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MOLYBDOENZYME PARTICIPATION IN PLANT BIOCHEMICAL PROCESSES

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ABSTRACT

Molybdenum is a key microelement in plant vital functioning. The microelement can be absorbed by the plants only in the form of molybdate-anion. The Molybdenum deficiency affects negatively to the most important agricultural growing. As molybdenum takes part in such vital mechanisms as nitrogen and sulfur metabolism, plant hormone biosynthesis, and purine banding catabolism. Molybdenum is included in enzyme content which is called molybdoenzymes. Having bonded with molybdopterin it creates molybdenum co-factor (Moco) and gets oxidation-reduction properties. Moco is included in active site of molybdoenzymes. They take part in sulfur and nitrogen metabolism, and detrimental compound detoxication. Molybdenum deficiency is characterized by the slow plant growth, low amount of chlorophyll ascorbic acid capacity. It was noticed that plants suffering from the molybdenum deficiency can be saved, sodium molibdate can be used, it can be put directly in the soil or plant leaves can be sprayed with the solution. There are five plant molibdoenzymes which are currently known: sulfite oxidase (SO), xanthine dehydrogenase (XD), nitrate reductase (NR), aldehyde oxidase (AO) and mitochondrial amidoxim-regenerative component. Nitrate reductase catalyzes the first stage of nitrate assimilation, eucariotic organisms contain three isoforms of the molybdoezimes: A NADH, A NAD(P)H и NADPH. Xanthine dehydrogenase regulates purine metabolism. XD increases plant antioxidant ability and slows down leaves aging. Molybdoenzymes are involved in the process of the stress adaptation, defining of the mechanisms and their reaction to environmental stress conditions is important for plant stress resistance.

Key words: molybdenum, molybdoenzymes, sulfite oxidase, nitrate reductase, molybdenum deficiency, abscisic acid.

INTRODUCTION

All over the world a wide range of soils suffers from the molybdenum deficiency. The deficiency of the element creates agrarian problem, as it influences crops quality and brings to loses of vital agricultural crops. The plants which suffer from the molybdenum deficiency, grow slowly, contain low amount of chlorophyll and ascorbic acid [1].

Tomato molybdenum deficiency appears as spots on the lower leaves, if the sickness progresses the necrosis of leaves edges appears, the leaves may roll, inflorescence drop, fruit do not develop [2]. Sugar beet molybdenum deficiency appears as light-green leaves, which later get yellow-green coloration, old leaves in the area of

the tip or leaf stock roll and die. The symptoms move from old to new leaves, the dying of the apical point is on the 7th or 9th week. *Hordeum molybdenum* deficiency appear as opaque bright-green leaves, their tips become ivory or light-brown, seeds become small. If the level of deficiency is critical the caulis are getting weaker, leaves dull-green with brown tips, which are becoming necrotic patches. New leaves are rolled with the chlorosis signs, seeds do not develop [3].

Leguminous plant molybdenum deficiency looks like nitrogen hunger. Critical molybdenum deficiency slows down the process of plant growth much, the plants become dull-green, lives lose their form and die. Tubercules are badly developed or absent at all [4].

The majority of the changes discussed above are connected to molybdoenzymes activity decrease. One of the first experiments connected to the molybdenum necessity for the adequate plant growth was demonstrated with help of tomato plants, which were grown on the plant culturing units with solution, which did not contain molybdenum. The plans grown with the molybdenum deficiency showed phenotypes, such as chlorosis, changes in limb morphology. The first case of molybdenum deficiency was registered in agriculture on the runs of the South Australia. Later it was noticed that plants suffering from the molybdenum deficiency can be saved, by using sodium molybdate in the soil or by spraying the leaves with the solution [5].

In plants molybdenum takes part in nitrogen and sulfur metabolism, plant hormone biosynthesis, and purine bonds catabolism. The physiosorption is influenced by soil pH, the ideal pH level for the molybdenum physiosorption is 4 and 5. In acidic sandy soils the level is not high, thus plants suffer from deficiency in current micronutrient. Adding of lime and phosphorous fertilizers increases molybdenum availability for plants [6].

Plant molybdoenzymes. Having bonded with molybdopterin, molybdenum forms molybdenum cofactor (Moco) (Fig.1.) and gets reductive-oxidative properties. Moco is included in active site of molybdoenzymes, for the work they use small strands of electron transfer and take part in sulfur and nitrogen metabolism, hormone synthesis, and detrimental compound detoxication [7].

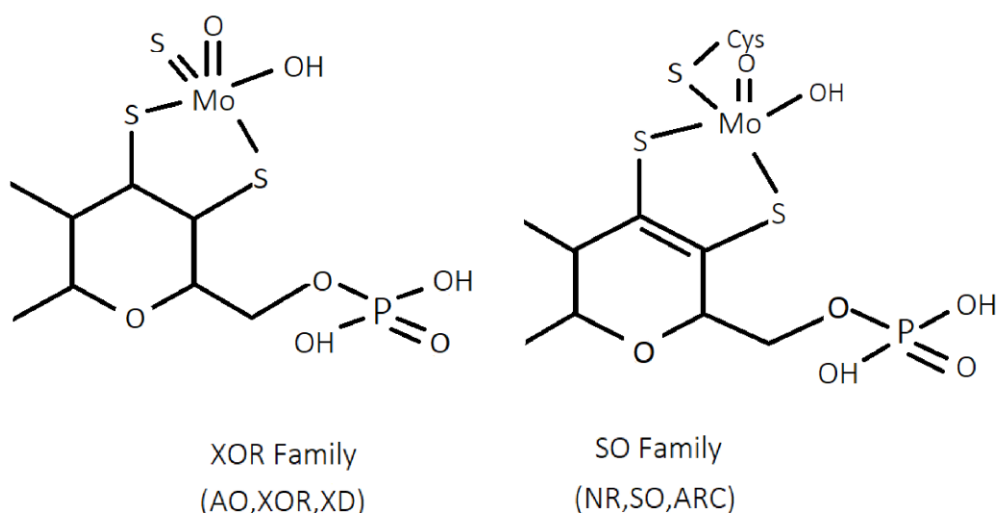


Fig.1. Two forms of Moco required for the transition in molybdoenzymes family

Molybdoenzymes X-ray crystallographic analysis shows that cofactor is not situated outside protein, it is in the depths of a molybdoenzymes, and thanks to its structure becomes available for the complying substrate. When the amount of wolframium increases, the activity of molybdoenzymes decreases. Wolframium is molybdenum's antagonist as it can change molybdenum in molybdoenzymes, creating catalytically-active or subactive analogue [8].

Molybdoenzymes in plants are the key molybdoenzymes in nitrate assimilation, purine metabolism, hormone biosynthesis, and most likely, sulfite detoxication. It is believed that they take part in the process of stress adaptation and, as a result understanding of the way they react in environmental stressful situations is vital for agriculture and for plant stress resistance improvement [9].

Molybdate anion is the only molybdenum form, appearing in soil, which is available for plants. More than fifty molybdoenzymes are depend on molybdenum (concentration), there are five types of such enzymes known in plants: sulfite oxidase, mitochondrial amidoxim-regenerative component, xanthine dehydrogenase, nitrate reductase, and aldehyde oxidase [10].

Nitrate reductase: functions, isoform, and factors influencing to its activity.

Nitrate reductase (NR) is a vital molybdoenzymes in plant life. It catalyzes the first stage of nitrate assimilation, turns nitrate into nitrite to be precise [11].

For a long time NR was considered to be the main molybdoenzymes responsible for nitrogen oxide production in most plants. Nitrogen oxide, regulating growth, developing metabolism, and leaf aging is incredibly vital in plant existence, it is also responsible for plant biotic and abiotic stress, protective processes in the fight with pathogenic agents. However, it is well known fact now that nitrate reductase is not able to produce nitrogen oxide from nitrite in vitro, when noitrate is in environment. NR is able to provide NADH electrons in mitochondrial amidoxim-regenerative component (which is renamed in NR-forming nitrite reductase) for nitrite recovery process up to nitrogen oxide. NR-forming nitrite reductase produces nitrogen oxide due to electron transport chain by nitrate reductase from NAD (P) H to heme [12].

There are three isoforms of nitrate reductase in eukaryotic organisms: A NADH-specific nitrate reductase peculiar to such plants as tomato, tobacco and water-inhabiting plants. A NAD(P)H is contained in monocotyledonous plants: rice, barley, and corn, also in coral bean and common birch, and NADPH is in mushrooms. There are all three forms of isoforms in soybeans. The most of the higher plant are characterized by A NADH specific isoform. NR is a dimerous protein which consists of two identical subunits; for the nitrate catalysis reduction process there are three prosthetic groups in each subunit: the first group is FAD which is located at C-terminus polypeptide, the second is a gem or Cytb557 which is located in the center, and the third one is MoCo which is at N-terminal end of a molybdoenzymes (Fig.2.). In the reduced form to ease the process of nitrate consumption, NR is used by a electron physiological donor, ferredoxin [13].

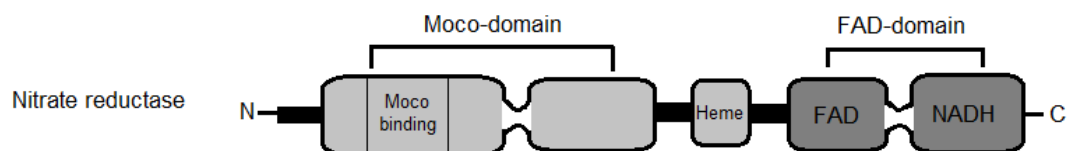


Fig.2. Nitrate reductase structure.

Transformation of non-organic into organic nitrogen form is a process of nitrate assimilation. About 25% of photosynthetic energy is spent for this process. The

production of ammonium in chloroplast includes two stages of transportation and two stages of reconstruction. Transportation stages mean getting of nitrate into a cell and nitrite into chloroplast. The first stage of nitrate reconstruction into nitrite is in cytosol, it catalyzes by nitrate reductase, the second stage is a change from nitrite to ammonium, catalyzes by nitrite reductase (Fig.3.) [13,14].

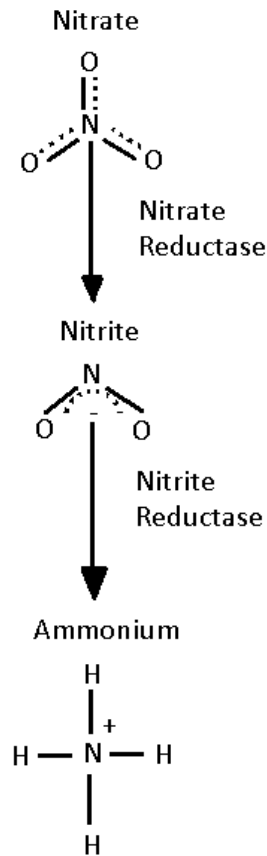


Fig.3. The production of ammonium

In the darkness or when the roots are located in anoxic environment nitrate reductase activity increases, but nitrite reductase activity decreases, nitrite is collected in cells, and later it is released into environment. Nitrite is transported either in the form of protons or in the form of ions. In acid environment nitrogen oxide is formed from the proton form of nitrite by nonenzymatic reaction: $2\text{HNO}_2 \leftrightarrow \text{NO} + \text{NO}_2 + \text{H}_2\text{O}$. Maximum activity of nitrite reductase appears if pH 6.1 is [15].

Light and carbohydrates influence nitrate reductase at the level of transcription and translation. It was proved that short non-stop green light exposure (48 hours) in combination with red and blue lights decreases the nitrate content. Thus, red and blue lights are photosynthesis promoting agents, while green light affects positively to nitrate reductase gene expression [16]. The same way, in darkness adjusted tobacco plants Tex-Mex, sucrose, glucose, and fructose strengthen nitrate reductase expression. During days and nights nitrate reductase gene expression changes with help of transcriptional or post-transcriptional regulations. The level of nitrate reductase informational rizi form increases at night, reaches its peak at the dawn, and gradually decreases during the day. Low temperatures and draught influence nitrate reductase gene expression and decreases daily activation of these genes in tomatoes, yet draught decreases the level of nitrate reductase informational rizi form in corn leaves. Apart from the environment factors, plant hormones also influence nitrate reductase expression [17]. Cytokinins increase the nitrate reductase activity in many plants. Thus, cytokinins

increased nitrate reductase activity in cabbage stem piths explants, wheat and barley germs, and cut out cucumber seed lobes [18].

Dormin also leads to nitrate reductase activity stimulation, if potato tuber pieces have been treated for 22 hours in advance, at zero ectogenous nitrates level the nitrate reductase activity increases and the content of endogenous nitrates increases as well. Pre-treatment with the solution containing dormin and actinomycin D, affects the best stimulation of NR [19].

Therefore, NR catalyzes the stage of nitrate transformation into nitrite. There are three isoforms of nitrate reductase in eukaryotic organisms: A NADH, A NAD(P)H и NADPH. Green light affects positively to nitrate reductase gene expression. Cytokinins and dormin increase activity of the enzyme as well. Environmental factors such as low temperature and draught decrease activity of NR in plant leaves.

The role of mitochondrial amidaxim reductase is not learned in detail yet, the well known fact is plant genomes contain two isoforms of the given molybdoenzyme [20].

Xanthine dehydrogenase: functions, construction, and role in plant life. Xanthine dehydrogenase (XD) is a molybdoenzyme which regulates purine metabolism. It catalyzes 2,6,8-trioxypurine formation from xanthine and hypoxanthine, and later allantoin and allantoat synthesis with help of chain of metabolic reactions (Fig.4.). Xanthine dehydrogenase activity increase boosts rice antioxidative capability and slows down the aging process of rice leaves. By doing so, this enzyme improves the photosynthesis products collection and increases the yield [21].

xanthine dehydrogenase

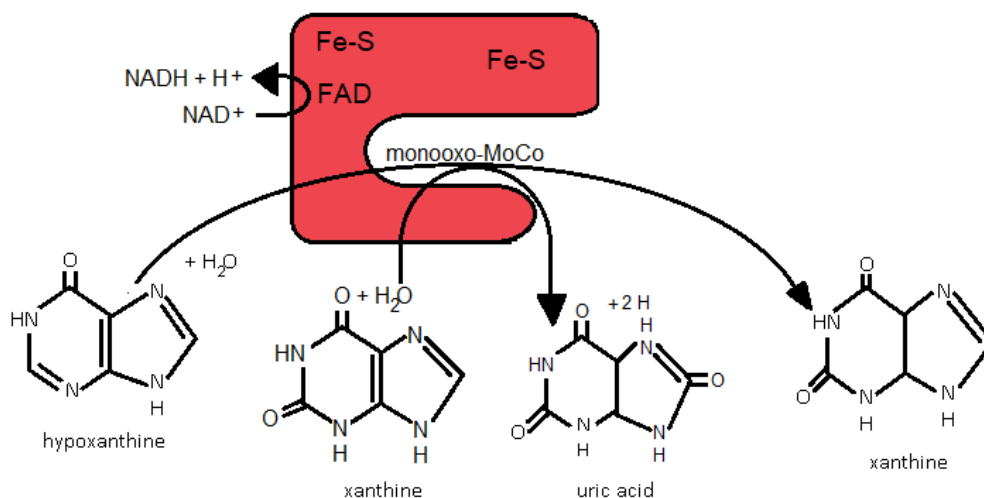


Fig.4. Xanthine dehydrogenase catalyzes uric acid formation

XD is a homodimeric enzyme, its molecular weight is 285,000; it consists of two subunits, molecular weight of each one is 141,000. Holoenzyme contains 1.7 (\pm 0.7) gram-mol of molybdenum and 8.1 (\pm 2.0) gram-mol of ferrum / gram-mol of enzyme, the enzyme itself contains FMN in the role of flavin, thus it is molybdo-ferro-flavo enzyme. Animal XD and mushroom XD is also molybdo-ferro-flavo enzyme with a FAD as a flavin [22].

Xanthine dehydrogenase is required for fixed nitrogen assimilation in grain-bean cultures. 2,6,8-trioxypurine, which is formed in the process of reaction, that is catalyzed by xanthine dehydrogenase, it is precursor substance for ureide, allantoin, allantoat. In turn these elements transfer nitrogen in bean cultures. Conducted researches, *in vitro*

have shown that in kidney beans xanthine dehydrogenase can act as dehydrogenase or as oxidase. To be precise it can either protect from oxidative radicals, or vice versa, produce them [23]. The same way, in the pattern plant, *Arabidopsis thaliana*, affected by powdery mildew, xanthine dehydrogenase, plays two roles, functions as oxidase along with NADPH oxidases RbohD and RbohF, producing superoxide, which transforms into hydrogen peroxide. Hydrogen peroxide supports resistance of the harmed cells to the powdery mildew. At the same time this molybdoenzyme functions as dehydrogenase which is producing 2,6,8-trioxypurine to capture hydrogen from chloroplasts, which were under stress, thus, it protects a plant from oxidative damage caused by stress [24].

Above all mentioned before in transgenic plants *Arabidopsis thaliana* with “silent genes” xanthine dehydrogenase AtXDH1 and AtXDH2 there was the fact, that sudden decrease of XD protein level leads to quick extra xanthine accumulation and slow growth phenotype, in this case development of fruit and seed crop-producing power is worsen even in normal conditions of growing. XD inactivation leads to early leaves ageing process and quick chlorophyll cleavage. This experimental work proves the importance of XD at the time of plant growing and development, and also in physiological processes of leaf ageing [25].

XD plays an important role in adaptation of *Arabidopsis thaliana* in the period of draught, as enzyme knock down leads to accumulation of extra hydrogen peroxide level in transgenic plantlets in comparison with wild plantlets. Increasing of the level oxygen active forms (OAF) influences to lower resistance level in the periods of draught, as OAF level exceeds the tolerance level of XD suppress lines, which leads to remediless oxidative damage. This damage leads to intense cells death. Therefore, XD activity suppression creates arabidopsises sensitive to draught [26].

The experiment with barley, which was grown in Hoagland medium, showed that XD activity increases in all parts of a plant if sodium molybdate concentration increases up to 100 mcM/liter in nutritional medium, whilst activity in leaves does not change much. Activity of the enzyme in root extract increased a bit if the level of sodium tungstate increases up to 1mcM/liter, yet further increase of concentration leads to decrease of activity. In other words, activity of XD in barley increases if molybdate and some amount of concentration tungstate are added [27]. It does not metter which XD substrate catalyzes OAF, thanks to inner activity of NADH oxidase. XD produces OAF in a FAD-containing domain by NADH oxidation. Being supported in conditions of hypoxia the reaction depends on pH and the level of oxygen [28].

OAF is a side product of plant aerobic metabolism it forms in chloroplasts, mitochondrions, and peroxisomas. OAF causes remediless DNA damage and cells death, but also works as important signal molecules, which are regulatin normal plant growth and reaction to stress [29].

According to everything mentioned above, XD catalizes 2,6,8-trioxypurine formation from xanthine and hypoxanthine, and later allantoin and allantoat synthesis. This molybden enzyme is necessary for fixed nitrogen assimilation in a grain of a bean plant. It increases plant antioxidative capability and slows down leaves ageing, influences directly to fruit development and seed fertility. XD helps to draught adaptation process if small amount of molybdate and tungstate concentration are added.

CONCLUSION

To sum up the digest, the importance of molybdenum for plants was shown. In case of molybdenum deficiency plant leaves morphology changes, seeds develop poorly, flowering is broken, growth of plants slows down. The micro element is included in several enzymes which are called molybdoenzymes. Having bonded with

molybdopterin, molybdenum form molybdenum cofactor (Moco). It gets reductive-oxidative properties. Moco is included in the active site of molybdoenzymes, they take part in sulfur and nitrogen metabolism, hormone synthesis, harmful bonds detoxification.

Molybdoenzymes take part in the processes of stress adaptation and as a result play important role for the agriculture.

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МОЛИБДОФЕРМЕНТТЕРДІҢ ӨСІМДІКТЕРДІҢ БИОХИМИЯЛЫҚ ПРОЦЕСТЕРІНЕ ҚАТЫСУЫ

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АБСТРАКТ

Молибден өсімдіктердің тіршілігінде негізгі микроэлемент болып табылады. Өсімдіктер осы микроэлементті тек молибдат-анион түрінде сіңіреді. Молибденнің жетіспеушілігі аса маңызды ауыл шаруашылығы дақылдарына зиянды әсер етеді, себебі молибден өсімдіктерде азот, күкірт метаболизмі, өсімдік гормондарының биосинтезі мен пурин қосылыстарының катаболизмі сияқты маңызды механизмдерге қатысады. Молибден молибдоферменттер деп аталатын ферменттердің құрамына кіреді. Ол молибдоптеринмен байланысып, молибден кофакторын (Мосо) құрайды және тотығу-тотықсыздану қасиеттеріне ие болады. Мосо молибдоферменттердің активті сайтының құрамына кіреді. Олар күкірт пен азот метаболизміне, гормондар синтезіне, зиянды қосылыстарды уытсыздандыруға қатысады. Молибденнің жетіспеушілігі өсімдіктердің баяу өсуімен, хлорофилл мен аскорбин қышқылы мөлшерінің аз болуымен сипатталады. Топыраққа натрий молибдатын қолдану немесе осы ерітіндіні жапырықтарға шашу арқылы молибденнің жетіспеушілігі байқалатын өсімдіктерді сақтап қалуға болатындығы анықталды. Бес өсімдік молибдоэнзимдері белгілі: сульфит оксидаза (СО), ксантин дегидрогеназа (КДГ), нитратредуктаза (НР), альдегид оксидаза (АО) және митохондриялық амидоксим-қалпына келтіруші компонент. Нитратредуктаза нитраттар ассимиляциясының бірінші сатысын катализдейді, эукариоттық ағзаларда осы молибдоферменттің үш изоформасы қамтылған: А NADH, А NAD(P)H и NADPH. Ксантиндегидрогеназа пуриндер метаболизмін реттейді. КДГ өсімдіктердің антиоксиданттық қабілетін арттырады және жапырақтардың ескіруін баяулатады.

Молибдоферменттер күйзеліске бейімделу процесіне тартылады, олардың сыртқы ортаның күйзеліс жағдайларына реакциясының механизмдерін анықтау өсімдіктердің күйзеліске төзімділігін жақсарту үшін маңызды.

Негізгі сөздер: молибдоферменттер, сульфит оксидаза, нитратредуктаза, молибден жетіспеушілігі, абсциз қышқылы.



УЧАСТИЕ МОЛИБДОФЕРМЕНТОВ В БИОХИМИЧЕСКИХ ПРОЦЕССАХ РАСТЕНИЙ

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АБСТРАКТ

Молибден является ключевым микроэлементом в жизнедеятельности растений. Данный микроэлемент может быть усвоен растениями в лишь форме молибдат-аниона. Нехватка молибдена оказывает пагубное воздействие на первостепенные сельскохозяйственные культуры, поскольку у растений молибден принимает участие в таких важных механизмах как метаболизм азота, серы, биосинтез растительных гормонов и катаболизм пуриновых соединений. Молибден входит в состав ферментов, названных молибдоферментами. Он, связываясь с молибдоптерином образует кофактор молибдена (Мосо) и приобретает окислительно-восстановительные свойства. Мосо входит в состав активного сайта молибдоферментов. Они участвуют в метаболизме серы и азота, синтезе гормонов, детоксикации вредных соединений. Дефицит молибдена охарактеризован медленным ростом растений, содержанием низкое количество хлорофилла и аскорбиновой кислоты. Было обнаружено, что растения, страдающие дефицитом молибдена можно спасти, применяя молибдат натрия в почву или опрыскивая листья этим раствором. Известно пять растительных молибдоэнзимов: сульфит оксидаза (СО), ксантин дегидрогеназа (КДГ), нитратредуктаза (НР), альдегид оксидаза (АО) и митохондриальный амидоксим-восстанавливающий компонент. Нитратредуктаза катализирует первую стадию ассимиляции нитратов, эукариотические организмы содержат три изоформы данного молибдофермента: А NADH, А NAD(P)H и NADPH. Ксантиндегидрогеназа регулирует метаболизм пуринов. КДГ повышает антиоксидантную способность растений и замедляет старение листьев. Молибдоферменты вовлечены в процесс адаптации к стрессу, определение механизмов их реакции на стрессовые условия внешней среды важны для улучшения стрессоустойчивости растений.

Ключевые слова: молибдоферменты, сульфит оксидаза, нитратредуктаза, дефицит молибдена, абсцизовая кислота.