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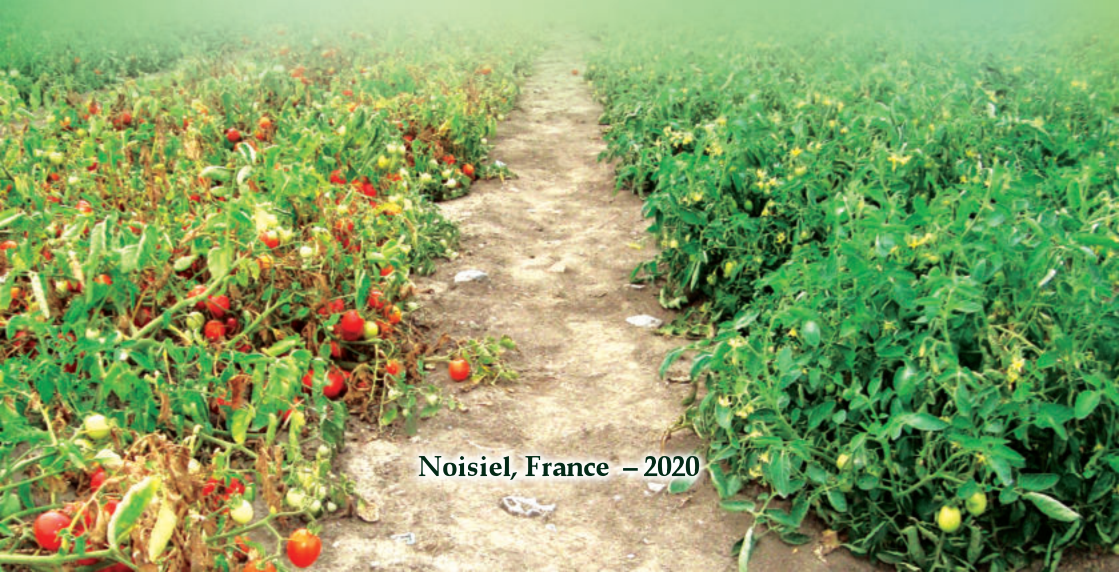

Noisiel, France – 2020

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UDC 581.1:[661.162.65/.66:582.930.12](043.5)

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Physiological bases of growth regulation and morphogenesis of tomatoes under gibberellin and retardants treatment / O. O. Kravets, V. G. Kuryata. – Noisiel, France, 2020. – 122 p.

In the monograph it was studied the features of growth processes, morphogenesis and functioning of donor-acceptor system of tomatoes (*Solanum lycopersicum* L.) under the influence of gibberellin (gibberellic acid, GA_3) and its antagonists – triazole derivative tebuconazole and ethylene releasing compound esphon in the formation of crop productivity.

Gibberellic acid (GA_3) and retardants caused a clear growth regulating effect on the intensity of plant growth, accompanied by changes in relative proportion of vegetative organs weight. Application of tebuconazole resulted on the formation of a more powerful donor sphere, where relative proportion of leaf weight in the total vegetative weight of plant was higher during whole vegetation stage.

The mesostructure measurement of leaves was optimized under gibberellin and tebuconazole treatment: thickness of leave increased by enhancement of linear dimention of spongy parenchyma cells and volume of palisade parenchyma cells.

It was found that leaves of tebuconazole and gibberellin treated tomatoes were characterized by the highest measurements of leaf area density value, chlorophyll content and net photosynthetic productivity which created the prerequisites to enhance a gross photosynthetic crop production.

It was established that stems and roots are characterized by intensive depositing possibilities of nonstructural carbohydrates that remobilized to carpogenesis needs (fruit formation and growth). Reducing of sucrose content in leaves of treated plants with a simultaneous increase of reducing sugars content at the fruitification stage (brown ripeness) indicated that transport of sugar from leaves to fruits ceased earlier than from root and stem. Preparations treatment significantly influenced on the reutilization of nitrogen, phosphorus and potassium from stem and leaves. This process was more intensive under gibberellin and triazole derivative compound tebuconazole.

The most effective in the field condition was the application of 0,025 % tebuconazole. The maximum value of this indicator was under gibberellin in the greenhouse growing condition which indicates the dependence of the growth stimulator on sufficient water supply. Application of ethylene releasing compound esphon at the stage of 25 % fruit ripeness significantly accelerated the rate of fruit ripening, that led to a reduction in the number of harvests and an increase in the share of early crop production. The maturation of tomato fruit was largely determined by the intensity of maceration of fruit tissues, which is based on the processes of hydrolysis of cell wall polysaccharide components – hemicelluloses and pectins.

Key words: donor-acceptor system, retardants, gibberellins, morphogenesis, productivity, tomatoes (*Solanum lycopersicum* L.).

CONTENS

ABBREVIATIONS USED IN THE MONOGRAPH

2-CEPA	2-chloroethylphosphonic acid
ABA	abscisic acid
ACA	1-aminocyclopropane-1-carboxylic acid
HMA	hydrazide maleic acid
DA_3	gibberellic acid
DNA	deoxyribonucleic acid
DCIB	2,3-dichloroisobutyrate sodium
DSA	N,N-dimethylhydrazine succinic acid
IAA	indolylacetic acid
LI	leaf index
LADV	leaf area density value
CI	chlorophyll index
CCC	chlorocholine chloride
CHD	cyclohexadione
NPP	net photosynthetic productivity

INTRODUCTION

In modern plant physiology, the regulation of donor-acceptor relations («source-sink» system) is considered as the highest level in hierarchy of processes that ensure the functioning of a plant as an integral system [18, 39]. The regulation of these relationships, as a system of assimilates redistribution between the organs and tissues of a plant during ontogenesis can be carried out at different levels of plant organism organization with the participation of various regulatory mechanisms [141, 279]. This concept is used as for analysis of heterotrophic growth phases (seed germination) under conditions of sckoto- and photomorphogenesis, as for the actions of various growth regulators groups and abiotic environmental factors [183], and for analyzing the ratio of photosynthetic intensity and growth processes, where the first act as the main donor, and the last as an acceptor of assimilates [113, 207]. It is also known that various types of reserve substances play the role of a buffer between photosynthesis as a «source» of assimilates and growth of structural substance of vegetative, storage and reproductive organs as a «sink» of assimilates, which determines the independence of growth processes from photosynthesis [187]. At the same time, it have not been studied enough the features of intermediate deposit assimilates in vegetative organs of the plant as an additional reserve, that is used in common with the newly formed forms of nonstructural carbohydrates in fruit growth development.

Application of phytohormones and synthetic growth regulators can artificially change the morphogenesis, activity of growth and photosynthetic processes, regulate plant loading with fruits and seeds. In essence, the application of such drugs with the opposite mechanism of action 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.

It is known that changes in growth intensity are realized under phytohormones actions, in particular gibberellins, that significantly enhance growth processes [195]. Besides, in modern plant cultivation, it is widely used a group of synthetic growth inhibitors with antigibberellin mechanism of action (retardants), that either reduce the synthesis of this phytohormone or block the formation of hormone-receptor complex that maked impossible the effect of already synthesized gibberellin [115, 172, 276]. The application of retardants leads to a significant increase in crop production [61, 147, 161, 201], at the same time, the analysis of literature data indicates that studies in which the simultaneous effect of gibberellin and antigibberellin compounds on morphogenesis and functioning of donor-acceptor system of tomato plants are practically absent, which does not allow us to fully assess the effect of these groups of growth regulators on the plant physiological processes.

Tomatoes occupy one of the leading places among vegetable crops. In Ukraine, this crop is grown mainly in the southern areas of the steppe zone (65-70 % of the total area) and in the forest-steppe zone (about 20 %) [213]. This vegetables are widely used for food in fresh and processed form, canning industry, due to their ecological plasticity, high yield, versatility in the use of fruits, biological value and taste. Tomato fruits contain: dry matter – from 4,8 to 7,0 % (soluble sugars are more than half of the total weight), organic acids – 0,4-0, 6%, cellulose – 0,75-0,84 %, pectin substances – 0,10-0,14 %, raw protein – 0,95 %, fats and essential oils – 0,2 %, minerals – 0,6 %. Vitamins also play an important role: vitamin C (ascorbic acid) – 200-300 mg/ kg per fresh matter weight, β-carotene – 15-17, vitamin B_1 (thiamine) - 1,0-1,2, vitamin B_2 (riboflavin) – 0,5-0,6, vitamin PP (nicotinic acid) – 4,1-4,5, vitamin I (lycopene) – 30-35, vitamin B_9 (folic acid) – 0,75, vitamin H (biotin) – 0,04 [17, 164]. Tomatoes contain pigment lycopene that causes a red color of tomatoes and is a strong antioxidant, as it blocks the negative effects of free radicals on the human body [11]. The study of donor-acceptor relations on tomato crop is advisable, since their acceptor zone – fruits constitute a significant part of the whole plant weight, that makes it possible to effectively evaluate the redistribution of substance flows between donor and acceptor spheres under the various factors effects.

However, the analysis of literature data presents only a few amount of gibberellins and various types of retardants actions on morphogenesis, features of formation and functioning of photosynthetic apparatus, assimilates redistribution and mineral nutrition elements between the organs of tomato plants in connection with crop production.

In this case, **the issue of this study** was to establish the functioning of donor-acceptor system and morphogenesis of tomatoes plants (*Solanum lycopersicum* L.) under gibberellin (gibberellic acid, GA_3) and its antagonists – triazole derivative tebuconazole and ethylene releasing compound esphon treatment on the formation of crop productivity.

The tasks of the study are:

1. Ontogenetic changes of histo- and morphogenesis of tomato plants under the influence of gibberellin and retardant tebuconazole and esphon.
2. Features of formation and functioning of photosynthetic apparatus of tomato plants under the actions of these growth regulators.
3. Features of redistribution of carbohydrates, nitrogen-containing compounds and elements of mineral nutrition between the organs of tomato plants under the influence of gibberellin and compounds with antigibberellin mechanism of action.
4. Effect of ethylene producer esphon on the restructuring of polysaccharide complex of the cell wall and characteristics of product quality in the process of fruit ripening of tomato plants.

The object of the study is a donor-acceptor relationship between assimilative apparatus and competing attracting centers of tomato plants for the stimulator and growth inhibitors interaction.

The subject of the study is morphogenesis, redistribution of assimilates and trophic support for the growth and development of tomato plants under the influence of gibberellin and retardant.

CHAPTER 1

PHYSIOLOGICAL BASES OF GIBBERELLIN AND VARIOUS TYPE OF RETARDANTS APPLICATION IN PLANT GROWING

1.1. General characteristics of growth regulators with antigibberellin mechanism of action

The determination of mechanisms formation and donor-acceptor («source-sink» relation) system functioning is seen as 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 [39, 279]. 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) [99, 182, 183], and for analyzing the relationships between growth processes and photosynthesis in autotrophic phase development at the different vegetation stages [18, 140, 279]. 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 [95, 128, 172, 201].

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 [22, 61, 79]. 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 [268, 270, 271].

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 [115, 216]. It is known that these synthetic substances are used to inhibit growth processes [22, 61], accelerate the transition to a resting state [115], increase plant resistance to adverse environmental factors [9, 37, 272]. These compounds differ significantly in their chemical structure, however, they cause the same effect – they slow down cell division and stretching, which leads to inhibition of growth in general, without causing abnormal deviations. Artificial restriction of the vegetative organs growth under the influence of retardant leads to a redistribution of assimilates in the direction of fruit formation with sufficient assimilation apparatus activity, that resulting in increased yields and improved quality of crops [6, 46, 144, 170]. At the same time, it is not enough understood the physiological mechanisms of growth reduction and increasing plant productivity under the actions of retardants.

The five groups of substances are the most commonly used plant growth regulators with retardant properties:

1. Onium compounds – quaternary ammonium salts, sulfonium and phosphonium. Compounds of this group include AMO-1618, phosphon-D, morphol, pix, chlorocholine chloride, chloromequate chloride, 17-DMC, 3-DEC [3, 150, 214, 218, 282].
2. Hydrazine derivative conpounds – hydrazine maleic acid (GMA, MH-sodium), NN-dimethylhydrazide succinic acid (DSA, B-9, Alar-85, Kilar-85) [145, 178, 265].
3. Triazole- and pentanol derivative compounds – paclobutrazole, uniquezole, pyridazine (BAS-111), tebuconazole (folicur), azovit, flupiramidol [36, 235, 240, 271, 272, 278].
4. Ethylene producers (ethylene releasing compound) – 2-HEPA, ethephone, hydrel, dihydrel, camposan M, dexterel, etrel, zeron [2, 62, 148, 208, 259, 283].
5. Isobutyrates – DCIB, FV-450, MENDOA [32, 72, 234].

These drugs cause similar anatomical and morphological changes, but differ in the mechanism of action. Retardants can be divided into 2 groups according to this principle: substances that interrupt the gibberellins biosynthesis and substances that neutralize the stimulating effect of gibberellins without interrupting biosynthesis [158].

The analysis of the physiological and biochemical mechanisms of growth inhibitor action of quaternary ammonium compounds indicates that they interrupt the biosynthesis of gibberellins in only one link [190]. In particular, AMO-1618 inhibits the activity of ent-cauren synthase at the stage of conversion of geranylgeraniol diphosphate to copalylpyrophosphate, as does chlorcholine chloride (CCC) [54, 157], unlike phosphon D, which does this at the ent-cauren to ent-caurenol stage [54, 191].
Onium compounds, as a rule, cause shortening and thickening of the stem, a change in the area of leaf blades and increased accumulation of photosynthetic pigments in the leaves [192], an increase in the female flowers in plants [94, 159]. Thus, treatment of cotton seeds with a chemical structure similar to CCC with mepiquat chloride led to inhibition of plant growth, a decrease in leaf surface area, and the fresh and dry plant matter weight [222]. TUR compound treatment on tomato plants increased the transpiration rate, the number of vascular-fibrous bundles and their water supply, which eliminated water deficiency in leaf tissues [260]. Applicatiom of the drug increased the dry weight of jasmine plants, number of shoots, flowering time of the plant, but decreased the plant growth and the leaf surface area. It was found that low drug concentrations significantly decreased, while moderate concentrations increased the chlorophyll concentration in the jasmine leaf [278].

Hydrazine maleic acid (HMA) or 6-hydroxy-3(2H)-pyridazinone and compounds synthesized based on it (Alar-85, Kilar-85, DYAK, GMK-sodium) also exhibit growth inhibitor properties. The physiological activity of this group of drugs is due to their ability to affect certain groups of cell cycle genes and inhibit the processes of nucleic acid biosynthesis [58]. It is important to note the structural similarity of the drug with phenolic compounds of plant cells involved in utilization of auxin, as well as the ability of HMA to form stable complexes with β-D-glucosides of phenolic compounds, humic and fulvic acids [241].

Hydrazine derivatives were widely used in crop production to increase the yield of tomatoes and apple trees, to slow the growth of stems and compact formation of the crown and to stimulate the laying of fruit buds [115, 145]. At the same time, the practical application of drugs of this group is now recognized as inappropriate for the production of food products of plant origin, since it has been established their significant mutagenic and carcinogenic effects on animal organisms. The application of GMAs and other drugs of this group remains perspective in decorative gardening and floriculture [265].

Triazole derivatives compound is a special group of retardants. The effect of triazole derivatives on the growth of axial organs of plants is based on the inhibition of ent-cauren synthetase activity and the suppression of gibberellins biosynthesis in three parts of this process: at the stage of conversion of geranylgeranioldiphosphate to copalylpyrophosphate and further to ent-cauren, like some quaternary ammonium salts [158, 195]. In addition, triazole derivatives inhibit the conversion of ent-cauren to ent-caurenol, ent-caurenol via ent-caurenal to caurene acid, and provide extremely high and stable retardant activity with respect to stem growth and seed germination of many plants by suppressing α-amylase activity [23, 192, 194]. The physiological functions of triazoles are manifested in the suppression of brassinosteroids biosynthesis [12], to a lesser extent of ethylene [41], as well as some cytokinins [193].

The physiological activity of triazole derivatives is shown to suppress the growth of stems [248], axial organs of cereal grains [23], legumes [105, 275], vegetables [118], one-, perennial crops [232], increased productivity, and resistance to the pathogens action and less environmental burden per hectare [244]. An important characteristic of retardants is environmental safety and low toxicity.

One of the typical representatives of this group is paclobutrazole. It was established that the level of 1-aminocyclopropane-1-carboxylic acid (ACC) increases and decreased the level of ethylene in the primary bean leaves at the light under the influence of paclobutrazole [242], while the content of ACC did not change for the actions of BAS 111W on rapeseed plants, and the ribosid zeatin and dehydrozeatin content increased by 3-4 times [41]. It was found that uniquezole treatment increased the resistance of wheat seedlings to high temperatures due to the preservation of turgor and less formation of ethylene. The physiological effect of drug is manifested exclusively in small doses. So, the rate consumption of uniquezole working solution decreased by more than 100 times compared to chlorcholinchloride (per hectare) to prevent the state of rice [191].

Triazole derivative compounds exhibit both inhibitor and fungicidal properties. If triazole exists in the form of enantiomer with an R configuration of chiral carbon atom that carries an OH group, this determines their fungicidal properties. If the enantiomer with the S configuration is at the same carbon atom, then such triazoles are inhibitors of gibberellins [194].

The preparations paclobutrazole, uniconazole, and azovite (triadimephone) are characterized by low toxicity, the ability to act in small doses and environmental safety [190]. The study of the paclobutrazole transport in the stem of apple seedlings suggest that more than half of the 14C activity was in the phloem and xylem 27 weeks after treatment, and only 23 % of the 14C activity was in the part where there was a clear inhibition of stem growth [190].

It was noted the ability of triazole derivative compound to inhibit the sterols and terpenoids synthesis [194]. So, paclobutrazole suppressed the synthesis of sterols in celery cell culture [93], and fenpropimorph is used as a fungicide on grape plants, since it inhibits the ergosterol biosynthesis – main component of fungal membranes [184].

It was very successful the creation of growth regulators of based on 2-chloroethylphosphonic acid (2-HEPA) – ethylene producer, which, unlike quaternary ammonium compounds and triazole derivatives compounds, does not affect the synthesis of gibberellins, but by blocking the formation of hormone-receptor complex, is able to inhibit the activity of already synthesized hormones of this class [58, 115].

The effect of ethylene producers is related to the fact that these drugs are environmentally friendly, since they decompose in plants with the release of free ethylene, a plant's native metabolite that accumulates in the cytoplasm and causes changes in the auxin-ethylene balance. It was established that the IAA content in pea plants decreased [139, 211], while the activity of auxins in winter rye decreased under the influence of etrel [210].

Ethylene causes a delay in the mitotic process in the meristems of vegetative organs, and is caused by blocking the synthesis of nuclear DNA [26]. The application of ethylene producer leads to a decrease in cell size in length and an increase in its isodiametric sizes, which leads to a shortening and thickening of the internodes [263]. These drugs accelerate the fruit ripening of apple trees [163], plums [40], tomatoes [64], which is necessary for mechanized harvesting. The etrel treatment makes it possible to obtain a greater number of female flowers on cucumber and pumpkin plants [215, 259]. Ethylene producers increase seed germination and energy of seed germination, disk maturation, which allows harvesting sunflower without loss [31], stimulate root growth, provide defoliation on cotton plants (80 % of leaves fall) [151]. It has been established that ethylene producers increased the activity of polygalacturonase and cellulases, due to accelerate the maturation of fruit [47, 107, 186].

A relatively new group of retardants is isobutyrates, which include 2,3-dichloroisobutyric acid (DCIA) and its sodium salts (PV-450, mendec). Two mechanisms of the retardant action of DCIA have been identified [32]. The first is the direct inhibition of HA biosynthesis from oxidative units after kauren and through the reduction of hydroxycarrenic carboxylic acid to the GA_3 and GA_1 contents. High doses of DCIA affected on the synthesis of GA, inhibits the enzyme activity, involved in the conversion of pantoin into pantothenic acid, thereby affecting on the formation of coenzyme A (K_oA). The second mechanism is associated with metabolism and is realized through interruption of gibberellin biosynthesis at the stage of formation of cauren acid from cauren [32]. The analysis of the labeled carbon content showed a decrease in the label in the free forms of GA_1 and GA_3 of treated young wheat plants, in particular, DCIA reduced the GA_3 formation by 2 times, and CCC – GA_1. It is also known that DCIA inhibits not only formation, but also the transport of GA. Thus, the inhibitor effect of this group of drugs is depended of the structure and is determined by blocking the synthesis or decreasing the activity of already synthesized gibberellins [115].

The effective retardants have also been found among the graminicides derivatives compound of cyclohexadione class (CHD), particularly – acyl-CHD, which effectively block the pathway of biosynthesis of GA, reduce the content of active gibberellins GA_1 and GA_4 and are widely used in modern crop production [36, 148]. Acyl-CHD suppresses the final stages of GA biosynthesis, namely the hydroxylation of GA_{20} in GA_1. Trinexapac-ethyl, prohexadion-Ca and daminoside inhibit mainly 3β-hydroxylation and formation of highly active gibberellins from inactive derivative compounds [194, 195, 220]. This is confirmed by detailed studies of the mechanism of acyl-CHD action [36], which showed that the structure of prohexadione molecule is similar to 2-oxoglutaric acid (co-substrate of deoxygenases that catalyze the hydroxylation of late stages of GA biosynthesis). Therefore, the primary site of calcium prohexadione action may be precisely 3β-hydroxylation. As a result of prohexadione application, there is a decrease in the level of GA_1 accumulation, which causes the accumulation of its predecessor – GA_{20} (inactive form). At the same time, it was shown the absence of transcriptional response to the phytohormones action, including prohexanedione-Ca on a genetically close to wheat and other cereal crops type – purple false brome (*Brachypodium distachyon* L. P. Beauv) [57, 152].

Retardants of acyl-CHD derivative class are easily absorbed through the leaf surface and cropetally move along the plant, the basipetal movement is limited. They can be effective both for introduction in the tillering phase, at the beginning of plant exit into the tube and in the flag leaf phase, when the growth of the last spike internode is activated. It is important that during this period all the elements of the spike are already laid, therefore, the introduction of CHD derivative compoun does not have a pronounced negative effect on the plants productivity [34, 155]. Retardant activity of new growth regulators is an important feature to reduce the dependence of growing cereal crops technology on adverse conditions of growing season, in particular moisture deficiency, high temperatures during the second part of growing season. It is the unfavorable conditions of vegetation seasons in recent years that often reduce the effectiveness of retardants application of onium compounds class; it also causes a decrease in yield of grain crops [152].

The retardant effectiveness is largely determined by the soil and climatic conditions, species and varietal specificity, the phase of plant development, the regulations of drugs application. Different groups of retardants have different effects on individual plant species and varieties [59]. Application of quaternary ammonium salts is more effective on legumes, asteraceae and cereals [50, 109, 111, 147], triazole derivative compounds on fruit, industrial and ornamental crops [10, 105, 113], ethylene producers on cereals and vegetables [38, 96, 264]. However, the physiological basis for application of various classes of retardants on tomato plants not adequately explored.

1.2. Physiological and biochemical changes in plants under the actions of retardants

The development of donor-acceptor («source-sink») systems of plant opens the prospects of artificially redistributing of assimilates flows from vegetative growth processes to the carpogenesis needs (the fruit formation and growth) and therefore, it is a potential factor in increasing the agricultural crops productivity

The application of plant growth regulators permit to artificially change the rate of growth processes. Thus, the artificial change in growth rate under the phytohormones and synthetic growth regulators treatment on the plant allows to simulate the different degrees of tension between donor (source) and acceptor (sink) zones in order to determine the features of formation and donor-acceptor functioning at different periods of ontogenesis [99, 183]. The plant growth regulators have a significant effect on morphogenesis that originate to analyse the depositing process of assimilates to different organs and tissues of the plant due the anatomical-morphological and physiological changes.

It has been established that the mechanism of retardants action is associated with the suppression of enzymatic gibberellin biosynthesis [231]. It is known that one of the most important functions of gibberellins in the process of cereal seeds germination is the ability to stimulate the embryo to secrete α-amylase in the endosperm, which contributes to the breakdown of starch [7, 13]. Gibberellin antagonists – quaternary ammonium salts and triazole derivative compounds, on the contrary, significantly block the activity of this enzyme. The α-amylase test is based on determining the activity of retardants [115].

The analysis of the related forms of gibberellins activity in raspberry shoots indicates that the content of this forms was less retardant dextrel and paclobutrazole treated trials. In the leaves, the activity of related forms of gibberellins increased under paclobutrazole interaction and decreased under the actions of dextrel (as compared to control) [107]. Similar results were obtained in other cultures. In particular, it was noted a decrease in the content of related forms of gibberellins in rapeseed leaves, the difference between control and paclobutrazole treated variant was minimal in potatoes and lucerne, and the content increased in soy and sugar beets [103]. Thus, the effect of retardants is not obviously associated with the inactivation of gibberellins by conversion to conjugated forms [115].

The results of the studies indicate a significant effect of retardants on the gibberellins activity in plants [54, 277]. Balance, ratio and sequence of different class of phytohormones play a decisive role in morphogenesis of the plant, consequently it would be incorrect to reduce the reaction of plants in the content and activity of gibberellin under growth regulators application [115]. Therefore, it is important to study changes in the content and ratio of other classes of phytohormones in plant tissues during artificial growth inhibition under retardants treatment.

The content of ethylene and ACC temporary increased under application of growth inhibitor chlormequat chloride on various plants, which is explained as a stressful reaction of plants to the interaction of drug, and it was not associated the effect of retardant CCC with significant changes in ethylene biosynthesis [208].

The nature of retardants action on auxin metabolism is species specific. Thus, auxin activity decreased under the influence of CCC and AMO-1618, which can be explained by both inhibition of its synthesis and an increase of IAA-oxidase [26, 192], while the auxin content increased of chlorocholine chloride treated beans and grapes, which can occur due to the formation of new lateral stems, while the apical meristems act as auxin synthesis centers [191, 192].

It has been established that application of triazole derivative compound caused the suppression of gibberellins synthesis and an increase in activity of natural growth inhibitors occurs, namely, ABA, which indicates the connection of the retardant action of drug and the hormonal regulation system [190, 192]. That can be explained by the fact that the synthesis of gibberellins and abscisic acid is a single pathway for the terpenes synthesis in a plant [29].

The results indicate a clear increase in the free form content of ABA under the influence of paclobutrazole on rapeseed [103], potato [121] and soy [51], however, the related form content of hormone decreased in the experimental trial of sugar beet plants [233]. Such morphological features of the crop can be explain by the rosette nature and stems absence, the intensity of hormone redistribution between leaves and powerful acceptor zone – root crop [227].

It has been established that the relative proportion of abscisic acid increases in the sprouts under the retardants actions during the germination of potato tubers, the content of free forms of cytokinins, indolylacetic acid and gibberellins decreased [121, 103], and the hormonal complex changes determine the features of meristems functioning and differentiation of organ tissues [160, 239].

The majority of agricultural crops are characterized by lodging [263]. The literature data indicates that application of antigibberellin compounds is effective to prevent the lodging of plants [8, 264], due an increase in the mechanical strength of a stem. It was established that 0,025 % paclobutrazole treatment of winter rapeseed plants predetermined inhibition of linear shoot growth with increased the stem branching and the formation of additional first-order branches that was accompanied by a significant thickening of stem due to the primary parenchyma of cortex, an increase in the transverse dimensions of sclerenchymal fibers and thickening of their cell walls. Such changes contributed to the enhancement of stem mechanical strength and reduced lodging that created technological advantages during harvesting [206]. It was noted a similar thickening of the stem under the action of chlormequat chloride on soybean plants [49, 134], sunflower [173] and oil poppy [175]. Thus, the results of the study were shown that chlormequat chloride treatment increased the diameter of the flax stem by 10-30 %, the number of xylem vessels in a row by 34-70 %, the bark was shed by 23-30 %, the diameter of the bast fiber by 24-35 %, which improved the resistance of flax plants to lodging and provided technological advantages in harvesting [66].

The restructuring of hormonal complex and inhibition of apical dominance under the influence of retardant caused strengthing of the stem branching that is an important part for the regulation of plant productivity. In particular, the actions of folicur increased the number of shoots in oil poppy [117], chlormequat chloride and paclobutrazole treated winter rapeseed [202], chlormequat chloride treated oilseed [66], paclobutrazole treated white mustard [221]. A greater number of leaves, flowers and fruits were laid due to increase in the stems branching of these crops, that is an important prerequisite to increase plant productivity. However, it is practically unstudied the possibilities of antigibberellin compound application in the cultivation of nightshade cultures to regulate the processes of organo- and histogenesis [106].

Photosynthetic activity has an important implication on the plant productivity, which is determined by the area of leaf surface, the leaves number and functioning duration, the mesostructure of leaves. The analysis of recent studies has shown that artificial restraint of plant growth processes is accompanied by significant changes in morphogenesis that related to the different levels of photosynthetic apparatus organization under retardants of various classes treatment [113, 137]. Chlormequat chloride treatment on oilseed flax increased the number of leaves on the plant without a noticeable enhancement of the leaf surface area due the smaller sizes of individual leaves [110]. The number of leaves and their total area increased of treated soybean plants [49]; the number of leaves decreased under the influence of chlormequat chloride on sunflower, however, due to a significant increase in the total leaf surface area [199]. The total leaf surface area of winter rapeseed plants decreased, but the leaves thickened [206]. The leaf surface area, the leaf fresh and dry matter weight increased and the life span was extended due to the action of triazole derivative folikur on oil poppy plants [175]. In the case of retardants application on oilseeds, the total area of leaf surface can increase without changes or even with a decrease in the area of individual leaf through more intensive stem branching and laying of more leaves [106].

The study of the etardants effect with different mechanisms of action on raspberry plants indicates a decrease in the leaf area and weight due to a decrease in the frequency of cell divisions and activity of free gibberellins in the leaves [107].

The leaf area density value is an important indicator of assimilative activity that characterized by the ratio of the leaf dry matter weight to the leaf area. It is explained a positive correlation between the rate of photosynthesis and this indicator by an increase in the number of basic structural elements and photosynthetic pigments that contributed to CO_2 assimilation. A positive changes of photosynthetic apparatus is the increase in the leaf density value and thickening of leaves under the action of retardants on crops. It has been established that the leaf area density value of chloromequate hlcoride and folicur treated poppy leaves increased [175]. Similar results were obtained by other researchers on crops of sunflower [198] and oil flax [66].

Mesostructural changes caused an increment of the leaf area density value under the action of drugs. Analysis of the mesostructural structure indicates an increase in the leaf thickness due to the thickening of photosynthetic tissue layer – chlorenchyma, an increase in the size and volume of columnar cells and spongy parenchyma of sugar beet [228], potato [201, 246], winter rape [104] leaves due to the effects of CCC, dextrel, paclobutrazole. It was observed an increase in cell volume of columnar parenchyma by 1,5 times [228]. The application of chlormequat chloride also contributes to an increase in the volume of chloroplasts in the columnar parenchyma cells of oil flax by 14-15 % and the size of spongy parenchyma cells by 21-27 % compared to control [66].

The action of various classes of retardants on the pigment system of leaves is quite complex and depends on the characteristics of the object of the study, the specifics of the drug and the conditions of its application. At the same time, it was revealed a positive effect of antigibberellin compounds on the chlorophyll content in leaves of experimental plants. So, paclobutrazole increased the content of chlorophylls in gerbera leaves [10], folicur – in oil poppy [113], chlorcholinchloride – in ginkgo biloba [282], flupiramidol – poinsettia [172] leaves.

Mixture of ethylene producer DCPTA and quaternary ammonium salt CCC increased the leaf area, the dry matter weight and the chlorophyll content in leaves [268]. The analysis of uniquizole interaction on soybean seeds indicates a similar effect of drug on the leaf photosynthetic apparatus [272].

The leaf index (LI) is an important cenotic indicator of the photosynthetic apparatus power [188]. It was established that LI increased in oil poppy [175], soy [51], and sunflower [206] plants under the action of retardants with different chemical structures. At the same time, an increase in the leaf index in the cenosis is not always a positive phenomenon, since thickening of crops and the formation of excess leaf surface can lead to shading of neighboring plants and, as a result, to a decrease in crop yield [113]. The application of retardants on these crops did not lead to such consequences, their productivity increased [104, 120, 123].

The ratio of respiration and photosynthesis in the ontogenesis of individual organs and the plant as whole has an important place in the growth functions of a plant, the structural features and photosynthetic apparatus power [52]. Respiration is considered as a powerful metabolic carbon acceptor, and the respiration to photosynthesis ratio largely characterizes the tension of donor-acceptor relations in the plant [48]. At the same time, the literature analysis of the retardants effect on the respiration of plants is fragmented. Thus, it was found that exogenous ethylene enhances the respiration of individual separated leaves of experimental trials [262], and the rate of respiration of chickpea plants decreased under the influence of chlorcholine chloride in the conditions of high humidity [92]. Similar results were obtained for the actions of dextrel and paclobutrazole on raspberry plants [107].

The changes in the donor- acceptor balance of germinating potato tubers under the influence of triazole derivative paclobutrazole led to an increase in the rate of respiration and the effect was enhanced under the light action. This is explained by the fact that the acceptor acted as an alternative growth for the retardants action in the conditions of respiratory photomorphogenesis, which utilizes an excess of soluble sugars in the sprouts [98].

It was found that the rate of photosynthesis decreased with a simultaneous increase in dark photorespiration when a part of the leaf blade (acceptor) was removed surgically of sugar beet plants [73].

The analysis of the obtained results has shown that the treatment of retardants with different mechanisms of action - paclobutrazole and dextrel contributed to the changes in the gas exchange of sugar beet plants, and there was an increase an increase in costs of photorespiration and dark respiration of leaves [228].

So, the photosynthesis rate of experimental trials decreased due to in the mesophilic resistance of leaves that depends on the volume of intercellular spaces, size of free mesophyll cell surface, physicochemical conditions of carbon dioxide exchange from cell surface to chloroplast and activity of ribulose bisphosphate-carboxylase despite the increase in the chlorophyll content of leaf tissues [153, 228].

The functioning of donor-acceptor relations are studied mainly by analyzing the ratio of the growth and photosynthesis rate, where growth processes act as the main acceptor and photosynthesis as a donor of assimilates [113, 207]. Assimilates include various compounds of carbon assimilated by the plant during photosynthesis, primarily transport and storage forms of carbohydrates, which are the basis of energy and metabolic processes, as well as «building material» in the processes of growth and development at all levels of plant organism organization [39]. It is known that various types of reserve substances play the role of a buffer between photosynthesis as a «source» of assimilates and growth of the structural substance of vegetative, storage and reproductive organs as a «sink» of assimilates that determines the independence of growth processes from photosynthesis [187].

The analysis of the various forms of carbohydrates content in plant organs suggests that the total content of sugars and starch in leaves and stems of winter rape [205], oil poppy [175], oil flax [69] and sunflower [198] gradually decreased during the growing season, moreover, the process intensified under the actions of retardants. Since, the growth processes in the vegetative organs significantly slow down and new powerful acceptor zones (fruits) appear at the same time after the budding phase, the main flow of assimilates is directed to the processes of carpogenesis, which are associated with a gradual decrease in the carbohydrate content in the vegetative organs and increase in crop yield under the influence of retardants [201] .

The productivity of sugar beets is associated with the accumulation of a large amount of sucrose in the root crop, which is synthesized in the leaves by the enzyme sucrose phosphate synthetase. So, the total content of sugars and sucrose increased in the roots of sugar beets hybrid Robert for the actions of paclobutrazole, and dextrel treatment led to a decrease in these indicators [228]. It was noted a similar effect of retardants on the redistribution of various forms of carbohydrates between organs on nightshade plants. Thus, the paclobutrazole and dextrel treatment of potato tubers led to a slowdown in tuber germination at the resting state, the activity of amylase and invertase significantly decreased, that was accompanied by an increase in the content of main transport form of sugars – sucrose and the deposition of excess carbohydrates in the form of starch grains in sprouts [136].

It is known that there is a clear correlation between the intensities of growth, photosynthesis, respiration and nitrogen nutrition of plants [106]. It has been sufficiently studied the exchange of nitrogen compounds under the retardants treatment of berry [107], cereal [219, 226], industrial [70, 198], legumes, and several other crops [1, 51, 243]. It was established that the protein nitrogen content in the leaves and stems of sunflower increased due to the action of chloromequate chloride compared to control [198], and, its content in the tissues of vegetative organs decreased of paclobutrazole treated rapeseed [206]. It has been proven that the protein accumulation increased and the oil content in the seeds, the unsaturated fatty acids content decreased simultaneously with an excess of nitrogen in the tissues during the development of oilseed plants [174, 66]. It was established that the total nitrogen content decreased due to increase in the carbohydrate content in the vegetative organs of chlormequat chloride and folicur treated oilseed plants [176].

The maximum amount of nitrogen-containing substances in the leaves and roots was found at the initial stages of the study. The nitrogen content in the tissues of the vegetative organs decreased more actively under the influence of chlorematechloride and folicur, which, in our opinion, indicates intensive protein hydrolysis and the outflow of nitrogen-containing compounds into new attracting centers – pods, the number of which increased towards to the end of the growing season [175]. Other authors obtained similar results of the outflow of nitrogen from vegetative organs to generative organs of winter rape [206], cotton plants under the actions of retardant pix [1], and sugar beets under the effects of dextrel [228].

The analysis of donor-acceptor relations for leguminous plants cannot be limited only by the specifics of assimilates redistribution between vegetative and generative organs of plants, growth and photosynthesis, since legume-rhizobial complexes act as additional attracting centers of assimilates redistribution [51]. The rate of atmospheric nitrogen assimilation of leguminous plants is determined by the nature of the formation and development of relationships between plants and nitrogen-fixing bulb bacteria [76].

The key enzymes of nitrogen assimilation by legumes are nitrogenase and nitrate reductase [51, 76]. The mechanism of nitrate reductase regulation is associated with the induction / repression of nitrogen synthesis, at the stage of oxidation of nitrate to nitrite, and the activity of specific proteases, which play a significant role in the complex system of nitrate reductase activity. It was established that the nitrate reductase activity in the leaves increased during the flowering phase and nitrogenase activity of root bulb bacteria increased, while its peak shifted to a later stage of ontogenesis – at the green bean phase due to the action of 0,5 % chlormequat chloride in soybean plants inoculated with strains of *Bradyrhizobium japonicum* [51, 119].

Phosphorus-potassium nutrition affects on the photosynthetic activity of plants, the transport of sugars from leaf chloroplasts to generative organs, growth processes, maintenance of turgor and nitrogen metabolism.

A certain balance of nutrition elements contributes to the normal flow of plant ontogenesis phases, increasing crop productivity due to the influence of growth regulators. Thus, the phosphorus contents decreased in the leaves of chlormequate chloride treated sugar beet, and the potassium content increased both in the leaves and in the roots of research plants [227]. The phosphorus content in tubers was elevated in retardant-treated potato plants throughout the study. The phosphorus content increased in the leaves of experimental plants at the beginning of growing season and decreased at the end [243]. The potassium content in the leaves decreased at the beginning of the study, increased during flowering, and decreased again at the end of the study. In tubers, the potassium content increased only at the first stages of the study and subsequently decreased [243]. The potassium content in the leaves of black chokeberry was increased during fruitification stage under the influence of chlorcholine chloride [115].

The analysis of the study of mineral nutrition elements metabolism in the organs of oil flax plants indicates that the phosphorus content in the leaves increased at the beginning of the study under the action of antifibberellin compounds, that caused the optimization of phosphorus nutrition of plants under the influence of retardant. Its content gradually decreased the amplification of phosphorus outflow to the fruits, which are intensively formed at the end of growing season. It was noted the same pattern for the stem. Consequantly, the outflow of phosphorus to fruits increased due to an intensive increment in the concentration in fruits under retardant treatment in ontogenesis than in the control variant [68]. Similar patterns were established for winter rape [206], sunflower [198].

The content of nitrogen, phosphorus and potassium in the vegetative organs gradually decreased due to an increase in the outflow of these nutrients to the fruits, the amount of which increased under the actions of retardants during the growing season. Therefore, it is necessary to study the nature of assimilation and redistribution of the main flows of mineral nutrition elements by organs of vegetable crops for the actions of growth regulators with an antigibberellin mechanism of action.

The regulation of growth and development of crops with the retardants application directionally affect on the individual stages of ontogenesis and ultimately increase productivity and yield quality.

Retardants are able to regulate fruiting [149], accelerate crop ripening processes [4, 14], change the direction of assimilates and metabolites flow in the direction of their increased deposition in storage organs of plants, which leads to increased crop yields [98, 243], affect on the quality yield [69, 99], have a significant impact on the seed productivity of plants [71, 113, 161, 166].

It was found that the application 0,5 % chlormequat chloride led to an increase in seed productivity of flax cv. Debut by 21,2 %, and cv. Orphei by 12,0 %. The oil content increased, the quality of seeds improved (the content of related higher fatty acids, the ratio of unsaturated and saturated higher fatty acids increased) under the drug treatment [66].

The yield of quaternary onium compounds 3-DEC and 17-DMC treated rape plants increased by 10-27 %, due to the effect on the pods formation of main stem [150]. The application of paclobutrazole and dextrel on winter rape led to an increase in the number of first-order stems and pods, which increased the seed productivity of plant [206]. Similar results were obtained under triapentenol [20], modus [197] and ceron treatment at low concentrations before the budding stage [106].

It was established that the uniquezole treatment of corn seeds increased seed yield by 20-30 % [268], triapentanol – by 3,7-8,3 % [20]. The application of BAS 111-W on rapeseed increased seed yield by 6-15 % [41].

The application of retardants, ethylene producers and their derivatives compounds leads to increased the yields of fruit [58, 177], technical: starchy [123, 243], sugar-bearing [231], oil-bearing [116, 176, 206, 150], vegetable [118, 38] and berry crops [107, 62].

The management of the resting state allows solving important practical problems: it minimizes the loss of reserve compounds of root crops and tubers and increases their resistance to bacterial and fungal infections by microflora, in particular, the formation of sprouts at the end of resting period affects the quality of seed and yield of potatoes.

The formation of «source» for reserve assimilates by seedlings from different organs of stock (potato and artichoke, cotyledons of sunflower and pumpkin seeds) is largely determined by a change in the apical meristems activity, which is manifested in increased the seed germination energy, increased histogenesis for the actions of gibberellins and inhibitors of these processes – retardants [180]. So, , the germination of potato tubers was inhibited for the retardants actions, namely, the growth of stems was slowed due to the growth of primary cortex cells, which led to the secondary deposition of excess carbohydrates in the form of amyloplasts starch [179, 248]. The reduction of cotyledon oil application was determined by the corresponding changes in the lipase complex activity during germination of retardant treated sunflower seeds that containing oil as a reserve substance [135, 180].

Thus, the ways and mechanisms of functioning and regulation of the donor-acceptor system activity opens up new possibilities to optimize the crops production process by artificially redistributing of photosynthesis products to fruits, root crops, other reserve organs under the influence of phytohormones and various groups of synthetic growth regulators. At the same time, the effect of antigibberellin compounds on the morphological and physiological features of donor-acceptor system functioning of nightshade cultures has not been studied.

1.3. Physiology of ethylene releasing compounds action on carpogenesis

One of the most powerful acceptors of photosynthesis products is plant growth zones and processes of fruit formation and growth (carpogenesis) [115]. The increase in the number of fruits leads to improve the attracting ability of these zones, and a corresponding redistribution of assimilates flows from vegetative growth to the fruits formation and growth. This effect can be achieved by trimming of fruit-bearing stems, removing of much absorbing stems, etc. However, this requires significant physical costs and is not economically feasible. Application of exogenous hormones and growth regulators is widely used to change the growth rate of individual organs (and their acceptor potential), that allows to simulate a various degrees of stress in the «donor-acceptor» system [147, 161, 172].

It has acquired great environmental significance the creation and application of ethylene producers based on 2-chloroethylphosphonic acid – ethephon, hydrel, dihydrel, dextrel, camposan, which decompose in plants to free ethylene. It is known that the native metabolic product – ethylene plays an important role in the regulation of vegetative growth and aging of plant organs [16, 208, 283].

Ethylene releasing compounds not affect on the synthesis of gibberellins, but are able to inhibit the activity of already synthesized hormones of this class by blocking the hormonal-receptor complex formation unlike the retardants action of quaternary ammonium and triazole derivatives compounds [115, 158]. Therefore, the study of ethylene producers interaction on the features of carpogenesis and the donor-acceptor system functioning of plants is relevant.

It is believed that the primary mechanism of ethylene action is the dissociation of cytoskeleton bonds with membranes, and this causes a delay of the polar IAA transport in the cell. The organization of auxin polar transport provides an asymmetric arrangement of the IAA secretion apparatus at the two ends of each cell [139, 210].

It has been established that the key enzymes in ethylene biosynthesis are the enzyme 1-aminocyclopropane-1-carboxylic acid synthase (ACA-synthase, ACS) and 1-aminocyclopropane-1-carboxylic acid oxidase (ACA-oxidase, ACO) [209, 261]. At the beginning stages of biosynthesis, the enzyme ACA-synthase converts S-adenosyl-L-methionine to 1-aminocyclopropane-1-carboxylic acid (ACA), which is a precursor of ethylene, then in the presence of oxygen, ACA under the influence of ACA-oxidase decomposes with the formation of ethylene, ammonia, methanoic acid and CO_2 [63, 272]. These enzymes are encode by a series of Md-ACS and Md-ACO genes, express in different tissues and at the different stages of fruit ripening [217, 238]. Md-ACS1 and Md-ACO1 genes largely determine the level of ethylene synthesis in fruits during ripening, and also during storage, which determines their significant influence on the degree of fruit quality [280, 24, 44, 284].

The physiological effect of ethylene producers action depends on the features of the drugs income in the tissue, the speed of movement and their metabolism in the plant.

It was found in experiments with labeled ^{14}C 2-HEPA that the drug easily moves up and down from the place of application and accumulates in the growth and active metabolism zones [156, 212, 237], but the drug speed depends on the age of the plant. In experiments on annual apple tree seedlings, it was shown that within an hour after applying ^{14}C-etrel on a leaf, the drug could be found in all organs of the plant, with the highest activity observed in young, intensively growing leaves. On the fourth day, the label moved to the root system [91, 284]. Moreover, a significant part of drug remains on the surface of plant organs for several days and can be washed off with water [265]. Some researchers believe that 2-HEPA moves unchanged throughout the plant; in other studies, it has been established the appearance of conjugates with sugars [91, 156, 47]. It is suggested that the binding of ethylene producer in the cell can occur with the participation of enzymes, since it was observed a decrease in 2-HEPA binding in experiments with protein synthesis inhibitors [143, 267]. At the same time, the presence of such enzyme systems in plants has not yet been established; therefore, other researchers believe that binding to sugars can occur by a purely chemical route [91, 47].

It was found that the rate of ethylene excreation in 2-chlorethylphosphonic acid treated plants is directly dependent on the drug concentration [59], and the rate of 2-HEPA decomposition in both solutions and plants depends on temperature. The ethylene excreation of winter rye increases by 10 times with an increase in temperature from +10 to +30 °C and it stops completely at 40 °C [91].

Part of the drug introduced into the plant remains either unchanged or decomposed. ^{14}C-labeled 2-HEFA metabolites were found in fruits of a number of fruit crops (cherries, peaches, apple trees), and unchanged 2-HEFA was found after 65 days in peach fruits in a complex with sugars and other substances [156].

The ripening processes of juicy fruits, falling leaves, the formation of aerenchyma are associated not only with destructive processes, but also with synthesis processes. So, degradation of starch, pectins, destruction of chlorophylls increased. At the same time, the biosynthesis of proteins and RNA is activated, the enzyme system of ethylene biosynthesis is synthesized, and the formation of volatile compounds is enhanced [107]. Enzymes that destroy cell walls – cellulases, pectinases are synthesized under the influence of ethylene.

It is known that cellulose, hemicellulose and pectin substances are the main components of the cell wall. Cellulose, as an important component of the cell wall, is glucan, in which glucose residues are connected (β1→4) by glycosidic bonds, the synthesis of which is catalyzed by cellulose synthase [65]. In particular, changes in the molecular structure of cellulose in the cell walls of raspberries are shown in the study [115] during ripening. The author found that the ripening process of berries was accompanied by an increase in the degree of cellulose molecules polymerization, and it was concluded that cellulose partially hydrolyzed the outer layers of the cell wall during ripening, and the process was intensified due to the action of ethylene producer. The analysis of the studies of fruit softening both in vivo and in the tissues incubation with enzyme solutions has shown that maceration processes are localized in the middle plates and outer layers of the cell walls [122]. It was noted that the ripening of tomatoes, avocados, blackberries, pears, strawberries, papaya, peach, and apple is always associated with an increase in the cellulase activity [269]. These data are consistent with the results of studies by other authors; that studied changes in the cell wall after treatment of tissues with cellulase due to the application of an electron microscope. The amount of fibrillar material between the cells and in the outer part of the cell wall was significantly reduced, and its inner part was not exposed to this enzyme under the influence of drug.

There are various views on the relative direction of changes in the structure of pectin substances. It is known that pectin substances are include insoluble protopectin, soluble pectin polysaccharides and their corresponding galactans, arabinans and arabinogalactan. Pectin polysaccharides (pectins) are in a large group of glycanogalacturonans – acidic plant polysaccharides, where the 1,4-linked residues form the main carbohydrate chain α-D-galactopyranosyluronic acid [165].

Determination of the pectins molecular weight isolated from raspberries showed that the polyuronid complex undergoes significant changes: the average molecular weight of pectins decreased upon ripening of the berries, due to the transition of protopectin to soluble pectin within a week after the 0,1 % camposan M treatment. In addition, enhanced depolymerization of polyuronides and low molecular weight cellulose occurred under the drugs action; camposan M influenced on the quality of raspberries – it increased the content of sugars, anthocyanins and reduced total acidity [122].

It is known that the properties of pectins largely depend on changes in the degree of molecules esterification [156]. The analysis of the physicochemical constants of pectins of ripening cherry berries [250] indicates that the amount of free carboxyl groups grows in both soluble pectin and protopectin by the time the fruits ripening. The study of the pectins structural elements of control and ethylene producers treated raspberry berries during the ripening period indicates that the content of total, free and esterified carboxyl groups in pectin trials did not change during the period of intensive softening of the cell walls, during the period of rapid softening of the fruit, in fact, during aging, pectin esterases do not participate in the degradation of pectins [122, 182].

The application of ethephon on gooseberry plants 7 days before harvest indicates an increase in the total pectin polymers content, a higher accumulation of water-soluble and soluble fractions of pectin, and an increase in the polygalactorinase enzyme activity are necessary to maintain pectin degradation [62].

So, exogenous treatment of mangoes led to a decrease in starch content from 18 % to 0,1 %, pectin from 1,9 % to 0,5 %, cellulose from 2 % to 0,9 % and hemicellulose from 0,8 % to 0,2 %. At the same time, total soluble solids increased from 7 % to 20 %, total soluble sugars from 1 % to 15 %, and pH increased from 2,8 to 5,1 [53] and the content of free galacturonic acid increased from 36 to 168 mg/% per fresh matter at the ripening [185].

The process of germination of pumpkin seeds under conditions of scotomorphogenesis is accompanied not only by the application of reserve oil and nitrogen-containing substances of cotyledons, but also by a significant restructuring of polysaccharide complex. The study of the pectins content in fat-free material under germination conditions in the light and in the dark under the influence of gibberellin and retardants indicates that the growth processes are accelerated under conditions of scotomorphogenesis, there was a slight increase in the polysaccharides content in cotyledons [182].

At the same time, scotomorphogenesis was characterized by a lower content of free pectins, but a higher content of common and related carboxyl groups in comparison with photomorphic plants. Thus, the degree of pectin esterification increases in the dark, at higher plant growth rates, which is important for understanding the conformational changes in pectin macromolecules in the cell walls during seed germination. It is known that an increase in the degree of carboxyl groups esterification caused a transformation of coil structure into a spiral structure, and the macromolecule volume increased. The obtained data indicate an increase in the degree of cotyledon pectins esterification is accompanied by a significant decrease in the content of pentosans of cell walls in the dark, which indicates their partial inclusion in the polyuronides structure. This conclusion is consistent with modern ideas about the fundamental possibility of the carboxyl groups esterification of polygalacturonic acid with neutral polysaccharides [180].

Excess assimilates can be deposited not only in the form of starch, but also in the form of structural polysaccharides and lignin [107], retardants and phytohormones act opposite to these processes. In particular, it was noted an increase in the activity of enzymes that regulate the formation of cotton fibers – glucansynthetase and peroxidase for the actions of pix retardant, as a result of which the formation of cell walls was accelerated [1]. The reverse processes – an increase in the enzymes activity that destroy polysaccharides [107], significant changes in the structure of hemicellulose [53], the ratio of protopectin to soluble pectin and pectin depolymerization [62], cleavage of the glycoprotein complex of the middle plate, occur during fruits and berries ripening [53]. It has been established that pectin oligomers, which are released as a result of acid or enzymatic hydrolysis, can initiate rapid acceleration of ethylene synthesis [281], and oligosaccharides released from cell walls initiate the synthesis of other enzymes that destroy polysaccharides.

Thus, the research results presented in the literature indicate that different groups of retardants can improve the conditions for collection and storage of products, regulate the ripening time and increase the quality indicators of crop yields. Performance optimization associated with changes in hormonal status for the actions of growth regulators. However, the obtained data are controversial, which necessitates further research on the problem.

The creation of a new ethylene producer – retprol was a significant achievement [162]. This is the well-known calcium carbide CaC_2, simple in structure and cheap to use. It was found that it decomposes with the formation of calcium hydroxide and acetylene, which, with the participation of nitrogen-fixing microorganisms, restores the acetylene formed in the hydrolysis of CaC_2 into ethylene under the drug interaction into the soil in the moist conditions. The ethylene enters in vegetative plants through the roots. The drug is highly effective on tomatoes, cucumbers, potatoes, hemp, corn and soy [162].

It was developed new ethylene producers – ifonii and ifonilii to rationalize the technology for growing winter wheat to replace the CCC. These are drugs with antiseptic properties and significantly lower doses of use. So, the effective dose of chlorcholine chloride for wheat plants is 1300-4000 g ha, while for ifonii and ifonilii are 100-200 g/ha. It is assumed that ethylene producers of this type increase the efficiency and pesticidal discharge of winter wheat growing technology [56] and replace the CCC and fungicides and due the low toxicity and effectiveness of small doses of application. It is achieved the reducing of toxicity and sharpness of the odor by replacing the active CCC chlorine with «soft» antiseptic sulfur-containing fluorinated radicals. It was proved that the average degree of fungal infection of spike was manifested on ifonii treated winter wheat plants. It has been suggested that the fungicidal properties of ifonii also contribute to an increase in the yield since the drug was first patented as a plant fungicide [56].

Thus, the analysis of literature data indicates that compounds with antigibberellin mechanism of action realize the growth-regulating effect on the morphogenesis and production process of crops in the different ways. In this regard, it is an important theoretical and practical task to establish the features of retardants application with various mechanisms of action on the formation and functioning of donor-acceptor system of plants.

CHAPTER 2

MATERIALS AND RESEARCH METHODS

2.1. Agroclimatic conditions of experiments

The territory of Vinnitsa region is located in the temperate zone. The temperate continental climate of the Vinnitsa region is characterized by long, non-hot summers with sufficient moisture and relatively mild winters. During the warm periods, the region's climate is determined by the western and northwestern Atlantic air masses, which are saturated with moisture. In the cold season, the territory has a noticeable influence of the Siberian (Asian) anticyclone with south and southeast winds directions. To a lesser extent, the climatic conditions of the region depend on air masses from the Arctic and the Mediterranean [28, 171].

The territory of the Vinnytsia region according to the state agro-soil zoning of Ukraine is divided into two agro-soil regions in the northern and five agro-soil regions in the southern sub-province of the right-bank Forest-Steppe. Black soil (42,1 %) and gray forest soils (50,5 %) are wide spread in the region. As a rule, forests and loesslike loams are soil formation rocks [27].

Four seasons are clearly distinguished in the region. Average annual air temperatures range from + 7 °C in the north to + 9 °C in the south of Vinnytsia region. The average amplitudes of temperature changes during the year do not exceed 25 °C. The total of positive temperatures is 2500-3000 °C. The average duration of winter is 110 days. The coldest month of the year is January. A temperature drops to -32 ...- 38 °C on some days of the month under the influence of continental air masses. The maximum temperature reached 37 °C in July (the warmest month). The average monthly temperature is -6 ...- 4 °C in the winter months and +18 ... 20 °C in summer [43, 171].

The soil freezes to a depth of 55 cm in winter, the average monthly temperature on the surface fluctuates around 1,5...- 7,7 °C. The soil temperature rises to +21,5 ... 23,6 °C in the summer months [171] .

Weather conditions of the research areas are presented in a table 2.1.1. [255].

Table 2.1.1.

Air temperature and precipitation of the research area for 2015-2017

Year	Measerements	Month			
		May	June	July	August
Annual average precipitation, mm		48	88	85	79
Annual average daily air temperature, °C		14,2	17,2	19,4	18,4
2015	Average monthly precipitation, mm	34,54	35,81	14,23	4,07
	Monthly average daily air temperature, °C	15,2	19,2	21,2	21,3
	Monthly maximum daily air temperature, °C	20,7	25,2	27,5	28,2
	Monthly minimum daily air temperature, °C	9,5	13	14,8	14,1
2016	Average monthly precipitation, mm	54,11	53,6	43,7	31,75
	Monthly average daily air temperature, °C	15,1	20,1	21,3	20,3
	Monthly maximum daily air temperature, °C	19,7	24,5	26,9	26,4
	Monthly minimum daily air temperature, °C	9,2	14,4	15,2	13,2
2017	Average monthly precipitation, mm	27,43	16,79	50,29	35,82
	Monthly average daily air temperature, °C	14,6	19,5	20,3	21,7
	Monthly maximum daily air temperature, °C	19,6	24,6	25,8	27,3
	Monthly minimum daily air temperature, °C	8	13,1	14,2	15

The literature data indicates that tomato crop depends on many factors, primarily on the availability of moisture, heat, nutrients, especially in the critical period of development – from the mass formation of fruits to the first mass harvest [273].

An analysis of the May-August weather conditions indicates that 2015 and 2017 were the drier years of the study, since the average monthly daily air temperature in June was higher compared to the annual average daily temperature, while the amount of precipitation during this period was less and amounted in 2015 to 35,81 mm, and in 2017 to 16,76 mm compared to the annual average precipitation

– 88 mm (table 2.1.1.). The most optimal year for the growth and development of tomato plants was 2016, since the amount of precipitation in June was 53,6 mm compared to the annual average – 88 mm.

2.2. Hybrid characteristic

The Solerosso hybrid is the high-yield ultraprecocious deterministic hybrid of dutch selection tomatoes. Manufacturer – «Nunhems» (Bayer CropScience, Holland). The growing season is 90-95 days. Plant height up to 50 cm. Bush – determinant, moderately sprawling. The fruit is roundish, weight is 50-60 g, medium density, forms up to 6 seed chambers and is characterized by a good taste. The hybrid has a very high yield (about 100 t/ha), despite the small size of fruit. Tomatoes are characterized by amicable ripening (brushes of 5-6 pieces). It is used for whole-canning, processing for tomato products, as well as for the sale of early products on the market. The hybrid is tolerant to fusarium, verticidosis, cladosporiosis and is resistant to stressful growing conditions. It is recommended to be grown indoors and outdoors in regions with a temperate and warm climate [256].

2.3. Characteristics of drugs

Gibberellic acid (GA_3, $C_{19}H_{22}O_6$) is a terpenoid with a tetracyclic gibberellic skeleton with 19 or 20 C atoms, often with an additional lactone ring. Natural phytohormones exhibit the properties of growth regulators and inducers of the natural protective mechanisms of plant cells and are used in agronomic technologies for growing crops [15, 274].

Gibberellins are natural phytohormones, they are present in all plants and the diet of herbivorous macro- and microorganisms, their metabolism occurs naturally. According to the «Hygienic Classification of Pesticides by Hazard» (State Sanitary Rules and Regulations 8.8.1.002-98), GA_3 in terms of acute oral, transdermal toxicity belongs to 4th hazard class, acute inhalation toxicity – up to grade 2-3, does not irritate the skin, is a moderate irritant to mucous membranes membranes of the eyes with a lack of allergenic potential. It was established that gibberellins exert a general toxic effect on the body with a predominant effect on renal function in the subchronic and chronic effects regime. Gibberellins are unstable in soil and moderately stable in water, quickly decompose in air, safe for bees and beneficial entomofauna, soil microorganisms, birds. They are not toxic to aquatic organisms and do not accumulate in plants and environment [274]. According to the EFSA [35], for gibberellic acid, the ADI value (acceptable daily intake) is 0,68 mg/kg, based on the NOEL value for rats – 680 mg/kg, in subchronic toxicity and safety factor is 1000 [258]. However, according to ERA experts, there is no need to justify the allowable daily dose of gibberellins, since under the current regulations for the application of gibberellin-based compounds, the risk of exceeding residual gibberellins in foods above the level of 1 ppm is not expected.

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, triazole derivative compound. The manufacturer is Bayer Crop Science AG (Germany). Transparent crystalline substance with a molecular weight of 307,8 Da, melting point – 104,7 °C. The vapor pressure (20 °C) is $1{,}7 \cdot 10^{-3}$ hPa ($1 \cdot 10^{-3}$ mm). Solubility in organic solvents (20 °C, in g/l): in hexane – 0,1-1, propanol – 50-100, toluene – 50-100, in dichloromethane – 200-500. Solubility in water (20 °C) is 32 mg/l (0,032 %). It is resistant to hydrolysis [254].

LD_{50} for rats is 3933>5000 mg/kg; for birds – 1000-4488 mg/kg, for earthworms – 100-1000 mg/kg per dry weight. It does not irritate the skin and eyes of rabbits. The 3d hazard class. The drug is not toxic to bees in the recommended consumption rates [138].

It is used in all European countries as a standard for growing winter rape due to its pronounced growth-regulating action., The plants stop growing their ground mass under drug treatment on winter rape in the autumn period at the 3-5 leaves phase. Photosynthesis continues simultaneously with the inhibition of growth processes that promotes the accumulation of assimilates in the root part and leads to the growth of long and well-branched roots, improves winter hardiness of plants. The application of tebuconazole as a fungicide in spring ensures plant resistance to lodging and promotes better formation of lateral shoots [249].

Tebuconazole provides an even acropetal distribution of the fungicide in the middle of plant leaf over a long period of time. Tebuconazole penetrates into the plant in 1-2 hours, so it remains effective even of a possible rain after application. It is used both prophylactically and after the defeat of disease, since it remains effective for several weeks. It is recommended the application of compound in the form of small-droplet spraying with a flow rate of 300 l/ha. It can be used in compositions with many herbicides, growth regulators, liquid fertilizers, insecticides, as well as with other contact and systemic fungicides. It should be checked for miscibility before preparing the working solution [257].

It is used as a broad-spectrum systemic fungicide to combat diseases of leaves and ears of grain (fusarium, septoria, rust, powdery mildew and others), gray rot of grapes, some diseases of soy, rape, sunflower, vegetable, fruit stone fruits (drug tebuconazole) at normal costs 125-1000 g/ha by spraying and seed treated to combat with smut, cereal septoria with a consumption rate of 2-25 g/10 kg of seeds. It has a wide range of biological activity: prophylactic and therapeutic application, a well-defined stop effect, long-term protection of leaves, stems and spike from the main diseases, kindness with other drugs, absence of phytotoxicity [254].

Esphon (ethephon, etrel, 2-HEPA) – 65 % solution of dichloroethylphosphonic acid (HEPA, $C_2H_6ClO_3P$). Manufacturer – LLC Agrosintez (Russia). Esphon belongs to ethylene releasing compound according to the mechanism of action. The active substance quickly penetrates into the plant and decomposes in its tissues with the formation of ethylene. In turn, ethylene inhibits the action of growth phytohormones gibberellins and stimulates the synthesis of solid substances (lignin, pigments, sugars, etc.). The dynamics of biomass accumulation of plant in the direction of fruit is changed. The effect of ethylene producers is significantly dependent on air temperature. The temperature range should be from +12 to +30 °C. It is recommended the maximum dose treatment at a temperature below 16 °C. Resistance to rinsing is acquired 4-5 hours after treatment [264].

2-chloroethylphosphonic acid – has a molecular weight of 144,5 Da and a melting point of 74-75 °C. It is a solid white waxy substance. 2-HEPA is a hygroscopic, readily soluble in water, ethyl and isopropyl alcohols, acetone, propylene glycol. It hydrolyzes to ethylene, hydrochloric and phosphonic acid in water at pH above 4,1-4,5. It is slightly soluble in non-polar solvents – benzene, propylene glycol, insoluble in kerosene, does not work in the air, incompatible with alkali metal salts in solution. It easily forms mono- and diesters with aliphatic and aromatic alcohols.

It has low toxicity for warm-blooded – 3d toxicity class (low toxicity) LD_{50} for rats and at first administration is 4220 mg/kg [280, 16, 283].

Esphon is used as a plant growth regulator in many crops. It is also recommended to increase productivity, frost resistance, accelerate fruit ripening and increase sugar content of sugar beet root crops [252]. A single spraying should begin when the fruit ripens to 20 % in order to increase friendliness and accelerate fruit ripening, while the number of fruits that started to grow is at least 50 %, since green fruits can dry out. Esphon is compatible with many herbicides, insecticides, fungicides, micro and macro fertilizers, except of preparations based on dithiocarbonates, sulfur and copper [253].

2.4. Research methods

Tomato plants were grown in field and in greenhouse growing conditions. A field-based micro-trial setup was established at a specialized farm FG «Solskyi» in Vinnitsa region from 2015 to 2017. Seeds of the high-yield ultraprecocious deterministic hybrid of dutch selection tomatoes Solerosso were sown for seedlings in greenhouses 02/03/2015, 05/03/2016 and 12/03/2017. Seedlings were planted on 18/05/2015, 22/05/2016 and 27/05/2017 by a tape method with the planting formula 50+50+ 50 × 50. It was used a mineral fertilizers $N_{50}P_{40}K_{30}$. The experiment followed a randomized block design (33 m^2) with five replication. In the greenhouse growing conditions, plants were grown in 15 kg vessels with introduced of nutrient mixture «VNIS». Soil moisture was maintained at 60% of total moisture capacity. The repeatability of the experiment is fivefold. The treatment was applied via foliar spraying OP-2 with aqueous solution of 0,005 % solution of gibberellin (gibberellic acid, GA_3), 0,025 % tebuconazole and 0,05 % esphon (per active compound) once at the time of budding initiation to complete wetting of leaves – 06/06/2015, 16/06/2016 and 29/06/2017. 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 every 10 days. 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, than for 4 hours at 85 ° C and dried in air to an air-dry state.

Mesostructural organization of leaves and anatomical structure of stem were studied at the fruit formation phase on a fixed material [154]. It was used a mixture of equal parts of ethanol, glycerol and water with addition of 1 % formalin for its preservation. Measurement of cells sizes, individual tissues and organs was performed by using a microscope "Mikmed-1" and ocular micrometer MOB-1-15x. It was used a partial maceration of leaf tissue [100]. Determination of individual cells size was carried out after the maceration of leaf tissues with a 5% solution of acetic acid in 2 mol/l hydrochloric acid. It was analyzed the middle-layer leaves and stems of the shoots on the same stage of plant growth development for anatomical structure.The frequency of microscopic studies is twenty times.

The chlorophyll content (per leaf fresh matter weight) was determined by spectrophotometric method on the spectrophotometer SF-16 [45].

It was determined the coenotic indicator – leaf index (LI), as the green leaf area per unit ground surface area and chlorophyll index (CI) as the total chlorophyll content of the leaves [189].

It was determined the total of sugars, reducing sugars and starch in vegetative organs by the using iodometric method of Pochinok [173]. The phosphorus content was determined by the formation of phosphorus - molybdenum complex, the potassium content by the flame photometric method [196] and the total nitrogen content by the Kjeldahl method [173]. In mature fruits, it was determined the product quality – sugar content [173], ascorbic acid [224] and total acidity [33].

Pectin preparations were isolated by extraction from dry material, extracted with 0,03 N HCl for 1 hour at a temperature of 80 °C. The resulting extract was filtered, and the residue was washed with 0,03 N HCl. The resulting extract was precipitated with ethyl alcohol (three times of the total volume – 1:3). After decantation, the precipitate was centrifuged, dissolved in water, reseparated with alcohol (three times of the volume), centrifuged, washed with acetone until negative reaction with chlorine ions and dried [122]. In the obtained preparations, it was determined the content of total, free and esterified carboxyl groups [142]. The hemicellulose content was determined by the iodometric method, the quantitative content of pentosans was determined colorimetrically at a wavelength of 610-660 nm by a qualitative reaction with an orcine reagent [173].

Statistical analysis of experimental data was performed by computer program «STATISTICA-6» StatSoft Inc. The reliability of obtained results between control and experiment varient was assessed with the use of Student's t-test. Tables and figures show average values for the years of research and their standard errors.

CHAPTER 3

ANATOMO-MORPHOLOGICAL CHARACTERISTICS OF TOMATO GROWTH FUNCTIONS UNDER GIBBERELLIN AND VARIOUS TYPE OF RETARDANTS TREATMENT

3.1. Changes in growth characteristics of tomatoes under gibberellin and retardants application

The possibility of gibberellin and retardants application for targeted regulation of growth, development and metabolism has been shown in a number of crops [97, 229], however, the question of anatomical structure features of organs, ratio of shoot growth rates and leaf surface area with artificial stimulation and inhibition of growth, as one of the central components of the donor-acceptor system, remain largely unexplored.

Regulation of agricultural plants growth and development realized by application of retardants – different quaternary ammonium compounds in crop production [130, 146, 200]. However, the analysis of literature data presents only a few amount of retardant effects of new generation – the triazole derivative compounds and ethylene releasing compounds on morphogenesis and physiological and biochemical processes of vegetable cultures [118, 131].

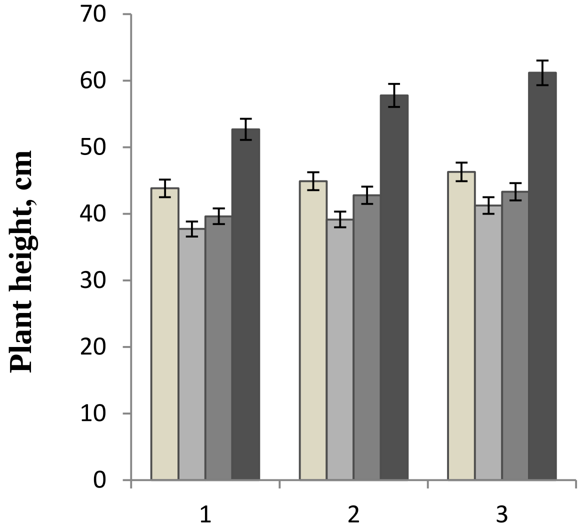
The necessity to study the mechanism of action of these groups of drugs is due to the fact that representatives of triazole derivatives compounds (unicazole, tebuconazole and others) are widely used for practical purposes [113, 133, 271], while the action of ethylene releasing compounds based on 2-chloroethylphosphonic acid is realized through a native product metabolism – ethylene, not carry toxicological and environmental hazards to the environment [90]. Since the representatives of these groups of retardants are antigibberellins, it is advisable to compare the effect of these drugs with the action of gibberellin when analyzing growth function.

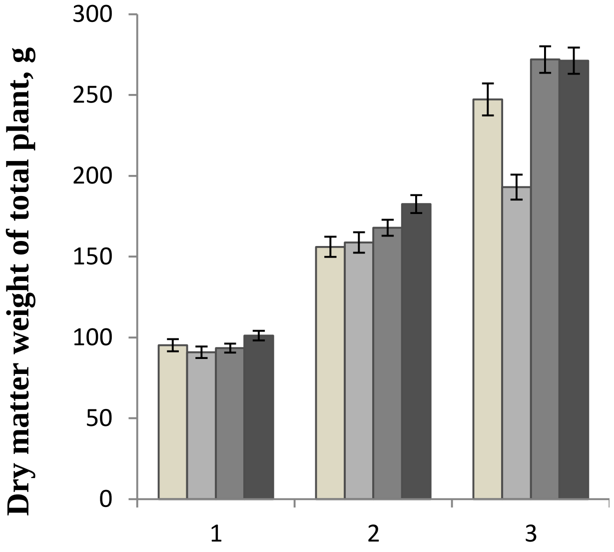
Our research results indicate that gibberellin and retardants used in the work show a clear growth-regulating effect on plant growth intensity. The height of treated plants significantly increased under the influence of gibberellic acid (GA_3), and decreased compared to control under the actions of both retardants (Fig. 3.1.1.).

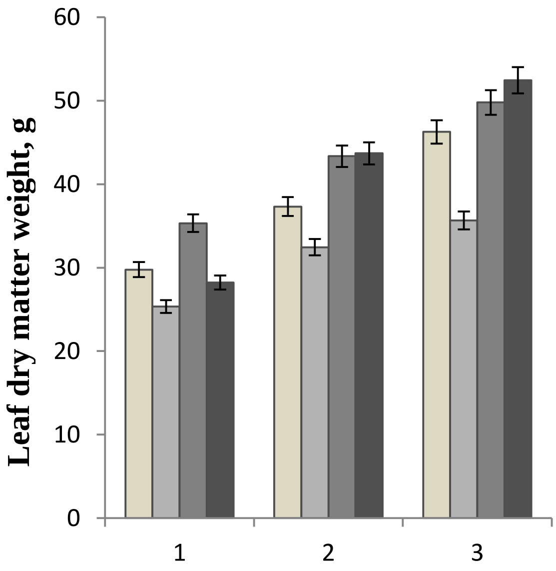
It has been established that changes in the intensity of growth processes due to growth regulators application are accompanied by the redistribution ratio of dry matter weight between plant organs. Analysis of the average data for the years of research indicates that the dry weight of root and stem of plants in all experimental variants decreased during whole growing season, however, the dry matter weight of root increased under ethylene producer treatment at the brown ripeness fruitification stage. At the stage of fruit formation and green ripeness of the fruits, it wasn't observed the significant differences of dry matter weight. At the same time, during the brown ripeness fruitification stage, a dry matter weight of the plant increased under tebuconazole and gibberellin application and under esphon treatment this indicatop was significantly less than the weight of the plant of control variant.

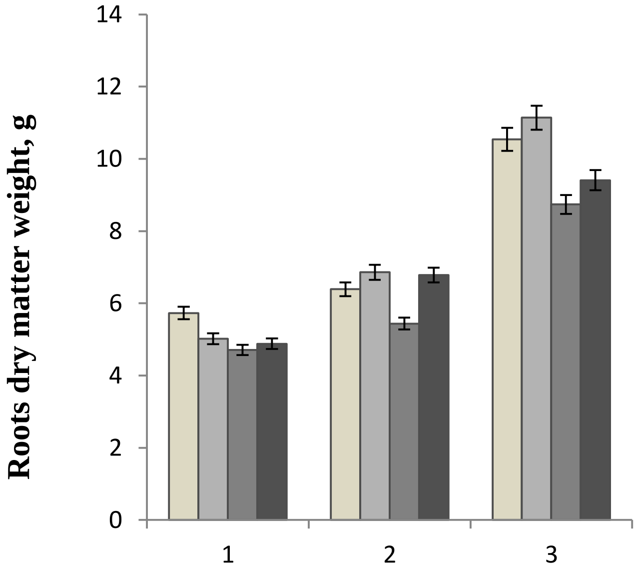
Accordingly to the results of our research, weather conditions influenced on the accumulation of dry matter by the vegetative organs of tomatoes. An analysis of this indicator in the wettest 2016 year of study shows that at the beginning of plant vegetation (stage of fruit formation), the total dry matter weight of root, stem and leaves decreased due to retardants treatments, while the effects of gibberellin were close to control. At the end of vegetation (stage of brown ripeness) of 2016 years, in all experimental variants, this indicator increased: control – 199,29 ± 6,38 g, esphon – 213,32 ± 4,81 g, tebuconazole – 208,24 ± 4,92 g, gibberellin – 201,66 ± 4,51 g. In dry 2017, at the end of vegetation, the total dry matter weight of plant's vegetative organs increased under the actions of tebuconazole and gibberellin, esphon application decreased it compared to control. So, at the end of vegetation, this indicator of tebuconazole treated plants was 31,48 ± 1,03 g, gibberellin treated – 37,65 ± 1,28 g, esphon treated – 21,43 ± 0,67 g against to control – 25,97 ± 0,81 g.

It was found that at the fruitification stage (brown ripeness) a decrease of plant weight under 0,05 % esphon treatment is partly due to phytotoxic effects: leaves were twisted, ovaries fell off, leaf edge turned yellow. Signs of a phytotoxic effect by drug application were manifested on growth processes and plant development in the 3 following weeks after treatment.









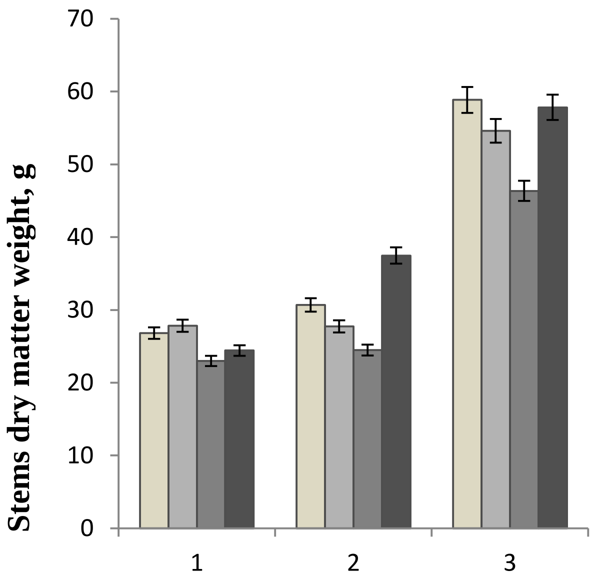


Fig. 3.1.1. Influence of gibberellin and retardants on growth processes and accumulation of dry matter weight by vegetative organs of tomatoes hybrid Solerosso:

1 - fruit formation stage;

2 - fruitification stage (green ripeness);

3 - fruitification stage (brown ripeness).

– control; – 0,05 % esphon; – 0,025 % tebuconazole; – 0,005 % gibberrelin

In separate studies, it was noted that application of ethylene producer compounds in the juvenile period of development is impractical [264], precisely because of desiccant action, which is often used in technology of growing agricultural plants [60]. However, in some cases, the application of ethylene releasing compounds leads to a typical growth inhibitory effect without signs of phytotoxicity, which is accompanied by an increase in crop yields, in particular raspberries [107], which indicates the necessity for a detailed exploration of this issue.

Leaf apparatus that performs the processes of photosynthesis plays the main role in the formation of crop production [137]. An important indicator of the production process is a number of leaves on the plant, their total area, weight, structural features and life expectancy. It is known that leaf growth realized due to activity of their marginal meristem. The obtained results indicate a significant effect of drugs on the formation of leaf apparatus of tomato plants (Fig. 3.1.2.).

The analysis of the data indicates that at the fruit formation and fruitification stage (green ripeness) the largest number of leaves was formed due to increase stem branching under esphon and tebuconazole application. The number of leaves in the variant of gibberellin treated plants significantly increased from green to brown ripeness of fruitification stage that can be explained by the general positive effect of phytohormone on plant growth.

The retardation in growth processes is accompanied by changes in the formation of surface assimilation. The area of surface assimilation is one of the cardinal components in the provision formation of the plant organism by plastic material for growth and respiratory processes. The size of surface assimilation during the growing season largely determines the nature of production process and crop productivity [74]. The obtained results indicate that an increase in the number of leaves was accompanied by a significant increase in the area of leaf surface. Maximum leaf surface area was observed under tebuconazole and gibberellin treatment at the fruit formation and green ripeness fruitification stage. At the brown ripeness fruitification stage, an increase in leaf area of esphon treated plants was observed due to the removal of phytotoxicity symptoms.

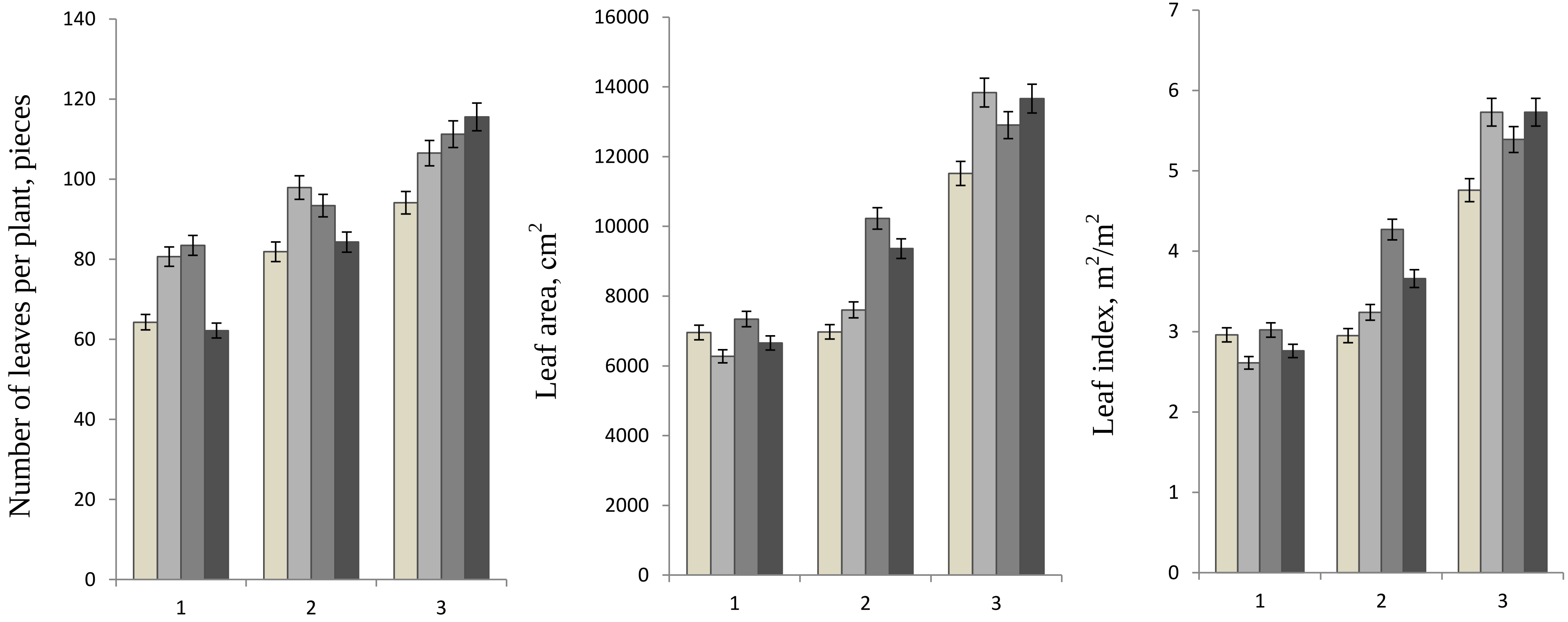


Figure 3.1.2. Formation of leaf apparatus of tomatoes hybrid Solerosso under retardants and gibberellin treatment:

1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness)

– control; – 0,05 % esphon; – 0,025 % tebuconazole; – 0,005 % gibberellin

The specificity of this drug action was the fact that it influenced on the duration of individual vegetation phases of plant development. In particular, the flowering of esphon treated tomato bushes increased at a time when other variants of growth regulators caused an intensive growth and fruit formation of experimental trials.

Leaf index is an important cenotic index for the total crop yield, which is defined as the green leaf area per unit ground surface area [188].

The analysis has shown that gibberellin and retardants application increased the leaf index compared to control at the fruitification period (Fig. 3.1.2.).

Accordingly, it was noted that the leaf surface of an individual plant and agrocenosis increased by the actions of growth regulators. This contributes to the formation of a powerful assimilation apparatus and more active accumulation of dry matter weight, which is an important prerequisite for increasing the crop yield.

It is known that growth regulators are able to changes the assimilative potential of organs that influence on the redistribution of plastic substances between plant organs. It was found that the ratio of accumulation and distribution of plant organs weight were changed by the actions of drugs. This is an evidence of a general restructuring of the plant's donor-acceptor system under gibberellin and retardants application (Fig. 3.1.3.).

The results of the study indicate that application of retardant tebuconazole led to forme a more powerful donor sphere of the plant where the relative proportion of leaves in the total weight of a plant was increased during whole period of carpogenesis (fruits growth and formation). Moreover, the proportion of vegetative organs (roots and stems) was less than in other experimental trials.

Thus, gibberellin and tebuconazole treatment enhanced the donor sphere of tomato plants due to an increase in the number of leaves and leaf index. The most effective was application of tebuconazole that characterized by a maximal proportion of leaves weight from the total plant weight and created the prerequisite for improving the crop yield.

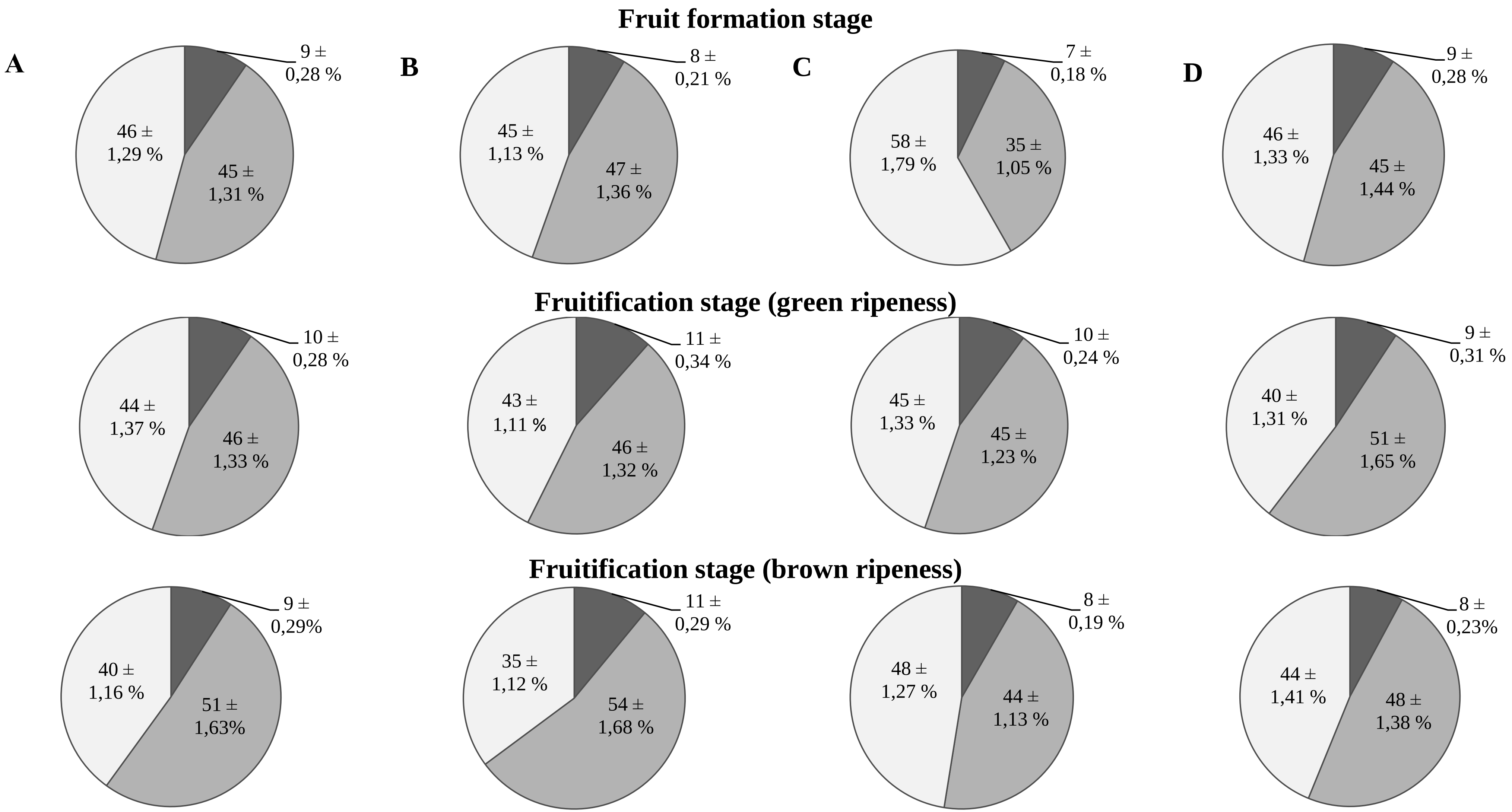


Fig. 3.1.3. Relative proportion of dry matter weight of vegetative organs under retardants and gibberellin application on tomatoes hymbrid Solerosso: A – control; B – 0,05 % esphon; C – 0,025 % tebuconazole; D – 0,005 % gibberellin – roots, – stems; – leaves.

3.2. Influence of gibberellin and retardants on anatomical structure of stem and mesostructural organization of tomato leaf

The regulation of donor - acceptor relations is an important component of optimization of agricultural crop production process, in particular by artificially redistributing of assimilates flows to economically important organs (fruits, storage root). This effect achieved through morphophysiological changes – the formation of a powerful leaf surface, effective mesostructure, acceleration of the rate of photosynthetic apparatus formation and prolongation of leaf life as the main donor of assimilates [115, 236].

The main property of gibberellin and retardants is the ability to stimulate or inhibit stem growth in length, mainly due to the effect on subapical meristem, which is responsible for stem formation and growth. It is believed that the apical meristem continues to function normally, due to which the leaf is not significantly affected and reaches its normal size [192]. In this regard, it is advisable to establish the influence of these compounds on the formation of anatomical organization of tomato crop.

Antigibberellin compounds are widely used on cereal plants in order to increase the resistance of crops to lodging due to increase mechanical strength of stem. It was found that the thickening of cell walls under the influence of chlorocholine chloride is associated with an increase in the sclerenchyma layer size, while some researchers noted a cell walls thickening of sclerenchymal fibers [3], while others noted a decrease in the final sizes of parenchymal, sclerenchymal and epidermal cells under CCC and ethephone treatments [96], or an increase in the sclerenchyma cells number of layers without changing the size of individual cells [167].

The comparative analysis of gibberellin, esphon and tebuconazole interaction on stem anatomical structure of tomatoes indicates that treatment with drugs led to changes in the histogenesis of this plant organ (Table 3.2.1.). In particular, the more intensive growth of gibberellin treated plant was accompanied by the formation of a thinner stem due to a decrease in the thickness of bark, wood, core and epidermis. The obtained results indicate that gibberellin application caused formation of more developed tissues of primary origin: hypodermis and collenchyma. In this variant it was noted the formation of a larger number of vessels (xylem) in a layer of wood however, those elements were smaller compared to control. Similar tendencies were noted for the shoot core: the linear dimensions of central parenchymal cells and the cells of perimedular zone were smaller compared to control.

Triazole derivative compound and ethylene producer affected oppositely to the formation of stem. It was noted that tebuconazole influenced on the thickening of stem due to an increase in the thickness of bark and core. Similar results of triazole derivatives interaction were noted by other researchers [206, 243]. In most cases, it was noted that application of both compounds affected to the formation of a thinner layer of wood, although the number of xylem vessels in a layer of wood was significantly larger compared to control and gibberellin treated trial. This discrepancy between the thickness of a wood layer and the number of xylem vessels in a number of woods is due to the fact that the compounds significantly reduced a thickness of vessels. Similar changes in shoot anatomy were noted on the triazole derivative compound paclobutrazole and ethylene releasing dextrel treated winter rape plants, which contributed to the enhancement of mechanical strength of the stem and created technological advantages of harvesting [104]. So, application of gibberellin and retardants most significantly affected to the functioning of lateral meristem during stem formation, that consequently caused the greatest changes in the formation of xylem (table 3.2.1.). It is known that physiological state of leaf is in close interaction with its structural features, defined in the scientific literature as a “mesostructure” [154]. In most cases, the study of synthetic growth inhibitors with antigibberellin mechanism of action on the leaf photosynthetic function is rarely carried out by its mesostructural characteristics [66]. It has been established that retardants inhibit the growth of subapical meristem, which is responsible for the formation and growth of stem [26, 115]. However, in developing of general scheme of retardants interaction, it is not adequetly explored the question of features of retardants influence on the marginal meristem, the functioning of which determines the size and shape of leave, accordingly, the total area of surface assimilation.

Table 3.2.1.

Anatomical structure of stem under retardants and gibberellin treatment on tomatoes hymbrid Solerosso (average values for 2015 - 2017 years of research)

Indicators	Control	0,05 % esphon	0,025 % tebuconazole	0,005 % gibberellin
Stem thickness of, µm	9619,34 ± 239,02	9285,56 ± 244,73	10064,73 ± 209,37	9239,18 ± 204,29
Bark thickness, µm	448,79 ± 8,62	*509,86 ± 6,98	467,03 ± 5,67	*393,67 ± 2,68
Wood thickness, µm	864,28 ± 7,86	*766,87 ± 8,18	*821,11 ± 8,09	*792,82 ± 5,13
Core thickness, µm	6932,68 ± 203,61	6663,87 ± 211,88	*7427,74 ± 179,44	6816,88 ± 185,98
Epidermis thickness, µm	30,26 ± 0,97	*34,12 ± 1,07	30,35 ± 0,97	*24,67 ± 1,08
Hypodermis thickness, µm	35,99 ± 1,17	*40,72 ± 1,31	*39,94 ± 1,04	35,21 ± 1,41
Collenchyma thickness, µm	212,71 ± 8,19	*272,41 ± 9,14	*251,49 ± 12,69	*242,94 ± 4,96
Collenchyma cell wall thickness, µm	0,57 ± 0,01	*0,71 ± 0,03	0,55 ± 0,01	*0,76 ± 0,02
Diameter of a collenchyma cell, µm	9,73 ± 0,14	*11,78 ± 0,28	9,31 ± 0,31	*8,89 ± 0,27
Number of xylem vessels in a wood layer, pcs.	13,21 ± 0,34	*16,05 ± 0,34	*17,71 ± 0,36	*14,61 ± 0,49
Diameter of a xylem vessel, µm	81,47 ± 3,17	*54,82 ± 1,67	*66,61 ± 2,83	77,37 ± 2,56
Linear dimensions of central parenchymal cells, µm	207,33 ± 4,63	*243,81 ± 7,81	214,91 ± 6,63	*184,24 ± 3,68
Linear dimensions of perimedular zone cells, µm	76,58 ± 2,07	*83,58 ± 2,65	*71,57 ± 2,08	*68,41 ± 2,09

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

In some cases, thickening of lamina of plants under the influence of retardant was observed due to the growth of epidermal and mesophyllic cells [110, 198], in other works it was noted that compouds either not affected to the total number of cells per unit leaf area, or caused an increase in the number of cells in mesophyll of the treated plants [21]. Since in some cases a decrease in the area and weight of laminas under the influence of retardants is not accompanied by a decrease in the size of mesophyll cells, it can be assumed that this is due to a decrease in the frequency of anticlinal devision and a general inhibition of marginals activity [107].

Analysis of leaf mesostructure organization testified that changes in the thickness of leaf blade of drugs treated plants are due to the growth of photosynthetic tissue – chlorenchyma (table 3.2.2.). Thus, 0,025 % tebuconazole and 0,005 % gibberellin treatment leads to an increase in the linear dimensions of spongy and cell volume of the columnar parenchyma – the main assimilation tissue of the leaf. A similar thickening of leaves due to the growth of chlorenchyma was observed in other triazole derivatives treated crops [51, 180, 228]. However, those indicators of 0,05 % esphon application were less control and can be concluded about changes in the nature of marginal meristem activity of the leaf under under antigibberellin compounds action.

Significant changes have occurred in epidermal tissue of the leaf. The analysis of the research results suggest that tebuconazole application resulted in an increase in the thickness of leaf's upper and lower epidermis compared to control. The opposite effect was observed for esphon and gibberellin treated trials – the thickness of epidermal cells decreased.

It is well known that inhibitors and growth stimulators affect on the number of stomata per unit of abaxial leaf surface [26, 242]. The area and number of stomata increased of oil poppy seed plants cv. Berkut [175] and potatoes cv. Nevskaya [243] under chlormequat chloride and triazole derivatives tebuconazole and paclobutrazole applications while the area of epidermal cells of potato not changed.

Table 3.2.2.

Influence of retardants and gibberellin on leaf mesostructural organization of tomatoes hybrid Solerosso (mean values for 2015 - 2017 years of research)

Indicators	Control	0,05 % esphon	0,025 % tebuconazole	0,005 % gibberellin
Thickness of leave, μm	247,69 ± 7,43	*198,46 ± 6,94	*272,35 ± 7,28	*264,46 ± 6,25
Thickness of chlorenchyma, μm	211,27 ± 6,74	*168,06 ± 5,21	*227,77± 7,18	*228,92 ± 6,35
Volume of palisade parenchyma, $μm^3$	46299,25 ± 1435,28	*42279,95 ± 1310,68	*58613,09 ± 1817,01	*55750,79 ± 1512,05
Length of spongy cells, μm	20,77 ± 0,44	*22,31 ± 0,69	*23,17 ± 0,75	*22,07 ± 0,46
Width of spongy cells, μm	15,49 ± 0,48	14,07 ± 0,43	14,71 ± 0,45	15,15 ± 0,43
Thickness of upper epidermis, μm	20,39 ± 0,59	*16,49 ± 0,47	*24,61 ± 0,75	18,33 ± 0,56
Thickness of lower epidermis, μm	16,02 ± 0,46	*13,92 ± 0,45	*19,98 ± 0,67	*17,22 ± 0,45
Number of stomatas on 1 mm^2 of the abaxial leaf surface, pieces	27,23 ± 0,68	*30,88 ± 0,98	*37,05 ± 1,19	*41,11 ± 1,21
Area of a stomata, mcm^2	397,01 ± 10,91	391,87 ± 9,75	*365,23 ± 9,68	*307,33 ± 1-,25
Stomatal index	0,35 ± 0,01	0,36 ± 0,01	*0,39 ± 0,01	*0,41 ± 0,01

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

The results of the research suggest that the number of stomatas per unit leaf area of experimental plants increased with reducing of area of one stomata. The calculation of stomatal index, which characterizes the ratio of number of stomata form to the total number of epidermal cells on the same leaf area, indicates that tebuconazole and gibberrelin increased this measurement, while influence if esphon was close to control. It can be concluded that such anatomical component of the photosynthetic apparatus functioning can positively influenced on the intensity of transpirational processes.

The obtained results suggest that gibberellin (stimulator of growth processes) treatment improved the donor potential of leaf growth due to the increase in linear growth, accompanied by the formation of new leaves. Application of tebuconazole and esphone, inhibitors of gibberellin biosynthesis, led to an increase in the number of leaves and leaf surface area due to inhibition of linear growth and enhancement of stem branching.

The analysis of morphogenesis of tomato plants under gibberellin and antigibberellin compounds treatment indicate significant changes in histogenesis and leaf apparatus formation of the plant. In particular, gibberellin and retardants interaction significantly increased in the number of leaves, their weight and total leaf surface due to general stimulation of growth under the influence of phytohormone and increased stem branching due to the action of triazolederivative and ethylene realizing compounds. Leaf mesostructure of tomato plants was optimized under gibberellin and tebuconazole interaction, while the tebuconazole treatment was more effective. The application of esphon led to a deterioration in the anatomical characteristics of leave compared to control.

Consequently, the application of 0,025 % tebuconazole and 0,005 % gibberellic acid led to the formation of a more powerful donor sphere of the plant compared to control, which is an important prerequisite for increasing the crop yields. The most effective for crop production was the application of triazolederivative compound tebuconazole.

CHAPTER 4

STRUCTURAL AND FUNCTIONAL ORGANIZATION OF PHOTOSYNTHETIC APPARATUS AND TROPHIC SUPPORT OF MORPHOGENESIS UNDER GIBBERELLIN AND VARIOUS TYPES OF RETARDANTS TREATMENT ON TOMATO PLANTS

4.1. Formation of photosynthetic apparatus, accumulation and redistribution of assimilates between the organs of tomato plants under growth regulators action

Regulation of donor-acceptor system of a plant by phytohormones or modifiers of their action opens up prospects for artificial redistribution of assimilates (products of photosynthesis) to economically valuable organs, which plays an important role in increasing the productivity of agricultural crops [18, 67]. It is known that the regulation of donor-acceptor relations in plant is determined by a system of direct and inverse connections [126, 279], where the processes of photosynthesis serve as the main donor, and the processes of growth – deposition of substances in the reserve, and zones of active metabolism are the acceptors of assimilates [39, 61, 182, 230].

Leaf surface formation is one of the central factors that determining plant productivity. The results of the influence of growth regulators with different mechanisms of action on the morphogenesis of tomato plants indicate that an increase in the number of leaves, their weight and leaf surface area is accompanied by changes in important indicators that characterize the potential productivity of a unit leaf surface:, chlorophyll content and net photosynthetic productivity.

It is known that the positive correlation between the rate of photosynthesis and the leaf area density value (LADV), which characterizes the ratio of the leaf dry matter weight to the leaf area, is due to an increase in the concentration of the main structural elements (chlorenchima cells, chloroplasts) and photosynthetic pigments, with the direct participation of which CO_2 assimilation is carried out [55].

The obtained results of the research show that the index of leaf area density value gradualy increase in all variants of the experimental trials during the period of fruit formation (table 4.1.1.). The leaves of tebuconazole treated tomatoes were characterized by the highest value of this indicator. This correlates well with the results of mesostructural characteristics of triazole derivative retardant treated plants where the leaf thickness increased at the end of vegetation. It was noted that the maximum value of this indicator under gibberellin application was at the brown ripeness stage at the end of fruit vegetation, while under the influence of esfon, the LADV index was the lowest during the whole vegetation period, which also correlates with the thickness of leaf blade of the experimental trials (table 3.2.2.).

Analysis of literature data shows that the effect of retardants is determined by the dose of the active compound of drug, the specifics of its action and weather conditions [107]. It was observed an increase in the chlorophyll content in leaves of paclobutrazole and dextrel treated potato plants by researcher [243], in leaves of folicur treated oilseed poppy [175]. In other works it was noted a decrease in chlorophyll content in the leaves of dihydrel and chlorocholine chloride treated tomatoes due to the negative influence of retardants on thylakoid of chloroplasts and reduced accumulation of chlorophyll «*a*» in leaves [266]. It based on the reduction of chlorophyll content in leaves may be partial destruction of chloroplasts of camposan M and dextrel treated raspberry [107] or increase of chlorophyllase activity at the initial part after plant treatment period [25, 266].

The literature data suggested that the chlorophyll content in tomato leaves decreased under the influence of ethylene producer due to the conversion of chlorophyll *a* into pheophytin during acidification of the medium with decomposition products of derivatives of 2-chlorethylphosphonic acid compounds [107]. Our data indicates that drugs treatment, including ethylene producer esphon application does not lead to significant changes in the chlorophyll content, this indicator was close to control at the stage of fruit formation (table 4.1.1.). However, it should be noted that the chlorophyll content in leaves of retardants and gibberellin treated trials remained higher compared to control at the end of the growing season.

A similar effect of retardants application on the chlorophyll content was obtained on raspberry plants during the activity of chlorophyllase studying [107].

Table 4.1.1.

Anatomo- and physiological parameters of leaf apparatus of gibberellin and retardants treated tomatoes hybrid Solerosso

Vegetation period	Indicators	control	0,05 % esphon	0,025 % tebuconazole	0,05 % gibberellin
Fruit formation stage	Leaf area density value, mg/cm^2	1,79±0,06	1,78±0,03	*2,12±0,05	1,71±0,03
	Total chlorophyll content (*a*+*b*), % per leaf fresh matter weight	0,72±0,022	0,72±0,021	0,74±0,021	0,71±0,020
	Chlorophyll index, g/m^2	1,92±0,05	1,79±0,05	*2,79±0,09	1,82±0,05
	Net photosynthetic productivity, $g/(m^2 \cdot day)$	6,41±0,16	*4,70±0,12	*10,83±0,43	*6,37±0,18
Fruitification stage (green ripeness)	Leaf area density value, mg/cm^2	2,88±0,09	*2,22±0,07	*2,93±0,07	2,74±0,08
	Total chlorophyll content (*a*+*b*), % per leaf fresh matter weight	0,71±0,011	0,73±0,012	*0,76±0,021	*0,77±0,021
	Chlorophyll index, g/m^2	2,01±0,06	*1,79±0,04	*2,23±0,07	2,06±0,06
	Net photosynthetic productivity, $g/(m^2 \cdot day)$	7,32±0,17	7,23±0,19	8,29±0,31	*9,52±0,27
Fruitification stage (brown ripeness)	Leaf area density value, mg/cm^2	3,57±0,08	*2,92±0,08	*4,54±0,13	*4,34±0,12
	Total chlorophyll content (*a*+*b*), % per leaf fresh matter weight	0,54±0,011	*0,79±0,022	*0,71±0,021	*0,71±0,021
	Chlorophyll index, g/m^2	1,54±0,04	1,49±0,04	*2,13±0,06	1,62±0,06
	Net photosynthetic productivity, $g/(m^2 \cdot day)$	6,54±0,19	*4,41±0,11	*9,36±0,21	6,44±0,11

Note. * – difference is significant at $p<0,05$.

One of the important cenological indicators related to the improvement of photosynthetic productivity of the plants is chlorophyll index. Changes in the chlorophyll accumulation and significant morphological changes in the leaf apparatus under drugs application lead to a significant changes in the chlorophyll index of plants according to the experimental trials (table 4.1.1.). Our data indicates that this indicator was higher under the actions of tebuconazole and gibberellin, and for the esphon application was lower compared to control during the fruiting period.

It is known that the indicator of the net photosynthetic productivity is characterized by photosynthetic productivity of unit leaf surface. Analysis of the obtained data shows that this indicator was highest in the tebuconazole and gibberellin variants and for the actions of esphon it was lower compared to control (table 4.1.1.). In our opinion, a significant increase in the rate of net photosynthetic productivity with an increase in the leaf surface area due to the tebuconazole and gibberellin application created the prerequisites to enhance gross photosynthetic crop production and accumulation of a greater number of photoassimilates in the plant.

It is known that the part of assimilates can be temporarily deposited in the organs of reserve with subsequent reutilization for the processes of carpogenesis. At the same time, the assimilative capability of vegetative organs of the plant due to the actions of phytohormones and synthetic growth regulators are not well analysed. In our opinion, it is expedient to determine the dynamics and ratio of non-structural carbohydrates in the plant organs at different stages of fruit formation to analyse the depositing capacity of the vegetative organs according to the experimental trials. The obtained results indicate that in the vegetative organs of tomato plants – roots, stems and leaves at the fruit formation stage are accumulated more nonstructural carbohydrates (sugars + starch) than in the control due to formation of a more powerful donor sphere of leaf apparatus under plants grows regulators treatment (fig. 4.1.1). Obviously, this is a consequence of the enhanced photosynthetic work of leaf apparatus of treated plants. The highest content of carbohydrates in all stages of the fruitification phase was noted in stems of tomato plants, that indicates the powerful depositing capabilities of this vegetative organ.

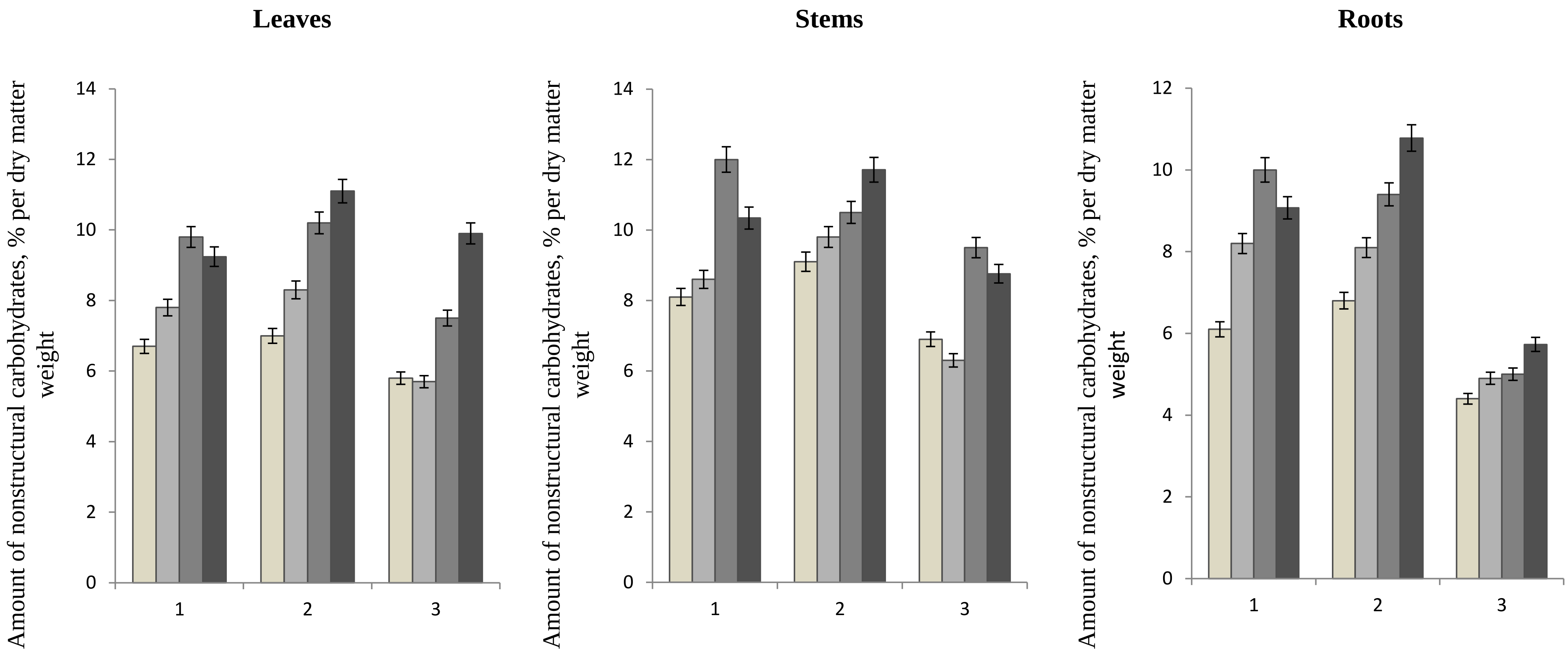


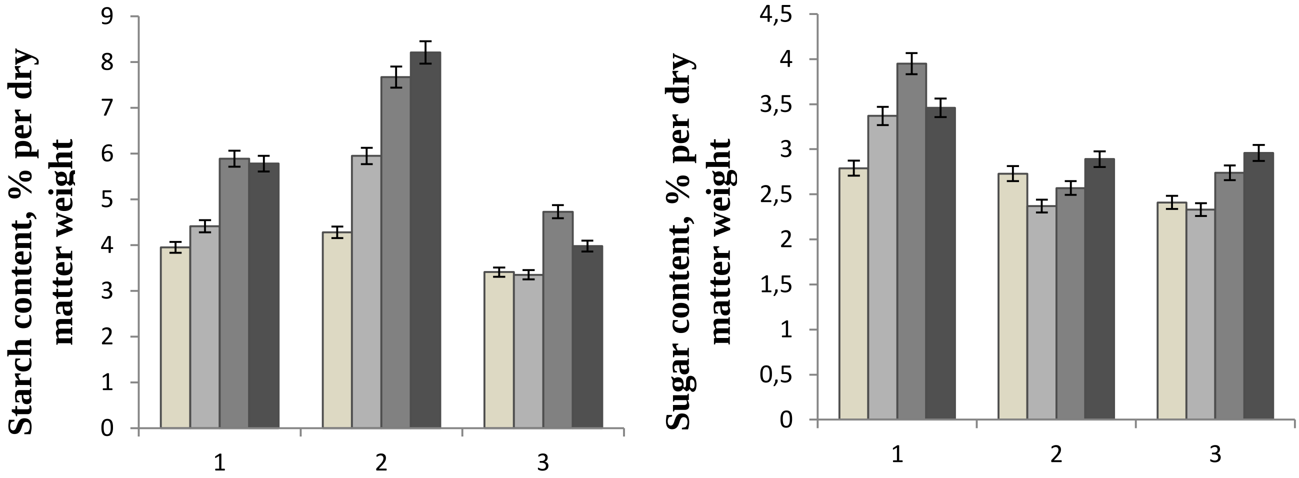
Fig. 4.1.1. Amount of nonstructural carbohydrates (sugar+starch) in vegetatives organs of tomatoes hybrid Solerosso under application of growth regulators (% per dry matter weight): 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness). – control; – 0,05 % esphon; – 0,025 % tebuconazole; – 0,005 % gibberellin

At the same time, tebuconazole and gibberellin application increased the amount of sugars and starch in the roots, stem and leaves of plants during the whole fruitification stage. It can be concluded that this indicates some of their redundancy, which is not fully spent on the fruits formation and growth, but is temporarily accumulated to reserve that is deposited in vegetative organs and then used at the stage of transition from green to brown ripeness.

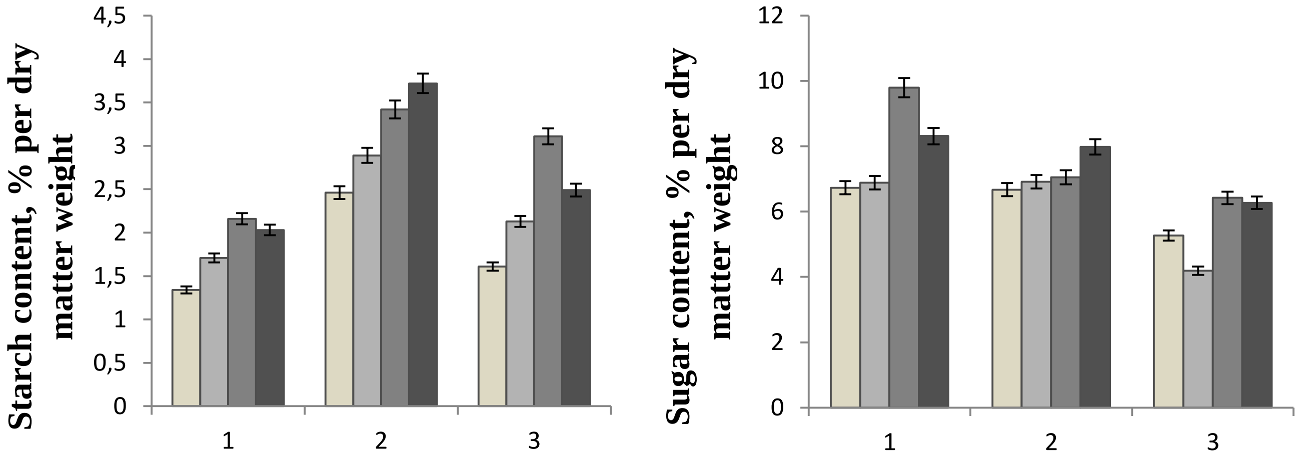
It is known that the attracting factor affects on the concentration of metabolites that are located in the chloroplast or around the plastid space and which exert an effect on enzymes of photosynthesis («feed back – mechanism»), regulating the ratio of the rates of synthesis and transport of substances from the phototrophic cell. Sucrose-phosphate synthetase is a key enzyme that opens the way for transport and distribution of assimilates in a plant [78]. Moreover, the enzyme activity is inhibited by an excess of sucrose by 20-40 %, therefore, with an increase in the concentration of sucrose in the biosynthesis zone, its new formation slow down until an excess of sucrose is used in the cell itself. This simple but radical regulatory mechanism provides a balance between the primary synthesis of transport sucrose and the need for plants. Thus, the accumulation of photosynthetic products in chloroplasts and cells due to a decrease in their outflow to the attracting centers largely regulates the activity of the photosynthetic apparatus.

The accumulation of starch in plastids to a certain extent does not significantly affect on photosynthesis, however, an increase in its concentration with changes in the levels of donor-acceptor relations of plant suppresses CO_2 fixation and blocks the activity of photosynthetic enzymes [153]. Analysis of the total amount of sugars and starch in vegetative organs of tomato plants indicates that during the fruiting period, the intensity of carbohydrates and starch applying was different (fig. 4.1.2.). A decrease in the total carbohydrates content in the vegetative organs of research plants starting from the stage of green ripeness of fruits can be explained by a more intense polymerization of excess sugars and formation of a stored carbohydrate – starch, the content of which in this stage still increased. At the end of fruit growth (brown ripeness), the sugars and starch content in vegetative organs is significantly reduced.

Leaves



Stems



Roots

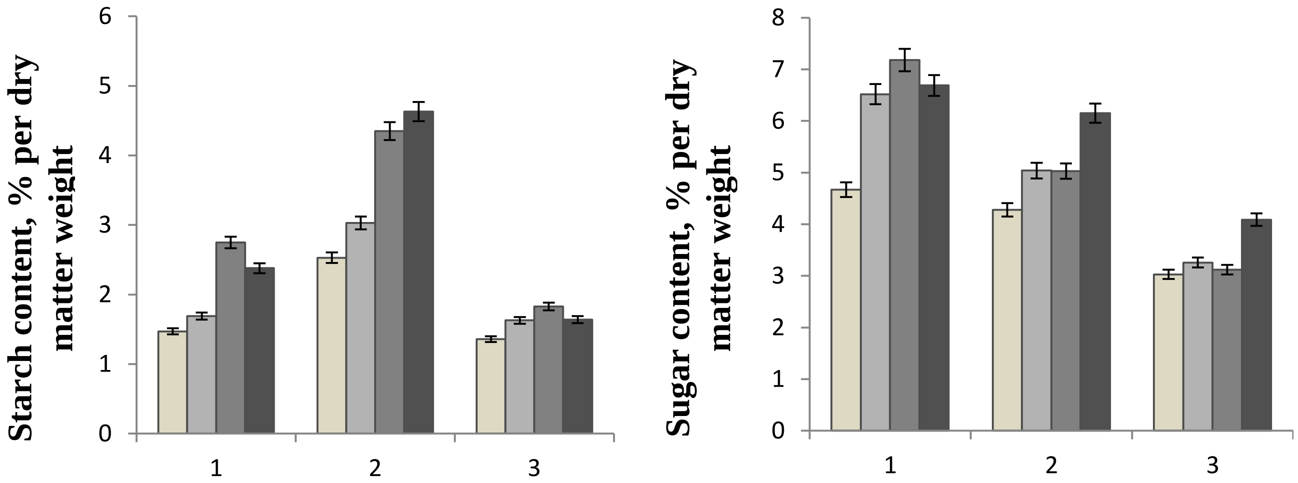


Fig. 4.1.2. Sugar and starch content in vegetatives organs of tomatoes hybrid Solerosso under application of growth regulators (% per dry matter weight) at the fruitification stage: 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness). ▭ – control; ▭ – 0,05 % esphon; ▭ – 0,025 % tebuconazole; ▭ – 0,005 % gibberellin

In our opinion, this is the result of a decrease in the attractive capability of acceptor zones due to the complete cessation of fruit growth processes and their transition to final ripening, which leads to a slowdown in the photosynthetic fixation of carbon dioxide in the donor sphere, a decrease in the share of transport forms (sucrose) and the outflow of assimilates from leaves to carpogenesis needs.

Analysis of the content of various forms of carbohydrates in the organs of tomatoes indicates that during the entire fruiting period (from the stage of fruit formation to the brown ripeness stage), the content of reducing sugars decreased in the roots and stems of research tomato plants (table 4.1.2.). However, unlike other vegetative organs, the following clear pattern was observed for the leaves. It was found an increase in the content of reducing sugars and a more significant decrease in the sucrose content in the leaves of the experimental plants compared to control from green ripeness stage, when the fruit was already fully formed and growth processes were stopped to the brown ripeness stage. Since sucrose is the main transport form of carbohydrates in the plant, the transport of sugars from leaves to fruits stops earlier than from roots and stem, resulting in an increase in the reducing sugars content.

Thus, application of gibberellin and retardants leads to a more intensive accumulation of nonstructural carbohydrates (sugars and starch) in the vegetative organs of research tomato plants with subsequent active reutilization of these substances on the fruits formation and growth needs. The deposited carbohydrates in the roots, stems and leaves are used with different intensities, the transport of sugars from leaves to fruits stops earlier than from roots and stem of tomato plants.

4.2. Redistribution of nitrogen, phosphorus and potassium between the vegetative organs of tomato plants under gibberellin and retardants application

The main regularities of photosynthetic processes and redistribution of assimilate flows throughout a plant with varying growth rates of individual organs have been studied sufficiently within the framework concept of donor-acceptor system functioning [18, 39, 115].

Table 4.1.2.

Effect of gibberellin and retardants on the carbohydrates content in the vegetative organs of tomatoes, % per dry matter weight (average values for 2015-2017)

Indicators		control	0,05 % esphon	0,025 % tebuconazole	0,05 % gibberellin
Fruit formation stage					
Root	reducing sugars, %	3,12±0,04	*5,05±0,12	*5,32±0,09	*4,48±0,08
	sucrose, %	1,48±0,02	*2,39±0,07	*1,78±0,01	*2,11±0,04
Stem	reducing sugars, %	4,99±0,09	5,31±0,21	*7,25±0,13	*6,22±0,27
	sucrose, %	1,68±0,02	*1,79±0,02	*2,71±0,03	*2,25±0,05
Leaves	reducing sugars, %	1,86±0,04	*2,04±0,07	*2,41±0,03	*2,28±0,06
	sucrose, %	0,89±0,02	*1,39±0,02	*1,59±0,02	*1,22±0,02
Fruitification stage (green ripeness)					
Root	reducing sugars, %	2,29±0,04	*3,61±0,04	*3,43±0,07	*3,73 ±0,09
	sucrose, %	1,88±0,01	*1,38±0,02	*1,52±0,02	*2,36 ±0,04
Stem	reducing sugars, %	4,24±0,09	*4,77±0,17	*4,93±0,16	*5,78±0,17
	sucrose, %	2,32±0,02	*2,07±0,08	2,13±0,09	*2,16±0,05
Leaves	reducing sugars, %	1,96±0,04	*1,37±0,04	*1,81±0,05	*1,74±0,02
	sucrose, %	0,79±0,02	*1,02±0,02	0,82±0,02	*1,15±0,01
Fruitification stage (brown ripeness)					
Root	reducing sugars, %	1,71±0,02	*2,26±0,08	*2,29±0,03	*2,87±0,05
	sucrose, %	0,87±0,01	*1,02±0,05	*0,79±0,01	*1,16±0,02
Stem	reducing sugars, %	3,64±0,02	*3,05±0,11	*4,87±0,09	*4,99±0,14
	sucrose, %	1,55±0,01	*1,15±0,04	*1,64±0,04	*1,43±0,02
Leaves	reducing sugars, %	1,94±0,06	*1,65±0,02	*2,32±0,05	*2,36±0,07
	sucrose, %	0,47±0,01	0,59±0,01	*0,39±0,01	*0,51±0,01

Note. * – difference is significant at $p<0,05$.

However, the specific features of mineral nutrients assimilation and their redistribution through the plant organs for the gibberellin and retardants application have not been systematically studied in connection with productivity of crop.

Effective regulation of the mineral nutrition elements ratios is a necessary condition for the normal growth and development of plants. The sufficient evidence from the literature suggest that there is a clear relationship between the growth rate, photosynthesis and nitrogen nutrition of the plant. It was observed a positive correlation between the protein nitrogen content and the rate of photosynthesis [175] and respiration of plants [52], as well as the protein nitrogen redistribution during the growing season from vegetative to generative organs of the plant [49], which is associated with changes in the rate of photosynthesis and respiration of organs in ontogenesis [48].

It has been fully studied the dynamics of the nitrogen compounds content and redistribution in berry crops under chlorocholine chloride treatment. It was revealed that the total and protein nitrogen content increased in the leaves and stems of drug-treated raspberries and gooseberries plants, while it was noted a contrary effect, the content of non-protein nitrogen decreased in strawberry leaves and stems of raspberries. This should obviously be explained by the intensive flow of this fraction for protein formation with a general increase in the nitrogen content [107].

It has been suggested in a number of studies [59] that the effect of chlorocholine chloride on the nitrogen metabolism in a plant is realized not only through the regulation of activity of amino acids and proteins synthesis, but also due to a change in the donor-acceptor relations, due to the influence on the formation and functioning of attracting nitrogen compounds centers. The outflow of free amino acids from the vegetative organs to growing berries increased due to intensive loading of raspberry bushes by yield under the chlorocholine chloride influence in the second half of growing season. The free amino acids content increased in vegetative organs compared to control while their content reducing in fruits as a result of the formation of small fruits under retardant treatment on black chokeberry plants [107].

The literature data indicates that antigibberellin compounds have different effects on the nitrogen accumulation by leguminous plants. It has been established that the activity of nitrate reductase – a key enzyme of nitrogen assimilation, carries out the first reaction of of nitrate to nitrite conversion decreased under retardant application, it was compensated by increased activity of nitrogenase complex in soy vegetative organs during the period of beans formation. The content of nitrogen compounds increasedat the flowering phase and the phase of bean formation and its sharp decrease at the green bean phase in the leaves and stems of soybean due to the action of *Bradyrhizobium japonicum* strains and chlormequat chloride and dextrel retardant treatment as a result of nitrogen outflow for carpogenesis needs [51].

Analysis of total nitrogen content in the vegetative organs of tomato plants treated by growth regulators indicates significant differences in the accumulation and redistribution of this nutrient according to the trials of experience. Application of drugs had insignificant effect on the nitrogen content in the roots of plants (fig. 4.2.1.), it was more clear the fluctuations of this indicator in the stems of tomatoes. It was noted a significant decrease in the nitrogenous compounds content of all treated trials from fruit formation stage to green ripeness fruitification stage. In our opinion, such a decrease in the nitrogen content cannot be explained by biodilutions, since the vegetative growth of tomatoes slows down significantly during the period of growth and fruit formation. In this regard, we assume that changes in the element content of treated plants compared to control are determined by the outflow of nitrogen-containing compounds from stem to fruit formation.

It was established that the main donor of nitrogen in tomato plants were leaves. The most significant changes in the content of this element were in the control – from 3,29 ± 0,02 % at the stage of fruit formation to 2,34 ± 0,01 % at the brown ripeness fruitification stage, as well as in esphon – from 3,51 ± 0,02 % to 2,68 ± 0,06 % and gibberellin – from 3,37 ± 0,07 % to 2,67 ± 0,04 % by dry weight matter, respectively, due to intensive nitrogen outflow during the whole vegetation period on the fruits formation.

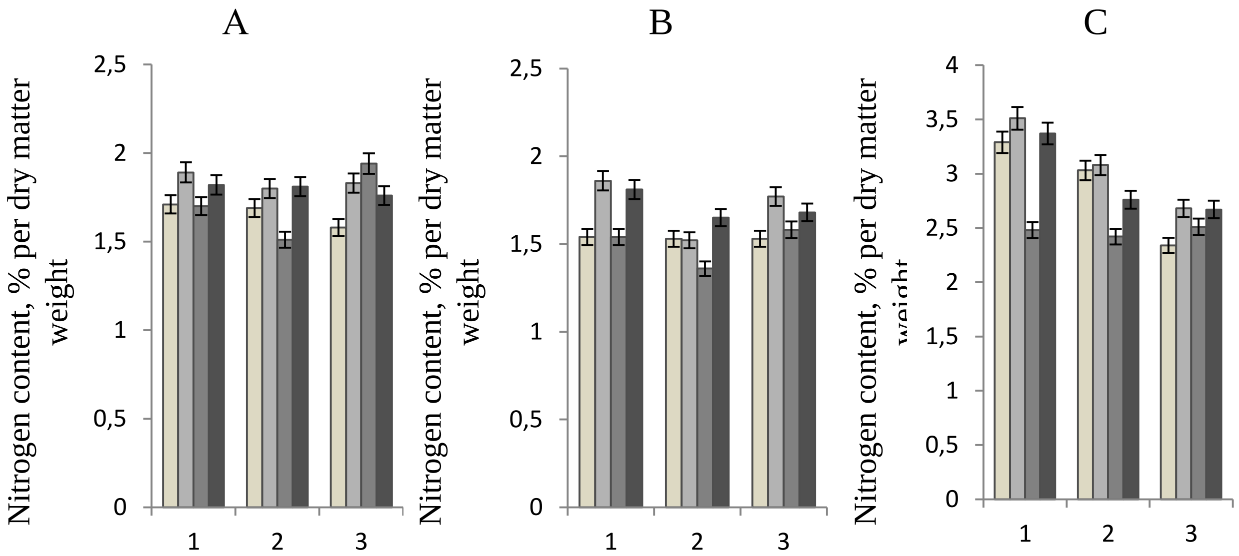


Fig. 4.2.1. Nitrogen content in vegetative organs of tomato plants under gibberellin and retardants application: 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness). A – root, B – stem, C – leaves. – control; – 0,05 % esphon; – 0,025 % tebuconazole; – 0,005 % gibberellin

Less intense fluctuations in the content of this element under triazole derivative tebuconazol application, apparently, is connacted with the fact that plant developed the largest leaf surface and leaf weight that led to forme high gross accumulation of nitrogen in them, and therefore the carpogenesis needs are covered. Similar results of the retardants effect on the redistribution of nitrogen compounds towards the generative organs were obtained in the works of other authors on oilseeds: winter rape [206], sunflower [198] and oil poppy [174].

It is known that the phosphorus and potassium supply is an important prerequisite for increasing crop productivity. These elements play a key role in the process of photosynthesis and the movement of sugars from leaf chloroplasts to root crops and generative organs.

The analysis of the literature data indicates the contradictory nature of the influence of various growth regulators on the phosphorus and potassium content of crops. Thus, the application of chlormequat chloride on sugar beet plants caused a decrease in the content of phosphorus compounds in leaves and root crops with a simultaneous increase in the potassium content [55], while the action of triazole derivative paclobutrazole increased the phosphorus and potassium content in the leaves and decreased in the roots [228]. This compound caused an increase in the phosphorus and potassium content at the beginning of growing season and decreased in their content at the end of Nevskaya potato plants [243]. The application of paclobutrazole on rapeseed plants not caused changes in the potassium content in the leaves of experimental plants [206].

Thus, it is advisable to study the interaction of retardants and gibberellin on the redistribution of mineral nutrition elements by tomato plants.

The results of the study indicate that the phosphorus content in the roots of esphon and gibberellin treated plants was higher compared to control during fruitification stage, while under tebuconazole application, the phosphorus content decreases significantly from fruit formation to brown ripeness fruitification stage, which indicates an increased outflow of this element to the fruits (fig. 4.2.2.).

A B C

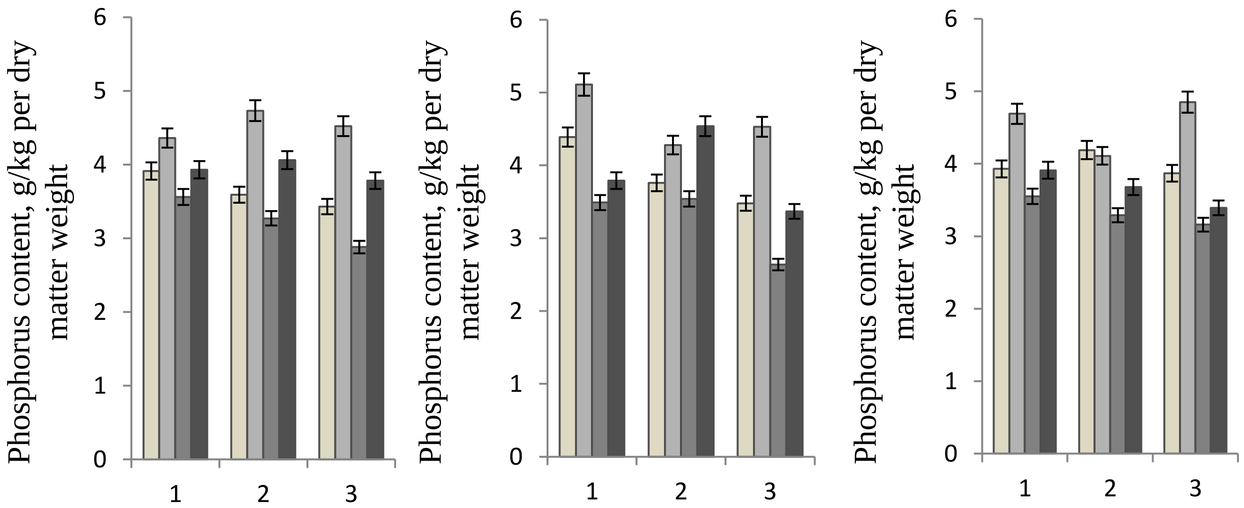


Fig. 4.2.2. Phosphorus content in vegetative organs of tomato plants under gibberellin and retardants application: 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness).

A – root, B – stem, C – leaves. ▭ – control; ▭ – 0,05 % esphon; ▭ – 0,025 % tebuconazole; ▭ – 0,005 % gibberellin

Similar changes occurred in the stem and leaves in the trials treated by triazole derivative compounds. The content of phosphorus compounds of tebuconazole treated trials in terms of the dry weight matter in stem also decreases significantly during the whole fruitification stage from 3,49 ± 0,05 g/kg to 2,64 ± 0,05 g/kg, in leaves – from 3,55 ± 0,07 g/kg to 3,16 ± 0,07 g/kg, as well as for gibberellin treatment – in stems from 3,79 ± 0,05 g/kg to 3,37 ± 0,05 g/kg, in leaves – from 3,91 ± 0,06 g/kg to 3,39 ± 0,09 g/kg, that indicates an intensive reutilization of this element on the formation, growth and ripening of fruits.

It is known that the optimal provision of plants with potassium improves photosynthesis, loading of phloem by newly synthesized assimilates and their transport along the phloem, which contributes to the growth of crop production and its quality [77]. The potassium content in roots of gibberellin, tebuconazole and esphon treated plants at the stage of green and brown ripeness was higher compared to control (fig. 4.2.3.).

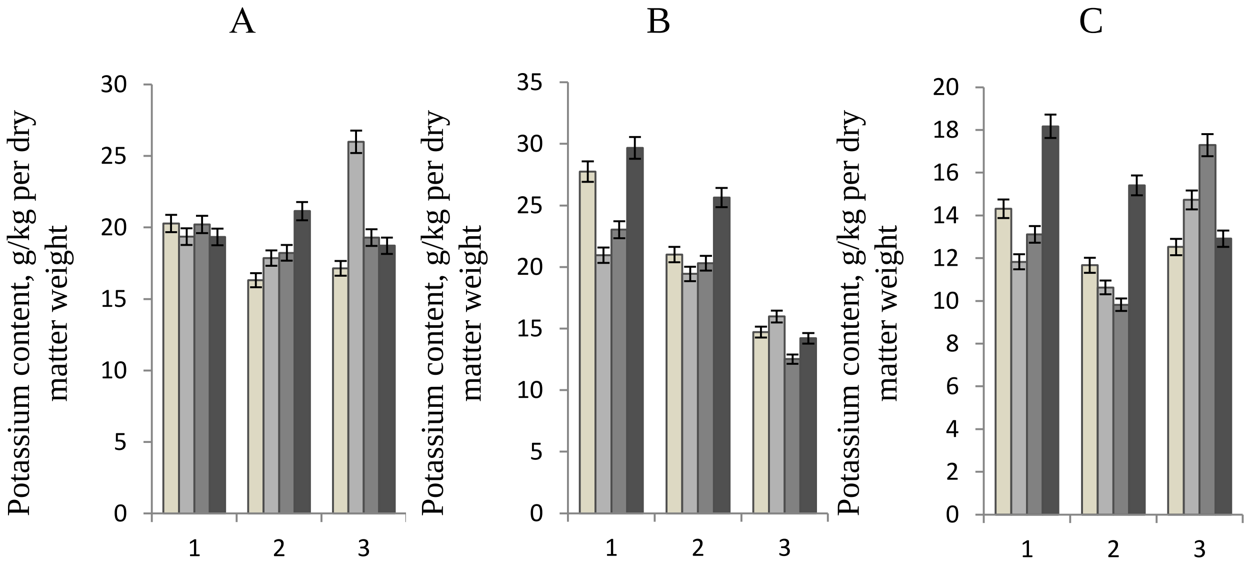


Fig. 4.2.3. Potassium content in vegetative organs of tomato plants under gibberellin and retardants application: 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness).

A – root, B – stem, C – leaves. – control; – 0,05 % esphon; – 0,025 % tebuconazole; – 0,005 % gibberellin

In the stem, it was noted a gradual decrease of potassium content for all experimental trials, and at the end of fruitification stage, the content of this element in organs was minimal. The lowest value of this indicator was noted in stems of research plants under application of gibberellin and tebuconazole against to control. It was observed a similar decrease in the potassium content in the leaves from growth and fruit formation stage to green ripeness fruitification stage. If there was a decrease in the element content in the leaves of gibberellin treated plants during the whole fruitification stage, then esphon and tebuconazole application increased in the potassium content from the green ripeness to brown ripeness fruitification stage, especially in tebuconazole treated trials. An enhancement of the potassium content in leaves in tebuconazol variant is explained, obviously, by an increase in the relative proportion of element on the background of reducing sugars content, nitrogen-containing compounds due to their outflow to the growing fruit.

Thus, the vegetative organs of plant – root, stem and leaves are an important source of nitrogen, phosphorus and potassium supply to the fruits that form during fruitification stage. The reutilization of main nutrients from stem and leaves of the plant was more intense in gibberellin and triazole derivative compound tebuconazole treated trials.

CHAPTER 5
FEATURES OF PRODUCTION PROCESSES UNDER INFLUENCE OF GROWTH REGULATORS ON TOMATOES
5.1. Influence of gibberellin and retardants on yield and quality of tomato products

Processes of growth, photosynthesis and deposition of substances in the stock are played a main role in the formation of plant productivity, therefore the features of donor-acceptor system formation and functioning of agricultural plants with exogenous regulation of growth processes are very important. The analysis of literature data contains information about application of gibberellin and antigibberellin compounds in order to increase crop yields by anatomical, morphological, and physiological and biochemical changes in leguminous [41, 99, 271], oilseeds [102, 110, 129], vegetables [19, 118, 125], technical [268, 272], ornamental [42, 277, 282] and other agricultural plants [5, 168, 169].

The experimental data obtained in the previous chapters indicate the significant role of morphological and mesostructural components of donor-acceptor system of tomato plants under the actions of gibberellin and various types of retardants. In particular, the application of triazole derivative compound tebuconazole led to more significant anatomical and morphological changes in the formation of leaf apparatus: the indicators of number of leaves, weight, leaf surface area and leaf index were higher in this experimental trial (fig. 3.1.1.; 3.2.2.). The mesostructural indicators of leaves also changed in a similar way – the thickness of leaf, the main photosynthetic tissue of chlorenchyma, the sizes of assimilative cells of columnar and spongy parenchyma increased under tebuconazole interaction (table 3.2.2.). Analysis of depositing capabilities of vegetative organs of plants at the fruiting period indicates that the treatment of 0,005 % gibberellin and 0,025 % tebuconazole contributed to the formation of a more powerful donor sphere of tomato plants increased photosynthetic activity as a unit of the leaf area and of the plant as a whole, increased in the deposition of photoassimilates and mineral nutrition elements in vegetative organs of the plant with subsequent active reutilization of these substances on carpogenesis needs compared to 0,05 % esphon treated tomato plants (fig. 4.1.1; 4.2.1;. 4.2.2;. 4.2.3.).

Analysis of various types of growth regulators interaction on the tomatoes plants in the field condition indicate that the triazole derivative telaconazole treatment enhanced the crop yield by 28 % due to an increase in the average weight of one fruit table 5.1.1), the yield of growth stimulator gibberellin treated plants was close to control – the average weight of one fruit decreased with simultaneous increase in the number of fruits per bush.

Table 5.1.1.

Influence of gibberellin and retardants on productivity and quality of tomato products in field condition

Indicators	Control	0,05 % esphon	0,025 % tebuconazole	0,005 % gibberellin
Yield, t/ha	68,16±1,71	67,01±1,51	*87,78±1,69	69,03±1,07
Weight of fruits per one bush, kg	1,61±0,03	1,57±0,03	*2,08±0,04	1,62±0,04
Number of fruits per a bush, pieces	35,41±1,07	33,48±1,24	36,41±1,29	*40,79±1,09
Weight of one fruit, g	41,54±1,05	43,33±1,18	*51,15±1,21	37,16±1,93
Content of ascorbic acid, mg/100 g	26,38±0,82	26,59±0,73	*22,95±0,58	*21,32±0,63
Titrated acidity, g /100 g	0,58±0,02	*0,69±0,02	*0,81±0,02	*0,77±0,02
Reducing sugar, % per fresh matter	0,95±0,02	*1,13±0,03	*1,27±0,03	*1,02±0,02
Sucrose, % per fresh matter	0,68±0,01	*0,35±0,01	0,69±0,02	*0,75±0,01
Total sugars, % per fresh matter	1,65±0,03	*1,49±0,04	*1,94±0,05	*1,79±0,03

Note. * – difference is significant at $p<0,05$.

It was found that the productivity of gibberellin treated tomato plants is largely determined by the water supply conditions. The results of the study conducted in the greenhouse conditions of growing experience show that the application of tomatoes by multidirectional growth regulators caused similar anatomical and morphological changes in leaf and stem parameters compared to obtained values in the field condition. So, the highest yield increase was obtained precisely due to the gibberellin action - the weight of fruits per one bush increased in comparison with control and tebuconazole im the greenhouse growing conditions (table 5.1.2.).

Table 5.1.2.

Influence of tebuconazole and gibberellin on productivity of tomatoes in greenhouse growing condition

Indicators	Control	0,025 % tebuconazole	0,005 % gibberellin
Yield, t/ha	1666,01 ± 64,65	*2074,62 ± 57,15	*2400,17 ± 52,83
Weight of fruits per one bush, kg	27,51 ± 0,51	*31,51 ± 0,45	*34,51 ± 1,01
Number of fruits per a bush, pieces	60,56 ± 1,59	*65,84 ± 1,61	*69,55 ± 1,78
Weight of one fruit, g	20,05 ± 0,58	*31,05 ± 0,75	*17,55 ± 0,32
Content of ascorbic acid, mg/100 g	0,41 ± 0,01	*0,43 ± 0,01	*0,38 ± 0,01
Titrated acidity, g /100 g	1,31 ± 0,04	*1,26 ± 0,03	*1,51 ± 0,06
Reducing sugar, % per fresh matter	0,42 ± 0,01	*1,09 ± 0,03	*0,96 ± 0,02
Sucrose, % per fresh matter	1,81 ± 0,02	*2,41 ± 0,07	*2,61 ± 0,09

Note. * – difference is significant at $p<0,05$.

In our opinion, the enhancement of productivity in these conditions is determined by stability of the water regime, when the soil moisture in the vessels was maintained at 60 % of the total moisture capacity compared to the dry field conditions of the years of research. In the conditions of field experiment, the yield of growth stimulator gibberellin treated plants was close to control – the average weight of one fruit decreased with simultaneous increase in the number of fruits per bush.

Application of ethylene releasing compound as retardant in order to increase the crop yield at the budding phase was ineffective, productivity of tomato plants decreased both in the field and in the greenhouse growing condition.

It can be noted that under drugs treatment, the total acidity in all experimental trias was significantly increased, the sugar content increased and the ascorbic acid content decreased under the tebuconazole and gibberellin interaction, and the sugar content decreased due to esphon application compared to control (table 5.1.1.). Our results of the decrease in the ascorbic acid content in products under retardants interaction is consistent with the results of experiment on raspberry [107] and cherry [75] crops. Whereas, the ascorbic acid content and total acidity increased under the actions of triazole derivative compound tebuconazole in the greenhouse growing experiment, and these indicators decrease for the actions of gibberellin compared to control in the sufficient soil moisture conditions (Table 5.1.2.). However, fluctuations in product quality of treated tomato plants are without significant changes compared to typical product quality values for this crop.

The concept of donor-acceptor system functioning [107, 115] suggests that the activation of photosynthetic processes is largely determined by the «source» of assimilates from the acceptor. Our research results show that the capacity of acceptor zone of tomatoes increased under the influence of tebuconazole compared to control, esphon and gibberellin (fig. 5.1.1.).

Thus, the analysis of the data obtained in the field conditions testifies that the activity of photosynthetic apparatus increased under the action of triazole derivative compound at the brown ripeness fruitification stage. It was noted that the net photosynthetic productivity increased by 1,4 (table 4.1.1.). The transport of assimilate to fruit formation is also increasing, where the relative proportion of fruits to the vegetative organs weight was the highest in the variant of tebuconazole. This indicator was lower of gibberellin and esphon treated plants compared to control, which is consistent with a decrease of the net photosynthetic productivity at the brown ripeness fruitification stage.

The analysis of the carbohydrate content in the fruits of the experimental plants during the ripening period indicates that the starch content and the amount of sugars significantly increased from the stage of fruit formation to the green ripeness stage of gibberellin and retardant treated trials compared to control (table 5.1.3.).

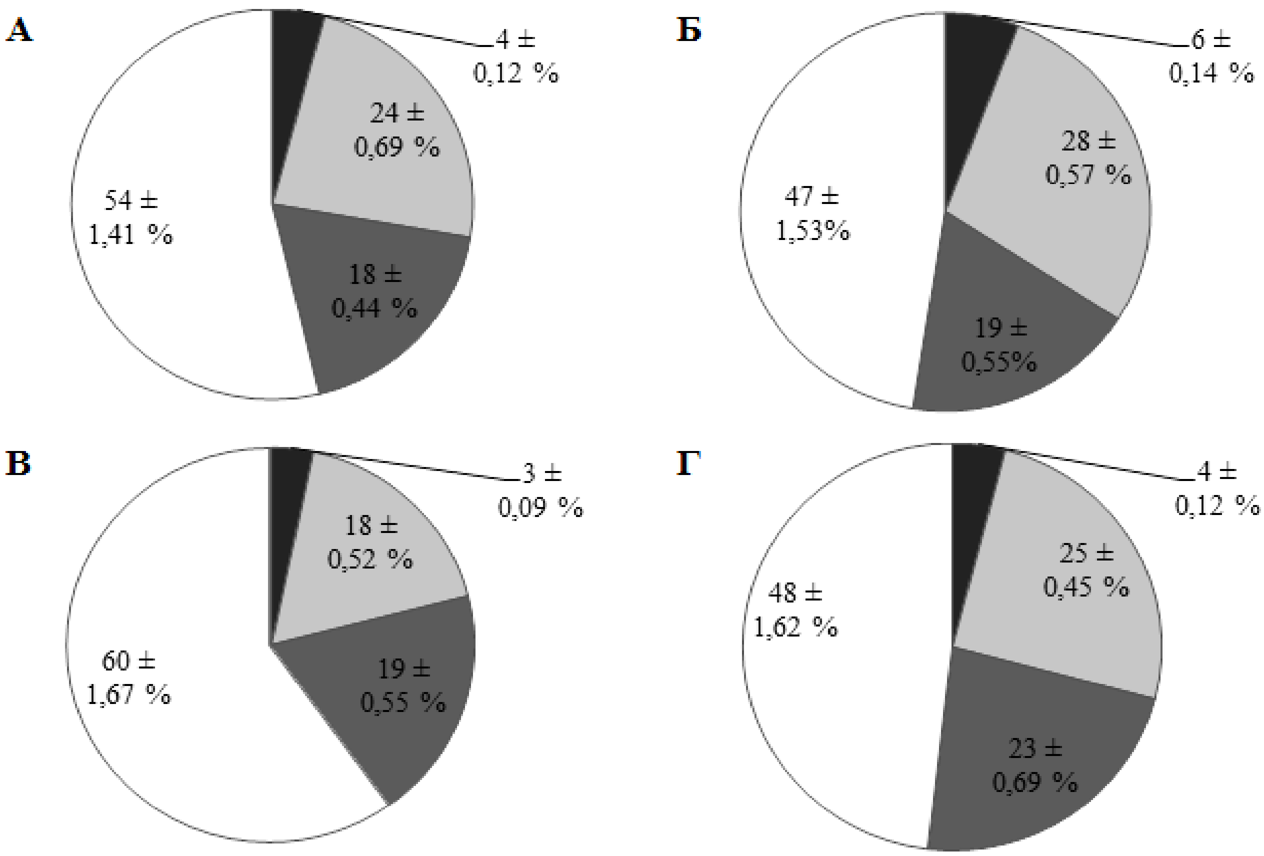


Fig. 5.1.1. Relative proportion of dry matter weight of organs under retardants and gibberellin application: А – control; Б – 0,05 % esphon; В – 0,025 % tebuconazole; Г – 0,005 % gibberellin.

– roots; – stems; – leaves; – fruits

The content of non-structural carbohydrates (starch + sugar) decreased not due to decrease in the reducing sugars content but due to decrease in the starch content, where this indicator decreased by 1,96 times under the actions of tebuconazole as a result of intensive hydrolysis at the brown ripeness fruitification stage.

Table 5.1.3.

Dynamics of carbohydrates accumulation by fruits under gibberellin and retardants treatment on tomatoes hybrid Solerosso, % per dry matter weight (average values for 2015-2017)

Indicators	control	0,05 % esphon	0,025 % tebuconazole	0,005 % gibberellin
Fruit formation stage				
reducing sugars, %	12,21±0,15	*13,71±0,35	12,78±0,38	*13,14±0,21
sucrose, %	4,78±0,09	*4,31±0,08	*3,13±0,04	*3,54±0,07
amount of sugars, %	17,04±0,18	*17,82±0,15	*15,57±0,32	16,39±0,45
starch, %	9,74±0,09	10,03±0,28	*15,33±0,45	*13,59±0,33
amount of nonstructural carbohydrates, %	26,78±0,27	27,85±0,43	*30,90±0,77	*29,98±0,78
Fruitification stage (green ripeness)				
reducing sugars, %	15,11±0,38	15,76±0,34	*17,78±0,64	*18,37±0,66
sucrose, %	5,48±0,14	*6,07±0,13	*6,26±0,16	5,26±0,17
amount of sugars, %	20,38±0,53	21,51±0,55	*23,58±0,62	*23,79±0,61
starch, %	8,02±0,21	*9,87±0,19	*12,34±0,32	*10,13±0,29
amount of nonstructural carbohydrates, %	28,40±0,74	*31,98±0,74	*35,92±0,94	*33,93±0,90
Fruitification stage (brown ripeness)				
reducing sugars, %	19,99±0,52	*17,71±0,45	*21,91±0,54	20,47±0,55
sucrose, %	6,84±0,18	*7,99±0,25	7,03±0,12	*6,32±0,09
amount of sugars, %	27,18±0,64	*25,33±0,55	28,27±0,47	26,22±0,39
starch, %	8,59±0,25	*7,64±0,09	*6,31±0,19	*6,63±0,12
amount of nonstructural carbohydrates, %	35,77±0,89	*32,97±0,64	34,58±0,66	*32,85±0,51

Note. * – difference is significant at $p<0,05$.

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It has been established that retardants was exercised a similar effect on the content of various forms of sugars in the vegetative organs of potatoes [247], sugar beets [228] and sunflower [198].

It was found that application of drugs influenced the content of mineral nutrition elements in the generative organs of tomatoes. The obtained results indicate that the nitrogen content in the fruits of treated plants decreased, and the potassium content increased due to the effects of gibberellin and retardant from the stage of fruit formation to the green ripeness stage. Application of growth stimulator gibberellin and antigibberellin compounds tebuconazole and esphon not significantly affected on the nitrogen and potassium content in fruits of plant at the end of fruitification stage (fig. 5.1.2.).

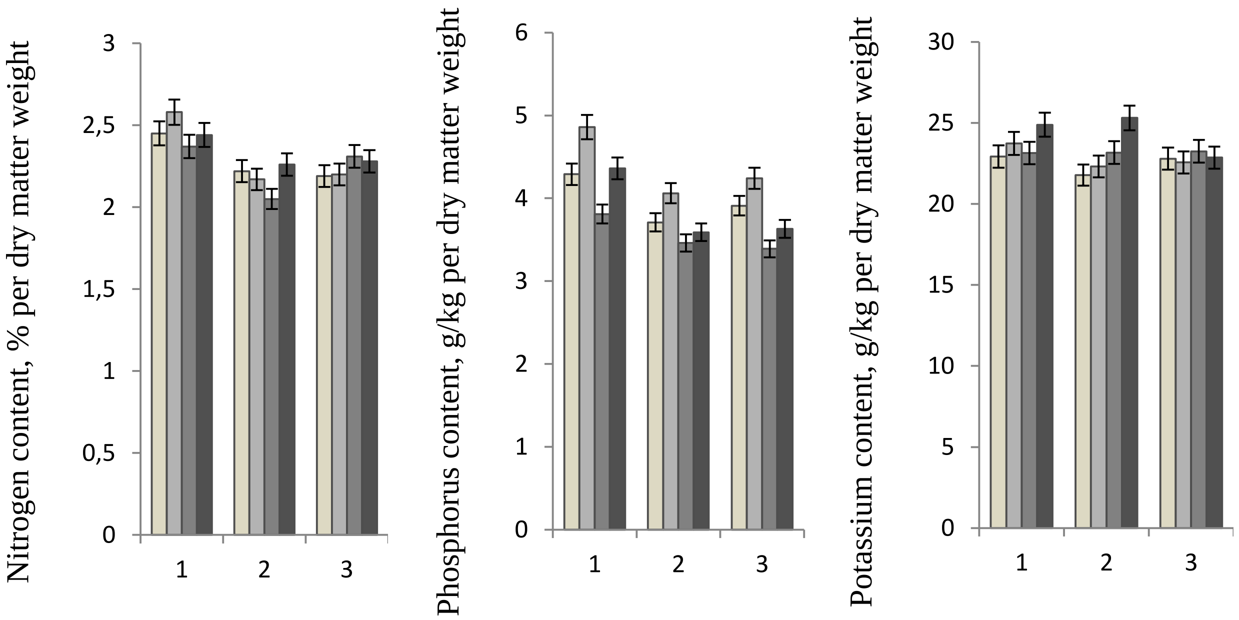

Fig. 5.1.2. Content of mineral nutrition elements in fruits of tomatoes hybrid Solerosso: 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness).

– control; – 0,05 % esphon; – 0,025 % tebuconazole;

– 0,005 % gibberellin

The analysis of the phosphorus content indicates that from the stage of fruit formation to the brown ripeness fruitification stage (period of intensive growth and ripening of fruits) under the influence of tebuconazole and gibberellin, the phosphorus content in tomato fruits significantly decreased. In our opinion, such decrease in the element content can be explained by biodilution due to increased of fruit yield.

Thus, application of gibberellin and retardants leads to the reconstruction of donor-acceptor relation system of the plant, formation of a more powerful photosynthetic apparatus, redistribution of assimilate flows to the fruit growth processes, more intensive use of reserved compounds from vegetative organs to carpogenesis needs, that lead to improve crop productivity. The triazole derivative compound tebuconazole proved to be the most effective for increasing the productivity of tomato plant in the field condition. The maximum value of this indicator was under the growth stimulator gibberellin in the greenhouse growing condition which indicates the dependence of the action of this drug on sufficient water supply.The yield of gibberellin treated plants was close to control in the field experience. Application of ethylene releasing compound as retardant in order to increase the crop productivity was ineffective both in the field and in the greenhouse growing condition.

5.2. Application of ethylene releasing compound esphon to accelerate the ripening of tomato fruits

The synthesis of compounds that can break down with the release of ethylene, opens up broad prospects for their application in crop production with the aim of mechanized harvesting, to avoid adverse weather conditions and early frosts.

It is known that ethylene producers facilitate the separation of fruits and berries from the mother plant; therefore, pre-harvest treatment with these drugs is recognized as a prerequisite for the effective application of fruit machines. In this case, one of the results of pre-harvest spraying is the acceleration of ripening, improving a colour of fruits and berries. Compounds can be used to reduce the number of harvests, post-harvest treatment of fruits to accelerate their ripening.

At the same time, it is remain largely unexplored the physiological changes in fruits and berries after ethylene releasing compound treatment, so there is important implication to study the effect of ethylene producer esphon on the features of carpogenesis of tomato plants.

The obtained results indicate that application of 0,05 % esphon as retardant in order to increase the crop yield was ineffective at the budding phase. However, the treatment of ethylene releasing compound esphon at the stage of 25 % fruits ripeness stage significantly accelerated the rate of their ripening and reduced the number of harvests from three to two which created economic advantages in the early yield production (fig. 5.2.1, 5.2.2.).

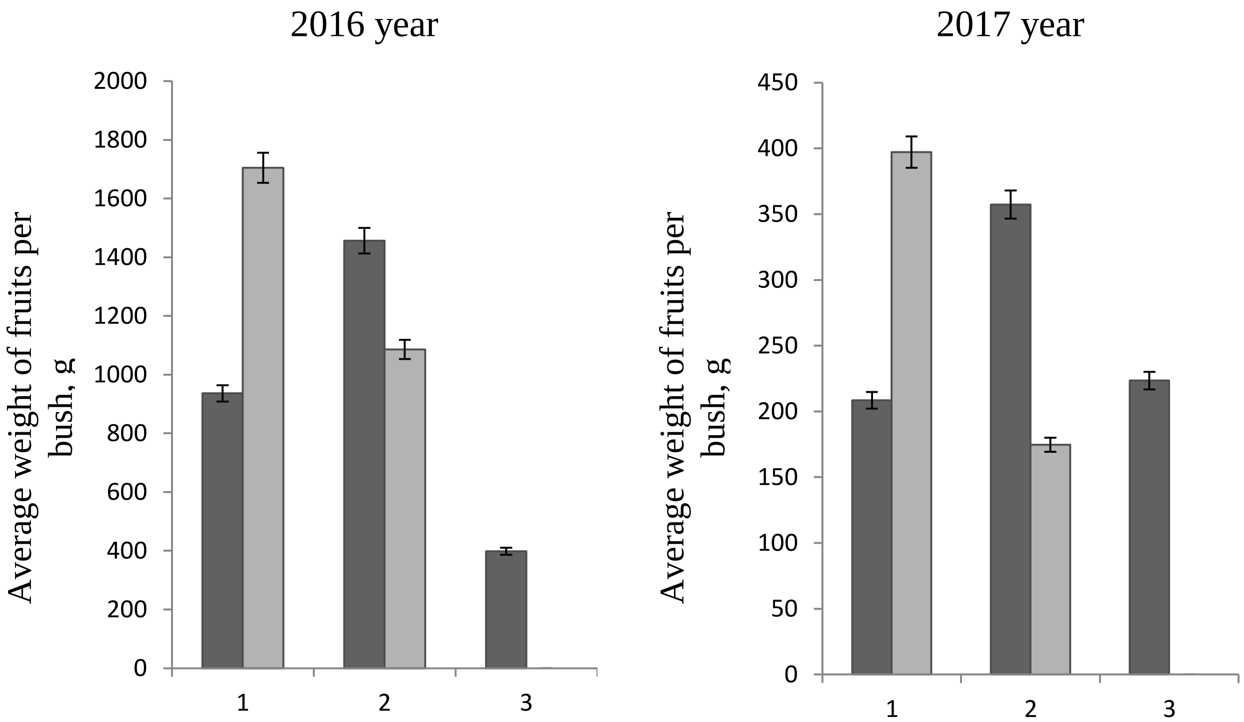

Fig. 5.2.1. Influence of 0,3 % esphon on ripening rate of tomato fruits hybrid Solerosso. Treatment time: 2016 – 28th of july, 2017 – 3d of August.

Sampling time: 1 – after 3 days, 2 – after 6 days, 3 – after 9 days.

– control; – 0,3 % esphon.

Fig. 5.2.2. Application of 0,3 % esphon on ripening of tomato fruits hybrid Solerosso in field condition

It was found that the ripening of fruits and berries is accompanied by a deep structural and functional restructuring of the cell wall: a decrease in its thickness [47], increased enzymes activity that destroy polysaccharides [185], significant structural changes in hemicellulose [53], the ratio of protopectin to soluble pectin and pectin depolymerization [30, 182], cleavage of glycoprotein complex of the middle plates [122]. It has been established that pectin oligomers released as a result of acid or enzymatic hydrolysis are capable to initiate a rapid acceleration of ethylene synthesis [225, 47, 165].

The analysis of literature data shows that camposan M treatment of raspberries led to changes in the molecular structure of cell wall cellulose due to an increase in the polymerization degree of molecules [122]. It was also established that the degradation of cell wall structures during the maturation of fruits and berries begins with enzymatic cleavage of polyuronic polymers [156]. The determination of molecular weight of berry pectins within a week after 0,1 % camposan M treatment of raspberry showed that the polyuronid complex undergoes significant changes: the average molecular weight of pectins decreased upon ripening of berries, and the process was faster in the experimental trial [122]. It was revealed that the mass fraction of high molecular weight fractions of pectins decreased in the experimental trial compared to control. The author concluded that one of the reasons for transition of protopectin to soluble pectin is the predominant cleavage of polygalacturonase of high molecular weight fractions of pectins upon maturation [122, 156].

The study of the content and structural features of non-cellulose polysaccharides of tomato fruits at the maturation stage indicate the restructuring of polysaccharide complex of the cell walls during this period. The obtained analysis of the structural elements of pectins extracted at the different stages of ripening indicate significant structural changes in these polysaccharides throughout the entire ripening period both in the control and in the variant of ethylene producer esphon treated plants (table 5.2.1.).

It was noted an increase in the free carboxyl groups content in the pectin fraction during the period of active ripening of fruit. It can be explained by the processes of deetherification, enzymatic cleavage of methoxyl and acetyl groups. At the same time, it was found that the content of total and esterified carboxyl groups of pectin increased during this period, which does not allow us to draw the following conclusion. In our opinion, the growth of total carboxyl groups in pectin is determined by the more intensive hydrolysis of the non-galacturonic fraction of pectin substances.

Table 5.2.1.

Content of free, esterified and total carboxyl groups of pectins under 0,3 % esphon treatment on tomato fruit during ripening

Indicators	Control	0,3 % esphon	Control	0,3 % esphon	Control	0,3 % esphon
	01.08.2016		04.08. 2016		07.08.2016	
Free carboxyl groups, мg·Eq/g	0,06 ± 0,001	*0,14 ± 0,004	0,19 ± 0,004	*0,24 ± 0,006	0,33 ± 0,001	*0,29 ± 0,001
Esterified carboxyl groups, мg·Eq/g	1,55 ± 0,021	*3,01 ± 0,072	2,89 ± 0,091	3,00 ± 0,081	3,23 ± 0,122	3,41 ± 0,091
Total carboxyl groups, мg·Eq/g	1,61 ± 0,022	*3,15 ± 0,081	3,08 ± 0,052	3,24 ± 0,092	3,56 ± 0,112	3,70 ± 0,111
	07.08.17		10.08.17		13.08.17	
Free carboxyl groups, мg·Eq/g	0,101 ± 0,002	*0,15 ± 0,003	0,151 ± 0,003	0,161 ± 0,004	0,211 ± 0,001	0,191 ± 0,006
Esterified carboxyl groups, мg·Eq/g	2,55 ± 0,081	*3,83 ± 0,132	3,59 ± 0,112	*4,42 ± 0,141	4,27 ± 0,131	4,75 ± 0,151
Total carboxyl groups, мg·Eq/g	2,65 ± 0,071	*3,98 ± 0,111	3,75 ± 0,122	*4,58 ± 0,152	4,48 ± 0,141	4,94 ± 0,163

Note: 1. Treatment time: 2016 – 28th of July, 2017 – 3d of August.

2. * – difference is significant at p<0,05.

The analysis of the hemicellulose and pentosan content at the different stages of fruit maturation indicates an intensive hydrolysis of these polysaccharides, while these processes occur more intensively of esphon treated trial (fig. 5.2.3.).

Thus, the ripening process is largely determined by the intense maceration of fruit tissues, which is based on the hydrolysis of polysaccharide components of the cell wall – hemicellulose and pectin. Moreover, the decrease in their content occurs more intensively under esphon application compared to control.

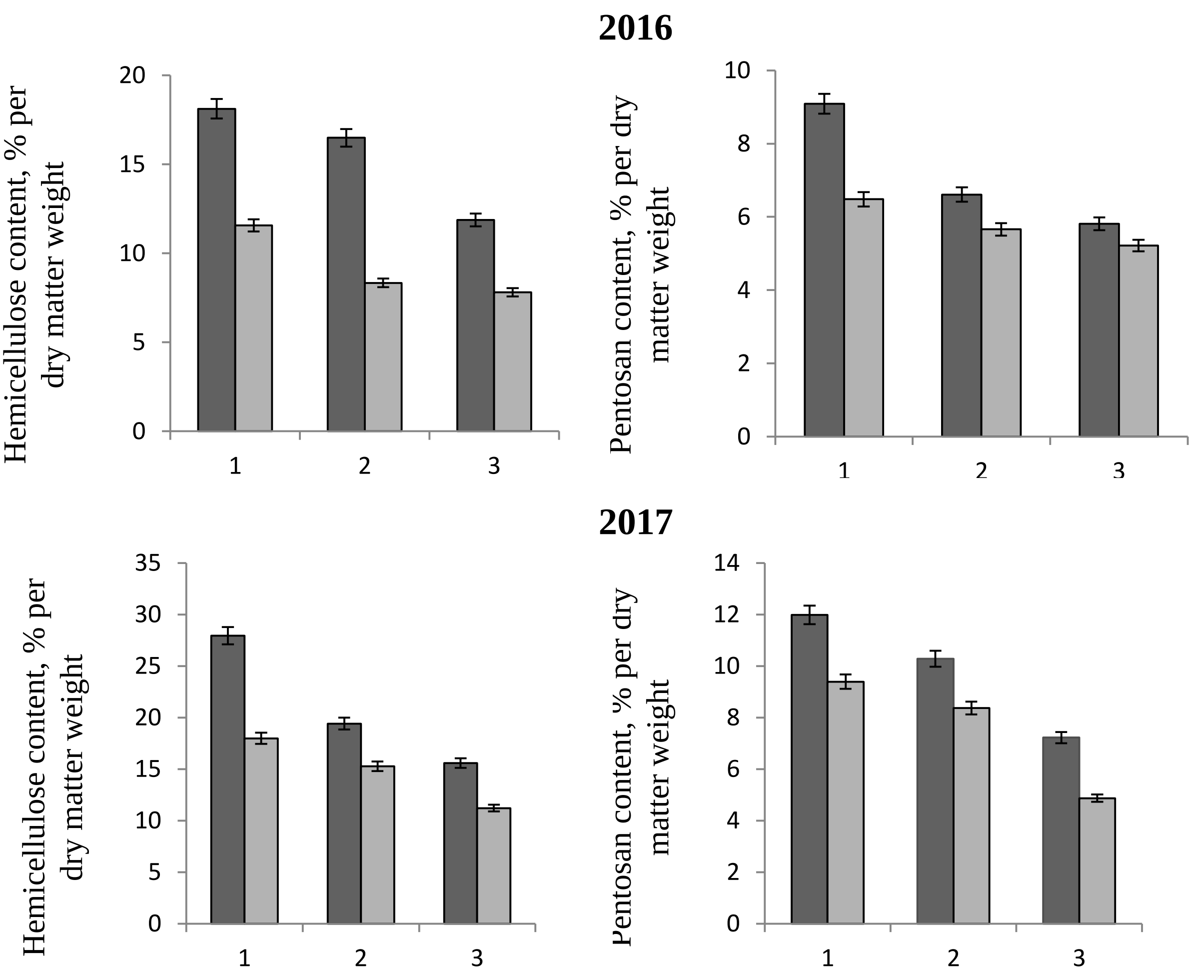

Fig. 5.2.3. Hemicellulose and pentosan content in tomato fruits under ethylene releasing compound application. Treatment time: 2016 – 28th of july, 2017 – 3d of August. Sampling time: 1 – after 3 days, 2 – after 6 days, 3 – after 9 days.

■ – control; □ – 0,3 % esphon.

It was found that forced ripening of tomato fruits is accompanied by changes in the quality of crop production. 0,3 % esphon pre-harvest treatment led to an increase in total acidity, a decrease in the content of carbohydrates and ascorbic acid in the fruits of research plants compared to mature fruits of tomatoes that ripened in vivo without the application of ethylene producers (table 5.2.2.). At the same time, these changes are within the range of fluctuations to typical product quality values for this crop.

Table 5.2.2.

Influence of esphon on product quality of tomatoes hybrid Solerosso (average values for 2016-2017)

Indicators	control	0,3 % esphon
Content of ascorbic acid, mg/100 g	26,38±0,82	26,02±0,69
Titrated acidity, g /100 g	0,52±0,02	*0,62±0,02
Reducing sugar, % per fresh matter	1,15±0,04	1,19±0,02
Sucrose, % per fresh matter	0,82±0,01	*0,62±0,01
Total sugars, % per fresh matter	2,07±0,03	1,83±0,03

Note. * – difference is significant at $p<0,05$.

Thus, the application of 0,3 % esphon at the stage of 25 % fruit ripeness significantly accelerated their ripening due to intensive maceration of fruit tissues, which is based on the hydrolysis of polysaccharide components of the primary cell wall – hemicellulose and pectins. As a result of such treatment, the number of harvests was reduced and the share of early production in the crop structure was increased.

DISCUSSION

Our many years of research have established that the action of gibberellin and retardants on tomato plants is realized through the reconstruction of donor-acceptor relation due to regulation of growth processes, accumulative activity of shoot and donor activity of leave, redistribution of assimilate and mineral nutrition elements flows between vegetative and generative organs of the plant.

Gibberellic acid (GA_3) and retardants caused a clear growth regulating effect on the intensity of plant growth, accompanied by changes in relative proportion of matter weight between organs of the plant. Application of tebuconazol resulted on the formation of a more powerful donor sphere, where relative proportion of leaf weight in the total weight of plant was higher during whole period of vegetation. Moreover, the proportion of other vegetative organs was less than in other experimental trials. The growth of the leaf donor potential under the actions of growth stimulator gibberellin occurred as a result of increased of linear growth, accompanied by formation of new leaves. While the application of tebuconazole and esphon led to an increase in the number of leaves and leaf surface area due to inhibition of linear growth and increased of stem branching.

It was found that the application of growth regulators with different directions of action significantly influenced on the histogenesis and formation of leaf apparatus of tomatoes. In particular, the mesostructure measurement of leaves was optimized under gibberellin and tebuconazol treatment: thickness of leave increased by enhancement of linear dimention of spongy parenchyma cells and volume of palisade parenchyma cells – main assimilation tissue of leave. Application of esphon resulted in deterioration of anatomical characteristics of leave compared to control.

It was established that in all experimental variants during the period of fruit formation there is a gradual increase of important indicators that characterize the potential photosynthetic productivity of unit leaf surface. The leaves of triazole derivative tebuconazol and growth promoter gibberellin treated tomatoes were characterized by the highest measurement of leaf area density value (LADV), chlorophyll content and net photosynthetic productivity created the prerequisites to enhance gross photosynthetic crop production and accumulation of a greater number of photoassimilates in the plant. The increase of important cenotic index – leaf (LI) and chlorophyll index (CI) under tebuconazole treatment lead to enhance the cenosis productivity.

Analysis of depositing possibilities of vegetative organs of the plants during fruitification phase showed the importance of temporarily accumulation of nonstructural carbohydrates in them with subsequent reutilization for carpogenesis needs. The obtained results indicate that in the vegetative organs of tomato plants are accumulated more carbohydrates (sugars + starch) due to formation of a more powerful donor sphere under tebuconazol and gibberellin treatment compared to control. Obviously, this indicates some of their redundancy, which is not fully spent on the fruits formation, but is temporarily accumulated to reserve. The highest content of carbohydrates in all stages of the fruitification phase was noted in stems of tomato plants, that indicates the powerful depositing capabilities of this vegetative organ. Sucrose is a main transport form of carbohydrates in the plant, a more significant reduction in its content in the leaves of experimental plants and the growth of reducing sugars content at the brown ripeness stage suggests that transport of sugar from leaves to fruits ceased earlier than from root and stem, consequently the reducing sugars content increased.

It was found that gibberellin and retardants treatment of tomato plants influenced on the accumulation and redistribution of mineral nutrition elements. The obtained results indicate that nitrogen provision of generative organs occurs first of all due to its reutilization from leaves. The most significant changes in the content of this element were in the control, as well as in esphon and gibberellin variants, due to intense outflow of nitrogen on fruit formation throughout the vegetation stage. Less intense fluctuations in the content of this element under triazole derivative tebuconazole application, apparently, is connacted with the fact that plant developed the largest leaf surface and leaf weight that led to forme high gross accumulation of nitrogen in them, and therefore the carpogenesis needs are covered.

It was established that the phosphorus content in stems and leaves of tebuconazol and gibberellin treated tomato plants is significantly reduced throughout the fruitification stage, which indicates the intensive reutilization of this element on the fruit formation, growth and maturation. An enhancement of the potassium content in leaves of tebuconazole treated plants is explained, obviously, by an increase in the relative proportion of element on the background of reducing sugars content, nitrogen-containing compounds due to their outflow to the growing fruit.

The results of the study indicate that 0,025 % tebuconazole treatment of plants enhanced the crop yield by increasing a weight of one fruit without significant changes in product quality of tomatoes compared to control. Analysis of relative proportion weight of vegetative and generative organs suggests that this indicator was the highest under tebuconazole application. Modern ideas about the functioning of donor-acceptor relation system are based on the fact that the intensity of photosynthetic processes is largely determined by the «source» for assimilates from the acceptor side. Obviously, the higher loading of tomato plants by fruits of tebuconazole treated tomatoes is an important additional factor for impoving the activity of photosynthetic apparatus of the plant, which explains the higher value of net photosynthetic productivity (NFP) in this variant.

It was found that the productivity of gibberellin treated tomato plants is largely determined by the stable water supply. Thus, in the greenhouse growing conditions, the greatest increment of yield was obtained precisely under gibberellin treatment. Enhancement of yield in these conditions in comparison with the arid field conditions of research years is determined, in our opinion, by the expense of a stable water supply, when the moisture content of soil in vessels was maintained at 60 % of the total moisture content. In the field conditions, the yield of growth stimulator gibberellin treated plants was close to control – the average weight of one fruit decreased with simultaneous increase in the number of fruits per bush.

Application of ethylene releasing compound as retardant in order to increase the crop yield at the budding phase was ineffective. However, the application of ethylene releasing compound esphon at the stage of fruits ripening to increase the share of early crop yield has created economic advantages in the fruit production. The treatment of 0,3 % esphon at the stage of 25 % fruits ripeness stage significantly accelerated the rate of their ripening and reduced the number of harvests.

Thus, application of gibberellin and retardants leads to the reconstruction of donor-acceptor relation system of the plant, formation of a more powerful photosynthetic apparatus, redistribution of assimilate flows to the fruit growth processes, more intensive use of reserved compounds from vegetative organs to carpogenesis needs, that lead to improve crop productivity. The triazole derivative compound tebuconazole proved to be the most effective for increasing the productivity of tomato plant in the field condition. The maximum value of this indicator was under the growth stimulator gibberellin in the greenhouse growing condition which indicates the dependence of the action of this drug on sufficient water supply. Application of ethylene releasing compound as retardant in order to increase the crop productivity was ineffective, but treatment of this compound at the stage of 25 % fruits ripeness stage significantly accelerated the rate of their ripening, the number of harvests was reduced and the share of early production in the crop structure was increased. The maturation of tomato fruit was largely determined by the intensity of maceration of fruit tissues, which is based on the processes of hydrolysis of cell wall polysaccharide components – hemicelluloses and pectins.

CONCLUSIONS

1. Growth regulators with different mechanisms of action – gibberellic acid and retardants affected on the donor-acceptor systems formation and functioning of tomato plants, its anatomical, morphological and mesostructural characteristics, assimilating activity, deposition and redistribution of carbohydrates, nitrogen-containing compounds and mineral nutrients between vegetative organs and fruits, that significantly affects on the crop production.
2. Growth regulators increased the assimilating surface area of plants compared to control, but this happened in various ways. Retardants increased the number of leaves and their area as a result of increased stem branching, whereas gibberellin increased it due to the intensification of linear growth.
3. Gibberellin and tebuconazole treatment increased in the volume of assimilative parenchyma cells, leaf thickness, its specific weight and the total chlorophylls content that with an increse in the number of leaves enhanced chlorophyll index and net photosynthetic productivity. Application of esphon negatively affected on those indicators.
4. The increase in photosynthetic productivity of tomato plants contributed to enhancement of assimilation to the plant organism under gibberellin and tebuconazole treatment, that was manifested an increase in the nonstructural carbohydrates content in vegetative organs compared to untreated plants.
5. The stem plays an important role of temporary reserve of assimilates, which is amplified under tebuconazole and gibberellin interaction. In the second part of fruitification stage, the nonstructural carbohydrates content in stem and roots decreased as a result of their reutilization to carpogenesis.
6. Gibberellin and tebuconazole treatment intensified the reutilization of nitrogen, phosphorus and potassium from vegetative organs to fruits of tomato plants. Esphon also influenced on the accumulation and redistribution of assimilates and nutrients in tomato plants, but to a lesser extent.

7. As a result of tebuconazole and gibberellin treatment increased productivity of tomato plants without significant changes in product quality. In the first case, this was due to an increase in a weight of one fruit, in the second, due to an increase in the weight and number of fruits on the plant. However, the positive effect of gibberellin was manifested only with optimal water supply in the greenhouse growing conditions; tebuconazole was effective in the field condition.

8. Application of ethylene releasing compound esphon as retardant in order to increase the crop yield at the phase of budding was ineffective, but at the stage of 25 % fruit ripeness it significantly accelerated the rate of their ripening. The maturation of tomato fruit was largely determined by the intensity of maceration of fruit tissues, which is based on the processes of hydrolysis of cell wall polysaccharide components – hemicelluloses and pectins. Such acceleration led to a reduction in the number of harvests and increase in the share of early crop production.

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