch in vegetative organs by the using iodometric method, the total nitrogen content – by Kjeldahl, chlorophylls – by spectrophotometric method on the spectrophotometer SF-16. It was determined the content of sugar and organic acids in fruits (AOAC, 2011). Sampling for analysis was carried out in the middle of day with five analytical replications of the research. The statistical processing of results was performed using the computer software *Statistica 6.0*. The reliability of obtained results between control and experiment variant 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

The results of the study indicate that application of retardants Folicur and Esphon caused a typical effect on the linear growth of tomato plants (Altintas, 2011). At the fruitification phase in the stages of green tomatoes ripeness, the average height of control plants was 50.6 ± 1.08 cm, after Folicur application – 46.3 ± 1.68 cm, and according Esphon application – 43.6 ± 1.19 cm, even so, the anatomical and morphological measurements of plants have significantly changed.
The formation of plant donor activity linked to the development of leaf apparatus, number, area and weight of leaves (Matsoukis et al., 2015; Kuryata, 2009, 2014). At the end of vegetation, at the fruitification stage (brown ripeness), it was analyzed the ratio of vegetative organs that indicates significant differences in the morphogenesis of tomato plants under applied drugs treatment (Fig. 1). Application of Folicur increased relative proportion of leaf weight in the total vegetative weight of plant and under

Esphon treatment – decreased.
It was found a significant difference in the number, leaf weight and their area under drugs treatment. The interaction of both retardants was a significant increase the number and area of leaves per plant (Table 1). Analogical changes in plants are typical under the retardants application, which is due to increase stem branching that occurs simultaneously with linear growth inhibition (Kuryata, 2009). At the same time, the leaf dry matter weight of Folicur treated plant was increased and under Esphon was decreased compared with control. The leaves of this variant were thinner with less developed chlorenchyma, smaller cell sizes of palisade and spongy parenchyma and a thinner epidermis (Table 1). However, application of Folicur contributed to increase the size of anatomical leave structures, in this variant also marked the greater total chlorophyll content per leaf fresh matter weight. Obviously, these changes are related to the differences in the index of net photosynthetic productivity, which characterizes the photosynthetic productivity per unit leaf surface: it was higher under Folicur treatment among all variants of experiment.

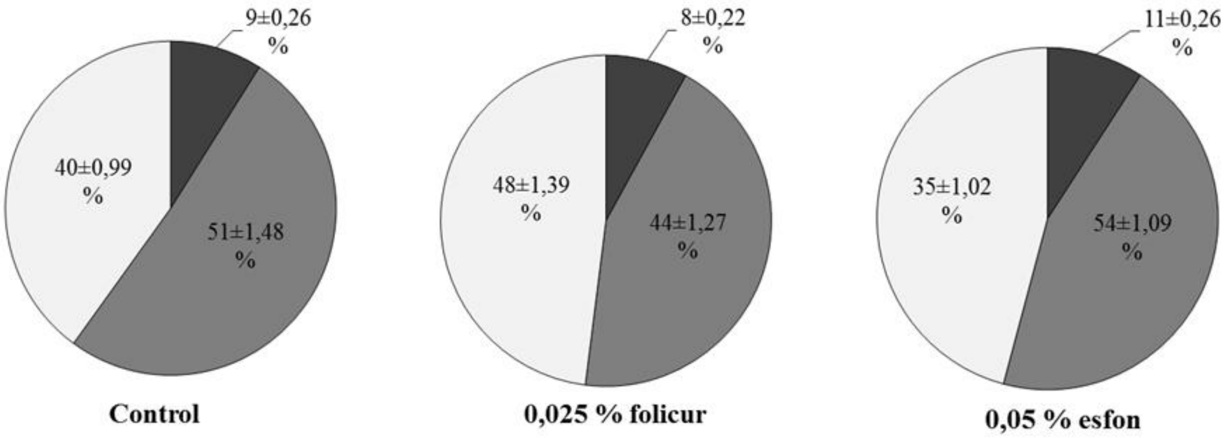

Figure 1. Relative proportion of vegetative organs dry matter weight at the fruitification phase after Folicur and Esphon treatments on tomatoes sv. Solerosso

In the theory of production process, special importance is attached to the important coenotic index - leaf index, which is defined as the green leaf area per unit ground surface area. The obtained results indicate that both drugs application increased the leaf index where the most significant effect was created by Folicur.

Table 1. Formation of photosynthetic apparatus of tomatoes sv. Solerosso under Folicur and Esphon treatment (stage of green ripeness)

Measurements	Control	Folicur	Esphon
Number of leaves, pieces	81.80±2.55	93.40±3.18*	97.90±2.23*
Area of leaf surface, cm^2	6975.0±163.2	10226.0±290.50*	7605.0±188.5*
Leaf dry matter weight, g	37.30±1.07	43.30±1.310*	32.50±0.94*
Leaf index, m^2/m^2	2.90±0.05	4.3±0.04*	3.20±0.04*
Thickness of leave, μm	247.70±3.13	272.40±3.75*	198.50±6.94*
Thickness of upper epidermis, μm	20.40±0.59	24.6±0.75*	16.50±0.47*
Thickness of lower epidermis, μm	16.0±0.45	20.0±0.67*	13.02±0.45*
Thickness of chlorenchyma, μm	211.30± 2.58	227.80± 1.95*	168.10±5.21*
Volume of palisade parenchyma, $μm^3$	46229±1435.30	58613.0±1445.20*	42279.0±1310.7
Length of spongy cells, μm	20.80±0.72	23.20±0.28*	22.30±0.69
Width of spongy cells, μm	15.50±0.48	14.7± 0.45	14.10±0.43*
Total chlorophyll content, % per leaf fresh matter weight	0.72±0.022	0.76±0.01*	0.63±0.02*
Net photosynthetic productivity, g/(m^2·day)	7.10±0.16	9.50±0.27*	7.10±0.18

Note: * - difference is significant at p<0,05

Thus, the donor potential improvement of Folicur treated plant increased the number, leaf weight, leaf surface, leaves mesostructural organization, which created the prerequisites to enhance crop productivity. Such changes in the leaves of tomato plants after Folicur application led to increase the leaf photosynthetic productivity that improved the NPP, which characterizes photosynthetic productivity per unit leaf area. Application of ethylene producer Esphon increased the area of leaf surface, but the total weight of leaves per plant decreased due to formation of more thin leaves. The results of research clearly indicate that Folicur created the optimal conditions for optimizing the production process of tomato plants due to increase the number and leaf area. At the same time, there are only a few works that analyze the issues of photosynthetic processes and carbohydrates content dependence after retardants application (Zhang et al., 2013; Sardoei et al., 2014).

It is explored that some of assimilates may be temporarily deposited in the stock organs with subsequent reutilization on the carpogenesis processes. At the same time, the depositing possibilities of plants vegetative organs after phytohormones and synthetic growth regulators application are not adequately explored. In our opinion, it is expedient to determine the dynamics and correlation of nonstructural carbohydrates content in plant organs at the different fruit formation stages to assess the depositary capacity of vegetative organs of experimental variants.

The obtained results suggest that at the period of fruit growth due to formation of a more powerful leaf apparatus donor activity, the low content of total nonstructural carbohydrates (sugars + starch) was higher in the vegetative organs of the plant - roots, stems, and leaves under Folicur compared with control and Esphon treatment (Table 2). Obviously, this is a consequence of the enhanced leaf apparatus photosynthetic work after retardants application on plants. The highest total content of carbohydrates at all fruit formation stages was noted precisely in the stems of tomato plants that indicates the powerful depositing possibility of this vegetative organ. At the same time, the total content of sugar and starch in roots, stems and leaves of Folicur-treated plants was the highest throughout the fruit formation phase. Analysis of obtained results indicated that the content of carbohydrates decreased in the leaves, roots and stems of tomatoes gradually throughout the fruit formation stage (from the stages of green to brown tomato ripeness), the most intense effect was marked by interaction of Folicur. In our opinion, this is an indication that at this period plant is over-assured with assimilated sugars and uses them not only for the growth and formation of fruits, but also for the creation of carbohydrates reserve, which is deposited in vegetative organs with followed their utilization at the stages of green to brown fruit ripeness.

Table 2. Content of nonstructural carbohydrates (sugars + starch) and nitrogen containing compounds in vegetative organs of tomatoes sv. Solerosso at the fruitification phase (% per weight of dry matter) under Folicur and Esphon treatment

Vegetation period	Organ of plant	Total nonstructural carbohydrates (sugars + starch)			Nitrogen containing compounds		
		Control	Folicur	Esphon	Control	Folicur	Esphon
Fruit formation stage	Root	6.10±0.06	10.0±0.09*	8.20±0.09*	1.70±0.01	1.70±0.01	1.90±0.03*
	Stem	8.10±0.07	12.0±0.08*	8.60±0.04*	1.50±0.02	1.50± 0.02	1.90±0.02*
	Leaf	6.70±0.10	9.80±0.14*	7.80±0.12*	3.30±0.02	2.50±0.03*	3.50±0.02*
Fruitification stage (green ripeness)	Root	6.80±0.07	9.40±0.13*	8.10±0.07*	1.70± 0.03	1.50±0.02*	1.80±0.04
	Stem	9.10±0.13	10.50±0.14*	9.80±0.11*	1.50±0.02	1.40±0.01*	1.50±0.03
	Leaf	7.0±0.10	10.20±0.10*	8.3±0.10*	3.0±0.07	2.40±0.02*	3.1± 0.07
Fruitification stage (brown ripeness)	Root	4.40±0.06	5.0±0.05*	4.90±0.06*	1.60±0.02	1.90±0.05*	1.80±0.02*
	Stem	6.90±0.07	9.50±0.14*	6.30±0.09*	1.50±0.03	1.60±0.03*	1.80±0.03*
	Leaf	5.80±0.09	7.50±0.09*	5.70±0.08	2.30±0.01	2.50±0.05*	2.70±0.06*

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

At the end of vegetation period (brown fruit ripeness), the content of sugars and starch in vegetative organs is significantly reduced. In our opinion, it testifies to the fact that this is the results of a decrease assimilates "request" due to the complete cessation of fruit growth and their transition to the final ripening.
Total nitrogen content analysis of tomatoes vegetative organs suggests a gradual decrease in experimental variants throughout the, which is particularly clearly observed in the leaves.
In our opinion, such decrease of the element content cannot be explained by biodegradation, because during the stage of fruit growth and formation, vegetative growth of tomatoes is significantly inhibit. In this regard, the changes of element content are determined by the outflow of nitrogen containing compounds to the carpogenesis needs. The most intense reduction of nitrogen containing compounds occurred throughout the fruit formation stage to the fruitification stage (green ripeness), in the roots and stem of the plant under Folicur and Esphon treatment. Consequently, the application of retardants leads to provide these organs as donors of reserve nitrogen to carpogenesis. However, at the fruitification stage (brown ripeness), the nitrogen content in the roots and stems of these variants increased due to the arrival of "fresh" nitrogen.
It was found that formation of a more powerful photosynthetic apparatus, intensification of synthesis, accumulation and intensive assimilates and nitrogen-containing compounds redistribution from vegetative organs to the fruits by Folicur increased the crop yield (Table 3).

Table 3. Yield and product quality of tomato plants sv. Solerosso under Folicur and Esphon treatment

Measurements	Control	Folicur	Esphon
Yield, t/ha	68.20±1.71	87.80±1.69*	67.01±1.51
Weight of fruits from one bush, kg	1.60±0.03	2.10±0.04*	1.60±0.03*
Number of fruits on a bush, pieces	35.40±1.07	36.40±1.29	33.50±1.24
Weight of one fruit, g	41.50±1.05	51.20±1.21*	43.30±1.13
Total sugars, % per fresh matter	1.70±0.03	1.90±0.05*	1.50±0.04*
Titrated acidity, g /100 g	0.60±0.02	0.80±0.02*	0.70±0.02*

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

Application of ethylene producer as a retardant not lead to improve the yields of tomatoes. It is draw attention to certain differences of product quality - significantly increased the sugar content and acids under Folicur treatment and decreased the sugar content under Esphon treatment compared to control.

Discussion

The processes of photosynthesis play the main role in the formation of plant productivity; therefore, it is extremely important to study the features of formation and functioning of the donor sphere growth processes under exogenous regulation of agricultural plants. The obtained results testify to the significant role of the morphological and mesostructural components “source-sink” relation system of tomato plants under the various types retardants treatments. The application of triazole derivative Folicur resulted in more significant anatomical and morphological changes in the formation of leaf apparatus compared to ethylene producer Esphon: the measurement of number, weight, area of leaf surface and leaf index in this experiment were higher. The appropriate changes were noted in the mesostructure measurement of leaves: thickness of leave – main photosynthetic tissue of chlorenchyma, assimilatory cells size of palisade and spongy parenchyma. Analysis of depositing possibilities of plants vegetative organs at the fruitification stage indicates the importance of temporary postponement of nonstructural carbohydrates and nitrogen containing compounds in them followed by reutilization for carpogenesis needs. Application of Folicur resulted on the formation of a more powerful donor sphere and in the early fruit growth and formation stages are postponed more carbohydrates in vegetative organs of tomato plants compared to control. The content of sugars and starch in the roots, stems and leaves of plants under Folicur treatment was highest in all organs of the plant throughout the fruitification phase compared to control and variant with Esphon application. The obtained results also testify to the possibilities of nitrogen compounds remobilize from vegetative organs to carpogenesis needs. The obtained results also testify to the possibilities of nitrogen compounds remobilize from vegetative organs to carpogenesis needs. After Folicur treatment, the most intense decrease in the content of nitrogen containing compounds was observed during the transition from the fruit formation stage to green fruits stage in roots and stem of plant during the period of the most intense tomatoes growth. Thus, these organs acted as donors to provide carpogenesis with reserve nitrogen.
Consequently, the application of triazole derivative retardant Folicur contributed to the donor sphere formation of tomato plants, the enhancement of photosynthetic activity as unit of leaf area and plants in general, the temporary deposition of photoassimilate and nitrogen containing compounds in vegetative organs, followed by the active reutilization of these

substances for the fruit formation and growth needs. The result of such "source-sink" relation system restructuring was to increase the crop of tomato culture.

Conclusions

Application of Folicur is formed a more powerful donor sphere of tomato plants in comparison to Esphon due to increase the number, total leaf area and leaf index, mesostructural optimization that improved the index of net photosynthetic productivity and productivity of leaf apparatus in general. The main role in the carpogenesis processes is played by the intermediate deposition of assimilates and nitrogen containing compounds in the vegetative organs of tomatoes with followed their reutilization for the growth and fruit formation needs. The result of a more powerful donor sphere formation, reutilization of assimilates and nitrogen containing compounds of Folicur-treated plants lead to improve the tomato yield.

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