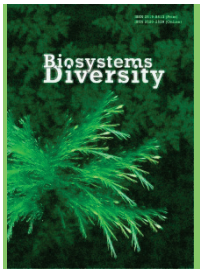

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Effect of antigibberellins on morphogenesis, photosynthetic apparatus, productivity and their residual content in tomato fruits

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The application of growth and development regulators on crops in order to optimize their production process is one of the leading tasks of modern plant physiology. Retardants – gibberellin inhibitors are widely used for this purpose. We investigated the effect of foliar treatment with EW-250, CCC-750 and 2-CEPA on morphogenesis, leaf apparatus, content of photosynthetic pigments, indices of chlorophyll fluorescence induction, CO_2 gas exchange, and residual amounts of drugs in the fruits of tomato (*Lycopersicon esculentum* Mill.) Bobcat hybrid. The field experiment was laid on plots with an area of 33 m^2. The treatment of the plants was carried out at the budding stage. Morphometric indices were determined at the stages of flowering and fruit formation. The chlorophylls content was determined in the raw material by the spectrophotometric method. Indices of photosystem II (PSII) photochemical activity were determined according to the parameters of chlorophyll fluorescence induction after a half-hour exposure of plants in the dark using a portable single-beam fluorimeter "Floratest". The determination of the residual content of retardants in the fruits was carried out on a Shimadzu GC gas chromatograph with a mass spectrometric detector – GCMS- QP2020 EI. All gibberellin inhibitors reduced linear plant size. The number of leaves on the plants decreased under 2-CEPA treatment, and increased after the application of EW-250. Treatment with 2-CEPA decreased, EW-250 significantly increased, and CCC-750 practically did not change the leaves' fresh and dry weight. Leaf area and leaf index decreased under 2-CEPA treatment, but practically did not change when EW-250 and CCC-750 were applied. All antigibberellin drugs increased the leaf specific leaf weight and thickened the leaf lamina due to the growth of chlorenchyma cells. At the same time, growth inhibitors increased the volume of columnar parenchyma cells and practically did not change the size of spongy parenchyma cells. Retardants increased the chlorophylls content in leaves, while the ethylene producer 2-CEPA did not change this index. The plants' chlorophyll index after treatment with drugs increased significantly. The whole plant dry weight increased under EW-250 treatment, decreased after 2-CEPA application, and did not change under CCC-750. It was established that the photosynthetic rate increased under the EW-250 treatment, both in the flowering stage and in the stage of fruit formation, while when using 2-CEPA and CCC-750, it occurred only at the stage of fruit formation. The most significant positive changes of PSII photochemical activity indices were observed under the use of EW-250. Under the action of the drug, the maximum and actual quantum efficiency of PSII increased, the linear electron transport accelerated, and the fraction of reaction centers that did not transfer electrons from the primary acceptor QA to QB decreased, at the same time the chlorophyll fluorescence decay coefficient significantly increased, which indicates an increase in the CO_2 assimilation intensity. Retardants increased the proportion of the fruit in the whole plant dry weight. All growth regulators increased net photosynthetic efficiency. A significant increase in fruit yield occurred under EW-250 treatment. When using CCC-750, the index tended to increase, while under the influence of 2-CEPA the yield decreased. The residual amounts of EW-250 and CCC-750 in the fruits did not exceed the maximum permissible concentrations.

Keywords: *Lycopersicon esculentum* Mill.; retardants; morphometry; leaf apparatus; leaf mesostructure; cenotic indices; photosynthesis; yield; retardants' residual quantities.

Introduction

Studying the patterns of growth and development of food group cultivated plants is an important theoretical basis for the conscious management of these processes in order to optimize their productivity. A significant role in such management is played by native and synthetic plant growth regulators, both stimulators (Rogach & Rogach, 2015; Rohach, 2017) and inhibitors (Kuryata et al., 2016; Polyvanyi et al., 2022). With the help of growth regulators, it is possible to influence the intensity and direction of physiological processes, increase the crop yield, and improve the product quality, speed up or slow down growth, budding, flowering and carpogenesis (Jabiret al., 2017; Kuryata et al., 2021). All these processes are under hormonal control (Rogach et al., 2020). That is why changes in the hormonal status of plants lead to the restructuring of almost all anatomical-morphological and physiological-biochemical processes in the plant organism (Rohach et al., 2021).

One of the most common groups of growth regulating compounds are gibberellin inhibitors – retardants, compounds that interrupt the synthesis of gibberellins in one or more links (Rademacher, 2016) and ethylene producers, which block the process of the hormone-receptor complex formation between the hormone and the receptor protein (Zemlyanskaya et al., 2016).

One of the most important features of retardants from the point of view of agricultural production is the ability to increase the crop yield

(Sarker et al., 2016; Yooyongwech et al., 2017). Inhibition of the activity of apical and intercalary meristems due to the inhibition of gibberellin synthesis under the influence of retardants led to a decrease in the plants' linear size and, as a result, reduced the demand for assimilates for the growth of one of the largest plant sinks – the stem (Kim & Hong, 2012). At the same time, a compensatory increase in the activity of lateral and marginal meristems led to increased branching of the shortened stem and redistribution of excess plastic substances to the growth and formation of the plant lateral organs – leaves and fruits (Kuryata et al., 2019). In particular, paclobutrazol, and prohexadione Ca in greenhouse conditions at concentrations of 40, 80 and 160 ppm inhibited linear growth and increased stem branching in linseed, accelerated seed maturation, and increased the number of fruits (Kuryata & Khodanitska, 2018). Under the influence of paclobutrazol, the oil content in seeds decreased, and under the influence of prohexadione it increased (Kim et al., 2018). Uniconazole reduced the height of magnolia plants by shortening internodes, did not affect stem diameter, and reduced the node number per plant (Shi et al., 2021). The same drug in doses of 0.5, 1.0, 1.5 and 2.0 mg/L caused a decrease in the linear dimensions of the stem and its thickening in rapeseed plants in direct proportion to the dose. The retardant at low and medium concentrations increased leaf area, and shoot and root dry weight (Zuo et al., 2020). Spraying of *Brassica campestris* L. plants with uniconazole solution inhibited growth, slowed down the processes of budding and flowering (Song et al., 2019). Gibberellin inhibitors paclobutrazol, uniconazole and ethephon inhibited the growth in height of corn plants, contributed to a better accumulation of dry matter and faster grain filling. The use of triazole-derived retardants turned out to be more effective than the ethylene producer ethephon (Ahmad et al., 2019).

The leading place in the formation of biological productivity and yield of crops belongs to the leaf apparatus. Double foliar treatment of sunflower plants on the 6th day after emergence with cycocel at concentration of 1500 and 3000 ppm, and mepiquat chloride 25 g/ha decreased the linear dimensions of the plants, increased the leaf number on the plant by 4–7%, decreased the leaf area and leaf index by 4–9%, and increased the leaves' dry weight by 5–13% (Secondo & Reddy, 2018). The use of uniconazole on barley plants in concentrations of 150 and 200 ppm under pot experiment conditions increased the number of leaves on the plant, their area, fresh and dry weight of the leaves and the plant as a whole. The concentration of 150 ppm was more effective (Jabiret al., 2017). In cucumbers, under the influence of hexoconazole, the leaf length decreased by 6–11%, their width – by 12–18%, and their area – by 4–9%, but leaf plates thickened by 13–37%. The retardant also reduced plant fresh and dry weight (Kim & Hong, 2012). Mango plants were treated with PP333 in concentrations of 7.5 and 10 g/L. The drug shortened shoots by 13–21%, reduced the leaf number by 26–33%, and leaf area by 4–17% (Sarker et al., 2016). Narcissus plants were treated by pentanol-derived retardant EL 500 and triazole-derived PP333 applied to the soil. The drugs reduced plant height, leaf length, and leaf area, but increased the ratio of leaf to plant weight and thickened leaf lamina (Demir & Çelikel, 2019). Under Indian conditions, foliar treatment of sugarcane with etrel on the 90th, 120th, and 150th day after planting increased the growth activity of all above-ground organs and slowed down the root development. The ethylene producer increased the linear dimensions of the plants due to the internode length, increased the internode number on the plant, and the number of shoots formed after planting. Under the influence of etrel, the leaf number on the stem, the leaf area, and the leaf surface index increased. Under the influence of the drug, the leaves' life expectancy and the maximum leaf surface area were extended (Rai et al., 2017).

The leaf mesostructure also changed under the influence of antigibberellin drugs. In particular, under pot conditions, on the 14th day after emergence, yellow passion fruit seedlings were treated through the root with paclobutrazol of various concentrations (40, 80, 120 and 160 mg/L). With increasing concentration, the gibberellin inhibitor decreased the leaf area, increased the epidermal cells number, thinned the abaxial epidermis, and thickened leaf plates due to the growth of both columnar and spongy mesophyll cells. The drug increased the stomata number and stomatal index, decreased or did not change cell density in leaves (Teixeira et al., 2019). Treatment of *Moringa oleifera* L. with paclobutrazol at a dose of 20 mg/L did not affect the thickness of the upper and lower epidermis cuticle, but thickened the spongy parenchyma of the leaves without changing the number of its cell layers and columnar parenchyma, increasing the length of columnar cells (Abou-Shlell et al., 2017).

Retardants and ethylene producers have a positive effect on the pigment content in leaves. Spraying winter wheat plants with Medax Top 1.0 L/ha (prohexadione Ca and mepiquat chloride) and Terpal, 1.5 L/ha (mepiquat chloride and ethephon) increased the chlorophyll content in the flag leaf (Miroshnichenko et al., 2017). As a result of the pre-sowing treatment of soybean seeds with uniconazole, the amount of chlorophyll in the leaves increased mainly due to chlorophyll a. The maximum value of the chlorophyll content was observed at the dose of 4 mg/kg, and the lowest – at the drug dose of 8 mg/kg (Yan et al., 2015). In order to grow sunflower as an indoor plant, it was treated three times (15, 30 and 45 days after sowing) with mepiquat chloride in concentrations of 2, 4, 6, 8 and 10 L/ha. The drug at low concentrations reduced the chlorophyll content at the initial stages after treatment. Higher retardant concentrations increased the pigment content in leaves (Suzuki et al., 2018). Different concentrations of paclobutrazol (from 25 to 125 mg/L in steps of 25 mg/L) were applied to the soil under *Camelina sativa* plants at the beginning of the flowering stage. The retardant increased the content of chlorophylls *a* and *b* in the leaves. The most effective drug concentration was 100 mg/L. Under its influence, the chlorophyll content increased by 54% compared to the control. The chlorophyll a/b ratio also increased. The same drug concentration increased the carotenoid content in the leaves by 3%. Other drug concentrations were less effective (Kumar et al., 2012). However, treatment of maize hybrids ZhengDan 958 and DongNong 254 with ethephon under Northeast China conditions reduced chlorophyll content in leaves (Li et al., 2019a). We have previously established that EW-250 reduced the linear size of tomato plants under the conditions of a pot experiment. Under the action of the drug, the leaf number on the plant, and the leaves' fresh weight increased, the chlorenchyma thickened, the volume of columnar parenchyma cells increased, and the chlorophyll content in the leaves increased. Such changes in the leaf apparatus under the influence of EW-250 led to an increase in the quantitative indices of tomato productivity (Rogach et al., 2022).

Gibberellin inhibitors significantly affect the leaves' photosynthetic capacity and the efficiency of PSII functioning. Thus, in order to prevent lodging of corn crops, the plants were treated with retardants CCC and 2-diethylaminoethyl-3,4-dichlorophenyl ether. Under the action of the drugs, the coefficient of chlorophyll fluorescence photochemical quenching increased and the coefficient of non-photochemical quenching decreased. When using CCC, the primary (F_0) chlorophyll fluorescence tended to decrease or did not change reliably, the maximum quantum yield of photochemical reactions in PSII, and the actual quantum yield tended to increase or reliably increased. During treatment with 2-diethylaminoethyl-3,4-dichlorophenyl ether, the primary chlorophyll fluorescence significantly decreased, and the quantum efficiency of PSII photochemical reactions increased (Wang et al., 2016).

Foliar treatment of sweet potato PP333 in doses of 17, 34, and 51 μM under drought conditions led to an increase in variable chlorophyll fluorescence. A positive correlation was found between the photon yield of PSII and the net photosynthetic rate (Yooyongwech et al., 2017). Spraying cassava plants with triadimefon and hexaconazole at doses of 20 and 15 mg/L increased the net CO_2 assimilation. The effect of triadimefon was more significant (Gomathinayagam et al., 2007).

Other researchers showed that critically high temperatures reduced the photosynthetic rate of radish hypocotyls, and under the influence of uniconazole, the photosynthetic processes intensity returned to the control level (Kaneko & Suzuki, 2006). Spraying potatoes with chlormequat chloride and mepiquat chloride increased the chlorophyll content in leaves, increased the CO_2 assimilation, and the whole plant dry weight. Such changes led to an increase in the yield of tubers (Tavares & Lucchesi, 1999). At the same time, the use of ethephon on corn crops reduced the indices of leaf area, leaf dry weight, CO_2 assimilation rate, and crop yield (Li et al., 2019a).

It is known that the use of retardants must be determined by strict toxicological and hygienic requirements. They should not accumulate in plants or in the soil, and should not affect the soil microflora. When applying synthetic growth regulators, it is necessary to take into account the

specificity of the culture, varietal characteristics, and the ecological load on the agrocenosis. Therefore, it is important to search for new promising anti-gibberellin substances and improvement of their use in agricultural practice.

The effectiveness of growth regulators and the ecological load on the environment are largely determined by soil and climatic conditions, species and variety specificity, the stage of plant development, and compliance with the regulations for the use of drugs. Now, plant growth regulators of a new generation are being created, which are characterized by high efficiency and environmental safety, therefore, the search for optimal conditions of use, taking into account the complex features of their action on various agricultural plants, is an important practical task of modern plant physiology (Kuryata et al., 2016; Rohach et al., 2020).

Modern literary sources contain information on the toxicological characteristics and effects of the growth regulators used in our study, as well as on the determination of the drugs' residual content in the soil, economically valuable plant organs and animal and human organisms. In particular, an efficient method was developed for the simultaneous determination of 11 plant growth inhibitors in *Ophiopogon japonicus* samples and soil using high-performance liquid chromatography and triple quadrupole tandem mass spectrometry (UPLC-QqQ-MS/MS). Extraction was carried out with acetonitrile containing 1.0% acetic acid with ultrasonic treatment. Limits of quantification varied from 0.03 to 3.54 μg/L. The highest frequency of detection was established after the use of paclobutrazol and CCC. In addition, paclobutrazol showed high residual content in soil (>1100 μg/kg) (Zhao & Yang, 2018). In other studies a simultaneous method was used for the detection of 6 types of growth regulators, including gibberellin inhibitors paclobutrazol and chlormequat chloride, in five types of fruit (apples, grapes, kiwi, peaches, and oranges) with a modified QuEChERS procedure and analysis by high-performance liquid chromatography with by tandem mass spectrometry (Yan et al., 2016). The method of liquid chromatography with tandem mass spectrometry was developed for the determination of eight pesticides, including the retardants EW-250 and difenoconazole, in *Lycium barbarum*. The samples were extracted with acetonitrile, then purified with a secondary amine. The results showed that at concentration levels of 0.01–10 mg/kg, the average extraction of these pesticides ranged from 82.1 to 96.2% with a relative standard deviation of less than 7%. The half-life of EW-250 was 14 day (Fu et al., 2017).

From the point of view of establishing the environmental safety of the use of growth regulators it is important to investigate the drugs' toxicological effect on plants, animals, fungi and bacteria. In particular, the use of EW-250 in concentrations of 5, 50 and 500 mg/kg reduced soil microbial biomass. It was shown that the half-life of the drug in the soil varied from 9 to 263 days, depending on the concentration. The retardant inhibited basal respiration, substrate-induced respiration, microbial biomass and enzyme activity throughout the study period, and nitrification rate during the first 30 days (Muñoz-Leoz et al., 2011). In other data, EW-250 significantly reduced soil microbial biomass and bacterial diversity, and this decreasing trend became more pronounced with increasing treatment frequency and drug concentration. In addition, EW-250 significantly simplified the complexity of the trophic network of soil bacteria, especially when treated with high concentrations of the retardant (Han et al., 2021). At the same time, the use of EW-250 in doses that correspond to the rules of agricultural technology did not significantly disturb the biological homeostasis of the soil and did not reduce its fertility. It was established that this drug stimulated the reproduction of organotrophic bacteria and fungi, and also increased the activity of soil enzymes responsible for phosphorus, sulfur and carbohydrate metabolism. It did not disrupt the activity of urease, which is responsible for the hydrolysis of urea, and did not cause significant changes in the structure of bacterial cenoses (Bácmaga et al., 2022).

One-, two-, and three-time treatment of rice crops with different EW-250 concentrations affected the indices of grain quality and the residual drugs' content in it. An increase in the number of treatments and the working solution concentration led to a decrease in the content of proteins, amylose and valuable amino acids, and an increase in the content of sugars, which indicates a decrease in grain quality. At the same time, the drug residual content in the seeds increased in direct proportion to the number of treatments (from 16.23 to 31.12 μg/kg), which is significantly below the maximum permissible hygienic indices (Li et al., 2022). *Lactuca sativa* seedlings with a root length of 2 mm were exposed to EW-250 at different concentrations (0.025, 0.05, 0.10, 0.20, 0.40 g/L) for 24 h. The growth regulator treatment led to impaired root growth and mitotic index, contributed to a high frequency of chromosomal aberrations. In addition, signs of cell death due to DNA fragmentation were observed (Aragão et al., 2021).

In other studies, EW-250 at a dose of 0.2–0.5 mg/L reduced the content of thyroxine and triiodothyronine in female Danio rerio fish (Li et al., 2019b). Studies of the toxic effects of EW-250 on rat heart tissues indicate that 28-day addition of the drug n the diet led to a decrease in the activity of cardiac acetylcholin esterase, an increase in serum marker enzymes (creatinine phosphokinase, lactate dehydrogenase, cholesterol, low-density lipoproteins), and a decrease in high-density lipoproteins, which may be a background for atherosclerosis of coronary arteries. In addition, the retardant increased the level of p53 protein, one of the main apoptosis-inducing factors, and the ratio of Bax/Bcl2 proteins, which open mitochondrial channels and trigger the mitochondrial branch of apoptosis from within. At the same time, cytochrome C was released from mitochondria to the cytosol, and caspase-9 and caspase-3, which are the triggering factors of the caspase cascade in apoptosis from within, were activated. In addition, EW-250 caused genotoxic effects. It induced DNA fragmentation and increased the frequency of micronucleated cells in the marrow. Moreover, myocardial fibrosis was observed when the drug was used on rats (Othmène et al., 2020). According to other data, the drug reduced the viability of cells, disrupted the normal division of the cell cycle and induced apoptosis of the human placental trophoblast cell line HTR-8. The expression of the anti-apoptogenic protein Bcl-2 decreased, and the level of the pro-apoptogenic protein Bax increased after the use of the drug on HTR-8 cells. Induction of apoptosis in trophoblast cells occurred through the mitochondrial pathway. The drug changed the expression of key regulatory genes involved in the modulation of trophoblast functions. Generally, the plant growth regulator suppressed the invasion and migration of human trophoblasts by affecting the expression of proteases, hormones, angiogenic factors, growth factors, and cytokines. Since the invasive and migratory properties of the trophoblast are necessary for successful placentation and fetal development, this suggests a potential risk of triazole fungicides in human pregnancy (Zhou et al., 2016). It is known that EW-250 caused a stress effect on the endoplasmic reticulum of intestinal cells and stimulated the initiation of the mitochondrial branch of apoptosis in these cells (Othmène et al., 2022).

So, the analysis of the literature proved that the use of gibberellin inhibitors – retardants and ethylene producers, especially from the triazole group, leads to the optimization of agricultural crops' performance, and increases their yield due to positive changes in the leaf apparatus of plants and their photosynthetic processes. At the same time, there are practically no comparative systematic studies of the regulation of growth rate, morphogenesis, formation of leaf apparatus, and photosynthetic activity of vegetable nightshade plants under the action of retardants and ethylene producers. Also, the components of ecologically safe technologies for the use of antigibberellins and the determination of residual drug content in the economically valuable organs of agricultural crops of the Solanaceae family remain undetermined.

In relation to the above, the aim of work was to study the effects of retardants EW-250, CCC-750, and ethylene producer 2-CEPA on the morphogenesis, leaf apparatus, mesostructural organization of leaf laminae, pigment content, indices of chlorophyll fluorescence induction and CO_2 assimilation, and productivity of tomatoes *Lycopersicon esculentum* Mill., as well as determining the content of residual amounts of gibberellin inhibitors in their fruits.

Materials and methods

Small-scale field experiments were conducted on the lands of the farm "Berzhan P. G." village Gorbanivka, Vinnytsia district, Vinnytsia region in the growing seasons of 2013–2016 and 2018. Seedlings of Bobcat hybrid tomatoes were planted by the tape method according to the formula 80 + 50 + 50 × 50. The area of the plots was 33 m^2, the repetition was fivefold. The plants were treated in the morning with a backpack

sprayer CO-12 "Marolex" (Poland) until the leaves were completely wet with a 0.15% solution of esphon (2-CEPA) (Ukraine), a 0.025% solution of tebuconazole (EW-250) (Bayer, Germany) and with a 0.25% solution of chlormequat chloride (CCC-750) (BASF, Germany) at the budding stage on June 14, 2013; June 17, 2014; June 19, 2015; June 21, 2016; and June 8, 2018. Control plants were sprayed with tap water. Phytometric parameters (plant height, fresh and dry weight of plants and leaves, leaf area) were determined on ten plants at the stages of flowering and fruit formation.

To determine the weight of individual organs laboratory scales were used. The leaf area was determined by the die cutting method (AOAC, 2010). The selection of samples for the study of the leaf mesostructural organization was carried out at the stage of fruit formation. The leaf mesostructure was analyzed during the period of carpogenesis (30th day after treatment) on fixed material. For anatomical analysis, the middle tier leaves, which had completely finished growing, were selected. The plant material was stored in a mixture of equal parts of ethyl alcohol, glycerin, and water with the addition of 1% formalin. The sizes of individual chlorenchyma cells were determined on preparations obtained by the method of partial maceration of leaf tissues. The macerating agent is a 5% solution of acetic acid in hydrochloric acid (2 mol/L). The dimensions of anatomical elements were determined on a MB-130 40×-1600× LED Mono microscope (SIGETA, Ukraine) using an MOV-1-15× eyepiece micrometer (Lomo-Mikrosistemy, RF). The repetition of microscopic measurements was thirty-five times.

The carbon dioxide gas exchange parameters were measured on the middle tier leaves that had finished growing, not separated from the plant, under controlled conditions on a device mounted on the basis of an infrared optical-acoustic gas analyzer GIAM-5M (RF). The area of leaf was placed in a thermostatted (25 °C) leaf chamber (3 × 7 cm). The leaf was illuminated with a KG-2000 incandescent lamp through a water filter. Lighting intensity was 400 W/m^2 PAR. Atmospheric air with a natural CO_2 concentration was blown through the chamber at a rate of 1 L/min. The net photosynthetic rate was recorded after 45 minutes of the start of leaf illumination in the chamber, when the gas exchange indices reached a stationary level. The transpiration rate was determined by a thermoelectric micropsychrometer based on the difference in air humidity at the entrance and exit from the chamber. The photorespiration rate was assessed by the CO_2 postillumination burst from leaf within 1 min after turning off the light. Gas exchange parameters were calculated according to the standard method (Mokronosov & Kovalev, 1989). Measurements were repeated three times.

The content of total chlorophyll was determined in the fresh leaves by the spectrophotometric method on a ULAB 102UV spectrophotometer (Shanghai Metash Instruments Co., China) in five replicates (AOAC, 2010). During the growing season, the net photosynthetic efficiency (NPE) was determined as the increase in the mass of dry matter per unit of leaf area per unit of time, the leaf index (LI) as the ratio of the total leaf area to the unit of crop area, the chlorophyll index (ChlI) as the product of the plant leaf area and the content of total chlorophyll in them, and the specific leaf weight as the ratio of leaves dry weight of to their area.

To determine the chlorophyll fluorescence induction parameters, a portable single-beam fluorimeter "Floratest" developed by the V. M. Hlushkov Institute of Cybernetics of the National Academy of Sciences of Ukraine was used. The remote optoelectronic sensor contains an LED with maximum radiation intensity at λ = 470 + 20 nm. Indices of irradiation in the sensor: wavelength of irradiation 470 + 15 nm; the area of the irradiated spot is not less than 15 mm^2; illuminance within the spot is not less than 2.4 W/m^2. Indices of signal reception in the optoelectronic sensor: spectral range of fluorescence intensity measurement – from 670 to 800 nm; the area of the reception window – 9 mm^2; the sensitivity of the photodetector at λ = 650 nm – 0.45 A/W. The device recorded data 90 times according to the 5$\sqrt{t}$ law. Exposure time – 240 s. The results were obtained in the form of a Kautsky curve, which reflects the time dependence of the chlorophyll fluorescence intensity (Fig. 1) (Brayon et al., 2000; Golcev et al., 2016).

In order to determine the residual amounts of growth regulators in tomato fruits, 250 g of fruits were extracted. To extract CCC-750, sample preparation was carried out as follows. The homogenate was placed in a 500 cm^3 separatory funnel and 30 cm^3 of dichloromethane was added, vigorously shaken for 1 min. After complete stage separation, the lower organic layer was separated and discarded. 1 cm^3 of sodium tetrafluoroborate solution was added to the aqueous phase in the separatory funnel, 30 cm^3 of dichloromethane was added, vigorously shaken for 1 min, the lower organic layer was separated and collected in a 200 cm^3 flat-bottomed flask. The aqueous phase extraction operation was repeated with a new portion of 30 cm^3 dichloromethane. The settled organic layer (lower phase) was combined with the previously obtained extract. The aqueous phase was discarded.

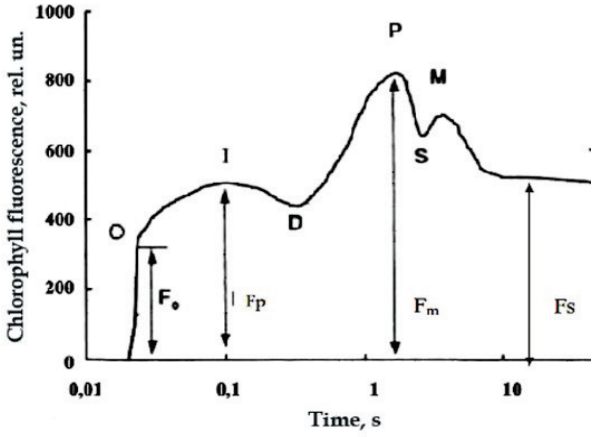

Fig. 1. Typical curve of chlorophyll fluorescence induction (Holoborodko et al., 2022)

The combined extract was transferred to a 250 cm^3 separatory funnel, 25 cm^3 of a 2 M hydrochloric acid solution was added, and it was vigorously shaken for 1 min. After complete phase separation, the lower organic layer was separated and discarded. Then 25 cm^3 of dichloromethane was added to it, vigorously shaken for 1 min. After complete phase separation, the lower organic layer was separated and discarded. The aqueous phase was transferred to a 150 cm^3 round-bottom flask and evaporated on a vacuum rotary evaporator at a temperature of 60 °C to a dry fraction. 25 cm^3 of deionized water was added to the flask with the dry extract, and evaporated to dryness again. For complete removal of hydrochloric acid, the evaporation operation with an additional 25 cm^3 portion of water was repeated twice. The resulting residue was dissolved in a 10 cm^3 flask in an acetonitrile-methanol mixture (95:5) and introduced into the prepared column. After that, the flask was washed with 5 cm^3 of this mixture of solvents, which are also introduced into the column. After complete absorption of the solvent, the substance was eluted from the column with 85 cm^3 acetonitrile-methanol mixture (95:5) at a flow rate of 1–2 drops per second, collecting the eluate in a 250 cm^3 evaporating flask. The solution was evaporated to dryness on a rotary vacuum evaporator at a temperature of 45 °C, the residue was subjected to pyrolysis.

The residue contained in the flask was transferred to a vial by the 3 1 cm^3 portions of methanol, subjecting each portion of the solvent in the vial to a stream of nitrogen (the vial was placed in a thermostat heated to 45–50 °C). Add 50 mm^3 10% sodium hydroxide solution. The vial was closed with an aluminum cap with a silicone gasket, the cap was crimped with a crimper and additionally strengthened with the wire. The vial was placed for 15 minutes in a thermostat heated to 200 °C. After the specified time, it was removed from the thermostat and cooled to room temperature. 0.5 cm^3 of the gas stage was taken with a syringe (through a silicone gasket) and analyzed under chromatography conditions.

To extract EW-250, sample preparation was carried out as follows. 10 g of plant material crushed in a homogenizer was placed in a 250 mL conical flask, 50–100 mL of acetone-water solvent mixture (1:1) was poured in, and EW-250 was extracted in an ultrasonic bath for 10 minutes. The extract was filtered through a paper filter ("red tape"). The extraction was repeated twice in portions of 30 mL of the same mixture. The combined filtrate was placed in a separatory funnel and re-extracted with dichloromethane three times in portions of 30 mL each. To speed up the delamination, 5 mL of saturated sodium chloride solution was added.

The combined dichloromethane extracts were filtered through a layer of anhydrous sodium sulfate. The obtained solution was evaporated on a rotary evaporator at a temperature of 50 °C until complete removal of dichloromethane. Next, the extracts were purified in a silica gel column.

Determination of the retardants' residual quantities was carried out on a Shimadzu GC gas chromatograph with a mass spectrometric detector – GCMS-QP2020 EI (calibration certificate dated August 12, 2022 No. 01/7132/22). The obtained organic solutions were analyzed on a chromato-mass spectrometer under the following conditions: capillary column – Rxi-5ms (Serial No. 1544328), length – 30 m, diameter – 0.25 mm, phase – 0.25 μm, constant flow – 1.2 mL/min, carrier gas – helium. Injector – auto-injector AOS-20i+s, Split 20:1, evaporator temperature T = 250 °C. Thermostat – T_{start} = 100 °C (2 min), heating – 15 °C/min to T_{end} = 280 °C (10 min). The detector was mass-selective, the temperature of the interface was T = 280 °C, ionization was by electron impact, the temperature of the ion source was T = 280 °C. Sample – 5.0 μL, automatic input. The study was conducted under the condition of registration of full ion current chromatograms (m/z = 50–550).

Analysis of mass chromatograms was performed using LabSolutions software using the NIST14.lib mass spectral database.

The percentage content of the active substance was calculated according to the formula:

$$\omega = \frac{c}{r} \times \frac{s}{p} \times 100\%,$$

where ω – percentage content of the active substance (%), c – concentration of the solution of the active substance standard sample (mg/cm^3), r – the ratio of the weight of the investigated substance to the volume of the extractant (mg/cm^3), s – the area of the peak of the investigated substance (c.u.), p – peak area of the standard sample of the active substance (c.u.).

The mass of the active substance in the sample provided for research was calculated according to the formula:

$$m = \frac{\omega \times n}{100\%},$$

where m – the mass of the active substance in the sample provided for the research (g), ω – percentage content of the active substance (%), n. – the mass of the substance provided for research (g).

The results were processed statistically using the Statistica 6.0 computer program (StatSoft Inc., USA). Univariate analysis of variance was used (differences between mean values were calculated by ANOVA with Bonferroni's correction, they were considered significant at $P < 0.05$).

Results

Foliar treatment of tomatoes at the budding stage with aqueous solutions of 2-CEPA, EW-250 and CCC-750 slowed down the linear growth of the plants. At the stage of fruit formation, the height of plants treated with 2-CEPA, EW-250, and CCC-750 was lower than in the control by 26.6%, 14.8%, and 19.6%, respectively (Table 1).

Table 1

Effect of foliar treatment with antigibberellins on morphometric and cenotic indices, and pigment content in leaves of *Lycopersicon esculentum* Mill. Bobcat hybrid (mean data for 2013–2016 and 2018, x ± SE, n = 10)

Index	Control		2-CEPA		EW-250		CCC-750	
	1	2	1	2	1	2	1	2
Plant height, cm	59.6 ± 1.9	63.8 ± 2.1	40.8 ± 1.3***	46.8 ± 1.7***	50.6 ± 1.8**	54.3 ± 1.9**	47.1 ± 1.5***	51.3 ± 1.6**
The number of leaves on a plant, pcs.	48.1 ± 1.2	71.2 ± 2.7	37.4 ± 1.1***	46.4 ± 1.8***	58.8 ± 2.0***	79.5 ± 2.3*	50.9 ± 1.9	74.3 ± 2.2
The number of leaf plates on a leaf, pcs.	6.95 ± 0.21	5.77 ± 0.20	5.97 ± 0.20***	6.47 ± 0.25	6.11 ± 0.24*	5.91 ± 0.21	6.82 ± 0.27	6.12 ± 0.26
Leaves fresh weight, g	163.3 ± 7.1	157.2 ± 6.7	111.1 ± 4.5***	129.4 ± 5.3*	185.5 ± 8.2	218.4 ± 9.9***	154.4 ± 6.6	183.3 ± 8.1*
Leaves dry weight, g	32.4 ± 1.5	38.6 ± 1.9	22.4 ± 1.0***	31.4 ± 1.3*	38.1 ± 1.8*	52.0 ± 2.2***	31.7 ± 1.4	42.9 ± 2.0
Leaf area, cm^2	6641 ± 332	6332 ± 303	3824 ± 166***	4140 ± 199***	6261 ± 311	7028 ± 332	4938 ± 222**	5927 ± 267
Leaf index, m^2/m^2	2.21 ± 0.11	2.11 ± 0.10	1.27 ± 0.05***	1.38 ± 0.07***	2.09 ± 0.10	2.34 ± 0.12	1.64 ± 0.08**	1.97 ± 0.10
Leaf specific weight, mg/cm^2	4.37 ± 0.21	6.25 ± 0.30	6.17 ± 0.30***	8.06 ± 0.40**	5.97 ± 0.29**	7.41 ± 0.37*	6.22 ± 0.31***	7.47 ± 0.37*
The total chlorophyll *a* + *b* content, % f.w.	0.462 ± 0.023	0.453 ± 0.022	0.471 ± 0.023	0.466 ± 0.023	0.542 ± 0.027*	0.529 ± 0.026*	0.535 ± 0.022*	0.472 ± 0.023
Chlorophyll index, g/m^2	1.01 ± 0.05	1.13 ± 0.05	1.51 ± 0.07***	1.52 ± 0.07**	1.48 ± 0.07***	1.58 ± 0.08***	1.52 ± 0.07***	1.45 ± 0.07**

Note: differences between mean values were calculated using the ANOVA test, with Bonferroni's correction, which is considered significant at * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$ compared to the control at this stage of vegetation; 1 – flowering stage; 2 – fruit formation stage; 2-CEPA – 0.15% solution of esphon, EW-250 – 0.025% solution of tebuconazole, CCC-750 – 0.25% solution of chlormequat chloride.

Since the main donor of plastic substances in the plant are leaves, the impact of growth inhibitors on the plants leaf apparatus was analyzed. Due to the fact that tomatoes have complex leaves, the number of leaves on the plant was calculated. During the 2-CEPA treatment at the beginning of the fruit formation stage, the number of leaves on the plant was 34.9% less than in the control. Under the action of EW-250, the number of leaves on the plant increased significantly (by 11.7%). When using CCC-750, the number of leaves only tended to increase compared to the control. We found that 2-CEPA decreased, EW-250 significantly increased, and CCC-750 practically did not change the leaves fresh and dry weight (Table 1).

One of the main indices that affect crop yield is the leaves' area on a plant. It was found that under treatment, this index significantly decreased both at the flowering fruiting stages. Under the influence of 2-CEPA the leaf area at flowering significantly decreased significantly decreased, and at the stage of fruit formation it only tended to decrease. After the application of CCC-750, a tendency to leaf area decrease was observed at flowering, and at the fruit formation it had a tendency to increase. At the same time, the ethylene producer (2-CEPA) reduced the LI by 34.7%, the triazole-derived drug (EW-250) increased it by 10.9%, and the onium retardant (CCC-750) practically did not change this index (Table 1). The SLA indicates the provision of a leaf with structural elements that participate in photosynthetic processes, essentially reflects the efficiency of photosynthetic processes on a leaf surface unit, and is indirectly related to the thickness of leaf plates. The results of our research show that all gibberellin inhibitors increased the SLA both at the flowering and fruiting stages. Thus, at the stage of fruit formation, 2-CEPA increased this index by 28.9%, CCC-750 – by 19.5%, and EW-250 – by 18.6% (Table 1).

These results are fully consistent with the data of the mesostructural analysis of leaf laminae. Antigibberellin drugs thickened the tomatoes' leaf laminae due to the growth of parenchyma assimilation cells (Table 2). The maximum increase in the thickness of the chlorenchyma was observed under treatment with EW-250 (30.1 %). The use of 2-CEPA thickened the assimilation parenchyma layer by 28.5%, and CCC-750 – by 21.5%. The growth inhibitors 2-CEPA, EW-250, and CCC-750 increased the volume of columnar parenchyma cells by 39.0%, 61.5%, and 55.7%, respectively. The drugs did not change the width of spongy parenchyma cells, and 2-CEPA and EW-250 significantly increased the length of these cells. The upper epidermis was thinner only under 2-CEPA treatment, and the lower epidermis was thinner compared to the control after the application of all three growth regulators.

The content and ratio of photosynthetic pigments is an index of the assimilation apparatus functioning efficiency (Morgun et al., 2019). It turned out that under the action of EW-250, the amount of chlorophyll in leaves increased significantly. At the stage of fruit formation, this index exceeded the control by 16.8%, and at the flowering stage – by 17.3%. Under the influence of 2-SEPA, the total chlorophyll content did not change significantly, but after treatment with CCC-750, it significantly increased at the flowering stage by 15.8% (Table 1). All drugs with anti-gibberellin action significantly increased the plants' CII. In particular, after the application of 2-CEPA, it exceeded the control at the stages of flowering and fruit formation by 48.5% and 34.9%, respectively. Under treatment with EW-250, the index increased by 46.5% and 39.5%, and after spraying CCC-750 – by 50.5% and 28.5%, respectively (Table 1). Gas exchange processes in the leaves are important indices of the plants' photo-

synthetic apparatus performance. The results of measuring tomato leaves' gas exchange rate after treatment with antigibberellins indicates that under the influence of EW-250, the net photosynthetic rate at the end of the flowering stage had a clear tendency to increase (Table 3). However, at the beginning of the fruit formation stage, all growth regulators significantly increased the photosynthetic rate. The action of EW-250 turned out to be the most effective. The increase was not so significant when treated with CCC-750 and 2-CEPA.

Table 2

Effect of foliar treatment with antigibberellins on mesostructural parameters of leaves of *Lycopersicon esculentum* Mill. Bobcat hybrid (x ± SE, n = 35)

Index	Control	2-CEPA	EW-250	CCC-750
Leaf thickness, μm	239.1 ± 3.2	282.2 ± 3.3***	295.3 ± 9.0***	270.1 ± 5.3***
Upper epidermis thickness, μm	29.2 ± 0.8	26.0 ± 0.6**	31.0 ± 0.8	28.3 ± 0.7
Chlorenchyma thickness, μm	186.3 ± 1.6	239.1 ± 2.2***	242.2 ± 7.7***	226.4 ± 4.0***
Lower epidermis thickness, μm	24.1 ± 0.8	16.6 ± 0.5***	21.9 ± 0.5*	16.3 ± 0.5***
Columnar parenchyma cells volume, μm^3	6228 ± 301	8658 ± 432***	10057 ± 495***	9694 ± 319***
Spongy parenchyma cells length, μm	30.3 ± 1.5	39.9 ± 0.6***	36.1 ± 1.3**	31.6 ± 1.0
Spongy parenchyma cells width, μm	23.6 ± 1.4	25.8 ± 1.3	25.5 ± 0.6	23.7 ± 0.8

Note: differences between mean values were calculated using the ANOVA test, with Bonferroni's correction, which is considered significant at * – P < 0.05; ** – P < 0.01; *** – P < 0.001 compared to the control at this stage of vegetation; 2-CEPA – 0.15% solution of esphon, EW-250 – 0.025% solution of tebuconazole, CCC-750 – 0.25% solution of chlormequat chloride.

Table 3

The effect of growth regulators on the photosynthetic, photo- and dark respiration rates of *Lycopersicon esculentum* Mill. Bobcat hybrid leaves at the end of flowering (1) and the beginning of fruit formation stages (2) (x ± SE, n = 3)

Treatment	Photosynthesis, mg $CO_2/(dm^2 \cdot h)$		Photorespiration, mg $CO_2/(dm^2 \cdot h)$		Dark respiration, mg $CO_2/(dm^2 \cdot h)$		Transpiration, g $H_2O/(dm^2 \cdot h)$	
	1	2	1	2	1	2	1	2
Control	19.0 ± 0.81	10.6 ± 0.42	2.0 ± 0.09	1.4 ± 0.06	1.7 ± 0.08	1.2 ± 0.05	2.1 ± 0.09	1.3 ± 0.05
2-CEPA	16.4 ± 0.72	13.8 ± 0.64*	1.5 ± 0.07*	1.8 ± 0.08*	1.0 ± 0.03**	1.6 ± 0.07*	1.8 ± 0.07	1.4 ± 0.06
EW-250	20.7 ± 0.93	20.7 ± 0.90**	0.9 ± 0.04**	2.5 ± 0.11**	1.2 ± 0.05*	2.3 ± 0.11**	1.8 ± 0.08	1.9 ± 0.08**
CCC-750	19.6 ± 0.82	15.2 ± 0.73*	1.9 ± 0.09	2.1 ± 0.09**	1.0 ± 0.04**	1.8 ± 0.08**	1.9 ± 0.09	1.5 ± 0.07

Note: see Table 1.

All gibberellin inhibitors decreased the photorespiration and dark respiration rates at the flowering stage, and increased them at the beginning of fruit formation. The most significant decrease at the first stage and increase at the second occurred under EW-250 treatment. All growth regulators reduced the transpiration at the flowering stage and increased it at the beginning of fruit formation stage.

The light photosynthetic reactions' rate, the level of chlorophyll fluorescence, the chlorophyll fluorescence photochemical and non-photochemical quenching rate, the efficiency and quantum yield of PSII, the electron transport rate in photosystems are important indices of the photosynthesis efficiency (Korneev, 2002, Golcev et al., 2016). The results of our research show that gibberellin inhibitors changed the parameters of the Kautsky curve (Table 4).

Antigibberellin drugs increased or did not change the minimal level of chlorophyll fluorescence induction (F_0) both at the flowering and fruit formation stages. All gibberellin inhibitors reduced the fluorescence level at the time of reaching a temporary slowdown in its increase (F_p) and steady-state terminal fluorescence (F_s) at the flowering stage and significantly increased them compared to the control at the fruiting stage. Under treatment with all drugs, the maximal fluorescence (F_m) at the flowering stage was lower than the control, and at the stage of fruit formation it exceeded the control value under treatment with EW-250. The level of variable fluorescence (F_v) under the treatment with EW-250 significantly exceeded the control at the fruiting stage, and was significantly reduced under the application of CCC-750 at both stages of vegetation.

The most important parameter of the chlorophyll fluorescence induction is the maximum quantum efficiency of PSII photochemical reactions (Kl). It is used as a critical index of the plants' photosynthetic apparatus efficiency with optimal values of about 0.83. All growth regulators significantly increased this index at the flowering stage, and under the action of 2-CEPA and EW-250 it tended to increase at fruit formation stage. Kl values under the action of all drugs were closer to the optimal compared to the control, except for the variant with CCC-750 at the fruiting stage, and in the variant with the use of EW-250 it was 0.83 at the flowering stage.

The coefficient of chlorophyll fluorescence decay, which correlates with CO_2 assimilation rate (K_g), significantly exceeded the control under EW-250 treatments both at the flowering and fruiting stages. Under the influence of other drugs, it practically did not change compared to the control or decreased (at the fruiting stage under CCC-750 treatment). The actual quantum efficiency of PSII photochemistry, which characterizes the rate of linear electron transport (K_f), indicates the level of photosynthetic processes activity. We found that under the EW-250 treatment, it reliably increased at flowering and tended to increase at fruiting. When treated with other growth regulators, the index did not change significantly, with the exception of the variant with CCC-750 at the fruit formation stage. The coefficient of chlorophyll fluorescence photochemical quenching, which characterizes the share of open PSII reaction centers (Kq), did not undergo significant changes after treatment with growth regulators.

The index of the PSII (reaction centers) RC fraction that does not reduce the QB acceptor (K_n) characterizes the relative number of inactive reaction centers that do not participate in the electron transport to the plastoquinones pool. In control plants, the share of QB-non-reducing centers at the fruiting stage was significantly lower than at the flowering stage. In the treated plants at the flowering stage, this index did not reliably change under the use of 2-CEPA and CCC-750, and decreased after treatment with EW-250. At the fruiting stage, under treatment with CCC-750 and 2-CEPA, the index was significantly higher than in the control variant, and after the use of EW-250 showed a downward trend.

Changes in the growth processes rate, the leaf apparatus formation and functioning, and changes in photosynthetic processes affected the accumulation of dry matter mass by plants and the net photosynthetic efficiency (NPE). Under the treatment of 2-CEPA, EW-250 and CCC-750, the NPE increased both at the flowering and fruit formation stages. On average, the increase in the NPE when treated with antigibberellins was about 40% (Table 1). EW-250 caused an increase in the whole plant dry weight at flowering and fruiting by 18.1% and 25.3%, respectively. Under treatment with 2-CEPA, the dry weight decreased by 33.9% and 31.8% compared to the control. Under the influence of CCC-750, this index did not change significantly (Table 5).

The analysis of the dry weight ratio of vegetative and generative organs of tomatoes revealed that the treatment with retardants led to the redistribution of plastic substances towards the generative organs – fruits, due to a decrease in the stem dry weight both at the flowering and fruit formation stages. The use of drugs also increased the share of dry weight of leaves at the flowering stage compared to the control, and the share of roots also increased under the action of the ethylene producer (Fig. 2).

Table 4

Effect of foliar treatment with antigibberellins on chlorophyll fluorescence parameters in leaves (relative units) of *Lycopersicon esculentum* Mill. Bobcat hybrid at the stages of flowering (1) and fruit formation (2) (x ± SE, n = 3)

Index	Control		2-CEPA		EW-250		CCC-750	
	1	2	1	2	1	2	1	2
Minimal fluorescence (F_o)	648 ± 32	452 ± 22	288 ± 14**	456 ± 21	216 ± 10**	480 ± 22	296 ± 14**	482 ± 23
The level of fluorescence at the time of reaching a temporary slowdown in its increase (F_p)	1352 ± 67	620 ± 29	992 ± 49*	1088 ± 49**	624 ± 29**	536 ± 25	864 ± 39**	976 ± 49**
Maximal fluorescence (relative units), which is proportional to the total amount of chlorophyll (F_m)	1768 ± 88	1452 ± 70	1344 ± 66*	1624 ± 77	1296 ± 63*	1928 ± 96*	1112 ± 55**	1160 ± 55*
Steady-state terminal fluorescence (relative units), which is defined by the dynamic balance of photosynthetic processes (F_s)	984 ± 48	704 ± 29	712 ± 32*	768 ± 35	528 ± 26**	848 ± 33*	624 ± 30**	812 ± 38
Variable fluorescence – the level of which characterizes the activity of primary photochemical processes in PSII ($F_v = F_m - F_o$)	1120 ± 55	1000 ± 49	1056 ± 51	1168 ± 57	1080 ± 55	1448 ± 70**	816 ± 39*	678 ± 32**
Maximum quantum efficiency of PSII photochemical reactions (index of the photosynthesis light phase overall efficiency), ($Kl = F_v/F_m$)	0.63 ± 0.03	0.69 ± 0.03	0.78 ± 0.04*	0.71 ± 0.03	0.83 ± 0.04*	0.75 ± 0.03	0.73 ± 0.03*	0.58 ± 0.03
Index of the PSII RC fraction that does not reduce acceptor Q_B ($Kn = (F_p - F_o)/Fv$)	0.629 ± 0.018	0.168 ± 0.038	0.667 ± 0.015	0.541 ± 0.022**	0.378 ± 0.028**	0.039 ± 0.042	0.696 ± 0.014	0.729 ± 0.011***
The coefficient of chlorophyll fluorescence decay, which correlates with CO_2 assimilation rate ($Kg = (F_m - F_s)/F_s$)	0.79 ± 0.03	1.06 ± 0.04	0.88 ± 0.04	1.11 ± 0.06	1.46 ± 0.07**	1.27 ± 0.05*	0.78 ± 0.04	0.43 ± 0.02***
The actual quantum efficiency of PSII photochemistry, which characterizes the rate of linear electron transport ($Kf = (F_m - F_s)/F_m$)	0.44 ± 0.02	0.52 ± 0.02	0.47 ± 0.02	0.53 ± 0.02	0.59 ± 0.03*	0.56 ± 0.03	0.44 ± 0.02	0.31 ± 0.01**
The coefficient of chlorophyll fluorescence photochemical quenching, which characterizes the share of PSII open reaction centers ($Kq = (F_m - F_s)/(F_m - F_o)$)	0.700 ± 0.032	0.748 ± 0.035	0.598 ± 0.028	0.733 ± 0.035	0.711 ± 0.032	0.746 ± 0.033	0.598 ± 0.025	0.513 ± 0.022*

Note: see Table 1.

Table 5

Effect of foliar treatment with antigibberellins on biological productivity of *Lycopersicon esculentum* Mill. Bobcat hybrid (mean data for 2013–2016 and 2018, x ± SE, n = 10)

Index	Control		2-CEPA		EW-250		CCC-750	
	1	2	1	2	1	2	1	2
Plant dry weight, g	107.2 ± 5.3	136.5 ± 6.7	70.8 ± 3.3***	93.0 ± 4.5***	126.6 ± 6.1*	170.9 ± 8.2**	107.9 ± 5.3	144.8 ± 7.1
Net photosynthetic efficiency, g/m^2×day	1.12 ± 0.05	0.78 ± 0.04	1.78 ± 0.09***	0.99 ± 0.05**	1.44 ± 0.07**	1.15 ± 0.06***	1.56 ± 0.07***	1.17 ± 0.06***

Note: see Table 1.

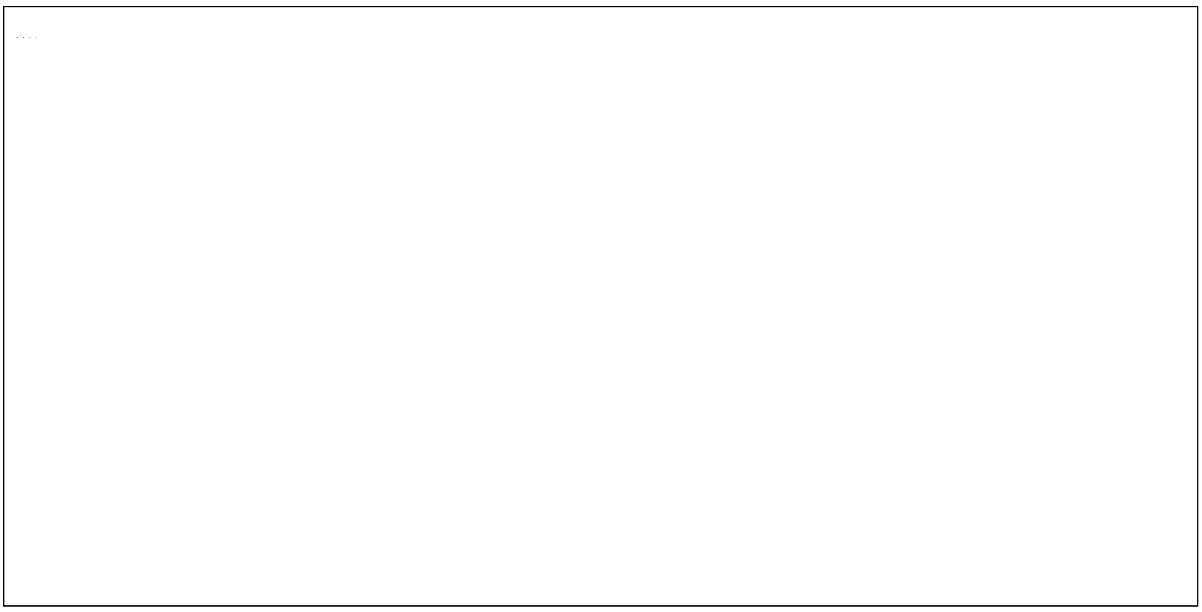

Fig. 2. Effect of foliar treatment with antigibberellins on the dry weight ratio of whole plant organs of *Lycopersicon esculentum* Mill. Bobcat hybrid: treatment at the budding stage; x ± SE, n = 10; on the left – at the flowering stage, on the right – at the fruiting stage; differences between mean values were calculated using the ANOVA test, with Bonferroni's correction, which is considered significant at * – P < 0.05, ** – P < 0.01, *** – P < 0.001 compared to the control at this stage of vegetation; on the right – flowering phase; on the left – the fruiting phase; 2-CEPA – 0.15% solution of esphon, EW-250 – 0.025% solution of tebuconazole, CCC-750 – 0.25% solution of chlormequat chloride

The results of our research indicate changes in the tomatoes' productivity. The most effective was the use of EW-250. Treatment with triazole increased the fruit number per plant by 16.4%, which led to an increase in the weight of fruits per plant by 25.1% (Table 6). 2-CEPA reduced the fruit number per plant by 15.1%, which resulted in a 15.2% decrease in yield. Treatment with CCC-750 did not reliably affect the elements of productivity, and the weight of fruits from one plant tended to increase. Analysis of the residual content of growth regulators in tomato fruits showed that EW-250 content was 0.0006 mg/kg, and CCC-750 – 0.046 mg/kg. According to this results, no excess of the maximum permissible concentration of residual amounts of retardants in agricultural products was found (in accordance with State Sanitary Rules and Regula-

tions 8.8.1.2.3.4-000-2001 dated September 20, 2001, residual amounts of this drug should not exceed 0.01 mg/kg and 0.05 mg/kg, respectively).

Table 6
Effect of foliar treatment with antigibberellins on plant productivity elements of *Lycopersicon esculentum* Mill. Bobcat hybrid (mean data for 2013–2016 and 2018, x ± SE, n = 10)

Index	Control	2-CEPA	EW-250	CCC-750
Number of fruits per plant, pcs.	13.6 ± 0.6	11.6 ± 0.5*	15.9 ± 0.8*	14.3 ± 0.7
The average weight of one fruit, g	164 ± 8	164 ± 8	176 ± 9	175 ± 9
Weight of fruits from one plant, g	2236 ± 111	1898 ± 92*	2796 ± 133**	2515 ± 123

Note: treatment of plants at the budding stage, determining of indices at the fruit ripening stage; * – P < 0.05; ** – P < 0.01; *** – P < 0.001, comparison to control in one row was carried out by the method of difference between average values calculated according to the ANOVA criterion with Bonferroni's correction; 2-CEPA – 0.15% solution of esphon, EW-250 – 0.025% solution of tebuconazole, CCC-750 – 0.25% solution of chlormequat chloride.

Discussion

The growth rate greatly affects the morphogenetic, photosynthetic and production processes in the plant organism. Quite interesting from the point of view of plant physiology is the inhibition of linear growth with the subsequent redistribution of excess plastic substances to economically valuable organs, both vegetative (leaves, roots) and reproductive (fruits, seeds). Slowing down of growth processes under the influence of gibberellin inhibitors is indicated by the vast majority of researchers (Kim et al., 2018; Zuo et al., 2020; Shi et al., 2021).

The basis of a plant's biological productivity is the leaf. In our studies after the application of retardants there were changes in the leaf apparatus that determined optimization of the production process. Slowdown of stem growth due to inhibition of the apical meristem's activity under the action of antigibberellins causes compensatory activation of other meristematic tissues – lateral and marginal. As a result, in plants exposed to retardants, stem branching and additional laying of leaves increased. Data on such effects after treatment with retardants and ethylene producers are quite often found in literature sources (Hua et al., 2014; Koutroubas & Damalas, 2016). The excessive inhibitory impact of ethylene producers had a repressive effect on the formation of the leaf apparatus. As a result, the leaf surface area and the plants' leaf index significantly decreased after the application of 2-CEPA, and practically did not change under treatment with retardants EW-250 and CCC-750 compared to the control. Other researchers point out the inefficiency of the use of compounds whose active substance is 2-CEPA in terms of optimizing the leaf apparatus quantitative parameters (Li et al., 2019a).

Activation of marginal meristems under the action of retardants, in our opinion, led to the growth of the leaf assimilation parenchyma, which led to its thickening, and an increase in the fresh and dry weight compared to the control. The confirmation of our hypothesis is an increase in the specific leaf weight, and a thickening of the leaf due to an increase in the size of the chlorenchyma. At the same time, the drugs increased the volume of columnar parenchyma cells – the main cells where photosynthesis takes place. The increase in the number of structures that provide photosynthesis simultaneously with the increase in the amount of chlorophyll in the leaves and the chlorophyll index of the plants created the prerequisites for increasing the tomato biological productivity, which was manifested in the increase in the whole plant dry weight. This can be especially clearly observed at the fruiting stage in plants treated with EW-250. Moreover, the growth of plant dry weight occurred in the reproductive organs – fruits, with a simultaneous decrease in the share of the stem dry weight. In this case, it is extremely important that in plants treated with gibberellin inhibitors the share of the main donors of plastic substances – leaves at fruiting did not decrease, and at the flowering stage even increased compared to the control. Instead, the share of the stem – a powerful sink of plant assimilates and competitor of the main sink of the economic and valuable organ – the fruit – decreased. Similar results regarding changes in the leaf mesostructural organization (Teixeira et al., 2019; Shevchuk et al., 2020), the pigments' content (Ahmad et al., 2019; Gao et al., 2019) and the fresh and dry weight accumulation in experimental plants are also indicated by other scientists (Taherpazir & Hashemabadi, 2016; Gao et al., 2019; Zuo et al., 2020).

A clear index of the production process performance in plants is the increase in the net photosynthetic efficiency. Treatment with all antigibberellin drugs significantly increased this index. Other researchers recorded similar results under the action of retardants (Kuryata & Khodanitska, 2018). However, it is worth paying attention to the fact that increase in the net photosynthetic efficiency after treatment of plants with the ethylene producer 2-CEPA, which occurred due to a decrease in the quantitative indices of the leaf apparatus development, was accompanied by a decrease in biological productivity (plant dry weight) and was, obviously, the result of a compensatory increase in the productivity of photosynthetic apparatus against the background of reducing its size. In our opinion, this was facilitated by positive changes at the tissue and cellular levels – a tendency to increase in the chlorophyll content in leaves, thickening of the chlorenchyma, and an increase in the columnar parenchyma cells' volume, but they could not fully compensate a significant decrease in the leaves' area. It is important to note the preservation of high values of leaf surface area and an increase in net photosynthetic efficiency while an increase in the fruits' number led to a greater biological and economic productivity of plants under treatment with EW-250 compared to the control.

All growth regulators increased the photorespiration rate simultaneously with the intensification of the photosynthetic processes (Table 3). On the one hand, this can be explained by the fact that photosynthetic CO_2 assimilation and photorespiration are manifestations of the carboxylase and oxygenase activity of the same enzyme – Rubisco. On the other hand, the results indicate that treatment of tomato plants with growth regulators in most cases contributed to increasing the photosynthetic apparatus capacity at the tissue and organ levels, as well as the whole plant, which, without a doubt, should have increased its provision of assimilates, primarily carbohydrates, which, in fact, are the main substrate of respiratory processes. This is indirectly confirmed by a significant increase in the dark respiration rate at the stage of fruit formation under the influence of growth regulators. At flowering, almost all growth regulators reduced the dark respiration rate, which can be explained by the lack of use of assimilates for form-forming processes associated with carpogenesis. With the appearance of new sinks of assimilates – fruits, the dark respiration exceeded the control index.

Reduction in the transpiration rate at the flowering stage and its increase at the beginning of the fruit formation stage, in our opinion, is clearly related to the activation of all metabolic processes in the plant against the background of carpogenesis, especially since the fruit formation occurred more intensively under treatment with growth regulators. It is also worth noting that the greater the plant's biological productivity, the more intensive the photorespiration, dark respiration, and transpiration.

The net photosynthetic efficiency as an integral index of the photosynthetic apparatus activity largely depends on the total leaf surface area, the leaves' physiological state, and the strength of the demand for assimilates from the sinks (Stasik & Kiriziy, 2011). At the same time, some of the leaves, depending on the location on the plant (including the distance from the sink), may actively photosynthesize and be a source of assimilates, or may, while maintaining a green colour, be photosynthetically inactive due to the absence of assimilates translocation to sink.

The changes in the photosynthetic apparatus at the organism level under the action of antigibberellins, respectively, are reflected at the level of photochemical processes in the chloroplast thylakoids, in particular in changes in the fluorescence induction parameters. Retardants increased or tended to increase the chlorophyll content in leaves, however, the index characterizing the effectiveness of PSII functioning varied under the influence of different drugs. In particular, all drugs increased the PSII maximum quantum efficiency. However, the PSII actual quantum efficiency (K_f), which reflects the linear electron transport rate in chloroplasts, increased statistically significantly only under treatment with EW-250, and in plants treated with CCC-750 it even significantly decreased (Bjorkman & Demmig, 1987; Korneev, 2002). This inconsistency of changes in the maximum and actual quantum efficiencies is associated with a decrease in

the share of PSII reaction centers (RC) that does not reduce the QB acceptor (K_n coefficient) in plants under the action of EW-250, and their increase under the treatment with 2-CEPA and CCC-750, indicates a decrease in photodamage of PSII RC in plants after treatment with the first drug and increase after treatment with the last two. At the same time in plants treated with retardants, changes relative to the control of the chlorophyll fluorescence decay coefficient (K_g), which correlates with CO_2 assimilation rate, were also in good agreement with the changes in the coefficients K_f and K_n. It can be assumed that such optimization of the chloroplasts' photosynthetic apparatus of plants treated with EW-250 was facilitated by an increase in the CO_2 assimilation activity due to an increase in plants' economic and biological productivity (assimilates sink). On the contrary, the insufficient strength of the demand for assimilates under the action of 2-CEPA and CCC-750 along with a high chlorophyll content and significant development of the photosynthetic apparatus at all levels did not allow the full use of its potential, which is accompanied by the inhibition of photosynthetic processes and greater photodamage of the PSII RC.

Conclusions

Treatment of *Lycopersicon esculentum* Mill. Bobcat hybrid with antigibberellin plant growth regulators 2-CEPA, EW-250, CCC-750 induced changes in the morphogenesis, structure and functioning of the leaf and photosynthetic apparatus, changed the culture productivity, and at the same time did not exceed the maximum permissible concentration of retardants residual amounts in ripe fruits.

All preparations reduced the plants' linear dimensions and caused changes in the leaf apparatus. The number of leaves decreased after the application of 2-CEPA, and increased under the action of EW-250. 2-CEPA decreased, EW-250 increased, and CCC-750 did not change the leaves' fresh and dry weight. The leaf area and the leaf index of plantations did not change practically when retardants were applied, but they decreased under treatment with 2-CEPA. All antigibberellin drugs increased the specific leaf weight and thickened the leaf plates due to the growth of assimilating parenchyma cells. At the same time, the volume of columnar parenchyma cells increased under the influence of the drugs, and the size of spongy parenchyma cells practically did not change. EW-250 and CCC-750 increased the chlorophyll amount in leaves, while 2-CEPA did not change it. The chlorophyll index of plants after treatment with drugs increased significantly. The whole plant dry weight increased under EW-250 treatment, decreased after 2-CEPA treatment, and remained unchanged under CCC-750 treatment. It was found that under EW-250 treatment the photosynthetic rate increased at the stages of flowering and fruit formation, and under 2-CEPA and CCC-750 treatment – only at the stage of fruit formation. EW-250 and CCC-750 increased the proportion of fruits in the whole plant total dry weight. All drugs increased the net photosynthetic efficiency. Antigibberellin drugs affected the indices of PSII photochemical activity, and the electron transport activity in chloroplasts, which are calculated according to the parameters of chlorophyll fluorescence induction. The most effective was the use of EW-250. The drug increased the maximum and actual PS II quantum efficiency, accelerated the linear electron transport and reduced the share of reaction centers that do not transfer electrons from the primary acceptor QA to QB, significantly increased the coefficient of chlorophyll fluorescence decline, which indicates an increase in the CO_2 assimilation rate.

A significant increase in fruit yield occurred under EW-250 treatment. With the use of CCC-750, the index tended to increase, while under the action of 2-CEPA it decreased. The residual amounts of EW-250 and CCC-750 did not exceed the maximum permissible concentrations.

Therefore, anatomical-morphological and structural-functional changes in tomato plants under the action of gibberellin inhibitors were conditioned due to changes in the activity of different types of meristematic tissues. Enhancement of photosynthetic activity due to an increase in the chlorophyll content and changes in photophysical and photochemical processes in PSII increased the biological productivity of the culture. The obtained results provide a new practical approach to increasing tomato yield. At the same time, certain questions regarding the molecular and physiological mechanisms of influence of the investigated gibberellin inhibitors require further study.

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