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ANATOMIC-PHYSIOLOGICAL CHANGES IN HORSE BEAN SEEDLINGS UNDER THE INFLUENCE OF GIBBERELLIN AND TEBUCONAZOLE AT CONDITIONS OF PHOTO- AND SCOTOMORPHOGENESIS

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The combination of light/dark external factor, GA₃ and GA₃ synthesis inhibitor tebuconazole significantly changed the pattern of the source-sink relationship in sprouts of horse bean during seed germination. The usage of gibberellin at light leads to increase of reserve starch hydrolysis in germinating horse bean seeds. The absence of light was a more significant factor for the starch hydrolysis than the exogenous use of gibberellin and the antigibberellin substance tebuconazole. The nitrogen-containing compounds content and reserve fats at early stages of germination in cotyledons did not change significantly, indicating less intensive use of these compounds for morphogenesis during this period. Seed germination was accompanied by a decrease under the action of gibberellin at light, and under the action of tebuconazole — an increase, in root and epicotyl diameter due to the peculiarities of histogenesis. Under the influence of gibberellic acid, total epiblem and the primary root cortex thickened at light, and the epidermis and the primary cortex of hypocotyl — at light and dark. The opposite change was caused by tebuconazole — the increase of tissue complex thickness occurred under both photo- and scotomorphogenesis conditions. The number of xylem vessels in the vascular-fibrous bunches in roots increased under the influence of tebuconazole in dark. In epicotyls, the increase occurred in the number of vessels in bunches under the action of tebuconazole both at light and in dark. Insofar as histogenesis is controlled by phytohormones, established histological changes indicated a significant re-structuring of the entire hormonal complex of seedlings.

Key words: *Vicia faba* L., morphogenesis, source-sink system, seed germination, light, gibberellins, retardants.

One of the most important external factors that significantly affect morphogenesis is light. The ability to switch between scotomorphogenetic and photomorphogenetic development is essential for seedling survival. Central to this mechanism is the photoreceptor system (including phytochromes, cryptochromes and phototropin), which regulate the activation of photomorphogenesis [1]. In this case, the excitation of one photoreceptor can enhance or inhibit the action of another [2]. The light spectral composition and intensity have a significant effect on seedling growth. Destruction

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of the leaf columnar parenchyma was observed during prolonged exposure to red rays in cucumber plants, while the spongy parenchyma, which assumes the main functional load, undergoes minor changes [3]. Plants that germinate in complete darkness develop a program of scotomorphogenesis, characterized by elongation of the epicotyl or hypocotyl, the formation of a hypocotyl loop, yellowing of cotyledons and corrugated first leaves formation, reducing the leaves number in future [4, 5]. In dark, plants form underdeveloped conductive structures; the apical meristem contains proplastids and etioplasts instead of full-fledged chloroplasts. In this case, monocotyledonous and dicotyledonous plants differ in the morphology of seedlings that are grown at light and dark [6].

Today it is known that light can modify the growth and morphogenesis of plants through the restructuring of the hormonal complex, which is a mechanism of influence on source-sink system [7, 8]. The initial stages of photomorphogenesis are accompanied by active metabolic changes, phytochrome modification of the hormonal status of seedlings, transport and formation of phytohormones gradients, in particular gibberellins, in the plant, and changes in the rate of natural inhibitors [9, 10]. The use of gibberellic acid biosynthesis inhibitors reduces the cells number and longitudinal growth of stem cells, roots, leaves narrow, reducing the ratio of linear size of shoots relative to roots, leaves become dark green and delayed aging in phototropic plants [11,12].

On the soil surface, light acts as the main exogenous agent that inhibits the activity of the main protein-suppressor of photomorphogenesis COP1, which is synthesized in the nuclear space. Light determines the activity of other transcriptional regulators that provide the realization of gibberellin (DELLA) and brassinosteroids (BZR1/BES1) signals, as well as activate trans-factors such as HY5, which initiate the transition to autotrophic nutrition [13]. Because phytohormones are included in the light signal transduction system, many of the light-regulated plant development factors also respond to the treatment of plants with hormones [14].

Changes in the growth rate of different seedling organs under conditions of photo- and scotomorphogenesis are obviously accompanied by differences in the rate of use of reserve substances deposited in the cotyledons, resulting in changes in the degree of tension between source and sink activity. In some works, data are presented that indicate the possibility of regulating the rate of reserve compounds utilization for the needs of growth and development by external and internal factors [7, 15, 16].

The aim of our study was to establish the effects of gibberellin and its antagonist tebuconazole on the functioning of the system depot of assimilates—growth during the germination of horse bean seeds under conditions of photo- and scotomorphogenesis.

Materials and methods

The work was carried out on seedlings of horse beans (*Vicia faba* L.) of Vivat variety. This is a medium-ripe variety with a growing season of 100—105 days. It is high-yielding — potential seed yield is 4.9 t/ha. Grain protein content is 34.3 %. Vitamin C content is 1.4 mg per 100 g. Total sugar

content is 5.7 %. It is technological, resistant to major diseases. It has high resistance to lodging, shedding of beans and spalling.

The combined effect of light or darkness, gibberellic acid and gibberellin antagonist tebuconazole was used to create different tensions of source-sink relations during horse bean seeds germination. The seeds were soaked for 24 hours in a 0.025 % aqueous solution of gibberellic acid (GA₃) or tebuconazole (TBZ) at concentration 0.05 %. Gibberellic acid is a white crystalline substance with a molecular weight of 346.2 Da, the molecular formula is C₁₉H₂₂O₆. Melting point is 227 °C. The substance is poorly soluble in water and soluble in organic solvents. Gibberellic acid is a low-toxic compound and belongs to the 3rd class of toxicity. LD₅₀ for rats is 15630 mg/kg. It does not show carcinogenic, blastomogenic, skin-resorptive and embryotoxic properties. The residual content of the substance is not normalized, due to its presence in plants as a native metabolite.

Tebuconazole (C₁₆H₂₂ClN₃O, 4,4-dimethyl-3-(1H-1,2,4-triazol-1-ylmethyl)-1-n-chlorophenyl-pentan-3-ol) [26]. It is a transparent crystalline substance with a molecular weight of 307.8 Da and a melting point of 104.7 °C. It is low-toxic for warm-blooded animals, and the LD₅₀ for rats is 3.9–5.0 g/kg. It is the drug of 3rd danger class. In control variant, the seeds were soaked in distilled water.

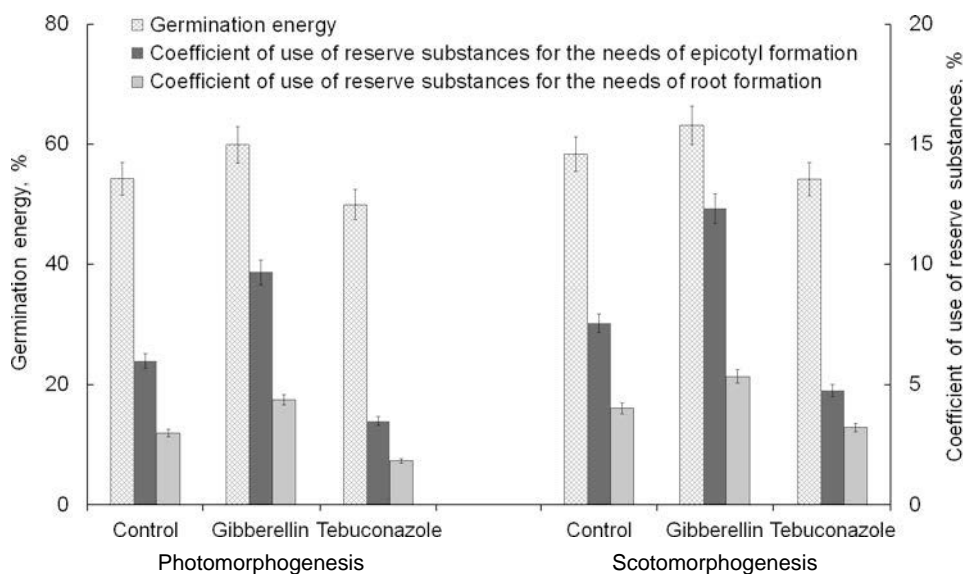
Seeds were sown in ditches with damp sand. Biological repeatability was fivefold. The experiment was performed at the action of light (about 500 lux) and in dark in order to study the implementation of programs of scoto- and photomorphogenesis. Microscopic investigations were performed using a microscope «Mikmed-1» and an ocular micrometer MOV-1-15x. The analytical repeatability of anatomical measurements was twentyfold. Germination energy was determined on the 3rd day of germination. The coefficients of seed reserve substances use for the needs of epicotyl and root formation were defined as the ratio (in percent) of dry matter mass of organ and total seedling dry matter mass on the 18th day.

At the same time, the content of reserve compounds in cotyledons was determined according to the variants of the experiment. Determination of starch content in cotyledons was performed by iodometric method, fat content — by quantitative extraction using Soxhlet extractor, total nitrogen — by Kjeldahl [17].

The analytical repeatability of studies was fivefold. Statistical processing of the results was performed using the software package Statistica 6.0. The reliability of the difference between control and experiment was determined by Student's t-test. The tables and graphs show the arithmetic mean values and their standard errors.

Results and discussion

The results of the study show that dark stimulated seed germination — this process occurred faster than at light. The treatments significantly affected the rate of seed reserves utilization for growth processes (Figure). The indices of germination energy and the coefficients of seed substances use for the needs of epicotyl and root formation had the opposite effect under the action of gibberellin and retardant tebuconazole.



The effect of light, gibberellin and tebuconazole on germination energy and the rate of seed reserves use on the formation of seedling organs

Starch is the basic reserve substance of horse bean seeds, so it is essential to analyze the dynamics of shifts in this reserve polysaccharide content in cotyledons during germination under the growth regulators (GR) action. Among other leading factors of gibberellins influence on seed germination is the ability to stimulate α -amylase release by the embryo into the endosperm, which contributes to starch grains splitting [18]. Our results indicate a significant light effect on the starch hydrolysis rate during seed germination (Table 1). The starch use rate in seed was much higher under conditions of germination in the dark. Gibberellin stimulated starch breakdown simultaneously in light and in dark, but the effect of the antigibberilline substance TBZ on the polysaccharide hydrolysis rate has not been established. It is known that triazole compounds, include TBZ, do not affect the activity of previously synthesized gibberellin, but only block its neoplasm [19]. Obviously, the horse bean seeds have a sufficient amount of gibberellins reserved for rapid starch hydrolysis at the early stages of seedling germination.

Previously, we found a significant accumulation of sugars at light and under TBZ action in cotyledons [20]. This may indicate that the slower epicotyl and root formation in TBZ-treated seedlings is associated with not only a deceleration of starch hydrolysis, but also with an inhibition of the use and outflow of sugars under retardant influence. However, it should be noted that light presence or absence during germination was a much more significant factor for the hydrolysis of starch than the use of GR.

There are only limited details on gibberellins and retardants effect on the use of non-starch reserve substances during germination, in particular proteins and lipids [21, 22]. Our results indicate a slower use of nitrogen-containing compounds compared to reserve carbohydrates in germination of bean seeds. Changes in nitrogen content in cotyledons of scotomorph and photomorph plants on the 18th day of germination were much smaller than changes in starch content. The use of gibberellin and tebu-

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TABLE 1. The effect of light, gibberellin and tebuconazole on the content of starch, total nitrogen and oils in cotyledons of horse beans (% of dry weight)

Treatment	Starch		Total nitrogen		Fat	
	a	b	a	b	a	b
Control	24.17±1.11	15.20±0.76	4.74±0.24	4.26±0.21	0.68±0.03	1.04±0.05
GA ₃	22.31±0.11*	15.20±0.75	4.54±0.23	4.57±0.22	0.92±0.05*	0.57±0.03*
Tebuconazole	22.17±1.20	15.52±0.56	4.04±0.20*	3.64±0.18*	0.50±0.02*	0.49±0.02*

Notes: * the difference is significant at $p \leq 0.05$; a — photomorphogenesis; b — scotomorphogenesis.

conazole did not lead to considerable changes in nitrogen content in cotyledons. According to previously data obtained, deep protein hydrolysis and nitrogen-containing compounds use for the processes of organogenesis is started after intensive starch hydrolysis. In particular, this trend was established during the germination of maize seeds: starch is used primary, and protein compounds are used at later stages of germination [23].

Horse bean seeds contain a small amount of oil. Analysis of the residual fat content in cotyledons shows that germination at light was accompanied by an increase in oil content under the action of gibberellin and a decrease in it under the action of TBZ compared to control. In our opinion, this is due to the peculiarities of the substance biodilution under the action of GR: the relative fat content increases due to the more intensive starch use under the action of gibberellin. The opposite trend was observed under tebuconazole action. Oil content decreased in cotyledons under the action of both GA₃ and TBZ, at conditions of scotomorphogenesis. This specificity of the seeds reserve oil use in dark requires further study.

Changes in the reserves use in germinating seed are determined by the growth centers demand, and the processes of organogenesis, which are the main sink of these substances during heterotrophic development. It is established that the use of antigibberellin GR (retardants) leads to inhibition of linear growth and changes in morpho — and histogenesis of plants [24–26]. In particular, structural changes in the anatomy of the tobacco plants stem were detected both under the light influence and under the action of GA₃. The accumulation of lignin in cell walls was regulated primarily by light, regardless of gibberellin effect and its concentration [27]. It should be noted that the effect of gibberellins and retardants was studied mainly on the growth processes rate and the formation of secondary stem structure [8, 28], the features of the primary structure of vegetative organs remain barely explored.

Gibberellins are known to regulate the synthetic processes, transport and biological activity of apical meristem, activating hormones, and inhibit the development of lateral meristems. The primary and secondary growth sites are spatially separated, and cellular hormonal signals coordinate the growth rate between the apical and lateral populations of meristematic cells [27]. Therefore, insofar as the action of gibberellin and tebuconazole changes the growth rate of seedlings at light and in dark, it is relevant to analyze the histological and anatomical changes in them during germination (Table 2).

TABLE 2. The effect of gibberellic acid and tebuconazole on the anatomical structure of horse bean seedlings under conditions of photo- and scotomorphogenesis

Indices	Control		Gibberellin		Tebuconazole			
	a		b		a		b	
	a	b	a	b	a	b	a	b
Root thickness, μm	Root							
	3133 \pm 141	3085 \pm 139	2555 \pm 122*	2967 \pm 159	3579 \pm 166*	2937 \pm 127		
Total thickness of epiblem and primary bark, μm	758 \pm 33	771 \pm 33	721 \pm 32	837 \pm 32	945 \pm 42*	874 \pm 38*		
Stele diameter, μm	1617 \pm 80	1543 \pm 77	1113 \pm 55*	1292 \pm 64*	1689 \pm 84	1189 \pm 59*		
Quantity of vessels in xylem bundles, units	6.1 \pm 0.3	6.8 \pm 0.34	6.3 \pm 0.3	5.5 \pm 0.2*	5.7 \pm 0.2	8.3 \pm 0.4*		
Diameter of xylem bundles, μm	35.9 \pm 1.7	27.9 \pm 1.3	35.5 \pm 1.2*	36.4 \pm 1.8*	54.7 \pm 2.7*	37.0 \pm 1.8*		
Epicotyl thickness, μm	Epicotyl							
	3177 \pm 127	3320 \pm 125	2811 \pm 121*	2367 \pm 113*	3742 \pm 145*	2872 \pm 147*		
Total thickness of epidermis and primary bark, μm	627 \pm 25	822 \pm 36	541 \pm 23*	634 \pm 28*	831 \pm 36*	860 \pm 38		
Stele diameter, μm	1923 \pm 96	1677 \pm 83	1729 \pm 86*	1098 \pm 54*	2080 \pm 104*	1152 \pm 57*		
Quantity of vessels in xylem bundles, units	6.4 \pm 0.3	9.8 \pm 0.4	6.2 \pm 0.3	8.46 \pm 0.4*	11.0 \pm 0.5*	10.6 \pm 0.5		
Diameter of xylem bundles, μm	35.8 \pm 1.7	23.5 \pm 1.1	28.6 \pm 1.4*	26.2 \pm 1.3*	32.6 \pm 1.6	29.8 \pm 1.4*		

Notes: * the difference is significant at $p \leq 0.05$; a — photomorphogenesis; b — scotomorphogenesis.

Analysis of the anatomical structure of scoto- and photomorphogenic seedlings indicates a significant effect of gibberellin and antigibberellin substance tebuconazole on root and epicotyl primary structure. Under the conditions of photomorphogenesis, there was an apparent decrease in root thickness at GA3 action and its thickness increase under the influence of tebuconazole. The same formation process direction was observed for epicotyl. Significant difference was not observed in root thickness under gibberellin action in seedlings developed in dark, but epicotyl thickness decreased under the TBZ action. The changes were determined by the peculiarities of stele and cortex histogenesis of organs. Under gibberellin action, the total epiblem and primary bark thickness of root, and epidermis and primary bark of epicotyl decreased, however these indices increased in photomorphogenic seedlings under tebuconazole action. Similar changes occurred in stele of root and epicotyl under the action of GR. The decrease in stele diameter was observed under gibberellin action in scotomorphogenesis conditions. The same peculiarities were observed only in dark under tebuconazole action, but at light the thickness of this tissue complex even increased. During photomorphogenic development, the number of vessels in vascular-fibrous bundles of root did not change under the action of gibberellin, but increased under tebuconazole influence. The number of vessels under the influence of gibberellin in epicotyl also did not change under photomorphogenesis conditions, but increased under the action of tebuconazole. A similar effect of another triazole substance paclobutrazol on the xylem formation was found in potatoes [29]. During development in dark, the number of vessels in root under gibberellin treatment was smaller compared to control, but increased by the action of tebuconazole. A similar pattern was established for the development of epicotyl under scotomorphogenesis conditions. At the same time, diameter of root xylem vessels significantly increased both at light and in dark due to tebuconazole action, and under gibberellin action diameter increased only during development in dark. Vascular diameter in epicotyls increased both under the action of gibberellin and tebuconazole during development in dark.

Thus, the use of gibberellin under the presence of light leads to increased reserve starch hydrolysis in germinating horse bean seeds. The absence of light was a more significant factor for the hydrolysis of starch than the exogenous use of gibberellin and antigibberellin drug tebuconazole. The content of nitrogen-containing compounds and reserve fats (oils) at the early stages of germination in cotyledons did not change significantly, indicating less intensive use of these compounds for morphogenesis during this period. Seed germination at light under the action of gibberellin was accompanied by a decrease, and under the action of tebuconazole — by an increase in the root and epicotyl diameter due to the peculiarities of histogenesis. Total thickness of epiblem and primary root cortex at light, and epidermis and primary cortex of epicotyl at light and in dark decreased under the influence of gibberellic acid. Tebuconazole caused the opposite change — the thickness increase in this tissue complex occurred under both photo- and scotomorphogenesis conditions. Under the influence of tebuconazole in dark, the number of xylem vessels in vascular-fibrous bundles of root increased. In epicotyls, the increase in the number of vessels in

bundles under the action of tebuconazole occurred both at light and in dark. Insofar as histogenesis is controlled by phytohormones, the established histological changes indicate a significant re-organization of the entire hormonal complex of seedling under the light, exogenous gibberellin and its antagonist tebuconazole action.

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АНАТОМО-ФІЗІОЛОГІЧНІ ЗМІНИ У ПРОРОСТКАХ КІНСЬКИХ БОБІВ ПІД ВПЛИВОМ ГІБЕРЕЛІНУ І ТЕБУКОНАЗОЛУ В УМОВАХ ФОТО- І СКТОМОРФОГЕНЕЗУ

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Комбінування зовнішнього (світло/темрява) чинника, гіберелової кислоти та інгібітора синтезу гіберелінів тебуконазолу в період проростання насіння істотно змінювало характер донорно-акцепторних відносин у проростках кінських бобів. Застосування гібереліну за наявності світла приводить до посилення гідролізу резервного крохмалю проростаючого насіння кінських бобів. Відсутність світла виявилася для гідролізу крохмалю істотнішим чинником, ніж екзогенне застосування гібереліну та антигіберелінового препарату тебуконазолу. Вміст азотовмісних сполук та резервних жирів у сім'ядолях на перших етапах проростання істотно не змінювався, що свідчить про менш інтенсивне використання цих сполук на потреби морфогенезу в цей період. Проростання насіння на світлі за дії гібереліну супроводжувалося зменшенням, а за дії тебуконазолу — збільшенням діаметра кореня й епикотилія внаслідок особливостей

гістогенезу. Під впливом гіберелової кислоти сумарна товщина епіблеми та первинної кори кореня на світлі, а в гіпокотилі — епідермісу та первинної кори на світлі і в темряві зменшувалася. Тебуконазол спричинював протилежну зміну — зростання товщини цього тканинного комплексу відбувалося як за умов фото-, так і скотоморфогенезу. Під впливом тебуконазолу в темряві зростала кількість судин ксилеми в судинно-волокнистих пучках кореня. В епикотилі зростання кількості судин у пучках за дії тебуконазолу відбувалося як на світлі, так і у темряві. Оскільки гістогенез контролюється фітогормонами, встановлені гістологічні зміни свідчать про істотну перебудову всього гормонального комплексу проростка.

Ключові слова: *Vicia faba* L., морфогенез, донорно-акцепторна система, проростання насіння, світло, гібереліни, ретарданти.