REGULATION OF MORPHOGENESIS AND PROCESS OF AGRICULTURAL CROP PRODUCTION BY MEANS OF PHYTOHORMONE ANALOGUES AND MODIFIERS OF THEIR ACTION

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Regulation of morphogenesis and process of agricultural crop production by means of phytohormone analogues and modifiers of their action

The monograph examines the literature and experimental data on the influence of synthetic growth regulators with different mechanisms of physiological action on growth processes, morphogenesis, formation and functioning of the source-sink system of crops in connection with their productivity.

For plant physiologists, agronomists, teachers, postgraduate students and students of biological specialties.

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CHAPTER 1.
EFFECT OF GIBBERELLIN AND RETARDANTS ON GROWTH PROCESSES, LEAF APPARATUS FORMATION, REDISTRIBUTION OF ASIMILATES AND NUTRITIONS IN CONNECTION WITH CROP PRODUCTIVITY OF GOOSEBERRY PLANTS

Introduction

The current status of development of plant physiology allows analyzing the processes of accumulation and redistribution of photoassimilates between plant organs from the standpoint of the concept of source-sink relations (source-sink system). The source and sink spheres of the plant are connected by a system of direct and feedback (hormonal, trophic), which provides mutual correction of growth and photosynthesis. The processes of photosynthesis are considered as a source, and the processes of growth, accumulation of reserve substances and zones of active metabolism during autotrophic nutrition are considered as a sink [37, 73], or interaction between reserve organs and growth processes at the heterotrophic stage of seedling development [35,46]. It is also known that different types of reserve substances play the role of a buffer between photosynthesis as source of assimilates and the growth of the structural substance of vegetative, storage and reproductive organs as sink of assimilates. This determines to some extent the independence of growth processes from photosynthesis [37]. The issues of intermediate deposition of assimilates and mineral nutrients in the vegetative organs of the plant as an additional reserve used for the processes of carpogenesis (fruit and seed formation) are insufficiently studied. The usage of phytohormones and synthetic growth regulators makes it possible to change artificially the activity and ratio of growth and photosynthetic processes, morphogenesis, fruit loading of plants [3, 11,15]. The use of drugs with opposite mechanism of action allows to artificially simulate different tension degrees of source-sink relations and to find out what morphological and physiological changes cause redistribution of assimilate flows between plant organs [19, 29,70].

It is known that gibberellins significantly enhance the processes of vegetative growth [49]. Among exogenous phytoregulators, a group of synthetic growth inhibitors – retardants is also actively used. The mechanism of physiological action of this group members is that being antihiberellins they block the synthesis or physiological activity of synthesized gibberellin in the plant [49, 57]. Numerous studies have confirmed that the use of retardants causes artificial changes in morphogenesis [1,54,71], regulates the activity of growth processes [3,7,11], photosynthetic productivity as a unit of leaf surface as plants and coenosis in general [18,32,34], affects the processes of carpogenesis, loading of plants with fruits and seeds [11,15,75]. The use of retardants often leads to a significant increase in crop productivity [31, 32, 51]. In modern horticulture and viticulture, gibberellins and inhibitors of their biosynthesis are widely used, and the global market for these drugs is in the range of 500 million dollars [49]. The effect of different types of retardants on berry crops has not been studied enough. In particular, there are no studies on the influence of gibberellins and different types of retardants on morphogenesis, features of photosynthetic apparatus formation, accumulation, redistribution of assimilates and mineral nutrients between organs of gooseberry plants. In this regard, the main purpose of this work was to establish the influence of gibberellins and various types of retardants – tebuconazole and esfon on the formation and functioning of the source-sink system of gooseberry plants (*Grossularia reclinata* (L.) Mill) in connection with crop productivity.

Research methods

The work was performed on production plantations of gooseberry variety Mashenka.

The variety was bred by Belarusian breeders. It has the appearance of a compact lush bush with thick straight shoots. The height of the bush is 120-150 cm. The stems have single spikes of light brown color. Berries weigh varies from 6 to 8 g. The shape is round-oval, ripeing color change from light green to orange-red hue. The fruits have a sweet and sour taste. Shrubs begin to bear fruit in the 3^{d}-4^{th} year after planting. One-yearly, it is possible to gather 2,5-5 kg from one bush. Under proper care, shrubs can bear fruit for 16-20 years [58].

Field experiment was conducted in a specialized farm FP "Dagor" (2015-2017) village Rakovo, Tomashpil district, Vinnytsia region. The plot area is 30 m^2. The repeatability is fivefolded.

Treatment of plants was carried out with a knapsack sprayer OP-2 with 0.005% solution of gibberellin (gibberellic acid, GA_3), 0.025% aqueous solution of tebuconazole, 0.1% solution of esfon (rated for the active substance) once in the budding phase until complete wetting.

The following drugs were used in the experiment.

Tebuconazole - ($C_{16}H_{22}ClN_3O$) -RS) -1β-chlorophenyl-4,4-dimethyl-3- (1H-1,2,4-triazol-1-yl-methyl) pentan-3-il, triazole derivative substance. Manufacturer – Bayer Crop Science AG (Germany). Tebuconazole is colorless crystal substance that dissolves well in organic solvents (20 ° C, in g/l): in hexane it is 0.1-1, in propanol – 50-100, in toluene – 50-100, in dichloromethane – 200-500. Water solubility is (20° C) 32 mg/l (0.032%). The half-life at 20 ° C is over a year. The substance is stable at elevated temperatures and in light. Resistant to hydrolysis in clean water at pH 5-9 and photolysis. Molecular weight is 307.8 D, melting point is 104.7° C. Tebuconazole is also used as a systemic fungicide with a broad spectrum of action to control diseases of leaves and ears of cereals (fusarium wilt, septoria, rust, powdery mildew and others), gray rot of grapes, some diseases of soybeans, canola, sunflower, vegetables, fruits and vegetables by spraying standart of 1000 g/ha. It is seed disinfectant to combat solid smut, septoria cereals at a rate of 2-25 g per 10 kg of seeds. It has protective and medicinal properties, a well-defined stop effect, provides long-term protection of leaves, stems and ears from major diseases, mixes well with other drugs, has no phytotoxicity.

Esfon (ethephon, etrel, 2-HEPA) is a 65% solution of dichloroethylphosphonic acid (HEPA, $C_2H_6ClO_3P$). Manufacturer – PLC Agrosynthesis (Russia). It is solid, white, hygroscopic, waxy substance, well soluble in water, ethyl and isopropyl alcohols, acetone, propylene glycol substance, less soluble in nonpolar solvents – benzene, toluene. Molecular weight is 144.5 D, melting point is 74° C. It is not flammable. In solution it is not compatible with alkaline salts. It has low toxicity for warm-blooded animals: LD50 for white rats prerorally is 4220 mg/kg. The drug and its metabolites are excreted in the urine within 7 days. It does not cause embryotoxic, hepatogenic and mutagenic effects, has no cumulative properties. Aqueous solutions with pH value of 4.1-4.5 are stable, at higher pH values, which are characteristic of plant cell sap, spontaneous non-enzymatic breakdown of esfon begins with the release of free ethylene, with regulatory functions.

The mechanism of action of esfon belongs to ethylene producers. The active substance quickly penetrates the plant and decomposes in its tissues with the formation of methylene. In turn, ethylene inhibits the action of phytohormones, the growth of gibberellins and stimulates the synthesis of solids (lignin, pigments, sugars, etc.). The action of ethylene producers significantly depends on air temperature. The recommended maximum dose for use at temperatures below +16° C. Resistance to washing is acquired in 4-5 hours after treatment [66].

Treatment with ethephon facilitates mechanized harvesting of apples, cherries, citrus, sea buckthorn, grapes, etc. The drug is used to increase yields, frost resistance, accelerate fruit ripening and increase the sugar content of sugar beet roots. Esfon is compatible with many herbicides, insecticides, fungicides, micro- and macro-fertilizers, with the exception of preparations based on dithiocarbonates, sulfur, copper [67].

Gibberellic acid (GA_3, $C_{19}H_{22}O_6$) is a white crystalline substance with a molecular weight of 346.2 D. Melting point is at 227° C. The substance is poorly soluble in water and soluble in organic solvents. Gibberellic acid is a low-toxic compound, belongs to the 3rd class of toxicity, does not irritate the skin, but is a moderate irritant to the mucous membranes of eyes without allergenic potential. LD_{50} for rats is 15 630 mg/kg.

Gibberellins are moderately resistant in water and low in soil, decompose rapidly in air, safe for bees, soil microorganisms and birds. Do not accumulate in plants and the environment, are not toxic to aquatic organisms [72].

Gibberellins are natural phytohormones, have the properties of growth regulators, are present in all plants and common diet of herbivorous macro- and microorganisms, their metabolism occurs naturally. According to the "Hygienic classification of pesticides by degree of danger" (DerzhSanPiN 8.8.1.002-98), GA_3 on the parameters of acute oral and dermal toxicity belongs to the 4th class of danger, its acute inhalation toxicity is up to 2d-3d class. It does not irritate skin, but irritating ability to the skin and mucous membranes of eyes is without allergenic potential. According to EFSA [8], the value of ADI (acceptable daily intake – acceptable consumption rates) for gibberellic acid is 0.68 mg/kg. However, according to experts, there is no need to justify the permissible daily dose of gibberellins, because according to current regulations for the use of gibberellin-based drugs, the risk of excess residual amounts of gibberellins in food above 1 ppm is not expected.

The mesostructural organization of the leaf was determined at the end of the growing season on a fixed material [38]. For preserving the material a mixture of equal parts of ethyl alcohol, glycerin, water with the addition of 1% formalin was used. The size of individual chlorenchyma cells was determined on drugs obtained by partial maceration of leaf tissues [20]. The macerating agent was a 5% solution of acetic acid in hydrochloric acid 2 mol/L.

Leaves and the middle part of one-year shoots at the end of the growing season were selected for anatomical analysis. The study of the size of the anatomical elements was performed using a microscope «Mikmed-1» and an ocular micrometer MOV-1-15X. The content of chlorophyll was measured in fresh material by spectrophotometric method on a spectrophotometer SP-16 [9]. The area of the leaf blade was determined by Polyakov method [39].

For biochemical analysis, the materials were fixed with liquid nitrogen, dried for 4 hours at 85° C in oven, dried in the air till air-dry state.

The content of total sugars, reducing sugars and starch in vegetative organs and fruits was determined by iodometric method [42]; phosphorus – by phosphorus-molybdenum complex formation with ammonium iron molybdate, potassium – by the flame-photometric method [50], the total nitrogen content – by Kjeldahl [43]. In mature fruits as indicators of product quality were set sugar content [42], ascorbic acid content [59] and total acidity [6]. Statistical processing of the results was performed using software package Statistica-6. The reliability of the difference between control and experiment was determined by Student's t-test. The tables and figure show the arithmetic mean values and their standard errors.

1.1. Influence of gibberellin and retardants on growth processes and morphogenesis of gooseberry

Many scientific investigations are devoted to the formation of the leaf apparatus of plants under the action of growth regulators. In particular, the influence of chlormequat chloride on the formation of the mesostructure of raspberry leaves [18], sugar beet [60,61], potatoes [64]; paclobutrazol – on the mesostructural organs of oilseeds: poppy [33,45], flax [13], rapeseed [55]. These studies showed that the use of these groups of retardants modified the activity of marginal meristems of the leaf, and therefore contributed to its thickening and adjusted the ratio of individual tissues of the leaf. The results of research confirm the strengthening of the production process due to the increase in photosynthetic activity per unit leaf area, which is determined by the increase in concentrations of structures involved in photosynthesis. However, the effect of the new triazoles of tebuconazole and ethylene producers on leaf formation and function remains actually unclear. In this regard, we investigated the anatomical-morphological and mesostructural characteristics of gooseberry leaves under conditions of different tension in source-sink relations under the influence of gibberellin and these retardants.

It is known that the production process of plants depends on the ratio of the source and sink spheres' activities of the plant [23,25,36]. The source sphere is primarily represented by the leaf apparatus and the process of photosynthesis, which provide morphogenesis by assimilates. The mesostructural features of the leaf are essential for the functioning of the source sphere of plants [27, 55]. Earlier it was found that different types of retardants affect not only the activity of lateral and apical meristems but also the marginal meristems of the leaf, which can lead to a significant restructuring of its organization [27,48,64].

The obtained research data prove the typical restrictive effect of gibberellin and retardants on the growth processes of gooseberry plants. Under the influence of gibberellic acid, the length of one-year shoots at the end of the growing season were 32.2 ± 0.6 cm, tebuconazole – 22.2 ± 0.4 cm, esfon – 18.2 ± 0.4 cm compared to 27.7 ± 0.56 cm in control. The leaf area differed significantly: under the action of gibberellin the average leaf area was 20.8 ± 0.4 cm^2, tebuconazole – 16.6 ± 0.3 cm^2, esfon –15.2 ± 0.3 cm^2 compared to the control of 18.4 ± 0.4 cm^2.

We found that the use of all drugs caused significant changes in the anatomical structure of gooseberry leaves (Table 1).

Table 1.

Influence of gibberellin and retardants on the mesostructural organization of formed gooseberry leaves variety Mashenka (average values for 2015–2017)

Indicator	**Control**	**Gibberellin**	**Tebuconazole**	**Esfon**
Leaf thickness, µm	244.0±8.1	287.6±8.6*	317.7±7.3*	293.7±10.1*
The thickness of the chlorenchyma, µm	208.2±5.4	237.9±3.9*	265.5±1.7*	243.1±4.1*
The thickness of the upper epidermis, µm	18.1±0.6	26.2±0.2*	27.0±0.8*	25.3±0.8*
The thickness of the lower epidermis, µm	17.7±0.4	23.5±0.5*	25.1±0.8*	24.1±0.8*
Columnar parenchyma cell volume, μm^3	10305.5± 355.2	13446.6± 222.9*	14795.1± 371.4*	11885.3± 499.1*
The length of the cells of the spongy parenchyma, µm	28.1±0.5	33.0±0.3*	35.1±1.5*	31.0±0.9
The width of the cells of the spongy parenchyma, µm	23.6±0.5	24.23±0.6	26.1±0.5*	22.5±0.3
Chlorophyll content (a + b),% by weight of crude matter	0.56±0.01	0.51±0.01*	0.63±0.02*	0.50±0.01*

Note*:* *– the difference is significant at $p \leq 0.05$.

There was a significant thickening of the leaves of plants of the experimental variants, which indicates an increase in the concentration of structures that provide photosynthesis per leaf area unit.

The obtained data show that the thickening of the leaf occurred both due to the increase in the thickness of the main photosynthetic tissue as chlorenchyma and due to the thickening of the adaxial and abaxial epidermis. Treatment of plants with gibberellin and retardants increased the linear size of the spongy parenchyma and the volume of the main assimilation tissue of the leaf – columnar parenchyma. The most efficient effect on the mesostructure of the leaves was seen due to triazoles drug tebuconazole.

The positive effect of tebuconazole in comparison with the control and other drugs was manifested in the chlorophyll accumulation. The use of gibberellin and ethylene-producing esfon had the opposite effect: it decreased the chlorophyll content in the leaves compared to the control.

Thus, under the influence of gibberellin and retardants, the source potential of leaves increased due to the optimization of their mesostructure, as a result increasing the productivity of gooseberry culture.

Similar results were obtained during the study of the effect of retardants of different chemical structure on other crops.

Thus, the thickening of leaves and improved development of the assimilative chlorenchyma under the action of paclobutrazol was found on sugar beet plants [60]. It was found that the use of triazole-derived follicur preparation on tomatoes led to more important anatomical and morphological changes in the formation of the leaf apparatus compared to ethylene-producing esfon: the number of leaves, weight, leaf surface area and leaf index in this variant of the experiment were higher. Similarly, the mesostructural parameters of the leaves changed: the thickness of the leaf, the main photosynthetic tissue of the chlorenchyma, the size of the assimilation cells of the columnar and spongy parenchyma under the action of tebuconazole increased [21,22].

It is known that gibberellins enhance and retardants inhibit the linear growth of shoots [25,49,69]. At the same time, there is a significant restructuring of the anatomical structure of the shoots. The use of chlormequat chloride on oilseed flax plants led to thickening of the stem, increase in the number of xylem vessels in a row, increase in the thickness of the cell walls of bast fibers, which improved the resistance of flax plants to lodging [13]. Under the action of paclobutrazol on winter rape plants, the linear growth of shoots was inhibited with a simultaneous increase in the stem branching and the additional branches of the first order formation. This is contributed to a significant thickening of the stem due to the parenchyma of the primary cortex, increasing the transverse size of the sclerenchymal fibers and thickening of their cell membranes [55]. Similar changes occurred with the use of retardants on plants of potatoes [64], soy [10], oil poppy [44,45], corn [2,68]. The effect of drugs on woody plants has been much less studied. In particular, the use of chlorocholine chloride, paclobutrazol and dextrel led to a decrease in the thickness of one-year shoots of raspberries when spraying plants in the budding phase [24].

Anatomical structure analysis of one-year gooseberry shoots at the end of the growing season shows that the drugs had a typical restrictive effect: under the influence of gibberellin shoots were longer and thinner and under the action of tebuconazole – shorter and thicker (Table 2).

Changes in shoot thickness in the experimental variants were determined by the peculiarities of bark, wood and core formation of one-year shoots: under the action of tebuconazole the thickness of these histological complexes increased, and under the action of gibberellin indexes decreased compared to control. Similar results of the effect of gibberellic acid have been observed by other researchers [17].

It was found that under the action of tebuconazole retardant a larger number of vessels in the wood compared to the control and other variants of the experiment were formed. The increase in the number of vessels in bundels of xylem was accompanied by a decrease in their diameter.

Similar trend is characteristic for the action of ethylene-producer esfon. It is proved that the use of drugs contributed to the thickening of the sclerenchymal fibers of the cortex, and the greatest rates of thickening were observed under the action of tebuconazole. Gibberellin usage made thinner cell walls of sclerenchymal fibers compared to controls and retardant variants. The increase in the size of the perimedullar zone cells of the core was noted in the variant under the use of tebuconazole.

Table 2.

Anatomical and morphological structure of one-year shoots of gooseberry variety Mashenka at the end of the growing season (average values for 2015-2017)

Indicator	**Control**	**Gibberellin**	**Tebuconazole**	**Esfon**
Shoot length, см	27.7±0.8	32.2±0.9*	22.16±0.6*	18.16±0.4*
Shoot thickness, mm	5.1±0.1	4.4±0.1*	6.2±0.2*	5.2±0.1
Cortex thickness, μm	579.1±17.4	488.5±14.7*	692.5±20.8*	753.1±12.6*
Wood thikness, μm	822.4±24.6	770.5±23.1	866.6±26.1	693.0±20.8*
Core diametr, μm	2371.8±72.2	1894.4±56.8*	3147.2±94.4*	2165.5±65.6
Quantity of vessels per xylem bundels, unit	16±0.2	21±0.3*	24±0.3*	20±0.4*
Diametr of xylem vessels, μm	58.1±1.8	52.2±1.6*	50.8±1.5*	44.6±1.3*
Cell wall thickness of sclerenchymal fibers in cortex, μm	5.4±0.1	4.8±0.1*	6.1±0.1*	5.8±0.1*
Diameter of the cells of the perimedullar zone, μm	49.21±0.9	54.82±0.8*	57.96±1.1*	52.74±0.8*

Note*:* *– the difference is significant at $p \leq 0.05$.

The formation of massive wood, thickening of the cell walls of sclerenchymal fibers and trachea are the indicators of more complete maturation of shoots, which is important given the preparation of plants for the period of autumn-winter dormancy and their frost resistance. We found that anatomical changes in completely formed shoots (in October) were accompanied by biochemical composition changes of both reserve carbohydrates and structural biopolymers of shoots (Table 3).

It is known that the differentiation of sclerenchyma and xylem completes with the formation of a powerful secondary envelope due to the intensive deposition of cellulose layers and lignification of cell membranes.

Lignin provides strength to stems and leaves and, in addition, mechanical tension and protection against infection, reducing the permeability of cell walls to water. It is a complex macromolecular compound that contains a number of functional groups, in particular hydroxyl phenolic, methoxyl, etc. [41]. Lignin is localized in the cell membranes of mechanical and conductive tissues, forming in the matrix of the cell wall, filling the gaps between hemicelluloses and microfibrils of cellulose. Cell wall peroxidases are involved in lignin biosynthesis [46].

Table 3.

Gibberellin and tebuconazole influence on chemical composition of gooseberry shoots of Mashenka variety at the end of the growing season (% by weight of dry matter, average values for 2015-2017)

Substance	**Control**	**Gibberellin**	**Tebuconazole**	**Esfon**
Cellulose	23.61±0.71	27.46±0.82*	30.21±0.90*	25.68±0.68
Lignin	14.92±0.45	15.11±0.37	17.42±0.53*	16.14±0.24*
Hemicellulose	17.28±0.52	22.66±0.68*	18.99±0.56	18.09±0.54
Pentosans	12.03±0.36	12.92±0.38	12.50±0.37	11.28±0.34
Pectins	6.97±0.10	5.86±0.08*	6.96±0.11	6.44±0.04*
Sugar content (sugar+starch)	7.25±0.22	11.27±0.34*	11.60±0.35*	9.32±0.28*
Reducing sugar	2.55±0.08	3.96±0.12*	4.50±0.14*	3.24±0.09*
Sucrose	2.66±0.05	4.94±0.09*	4.93±0.09	4.02±0.08*
Total sugar	5.35 ±0.16	9.16±0.27*	9.69± 0.29*	7.47±0.29*
Starch	1.90±0.05	2.11±0.08	1.91±0.05	1.85±0.07

Note*:* *– the difference is significant at $p \leq 0.05$.

Under the action of tebuconazole, the content of the main structural biopolymers like cellulose and lignin in the shoots of this variant was the highest. The lignin content is a test indicator of wood maturation, which is important for increasing the frost resistance of gooseberry plants [25]. Under the action of gibberellin, a more intensive accumulation of hemicelluloses and a decrease in the content of pectin substances was found in comparison with tebuconazole, and under the action of both drugs the content of these biopolymers was increased in comparison with the control.

The results of the study indicate that the main fraction of hemicelluloses of gooseberry shoots were pentosans. Its content increased under the action of gibberellin and tebuconazole in comparison to control. This has a positive effect, because of its possible hemicellulose use as a reserve substance during critical periods of plant growth and development [47].

Previously, significant depositional potential of the vegetative organs of tomato plants – stems and roots in the temporary accumulation of reserve carbohydrates and their subsequent use for fruit formation and growth [26,32]. The data obtained in this study indicate a significant deposit role of gooseberry stem in preparation for autumn-winter dormancy. Under the action of tebuconazole and gibberellin retardant, the content of sugars, starch and their total content in one-year shoots of gooseberry plants of the experimental variants was higher compared to the control (see Table 3).

1.2. Accumulation and redistribution of various forms of carbohydrates in gooseberries under the action of gibberellin and retardants

It is known that part of the assimilates can be temporarily deposited in the reserves with subsequent re-utilization for the processes of carpogenesis [37, 51]. In our opinion, for assessing the source and deposit capacity of vegetative organs according to the experimental options, it is advisable to determine the dynamics and ratio of non-structural carbohydrates in plant organs at different stages of fruit formation. Our results show that during the whole period of development due to the formation of a stronger mesostructure under the influence of drugs, the content of nonstructural carbohydrates (sugars + starch) in the leaves was consistently higher than in control (Table 4). In the variant of tebuconazole, the content of non-structural carbohydratesin leaves was maximum compared to other variants at the phase of formation and complete fruit ripeness. In our opinion, this indicates greater photosynthetic and source activity of the leaves under the action of this drug due to the formation of the optimal mesostructure and growing chlorophyll content.

Table 4.

The effect of gibberellin and retardants on the content of sugars and starch in leaves and stems of gooseberry Mashenka variety at different phases of development (% by weight of dry matter, average values for 2015-2017)

Development phase	**Sugar content (total sugar+starch)**				**Total sugar**				**Starch**			
	Control	**Gibberellin**	**Tebuconazole**	**Esfon**	**Control**	**Gibberellin**	**Tebuconazole**	**Esfon**	**Control**	**Gibberellin**	**Tebuconazole**	**Esfon**
	Leaf											
Flowering	11.30± 0.24	13.30± 0.28*	11.90± 0.24	11.91± 0.24	10.01± 0.20	11.70± 0.24*	10.71± 0.21	10.50± 0.22	1.31± 0.02	1.60± 0.04*	1.22± 0.02*	1.40± 0.03*
Fruit formation	10.30± 0.21	12.40±* 0.24	12.90± 0.26*	11.70± 0.24*	10.20± 0.20	10.60± 0.22	11.20± 0.22*	10.31± 0.22	1.50± 0.03	1.81± 0.04*	1.70± 0.03*	1.42± 0.02
Complete fruit ripeness	11.40± 0.22	11.71± 0.24	13.30± 0.27*	12.50± 0.26*	10.30± 0.21	9.50± 0.20*	11.20± 0.22*	10.21± 0.21	1.10± 0.02	2.21± 0.05*	2.11± 0.06*	2.30± 0.05*
	Stem											
Flowering	12.10± 0.24	12.70± 0.26	12.81± 0.26	11.40± 0.23	10.80± 0.22	11.40± 0.23	11.30± 0.18	10.20± 0.22	1.31± 0.02	1.34± 0.02	1.51± 0.02*	1.20± 0.02*
Fruit formation	8.40± 0.16	10.71± 0.26*	9.10± 0.18*	10.10± 0.20*	6.70± 0.14	8.70± 0.18*	7.10± 0.16	8.50± 0.18*	1.72± 0.04	2.02± 0.04*	2.01± 0.04*	1.60± 0.04
Complete fruit ripeness	8.30± 0.18	9.90± 0.20*	10.70± 0.22*	9.20± 0.18*	7.10± 0.16	8.10± 0.16*	8.60± 0.17*	7.51± 0.16	1.20± 0.02	1.82± 0.04*	2.11± 0.06*	1.72± 0.03*

Note: *– the difference is significant at $p \leq 0.05$.

It is known that the excess of assimilates can be temporarily deposited not only in the leaves but also in other organs of the plant, followed by their acceptance by the processes of vegetative growth or carpogenesis.

The results of the study indicate a powerful deposit role of gooseberry stem in the regulation of growth and fruit formation of plants. The content of sugars and starch and their total content was close to the content of these carbohydrates in photosynthetic organs, ie in leaves. In general, similar pattern to the leaves was observed: the content of non-structural carbohydrates in plants of the experimental variants was higher compared to control.

In our opinion, the enhancement of source function of the leaves of the variant under the use of tebuconazole was evidenced by the fact of increased content of nonstructural carbohydrates in both leaves and stems of gooseberry experience at the phase of full ripeness of fruits due to cessation of vegetative growth and end of carpogenesis. At the same time, in one-year stalks it was accumulated more starch and sugars in comparison with other variants of experiment. The results of study of the dynamics of the reducing sugars content and sucrose content in leaves and stems of gooseberries at different phases of plant ontogenesis give a fairly clear idea of the peculiarities of sugars accumulation and redistribution between plant organs (Table 5).

Thus, generally, leaves accumulated more reducing sugars and sucrose at the flowering and fruit formation phase. During the transition to the phase of complete ripeness, the content of both forms of sugars decreased in the variants with gibberellin and retardants compared to the control, which, in our opinion, indicates the better provision of carpogenesis process with carbohydrates. The most intense outflow of reducing sugars and sucrose was in the variant with tebuconazole.

In the control variant, the reducing sugar content did not change during this period. A similar correlation in the different forms of sugars' dynamics under the action of used drugs was found for the stem.

Re-utilization of deposited sugars from the stem for the needs of growth and fruit formation starting from the fruit formation phase to the phase of complete ripeness took place both in the variant treated with gibberellin and with retardants.

Table 5.

The effect of gibberellin and retardants on the content of various sugars in leaves and stems of gooseberry variety Mashenka at different phases of development (% by weight of dry matter, average values for 2015-2017)

Development phase	**Reducing sugar content**				**Sucrose content**			
	Control	**Gibberellin**	**Tebuconazole**	**Esfon**	**Control**	**Gibberellin**	**Tebuconazole**	**Esfon**
Flowering	Leaf							
	8,80±0,24	10,52±0,31*	9,60±0,29	9,71±0,27*	0,91±0,03	1,40±0,04*	1,31±0,04*	0,80±0,02*
Fruit formation	9,11±0,28	9,31±0,27	10,40±0,32*	9,22±0,28	1,33±0,05	1,43±0,04	1,52±0,04*	1,40±0,04
Complete fruit ripeness	9,20±0,28	8,71±0,25	9,82±0,29	8,84±0,28	1,11±0,03	1,01±0,03*	1,23±0,02*	1,20±0,04
Flowering	Stem							
	10,51±0,31	10,60±0,32	11,33±0,34	10,11±0,30	0,80±0,02	1,02±0,03*	1,10±0,03*	0,81±0,02
Fruit formation	6,12±0,18	8,20±0,25*	7,31±0,22*	7,01±0,22*	0,71±0,02	1,14±0,03*	1,12±0,03*	1,01±0,02*
Complete fruit ripeness	6,60±0,20	7,32±0,22	7,60±0,23*	6,50±0,20	0,72±0,02	0,90±0,03*	0,81±0,02*	0,80±0,02*

Note*:* *– the difference is significant at $p \leq 0.05$.

While in control the sucrose and reducing sugar content either did not change or even increased. Since sucrose is the main form of transport of sugars in the plant, this, in our opinion, indicates an earlier cessation of carbohydrates transport to the fruit in the last phase of their development in plants of the control variant.

Thus, under the action of gibberellin and retardants, the outflow of all forms of sugars from leaves and stems of gooseberry plants to a powerful sink zone of fruit formation and growth increases. The results of the research also indicate that the optimization of the mesostructural organization of leaves, increasing the accumulation of carbohydrates in them under the action of the drugs creates not only an excess of assimilates used during carpogenesis. Significant difference in reserve carbohydrates content in stems is maintained between the experimental variants and control throughout the one-year development cycle. Thus, at the end of the growth period and the transition to the autumn-winter dormancy state (late October), the stems of plants treated with tebuconazole, gibberellin and esfon contained more non-structural carbohydrates (sugars and starch) than the control (see Table 3).

That is essential because the accumulation of reserve carbohydrates in wintering tissues is an important prerequisite for higher frost resistance of woody plants.

The most effective in this aspect was also the use of triazole retardant tebuconazole.

1.3. The effect of gibberellin and retardants on the content of nitrogen, phosphorus and potassium in vegetative organs of gooseberry plants during the growing season

The main patterns of photosynthetic processes and redistribution of assimilate flows through the plant during the growth rate changing of individual organs are sufficiently studied within the concept of source-sink system functioning in plant [37].

Maintaining of certain ratios of nutrients is a necessary condition for proper growth and development of plants. Since retardants are modifiers of hormonal-inhibitory balance in the plant, the question about changes in the redistribution of mineral nutrients between plant organs under the action of drugs in this group arises.

Scientists argue that there is a strong correlation between growth rate, respiration, photosynthesis, production process and nitrogen nutrition of plants. It is established that under the action of retardants and other growth regulators, the change in the activity of growth processes may be accompanied not only by plastic substances' redistribution between the source and sink spheres of the plant but also by nutrients [32]. It was found that the photosynthetic activity and nitrogen status of the plant affect the accumulation of dry matter and nitrogen in wheat ear before and during flowering, and both parameters correlate with the number of ovaries [5]. It has been suggested that earlier flowering may play a role in age deceleration. The yield increase in correlated in time with a decreasing in stoma resistance and specific nitrogen content in leaves. It is believed that a systematic approach to improving the quality of wheat grain should be connected with use measures to improve the absorption and distribution of nitrogen between plant organs, intensify the photosynthetic apparatus and its coordination with the re-mobilization of nitrogen from vegetative parts to grain during its filling, as well as maintaining ability to nitrogen uptake during grain growth. It is necessary to increase the efficiency of re-mobilization of nitrogen-containing compounds from the vegetative organs at the end of the growing season and control the fractionation of nitrogen-containing compounds in grain between different forms of protein to improve the baking quality of flour.

Metabolism of nitrogen compounds under the influence of retardants is sufficiently studied in potato plants [62, 63], oil poppy [45], tomatoes [32], oil flax [12], etc. In treated potato plants under the action of retardants in the early stages of vegetation increased nitrogen content in all organs of the plant. During the growing season there was a gradual decrease in the element content in organs, due to the intensity of organic matter accumulation and biodilution of the element content [62,64]. In the case of absence of nitrogen nutrition, plant organs are overfilled with carbohydrates, which, in its turn, causes plant growth and development decelerations.

Negative is the excess of nitrogen, which does not correspond to the level of phosphorus-potassium nutrition as it leads to an increase of non-protein nitrogen in the organs [65]. It was found that the high supply of alfalfa plants with phosphorus and nitrogen in the initial period of development significantly improves the further growth of the plant [16].

Under the action of chlormequat chloride in oilseed flax plants, the maximum amount of nitrogen-containing substances in leaves and stems was noted during the initial stages of development, while the leaves had a higher nitrogen content compared to other organs. The total nitrogen content in tleaves was in 2.6-3 times higher than in stems, protein fraction of nitrogen was in 3.2-3.5 times higher [12]. Similar results were obtained by other researchers on sunflower plants [52,53], rape [56].

Analysis of scientific sources shows that under conditions of photo- and scotomorphogenesis there was a significant outflow of nitrogen from the cotyledons to seedlings, ie cotyledon protein was used more intensively for growth processes in the formation of seedling structures under photomorphogenesis. At the same time, inhibition of growth by retardant slowed down, and acceleration by gibberellin intensified this process both under conditions of photo- and scotomorphogenesis [48].

Much less information on the retardant's effect on nitrogen metabolism of fruit and berry crops. It was found that under the action of chlorocholine chloride from the start of shoot growth there was an increase in total and protein nitrogen content in stems and leaves of raspberries. There was a decrease in the non-protein nitrogen content in leaves of strawberries and raspberry stems, which with the overall nitrogen content increase was due to the intensive use of this fraction for protein formation [24]. However, the peculiarities of the mineral nutrients supply and their re-distribution in plant organs under the action of gibberellin and retardants in connection with the productivity of crops have not been studied enough.

Our analysis of the dynamics of nitrogen-containing compounds in leaves and one-year stems of gooseberries at different phases of plant development shows that under the action of all drugs there was a more intense accumulation of nitrogen in the vegetative organs of the plant – leaves and stems (Fig. 1).

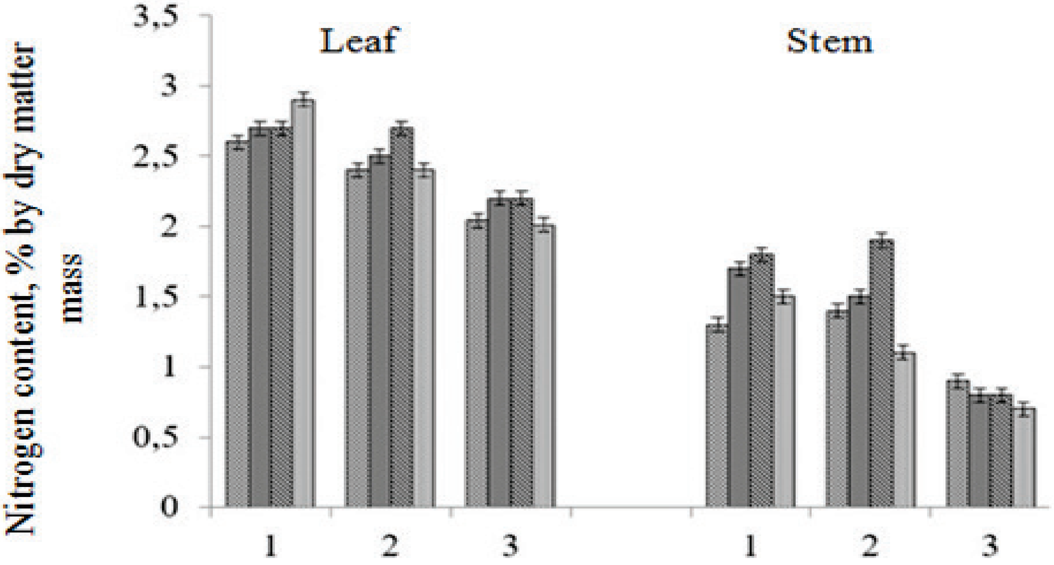


Figure 1. Influence of gibberellin and retardants on nitrogen content in vegetative organs of gooseberry plants of variety Mashenka at different phases of development: 1 - flowering phase; 2 - fruit formation phase; 3 - phase of complete ripeness. ▦ - control; ▩ - 0,005 % gibberellin; ▧ - 0,025 % tebuconazole; ▦ - 0,1 % esfon.

The deposit role of the stem in the accumulation of nitrogen is significant. Under the action of drugs, the nitrogen content significantly exceeded the control variant.

Tebuconazole was the most effective when the nitrogen content was the highest in plants. In all variants of the experiment there was a gradual decrease in the nitrogen content in tissues of leaf and stem at fruit formation and complete ripeness phases. In our opinion, such significant decrease in the content of nitrogenous substances in the vegetative organs during ontogenesis indicates intensive re-utilization and outflow of these compounds for the needs of carpogenesis – the formation and development of fruits. The most significant decrease in nitrogen content occurred under the action of tebuconazole and gibberellin.

There is significantly less data on the effect of retardants on the intake and metabolism of phosphorus in plants. The use of chlorocholine chloride on corn seedlings increased the absorption of phosphorus by the roots, and also accelerated their movement up the plant [4]. An increase in the phosphorus content in leaves and a decrease in roots were observed in sugar beet due to the action of dextrel and paclobutrazol [60]. It was found that the action of inorganic phosphorus in the composition of nucleotides was inhibited by the action of chlorocholine chloride on wheat and oats [74].

Peculiarities of phosphorus re-distribution between plant organs in ontogenesis are similar to nitrogen one. Our data show that the phosphorus content throughout the fruiting period was decreased in leaves and stems of experimental plants of gooseberry under the action of drugs (Fig. 2).

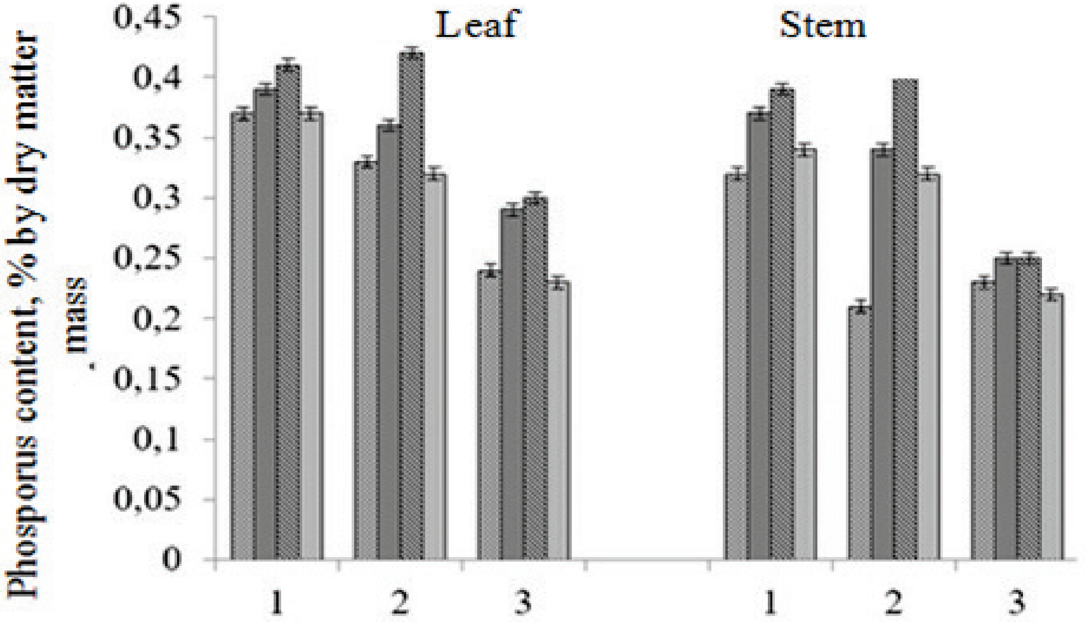


Figure.2. Influence of gibberellin and retardants on phosphorus content in vegetative organs of gooseberry plants of variety Mashenka at different phases of development: 1 - flowering phase; 2 - fruit formation phase; 3 - phase of complete ripeness. ▒ - control; ▓ - 0,005 % gibberellin; ▧ - 0,025 % tebuconazole; ░ - 0,1 % esfon.

In our opinion, a similar mechanism of nitrogen and phosphorus accumulation in plant organs indicates a close connection between the metabolism of these elements. Under the action of tebuconazole and gibberellin, the phosphorus content in the vegetative organs of gooseberry was maximum in comparison with the control and the esfon variant. It is also noteworthy that the significant storage capacity of gooseberry plants' stem in relation to phosphorus: the content of this element did not differ from its content in leaves. As for nitrogen-containing compounds, it was observed more intense outflow of phosphorus in the phase of fruit formation and full ripeness under the action of tebuconazole and gibberellin.

It is known that potassium significantly affects the transport of assimilates through the plant, the synthesis of reserve polycarbohydrates [14]. The increase in potassium content in leaves under the action of retardants is a prerequisite for higher metabolism rates in them. The obtained data indicate that the use of drugs significantly affected the supply of potassium to the vegetative organs of gooseberry plants (Fig. 3).

Tebuconazole and gibberellin had the most significant effects. In these variants it was the highest potassium content in leaves and stems of gooseberry plants recorded during the flowering phase. At the same time, there was no significant effect of drugs on the dynamics of element reduction in tissues of leaves and stems during ontogenesis.

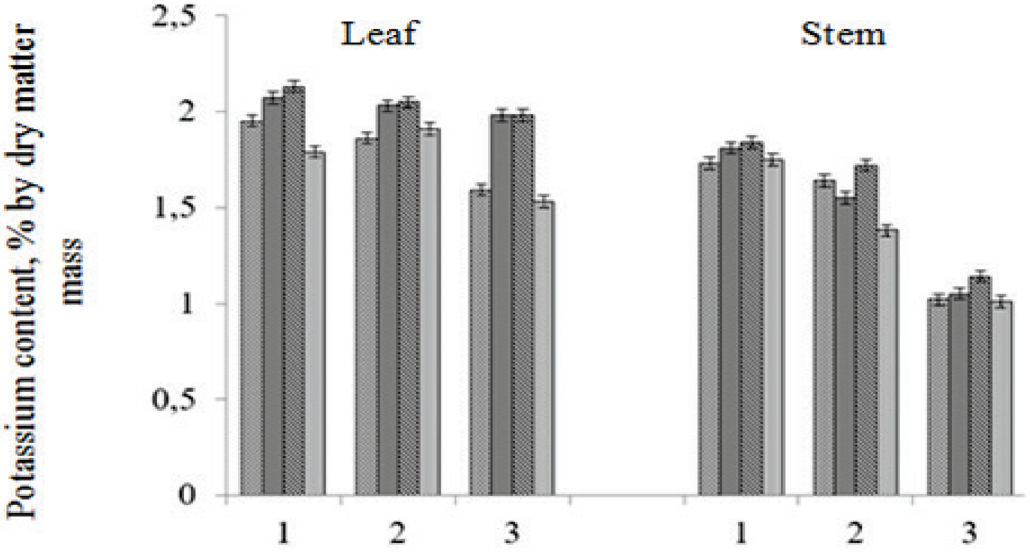


Figure 3. Influence of gibberellin and retardants on potasium content in vegetative organs of gooseberry plants of variety Mashenka at different phases of development: 1 - flowering phase; 2 - fruit formation phase; 3 - phase of complete ripeness. ▦ - control; ▩ - 0,005 % gibberellin; ▧ - 0,025 % tebuconazole; ░ - 0,1 % esfon.

Thus, the obtained data prove the effectiveness of the use of growth regulators for the accumulation and redistribution of the main nutrients as nitrogen, phosphorus and potassium. The action of tebuconazole and gibberellin intensified the accumulation of these elements in leaves and stems of gooseberry plants. The stem also plays a significant deposit function in accumulation of these elements in the plant.

1.4. Yield of gooseberries under the action of gibberellin and retardants of different types

The important component in the technology of yield increasing of agricultural products is the use of plant growth regulators, which in very small doses can significantly increase plant viability, increase their resistance to diseases, pests, adverse environmental conditions, ie increase productivity and improve crop quality. The main role in the forming of plant productivity is played by the processes of photosynthesis, growth and deposition of substances in reserve, that is why the peculiarities of the functioning of the source-sink system of crops in exogenous regulation of growth processes is extremely important.

The experimental data presented in the previous chaptes show that the use of gibberellin and various types of retardants for optimizing of growth processes and development of gooseberry plants leads to significant changes in the organization of the photosynthetic apparatus, growth changes, morphogenesis and the nature of source-sink relations. In particular, the use of gibberellin and tebuconazole led to the optimization of the leaves' mesostructure. Under the action of the drugs, the mesostructural parameters of gooseberry leaves changed: the leaf thickness increased due to the increase of the main photosynthetic tissue – chlorenchyma, thickening of the upper and lower epidermis, increase of linear size of spongy paremchima and volume of the main assimilation tissue of the leaf – columnar paremchima. The most impactful effect on the leaf mesostructure was carried out by the triazole drug tebuconazole (see Table. 1). Inhibition of linear shoot growth with simultaneous rearrangement of leaf mesostructure under the action of retardants enhanced the synthesis of nonstructural carbohydrates and their accumulation in the vegetative organs of gooseberry plants, which increased the carbohydrate reserve for fruit formation and growth (see Table 4). The results of studying the effect of gibberellin and retardants on the content of nitrogen, phosphorus and potassium in leaves and stems of gooseberries during ontogenesis indicate that the drugs cause significant changes in the accumulation of these elements. Under the action of tebuconazole and gibberellin there was an accumulation of nitrogen, phosphorus and potassium in the tissues of leaves and stems of gooseberry plants (see Fig. 1, 2, 3.), which was a prerequisite for increasing crop yields.

Restructuring of source-sink relations under the action of retardants, changes in the formation and functioning of the photosynthetic apparatus, the peculiarities of the accumulation of assimilates and their distribution between plant organs significantly affected the yield of crops.

The influence of different types of retardants and gibberellin on productivity and quality indicators of crop products are analyzed in separate scientific publications. It was found that the use of chlormequat chloride in oilseed flax culture contributed to yields and significantly changed of quality indicators. In the experimental variants, the number of capsules per plant was increased. The maximum number of seeds in fruit was noted by the action of chlormequat chloride and its mixture with treptolem. Under the effect of growth regulators, seed weight increased by 2.5 - 4%. The greatest increase in yield was provided by the use of retardant and its mixture with a growth stimulant (by 0.15-0.26 t / ha) [13]. A similar effect was exerted by the use of retardants on oil poppy culture. During treatment with drugs there was a significant increase in the number of capsule fruits per plant. At the same time, weight of 1000 seeds and the weight of seeds per capsule grew. The most effective was the use of treptolem and chlormequat chloride mixture [45]. The use of growth regulators on sunflower plants improved oil quality due to the increase in unsaturated fatty acids content due to linoleic acid. The most effective in improving of sunflower oil quality characteristics was the integrated use of chlormequat chloride and treptolem [52]. It was found that treatment of plants with retardants increased soybean productivity. In particular, the number and weight of seeds per plant increased. There were changes in oil quality, namely increase of the ratio of unsaturated to saturated fatty acids [10].

Analysis of the effect of retardants on the productivity of tomatoes shows that the treatment of plants with triazole drug folicur increased crop yields by increasing the average fruit weight. It should be noted that the use of drugs significantly increased the total acidity in all experimental variants, while increasing sugar content and decreasing ascorbic acid content under the influence of tebuconazole. There was a decrease in sugar content under the action of esfon compared to control [32]. On sugar beet plants it was found that 0.025% paclobutrazol treatment of plants during the 14 - 16 and 38 - 40 leaves formation increased the yield of root vegetables by 22% and sugar content by 1%. This reduces the ratio of dry matter of greens and roots, which indicates an increase in the economic efficiency of the crop. It is proved that the treatment of sugar beet plants in the first year of development with 0.3% dextrel, 0.025% and 0.05% paclobutrazol increases the seed productivity of seedlings in the transplanting method of cultivation and increases the fruit weight of the smallest fraction. In raspberry plants, the use of retardants at early stages of development caused a significant yield increase due to changes in plant architecture, growth deceleration of substitutive shoots, improving of fruiting shoots conditions and open placing of flowers and berries of raspberry plants [18].

It is known that the deep physiological rearrangement of plants under the action of drugs can significantly affect the productivity of berry crops. Accordingly, one of the prerequisites for the use of gibberellin and various types of retardants on gooseberry plants is to control the yield rates and its quality.

The use of gibberellin and retardants in gooseberry culture at early stages of development had different effects on yield and product quality (Table 6).

Treatment of gooseberry plants with tebuconazole and gibberellin significantly increased yields, both from the bush and the coenosis in general. The most effective was the use of tebuconazole: in this variant the yield was increased by 29%. Close to this value was the effectiveness of gibberellin as yield was increased by 22%.

Table 6.

Influence of gibberellin and retardants on yield and quality of gooseberry output of variety Mashenka (average values for 2015 - 2017)

Indicators	**Control**	**Gibberellin**	**Tebuconazole**	**Esfon**
Yield, t/ha	14.21±0.28	17.33±0.42*	18.32±0.38*	14.70±0.26
Yield per bush, kg	2.90±0.05	3.50±0.06*	3.70±0.07*	3.10±0.04*
Acidity, %	1.90±0.07	1.89±0.03	2.20±0.06*	2.01±0.04
Ascorbic acid, mg/100g	20.82±0.41	23.10±0.45*	24.21±0.48*	21.30±0.42
Sugar content, % by crude matter	7.40±0.16	8.40±0.17*	9.01±0.18*	8.31±0.16*

Note*:* *– the difference is significant at $p \leq 0.05$.

Important indicators of retardant use are the qualitative characteristics of the product, ie the content of ascorbic acid, the amount of sugars and total acidity. The results show that the drugs' use increased the content of ascorbic acid and sugars in berries, ie it helped to improve product quality. A slight increase in the acidity of the berries is within the range of fluctuations that are typical for gooseberries in different climatic conditions. The use of ethylene producer as a retardant to increase yields was ineffective.

Thus, the obtained data show that the yield of gooseberry culture was increased due to the formation of a more powerful source sphere, accumulation and redistribution of assimilate flows and basic nutrients from vegetative organs to fruits under the action of drugs. The most viable was the use of triazole drug tebuconazole for increasing the productivity of gooseberry plants.

Conclusions

On the basis of the conducted experimental researches and received data were formulated following conclusions:

1. Treatment of gooseberry plants with gibberellin and retardants of different

types at budding phase led to modification of source-sink relations in plant, which was realized through anatomical and morphological changes of vegetative organs, redistribution of assimilates and minerals towards berry formation.

2. The use of drugs had a significant impact on the organo- and histogenesis of gooseberry plants. The action of tebuconazole inhibited the linear growth of shoots with simultaneous thickening of the stem. Esfon did not cause the thickening, and the use of gibberellin had the opposite result: elongation and thinning of the stem. The action of tebuconazole formed a larger number of xylem vessels compared to the control and gibberellin, while increasing the cell wall thickness of the sclerenchymal fibers of cortex. The consequence of such a re-structuring under the action of retardants was cellulose, hemicellulose and lignin accumulation in one-year shoots of gooseberry in comparison to control, which is evidence by a more complete shoot maturation.

3. The use of gibberellic acid and retardants led to the formation of a more powerful photosynthetic apparatus. The leaf area decreased under the action of retardants, and gibberellin increased it compared to control. However, in all variants of the experiment, a thickening of the leaf blade was noted due to the formation of a stronger chlorenchyma, and volume and linear size increase of its cells. The most effective was the use of tebuconazole. Under the action of this drug there was a significant increase in the content of chlorophyll in leaf tissues.

4. Optimization of the mesostructural organization of the leaf enhanced the provision of morphogenesis processes by assimilates, which manifested itself in an increase of nonstructural carbohydrates (sum of sugars + starch) content in leaves compared to untreated plants at all development phases.

5. It has been established the important deposit function of stem in the regulation of source-sink relations of gooseberry. Carbohydrates content in this vegetative organ was close to the content in leaves. Under the action of drugs, the carbohydrate content in gooseberry stem increased compared to control. During fruiting, the content of non-structural carbohydrates in stem decreased due to re-utilization to the processes of carpogenesis.

6. The use of growth regulators significantly affected the accumulation and redistribution of basic nutrients – nitrogen, phosphorus, potassium. There was a more intensive accumulation of these elements in the leaves and stems of gooseberry plants under the action of tebuconazole and gibberellin. Stem plays a significant deposit function of the elements' accumulation in plant.

7. Yield of gooseberry culture increased due to the formation of a more powerful source sphere, accumulation and redistribution of flows of assimilates and basic nutrients from vegetative organs to fruit. The use of triazole drug tebuconazole was the most effective for increasing of productivity without significant changes in product quality.

CHAPTER 2.
EFFECT OF PHYTHORHORMON ANOLOGUES AND RETARDANT TEBUCONAZOLE ON GROWTH PROCESSES, MORPHOGENESIS AND YIELD OF SWEET PEPPER

Introduction

Analysis of world crop production trends shows that one of the ways to solve the problem of high and stable yields is the use of new technologies basing on plant growth regulators [11,44]. The list of these substances that are able to change the intensity of physiological processes of plants in the correct direction is annually updated. Low consumption rates of growth regulators affect morphogenesis, increase plant resistance to external factors and increase yields, which determines the feasibility of their use [2,49,58]. Such drugs are either anologues of phytohormones or modifiers of the hormonal status of plants by their nature [5,12,44].

Due to this, synthetic growth regulators have a wide range of effects on the plant, and their use allows to target individual stages of growth and development in order to mobilize the potential of the plant organism [19, 31]. The first application of these compounds is associated with the intensification of growth and development due to increased cell division and stretching, resulting in a more powerful assimilation apparatus of the plant with the subsequent creation of bigger amount of nutritive compounds in it, which will be sent to productive organs. For this purpose, phytohormones-stimulators and their synthetic anologues are used. The second direction is related to the inhibition of growth processes, which is accompanied by the accumulation of excess assimilates and their re-distribution between the organs of the plant organism. Usually it occurs in the direction of economically important organs, against the background of changes in source-sink relations in the whole plant. For this purpose, growth inhibitors are used – retardants [25,51].

Under the influence of growth and development regulators the hormonal status of the plant organism [4, 32,39], carbohydrate and nitrogen metabolism [20, 28, 47] are changed, increases cold resistance [17], salt-resistance [1] and drought resistance

[14, 22,43,44,56], and plant resistance to phytopathogens improves [15]. The effectivety of growth regulators largely depends on soil-climatic conditions, species and varietal specificity, phases of plant development, regulations for the use of drugs.

The search for optimal conditions for the use of restrictive substances, taking into account the complex features of their action on various agricultural plants remains an important practical task of modern phytophysiology. Regulations for the use of growth regulators have been developed for many food, technical, fodder and ornamental crops [24].

Increasing the yield of vegetable crops is possible due to many factors: the introduction into production of new, more productive varieties, the introduction of varietal zoning, in which the placement of different early varieties is carried out taking into account the agro-climatic resources of the territory to biological characteristics of these crops. At the same time, the influence of synthetic analogues of phytohormones and modifiers of their action on morphogenesis, photosynthetic activity, supply and redistribution of mineral nutrients and yield of vegetable nightshade crops, in particular sweet pepper, remains poorly understood. In this regard, the aim of the study was to determine the effect of different directions of action of growth and development regulators – stimulants (gibberellic acid, 1-naphthylacetic acid and 6-benzylaminopurine) and growth inhibitor (tebuconazole retardant) on the morphogenesis and yield of sweet pepper crops, as well as to develop effective regulations for their use in the Right-bank forest-steppe of Ukraine.

Research methods

The experimental part of the work was carried out in the laboratory of plant physiology and biochemistry of the Department of Biology of Vinnytsia State Pedagogical University named after Mykhailo Kotsyubynsky and in the peasant farm «Berzhan P.G.» v.Gorbanivka, Vinnytsia district, Vinnytsia region, vegetation periods of 2013–2015. The effect of 1-NAA (1-naphthylacetic acid), GA_3 (gibberellic acid), 6-BAP (6-benzylaminopurine) and tebuconazole on the morphogenesis and productivity of sweet pepper Antey variety was examined during the experiments.

1-Naphthylacetic acid is a white powdery substance with a molecular weight of 186.21 D and the molecular formula $C_{12}H_{10}O_2$. Melting point is 126–133.5°C, boiling point is 372°C, ignition temperature is 270.1°C. It decomposes at temperature of 360°C. Technical name of compound is 1-NAA.

1-Naphthylacetic acid is a low-toxic compound and belongs to the 3rd toxicity class. The LD50 for white rats is 1753 mg/kg. The drug is practically non-toxic to bees and low-toxic to fish. The drug is used as a growth regulator of stimulating action. The plant is absorbed through the roots and leaves. 1-NAA is an analog of the natural phytohormones’ action – auxins. The drug is poorly soluble in water and soluble in organic solvents [59].

Gibberellic acid (GA) is a white crystalline substance with a molecular weight of 346.2 D, with the molecular formula $C_{19}H_{22}O_6$. Melting point is 227°C. The substance is poorly soluble in water and well soluble in organic solvents. Gibberellic acid is a low-toxic compound and belongs to the 3rd toxicity class. LD50 for rats is 15630 mg/kg. It does not show carcinogenic, blastomogenic, skin-resorptive and embryotoxic properties. Residual amounts are determined by high performance thin-layer chromatography. The residual content of the drug is not normalized, because in plants it is present as a natural metabolite. The drug is non-toxic to bees and other insects, low-toxic to fish. It is used as plant growth regulator. The drug is obtained by fermentolysis of fungi of the species Gibberella fuljukoi and Fusarium moniliforme.

6-benzylaminopurine (benzyladenine) is a yellowish-white powdery substance with a molecular weight of 225.25 D and the molecular formula $C_{12}H_{11}N_5$. Melting point is 229.51°C. It decomposes at a boiling temperature of 245°C. The technical name of the compound is 6-BAP. The drug is poorly soluble in water and soluble in organic solvents. It is used as a growth regulator of stimulant action. It enters the plant through the roots and leaves. 6-BAP is an analog of natural phytohormones – cytokinins [57].

Tebuconazole is a triazole-derived retardant. It is also used as a systemic fungicide with a broad spectrum of action to protect rapeseed and cereals from a complex of diseases. It has the properties of a growth regulator on winter oilseed rape. Active substance of tebuconazole – 4,4-dimethyl-3-(1H-1,2,4-triazol-1-ylmethyl)-1-n-chlorophenylpentan-3-ol. It is transparent crystalline substance with a melting point of 104.7°C. It is poorly soluble in water, good soluble in organic solvents. It is not hydrolyzed at pH from 4 to 7 in water at 20°C for more than a year [30].

Pepper seeds for seedlings were sown in greenhouses on the 20th of February, 2013, on the 18th of February, 2014 and on the 22th of February, 2015. Seedlings were planted on the 22th of May, 2013, on the 8th of May, 2014 and on the 15th of May, 2015 in a tape method according to the 80+50+50×25 formula. The location of the plots is randomized. The area of the plots is 10 m2. The frequency is fivefold. Morphological parameters (plant height, stem thickness, crude and dry weight of plants) were determined every 10 days, the area of leaves was determined by weight [18].

Plants were treated in the morning with a knapsack sprayer OP-2 until complete wetting of the leaves with 0.005% solution of 1-NAA, 0.005% solution of GA_3, 0.005% solution of 6-BAP and 0.025% solution of tebuconazole. The location of the plots is randomized, the area of the plots is 10 m2, the frequency is fivefold. The mesostructural organization of leaves was studied at the end of the growing season on fixed material. The leaf index was studied as the area of all green leaves per unit of soil surface. It was calculated according to the recommendations by Pryadkina G.A. [42]. The chlorophyll content in fresh material was determined by spectrophotometric method on a spectrophotometer SP-16, the content of sugars, reducing sugars and starch in the vegetative organs was determined by iodometric method, phosphorus – by the formation of phosphorus-molybdenum complex with photo-molybdenum method, total nitrogen was determined by using Kjeldahl method [3]. Statistical processing of the results was performed using the software package Statistica-6. The tables and figures show the arithmetic mean values for 3 years of the experimenent and their standard errors.

2.1. Anatomical and morphological changes of sweet pepper plants under the action of phytohormone anologues and tebuconazole retardant

Anatomical and morphological changes of the plants under the action of growth regulators significantly affect the productivity of crops. This effect is manifested in the change in the ratio of the source and sink spheres' activity of the plant [6,7,8,41]. The processes of photosynthesis, which constitute the essence of the source function of the leaf, depending on the physiological and mesostructural features of the leaf, and on the total leaf area at the level of coenosis.

The obtained results indicate a significant effect of phytohormone anologues and a representative of the class of retardants – tebuconazole on the rate of growth processes [36]. It was found that the more intensive plant growth occurred under the action of gibberellic acid, which is a typical reaction to this phytohormone [45]. Similar results were obtained under the action of gibberellic acid on the growth of tomatoes of different varieties [23,30].

In many cases, there was an increase in crop productivity with the use of drugs of the retardant group, which are antigiberellins by the action mechanism. It is known that they block the synthesis or action of already synthesized gibberellin [30]. The results confirm the typical effect of the retardant of the triazole series tebuconazole on the growth of sweet pepper. Under the action of the drug, plant height was the lowest among all variants of the experiment. The use of 1-NAA and cytokinin analog 6-BAP did not lead to significant changes in the length of sweet pepper plants compared to the control [36]. The use of drugs led to thickening of the stem. In particular, it was 1.3±0.07 cm in the variant with auxin, with gibberellin – 1.2±0.06 cm, with cytokinin – 1.3±0.07 cm, in the variant with tebuconazole – 1.4±0.08 cm, contrary to 1.1±0.05 cm in control variant. The most effective was the use of the drug tebuconazole. This effect of the retardant on the stem growth in thickness is typical and recorded in many crops: winter rape [48], potatoes [53], oil flax [20], sunflower [46], soybean [13], oil poppy [41] and others.

It is known that growth regulators affect the formation of the leaf blade [30], and accordingly the photosynthetic productivity of crops. At the same time, there is lack information in the scientific literature on the comparative effect of synthetic growth regulators of different chemical nature on the morphological parameters and anatomical structure of sweet pepper leaves. Our results indicate that the used drugs increased the number of leaves per plant [36]. It was found that tebuconazole increased the number of sweet pepper leaves most effectively. Significantly increased the rate of application, 6-BAP and GA_3. Action 1-NAA was the least effective compared to other drugs.A similar increase in the number of leaves under the action of retardants was observed in other crops, which is explained by more intensive branching of the stem under the action of these drugs compared to the control [30].

A similar trend is generally established for the indicators of dry and crude matter mass of leaves. The use of all drugs led to the growth of crude and dry matter of the leaves. The largest leaf mass was under the action of tebuconazole [36].

It is known that one of the most important indicators of potential photosynthetic productivity of plants is the leaf area. Analysis of the obtained data shows that the leaf area increased under the action of all drugs, and it was the largest in the tebuconazole variant (Figure 1). Similar results were obtained studying the effect of retardants on other crops: sugar beet [52], sunflower [42], oil poppy [41], tomatoes [23], soy [13].

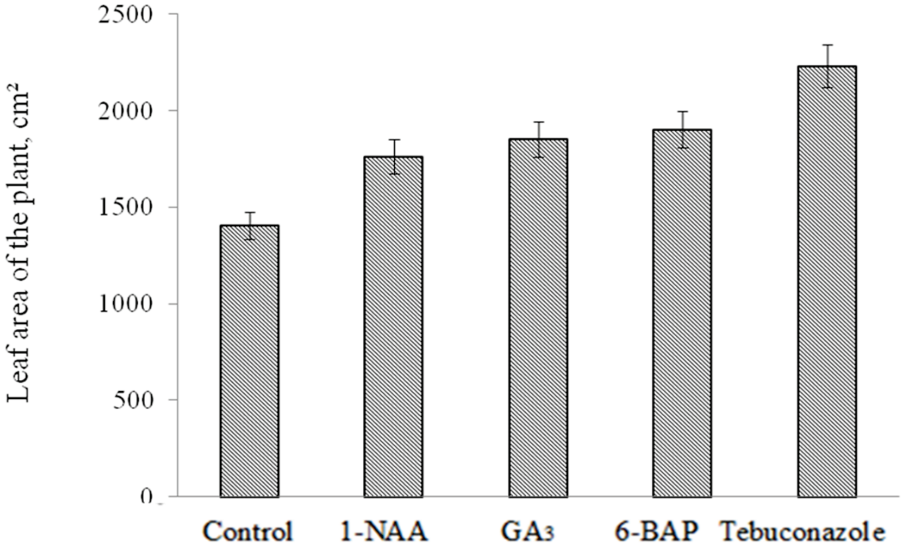


Figure 1. Influence of phytohormone anologues and tebuconazole retardant on the leaf area of sweet pepper Antey variety, fruit ripening phase

Thus, the obtained results indicate the stimulation of the formation of the leaf apparatus of sweet pepper under the action of all drugs of the regulating type (1-NAA, GA_3, 6-BAP) and antigibberellin tebuconazole. The most effective was the use of triazole derivative of tebuconazole.

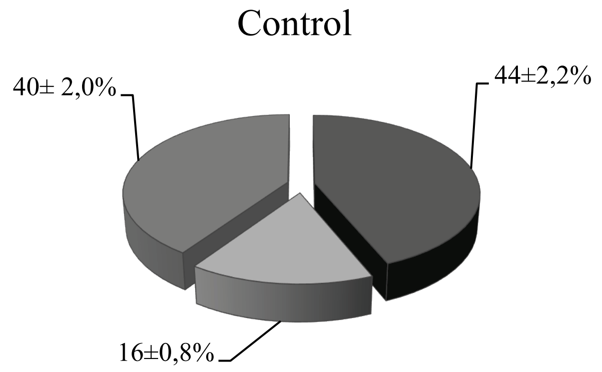
It is known that a significant role in the formation of overall productivity and crop yield is played by the source-sink system of plants. One of the promising areas of the production process regulation is the redistribution of assimilates in the plant. In particular, it was found that a partial restriction of the intensity of vegetative organs' growth of plants contributes to the formation of an excess of assimilates, which in its turn to contribute to the formation of economically valuable parts of the plant – fruits, seeds, roots [30,37]. Plant productivity is determined by both the capacity of the source sphere and the capacity of the sink zones.

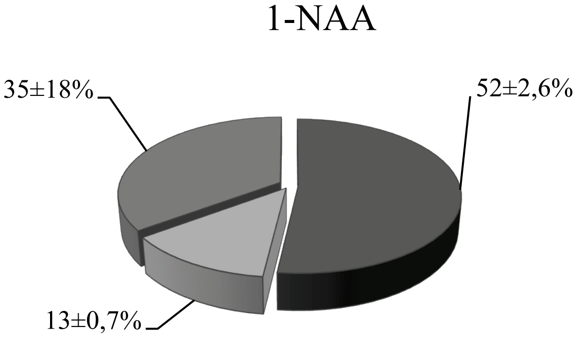
Estimation of the ratio of masses of vegetative organs of the plant in the phase of fruit ripening indicates that the relative proportion of leaves increased among the plant organs in the variants of experiments with the use of growth stimulants and inhibitor tebuconazole compared to control (Figure 2).

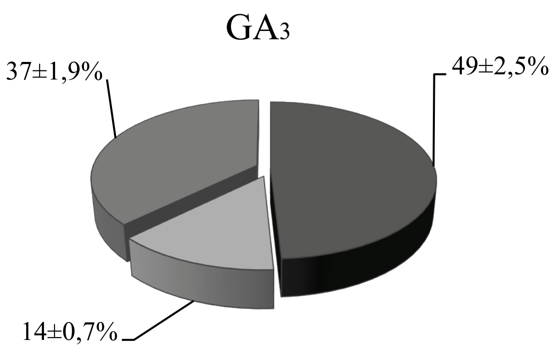
This indicates an increase in the share of the source sphere of the plant and better support for the processes of growth, development and crop formation. A similar relationship was observed between the vegetative organs of tomato plants [21].

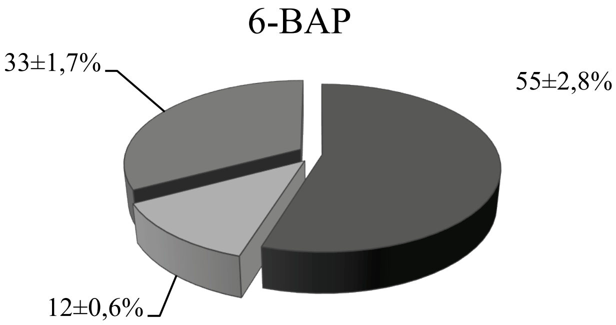
Leaf index – this is an important indicator of the production process of the crop, which is defined as the leaf area of a soil surface unit. The obtained data indicate that the use of all drugs led to an increase in this indicator (Figure 3).

Thus, our results from the anatomical and morphological changes of sweet pepper plants study indicate: the use of growth regulators (1-NAA, GA_3, 6-BAP) and antigibberilline drug tebuconazole at the budding phase leads to important changes in morphometric parameters of plants of this crop: more powerful leaf apparatus, increasing the total leaf area of both plants and coenoses in general. This is an important prerequisite for increasing the yield of sweet pepper.


Control


1-NAA


GA3


6-BAP

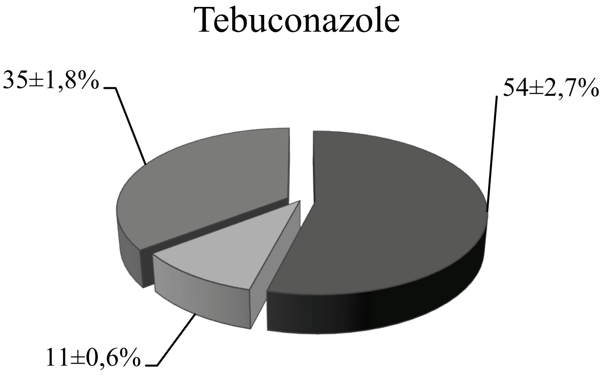

Tebuconazole

Figure 2. Influence of phytohormone anologues and tebuconazole on the ratio of dry matter masses of vegetative organs of sweet pepper at the phase of complete fruit ripeness

■ – leaf dry matter mass;
▨ – stem dry matter mass;
□ – root dry matter mass

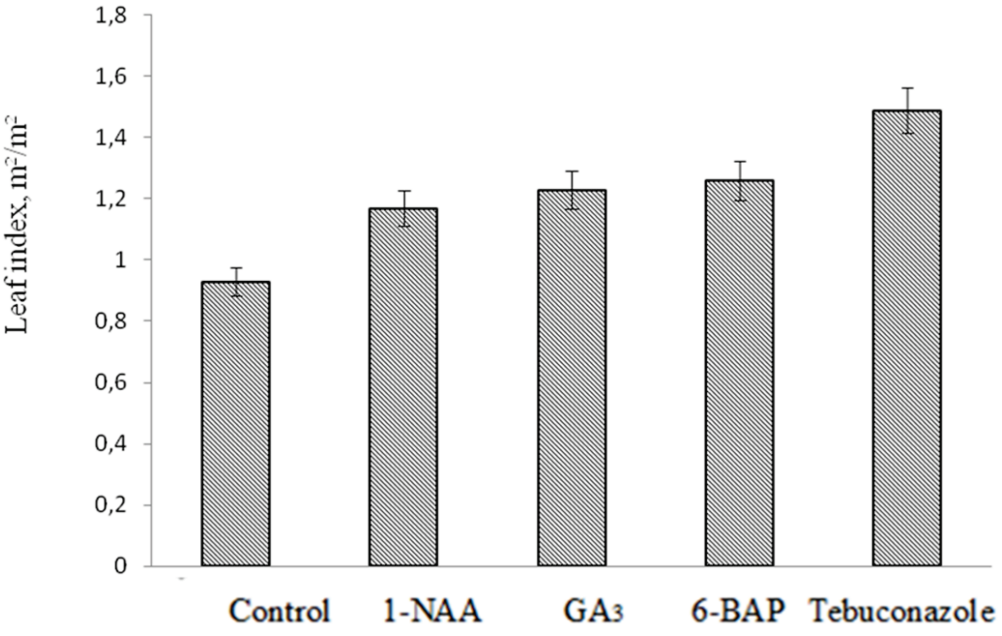


Figure 3. The effect of drugs on the leaf index of sweet pepper plants of Antey variety, the phase of fruit ripening

2.2. Formation and functioning of the photosynthetic apparatus under the influence of phytohormone anologues and tebuconazole retardant

Regulation of the source-sink system of the plant with the help of synthetic growth regulators allows to redistribute artificially the products of photosynthesis to economically valuable organs, and thus increase the yield of crops [9,29,43,47]. In our opinion, the results obtained on changes in the morphological features of the plant under the influence of drugs should be supplemented by data on changes in the anatomical features of the leaf (mesostructure), which largely depends on the synthetic activity of plants [10,32,33]. The use of growth stimulants and retardant changed the mesostructure of sweet pepper leaves. These data show that the action of drugs 1-NAA, GA_3, 6-BAP and tebuconazole thickened the leaf, and the most effective was the use of gibberellic acid and tebuconazole. Leaf thickening occurred primarily due to the main photosynthetic tissue – chlorenchyma, as well as due to thickening of the upper and lower epidermis (Table 1).

It is known that the columnar assimilative parenchyma plays a key role in photosynthesis. The results show that using 1-NAA, GA_3, 6-BAP and tebuconazole, the columnar parenchyma cell volume increased significantly. Similar results were obtained using retardants of different chemical nature on other crops [8,9,11,38].

Table 1.

Influence of synthetic growth regulators on mesostructural organization of Antey sweet pepper leaves

Experimental variant	**Control**	**1-NAA**	**GA_3**	**6-BAP**	**Tebuconazole**
Leaf thickness, µm	263.7 ±13.18	274.4 ±13.72	*327.4 ±16.37	298.6 ±14.93	*353.9 ±17.69
The thickness of the upper epidermis, µm	23.3 ± 0.62	22.9 ± 0.57	*31.1 ±0.21	*28.7 ± 0.73	*35.2 ± 0.26
The thickness of the chlorenchyma, µm	216.5 ±1.68	*227.6 ±2.91	*266.7 ±5.79	*244.9 ±4.13	*282.3 ± 5.58
The thickness of the lower epidermis, µm	23.9 ±0.49	23.9 ±0.62	*29.6 ±0.53	25.1 ±0.85	*36.4 ± 0.35
Columnar parenchyma cell volume, µm3	19857.1 ±896.32	20637.7 ± 817.57	*26688.8 ±1117.20	*23058.6 ±1147.19	*24366.1 ± 787.69
The length of the cells of the spongy parenchyma, µm	33.3 ±0.95	*42.8 ±0.74	*39.8 ±0.78	34.1 ±1.30	*40.2 ± 0. 57
The width of the cells of the spongy parenchyma, µm	24.9 ±0.75	*33.4 ±0.82	*32.4 ±0.89	26.9 ±1.04	*31.9 ±0.57
Specific leaf surface density, mg/cm2	7.9±0.39	8.7±0.43	*9.6±0.47	*9.1±0.45	*11.2±0.55

Note:* – the difference is significant at $p \leq 0.05$.

The specific leaf surface density (SLSD) is characterized by the ratio of leaf dry matter to its area. The importance of the indicator is determined by the fact that it characterizes the concentration of structural elements that are directly involved in the processes of photosynthesis. The results show that changes in the mesostructural organization of the leaf led to an increase in this indicator.

This correlates well with the leaf thickness, the maximum value is set for the option using gibberellic acid and tebuconazole. In these variants the maximum thickness of the chlorenchyma, the main photosynthetic tissue of the leaf, is observed. Similar changes in the formation of mesostructure and SLSD index under the action of GA_3 and retardants of different types were found by other researchers on crops of oil poppy [41], soy [13,26], tomatoes [23], sugar beet [52].

Optimization of the mesostructure formation is accompanied by the formation of large cells of the columnar and spongy parenchyma and an increase in chlorophyll content in leaves. The maximum chlorophyll content was observed under the action of a triazole-derived drug tebuconazole (Table 2).

Table 2.

The effect of drugs on the chlorophyll content and pure photosynthesis productivity of sweet pepper Antey

Experimental variant	Chlorophyll content (a + b),% by weight of crude matter	Pure photosynthesis productivity, r/(m2×day)
Control	0.62±0.03	1.73±0.08
Auxin	0.66±0.03	*1.24±0.06
Gibberellin	0.59±0.02	*2.24±0.11
Cytokinin	*0.69±0.03	*2.07±0.10
Tebuconazole	*0.71±0.04	*2.69±0.13

Note:* – the difference is significant at $p \leq 0.05$.

A similar increase in the chlorophyll content under the action of triazole-derived drugs was found for the culture of tomatoes [27], raspberries [24].

An important consequence of changes in the leaf mesostructure and an increase in the chlorophyll concentration under the action of drugs was an increase in pure photosynthesis productivity (PPP) of pepper plants [34,35]. As can be seen from table 2, these indicators clearly increased in the variants with the use of GA_3, 6-BAP and tebuconazole. Under the action of gibberellin and tebuconazole, these indidators were maximum.

The PPP index characterizes the photosynthetic productivity per leaf area unit. Given that the total area of the leaf surface of an individual plant and the phytocenosis increases under the action of the applied growth regulators, this indicates an increase in the gross productivity of plant photosynthesis and coenosis in general.

Therefore, using growth regulators, the mesostructure of the leaf is optimized, the content of pigments increases, as a result of that the photosynthetic activity per leaf area unit increases. Given the growth of the total leaf area, it can be stated that the use of synthetic growth regulators creates the preconditions for optimizing of sweet pepper production process.

2.3. Accumulation and redistribution of non-structural carbohydrates under the action of growth stimulants and tebuconazole retardant during the ontogenesis of sweet pepper plants

The main product of photosynthesis is carbohydrates, which form the crop. Therefore, in our opinion, it was necessary to study the peculiarities of accumulation of spare substances in leaves, their re-distribution between plant organs in the processes of ontogenesis, the importance of individual vegetative organs in temporary deposition of carbohydrates followed by their re-utilization for growth and fruit formation. The obtained research results indicate the influence of the applied growth regulators on the dynamics of non-structural carbohydrates content (sugars and starch) in the organs of sweet pepper plants (Table 3). It was found that at fruit formation phase the content of non-structural carbohydrates in leaves of sweet pepper plants under the action of GA_3 and tebuconazole was higher than in control and in 1-NAA and 6-BAP variant.

Table 3.

Peculiarities of accumulation and redistribution of various forms of non-structural carbohydrates in sweet pepper Antey variety under the action of phytohormone anologues and tebuconazole retardant (% by dry matter weight)

Experimental variant	**Total sugar**	**Starch**	**Non-structural sugar content**	**Total sugar**	**Starch**	**Non-structural sugar content**	**Total sugar**	**Starch**	**Non-structural sugar content**
	Fruit formation phase			**Fruit ripening phase**			**Mature fruit phase**		
	Leaf								
Control	4.66 ±0.02	6.44 ±0.01	11.1 ±0.55	6.02 ±0.30	7.34 ±0.02	13.36 ±0.66	5.64 ±0.28	7.12 ±0.01	12.76 ±0.63
1-NAA	4.1 ±0.20	*5.94 ±0.01	10.04 ±0.50	5.39 ±0.26	*5.86 ±0.01	11.25 ±0.56	5.32 ±0.26	*5.64 ±0.01	10.96 ±0.54
GA$_3$	4.14 ±0.20	7.36 ±0.02	11.5 ±0.23	5.84 ±0.29	*6.96 ±0.01	12.8 ±0.64	5.76 ±0.28	*6.49 ±0.01	12.25 ±0.61
6-BAP	4.54 ±0.22	*6.19 ±0.02	10.73 ±0.53	5.32 ±0.26	*5.82 ±0.01	11.14 ±0.55	4.84 ±0.24	*5.4 ±0.01	*10.24 ±0.51
Tebuconazole	4.41 ±0.22	6.92 ±0.02	11.33 ±0.56	5.56 ±0.27	*6.83 ±0.02	12.39 ±0.61	*5.43 ±0.27	6.01 ±0.01	11.44 ±0.57
Stem									
Control	7.06 ±0.35	3.64 ±0.02	10.7 ±0.53	6.79 ±0.33	5.09 ±0.02	11.88 ±0.59	6.39 ±0.31	5.78 ±0.01	12.17 ±0.60

Table 3 continuation

1-NAA	6.67 ±0.33	*3.46 ±0.01	10.13 ±0.50	6.49 ±0.32	5.19 ±0.01	11.68 ±0.58	6.34 ±0.31	*5.63 ±0.01	11.97 ±0.59
GA_3	6.14 ±0.30	3.82 ±0.01	9.96 ±0.49	5.84 ±0.29	5.46 ±0.02	11.3 ±0.56	5.55 ±0.27	*5.38 ±0.01	10.93 ±0.54
6-BAP	*5.61 ±0.28	*3.41 ±0.02	9.02 ±0.45	5.81 ±0.29	*4.40 ±0.02	10.21 ±0.51	5.9 ±0.29	*4.74 ±0.01	10.64 ±0.53
Tebuconazole	7.37 ±0.36	5.07 ±0.02	12.44 ±0.62	5.56 ±0.27	5.58 ±0.02	11.14 ±0.55	5.49 ±0.27	*5.69 ±0.01	11.18 ±0.55
Root									
Control	3.08 ±0.15	3.52 ±0.01	6.6 ±0.33	3.39 ±0.16	2.56 ±0.01	5.95 ±0.29	3.39 ±0.16	2.18 ±0.01	5.57 ±0.27
1-NAA	3.05 ±0.15	*3.24 ±0.01	6.29 ±0.31	2.92 ±0.14	2.6 ±0.01	5.52 ±0.27	2.99 ±0.15	2.47 ±0.02	5.46 ±0.27
GA_3	2.97 ±0.14	*3.19 ±0.02	6.16 ±0.30	3.27 ±0.16	*2.48 ±0.02	5.75 ±0.28	3.37 ±0.16	*2.12 ±0.01	5.49 ±0.27
6-BAP	3.61 ±0.18	*3.16 ±0.01	6.77 ±0.33	3.49 ±0.17	*2.36 ±0.023	5.85 ±0.29	3.41 ±0.17	2.31 ±0.01	5.72 ±0.28
Tebuconazole	2.87 ±0.14	3.72 ±0.02	6.59 ±0.32	2.86 ±0.14	2.69 ±0.01	5.55 ±0.27	2.88 ±0.14	2.21 ±0.01	5.09 ±0.25

Note:* – the difference is significant at $p \leq 0.05$

In our opinion, this is a consequence of the formation of optimal mesostructure of the leaves in these variants and increase in pure photosynthesis productivity. The most significant was the increase in starch content, the main reserve polysaccharide.

Analysis of the results shows that at subsequent phases of fruit development there is an outflow of assimilates from the leaves. The most significant was the decrease in non-structural carbohydrates content starting from the ripening phase to the mature fruit phase under the action of tebuconazole and 6-BAP. The decrease in the carbohydrates content in all variants of the experiment occurred both due to sugars and due to starch. It should be noted that significant changes occurred in the content of sugars and starch in the vegetative organs of the plant – stems and roots. The maximum content of the nonstructural carbohydrates was observed in the variant with tebuconazole at the phase of fruit formation also both due to the increase in sugar content and due to starch content. Higher starch content in the stem was observed with the use of gibberellic acid and tebuconazole. 1-NAA and 6-BAP treated variants either did not differ from the control or contained less sugars and starch. At this phase, the higher starch content in root was noted under the influence of tebuconazole.

The results indicate significant depositing potential of the stem and root. The content of sugars and starch in the stem did not differ from the content of these substances in the leaf. It is known that in the implementation of source-sink relations in plants, a significant role can be played by temporary reservation of substances in the vegetative organs. The roots are characterized by a decrease in the content of non-structural carbohydrates during ontogenesis from the phase of fruit formation to the mature fruit phase. The maximum decrease was observed in the variant under tebuconazole action.

The decrease in sugar and starch content from the phase of fruit formation to the mature fruit phase was also observed in stem in tebuconazole use variant. In all other variants, there was an increase in non-structural carbohydrates content starting from the fruit formation phase to mature fruit phase.

In our opinion, this is due to the fact that the transport of assimilates to fruits lasts longer in the variant of application of tebuconazole than using of other drugs. The increase in carbohydrate content in variants treated with 1-NAA, GA_3 and 6-BAP is associated with the cessation of outflow to the fruit at the phase of fruit ripening lasting to the mature fruit phase.

It is known that the main transport sugarform is sucrose. Analysis of the results of the study of the content of this disaccharide in the organs of sweet pepper plants by stages of development shows the influence of regulators on the accumulation and redistribution of this sugar (Table 4).

During ontogenesis, in general, according to the experimental variants, the increase in the sucrose content was observed in leaves of plants. The maximum increase in this transport sugar form content was in tebuconazole variant comparing to the control. This indicator also increased in 1-NAA and GA_3variants, the growth was less effective in 6-BAP variant. Another trend was observed in sucrose accumulation in stem and root of the plant. In particular, in roots of control plants, sucrose content decreased from the phase of fruit formation to mature fruit phase.

Sucrose levels remained virtually unchanged in the 6-BAP and 1-NAA variants, and sucrose increases were observed in GA_3 and tebuconazole variants. In the stem of control plants and in the 1-NAA variant there was no difference in sucrose accumulation during the growing season. The increase in sucrose content in stem of sweet pepper occurred under the use of 6-BAP, GA_3 and tebuconazole. The maximum increase was observed in the GA_3 and tebuconazole variants.

Table 4.

The effect of growth regulators on the sugar content in the vegetative organs of the sweet pepper plant Antey (% by dry matter weight)

Experimental variant	Fruit formation phase			Fruit ripening phase			Mature fruit phase		
	Leaf								
	Total sugar	Reducing sugar	Sucrose	Total sugar	Reducing sugar	Sucrose	Total sugar	Reducing sugar	Sucrose
Control	4.66 ±0.02	2.46 ±0.02	2.14 ±0.01	6.02 ±0.01	3.38 ±0.02	2.56 ±0.01	5.64 ±0.02	3.18 ±0.01	2.42 ±0.01
1-NAA	*4.1 ±0.02	*2.23 ±0.02	1.8 ±0.01	*5.39 ±0.02	*2.27 ±0.01	3.1 ±0.04	*5.32 ±0.02	*2.05 ±0.01	3.23 ±0.01
GA_3	*4.14 ±0.02	*2.43 ±0.02	1.64 ±0.01	*5.84 ±0.01	*3.05 ±0.02	2.7 ±0.02	5.76 ±0.02	*2.84 ±0.01	2.86 ±0.01
6-BAP	*4.54 ±0.02	2.57 ±0.02	1.9 ±0.01	*5.32 ±0.01	*2.89 ±0.01	2.35 ±0.02	*4.84 ±0.011	*2.64 ±0.02	2.16 ±0.01
Tebuconazole	*4.41 ±0.02	2.48 ±0.02	1.86 ±0.01	*5.56 ±0.02	*2.2 ±0.02	3.14 ±0.01	*5.43 ±0.02	*2 ±0.01	3.38 ±0.02
Stem									
Control	7.06 ±0.02	5.94 ±0.01	1.09 ±0.01	6.79 ±0.02	5.68 ±0.01	1.09 ±0.01	6.39 ±0.01	5.29 ±0.01	1.06 ±0.01

Table 4 continuation

1-NAA	*6.67 ±0.01	*5.45 ±0.02	1.18 ±0.04	*6.49 ±0.02	*5.34 ±0.02	5.15 ±0.021	*6.34 ±0.01	*1.12 ±0.02	1.15 ±0.01
GA$_3$	*6.14 ±0.02	*5.13 ±0.02	*0.98 ±0.03	*5.84 ±0.01	*4.63 ±0.02	1.18 ±0.01	*5.55 ±0.03	*4.28 ±0.01	1.24 ±0.02
6-BAP	*5.61 ±0.02	*4.5 ±0.02	*0.9 ±0.01	*5.81 ±0.02	*4.7 ±0.01	1.09 ±0.01	*5.9 ±0.01	*4.8 ±0.01	1.06 ±0.02
Tebuconazole	7.37 ±0.02	6.17 ±0.02	1.18 ±0.01	*5.56 ±0.03	*4.24 ±0.01	1.28 ±0.02	*5.49 ±0.03	*4.14 ±0.02	1.32 ±0.01
Root									
Control	3.08 ±0.02	2.27 ±0.01	1.59 ±0.01	3.39 ±0.01	2.26 ±0.013	1.1 ±0.009	3.39 ±0.02	2.21 ±0.01	1.16 ±0.01
1-NAA	3.05 ±0.02	*2.15 ±0.02	*0.86 0.01	*2.92 ±0.02	*1.99 ±0.01	*0.91 ±0.007	*2.99 ±0.02	*2.02 ±0.01	*0.94 ±0.01
GA$_3$	*2.97 ±0.02	*2.15 ±0.01	*0.79 ±0.01	*3.27 ±0.02	*2.17 ±0.01	1.06 ±0.012	3.37 ±0.02	*2.15 ±0.02	1.19 ±0.01
6-BAP	3.61 ±0.03	2.57 ±0.01	*1.0 ±0.02	3.49 ±0.01	2.47 ±0.01	*0.99 ±0.001	3.41 ±0.01	2.44 ±0.01	*0.95 ±0.01
Tebuconazole	*2.87 ±0.02	*2.1 ±0.01	*0.75 ±0.01	*2.86 ±0.02	*1.94 ±0.01	*0.9 ±0.007	*2.88 ±0.02	*1.89 ±0.01	*0.96 ±0.01

Note:* – the difference is significant at $p \leq 0.05$

2.4. The content of nutrients in the organs of sweet pepper under the action of phytohormone anologues and tebuconazole

It is known that the total productivity and yield of crops depend on the peculiarities of nitrogen metabolism in the plant. We analyzed the dynamics of nitrogen content in the vegetative organs by growth phases under the influence of growth regulators. It was found that the use of growth regulators significantly affects the dynamics of total nitrogen and its forms (protein and non-protein) during ontogenesis (Table 5).

In particular, at the fruit formation phase in leaves was found no significant difference in total nitrogen content according to the experimental variants. At fruit ripening and mature fruit phases, the nitrogen content decrease was found in leaves in all experimental variants. Since the leaf growth intensity slows down during this period, it is impossible to explain this by biodilution processes.In our opinion, the decrease indicates that accumulated nitrogen in leaves is used for fruit formation and growth processes.

It is known that assimilates synthesized by the plant can be temporarily deposited in other organs, followed by re-utilization for the carpogenesis processes. The results indicate a significant depositing stem and root capacity of sweet pepper plants.

During the growing season, nitrogen compounds content decreased in these organs, indicating their use in fruit growth and development processes. The maximum nitrogen content during ontogenesis was observed in the variant under tebuconazole use. A similar effect of this retardant on nitrogen accumulation was found for gooseberry crop [50]. That's it the variant where the maximum reduction of nitrogen content is also noted during ontogenesis, testifying, in our opinion, the intensive use for fruit formation and growth. A significant decrease in nitrogen content was recorded in stems in the variant treated with gibberellic acid.

Table 5.

Effect of growth stimulants and tebuconazole retardant on nitrogen content in vegetative organs plants of sweet pepper

Antey

Experimental variant	**Fruit formation phase**			**Fruit ripening phase**			**Mature fruit phase**		
	Total nitrogen	**Protein nitrogen**	**Non-protein nitrogen**	**Total nitrogen**	**Protein nitrogen**	**Non-protein nitrogen**	**Total nitrogen**	**Protein nitrogen**	**Non-protein nitrogen**
	Leaf								
Control	4.07 ±0.02	3.14 ±0.02	0.87 ±0.02	3.32 ±0.01	2.7 ±0.02	0.61 ±0.02	3.1 ±0.02	2.71 ±0.02	0.39 ±0.02
1-NAA	4.11 ±0.02	3.34 ±0.01	*0.75 ±0.02	3.72 ±0.02	3.08 ±0.02	0.64 ±0.02	3.11 ±0.02	2.72 ±0.01	0.39 ±0.02
GA_3	4.0 ±0.02	3.23 ±0.02	*0.78 ±0.02	3.59 ±0.01	3.01 ±0.01	0.58 ±0.01	*3.02 ±0.02	2.66 ±0.01	0.36 ±0.02
6-BAP	4.01 ±0.02	3.3 ±0.01	*0.65 ±0.02	3.75 ±0.03	3.07 ±0.02	0.67 ±0.03	3.45 ±0.03	3.02 ±0.01	0.42 ±0.02
Tebuconazole	4.05 ±0.02	3.3 ±0.01	*0.75 ±0.02	3.68 ±0.01	3.03 ±0.02	0.64 ±0.02	3.51 ±0.03	2.88 ±0.01	0.47 ±0.02
Stem									
Control	2.06 ±0.01	1.63 ±0.02	0.53 ±0.01	1.61 ±0.02	1.17 ±0.01	0.44 ±0.01	1.6 ±0.01	1.18 ±0. 02	0.42 ±0.02
1-NAA	2.25 ±0.01	*1.54 ±0.01	0.71 ±0.01	1.75 ±0.01	1.2 ±0.01	0.55 ±0.01	1.57 ±0.01	1.14 ±0.01	0.43 ±0.01

Table 5 continuation

GA_3	2.09 ±0.02	*1.55 ±0.01	0.53 ±0.01	1.57 ±0.01	1.15 ±0.01	0.42 ±0.01	*1.35 ±0.01	*1.04 ±0.02	*0.31 ±0.02
6-BAP	*1.92 ±0.02	*1.48 ±0.03	*0.44 ±0.03	1.94 ±0.02	1.38 ±0.01	0.54 ±0.01	2.02 ±0.01	1.4 ±0.01	0.61 ±0.01
Tebuconazole	2.76 ±0.01	2.24 ±0.01	0.51 ±0.01	1.71 ±0.01	1.42 ±0.01	*0.28 ±0.01	1.6 ±0.01	1.27 ±0.02	*0.3 ±0.02
Root									
Control	1.62 ±0.01	1.19 ±0.01	0.42 ±0.01	1.26 ±0.01	0.99 ±0.01	0.27 ±0.01	1.17 ±0.02	0.95 ±0.01	0.22 ±0.02
1-NAA	1.58 ±0.02	1.23 ±0.01	*0.35 ±0.02	1.51 ±0.01	1.27 ±0.01	*0.23 ±0.01	1.44 ±0.02	1.22 ±0.02	0.21 ±0.02
GA_3	1.73 ±0.01	1.28 ±0.01	0.44 ±0.01	1.49 ±0.01	1.16 ±0.01	0.32 ±0.01	1.32 ±0.01	1.03 ±0.01	0.28 ±0.01
6-BAP	1.61 ±0.02	1.3 ±0.02	*0.31 ±0.02	1.71 ±0.01	1.26 ±0.02	0.44 ±0.01	1.56 ±0.02	1.28 ±0.01	0.28 ±0.01
Tebuconazole	2.2 ±0.02	1.62 ±0.02	0.57 ±0.01	1.72 ±0.01	1.35 ±0.01	0.37 ±0.01	1.66 ±0.02	1.33 ±0.01	0.33 ±0.01

Note:* – the difference is significant at $p \leq 0.05$

Nitrogen content analysis in roots indicates the gradual use of deposited nitrogen during the processes of carpogenesis: in all variants of the experiment noted a decrease in this element content. During ontogenesis, the nitrogen content was maximal under the action of tebuconazole. Similar changes under the action of drugs have been found during ontogenesis of tomato plants [27].

The positive role of all used drugs should be noted for the content of protein nitrogen in the vegetative organs: in leaves and roots of sweet pepper plants, the content of this nitrogen form was consistently higher in comparison to control. This pattern for stems was observed only in tebuconazole variant.

It is known that phosphorus and potassium play an important role at the period of fruit formation. Analysis of the content of these elements in the vegetative organs of plants in the ontogenesis of sweet pepper indicates a significant effect of growth stimulants and retardant on the accumulation and redistribution of phosphorus and potassium between plant organs.

The obtained data show that there was a decrease in the content of this element in experimental variants during ontogenesis starting from the fruit formation phase to mature fruit phase in leaves and stems of plants (Figure 4). The maximum phosphorus content was observed in 1-NAA and retardant tebuconazole variants. In our opinion, the decrease in the phosphorus content in vegetative organs indicates the intensive re-utilization of the element for the carpogenesis needs for the formation of fruit growth.

The significant depositive value of roots of sweet pepper plants has been established in the process of phosphorus use. The decrease in the content of this element was observed in the experimental variants from the phase of fruit formation to the phase of fruit ripening, with subsequent increase in phosphorus content in the variants treated with growth stimulants. The tebuconazole variant was characterized by another tendency: the phosphorus content in roots decreased at the last phase of ontogenesis. In our opinion, this is due to the continued supply of phosphorus to the fruits due to the increased crop load of plants of this variant by phases.

Potassium is known to be important during fruiting. It is an activator of more than 60 different enzyme systems [40]. A large amount of potassium is contained in areas of active growth, but it is quite small in old organs of the plant. The early stages of its growth are particularly important periods for ensuring of plant with the element.

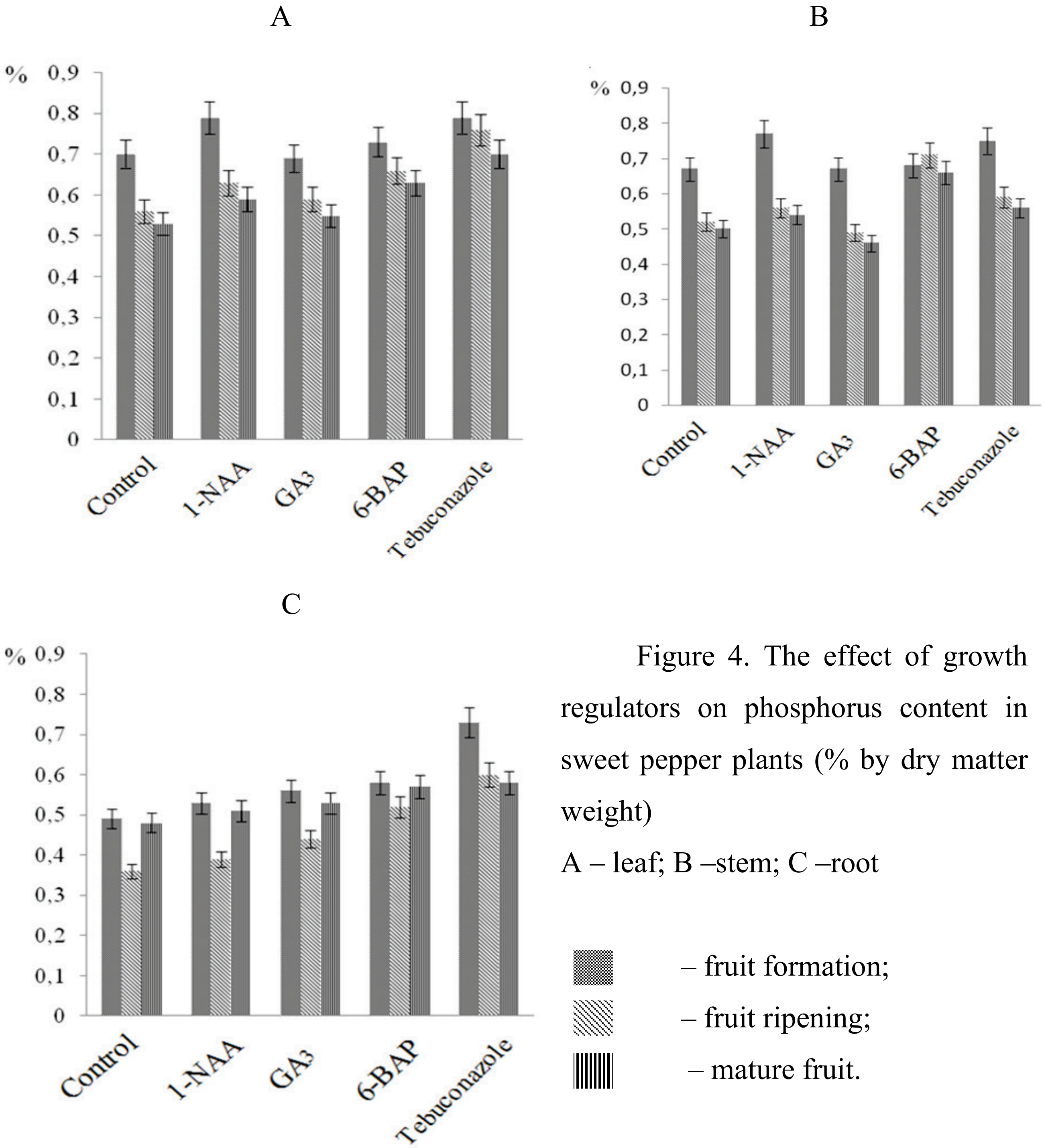
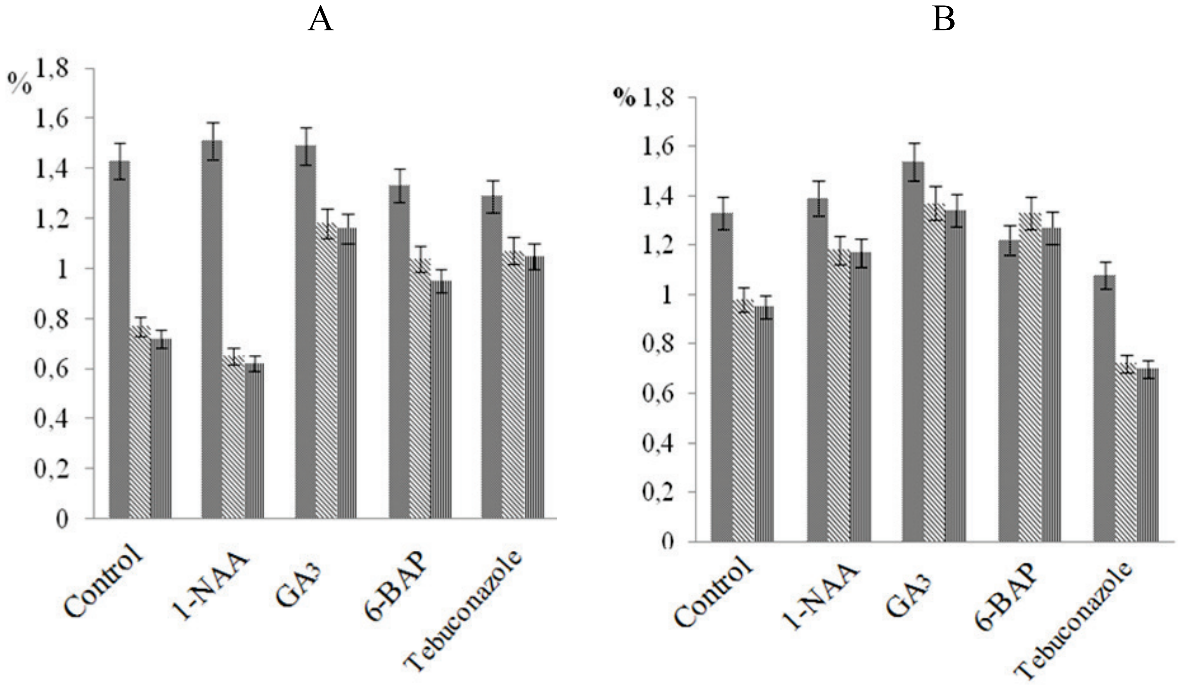


Figure 4. The effect of growth regulators on phosphorus content in sweet pepper plants (% by dry matter weight)

A – leaf; B –stem; C –root

Potassium is the main part of the cations of cell sap, affects the properties of the cytoplasm. It is necessary for the absorption and transport of water and the work of the stoma. The lamellar and granular structure of chloroplasts is not formed under conditions of deficiency of this element, photosynthesis and plant growth are stopped. The biosynthesis of polysaccharides, starch in potato plants, sucrose in sugar beet, monosaccharides in fruits is enhanced under the influence of potassium [16,54,55].

There was a gradual decrease in the element content during the ontogenesis from the phase of fruit formation to mature fruit phase of sweet pepper plants according to the variants of the experiment (Figure 5). Obviously, this is due to the re-utilization of potassium for fruit formation and growth. The highest content of potassium was observed in leaves and stems of sweet pepper plant.



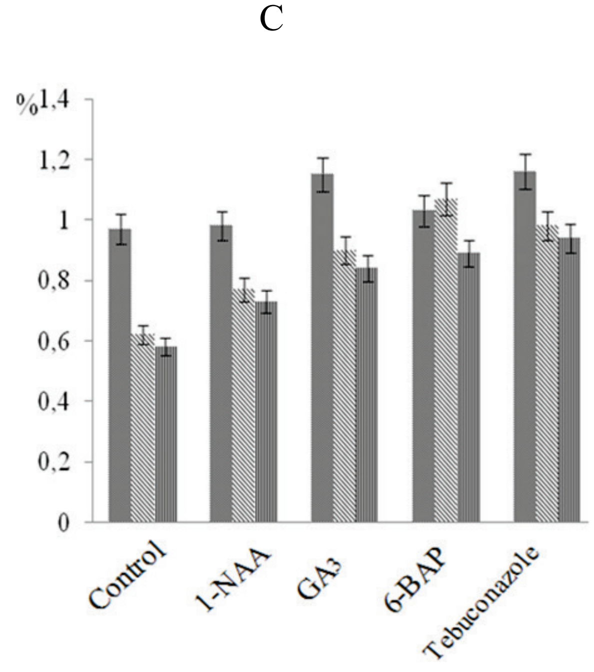


Figure 5. The effect of growth regulators on potassium content in sweet pepper plants (% by dry matter weight)

A – leaf; B –stem; C –root

▩ – fruit formation;

▧ – fruit ripening;

▥ – mature fruit.

At the same time, the significant depositive potential of roots of sweet pepper plants should be noted, while the accumulation of potassium was observed during the growing season. The maximum content of potassium in vegetative organs of sweet pepper plant accumulated under the action of gibberellin.

Thus, the use of drugs led to a re-distribution of potassium and phosphorus in the plant with the most effective changes that occurr under the action of tebuconazole. This drug generally increased the content of important nutrients in vegetative organs of the plant during ontogenesis.

2.5. Influence of growth regulators on sweet pepper yield

The analyzed data show that under the action of drugs significantly changed the anatomical and morphological structure of sweet pepper plants, improved coenological characteristics of plantations, optimized photosynthetic activity of both individual plants and coenoses in general. This creates important prerequisites for increasing the yield of sweet peppers. However, in literature there is no data on the peculiarities of carpogenesis (growth and fruit formation) of this culture under the action of the used drugs. This determines the in-depth study requirement of the problem.

The results of 3-year research within 2013-2015 growing season show that the use of growth regulators 1-naphthylacetic acid, gibberellic acid, 6-benzylaminopuric acid and tebuconazole retardant contributed to the growth of fruit number and fruit weight unit per plant (Figure 6) [36].

The maximum value of fruit weight at the end of the growing season was recorded under the influence of the drug tebuconazole, and the largest number of fruits per plant was in gibberellic acid variant. Similar data were obtained during the study of these drugs' effect on tomato plants [21]. The highest fruit load was observed in gibberellic acid and tebuconazole variant, that is in a good agreement with the enhancing of photosynthetic processes, the use of assimilates for carpogenesis, as well as the accumulation and reutilization of nutrients by drug action.

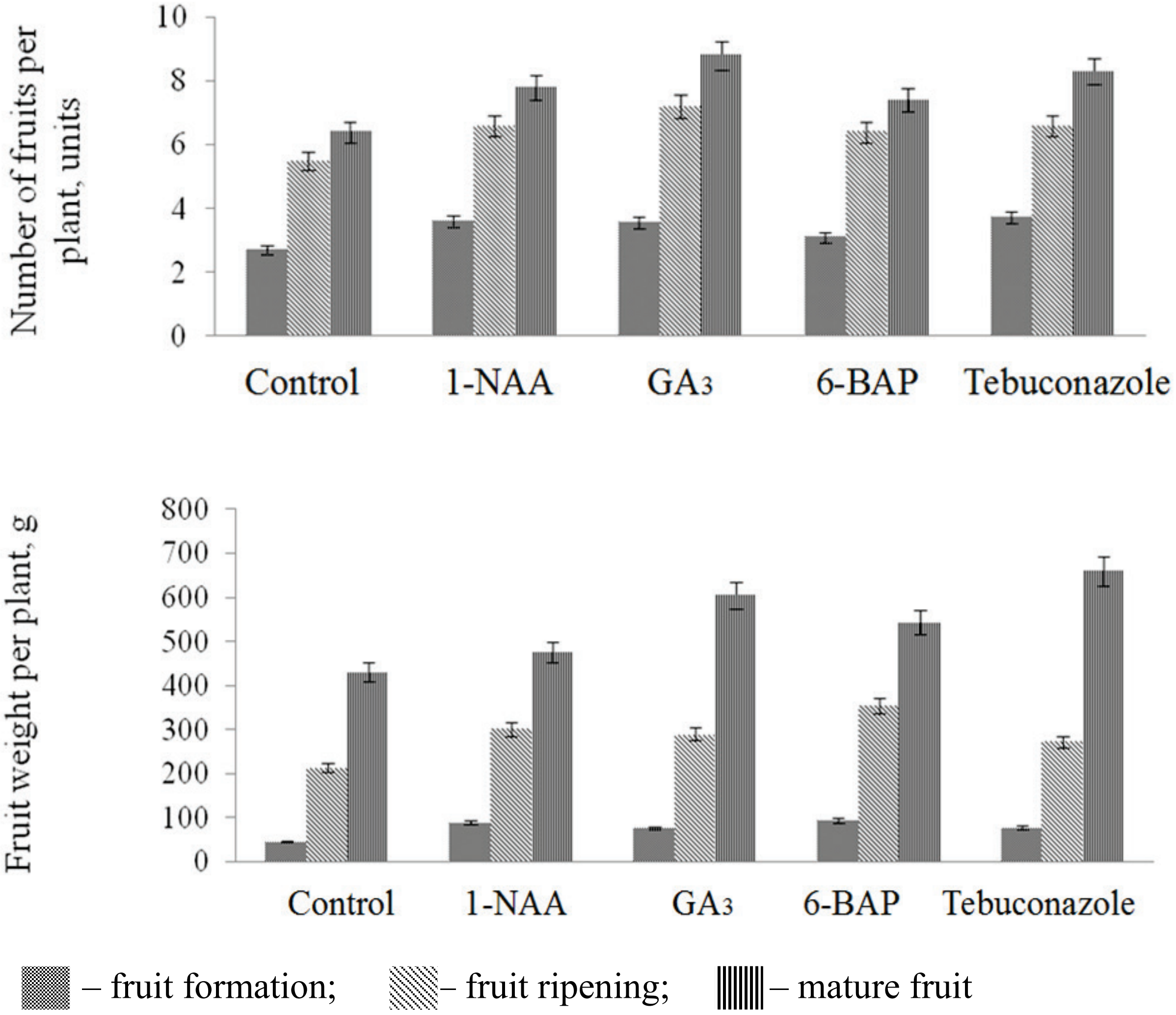


Figure 6. Influence of growth regulators on the number of fruits and fruit weight unit per plant of sweet pepper Antey

Thus, the results of our investigation indicate that the use of growth inhibitor tebuconazole and plant growth stimulants improve the productivity of sweet pepper. The use of gibberellic acid and tebuconazole retardant was the most effective.

Conclusions

1. Growth regulators with different mechanism of action (GA_3, 1-NAA, 6-BAP and tebuconazole retardant) affect the formation and functioning of the source-sink system of sweet pepper plants, its anatomical, morphological and mesostructural

characteristics, assimilation activity, deposition and re-distribution of carbohydrates and mineral nutrients between vegetative organs and fruits, associating with crop yields.

2. The use of drugs led to the formation of a more powerful photosynthetic apparatus of the plant: the number of leaves their weight, total leaf area increased, an important cenological indicator, leaf index also increased, creating favourable conditions for increasing crop productivity. Gibberellic acid and tebuconazole had the most effective effect on the formation of the leaf apparatus of plants.

3. The mesostructure of leaves changed significantly under the influence of the applied growth regulators: thickened, stronger assimilative parenchyma was formed due to the increase in the volume and size of the cells of the columnar and spongy parenchyma. The consequence of such changes was an increase in specific leaf surface density and an increase in pure photosynthesis productivity. The largest increase in pure photosynthesis productivity occurred under the action of gibberellic acid and tebuconazole.

4. The use of anologues of phytohormones 1-NAA, 6-BAP, GA_3 and tebuconazole retardant increased the crop load per bush, stimulating the outflow of assimilates from leaves. The most significant was the decrease in non-structural carbohydrates content starting from the fruit ripening phase to mature fruit phase under the action of tebuconazole and 6-BAP. The reduction of carbohydrates content in experimental variants was due to both sugars and starch.

5. A significant depositive function is performed by non-leaf vegetative organs of the plant (stem and root), the carbohydrate content of which was close to the carbohydrate content in leaves. There was a decrease in non-structural carbohydrates content in roots from fruit formation phase to the mature fruit phase. The maximum decrease was observed in tebuconazole-treated variant. In the stem, The reduction of sugar and starch content from fruit formation phase to mature fruit phase also occurred in plants of the variant with the use of this drug. In all other variants, there was an increase in non-structural carbohydrates content from the fruit formation phase to mature fruit phase. This indicates that transport of assimilates to the fruits

takes longer in the variant with the tebuconazole use in comparison to other drugs.

6. The use of growth regulators significantly affected the dynamics of nitrogen content during ontogenesis. At the phase of fruit formation in leaves of plants was found no significant difference in total nitrogen content, and at the phase of fruit ripening and mature fruit phase the nitrogen content decreased in leaves in all variants of the experiment. This indicates that accumulated nitrogen of leaves was used for the formation and growth of fruits. The maximum reduction of nitrogen content was found under the action of GA_3 and 1-NAA drugs during ontogenesis.

7. The use of phytohormone anologues and tebuconazole retardant led to the accumulation of higher levels of phosphorus and potassium in vegetative organs of sweet pepper – leaves, stems and roots at the ripening phase and fruit ripening phase. Tebuconazole had the most significant effect on phosphorus content and gibberellic acid – on potassium content.

8. The use of drugs changed the structure of the crop in all variants of the experiment: the number of fruits and the average weight of the fruit per plant compared to the control. As a result, the total crop yield increased in all variants of the experiment. The most effective was the use of gibberellin and tebuconazole.

CHAPTER 3.
INFLUENCE OF GROWTH REGULATORS ON MORPHOGENESIS AND PRODUCTIVITY OF OIL FLAX

Introduction

The main task of modern agricultural production is finding of effective methods to improve crop productivity [2, 46, 55]. Analysis of trends in world crop production shows that one of the ways to solve the problem of high and stable yields is the use of new technologies using synthetic plant growth regulators [5, 43, 57]. This group of compounds makes it possible to regulate the individual stages of ontogenesis in order to mobilize the potential of the plant organism, which affects the yield and quality of agricultural products [31, 40].

It is known that growth regulators based on phytohormones and modifiers of their action affect the functioning of source-sink relations in plant, and the establishment of growth and development patterns under the action of physiologically active compounds contributes to the development of effective methods for increasing yields and improving the quality of agricultural products [2].

By their nature, growth regulators are anologues or modifiers of the hormonal status of plants [3, 10]. These drugs include natural phytohormones, their synthetic anologues or composite drugs that contain a balanced complex of phytoregulators, biologically active substances, microelements that are actively involved in metabolism and lead to visible growth and development changes [9, 23, 29].

In order to intensify the processes of histo- and morphogenesis, growth stimulants are used [24, 35]. Phytohormones and their synthetic anologues cause acceleration of cell proliferation and differentiation, as a result of this a more branched root system is formed, the anatomical and morphological organization of the leaf is changed. A powerful assimilative apparatus is able to provide active synthesis of plastic compounds, the flow of which is directed to the generative organs, which increases crop yields [50, 54, 59].

In agricultural practice both stimulants and inhibitors of plant development (retardants) are used [1, 7]. As a rule, amid the changes in source-sink relations in plant, retardants slow down the growth process. Reduction of the need for spare substances for vegetative growth leads to the accumulation of assimilates and their subsequent re-distribution towards economically important organs [25, 26]. The use of synthetic growth regulators affects the intensity and direction of physiological processes [27, 30], the quantity and quality of the crop, resistance to water deficit [11, 19] and extreme temperatures [53].

Using synthetic growth-regulating compounds, it is necessary to take into account the species specificity of the crop, varietal differences, phases of plant development and soil-climatic conditions [37, 62]. The efficiency of the use of growth regulators and environmental impact on the environment is determined by compliance with the regulations of drug administration [33, 73]. Today, new generation of plant growth regulators have been created, which are characterized by high efficiency and environmental safety [60, 70, 71]. They activate the main processes of plant life: membrane processes, cell division, enzyme systems, photosynthesis, respiration and nutrition, as well as increasing the biological and economic efficiency of crop production [51, 54, 74].

The data from literature on the effect of stimulants and inhibitors of plant development on the growth and yield of many oilseeds and industrial crops, as well as regulations for the drug use are contradictory [47]. At the same time, a comprehensive study of the influence of different types of regulating compounds and their mixtures on physiological and biochemical processes, features of morphogenesis, productivity of these cultures was practically not carried out.

For many decades, the leading oil crop in Ukraine has been sunflower, to a lesser extent rapeseed [45]. However, their crops are too depleting of the soil, which leads to a violation of mineral supply, changes in the microbiological backdrop [65]. A possible alternative to sunflower is oil flax being a valuable profitable crop and a good precursor for many agricultural plants. The short growing season and drought resistance of flax allow to expand crops, to increase the production of vegetable oils without deteriorating of soil condition [63].

Oil flax (curly) is a drought-resistant, precocious plant that can give high seed yields, from which, at the same time, fiber is obtained [34]. Flaxseed contains up to 50% of valuable oil, rich in unsaturated fatty acids, about 20-30% of protein, 12-20% of carbohydrates, as well as carotene, potassium, calcium, magnesium, iron, zinc [64]. Recently, from short-fiber flax is obtained cottonized, cotton-like fiber for the production of mixed flax-cotton fabrics and medical cotton wool. The products of its processing are used in food, pharmaceutical, chemical, light, perfume, electrical, aviation industries, for the manufacture of dietary products, textiles, varnishes, paints, and as a raw material base for biofuels [16, 50]. Flax has fodder value: the pomace or marc (oil cake) contains 6-12% of fat and 38% of protein. Its 1 kg nutritional value is 1.2 fodder units. Flaxseed grist contains a number of essential amino acids and does not require extrusion [4].

Due to the small domestic demand for flaxseed oil, the Ukrainian flax trade is more export-oriented. Gradually, the area under oilseed flax increase in the steppe and forest-steppe [64, 75].

The current state of development of the production and processing of flax products in Ukraine is quite complex [45]. The development of the flax industry is impossible without the production of high quality competitive products [38]. This depends largely on the use of new flax varieties and cost-effective cultivation techniques that can provide high seed yields. At the present stage, it is necessary to use affordable and inexpensive means of mineral nutrition and optimization of cultivation technology, an important element of which is the use of plant growth and development regulators [51].

Modern varieties of oil flax are characterized by a reduction of the growing season, drought resistance, no shedding and an increase in seed oil content [47]. In this regard, it is of great practical interest to study the possibility of the influence of growth regulators on the productivity, oil content of flax seeds and quality characteristics of oil. However, the influence of growth regulators with different mechanism of action on the morphological parameters of flax plants, the dynamics of spare substances accumulation, yield and oil content of seeds, its qualitative characteristics remain virtually unexplored.

Accordingly the aim of our work was to find out the influence of growth and development regulators of different action chlormequat chloride and treptolem on the growth processes, development and productivity of flax seeds.

Research methods

Oil flax was grown according to standard technology, according to the technological map on cultivation [15]. Plants were treated once with a 0.5% aqueous solution of chlormequat chloride, aqueous solution of treptolem (0.033 ml/l) and a mixture of these drugs of same concentrations at the budding phase until complete wetting of leaves. Control plants were sprayed with tap water. The consumption of the working solution was 300 l/ha.

Chlormequat chloride is β-chloroethyltrimethylammonium chloride ($[ClCH_2CH_2N(CH_3)_3]^+Cl^-$). It blocks the biosynthesis of gibberellin, penetrating the plant mainly through the leaves and is partially absorbed by the root system from the soil. Treptolem is a complex preparation of 2,6-dimethylpyridine-1-oxide with succinic acid and phytohormones of gibberellin, auxin, cytokinin nature, amino acids, carbohydrates, obtained by culturing endophyte fungi from the root system of plants on synthetic nutrient medium.

The research was carried out on oil flax crops of early-ripening Debut variety and medium-ripening Orpheus variety, which are suitable for growing in the Steppe and Forest-Steppe zone.

The hydrothermal coefficient was 1-1.5 during the growing season in research areas. The soil cover in the area of the experiments is represented by gray and light-gray forest podzolic soils with coarse-grained medium-loam mechanical composition, slightly acidic (pH 6.6).

Morphological parameters (plant height, stem diameter in the central part, number of leaves, dry weight of the whole plant and its organs) were studied every 10 days. The leaf area was determined by the print method. The mesostructural organization of leaf and the anatomical structure of stem were studied during field studies at the ripening phase. The mesostructural organization of leaf of the experimental plants was studied by Mokronosov method [45]. A mixture of ethyl alcohol, glycerin, water in equal parts with adding of 1% formalin was used to preserve the biological material. Determination of cell size, seperate tissues, organs, vascular diameter was performed using ocular micrometer MOV-1-15x and digital camera for the microscope ScienceLab DCM 250. For this purpose, partial maceration of leaf tissues was used. A 5% solution of acetic acid in 2 mol/l hydrochloric acid was chosen as the macerating agent. Leaves of the same age and storey were selected for mesostructural analysis, and studies of the anatomical structure of the stem were performed in the middle part of the organ.

The total oil content in seeds was determined by extraction in Soxhlet apparatus. Petroleum ether with a boiling point of 40-65°C was used as an organic solvent. In the extracted oil samples, its qualitative characteristics were determined: acid number – by the indicator method for dark oils, iodine number - by the Gengrinovich method, saponification number, ether number, glycerol content – by conventional methods.

Quantitative content and qualitative composition of saturated and unsaturated fatty acids were determined by gas-liquid chromatography on a chromatograph "Chrom-5" (Czech Republic). Chromatography conditions were: 3.5 m glass columns with an inner diameter of 3 mm, filled with Chromosorb W AW 100-120 mesh sorbent with a mixture of stationary phases SP-2300 and 2% SP-2310 and 3%. Gas flow rate is 50 ml/min, gas-carrier is nitrogen. The temperature of the column was 200°C, the evaporator was 230°C, and the flame ionization detector was 240°C.

The content of residual chlormequat chloride quantities was determined by thin-layer chromatography on plates of the brand «Silufol UV-254» company Kavalier (Czech Republic). The method is based on the extraction removal of chlormequat chloride with acetone, following by purification in chromatographic column with silica gel. The quantity of chlormequat chloride was determined by measuring the optical density of the chromatogram of the analysed sample and standard solutions, which were measured on SP-46 spectrophotometer in sequential light of 730 nm wavelength. In parallel, the quantity of chlormequat chloride was determined by comparing of the sample and standard solutions spots of the chromatograms. Determination of the residual quantities of treptolem was implemented by high-performance gas-liquid chromatography on Crystal 2000M chromatograph made by company SCB (Technical Design Office) Chromatek. Extraction of residual treptolem quantities of from flax seeds was performed according to the method "Method for determining the residual pesticides" in accordance with DSTU (National Standard of Ukraine) 13496.20-87.

The obtained research results were processed statistically [14] and with the use of computer software package Statistica 6.0. The tables and graphs present the average values of three-year research.

Results and discussion

The key role in regulation of plant morphogenesis is played by the hormonal system, while the physiological effect depends not on the concentration of individual phytohormones, but on their ratio [12]. Ontogenetic changes in the ratio of gibberellins, cytokinins and auxins significantly affect the growth processes and features of the histogenesis of vegetative and generative organs of plants [48]. It is known that inhibitors and stimulators of development, influencing growth processes, may change the habit, anatomical structure and productivity of plants [36, 66]. We found that there were significant changes in morphogenesis and productivity of the culture in oilseed flax plants under the action of chlormequat chloride, treptolem and a mixture of drugs.

The results of our studies show that the use of antigibberelliine growth regulator chlormequat chloride led to a decrease in the linear size of flax plants of both varieties. That is a typical response of plants to the effects of retardants (Figure 1.). Thus, the height of the flax steam decreased by 12-14% and was 45-47 cm.

Treatment of plants with growth stimulators caused an increase in stem height to 59-62 cm, which is 13-14% higher than control. The effect of the mixture of drugs was insignificant – the plant height increased by 2-4% in comparison to the control.

The resistance to lodging issue is important for flax cultivation. Despite the widespread use of growth regulators of the retardant class for grain lodging prevention [39, 49], data on increasing the stability of oil seeds is found only in some publications [41, 42].

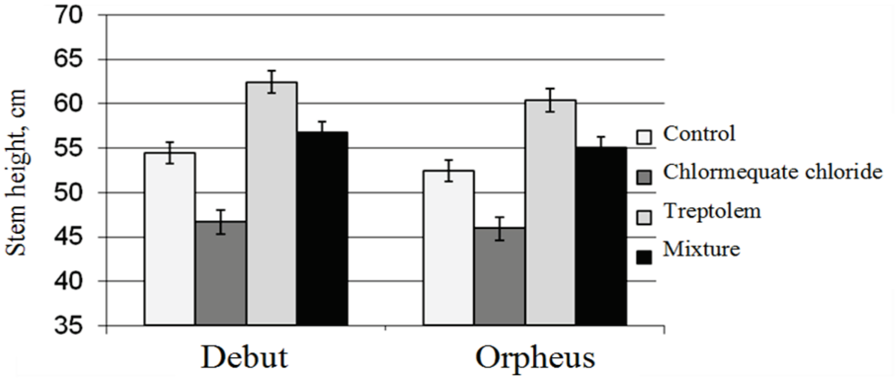


Figure 1. The effect of growth regulators on the stem height of oilseed flax plants

The results of our studies indicate that the use of growth regulators was a stem thickening of the experimental plants of all variants (Figure 2). The maximum diameter of the stem increased under chlormequat chloride use – an average of 27% for Debut variety and 33% for Orpheus variety. Under the influence of a mixture of retardant and stimulant, the transverse dimensions of the stem increased by 18 and 24%, respectively. The use of treptolem separately led to an increase in stem diameter of plants of Debut variety by 8% and by 14% for Orpheus variety. Namely, flax plants of Orpheus variety are more responsive to the introduction of exogenous growth regulators.

Anatomical studies show that stem thickening was due to increased bark and xylem development (Table 1, Figure 3.). Thus, under the action of growth regulators the number of xylem vessels in a set was increased by 1.3-1.7 times, leading to a significant thickening of its layer. The most effective was the use of chlormequat chloride and a mixture of retardant with treptolem, under the action of which the xylem layer increased by 1.8-1.9 times.

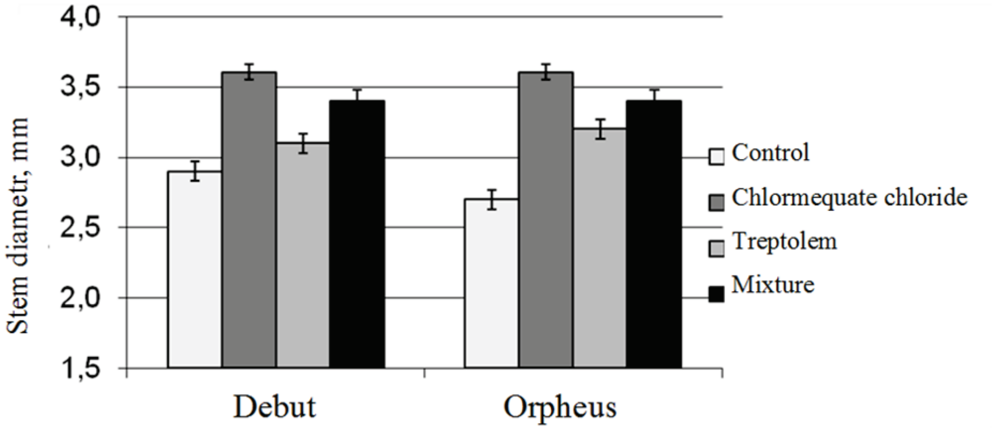


Figure 2. The effect of growth regulators on the stem diametr of oilseed flax plants.

Table 1.

Influence of growth regulators on the anatomical structure of the oil flax stem of Orpheus variety

Experimental variant / **Indicator**	**Control**	**Chlormequat chloride**	**Treptolem**	**Mixture**
The thickness of the epidermis, µm	18.5±0.4	20.8±0.5*	19.8±0.4*	21.3±0.6*
Cortex thickness, µm	241±8	320±12*	298±12*	311±14*
Xylem thikness, µm	541±10	1016±12*	769±13*	956±11*
Quantity of vessels per xylem set, unit	23±0.5	40±0.6*	31±0.8*	36±0.8*
Quantity of vessels per bast bundels, unit	32±2.1	32±3.8	33±3.6	34±2.0
Diametr of bast vessels, µm	29±0.5	39±0.6*	36±0.5*	39±0.9*
Cell wall thickness of bast fibers, µm	11.3±0.5	16.8±0.4*	14.7±0.4*	15.8±0.7*

Note*:* *– the difference is significant at $p \leq 0.05$.

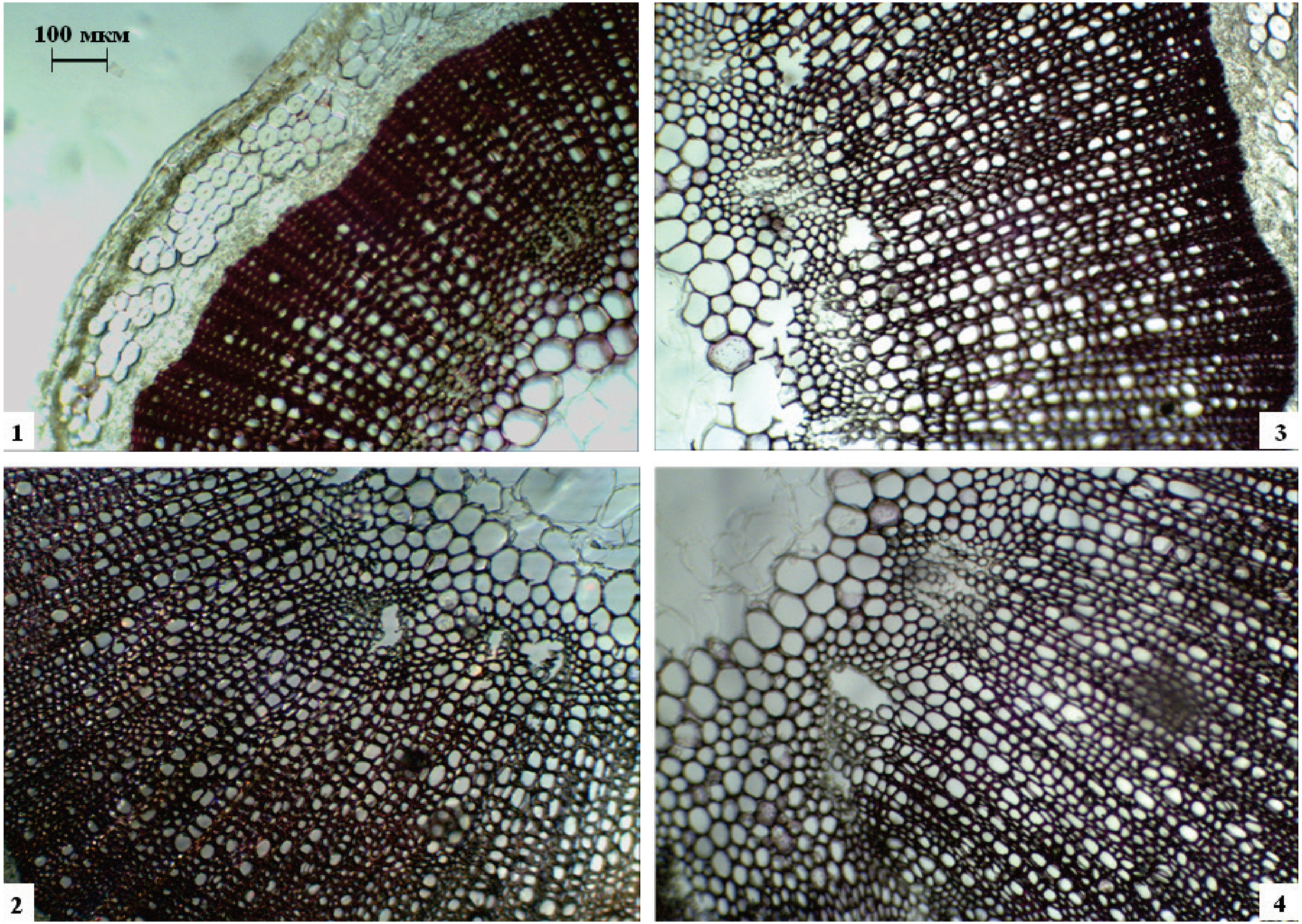


Figure 3. The effect of growth regulators on the stem xylem of oilseed flax plants Orpheus variety. **1** – control, **2** – chlormequat chloride, **3** – treptolem, **4** – mixture.

Using growth regulators, the number of bast fibers per bunch did not change, but diameter increased, the number of fibers with a severe thickening type of cell membranes increased. In particular, under treptolem influence, the cell wall thickness of the bast fiber increased by 30%, under the influence of stimulant and retardant mixture – by 40%. The maximum thickening was observed using chlormequat chloride – by 46% in comparison to control. The transverse dimensions of the fibers increased by 25-33% as a result (Figure 3).

Thus, the use of drugs led to stem thickening, increasing in the number of xylem vessels in a set and cell wall thickness of bast fibers, which improved the resistance of flax plants to lodging and provided technological advantages in harvesting.

Modern plant physiology considers the plant as an integral self-regulating system, where the source of assimilates are photosynthetic organs, especially leaves, all other organs are the sink [6]. Particularly, an important role in plant productivity is played by photosynthetic activity, which is largely determined by leaf area and anatomical features of the leaves, as well as the formation of demand for assimilates by acceptor zones [60, 67].

The results of our research show that the use of growth regulators with different mechanisms of action caused changes in leaf area formation of oilseed flax plants (Figure 4). Thus, the number of leaves on the plant under the action of the antigibberellin drug chlormequat chloride increased (Figure 5), but the total leaf area did not differ from the control. This indicates a decrease in the area of one leaf under the action of the drug, that is a typical response of plants to gibberellin deficiency [12, 26].

The action of a complex growth stimulator treptolem with cytokinin and auxin activity, as well as in a mixture with a retardant on the plant formed a larger number of leaves and significantly increased total leaf area. This confirms the opinion that leaf growth rate is positively correlated with the content of these phytohormones. Not only the size of the leaf surface but also the rapidity of leaf death is essential for the formation of the flax plant crop. The results show that the use of retardant and growth stimulant prolonged the life of the leaves (Figure 5).

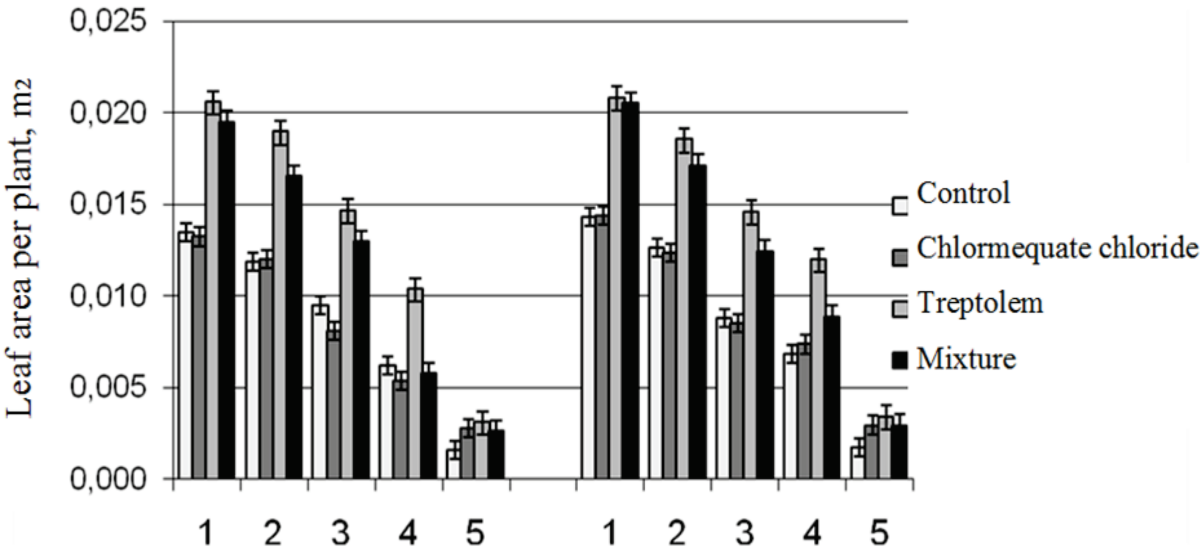


Figure 4. The effect of growth regulators on the leaf area of oilseed flax plants
Period after treatment: 1 – the day of 10, 2 – the day of 20, 3 – the day of 30, 4 – the day of 40, 5 – the day of 50.

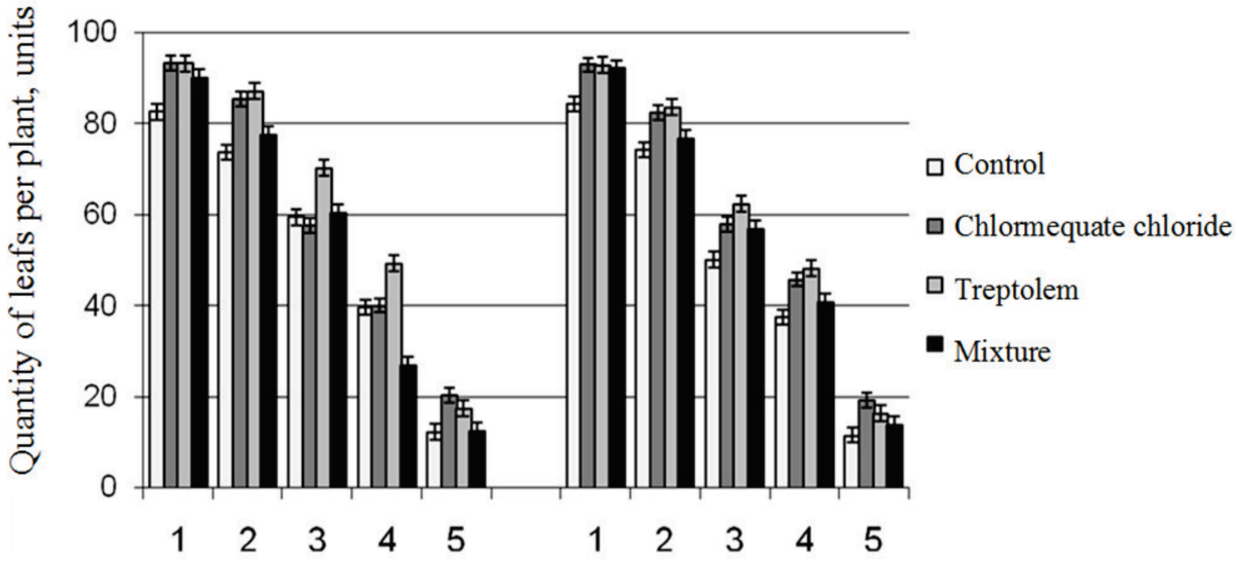


Figure 5. The effect of growth regulators on the leaf number of oilseed flax plants
Period after treatment: 1 – the day of 10, 2 – the day of 20, 3 – the day of 30, 4 – the day of 40, 5 – the day of 50.

It has been noted in publications that a decrease in leaf area was not definitely accompanied by a decrease in photosynthetic productivity [28, 58]. The results of our research show that the photosynthetic activity of flax leaves increases under the action of growth regulators, and the largest increase in source potential per unit leaf area occurred in a variant using a mixture of treptolem and chlormequat chloride, as well as separated growth stimulator (Figure 6).

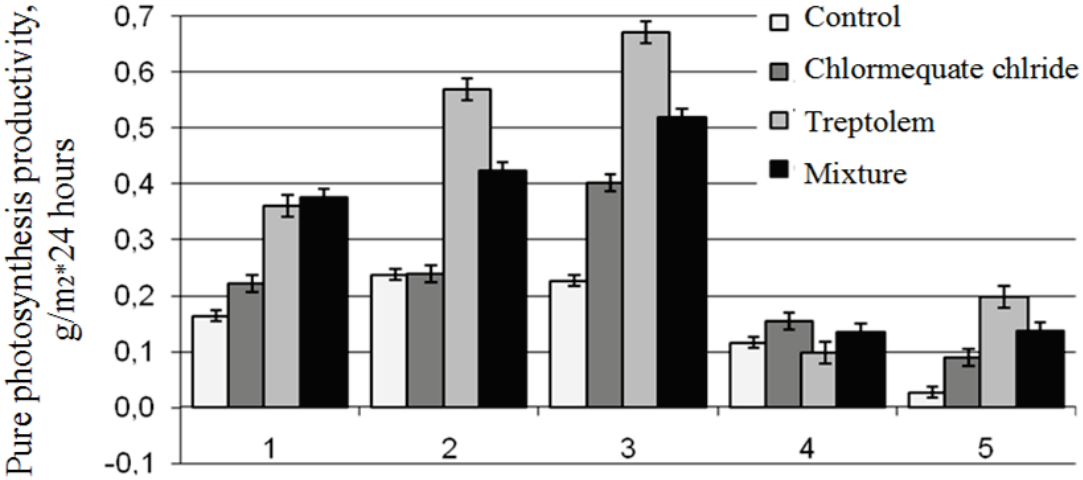


Figure 6. Pure photosynthesis productivity of oilseed flax plants under the effect of growth regulators. Period after treatment: 1 – the day of 10, 2 – the day of 20, 3 – the day of 30, 4 – the day of 40, 5 – the day of 50.

Increasing the number and area of leaves in flax plants under the action of treptolem and in a mixture with a retardant, promotes the formation of a more powerful assimilating surface, leading to photosynthetic productivity increase and more active accumulation of dry matter. Thus, under the influence of a mixture of regulators, the total dry matter mass of flax plants of Debut variety increased to 4.31±0.18 g and to 4.55±0.21 g for Orpheus variety, under the action of a growth stimulator – 4.07±0.22 g and 4.45±0.19 g, respectively, while in control this indicator was 3.77±0.22 g and 3.55±0.20 g, respectively. Using chlormequat chloride, the dry matter mass of Debut variety flax plants was 4.67±0.20 g, and the same of Orpheus variety was 4.37±0.20 g.

The nature of the photosynthetic process and the substrate support of growth processes was largely determined by the anatomical and morphological features of the leaf [32, 69, 78].

Studies of leaf anatomical structure show that the use of drugs during vegetation and field experiments significantly affected the mesostructural characteristics of flax leaves (Table 2).

We investigated that the decrease in leaf area in flax plants treated with retardant was accompanied by thickening of the leaf blade to 170.7±3.4 µm against 144.7±1.5 µm in control, which is a typical reaction of plants to the effects of retardants [45, 68]. A similar thickening of the leaves occurred under the action of treptolem and mixture. Leaf thickness under the action of treptolem and mixture with a growth inhibitor was 170.3±2.1 and 168.4±4.2 µm, respectively. Similar results have been established by other researchers on sunflower, potato, tomato crops [9, 18, 26, 52].

We found that the thickening of the leaf blade in plants of the experimental variants is due to the growth of chlorenchyma. There was a significant increase in cell volume of columnar assimilating tissue – the main leaf photosynthetic tissue under the action of the drugs. Thus, under the action of growth regulators, the cell volume of columnar parenchyma increased by 1.4-1.5 times. The size of spongy parenchyma cells did not change significantly.

The influence of growth regulators on photosynthetic productivity was realized through chloroplastogenesis. Our results indicate that treatment with the drugs increased the content and volume of chloroplasts in cells of chlorenchyma, in opposite to control.

Thus, the use of retardant and stimulant increases the volume of chloroplasts in cells of columnar parenchyma by 14-15%, and in cells of spongy parenchyma – by 21-27% in comparison to control. In our opinion, this changes of similar nature under the influence of physiologically opposite drugs is a consequence of the fact that the same ratio of auxins + cytokinins / gibberellins was formed in both cases, increasing in comparison to untreated plants.

Analysis of the mesostructural parameters of the photosynthetic apparatus of oilseed flax plants shows that under the influence of treptolem and a mixture with chlormequat chloride was formed a more powerful photosynthetic apparatus: leaf area and number of leaves increased, chlorenchyma contained more chloroplasts than in chlormequate chloride treated variant.

Table 2.

Leaf mesostructural organization of oil flax plants Orpheus variety under the action of growth regulators

Indicator / **Experimental variant**	**Control**	**Chlormequat chloride**	**Treptolem**	**Mixture**
Columnar parenchyma				
The length of the cell, μm	35.6±2.1	39.9±2.0	40.8±1.9	39.3±1.7
The width of the cell, μm	13.9±0.8	15.4±0.7	15.9±0.7	15.2±0.8
Cell volume, μm^3	3824±171	5327±196*	5727±215*	5317±224*
Quantity of chloroplasts per cell, units	12.9±0.5	14.5±0.6	14.7±0.7	14.9±0.6*
Chloroplast volume, μm^3	38.3±1.8	43.6±1.8*	43.9±2.0*	43.9±2.1
Spongy parenchyma				
The length of the cell, μm	19.4±0.7	17.5±0.8	18.4±0.9	18.9±0.8
The width of the cell, μm	16.2±0.6	14.2±0.6	14.8±0.7	14.1±0.7*
Quantity of chloroplasts per cell, units	6.2±0.3	8.9±0.3*	10.4±0.4*	10.8±0.5*
Chloroplast volume, μm^3	30.7±1.4	37.1±1.6*	38.9±1.6*	37.8±1.7*

Note:* – the difference is significant at $p \leq 0.05$.

Thus, flax oil plants treatment with chlormequat chloride, treptolem and a mixture of drugs led to changes in growth processes: the retardant inhibited the linear growth of plants, stimulator and a mixture of growth regulators enhanced stem growth. Under the influence of growth regulators, the stem diameter increased due to changes in anatomical organization: the bark thickened, the number of xylem vessels in a set increased, the diameter of bast fibers increased, improving the resistance of flax plants to lodging and providing technological advantages in harvesting. The use of regulators led to better development of columnar leaf parenchyma, increase in size and number of chloroplasts, prolongation of leaf life, resulting in increased photosynthesis productivity, more intensive accumulation of dry matter mass of experimental plants.

It is known from the literature that plant growth regulators affect the nature of source-sink relations in plant organism. As a result, there are changes in the structural organization of vegetative organs, the restructuring of the assimilation apparatus, the formation of additional centers of attraction [3, 13]. Increasing the attractiveness of sink zones leads to increasing of photosynthesis productivity and photosynthetic fixation of carbon dioxide, as well as the share of transport forms (sucrose) and the outflow of assimilates from leaves.

The rapidity and direction of transport of assimilates is determined by the formation processes, so the composition of compounds transported from the leaves, and the nature of their secondary use at growth zones and store tissues are changed during ontogenesis of the plant [31].

Changes in the functioning of the source-sink system occur due to the re-distribution of assimilate flows between plant organs. Therefore, the development of effective methods for the regulation of ontogenesis with the help of phytohormonal drugs requires a study of the dynamics of spare substance accumulation in plant.

The literature presents single and disparate data on the effect of growth stimulants and inhibitors on the accumulation and metabolism of carbohydrates in plant organs during ontogenesis.

The results of our research show that under the influence of growth regulators there are changes in the accumulation and re-distribution of carbohydrates between the organs of flax plants during the growing season.

Total carbohydrates (sugar+starch) content in leaves in all experimental variants was higher compared to the control during the growing season (Figure 7). Apparently, this was due to the retardant blocking the sink activity of the growth zones in vegetative organs and reducing the outflow of assimilates thereto in the variants with chlormequat chloride and drug mixture. In the case of treptolem use, this was due to the stimulating effect of the growth regulator on the synthesis processes and more intensive development of the plant organism.

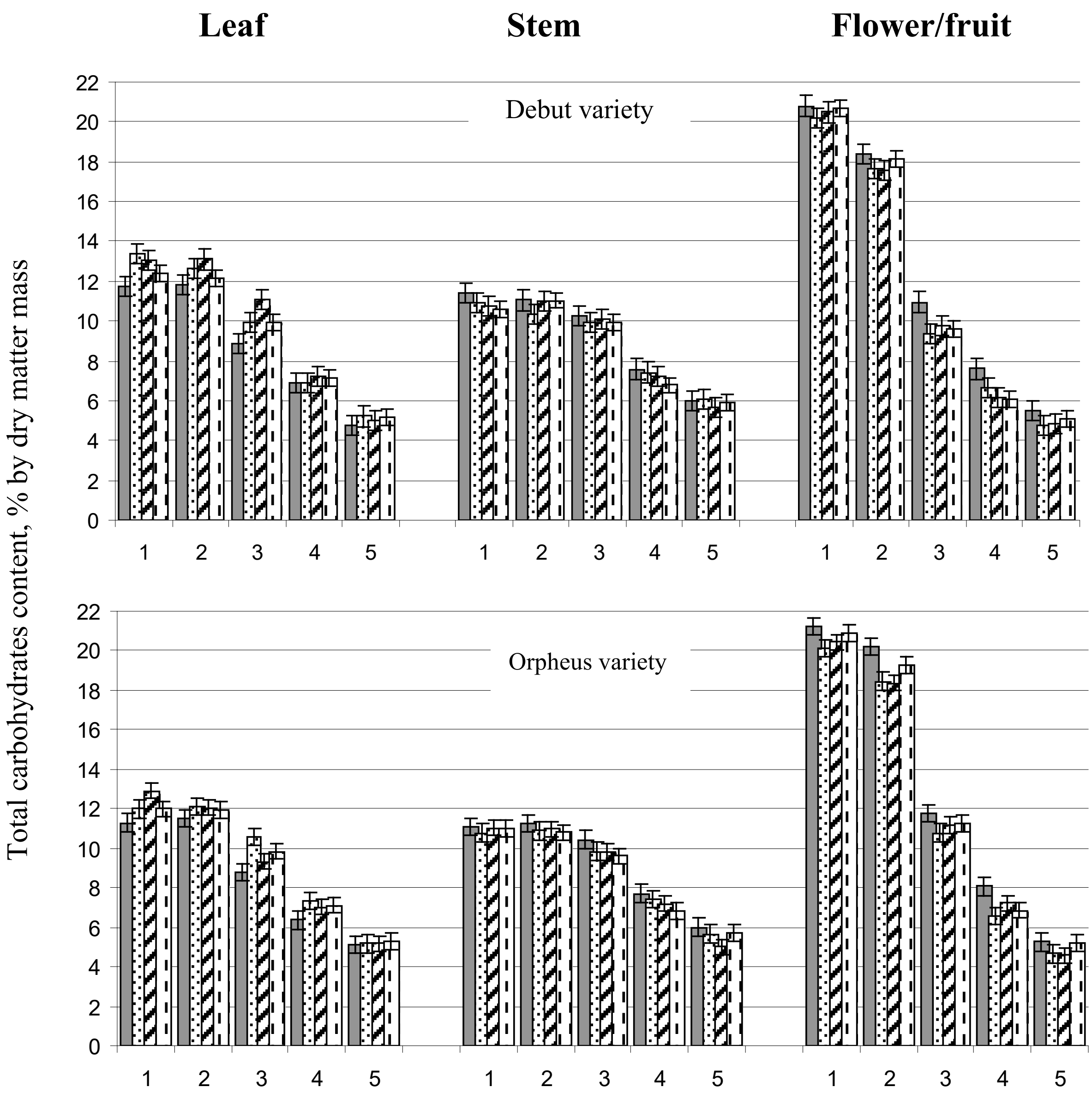


Figure 7. Dynamics of total carbohydrates content (sugar+starch) in aboveground parts of oilseed flax plants under the effect of growth regulators.

■ – control; ░– chlormequat chloride; ▨ – mixture of drugs; □ – treptolem.

Time of sampling: 1-5 – the day of 10, 20, 30, 40, 50 after treatment.

The accumulation of carbohydrates excess in leaves of experimental variants was positive, because a powerful reserve fund of assimilates was created, which was used for the formation and growth of flax fruits, increasing their quantity. Thus, according to the results of three-year research, the number of capsules per plant was 34-36 in chlormequat chloride-treated variant, and it was 29-31 under the action of treptolem and drug mixture, while 25-27 fruits were formed by plant in control variant.

In stems of plants treated with the drugs, the total carbohydrate content either did not differ in comparison to experimental variants, or was lower than in control. This was in good agreement with the anatomical and morphological data presented in Table 1, Figures 2-3. There was a thickening of the stem in all experimental variants, mainly due to the xylem, the carbohydrate excess coming from the leaves, obviously, can be used for the formation of its structural polysaccharides.

The processes of fruit formation and growth were accompanied by a significant reduction in free sugars and starch content in all variants of the experiment.

During the beginning and mass flowering (late June) there was no significant difference in carbohydrate content in generative organs under the influence of plant growth regulators. During the ripening phase, the difference in the concentration of carbohydrates in tissues begins to appear, sugar content decreases in all experimental variants in comparison to control, which is obviously due to the possible accumulation of other substances (protein and oil) in seeds. We have established similar patterns on the content of separate fractions of carbohydrates for flowers and fruits.

As can be seen from Figure 8, a gradual decrease in total sugar content occurs due to both starch and reducing sugars. During the period of flowering, fruit formation and its filling, the concentration of starch decreases by 1-2% in vegetative organs. The maximum decrease in the content of this polysaccharide was observed in leaves, using chlormequat chloride on plants of Debut variety, and in stems using mixture of drugs for Orpheus variety. Obviously, this was due to the use of carbohydrates for oil biosynthesis in seeds and the accumulation of protein compounds in fruits.

Thus, under the influence of growth regulators, the source potential of leaves of experimental plants increased. There was an increased sugars and starch content. The excess of carbohydrates was used for formation of a stronger stem of plants and fruit growth, which quantity increased under the action of drugs.

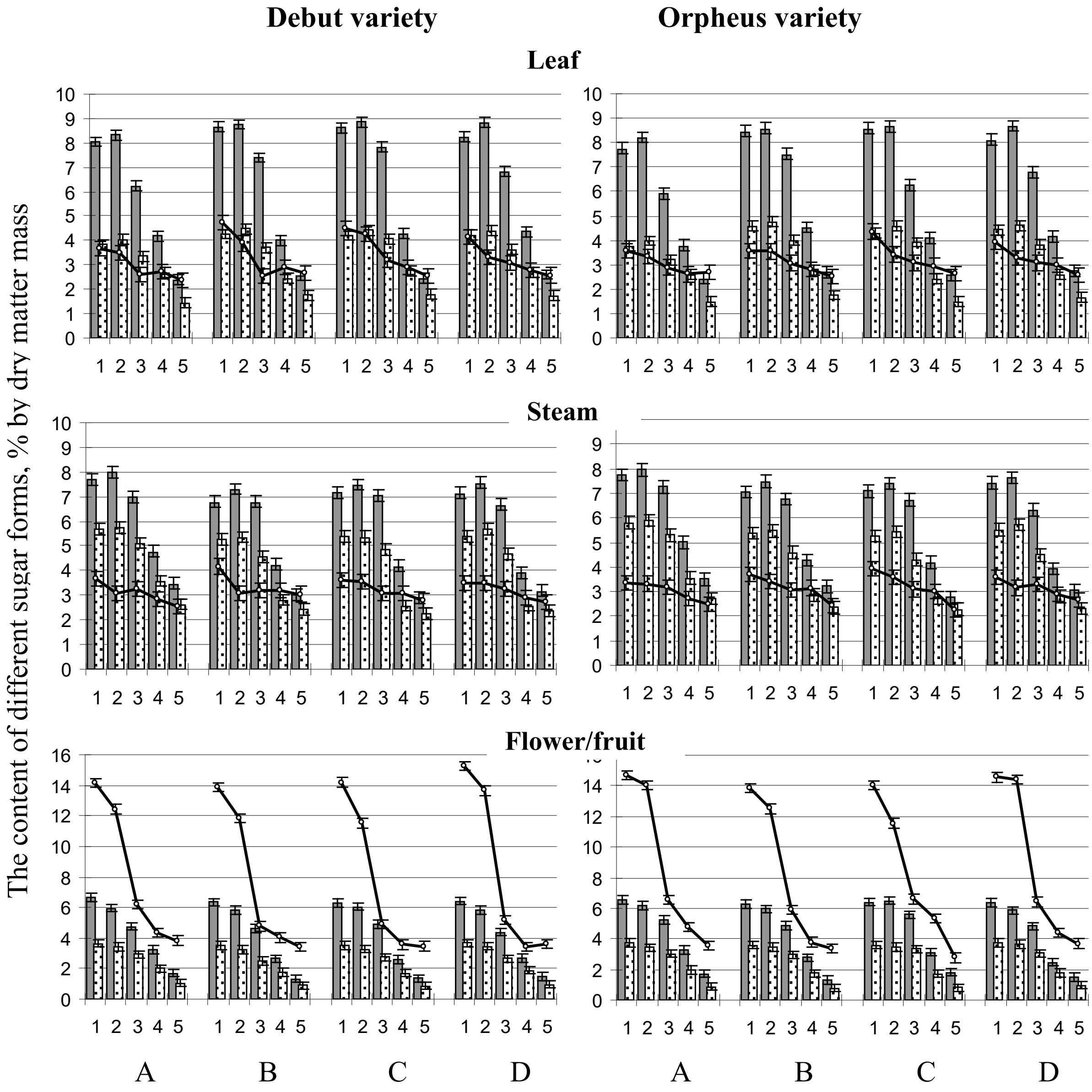


Figure 8. The effect of growth regulators on deposition of different sugar forms in oilseed flax plants. **A** – control; B – chlormequat chloride; C – mixture; D – treptolem.
Time of sampling: 1-5 – the day of 10, 20, 30, 40, 50 after treatment.

▨– total sugar; ⁙- reducing sugar; ●━━● – starch.

The use of phytohormonal drugs was accompanied by an increase in oilseed productivity as a result of re-distribution of excess assimilates to seeds or storage organs. Growth regulators based on natural or synthetic phytohormones provide the ability to control the duration of some phases of development, which allows to realize the genetic potential of the plant organism and provide conditions for the formation of higher yields and quality of agricultural products.

The results of our research show that the use of a retardant of the group of quaternary ammonium compounds chlormequat chloride, a complex stimulator of development treptolem with cytokinin and auxin activity, as well as their mixtures caused an increase in yield of oil flax. The effect of drugs on the flax productivity was manifested in crop structure changes. Thus, there was an increase in the number of capsules per plant, the number of seeds per fruit and seed weight under conditions of small-plot experiment for drug treatment (Tables 3, 4).

Table 3.

The effect of growth regulators on yield of oilseed flax plant

Experimental variant	**Debut variety**	**Orpheus variety**
Conrtol (water)	1.82±0.05	1.88±0.06
Chlormequat chloride	2.08±0.04*	2.13±0.05*
Treptolem	1.89±0.06	1.95±0.05*
Mixture	2.07±0.05*	2.03±0.05*

Note:* – the difference is significant at $p \leq 0.05$.

The use of chlormequat chloride leads to blocking of gibberellin synthesis and partial removal of the apical dominance effect, resulting in increased stem branching and laying of more capsules. Thus, under the action of drug, this indicator increased by 35-39% in average in comparison tocontrol, while the mixture of growth regulators use showed the increase by 22-31%. In all experimental variants, the weight of 1000 seeds increased by 2.3-4.1%. The weight of seeds per plant changed the most significantly under the treatement with chlormequat chloride – by 0.4-1.3 g, as well as in mixture variant – by 0.5-0.9 g, using treptolem – by 0.2-0.5 g.

Meteorological conditions during the growing season can affect crop productivity. It is confirmed by studies of other authors [15, 16]. In particular, in a more typical year in terms of precipitation, the yield of plants treated with chlormequat chloride increased the most significantly – by 14.8% for Debut variety and by 15.4% compared to control for Orpheus variety.

Table 4.

The effect of growth regulators on productivity of oilseed flax plant

Experimental variant	**Fruit quantity per plant, units**	**Seed quantity per capsule, units**	**1000 seeds weight, g**	**Seed weight to plant weight ratio**	**Seed weight per plant, g**
Debut variety					
Conrtol (water)	25.03 ±0.72	8.23 ±0.25	7.65 ±0.08	0.451	1.58 ±0.09
Chlormequat chloride	34.74 ±0.77*	9.10 ±0.21*	7.94 ±0.04*	0.529	2.31 ±0.15*
Treptolem	29.04 ±0.68*	8.33 ±0.25	7.82 ±0.07	0.471	1.81 ±0.11
Mixture	30.22 ±0.65*	9.13 ±0.13*	7.86 ±0.05	0.503	2.17 ±0.12*
Orpheus variety					
Conrtol (water)	27.00 ±1.03	8.25 ±0.22	7.86 ±0.02	0.461	1.75 ±0.08
Chlormequat chloride	36.49 ±1.22	9.17 ±0.16*	8.18 ±0.02*	0.598	2.55 ±0.11*
Treptolem	30.73 ±1.14*	8.41 ±0.18	8.09 ±0.03*	0.468	2.09 ±0.13
Mixture	30.82 ±1.22*	9.08 ±0.17*	8.13 ±0.02*	0.510	2.27 ±0.14*

Note:* – the difference is significant at $p \leq 0.05$.

The results of our research show that the yield of oilseed flax is most correlated with the number of fruits and seeds (Figure 9).

Despite the fact that the most effective way to increase the yield was the use of chlormequat chloride, the obtained results for optimization of production process using treptolem and a mixture of drugs were valuable in practical terms, too. Thus, from short straw of oil flax fiber it is possible to obtain cotonised, cotton-like fiber for the production of mixed flax-cotton fabrics, medical cotton wool [8, 64].

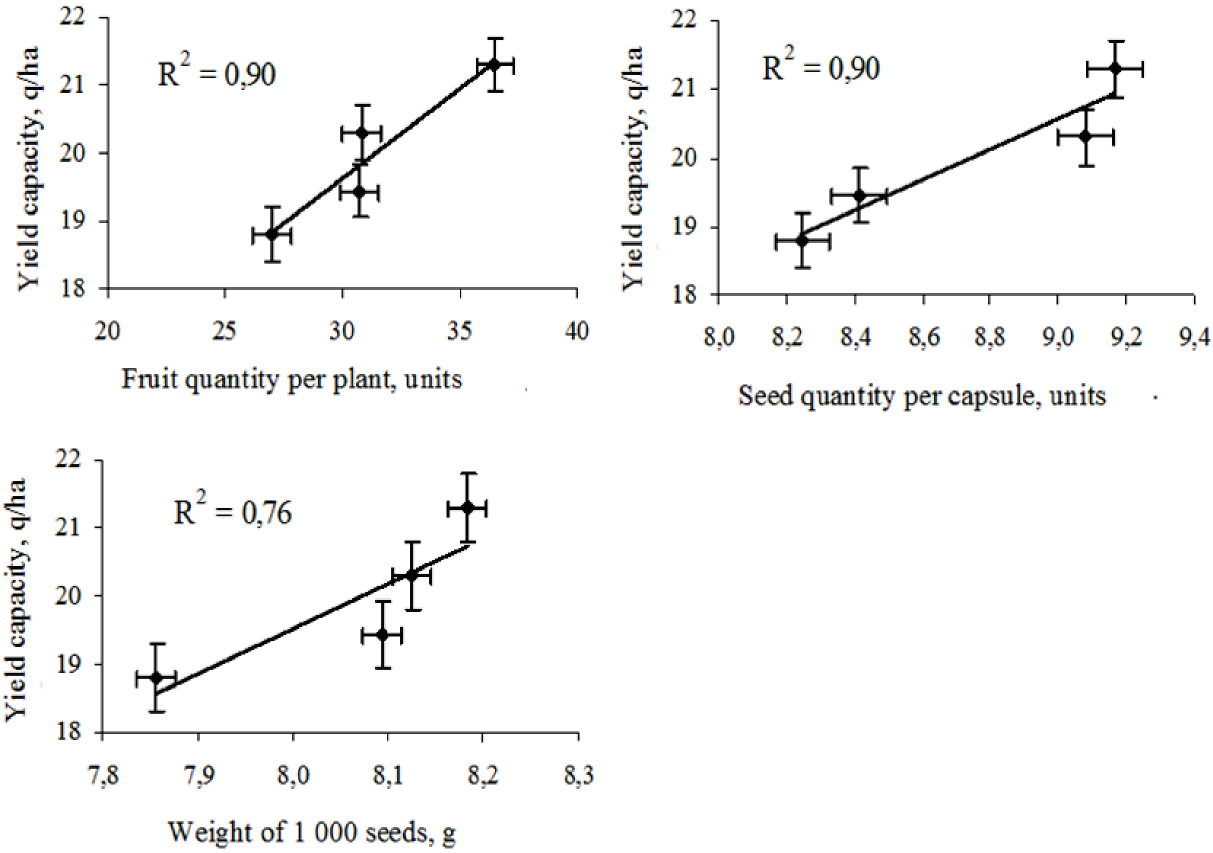


Figure 9. The relation between structural elements and yield of oilseed flax Orpheus variety

Under the influence of treptolem the growth of flax plants increased, the stem length increased (Figure 1.). At the same time, under the action of the stimulator a thinner fiber was formed in comparison to plants treated with retardant (Table 1). Thus, the use of the drug leads to a double positive effect – yield increase, while improving the fiber quality.

Over the years, the treptolem treatment of flax crops led to a stable yield growth by 2.7-4.1% for both varieties. Due to the content of hormones of cytokinin and auxin nature , treptolem can be included in physiological processes in plant and enhances growth. Intensive protein hydrolysis in vegetative organs promotes the outflow of nitrogen-containing compounds to new attracting centers – fruits.

The use of inhibitor and growth stimulator mixture was the most effective for Debut variety flax. Thus, in some years the seed productivity of the crop increased by 21.2%. For Orpheus variety, the increase was 12.0% relative to control. Based on current data on the nature and mechanisms of action of these growth regulators, it can be noted that the use of chlormequat chloride and treptolem allows to optimize the ratio of auxin+cytokinin/gibberellin in flax plants [24, 61, 72]. Similar changes in the balance of physiologically active substances and the functioning of the source of assimilates – sink system led to a more active flow of spare substances to the generative organs.

Analysis of yield indicators shows that the ratio of seed weight to plant weight increased under the treatment with growth regulators (Table 3). The most significant increase in the ratio for plants of Orpheus variety was observed in chlormequat chloride-treated variant, while for plants of Debut variety – under the action of a mixture of drugs. Despite the increase in seed weight from the treptolem-treated plants, the ratio changed slightly or was lower in comparison to control. This is due to the increase in the total plant weight and active stem growth under the action of growth stimulator.

Thus, the results of our research show that the use of growth inhibitor chlormequat chloride, development stimulator of treptolem and a mixture of these drugs improves the productivity of flaxseed. The most effective was the use of retardant and its mixture with stimulator.

Flax seeds contain a significant amount of lipids, proteins, fiber, carbohydrates, as well as the most important elements – potassium, calcium, phosphorus, magnesium, sodium, copper, iron, manganese. Among the vitamins ascorbic acid, thiamine, riboflavin, pyridoxine, nicotinic and pantothenic acids, biotin, folic acid, tocopherols were found [4, 47]. This permits the use of flaxseed and oil in the diet of patients with obesity, atherosclerosis, coronary heart disease, hypertension, diabetes, cirrhosis, hepatitis, fatty liver disease. Flax seeds also have fodder value: the marc contains 6-12% fat and 38% protein, and its 1 kg nutritional value is 1.2 fodder units. Flaxseed grist contains a number of essential amino acids and it does not require extrusion [15, 63].

Flaxseed oil is a mixture of triglycerides of fatty acids: 9-11% palmitic and stearic, 13-29% oleic, 15-30% linoleic, 44-61% linolenic acids. Flaxseed oil is an extremely biologically valuable product. It is characterized by a high content of mono- and polyunsaturated fatty acids, in particular linoleic and linolenic acids, which are essential for humans [34]. Polyunsaturated essential fatty acids are precursors of long-chain fatty acids and are part of cell membranes. Of particular importance is α-linolenic acid, which content in some flax varieties can reach 50% [20, 22].

Due to the high unsaturated acids content and their ability to oxidize rapidly, linseed oil is fast-drying, which leads to its use in the high quality production of drying oils, alkyd resins, oil varnishes, mild soaps, as a component of linear fixers, printing inks and others.

Given the widespread use of flax products in the national economy and the possibility of influence on the accumulation of reserve compounds in seeds due to the use of plant growth regulators [22, 30, 32], among the aims of our work was to determine the effectivity of drugs with different directions of action to improve the quality composition of flaxseed oil.

The results of our research show that oil content in flax seeds increased under the action of chlormequat chloride, treptolem, as well as their mixture (Table 5).

The largest increase in seed oil content was observed using a retardant and its mixture with a growth stimulant in comparison to control.

We found that the treatment of flax plants with retardant and stimulator of development led to quality changes in oil in comparison to control (Table 5). In particular, saponification value, ether and iodine values, glycerol content increased in the vast majority of variants under the influence of drugs.

The acid value as an indicator of free fatty acids content did not exceed the permissible concentrations (not more than 2.5 mg KOH/g) for linseed oil in all experimental variants. The content of free acids was most significantly reduced under the treptolem use.

We found an increase in saponification value (characterizing total free and bound fatty acid content) and ether number (characterizing bound fatty acid content) of oil using plant growth regulators on both varieties of flax. Treatment of plants with chlormequat chloride and treptolem led to a stable growth of these indicators over the years.

Flaxseed oil is characterized by a relatively high iodine value (an indicator of unsaturated fatty acid content). The effect of drugs on this indicator was insignificant – by 6-12 g of iodine per 100 g of oil above the control under the retardant and its mixture with a stimulant, and by 2-9 g of iodine above the control under the influence of treptolem.

Table 5.

Influence of growth regulators on the content and qualit

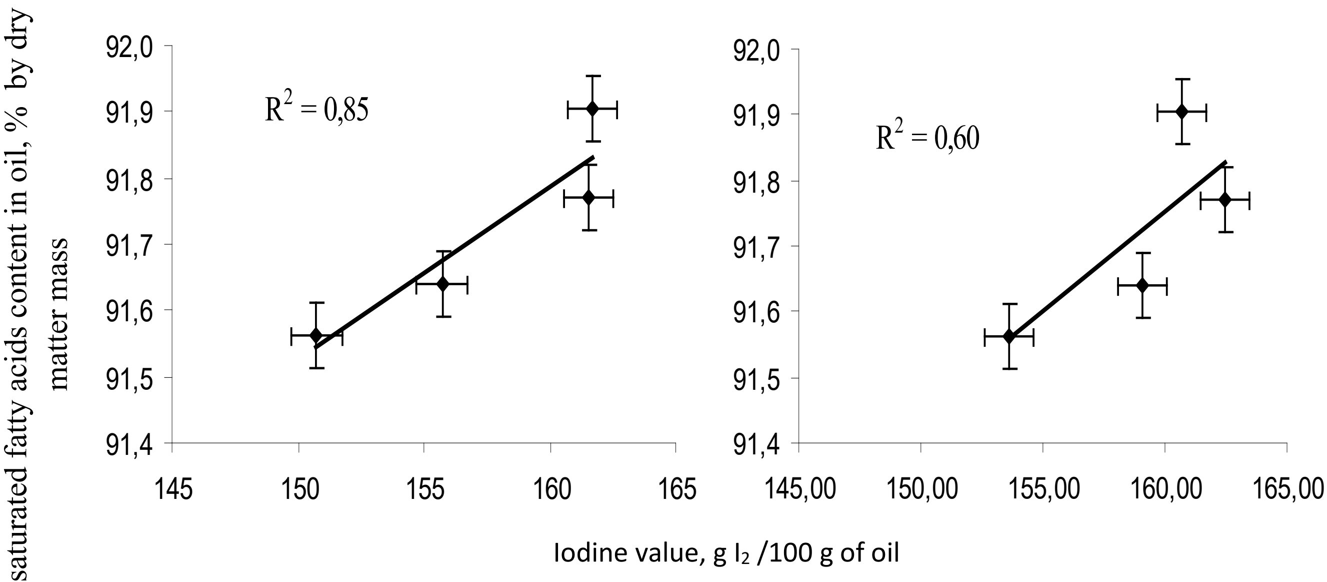
Table 5 continuation

Indicator / **Experimental variant**	**Oil content in seeds, %**	**Acid value, mg KOH/1 g of oil**	**Saponification value, mg KOH/1 g of oil**	**Ether value, mg KOH/1 g of oil**	**Iodine value, g I_2/100 g of oil**
Debut variety					
Conrtol (water)	34.3 ±0.3	1.87 ±0.14	161.73 ±2.25	159.90 ±2.25	150.73 ±2.40
Chlormequat chloride	36.7 ±0.2*	1.65 ±0.04	178.37 ±2.65*	176.67 ±2.45*	161.53 ±4.70
Treptolem	36.0 ±0.2*	1.63 ±0.03	180.00 ±1.87*	178.37 ±2.21*	155.73 ±4.80
Mixture	36.9 ±0.2*	1.77 ±0.15	176.50 ±1.85*	174.75 ±2.80	161.70 ±2.92*
Orpheus variety					
Conrtol (water)	36.8 ±0.2	1.71 ±0.03	162.50 ±1.92	160.80 ±2.82	153.65 ±4.62
Chlormequat chloride	39.1 ±0.1*	1.54 ±0.07	170.57 ±2.72	168.84 ±2.12	162.43 ±1.47*
Treptolem	38.5 ±0.3*	1.57 ±0.03	185.57 ±2.09*	184.00 ±2.03*	159.06 ±5.70
Mixture	39.3 ±0.3*	1.93 ±0.04	181.56 ±1.76*	179.64 ±2.30*	160.72 ±4.71

Note:* – the difference is significant at $p \le 0.05$.

The quality of oil also largely depends on the ratio of fatty acids in it [44]. Chromatographic analysis of flaxseed oil revealed seven major higher fatty acids – palmitic, palmitoleic, stearic, oleic, linoleic, α-linolenic, gondoic (Table 6). The results of our research show that the use of growth regulators affects the fatty acid composition of flaxseed. Thus, treatment of plants with chlormequat chloride and treptolem caused a decrease in saturated acid content. The use of drug mixture on plants of Orpheus variety led to the most significant decrease in concentration of palmitic and stearic acids. The lowest values of saturated acid content in flaxseed oil of Debut variety were observed after treatment with growth inhibitor.

Under the use of growth regulators, the total content of unsaturated higher fatty acids increased, correlating with the iodine value (Figure 10). In major cases, the ratio of unsaturated to saturated fatty acids increased in comparison to control, indicating improvement of oil quality. The maximum increase in this ratio was found under the action of a mixture of chlormequat chloride and treptolem. It was 12.09 for Debut variety and 12.42 for Orpheus variety, as well as after the use of retardant it was 12.28 and 11.61, respectively.



Debut variety **Orpheus variety**

Figure 10. The relation between unsaturated fatty acids content and iodine value of flax oil

Taking into account the requirements of environmental safety using synthetic and complex plant growth regulators, the necessary condition was the study of toxicological risk and control of the content of residual quantities of drugs in final product [17, 21, 24].

Table 6

Influence of growth regulators on higher fatty acids content in flaxseed oil of Orpheus variety (% by dry matter mass)

Experimental variant / **Fatty acid**	**Debut variety**				**Orpheus variety**			
	Control	**Chlormequate chloride**	**Treptolem**	**Mixture**	**Control**	**Chlormequate chloride**	**Treptolem**	**Mixture**
Palmitic	5.01±0.02	4.94±0.09	4.96±0.01	4.90±0.07	4.85±0.22	4.63±0.07	4.66±0.01	4.42±0.01
Palmitoleic	0.06±0.003	0.06±0.005	0.06±0.005	0.07±0.002	0.05±0.006	0.06±0.005	0.05±0.005	0.06±0.005
Stearic	3.43±0.01	3.30±0.09	3.41±0.04	3.21±0.01	4.02±0.07	3.87±0.07	3.88±0.18	3.58±0.04*
Oleic	18.95±0.01	19.05±0.11	19.11±0.18	18.54±0.11	19.15±0.32	20.10±0.12	18.58±0.41	20.65±0.24*
Linoleic	14.05±0.02	13.68±0.08*	13.89±0.14	13.87±0.08	14.00±0.16	13.91±0.03	14.16±0.33	14.04±0.18
α-Linoleic	58.16±0.06	58.88±0.12*	58.42±0.01	59.35±0.14*	57.78±0.30	57.34±0.30	58.59±0.62	57.14±0.56
Gondoic	0.34±0.01	0.10±0.01*	0.16±0.01*	0.09±0.01*	0.13±0.01	0.09±0.01	0.09±0.01	0.14±0.01
Saturated acids content	8.44	8.24	8.37	8.11	8.87	8.50	8.54	8.00
Unsaturated acids content	91.56	91.77	91.64	91.90	91.12	91.51	91.48	92.01
The ratio of unsaturated / saturated acids	10.88	11.18	10.97	11.38	10.28	10.80	10.73	11.56

Note:* – the difference is significant at $p \leq 0.05$.

The content of residual quantity of growth regulators was determined by chromatography (research method according to NTD–MD № 1909-78). According to DSanPiN. 8.8.1.2.3.4.-000-2001 the residual quantities of chlormequat chloride in seeds should not exceed 0.1 mg/kg. In the sample of Orpheus variety flax seeds treated with this retardant, the concentration was 0.042 mg/kg.

Extraction of residual quantity of treptolem from flax seeds was performed in accordance with GOST 13496.20-87. The residual quantity of growth regulator in Orpheus variety flax seeds was 0.0073 mg/kg. It did not exceed DSanPiN. 8.8.1.2.3.4.-000-2001 norm for flax seeds – 0.03 mg/kg.

Therefore, the use of chlormequat chloride, treptolem and their mixture caused an increase in the oil content in flax seeds, improving its quality characteristics, increasing the content of unsaturated fatty acids. The residual quantities of these growth regulators in the seeds did not exceed the maximum allowable concentrations (MACs) set by toxicological and hygienic standards.

Conclusions

1. The use of chlormequat chloride, treptolem and their mixture in oilseed flax culture led to the modification of source-sink relations in plant, being realized through anatomical and morphological changes of vegetative organs, re-distribution of assimilates and minerals towards the formation of capsules.

2. Treatment of flax oil plants with chlormequat chloride, treptolem and drug mixture led to changes in growth processes: the retardant inhibited the linear growth of plants, stimulant and mixture of growth regulators enhanced stem growth. Under the influence of growth regulators, the stem diameter increased due to changes in anatomical organization: the bark thickened, the number of xylem vessels in a set increased, the diameter of bast fibers increased, improving the resistance of flax plants to lodging and providing technological advantages in harvesting.

3. Under the action of chlormequat chloride, treptolem and their mixture increased the number of leaves per flaxseed plant. Under the influence of the stimulant and its mixture with the retardant, the total leaf area per plant increased,

contributing to the formation of a powerful assimilation surface. The use of growth-regulating drugs led to improoved development of the columnar parenchyma of the leaf, increasing the size and quantity of chloroplasts, resulting in increased photosynthesis productivity, more intensive accumulation of dry matter mass of experimental plants.

4. There were changes in carbohydrate accumulation and re-distribution between the organs of flax plants under the influence of growth regulators. The accumulation of excess carbohydrates in leaves of experimental variants creates a powerful reserve stock of assimilates, used for the formation of a more developed stem and fruit growth. The reduction in free sugars and starch content in capsules was due to the use of carbohydrates for oil biosynthesis in seeds and the accumulation of protein compounds in fruit.

5. The effect of drugs on the productivity of flax was manifested in changes in crop structure. The number of fruits per plant increased in the experimental variants. The maximum number of seeds per fruit was observed under the action of chlormequat chloride and its mixture with treptolem on both varieties. The use of growth regulators increased the weight of seeds. The largest increase in yield was provided by the use of retardant and its mixture with growth stimulant.

6. The use of chlormequat chloride, treptolem and their mixture caused an increase in oil content in flax seeds, improving its quality characteristics. Saponification, ether and iodine values were increased under the influence of drugs, and the acid value decreased. The rates of unsaturated fatty acid content were increased.

7. The residual quantities of growth regulators in seeds did not exceed the maximum permissible concentrations established by toxicological and hygienic standards.

CHAPTER 4.
FUNCTIONING OF THE SOURCE-SINK SYSTEM UNDER THE ACTION OF GROWTH REGULATORS

Introduction

The main task of the crop industry is to ensure the possibility of influencing on yields by changing the major characteristics of crops directly or indirectly [54].

According to the modern notion, higher plants are a single source-sink system, which mainly depends on genetic development programs. It is known that a characteristic feature of the most high-productive crops is the saturation of assimilating tissues with pigments [17, 84]. However, even the experience of using transgenic plants with changes of only one or several molecular determinants in majority does not lead to a significant and reliable increase of yields [33]. Instead, the possibility of correcting of the production process in epigenetic ways is the main advantage of the approach to crop production in terms of regulation of source-sink relations.

4.1. The main aspects of the concept of source – sink

The concept of source – sink relations began its formation in the 60s of the last century and became well-developed in the 80s due to the works of A.L. Kursanov, A.T. Mokronosov, D. Heyder and I. Wardlow. Today the concept covers different levels of organization of the plant organism starting from tissue to organism, in particular at the level of a single organ, such as a leaf, source-sink connections can function between photosynthetic tissues (source) and the conduction system (sink), as well as at cellular level – between the chloroplast and the cytosol. The coordination of the activity of plastic fluxes between the source and the sink occurs mainly due to the system of regulatory signals, which may be primarily the assimilates, phytohormones and other signaling molecules [52].

For regulation of the source–sink system of cultivated plants, both genetic and technological ways are used, working in a complex, complementing each other. That makes it possible to reduce the amount of fertilizer required to obtain a unit of crop production, its cost and reduce the negative pressure on the environment [1, 11, 29, 80].

Regulation of source-sink relations is considered as the highest level in the hierarchy of processes that ensure the functioning of the plant as a whole system [39, 42]. It is believed that the evolutionary prerequisite for the ejection of the source – sink system is the formation of the vascular system, which provides not only the vertical position of the plant in space, but also the transport, mechanical and spare functions in the plant. As the phloem is the major transport pathway for aminoacids and organic nitrogen from source to sink [10, 79], it eliminates the possibility of regulating the source-sink pressure gradient by altering the activity of transport proteins that mediate cellular export and import through the apoplast. Such transport is effective in highly specialized sieve-like elements of the phloem, even in the tallest trees [8, 54]. In particular, it was found that exogenous effects (temperature, carbon dioxide) on the phloem of Brutus pine (*Pinus brutia* Ten.) [3], oak (*Quercus robur* L.) [15], poplar seedlings (*Populus cathayana* L.) [93] caused changes in carbohydrate and protein metabolism in photosynthetic organs. Changes in metabolism were also observed as a result of exposure to xylem, although the latter was more stable.

Establishing of the key features of source –sink relations is important to clarify the processes of crop growth, adaptation and overcoming environmental constraints [16]. In particular, for new varieties of Salix spp the optimizing model of the balance between source (photosynthesis) and sink (morphogenesis) was investigated. It led to an increase in the productivity of broadleaf varieties by 20%, and narrow-leaved – by 47% [8]. It is proved that the regulation of source-sink relations by creating conditions of temperature stress also had a positive effect on the productivity of bell pepper culture, contributing to an increase in the number of flowers on the plant (65%) during budding, as well as mesocarp cell size and proportion by fruit weight

[14, 29]. In this case, it should be borne in mind that the attractive tension of organs depends primarily on the number of cells, rather than their size [52]. It is likely that the increase in crop productivity is associated with an increase in the intensity of photorespiration under stress, which, in contrast to dark respiration, does not lead to unproductive losses of assimilated carbohydrates [50, 86].

Increasing the yield and stability of the crop under stress conditions is the primary goal of growing crops such as wheat (*Triticum spp.*) [49, 86] and rice (*Orýza spp.*) [5, 16]. It was found that high temperature had a negative impact on the productivity of wheat at the stage of pollination and ear filling, inhibiting the activity of the acceptor sphere (sink), namely the process of grain formation [18, 27, 54, 56]. The established features of the functioning of the source-sink system is an important mechanism for the redistribution of assimilates between plant organs in ontogenesis in order to improve productivity.

4.2. The use of retardants and other plant growth regulators to regulate the functioning of source-sink relations

It should be noted that according to modern ideas, the basic concepts of the concept of "source" and "sink" can be applied not only to specific organs, but also to processes. It is known that the realization of source-sink relations can occur in different systems: photosynthesis–growth, depot of assimilates–growth, macro- and microsymbionts – processes of symbiotic nitrogen fixation. Accordingly, there are traditionally three types of attracting centers, which differ in the nature of activity: growth points, places of deposition of substances for reserve and places of active metabolism [42].

4.2.1. Functioning of the photosynthesis - growth system from the point of concept view of source-sink relations.

Since light is one of the most important external factors that significantly affect morphogenesis, the main focus of research is on the processes of functioning of the system «photosynthesis-growth». The first is assigned the role of producer of assimilates, the second process plays the role of consumer of assimilates, where the assimilate may be understood as a substance formed as a result of photosynthesis as the primary organic compound. The number of assimilates is directly proportional to the photosynthetic activity, which is determined by the enzymatic potential of chloroplasts, the area of the assimilating organ and the productivity of the process[34, 35]. This is confirmed by modern studies, which indicate the peculiarities of relationship between the decrease in leaf area and the decrease in the dry matter mass of leaves and stems of raspberries under the action of gibberellin. In addition, the functioning of the leaf apparatus significantly affects the productivity of the plant, where an additional powerful sink of assimilates is the processes of carpogenesis [39].

The improvement of the assimilation process positively correlates with the values of morphometric parameters, the formation of which occurs due to the activity of marginal meristems, which are the main acceptors during vegetative growth, being under molecular control [9, 36, 42].

The determining factor of source functioning is the mesostructural organization of the leaf, namely leaf thickness, columnar parenchyma volume, linear size of the spongy parenchyma and chlorophyll content in tissues, which determines the efficiency of photon energy use and its absorption [60, 61]. Reorganization of the leaf apparatus, optimization of the anatomical and morphological structure of the chlorenchyma and changes in the chlorophyll index lead to increased values of pure photosynthesis productivity, which is confirmed by experimental studies of «source» of a number of plants: potatoes [90], sugar beets [84], rapeseed [76], sunflower [73], oil flax [32], oil poppy [67], soy [26, 41].

It is known that the intensity of photorespiration determines the resistance of the photosynthetic apparatus to photoinhibition while reducing the assimilation of CO_2. As a result of inhibition of carbon dioxide assimilation in bright light, photoinhibition of PSII occurs. In wheat plants, high rates of photorespiration intensity contributed to the preservation of the activity of the photosynthetic apparatus due to changes in metabolism of glycolate, which enhance the decarbonization of its intermediates and the loss of assimilated carbon [49]. Photorespiration as an electron acceptor reduces photoinhibition, also supporting the activity of linear electron transport in chloroplasts [17, 30], which helps maintain high productivity during the generative period during ontogenesis, stimulates nitrogen metabolism and ensures high adaptive potential of varieties under adverse conditions [72]. It is also known that the inhibition of photosynthesis can occur due to an excess of assimilates. Since growth processes are associated with metabolic processes, redistribution of plastic substances, energy transformations, it is necessary to take into account all mechanisms of improving photosynthetic assimilation [49], which allow not only to reorient assimilate flows, but also to use them effectively, preventing their surpluses formation.

Recent studies suggest that changes in the source-sink system of the plant caused by surgical removal of part of the sink not only inhibit photosynthesis, increasing competition from acceptors for assimilates, but can also increase dark respiration [9, 14, 61]. During experiment involving the treatment of oil palm inflorescences (*Elaeis guineensis Jacq*.) with growth regulators or partial defoliation, it was possible to influence the redistribution of assimilates in the source-sink system. The attractive properties of heterotrophic organs during retardant treatment changed significantly: the number of flowers in the inflorescence increased, the number of fruits obtained from one inflorescence, the amount of oil in the dry material of each fruit. The change in the ratio between the supply of the source and the growing demand for carbohydrates in the organs was confirmed by a decrease in the fall of flowers rate due to reduced demand for nutrients by the vegetative organs [6, 60]. Other researchers have found that the optimization of winter rapeseed cultivation depends on the regulation of the availability of resources for seed formation during the reproductive phase of development by correcting the number of branches that are "extra" acceptors of assimilates [28, 74, 76].

Taking into account the above, there is a need to use alternative ways to reduce the activity of growth centers without creating conditions of additional stress (defoliation), namely the use of growth inhibitory drugs – retardants. The literature presents comprehensive information on the peculiarities of the processes of photosynthesis and respiration under the influence of retardants [30, 31, 44, 50, 75]. The use of growth inhibitors allows to influence the functioning of the source, as well as to simulate the activity of the sink sphere, which reduces the demand for assimilates by the main sink – the developing sprout. Thus, due to the suppression of the activity of apical meristems, there is a redistribution of plastic substances for the needs of more priority processes, the development of other organs [33]. For example, during the experiment, due to foliar application of growth regulators, changes in the system of source-sink relations were achieved - it was possible to overcome low productivity and quality of sesame seeds (*Sesamum indicum* L.), as well as degrading yields due to late carpogenesis in rainy areas [92].

The effectiveness of retardants has also been proven for other cultures. In particular, treatment with treptolem had a significant effect on growth processes, mesostructure of leaves, redistribution of assimilates and mineral elements between the organs of oil poppy (*Papaver somniferum* L.). As a result of source-sink system restructuring, morphogenesis was enhanced at the beginning of the growing season, which led to the formation of more leaves and an increase in their surface area, optimization of leaf mesostructure and an increase in the level of carbohydrate reserves deposited in the vegetative organs. The formation of a stronger acceptor sphere was determined by increased branching of the stem and, accordingly, the laying of more fruit in the second half of the growing season, which led to a more intense flow of nonstructural carbohydrates, nitrogen compounds and nutrients, which ultimately increased seed yield [38, 45, 67].

It is known that during the fruiting period of sweet peppers [44] and tomatoes [6] the consumption of assimilates for the growth of vegetative organs decreased significantly, which contributed to the laying of more fruits on the plant and increased yields of nightshade. The use of tebuconazole caused a significant rearrangement of the mesostructure of the leaves, their thickening due to the growth of chlorenchyma, an increase in the volume of cells of the columnar parenchyma and the linear size of the cells of the spongy parenchyma. At the same time, the specific surface density of leaves increased, the content of chlorophyll and the content of nitrogen (primarily protein) increased significantly in comparison with the control and the variant with the use of gibberellin. Due to the action of the retardant, the activity of the source (leaves) in peppers and tomatoes significantly increased, and the indicators of pure photosynthesis productivity were improved [40].

According to the concept of "source-sink" spare substances of different types play the role of a buffer between photosynthesis and growth of vegetative, storage and reproductive organs, which to some extent determines the dependence of growth processes on photosynthesis, and vice versa – photosynthesis on growth [4, 51, 58, 59]. It is typic that under the action of growth inhibitors the mass fraction of fruits (sink sphere of the plant during fruiting) increases and, at the same time, the mass fraction of the source of assimilates increases, mainly due to optimization of mesostructure. Instead, the formation of a larger leaf area is the main way to increase the efficiency of the source during treatment with phytohormones [68].

It is obvious that the formation and growth of fruits occur due to partial re-utilization of carbohydrates from the vegetative organs of the plant to the processes of carpogenesis [19,34], the formation of roots [26, 83, 85], other economically valuable plant organs [81]. It is proved that the increase in sugar content in the leaf blade is accompanied by an increase in the activity of photorespiration relative to photosynthesis. Reducing the intensity of assimilation in grapes reduced the outflow of assimilates from the leaf (source) to the bunch, increasing their accumulation in the stem and root [50, 51].

There is evidence that the functioning of the source-sink system depends on the individual characteristics of the culture. For example, the yield of wheat (*Triticum aestivum* L.*),* the grain of which is formed mostly in the presence of a saturated source of assimilates, is mainly limited by growing conditions or a combination of phenotypic properties [20]. This allows us to conclude that different species are sensitive to resource constraints during fruit formation. In particular, the limitation of source resources in soybean plants (*Glycine max* (L.) Merrill*)* causes a significant aggravation of bean formation [7, 13, 23, 62]. Similar results were obtained for maize (*Zea mays L.*)[12, 24], however, it should be noted that the response to changes in source potential was less pronounced [2, 13].

4.2.2. Functioning of source-sink relations in the system "macro-, microsymbionts - nitrogen fixation"

In addition to studies of the mechanisms of functioning of source-sink relations within the system "photosynthesis – growth", there are fewer data based on the establishment of regulation aspects of plant production process in terms of "macro-, microsymbionts – nitrogen fixation".

The available literature on the functioning of the bacteroid as a consumer of assimilates contains information on the improvement of photosynthesis due to the influx of plastic substances and energy to the bacteroid in the process of symbiotic nitrogen fixation. It has been established that the nitrogen fixation process is closely complementary to the expression of bacterial genes that affect the plant genome [25]. The influence of inoculum growth substances is a powerful tool for modifying the growth of the root system according to the needs of the plant and the development phase: the number of tubers on the roots began to grow in the budding phase, and the maximum mass was recorded in the bean formation phase. Such a positive effect on source-sink system and improvement of the production process in legumes was achieved with the combined effect of inocula and retardants [47].

First of all, the optimization occurs due to the re-orientation of the flows of plastic substances to new acceptor centers, which arise due to the reduction of growth activity of meristems and the formation of new "consumers" – bean-rhizobial symbiosis. In addition, a positive correlation was found between the indicators of photosynthetic activity and the growth of tubers, inhibition of their acetylene-reduction activity. The results of inoculation of soybean plants with *Bradyrhizobium japonicum* strains were an increase in the number of leaves per plant, as well as their area, pigment content and nitrate reductase activity in leaves and root nodules.

Due to bacterization of *B. japonicum* strains, the yield of the crop was expanded by increasing the mass of beans per plant and their number: there was an accumulation of dry matter mass of soybeans in the green bean phase and simultaneous optimization of soybean stem structure, which prevented plant lodging. The increase in oil content and the ratio of unsaturated and saturated fatty acids in the seeds contributed to improved product quality [25, 46].

It is noted above that the trophic supply of plants during artificial growth inhibition is determined not only by the receipt of assimilates, but also by the assimilation of elements, ie, the complete re-utilization of already deposited compounds in storage tissues. Under the conditions of any deficit, the metabolism, intake and redistribution of other elements undergo significant changes. However, energy flow rate due to inhibition or stimulation of morphogenesis under the influence of growth regulators and light regime remain little known, which significantly limits the ability to analyze the effect of retardants on the formation of the plant source system, given their different chemical nature [70].

It is a well-known fact that the main group of plant assimilates are carbohydrates such as starch. The polysaccharide plays a dual role in the distribution of carbon. Releasing carbohydrate reserves for growth and development, starch serves as a source, and in seeds, tuberous roots it functions as runoff or depot, which helps to provide the generative organs with energy as needed. That is, the biological role of starch varies depending on the ontogenetic period and in response to exogenous influences [15, 57].

The synthesis and degradation of starch regulate the content of compound sugars. Since the long exploitation of the leaves allows the plant to maintain vegetative growth longer, it leads to an increase in the toxic properties of the sink. It was found that starch accumulates more slowly in the bulbs and tubers of *Erythronium americanum* due to the degradation of sucrose, which leads to an increase in cell capacity: there is a rapid accumulation of starch – decreases the capacity of the sink. Accumulation of carbohydrate causes the decrease in the activity of fructose-1,6-bisphosphatase in the bulb and the decrease in the use of glyceraldehyde-3-phosphate in the leaf, which causes the induction of its aging [21].

Regulation of source-sink in sugar cane plants (*Saccharum* spp.) has been an effective mechanism for influencing the onset of vegetative growth and its duration, as well as the activity of deposition and the dynamics of the amount of sucrose in the stem [79]. It is known that the regulation of key mechanisms of source-sink system occurs mainly due to the optimization of the signaling pathway of trehalose-6-phosphate, which regulates the release of carbohydrates, which is key to many features of crop yields [65,77,79].

It is known that an excess of non-structural carbohydrates does not regulate photosynthesis, but contributes to the further accumulation of their forms in the petioles of *Raphanus sativus* and increasing nitrogen levels regardless of the needs of organs [77,87]. In wheat, the deposition of reserve substances in the stem plays a dual role – the temporary storage of assimilates for further use in filling the ear, as well as the role of an alternative sink, whose attractiveness stimulates the activity of the photosynthetic apparatus before the appearance of grains. In this case, the new varieties have a much higher attractiveness of ear than the old varieties of wheat [72]. Similar data indicating the possibility of temporary deposition of carbohydrates in the shoots were obtained for gooseberries under conditions of treatment with tebuconazole [82].

4.2.3. Regulation of source-sink relations in the system "depot of assimilates – growth"

Modern literature contains a small amount of information concerning the characteristics of the third type of sink center – places of deposition of substances in stock. Deposition processes play a crucial role in the formation of a reserve source of nutrients used for morphogenesis in the heterotrophic phase of plant development. At the same time, the problem of establishing the patterns of functioning of the source-sink relations in the system of "depot of assimilates – growth" acquires special significance.

It is known that phytohormones play a leading role in the regulation of growth processes, distribution of assimilates and regulation of the relationship between source and sink based on the coordination of the activity of invertase- and hexose-transporter [53, 59, 80]. Understanding the metabolic dynamics in terms of source-sink relations gives an advantage for the selection of seed [63, 91] or young plants that can maintain high yields of cereals and legumes [1, 19, 55].

It is proved that the level of hormones has a positive correlation with indicators of pure photosynthesis productivity, processes of absorption, motion and inclusion in the metabolic processes of mineral nutrients and nutrients [19, 27, 55], the transition of seedlings to autotrophic nutrition [36, 82]. Such data proved to be the basis for the use of antigibberellins as a driving force for the formation of source-sink potential of seedlings. Treatment of bean seeds with an aqueous solution of tebuconazole reduced seed germination rate and the use of cotyledons reserve substances, while the effect of gibberellin and lack of light had the opposite effect [69].

Studies have shown that in dark, the action of gibberellin increases the demand for plastic substances, while in light and under treatment with retardants, the sink activity of seedlings and seed germination energy decreases [37]. The formation of seedlings reques for reserve compounds from different origins of the reserve organs (potato and Jerusalem artichoke tubers, cotyledons of sunflower seeds and pumpkin) is largely determined by the activity of apical meristems during germination, manifested in increased histogenesis by gibberellin and weakening of these processes under the influence of retardants. It is known that under the action of the latter there was a thickening of seedlings due to the growth of the parenchyma of the primary cortex and pith with a simultaneous significant slowdown in their linear growth [69, 71].

Under conditions of photomorphogenesis, the action of light has an inhibitory effect on the indicators of linear growth of both coleoptile and root system, the processes of use of reserve substances, in particular, starch. Treatment of maize seeds with gibberellin stimulated the intensity of seed germination, increased the activity of acceptors (seedling growth) and the rate of use of reserve starch under conditions of scotomorphogenesis. The effect of tebuconazole retardant was the opposite – there was a slowing of germination, reducing the length of seedlings and reducing the intensity of starch use for the needs of sink [40].

It is well known that an excess of assimilates can be deposited not only in the form of starch, but also in the form of proteins and fats, as well as structural polysaccharides that are part of cell walls [71]. It has been found that in most plant species aminoacids are the predominant form in which nitrogen is transported, however, in tropical or subtropical legumes the main compounds of nitrogen transport are ureides, which demonstrates their fundamental difference and may indicate the peculiarities of metabolism and catabolism in legumes [88, 89].

In addition to the influence on protein metabolism during the heterotrophic phase of development, the influence of growth regulators on morphogenesis, rapidity and intensity of utilization of deposited oil in pumpkin cotyledons in light and in dark was noted. It was found that the rate of use of reserve cotyledon fats for organogenesis was higher under conditions of scotomorphogenesis [36].

It is known that structural polysaccharides make up the bulk of the plant and in critical periods of growth and development can be incorporated in metabolism, probably providing a photosynthesis-independent flow of carbohydrates to the sink centers [22, 79]. The possibility of re-structuring the cell walls confirms the study of their structure in *Brachypodium distachyon*, which showed clear changes in the number and structure of polymers: cellulose, lignin, pectin and hemicelluloses. The supply of various forms of nitrogen led to the remodeling of cell walls of type II [22]. Given the scale and importance of the process, the source and sink properties of cell membranes require more detailed study, as changes in their polysaccharide complex during seed germination remain little known.

Single research studies contain data on the influence of growth regulators gibberellin (GA_3) and chlormequat chloride (CCC) on the process of seed germination, which is accompanied by a significant restructuring of the polysaccharide complex [71]. It was found that pentosans of cell walls are used as a reserve substance of the plant, as a result of which there is a modification in conformation and a partial molecular weight increase of pectins due to the esterification processes of carboxyl groups of these polysaccharides [69].

Conclusions

The analysis of data sources showed a limited amount of data on the influence of an artificial combination of exogenous and endogenous factors on the functioning of the source and sink in individual plant organs at the stage of germination [43, 48]. However, the characteristics of source-sink relations functioning in plants with different types of reserve compounds and the establishment of redistribution and the ratio of proteins, fats and carbohydrates to histogenesis in the phase of heterotrophic development remain poorly understood, which serves as a basis for further research.

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Chapter 1.

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