IRSTI 34.29.25 https://doi.org/10.26577/eb.2024.v98.i1.06

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EVALUATION OF EFFECT OF EXOGENOUS MOLYBDENUM AND TUNGSTEN ON SEED GERMINABILITY AND ON SYMPTOMS OF VIRUS INFECTION IN PLANTS

Crop production is the basis of agriculture in Kazakhstan. Soils in Kazakhstan suffer from molybdenum deficiency. Molybdenum deficiency in plants is characterized by the stunted growth, poor seed setting, fruit deformation and reduced plant resistance to diseases. Molybdenum catalyzes key steps in the metabolism of nitrogen, carbon and sulfur. It promotes the biosynthesis of the phytohormones of abscisic acid and indole-3-butyric acid. An increase in molybdenum concentration leads to an increase in aldehyde oxidase activity. Aldehyde oxidase generates hydrogen peroxide during viral infection; hydrogen peroxide triggers a hypersensitive response, strengthens cell walls and prevents the spread of viral infection. Molybdenum is biologically inactive until a special complex called molybdenum cofactor is formed. For the formation of the latter it is necessary for molybdenum to be in the state of molybdate anion. There are five known plant molybdoenzymes: aldehyde oxidase, sulfite oxidase, nitrate reductase, xanthine dehydrogenase and mitochondrial amidoxime resuctase. The aim of this work is to find the optimal concentration of molybdenum for aldehyde oxidase activation. The objectives of the conducted experiment are: – to apply an efficient and cost-effective method to replenish molybdenum deficiency in the experimental plant; – to demonstrate the effect of molybdenum on the development of virus infection of the infected plant. As a result, it was proved that with the increase of concentration from 0.1 mM to 1 mM, the activity of aldehyde oxidase increases, which contributes to the increase of seed germination. The optimal concentration for seed germination is 1 Mm molybdenum concentration. As the concentration of molybdenum increases, the resistance of adult plants to virus infection also increases. Thus, 1 mM molybdenum concentration is optimal for seed germination and resistance to virus infection.

Key words: molybdenum; tungsten; N. benthamiana; spraying; aldehyde oxidase.

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Тұқымдардың өнгіштігіне вольфрам мен молибденнің әсерін анықтау және осы металдардың өсімдіктерінде вирустық жұқпа белгілері дамуына экзогендік әсерінің нәтижесі

Өсімдік шаруашылығы Қазақстан ауыл шаруашылығының негізі болып табылады. Қазақстан аумағындағы топырақ молибден тапшылығынан зардап шегіп отыр. Өсімдіктердегі молибден тапшылығы өсудің тежелуінен, нашар тұқым салуынан, жемістердің деформациясы мен өсімдіктердің ауруларға төзімділігінің төмендеуінен байқалады. Молибден азот, көміртек және күкірт алмасуының негізгі қадамдарын катализдейді. Ол абсциз қышқылы мен индол-3-май қышқылы фитогормондарының биосинтезіне ықпал етеді. Молибден концентрациясының жоғарылауы альдегидоксидаза белсенділігінің жоғарылауына әкеледі. Альдегидоксидаза вирустық инфекцияға ұшыраған кезде сутегі асқын тотығын тудырады, сутегі асқын тотығы жоғары сезімталдық реакциясын тудырады, жасуша қабырғаларын нығайтады және вирустық инфекцияның таралуын болдырмайды. Молибден кофакторы деп атау берілген арнайы кешен пайда болғанға дейін молибден биологиялық белсенді емес. Молибден кофакторы қалыптасу үшін молибден анион молибдаты күйінде болуы керек. Өсімдік молибдоферменттерінің бесеуі белгілі – альдегидоксидаза, сульфитоксидаза, нитрат редуктаза, ксантиндегидрогеназа және митохондриялық амидоксимарезуктаза. Бұл жұмыста біз альдегидоксидазаның екі негізгі қызметін қарастырдық: тұқымның өнгіштігі мен вирустық инфекцияға төзімділігіне әсері. Бұл жұмыстың мақсаты АО белсендіру үшін молибденнің оңтайлы концентрациясын іздеу болып табылады.

Өткізілген эксперименттің міндеттері: – эксперименттік өсімдіктегі молибден тапшылығын толтыру үшін тиімді және экономикалық ұтымды әдісті қолдану; – жұқтырылған өсімдіктің вирустық инфекциясының дамуына молибденнің әсерін көрсету болып табылады. Нәтижесінде концентрацияның 0,1 мМ-ден 1 мМ-ге дейін жоғарылауы нәтижесінде АО белсенділігі де жоғарылайтыны дәлелденді, бұл тұқымның өнгіштігінің жоғарылауына ықпал етеді. Тұқымның өнуі үшін оңтайлы концентрация – 1 мм молибден концентрациясы. Молибден концентрациясы жоғарыласа, ересек өсімдіктердің вирустық инфекцияға төзімділігі де артады. Осылайша, 1 мм молибден концентрациясы тұқымның өнуі және вирустық инфекцияға төзімділігі үшін оңтайлы болып табылады.

Түйін сөздер: Молибден, вольфрам, N. benthamiana, су бүрку, альдегид оксидаза.

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Определение влияния вольфрама и молибдена на всхожесть семян и эффект экзогенного воздействия данных металлов на развитие вирусного инфицирования в растениях

Растениеводство является основой сельского хозяйства Казахстана. Почвы на территории Казахстана страдают дефицитом молибдена. Дефицит молибдена у растений характеризуется задержкой роста, плохой закладкой семян, деформацией плодов и снижением устойчивости растений к заболеваниям. Молибден катализирует ключевые этапы метаболизма азота, углерода и серы. Он способствует биосинтезу фитогормонов абсцизовой кислоты и индол-3-масляной кислоты. Увеличение концентрации молибдена приводит к увеличению активности альдегидоксидазы. Альдегидоксидаза при воздейсвие вирусной инфекции генерирует перекись водорода, перекись водорода запускает гиперчувсивительный ответ, укрепляет клеточные стенки и предотвращает распространение вирусной инфекции. Молибден катализирует ключевые этапы метаболизма азота, углерода и серы. Он способствует биосинтезу фитогормонов абсцизовой кислоты и индол-3-масляной кислоты. Увеличение концентрации молибдена приводит к увеличению активности альдегидоксидазы. Альдегидоксидаза при воздействии вирусной инфекции генерирует перекись водорода, перекись водорода запускает гиперчувсивительный ответ, укрепляет клеточные стенки и предотвращает распространение вирусной инфекции. Молибден биологически неактивен до тех пор, пока не сформируется специальный комплекс, названный кофактор молибдена. Для формирования последнего необходимо, чтобы молибден находился в состоянии молибдат аниона. Известно пять растительных молибдоферментов – альдегидоксидаза, сульфитоксидаза, нитратредуктаза, ксантиндегидрогеназа и митохондриальная амидоксимарезуктаза. В данной работе мы рассмотрели две главные функции альдегидоксидазы: влияние на всхожесть семян и устойчивость к вирусной инфекции. Цель данной работы является поиск оптимальной концентраций молибдена для активации АО. Задачами проведенного эксперимента является: – применение эффективного и экономически выгодного метода для восполнения дефицита молибдена в экспериментальном растении; – продемонстрировать влияние молибдена на развитие вирусной инфекции зараженного растения. В результате было доказано, что с повышением концентрации от 0,1 мМ к 1 мМ повышается активность АО, что способствует повышению всхожести семян. Оптимальной концентрацией для всхожести семян является 1мМ концентрация молибдена. С повышением концентрации молибдена повышается и устойчивость взрослых растений к вирусной инфекции. Таким образом, 1 мМ концентрация молибдена является оптимальной для прорастания семян и устойчивости к вирусной инфекции.

Ключевые слова: Молибден, вольфрам, N. benthamiana, опрыскивание, альдегид оксидаза.

Introduction

It has long been known that molybdenum is important for the nutrition of higher plants [1]. Molybdenum in small quantities improves the growth of barley, lettuce, asparagus, tomato and other agriculturally important plants [2].

Free molybdenum ions are inactive. Molybdenum in plants occurs in the form of Mo042- anion [3]. In all organisms, molybdenum binds to pterin in a complex called molybdenum cofactor (MoCo) [4]. MoCo is identical in all molybdoenzymes (except for nitrogenase) [5]. The main function of MoCo is catalytic [6, 7].

The antagonist of molybdenum is tungsten (W) [8]. Despite its similarity to molybdenum, tungsten has a toxic effect on plants [9]. It leads to the stunted growth of seedlings, reduced biomass of roots and shoots and dysregulation of gene expression associated with the planned cell death (apoptosis) [10]. Tungsten and molybdenum bind to the same ligand in enzymes. Tungsten as a chemical analogue of molybdenum can substitute molybdenum in the active center of molybdoenzymes, making them inactive. This function of tungsten is used to study the structure and properties of molybdoenzymes [11].

Molybdenum deficiency in young plants is characterized by chlorosis, leaf deformation, grayish discoloration, leaf rot and stunted growth [12]. Deficiency also leads to seed deformation in oats and wheat, undergrowth of berries in grape clusters, undergrowth of pollen grains in corn, and poor pollen germination [13].

Molybdenum is a vital trace element as it is required for the normal plant growth and development [14]. The results of many years of research at the Institute of Soil Science of the National Academy of Sciences of the Republic of Kazakhstan confirmed that the molybdenum content in our soils is three times less than the necessary critical concentration (0.1 mg Mo/kg for temperate zone soils) for the normal plant development [15]. Molybdenum is necessary for the work of five plant enzymes – sulfite oxidase, mitochondrial amidoxime reducing component, xanthine dehydrogenase, nitrate reductase and aldehyde oxidase [16, 17].

In this work, functions of aldehyde oxidase were considered.

Aldehyde oxidase (AO) is an enzyme containing flavin adenine dinucleotide (FAD), a cofactor of iron and molybdenum, as prosthetic groups [18]. It belongs to the family of molybdenum-containing hydroxylases [19]. Aldehyde oxidase plays an important role in plant life as it is involved in the defense response to *TBSV (tomato bushy stunt virus*) attack. The mechanism of reduction of viral infection by aldehyde oxidase is associated with the generation of hydrogen peroxide, which initiates intense oxidative stress that causes damage and cell death at the site of virus entry [20]. H202 promotes cell wall strengthening: papillae are formed, lignification process is activated, and hydroxyproline/proline-rich proteins are cross-linked. These processes limit the spread of viral infection [21].

It has been previously proven that an increase in molybdenum concentration leads to an increase in aldehyde oxidase activity and, consequently, positive growth and development of barley is observed [22].

The object of study of our work is a plant of the nightshade family *(Solanaceae) – Nicotiana benthamiana*.

The aim of this work is to find the optimal concentration for aldehyde oxidase activation.

Main objectives are:

- to apply an efficient and cost-effective method to replenish molybdenum deficiency in the experimental plant;

- to demonstrate the exogenous effect of molybdenum on aldehyde oxidase activity against virus infection.

Materials and methods

Seed priming and planting.

Priming of *Nicotiana benthamiana* seeds in 0.1; 0.5 and 1 mM concentration of sodium molybdate dihydrate ($Na_2MoO_4•2H_2O$), sodium tungstate dihydrate ($Na_2WO_4•2H_2O$) and molybdate with sodium tungstate dihydrate was performed. Distilled water was used as a control [23]. Since the seeds are small, priming was carried out for 1.5 hours.

After the seeding process, the seeds were dried, thirteen seeds were selected from each group and sown in pre-moistened soil in a specially equipped growth chamber. Universal soil ("Terravita", Russia) for sowing seeds was sterilized in an autoclave for 30 minutes at a pressure of 1 atmosphere. Optimal conditions for seed germination were maintained in the growth chamber: air humidity of about 78% and air temperature of 28 ºC. All pots were sealed with parafilm and covered with foil to create the best conditions for seed germination: darkness and humidity. After seven days, the germinated seeds were counted.

Performing native gel electrophoresis of seeds.

The remaining seeds were homogenized in pre-cooled porcelain mortars with the addition of the extraction buffer at 1:3 ratio to perform native gel electrophoresis under the non-denaturing conditions. The extraction buffer included 250 mM sucrose, EDTA, L-cysteine, DTT and TRIS-HCl, pH 8.5 [24]. The separation and loading gels were used for electrophoresis.

The separation gel consisted of acrylamide, bisacrylamide, TRIS-HCl pH 8.5, TEMED, APS, and distilled water. The loading gel also consisted of acrylamide, bisacrylamide, TRIS Base pH 6.8, TEMED, APS and distilled water. Samples were loaded into these gels at 4:1 ratio using the loading buffer, and the process itself was performed in the electrode buffer containing TRIS-HCl, TRIS-base and glycine solution with pH 8.89 [25]. Before the main electrophoresis, "pre-phoresis" was performed on an idle gel for 30 minutes under the same conditions as the main electrophoresis (110 V and 50 mA). "Pre-phoresis" was necessary to clear the gel of residual unpolymerized reagents. Electrophoresis was performed at 110 V and 50 mA current for 3.5 hours.

Determination of aldehyde oxidase activity of seeds.

To determine the aldehyde oxidase activity of seeds in gel that had undergone the seeding process in the previously mentioned solutions, a reaction mixture was prepared. This mixture included 2.5 ml of 50 mM TRIS-HCl (pH 7.4); 15 mg vanillin, 10 mg indole-3-carboxaldehyde, 6 mg thiazolyl blue tetrazolium bromide (MTT), and 1 mg phenazine methosulfate (PMS). The total volume was brought to 25 ml with distilled water. The gel was incubated in the prepared substrate in a thermal shaker for 30 minutes at 37°C in the dark until violet bands appeared. These bands characterized the activity of aldehyde oxidase [22].

Cultivation of Nicotiana benthamiana plants in soil.

After counting the germinated seeds, twelve seedlings were replanted into individual pots with soil mixed with vermiculite. Plants were grown in the same specially equipped growth chamber under conditions simulating a 17-hour day and a 7-hour night. Artificial lighting was provided by Klaus LED lamps with a spectrum of 6400 K. Watering was carried out every 3 days with 40 ml of distilled water for each plant [26].

Cultivation of Nicotiana benthamiana plants on a hydroponic unit.

Twelve seedlings were placed on small pieces of mineral wool and put in plastic boxes with pre-prepared solution for "Tripart/Flora Series" hydroponic unit made in France.

The" Tripart/Flora Series" solution contains total nitrogen, potassium oxide, calcium oxide, iron chelate 6% EDDA – 11% DPTA, copper chelate EDTA, zinc chelate EDTA, boron and manganese chelate EDTA.

Treatment of plants with tungsten, molybdenum and tungsten-molybdenum solutions and inoculation of wild-type Tomato bushy stunt virus (TBSV).

Month-old *N. benthamiana* plants with initially similar morphological characteristics such as height, lamina development and total vegetative mass were selected for infection.

Ten month-old *N. benthamiana* plants with similar morphological features were sprayed with three pre-prepared concentrations of molybdate dihydrate, tungstate dihydrate and a combined concentration of 14 ml per plant. Distilled water was used as a control. Spraying was performed one day before infection. Infection of wild-type *Tomato bushy stunt virus (TBSV*) plants was carried out through the mechanical damage to the mid-tier leaves.

Infected plants were grown under identical conditions until symptoms appeared. Morphological changes were observed on the third and seventh day after infection.

Homogenization of samples for horizontal gel electrophoresis.

300 mg of each of the leaves of control and inoculated *N. benthamiana* plants with wild-type TBSV were homogenized in TE buffer consisting of TRIS pH 7.4 and EDTA pH 8 at 1:2 ratio (mg/µl buffer sample) on ice in sterile porcelain mortars. After homogenization, the samples were centrifuged [20].

Results and discussion

Determination of aldehyde oxidase activity in native gel after seeding at 0.1; 0.5 and 1 mm concentrations

As a result of enzymatic staining, three isoforms of aldehyde oxidase (AO1, AO2 and AO3) were detected in the seeds. Figure 1 shows that all three concentrations of tungsten decreased the activity of AO1 isoform.

The effect of aldehyde oxidase activity enhancement was more intense in samples incubated in molybdenum solutions compared to combined concentrations and concentrations with tungsten.

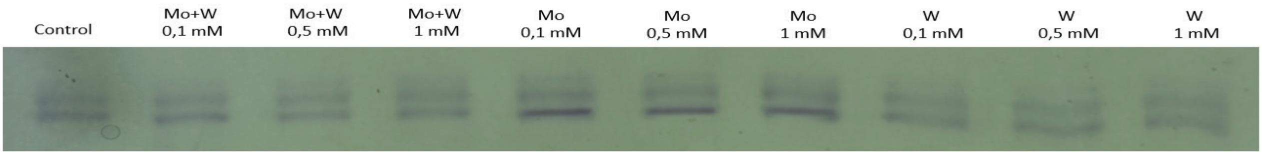

Figure 1 – Determination of aldehyde oxidase activity in gel after electrophoresis in non-denaturant conditions in *N. benthamiana* seeds

Previously, three AO isoforms in pea plants (PAO1, PAO2 and PAO3) were identified by a number of scientists. PAO1 was most active in the leaves of seedlings and young leaves of adult plants. In roots, PAO1 was found only in seedlings. As pea plants aged, this isoform disappeared. PAO1 plays an important role in the germination and development of pea plants [27]. The above-mentioned article supports our findings, since with increasing tungsten concentrations, the intensity of staining of AO1 isoform decreases, and after planting, the germination of seeds incubated in tungsten concentration decreases (Fig. 2).

The opposite result was obtained when seeds were incubated in molybdenum solutions. Increasing the molybdenum concentration increased the activity of aldehyde oxidase. Also, molybdenum had a positive effect on seed germination (Fig. 2). The data obtained by us are consistent with earlier studies [28, 29], according to which molybdenum is vital for the normal growth and development of plants.

Seed germination results

Priming is a cost-effective way to replenish the lack of essential trace elements for the good plant growth and development [30]. Therefore, we applied this method to replenish trace element deficiency.

A week after sowing the seeds that had undergone the seeding process, the germinated seeds were counted in comparison with the control. Thirteen seeds were planted in each pot (Fig. 2).

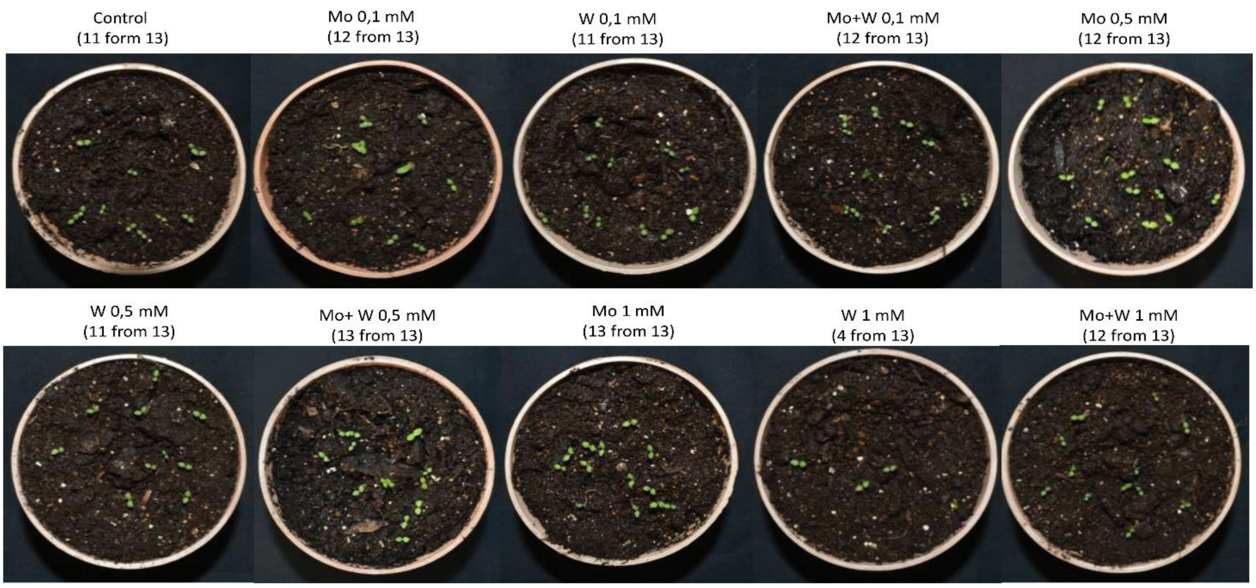

Figure 2 – The growth of *N. benthamiana* after priming with various concentrations of Mo, W and Mo+W on day 7 of cultivation

From the result obtained (Fig. 2) it follows that the most optimal concentration for seeding is 1 Mm concentration of sodium molybdate dihydrate (Na_2MoO_4•$2H_2O$), i.e. at this concentration, absolute seed germination is observed (13 out of 13). Studies conducted on barley confirmed that molybdenum has a beneficial effect on the growth and development of seedlings [22].

Morphological signs of infection of plants with wild-type TBSV grown in soil

Three days after inoculation, the first signs of infection appeared in the form of slight curling of the upper tier leaves. Symptoms were weakly manifested, the only exceptions being 0.5 and 1 mM concentrations of Mo and 1 mM concentration of W. Plants sprayed with the above mentioned concentrations showed necrosis of the mid-tier leaves (Table 1, Fig. 2). It is difficult to predict the dynamics of virus infection spread based on the results of the third day.

Subsequent observation of the development of symptoms was performed on the day after inoculation.

On the seventh day, there was an increase in infection symptoms. Control plants showed standard infection symptoms characteristic of wild-type TBSV (Fig. 4, Table 2) [31].

Table 1 – Symptoms of virus infection on the third day after inoculation of soil-grown plants

Metattes / Concentrations	**0.1 мM**	**0.5 мM**	**1 мM**
Control	Curling of the upper tier leaves, chlorosis of the lower tier leaves		
Mo	Slight curling of the upper tier leaves	Necrosis of the mid-tier leaves	Necrosis of the mid-tier leaves
W	Slight curling of the upper tier leaves	Slight curling of the upper tier leaves	Necrosis of the mid-tier leaves
Mo + W	Slight curling of the upper tier leaves	Slight curling of the upper tier leaves	Curling of the upper tier leaves, chlorosis of the lower tier leaves

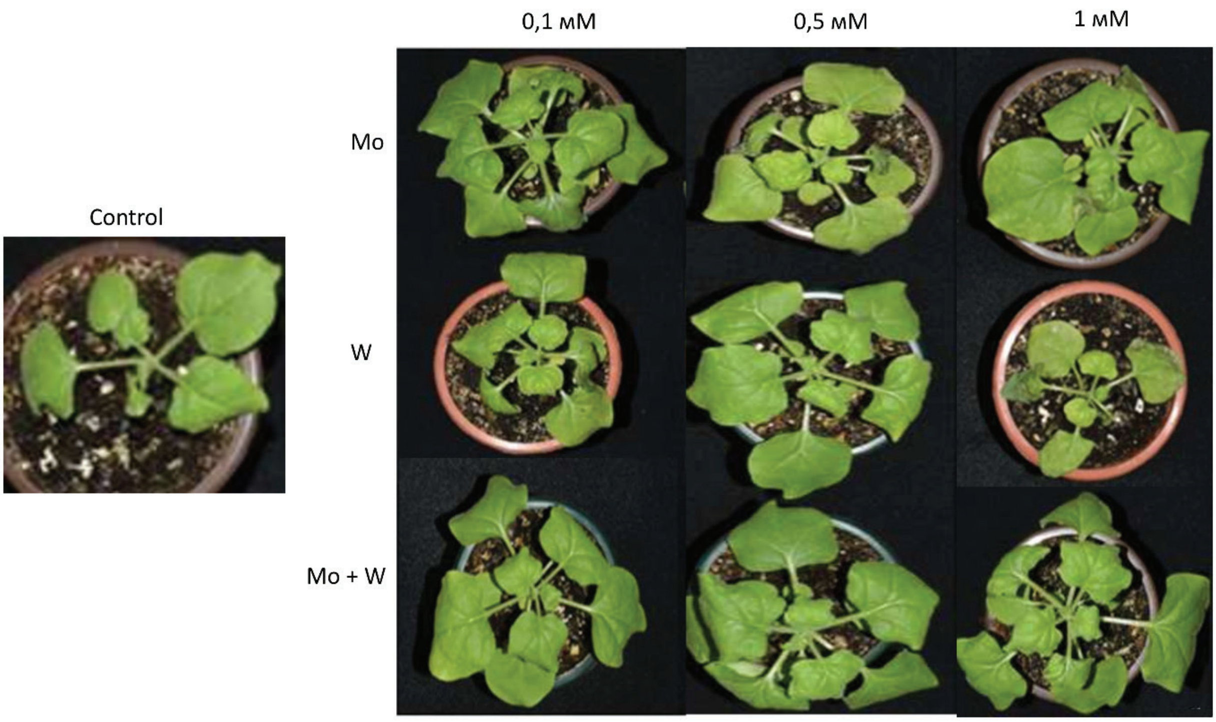

Figure 3 – The morphological signs of plant infestation treated with 0.1, 0.5, 1 mM concentrations of Mo and Mo+W 3 dpi.

Plants sprayed with 1 mM tungsten concentration showed the most striking symptoms of infection: apical necrosis, death of the mid- and lower tier leaves, curling and mosaic of the upper tier leaves. With the increase of tungsten concentration, plant resistance to virus infection decreases (Table 2, Fig.

4). The obtained result is supported by research data, according to which tungsten has a deleterious effect on plants: it causes deformation of cell components, disrupts the cell cycle and gene expression [32, 33].

An increase in molybdenum concentration from 0.1 to 1 mM increases plant resistance to virus infection. Plants sprayed with 1 mM concentration of molybdenum showed minimal symptoms of infection (Table 2, Fig. 4).

It has already been proven that molybdenum helps to increase yield and improve the quality of fruits [34], so it is often used as a fertilizer [35]. Batyrshina states that molybdenum increases the activity of AO in barley leaves [22]. According to Yergaliyev, virus infection also increases the activity of AO enzyme in *N. benthamiana* leaves, which leads to an increase in H_2O_2 production. This was the first demonstration of the participation of plant AO in defense mechanisms against virus infection [20].

Thus, molybdenum promotes aldehyde oxidase activation, increasing plant resistance to biotic stress (virus infection).

Plants sprayed with combined solutions showed a slight increase in symptoms toward increasing concentrations. In general, the symptoms of infection of the combined concentrations were similar to those of the control plant.

Detection of virus infection in inoculated soil plants by agarose gel electrophoresis

Virions are infectious virus particles. They consist of proteins, envelope (lipid membrane) and nucleic acid: DNA or RNA [36].

Virions were detected in infected plants by agarose gel electrophoresis (Fig. 5) [37].

Detection of genomic RNA virus in gel under UV light was performed using the Mego Bio-print-1100/20M gel documentation system and ECX Vilber Lourmat ECX transilluminator (France).

This gel analysis showed that all inoculated plants were infected. This method is particularly important for infected plants pretreated with three molybdenum concentrations, since wild-type TBSV causes mild symptoms of infection compared to tungsten-treated and control plants.

Table 2 – Symptoms of virus infection on the seventh day after inoculation of soil-grown plants

Metattes / Concentrations	**0.1 мM**	**0.5 мM**	**1 мM**
Control	Curling of the upper and mid-tier leaves, death of the lower tier leaves		
Mo	Curling of the upper tier leaves and small areas of necrosis on the mid-tier leaves	Curling of the upper tier leaves and mosaic pattern on the mid-tier leaves	Slight curling of the upper tier leaves
W	Curling of the upper tier leaves, wilting of the lower tier leaves	Curling of the upper and mid-tier leaves, death of the lower tier leaves	Apical necrosis, death of the mid- and lower tier leaves, curling and mosaic of the upper tier leaves
Mo + W	Curling of the upper tier leaves and small areas of necrosis on the mid-tier leaves	Curling of the upper and mid-tier leaves, small areas of necrosis on the mid-tier leaves	Curling of leaves and mosaic pattern on the mid-tier leaves, necrosis of the lower tier leaves

Morphological signs of infection of plants with wild-type Tomato bushy stunt virus (TBSV) grown on a hydroponic unit

On the third day after infection, the main characteristic of virus infection spread is the appearance of numerous side shoots (Table 3, Fig. 4). This sign of virus infection spread is an indicator specifically for TBSV [38].

After spraying with three tungsten concentrations, plants were characterized by the stunted growth.

Plants sprayed with molybdenum and combined concentration continued to grow even after inoculation. It has already been proven that molybdenum enhances the oxidative tolerance of plants by increasing the activity of antioxidant enzymes and the production of abscisic acid (ABA) [39]. Therefore, plants treated with molybdenum continued to grow. The stunted plant growth after spraying with tungsten is a toxic effect characteristic of this metal [40].

Subsequent observation of the development of symptoms was performed on the day after inoculation.

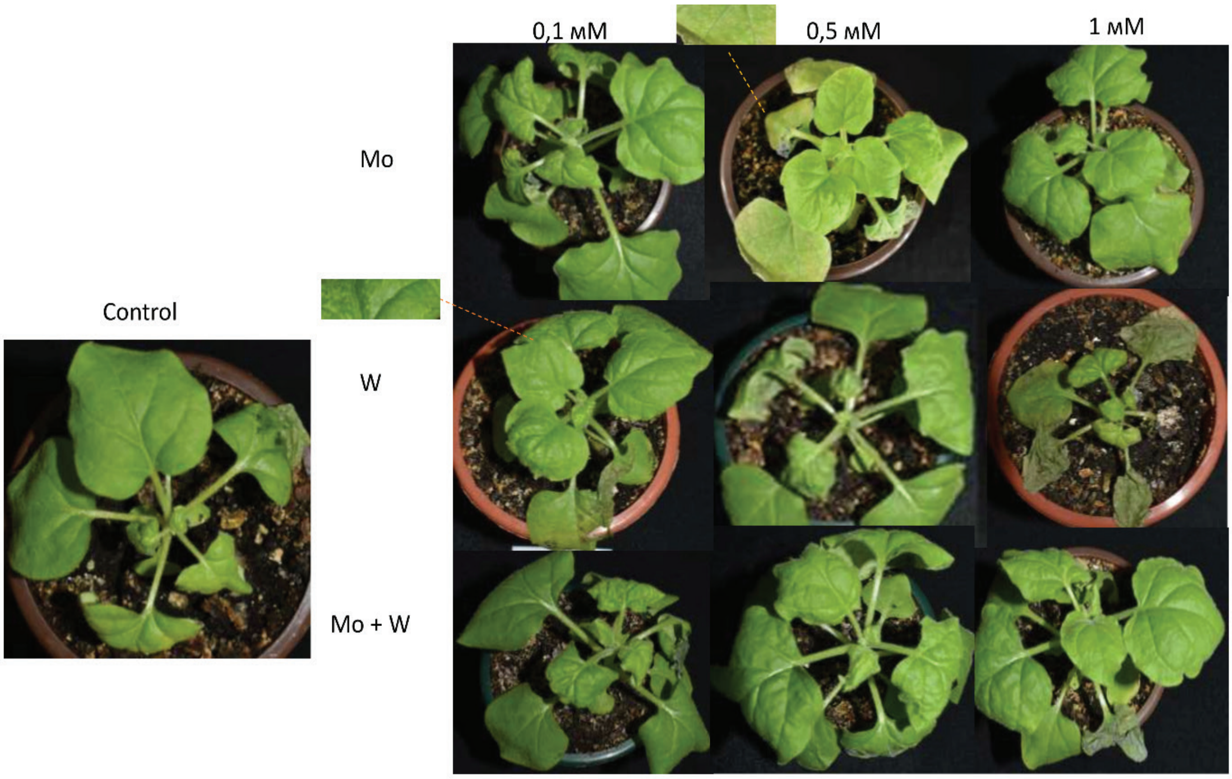

Figure 4 – The morphological signs of plant infestation treated with 0.1, 0.5, 1 mM concentrations of Mo , W and Mo+W 7dpi

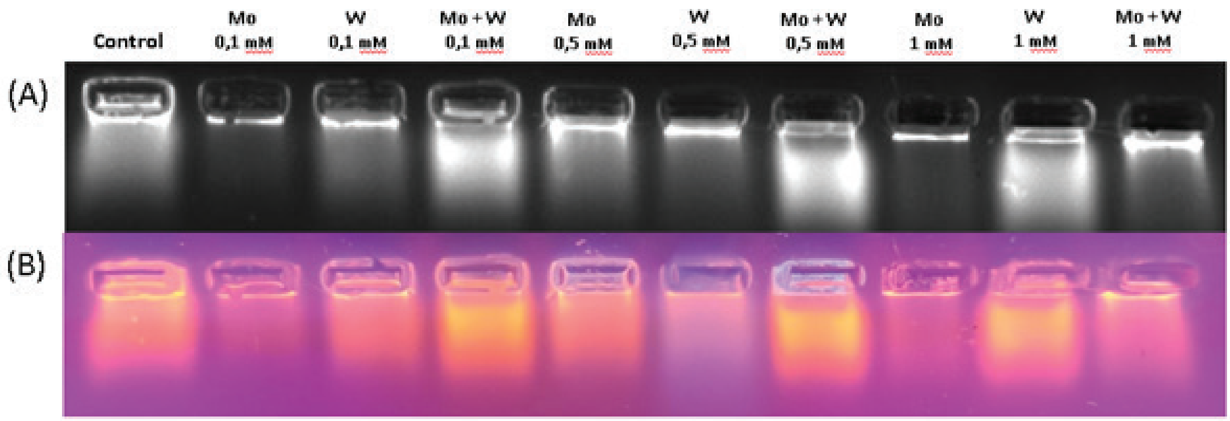

Figure 5 – Detection of RNA molecules in agarose gel from soil-grown plant samples: (A) using gel-documenting system Mego Bio-print-1100/20M, (B) using transilluminator ECX Vilber Lourmat (France)

On the seventh day after inoculation, plants treated with 1 mM concentration of tungstate showed clear symptoms of infection. The lower tier leaves died. It has been documented that excess tungsten can cause programmed cell death (PCD) [41].

Tungsten is a heavy metal [42]. Heavy metals (such as lead and copper) stimulate virus infection and lead to the virus population doubling [43]. Perhaps tungsten has a similar effect on the plant defense system.

Table 3 – Symptoms of virus infection on the third day after inoculation of hydroponically grown plants

Metattes / Concentrations	0.1 мM	0.5 мM	1 мM
Control	Curling of the upper tier leaves, necrotic lesions on inoculated leaves		
Mo	Appearance of numerous side shoots (bushy appearance), curling of the upper tier leaves, necrotic lesions on inoculated leaves	Appearance of numerous side shoots (bushy appearance), curling of the upper tier leaves, necrotic lesions on inoculated leaves	Appearance of numerous side shoots (bushy appearance), curling of the upper tier leaves, necrotic lesions on inoculated leaves
W	Stunted growth, curling of the upper tier leaves and necrotic lesions on inoculated leaves	Stunted growth, curling of the upper tier leaves and necrotic lesions on inoculated leaves, appearance of numerous side shoots (bushy appearance)	Stunted growth, increased curling of the upper tier leaves, presence of necrotic areas on the upper tier leaves, appearance of numerous side shoots (bushy appearance)
Mo + W	Appearance of numerous side shoots (bushy appearance), curling of the upper tier leaves, necrotic lesions on inoculated leaves	Appearance of numerous side shoots (bushy appearance), curling of the upper tier leaves, necrotic lesions on inoculated leaves	Appearance of numerous side shoots (bushy appearance), curling of the upper tier leaves, necrotic lesions on inoculated leaves

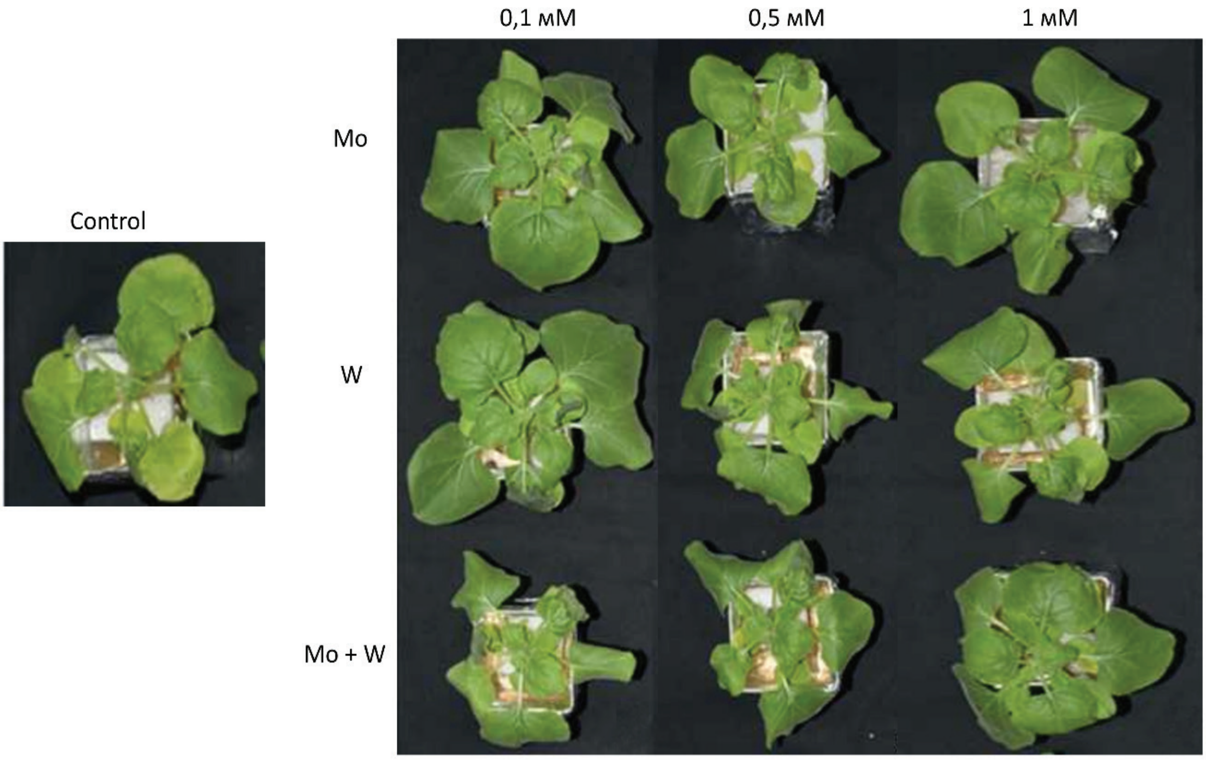

Figure 6 – Morphological signs of infection in *N. benthamiana* plants grown on a hydroponic unit and treated with 0.1, 0.5, 1 mM concentration 3 dpi.

The symptoms of infection of plants sprayed with the combined concentration are similar to the symptoms of virus infection in the control plant. Chlorosis of the lower leaves in plants treated with 0.5 and 1 mM concentrations of Mo+W is a characteristic sign of heavy metal impact on plants [44].

Plants sprayed with three concentrations of molybdenum also showed symptoms of infection. Despite this, we discovered a trend: the higher the concentration, the weaker the symptoms of infection. The weakest symptoms of infection were characteristic of 1 mM concentration of molybdenum.

It has already been proven that treatment of plants with non-toxic concentrations of the heavy metal cadmium can inhibit the spread of virus infection by blocking virus exit from the vascular tissue [45]. This experiment demonstrated that a 1 mM concentration of molybdenum is capable of delaying the spread of viral infection. This fact is explained by the activation of the aldehyde oxidase enzyme, which has a defense property against virus infection [46].

Necrosis of inoculated leaves of plants treated with 0.5 and 1 mM concentrations of molybdenum is a defense mechanism to block the spread of virus infection. According to Tapan K. and Yergaliyeva T., AO can serve as an important biological source of reactive oxygen species (ROS), which perform defense functions during the pathogen invasion by blocking the spread of virus infection [20].

Table 4 – Symptoms of virus infection on the third day after inoculation of hydroponically grown plants

Metattes / Concentrations	0.1 мM	0.5 мM	1 мM
Control	Curling and mosaic of the upper tier leaves, complete necrosis of inoculated mid-tier leaves and wilting of the lower tier leaves		
Mo	Curling of the upper tier leaves, increased shoot growth, necrosis of shoot leaf tips, mosaic and increased curling of the upper tier leaves	Slight curling of the upper tier leaves and necrosis of inoculated leaves	Slight curling of the upper tier leaves and necrosis of inoculated leaves
W	Mosaic and increased curling of the upper tier leaves, increased shoot growth, necrosis of shoot leaf tips	Curling of the upper tier leaves, shoot leaves curling, necrosis of inoculated leaves. Intense chlorosis of the lower tier leaves.	Increased curling of the upper tier leaves, curling and necrotic lesions on the mid-tier leaves, dying off of the lower tier leaves
Mo + W	Mosaic and increased curling of the upper tier leaves, increased shoot growth, necrosis of shoot leaf tips	Curling of the upper tier leaves and necrosis of inoculated leaves. Intense chlorosis of the lower tier leaves.	Curling of the upper tier leaves, necrotic lesions on inoculated mid-tier leaves. Intense chlorosis of the lower tier leaves.

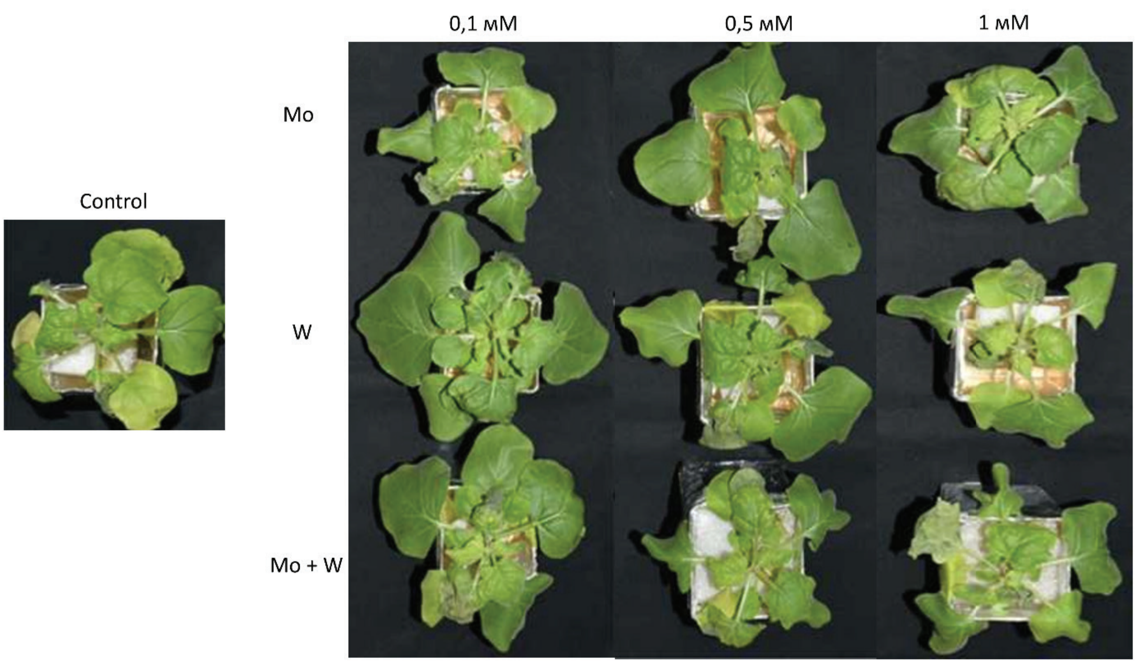

Figure 7 – Morphological signs of infection in *N. benthamiana* plants grown on a hydroponic unit and treated with 0.1, 0.5, 1 mM concentration 7 dpi.

Detection of virus infection in inoculated plants grown on a hydroponic plant using agarose gel electrophoresis

Virus particles acids that glow under UV light. Wild-type TBSV can be seen as single bright bands on traces with samples isolated from leaves of infected *N. benthamiana* plants (Fig. 8).

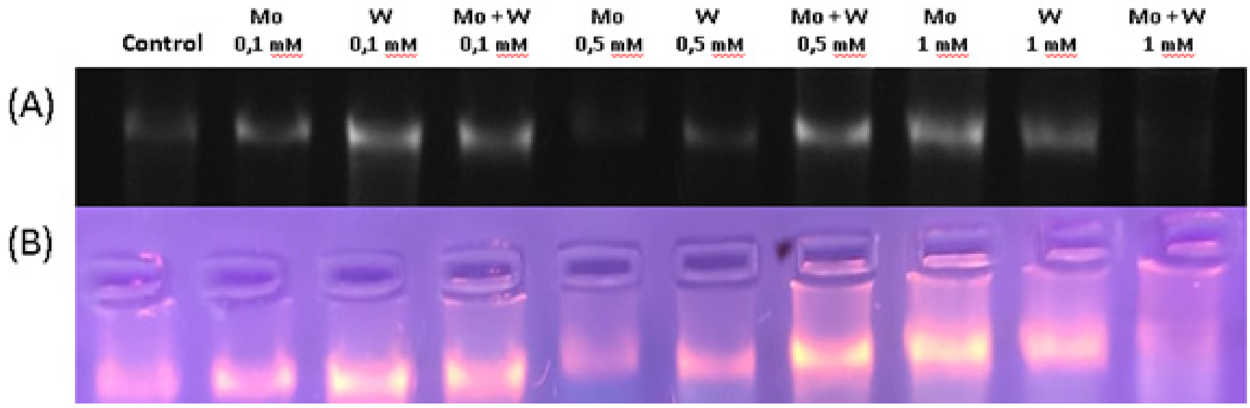

Figure 8 – Detection of RNA molecules in agarose gel from plant samples grown on a hydroponic unit: (A) using gel-documenting system Mego Bio-print-1100/20M, (B) using transilluminator ECX Vilber Lourmat (France)

Conclusion

Molybdenum deficiency leads to deterioration in the quality of crop products, and the impact of such abiotic stress as virus infection damages the entire agriculture of the Republic of Kazakhstan. Exposure to one stress affects the response of plants during another stress. These two issues formed the basis of our article.

Molybdenum deficiency in plants was replenished by priming. The optimal concentration for seed saturation is 1 mM molybdenum concentration, since it is this concentration that promotes absolute seed germination.

Plants deficient in a vital trace element such as molybdenum become the most vulnerable to virus infection.

Our study confirmed that molybdenum application can enhance plant defense mechanisms against virus infection by activating the molybdoenzyme, aldehyde oxidase. Aldehyde oxidase promotes the production of hydrogen peroxide, which helps to inhibit the spread of virus infection in experimental plants.

Aldehyde oxidase produces H2O2 during the oxidation of aromatic and aliphatic aldehydes. Oxidation electrons are transferred to molecular oxygen in a two-electron transfer step, resulting in the reduction of molecular oxygen to H2O2.

H2O2 performs several sequential functions: it initiates intense oxidative stress, accompanied by damage and cell death at the site of virus penetration, then peroxide acts as signaling molecules, induction of plant protective genes, glutathione S-transferase (GST) and glutathione peroxidase (GPx), which contribute to the formation of adaptive mechanisms and strengthen the cell wall: papillae are formed, lignification process is activated. As a result, the supply of nutrients to neighboring tissues is restricted, which leads to inhibition of the spread of viral infection.

In this case, even infected plants continue their growth and development. The optimal concentration for increasing plant resistance to virus infection is also 1 mM concentration of molybdenum. This study confirmed that 1 mM concentration is optimal for seed germination and resistance to virus infection.

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Received February 6, 2023
Accepted February 20, 2024