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VINNYTSIA MYKHAILO KOTSIUBYNSKYI STATE
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KURYATA VOLODYMYR GRYGOROVYCH
POPROTSKA IRYNA VOLODYMYRIVNA

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Translated by KRAVETS OKSANA OLEKSIIVNA

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Authors:
Kuryata V.G., Poprotska I.V.

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Reviewers:
Korniychuk O. V., PhD in agricultural sciences, director, Institute of Feed Research and Agriculture of Podillya NAAS of Ukraine;

Furman Yu. M., Doctor of Biological Sciences, Full Professor of Vinnytsia Mykhailo Kotsiubynskyi State Pedagogical University.

Physiological and biochemical basics of application of retardants in plant growing

The monograph summarizes the results of the study of the effect of different groups of retardants on the morphogenesis, formation and functioning of the donor-acceptor system of plants in connection with productivity of agricultural crops. It is discussed the mesostructural features of leaves and the activity of photosynthetic processes under artificial inhibition of linear growth and different plant loads with fruits and seeds. The influence of retardants on the donor-acceptor relations at the heterotrophic phase of development in the conditions of skoto- and photomorphogenesis was investigated. Issues of hormonal regulation of plant morphogenesis, features of accumulation, temporary storage and distribution of assimilates and nutrients between acceptors – processes of vegetative growth and carpogenesis are considered under the influence of retardant with various mechanisms of action.
The monograph is for plant physiologists, graduate students, students of higher education institutions.

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Content

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INTRODUCTION

One of the central directions of solving the problem of obtaining high and stable yields in world crop production is the application of intensive technologies using synthetic plant growth regulators. These drugs are either analogs of phytohormones, or modifiers of the hormonal status of plants. Synthetic growth regulators are not phytotoxic and are significantly less toxic to humans and animals compare to pesticides. The application of growth regulators has become an important component of measures that reduce the cost of manual labor and provide mechanization of care and collection of products, a stable harvest and its high quality. The analysis of chemicalization tendencies of the global crop production shows that the use of plant bioregulators at this stage of development is effective and economically profitable, and the regulation of physiological processes by drugs of this group is highly specific and cannot be achieved by other methods of influence [44, 129, 135]. Growth regulators surpass all other drugs used in agriculture in terms of expansion of production and sales. The creation of national programs for plant growth regulators, the restructuring of policies in the field of agricultural research in many countries of the world has ensured that this direction has reached a qualitatively new level, which is marked by the creation of new highly effective and environmentally sound, directional growth regulators.

Retardants are the greatest compounds in agricultural production - synthetic plant growth inhibitors with an antigibberellinic mechanism of action among the known growth regulators [141]. In modern agriculture, horticulture and viticulture, gibberellins and inhibitors of their biosynthesis are widely used, and the global market for these drugs is in the range of US $ 500,000,000 [171]. Almost seventy years have passed since the invention of the first chemical compounds with retardant properties (AMO-1618), but during this time only a few dozen compounds with this type of radical action have been synthesized and used in industrial directions [53]. The physiological mechanism of action of this compouns is the blocking of synthesis or physiological action of the already synthesized gibberellin in the plant [76, 171, 192]. The results of the data of recent years have established that the application of retardants makes it possible to change artificially morphogenesis [2, 6, 131, 232], regulate the activity of the growth function [14, 24, 58], the intensity of photosynthetic processes both per leaf area unit and the whole plant and cenosis in general [68, 92, 238], influence the processes of carpogenesis, load of plants with fruits and seeds [14, 58, 66, 67, 151], increase plant resistance to unfavorable environmental factors [7, 25, 117, 154], regulate product quality [122, 148, 207]. It is known that the functioning of the donor (photosynthetic tissues and organs) and acceptor (growth zones, substances reserve deposition and zones of active metabolism) spheres in a plant are interconnected by various regulatory systems in such a way that the growth rate determines the photosynthetic activity of the donor sphere [9, 62, 234]. It becomes possible to establish through which anatomo-morphological and physiological changes increase or decrease the transport of assimilate flows to various plant organs and tissues since growth regulators significantly affect morphogenesis [76, 180, 181].

The starting point for the retardants introduction in agricultural practice was the ability to solve effectively the complex problem of combating the lodging of cereals [57, 171]. However, the effect of retardants is multifunctional and not limited to inhibition of linear growth, including retardants are capable of significantly increasing plant resistance to extreme temperatures [82, 85, 109, 120], drought [3, 166, 167, 169, 170, 224], waterlogging of the soil [63], the effect of phytopathogenic microorganisms [64, 210] and others limiting factors of the high productivity formation of agricultural crops [201, 206, 231]. At the same time, retardants are not a universal method that causes the appearance of new properties inherent in the plant. Their action is limited by the capabilities of the plant genotype and retardants only help the plant to better reveal the inherited life potential, which, through a number of conditions, remains unrealized.

The application of retardants, ethylene releasing compounds and their mixtures in many cases leads to a significant increase in productivity and determines their introduction into complexes of measures for the cultivation of various crops - cereals [57, 146, 171], legumes [83, 84, 226], vegetables [90, 104, 152], technical [60, 183, 199, 202, 204, 213], widespread use in meadow growing [58, 193] and floriculture [46, 187]. The high efficiency of retardant treatment on fruit and berry crops has been proven [1, 73, 176, 186].

The effectiveness of retardants is largely determined by soil and climatic conditions, species and varietal specificity, the phase of plant vegetation, doses and periods of the drug application. In addition, certain groups of retardants show selectivity in relation to certain species and varieties of plants: AMO-1618 acts most effectively on legumes and Asteraceae, paclobutrazol - on fruit, grain and ornamental crops, CCC - on cereals, vegetables and industrial crops [76]. Therefore, the search for optimal regulations for the application of various groups of retardants on agricultural crops in specific soil and climatic conditions remains an important practical task.

The analysis of scientific literature shows that a lot of works are specifically devoted to the practical application of this group of growth regulators. The theoretical foundations of the exogenous regulation of plant growth and development by retardants have not been sufficiently developed, the available information is scattered and highlights only certain aspects of the problem. Crop productivity is largely determined by the assimilate redistribution strategy, the ratio of growth and photosynthesis processes, between which a dynamic state is established with a constant correction of the donor-acceptor ratio depending on various external influences [9]. The application of retardants makes it possible to simulate different tension of donor-acceptor relationships in a plant artificially. The reduction of the "request" of attracting centers for assimilates under the influence of growth inhibitors creates a unique opportunity for the analysis of donor-acceptor connections, knowledge of the patterns of integration of growth and photosynthesis, other plant functions, the role of a hormonal factor in regulating the integrity of the plant organism.

Despite a significant number of studies devoted to the effect of retardants on photosynthetic processes, the obtained results relate to changes in the structure and functioning of only individual levels of organization of the photosynthetic apparatus; they cannot be recognized as a sufficient scientific basis for understanding the mechanisms of donor-acceptor regulation in a plant during artificial growth inhibition. In addition, the transition to a new level of donor-acceptor relations under the influence of various external and internal factors is accompanied by changes in the intensity of plant respiration. This physiological process is considered as a powerful metabolite carbon acceptor in a plant [35, 36, 62], however, the effect of retardants on the respiration processes of plants remains practically unexplored. In this regard, analyzing the features of the formation of donor-acceptor relations in plants with retardant effects, there is an urgent need for a comprehensive study of the photosynthetic function of a plant under the influence of retardants of various chemical nature and their influence on the ratio of photosynthesis and respiration processes.

The regulation of donor-acceptor relations is considered as the highest level in the hierarchy of processes that ensure the functioning of a plant as an integral system. The main regularities of the functioning of donor-acceptor relations (the concept of source-sink relation) are mainly studied in the analysis of the ratio of growth and photosynthesis intensity, where growth processes act as the main acceptor, and photosynthesis – as an assimilate donor [99, 183, 234]. At the same time, the role of intermediate deposition of plastic substances, the features of utilization of different chemical compounds deposited in organs during the heterotrophic period of growth (germination period), the initial stages of the photosynthetic apparatus formation and the switching of relations in the donor-acceptor system have been insufficiently studied [111]. The regulation of these relations, as a system of assimilate redistribution between organs and tissues of a plant in the ontogenesis, can be carried out at all levels of organization of a plant with the participation of various regulatory mechanisms [9, 119, 194].

Assimilates mean various compounds of carbon assimilated by a plant in the process of photosynthesis, primarily transport and storage forms of carbohydrates, which are the basis of energy and metabolic processes, as well as "building materials" in the processes of growth and development at all levels of organization of the plant organism [62]. The functioning of the donor-acceptor system and the redistribution of lipids, nitrogen-containing compounds and other substances during the period of heterotrophic phases of plant development (germination) have been much less studied. The issues of their utilization remain practically unexplored under conditions of photomorphogenesis (development in the light) and scotomorphogenesis (development in the dark).

An effective symbiosis of nodule bacteria with a host plant is established under the condition of sufficient supply of photosynthetic products from the macrosymbiont to the microsymbiont, which are a source of energy for the processes of nitrogen fixation and assimilation of ammonia [65]. It has also been established that the application of growth regulators with growth inhibition action (retardants) leads to changes in plants and the growth rate of particular organs. The formation of an excess of assimilates during the inhibition of the plant linear growth ensures the redistribution of the photosynthetic products to towards economically valuable organs, contributes to an increase in crop yields [93, 95, 96]. The analysis of donor-acceptor relations for leguminous plant cannot be limited only by the specificity of the assimilate redistribution between the vegetative and generative organs of plants, the processes of growth and photosynthesis, since legume-rhizobial complexes act as additional attracting centers of the assimilate redistribution. At the same time, the features of symbiotic nitrogen fixation were not studied within the framework of the source-sink system.

The exogenous regulation of donor-acceptor relations of plants in the systems of photosynthesis - growth, depot of assimilates - growth and macro - microsymbiont under various conditions of strain of symbiotic nitrogen fixation under the influence of hormonal status modifiers of various types will allow directing of the flows of assimilates to the processes of carpogenesis (fruit formation and growth) and optimize the crop production process. A common technique for studying the patterns of growth and development is the treatment of plants with exogenous hormones, followed by analysis of fast and slow reverse reactions, changes in the metabolism and hormonal status of plants. However, at the present stage, this approach should be recognized as insufficient, since changes in the ratio of various groups of hormones can lead to changes in morphological and physiological programs [74,76,77]. The application of retardants, drugs with antigibberellic action, allows us to approach the study of the problem "by contradiction" – to establish relationships in the hormonal complex of plants when blocking the synthesis of gibberellins, the role of individual phytohormones and their ratios in morpho- and histogenesis, the formation of donor and attracting organ power. In the literature, there are only a few works in which changes in the hormonal complex are analyzed during the growth inhibitor treatment [94, 107].

An increase in the scale of production and application of synthetic growth regulators, including retardants, increases the risk of their pollution of the environment and agricultural products. In this regard, the requirements for the environmental and toxicological-hygienic safety of the new technologies are increasing, there is a need for such regulations for the application of drugs that allow you to get the maximum effect with the minimum doses of retardant. Thus, the study of the physiological and biochemical mechanisms of action of various groups of retardants is a prerequisite for determining the methods to increase the efficiency and safety of the growth regulators, which the modern global practice of plant growing assigns one of the leading places in agricultural production.

CHAPTER 1.
MAIN COMPOUNDS, MECHANISMS OF ACTION, TRANSLOCATION AND METABOLISM OF RETARDANTS IN A PLANT

1.1. General characteristics of the main groups of retardants.

Retardants include synthetic inhibitory-type growth regulators that can slow down plant growth without causing abnormalities in them [141,143]. These drugs differ significantly in their chemical structure, but they cause the same effect - they slow down cell division and elongation, which leads to inhibition of growth in general.

In agricultural practice and research work, the following groups of compounds with retardant properties are mainly used:

1. Quaternary ammonium compounds – AMO-1618, phosphon D, morfol, pix, chlormequat chloride (chlorocholine chloride, CCC), bromcholine chloride (BCC).

2. Hydrazine derivative conpounds – hydrazide maleic acid (MMC, MG-sodium), N, N-dimethyl succinic acid hydrazide (DSA, V-9, Alar-85, Kilar-85).

3. Triazole derivative compounds – paclobutrazol, uniconazole, tebuconazole.

4. Ethylene producers (ethylene releasing compound) – 2-CEPA, ethephon, hydrel, dihydrel, kamposan M, dextrel.

Among the quaternary ammonium salts, the most widely used is chlormequat chloride (C5H13Cl2N) – (*β*-chloroethyltrimethylammonium chloride), a derivative of quaternary ammonium salts.

It is a white crystalline substance, molecular weight is 158,07 *D*, decomposition temperature is 300 °C, solubility in water is 74 % at 20 °C. It dissolves well in alcohols, acetone and poorly in hydrocarbons. LD_{50} for white rats is 600-700 mg/kg, low-toxic for fish, the maximum permissible level of the drug in food is 2 mg/kg, the maximum daily dose for humans is 0,08 mg [125, 218]. When dissolved in water, chlorocholine chloride is completely dissociated into chlorine ion and *β*-chloroethyltrimethylammonium ion. It is obtained by the interaction of dichloroethane with trimethylamine, the reaction proceeds in one stage under pressure at 80-90 °C [236].

The retardant properties of chlorocholine chloride were discovered in the late 1950s by the American biochemist N. Tolbert in the process of studying of phosphate metabolism in plants using choline derivative compound [216]. About 200 derivatives of choline compounds were studied in N. Tolbert's laboratory by 1965. It was found that the trimethylamino group confers activity on the compounds. Replacing it with dimethylamine, as well as with other trialkylamine groups, leads to a sharp decrease or loss of activity. Allyltrimethylammonium chloride (AMAC) and the corresponding bromide (AMAB), 2-chlorallyltrimethylammonium chloride (CAC), and bromocholine bromide (BCB) exhibit similar properties to chlorocholine chloride. The activity disappears when the chlorocholine chloride – CH_2-Cl is replaced by – CH_2-OH or - COOH, as well as in analogue with the bromobutyl group [173]. Different countries produce different preparations of chlorocholine chloride –

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CCC, Cycocel, WR-62 CCC, Cykocel-750 A, AMV Chlormequat 40, Arotex, Retacel etc. The density of the drug is 1,135-1,145 g/cm^3, viscosity is about 10 cP at 20 °C, and at a temperature of - 8 ° C almost completely solidifies, has a neutral or weak alkaline reaction (pH is up to 8), does not lose its properties for a long time, is not flammable. The drug is low-toxic, does not have carcinogenic and blastomogenic properties, does not accumulate and does not decompose in the body, and is excreted from it after 48 hours. The period of depression in the soil, depending on the temperature and the moisture content of the soil, ranges from 3 to 43 days. The optimal conditions for the decomposition of the drug in the soil are a temperature of 25 °C and a soil moisture content of about 60 % [218]. In the soil, the drug is decayed with the formation of carbon dioxide, water, nitrogen and hydrochloric acid, neutralized by soil carbonates. Insects, as well as other animals do not die in the treated areas, the activity of microorganisms is not inhibited even at high doses [162]. The drug can induce the activity of such groups of microorganisms as ammonifiers, neutralizing and denitrifying bacteria in the soil. At the same time, the activity of other groups of bacteria is stimulated, so their total number does not change, and the cycles of development of microorganisms are quickly restored [146]. The corrosive properties of the drug are low, they increase significantly when heated, therefore, it is advisable to store the drug in the shade in summer. The drug retains its properties when stored in a cold room for more than three years, a prerequisite for use is intensive preliminary mixing to prevent possible sedimentation.

Hydrazide maleic acid (HMA), 1,2-dihydropyridazine-3,6-dione, is a colorless crystalline compound with a melting point of 296-298 °C. The drug is a white crystalline powder. Its molecular weight is 112,1 *D*. Solubility in water at 25 °C is 6 g/l. HMA behaves like a weak monobasic acid and therefore readily soluble salts with K^+, Na^+, $NH4^+$ ions. The drug is most often used in practice in this form. The sodium salt of HMA is readily soluble in water, which made it possible to create highly effective preparative forms of retardants on its basis. It is practically non-toxic for warm-blooded animals (LD_{50} for rats is 6900 mg/kg). However, HMA can be assigned to the group of retardants only conditionally, since it reduces the intensity of cell division both in the subapical and in the apical meristem, that is, it inhibits the activity of both gibberellins and auxins, which can cause disruption of leaf initiation [146]. In experiments on a model culture of the fungus *Giberella fujicuroi*, which has common main stages in the biosynthesis of gibberellins with higher plants, it was found that the growth inhibition effect of HMA and preparations based on, it is not associated with blocking hormone synthesis and is removed by the introduction of exogenous gibberellic acid [56]. These preparations were widely used in plant growing to increase the yield of tomatoes, apple trees, slow down the growth of shoots and compact crown formation, and stimulate the setting of fruit buds. These preparations were used to treat potatoes, onions and other vegetable crops for long-term inhibition of meristematic activity, which made it possible to reduce losses and improve the quality of preserved products. At the same time, the practical application of drugs of this group for the food production of plant origin is now recognized as inappropriate, since a significant mutagenic and carcinogenic effect of hydroside-containing drugs on animal organisms has been established [218]. The application of

HMA and other drugs of this group remains promising in ornamental gardening and floriculture.

Paclobutrazol ($C_{15}H_{20}ClN_3$ O) - 4,4-Dimethyl-1(1,2,4-triazolil-1)-1(4-chlorophenyl)pentanol-3, derivative of 1,2,4-triazole. Synonyms are P333, clipper, cultar, 'parley'. The molecular weight is 293,5 *D*. It is characterized by low solubility in water – 0,035 g/l, melting temperature 165-166 °C. LD_{50} for white rats is 1356-1953 mg/kg [126]. The high activity of paclobutrazol is associated with the stability of its molecules. By the method of bioprobes, the inhibition of the growth of strawberry shoots was observed even 11 weeks after the drug application. The drug was synthesized at ACI (Great Britain) in the study of the retardant activity of triazole compounds. On the basis of paclobutrazol, the company has created commercial preparative forms in the form of granules – oryza and emulsion – kultar, as the most effective preparation for fruit crops among all other triazole-based preparations. Systemic retardant and fungicide to combat powdery mildew and apple scab. It is used in concentrations of 0,125-4 kg/ha as a retardant and in concentrations of 0,125-0,2 kg/ha as a fungicide.

Tebuconazole ($C_{16}H_{22}ClN_3O$) - 4,4-dimethyl-3-(1H-1,2,4-triazol-1-lmethyl)-1-n-chlorophenyl-pentan-3-ol. Synonyms are Fenetrazole, Colossal, Trademan, AGROSILA, Horizon, Folicur, Raxil, Pharaon. It is a transparent crystalline substance, the molecular weight is 307,8 *D*, melting point is 104,7 °C. It is poorly soluble in water, highly soluble in organic solvents. It does not hydrolyze at pH 4 to 7 in water at 20 °C more than a year. It has a low toxicity for warm-blooded animals, LD_{50} for white rats is 3900-5000 mg/kg, it is of 3d hazard class. The drug is not toxic to bees in an amount that does not exceed the recommended consumption rates. It is manufactured by Bayer Crop Science AG (Germany).

Tebuconazole ensures uniform acropetal distribution of the drug in the middle of the plant leaf over a long period of time. The substance penetrates into the plant in 1-2 hours, so the drug remains effective even in the event of possible rain after application, retains its effectiveness for several weeks. It is recommended to use the drug in the form of drip spraying with a working fluid flow rate of 300 l / ha. It can be used in compositions with many herbicides, growth regulators, liquid fertilizers, insecticides, and other contact and systemic fungicides. It should be checked for miscibility before preparing the working solution,

Uniconazole ($C_{15}H_{18}$ ClN_3O) – (1E, 3R) – 1 - (4-chlorophenyl)-4,4-dimethyl-2 (1H-1,2,4-triazol-1-yl)pent-1-ene-3-ol. The molecular weight is 291,78 *D*. It is a white crystalline substance, melting point is 162,5 °C, solubility in water is 8,41 mg/l (25 °C). LD_{50} for white rats is 4000 mg/kg. The drug has second hazard class. It is widely used on crops such as rice, wheat, fruit trees, improving flower bud differentiation and flowering.

2-Chloroethylphosphonic acid (2-CEPA) ($C_2H_6ClO_3P$). Synonyms are Esphon, Etrel. It is a solid, white, hygroscopic, wax-like substance, readily soluble in water, ethyl and isopropyl alcohols, acetone, propylene glycol, less soluble in non-polar solvents - benzene, toluene. The molecular weight is 144,5 *D*, melting point is 74 °C. It does not dissolve in kerosene, hydrocarbon. It is incompatible with alkaline salts in a solution. It easily forms mono- and diesters with aliphatic and aromatic alcohols. It has a low toxicity for warm-blooded animals. LD_{50} for white rats orally 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 accumulative properties [184,185].

The drug was first synthesized in 1946 [55], but as a growth regulator it was put on the market in the form of a branded preparation of etrel by American companies in 1969. At the present time, a whole group of preparations based on 2-CEPA has been created (etephon, 2-CEPA, flordimex, amkem 68-250, amkem 66-329, hydrel, dihydrel, kamposan, dextrel). The stability of 2-chloroethylphosphonic acid depends on the pH value. Aqueous solutions with a value of pH <3,5 are stable, at higher pH values, which are characteristic of plant cell sap, spontaneous non-enzymatic fission of 2-CEPA begins with the release of free ethylene, which manifests its regulatory functions. Other drugs were created on the basis of 2-CEPA, which were used for a long time in crop production:

Dihydrel - BIS (2-chloroethylphosphonate) - N,N- dimethylhydrazine. It was formed by the interaction of 1,1-dimethylhydrazine with 2 moles of 2-CEPA. The molecular weight is 349 *D*. It is a glassy mass, water solubility is over 50 %. LD_{50} for white rats is 2500 mg/kg [125]. The form of the drug is represented by 40-50% aqueous solutions. It was most widely used as a retardant on rye crop with a rate of use 0,8-1,5 kg/ha. This ethylene producer has been classified as toxic in terms of toxicological indicators, taking into account the long-term effects of the hydrazinium component. In recent years, its use has been prohibited for treatment of plant objects that are used for human nutrition and for feeding animals [8].

Kamposan M. The drug 2-chloroethylphosphonic acid was first synthesized in the German Democratic Republic by the chemical plant in Bitterfeld and at the Institute of Organic Chemistry. It is green liquid containing 34 % 2-CEPA, 2,37 % CuSO4, 6,2 % PO_{4-3}, 57,43 % water. The green color of the drug is due to Cu^{2+} ions, which, being absorbed, are used by the plant as trace elements. The pH of the drug is 1,0-1,5, the LD_{50} for white rats is 3390 mg/kg. The drug is not toxic to bees, low toxic to fish [200]. The decay period of kamposan M in the soil is 18-72 days, depending on the temperature and the acidity of the soil, the process is slightly delayed in the soil with a high humus content [218]. The preparation possesses well-pronounced acidic properties, corrodes metals and varnishes, and therefore it is not recommended to fill the tanks with undiluted preparation.

Dextrel - D-(+)-threo-1-(n-nitrophenyl)- 1, 3-dioxyisopropylamonic, 2-chloroethylphosphonic acid. Dextrel is a solid crystalline substance, yellowish in color, not hygroscopic, not explosive. The content of the active substance in the technical product is 95-96 %, the water content is 3,95-4,95 %. The melting point is 150-153 °C. The compound is highly soluble in water. It can be stored up to 3 years. The drug and its aqueous solutions are corrosive storing in the dark,. Working solutions remain stable in the pH range 4,6-7,1. The retention period of the working solution is two days. The pH of the 1 % solution changes from 4,96 to 4,06 after 7 days of storage. In practice, 0,25 % solution of dextrel is most often used, changing its acidity from 5,60 to 4,61 per week of storage. Dextrel refers to low-toxic compounds. LD_{50} for oral administration for white rats is 6000 mg/kg. The drug has no accumulative properties, does not exhibit membrane toxicity and teratogenicity [218].

The Institute of Organic Chemistry and the Institute of Bioorganic Chemistry and Petrochemistry of the National Academy of Sciences of Ukraine synthesized new ethylene producers ifonium and ifonilium, which have high retardant activity and are considered as highly effective drugs in the technology of growing winter wheat [135].

1.2. Mechanisms of retardant action.

The study of the action of one of the first synthesized retardants – AMO-1618 and other quaternary ammonium compounds showed that under their influence the plants acquire rosette habit, which is associated with the almost complete absence of cell division in the subapical zone of the stem meristem. Growth inhibition action of drugs was removed under the influence of exogenous gibberellin. In this case, the meristematic activity increased several times, which led to a rapid elongation of the stem [188, 189]. The works of subsequent years have confirmed that retardants are substances of antigibberellin action [138, 139, 140, 171]. It was found that both quaternary ammonium compounds and triazole derivative drugs inhibit the synthesis of gibberellins, and the more links in the biosynthesis of gibberellins they block, the higher their activity. Thus, quaternary ammonium compounds (CCC, phosphon D, AMO-1618) inhibit the activity of ent-kauren synthase in the formation of copalyl pyrophosphate with geranyl geraniol diphosphate, and paclobutrazol interrupts the synthesis of gibberellin at three points at once, which is associated with its higher activity [141, 167].

A very great success was the development of growth regulators - methylene producer based on 2-chloroethylphosphonic acid (2-CEPA) [142]. Ethylene producers do not affect the synthesis of gibberellins, but they are able to inhibit the activity of already synthesized hormones of this class by blocking the formation of a hormone-receptor complex, unlike quaternary ammonium compounds and triazolederivative retardants [167]. This is evidenced by the fact that the growth inhibition effect of the ethylene producer is not removed by the administration of exogenous gibberellic acid [56, 142].

Ethylene, as a native metabolic product, takes part in the regulation of the processes of vegetative growth and aging of plant organs, however, the artificial ethylene treatment to regulate growth and development is associated with the inconveniences that arise working with gases. The promising application of ethylene producer is determined by the fact that preparations based on 2-CEPA decompose in plants, with free ethylene release. The change in the concentration of this gaseous phytohormone also causes a physiological reaction. It was found that the rate of non-enzymatic degradation of chlorethylphosphonic acid increases with an increase in the pH of cell sap in experiments with *Bryophyllum cruetrum* [225]. So, with an increase in the pH of the cell sap as a result of growing a plant on a long day to 4,6, the amount of ethylene released from 2-CEPA was three times higher than in plants that had a pH = 4,0 as a result of growing them on a short day.

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Ethylene causes a delay in the mitotic process in the meristems of the vegetative organs. Inhibition of mitosis by ethylene is caused by blocking the synthesis of nuclear DNA; when ethylene is removed, the frequency of mitosis increases. The study of the ethylene effect on mitosis of pea root cells made it possible to establish that cell proliferation is delayed at the boundaries of the G_1/S and G_2/M phases of the mitotic cycle [43]. On the example of the growth of winter rye, it has also been shown that the resistive effect of 2-CEPA is associated with a decrease in the proliferative function of the intercalary meristem and a subsequent decrease in the number of cells along the length of the vegetative organ of the cereal, and the effect of ethylene on the stretching phase of the cells of the leaf blade was determined by the concentration of methylene producer. The length of short epidermal and parenchymal cells even grew under the low concentrations of 2-CEPA, and a clear retardant effect was observed only after an increase in the drug concentration by 10^{-1} M [136].

A decrease in cell size in length under the ethylene action may be accompanied by an increase in its isodiametric size, which leads to shortening and thickening of internodes [156, 158]. Over-optimal concentrations of indolilacetic acid (IAA) lead to a similar effect. This is due to the fact that high concentration of auxin stimulates ethylene biosynthesis at the stage of conversion of S-adenosylmethionine to the immediate precursor of ethylene-1-aminocyclopropane-1-carboxylic acid (ACPA) [190]. It has been suggested that a change in the direction of cell growth may be associated with changes in the location of microtubules. It is known that phytohormones affect the orientation of microtubules in plant cells, which determine the location of cellulose microfibrils in the cell wall and the polarity of cell growth. It was found that in the parenchymal cells of the pea stem, the microtubules are oriented radially to the plasmalema using electron microscopy; however, their reorientation occurs under the influence of ethylene, which obviously leads to changes in the polarity of cell growth [208].

It was hypothesized that the primary mechanism of ethylene action consists in the dissociation of the bonds of the cytoskeleton with membranes, and this causes a delay in the polar transport of IAA in the cell. The organization of polar transport of auxin is provided by the asymmetric arrangement of the IAA secretion apparatus at the two ends of each cell. If this asymmetric arrangement of permeases in the cell membrane is supported by microtubules and microfilaments, and if this attachment apparatus is disintegrated by ethylene, then the treatment will stop organ elongation [147].

An attempt has been made to explain the action of other retardants, which differ in chemical structure from ethylene producer, by their ability to release ethylene upon cleavage in the cell. It was found that aqueous solution of chlorocholine chloride can be cleaved with the release of free ethylene, while cleavage is significantly accelerated with an increase in the pH of the medium. This allowed the author to suggest that the biological effect of CCC is due to the in vivo formation of ethylene [69]. At the same time, other authors, observed also a temporary increase in the content of ethylene and its precursor, ACpA under the influence of retardants, studying the biosynthesis of ethylene during the inhibition of the growth of winter wheat and bean by chlorocholine chloride. They concluded that an increase in the content of ethylene and its precursor is a stress response to processing and CCC intake to the tissues. The effect of CCC is not associated with significant changes in the biosynthesis of ethylene [184, 185]. The physiological effect of the ethylene action depends on the characteristics of the intake of drugs to the tissues, the speed of movement and their metabolism in the plant. In experiments with labeled 2-CEPA, it was found that the drug quickly passes through the integument of leaves, shoots, fruits and berries, easily moves up and down from the site of application, and accumulates in the zones of growth and active metabolism [33]. 2-CEPA decomposes in a plant in 3-4 weeks into its constituent parts – ethylene, phosphate and chloride, and the intensity of the breakdown of 2-CEPA both in solutions and in plants depending on temperature. In winter rye, when the temperature rises from 10 to 30 °C, the release of ethylene increases by a factor of 10, and at a temperature of 40 °C it stops completely [185].

The hormonal system plays an extremely important role in the regulation of the cell cycle, but it was noted that the role of endogenous phytohormones in the regulation of individual phases of the cycle has been almost studied. This is due to the fact that the main results were obtained when studying the effect of exogenous hormones. Considering that retardants are modifiers of the hormonal balance of a plant, their action can be realized through changes in the concentration and ratio of hormones. This determines the need for further study of changes in the hormonal status of a plant under the influence of retardants with different mechanisms of action.

CHAPTER 2. HORMONAL REGULATION OF PHYTOMORPHOGENESIS UNDER THE INFLUENCE OF RETARDANTS WITH DIFFERENT MECHANISM OF ACTION

2.1. Hormonal changes in plant shoots under retardant action.

The hormonal system is one of the most important factors in regulating the order and morphogenesis of plants. The treatment of organs with exogenous hormones is used to study the mechanisms of phytohormones action, followed by analysis of fast and slow reverse reactions, changes in metabolism and hormonal status of the plant. At the same time, the insufficiency of experiments only with exogenous hormones is obvious, since there is a complex interaction between individual hormones in an intact plant, and the treatment of plants with one or another hormone leads to changes in the synthesis and metabolism of others, the ratio of hormonal complex components [76, 77]. This can lead to change in morphological and physiological programs in a plant [157]. It is logical to assume that the study of relationship between the entire hormonal complex components under the treatment of plants with inhibitory action of certain phytohormones can be quite informative [76]. It is known that the inhibitory effect of retardants, depending on the chemical structure, is determined by the blocking of synthesis, or a decrease in the activity of already synthesized gibberellins [171]. However, only a few works are presented in the timely literature, in which changes in the hormonal complex of retardants treated plants are analyzed [94]. There are practically no comparative data on the effect of retardants with different mechanism of action - chlormequat chloride, triazole derivative compounds and etyleneproducer on the hormonal system of the plant, hindering the acquisition of new knowledge about the mechanisms of regulation of phytomorphogenesis under retardant effects. In this regard, the effect of retardants is expediently analyzed from the position of complex hormonal planning, analysis in the balance of various groups of phytohormones under the action of drugs.

It is known that the growth rate of the stem depends on the meristematic activity of the subapical zone, which is largely controlled by gibberellins. Gibberellins play an important role in genetic dwarfism, because numerically dwarf mutants, such as corn and beans, have fewer gibberellins than normal forms and clearly respond to the gibberellin application. The work of J.Sachs showed that rosette plants and plants that acquired rosette habitus under the treatment of one of the first synthesized retardants - AMO-1618 and other quaternary ammonium compounds, differ from normal tall plants by the almost complete absence of cell division in the subapical meristem of the stems, gibberellins quashed the retardant action. At the same time, it was found that the meristematic activity of this zone for phytohormone treatment increased several times, reduced the number of cells and their amount, which resulted in an elongation of the stems [188, 189].

Gibberellin also enhances the growth of hydrazide maleic acid (HMA) treated plants, but this does not completely remove the inhibitory effect of hydrazide. HMA blocks cell division in the apical and subapical zones of the stem, while gibberellin stimulates division only in the subapical zone. Inhibition of mitosis in the apical zone stops the adjunction of subapical zone with new cells; therefore, gibberellin can partially affect the growth and elongation of stem cells treated by HMA [146].

The data presented in the literature relate mainly to the study of the gibberellin free forms activity .in the plants under the influence of ammonium and phosphonium compounds (AMO-1618, CCC, phosphon-D). The influence of modern retardants of other groups on the activity of various forms of gibberellins remain poorly studied. Our study of free gibberellins activity during the period of active growth of the raspberry shoot testifies to a close relationship between changes in growth characteristics and the hormone activity under retardant inhibitory effect: a significant decrease in the activity of free gibberellins was noted under the influence of gibberellins at the field experiment, and at the same time exogenous gibberellic acid significantly increased their activity in stem tissues [74, 77]. A similar decrease in the biological activity of gibberellins was also observed under the influence of chlorocholine chloride during all phases of development of barley plants [205], and the content of individual gibberellins in rape seedlings decreased under the influence of BAS-111 [48]. The study of the paclobutrazol and dextrel interaction on the activity of free forms of gibberellins in raspberry shoots, carried out under the conditions of a vegetation experiment, confirmed the noted pattern. However, the difference between the options was less dramatic due to the optimal water supply and higher temperatures during the study period [77]. Determination of the gibberellin free forms activity in germinating bean seeds made it possible to establish that the mechanism of retardant action cannot always be associated with inhibition of gibberellin biosynthesis *de novo*, since an increase in the content of free gibberellins is possible due to their release from bound forms [144]. The formation of gibberellin glycosides is considered as one of the gibberellin inactivation mechanisms in ripening seeds, and the conjugation of the hormone form serves as a "reserve" for the regeneration of free gibberellins during germination [18]. However, it should be noted that there are practically no data in the literature on the accumulation of gibberellin conjugated forms in the vegetative organs of plants, which growth is inhibited by retardants. On raspberry plants, it was found that the activity of gibberellin-bound forms was lower in variants with the dextrel and paclobutrazol application [74]. So, the retardant action is obviously not associated with the inactivation of gibberellins by converting them into the conjugation form.

Our research results indicate a significant effect of retardants on the gibberellin activity in plants; however, it would be wrong to reduce the plant response to decelerating drugs with changes in the content and activity of only this class of phytohormones, in our opinion, since balance, ratio and sequence of various groups of phytohormone action play a decisive role in the regulation of plant growth and development. Therefore, it is important to study changes in the content and ratio of other classes of phytohormones in plant tissues during artificial growth inhibition under the retardants action.

It is known that the period of intensive growth of the stem coincides with a high level of activity of gibberellins and indolylocytic acid, the action of which is interrelated. In a number of crops, for example, pea seedlings, growth acceleration under the influence of gibberellin is associated with an increase in the content of auxins (IAA), and an increase can be very significant: the content of auxin can exceed the norm by 40-50 times [18]. It has been suggested that the effect of gibberellins can be manifested by an increase in the content of IAA phenolic inhibitors - oxidase, release of IAA from bound forms, since gibberellins increase the activity of hydrolases in tissues, activation of transport and enhancement of IAA biosynthesis under the influence of gibberellins [156]. At the same time, it should be noted that the effect of antigibberellic drugs on the content of indole acetic acid has been insufficiently studied, and the data obtained are scattered and contradictory. A decrease in the content of auxin in pea tissues was observed under the influence of unicanazole [115], while in rice shoots didn't change in the content of IAA occurred due to the action of this retardant [54]. There was also a decrease in the indole acetic acid content in the apical zone of bean seedlings under the action of CCC [144]. It should be noted, however, that the retardant effect on the content of indole acetic acid in the tissues of perennial woody plants has obviously not been studied.

Our study of the free IAA content in raspberry shoots decreased under the influence of antigibberellic drugs in the field experiment conditions during the period of active growth (Table 2.1) [77].

Table 2.1.

Influence of retardants on phytohormone content in shoots of raspberry cv. Novokitaivska on the day of 7 after spraying (1990), ng/g per wet matter.

Indicators	Control (water)	0,3 % Dextrel	1,2 % CCC	0,05 % Paclobutrazol
Total ABA content	1675	2762	520	2889
Free ABA	1350±14,5	*2000±12,2	*250±11,7	*2450±12,5
Bound ABA	250±5,4	*137±5,8	220±5,1	*89±.4,7
t-isomer of ABA	75±2,3	*625±8,2	*50±2,1	*350±5,8
Free IAA	63±0,2	*18±0,3	*21±0,1	*16±0,2
Zeatin	35±0,3	*133±0,8	*400±0,6	*traces
Zeatin riboside	traces	traces	*250±0,3	*235±0,3

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

The content of free IAA decreased under the influence of dextrel in the conditions of the 1997 growing experiment (Table 2.2). Obviously, the effect of retardants on the indole acetic acid content in shoots was mediated by a decrease in the activity of gibberellins, the positive inhibitory effect has been proven on the content of auxin in plants [18].

Table 2.2.
Influence of dextrel on phytohormone content in the shoots of raspberry cv. Novokitaivska in the conditions of vegetation experiment on the day of 11 after spraying (1997), ng/g per wet matter.

Indicators	Control (water)	0,3 % Dextrel
Total ABA content	2562	1376
Free ABA	1825±11	*763±8
Bound ABA	737±9	*613±8
t-isomer of ABA	150±12	*110±7
Free IAA	traces	*24,4±0,7
Zeatin	569±2,8	*traces

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

Thus, the content of main hormones (auxins and gibberellins) regulating the shoot growth in length decreases under the retardant influence, explaining the slowdown in the growth rate of raspberry shoots.

It is known that the ratio between the hormonal complex elements significantly affects the trophic situation in a particular organ. Obviously, a decrease in the content and activity of IAA and gibberellins in young shoot tissues due to the action of retardants determines a decrease in the "source" for assimilates, which, along with a decrease in the proliferative activity of the meristematic cells of subapical meristem, is one of the factors slowing down the growth rate of the shoot.

One of the main effects of auxin action on plants is the stimulation of the cambium activity, due to which the secondary growth of the shoot in thickness occurs. Preparations of active cambium are rich in auxins, and there is a parallelism between the amount of extracted auxin and the activity of this lateral meristem [28].

Comparison of the data obtained on the content and activity of IAA and gibberellins in tissues by the results of studying the histological parameters of the secondary growth of raspberry shoots under the influence of retardants indicates that there is a clear relationship between the content of these phytohormones and a decrease in the radial population of cells and their size [74]. Thus, the inhibitory effect of retardants on the activity of meristematic stem tissues is mediated by changes in the hormonal complex. It should also be borne in mind that phytohormones can affect the trophic situation in the organs not only due to the formation of the attracting power of the organ, but also through the formation of pathways. A decrease in the number and size of vessels in the xylem of raspberry and black chokeberry, more intensive and early formation of mechanical tissues in the xylem, leads to a deterioration in the provision of zones of apical and lateral growth of the stem with water and nutrients [72].

The participation of cytokinins in the regulation of stem growth in length and thickness is still far from clear; however, a high interaction of cytokinins and auxins was noted. In typical systems with cellular stretch, such as oat coleoptile and pea epicotyl, kinetin typically inhibits auxin-stimulated longitudinal growth and stimulates transverse growth. There is a sharp decrease in the content of cytokinins with a simultaneous increase in the content of IAA during the cells transition of maize seedlings to elongation. Cytokinins are extremely active in initiating separation of plant cells in tissue culture in the presence of auxin, and mitotic activity increases with an increase in the cytokinin / IAA ratio [137]. In the mitotic cycle, there are phases, their passage depends on auxins, and phases are required for cytokinins, which determines the need for these two phytohormones for cell division. However, there are data that do not agree with this theory. Thus, with an increase in the concentration of cytokinins, the efficiency of auxin action increases, and the tissue requirement for cytokinins decreased at higher concentrations of auxins [29].

Cytokinins were found in extracts from cambium of various plants, in tests they stimulate both the activity of cambium and the lignification of xylem elements. However, the question of the retardant effect on the content of cytokinins in shoots of agricultural crops has not been studied enough. At the same time, artificial inhibition of growth by retardants makes it possible to analyze the relation between the content of cytokinins and the rate of longitudinal growth of the shoot, the activity of cambium, and the attractive ability of tissues. Our research results indicate that the growth of raspberry shoots was inhibited by retardants, there was no clear relationship between the growth rate and the cytokinin content. A decrease in the intensity of growth processes was accompanied by an increase in the cytokinin content with a simultaneous decrease in the content of IAA in the stem tissues (Table 2.1). Differences in the dominance of cytokinin forms were observed: residual amounts of zeatin and a high content of the transport form, zeatin riboside, were found in the paclobutrazol variant, while in the variants with dextrel and chlorcholine chloride, zeatin dominated. The question of the possibility of cytokinin synthesis in shoot meristems remains open [18], however, the presence of a large number of transport forms of cytokinins is evidently explained by the intensive influx of phytohormones of this group from the root system, which is the main site of their synthesis.

It is known that cytokinins are capable of delaying the degradation of proteins and RNA, thereby maintaining the general ability of cells for synthetic activity and causing the attracting effect [18]. However, our results indicate that the cytokinin content cannot definitely characterize the activity of tissues, since a higher content of these hormones in the experiment was accompanied by a decrease in the weight and size of the stem [77]. There was a decrease in the content of both cytokinins and IAA in the shoot tissues in the conditions of the growing experiment under the influence of dextrel (Table 2.2). Obviously, the ability of tissues to attract is determined not by the content of this or that phytohormone, but by a complex interaction between all components of the hormonal complex.

The regulatory function of abscisic acid also remains largely unclear in the growth processes. ABA can inhibit the synthesis of DNA, RNA, proteins, stop cell division, it acts in the cell as an antagonist of gibberellins, auxins, cytokinins, which can lead to creeping effects. However, it would be wrong to consider ABA only as an inhibitor, since it can also cause the phenomenon of activation of growth processes. Thus, in yuvenile, fast-growing plants, it was noted an increased content of ABA; some tissues react to the introduction of ABA by increasing mitotic activity [18].

Information on the effect of retardants on the abscisic acid content is contradictory. According to some authors, chlorocholine chloride, in contrast to ethylene-releasing compounds, increased the phytohormone activity in barley stems [167], however, the phytohormone content in wheat seedlings decreased under the influence of paclobutrazol [13].

The results of our research indicate that the dependence of the growth processes to the ABA content is rather complex of retardant treated raspberry shoots. The total content of all forms of abscisic acid under the influence of paclobutrazol increased by 1,72 times, under the influence of dextrel - by 1,65 times, however, chlorocholine chloride caused a significant decrease (by 3,2 times) in the content of phytohormones compared to control (Table 2.1.). The total content of various ABA forms in dextrel treated raspberry stems was significantly lower than in control (by 1,87 times) in the conditions of the growing experiment. However, it should be noted that the decrease in the ABA content in the stem in these cases was accompanied by a significant increase in the phytohormone content in the leaves [76, 77]. If we proceed from the modern concepts that the main site of ABA synthesis is the leaves and the ability of this hormone to transport along the phloem [18], the difference in the ABA content in the stem and leaves can be explained by the slowing down of hormone outflow from the leaves to the stem.

Thus, the effect of retardants on the intensity of growth processes, the anatomical and morphological structure of raspberry shoots is not limited only to the antigibberellinic action of the growth inhibitory drugs, but is determined by changes in the entire hormonal complex, the complex interaction of its components.

A significant effect of paclobutrazol on the germination rate and anatomical structure of potato shoots was established. The "sprout dry matter weight/ tuber dry matter weight" indicator decreased at the first stages of germination compared to control under retardant. There was a significant inhibition of shoot growth (Figure 2.1) and profound changes in the anatomical structure of the shoots under the influence of retardant. The decrease in the length of potato sprouts due to the action of the retardant was accompanied by their significant thickening. Along the entire length of the sprout, the volume of parenchyma cells in the shoot tissues of tubers treated with retardant was higher than in the control both in the primary cortex and in the core. In our opinion, a decrease in the length and weight of shoots with a simultaneous increase in the size of parenchymal cells indicates retardant inhibition of the meristematic activity of growth zones, which was determined by the rearrangement of the hormonal complex (Table 2.3.) [107].

Paclobutrazol significantly influenced the content of various forms of gibberellins in potato sprouts. The content of free forms decreased by 1,7 times and the content of gibberellin bound forms increased by 1,2 times compared to control under the influence of 0,05 % paclobutrazol (Table 2.3). The ratio "free / bound" gibberellins in the control was 1,25, and in the experimental variant was 0,69. Thus, the action of paclobutrazol was realized primarily due to a decrease in the free

Control 0,05 % paclobutrazol

Figure 2.1. Effect of paclobutrazol on the germination of Ikar potatoes

gibberellin activity in the sprouts. This is in good agreement with modern concepts of blocking the synthesis of gibberellins with triazole-derivative drugs [171].

Table 2.3.

Influence of 0,05 % paclobutrazol on phytohormone content in potato sprouts cv. Ikar, ng/g per wet matter

	ABA		IAA		Cytokinins		$\frac{IAA+Z+ZR}{ABA}$	Gibberellins	
	free	bound	free	bound	Zeatin	Zeatin-riboside		free	bound
Control	23 ±0,1	133 ±1	216 ±1	241 ±7	50 ±1	65 ±1	3,7	424 ±1	336 ±16
0,05 % PB	*39 ±1,7	*180 ±2	*89 ±1	*141 ±2	*69 ±1	*131 ±1	2,0	*251 ±1	*395 ±19

Note: * - difference is significant at $p<0.05$; the gibberellin content is in equivalent to gibberellic acid (GA_3)

The slowdown in the growth of potato shoots under the retardants action was largely determined by changes in the abscisic acid content under the 0,05 % paclobutrazol influence, the potato sprouts of the trial variant contained 1,7 times more free ABA and 1,4 times more bound ABA compared with control. The hormone play the important role in maintaining deep dormancy in tubers. The obtained results indicate that there is a dependence of the growth processes activity on the state of abscisic acid in tissues.

The shoot growth rate of control variant was significantly higher, the ratio of bound to free ABA was 5,8, this indicator of trial variant was 4,5 where the growth was inhibited by the retardant. Thus, the slowdown in growth is associated with an increase in the relative content of free ABA. The dependence of the depth of dormancy on free ABA content in buds is also indicated in study [153].

The role of indole acetic acid in the regulation of dormancy and its termination has not been finally clarified. Exogenous IAA reduced the ABA content in the meristematic cells of the growth points of potato tubers; however, the action of this phytohormone increased the duration of deep dormancy in tubers [21]. It is believed that the reason for the ineffective use of IAA for interrupting of dormancy of tubers is its stimulating effect on ethylene formation [64].

Our data indicate that the paclobutrazol treatment of tubers leds to an unambiguous decrease in free and bound IAA content in the sprouts compared with control (Table 2.3). We obtained similar results under the retardants effect on the growth of raspberry shoots [77]. A decrease in the content of IAA for the actions of uniconazole and 17-DMS in the organs of various plants was also established in the works of other authors [129, 239]. At the same time, there is a clear relationship between the slowdown in the growth rate of shoots for the action of retardants and the ratio of free and bound forms of IAA in the control trial was 0,9, and in the experiment it was 0,63. Thus, one of the reasons for the retardant growth inhibition is a decrease in the concentration of free IAA in the tissues of the retardant-treated sprouts.

The preliminary data presented in this chapter indicate that the cytokinins content in the raspberry shoots increased for the retardant action, although the shoot growth intensity of retardant treated plants was significantly lower than in the control (Tables 2.1, 2.2). A similar increase in cytokinins content of uniconazole-treated plant tissues was noted in other works [153,171]. Our datas indicate that in the processes of growth regulation, the main role is played not by the absolute concentration of a particular phytohormone, but by their ratio. Thus, there was a significant increase in the content of zeatin and zeatin riboside in the tissues of retardant-treated potato sprouts of variety Ikar compared with control, but this was not accompanied by an increase in cell division: a decrease in the length and weight of sprouts with a simultaneous increase in the size of parenchyma cells indicates inhibition of the retardant meristematic activity of growth zones.

Noteworthy is the fact that the ratio of zeatin-riboside to zeatin in the plants of the trial variant was higher (1,9) than in the control (1,3), which indicates a relative increase in the content of the less active transport form of the hormone (zeatin-riboside).

Analysis of the integral indicator characterizing the hormonal complex - the ratio of total IAA, zeatin and zeatin riboside to the ABA content in the tissues indicates that it was higher in the control (Table 2.3).

Thus, the slowdown in the growth of potato shoots due to the action of paclobutrazol is determined by an increase in the relative proportion of abscisic acid in the hormonal complex, a decrease in the relative content of free forms of cytokinins, indolyle acetic acid and gibberellins.

2.2. Retardant effect on hormonal complex of leaves.

The attention of researchers is focused, on the main property of retardant effect on a plant - the ability to inhibit the stem growth in length due to effect on the subapical meristem, which responds to the formation and growth of the stem. It is believed that the apical meristem continues to function normally, due to which the leaf is not significantly affected and reaches its normal size [167]. There are questions of the effect of these compounds on the structural and functional organization of the photosynthetic apparatus of plants, the donor function of the leaf during retardant effects in connection with a decrease in the attracting need for a shoot.

Our study of the free gibberellins activity in raspberry leaf tissues under the influence of chlorcholine chloride, paclobutrazol, dextrel, and exogenous gibberellin (GA_3) under the field conditions and growing conditions indicates a decrease in the hormone activity of treated plants with different types of retardants compared with control and gibberellin. The results obtained indicate a close relationship between a decrease in the activity of free gibberellins and a decrease in the leaf surface of the retardant treated shoot [74]. In some studies, it has been noted that associated gibberellins can exhibit functional activity, and at the same time it can be significant. There was no clear relationship between the retardant action of dextrel and paclobutrazol and the content of bound forms of gibberellins in raspberry leaves: with a decrease in leaf surface area in both experimental variants, paclobutrazol caused an increase in activity, and a decrease in the activity of bound forms of gibberellins inder dextral treatment [77].

It is known that the leaf with respect to its morphogenesis exhibits a certain autonomy, which has been proven in trials with young leaf rudiments in crops on artificial substrates, the final size and shape of the leaf are largely determined by the correlative influence of other plant organs. Thus, partial derisoidation of plants in a young leaf causes a stop in the division of mesophyll cells and a strong retardation of leaf growth. Thus, the hormonal control of phylogenesis is maintained by both endogenous and exogenous phytohormones in relation to leaf [18].

Four important components of the hormone-inhibitory system can be synthesized in chloroplasts: gibberellins, indolylocytic acid, phenolic inhibitors and ABA. Poor growth of mesophyll of root incision is explained by the fact that cytokinins enter the plant's aerial organs along with xylem sap from the root system, and this organ is obviously the main site of cytokinin synthesis. It has also been established that synthetic cytokinins can replace the root system in ensuring normal leaf growth. In general, cytokinins, along with gibberellins, play a central role in regulation of leaf growth; however, the effect of retardants on the hormone content in leaf tissues remains largely unexplored.

The data presented in Tables 2.4, 2.5, the effect of retardants on the content of cytokinins in raspberry leaf tissues under the field conditions and vegetation experiments indicate that there was a decrease in the content of active form of cytokinins, zeatin of treated plants compare with control. The cytokinin content decreased most significantly under the action of dextrel. Simultaneously, the appearance of zeatin-riboside (transport form of the hormone) was noted under paclobutrazol and chlorocholine chloride treatment. The study of the cytokinins content in the tissues of the dextral treated raspberry leaf under the vegetation experiment conditions also indicates that the zeatin content of experimental trial was much lower, and the specificity of the retardant action was that the ribosidezeatin was absent in the leaves of both experiments of dextrel-treated plants.

The role of auxin in the regulation of leaf blades formation and growth remains largely unclear. It was found that auxins in different concentration can stimulate the growth of the primary (midvein) and secondary leaf veins, but they practically do not affect the mesophyll tissues between the veins [18]. Our research results indicate that the relationship between the content of free IAA and the inhibition of leaf growth processes is rather complex.

Table 2.4.

Influence of retardants on phytohormone content in the leaves of raspberry cv. Novokitaivska on the day of 7 after treatment (1990), ng/g per wet matter.

Indicators	Control (water)	0,3 % Dextrel	1,2 % CCC	0,05 % Paclobutrazol
Total ABA content	554	733	3220	1611
Free ABA	275±11,4	*125±8,3	*2600±12,1	*1375±11,6
Bound ABA	129±5,8	*208±6,4	*75±2,1	*101±3,3
t-isomer of ABA	150±5,8	*400±8,8	*545±6,6	*135±4,3
Free IAA	14±0,1	*13±0,1	*32±0,2	*12±0,1
Zeatin	375±0,8	*25±0,1	*320±0,6	*125±0,3
Zeatin riboside	traces	traces	*125±0,3	*34±0,1

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

There was a slight decrease in the phytohormone content in the leaves under the influence of dextrel and paclobutrazol, but there was an increase in the phytohormone content under the influence of chlorocholine chloride under the field conditions. The content of IAA in leaf tissues was higher under the influence of dextrel under the vegetation condition of 1997 than in the field experiment (Table 2.5). Thus, it was observed no direct corelation between the IAA content and inhibition of growth processes.

Table 2.5.

Influence of retardants on phytohormone content in the leaves of raspberry cv. Novokitaivska on the day of 10 after treatment in the vegetation condition (1997), ng/g per wet matter.

Indicators	Control (water)	0,3 % Dextrel
Total ABA content	1625	2400
Free ABA	875±11	*1000±18
Bound ABA	750±9	*1400±12
Free IAA	145±22	*386±17
Zeatin	57,5±0,8	*traces
Zeatin riboside	traces	traces

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

It is known that the ratio of cytokinins to IAAs largely determines the meristematic activity of cells [157]. If we compare the ratio between total content of cytokinins and free IAA (Tables 2.4, 2.5), then the same pattern is observed – under the influence of retardants, this ratio decreased both in the field and vegetation conditions. Thus, one of the central factors determining the retardant effect is a decrease in the cytokinin to IAA ratio.

Data of the retardant effect on the various forms of ABA content are presented in the literature by isolated works, and their conclusions are contradictory. Thus, an increase in the content of abscisic acid was observed under the influence of various retardants for a number of crops [126, 222]; however, the content of abscisic acid decreased in wheat seedlings under the action of paclobutrazol [13]. Our study of the retardants effect with different mechanisms of action on the ABA content in young raspberry leaves indicates an increase in the total ABA content, and the pattern was confirmed both in the field and vegetation conditions (Tables 2.4, 2.5).

The study of the phytohormones interaction in the cell under the influence of one factor or another should include questions about whether one of them changes the content of the other. It was noted a more significant increase in the ABA content, primarily due to the free form under chlorocholine chloride and paclobutrazol that block the synthesis of gibberellins. This pattern should be obviously explained by the fact that the synthesis of abscisic acid and gibberellins is the only pathway for the formation of terpenes and in both cases proceeds from mevalonic acid [171]. In other words, there is metabolic branching in plant metabolism, at the ends of which

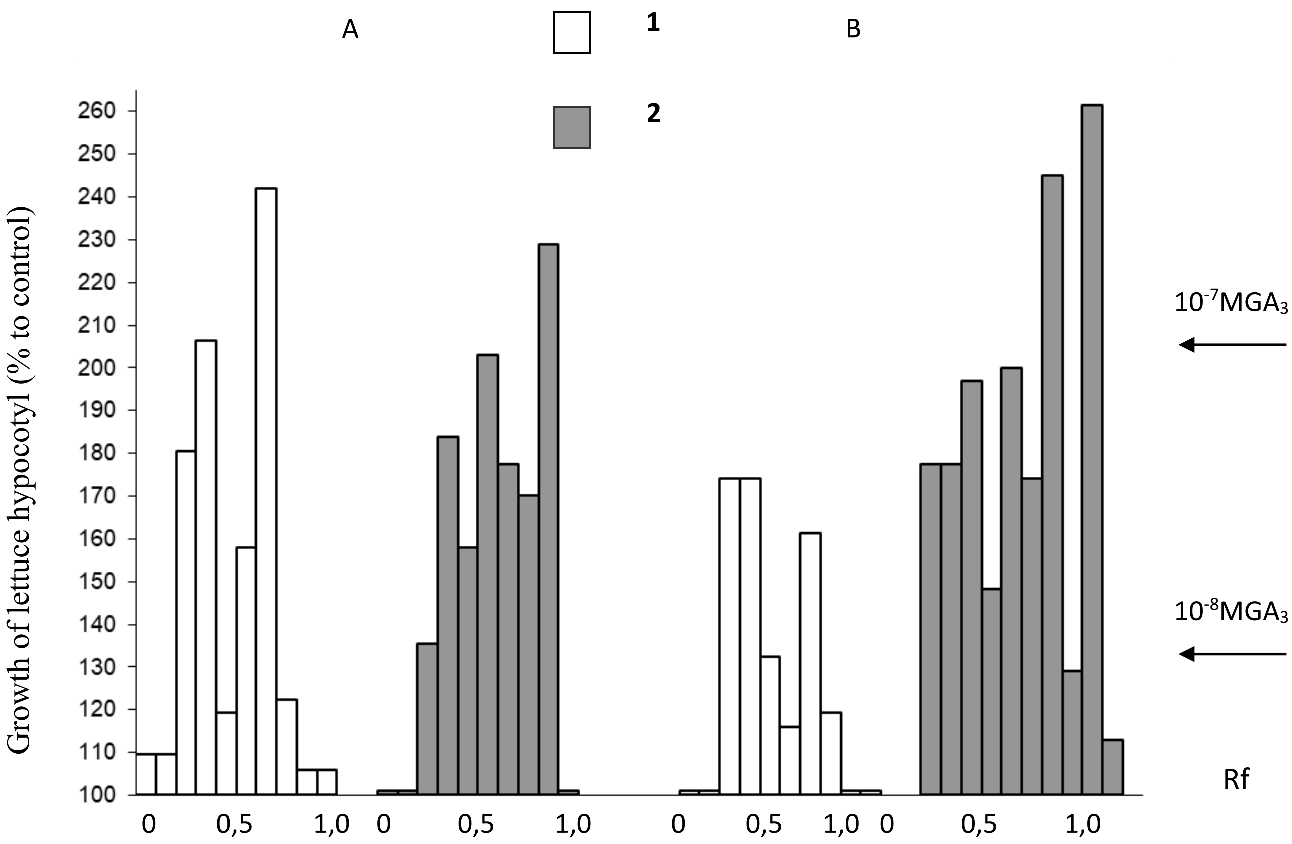

Figure 2.1. Effect of paclobutrazol on the activity of free and bound ABA in the leaves of sugar beet Robert's hybrid; A – control; B – 0, 25% paclobutrazol; 1 – free ABA; 2 – bound ABA

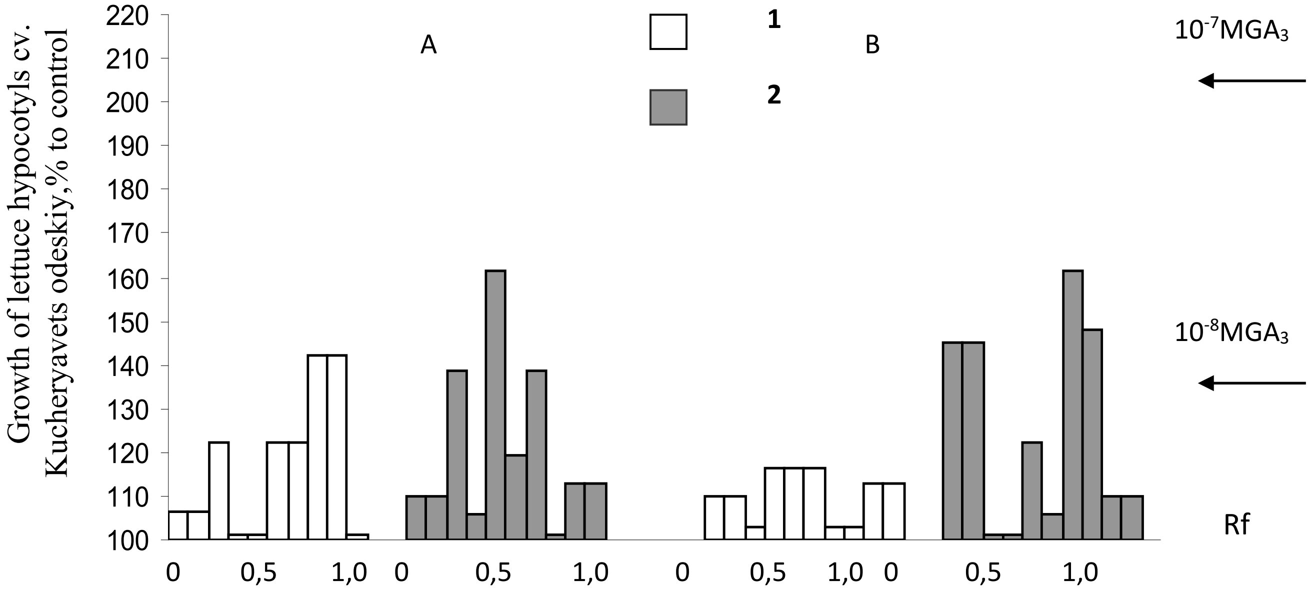

Figure 2.2. Effect of paclobutrazol on the activity of free and bound ABA in the leaves of potatoes cv. Nevska; A – control; B – 0, 25 % paclobutrazol; 1 – free ABA; 2 – bound ABA

hormones with different signs of action appear [40]. Thus, modern concepts of the biosynthesis of gibberellins in plants suggest the reason of the ABA accumulation in leaves under the influence of retardants: they do not block the formation of farnesyl pyrophosphate, a precursor of ABA, but show their effect at later stages of terpene biosynthesis, shifting biosynthesis towards the abscisic acid accumulation.

The nature of the retardants effect on endogenous growth regulators is largely determined by the specificity of the drug and environmental factors [167]. In contrast to CCC and paclobutrazol, it was observed a decrease in the content of the active hormone form, free ABA, in leaf tissues under the influence of ethylene producer dextrel in the field conditions (Table 2.4). This is obviously associated with a more intense outflow of the hormone into the growing stems, where its concentration significantly exceeded the content in the stems of control variant (Table 2.1). A significant increase in the content of free and bound forms of ABA in the leaves of the trial variant under the influence of dextrel clearly correlated with a decrease in the content of the hormone in the growing shoot in the vegetation conditions of 1997 (Table 2.2). The obtained results indicate that the concentration of hormones in certain tissues and organs is determined not only by the intensity of their formation, but also by the rate of their migration to other growth centers.

Our analysis of the effect of various retardants on the content of gibberellins and abscisic acid in the leaves of other agricultural crops in the vegetation condition indicates significant changes in the ratio of free and bound forms of these hormones [94]. In particular, in all crops there was an unambiguous decrease in the content of free forms of gibberellic substances in the experiment compared with control. Thus, a decrease in the activity of free gibberellins in leaf tissues is a universal plant response to paclobutrazol interaction. Similarly to raspberries, in these crops it also found that there was no clear relationship between the retardant action of dextrel and paclobutrazol and the content of bound forms of gibberellins in the leaves: in rapeseed, there was a decrease in the content of bound forms of gibberellins [180], in potatoes [215] between control and experimental trials was minimal, and in soybeans [39] and sugar beets [203] there was a sharp increase in the content (Figures 2.1, 2.2). Analysis of the histograms of the activity of free and bound gibberellins also indicates a redistribution of the activity of various fractions (according to Rf values) for the retardant action. Changes in the ratio of individual gibberellins under the influence of paclobutrazol in rape were also noted [49]. In our opinion, this may indicate that paclobutrazol affects not only the synthesis of precursors, but also the later stages of the individual gibberellins synthesis.

The obtained results indicate an increase in the content of free ABA under the influence of paclobutrazol in the leaves of all crops [94]. An increase in the content of bound ABA was noted for rapeseed, potatoes, lucerne and soybeans; however, it was noted a decrease in the bound form of the hormone content in the experimental variant of sugar beet plants due to the morphological features of the crop - rosette nature and the absence of stems, the intensity of hormone redistribution between leaves and a powerful acceptor zone - a growing root-crop.

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Thus, a typical plant response to paclobutrazol treatment is a decrease in the content of free gibberellins and an increase in the content of free ABA in the leaves of experimental plants.

Consequently, a decrease in the intensity of mitotic activity of marginal meristems is indirectly by changes in the hormonal complex: under the influence of retardants, the activity of free gibberellins decreases, the ratio of cytokinins to IAAs, while the abscisic acid content decreases. The processes of photosynthesis and growth form an interconnected and self-regulating system, it is expedient, in our opinion, to analyze structural and functional changes under the influence of retardants in the system of donor-acceptor relations, providing a theoretical basis for an integrated approach to the essence of the issue.

CHAPTER 3.
EFFECT OF GIBBERELLIN AND RETARDANTS ON GROWTH PROCESSES, LEAF APPARATUS FORMATION, REDISTRIBUTION OF

3.1. Effect of retardants on morphological and mesostructural characteristics of leaves.

The functional and regulatory interaction of photosynthesis and growth in production processes is becoming one of the central tasks of plant physiology. According to modern concepts, the plant is a single donor - acceptor system (source - sink), where the donor of assimilates is the photosynthetic organs, primarily leaves, and all other parts of the plant act as an acceptor. The regulation of donor - acceptor relations is considered as the highest level in the hierarchy of processes that ensure the functioning of a plant as an integral system [9, 62, 76].

Traditionally, three types of attracting centers are different in the nature of their functional activity: points of growth, places of substances deposition in a store and places of active metabolism. It was found that there is a positive correlation between the amount and activity of these acceptors and the photosynthetic activity of leaves [133, 134]. This was previously proved by means of model experiments with an artificial change in the "request" for assimilates by partial or complete removal of consuming organs, which leads to inhibition of photosynthesis [47], or by reducing the leaf area while maintaining the activity of attracting centers. This causes an increase in photosynthetic activity of leaf area unit due to the activation of chloroplasts at first, and then due to the formation of an additional photosynthetic surface [15]. The completion of the growth processes, or the termination of the substances deposition in the stock is accompanied by opposite effects [52]. Thus, epigenetic processes play a leading role in determining the characteristics of photosynthesis. Since there is a positive correlation between the rate of growth processes and photosynthetic activity of leaves, an important question arises about the levels at which self-regulation of donor - acceptor relationships of growth and photosynthesis processes occurs. In our opinion, the application of retardants to study donor-acceptor relationships can have a significant advantage over "acute" experiments with artificial removal of plant organs (partial or complete defoliation, derisoidation, etc.), since a decrease in the activity of growth centers is achieved without significant stress for plants.

The photosynthetic apparatus is a complex hierarchy of systems of various levels of organization, it is necessary to assess changes at the level of a plant, leaf, cell, and chloroplast under the influence of retardants.

The formation of the leaf surface is one of the central factors that determine plant productivity. The regularities of the leaf surface formation for the retardants action indicate significant anatomo- morphological changes in the ontogenesis of trial plants. At the same time, the power of the acceptor zone significantly influenced the creation and functioning features of the leaf apparatus. Some studies were carried out on annual shoots of raspberries, where only plant growth processes acted as an acceptor, and some on plants, where, in addition to growth processes, carpogenesis (fruit formation and growth) acted as a powerful donor of assimilates. Our study of the growth features of vegetative shoots of two raspberry varieties under the influence of retardant and exogenous gibberellin made it possible to establish that a decrease in the leaf surface area and shoot length was accompanied by a decrease in the dry weight of leaves and stem compared with control and the variant in which gibberellin was used. At the same time, the thickness of the leaf increased significantly and the leaf area density value increased [71].

Changes in the size of the leaf surface, the weight of leaves and stem of a growing shoot can make significant adjustments to the level of donor-acceptor ratios of the whole plant. This indicator is characterized by the ratio of dry matter of leaves to weight of stem dry matter, indicates its higher value in variants with different types of retardants in comparison with control, and a decrease in this indicator under exogenous gibberellin. Moreover, the greatest value of this indicator was noted in the variant with 0,05 % paclobutrazol, which also caused the most significant effect on growing [74]. Thus, despite the decrease in the total leaf surface area, the relative provision of the shoot with the leaf apparatus increases under the retardant influence. An increase in the "leaf dry matter / stem dry matter" indicator under the retardants influence creates the prerequisites for the accumulation of an excess of assimilates in intermediate funds of various levels, due to which the buffering of the bonds of photosynthesis and growth is achieved.

The physiological state of the leaf is in close interaction with its structural features, which are defined in the scientific literature as "mesostructure". Our data indicate that the thickening of leaves under the retardant influence occurred due to an increase in the proportion of chlorenchyma, the cell sizes of the main leaf tissues – palisade and spongy parenchyma, epidermis, practically did not change (Table 3.1). Comparison of these data with the results of morphological analysis allows us to draw a conclusion about changes in the nature of the marginal meristem activity under the influence of retardant. Since an increase in leaf thickness and an increase in specific leaf weight was observed in the trial, and the size of mesophyll cells did not change, this, in our opinion, indicates an increase in the number of layers of mesophyll cells, that is, the inclusion of periclinal sections of the marginal meristem [71]. At the same time, a comparison of the data on the absence of differences in the cell sizes of leaves of the control and experimental variants with a decrease in leaf area and weight in the experiment indicates a decrease in the frequency of anticlinal divisions and a general decrease in mitotic activity. Thus, morphophysiological changes in the leaf apparatus under the action of retardants are largely due to changes in the mitotic activity of marginal meristems and the features of differentiation of mesophyll cells.

It was found that regardless of the chemical structure of the retardant, the effectiveness of its action is determined by the weather conditions of the growing season, the formulation and concentration of the active substance, and the features of plant ontogenesis. In drier conditions of the growing season, the effect of the compounds was more pronounced and manifested itself longer than in years with a large amount of precipitation. The sensitivity of plants to retardants is largely determined by species specificity - plants with high growth rates (raspberries) exhibit a clearer effect-dose relationship than plants with an extended growth period (chokeberry). Inhibition of growth of the shoots replacing raspberries with the retardants interaction made it possible to change the architectonics of plantings and create better conditions for light conditions for fruiting shoots [74].

The leaf surface area of raspberry shoots decreased under the influence of retardants, but the relative supply of plants with the photosynthetic apparatus increased. A decrease in leaf area of retardant-treated plants is not associated with a decrease in the cells size, but is determined by a decrease in the activity of marginal meristems. It was observed a decrease in the area of individual leaf under the influence of chlorocholine chloride with a simultaneous thickening due to the proliferation of mesophilic and epidermal cells in potato plants [215], oil flax [61], and sugar beet [203]. The number of chloroplasts in chlorenchyma cells was either at the level or lower under retardants compare to the control variant. An important regularity was observed that the cell volume corresponding to one chloroplast was significantly greater during the entire period of trial than in the control, which indicates significant metabolic, energetic and informational changes in the relationship between the plastome and the cytoplasm. The decrease in the chloroplasts number and the "chloroplast to cell volume" ratio under the retardant clearly correlated with an increase in ABA concentration with a decrease in cytokinin content of experimental trial (Tables 2.4, 2.5).

The 0,3 % kamposan M, 0,3 % dextrel and 0,05 % paclobutrazol application caused a effect without phytotoxicity signs. The retardant effect of 1,2-2,4 % chlorocholine chloride solutions on berry plants was more severe – the growth inhibitory effect was accompanied by the appearance of significant chlorotic spots on the leaves of raspberries, chokeberries and strawberries [100, 101].

Our electron microscopic study of mesophyll cells of chlorocholine chloride treated raspberry plants indicates that the drug caused various damages in a part of chloroplasts, up to their complete disintegration. In this case, the lamellar structure was destroyed, chloroplasts swelled, and a large number of osmiophilic globules appeared [108]. We noted that the structure of chloroplasts and the results of literature data under retardants treatment are similar to the changes that abscisic acid causes in plastids [212, 235]. Obviously, the accumulation of this stress hormone, which we noted in our experiment (Table 3.1) is one of the central factors leading to anomalies in the internal structure of chloroplasts under the influence of retardants.

The study of chlorocholine chloride effect on the pigment complex of raspberry and black chokeberry leaves indicates that the chlorophylls and carotenoids content in leaf tissues immediately decreased after retardants treatment with concentrations that provide a growth inhibitory effect [78, 103], which coincides with the appearance of chlorotic spots on the leaves of these crops. The difference in the pigment content of control and experimental variants of black chokeberry was less significant and leveled out faster than in raspberry plants. CCC application also caused a decrease in the carotenoid content of raspberry and black chokeberry leaves during the period of intensive shoot growth [74]. At the same time, it should be noted that the effect of retardants on the chlorophyll and carotenoid content through a change in the ABA to

Table 3.1.

Influence of retardants on mesostructural indicators of raspberry leaves.

Indicators	10/06/1996			30/09/1996		
	1	2	3	1	2	3
Partial tissue volume on the transverse leaf cut, (%)						
epidermis	24,4±3,2	20,5±2,1	20,8±4,0	21,8±2,4	*12,8±1,8	*13,2±2,9
chlorenchyma	75,6±4,1	79,5±4,2	79,9±3,8	78,2±4,0	87,2±3,4	86,8±4,1
Cell volume of upper epidermis,(μm^3)	2488±68	2502±61	2666±120	6620±104	6294±130	6848±45
Cell volume of lower epidermis,(μm^3)	2242±96	2254±91	2242±108	4648±96	4604±58	4810±56
Cell volume of palisade parenchyma,(μm^3)	524±22	496±18	561±16	1495±48	1479±81	1440±45
Cell volume of spongy parenchyma,(μm^3)	355±18	398±24	376±13	567±51	548±22	580±23
Chloroplasts number in a columnar parenchyma cell, (μm^3)	11,4±0,3	10,6±0,4	10,6±0,2	13,4±0,2	*11,6±0,3	*12,1±0,2
Chloroplasts number in a spongy parenchyma cell, (μm^3)	9,6±0,1	*8,5±0,2	*9,2±0,1	9,8±0,2	9,7±0,2	9,6±0,2
Cell volume of columnar parenchyma per chloroplast, (μm^3)	46,6	46,8	52,9	111,6	127,5	119
Cell volume of spongy parenchyma per chloroplast, (μm^3)	36,9	46,8	40,9	57,9	56,5	60,4

Note: 1 - control, 2 – 0,05 % paclobutrazol, 3 - 0,3 % dextrel. Plant treatment on May, 16 and 30. * - difference is significant at $p<0.05$.

cytokinin ratio is apparently not the only way to regulate the pigments accumulation. Thus, an increase in the ABA to cytokinin ratio in raspberry leaves was also observed under the action of triazole-derivative compound paclobutrazol, but our data indicate an increase in the chlorophyll content in leaf tissues under the retardant influence [74].

It was suggested in the literature that the decrease in the chlorophyll content of tomato leaves under the influence of ethylene producer can proceed in a non-enzymatic way due to the conversion of chlorophyll "a" into pheophytin upon acidification by the decomposition products of ethylene releasing compounds. Obviously, there is no reason to accept this reason as the main one. The data obtained by the studying of the chlorophyllase activity under the retardant influence indicate that there was a clear increase in the enzyme activity under the influence of chlorophyll chloride and dextrel, especially at the first stages of development [74, 108]. The difference between control and experiment trial decreased significantly after the ending of growth period. In addition, chlorocholine chloride has a slightly alkaline reaction and cannot cause acidification.

Thus, the analysis of the effect of retardants with different chemical structure (chlorocholine chloride, ethylene releasing compound, paclobutrazol), as well as an analysis of literature data, allows us to conclude that there is no unified mechanism of retardant action on the pigments biosynthesis: the nature of chlorophyllation is determined by the specificity of the drug and the conditions of its application. Regulation of leaf donor function during inhibition of vegetative growth is primarily determined by a decrease in the number of structural elements that take part in photosynthesis: the mass and area of leaves, the number of mesophyll cells, and the chloroplasts number in the cell.

Certain differences in the anatomical and morphological characteristics and mesostructure of leaves were established under the retardants action in plants that form a powerful donor sphere as a result of carpogenesis processes. In particular, the total leaf area increased as a result of increased branching of the stem under the influence of various retardants in plants of winter rape [216], soybeans [39], sunflower [177], oil flax [61,88], oil poppy [161], in contrast to vegetative raspberry shoots. Analysis of the ratio of the vegetative organs weights of tomato plants at the end of the growing season indicates that at the stage of brown fruit ripeness this indicator of folicur treated plants increased, and for the action of esphon the relative proportion of leaf weight in the total weight of plant was higher, which is an important prerequisite for improving the crop yield (Figure 3.1). An increase in leaf thickness was also established due to an increase in the volume of columnar and spongy assimilating parenchymal cells [92].

The results of the study indicate that in all experimental variants during the period of fruit formation there is a gradual increase of important indicators – leaf area density value that characterize the potential photosynthetic productivity of unit leaf surface (Table 3.2). Tebuconazole tomato leaves were characterized by the highest value of this indicator. This correlates well with the results of mesostructural characteristics of triazole derivative compounds treated plants, where at the end of growing season the leaf thickness was greatest, while the value of leaf area density of

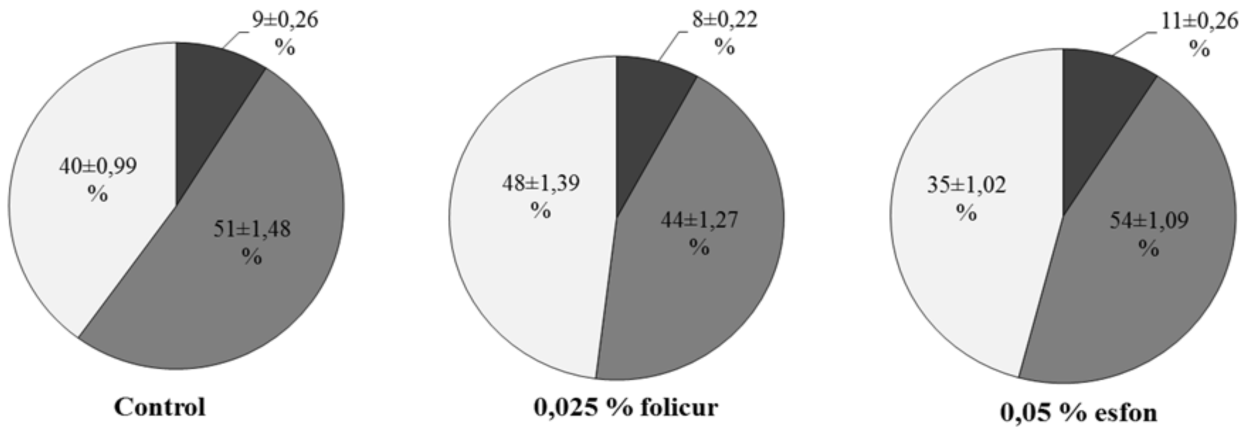

Figure 3.1. Relative proportion of dry matter weight of vegetative organs under folicur and esphon application on tomatoes hymbrid Solerosso: ▇ – roots, ▇ – stems; ▢ – leaves. Average values for 2015 - 2017 years of research

esphon treated plants was low during whole period of growing season that also correlated with the lamina thickness of ethylene releasing compound of applicated plants [92]. Plant growth regulators treatment does not lead to significant changes in the chlorophyll content, this indicator at the fruit formation stage was close to control in all experimental trials (Table 3.2). However, at the end of growing season, the chlorophyll content of both retardants treated plants remained higher compared to control. Changes in the accumulation of chlorophylls and significant morphological changes in the leaf apparatus due to the drugs interaction lead to significant differences in the chlorophyll index of plants according to the trials of experience. At the green ripeness fruitification stage, tebuconazole application increased in this indicator and esphon decreased it compared to control during the whole fruiting period. The obtained data indicated that tebuconazole increased in the net photosynthesis productivity and esphon decreased in this index compared to control at the green ripeness fruitification stage (Table 3.2).

Thus, net photosynthetic productivity is characterized by photosynthetic productivity of unit leaf surface, which with the increase in area leaf surface under tebuconazol and gibberellin action created the prerequisites to enhance gross photosynthetic crop production and accumulation of a greater number of photoassimilates in the plant.

Table 3.2.

Physiological parameters of leaf apparatus of retardants treated tomatoes hybrid Solerosso (average results for 2015 - 2017 years of research)

Indicators	Control	0,05 % esphon	0,025 % tebuconazole
Fruit formation stage			
Leaf area density value, mg/cm2	1,79±0,06	1,78±0,03	*2,12±0,05
Total chlorophyll content (a+b), % per leaf fresh matter weight	0,72±0,022	0,72±0,021	0,74±0,021
Chlorophyll index, g/m2	1,92±0,05	1,79±0,05	*2,79±0,09
Net photosynthetic productivity, g/(m^2 ·day)	6,41±0,16	*4,70±0,12	*10,83±0,43
Fruitification stage (green ripeness)			
Leaf area density value, mg/cm2	2,88±0,09	*2,22±0,07	*2,93±0,07
Total chlorophyll content (a+b), % per leaf fresh matter weight	0,71±0,011	0,73±0,012	*0,76±0,021
Chlorophyll index, g/m2	2,01±0,06	*1,79±0,04	*2,23±0,07
Net photosynthetic productivity, g/(m^2 ·day)	7,32±0,17	7,23±0,19	8,29±0,31
Fruitification stage (brown ripeness)			
Leaf area density value, mg/cm2	3,57±0,08	*2,92±0,08	*4,54±0,13
Total chlorophyll content (a+b), % per leaf fresh matter weight	0,54±0,011	*0,79±0,022	*0,71±0,021
Chlorophyll index, g/m2	1,54±0,04	1,49±0,04	*2,13±0,06
Net photosynthetic productivity, g/(m^2 ·day)	6,54±0,19	*4,41±0,11	*9,36±0,21

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

3.2. Accumulation and redistribution of carbohydrates in the plant under the action of retardants.

The data presented in the literature indicate the possible effect of triazole derivative compounds on the carbohydrate metabolism of plants [118]. The obtained results indicate that in the vegetative organs of tomato plants – roots, stems and leaves at the fruit formation stage are accumulated more nonstructural carbohydrates (sugars + starch) than in the control due to formation of a more powerful donor sphere under plants grows regulators treatment (Figure 3.2). Obviously, this is a consequence of the enhanced photosynthetic work of leaf apparatus of treated plants. The highest content of carbohydrates in all stages of the fruitification phase was noted in stems of tomato plants, that indicates the powerful depositing capabilities of this vegetative organ. At the same time, tebuconazole application increased the amount of sugars and starch in the roots, stem and leaves of plants during the whole fruitification stage. It can be concluded that this indicates some of their redundancy, which is not fully spent on the fruits formation and growth, but is temporarily accumulated to reserve that is deposited in vegetative organs and then used at the stage of transition from green to brown ripeness.

The analysis of various forms of carbohydrates content in tomato organs in terms of dry matter suggests that during the whole fruiting period (from the fruit formation stage to brown ripeness fruitification stage) the reducing sugars content in the roots and stalks of tomato research plants decreased. However, from the green ripeness fruitification stage, when the fruits was already fully formed and growth processes completed, to the brown ripeness fruitification stage for the leaf was observed not an decrease, but an increase in the reducing sugars content (esphon – from 1,37±0,04 % to 1,65 ± 0,02 %; tebuconazole – from 1,81 ± 0,05 % to 2,32 ± 0,05 %; compared to control – from 1,96 ± 0,04 % to 1,94 ± 0,06 %). It was also observed a strong decrease in the sucrose content in the leaves of experimental trials. Thus, this indicator under esphon treatment decreased from 1,02 ± 0,02 % at the green ripeness stage to 0,59 ± 0,01 % at the brown ripeness stage; under tebuconazole – from 0,82 ± 0,02 % to 0,39 ± 0,01 %; compared to control – from 0,79 ± 0,02% to 0,47 ± 0,01 %. Since sucrose is the main transport form of carbohydrates in the plant, the transport of sugars from leaves to fruits stops earlier than from roots and stem, resulting in an increase in the reducing sugars content.

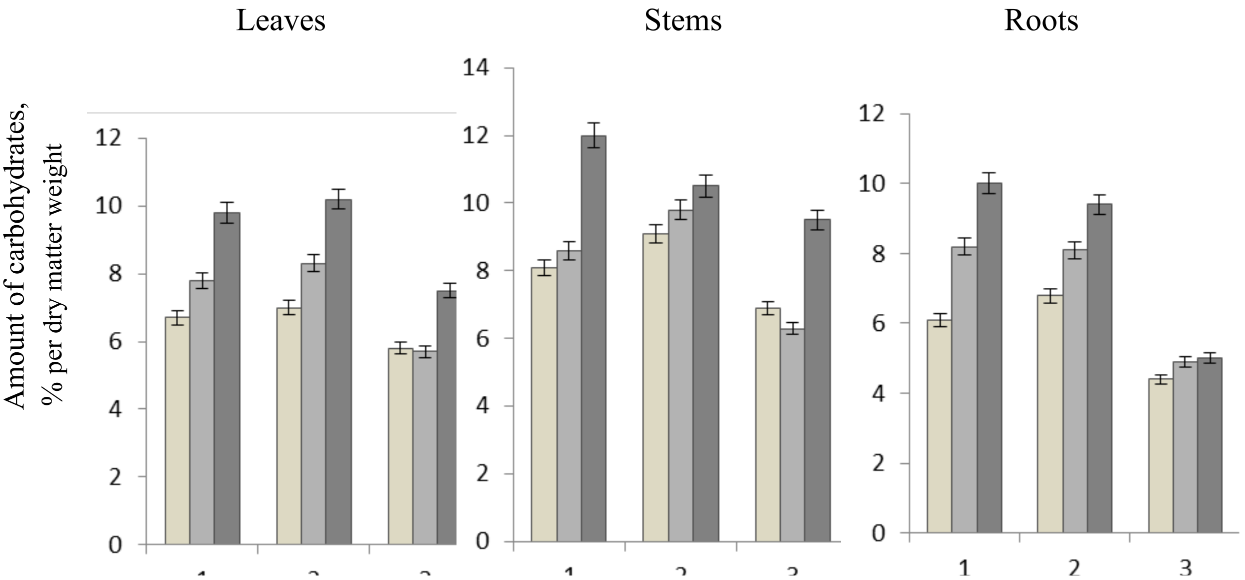

Figure 3.2. Amount of nonstructural carbohydrates (sugar+starch) in vegetatives organs of tomatoes hybrid Solerosso under application of growth regulators: 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness).

– control; – 0,05 % esphon; – 0,025 % tebuconazole. Average results of 2015-2017.

Thus, application of gibberellin and retardants leads to a more intensive accumulation of nonstructural carbohydrates (sugars and starch) in the vegetative organs of research tomato plants with subsequent active reutilization of these substances on the fruits formation and growth needs. The stem plays an important role of temporary assimilates depot, which is amplified under the influence of

Table 3.3.

Sugar and starch content in vegetatives organs of gooseberry cv. Mashenka under application of folicur (% per dry matter weight) (average values for 2015 - 2017 years of research)

Stages	Plant organs	Sugar content		Reducing sugars		Sucrose		Starch	
		Control	Folicur	Control	Folicur	Control	Folicur	Control	Folicur
Blooming stage	Leaves	10,01±0,81	10,7±0,84	8,8±0,51	9,6±0,62	0,9±0,02	*1,3±0,06	1,3±0,04	1,2±0,03
	Shoots	10,8±0,12	*11,3±0,18	10,5±0,16	*11,3±0,24	0,8±0,01	*1,1±0,06	1,3±0,01	*1,5±0,02
Fruit formation stage	Leaves	10,2±0,11	*11,2±0,26	9,1±0,48	*10,4±0,18	1,3±0,05	*1,5±0,01	1,5±0,06	*1,7±0,01
	Shoots	6,7±0,12	7,1±0,18	6,1±0,36	*7,3±0,11	0,7±0,07	*1,1±0,05	1,7±0,02	*2,0±0,04
Full ripeness stage	Leaves	10,3±0,11	*11,2±0,12	9,2±0,12	*9,8±0,09	1,1±0,01	*1,2±0,01	1,1±0,01	*2,1±0,02
	Shoots	7,1±0,07	*8,6±0,02	6,6±0,91	*7,6±0,17	0,7±0,03	*0,8±0,02	1,2±0,01	*2,4±0,01

Note: * – difference is significant at $p<0.05$.

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tebuconazole and gibberellin treatment. In the second half of fruiting period, the nonstructural carbohydrates content in the stem and roots decreased as a result of their utilization to carpogenesis [168].

Analysis of the non-structural carbohydrates content (sugar + starch) in gooseberry plants shows that changes in the photosynthetic apparatus organization for the folicur actions lead to a more intensive accumulation of assimilates in the tissues of vegetative organs. The results of the study indicate that the leaves of gooseberry treated plants during the entire period of ontogenesis contained a higher amount of sugars, reducing sugars and sucrose contant compared with control (Table 3.3). It is known that the growth restriction under retardants action caused an excess of assimilates and can be created not only in the leaves, but also in other vegetative organs. The reserve carbohydrates deposited in this way can be used in the formation of fruits, seeds, and reserve vegetative organs. The obtained data indicate that a significant part of the sugars is deposited in the shoots, which is close in content to their concentration in the leaves. At the same time, they obviously play a significant role in the carpogenesis processes (formation and development of fruits) – the decrease in the sugar content from the flowering phase to the phases of fruit formation and full ripeness was more significant than in the leaves, obviously associated with a more intense outflow into fruits. Similar changes were noted for the starch content in leaves and shoots - for the actions of folicur, the content of this reserve polysaccharide was higher than in the control during the entire period of development.

Thus, a more powerful donor sphere of plants is formed in the year under the drug treatment, which is an important prerequisite for increasing the productivity of agricultural crops.

3.3. Features of photosynthesis and respiration of plants under the treatment of compounds with antigibberellin activity.

The issues of photosynthetic support of plant epigenesis under the changes in donor-acceptor relations in a plant are quite fully presented in the literature, however, the features of respiration, the scale of respiratory expenditures in comparison with gross - photosynthesis during the transition to other levels of donor-acceptor relations in general, and it is still far from complete under the influence of retardants in particular. The ratio of the photosynthesis and respiration processes plays one of the central role in the mass accumulation of individual organs and total plant during ontogenesis. It is known that the total respiratory expenditure can be from 10 to 80 % of carbon assimilated during photosynthesis [35, 36], and a change in the ratio of the source-sink system of a plant by removing a part of the acceptor not only suppresses photosynthesis, but can also enhance dark respiration [133]. The obtained data determines the need for an in-depth study of the growth-inhibitory effect on the ratio of respiration and photosynthesis significantly reduces the possibilities of analyzing the influence of growth regulators on the formation of donor-acceptor system of plants.

The obtained results indicate that a decrease in the growth activity of raspberry shoots at the early stages of plant development under the influence of retardants in the growing experiment condition is accompanied by changes in the ratio of dark respiration and photosynthesis (Table 3.4).

Table 3.4.

Effect of retardants on growth processes, photosynthesis and dark respiration of raspberry plants on the day of 10 after treatment (vegetation experiment, 1997)

Indicators	Plant height(cm)	Intensity of dark respiration (R)	Apparent photosynthesis	Gross-photosynthesis (Pg)	R/Pg
		mg CO_2/(g of wet matter per h)			
Control	15,3±0,92	10,2±0,65	21,5±0,17	31,7±0,82	0,32
0,3 % dextrel	*9,1±0,64	10,0±0,39	*11,0±0,15	*21,0±0,54	0,48
0,05% paclobutrazol	*9,5±0,61	9,0±0,44	*15,7±0,68	*24,7±1,00	0,36

Note: * – difference is significant at $p<0.05$.

On the day of 10 the intensity of photosynthesis decreased, the respiratory costs (R/Pg) of treated plants increased and the growth inhibitory effect was clearly manifested after the 0,05 % paclobutrazol and 0,3 % dextrel application of raspberry plants. It should be noted that dextrel and paclobutrazol application didn't cause significant differences in the intensity of dark respiration compared to control. Similarly, according to the literature data, etrel influenced the respiration of tomato leaves — a decrease in the R/Pg ratio occurred due to a slowdown in the gross-photosynthesis of plants in experimental trials [227]. Thus, one of the reasons limiting the donor function of photosynthesis is an increase in respiratory expenditure, as a result of which the proportion of assimilates directed to the needs of epigenesis decreases.

It also found that changes occur in the gas exchange of the sugar beets plant under the influence of retardants [203]. The mesophilic resistance of the leaves (r_m) increased of the drug-treated sugar beet plants (Table 3.5), which was accompanied by a decrease in the intensity of photosynthesis, despite the increase in chlorophylls content in the leaf tissues.

The study of the mesostructural organization of sugar beet leaf indicate that one of the reasons to increase in mesophilic resistance under the retardants influence is the thickening of leaf and decrease in the intercellular spaces as a result of an earlier cessation of the epidermal cells growth. It is important to understand the functioning of donor-acceptor system of plants under the influence of retardants with different mechanisms of action - paclobutrazol and dextrel, there was an increase in the costs of photorespiration and dark respiration in leaves that were completely formed after drug treatment of experimental plants (Table 3.5).

Consequently, the factors limiting the donor function of the leaf for the retardant effects decrease in the leaf surface area due to a decrease in the meristems proliferative activity, an increase in mesophilic resistance to CO_2 diffusion, inhibite the rate of assimilates flows for growth processes in the leaf and their outflow to the leaves from the upper parts of plants. All these lead to decrease in the intensity of CO_2 assimilation and increase in the share of respiratory costs in carbon dioxide gas exchange, which is an excess of unused assimilates in the leaf.

Table 3.5.

Influence of retardants on the parameters of gas exchange in sugar beet leaves of Robert's hybrid (2003, vegetation experiment)

Indicators	Control	0,3 % Dextrel	0,05 % Paclobutrazol
Carbon dioxide gas exchange of leaf, mg $CO_2/(dm^2 \cdot h)$: Apparent photosynthesis P	21,5±0,02	*19,9±0,02	*18,2±0,04
Photorespiration Rp	6,5±0,03	*6,1±0,03	*6,0±0,03
Dark respiration Rd	3,5±0,03	*3,8±0,09	3,5±0,03
Rp/P	0,30±0,004	*0,32±0,003	*0,33±0,003
Rd/P	0,16±0,002	*0,20±0,003	0,19±0,003
Transpiration, g $H_2O/(dm^2 \cdot h)$:	2,77±0,005	*2,60±0,005	*2,74±0,002
Diffusion resistance, s/cm leaf r_l	3,76±0,009	*4,05±0,005	*3,68±0,002
Mesophyll r_m	6,14±0,05	*7,11±0,05	*8,13±0,02
CO_2 concentration in the intercellular spaces (C_i), mg/l	0,407	0,406	0,435

Note: plants treatment on the day of 70 of vegetation; * – difference is significant at $p<0.05$.

It should be noted that the studied drugs have different effects on the components of diffuse resistance. Leaf resistance r_l and mesophyll r_m of the leaves of dextrel treated plants increased simultaneously, while paclobutrazol treatment had practically no effect on r_l with a significant increase in r_m. Therefore, the concentration of CO_2 in the intercellular spaces (C_i) under dextrel treatment did not differ from the control due to the balanced change in diffusion resistance, and it increased under paclobutrazol, since the absorption of CO_2 by the mesophil was inhibited disproportionately to its diffusion through the leaf surface (C_i has become closer to atmospheric). It can be assumed that the effect of paclobutrazol on the photosynthetic apparatus is not limited to the inhibition of photosynthesis by an excess of assimilates (in this case, most likely, the effect manifested due to dextrel application is expected), but the drug can participate in the direct regulation of photosynthetic processes.

Thus, retardant drugs – dextrel and paclobutrazol affect the anatomical and physiological parameters of the photosynthetic apparatus of sugar beet, which is expressed in a decrease in the leaf surface area, apparent photosynthesis, and an increase in the proportion of respiration in the carbon dioxide balance. The data obtained indicate that retardants are a powerful method of regulation of the assimilation apparatus activity. It is one of the components of donor-acceptor system and can be used to purposefully regulate the redistribution of plastic substances in sugar beet plants.

Our results of the hormonal complex of raspberry and sugar beet leaves under the influence of retardants of different chemical structure indicate the same nature of changes in the hormonal status of the leaf: there was a decrease in the free gibberellin content with a simultaneous significant increase in the free ABA content [203]. Thus, it becomes possible to compare the changes in the functioning of photosynthetic apparatus under the influence of retardants with the known ratio of endogenous phytohormones in the experiment.

The unambiguous dependence of the functional activity of chloroplasts under the application of one or another retardant has not been established. In general, an increase in the activity of chloroplasts in raspberry leaves was observed at the beginning of the growing season under the influence of retardants with different chemical structure, in the first week - after the drug treatment of plants, followed by equalization between the control and experimental trials of the Hill reaction activity and non-cyclic photophosphorylation, or even a significant decrease them at the end of the growth period [74,81]. In our opinion, this issue requires a deeper study, since we observed inhibition of photosynthesis in plants of experimental raspberry trials, as well as a decrease in the pigments content, destruction of chloroplast structures under the drugs action which is not consistent with an increase in the plastids functioning. The indicators of the chloroplasts photochemical activity are normalized per unit of pigment content, the results obtained rather indicate not an increase in the functional activity of plastids, but rather the participation in these processes in vitro greater than in the control of the chloroplasts number, the pigments content under the retardants influence decreased, especially after the treatment period. It was established by the gradual leveling, and then the decrease in the chloroplasts activity in the control and experiment trials at the end of the growth period. Obviously, it is determined by the gradual leveling of the pigment content in the leaves tissues of control and experimental variants and even an increase in their content at the end of the growing season [74, 81]. Thus, the photochemical activity of chloroplasts cannot be recognized as a specific indicator of the photosynthetic apparatus activity under retardants, since this indicator is formed in different trials with a different chloroplasts number.

The remote influence of phytohormones on photosynthesis is realized through the regulation of epigenesis, transport and deposition of substances into the storage [134]. The data presented in Chapter 2 indicate that the decrease in the acceptor (growing shoot) capacity for assimilates due to inhibition of meristem activity by retardants is determined by changes in the hormonal complex: the gibberellin and auxin content decreased with a simultaneous increase in the ABA content, which significantly decreases. The attracting factor influences the concentration of metabolites in the chloroplast or perioplastic space and exerting an effector effect on the enzymes of photosynthesis ("feed back mechanism"), regulating the ratio of the rates of synthesis and transport of substances from the phototrophic cell [134]. Thus, it was found that the final product of photosynthetic restoration of photosynthesis is glucose, which functions as an effector. The regulatory effect of glucose in photosynthetic cells was demonstrated by the example of the synthesis of direct transcription products – messenger RNA ribulose bisphosphate carboxylase and specific suppression by glucose of the synthesis of the large subunit of this enzyme encoded in the plastid genome [196]. Thus, the accumulation of photosynthetic products in the chloroplast and the cell as a result of a decrease in their outflow to the attracting centers largely regulates the activity of photosynthetic apparatus.

The study of the various forms of sugars and starch content in the leaves of raspberry variety Novosty Kuzmina under the 1,2 % chlorocholine chloride treatment indicates that the growth inhibitory effect of the drug was accompanied by significant changes in the carbohydrate accumulation. There was a decrease in the total sugars, reducing sugars and sucrose content during the entire period of plant growth [74]. At the same time, the starch content increased significantly during the entire period of intensive shoot growth. The decrease in the sugar content in the leaves of experimental plants during the growing season, in our opinion, cannot be explained by their more intensive outflow into the acceptor zones, since the retardant inhibits the activity of shoot growth centers as the main acceptor of assimilates. Thus, free sugars, which are normally transported to the acceptor zones, under the retardant influence polymerize more intensively, forming a reserve starch. The possibility of storing assimilates in funds of different levels ensures the buffering of donor and acceptor bonds and a certain autonomy of the photosynthesis and growth processes [133].

Thus, the analysis of the photosynthetic apparatus functioning of raspberry plants under retardants action with various chemical nature on the vegetative growth of shoots indicate a decrease in the donor function of leaf due to inhibition of photosynthesis. Control over photosynthesis with a decrease in the “sink” for assimilates by the main acceptor - growing shoot is carried out by a feedback mechanism. This relationship is mediated by the effector effect of excess starch and changes in the balance of phytohormones – the accumulation of abscisic acid and a decrease in the activity and gibberellins and auxins content in leaf tissues.

An opposite pattern is observed in the functioning of the donor-acceptor system due to the fruits formation and growth during the formation of powerful acceptor zone in plants. The number and area of the leaf increased, the leaf mesostructure organization is optimized, the net photosynthetic productivity increased, which lead to an increase in yield [39, 90, 161].

CHAPTER 4.
ACCUMULATION AND REDISTRIBUTION OF MINERAL NUTRITION ELEMENTS IN AGRICULTURAL PLANTS UNDER RETARDANTS TREATMENT

The integrity of the plant organism is based on the interaction of organs and the active exchange of organic and mineral substances between them. It has been sufficiently studied the regularities of photosynthesis and redistribution of assimilate flows throughout the plant with a change in the growth rate of individual organs within the source-sink concept. However, the nature of mineral nutrition elements intake and their redistribution between plant organs with changes in the tension of donor-acceptor relations in general (and under the influence of retardants) remain largely unclear.

There is enough data in the literature that there is a clear relationship between the intensity of growth, photosynthesis, respiration and nitrogen nutrition of the plant. A positive correlation was observed between the protein nitrogen content and the intensity of photosynthesis and respiration of plants [62, 132]. There is no information in the literature on the effect of retardants on the exchange of nitrogen compounds for berry crops. In this regard, we studied the features of the various forms of nitrogen redistribution, as well as free and bound amino acids and their content in the leaves and stems of retardant treated berry crops in the different weather conditions of the growing season. It was found that the chlorocholine chloride treatment has a significant effect on the dynamics of nitrogen-containing compounds in the vegetative organs of berry crops. The first reaction of plants at the beginning of the growth of retardant treated rowan and raspberry shoots was an increase in the content of total and protein nitrogen both in the stems and in the leaves; it was not observed a definite pattern in the dynamics of non-protein nitrogen [102, 103]. The content of non-protein nitrogen in the stems and leaves of gooseberries, as well as in raspberry leaves increased under the influence of chlorocholine chloride. On the contrary, it was noted a decrease in the content of non-protein nitrogen in the strawberry leaves and raspberry stems, which, with a general increase in the nitrogen content, should obviously be explained by the intensive use of this fraction for the formation of protein. In our opinion, an increase in the content of nitrogen-containing compounds in the vegetative organs of berry crops is associated with a slowdown in their intake and use in growth centers, the activity of which is inhibited under the retardant influence. The results of the study of the hormonal complex of raspberry shoots under the influence of retardants of various chemical nature indicate that this decrease in the attracting activity of shoot growth zones is based on a decrease in the content and activity of indoleacetic acid and gibberellins (see Tables 2.1, 2.2).

We noted a significant decrease in the nitrogen content in vegetative organs in June - July. Obviously, this fact should be explained by the reutilization of proteins and the outflow of nitrogenous compounds into a new powerful acceptor zone – fruit formation. This conclusion is also confirmed by the fact that a clear increase in the total and non-protein nitrogen content was observed in the leaves of strawberries in August after the end of fruiting. Similar data on the decrease in the content of nitrogenous compounds in various crops during the growing season were obtained in other works [91]. It was observed a gradual leveling in the total and protein nitrogen content of experimental trials in June - July [103].

The nitrogen content in the organs of treated plants was significantly influenced by the concentration of the retardant in the working solution. The effect chlorocholine chloride in the higher concentrations of 1,1-2,4 % solutions turned out to be more significant on nitrogen metabolism. More intensive accumulation and reutilization of protein were observed in these variants. The specificity of retardant action should be noted. Chlorcholine chloride significantly inhibited the growth of raspberry shoots and caused the appearance of chlorotic spots along the edges of the leaves of raspberries, strawberries, and black chokeberries. In the gooseberry, there was no significant inhibition of stem growth and the appearance of chlorosis on the leaves. For the same crops, smaller differences were noted in the content of nitrogenous compounds in the leaves and stems of treated plants in comparison with other studied crops. In 1982, it was studied the content of bound and free amino acids, as well as their amount in the stems and leaves of raspberries, in May, immediately after spraying the plantings and in June, during the fruitification period. It was used 1,2 % retardant for experimental trials. The results indicate an increased in accumulation of amino acids and their incorporation into proteins under the action of chlorocholine chloride [74]. It was observed an increase in the total content of amino acids (primarily bound) in the leaves, and free amino acids for shoots (especially aspartic) after the treatment in May. The greatest changes occurred in the content of aspartic and glutamic acids, leucine, and alanine. The increase in the amino acids content in the experimental variant was mainly due to the fraction of bound amino acids, which indicates an increase in protein biosynthesis under the action of retardants. These data are in agreement with the results of studying the dynamics of protein nitrogen content.

The results of our studies indicate a close relationship between the change in the attracting power of organs under the influence of retardants and the redistribution of nitrogenous compounds in the organs of the plant. In this regard, it is necessary to study the features of nitrogen metabolism in black chokeberry under the influence of chlorocholine chloride. It was observed a decrease in the size and weight of berries and a decrease in yield [100]. It was found that the dynamics of the various nitrogen fractions content during the vegetative growth and fruiting of black chokeberry under the influence of retardant was largely determined by the weather conditions in the growing season. In drier growing conditions, there was a clear increase in total and protein nitrogen in the leaves and stems of experimental plants [102]. The content of non-protein nitrogen simultaneously decreased in leaves; a certain pattern in the non-protein fraction content was not observed for the stems. In more humid growing conditions, an increase in the total nitrogen content did not appear immediately after treatment in May, but later, in July. Thus, the increased accumulation of nitrogen-containing compounds in chokeberry under the influence of chlorocholine chloride is more pronounced against the background of insufficient moisture.

The accumulation of various forms of nitrogen in the experimental plants is confirmed by the data on the content of various fractions of amino acids in the leaves and stems of rowans immediately after treatment. An increase in the content of amino acids was observed in the leaves and stems of experimental plants, and mainly due to the fraction of free amino acids. The greatest changes occurred in the content of aspartic acid in the stems of experimental variant. The data obtained indicate that for black chokeberry there is no clear relationship between the concentration of the retardant in the working solution and the level of accumulation of various forms of nitrogen [102]. This is in good agreement with the lack of a clear growth dependence of the effect - dose in this crop under 0,6 – 2,4 % chlorocholine chloride treatment. The obtained results also indicate that during the growing season from May to September there was a decrease in the amount of total and protein nitrogen in the leaves. We explain this by the reutilization of proteins and the outflow of nitrogen-containing compounds into developing fruits.

It was noted a decrease in yield and the phenomenon of small-fruits under the influence of chlorocholine chloride on chokeberry plants. In this regard, the higher level of total and protein nitrogen during the entire growing season should obviously be explained by a decrease in the supply of nitrogen-containing compounds to growing fruits. The data on the content of free, bound amino acids and their amount in the stems and leaves of plants in the control and experimental variants during the period of fruitification generally confirm the conclusion about a slowed outflow of nitrogen compounds from vegetative organs into fruits under the retardant influence [74,102]. There was a higher level of total amino acid content in the leaves and stems of the experimental variant, and a decrease in the content of bound amino acids during the fruitification period. The higher content of free amino acids in the vegetative organs of the retardant treated plants in comparison with the control indicates a decrease in its outflow into the fruits. Thus, the regulation of nitrogen compounds exchange under the influence of retardants is mediated by changes in donor-acceptor relations. A decrease in the capacity of a new acceptor zone in the second half of the growing season – growing fruits, determines a slowdown in the outflow of nitrogenous compounds and an increase in their concentration in the vegetative organs of chokeberry under the influence of retardant.

It was noted a significant accumulation of free aspartic and glutamic acids, alanine, leucine, lysine, and arginine for the leaves. Free glutamic acid accumulated most significantly in the stems. Chlorocholine chloride treatment led to a decrease in the content of these amino acids in berries [74].

Thus, the obtained research results indicate that the effect of chlorocholine chloride on nitrogen metabolism of a plant is realized not only through the regulation of the activity of amino acids and proteins synthesis, but also a change in the donor - acceptor ratios of the plant due to the effect on the formation and functioning of centers that attract nitrogenous compounds.

The research materials presented in the previous chapter of the work indicate that retardants cause a different rate growth inhibition of the individual plant organs due to a decrease in the flow of assimilates into the growing organs, a quantitative decrease in the elements of the photosynthetic apparatus. At the same time, the trophic situation in individual plant organs during artificial growth inhibition is determined not only by the intake of assimilates, but also by the assimilation of mineral nutrition elements. The study of mechanism of the intake and redistribution of nutrients under the influence of retardants creates a theoretical basis for further predicting the removal of certain nutrients from the soil and the development of rational schemes for the application of fertilizers on industrial of crops under the action of compounds with growth inhibitory effect. Our research results indicate that the content of mineral substances in the shoots of black chokeberry did not remain constant, but changed according to the phases of the growing season, and the treatment with retardant had a significant effect on the dynamics of the content of individual elements [102]. A clear decrease in the content of phosphorus and potassium in stems and leaves was observed during the period of active growth of shoots – in May and June. We consider that during this growing season there is an intensive accumulation of organic matter, as a result of which there is a kind of dilution of minerals in organic matter, which accumulates at a higher rate. This also explains the higher level of potassium in the shoots treated with chlorocholine chloride at the first stages of the growing season [74]. It is obvious that the inhibition of growth by the retardant at the early stages of development leads to a slowdown in the accumulation of organic matter, against the background of which the relative content of potassium increased. The leaves of the control plants were better developed, had larger sizes, and uniform green color of the leaf blade. Chlorocholine chloride treated plants had smaller leaves, leaf blades were often irregular in shape, and significant chlorotic spots at the beginning of the growing season. The content of phosphorus and potassium increased significantly in the leaves in the second part of the growing season, after the end of the fruitification period, which we explain by the influx of elements into the leaves due to the completion of the growth period and the formation of fruits. In the autumn period, the content of phosphorus and potassium in the leaves significantly decreased due to their mobilization into the wintering plant organs. These data are in good agreement with the data on the high mobility of these elements in plant tissues [123, 233].

The dynamics of the phosphorus and potassium content is more common for stems. The high content of these elements during the period of intensive growth changed by its gradual decrease in the period of completion of growth processes and did not change significantly [102]. The phosphorus content in the shoots of black chokeberry was the lowest of all studied elements, and it was established no significant effect of chlorocholine chloride on the content of this element. These data differ from the results of studying the effect of chlorocholine chloride on the content of total phosphorus and its fractions in grape shoots, in which the retardant treatment of bushes led to an increase in the content of phosphorus in the tissues of plants varieties with medium strength of growth and a decrease for the variety Goruli with strong strength of growth [32].

Our studies indicate that chlorocholine chloride caused an increase in the calcium content and the number of bivalent cations (Ca^{++} + Mg^{++}), and also, in general, reduced the content of monovalent cations (Na^{+} + K^{+}) in the tissues of the chokeberry leaves during the entire growing season. Also it was found a clear decrease in the ratio of K^+ / Ca^{++} and K^++ Na^+ / Ca^{++}+ Mg^{++} in the experimental variant compared to the control in the same period. The study of the divalent cations content in chlorocholine chloride treated raspberry leaves indicates an increase in the calcium content in the experiment during the entire period of active growth of shoots [74, 103]. We did not find a clear pattern in the magnesium content in raspberry leaves under the influence of chlorocholine chloride, as in the leaves of black chokeberry.

In our opinion, the increase in the content of divalent cations, and primarily calcium under the influence of chlorocholine chloride, is largely associated with the biopolymers accumulation by cell wall. The presence in the cell walls of a significant number of negatively charged functional groups (primary carboxyl and hydroxyl) allows it to accumulate cations, and this ability increases with an increase in the ion charge. Calcium cross-linked intermolecular bonds carry a load in the cell walls, and their rupture during acidification of the cell wall is considered as one of the mechanisms of wall softening during cell growth in the stretching phase [221]. The increase in the content of bivalent cations in black chokeberry and raspberry plants under the influence of chlorocholine chloride is apparently associated with an increased accumulation of cell wall biopolymers due to the redistribution of assimilates during artificial growth inhibition, earlier and more intensive formation of mechanical and conductive tissues. Data on the dynamics of the biopolymers content in cell membranes of raspberries and black chokeberries vegetative organs indicate the growth of their particles from the total amount of the plant in ontogenesis, and chlorocholine chloride intensified this process. The results of studying the accumulation of cellulose and lignin in the leaves of chlorocholine chloride treated chokeberry also indicate an increase in the content of these substances in plants of the experimental trial [74].

The tomato plant is a fairly convenient object for studying the characteristics of the accumulation and redistribution of nutrients under the action of gibberellin and antigibberellin drugs - retardants on the formation of powerful acceptor zone – fruits.

Analysis of total nitrogen content in the vegetative organs of tomato plants treated by growth regulators indicates significant differences in the accumulation and redistribution of this nutrient according to the trials of experience. Application of drugs had insignificant effect on the nitrogen content in the leaves of plants (Fig. 4.1.) [2].

It was noted a significant decrease in the nitrogenous compounds content of all treated trials from fruit formation stage to green ripeness fruitification stage. In our opinion, such a decrease in the nitrogen content cannot be explained by biodilutions, since the vegetative growth of tomatoes slows down significantly during the period of growth and fruit formation. In this regard, we assume that changes in the element content of treated plants compared to control are determined by the outflow of nitrogen-containing compounds to fruit formation. It was established that the main donor of nitrogen in tomato plants was leaves.

At the stage of fruit formation, the nitrogen content in all plant organs under the action of gibberelic acid was higher than in other trials, which is explained by the greater intensity of growth processes under the action of phytohormone. At the same time, there is a gradual decrease in the nitrogen content in the vegetative organs during the entire fruitification phase. The most intense decrease in nitrogen-containing compounds occurred in the roots and stem of the plant under the action of the gibberellin antagonist – retardant folicur during the transition from the stage of fruit formation to the stage of green fruit, that is, during the period of the most intensive growth of tomato fruits. Consequently, these organs were the main donors for providing carpogenesis with reserve nitrogen. At the same time, at the stage of brown fruit ripeness, the nitrogen content in the roots and stem of plants of this variant increased, apparently due to the supply of "fresh" nitrogen.

The crop production increased under the action of both drugs as a result of formation of a more powerful photosynthetic apparatus, synthesis enhancement, accumulation and intensive redistribution of the flows of assimilates and nitrogen-containing compounds from the vegetative organs to the fruits [90, 91].

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

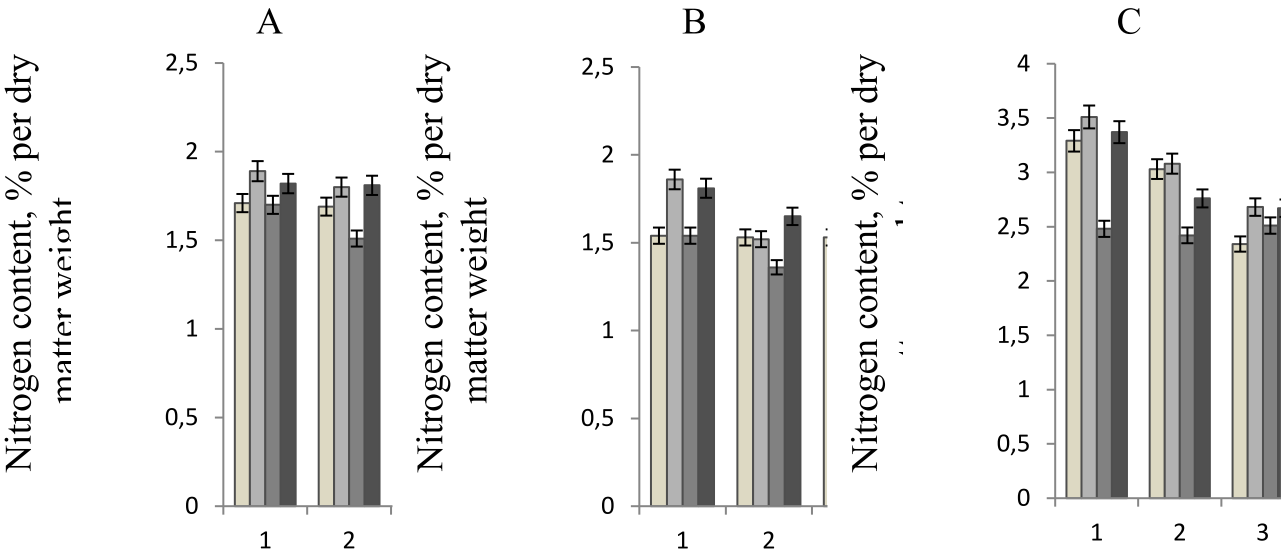

Fig. 4.1. Nitrogen content in vegetative organs of tomato plants under gibberellin and retardants application: 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness). A – root, B – stem, C – leaves. – control; – 0,05 % esphon; – 0,025 % folicur; – 0,005 % gibberellin

The analysis of the literature data indicates the contradictory nature of the influence of various growth regulators on the phosphorus and potassium content of crops. Thus, the application of chlormequat chloride on sugar beet plants caused a decrease in the content of phosphorus compounds in leaves and root crops with a simultaneous increase in the potassium content, while the action of triazole derivative paclobutrazol increased the phosphorus and potassium content in the leaves and decreased in the roots [203]. This compound caused an increase in the phosphorus and potassium content at the beginning of growing season and decreased in their

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content at the end of Nevskaya potato plants [214, 215]. The application of paclobutrazol on rapeseed plants not caused changes in the potassium content in the leaves of experimental plants [180]. Thus, it is advisable to study the interaction of retardants and gibberellin on the redistribution of mineral nutrition elements by tomato plants.

The results of the study indicate that the phosphorus content in the roots of esphon and gibberellin treated plants was higher compared to control during fruitification stage, while under tebuconazole application, the phosphorus content decreases significantly from fruit formation to brown ripeness fruitification stage, which indicates an increased outflow of this element to the fruits (Fig. 4.2.) [91]. Similar changes occurred in the stem and leaves in the trials treated by triazole derivative compounds. The content of phosphorus compounds of tebuconazole treated trials, as well as for gibberellin trials in terms of the dry weight matter in stem also significantly decreases during the whole fruitification stage that indicates an intensive reutilization of this element on the formation, growth and ripening of fruits.

It is known that the optimal provision of plants with potassium improves photosynthesis, loading of phloem by anew synthesized assimilates and their transport along the phloem, which contributes to the growth of crop production and its quality. The potassium content in roots of gibberellin, tebuconazole and esphon treated plants at the stage of green and brown ripeness was higher compared to control (Fig. 4.3.).

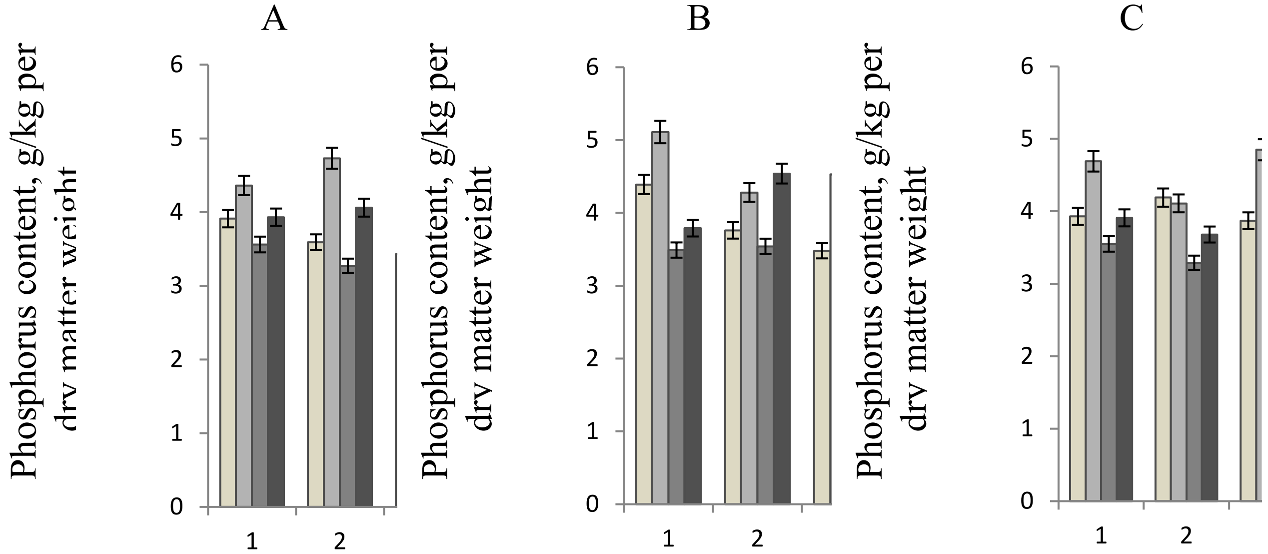

Fig. 4.2. Phosphorus content in vegetative organs of tomato plants under gibberellin and retardants application: 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness).

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

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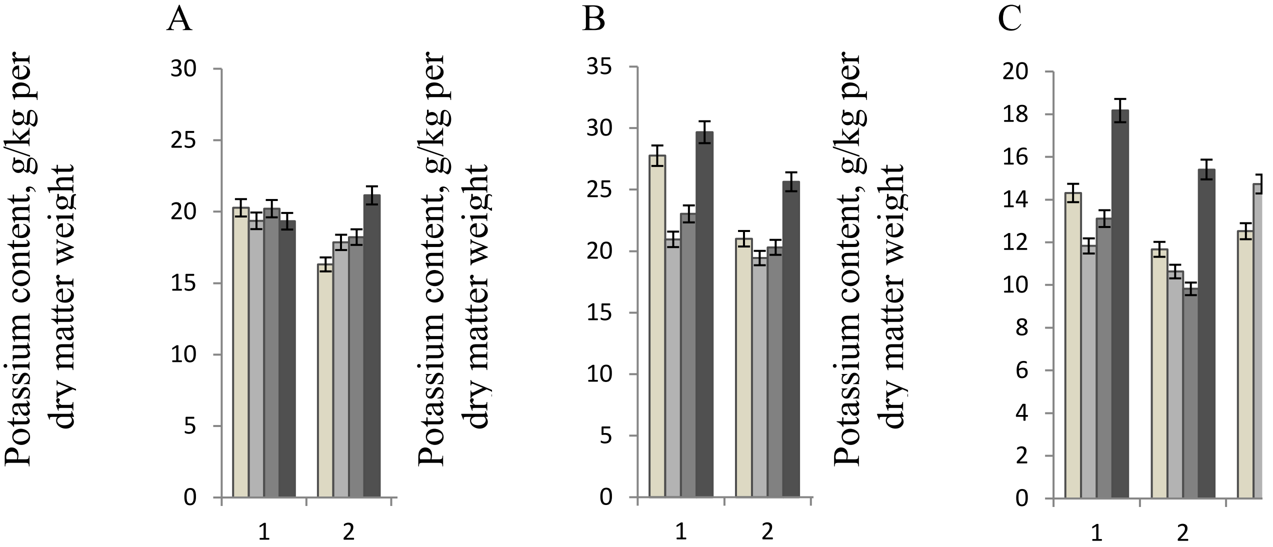

Fig. 4.3. Potassium content in vegetative organs of tomato plants under gibberellin and retardants application: 1 – fruit formation stage; 2 – fruitification stage (green ripeness); 3 – fruitification stage (brown ripeness).

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

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

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

The study of the folicur influence on the content of these elements in the gooseberry leaves and shoots during ontogenesis indicate that the folicur treatment (0,025 % solution) causes agnological changes in the nutrients accumulation (Table 4.1). With folicur, there was an increase in the content of nitrogen, phosphorus and potassium in the tissues of the leaves and stem of the gooseberry plants during the flowering phase, which created an additional reserve for the fruits formation and growth.

In our opinion, the reason for such changes is a decrease in the biodilution of elements concentration as a result of a reduction in growth processes. There is a gradual decrease in the content of these elements in the tissues of leaves and stems due to their reutilization for the needs of fruits formation and growth during ontogenesis.Thus, the vegetative organs of plants – the root, stem and leaves during the fruiting period are an important source of nitrogen, phosphorus and potassium supply to the developing fruits.

Table 4.1.

Influence of folicur on the content of mineral nutrition elements in vegetative organs of gooseberry cv. Mashenka (% per dry matter weight)

Stages of development	Organs of plant	Nitrogen content		Phosphorus content		Potassium content	
		Control	Folicur	Control	Folicur	Control	Folicur
Flowering stage	Leaves	2,6±0,03	2,7±0,05	3,7±0,08	*4,1±0,06	19,5±0,7	*21,3±0,9
	Stems	1,3±0,05	*1,8±0,04	3,2±0,07	*3,9±0,05	17,3±0,8	*18,4±0,2
Fruit formation stage	Leaves	2,4±0,02	*2,7±0,03	3,3±0,08	*4,2±0,01	18,6±0,6	*20,5±0,3
	Stems	1,4±0,02	*1,9±0,03	2,1±0,04	*4,1±0,01	16,4±1,2	*17,2±0,2
Fruit ripening stage	Leaves	2,04±0,01	*2,2±0,02	2,4±0,02	*3,0±0,04	15,9±0,2	*19,8±1,3
	Stems	0,9±0,03	0,8±0,01	2,3±0,02	*2,5±0,03	10,2±0,2	*11,4±0,7

Note: * – difference is significant at $p<0.05$.

CHAPTER 5. USE OF RESERVE SUBSTANCES BY SPROUTS AT THE HETEROTROPHIC PHASE OF DEVELOPMENT FOR GIBBERELLIN AND RETARDANTS ACTIONS

5.1. Effect of gibberellin and retardants on seed germination with different types of storage substances under skoto- and photomorphogenesis conditions.

The problem of artificial redistribution of assimilates and nutrients between plant organs is one of the central ones in modern phytophysiology, since the solution will effectively regulate the activity of plant physiological functions, purposefully redistribute the flows of assimilates to economically valuable organs [9, 84, 104]. Regulation of the donor-acceptor system is the highest level of maintaining the integrity of the plant organism. This regulation can be carried out at different levels of plant organization with the participation of different physiological and biochemical mechanisms [119, 194, 209]. Most of the studies on the donor-acceptor system of plants are devoted to the interaction of the photosynthesis and growth processes. The first process acts as a donor (source) of assimilates, and the second – as an acceptor (sink) [87, 97, 234]. At the same time, there is much less information on the functioning of this system during the germination of bulbs, tubers, and rhizomes in the heterotrophic phase of development [98, 99]. During this period, reserve compounds of various chemical structures – carbohydrates, nitrogen-containing compounds, vegetable oils, etc. are used for the needs of morphogenesis and deposited in the storage organs.

The development of plants in the light and in the dark during the germination period is characterized by differences in the intensity of use of reserve substances deposited in the organs, as a result of which the degree of tension between the activity of the donor and the acceptor changes. In some works, data are presented that indicate the possibility of regulating the rate of utilization of reserve compounds for the needs of growth and development by external and internal factors [2, 92, 114]. It has been established that light not only provides the process of carbon nutrition and determines the transition to reproductive development, but also through the system of photoreceptors (phytochromes, cryptochromes and phototropins) includes the program of photomorphogenesis [26, 27, 50, 228]. This ensures the differentiation of chloroplasts, the formation of full-fledged leaves and the transition to the phase of autologous nutrition. Plants germinating in the dark develop according to the program of scotomorphogenesis. They are characterized by an elongated hypocotyl and epicotyl, the formation of a hypocotyl loop, the first corrugated leaves, and yellow cotyledons. In seedlings of monocotyledonous plants, the axial organs and leaves stretch in length during etiolation. In dicotyledonous plants, the internodes of the stem are stretched, and the sizes of cotyledons and primary leaves change.

Changes in the nature of donor-acceptor relations during the transition from heterotrophic nutrition to the autotrophic stage of plant functioning should be studied on plant cotyledons, since the donor and acceptor (cotyledon - cotyledonous leaf) are

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represented by one organ and are separated only in time. It should be noted that the ratio of photosynthesis and respiration under the action of gibberellin and retardants during the germination period has been insufficiently studied. It is also known that storage substances of different types play the role of a buffer between photosynthesis as a "source" of assimilates and the growth of the structural substance of vegetative, storage and reproductive organs as a "sink" of assimilates, which determines to a certain extent the independence of growth processes from photosynthesis, in particular during the period germination [113]. At the same time, the influence of light and gibberellins on the specificity of utilization of plastic substances deposited in the cotyledons remains practically unexplored.

The hormonal system plays a key role among the internal factors regulating the tension of donor-acceptor relations [237]. It has been established that light can modify the growth and morphogenesis of plants due to the rearrangement of the hormonal complex [17, 51, 114, 228]. The AtGA3ox1 biosynthesis gene increases the level of bioactive gibberellins in germinating arabidopsis seeds. It was found that red light inhibits the formation of GA 2-oxidases, which leads to a sharp increase in the gibberellins content in germinating lettuce seeds under the influence of red light [59]. Blue light suppressed the growth in length of the hypocotyl of arabidopsis seedlings due to inhibition of enzymes of gibberellin biosynthesis and the activity of enzymes associated with the biosynthesis of cell wall biopolymers.

It is known that the most important function of gibberellins during germination of cereal seeds is to stimulate the release of α-amylase by the embryo, which leads to the degradation of starch grains in the endosperm [171]. It should be noted that the features of the seed germination and storing vegetative organs of plants by gibberellins, containing not starch as a reserve substance, but other compounds – proteins, lipids, inulin, etc., remain poorly studied.

Retardants with inhibitory mechanism of action are used to block the physiological action of giberelin [14, 66, 223, 230]. At the same time, although retardants lead to significant changes in plant ontogeny [124, 172], the features of their effect on plant development during skoto- and photomorphogenesis remain unknown and require intensive research.

It was studied the processes of temporary assimilates (carbohydrates) deposition in the functioning of the donor-acceptor system of plants due to the analysis of the ratio of photosynthesis (source) and growth (sink) of assimilates [62, 75, 76]. At the same time, the utilization of reserve substances from the storage tissues of seeds for the ontogenesis needs in the heterotrophic phase of growth, the participation of light and the role of the hormonal system in regulatory processes in the system "reserve compounds - growth" remains unknown. In our opinion, data on the features of the reutilization of not only carbohydrates, but also other basic substances of the reserve - proteins and oil of seeds of the corresponding plant species under conditions of photo- and scotomorphogenesis - are important.

The growth rate depends on the activity of the seedling meristematic zones, which is largely under the control of gibberellins. It was noted a significant decrease in the activity of free gibberellins in agricultural plants under the action of antigibberellin compounds paclobutrazol, chlormequat chloride, dextrel [77, 107].

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We found that the process of corn seeds germination in the light and in the dark under the action of gibberellin and the retardant tebuconazole during photo- and scotomorphogenesis was accompanied by significant changes in plant development. A more intensive stimulation of the growth of the aerial part and the root system of the seedling was noted under the action of gibberellin than in the control, and the process proceeded more intensively in the dark. The application of the antigibberellin drug tebuconazole significantly blocked the germination process in the light and in the dark (Table 5.1). The morphological changes in seedlings according to the experimental variants were determined by the different degree of reserve substances utilization of seeds during the germination period - the coefficient of reserve substances use under the action of tebuconazole was minimal both in the world and in the dark. The stimulating effect of gibberellin on germination under conditions of scotomorphogenesis was characterized by a higher value of this indicator. It is important to analyze the outflow of the reserve substance from the seeds to the acceptor zone (seedling) according to the variants of the experiment in connection with the formation of different requests for reserve metabolites since the growth and processes of morphogenesis of seedlings increased under the action of gibberellin in comparison with the retardant.

The main reserve substance of corn seeds is starch. Gibberellins are able to stimulate the processes of seeds germination of cereal crops as a result of the α-amylase release by the embryo into the endosperm, which leads to the hydrolysis of starch grains. Our results indicate that a higher value of the coefficient of utilization of reserve substances in the dark and under the action of gibberellin is determined by more intensive hydrolysis of the reserve polysaccharide - its content in these variants significantly decreased (Table 5.1). Germination of seeds, in which starch is the main reserve substance, is accompanied by *de novo* synthesis and release of amylase in the endosperm by the embryo under the action of gibberellin, which in turn leads to the degradation of starch in starch grains [171]. Treatment with exogenous gibberellin also enhances these processes and stimulates seedling growth. The application of retardants, which are gibberellin antagonists, can reduce the demand for assimilates due to blocking the synthesis of gibberellins, the activity of the amylase complex, and a decrease in the activity of the meristem functioning. As a result, tebuconazole had minimal effect on changes in starch content in germinated corn seeds in the light and in the dark. This is corelated with the lowest values of the coefficient of reserve substances utilization and low growth rates of seedlings in these variants.

The literature does not contain data on the redistribution of mineral nutrition elements between seed and seedlings during germination under the action of gibberellin and retardants in the light and in the dark. Analysis of the total nitrogen content in the seed of sprouted seeds indicates that under the conditions of photo- and skotomorphogenesis the differences were minimal.

At the same time, the application of gibberellin and retardant contributed to the increase in nitrogen content in the dark, contrary to the variant with light. In our opinion, this is clearly explained by the peculiarities of biodegradation: more efficient use of the main reserve substance, starch, led to an increase in the relative content of nitrogen. This also indicates that starch is primarily used, and protein compounds are

Table 5.1.

Influence of gibberellin and tebuconazole on germination rates of maize seed, hybrid Dostatok 300 MV, under the conditions of photo- and skotomorphogenesis

Indicators	Control		Gibberellin		Tebuconazole	
	light	dark	light	dark	light	dark
Length of above ground part, cm	3,0 ±0,05	*6,0± 0,18	4,0±0,11	*15,1±0,34	1,0±0,04	*1,4±0,07
Length of root system, cm	5,1±0,15	*7,9±0,18	4,8±0,14	*12,1±0,21	1,8±0,05	*4,3±0,12
Coefficient of use of reserve substances, %	12±0,5	*20±0,9	14±0,4	*25±0,8	6±0,3	*7±0,2
Starch content, % per dry matter weight	59,2±0,02	55,1±0,03*	52,0±0,02	*49,0±0,04	58,1±0,05	58,1±0,05
Total nitrogen content, % per dry matter weight	1,4±0,02	*1,3±0,01	1,2±0,03	*1,7±0,02	1,4±0,03	*1,4±0,02
Phosphorus content, % per dry matter weight	3,8±0,01	*3,3±0,01	3,6±0,04	*4,0±0,04	3,5±0,05	*3,7±0,02
Potassium content, % per dry matter weight	1,6±0,04	*1,2±0,01	1,5±0,02	*1,9±0,03	1,5±0,01	1,6±0,03

Note: * – difference is significant at $p<0.05$.

used at later stages of germination. A similar trend was observed for the use of reserve forms of phosphorus and potassium: in the control trial, utilization of mineral elements of seeds was more intensive in the dark, and in experimental variants the content of phosphorus was higher in the dark. Consequently, under the conditions of scotomorphogenesis, the growth-stimulating effect of gibberellin significantly increased. Antigibberellin action of tebuconazole resulted in significant inhibition of germination and the use of reserve compounds of maize seeds, both in the light and in the dark. This indicates the key role of gibberellin in seed germination processes that contain starch as a reserve substance.

In the analysis of the effect of gibberellin and retardant tebuconazole on the growth of bean seedlings under conditions of photo and skotomorphogenesis, it was established that gibberellin less stimulated the growth of these seedlings compared to maize sprouts (Table 5.2). In beans, a significant part of the reserve substances of cotyledons is nitrogen-containing compounds. The change in the growth characteristics and the coefficient of use of seed reserve materials was accompanied by a decrease in the content of total nitrogen, indicating the use of reserve nitrogen-containing compounds in the processes of morphogenesis. In this case, under the conditions of skotomorphogenesis, the content of protein nitrogen in the control was lower than in the photomorphic seedlings, and the opposite effect was noted in the actions of gibberellin and retardant.

On the other hand, in all variants of the experiment, the concentration of non-protein forms of nitrogen was reduced precisely in skotomorphic plants compared with photomorphic ones. In our opinion, this testifies that gibberellin and retardant have a weaker effect on the processes of hydrolysis of reserve proteins and a stronger effect on the transport of non-protein forms of nitrogen to the seedling tissue.

Table 5.2.

Influence of gibberellin and tebuconazole on the germination rates of bean seeds, variety Galaxy, under the conditions photo- and skotomorphogenesis

Indicators	Control		Gibberellin		Tebuconazole	
	light	dark	light	light	dark	light
Length of seedlings, cm	9,4 ±0,5	10,0± 0,5	9,3 ±0,46	*12,6±0,5	6,3± 0,31	*9,4±0,47
Coefficient of use of reserve substances, %	21 ±0,5	*28±0,3	25± 0,5	*37± 0,3	15± 0,3	*16± 0,4
Total nitrogen content, % per dry matter weight	4,57 ±0,04	*4,15± 0,02	4,14±0,02	*4,08±0,02	4,17±0,03	*4,07± 0,01
Protein nitrogen content, % per dry matter weight	3,21±0,03	*3,12±0,02	2,95±0,02	*3,07±0,03	3,04 ±0,02	*3,18 ±0,01
Non-protein nitrogen content, % per dry matter weight	1,36±0,01	*1,03±0,02	1,19±0,01	*1,01±0,01	1,13±0,02	*0,90±0,01
Phosphorus content, % per dry matter weight	7,19±0,07	*6,73±0,03	6,62±0,06	6,70±0,04	6,33±0,05	*6,72±0,03
Potassium content, % per dry matter weight	17,48±0,14	*17,07±0,16	17,39±0,15	17,42±0,17	15,59±0,13	*17,31±0,14

Note: * – difference is significant at $p<0.05$.

The dynamics of the content of other elements, phosphorus and potassium, was similar to that observed during the germination of maize seeds: in the control seed sample, there was a decrease in the content of these elements. The use of either preparation did not affect their content or even increased under the conditions of skotomorphogenesis. In our opinion, this testifies that the reserves of phosphorus and potassium under the effects of gibberellin and tebuconazole are used in the processes of morphogenesis in later stages of ontogeny.

It is known that light controls not only the process of photosynthesis (the donor function), but also the morphophysiological parameters of plants with a definite hierarchical structure of acceptors. Light changes the realization of plants' development programmes, which can be traced in changes in the speed and duration of plants' growth both on the level of the plant as a whole and and on the level of their separate parts (root, epycotyl, hypocotyl, leaf) [27]. These changes are realized through the restructuring of the hormonal complex. Phytohormones are included in the light signal transduction because many of the development reactions of plants which are controlled by light also react to the action on plants by hormones [34]. Results of genetic analysis of mutations of gibberellins and phytochromes indicate an interaction between these signaling systems under certain physiological conditions.

Our results show that plants that grew in the dark developed on the skotomorphogenesis model. They are characterized by longer hypocotyls, the presence of a hypocotyl loop and the yellow colour of the cotyledonary leaves. In the light, plants developed on the photomorphogenesis model: the hypocotyls were shorter, the hypocotyl loop straightened, the cotyledonary leaves grew and acquired an intense green colour (Figure 5.1.).

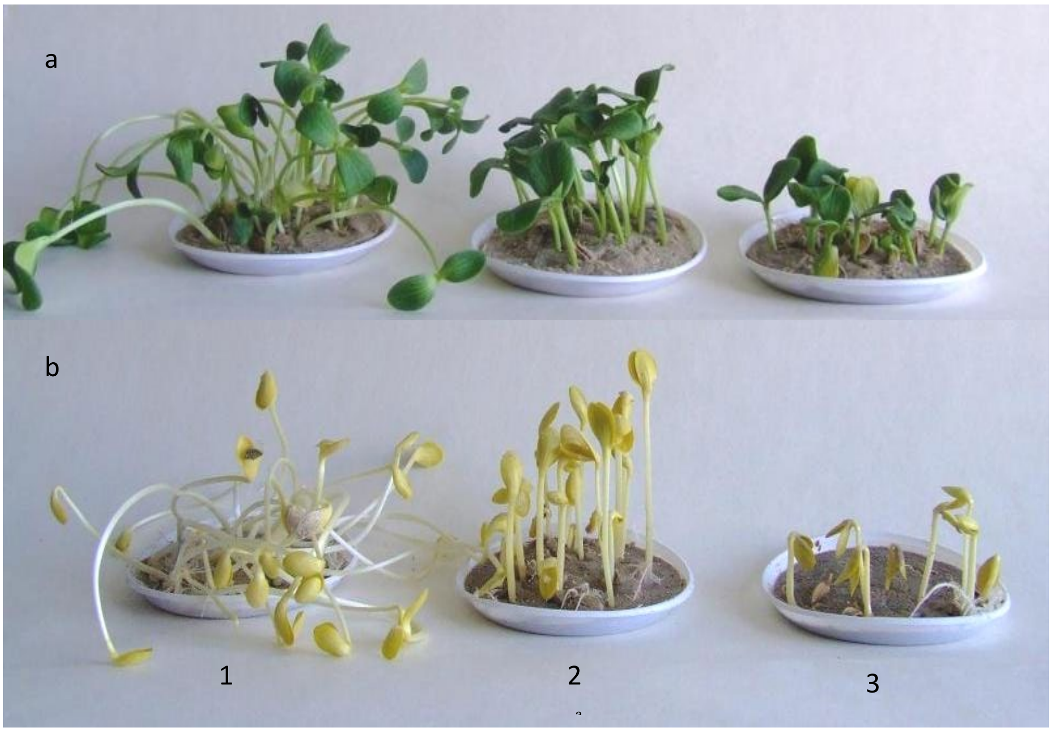

Figure 5.1. Action of gibberellin and chlormequat chloride on germination of pumpkin seeds, cv. Mozoliyivskyy 15, in the light (a) and in the dark (b): 1 – GA_3 (150 mg/l); 2 – control; 3 – CCC (0,25%); on the day of 12 day of germination

We have previously found that the growth of pumpkin seedlings was suppressed in the light, but the treatment of seedlings by gibberellic acid eliminated the effect caused by light. The growth inhibitory effect of light intensified in conditions of reduction of gibberellin synthesis under the action of the retardant, this indicates that gibberellins are the active modifiers of the photoreceptor system in plants [112, 113]. Similar conclusions have been made by other authors studying the interaction of light at different wavelengths and phytohormones in the processes of skoto- and photomorphogenesis of bean plants [34]. An important role in forming a "request" for assimilates is played by the processes of organ- and histogenesis because differentiation of various tissues of the developing organ requires the different costs of reserve metabolites. Analysis of the the anatomical structure of pumpkin seedlings shows that in both conditions of skoto- and photomorphogenesis the number of fibrovascular bundles in seedlings is almost unchanged. However, all the anatomical elements of structure differed in their larger dimensions with seedlings developed in the dark. This applies to linear dimensions of epidermal cells, collenchyma (in a cross section), the diameter and length of parenchyma cells.

Thus, in conditions of skotomorphogenesis the increasing of growth intensity accompanied by formation of larger anatomical elements of the primary structure and the use of gibberellin increased plant growth in the dark and eliminated the growth inhibiting effect of light in conditions of photomorphogenesis.

Our results indicate the significant effect of the gibberellin and retardant on germination and intensity of use of reserve compounds in the pumpkin seeds' cotyledons. Gibberellic acid and chlormequate chloride influenced the rate of reserve substances utilization in pumpkin seeds. The utilization coefficient was the highest under the action of gibberelic acid at the time of cotyledon opening, and it was the lowest compared to the control under the retardant action. It was noted a more intensive use of seed storage substances in seedlings growing in the dark during germination.

The results indicate that application of gibberellin and chlormequat chloride greatly influenced the character of use of the cotyledon's reserve substances. The main reserve substance of pumpkin seeds is an oil. The results obtained indicate that the most unused oil remained under the action of chlormequat chloride during the complete opening of cotyledons, which clearly correlated with the values of utilization coefficient of seed reserves (Table 5.3).

The integrity of a plant organism is based on interaction of the organs and active exchange of organic and mineral substances between them. However, the nature of income and redistribution of nitrogen-containing compounds between plant organs with changes in the source-sink relations during heterotrophic development in general and under the influence of gibberellin and retardants in particular remains largely unexplored. Since retardants are the modifiers of hormonal and inhibitory balance in plants, here the question arises of changes in the income and redistribution between organs of plant nitrogen compounds under the influence of this group of preparations. In our opinion, for the better understanding of the nature of changes in source-sink relations under the influence of retardants, it was expedient to analyze the dynamics of content of different forms of nitrogen and their proportion in different stages of growth and development with an artificial change of the acceptor activity for the actions of gibberellin and its antagonist. The use of cotyledon leaves as a research model to study the question of utilization of reserve nitrogenous compounds allows one to analyze the translocation of only reserve forms of nitrogenous compounds and exclude the "new" nitrogen, which comes from the root system by mineral nutrition.

Table 5.3.

Content of higher fatty acids in cotyledon oil of pumpkin seedlings, cv. Mozoliivsky 15, under the effect of gibberellic acid and chlormequat chloride under the conditions of photo- and skotomorphogenesis (%)

Indicators	Control		Gibberellin		Chlormequat chloride	
	light	dark	light	dark	light	dark
Length of hypocotyl, cm	10,4±0,6	*11,8±0,4	14,2±0,5	*16,8±0,3	4,7±0,5	*5,93±0,4
Coefficient of use of reserve substances, %	18,3±0,64	35,9±0,85*	22,2±0,35	*38,4±0,32	13,87±0,56	22,9±0,18*
Oil content, % mass of dry matter	8,8 ± 0,2	*7,6 ± 0,1	12,2 ± 0,3	11,6 ± 0,2	22,4 ± 0,3	22,4 ± 0,3
Total nitrogen content, % per dry matter weight	6,05±0,01	6,91±0,01*	5,99±0,02	*6,73±0,03*	7,13±0,02	*7,16±0,01
Protein nitrogen content, % per dry matter weight	4,04±0,01	4,75±0,01*	3,68±0,01	*4,76±0,01	4,94±0,04	5,09±0,02*
Non-protein nitrogen content, % per dry matter weight	2,01±0,04	2,16±0,05*	2,31±0,03	*1,97±0,02	2,19±0,02	2,07±0,01*

Note: * – difference is significant at $p<0.05$.

The analysis of our data shows that under the conditions of photo- and skotomorphogenesis, there was a significant outflow of nitrogen from cotyledons into sprouts, and the content of total and protein nitrogen in the non-fatty material of cotyledon leaves significantly differed: in particular, it was lower in the variant of development of seedlings on light (Table 5.3.). Obviously, this indicates a more intensive use of cotyledon protein for growth processes in the formation of seedlings structures under photomorphogenesis conditions. The different rate of the growth processes under the action of retardant and gibberellin was accompanied by different intensity of outflow of nitrogen-containing compounds from cotyledons. In particular, in the light, the smallest content of protein nitrogen remained in the variant with gibberellin, and the largest content in the variant with the use of its antagonist, chlormequat chloride. When germinating in the dark, protein nitrogen was least intensively used under the action of retardant. In the control and in the variant with the use of gibberellin, the intensity of the use of protein nitrogen was the same;

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however, the decrease in the total nitrogen content in cotyledons under the influence of phytohormones was more intensive due to non-protein fraction.

The chromatographic analysis of pumpkin oil revealed six higher fatty acids:palmitic, stearic, oleic, linoleic, linolenic and arachinic. It is known that the seed germination of crops containing oil as a reserve substance is accompanied by a decrease in the ratio of unsaturated/saturated higher fatty acids as a result of the saturation processes. We have not established a clear relationship between the use of preparation and the indicated ratio in the process of germination of seeds, which, in our opinion, indicates the absence of influence of gibberellins on the activity of saturases [164].

The results of the analysis of the oil content in cotyledons according to the experimental variants indicate that under the effect of gibberellin, the content of this substance remained higher at the end of the germination period compared with the control. In this case, the coefficient of use of seeds substances in this variant was the highest. In our opinion, this testifies that increased growth under the effect of phytohormon is determined not only by the rapid utilization of lipids, but also by possible increased hydrolysis of other reserve substances of cotyledons – nitrogen containing compounds.

Intensity of plant respiration is closely related to the growth processes, usually intensity of respiration is amplified with intensification of growth. The application of retardants allows one to explain clearly the significance of respiration components with the artificial change of donor and acceptor (source and sink) activity because it is possible to simulate this type of disbalance of the donor and acceptor activity in which a request to assimilates of the main acceptor (developing seedlings) is reduced due to inhibition its meristem activity. It must be emphasized that depending on the methodological approaches and the degree of research detail both the separate plant structures (organs, tissues, cells and organelles) and the processes (photosynthesis, respiration, storing, transportation) can act as a donor and as an acceptor. In this, the application of "donor and acceptor" concepts to particular organs or processes is not absolute and depends on the development phase of the separate organ or the whole plant [62].

The results obtained also show that the use of gibberellin and the antigiberrelic agent chlormequat-chloride under conditions of photo- and skotomorphogenesis influenced significantly the gas exchange of seedlings (table 5.4.) [164]. At present, respiration is seen as a powerful metabolic acceptor of carbon, and the total respiratory costs may reach 60% of the carbon assimilated in photosynthesis [35, 36]. The ratio of respiration/photosynthesis largely characterizes the tension of source-sink relations in plants, but the scale of respiratory costs compared with the true photosynthesis during the transition to other levels of source-sink relations has not been completely clarified.

Table 5.4.
Intensity of gas exchange of pumpkin seedling, cv. Mozoliyivskyy 15, under the influence of gibberellin (GA_3, 150 mg/l) and chlormequat chloride (0,25 % solution) under photo- and skotomorphogenesis (mg CO2/g of dry matter • h, the 12h day of germination)

Variant of experiment	Photomorphogenesis					Skotomorphogenesis	
	Utilization coefficient of reserve substances of seeds, %	Respiration intensity (R)	Apparent photosynthesis	True photosynthesis (Pg)	R / Pg	Utilization coefficient of reserve substances of seeds, %	Respiration intensity (R)
Control	18,3±0,64	1,70±0,07	0,95±0,02	2,65±0,09	0,59	35,9±0,85	2,03±0,08
GA_3	*22,2±0,35	*1,14±0,03	*0,81±0,03	*1,95±0,06	0,64	*38,4±0,32	*3,00±0,12
CCC	*13,87±0,56	*2,57±0,08	*0,32±0,01	2,89±0,09	0,89	*22,9±0,18	*2,94±0,10

Note: * – difference is significant at $p<0.05$.

The control variant was marked by the lowest intensity of dark respiration under conditions of skotomorphogenesis, and under the action of gibberellin and its antagonist chlormequat-chloride the intensity of respiration increased. In the seedlings that grew in the light, the highest intensity of respiration was observed in the variant with chlormequatchloride, and the lowest – in the variant with gibberellin. Generally, in all variants of the experiment the dark respiration intensity was lower in seedlings which passed on the light from heterotrophic to autotrophic nutrition than in seedlings, grown in the dark. The results obtained permit one to draw the conclusion that gibberellin and its antagonists have opposite effects on respiratory components: stimulation of growth under the action of GA_3 is accompanied by increased growth respiration, and support of cell homeostasis under the action of the growth inhibiting preparation chlormequat-chloride provided by increase of maintenance respiration [74]. In our view, the decrease in the intensity of true photosynthesis per unit weight of dry matter influenced by GA_3 compared to control can be explained by the lower proportion of the cotyledons' weight compared to the whole plant in this version. At the same time, the respiratory costs (R/Pg) greatly increased in the variant using chlormequat-chloride. We have previously been suggested that respiration plays the role of "safety valve" by removing the excess of assimilates in the form of CO_2 [113]. Thus the donor function of cotyledon leaves of photomorphic plants is limited by the increase of respiratory costs, therefore it decreases the proportion of assimilates that are directed to the needs of organogenesis.

Thus, a modification of regulatory relations in the source-sink system "depot of assimilates – growth" in the early development of seedlings by using exogenous gibberellin and retardant chlormequat chloride leads to changes in morphogenesis and growth rate, which affects the intensity of reserve compounds' use, respiration and photosynthesis during the transition to autotrophic nutrition. In the dark and using gibberellin the request for reserve substance increases, while in the light and with treatment by retardants the acceptor activity of seedlings decreases.

It is known that there is a close relationship between the changes in growth characteristics with the action of retardants and the activity of gibberellins. In particular, under the influence of paclobutrazol, chlormequat-chloride and dextrel a significant decrease was noted in the activity of free gibberellins in raspberry shoots in conditions of growing and field experiments, while the introduction of exogenous gibberellic acid raised significantly their activity in the tissues of the stem [74]. Our results indicate that gibberellin increased and chlormequat-chloride decreased the linear dimensions and volume of cells of the main parenchyma, but the use of preparations had no effect on the number of fibrovascular bundles in the stem. Thus, gibberellins and the absence of light increase growth processes, and therefore attractive activity in seedlings at the heterotrophic nutrition stage. The use of retardants and the effect of light in this period acts in the opposite way – reduces the intensity of the growth process and therefore the attractive activity of seedlings. Consequently, the formation by seedlings of "a request" for the reserve assimilates from cotyledons is largely determined by changes in subapical meristem activity, which is manifested in the acceleration of seed germination, amplification of histogenesis for the action of gibberellin and weakening of these processes under the influence of the retardant

Since the growth amplified and the activity of seedlings' meristems intensified under GA_3 compared with the action of retardants, it is important to analyze the features of redistribution of reserve substances in the acceptor zone (seedling) in the variants of the experiment in connection with formation of a different request for reserve metabolites. The results obtained for determining the content of different forms of nitrogen and oil in the cotyledons indicate that gibberellins are an important link of the unique regulatory mechanism of mobilization of reserve substances in germinating seeds, regardless of their chemical nature. The level of utilization of nitrogenous compounds from cotyledons was higher with the action of gibberellin. Previously, it was also found that the process of pumpkin seed germination was accompanied not only by use of typical reserve substances of oil crops – reserve oil and nitrogen-containing compounds, but also by a significant restructuring of polysaccharide complex of cell walls. The pentosans of cell walls use as a reserve substance and there is a change of conformation and a partial increase in the molecular weight of pectins. These processes were amplified in conditions of skotomorphogenesis as a result of intensive growth of seedlings in the absence of autotrophic nutrition and, consequently, a deeper utilization of the reserves of the donor plastic substances – the cotyledons [163,164].

Combined use of light, gibberellins, and retardants for artificial regulation of the tension of donor- acceptor relations in a plant can become an effective method for studying the role of phytohormones and finding out the features of the use of plant reserve compounds in experimental studies into germination processes. It was found that the growth of the above-ground part and the root system of seedlings of plants containing different types of reserve substances – starch (maize), proteins (beans) and oils (pumpkin) – is more intense under the effect of gibberellins, in comparison with the control. The process was faster in the dark. The application of antigibberellin preparation of tebuconazole substantially blocked the process of germination under the conditions of photomorphogenesis and skotomorphogenesis. The morphological changes of seedlings in the variants of experiment were determined by different degrees of the use of seed reserve substances during the period of germination: the coefficient of the use of reserve substances was maximal under the effect of gibberellin, and was minimal under the action of retardants (tebuconazole, chlormequat chloride) both in the light and in the dark.

5.2. Features of application of reserve lipids during seed germination under the action of retardants.

The mechanisms of utilization of reserve lipids is important for understanding the functioning of the donor-acceptor system of plants at the heterotrophic period of development, since it is lipids that are deposited as the main reserve substance of seeds in 75 % of flowering plant species. Hydrolysis of reserve lipids is carried out under the influence of lipases, which break down triacylglycerides into glycerol and higher fatty acids. These hydrolysis products can be converted into glucose in the processes of gluconeogenesis, as a result of which the processes of organogenesis and histogenesis of seedlings are provided. In our experiments, different strains of donor-acceptor relations between the zone of deposition of reserve compounds and the zone of growth of sunflower seedlings were artificially created in the experiment under growth stimulators (gibberelic acid, treptol) and growth inhibitors - retardants chlormequat chloride and paclobutrazol. This led to changes in the rate of seed germination and, accordingly, the use of different amounts of the main reserve substance. Our research results indicate that the application of gibberelic acid, synthetic growth stimulator treptolem, and growth inhibitors chlormequat chloride and paclobutrazol led to changes in the lipid metabolism of seedlings and the rate of their germination (Table 5.5). The germination energy under the action of gibberellin and treptolem did not significantly differ from the control On the third day of seed germination. At the same time, the application of growth inhibitors chlormequat chloride and paclobutrazol on sunflower varieties caused a significant decrease. Analysis of the oil content in seedlings on the sixth day of seed germination according to the experimental trial indicates a significant decrease in the control and under the influence of the used growth stimulants and a higher oil content under the action of chlormequat chloride and paclobutrazol, which is an indicator of a slowdown in the utilization of reserve lipids. It is known that the use of reserve oil during the germination of oilseeds occurs with the participation of lipases. Lipases are synthesized on the membranes of the endoplasmic reticulum and are transferred in the form of secretory vesicles to the spherosomes of cotyledons, where, after membrane destruction, acidic lipase breaks down triglycerides to glycerol and higher fatty acids. In addition, it is generally known that lipid cleavage can occur under the influence of alkaline lipases in glyoxisomes. Analysis of the activity of acidic and alkaline lipases according to the variants of the experiment indicates their higher activity under the action of gibberelic acid and treptolem and decrease in the activity of these enzymes under the influence of retardants [99, 176]. The growth intensity of control and growth stimulators did not differ significantly. In our opinion, this indicates sufficient provision of the germination process of sunflower seeds with synthesized endogenous gibberellins, and therefore the additional application of exogenous stimulants had an effect on the process. A similar situation was noted for the reserve oil content for these variants of the experiment – the difference was minimal. At the same time, the application of retardants of the quaternary ammonium salt of chlormequat chloride and the triazole-derivative compound paclobutrazol resulted in blocking the synthesis of endogenous gibberellins, which, in our opinion, slowed down the process of germination and the use of reserve lipids.

Table 5.5.

Effect of growth stimulators and retardants on the germination intensity, content and quality characteristics of oil in sunflower seedlings

Object	Experimental trial	Energy of germination (%)	Oil content, % mass of dry matter	Activity of acidic lipases *(ml 0,1N* NaOH/*g*)	Activity of alkaline lipase *(ml 0,1N* NaOH/*g*)
cv. Flagship	Control	74,0 ± 1,4	48,5 ± 0,5	2,3 ± 0,1	3,6 ± 0,2
	Treptolem (0,33 ml/l)	75,3 ± 3,4	46,2 ± 1,5	*3,9 ± 0,2	4,0 ± 0,2
	CCC (1%)	*60,7 ± 2,2	49,1 ± 0,6	*1,0 ± 0,1	*2,1 ± 0,1
Svitoch's Hybrid	Control	99,4 ± 1,3	43,2 ± 0,5	1,8 ± 0,1	1,9 ± 0,1
	GA (150 ml/l)	99,8 ± 1,1	42,9 ± 0,4	1,9 ±0,2	2,1 ± 0,1
	Paclobutrazol (0,05%)	*93,6 ± 1,2	*47,9 ± 0,3	*1,3 ± 0,1	*1,5 ± 0,1

Note: * – difference is significant at $p<0.05$.

The application of histochemical reaction with Lugol's solution for starch showed the absence of this polysaccharide in germinating seeds. Consequently, for the sunflower crop, the intensification of germination is not accompanied by the synthesis of amylase *de novo*, which is typical for cereals. It is known that the processes of maturation and germination of oilseeds are accompanied by significant qualitative changes in the composition of higher fatty acids, although the sequence of their transformation during seed germination remains largely unknown. Analysis of qualitative characteristics of the oil isolated from the seeds on the day of 6 of germination according to the experimental variants makes it possible to assess the general direction of the processes accompanying the germination of sunflower seeds. In particular, there were changes in the acid, alkaline and essential numbers of the oil under the action of GA_3 and various types of retardants in comparison with the control (Table 5.6.).

The acid value characterizes the total amount of free fatty acids in the oil. The data obtained indicate that the content of free fatty acids in the oil was less under the influence of retardant paclobutrazol than under GA_3 and control. This allows us to conclude that the hydrolysis of the seed storage oil is slower under the action of this growth inhibitory drug.

It was found that the saponification value was the highest under gibberellic acid, and the higher ether value of oil under the influence of GA_3 evidently indicates a slower use of glycerol for the formation of sugars in germinating seeds at the first stages of development than the use of fatty acids.

The indicator of unsaturated fatty acids content in the oil is the iodine value. The obtained data indicate that changes in this indicator occur under the action of drugs. In particular, on the day of 6 of germination, the iodine value increased under gibberellic acid and paclobutrazol treatment, which indicates a corresponding increase in the content of unsaturated higher fatty acids of the oil.

The content of sunflower oil under the action of drugs can be analysed by the chromatographic study of its fatty acid composition according to the experimental trial. It has been studied that the application of retardants during the budding period leads to a change in the profile of fatty acids and the ratio of unsaturated and saturated fatty acids in oilseeds. In particular, an increase was noted in sunflower [176], rapeseed [180], soy [39], and flaxseed [61] oils of the indicated ratio for the action of retardants that correlated with an increase in the iodine value. In soybeans, this ratio changed due to an increase in the content of linoleic acid and a decrease in palmitic and stearic acids. In sunflower plants it is also due to linoleic acid [98].

Table 5.6

Effect of GA_3 and paclobutrazol on the quality characteristics of Svitoch's hybrid sunflower seed oil on the day of 6 of germination

Indicator	Control	GA_3 (150 mg/l)	0,05 % Paclobutrazol
Acid value (mg KOH/g of oil)	4,1±0,2	3,9± 0,1	3,6±0,2
Saponification value (mg KOH/g of oil)	172,2±7,0	*189,7±4,2	177,3±5,1
Ether value (mg KOH/g of oil)	168,1±6,8	*185,8±4,1	173,7±4,9
Iodine value (g I/100 g oil)	118,3 ±1,3	*128,6±2,4	121,5±2,1

Note: * – difference is significant at $p<0.05$.

One of the important practical tasks is to reduce the linolenic acid content in the oil, which gives it a bitter taste during storage. The retardants caused a decrease in the content of this acid in rapeseed oil, which was accompanied, as a rule, by an increase in the linoleic acid content, which is a positive factor [98]. At the same time, it has been studied much less the issues of higher fatty acids utilization for the needs of seedling formation in the heterotrophic phase of development.

In the trials of sunflower oil, seeds of cv. Svitoch, on the day of six of germination, contain nine higher fatty acids: myristic, stearic, palmitic, palmitoleic, oleic, linoleic, linolenic, arachic and behenic. Oleic and linoleic acids dominated among unsaturated higher fatty acids (HFA) and palmitic acids – among saturated HFA. The application of gibberelic acid and paclobutrazol resulted in a change in the percentage of these acids in the oil (Table 5.7).

Table 5.7.

Effect of gibberellic acid and paclobutrazol on the fatty acid content in the seed oil of Svitoch's hybrid during germination (%)

Trials / Acids	Control	Gibberellic acid (150 mg/l)	Paclobutrazol (0,05 %)
Myristic acid	0,25 ± 0,002	*0,16 ±0,001	*0,15 ±0,002
Stearic acid	4.05 ±0,06	*4,41 ±0,04	*4,02 ±0,05
Palmitic acid	7,15 ±0,10	*5,94 ±0,15	*6,77 ±0,11
Palmitoleic acid	0,05 ±0,001	*0,04 ±0,001	0,05 ±0,002
Oleic acid	35,18 ±0,15	*35,69 ±0,11	*34,29 ±0,06
Linoleic acid	52,55 ±0,25	52,19 ±0,09	*53,17 ±0,06
Linolenoic acid	0,36 ±0,005	*1,13 ±0,002	*1,16 ±0,004
Arachic acid	0,20 ±0,003	*0,22 ±0,005	0,19 ±0,005
Behenic acid	0,21 ±0,002	*0,22 ±0.001	*0,20 ±0,002
Content of unsaturated higher fatty acids	88,14	89,05	88,67
Content of saturated higher fatty acids	11,86	10,95	11,33
Unsaturated/saturated fatty acids	7,4	8,1	7, 8

Note: * – difference is significant at $p<0.05$.

The oleic acid content decreased under the action of gibberellin compared to control, and the opposite changes were noted for linoleic acid under the action of paclobutrazol. The unsaturated linolenic acid content increased in both experimental variants against the control. Accordingly, the ratio of unsaturated / saturated HFA changed during germination under the action of drugs. This indicator increased in both experimental trials. Consequently, the application of exogenous gibberellin and the antigibberellin compound paclobutrazol leads to significant changes in the use of reserve oil and its fatty acid content during the germination of sunflower seeds.

The application of growth regulators with the opposite mechanism of action to create different tensions of donor - acceptor relations in a plant makes it possible to analyze the features of the redistribution of assimilates and reserve substances deposited in organs at different stages of ontogenesis. This approach allows to artificially redistribute the flows of photosynthesis products into economically valuable organs to optimize the production process of agricultural plants [90,105]. The application of retardants allows for the storage of products. In particular, the paclobutrazol and chlormequat chloride treatment of potato tubers significantly inhibits germination, which contributes to the preservation of production [110, 164, 182]. The application of this approach makes it possible to determine the efficiency of the use of reserve substances in seeds with different types of reserve compounds – starch, proteins and oil in the heterotrophic phase of development during the germination period, to establish possible regulatory mechanisms of this process. It is known that there is a close relationship between changes in the growth characteristics of the retardants action and the activity of gibberellins. In particular, a significant decrease in the activity of free gibberellins in raspberry shoots was noted under the influence of paclobutrazol, chlormequat chloride and dextrel in the conditions of vegetation and field experiments, while the introduction of exogenous gibberellic acid significantly increased their activity in the stem tissues. Previously, we found that the growth of pumpkin seedlings was suppressed in the light, however, gibberellic acid treatment of seedlings significantly removed the effect caused by light. The plant inhibitory effect of light increased with a decrease in the synthesis of gibberellins under the influence of retardant, which indicates that gibberellins are active modifiers of the plant photoreceptor system [164]. It is known that the formation of "sink" by seedlings for reserve assimilates from the cotyledons is largely determined by changes in the activity of subapical meristems, which is manifested in the acceleration of seed germination, increased histogenesis under the action of gibberellin and weakening of these processes under the influence of retardant. The obtained results of the various forms of nitrogen and oil content in pumpkin cotyledons indicate that gibberellins are an important link in the unique regulatory mechanism of mobilization of reserve substances in germinating seeds, regardless of their chemical nature [98]. At the same time, the features of utilization of reserve oil, higher fatty acids during acceleration or deceleration of germination of oilseeds under the action of gibberellin and antigibberellin drugs require in-depth study. The obtained results indicate that sunflower seeds during germination are sufficiently provided with endogenous gibberellins, as a result of which additional treatment with gibberellic acid and treptolem did not lead to a significant acceleration of germination. At the same time, the utilization of the reserve oil in the control and in the growth stimulantors treated plants was much more intensive than in the variants with chlormequat chloride and paclobutrazol.

In our opinion, the inhibition of germination and the use of reserve oil on the processes of morphogenesis under the influence of retardants was determined precisely by their blocking of the endogenous gibberellins synthesis. The hormone deficiency led to a decrease in the hydrolytic activity of reserve tissues due to inhibition of lipase synthesis and the activity of seedling meristems. The activity of donor and acceptor spheres of the plant was limited. The results obtained indicate that the difference in oil content during the period of seed germination under the action of growth and control stimulants was less than under the action of retardants. A similar pattern was observed when studying the germination of pumpkin seeds under the action of gibberellin and chlormequat chloride. In our opinion, the explanation for this fact is that during the germination period, other compounds are also used, first of all, reserve nitrogen-containing substances [165]. In addition, it was found that the process of germination of pumpkin seeds is accompanied not only by the use of reserve oil and nitrogen-containing compounds, but also by a significant restructuring of the polysaccharide complex of cell walls. At the same time, pentosans of the cell walls can be used as a reserve substance; conformation changes and a partial increase in the molecular weight of pectins occurs. The process intensifies under the conditions of scotomorphogenesis due to the intensive growth of seedlings in the absence of autotrophic nutrition and, as a consequence, deeper utilization of the donor's reserves of plastic substances of the cotyledons [163].

Consequently, the application of growth stimulators and antigibberellin drugs (retardants) is an effective technique for artificial reconstruction of donor - acceptor relations during the germination of oilseeds, and it makes it possible to establish the role of the hormonal factor in the utilization of reserve lipids in the heterotrophic phase of plant development. Blocking the synthesis of gibberellin by retardants led to a decrease in the activity of acid and alkaline lipases, a slowdown in the hydrolysis of the reserve oil, significant changes in the acid value and saponification value, iodine nvalue in oil during germination, a decrease in the activity of meristems, and a decrease in seed germination energy. The action of gibberellic acid and treptolem was opposite. The content of oleic acid decreased under the action of gibberellin compared to control, and the opposite changes were noted for linoleic acid under the action of paclobutrazol. Giberelic acid stimulated, and the retardant paclobutrazol slowed down the use of free higher fatty acids in the processes of morphogenesis.

CHAPTER 6.
REGULATION OF CROPS PRODUCTION PROCESS UNDER INFLUENCE OF RETARDANTS

Coordination of the processes of growth, photosynthesis and deposition of substances into the reserve has a direct impact on the crop productivity and formation of economic products. The quantitative ratios and qualitative direction of these processes are under genetic and hormonal control, which provides self-regulation of biological systems for more efficient use of productivity resources [62]. The experimental and literary data presented in the previous chapters indicate that the application of various types of retardants to optimize the growth processes and development of plants in agricultural crops leads to significant changes in the hormonal status of the plant, the organization of photosynthetic apparatus and nature of donor-acceptor relations. It is clear that such profound physiological restructuring can have a significant impact on performance. In addition, the application of one or another retardant must be justified from a toxicological and ecological point, which describes the need to control the residual amounts of drugs in products. Thus, one of the prerequisites for the application of various types of retardants on agricultural crops is to control the yield and quality of crops.

6.1. Productivity of oilseeds under the action of retardants.

Vegetable oils are one of the important components of the human diet. The production of vegetable fats has several advantages over animal fats. These include the relatively low cost and waste-free production, great health benefits, which is associated with the optimal profile of fatty acids and the fat-soluble vitamins content [30, 41]. The production of vegetable oils is one of the most important branches of the agro-industrial complex of Ukraine. In particular, Ukraine is the largest producer and exporter of sunflower oil. Sunflower occupies more than 90 % in the structure of production of all oilseeds, and 10 % in the structure of sown areas. The production of soybean oil is 2,7 %, rapeseed oil –1 % of the vegetable oils production and is constantly increasing [175]. The rapid growth in rapeseed cultivation in recent years is also associated with the production of biodiesel fuel for internal combustion engines. The production of flaxseed and poppy seed oil with valuable medicinal properties is increasing, and it is also an important raw material for the food and perfume industry [61,160]. The topical issues for all oilseeds are increasing the resistance to lodging, frost resistance, oil content in seeds and optimizing its chemical composition.

The application of this group of compounds makes it possible to establish the significance of the anatomical- morphological and mesostructural components in the realization of the dornor-acceptor relations of the plant and the optimization of the production process.

The overwhelming majority of agricultural crops are characterized by lodging of crops [16]. In the literature, there is a sufficient amount of information on the application of antigibberellins in order to prevent lodging of crops [195]. The increased resistance to lodging of crops is associated with an increase in the mechanical strength of the stem. Thus, the triazole derivative BAS 111 W treatment of rapeseed plants at a dose of 300–600 g/ha (in the spring at the stage of the beginning of stem growth) significantly inhibited stem growth and improved yield [48]. Otherwise, the triapentenol treatment (an active substance concentration of 245–320 g/ha) of spring rapeseed at the beginning of active stem growth inhibited its growth, but later treatment, at the end of budding and before the beginning of flowering, did not change the axial dimensions of the plant [145].

We found that a thickening of the stem occurs simultaneously with a decrease in plant height under the action of drugs and it was found out due to which tissues. Thus, the stem diameter of oil flax increased under the action of chlormequat chloride due to the enhancement of bark and xylem development [61]. The number of vessels in the xylem row increased by 1,3-1,7 times under the drug treatment, which led to a significant thickening of its layer. The number of bast fibers did not change, however, it was noted an increase in their diameter and a significant thickening of the cell walls. A similar stem thickening of soybeans [39], sunflower [176], winter rape [105] and oil poppy [161] occurred under the action of retardants due to an increase in the bark size, mainly due to the proliferation of mechanical tissues – collenchyma and sclerenchyma. Consequently, changes in the processes of differentiation of the subapical meristem under the action of retardants led to a better development of mechanical tissues, which contributed to an increase in the stem strength and increased plant resistance to lodging, and created technological advantages during harvesting.

The rearrangement of the hormonal complex and inhibition of apical dominance under the influence of retardants led to an increase in stem branching, which is important for the plant productivity regulation. In particular, the number of shoots in oil poppy increased under the action of folicur [159], winter rape under the action of chlormequat chloride and paclobutrazol [105], oil flax under the action of chlormequat chloride [61], white mustard under the action of paclobutrazol [198]. More leaves, flowers and fruits were laid as a result of increased stem branching of these crops, which is an important condition for increasing yields.

Photosynthetic activity plays a key role in plant productivity, which is largely determined by the leaf surface area, the number and lifespan of leaves, and the leaf mesostructural organization. Chlormequat chloride treatment of oil flax crops leads to an improvement in the number of leaves without significant growth of leaf surface area due to the smaller size of an individual leaf [61]. In a soybean plant, the leaf surface and the number of leaves increased [37], and the number of leaves decreased in chlormequat chloride treated sunflower due to a significant increase in leaf surface area [176]. The total leaf area decreased in winter rape plants, but the leaves thickened [180]. The leaf surface area, the wet and dry matter weight of the sheet and the leaf lifespan increased in the waste oil treated by triazole derivative compound folicur [160]. These changes are an important condition for increasing photosynthetic productivity.

The regularities of organic substances redistribution in plants with a change in the growth rate of individual organs have been sufficiently studied within the concept of donor-acceptor system function [62]. The action of various groups of retardants leads to a restructuring of the plant's assimilation apparatus, a change in habitus, the ratio of organs masses, the appearance of additional attracting centers and an increase or decrease in the functioning of already existing ones, this indicates a change in the nature of donor-acceptor relations in the plant. The nature of donor - acceptor relations is in the redistribution of flows of assimilates and nutrients between plant organs. Therefore, in order to develop measures of exogenous regulation of ontogenesis using retardants, it is necessary to have a clear idea of the dynamics of accumulation and redistribution of plastic and mineral substances in a plant under their action.

It was found that the total content of carbohydrates (sugar and starch) during the growing season under the action of paclobutrazol and chlormequat chloride was higher than in the control leaves and stems of winter rape [180]. The total carbohydrate content was also higher in the leaves and roots of folicur and chlormequat chloride treated oil poppy throughout the growing season [161]. The application of paclobutrazol and chlormequat chloride on sunflower and oil flax plants also led to this result [61, 177]. The same reaction is caused by the blocking of attracting activity of the growth zones of vegetative organs by retardants and a decrease in the outflow of assimilates to them. At the same time, the accumulation of excess carbohydrates in the leaves and other vegetative organs of the experimental plants has a positive value, since a powerful reserve fund of assimilates is created, which is used for the fruits formation and growth. Thus, the donor potential of experimental plants grows under the influence of growth regulators. An excess of carbohydrates is used for the formation of a more powerful stem of plants and the growth of fruits due to increase stem branching and increased under the action of drugs [12, 70, 178, 179].

The dynamics of the various forms of carbohydrates content in the organs of oilseeds plants suggests a gradual decrease in the total content of sugars and starch in the leaves and stems of winter rapeseed, oil poppy, oil flax and sunflower during the growing season, and the process intensified. Since, after the budding phase, the growth processes in the vegetative organs slow down significantly and at the same time new acceptor zones – fruits appear, the main flow of assimilates is directed to the carpogenesis processes. This is associated with a gradual decrease in the carbohydrates content in the vegetative organs and an increase in the crop yield under the influence of retardants.

There was a decrease in the protein nitrogen content in the tissues of vegetative organs of oil flax under the action of retardants, which, according to the author, is associated with the outflow of nitrogen-containing compounds to the fruits, the amount of which is increasing [61]. Similar results were obtained by us on winter rape plants [105].

Maintaining a certain balance of nutrients under the influence of growth regulators contributes to the normal passage of the phases of plant ontogenesis, improving the crop productivity. The literature contains a small number of works devoted to the retardant effect on the content and dynamics of plant nutrients.

It was studied the metabolism of mineral nutrition elements in the organs of oil flax plants. it was found that when using It was noted that application of drugs with antigibberellin activity increased in the phosphorus content in the leaves at the beginning of the study, which indicates the optimization of phosphorus nutrition of plants under the influence of retardant. At the same time, its subsequent gradual decrease at the end of the growing season took place, which indicates an increase in the outflow of this element into intensively fruit forming. The same pattern was observed for the stem. The consequence of such phosphorus outflow into fruits was that the phosphorus concentration in fruits under the action of retardants in ontogenesis increased more intensively than in control [61]. A similar pattern was noted for oil poppy [161], winter rape [177], and sunflower [176].

It was found that, there was an increase in the potassium concentration in the vegetative organs under the action of growth regulators compared to control, which indicates an increase in metabolic processes under the action of drugs. This tendency is more distinctly traced for the stems. In particular, the potassium content was higher by an average of 13-15 % in the stems of chlormequat chloride-treated flax plants during the entire study period [61]. The potassium content in the tissues of vegetative organs of flax plants was maximum during the flowering period. During the formation and ripening of fruits, the element content in the leaves and in the stems decreased, which is associated with an increase in the outflow of mineral compounds into the forming generative organs. According to the author, the temporary deposition of potassium in the stem makes it possible to reutilize it more actively in the future to ensure the formation and growth of fruits. At the same time, there is no significant accumulation of potassium in the pods of experimental plants, which is obviously associated with the biodilution of this element as a result of an increase in the fruit loading of the plant. It was noted a similar decrease in the potassium content in leaves and roots during the formation of pods under the action of folicur and chlormequat chloride in oil poppy [161]. The element content decreased in the leaves and in the roots by the end of the growing season due to increase in mineral compounds outflow into the generative organs that are being formed.

Thus, the retardants treatment of oilseed plants led to change in the assimilation and redistribution of basic nutrients. In general, the content of nitrogen, phosphorus and potassium in vegetative organs under the action of drugs gradually decreases due to an increase in the outflow of nutrients to fruits during the growing season. The number of fruits increased under the drugs treatment.

The concept of donor-acceptor relations functioning in a plant suggests that the activity of donor function of the photosynthetic apparatus is largely determined by the activity of the acceptor, the power of its “sink” for assimilates [62,76,86]. Growth zones, including the processes of carpogenesis, act as acceptor centers at the organismic level. The inhibition of linear growth of oilseed plants by retardants contributes to the intensification of branching and the establishment of a larger number of fruits - new acceptor centers. This stimulates the assimilates outflow to them, which in itself acts as an additional factor in stimulating the photosynthetic processes.

Regulation of oilseeds growth and development with retardants makes it possible to directly influence the individual stages of ontogenesis and, ultimately, to increase the productivity and quality of the oilseed crop. The restructuring of the hormonal complex of plants under the action of retardants, an increase in stem branching, an increase in the photosynthetic activity of leaf apparatus and the redistribution of assimilates and nutrients towards the formation of new fruit organs leads to an increase in plant productivity. It was noted that quaternary compounds 3-DES and 17-DMC spraying of spring rapeseed plants increased in yield by 10-27 % due to the effect on the formation of pods on the main stem [128]. The application of paclobutrazol and dextrel on winter rape resulted in an increase in the number of first-order shoots and pods, which increased the seed productivity of the crop [177]. Similar results were obtained on the plant treated by retardants before flowering, but other periods of application did not affect or reduced the productivity of winter rape [149]. Spring treatment of winter rape crops with triazole derivative compound Kultar and Baronet at the phase of seed maturation had an inhibitory effect on seed productivity [116]. A similar effect was observed under triapentenol to prevent lodging of rapeseed crops and did not affect plant productivity in the autumn treatment to improve winter hardiness [11].

The yield of sunflower crops increased under the action of chlormequat chloride and their mixture with treptolem [175]. The increase in yield was due to an increase in the number of achenes in the pods, their weight, and pod diameter [176]. Chlormequat chloride and dextrel treatment of soybean plants promoted more intensive accumulation of the weight of generative organs and yield by 5–12 % [83]. The most effective was the effect of 0,3 % dextrel and 0,5 % chlormequat chloride against the bacteriization with *Bradyrhizobium japonicum* M8 tATA 761T strains. The productivity of mustard plants increased under paclobutrazol treatment [197].

The application of chlormequat chloride and triazole derivative folicur resulted in an increment of the seed productivity of oil poppy. The folicur treatment resulted in a significant increase in the number of pods on the plants. At the same time, the weight of a thousand seeds and the weight of seeds in a pod grew, which led to an increase in the yield of the crop [161].

The oil content in oil flax seeds increased and the oil quality parameters changed under the action of chlormequat chloride in comparison with the control - the saponification value, the ether and iodine values and the glycerol content increased [61]. Similar changes in quality and an increase in the oil content by 1-4 % in sunflower seeds under the action of chlormequat chloride were noted in another work [177].

It was found that the application of retardants leads to a change in the fatty acid profile and the ratio of saturated and unsaturated fatty acids. In particular, there is an increase in the unsaturated fatty acid content in sunflower, rapeseed, soybean, flaxseed oils of the indicated ratio according to the action of retardants, which correlate with an increase in the iodine value. In soybeans, this ratio changed due to an increase in the content of essential linoleic acid and a decrease in palmitic and stearic acids [38,39]. In sunflower plants it is also due to linoleic acid [176]. In oil flax plants, the oleic and linolenic acid content significantly increased under the action of chlormequat chloride [61. At the same time, in oily poppy plants, the content of saturated and unsaturated fatty acids did not change [95].

One of the important practical tasks is to reduce the content of linolenic acid in the oil, which gives it a bitter taste during storage. The retardants caused a decrease in the content of this acid in rapeseed oil, accompanied by an increase in the content of linoleic acid, which is a positive factor [105]. The presence of erucic acid in rapeseed oil in a concentration of more than 2 % is undesirable, since it negatively affects the cardiovascular system and the liver, which significantly limits the use of rapeseed oil for human nutrition. At the same time, some literary sources contain information that erucic acid is important when using rapeseed oil in the production of biodiesel fuel for internal combustion engines. It was found that the application of paclobutrazol led to an increase in the content of erucic acid in comparison with the control, while chlormequat chloride and dextrel reduced or did not change its content. At the same time, the content of erucic acid did not go beyond 2 % under retardants, regardless of the weather conditions of the growing season, which is a high indicator of the oil food quality [180].

An intensification of production and application of synthetic growth regulators, including retardants, increase the danger of their pollution of the environment and agricultural products. In this regard, the use of retardants should be determined by strict toxicological and hygienic requirements. The drugs should not accumulate in plants, soil and affect its microflora. There is a need for such regulations for the use of drugs that would allow obtaining the maximum effect with the minimum doses of retardant. The study of physiological and biochemical mechanisms of action of different groups of retardants is a prerequisite for determining ways to increase the efficiency and safety of this group of growth regulators on oil crops. Taking into account the requirements of environmental safety of synthetic plant growth regulators application, it is necessary to study the toxicological risk and control the content of residual amounts of drugs in the finished product. The use of retardants in the recommended concentrations on oilseeds did not lead to the accumulation of drugs in products in excess of the established norms. It was found that in the seeds of winter rape, oil poppy, soybeans, oil flax and sunflower, the content of chlormequat chloride did not exceed the permitted concentration of 0,1 mg/kg (State Sanitary Rules and Regulations (8.8.1.2.3.4.-000-2001) in Ukraine) and paclobutrazol was present only in trace concentrations of winter rape [177]. Consequently, the application of drugs with an antigibberellin mechanism of action (retardants) leads to significant changes in the morphogenesis and functioning of the donor-acceptor system of oilseed plants, which leads to an increase in productivity, an increase in oil yield and an improvement in its quality.

The data of the retardants action on crops of winter and spring rape are contradictory. It was studied the formation of spring rape productivity and found that the quaternary ammonium compounds 3-DES and 17-DMC effectively affect the formation of pods of the main stem. The yield increased by 10-27 % after the plants treatment at the phase of four leaves. The number of seeds per pod and the weight of

1000 seeds did not change [128,129]. The results of our studies indicate that a triazole derivative – paclobutrazol and a quaternary ammonium compound – chlormequat chloride led to an increase in the yield of rapeseed due to an increase in the number of first-order branches, the number of pods on them and the number of seeds in one pod. At the same time, the weight of 1000 seeds did not change significantly (Table 6.1).

Table 6.1.
Influence of retardants on the biological productivity of winter rapeseed (micro-field trials)

Measurements	Number of pods per a plant, pieces	Number of seeds per a pod, pieces	Weight of 1000 seeds, g	Yield of a plant, g
2002, cv. Galitsky				
Control	24,60±0,45	24,69±0,31	5,03±0,06	3,06
0,025% paclobutrazol	*29,87±0,68	*26,26±0,30	*5,12±0,05	4,02
0,3% dextrel	*22,27±0,40	25,04±0,31	5,10±0,25	2,85
1% chlormequat chloride	24,17±0,51	*25,96±0,30	5,25±0,14	3,32
2003, cv. Wotan				
Control	27,99±0,71	14,14±0,19	4,57±0,12	1,81
0,025% paclobutrazol	*36,10±1,06	*15,49±0,33	4,76±0,08	2,66
0,3% dextrel	26,20±1,10	14,40±0,19	4,68±0,13	1,77
1% chlormequat chloride	29,04±0,90	*14,87±0,20	4,52±0,07	1,95
2004, cv. Galitsky				
Control	104,76±3,52	25,43±0,44	3,59±0,08	9,56
0,025% paclobutrazol	*120,60±4,60	*28,13±0,51	3,65±0,09	12,38
1% chlormequat chloride	*116,87±4,57	24,90±0,54	3,51±0,08	10,21
2004, cv. Wotan				
Control	93,29±4,32	26,48±0,54	3,51±0,08	8,79
0,025% paclobutrazol	103,92±3,14	27,31±0,48	3,56±0,04	10,22
1% chlormequat chloride	*129,50±4,53	*23,65±0,50	3,60±0,06	10,57

Notes:

1. Dates of treatment: 2002 – the 25th of April; 2003 – the 8th of May; 2004 – the 24th of April.

2. * – difference is significant at $p<0.05$.

The reason for this phenomenon is a change in the source - sink system due to inhibition of the activity of plant apical meristems under the influence of retardants. At the same time, an excess of assimilates entered the pods, the amount of which increased under the action of drugs. At the same time, the effect of the ethylene producer dextrel on the productive process was not effective, which, in our opinion, is explained by the rapid decomposition of the drug in the plant.

It was found that the weather conditions of the growing season had a significant impact on the yield of the crop (see Table 6.1). The highest yields were recorded in those years when the climatic conditions were moderately warm and moderately humid. Hot and dry vegetation conditions in 2002 and especially in 2003 caused a decrease in plant productivity both in control and experiment [177].

It was found that plants were sensitive to a lack of moisture and high temperatures in the period from the beginning of budding to the end of fruit formation (April-May). The lack of moisture at this time inhibited the growth and development of plants, and high temperature indicators caused burns of buds and flowers, which led to a decrease in plant productivity. In addition, in 2003 the plants were damaged and weakened by the ice crust, which also negatively affected the yield. At the same time, retardants treated plants turned out to be better adapted to unfavorable environmental factors and, as a consequence, were characterized by higher productivity. The most effective was the 0,025 % paclobutrazol under the condition of sufficient water supply and under dry growing conditions. The number of additional shoots of the first order increased by 10-20 %, the number of pods per plant by 10-30 %, the number of seeds in one pod by 3-10 % under the drug action which led to an increase in the yield of seeds. The application of 1 % chlormequat chloride was less effective. In this case, the weather conditions of the growing season significantly influenced the experimental plants in this case. The number of additional shoots increased by 5-20 %, the number of pods per plant by 5-35 %, the number of seeds in one pod by 1-5 % under the influence of chlormequat chloride., It was observed no increase in yield under 0,3 % dextrel which, in our opinion, makes further use of drugs of this group in rapeseed not promising. The application of retardants led to an increase in the content of vegetable oil in seeds [177].

The results of the study indicate that retardants effected on the content of higher fatty acids in rapeseed oil [177]. The oil of rapeseed cv. Wotan and cv. Galitsky contains palmitic, oleic, linoleic, linolenic, gadalenic and erucic acids, the nutritional value and significance of which for the human and animal body are different [191]. It was noted in the literature that during ripening during drought, the content of erucic acid in rapeseed oil increases [10]. Our data confirm this point of view – under the arid vegetation conditions in 2002 and 2003, its content in the seeds of the control variant was higher than in typical weather conditions in 2001 and 2004. It was found that the paclobutrazol led to an increase in the content of erucic acid in comparison with the control, and chlormequat chloride and dextrel reduced or did not change its content.

An important indicator of the quality of rapeseed seeds is the glucosinolates content. Their main representatives are gluconapine, glucobrasicanapine, progoitrin [31,219]. By themselves, they are not harmful to farm animals and humans. Their decay products are dangerous. The harm of these sulfur-containing compounds is that they cause loss of appetite, decrease in body weight gain, and inhibit growth. The causes of these disorders are thyroid hypertrophy due to iodine metabolism disorders.

It was found that dry and hot growing conditions increase their the content of glucosinolates in rapeseed crops of 2001-2004 (Table 6.2). The same pattern was observed by other researchers [10]. The application of retardants paclobutrazol and chlormequat chloride led to a decrease in their content in unfavorable growing conditions. At the same time, the compounds caused an increase in the thioglycosides content by 5-15 % under optimal growing conditions. A clear effect of the retardant ethylene producer dextrel on this indicator was not found.

Table 6.2.

Effect of retardants on the glucosinolates content in winter rape seeds (% per wet matter weight)

Year	Control	0,025 % paclobutrazol	0,3 % dextrel	1 % chlormequat chloride
2001	1,44±0,05	1,50±0,06	1,63±0,08	-
2002	2,51±0,13	2,29±0,12	*1,84±0,09	*1,85±0,07
2003	2,54±0,04	*2,01±0,11	2,54±0,03	*1,66±0,07
2004	1,41±0,05	1,62±0,06	-	*1,62±0,03

Notes: 1. Dates of treatment: 2002 – the 25th of April; 2003 – the 8th of May; 2004 – the 24th of April. 2. 2001, 2002 – cv. Galitsky, 2003, 2004 – cv. Wotan. 3. * – difference is significant at $p<0.05$.

Consequently, the application of 0,025 % paclobutrazol and 1 % chlormequat chloride led to an improvement in the productivity of winter rape plants. The use of 1 % chlormequat chloride increased the yield of oil from seeds and improved its quality characteristics. Residual amounts of these preparations in rapeseed did not exceed the maximum permissible concentrations, so their application in agricultural production is perspective [180].

The results of our research indicate that the application of retardant chlormequat chloride (0,25 %), a synthetic growth stimulator treptolem (0,33 ml/l) and their mixture (1: 1) had a positive effect on the productivity of sunflower crop [176]. The number of achenes in the pod, their weight and pod diameter increased under the influence of drugss in the conditions of micro-trial experiment (Table 6.3).

The highest results of the increase in the basket diameter cv. Chumak were observed under the influence of drugs mixture. The maximum basket size was recorded of chlormequat chloride treated plants cv. Flagman. The weight of seeds of one pod and the number of achenes in it increased more in the cv. Chumak after the application of chlormequat chloride, and in the cv. Flagman – after the action of treptolem [176]. The weight of 1000 seeds increased most significantly in cv. Chumak under the influence of chlormequat chloride and drugs mixture and in cv. Flagman under the action of treptolem. In general, the crop yield significantly depended on the weather conditions of the growing season and the applied drugs.

The highest yield was observed in 2006 on both sunflower varieties of retardant treated variants. Chlormequat chloride increased the crop productivity by 12-14 %. The yield of drugs mixture treated cv. Flagma increased by 12 %. In the arid conditions of the 2007 growing season, the application of chlormequat chloride and

Table 6.3.

Influence of growth regulators on structural elements of sunflower yield

Year	Experimental trials	Diameter of pod, cm	Seed weight in a pod, g	Number of seeds in a pod, pieces	Weight of 1000 seeds, g
cv. Chumak					
2006	Control	19,22 ±0,55	79,22 ±5,82	1236,25 ±58,85	58,91 ±1,15
	Chlormequat chloride	20,71 ±0,71	85,80 ±4,19	*1405,46 ±58,13	62,22 ±2,19
	Drugs mixture	*21,72 ±0,93	85,40 ±4,27	1339,87 ±44,01	*67,09 ±2,62
	Treptolem	19,42 ±0,81	79,56 ±3,81	1323,29 ±48,23	60,45 ±2,83
2007	Control	13,67 ±0,39	33,38 ±1,75	825,25 ±40,15	39,80 ±1,11
	Chlormequat chloride	*15,91 ±0,47	*46,31 ±2,62	*1061,41 ±50,98	41,64 ±1,36
	Drugs mixture	*15,12 ±0,43	*42,75 ±2,06	*965,14 ±46,62	42,21 ±1,29
	Treptolem	*15,28 ±0,47	*41,30 ±1,87	*993,94 ±49,10	*43,51 ±1,28
2008	Control	19,17 ±0,69	64,83 ±3,24	1244,16 ±49,93	48,25 ±1,88
	Chlormequat chloride	20,82 ±0,61	*76,95 ±3,85	1370,01 ±61,51	*54,43 ±1,95
	Drugs mixture	*21,19 ±0,60	*77,69 ±3,88	*1407,71 ±62,15	*54,25 ±1,93
	Treptolem	*21,34 ±0,45	73,73 ±3,67	1382,39 ±55,38	53,67 ±1,95
cv. Flagman					
2006	Control	16,55 ±0,49	49,91 ±2,15	983,45 ±43,86	51,63 ±2,07
	Chlormequat chloride	17,06 ±0,35	51,02 ±1,82	996,43 ±38,14	50,03 ±1,30
	Drugs mixture	17,16 ±0,33	51,66 ±2,36	1076,04 ±39,40	50,15 ±1,70
	Treptolem	17,29 ±0,44	50,84 ±2,13	999,46 ±49,49	54,12 ±1,64
2007	Control	14,90 ±0,46	40,89 ±1,85	905,59 ±44,76	42,95 ±1,22
	Chlormequat chloride	15,77 ±0,42	*48,37 ±1,84	*1085,44 ±45,88	43,40 ±1,27
	Drugs mixture	15,31 ±0,47	42,97 ±2,09	911,41 ±45,44	45,16 ±1,34
	Treptolem	16,17 ±0,46	*52,47 ±2,26	*1122,43 ±49,00	*48,49 ±1,54

Year	Experimental trials	Diameter of pod, cm	Seed weight in a pod, g	Number of seeds in a pod, pieces	Weight of 1000 seeds, g
2008	Control	18,25 ±0,45	67,24 ±2,60	1094,06 ±47,96	61,98 ±2,43
	Chlormequat chloride	*20,75 ±0,75	*77,05 ±3,73	1242,50 ±61,87	60,64 ±2,52
	Drugs mixture	*19,75 ±0,40	72,68 ±3,34	1185,27 ±55,50	62,84 ±2,26
	Treptolem	*19,95 ±0,38	*78,53 ±2,90	1210,15 ±45,09	*68,88 ±1,92

Note: * – difference is significant at $p<0.05$.

treptolem separately turned out to be the most effective. The yield increased by 17-18 % under the action of chlormequat chloride and by 25-33 % under the influence of treptolem.

In conditions of sufficient water supply (2008), cv. Chumak showed the best yield indicators under the influence of retardant and its mixture with a stimulator. The crop productivity increased by 17 and 15 % under the action of chlormequat chloride and mixture with treptolem respectively in comparison with the control. The yield of cv. Flagman increased by 14 % under the influence of retardant and by 17 % under the action of stimulator compared to control (Table 6.4.).

Table 6.4.

Influence of growth regulators on sunflower yield, cwt / ha

Variety / Experimantal trials	cv. Chumak			cv. Flagman		
	2006	2007	2008	2006	2007	2008 p.
Control	30,65 ±0,54	24,12 ±0,84	24,85 ±0,75	24,96 ±0,51	26,57 ±0,68	22,29 ±0,47
Chlormequat chloride	*34,29 ±0,47	*28,49 ±0,48	*29,02 ±0,58	*28,26 ±0,46	*31,01 ±0,52	*25,42 ±0,49
Drugs mixture	*32,55 ±0,64	*27,99 ±0,42	*28,68 ±0,56	*28,12 ±0,49	*28,90 ±0,51	*24,04 ±0,56
Treptolem	31,97 ±0,53	*30,12 ±0,54	*27,54 ±0,44	*26,63 ±0,77	*35,42 ±0,71	*26,14 ±0,50

Note: * – difference is significant at $p<0.05$.

Our studies have found that the application of stimulator, inhibitor of plant growth and development and their mixture led to an increase in the oil content in sunflower seeds by 1-4 % in both varieties, depending on the weather conditions of the growing season. The most effective was the mixture of chlormequat chloride and treptolem. In particular, the oil content increased on average by 1,6 %, under retardant – by 1,4 %, under treptolem – by 1,1 %.

Thus, growth regulators chlormequat chloride, treptol and their equivalent mixture optimize the productivity of sunflower crops. The effectiveness of the drug application depended on the type of growth regulator and the weather conditions of the growing season.

The analysis of our data indicates that chlormequat chloride, treptolem and their mixture against leads to changes in the ratio between unsaturated and saturated fatty acids, and, accordingly, in the quality indicators of production at the different weather conditions of the growing season (Table 6.5). There was a clear increase in the ratio of unsaturated to saturated higher fatty acids in the oil under typical weather conditions. This indicates a positive effect of the compounds on the quality of vegetable oil. There was a decrease in the ratio between fatty acids, when the weather conditions were atypically wet at the end of the growing season, the results for the experimental variants were mixed in 2008.

Among the experimental options, it was noted that the highest values of this indicator was under the treptolem and chlormequat chloride mixture, which indicates an improvement in the quality of oil obtained from plant seeds treated with a mixture of growth regulators (see Table 6.5.). The increase in the unsaturated fatty acids content was due to linoleic acid in the typical weather conditions. The difference in the content of this acid between the experimental variants leveled out under atypical growing conditions. Thus, the application of growth regulators under typical growing conditions led to an improvement in the quality oil content due to an increase in the content of unsaturated fatty acids. The highest quality oil, containing the maximum content of linoleic acid, was obtained under the mixture of growth regulators.

The application of chlormequat chloride and treptolem at the phase of 5-6 pairs of leaves did not lead to their accumulation in the seeds, and the residual amounts did not exceed the maximum permissible concentrations. The amount of chlormequat chloride in sunflower seeds cv. Chumak does not exceed the norm and is below 0,05 mg/kg. The residual amount of treptolem in the sunflower seeds cv.Chumak does not exceed the norm and is 0,0125 mg/kg [176].

The results of the study indicate that the yield of oil flax increased under the application of quaternary ammonium compounds chlormequat chloride, a complex stimulator treptolem with cytokinin and auxin activity and their mixture. The effect of these compounds on the flax productivity was manifested in changes in the crop structure: there was an increase in the number of pods per plant, the number of seeds in fruits and the weight of seeds [61].

The chlormequat chloride treatment leads to blocking of the gibberellin synthesis and partial removal of the apical dominance effect, as a result of which there is an increase in the stem branching and an establishment of a larger number of pods per plant. So, this indicator under the action of drug grew on average by 35-39 % compared with the control, under the use of growth regulators mixture by 22-31 %. In all experimental variants, the weight of 1000 seeds increased by 2,3-4,1 %. The weight of seeds from one plant changed most significantly of chlormequat chloride treated plants - by 0,4-1,3 g, and under mixture with treptolem – by 0,5-0,9 g, under treptolem – by 0,2-0,5 g.

Table 6.5

Influence of growth regulators on higher fatty acid content in sunflower oil cv. Chumak (% on dry matter weight)

Trials / Fatty acids	2006				2007				2008			
	Control	Chlormequat chloride	Drugs mixture	Treptolem	Control	Chlormequat chloride	Drugs mixture	Treptolem	Control	Chlormequat chloride	Drugs mixture	Treptolem
Myristic acid	0,04 ±0,002	*0,03 ±0,001	*0,02 ±0,001	*0,03 ±0,001	0,04 ±0,002	0,04 ±0,002	*0,03 ±0,001	*0,03 ±0,001	0,04 ±0,001	*0,03 ±0,001	*0,02 ±0,001	*0,03 ±0,001
Palmitic acid	5,19 ±0,219	5,15 ±0,181	4,97 ±0,150	5,45 ±0,220	5,92 ±0,288	6,18 ±0,313	5,94 ±0,204	5,78 ±0,200	5,41 ±0,234	5,34 ±0,212	5,18 ±0,228	5,63 ±0,237
Palmitoleic acid	0,06 ±0,003	*0,04 ±0,002	*0,04 ±0,002	*0,08 ±0,003	0,08 ±0,004	0,07 ±0,003	0,07 ±0,003	*0,06 ±0,003	0,08 ±0,003	*0,04 ±0,001	0,09 ±0,002	*0,04 ±0,002
Stearic acid	4,18 ±0,183	4,00 ±0,160	3,90 ±0,165	3,90 ±0,179	3,41 ±0,171	3,28 ±0,155	3,37 ±0,144	3,65 ±0,121	3,41 ±0,153	3,58 ±0,137	3,29 ±0,145	3,60 ±0,111
Oleic acid	18,56 ±0,531	16,64 ±0,363	16,93 ±0,397	*16,10 ±0,342	18,91 ±0,444	18,00 ±0,505	18,84 ±0,578	20,63 ±0,616	19,43 ±0,711	19,34 ±0,747	19,36 ±0,722	18,90 ±0,506
Linoleic acid	71,09 ±1,224	73,29 ±1,456	73,46 ±1,313	73,66 ±1,111	70,97 ±0,977	71,70 ±1,201	70,97 ±1,024	68,83 ±0,912	70,98 ±1,080	71,02 ±1,009	71,21 ±1,300	70,95 ±1,540
Linolenoic acid	0,01 ±0,001	*0,03 ±0,001	0,01 ±0,001	*0,02 ±0,001	0,02 ±0,001	*0,05 ±0,002	0,02 ±0,001	*0,04 ±0,002	0,03 ±0,001	0,03 ±0,001	0,03 ±0,001	*0,04 ±0,002
Arachic acid	0,22 ±0,009	0,17 ±0,008	0,13 ±0,006	0,17 ±0,008	0,22 ±0,010	*0,11 ±0,005	0,20 ±0,009	0,26 ±0,011	0,07 ±0,003	*0,11 ±0,005	*0,12 ±0,006	*0,17 ±0,008
Gondoic acid	0,12 ±0,006	*0,06 ±0,002	*0,07 ±0,003	*0,06 ±0,003	0,02 ±0,001	0,06 ±0,002	0,02 ±0,001	0,09 ±0,003	0,16 ±0,008	*0,03 ±0,001	*0,07 ±0,003	*0,05 ±0,002
Behenic acid	0,55 ±0,025	*0,59 ±0,027	*0,47 ±0,020	*0,52 ±0,019	0,40 ±0,018	0,49 ±0,024	*0,54 ±0,027	*0,63 ±0,031	0,39 ±0,033	0,49 ±0,024	*0,64 ±0,031	*0,60 ±0,030
Ratio of unsaturated to saturated fatty acids	8,83	9,06	9,54	8,93	9,01	8,90	8,92	8,66	9,73	9,47	9,81	8,97

Notes: 1. Dates of treatment: 2006 – the 25th of June; 2007 – the 6th of June; 2008 – the 22th of June. 2. * – difference is significant at $p<0.05$.

Meteorological conditions during the growing season can affect the crop productivity that confirming by the results of the research of other authors [22, 23]. In particular, in 2010, more typical in terms of the precipitation amount, the yield increased most significantly by 14,8 % for the cv. Debut and by 15,4 % compared to control for cv. Orfey under chlormequat chloride treatment [61].

The application of the mixture of growth inhibitor and growth stimulator turned out to be the most effective for flax cv. Debut. So, in 2011, the seed productivity of crop grew by 21,2 % and by 12 % for cv. Orphey compare to control. It can be stated that the application of chlormequat chloride and treptolem makes it possible to simulate an increase in the auxin+ cytokinin / gibberelin ratio due to a modern data on the nature and mechanisms of action of these growth regulators [61]. Such changes in the balance of physiologically active substances and in the functioning of source-sink system led to a more active flow of plastic substances into the generative organs.

Thus, the application of growth inhibitor chlormequat chloride, stimulator of plant development treptolem and mixture of these drugs improves the productivity of oil flax. The most effective was the use of retardant and its mixture with a stimulator.

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 indispensable for humans. Polyunsaturated fatty acids are precursors of long-chain fatty acids and are found in cell membranes. α-linolenic acid is particularly important, the content of which in some flax varieties can reach 50 % [20]. Linseed oil is a fast-drying oil due to the high content of unsaturated acids and their ability to quickly oxidize, which leads to its use in the production of high-quality drying oils, alkyd resins, oil varnishes, mild soaps, a component of linear fixers, printing inks, etc.

The results of our research indicate that the oil content in flax seeds increased under the action of chlormequat chloride (CCC), treptolem, as well as their mixture [61].

The oil quality also largely depends on the ratio of fatty acids in it. Chromatographic analysis of flax oil revealed seven main higher fatty acids - palmitic, palmitoleic, stearic, oleic, linoleic, α-linolenic, gondoic (Tables 6.6, 6.7). The obtained results indicate that the use of growth regulators affects the fatty acid content of oil flax seeds. Thus, the chlormequat chloride and treptolem treatment led to a decrease in the saturated acids content. The use of drugs mixture on cv. Orphey in 2011 led to the most significant decrease in the concentration of palmitic and stearic acids. The lowest values of the saturated acids content in flax oil cv. Debut were observed after growth inhibitor treatment in the same year.

The total unsaturated higher fatty acids content increased under the growth regulators treatment, as evidenced by an increase in the iodine value. In most trials, the ratio of unsaturated to saturated fatty acids increased compared to the control, which indicates an improvement in the oil quality. High values of this indicator were recorded in 2011 in control and in experimental trials.

The residual amount of chlormequat chloride in seeds should not exceed 0,1 mg/kg according to the State Sanitary Rules and Regulations (8.8.1.2.3.4.-000-2001) in Ukraine. The concentration of drug is 0,042 mg/kg in a trial of retardant treated flax seeds cv. Orphey. The residual content of growth regulator is 0,0073 mg/kg in flax seeds cv. Orpheus which does not exceed the norm 0,03 mg/kg for flax seeds.

Consequently, the application of chlormequat chloride, treptolem and their mixtures led to an increase in the oil content in flax seeds, an improvement in its quality characteristics, and an increase in the unsaturated fatty acids content. The residual content of these growth regulators in the seeds did not exceed the maximum permissible concentrations established by the toxicological and hygienic standards [88].

We found that the application of growth inhibitors (chlormequachloride and folicur) and growth stimulants (treptolem and emistim C) and drugs mixture led to an increase in the yield of oil poppy. The influence of compounds with growth inhibitory and growth-stimulating action on the oil poppy productivity turned out to be similar to the oil flax in changes in the crop structure . Thus, a significant increase in the number of fruits on a plant - pods was noted in the conditions of a micro-trial experiment under drugs pods grew. The most effective was the application of chlormequat chloride and treptolem mixture. The number of pods on the plant increased under the action of drug. At the same time, the weight of a thousand seeds and the weight of seeds in a pod increase. As a result, the yield of seeds increased on average by 18,5 % [88]. We believe that the reason for this phenomenon is blocking the gibberellins synthesis and partial removal of the apical dominance effect under the application of growth inhibitors chlormequat chloride and folicur. The stem branching and the laying of more pods occurs. Growth simulators treptolem and emistim treatment also led to an increase in yield of oil poppy crops. Treptol is included in the physiological processes in the plant and affects the growth and branching of the stem due to the hormones of cytokinin and auxin nature.

It was found that the weather conditions of the growing season had a significant effect on the yield of poppy. In particular, the highest poppy yields were recorded in 2010 and 2014, when the climatic conditions were moderately warm and moderately humid. The hot and dry 2011 in terms of vegetation conditions led to a decrease in plant productivity of control and treated plants.

Table 6.6

Influence of growth regulators on higher fatty acids content in seed oil of flax cv. Debut (%)

Fatty acids \ Trials	2009			2010				2011			
	Control	0,5 % CCC	Mixture of drugs	Control	0,5 % CCC	Mixture of drugs	Treptolem, 0,033 ml/l	Control	0,5 % CCC	Mixture of drugs	Treptolem, 0,033 ml/l
Palmitic acid	5,27 ±0,005	5,15 ±0,030	5,21 ±0,020	4,91 ±0,030	5,03 ±0,015	*5,15 ±0,020	4,88 ±0,020	4,85 ±0,180	4,65 ±0,130	4,64 ±0,240	4,79 ±0,050
Palmitoleic acid	0,04 ±0,005	0,05 ±0,005	0,05 ±0,005	0,09 ±0,005	*0,06 ±0,001	0,07 ±0,002	*0,06 ±0,002	0,06 ±0,010	0,07 ±0,005	0,06 ±0,001	0,06 ±0,002
Stearic acid	3,82 ±0,015	*3,66 ±0,020	3,67 ±0,040	3,43 ±0,002	3,36 ±0,010	3,42 ±0,005	3,40 ±0,020	3,05 ±0,060	2,88 ±0,190	3,00 ±0,040	3,17 ±0,060
Oleic acid	19,49 ±0,055	*18,58 ±0,125	*18,05 ±0,180	21,71 ±0,055	*22,95 ±0,125	21,89 ±0,140	*22,45 ±0,040	15,64 ±0,130	15,64 ±0,490	15,19 ±0,240	*16,83 ±0,170
Linoleic acid	12,76 ±0,070	12,78 ±0,005	13,08 ±0,160	14,74 ±0,015	*13,96 ±0,020	*13,99 ±0,055	*14,05 ±0,080	14,65 ±0,050	14,29 ±0,380	*13,74 ±0,010	14,55 ±0,260
α- linolenoic acid	58,53 ±0,135	*59,67 ±0,145	59,81 ±0,385	54,28 ±0,130	54,56 ±0,135	*55,36 ±0,060	54,87 ±0,120	61,68 ±0,400	62,40 ±0,170	63,33 ±0,510	60,58 ±0,010
Gondoic acid	0,11 ±0,010	0,13 ±0,015	0,14 ±0,010	0,83 ±0,015	*0,10 ±0,002	*0,13 ±0,003	*0,30 ±0,005	0,08 ±0,002	0,08 ±0,005	*0,05 ±0,001	*0,04 ±0,005
Content of unsaturated higher fatty acids	9,09	8,81	8,88	8,34	8,39	8,57	8,28	7,90	7,53	7,64	7,96
Content of saturated higher fatty acids	90,93	91,20	91,13	91,65	91,63	91,44	91,73	92,11	92,48	92,37	92,06
Ratio of unsaturated to saturated fatty acids	10,00	10,35	10,26	10,99	10,92	10,67	11,08	11,66	12,28	12,09	11,57

Note: * – difference is significant at p<0.05.

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Table 6.7.

Influence of growth regulators on higher fatty acids content in seed oil of flax cv. Orphey (%)

Trials / Fatty acids	2009			2010				2011			
	Control	0,5 % CCC	Mixture of drugs	Control	0,5 % CCC	Mixture of drugs	Treptolem, 0,033 ml/l	Control	0,5 % CCC	Mixture of drugs	Treptolem, 0,033 ml/l
Palmitic acid	4,79 ±0,020	4,78 ±0,145	4,82 ±0,010	4,78 ±0,025	4,74 ±0,090	4,65 ±0,075	4,66 ±0,015	4,98 ±0,220	4,36 ±0,070	4,19 ±0,010	4,49 ±0,020
Palmitoleic acid	0,05 ±0,002	0,04 ±0,002	0,04 ±0,002	0,05 ±0,003	0,07 ±0,005	0,05 ±0,002	0,06 ±0,005	0,06 ±0,006	0,06 ±0,005	0,06 ±0,005	0,06 ±0,005
Stearic acid	4,13 ±0,085	4,13 ±0,060	4,19 ±0,020	4,10 ±0,015	3,91 ±0,090	*3,90 ±0,010	*3,74 ±0,045	3,82 ±0,070	3,57 ±0,070	3,26 ±0,180	3,72 ±0,020
Oleic acid	18,74 ±0,085	18,66 ±0,004	*18,28 ±0,040	23,21 ±0,015	23,39 ±0,110	*24,44 ±0,110	*19,74 ±0,185	15,51 ±0,320	*18,26 ±0,120	16,86 ±0,410	*17,73 ±0,200
Linoleic acid	13,32 ±0,080	13,65 ±0,150	13,42 ±0,145	13,51 ±0,020	13,49 ±0,080	13,32 ±0,085	*14,23 ±0,140	15,18 ±0,160	14,59 ±0,030	14,75 ±0,330	14,82 ±0,040
α- linolenoic acid	58,82 ±0,270	58,63 ±0,510	59,14 ±0,115	54,14 ±0,060	54,30 ±0,380	*53,44 ±0,145	*57,51 ±0,015	60,39 ±0,300	59,10 ±0,300	60,83 ±0,920	59,13 ±0,150
Gondoic acid	0,16 ±0,010	0,12 ±0,005	0,12 ±0,002	0,18 ±0,005	*0,10 ±0,002	*0,22 ±0,005	*0,09 ±0,002	0,05 ±0,003	0,06 ±0,005	0,06 ±0,002	0,06 ±0,005
Content of unsaturated higher fatty acids	8,92	8,91	9,01	8,88	8,65	8,55	8,40	8,80	7,93	7,45	8,21
Content of saturated higher fatty acids	91,09	91,10	91,00	91,09	91,35	91,47	91,63	91,19	92,07	92,56	91,79
Ratio of unsaturated to saturated fatty acids	10,21	10,22	10,10	10,26	10,56	10,70	10,91	10,36	11,61	12,42	11,18

Note: * – difference is significant at $p<0.05$.

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At the same time, growth regulators treated plants turned out to be better adapted to unfavorable environmental factors and, as a consequence, were characterized by higher productivity. The most effective for increasing the yield turned out to be the use of mixture of drugs with sufficient water supply and in the arid growing conditions. Analysis of the ratio between unsaturated and saturated fatty acids indicates that treatment of plants with treptolem (0,035 ml/l) and a mixture of drugs with chlormequat chloride contributed to an increase in the unsaturated fatty acids content in seeds oil of the 2010 year of vegetation period. The application of retardant reduced the unsaturated fatty acid content. Similarly, the compounds influenced the ratio of acids in the oil of the 2011 year of vegetation period: growth inhibitors (chlormequat chloride and folicur) increased the saturated fatty acids content, and the application of growth stimulators (emistim C and treptol) led to an increase in the unsaturated fatty acid content in the oil.

The greatest increase in the unsaturated fatty acids content led to the application of chlormequat chloride and treptolem mixture throughout the entire growing season [161].

Narcotic alkaloids (morphine, codeine, thebaine) are contained in pods in low quantities, and the content of other alkaloids (papaverine, narcein, neopine, hydrocatarnine, xantholine, laudanine, laudanidine, codamine, laudanosine, oxynarcotine, protopapaverine) does not exceed 0,1%. It was found that the multidirectional growth regulators treatment of poppy plants had a significant effect on the content of alkaloids. It was higher in pods of experimental variants at the end of the growing season than in control (Table 6.8). The results indicate that the content of narcotic alkaloids morphine, codeine and thebaine increased under the influence of drugs.

Table 6.8

Influence of plant growth regulators on alkaloid content in oil poppy plants at the phase of waxy ripeness (% per dry matter weight)

Indicators	Morphine	Codeine	Thebaine	Neopine	Papaverine	Narcotine	Oripavine
Control	0,113± 0,01	0,017± 0,001	0,013± 0,001	0,012± 0,001	0,071± 0,002	0,084± 0,003	0,014± 0,001
Treptolem (0,035 ml/l)	*0,251± 0,02	*0,024± 0,001	*0,021± 0,002	0,016± 0,002	*0,093± 0,001	*0,093± 0,001	*0,031± 0,002
0,5 % CCC	*0,262± 0,01	*0,028± 0,002	*0,023± 0,002	*0,019± 0,001	*0,110± 0,003	*0,098± 0,002	*0,026± 0,005
Mixture of drugs	*0,321± 0,04	*0,041± 0,003	*0,026± 0,003	*0,022± 0,002	*0,113± 0,001	*0,110± 0,005	0,034± 0,002

Notes:
1. * – difference is significant at $p<0.05$.
2. Mixture – Treptolem (0,035 мл/л) + 0,5 % CCC;
3. CCC – chlormequat chloride

It was established the presence of non-narcotic alkaloids, such as neopine, papaverine, narcotine, oripovine in poppy pods at the phase of waxy ripeness, the content was insignificant in all variants of the experiment.

Analysis of the residual amounts of chlormequat chloride and treptolem mixture treated plants indicates that the content of chlormequat chloride in the pods was 0,0013 mg/kg. The residual amount of this drug should not exceed 0,1 mg/kg according to State Sanitary Rules and Regulations (8.8.1.2.3.4.-000-2001) in Ukraine. The residual amount of treptolem in the experimental sample was 0,005 mg/kg, which was less than the permitted norm of 0,03 mg/kg. Thus, the application of treptolem and chlormequat chloride in the technology of poppy cultivation does not lead to the accumulation of excessive amounts of the drug in seeds [161].

Analysis of donor-acceptor relations for leguminous plants cannot be limited only by the specificity of the assimilates redistribution between the vegetative and generative organs of plants, the processes of growth and photosynthesis, since legume-rhizobial complexes act as additional attracting centers for the assimilates redistribution. We found that the application of retardants paclobutrazol and chlormequat chloride at the budding phase of soybean plants with pre-sowing bacterization of seeds with highly effective strains *Bradyrhizobium japonicum* leads to the correction of donor-acceptor relations in the plant, promotes the formation of a more powerful donor sphere, enhanced formation of soybean- rhizobial complexes and increases their nitrogen-fixing activity.

Chlormequat chloride treatment of soybean plants at the 8-10th leaf increased the number and total weight of bubbles. The bubbles number of retardants treated soybean plants inoculated by strains 634b and M8 increased at all phases of plant development [39]. The crop productivity increased due to the increase of stem branching and the establishment of a larger number of flowers and beans, the formation of larger leaf surface and the increase of photosynthetic activity per unit leaf area, improved nitrogen nutrition due to the optimization of nitrogenase and nitrate reductase activity, the combined use of seed bacterization with tuberous bacteria and paclobutrazol treatment. Therefore, pre-sowing inoculation of soybean seeds by *Br. japonicum* was effective compared to untreated control. In all variants, the combined use of bacteriizations and retardants increased the productivity of plants (Table 6.9.).

The greatest increase in yield was obtained under the application of strains M8 and 0,3 % dextrel and 71t strain and 0,5 % chlormequat chloride for cv. Podilska 1 and standard strain 634b and 0,5 % chlormequat chloride and strain M8 and 3 % dextrel for cv. Agate.

Soybean oil production in Ukraine ranks third place after sunflower and corn oil. It is becoming important to improve the quality of soybean oil. At the same time, there is no information in the literature of the growth regulators effect on the oil content, its chemical and quality characteristics in the seeds of protein-oil crops. It is known that the effect of chlormequat chloride and mixture of treptolem and chlormequat chloride was positive for the oil content of sunflower [180], oil flax, [61], oil poppy [161].

Table 6.9.

Yield of soybean cv. Podilska 1 and cv. Agate under inoculation and retardant treatment (average data for 2004-2006)

Trials/ Indicators		Number of beans per a plant, pieces	Weight of 1000 seeds, g	Yield, cwt/ha
cv. Podilska 1	Control	16,3±0,64	130,3±0,42	20,8±0,84
	634 b	*21,6±0,82	*142,5±0,70	*26,6±1,22
	71 t	*22,8±0,34	*145,2±0,22	*28,0±1,13
	M 8	*21,5±0,83	*140,5±0,44	*26,2±1,33
	71t + 0,5 % CCC	**28,4±0,78	**152,1±0,86	**30,8±1,62
	M8+0,3 % Dextrel	**30,2±1,12	143,6±0,32	**32,0±1,43
cv. Agate	Control	12,2±0,72	169,5±0,10	16,9±1,65
	634 b	*15,7±0,88	*183,2±0,14	*20,3±1,24
	634b + 0,5 % CCC	**19,9±0,53	185,2±0,83	**24,13±1,7

Notes: 1. * – difference is significant at $p<0.05$ for control.
2. **– for strain 634b.

Analysis of the oil content in soybean seeds indicates that inoculation with three applied *B. japonicum* strains 634b, 71t, and M8 did not significantly affect its content in seeds, whereas dextrel and chlormequat chloride treatment with inoculation of 71t and M8 strains increased in the oil content (Figure 6.1.).

It is known that linoleic acid is an irreplaceable polyunsaturated fatty acid, a cholesterol antagonist, and arachidonic acid synthesized from it is a precursor of eicosanoids – a large group of biologically active substances with a wide spectrum of biological action. Linolenic acid plays an important role in the oxygen metabolism of nerve cells, but in edible oil it impairs its taste, so oil with a minimum amount is desirable. The results of the study have shown that the application of retardants leads to a change in the profile of fatty acids and the ratio of unsaturated and saturated fatty acids. In particular, there is an increase in the indicated ratio of the chlormequat chloride action in sunflower and rapeseed oil [177, 180].

Chromatographic analysis of soybean oil made it possible to establish the presence of palmitic (C16: 0), stearic (C18:0), oleic (C18:1), linoleic (C18:2),), α-linolenic (C18:3) and arachidic (C20:0) higher fatty acids [4].

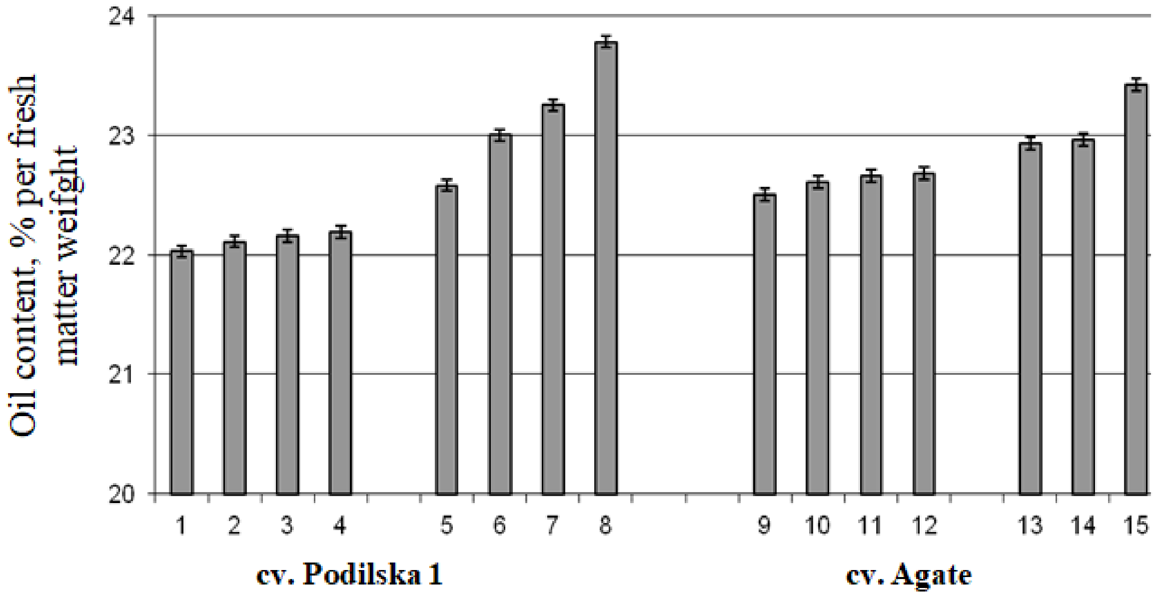

Figure 6.1. The effect of strains and retardants on the oil content in seeds of soybean cv. Podilska 1 (1–8): 1– control; 2 – strain 634 b; 3 – strain 71t; 4 – strain M8; 5 – 634b + 0,5 % CCC; 6 – 71t + 0,5 % CCC; 7 – M 8 + 0,5% CCC; 8 – M8 + 0,3 % dextrel; and cv. Agate (9–15) 9 – control; 10 – strain 634 b; 11 – strain 71t; 12 – strain M8; 13 – 634b + 0,5 % CCC; 14 – 71t + 0,5 % CCC; 15 – M8 + 0,5 % CCC. Average data for 2004-2006.

Our studies indicate changes in the content and ratio of higher fatty acids in soybean oil under inoculation and retardants (Table 6.10.). Analysis of the obtained data indicates an increase in the ratio of unsaturated to saturated fatty acids under the combined influence of strains and retardants, which is an important indicator of soybean oil. Changes in the ratio of higher fatty acids *Bradyrhizobium japonicum* 634b, 71m, M 8 followed by treatment of plants occurred due to an increase in the content of linoleic acid and a decrease in palmitic and stearic acids [39].

It was found the residual amount of chlormequat chloride was 0,006 mg/kg with an allowable rate of 0,1 mg/kg (State Sanitary Rules and Regulations (8.8.1.2.3.4.-000-2001) in Ukraine). Consequently, the proposed regulation for the chlormequat chloride treatment does not lead to the accumulation of excessive amounts of the drug in the seeds.

Thus, the application of chlormequat chloride and dextrel with inoculation had a positive effect on the fatty acid profile, increasing the ratio of unsaturated to saturated fatty acids. The highest quality soybean oil was obtained for the application of 0,3 % dextrel and 0,5 % chlormequat chloride with inoculation M8 strain.

Table 6.10

Fatty acid content in soybean oil of cv. Podilska 1 and cv. Agate under inoculation of *Bradyrhizobium japonicum* strains and retardants (%)

Indicators for cv. Podilska 1		16:0	18:0	18:1	18:2	18:3	20:0	Content of unsaturated higher fatty acids	Content of saturated higher fatty acids	Ratio of unsaturated to saturated fatty acids
2005	Control	9,69±0,04	4,53±0,02	20,22±0,03	55,01±0,03	10,23±0,03	0,32±0,01	14,54	85,46	5,88
	634b	9,47±0,02	4,28±0,06	*19,56±0,04	55,79±0,03	10,51±0,02	0,39±0,02	14,14	85,86	6,07
	634b+0,5% CCC	9,36±0,03	4,25±0,02	19,87±0,02	56,25±0,04	**10,05±0,02	0,22±0,02	13,83	86,17	6,23
	71t	*9,42±0,02	4,25±0,03	20,19±0,04	*56,33±0,02	9,55±0,02	0,24±0,01	13,92	86,07	6,18
	71t+0,5% CCC	9,34±0,04	4,21±0,02	**19,44±0,02	**57,61±0,02	**9,18±0,02	0,22±0,01	13,77	86,23	6,26
	M 8	9,41±0,05	4,40±0,03	19,35±0,04*	*56,20±0,02	10,40±0,01	0,23±0,01	14,04	85,96	6,12
	M 8+0,5% CCC	9,18±0,03	4,49±0,04	19,23±0,02	**57,19±0,03	9,79±0,02	0,12±0,01	13,79	86,21	6,25
	M 8+0,3% Dextrel	9,10±0,03	**3,75±0,02	**19,32±0,03	**57,31±0,03	10,36±0,03	0,15±0,01	13,00	86,99	6,69
2006	Control	9,80±0,04	3,98±0,03	18,58±0,04	57,29±0,04	10,23±0,04	0,12±0,01	13,90	86,10	6,19
	634b	9,70±0,03	3,94±0,03	18,18±0,04	57,90±0,03	10,16±0,02	0,13±0,02	13,77	86,24	6,26
	634b+0,5% CCC	9,36±0,02	3,63±0,01	18,66±0,02	*58,47±0,04	9,75±0,01	0,13±0,02	13,12	86,88	6,62
	71т	9,40±0,03	3,85±0,04	18,32±0,04	**57,77±0,05	10,52±0,02	0,14±0,01	13,39	86,61	6,47
	71t +0,5% CCC	9,22±0,04	3,90±0,04	18,37±0,02	**58,67±0,04	9,70±0,03	0,14±0,02	13,26	86,74	6,54
	M 8	9,61±0,03	3,95±0,03	*17,63±0,04	*58,53±0,02	10,14±0,05	0,13±0,01	13,69	86,30	6,30
	M 8+0,5% CCC	9,38±0,03	3,83±0,04	18,49±0,04	**58,60±0,03	9,66±0,02	0,14±0,01	13,35	86,75	6,50
	M8+0,3% Dextrel	**8,50±0,01	3,38±0,02	**19,62±0,04	**59,00±0,03	**9,36±0,04	0,15±0,01	12,03	87,98	7,31

Notes: 1. * – difference is significant at $p<0,05$ for control. 2. **– for strain 634b.

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6.2. Influence of retardants on yield and product quality of vegetable nightshade and industrial crops.

Our experimental data indicate a significant role of morphological and mesostructural components of donor-acceptor system of tomato plants under the actions of retardants. It was found that retardants with different chemical structures showed different effectiveness of influence on morphogenesis, accumulation and redistribution of carbohydrates and nutrients between plant organs. In particular, the application of triazole-derivative compound folicur on tomatoes led to more significant anatomical and morphological changes during the formation of the leaf apparatus as compared to the ethylene producer esphon: the indicators of the number of leaves, their weight, leaf surface area and leaf index in these experimental variants were higher. The mesostructural parameters of leaves changed in a similar way – the leaf thickness, the main photosynthetic tissue of chlorenchyma, the sizes of assimilative cells of the columnar and spongy parenchyma increase under folicur [90, 91]. Consequently, the 0,025 % folicur treatment of tomato plants in comparison with 0,05 % esphon promoted the formation of a more powerful donor sphere of tomato plants, increased photosynthetic activity of a unit of leaf surface area and a whole plant and an increase in the deposition of photoassimilates and mineral nutrients in vegetative organs of the plant with the subsequent active reutilization of these substances for the carpogenesis needs.

Analysis of the different types of retardants effect on the productivity of tomatoes indicates that the triazole derivative folicur treatment resulted in an increase in crop yield due to an increase in the average weight of one fruit (Table 6.11).

Table 6.11.

Product quality and productivity of tomatoes under retardants treatment in the field condition (average data for 2015-2017).

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

Note: * – difference is significant at $p<0.05$.

It should be noted that the application of drugs significantly increased the total acidity in all experimental variants, while the content of sugars increased and the content of ascorbic acid decreased under the influence of folicur, and the content of sugars decreased under the action of esphon in comparison with control. At the same time, fluctuations in the content of quality indicators of tomatoes under the influence of drugs are within the values typical for a given crops, which did not lead to significant changes in the product quality.

It has been established the positive effect of folicur retardant (active substance - tebuconazole) on the morphogenesis and productivity of sweet pepper. In particular, the number of fruits per plant, the weight of an individual fruit and number of fruits per plant increased and as a result the total fruit yield increased (Table 6.12).

Table 6.12

Influence of gibberellin and folicur on the yield of sweet pepper cv. Antey (average data for 2013-2015)

Indicators	Control	Folicur (0,025 %)
Number of fruits, units	5,8±0,29	*6,6±0,33
Weight of fruits per a plant, g	498,2±24,9	*626,8±31,3
Weight of a fruit, g	85,8±4,2	93,5±4,6
Total yield of fruits from the plot, t/ha	32,8±1,6	*41,7±2,1

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

It was found that the application of 0,025 % paclobutrazol at the budding period of potatoes led to decelaration in growth processes, which was accompanied by a decrease in the leaf area surface with a simultaneous restructuring of the leaf mesostructure. There was a leaf thickening due to the growth of columnar chlorenchyma, and increased in the number and area of stomata on the leaves. Varietal characteristics of potatoes had a significant impact on yield: the greatest increase in yield was observed in late-ripening varieties. No stable increase in yield was observed for early and mid-ripening varieties, however, the number of tubers per bush increased [215].

On sugar beet plants, it was found that the 0,025 % paclobutrazol treatment of plants at the formation of 14-16 and 38-40 leaves increases the yield of root crops by 22 % and sugar content by 1 %. At the same time, the ratio of the dry matter mass of the leaves and root crops decreases. This indicates an increase in the economic efficiency of the crop. It has been established that the treatment of sugar beet plants during the first year of development with 0,3 % dextrel, 0,025 % and 0,05 % paclobutrazol leads to an increase in the seed productivity in the planting method of growing and an increase in the weight of fruits of the smallest fraction. The application of 0,3 % dextrel according to this technology leads to an increase in the germination energy and germination capacity of all seed fractions [203].

6.3. Effect of retardants on yield and quality of berry crops.

The application of chlorocholine chloride on chokeberry, raspberry and strawberry at the early stages of plant development (before flowering) had different effects on the yield and product quality of these crops [101]. Observation of the development of control and experimental chokeberry plants showed that the retardant in the applied concentrations did not have a significant effect on the duration of individual phenophases. In the year of treatment and the year following the treatment, it was noted complete identity of the terms of vegetation, budding, flowering and fruiting. The only difference was that in the year of drug application there was a delay in fruit ripening in all experimental variants by four to six days. The direct effect of chlorocholine chloride on the growth rate of the chokeberry fruits has been established. 1,2 % CCC treatment led to inhibit fruit growth rates compared to controls and, ultimately, to small fruits (Table 6.13).

Analysis of the chokeberry fruits quality in the year of application and in the year following the treatment showed that the drug caused a number of changes in the chemical content and productivity of plants. Two-year data indicate that retardant spraying caused the phenomenon of small fruits, a decrease in the average weight of fruits and bunches in all variants of the experiment and, as a consequence, the yield decreased. The phenomenon of small fruits, later ripening of fruits under the chlorocholine chloride treatment was accompanied by a decrease in the content of sugars, ascorbic acid, and an increase in the total acidity of the fruits. A similar inhibition of plant development was noted on the pear fruits under the 0,1 % paclobutrazol treatment of trees at the flowering phase [19]. The retardant inhibited the development of the embryo sac, which was the reason for the inhibition of fruit development. It is known that the embryo sac is the site of the gibberelin synthesis, and the inhibition of fruit formation by paclobutrazol was associated with blocking the synthesis of these phytohormones.

The application of chlorocholine chloride on raspberry plants is temporarily suspended the intensive growth of replacement shoots and overgrowth and improve the light regime and fruitful nutrition of the shoots. The technology of retardant application involves two-fold processing of the replacement shoots with 1,2 % chlorocholine chloride at a consumption of 1100 l/ha of the working solution twice: the first time - at the height 15-20 cm of the replacement shoots (late April - early May), and the second time - at height 40 - 45 cm of replacement shoots (2 weeks after the first treatment). The study has shown that the application of 1,2 % chlorocholine chloride leads to a significant increase in the yield of industrial plantings of raspberries cv. Novosty Kuzmina and cv. Novokitaevska in the year of treatment and in the following year [101]. Chlorocholine chloride in the applied concentrations promoted the accumulation of sugars in raspberries and did not have a noticeable effect on the accumulation of sugars in strawberries (Table 6.14). The data on the retardant effect on other quality indicators of the product indicate the specificity of its effect. In the year of application, the drug had different effects on the size and weight of berries. Decrease in the size of berries and their weight was observed of strawberries (cv. Kievskuy early), similar to the chokeberry crops.

Chlorcholine chloride did not affect the totall acidity of raspberries. For strawberries, a decrease in this indicator was noted under the action of high concentrations of drug – 1,2 and 2,4 %. In the same crop, the content of ascorbic acid in berries decreased, which clearly correlated with an increase in the concentration of retardant. A decrease in the ascorbic acid content of raspberries was noticeably manifested with an increase in the concentration of the drug from 0,6 to 1,2 %. The subsequent increase in concentration by half (from 1,2 to 2,4 %) had practically no effect on the ascorbic acid content.

Thus, a change in the architectonics of raspberry plants under retardant due to growth inhibition of replacement shoots leads to an improvement in the light regime of fruiting shoots, an open arrangement of flowers and berries, and is an effective means of increasing the crop yield.

The question of the residual amount of retardant in berries is greatly simplified for our proposed method of chlorocholine chloride application of raspberry plants. There is no need for continuous treatment of plants with working solutions for this crop - an increase in plant productivity occurs under the treatment of young replacement shoots, which will bear fruit only the next year after treatment. This selective processing can easily be done on raspberries due to the biological characteristics of this crop. The development cycle of the aerial part of raspberries is two years old - in the spring, overwintered fruitful shoots no longer grow, and fruiting branches with leaves begin to form on them from a height of 40-60 cm with a total shoot length of 1,5-2 m. At the same time, rhizomes begin to develop from the buds annual replacement shoots of chlorocholine chloride treated plants at height of 15-20 and 40-50 cm.

Thus, vegetative shoots are spatially separated from that part of the fruiting shoot where the leaves are located, minimizing the amount of drug that gets on the fruiting shoot and the likelihood of CCC accumulation in the berries. At the same time, we considered it necessary to control the content of residual amounts of chlorocholine chloride in the berries, since there remains the possibility of partial penetration of the drug through the periderm of lower part of the fruitful shoot and through the soil due to the ingress of the working solution onto it. Our data indicate that when chlorocholine chloride treatment of raspberry plants with the proposed method (spraying with a 1,2 % solution of replacement shoots at the early stages of development), the drug does not accumulate in the berries. Chromatograms showed endogenous cholines with an Rf value of 0.44 and there was no specific reaction with 11% phosphoric-molybdic acid and 1 % stannous chloride at the zone of chlorocholine chloride [108].

We also tested ethylene releasing compounds – kamposan, dextrel, and 2-CEPA according to the scheme developed for chlorocholine chloride. The prospects for the drug treatment based on 2-chloroethylphosphonic acid are obvious, since their action is realized through an ethylene-native metabolic product. An increase in the productivity of raspberry plants under ethylene producers was not accompanied by a deterioration in the product quality either in the year of applicaion, or the year following after treatment. The results of the residual amounts of dextrel in raspberries indicate that the drug was used to inhibit the growth of vegetative shoots of

Table 6.13

Effect of chlorocholine chloride on yield and quality of chokeberry products

Concentration chlorocholine chloride, %	Yield of a bush, kg			Weight of berries, g		
	1982 - direct action	1983 - aftereffect	1983 - direct action	1982 - direct action	1983 - aftereffect	1983 - direct action
Control	5,62±0,24	4,70±0,32	4,70±0,23	1,02±0,053	0,94±0,041	0,94±0,041
0,6	*4,83±0,12	—	—	*0,78±0,048	—	—
1,2	*4,80±0,15	3,90±0,34	*3,60±0,34	*0,80±0,051	0,87±0,060	*0,81±0,048
2,4	*4,83±0,21	—	—	*0,82±0,042	—	—

Concentration chlorocholine chloride, %	Weight of a bunch, g			Sugar content, % (1982)	Content of ascorbic acid, g (1982)	Titrated acidity, % (1982)
	1982 - direct action	1983- aftereffect	1983 - direct action			
Control	21,20±3,52	20,60±2,43	20,60±2,43	8,1±0,02	22±0,1	4,26±0,01
0,6	17,90±1,96	—	—	*6,2±0,03	*18±0,2	4,26±0,03
1,2	17,82±2,03	18,20±2,54	17,20±2,13	*6,2±0,02	*17±0,3	*4,31±0,02
2,4	17,19±2,19	—	—	*6,2±0,04	*18±0,1	*4,58±0,04

Note: * – difference is significant at $p<0.05$.

Table 6.14

Chlorcholine chloride application on the fruit weight of raspberries and strawberries plants, titrated acidity, non-aggressive acids and sugars

Concentration chlorocholine chloride, %	Raspberry, cv. Novost Kuzmina					
	Berries weight, g			Titrated acidity, %	Content of ascorbic acid, mg %	Sugar content, %
	1982	1983	1983	1982		
Control	2,38±0,21	2,21±0,12	2,21±0,12	4,45±0,04	21,0±0,1	7,62±0,04
0,6	2,41±0,24	—	—	4,38±0,03	*18,5±0,1	*7,79±0,03
1,2	2,36±0,19	2,20±0,07	2,24±0,14	4,41±0,01	*11,5±0,2	*7,75±0,05
2,4	2,48±0,23	—	—	*4,42±0,02	*11,8±0,3	*7,78±0,01

Concentration chlorocholine chloride, %	Strawberries, cv. Kyivska early				
	Berries weight, g		Titrated acidity, %	Content of ascorbic acid, mg %	Sugar content, %
	1982	1983 (aftereffect)	1982		
Control	7,55±0,77	6,98±0,64	2,05±0,037	80,0±0,2	8,44±0,02
0,6	—	—	—	—	—
1,2	*5,49±0,69	7,10±0,24	*1,68±0,025	*70,0±0,1	8,43±0,04
2,4	*5,35±0,58	6,92±0,37	*1,61±0,019	*56,0±0,3	*8,55±0,03

Note: * – difference is significant at $p<0.05$.

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raspberries in our proposed regulations during the entire harvesting period, the drug was completely absent in berries [74].

The inhibition of the shoot linear growth under the simultaneous rearrangement of the leaf mesostructure for folicur promoted an increase in the synthesis of non-structural carbohydrates and their accumulation in the vegetative organs of gooseberry plants, which increased the carbohydrate reserve for the needs of fruit formation and growth (see Table 3.3). The results of the study indicated that the effect of folicur on the nitrogen, phosphorus and potassium content in the leaves and shoots of gooseberries caused significant changes in the accumulation of these elements. The content of nitrogen, phosphorus and potassium in the tissues of leaves and shoots of gooseberry plants increased under the action of folicur, (see Table 4.1), which contributed to an increase in crop yield (Table 6.15).

Table 6.15.

Influence of folicur on yield of gooseberry cv. Mashenka (average data for 2015-2017)

Indicators	Yield, t/ha	Yield of a bush, kg	Titrated acidity, %	Content of ascorbic acid, %	Sugar content, %
Control	14,2±0,08	2,9±0,92	1,90±0,15	20,8±0,70	7,40,05
Folicur	*18,3±0,05	*3,7±0,07	2,2±0,19	*24,2±0,51	*9,0±0,07

Note: * – difference is significant at $p<0.05$.

Important indicators of the retardant effectiveness are the qualitative characteristics of the product - the content of ascorbic acid, the amount of sugars and total acidity. The results obtained indicate that the application of folicur leads to an increase in the ascorbic acid and sugars content of berries, which is an indicator of improved product quality. A slight increase in the acidity of berries is within the range of fluctuations typical for gooseberries under the different climatic conditions of cultivation.

Therefore, the application of different types of retardants is effective for optimizing productivity and improving the production of berry crops.

CONCLUSIONS

1. The effect of retardants on agricultural plants is mediated by the rearrangement of donor-acceptor relations determined by profound changes in the hormonal complex, growth rate and morphogenesis, leaf mesostructure and the functioning of photosynthetic apparatus, accumulation, temporary deposition and redistribution of flows of assimilates.

2. The decrease in the growth rate of shoots under the influence of retardants with different chemical structures is determined by a significant restructuring of the hormonal complex of the stem. There is a significant decrease in the free gibberellin activity, while the introduction of exogenous gibberellic acid significantly increased this activity. The effect of retardants on the intensity of growth processes and the anatomical and morphological structure of shoots is not limited only to the antigibberellic effect of drugs, but is characterized by changes in the entire hormonal complex, a complex interaction of its components. There was no direct relationship between the content of indoleacetic acid and cytokinins and inhibition of growth processes; however, a decrease in the growth rate was accompanied by an increase in the cytokinins content with a simultaneous decrease in the content of IAA in the stem tissues under the influence of retardants. A clear relationship between the retardant applications and the abscisic acid content has not been established for different crops and the changes were opposite under the action of various drugs. At the same time, a decrease in the ratio of the indoleacetic acid content, gibberellin and cytokinins to the content of abscisic acid was noted under the action of retardant paclobutrazol.

3. Different types of retardants caused changes in the hormonal complex of the leaves. It was observed no direct relationship between the content of IAA and the inhibition of growth processes under the action of drugs, while the content of the active form of cytokinins, zeatin decreased compared to control. The ratio of cytokinin to IAA decreased under the action of retardants, while the content of antagonist of these phytohormones, abscisic acid, increased. The activity of free gibberellins was lower compared to control. Such changes in the hormonal complex contributed to changes in the activity of marginal meristems of plant leaves in a wide range of agricultural crops.

4. The power of acceptor zone had a significant effect on the features of formation and functioning of the leaf apparatus. If only the processes of vegetative growth (raspberry shoots) act as an acceptor of assimilates, the application of retardants led to a decrease in the weight and area of leaf surface of the shoot, a decrease in the number of chloroplasts in chlorenchyma cells. At the same time, an important regularity was observed: the cell volume corresponding to one chloroplast throughout the entire period of research under the influence of retardants was significantly greater than in the control, which indicates significant metabolic, energetic and informational changes in the relationships between the plastome and the cytoplasm. At the same time, the indicator of the ratio of leaf dry matter to stem dry matter increased, which created the prerequisites for the accumulation of an excess of non-structural carbohydrates (starch) in intermediate funds of different

levels. As a result, the share of photosynthetic products for the processes of vegetative growth decreases. The limitation of donor function of leaves under the retardant action is also due to a significant increase in respiratory costs. The acceptor sphere of plants is not limited only to vegetative growth, but also includes the processes of carpogenesis (winter rape, soybeans, sunflower, oil flax, oil poppy, tomatoes), under the influence of retardants, the weight of leaves and the total leaf area increased due to intensive stem branching. The thickness of chlorenchyma layer increased and the photosynthetic activity of a unit of leaf surface increased, which creates the prerequisites for increasing the productivity of agricultural crops.

5. The application of retardants leads to a more intensive accumulation of non-structural carbohydrates (sugars and starch) in the vegetative organs of plants during the fruitification period, followed by active reutilization of these substances for the formation and growth of fruits. The stem plays an important role as a temporary depot of assimilates, which is enhanced under the influence of drugs with an antigibberellin mechanism of action. In the second half of the fruitification period, the non-structural carbohydrates content decreases in the stem and roots as a result of their reutilization for the carpogenesis. The slowdown in the growth of vegetative barren shoots (raspberries) is accompanied by a decrease in the content of sugars, reducing sugars and sucrose during the entire period of plant growth with a simultaneous increase in starch content. Thus, free sugars, which are normally transported to the acceptor zones, polymerize more intensively, forming a reserve starch under the influence of retardant. Control over photosynthesis with a decrease in the "sink" for assimilates by the main acceptor - the growing shoot - is carried out according to the feedback mechanism. This relationship is mediated by the effector effect of excess starch and changes in the balance of phytohormones - the accumulation of abscisic acid and a decrease in the activity and content of gibberellins and auxins in leaf tissues.

6. Significant changes occur in the content and ratio of mineral nutrition elements in the tissues of the experimental plants under the action of retardants. There is a decrease in the ratio of monovalent and bivalent cations due to a slowdown in the supply of potassium tissue and an increase in the calcium content in raspberry shoots. The nitrogen content increases and the formation of protein in the vegetative organs of bush berry crops increases, while the regulation of the nitrogen compounds exchanges under the influence of retardants is mediated by donor-acceptor relations. A decrease in the capacity of acceptor zone of black chokeberry plants under the action of chlormequat chloride in the second half of the growing season as a result of small fruits of fruits slowed down the outflow of nitrogenous compounds and an increase in their concentration in the vegetative organs of the plant. An increase in the yield of gooseberry plants under the action of folicur promoted the outflow of nitrogen-containing compounds, phosphorus and potassium from the vegetative organs of the plant to the fruits. It has been established the essential role of the stem and roots in the temporary accumulation of nutrients in plants and the intensive use of these elements in the processes of carpogenesis.

7. The application of retardants paclobutrazol and chlormequat chloride at the budding phase of soybean plants with pre-sowing bacterization of seeds with highly

effective strains *Bradyrhizobium japonicum* leads to the correction of donor-acceptor relations in the plant, contributes to the formation of a more powerful sphere, enhanced formation of soybean-rhizobial complexes and an increase in their nitrogen-fixing activity. The application of retardants with *B. japonicum* strains promoted the activation of nitrogenase complex and nitrate reductase in leaves at the flowering phase and its decrease in the phase of bean formation. Nitrogenase activity in plants increased and the peak of activity shifted to a later stage of ontogenesis for compatible application of *B. japonicum* strains and retardants. The increased branching of stem and the establishment of a larger number of flowers and beans, the formation of a larger leaf surface and the growth of photosynthetic activity per unit leaf area improved nitrogen nutrition due to the optimization of nitrogenase and nitrate reductase activity, the combined use of seed bacterization with tuberous bacteria and strains.

8. Reorganization of donor - acceptor relations under retardants action, changes in the formation and functioning of the photosynthetic apparatus, the features of assimilates accumulation and their distribution between plant organs significantly influenced the productivity of agricultural crops. The formation of a more powerful photosynthetic apparatus was observed for oilseed plants (winter rape, soybeans, oil flax, oil poppy), due to increased stem branching, the formation of a larger number of leaves, an increase in the weight of leaves and leaf area, optimization of the mesostructure, chlorophyll and leaf indices growth of the plant. The consequence of such changes was an increase in the net photosynthetic productivity and an increase in crop yields, an improvement in product quality. The combined use of mixtures of retardants with synthetic growth stimulants (emistim C, treptol) turned out to be promising for optimizing the production process of oilseeds. Retardants caused similar morphological, anatomical and physiological changes in vegetable nightshade crops - sweet peppers, tomatoes, potatoes, which also led to an increase in yield. Treatment with retardants of various chemical structures of sugar beet plants during the formation of 14-16 and 38-40 leaves increased the yield of root crops and the sugar content in them. Such treatment led the next year to an increase in the seed productivity of mother plants in the planting method of cultivation, as well as to an increase in the germination energy and germination of all fractions of seeds. The use of retardants on plants of berry crops led to opposite effects. There was a decrease in yield due to the phenomenon of small-fruited chokeberry and strawberry, however, the yield of gooseberry significantly increased. In raspberry plants, the treatment of bushes at the early stages of development with retardants caused a significant increase in yield due to changes in the architectonics of plantings, a slowdown in the growth rate of replacement shoots, an improvement in the conditions for the existence of fruiting shoots and an open arrangement of flowers and berries. With the applied regulations for processing plants of agricultural crops with retardants, the residual amounts of drugs did not exceed the established norms.

9. The application of gibberellin and antigibberellic drugs is an effective method of artificial reconstruction of donor-acceptor relations during the period of germination of the vegetative organs (potatoes, onions, rhizomes) and seeds with various types of reserve compounds. The use of this approach makes it possible to

establish the role of the hormonal factor in the reserve substances utilization during the heterotrophic phase of plant development. The free forms of gibberellins content significantly decreased and the bound forms of gibberellins content increased under the action of paclobutrazol in potato sprouts. At the same time, the content of free and bound forms of abscisic acid increased simultaneously. Thus, the growth inhibitory effect of antigibberellin drug was realized primarily due to decrease in the activity of free gibberellins in sprouts, which makes it possible to apply retardant treatment of potato tubers to prolong the dormancy period and preserve their quality. Blocking the gibberellin synthesis by retardants in oil seeds (sunflower, pumpkin) led to a decrease in the activity of acid and alkaline lipases, a slowdown in the hydrolysis of the reserve oil, significant changes in the acid value and saponification value, and the iodine valuer in oil during germination. Gibberellic acid stimulated, and the retardant paclobutrazol slowed down the use of free higher fatty acids in the processes of morphogenesis. The higher value of the coefficient of use of reserve substances under the gibberellin action in the seeds of corn (reserve substance starch) and beans (reserve substance protein) was determined by more intensive hydrolysis of these biopolymers. As a result of the retardant action, the processes of using reserve substances and the rate of germination slowed down. The growth inhibitory effect of light increased with a decrease in the gibberellin synthesis under the influence of retardants, which indicates that gibberellins are active modifiers of the photoreceptor system of plants.

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SCIENTIFIC EDITION

MONOGRAPH

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Authors:
KURYATA VOLODYMYR GRYGOROVYCH

POPROTSKA IRYNA VOLODYMYRIVNA

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