

Effect of gibberellin on the use of reserve substances deposited in *Vicia faba* L. seeds at the phase of heterotrophic development under the conditions of photo- and skotomorphogenesis

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Under conditions of a combination of an external (light/dark) factor and a hormonal factor (gibberellic acid) during germination, changes in the functioning of the source-sink system in heterotrophic phase of horse beans development were studied. The increase in the epicotyl, root and seedling length, both in light and dark, as well as in the dry matter of the mass of the seedling organs, was found under drug action. Reserve substances were used more intensively under gibberellin and skotomorphogenesis influence. It is evidenced by the minimum dry matter of cotyledons and higher reserve utilization rates for root and epicotyl formation. Gibberellin stimulated starch breakdown in both, but during germination in dark, the rate of starch use was higher. Other content of sugars in skotomorphic seeds was associated with more intensive outflow for organogenesis needs: formation of root and epicotyl structures. The changes in the content of starch were higher than the changes in nitrogen content in skotomorphic and photomorphic seedlings. This indicates that gibberellin stimulates hydrolysis of reserve protein only after starch hydrolysis in dark. No specific gibberellin regulation of phosphorus and potassium outflow from seeds for organogenesis needs was found, suggesting sufficient mineral nutrients supply to ensure their re-utilization during germination, photo- and skotomorphogenesis processes.

Keywords: morphogenesis, source-sink system, seed germination, light action, gibberellins

INTRODUCTION

Understanding the mechanisms of regulation of the source-sink system of the plant is important due to the ability of eventual exogenous regulation of physiological processes as well as growth rate optimization, the assimilates redistribution of flow according to the needs of fruit formation and growth (Bonelli et al., 2016; Kuryata, Golunova, 2018). The interaction of growth and photosynthesis is the most studied aspect of this concept. Photosynthesis is considered a donor (source) of assimilates, and growth their acceptor (sink) (Yu et al., 2015; Kuryata, Kravets, 2018; Kuryata, Khodanitska, 2018). These relationships in plants are regulated at different levels (Matysiak, Kaczmarek, 2013; Savage et al., 2015; Sugiura et al., 2015; Humplík et al., 2015). At the same time, the issues of functioning of this system at the heterotrophic phase of plant development as the period of seeds germination and formation of other reserve organs remain practically undeveloped. The peculiarities of the use of spare substances of different chemical structures for the needs of organogenesis also remain little known.

Light is one of the external factors that have significant effect on morphogenesis and one of the most important ones. The discovery of light-sensitive photoreceptor proteins, which are activated by red, far-red, blue/UVA, and UVB light, helped to further understand the plants' response to light (Higuchi and Hisamatsu, 2016). Plants have four main groups of photoreceptor proteins: phytochromes (up to five different types with partially different functions), cryptochromes (two types), phototropins (two types), and UVR8. Signal transmission from them is not a simple circuit: they form a network, and the action of one photoreceptor can cause the enhancement or inhibition of the excitation of another (Jiang, Li, 2015). Spectral composition and light intensity have a significant effect on seedling growth. Thus, some studies noted that the strongest inhibition of growth of potato sprouts was caused by red light (660 nm) at low irradiation intensities, while red light with a wavelength of 735 nm at higher radiation doses

had the strongest inhibition effect on the growth (Molmann, Johansen, 2019). Another paper shows that a high calcium and pectin content was noted in the cell walls of tomato seedlings that grew under blue and white light contributing to the low cell wall elongation and growth retardation. A decreased level of calcium and pectin was found in seedlings grown in dark and in bright red light. Gibberellic acid enhanced the growth of epicotyl in blue light (Falcioni et al., 2020). Due to the activity of the photoreceptor system, light activates the photomorphogenesis programme (Hornitschek et al., 2012; Wu, 2014; Franklin, 2016) ensuring the structuring of chloroplasts, the formation of developed green leaves, and the transition to entire photosynthesis. In complete darkness, plants develop according to the programme of skotomorphogenesis: they form a hypocotyl loop, yellow cotyledons, and elongated epicotyl or hypocotyl. Rapid elongation of these organs is provided by the intense light output, and the tightly folded apical loop gives an opportunity for easy passage through soil or other substrates protecting small unfolded cotyledons and submeristematic tissues from damages. This strategy of growth guarantees that limited sources of seed are used as effectively as possible. It is a prerequisite for the survival of photoautotroph (Josse, Halliday, 2008). Monocotyledonous and dicotyledonous plants grown in light and in dark differ from one another in the morphology of seedlings. During the etiolation process, axial organs and leaves of dicotyledonous plants are stretched in length. In monocotyledonous plants, only the internodes of the stem (hypocotyl, epicotyl) are stretched, and the primary leaves and cotyledons are little changed (Bhatla, 2018).

Among the internal regulating factors of the tension in source-sink relations, the hormonal system plays the key role. Nowadays, it has been established that the growth and morphogenesis of plants can be modified due to light through the rearrangement of the hormonal complex (Kutschera, Briggs, 2013; Wu, 2014; de Wit, Pierik, 2016). In particular, it is known that the meristematic activity is controlled by the phytohormones gibberellins (Hedden,

Thomas, 2016). The *AtGA3ox1* biosynthesis gene has a positive effect on the phytochrome activity, by increasing the level of bioactive gibberellins. It was found that the formation of GA 2-oxidases is blocked by red light, which leads to a significant increase in gibberellin level during lettuce seeds germination under red light action (Nakaminami et al., 2003). The stretching of the etiolated hypocotyls of seedlings is suppressed by blue light, similar to the mechanism in arabidopsis. This mechanism depends on phytochrome photoreceptor and, in particular, on the encoding of enzymes of gibberellins biosynthesis and enzymes associated with cell wall metabolism. (Folta et al., 2003).

The changes in growth intensity in different organs of the seedling grown under photo- and skotomorphogenesis conditions are accompanied by differences in the intensity of the use of reserve substances in the stock organs, resulting in the changes in tension degree between source and sink activity. Some papers present data that indicate the possibility of regulating the utilization rate of reserve compounds for growth and development by external and internal factors (Kutschera, Briggs, 2003; Kuryata, Polyvanyi, 2018) In reference to that, the purpose of this work was to establish the influence of gibberellin on the deposit of assimilates – growth system functioning during the germination of horse bean seeds under conditions of photo- and skotomorphogenesis.

MATERIALS AND METHODS

The work was carried out with seedlings of horse beans (*Vicia faba* L.) of the variety Vivat. This is a medium-ripe variety with a growing season of 100–105 days; high-yielding, potential seed yield 4.9 t/ha, the grain content of protein 34.3%, vitamin C 1.4 mg per 100 g, total sugar 5.7%. It is technological, resistant to major diseases, has a high resistance to lodging, shedding of beans, and their cracking.

The combined effect of light and gibberellic acid was used to create different tensions of source-sink relations during the germination of horse bean seeds.

The seeds were soaked for 24 hours in an aqueous solution of gibberellic acid (GA3) at a concentration of 250 mg/l. Gibberellic acid is a white crystalline substance with a molecular weight of 346.2 D, the molecular formula is $C_{19}H_{22}O_6$. The 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 third class of toxicity. LD50 for rats is 15 630 mg/kg. It does not show carcinogenic, blastomogenic, skin-resorptive, or embryotoxic properties. The residual content of the drug is not normalized, because in plants it is present as a natural metabolite. The drug is non-toxic to bees and other insects and of low toxicity to fish. It is used as a plant growth regulator. The drug is prepared by fermentolysis of fungi of the species *Gibberella fuljukoii* and *Fusarium moniliforme* (Hedden, Thomas, 2016).

The seeds of the control variant were soaked in distilled water. Seeds were sown in ditches with wet sand, and the biological repeatability was fivefold. The experiment was performed under the action of light and in dark in order to study the implementation of programmes of skoto- and photomorphogenesis. Morphobiometric parameters (root length, seedling length, dry matter weight of individual organs and the whole plant) were determined on day 18 of germination.

Determination of the content of non-structural carbohydrates (sugars and starch) in the organs of seedlings was performed by the iodometric method, phosphorus content was determined by the intensity of the formation of phosphorus-molybdenum complex, potassium by flame-photometric method, and the content of total, protein and non-protein by the Kjeldahl method (AOAC, 2010). 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 figures show arithmetic mean values and their standard errors.

RESULTS AND DISCUSSION

The obtained data analysis shows that under conditions of skoto- and photomorphogenesis, gibberellic acid significantly affects the growth rate of seedling organs and the intensity of utilization of seed reserves for growth processes (Table 1).

There was a significant increase in the length of epicotyl, root, and seedling in general, both in light and in dark. The effect of phytohormone was more visible under the skotomorphogenesis condition. The mass of the dry matter of the organs of the seedling also increased. The use of seed reserves was slower in light than in dark, but these processes were stimulated by gibberellin. Spare substances of the seed were used more intensively under the gibberellin effect and conditions of skotomorphogenesis; it is evidenced by the minimum mass of cotyledon dry matter in plants of this variant and higher utilization rates of reserve substances for root and epicotyl formation on day 18 of germination.

Among the key features that demonstrate gibberellin's influence on the germination of starch-containing seeds is the ability to stimulate the release of α -amylase by the embryo into the endosperm that leads to the splitting of starch grains (Rademacher, 2016). The obtained

results of the study indicate a significant effect of gibberellic acid on the hydrolysis rate of starch under conditions of photo- and skotomorphogenesis (Table 2). The rate of reserve starch use was higher under conditions of germination in dark. Gibberellin stimulated the breakdown of starch in both light and dark. The total sugars and starch content were lower in the roots of skotomorphic plants and, especially, in the epicotyls of seedlings, or it did not differ significantly from photomorphic plants. In our opinion, this can be explained by more intensive growth rates and biodilution of non-structural carbohydrates among the structural polysaccharides of seedlings. The lower content of total sugar in the seeds of skotomorphic plants, both in the control and under the gibberellin action, is explained, in our opinion, by more intensive outflow for the needs of organogenesis – the formation of root and epicotyl structures.

It is known that sucrose is the main transport form of sugars in the plant. Noteworthy, the lowest content of this sugar in germinated seeds was observed in skotomorphic plants under the influence of gibberellin. The data about the highest coefficient of utilization of the reserves from cotyledons, in our opinion, indicates the stimulation of transport of sugars for the formation and growth of epicotyl and roots

Table 1. The effect of gibberellic acid on growth processes and the use of reserve substances by horse bean seeds under conditions of photo- and skotomorphogenesis

Indicator	Control		GA ₃	
	Photo-morphogenesis	Skoto-morphogenesis	Photo-morphogenesis	Skoto-morphogenesis
Length of above-ground part, cm	14.0 ± 0.86	19.5 ± 0.98*	18.0 ± 0.91	23.8 ± 1.18*
length of the root system, cm	8.1 ± 0.41	9.3 ± 0.47*	10.6 ± 0.52	14.3 ± 0.71*
Length of seedlings, cm	22.1 ± 1.26	28.8 ± 1.44*	28.6 ± 1.42	38.1 ± 1.9*
Mass of dry matter of above-ground part, g	0.034 ± .0017	0.039 ± 0.002*	0.048 ± 0.002	0.057 ± 0.002*
Mass of dry matter of root system, g	0.017 ± 0.001	0.021 ± 0.001*	0.022 ± 0.001	0.025 ± 0.001*
Mass of dry matter of cotyledons, g	0.513 ± 0.011	0.449 ± 0.020*	0.425 ± 0.024	0.377 ± 0.023*
Coefficient of use of reserve substances for the needs of above-ground part, %	6.0 ± 0.33	7.7 ± 0.38*	9.7 ± 0.48	12.4 ± 0.62*
Coefficient of use of reserve substances for the needs of the root system, %	3.0 ± 0.15	4.1 ± 0.22*	4.4 ± 0.22	5.4 ± 0.27*

Notes: * – the difference is significant at $P \leq 0.05$.

Table 2. The effect of gibberellin on the content of non-structural carbohydrates in the organs of seedlings of horse beans under conditions of photo- and skotomorphogenesis (day 18 of germination, % by weight of dry matter)

Plant organs	Variant of the experiment	Total sugar, %		Sucrose, %		Starch content, %	
		a	b	a	b	a	b
Root	Control	1.34 ± 0.07	1.27 ± 0.06	0.35 ± 0.02	0.33 ± 0.17	1.13 ± 0.06	1.06 ± 0.06
	GA ₃	1.08 ± 0.05*	1.07 ± 0.05*	0.28 ± 0.01*	0.27 ± 0.01*	1.07 ± 0.05	0.38 ± 0.02*
Epicotyl	Control	3.43 ± 0.16	1.78 ± 0.09	0.84 ± 0.04	0.80 ± 0.04	0.47 ± 0.02	0.38 ± 0.02
	GA ₃	5.42 ± 0.27*	3.36 ± 0.16*	1.41 ± 0.07*	1.48 ± 0.07*	0.38 ± 0.02*	0.39 ± 0.01
Cotyledons	Control	10.54 ± 0.53	8.76 ± 0.44	3.14 ± 0.16	4.12 ± 0.21	24.17 ± 0.20	17.53 ± 0.88
	GA ₃	15.13 ± 0.75*	9.84 ± 0.49	6.93 ± 0.34*	1.72 ± 0.08*	22.31 ± 0.11*	15.2 ± 0.75*

Notes: * – the difference is significant at $P \leq 0.05$; a – photomorphogenesis, b – skotomorphogenesis.

of skotomorphic seedlings in the variant of gibberellic acid.

The principal stock of horse beans is featured by both starch and protein. The literature presents only limited data on the use of deposited proteins and lipids under the effect of gibberellins (Poprotska et al., 2019).

Slower use of nitrogen-containing compounds compared to reserve carbohydrates in the germination of bean seeds was indicated as a result (Table 3). Changes in the nitrogen content in the seeds of skotomorphic and photomorphic plants on day 18 of germination were much smaller than changes in the starch content. The content of the protein fraction of nitrogen was significantly decreased under the action of gibberellin only in skotomorphic plants,

while the content of the non-protein fraction in the seeds was increased. In our opinion, this indicates that the hydrolysis of the seed reserve protein was stimulated by gibberellin in dark, but the process is started after intensive hydrolysis of starch. A similar trend is found in the germination of corn seeds: primarily the use of starch and protein compounds are used at later stages of germination (Poprotska et al., 2019).

The decrease in the total content of nitrogen and its fractions in the epicotyl and the root of skotomorphic seedlings, as well as under the action of gibberellins, were observed. In our opinion, this is due to the biodilution of the element by the organic matter of these organs caused by more intensive growth rates of skotomorphic plants.

Table 3. The effect of gibberellin on the content of nitrogen compounds in the organs of seedlings of horse beans under conditions of photo- and skotomorphogenesis (day 18 of germination, % by weight of dry matter)

Plant organs	Variant of the experiment	Nitrogen forms					
		Total nitrogen		Protein nitrogen		Non-protein nitrogen	
		a	b	a	b	a	b
Root	Control	3.16 ± 0.16	2.74 ± 0.14	1.9 ± 0.09	1.5 ± 0.08	1.26 ± 0.06	1.24 ± 0.06
	GA ₃	4.08 ± 0.02*	1.55 ± 0.07*	2.0 ± 0.40	1.01 ± 0.05*	2.03 ± 0.04*	0.54 ± 0.03*
Epicotyl	Control	7.56 ± 0.38	5.57 ± 0.28	3.47 ± 0.17	1.53 ± 0.08	4.09 ± 0.20	4.04 ± 0.20
	GA ₃	7.00 ± 0.35*	6.97 ± 0.34*	2.06 ± 0.04*	1.96 ± 0.04*	4.94 ± 0.03*	5.01 ± 0.03*
Cotyledons	Control	4.74 ± 0.24	4.21 ± 0.21	2.80 ± 0.14	2.60 ± 0.13	1.94 ± 0.09	1.61 ± 0.08
	GA ₃	4.58 ± 0.03*	4.57 ± 0.02*	2.55 ± 0.13*	2.18 ± 0.10*	2.03 ± 0.10	2.39 ± 0.11*

Notes: * – the difference is significant at $P \leq 0.05$; a – photomorphogenesis, b – skotomorphogenesis.

It was previously found that the change in growth characteristics and the rate of the utilization of reserve substances of bean seeds were accompanied by a decrease in total nitrogen content, which indicates the use of reserve nitrogen-containing compounds for morphogenesis (Poprotska et al., 2019). Our data indicate that under conditions of skotomorphogenesis, the content of protein nitrogen in the control was lower than in photomorphic seedlings, and under the action of gibberellin the content of protein fraction of nitrogen decreased and the content of non-protein fraction significantly increased. Earlier we also found the increasing action of gibberellin on the growth of the above-ground part and the root system of plant seedlings, which contained different types of reserve substances: starch (maize), protein (beans), and oil (pumpkin) compared to the control. At the same time, the process took place predominantly in the dark. Under the action of retardants, which block the formation of gibberellins, the germination process was blocked both in light and in dark. The rate of the utilization of reserve substances under the action of gibberellin was maximal, and under the action of anti-gibberellin drugs tebuconazole and chlormequat chloride was minimal in both skotomorphic and photomorphic seedlings (Kuryata et al., 2017; Poprotska et al., 2019). Thus, gibberellin plays a universal role in germination processes, regardless of the type of seed reserve; its effect is enhanced in dark.

The main patterns of the redistribution of plastic fluxes in the plant when changing the growth rate of individual organs are fully studied within the concept of the functioning of the source-sink system of plants (Yu et al., 2015; Bonelli et al., 2016; Rogach et al., 2020). However, the peculiarities of the redistribution of mineral nutrients in plant organs under the influence of gibberellin under conditions of photo- and skotomorphogenesis remain virtually unexplored.

Our analysis of the phosphorus content in the organs of seedlings of skoto- and photomorphic plants indicates the absence of a significant difference in the content of this element in the seed on day 18 of germination (Fig. 1). At the same time, in the roots and epicotyls of plants that formed in dark, in general, a lower content of the element was observed in comparison with photomorphic seedlings. In our opinion, this is similar to nitrogen and it is also related to biodilution. Also, gibberellin does not produce a significant effect on the evacuation of phosphorus from seeds to the needs of epicotyl and root formation.

Generally, similar patterns were observed for potassium: due to biodilution, skotomorphic plants were characterized by a lower potassium content in epicotyls and roots of seedlings and a slight decrease in the content of the component in seeds (Fig. 2). Gibberellin did not significantly affect the potassium content in skotomorphic seedlings.

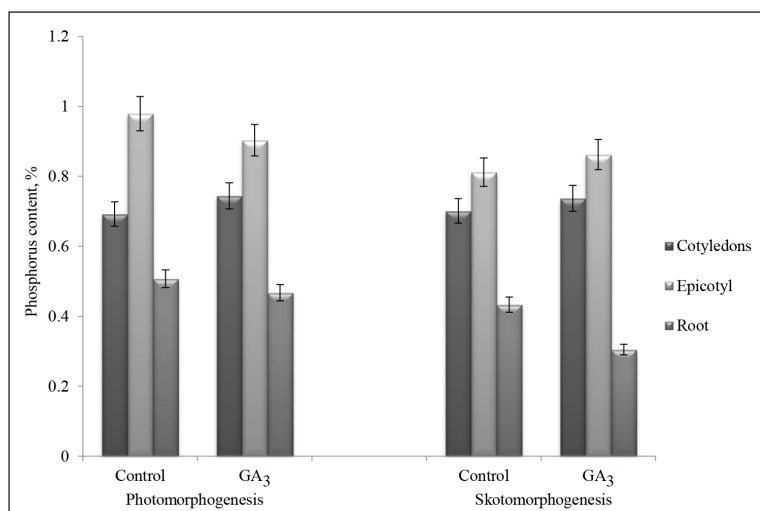


Fig. 1. The effect of gibberellic acid on the phosphorus content in the organs of horse bean seedlings under conditions of photo- and skotomorphogenesis (% by weight of dry matter)

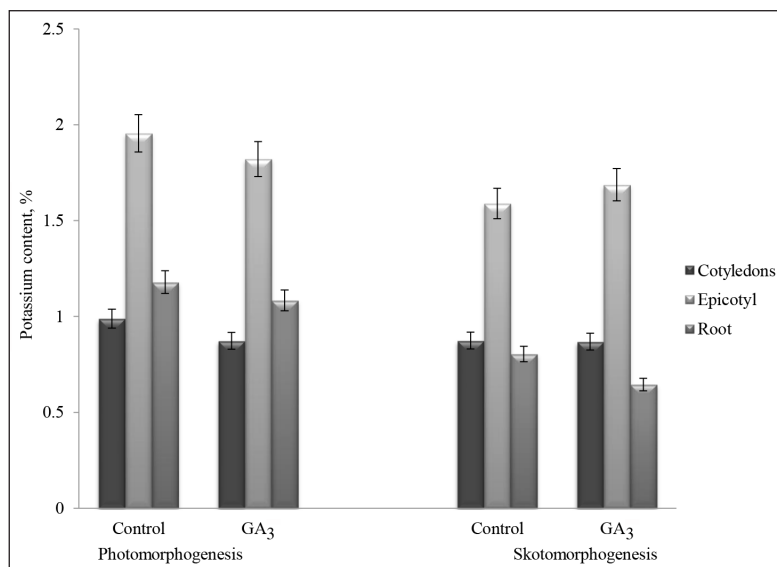


Fig. 2. The effect of gibberellic acid on the potassium content in the organs of horse bean seedlings under conditions of photo- and skotomorphogenesis (% by weight of dry matter of the plant)

This, in our opinion, indicates a sufficient supply of seeds with phosphorus and potassium to ensure the processes of photo- and skotomorphogenesis by these nutrients and a lack of specific gibberellin regulation of their re-utilization in germination processes.

CONCLUSIONS

The combination of external (light/dark) factor and hormonal factor (gibberellic acid) during seed germination significantly changed the nature of the donor-acceptor relationship in horse bean seedlings. The length of epicotyl, root, and seedling in general increased significantly under the action of the drug, both in light and in dark. Similarly, the mass of dry matter of the organs of the seedling increased. Seed reserve substances were used more intensively under the influence of gibberellin under conditions of skotomorphogenesis as evidenced by the minimum dry matter of cotyledons in plants of this variant and higher rates of reserve utilization for the formation of roots and epicotyl during germination.

Gibberellin stimulated the breakdown of starch in both light and dark, but under conditions of germination in dark, the rate of the use of reserve seed starch was higher. The lower content of the number of sugars in the seeds of skotomorphic plants, both in control and under

the action of gibberellin, is explained by a more intensive outflow for the needs of organogenesis: the formation of root and epicotyl structures. Quantitative changes in the nitrogen content in the seeds of skotomorphic and photomorphic plants during germination were much smaller than changes in the starch content. This indicates that in dark, gibberellin stimulates the hydrolysis of reserve protein in seeds, but the process is started after intensive hydrolysis of starch. It no specific gibberellin regulation of the outflow of mineral nutrients, phosphorus and potassium deposited in the seeds for the needs of organogenesis, was found.

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NEZÈS SĄLYGOMIS**

Santrauka

Derinant išorines (šviesa – tamsa) ir hormonines (giberelino rūgštis) sąlygas dygimo metu, buvo tiriama augavietės pokyčių, veikiančių heterotrofinę pupų vystymosi fazę, poveikis. Didėjant epikotiliui, šaknies ir daigų ilgiui tiek šviesoje, tiek tamsoje, daigų organų masę padidino ir giberelinas. Tiek giberelinas, tiek ir skotomorfogenezė turėjo įtakos intensyvesniam rezervinės medžiagos naudojimui – tai rodo minimali skilčialapių sausoji medžiaga ir didesni atsargų panaudojimo koeficientai formuojantis šaknims ir epikotiliams. Giberelinas skatino krakmolo skilimą, tačiau daiginant tamsoje krakmolo sunaudojama daugiau. Kitas cukraus kiekis skotomorfinėse sėklose buvo susijęs su intensyvesniu nutekėjimu organogenezės poreikiams tenkinti – šaknų ir epikotilio struktūrų formavimuisi. Krakmolo kiekis skotomorfiniuose ir fotomorfiniuose daiguose buvo didesnis nei azoto. Giberelinas stimuliuoja rezervinių baltymų hidrolizę tamsoje, tačiau procesas prasideda po krakmolo hidrolizės. Nenustatyta jokie specifinio giberelino reguliuojamo mineralinių medžiagų nutekėjimo – fosforo ir kalio, nusėdusių sėklose organogenezės reikmėms, nenustatyta, ar fosforo ir kalio atsargų pakanka foto- ir skotomorfogenezėi bei specifiniam giberelino reguliavimui daigumo procesuose.

Raktažodžiai: morfogenezė, augavietės pokyčiai, sėklų daigumas, lengvas veikimas, giberelinas