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INTENSITY OF PHOTOSYNTHESIS AND TRANSPORT OF ASSIMILATES IN *Solanum tuberosum* UNDER THE ACTION OF 24-EPIBRASSINOLIDE

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Abstract

Brassinosteroids are a unique class of steroid hormones. They have a wide functional activity, combining the properties of growth stimulants and inducers of protective reactions that reduce the damaging effect of stressors on the plant organism. They regulate the processes of ethiolation, the synthesis of other groups of phytohormones. There is information about the participation of brassinosteroids in the expression of light-regulated photosynthetic genes and regulation of the functioning of the photosynthetic apparatus. Nevertheless, information regarding the content of pigments is conflicting. Activation of the enzymes of the Calvin cycle is shown. Some researchers noted stimulation of CO_2 uptake and a positive effect on the yield of various crops. However, there are practically no data on the effect of brassinosteroids on the transport of assimilates to the attracting centers of plants. In this work, we established the effect of brassinosteroids on the rate of photosynthesis of potato plants and for the first time revealed their participation in the regulation of the transport of assimilates to tubers through changes in the content of ABA in the basal zone of the stem and cytokinins in tubers. Our work aimed to study the effect of 24-epibrassinolide on the intensity of the photosynthesis process, the content of assimilates in different zones of the stem, and to reveal the participation of ABA and cytokinins in the outflow of assimilates into tubers in potato plants. The *Solanum tuberosum* L. cv. Skoroplodny plants were grown in a growing house in soil culture. At flowering phase, the plants were sprayed with a 1.47×10^{-8} M solution of 24-epibrassinolil (Institute of Bioorganic Chemistry of the National Academy of Sciences of Belarus); the control plants were sprayed with water. The intensity of photosynthesis was assessed using the ^{14}C radioactive isotope generated in a gasholder from a mixture of radioactive and non-radioactive sodium bicarbonate. At the end of flowering, a clothespin chamber was attached to an intact leaf of the eighth layer. In the chamber, the leaf was exposed to $^{14}CO_2$ atmosphere (10 ml, 0.6% $^{14}CO_2$, 0.0334 mBq/nM) for 10 minutes. To determine the content of ^{14}C-assimilates, sections of the stem zones were fixed 48 hours after exposure to the $^{14}CO_2$ atmosphere. The radioactivity was measured (a T-25-BFL end counter, Isotope, Russia). The sucrose content was measured refractometrically (an RPL-3 refractometer, OAO Kyiv plant "AnalytPribor", Ukraine). The concentration of abscisic acid (AA) in the zones of the stem and cytokinins in the tubers were determined by enzyme-linked immunosorbent assay (ELISA) method. AA and zeatin (Serva, Germany) served as standard solutions of phytohormones. The content of chlorophylls a, b and carotenoids was determined in 80% acetone extracts (a KFK-3-01 photometer, AO ZOMZ, Russia). The thickness of the phellema was measured on intravital cross sections in the middle part of the tuber using an eyepiece micrometer (a Biolam microscope, LOMO, Russia). After the end of flowering, epibrassinolide increased the intensity of $^{14}CO_2$ assimilation by 23 % ($p \le 0.05$). The treated leaves exposed to $^{14}CO_2$ contained more sucrose as compared to the control leaves. An increase in the content of chlorophylls a, b and carotenoids occurred. The concentration of sucrose and ^{14}C-assimilates differed between various stem zones. In the basal zone, the concentrations were lower than in the middle part. Epibrassinolide increased the gradient of ^{14}C- assimilates and sucrose between the zones of the stem, which may indicate an increase in their outflow into tubers. Simultaneously, the level of endogenous abscisic acid in the basal zone increased, which facilitates unloading of phloem endings. Under the influence of epibrassinolide, the AA gradient between the zones was 41 % vs. 26 % ($p \le 0.05$) in the

control. In tubers, due to the exogenous epibrassinolide, the level of cytokinins which exhibit an attracting effect was higher compared to the control. The brassinosteroid increased the productivity of potato plants by 25 % ($p \leq 0.05$) and stimulated phellema formation in the tubers. The research data obtained suggest that epibrassinolide regulates the intensity of the photosynthesis process, the outflow of assimilates into the forming tubers through the participation of AA in the creation of a gradient of assimilates in the stem zones and an increase in cytokinins in tubers, which attract assimilates. This ultimately affects the productivity of potato plants.

Keywords: 24-epibrassinolide, photosynthesis, pigments, sucrose, ^{14}C-assimilates, abscisic acid, cytokinins, stem zones, *Solanum tuberosum*

Brassinosteroids are a unique class of steroid hormones. They have a wide functional activity, combining the properties of growth stimulants [1, 2] and inducers of protective response that reduce the damaging effect of stressors on the plant [3-5], and also regulate etiolation [6-8] and the synthesis of other groups of phytohormones. [9]. There is information about the participation of brassinosteroids in the expression of light-regulated photosynthetic genes [10] and the regulation of the functioning of the photosynthetic apparatus [11]. In particular, a significant increase in the content of chlorophylls a, b and carotenoids was shown due to the activation of enzymes involved in the biosynthesis of chlorophylls [10]. In studies on corn seedlings [12] and rhododendron plants [5], there is a slight effect of epibrassinolide on the content of pigments.

A positive effect of brassinosteroids on increasing the photochemical efficiency of photosystem II was established [5, 10, 13], which is confirmed mainly by the parameters of chlorophyll fluorescence. In some works, there are data on the activation of the enzymes of the Calvin cycle, carbonic anhydrase and RuBisCO [10, 13-15]. According to E.O. Fedina [16], the effect of the hormone on the activity of RuBisCO is due to the reduction of tyrosine phosphorylation of its subunits.

Few studies have shown stimulation of CO_2 uptake when plants are treated with epibrassinolide [5, 15]. The authors attribute this effect to an improvement in stomatal conductance. A positive effect of brassinosteroids on the productivity of various types of crops has been established]17]. However, there is practically no information in the special literature on the effect of phytohormones of a steroid nature on the transport of assimilates in plants. C. Wu et al. [18] in their work on transgenic rice plants with increased synthesis of brassinosteroids revealed an increase in the outflow of assimilates into underdeveloped grains of the upper part of the inflorescence. The participation of brassins in the control of sucrose transport into grapes is also noted [19].

This work shows for the first time the participation of 24-epibrassinolide in the regulation of assimilate transport into potato tubers through changes in the content of abscisic acid (AA) in the basal zone of the stem and cytokinins in tubers.

Our goal was to study the effect of 24-epibrassinolide on the intensity of the photosynthesis process, the content of assimilates in the stem zones, and to reveal the involvement of AA and cytokinins in the outflow of assimilates into potato tubers.

Materials and methods. Potato plants (*Solanum tuberosum* L.) of the Skoroplodny variety (selection of the Lorkh FRC of potato, Russia) were grown in a growing house (agro-bio station of the Turgenev Oryol State University, 2018-2019) in soil culture. Soil was gray forest medium loamy. Nitrogen, phosphorus and potassium were added in the amounts optimal for potatoes, 230, 70, and 310 mg/kg of soil, respectively. Each plant was grown in individual pot with 10 kg of soil, the humidity was maintained at 60% of full moisture content.

Plants at flowering stage were sprayed with a 1.47×10^{-8} M solution of 24-

epibrassinolide (Institute of Bioorganic Chemistry, National Academy of Sciences of Belarus); control plants were sprayed with water.

At the end of flowering, average samples of leaves of the 8th tier and stem zones 7 cm long (medium part between leaves of the 7th-8th tiers and basal part between leaves of the 1st-2nd tiers) were collected for analysis:; at the end of the growing season, tubers were collcted.

The intensity of photosynthesis was studied using the radioactive isotope ^{14}C [20] which was obtained in a laboratory gas holder from a mixture of 4 mg of radioactive and 2525 mg of non-radioactive sodium bicarbonate. At the end of plant flowering, an intact leaf of the 8th tier was exposed for 10 min to $^{14}CO_2$ under natural conditions (at 11.00 am and a temperature of 17-19 °C, a clothespin chamber into which 10 ml of $^{14}CO_2$ was injected from a gas holder using a medical syringe). Air humidity was 49%, illumination was 340 μmol photons $\cdot m^{-2} \cdot s^{-1}$. The specific radioactivity in the $^{14}CO_2$ atmosphere was 0.0334 mBq/nM, the $^{14}CO_2$ concentration $^{14}CO_2$ was 0.6%. To determine the rate of photosynthesis in a leaf that received $^{14}CO_2$, the extreme part of the leaf was split off, fixed for 30 min at 105 °C and dried at 60 °C. To assess the content of 1^4C-assimilates, segments of stem zones were fixed for 48 h after exposure to $^{14}CO_2$. Radioactivity was measured on a T-25-BFL end counter (Isotope, Russia).

The content of sucrose was estimated refractometrically (an RPL-3 refractometer, JSC Kiev Plant AnalytPribor, Ukraine), taking into account the refractive index of cell sap. The amount of abscisic acid (AA) in stem zones and the content of zeatin in tubers were measured by enzyme-linked immunosorbent assay [21]. After binding protein conjugate of the hormone, serum with antibodies and the experimental samples were added into the wells of the polystyrene plate. The amount of antibodies specifically bound to the protein conjugate of the hormone was determined using ram antibodies against rabbit immunoglobulins, labeled with peroxidase. Ortho-phenylenediamine was used to assess the activity of bound peroxidase. The intensity of the chromophore response was determined (a Dombi plate microphotometer, Latvia; $\lambda = 492$ nm). Reagents from Uralinvest (Russia) were used for the analyses. AA and zeatin (SERVA Electrophoresis GmbH, Germany) were standard solutions of phytohormones.

The pigments were extracted from the leaves with 80% acetone solution. The content of chlorophylls a, b and carotenoids was determined (a KFK-3-01 photometer, AO ZOMZ, Russia) [22].

The thickness of the phellema (cork) was measured on lifetimt transverse sections in the middle part of the tuber (an ocular micrometer MOV-1-15x, a Biolam microscope, LOMO, Russia).

Statistical processing of the experimental data was carried out using the Microsoft Excel 2010 program. The figures and the table show the arithmetic mean values (*M*) and their standard errors (±SEM) from five biological replicates. Analytical repetition is 5-fold. The significance of the results was assessed using the Student's *t*-test at a confidence level above 0.95.

Results. Spraying potato plants at the end of flowering with a solution of 24-epibrassinolide increased the intensity of $^{14}CO_2$ assimilation (Fig. 1) by 23% ($p \leq 0.05$). As a result, the leaves of the 8th tier, which received $^{14}CO_2$, contained 34% more sucrose compared to the control ($p \leq 0.05$).

An increase in the intensity of photosynthesis occurred with an increase in the pigment content in leaves (Fig. 2). The amoint of chlorophylls a and b increased by 25%, while carotenoids by 14% ($p \leq 0.05$). I.F. Golovatskaya et al. [11] reported that the enhancement of photosynthesis in regenerated potato plants upon root treatment with 10 nM epibrassinolide is associated with a significant

increase in the assimilation index. The effect of brassinosteroids on the intensity of photosynthesis could be due to their effect on the hormonal balance in the plant. An increase in the content of cytokinins in wheat plants was shown under the influence of treatment with a 0.4 μM solution of epibrassinolide [9]. Cytokinins are known to increase the intensity of photosynthesis [23].

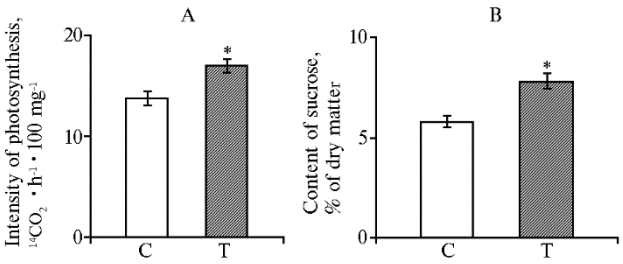

Fig. 1. Intensity of photosynthesis (A) **and sucrose content** (B) **in leaves of potato (*Solanum tuberosum* L.) cv. Skoroplodny plants in control** (C) **and upon spraying plants with 1.47×10^{-8} M 24-epibrassinolide** (T) **at blossoming** ($M\pm$SEM, $n = 5$, $N = 5$).
* Differences with control are statistically significant at $p \le 0.05$.

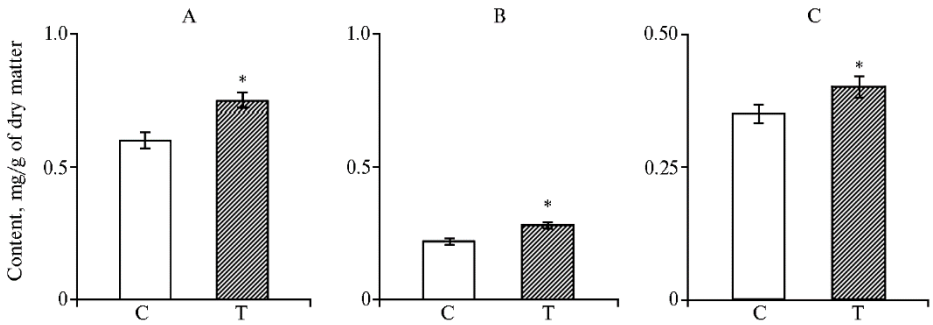

Fig. 2. Content of chlorophyll a (A)**, chlorophyll b** (B) **and carotenoids** (C) **in leaves of potato (*Solanum tuberosum* L.) cv. Skoroplodny plants in control** (C) **and upon spraying plants with 1.47×10^{-8} M 24-epibrassinolide** (T) **at blossoming** ($M\pm$SEM, $n = 5$, $N = 5$).
* Differences with control are statistically significant at $p \le 0.05$.

For the formation of economically valuable plant organs, it is important not only the prodution of assimilates in photosynthesis, but also their directed transport [24]. It is known that the distribution of photosynthesis products into attracting centers is determined by donor-acceptor interaction. We studied the distribution of ^{14}C-assimilates and sucrose which is the main transport form of assimilates in the middle and basal zones of the potato stem. Differences in the content of sucrose in the stem zones were found 48 h after the leaf exposure to $^{14}CO_2$ (Fig. 3). In the basal zone, the sucrose concentration was 24% less than in the middle zone ($p \le 0.05$). The value of the sucrose gradient between the middle and basal zones of the stem increased under the influence of 24-epibrassinolide to 44% ($p \le 0.05$).

A decrease in the content of sucrose in the basal zone could indicate an increase in its outflow. The distribution of ^{14}C-assimilates over stem zones turned out to be similar to the sucrose gradients in the control and in upon the variant with 24-epibrassinolide. That is, a basipetal gradient of sucrose and ^{14}C-assimilates was revealed in the stem.

The mechanisms of assimilate transport are widely discussed with special attention also paid to phytohormones. First of all, their role in attracting centers is considered {25}. Less attention is paid to the stem, although it is there that the redistribution of the outflow of assimilates to different organs occurs. There is no

information about the effect of brassinosteroids on the content of phytohormones in different zones of the stem. In our experiment, after the flowering, when there was an intensive growth of young potato tubers, abscisic acid accumulated in the basal zone of the stem, and to a greater extent under the influence of 24-epibrassinolide (Fig. 4).

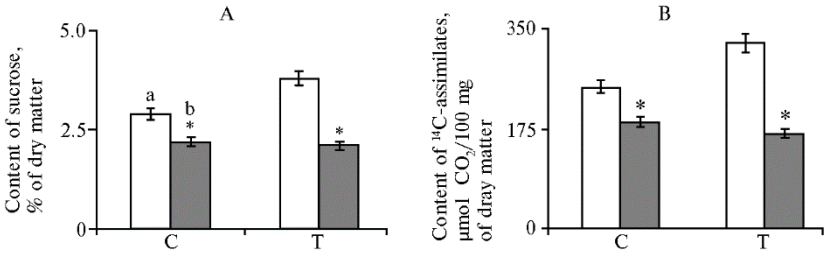

Fig. 3. Content of sucrose (A) **and ^{14}C-assimilates** (B) **in middle** (a) **and basal** (b) **stem zones in leaves of potato (*Solanum tuberosum* L.) cv. Skoroplodny plants in control** (C) **and upon spraying plants with 1.47×10^{-8} M 24-epibrassinolide** (T) **at blossoming** ($M\pm$SEM, $n = 5$, $N = 5$).
* Differences with control are statistically significant at $p \le 0.05$.

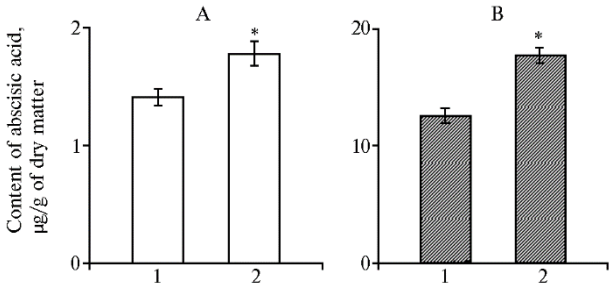

Fig. 4. Content of abscisic acid (AbA) in middle (1) **and basal** (2) **stem zones of potato (*Solanum tuberosum* L.) cv. Skoroplodny plants in control** (A) **and upon spraying plants with 1.47×10^{-8} M 24-epibrassinolide** (B) **at blossoming** ($M\pm$SEM, $n = 5$, $N = 5$).
* Differences with control are statistically significant at $p \le 0.05$.

Thus, in the control, the accumulation of endogenous AA in the basal zone was 26% higher than in the middle zone, and with 24-epibrassinolide, it was 41% higher ($p \le 0.05$). As a result, the AA gradient between the middle and basal zones was almost 2 times higher than that in the control.

According to T.H. Thomas [26], abscisic acid contributes to the unloading of phloem endings and, as a result, stimulates the accumulation of assimilates in the storage organ [27]. It should be noted that the formation of a positive sucrose gradient in the stem in the second half of the plant vegetation is facilitated by the accumulation of not only AA, but also auxins in the basal zone. Such data were obtained by us earlier [28]. According to the hypothesis put forward by E. Munch [29] and currently recognized, the osmotic pressure gradient is the driving force for the directed transport of assimilates.

Strengthening the outflow of assimilates into growing tubers under the influence of 24-epibrassinolide increased the productivity of potato plants grown in soil culture by 25% ($p \le 0.05$) (Fig. 5). An increase in the mass of tubers upon 24-epibrassinolide treatment may have been associated not only with an increase in the transport of assimilates, but also with the content of cytokinins in tubers, which are known to have an attracting effect. When plants were enriched with 24-brassinosteroid, a significant (more than 2-fold) increase in the content of zeatin cytokinin in tubers occurred (see Fig. 5).

For potato tubers, the formation of the secondary integumentary tissue of the periderm, primarily the phellema (cork) which regulates gas exchange and

protection against pathogens, is of great importance. Treatment of plants with 24-epibrassinolide increased the thickness of the phellema by 40% compared to the control ($p \leq 0.05$). Apparently, in this case, the influence was exerted by an increase in the content of cytokinons in tubers, which regulate cell division of phellogen, a secondary tissue that lays phellema layers outside the tuber.

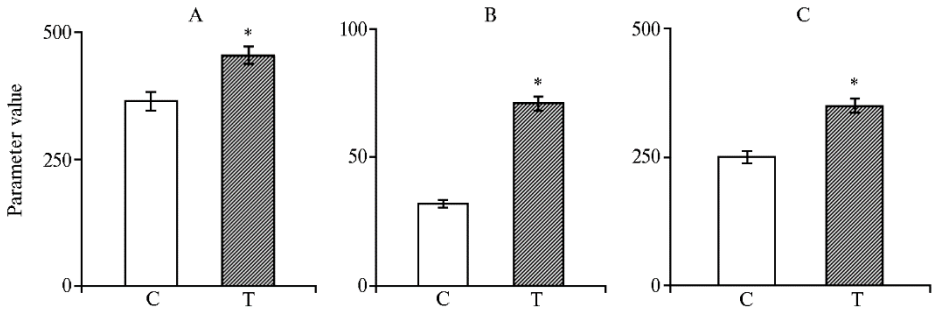

FIg. 5. Weight (g/plant, A)**, content of zeatin** (ng/g of dry weight, B) **and .phellema thickness** (μm, C) **in tubers of potato (*Solanum tuberosum* L.) cv. Skoroplodny in control** (C) **and upon spraying plants with 1.47×10^{-8} M 24-epibrassinolide** (T) **at blossoming** ($M\pm$SEM, $n = 5$, $N = 5$)**.**
* Differences with control are statistically significant at $p \leq 0.05$.

Thus, spraying potato plants of cv. Skoroplodny with a 1.47×10^{-8} M solution of 24-epibrassinolide at flowering stage of growth leads to an intensification of $^{14}CO_2$ absorption and an increase in the content of pigments in the leaves. At the end of flowering, with an increase in the content of abscisic acid (AA), the amount of ^{14}C-assimilates and sucrose decreased in the basal zone of the stem compared to the middle zone, which indicates the participation of AA in the unloading of phloem endings. The influx of assimilates into tubers under the influence of epibrassinolide was due to an increase in the content of cytokinins in the tubers. The data obtained allow us to conclude that 24-epibrassinolide regulates the intensity of the photosynthesis and outflow of assimilates into the developing tubers through the participation of AA in the formation of an assimilate gradient in stem zones and an increase in the content of cytokinins in tubers, which ultimately affects the productivity of potato plants.

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