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RESEARCH ARTICLE | НАУЧНАЯ СТАТЬЯ

# TRANSPORT OF BACTERIAL CYTOKININS TO SHOOT AND THEIR INFLUENCE ON GROWTH OF BARLEY PLANTS

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***Аннотация***

One important mechanism underlying the promotive action of rhizosphere bacteria on plants is their ability to produce plant hormones, particularly cytokinins. Cytokinin must be delivered from the roots to stimulate plant growth and exert beneficial effects on the shoots. This work aimed to study the transport of bacterial cytokinins in barley plants. We studied the effects of cytokinin-producing bacteria on the growth, cytokinin content, and expression of the *HvABCG* gene, a homolog of the rice *OsABCG18* and Arabidopsis *AtABCG14* genes encoding transporters of these hormones. Rhizosphere of 3-days-old barley seedlings were inoculated with Bacillus subtilis IB-22, and cytokinins were immunoassayed on the sixth day after bacterial treatment. On day 11, leaf growth stimulation was detected under the bacterial treatment, indicating that bacterial cytokinins affect shoot performance. This hypothesis was confirmed by a 1.5 increase in zeatin riboside levels registered in the shoots of bacteria-treated plants. Estimating the expression of the *HvABCG* gene showed its upregulation in the roots of bacteria-treated plants, suggesting the involvement of this transporter in the delivery of cytokinins to the shoots.

***Keywords:***

*Bacillus subtilis; Hordeum vulgare*; cytokinins, transporters

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# ТРАНСПОРТ БАКТЕРИАЛЬНЫХ ЦИТОКИНИНОВ В ПОБЕГ И ИХ ВЛИЯНИЕ НА РОСТ РАСТЕНИЙ ЯЧМЕНЯ

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***Abstract***

Одним из важных механизмов, лежащих в основе стимулирующего действия ризосферных бактерий на растения, является их способность продуцировать растительные гормоны, в частности цитокинины. Для стимуляции роста растений необходимо, чтобы цитокинин доставлялся из корней и оказывал благотворное воздействие на побеги. Целью данной работы было изучение транспорта бактериальных цитокининов в растениях ячменя. Мы исследовали влияние продуцирующих цитокинины бактерий на рост, содержание цитокининов и экспрессию гена *HvABCG*, который является гомологом гена *OsABCG18* риса и гена *AtABCG14* арабидопсиса, кодирующих транспортеры этих гормонов. Ризосферу 3-дневных проростков ячменя инокулировали *Bacillus subtilis* IB-22 и на шестой день после бактериальной обработки проводили иммуноферментный анализ цитокининов. На одиннадцатый день было обнаружено стимулирование роста листьев при бактериальной обработке, что свидетельствует о положительном влиянии бактериальных цитокининов на состояние побегов. Эта гипотеза была подтверждена 1.5-кратным увеличением уровня зеатинрибозида, зарегистрированным в побегах растений, обработанных бактериями. Оценка экспрессии гена *HvABCG* показала ее повышение в корнях растений, обработанных бактериями, что указывает на возможное участие этого транспортера в доставке цитокининов в побеги.

***Ключевые слова:***

*Bacillus subtilis; Hordeum vulgare*; цитокинины, транспортеры

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## INTRODUCTION

Rhizosphere bacteria are increasingly used in crop production as growth promoters, increasing yield and plant resilience. One of the important mechanisms underlying the stimulating effect on plants is their ability to produce plant hormones, in particular cytokinins. We previously demonstrated that presowing seed treatment with cytokinin-producing bacteria accelerates growth and increases yield in wheat plants [Arkhipova *et al.* 2019]. To stimulate plant growth, cytokinin must be delivered to the shoots, as these hormones exert their beneficial effects on the leaves [Wu *et al.* 2021]. Experiments with rice and Arabidopsis plants have shown that cytokinin delivery to the shoot depends on so-called ABC transporters, a superfamily of membrane channels that actively transport various substances through ATP hydrolysis [Zhang *et al.* 2014; Zhao *et al.* 2019]. It was important to verify the dependence of cytokinin influx into the shoot on cytokinin transporters in other plant species. This work aimed to study the transport of bacterial cytokinins in barley plants. The choice of this species was dictated by the sufficient knowledge of its genome, which made it possible to identify genes encoding cytokinin transporters and study their expression. We studied the effects of cytokinin-producing bacteria *Bacillus subtilis* IB-22 on the growth, nitrogen balance index, cytokinin content and expression of the *HORVU.MOREX.r3.7HG0645770* gene, which is a homologue of the rice *OsABCG18* and Arabidopsis *AtABCG14* genes [Mahalingam *et al.* 2022], in shoots and roots of barley.

## MATERIALS AND METHODS

Barley (*Hordeum vulgare* L.) seeds of the Prairie variety were sterilized with a 40% aqueous solution of sodium hypochlorite, diluted twofold. The seeds were laid out on filter paper moistened with tap water, covered with a second layer of filter paper, shaded, and transferred to a refrigerator for stratification at +5°C. The next day, the seeds were exposed to the dark at an ambient temperature of 21°C. On the third day, the seedlings were transplanted into sand saturated with Hoagland-Arnon nutrient medium at 80% of the total moisture capacity of the substrate, a 14-hour photoperiod, an illumination of 400 mol $m^2$ $s^{-1}$ PAR, and a temperature of 25/20°C (day/night). On the day following planting of the seedlings in the sand, 1 ml of a suspension of Gram-positive aerobic spore-forming cytokinin-producing bacteria *Bacillus subtilis* IB-22 (GenBank MT590663) (CFU $10^8$ $ml^{-1}$) was introduced into the rhizosphere of each plant.

Gram-positive aerobic cytokinin-producing bacterium *Bacillus subtilis* IB-22 (GenBank MT590663) [Kudoyarova *et al.* 2014] from the collection of microorganisms of Ufa Institute of Biology, RAS, was used for bacterial treatment. Inoculates for bacterial treatments were obtained by cultivating *B. subtilis* IB-22 on K1 medium as described [Arkhipova *et al.* 2020]. The strain of microorganisms was cultured in Erlenmeyer flasks on a shaker (160 rpm) for 72 h at 37°C, and bacterial biomass was applied to the rhizosphere as described above.

On the third day after bacterial treatment, cytokinins were extracted and purified from shoots and roots, and their concentrations were determined by immunoassay using antibodies against zeatin riboside after separation of cytokinin derivatives by thin-layer chromatography, as described [Kudoyarova *et al.* 2014]. Shoots and roots were homogenized, and cytokinins were extracted with 80% ethanol. The extract was separated from plant debris by centrifugation, and the ethanol was evaporated to leave an aqueous residue. They were loaded on a C18 cartridge (500 mg, Varian, Middelburg, The Netherlands), which was then washed with 20 ml of distilled water. Cytokinins were eluted with 70% ethanol, the eluate evaporated to dryness, and the residue dissolved in a minimum of 80% ethanol. The solution was loaded on precoated 5 × 20 cm, 0.25 mm thick silufol 60 F-254 plates (Merck, Darmstadt, Germany) for thin layer chromatography in the solvent system of butanol, ammonium hydroxide, and water (6:1:2). After ultraviolet detection of standard zeatin, its nucleotide, glucoside and riboside in a separate track for standards, the corresponding zones from the plant material were eluted with 0.1 M phosphate buffer (PB, pH 7.2–7.4). This protocol successfully separated and assayed zeatin nucleotide (Rf 0–0.1), zeatin glucoside (Rf 0.1–0.2), zeatin riboside (Rf 0.4–0.5), and zeatin (Rf 0.6–0.7) [Vysotskaya *et al*. 2009]. More than 90% recovery was obtained for zeatin, its riboside and glucoside standards. Anti-cytokinin antibodies with high immunoreactivity towards trans-zeatin, its riboside, N9-glucoside and nucleotides showed an inherently low cross-reactivity to dihydrozeatin and isopentenyladenine (iPA) and their derivatives. The aforementioned method was validated for our plant material by LC-MS/MS [Veselov *et al*. 2018].

At the same time, the nitrogen balance index (NBI), which is the ratio of chlorophylls and flavonoids, was measured in the leaf epidermis using the DUALEX SCIENTIFIC+ (FORCE-A, France) device. NBI provides the earliest information on the nitrogen status of a plant.

RNA extraction and transcript analysis of the *HORVU.MOREX.r3.7HG0645770* gene, encoding the cytokinin-transporting protein [Mahalingam *et al*. 2022], was performed as follows. Since this gene product is an ABCG transporter homologous to the rice gene OsABCG18, we will henceforth refer to it as *HvABCG*. Total RNA was isolated from control and experimental 6-day-old barley plants using the Lira reagent according to the supplier's protocol (Biolabmix, Russia). Nucleic acid concentration was measured using a Smart Spec Plus spectrophotometer (Bio-Rad, USA). To synthesize cDNA, a reverse transcription reaction was performed using M-MuLV reverse transcriptase (Synthol, Russia) on a TP4-PCR-01-Tercik amplifier (DNA-Technology, Russia). Expression of the ABC transporter gene was analyzed by quantitative real-time PCR on a CFX Connect real-time PCR Detection System (BioRad Laboratories, USA) using the SYBR Blue intercalating dye (Biolabmix, Russia). The qPCR protocol was as follows: 95°C for 5 min; 40 cycles at 95°C for 15 sec, 60°C for 20 sec, and 72°C for 30 sec. The following primer set (5'-3') was used in this study: HvABCG (XM_045104931.1); F - TAGCACCGCCATCAACTTTG, R - GCTAGGGTTTGATGCACAGC). The β-tubulin gene (X54844.1; F - GCTCCCAGCAGTACAGGACTCT; R - TGGCATCCCACATTTGTTGA) was used as an internal control to normalize the amount of total RNA present in each reaction. Changes in gene expression were determined by calculating the normalized gene expression level using the CFX Connect real-time PCR Detection System software (BioRad Laboratories, USA).

On the fourteenth day, shoot and root weights were measured.

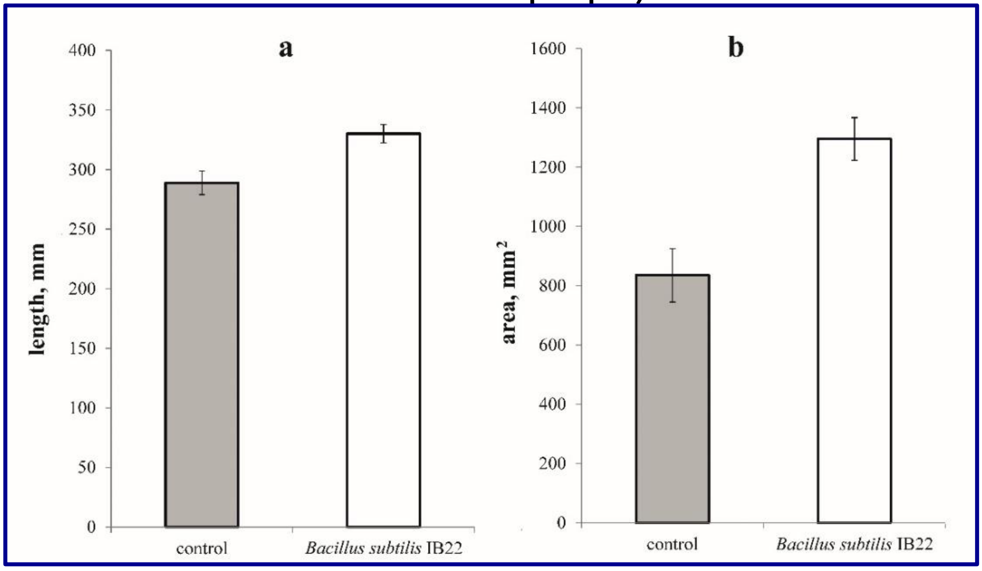
The data were processed using MS Excel software. Data in figures are presented as mean values ± standard error. The number of biological replicates (n) is provided in the figure’s legends.

## RESULTS AND DISCUSSION

An assessment of leaf size revealed stimulation of leaf growth under the influence of bacterial treatment, most noticeable in the third young leaf, the area of which was one and a half times larger compared to the control (plants not treated with bacteria) (Fig. 1). Thus, bacterial treatment promoted the growth of barley plants in the present experiments.

**Fig. 1. Effect of inoculation of barley rhizosphere with *Bacillus subtilis* IB-22 on the length, (a) and area, (b) of the third leaf measured 11 days after treatment. Mean values of control and treated plants are statistically different (n=50, p<0.05, t-test)**

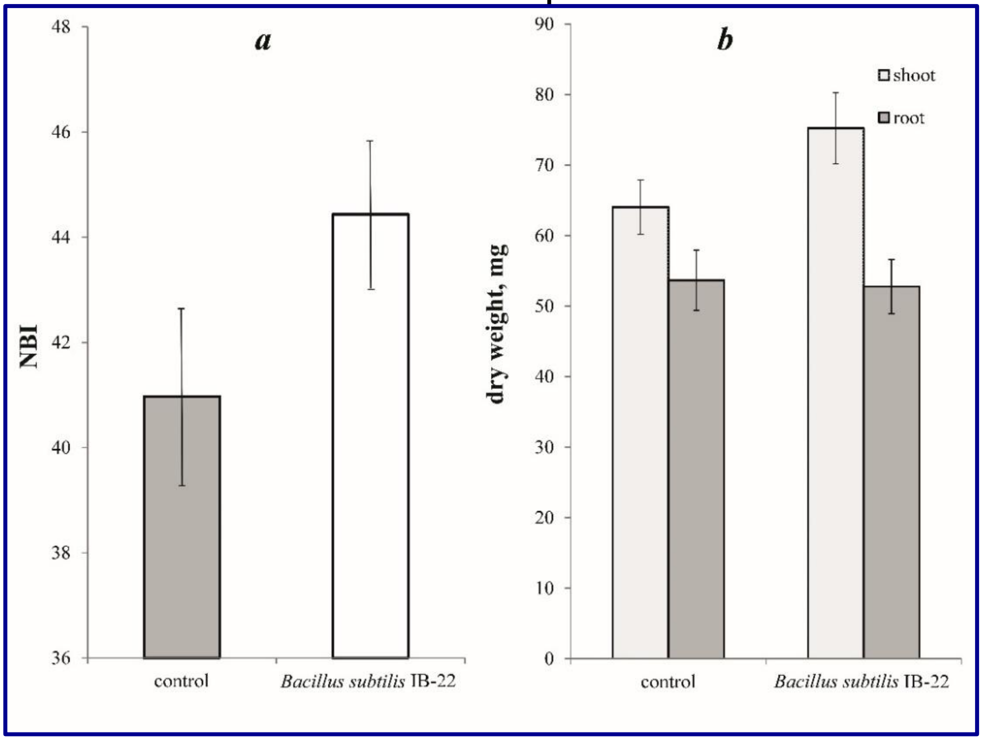
**Рис. 1. Влияние инокуляции ризосферы ячменя *Bacillus subtilis* IB-22 на длину (a) и площадь (b) третьего листа, измеренную через 11 дней после обработки. Средние значения для контрольных и обработанных растений статистически различаются (n=50, p<0.05, t-критерий)**




Moreover, the nitrogen index in leaves increased by 10% under the influence of the treatment (differences compared to the control are significant at $p<0.05$, t-test) (Fig. 2a). Since nitrogen uptake by plants is important for maintaining photosynthesis, it is not surprising that the dry mass of shoots of bacteria-treated plants was 20% higher compared to the control (differences compared to the control are significant at $p<0.05$, t-test) (Fig. 2b). However, no reliable effect of treatment on root mass and length was found.

**Fig. 2. Effect of inoculation of barley rhizosphere with *Bacillus subtilis* IB-22 on the nitrogen balance index (n= 36) (a) and dry weight of shoots and roots (n=40) (b) measured 11 days after treatment**

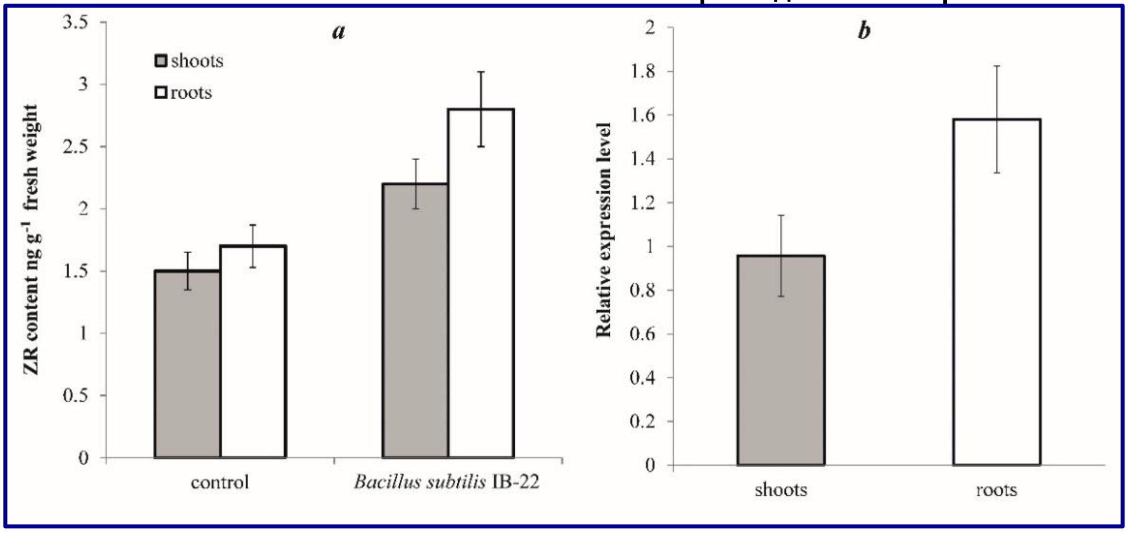
**Рис. 2. Влияние инокуляции ризосферы ячменя *Bacillus subtilis* IB-22 на индекс баланса азота (n= 36) (a) и сухую массу побегов и корней (n=40) (b), измеренные через 11 дней после обработки**



Since cytokinins are known to stimulate shoot growth [Wu *et al.* 2021] and photosynthesis [Cortleven, Schmülling 2015], the promotion of these characteristics in barley shoots by bacteria capable of synthesizing cytokinins suggests that in our experiments these hormones were delivered to the shoot. The results of cytokinin determination confirmed this hypothesis (Fig. 3a).

**Fig. 3. Effect of inoculation of barley rhizosphere with *Bacillus subtilis* IB-22 on the content of zeatin riboside (ZR) in shoots and roots (n=9) (a) and transcript level of *HvABCG* gene in bacteria-treated plants (n=9) expressed as fold change compared with control samples (b) measured 3 days after treatment**

**Рис. 3. Влияние инокуляции ризосферы ячменя *Bacillus subtilis* IB-22 на содержание рибозида зеатина (ZR) в побегах и корнях (n=9) (a) и уровень транскрипции гена *HvABCG* в растениях, обработанных бактериями (n=9), выраженный в виде кратного изменения по сравнению с контролем(b); образцы были взяты через 3 дня после обработки**




It showed a one-and-a-half-fold increase in zeatin riboside levels in the shoots of bacteria-treated plants compared to the control (differences compared to the control are significant at $p<0.05$). Since cytokinin ribosides are considered the primary form for transporting these hormones from roots to shoots [Sakakibara 2021], these results confirmed activation of cytokinin export from roots to shoots in bacteria-treated plants. An alternative explanation, according to which the bacteria stimulated cytokinin synthesis by the plants themselves, cannot be ruled out, but in our view, it seems less likely. Plants are known to absorb cytokinins from the soil, and the bacteria used in this study are known to produce cytokinins [Kudoyarova *et al.* 2014]. Therefore, the increased cytokinin content in the shoots of bacteria-treated plants most likely results from bacterial uptake and delivery of cytokinins to the shoots.

Previous experiments with the expression of the rice *OsABCG18* gene in tobacco leaves revealed the ability of this transporter to support the export of various forms of cytokinin from cells and their delivery to the shoots [Zhao *et al.* 2019]. Therefore, it was of interest to evaluate possible involvement of similar transporters in the delivery of cytokinins to barley shoots.

Genes with a high level of homology to known cytokinin transporter genes in Arabidopsis and rice were found in the barley plant genome [Mahalingam *et al.* 2022]. Based on this analysis, primers were designed to assess the expression of one of these genes (*HvABCG*), enabling testing of its putative role in controlling cytokinin distribution in bacteria-treated plants. As shown in Fig. 3b, the transcript level of this gene almost doubled in roots after bacterial treatment but remained unchanged in shoots. In rice and Arabidopsis plants, the amount of cytokinins accumulated in the shoot was positively correlated with the expression levels of OsABCG18 in roots of rice suggesting its role in the long-distance transport of cytokinins [Zhao *et al.* 2019]. In our experiments increased accumulation of cytokinins in bacteria treated plants was accompanined by increased expression in roots of HvABCG transporter, which is a homolog of rice and arabidopsis cytokinin transporters [Zhang *et al.* 2014; Zhao *et al.* 2019], indicating its possible involvement in the transport of bacterial cytokinins from roots to shoots.

Thus, we have shown that stimulation of barley plant growth by bacteria capable of synthesizing cytokinins is accompanied by, and apparently results from, an increase in cytokinin levels in plant shoots likely due to the transport of bacterial hormones from roots to shoots. These results suggest involvement of HvABCG transporter in the delivery of cytokines to plant shoots and support the proposal that bacterial cytokinins not only penetrate plants but are also transported to the shoot, where they stimulate growth and photosynthesis.

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## *Conflicts of Interest* | *Конфликт интересов*

The authors declare no actual or potential conflicts of interest related to the publication of this article.

Авторы декларируют отсутствие явных и потенциальных конфликтов интересов, связанных с публикацией настоящей статьи.

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