Ukrainian Journal of Ecology

Ukrainian Journal of Ecology, 2021, 11(3), 46-51, doi: 10.15421/2021_140

ORIGINAL ARTICLE

Features of leaf mesostructure rearrangement and redistribution of assimilates of sweet pepper plants under the action of gibberellic acid in connection with crop productivity

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Received: 27.04.2021. Accepted: 27.05.2021.

We have studied the gibberellic acid (GA3) effect on the formation and functioning of the donor-acceptor system of sweet pepper plants (*Capsicum annuum* L.) sv. Antey in connection with crop production. The donor-acceptor system of plants was rearranged under the treatment of 0.005 % aqueous growth regulator gibberellic acid solution during the budding period. As a result, the amount of leaf dry and fresh weight and leaf surface area increased, a more powerful donor sphere of the plant was formed. The internal structure of leaves changed under the influence of growth regulator. The leaf thickness of treated plants and the thickness of the upper and lower epidermis, the primary photosynthetic tissues - chlorenchyma, columnar and spongy assimilative size parenchyma cells increased — an important coenotic indicator of plants – leaf index was increased. At the same time, the growth regulator did not affect the chlorophyll content of leaves. Mesostructure rearrangement enhanced the indicator of specific leaf area density and net photosynthetic productivity characterized by the photosynthetic productivity of the unit leaf surface. More photoassimilates (free sugars and starch) accumulated in the leaves of treated plants compared to the control that ensured the growth and formation of fruits. The enhancement of total leaf area intensified gross photosynthetic productivity and phytocenosis, increasing the yield of sweet pepper plants.
Keywords: sweet pepper (*Capsicum annuum* L.), gibberellic acid, donor-acceptor system, mesostructure, productivity.

Introduction

Analysis of trends of the global crop production development indicates that one way to solve high and stable yields is to use the latest technologies of growth regulators application (Koutroubas and Damalas, 2016; Panyapruek et al., 2016). Low consumption rates of growth regulators affect morphogenesis, increase plant resistance to external factors, and increase productivity that determines their application's feasibility (Zhang et al., 2013; Carvalho et al., 2016; Tsygankova et al., 2019). The effectiveness of growth regulators largely depends on soil and climatic conditions, species and varietal specificity, phases of plant development, and drug treatment regulations (Pavlista 2013; Macedo et al., 2017; Kuryata and Golunova, 2018.) Such drugs are or analogs of phytohormones or modifiers of the hormonal status of plants (Kuryata and Khodanitska, 2018). Consequently, growth regulators have a broad spectrum of action on the plant, and their application allows for the targeted regulation of individual stages of growth and development to mobilize the potential possibility of the plant organism (Yang et al., 2016).
An essential practical task of modern phytophysiology is the search for optimal conditions for applying the growth-regulating compound, taking into account the complex features of their effect on various agricultural plants (Liu et al., 2006; Peng et al., 2014; Ahammed et al., 2020). The central aspect of the plant growth regulators' action is their ability to influence the donor-acceptor system, making it possible to redistribute the artificially assimilates flows to economically valuable organs (Yu et al., 2015; Bonelli et al., 2016; Kuryata et al., 2019a). The application of drugs that can artificially change the attracting ability of organs and regulate transport flows in a plant is of theoretical value and has great practical importance (Fagherassi et al., 2017; Abeledo et al., 2020).
Modern theoretical concepts of the mechanisms of functioning and relationship of donor and acceptor spheres in a plant under the effect of growth regulators application can be achieved due to morphophysiological changes: the formation of a thick leaf surface, an effective mesostructure, an accelerated rate of photosynthetic apparatus formation and an extension of the life span of leaves as the primary source of assimilates (Bai et al., 2016; Kuryata et al., 2019b; Shevchuk et al., 2019). The efficiency of this system depends on the power of acceptor centers; the formation of a "sink" for assimilates. One of the most powerful assimilate acceptors is vegetative growth and the formation and growth of the fruits (carpogenesis). Artificial change in the growth of vegetative organs leads to a redistribution of the assimilates flows between the vegetative organs and the fruit formation due to the sufficient activity of the assimilative apparatus. Scientific sources present the positive results of applying phytohormone analogs and modifiers of their action to increase the yield of a wide range of crops. However, very few works in which the results of studying the ways and mechanisms of these drugs' functioning on the functioning of the donor-acceptor system in connection with optimization of the production process of these crops would be generalized (Kuryata and Polyvanyi, 2018). The list of substances that can change the

intensity of the physiological processes of plants in the right direction is updated annually. It should consider the risks of increasing the pesticide load on the environment and use drugs of natural origin more widely to develop technologies that use synthetic drugs. It is known that gibberellins are a native metabolic product of plants, have a hormonal effect on the plant, and are widely used in plant growing (Sugiura et al., 2015; Rademacher, 2016; Hedden and Thomas, 2016). At the same time, the features of the effect of this drug on the formation and functioning of the donor-acceptor system, morphogenesis, photosynthetic activity, intake and redistribution of mineral nutrition elements, and the yield of crops, in particular vegetable solanaceous plants, remains poorly understood (Kuriata et al., 2016, 2017; Rogach et al., 2018).
In this regard, the main task of this work was to establish the effect of exogenous gibberellic acid (GA3) on the functioning of the donor-acceptor system of sweet pepper in connection with crop productivity.

Materials and methods

Field-based micro-trial experiments were established at a specialized agricultural farm, "Berzhan P." in Gorbanovka, Vinnytsia region (Ukraine), from 2013 to 2015 vegetation periods. We studied gibberellic acid (GA3) effect on the morphogenesis and assimilated redistribution in sweet pepper plants sv. Antey. This is a mid-season pepper variety that belongs to its sweet varieties. It needs 4-5 months to reach the full maturity from the date of sowing. The weights of fruits were 200-300 g; the productivities were 60-70 t/ha.
Gibberellic acid is a white crystalline substance with a molecular weight of 346.2 D, molecular formula $C_{19}H_{22}O_6$. The melting point is 227 °C — substance poorly soluble in water and well soluble in organic solvents. Gibberellic acid is a low-toxic compound and belongs to the 3rd class of toxicity. LA for rats 15630 mg/kg. It does not show carcinogenic, blastogenic, skin resorptive, and embryotoxic properties. The residual content of the drug is not standardized since it is present in plants as a natural metabolite. The drug is non-toxic to bees and other insects. It has low toxicity to fish. It is used as a plant growth regulator. The preparation is obtained by enzymolysis of fungi *Gibberella fuljukoi* and *Fusarium moniliforme* (Hedden and Thomas, 2016). Seedlings were planted on May 22, 2013, May 8, 2014, and May 15, 2015, by a tape method with the planting formula 80 + 50 + 50 × 25. The treatment was applied via foliar spraying OP-2 with an aqueous solution of 0.005% gibberellic acid to complete wetting leaves at the beginning of the budding phase on July 17, 2013, July 10, 2014, and July 9, 2015, respectively. The area of the experimental sites is $10m^2$. The location of the plots was not randomized; the experiment was carried out with five repetitions.
Morphological parameters (plant height, dry and fresh weight, leaf area) were determined in each phase of the growing season. The leaf mesostructure organization was studied at the phase of fruit formation on fixed material. It used a mixture of equal parts of ethanol, glycerol, and water with a 1% formalin for its preservation. Measurement of cell sizes, individual tissues, and organs was performed by using a microscope "Mikmed-1" and ocular micrometer MOB-1-15x. Determination of individual cell size of chlorenchyma was carried out after the maceration of leaf tissues with a 5% solution of acetic acid in 2 mol/l hydrochloric acids. Repetition of microscopic examinations - twenty times. The specific leaf area density (LAD) was determined as the dry matter weight per unit leaf area. The content of various forms of non-structural carbohydrates was detected by the iodometric method, chlorophyll (in % per leaf fresh matter weight) was registered by spectrophotometric method on the spectrophotometer SF-16 (AOAC, 2010). The coenotic indicator – leaf index (LI) was defined as the green leaf area per unit ground surface area. Net photosynthetic productivity (NPP) was fixed as the increase in dry matter weight per leaf area unit per day. The tables and charts show the average values of indicators for three years of research and their standard errors. Tables and figures show average values for the years of research and their standard errors. Statistical analysis of data was performed by Statistica v. 6.0 software.

Results and discussion

It is known that the primary manifestation of gibberellin phytohormones action is the stimulation of the plant axial organs growth due to the acceleration of the cell extension phase (Hedden and Thomas, 2016). The study results indicate that gibberellic acid typically influenced the linear dimensions of sweet pepper plants: at the end of the vegetation, the length of treated plants was 45 ± 2.3 cm compared to control 38 ± 1.8 cm.
The morphological component plays a vital role in the functioning of the donor-acceptor system of the plants. The number of leaves and their weight, the total leaf area of the plant, and the cenosis, in general, are essential indicators of the photosynthetic potential (Rogach et al., 2018; Khodanitska et al., 2019). We found that gibberellic acid treatment caused critical morphological changes in the leaf apparatus that occurred in the number of leaves, the dry and fresh matter weight, the leaf surface area of an individual plant, and an essential coenotic indicator - the leaf index (Fig. 1)
The ratio of the organ's weight of sweet pepper also changed for the action of gibberellic acid. The growth of relative weight of leaves in the weight of the whole plant has been established (Fig. 2). This indicates an increase in the share of the plant donor sphere and a better provision of growth, development, and formation of the crop with photosynthetic products.
At the same time, the growth of leaf area and leaf index is not always a reliable indicator for predicting crop yield. In particular, if an excessive leaf surface is formed, this can lead to shading of neighboring plants, a decrease in the intensity of photosynthesis, and, as a consequence, a decrease in crop yield. It is also essential to analyze possible changes in the anatomical structure of leaves, the photosynthetic pigments content, indicators of the photosynthetic productivity due to the drug treatment. Therefore, the results obtained regarding changes in the morphological characteristics under the influence of growth regulators should be supplemented by data on changes in the mesostructure of leaves that influenced the photosynthetic activity of plants.
The application of gibberellic acid changed the mesostructure of sweet pepper leaves. The leaf was significantly thickened under drug treatment. The thickening of a leaf occurred primarily due to the primary photosynthetic tissue - chlorenchyma and the thickening of the upper and lower epidermis (Table 1).

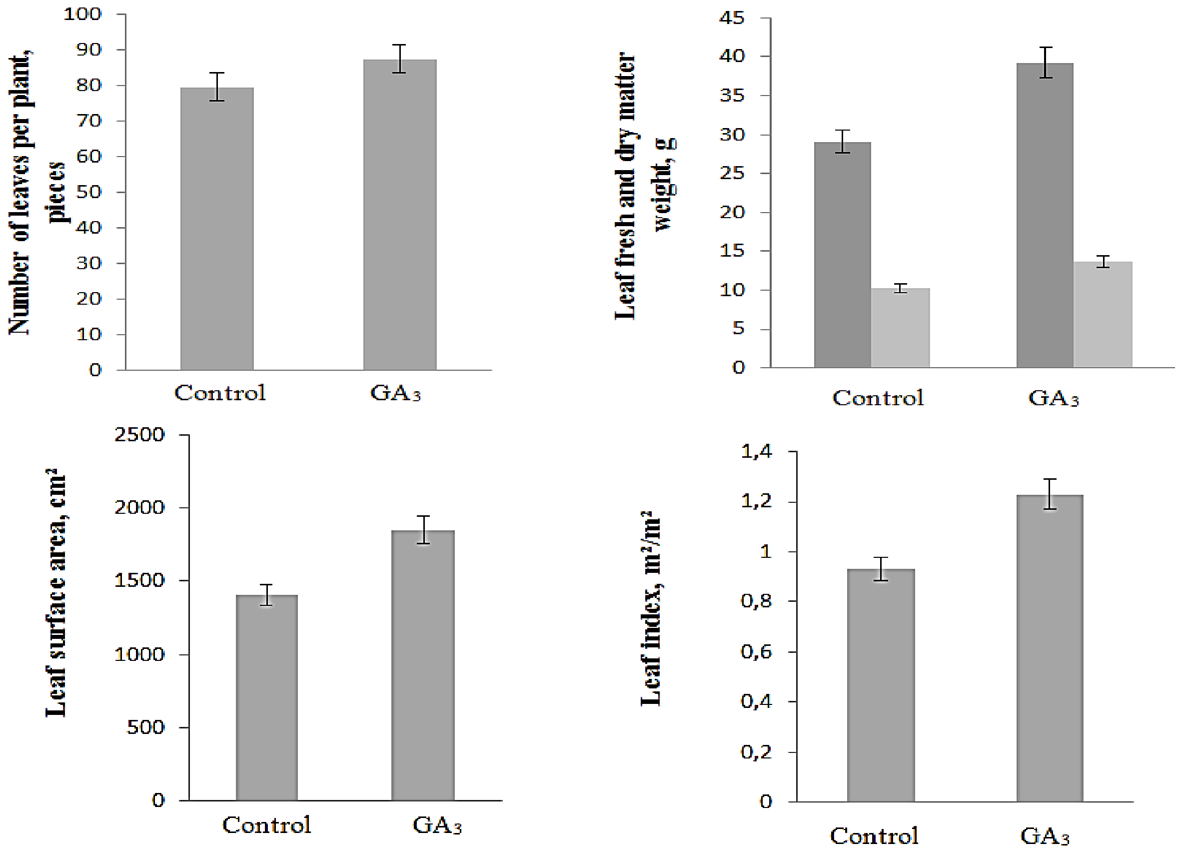

Fig. 1. Effect of gibberellic acid on morphological parameters and leaf index of sweet pepper plants.
Matter weight of plant: - fresh matter weight; - dry matter weight

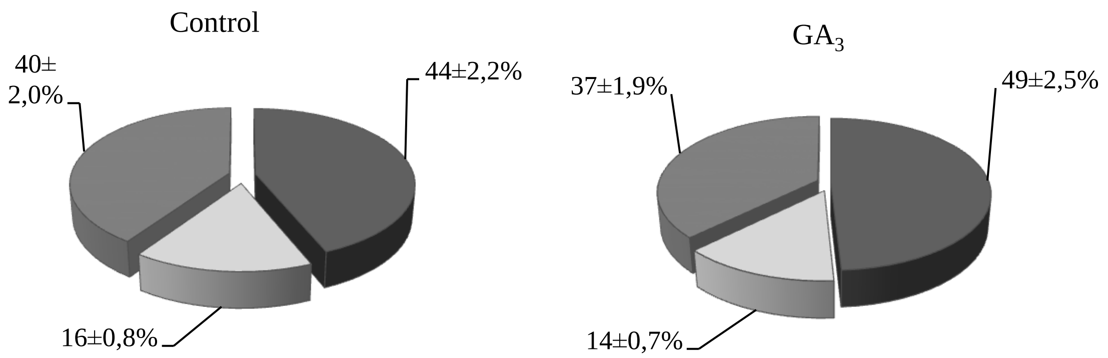

Fig. 2. Influence of gibberellic acid on the ratio of dry matter weight of vegetative organs of sweet pepper at the fruit's full maturity.
- dry matter weight of leaves; - dry matter weight of stems; dry matter weight of roots.

Table 1. Effect of synthetic growth regulators on mesostructural organization of sweet pepper leaves.

Indicators	Control	GA_3
The thickness of leaves, μm	263.7 ±13.18	*327.4±16.37
Thickness of upper epidermis, μm	23.3 ± 0.62	*31.1±0.21
Thickness of chlorenchyma, μm	216.5±1.68	*266.7±5.79
Thickness of lower epidermis, μm	23.9±0.49	*29.6±0.53
Volume of palisade parenchyma, μm^3	19857.1±896.32	*26688.8±1117.20
Length of spongy cells, μm	33.3±0.95	*39.8±0.78
Width of spongy cells, μm	24.9±0.75	*32.4±0.89
Leaf area density value, mg/cm^2	7.9±0.39	*9.6±0.47

Note. *Difference is significant at $p<0.05$.

It is assumed that the columnar assimilation parenchyma plays a crucial role in photosynthesis (Rogach et al., 2018). This tissue has a compact structure; the cells are tightly closed, the correct shape, no intercellular spaces. The internal volume of the tissue is fully used due to this structure. The cells of columnar assimilative parenchyma contain the maximum number of chloroplasts, photosynthetic pigments and are characterized by the highest activity of one of the key enzymes of the dark phase of photosynthesis - ribulosebisphosphatecarboxylaseoxygenase. The studies show that the tissue of gibberellin-treated plants was better developed, the volume of columnar assimilation parenchyma cells significantly increased.
The specific leaf area density (LAD) characterizes the ratio of the leaf dry matter per leaf area. The importance of this indicator is determined by the fact that it characterizes the concentration of structural elements that are directly involved in the photosynthetic processes. The changes in the leaf mesostructural organization under the drug action led to an increase in this indicator. This correlates well with the leaf thickness, the maximum value set for the experimental variant. Under the action of gibberellic acid, the maximum thickness of chlorenchyma, the primary photosynthetic tissue of the leaf, is observed. Optimization of mesostructure formation is accompanied by the formation of large cells of columnar and spongy parenchyma in the assimilation tissue of the leaf.
Analysis of the obtained data indicates the absence of a significant effect of the drug on chlorophyll synthesis in sweet pepper leaves (Table 2).

Table 2. Chlorophyll content and net photosynthetic productivity of sweet pepper under application of gibberellic acid.

Indicators	Total chlorophyll content (*a+b*), % per leaf fresh matter weight	Net photosynthetic productivity, g/(m^2 ·day)
Control	0.62±0.03	1.73±0.08
GA_3	0.59±0.02	*2.24±0.11

Note.*Difference is significant at p<0.05.

An essential consequence of changes in the leaf mesostructure was an increase in the net photosynthetic productivity (NPP) of sweet pepper plants treated by gibberellic acid. The NPP index characterizes the photosynthetic productivity per unit leaf area. Given that the drug's action increases the total leaf area of an individual plant and phytocenosis, this indicates an increase in gross productivity of photosynthesis of sweet pepper plants and coenosis in general.
The main product of photosynthesis is carbohydrates transported from the places of formation - leaves to the processes of growth, active metabolism, and storage. Therefore, it is necessary to establish the accumulation of the plastic substance in the leaves and the dynamics of their content at different stages of development to analyze the changes in donor-acceptor relations in the plant under the action of gibberellic acid. The obtained results indicate a significant effect of the drug on the dynamics of the non-structural carbohydrates content (sugars and starch) in sweet pepper leaves (Table 3). At the fruit formation phase, the non-structural carbohydrates content was higher in the leaves of sweet pepper plants under the drug's action than in control. In our opinion, this is a consequence of forming the optimal mesostructure of the leaves in these variants and increasing the net photosynthetic productivity. The most significant was the increase in the starch content - the main reserve of polysaccharides. The content of starch and non-structural carbohydrates in general in the experimental variant decreased compared to the control at the fruit ripening phase and the mature fruit phase. As the growth of vegetative organs stops at this time, this indicates a more intense outflow of photoassimilates to the fruit.
Thus, the growth stimulator gibberellic acid application-optimized the leaf mesostructure, resulting in increased photosynthetic activity per unit leaf area and increased gross photosynthetic productivity, accumulated non-structural carbohydrates in the leaves. The result of such changes was a significant increase in the yield of sweet pepper plants. The yield of gibberellic acid-treated plants was 41 t/ha against 31 t/ha in control. We revealed that the application of gibberellic acid at a concentration of 0.005% by foliar spraying during budding is a highly effective way to increase the productivity of sweet peppers.

Table 3. Dynamics of various forms of non-structural carbohydrates content of sweet pepper plants sv. Antey under gibberellic acids action (% per dry matter weight).

Indicators	Fruit formation stage			Fruitification stage			Full maturity fruit stage		
	Sugar content	Starch content	Amount of non-structural carbohydrates	Sugar content	Starch content	Amount of non-structural carbohydrates	Sugar content	Starch content	Amount of non-structural carbohydrates
Control	4.66±0.02	6.44±0.01	11.1±0.55	6.02±0.30	7.34±0.02	13.36±0.66	5.64±0.28	7.12±0.01	12.76±0.63
GA_3	4.14±0.20	7.36±0.02*	11.5±0.23	5.84±0.29	6.96±0.01*	12.8±0.64	5.76±0.28	6.49±0.01*	12.25±0.61

Note.* - Difference is significant at p<0.05.

Conclusion

The donor-acceptor system of sweet pepper plants sv. Antey was restructured under the treatment of 0.005% aqueous growth regulator gibberellic acid solution during the budding period. A powerful donor sphere of the plant was formed due to the increase in the number, leaf weigth and leaf surface area. The internal structure of the leaves changed, the leaf thickness and the thickness of the primary photosynthetic tissue - chlorenchyma and the columnar and spongy assimilative parenchyma cells size increased under the drug's application. The thickness of the upper and lower epidermis increased. The drug did not affect the chlorophyll content of leaves. The indicators of specific leaf area density and the net photosynthetic productivity increased due to rearrangement of leaf mesostructure. The leaves of drug-treated plants accumulated more photoassimilates and provided the processes of growth and fruit formation. The enhancement of the total leaf area provided an increase in the gross photosynthetic productivity and phytocenosis, increasing the yield of sweet pepper plants.

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Citation:
Kuryata, V.G., Kushnir, O.V., Kravets, O.O., Poprotska, I.V., Golynova, L.A., Shevchuk, O.A., Khodanitska, O.O., Tkachuk, O.O., Baiurko N.V. (2021). Features of leaf mesostructure rearrangement and redistribution of assimilates of sweet pepper plants under action of gibberellic acid in connection with crop productivity. *Ukrainian Journal of Ecology, 11* (3), 46-51.