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Production of Indolic Compounds by Rhizobial Bacteria

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Abstract

Rhizobial bacteria, besides nitrogen fixation in symbiosis with legumes, can colonize the roots of non-legumes and promote their growth by different mechanisms, independently of N_2 fixation. Owing to this, rhizobia are considered a plant growth-promoting rhizobacteria (PGPR). Some of the mechanisms of PGPR activity are phytohormone production. Selection of rhizobia which possess some of PGP traits *in vitro* is an important step prior to testing their effects on plants in controlled conditions or field. In this work the ability of indole-3-acid (IAA) production, one of the most important phytohormone of the auxin class, was evaluated in different rhizobial strains. The investigated rhizobial strains were isolated from alfalfa (belonged to the genera *Ensifer* and *Rhizobium*) and from soybean (*Bradyrhizobium* and *Rhizobium*). Strains of all investigated genera produced IAA in the presence of L-tryptophan as precursor, where *Ensifer* strains produced the highest amount of IAA (more than 200 μg ml^{-1}), followed by *Rhizobium*, while *Bradyrhizobium* strains produced the least amount of IAA (with some exceptions up to 15 μg ml^{-1}). With the increase of L-tryptophan concentration, the amount of IAA produced usually grew. Strains with high IAA production indicate their plant growth promoting potential and represent the candidates for evaluation of their effects in non-legumes in controlled and field conditions.

Keywords: rhizobia, phytohormones, inodole-3-acetic acid,

Introduction

Auxins or growth hormones are a group of plant hormones that are produced in the top parts of the tree and roots, transferred to the zone of cell elongation where they enhance the growth of plant organs. In addition to affecting the growth of plant organs, they have many other physiological effects, such as stimulation of flowering or parthenocarpy (Davies, 2013). Representatives of natural auxins all contain indole, and indole-3-acetic acid (IAA) is the most important and widespread type of natural auxin, 4-chloroindole-3-acetic acid (4-Cl-IAA), phenylacetic acid (PAA), indole-3-butyric acid (IBA), and indole-3-propionic acid (IPA) (Casanova-Sáez et al., 2021). The plant can degrade natural auxins with the enzyme auxin oxidase, which allows it to better regulate the growth process.

Today, in addition to natural auxins that are synthesized by the plants themselves, synthetic auxins are also used. With their help, it is possible to influence the course of physiological processes in the plant, which has found practical application in agriculture (Grossmann, 2007). Synthetic auxins are very difficult for the plant to break down with its enzyme auxin oxidase, or it cannot break them down at

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all, so the use of such hormones has a long-lasting effect (Hayashi, 2021). In addition to enabling the growth and elongation of individual cells, and thus whole plants, auxins have many other effects, of which the most important are: stimulation of seed germination, flowering, fruit formation without seeds (the so-called parthenocarpia), controls adventitious and lateral rooting, development of apical dominance, retention of leaf and pistil decline, modulates plant responding to light and gravity (phototropism and geotropism) and increases resistance to stress factors (Duca and Glick, 2020). The effect of auxin depends on their concentration, but also on other factors, such as temperature.

The ability of microorganisms to synthesize auxins has been known for a very long time (Spaepen and Vanderleyden, 2011). IAA production has been detected in many bacteria and it is estimated that over 80% of bacteria isolated from the rhizosphere have this ability (Patten and Glick 1996; Khalid et al. 2004). IAA acts as a signaling molecule in bacteria and affects the expression of bacterial genes. In addition to their regulatory role in their own cells, auxins produced by bacteria can also cause changes in plant development processes. Thus, auxins act as reciprocal signals and can have a great influence on plant-bacterial interactions. The main precursor for IAA synthesis is tryptophan, and the addition of tryptophan to the bacterial growth medium *in vitro* generally stimulates bacterial IAA production. Starting from tryptophan, at least 5 different pathways of IAA synthesis have been described, most of which are similar to plant synthesis pathways, but some intermediates differ (Spaepen et al., 2007). IAA formation via indole-3-pyruvic acid exists in most bacteria, both pathogenic and PGP bacteria, including the genera *Bradyrhizobium* and *Rhizobium*. It is also known that in some rhizobia the synthesis is performed via indole-3-acetaldehyde. The main source of triprophane for rhizobacteria are plant root exudates. Bacterial-synthesized IAAs may play a role in different levels of plant-bacterial interactions. Plant growth and nodulation (root nodule formation) have been controlled, among other things, by IAA synthesis by bacteria (Glick, 2012). IAA increases both surface area and root length and thus allows the plant greater access to nutrients in the soil (Ahemad and Kibret, 2013). Leguminous nodules contain more auxin than unnodulated roots. The nitrogen fixation potential of auxin-producing rhizobia-induced nodules is increased (Camerini et al. 2008). Also, rhizobia can modify auxin homeostasis by modifying auxin transport in plants (Mathesius 2008).

The importance of bacterial IAA production can be seen from the following examples: *Sinorhizobium meliloti* strains with IAA hyperproduction showed multiple tolerance to stress factors, but also increased *Medicago truncatula* tolerance to salt-induced stress (Bianco and Defez 2009). Also, inoculation of *M. truncatula* with rhizobia with hyper IAA production increased plant growth under phosphorus deficiency conditions, due to the release of organic acids by bacteria (Bianco and Defez 2010). All this indicates the advantages of rhizobia strains that produce larger amounts of auxins, so the selection of IAA hyper-producing rhizobia strains is of special importance for leguminous and non-leguminous plants.

In this work we tested the indolic compounds production by strains isolated from alfalfa (*Medicago sativa* L.) belonging mainly to the genus *Ensifer* (*Sinorhizobium*) and soybean (*Glycine max* L.) genus

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Bradyrhizobium under different concentrations of a triptophan as a precursor for IAA synthesis. The detection of IAA produced was measured during time and the number of viable cells was determined. In addition, the use of two different reagents in IAA determinations was compared.

Material and methods

The strains used, species of *Ensifer (Sinorhizobium)* spp., *Rhizobium* spp., *Bradyrhizobium* spp. originate from the collection of bacteria of the Institute of Soils Science. The method used two version of Salkowski reagents, Salkowski reagent with H_2SO_4, which can detect the presence of indole compounds at a concentration of 5-200 μg ml^{-1} (Glickmann and Dessaux, 1995), and the Salkowski reagent with $HClO_4$ which can detect indole compounds at a concentration of 0.2-45 μg ml^{-1} (Gordon and Weber, 1951). Therefore, the sulfuric acid method is recommended for screening a large number of strains of unknown indole production compounds, while the perchloric acid method can be used to more accurately determine indole compounds at higher concentrations.

The bacterial cultures developed in yeast mannitol broth supplemented with 0, 1, 2, 4 or 6 mg l^{-1} L-Trp were extracted via centrifugation. The supernatants of 1 ml was mixed with 2 ml of reagent with H_2SO_4 or with 2 ml of $HClO_4$ reagent (Salkowski reagents according to Glickmann and Dessaux (1995) and Gordon and Weber (1951), respectively). The mixtures were left in the dark at ambient temperature for 25 min until color development and absorbances were recorded at 535 nm with a spectrophotometer. The amount of auxin produced by bacterial strains was determined using a standard curve for IAA prepared in the range of 0–200 μg ml^{-1} or 0-100 μg ml^{-1}. The number of viable cells in cultures (CFU) was determined by plating the appropriate decimal dilutions on yeast mannitol agar plates.

Results and Discussion

Screening of fifty rhizobial strains nodulating alfalfa showed the indolic compounds production (IAA) by all strains, in the YMB medium supplemented with 2 mg ml^{-1} Trp and H_2SO_4 reagent (Figure 1). Most of the strains belonging to *Ensifer meliloti* species (Stajković-Srbinović et al., 2012) reached the highest detectable level of IAA of 200 μg ml^{-1} (designated as ≥200 μg ml^{-1}), while the lowest detected concentration was 15 μg ml^{-1}. The strains producing 15 μg ml^{-1} of IAA belong to *Rhizobium tibeticum* species, whereby visual observation IAA production could not be detected (color change). At this stage of screening the dilutions of bacterial cultures for IAA determinations were not made.

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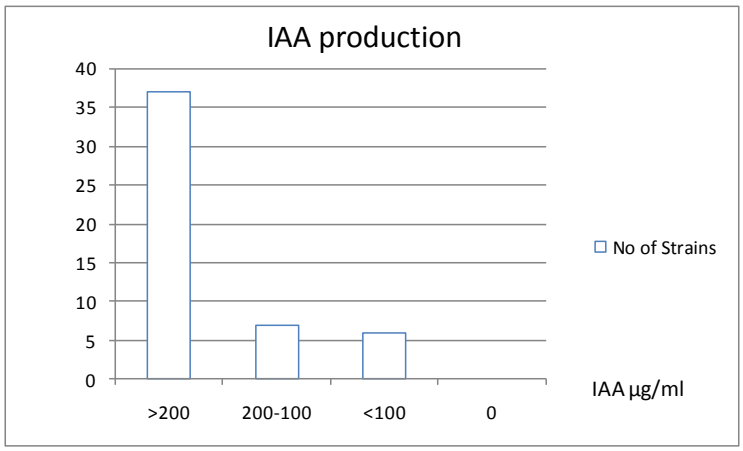

Figure 1. The indole production by alfalfa nodulating strains in the yeast mannitol medium supplemented with 2 mg ml^{-1} Trp determined using H_2SO_4 as reagent.

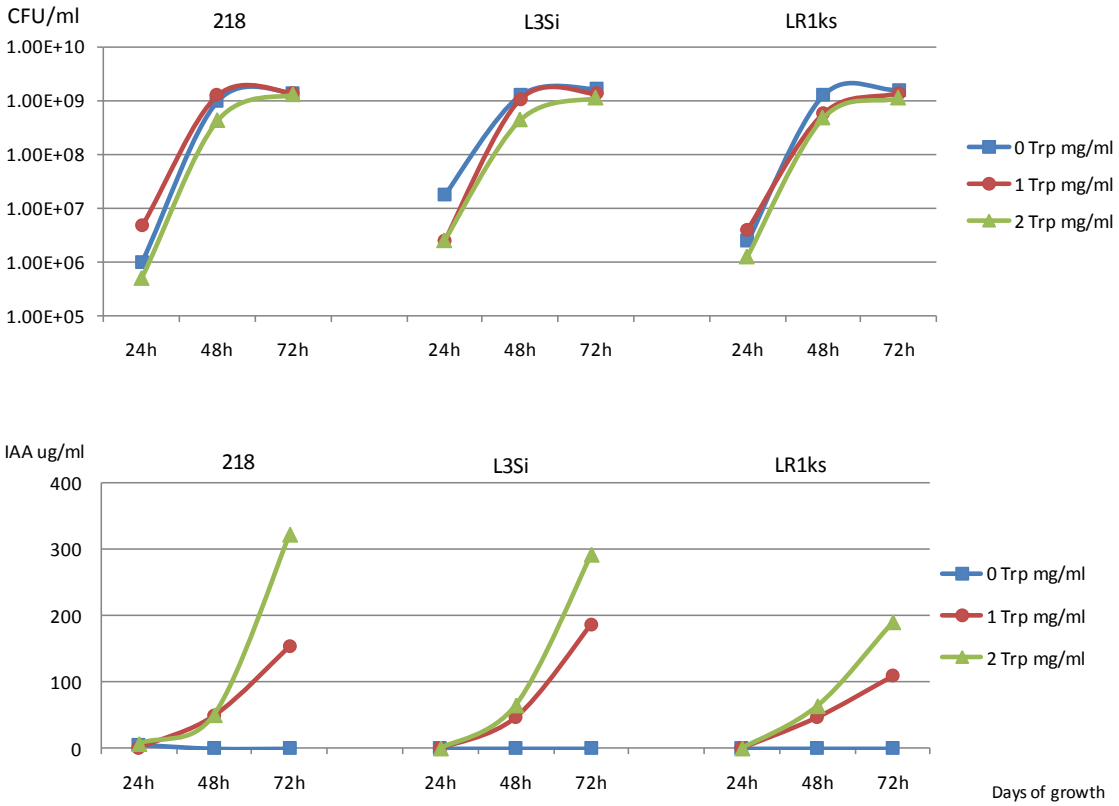

Figure 2. Growth and production of IAA by selected *Ensifer* strains depending on the L-Trp concentrations.

In the next step the production of IAA was measured in the medium supplemented with 0.0, 1.0, and 2.0 mg ml^{-1} L-Trp and using H_2SO_4 as a reagent, and the dilution of cultures for IAA determination was done. At the same time the number of viable cells (CFU-colony forming units) was determined. The CFU of *E. meliloti* strains reached the highest values after 48h and stayed the same in the next

72h. There were no differences in CFU numbers between different concentrations of L-Trp. The IAA production grew linearly, it was higher at higher L-Trp supplementation (Figure 2) and reached up to 300 μg ml^{-1} (or more) after 72h of cultivation.

Screening of forty *Bradyrhizobium* spp. strains showed IAA production in almost all strains, in the YMB medium supplemented with 2 mg ml^{-1} Trp and using H_2SO_4 as reagent. Most of the strains belonging to *Bradyrhizobium* species reached up to 51.10 μg ml^{-1} of indole compounds, while the lowest detected concentration was 5.81 μg ml^{-1} (data not shown).

In the next step the production of IAA was measured in the medium supplemented with 0.0, 0.5, 1.0, and 2 mg ml^{-1} Trp. At the same time the number of viable cells was determined. The CFU of *Bradyrhizobium* spp. reached the highest values after 72h of cultivation, and stayed the same in the next 96h, there were no differences in CFU numbers between different concentrations of L-Trp.

On the other hand, although the concentration of L-Trp influenced the IAA production positively, no clear pattern can be observed, i.e. the response of *Bradyrhizobium* strains to increased L-Trp concentrations as well as during the time of cultivation (Figure 3). The IAA production linearly grew for strain 503 and reached the highest level of 35 μg ml^{-1} , when 1 mg ml^{-1} Trp was added (Figure 3).

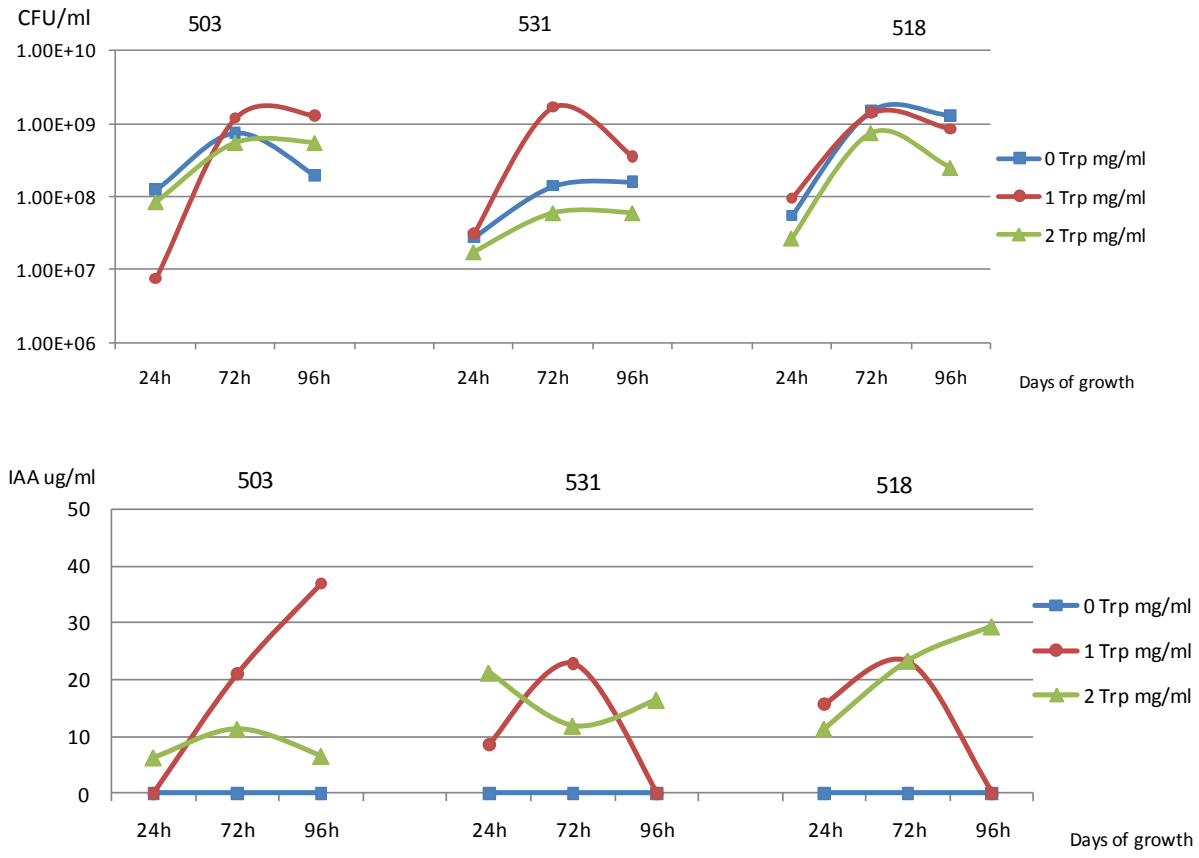

Figure 3. Growth and production of IAA by selected *Bradyrhizobium* strains depending on the L-Trp concentrations.

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Although *Bradyrhizobium* produces an incomparably lower amount of IAA compared to *Ensifer* strains, the amount of IAA produced mainly depends on the concentration of L-Trp and the day of incubation, while it varied slightly between strains. To check whether *Bradyrhizobium spp.* can produce more auxin in the presence of larger amounts of substrate, the production of IAA in medium with higher concentrations of L-Trp (2, 4, 6 mg ml^{-1}) was investigated for selected strains. However, the obtained results showed that the increase of the L-Trp concentration over 2 mg ml^{-1} does not affect the IAA production (Table 1).

Table 1. Production of IAA by *Bradyrhizobium* strains in the presence of high L-Trp concentrations and H_2SO_4 as reagent.

Bradyrhizobium strains	Production of IAA* µg ml^{-1}			
Trp mg ml^{-1}	0	2	4	6
505	nd	25.89	26.75	nd
525	nd	25.52	21.75	nd
527	nd	29.09	26.75	nd
529	nd	28.56	26.75	nd
531	nd	16.46	23.49	nd
532	nd	28.79	26.75	nd
540	nd	16.77	24.91	nd

nd-below the detection limit of 5 µg ml^{-1}

As the IAA concentration detected for *Bradyrhizobium spp.* was low or below the detection limit (5 µg ml^{-1}) in the experiments in which the Salkowski reagent containing sulfuric acid was applied, further experimental work examined whether the sensitivity could be increased by applying the Salkowski reagent containing perchloric acid test, that is more precise in determination of IAA concentrations produced. Namely, it is known from the literature that the application of Salkowski reagent containing perchloric acid enables greater precision in the detection of IAA concentration, but in the range from 0.2 to 45 µg ml^{-1} (Gordon and Weber, 1952). Considering the results obtained in experiments with Salkowski reagent with sulfuric acid, concentrations of L-Trp up to 2 mg ml^{-1} were used in further experiments, and the concentration of IAA was determined at the end of the incubation period. In these experiments, the production of IAA was measured comparatively using both types of reagents (Salkowski with sulfuric acid and with perchloric acid), and in addition to *Bradyrhizobium* strains, several strains of the *Sinorhizobium* genus were tested as well, which served as controls.

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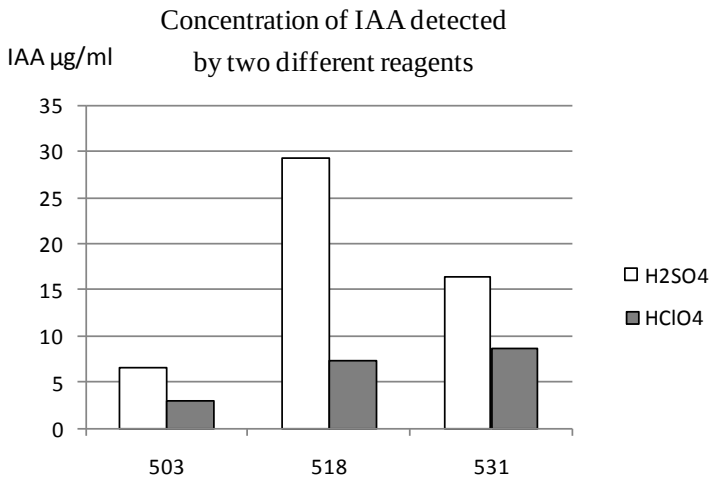

Figure 4. The IAA production by soybean nodulating strains in the yeast mannitol medium supplemented with 2 mg ml^{-1} Trp determined using H_2SO_4 or $HClO_4$ as reagent.

The obtained results for *Bradyrhizobium spp.* showed that the concentration of IAA detected in the presence of 2 mg ml^{-1} L-Trp using the sulfuric acid reagent, was higher than in using the reagent with perchloric acid (Figure 4). The interval of IAA production for all *Bradyrhizobium* spp. strains detected by reagent with perchloric acid was from 0.2 to even 95 µg ml^{-1} (Stajković-Sbinović et al., 2020), whereby the detected concentration for most strains was in the range of 2-10 µg ml^{-1}.

The concentrations of detected IAA for *Ensifer spp.* were the highest at the L-Trp concentration of 2 mg ml^{-1}, and the comparison of the values obtained for different reagents indicates that higher concentrations were obtained in the case of the Salkowski reagent with sulfuric acid application (Figure 5). The highest concentration of produced IAA was recorded in strain 218 after 5 days of incubation and it was 690 µg ml^{-1}.

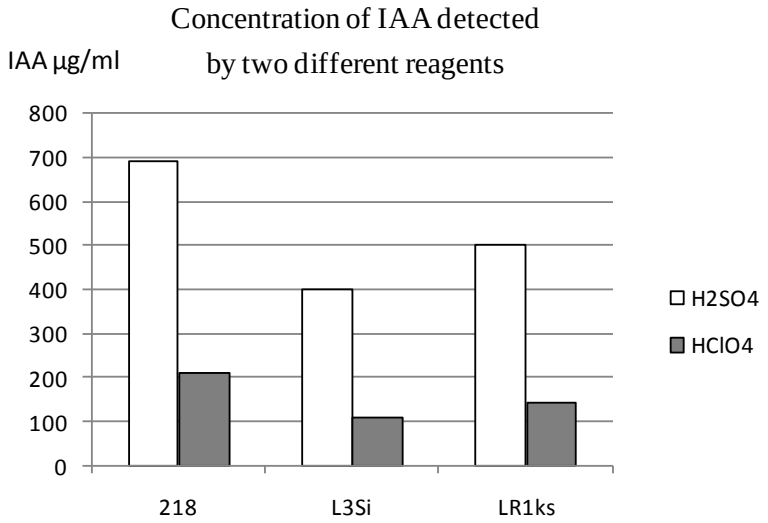

Figure 5. The IAA production by alfalfa nodulating strains in the yeast mannitol medium supplemented with 2 mg ml^{-1} Trp determined using H_2SO_4 or $HClO_4$ as reagent.

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The IAA detection using two types of Salkowski reagents in selected strains of *Bradyrhizobium* and *Ensifer* indicates that the concentration of IAA detected by the reagent with perchloric acid is lower, but the production trend was maintained (Figure 4 and 5).

Comparing the detected concentrations of IAA in *Bradyrhizobium* and *Ensifer* strains indicates a clearly lower production in representatives of the genus *Bradyrhizobium*. These results are in agreement with the findings of Stajković-Srbinović et al., (2012; 2020), which showed a weaker production of auxin by *Bradyrhizobium spp*. strains compared to *Sinorhizobium spp.*. *B. japonicum* strains are known to synthesize IAA, both as free-living forms in soil and as bacteroids in soybean nodules (Hunter, 1987; Minamisawa and Fukai, 1991). In addition, *B. japonicum* can use exogenous IAA as a carbon source and degrade it. It is also known that in the presence of certain amounts of IAA, the growth of bradyrhizobia is slowed down in a concentration-dependent manner (Donati et al., 2013). The two main techniques widely used for the detection of IAA are the colorimetric reaction using the Salkowski reagent and HPLC (high performance liquid chromatography). It was observed that the concentrations detected by the Salkowski reagent are always higher than in the case of using HPLC, which is explained by the fact that HPLC detects specifically IAA, while the method according to Salkowski detects some other indole derivatives that may or may not be related to the synthesis of IAA (Kuang- Ren et al., 2003). Although the fact speaks in favor of the HPLC method, the application of the Salkowski method is valid, since it was proven that a positive Salkowski reaction was always accompanied by a positive HPLC finding for IAA (Naqqash et al., 2016, Glickmann and Dessaux, 1995). Therefore, due to the cost-time ratio of these two analyses, the Salkowski reaction is still widely used. It is known that the concentration of produced IAA varies in strains depending on the concentration of added L-Trp (Gutierrez et al., 2009; Naqqash et al., 2016), which was also detected in our work. The production of IAA by *Ensifer spp.* and *Bradyrhizobium spp.* strains obtained in our work agrees with literature data. Namely, Ghodake et al. (2008) detected that *S. meliloti* strains produce IAA only in the presence of L-Trp and the concentration of IAA increases with increasing Trp concentration in the medium. The study by Singh et al. (2012) showed that about 50% of *Sinorhizobium* strains produce IAA. The lower production of IAA by *Bradyrhizobium spp.* strains also agrees with the available literature. Boeiro et al. (2007) showed for three commercial strains of genus *Bradyrhizobium* that the production of IAA in low concentrations, as well as other hormones (gibberellic acid and abscisic acid). However, in the work of Prevost et al. (2012) from a total of 216 *Bradyrhizobium* strains tested, only 33 synthesized IAA, which differs from our results.

The significance of the obtained results is reflected in the fact that strains producing IAA achieve better nodulation and nitrogen fixation in legumes and increase tolerance to stressful environmental conditions (Camerini et al., 2008). In addition, numerous authors have shown that hormone-producing strains of rhizobia can improve the growth of non-leguminous plants upon seed inoculation (Biswas et al., 2000; Yanni et al., 2001; Hafeez et al., 2004; Matiru and Dakora, 2005; Mishra et al., 2006; Pena and Reyes, 2007). Therefore, the strains that showed a high production of IAA *in vitro* in this work

indicate the existence of PGPR potential and make good candidates for additional tests with more plant cultures, first in semi-controlled, and then in field conditions.

Acknowledgments

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Produkcija indolnih jedinjenja od strane rizobijalnih bakterija

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Izvod

Abstract

Rizobijalne bakterije, pored fiksacije azota u simbiozi sa mahunarkama, mogu da kolonizuju korenje neleguminoznih biljaka i podstiču njihov rast različitim mehanizmima, nezavisno od fiksacije N_2. Zbog toga se rizobije smatraju rizobakterijama koje podstičeu rast biljaka (PGPR). Neki od mehanizama aktivnosti PGPR-a su proizvodnja fitohormona. Selekcija rizobija koje poseduju neke od osobina PGP in vitro je važan korak pre testiranja njihovog dejstva na biljke u kontrolisanim uslovima ili na polju. U ovom radu je procenjena sposobnost proizvodnje indol-3-sirćetne kiseline (IAA), jednog od najvažnijih fitohormona, kod različitih rizobijalnih sojeva. Ispitivani sojevi rizobija su izolovani iz lucerke (rodovi *Ensifer* and *Rhizobium*) i sojevi rizobija izolovani iz soje (*Bradyrhizobium* i *Rhizobium*). Sojevi svih ispitivanih rodova proizvode IAA u prisustvu L-triptofana kao prekursora, pri čemu sojevi roda *Ensifer* proizvode najveću količinu IAA (više od 200 µg ml^{-1}), a potom sojevi *Bradirhizobium* koji proizvode najmanju količinu IAA (sa nekim izuzecima do 15 µg ml^{-1}). Sa povećanjem koncentracije L-triptofana, količina proizvedene IAA obično raste. Sojevi sa visokom produkcijom IAA ukazuju na njihov potencijal za podsticanje rasta biljaka i predstavljaju kandidate za procenu njihovog dejstva na neleguminozne biljke u kontrolisanim i poljskim uslovima.

Ključne reči: rizobija, fitohormoni, inodol-3-sirćetna kiselina

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