International Journal of Agriculture and Biosciences 2026 15(4): 1746-1759.
https://doi.org/10.47278/journal.ijab/2026.095

RESEARCH ARTICLE
eISSN: 2306-3599; pISSN: 2305-6622

Interactive Effects of Viral Infection and Drought Stress on Biochemical and Molecular Stress Responses in Potato (*Solanum tuberosum* L.)

Aisarat Gajimuradova [1,2]*, Rauza Turpanova [1], Dmitriy Silayev [3], Irina Kirgizova [4], Nurtay Gubaidullin [2], Fariza Zhagipar [2], Gulzhamal Ismukanova [2], Alfiya Syzdykova [2], Aibek Zhumalin [2], Gulshat Bailina [2] and Rustem Omarov[1]

[1]Non-commercial Joint-Stock Company L.N. Gumilyov Eurasian National University, 010000 Astana, Kazakhstan
[2]Non-commercial Joint-Stock Company S.Seifullin Kazakh Agrotechnical Research University, 010000 Astana, Kazakhstan
[3]National Center for Biotechnology LLP, 010000 Astana, Kazakhstan
[4]Makinsk Poultry Farm LLP, 020000 Makinsk Town, Akmola region, Kazakhstan
*Corresponding author: aisarat3878@mail.ru

ABSTRACT

Potato productivity (*Solanum tuberosum* L.) is strongly affected by biotic and abiotic stresses, particularly viral infections and water deficit, which disrupt physiological processes and impair photosynthesis. This study investigated the physiological, biochemical, and molecular responses of five potato cultivars (Aliyans, Ulan, Narli, Babayev, and Tokhtar) to Potato virus M (PVM) infection, osmotic stress, and their combined impact (PVM+D). Antioxidant enzyme activities (peroxidase, catalase, and superoxide dismutase), photosynthetic pigment content (chlorophyll a, chlorophyll b, and total chlorophyll), and the expression of the stress-induced transcription factor *StDREB2* were assessed at 3, 5, and 7 days after treatment. The results showed that drought imposed the most intense and prolonged stress, largely determining the magnitude of antioxidant and photosynthetic responses, whereas PVM infection triggered a rapid but transient stress reaction. *StDREB2* expression was closely associated with overall physiological stress tolerance, integrating antioxidant defense and photosynthetic performance, while *Rm* primarily reflected cultivar-specific viral resistance. Cultivars Ulan and Tokhtar displayed high stress responsiveness, Aliyans exhibited a balanced adaptive strategy, and Narli and Babayev showed reduced tolerance across most parameters. Overall, drought exerted a stronger and more persistent effect on potato physiology than PVM infection, while combined stress induced an intermediate response. The identified cultivar-specific biochemical and molecular traits serve as valuable markers for assessing stress tolerance and potato breeding.

Keywords: Antioxidant enzymes, Drought stress, Gene expression, Photosynthetic pigments, Potato, *Rm* gene, *StDREB2* gene, Stress tolerance, Viral infection.

Article History
Article # 26-036
Received: 14-Jan-26
Revised: 17-Mar-26
Accepted: 24-Mar-26
Online First: 07-Apr-26

INTRODUCTION

Potato (*Solanum tuberosum* L.) is the third most important food crop worldwide after rice and wheat and serves as a staple food for approximately 1.3 billion people (Devaux et al., 2021). In 2023, global potato production reached approximately 383 million tons. During the same year, the total harvested area amounted to about 16.8 million hectares, yielding ≈383 million tons, of which 93.5 million tons were produced in China, followed by India (60.1 million tons), the United States (20.0 million tons), and Russia (19.3 million tons) (Hu et al., 2025). In Kazakhstan, potato is the second most important food crop, with an average per capita annual consumption exceeding 100kg. In 2023, national potato production amounted to approximately 2.1 million tons, while preliminary data for 2024 indicate a gross harvest of about 2.9 million tons (Ministry of Agriculture of the Republic of Kazakhstan, 2024). The average yield was approximately 213.4 c/ha. Low potato productivity in Kazakhstan is primarily associated with the widespread use of repeatedly reproduced seed material carrying high viral loads (Argynbayeva et al., 2023), insufficient phytosanitary protection, and suboptimal agrotechnical practices, including Limited irrigation and

Cite this Article as: Gajimuradova A, Turpanova R, Silayev D, Kirgizova I, Gubaidullin N, Zhagipar F, Ismukanova G, Syzdykova A, Zhumalin A, Bailina G and Omarov R, 2026. Interactive effects of viral infection and drought stress on biochemical and molecular stress responses in potato (*Solanum tuberosum* L.). International Journal of Agriculture and Biosciences 15(4): 1746-1759. https://doi.org/10.47278/journal.ijab/2026.095

A Publication of Unique Scientific Publishers

imbalanced plant nutrition (Gervais et al., 2021). Additional constraints include climatic stresses (Nasir & Toth, 2022; Murtaza et al., 2026), soil compaction, limited mechanization, and substantial post-harvest losses, which together maintain average yields at only 20-23 t/ha (Sinton et al., 2022).

Potato is affected by more than 50 different viruses (Verchot, 2022). As obligate parasites, viruses interfere with plant metabolism, disrupt physiological processes, reduce yield, and alter the biochemical composition of tubers (Lal et al., 2021). Potato virus M (PVM) is considered one of the most widespread and economically important potato viruses worldwide (Kumar et al., 2023; Rakesh et al., 2024; Yusubakhmedov et al., 2024). PVM infection can reduce potato yield by 15-45%, and in some regions cultivar infection rates may reach 100% (Zhao et al., 2022). Virus-induced seed degeneration is one of the most critical factors limiting potato productivity, with yield losses ranging from 10% to 80% (Kumar et al., 2020). Fig. 1 presents a general schematic overview of the effects of combined stress on potato plants.

In addition, contemporary studies consistently demonstrate that viral infections substantially reprogram plant metabolism. For example, infections caused by Potato virus Y (PVY), Potato virus S (PVS), and Potato virus M (PVM) lead to reductions in dry matter and starch content in potato tubers. Notably, PVM infection, particularly in combination with PVY, markedly deteriorates starch quality in tubers (Ospankulova et al., 2023). Metabolomic analyses further revealed that PVY infection induces pronounced alterations in amino acid, energy and fatty acid metabolism in potato leaves (Manasseh et al., 2023), highlighting the extensive impact of viral pathogens on plant biochemical processes and physiological functioning.

At the same time, changing climatic conditions must be considered as an additional stress factor that increasingly co-occurs with viral and bacterial infections, thereby intensifying metabolic and developmental constraints in potato. Although most potato-growing areas are irrigated, the overall availability of water resources is declining annually, and the high-water demand of potato cultivation contributes to rising production costs of this socially important crop. Potato is classified as sensitive or moderately sensitive to drought, depending on the criteria used. Drought stress in potato delays emergence, suppresses plant growth, reduces biomass accumulation, and severely decreases tuber number, size, and overall yield (Zaki & Radwan, 2022).

Evidence for combined stress effects on potato has already emerged in recent literature. In the field, potatoes face both biotic (viruses) and abiotic stressors (drought, high temperatures, etc.) and their combined effect often leads to non-additive effects – increased symptoms, changes in virus accumulation, and variability in responses between varieties. A review by Prakash et al. (2024) summarizes that viral infection in a number of systems can increase plant resistance to drought, so virus-induced effects are considered not only as a damaging factor, but also as a potential resource for reducing yield losses during water shortages. Using the tomato model, Sacco Botto et al. (2023) demonstrated that during severe drought, plants infected with TYLCSV wilted more slowly and recovered more quickly after rehydration compared to healthy plants, confirming phenotypically expressed virus-associated drought tolerance. A refinement of the mechanism is proposed in the work of Pagliarani et al. (2022): in an experiment with transgenic tomatoes expressing the viral protein C4 (TYLCSV), it was shown that C4 "priming" the response to moisture deficiency, and the effect manifests itself through morphological and water-physiological changes, indicating that a separate viral factor may play a key role, and not just the infection as a whole. A similar principle of "from viral protein to increased drought resistance" has also been demonstrated for the related begomovirus TYLCV in a study by Corrales-Gutierrez et al. (2020) found that the C4 protein increases drought resistance in Arabidopsis and that this effect is achieved through an ABA-independent mechanism, broadening our understanding of the pathways of resistance formation during viral infection. Overall, the data emphasize that the severity of virus-induced drought tolerance is context-dependent and determined by the combination of "virus strain × host genotype". Therefore, the authors consider the systematization of mechanisms to be the basis for approaches to improving crop drought tolerance.

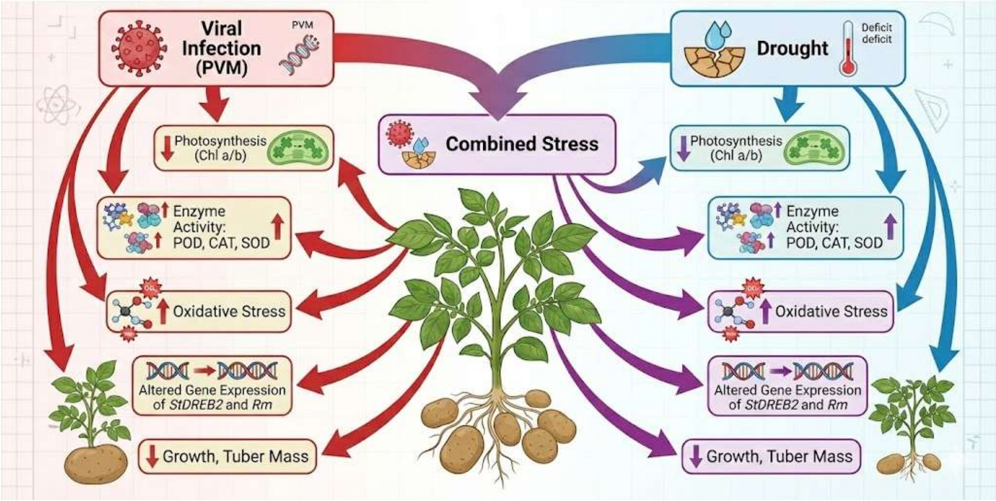

Fig. 1: Integrated effects of Potato virus M (PVM) infection and drought stress on the physiological and biochemical responses of potato plants.

These findings underscore the dual nature of virus-plant interactions under abiotic stress conditions: depending on the pathosystem and environment, abiotic stress can either exacerbate viral disease (e.g., via stronger symptom expression and higher virus accumulation) or, in some cases, viral infection/viral factors may be associated with improved drought-related performance (Prakash et al., 2024). However, such combined-stress effects remain insufficiently characterized in potato, and the evidence base is especially thin for Potato virus M (PVM) most work on PVM focuses on incidence/diagnostics/seed health, while mechanistic studies linking PVM outcomes to specific abiotic stressors are comparatively rare; one example illustrating environment sensitivity is temperature-dependent resistance to PVM reported for introgressed resistance from *Solanum megistacrolobum* (Tatarowska et al., 2020). Importantly, cultivar adaptation to specific regional environments must also be considered: modern potato improvement increasingly emphasizes target-environment testing, participatory/partner-based selection, and "best-bet" variety portfolios tailored to local agro-ecologies to improve adoption and performance under climate variability (Lindqvist-Kreuze et al., 2023).

Despite the availability of studies addressing potato responses to viral infections and drought stress individually, integrated investigations assessing their combined effects on biochemical mechanisms of stress tolerance remain extremely limited. Under conditions of climate change and increasing water scarcity, understanding how the interaction between viral infection and water deficit influences physiological and biochemical processes in plants represents a critical step toward improving yield prediction accuracy and developing more stress-tolerant cultivars. The aim of the present study was to experimentally evaluate the effects of Potato virus M (PVM) on growth, development, and biochemical and molecular indicators of drought tolerance in potato plants under *in vitro* conditions, as well as to elucidate the nature of interactions between viral and water-related stresses.

MATERIALS & METHODS

Subjects of Research

The study was conducted during 2022-2023 at the Scientific and Production Platform of Agricultural Biotechnology, Non-commercial Joint-Stock Company "S. Seifullin Kazakh Agrotechnical Research University", Astana, Kazakhstan.

In vitro potato plants of Kazakh breeding cultivars Ulan, Narli, Tokhtar, Aliyans, and Babayev were used as the experimental material. Virus-free *in vitro* potato plantlets were kindly provided by the Kazakh Research Institute of Potato and Vegetable Growing, Almaty, Kazakhstan. Micropropagation was performed according to a standard protocol using a modified Murashige and Skoog (MS) medium supplemented with 6-benzylaminopurine (6-BAP, 1m g L^{-1}) and indole-3-acetic acid (IAA, 0.5m g L^{-1}). Planting and cultivation were carried out in a phytotron chamber under controlled environmental conditions in accordance with the specified growth regimes (Fig. 2) (Gajimuradova et al., 2023).

Plant Infection with Potato Virus M (PVM)

Potato plants were inoculated with Potato virus M (PVM) by introducing SAP extracted from naturally infected potato plants into the liquid nutrient medium of culture tubes containing 3-week-old *in vitro* potato plantlets. Leaf tissue from naturally infected plants was homogenized in a mortar with 10 mM sodium phosphate buffer (pH 6.9-7.0, measured using a Consort C931 pH meter, Belgium) and carborundum powder (particle size d=0.037 mM). The resulting sap was filtered 0.2 µm sterile syringe filter (Corning, USA), and 5% (v/v) of the extract was added to 3 mL of liquid growth medium. For control samples, leaves were mechanically wounded without virus application. Three days after inoculation, leaves located one to two tiers above the inoculation site were excised and homogenized in 1mL of 1× phosphate-buffered saline. Viral infection was confirmed by PCR using specific primers. All experiments were conducted in duplicate.

Fig. 2: *In vitro* potato plants (A) and potato microcuttings of the Tokhtar variety (B).

PCR Identification of Viral Infection

Total RNA was extracted from infected and uninfected leaf samples using TRIzol reagent with modifications (Yusubakhmedov et al., 2024). A single-step RT-PCR reaction was performed using an RT-PCR Kit (Thermo Fisher Scientific, USA). Reverse transcription was carried out at 45°C for 30min, followed by denaturation at 94°C for 5min. PCR amplification consisted of 30 cycles of 94°C for 30s, 50.7°C for 30s, and 72°C for 30s, with a final extension at 72°C for 5min. Amplification products (5 µL) were analyzed by electrophoresis in a 1.5% agarose gel. The capsid protein (CP) gene sequence was used as the amplification target.

The following primers were used for RT-PCR and real-time RT-PCR to generate a 755bp amplicon:
PVM4_CP_F: GGGAGATTCAACGAAGAAAGC
PVM4_CP_R: GTCGCCTGATCAATCCCTCTA (Xu et al., 2010).

PCR was carried out in a VeritiPro thermal cycler (Applied Biosystems) in a 20 µL reaction volume containing 2 µL 10×PCR buffer, 1.5 µL 25 mM $MgCl_2$, 2 µL 2 mM dNTPs, 0.2 µL Taq DNA polymerase (Thermo Fisher Scientific, USA), and 1 µL cDNA. PCR conditions were as follows: initial denaturation at 94°C for 1.5min; 38 cycles of 94°C for 45s, 53°C for 45s, and 72°C for 1min; final extension at 72°C for 5min. PCR products (10 µL) were separated on a 2% agarose gel.

In vitro Drought Stress Conditions

Drought stress was simulated by supplementing the liquid nutrient medium with polyethylene glycol (PEG 6000) at a concentration of 30 g L^{-1}. Three-week-old potato plantlets of uniform age were cultured individually on filter paper bridges in test tubes containing 3mL of liquid Murashige and Skoog (MS) medium with 30 g L^{-1} sucrose (control) or supplemented with PEG 6000 at pH 5.7. Leaf samples were collected at 3, 5, and 7 days after stress initiation. Plants were maintained under a 16h photoperiod at 25 ± 2°C using cool white, fluorescent lamps providing approximately 90µmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD).

Combined Stress Treatment

Combined stress was imposed by simultaneous inoculation with PVM sap and the addition of PEG 6000 (30 g L^{-1}) to the nutrient medium. Viral infection was verified three days after inoculation; plants lacking confirmed infection were discarded. Sampling was conducted at 3, 5, and 7 days after stress initiation. Leaf samples were subsequently used for determination of antioxidant enzyme activities and photosynthetic parameters.

Antioxidant Enzyme Activity Assays

Leaf samples were collected at 3 dpi, 5 dpi, 7 dpi under drought stress, virus infection and combined stress and immediately processed for determination of peroxidase (POD), catalase (CAT) and superoxide dismutase (SOD) activities.

Peroxidase (POD) Activity

POD activity was determined based on the rate of H_2O_2 degradation at 590nm over 120s. Enzyme extracts were prepared with the addition of 20 µL of 100 mM PMSF (phenylmethylsulfonyl fluoride). Reaction mixtures contained 0.01% benzidine hydrochloride, and the reaction was initiated by adding 0.3% H_2O_2 (Masoud et al., 2025).

Catalase (CAT) Activity

CAT activity was measured by monitoring H_2O_2 decomposition at 240nm (Riseh et al., 2024). The reaction mixture contained 50 µL enzyme extract and 1mL potassium phosphate buffer (25 mM, pH 7.0) with 10 mM H_2O_2. Activity was expressed as µmol g^{-1} fresh weight (FW).

Superoxide Dismutase (SOD) Activity

SOD activity was assayed based on inhibition of nitroblue tetrazolium (NBT) photoreduction (Zhou et al., 2025). The reaction mixture contained KH_2PO_4 (50 mM, pH 7.8), NBT (75 mM), L-methionine (10 mM), EDTA (0.1 mM), riboflavin (20 mM), and 100 µL enzyme extract. After illumination for 15min, absorbance was measured at 560nm. Results were expressed as µmol g^{-1} FW.

Chlorophyll Content Determination

Chlorophyll a and b contents were determined spectrophotometrically. Leaf tissue (0.3-0.5g) was homogenized in 80% acetone with quartz sand, filtered, and extraction was repeated until the residue became colorless. Absorbance was measured at 649 and 665nm. Chlorophyll concentrations were calculated using Vernon's equations (1960) (Masoud et al., 2025).

Gene Expression Analysis

Total RNA was extracted using the RNeasy Plant Mini Kit (Qiagen, USA) following the manufacturer's protocol. First-strand cDNA synthesis was performed in a 20 µL reaction using SMARTScribe™ III reverse transcriptase (Clontech, USA). PCR amplification was conducted using Taq DNA polymerase (Thermo Fisher, USA) under the following conditions: 35 cycles of 98°C for 10s, 53-60°C for 45s, and 72°C for 1min, with a final extension at 72°C for 10min.
Target genes and primers:
Housekeeping gene: *StActin* (XM_006345899), 200bp (57°C)
F: GTGTGATGGTGGGTATGGGT
R: GGCTTCAGTTAGGAGGACAGG
Drought tolerance gene: *StDREB2* (JN125858), 128bp (60°C)
F: AAAGCAGAGGGAACACCAAC
R: GGGAAGAATAAGAACCAAGCCA
Virus resistance gene: *Rm* 768bp (53°C)
F: TGCCAGCCTAACACCCAAAA
R: TTGGATGCCGATGGGATCTG
Relative gene expression was calculated using the $2^{-\Delta\Delta Ct}$ method. Statistical analysis of expression levels was performed on ΔCt values.

Statistical Analysis

All experiments were conducted in triplicate. Statistical analysis included calculation of means, standard deviations, Student's t-test ($p < 0.05$), and Pearson correlation coefficients. Data processing was performed using Microsoft Excel 2010 and GraphPad Prism version 8.0.1. Each treatment included two biological replicates (n = 2; independent repetitions of the experiment). Within each replicate, five independent biological units (e.g., plants/tubers) were analyzed per treatment (n = 5).

RESULTS

Molecular Identification of the Virus

In vitro-grown potato plants were examined for the presence of Potato virus M (PVM) three days after inoculation in accordance with the experimental protocol. On the same day, the first samples were collected for the analysis of antioxidant enzyme activity. PCR analysis confirmed viral infection in all inoculated intact plant samples following co-cultivation with viral particles; the results are shown in Fig. 3.

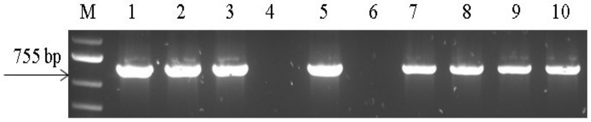

Fig. 3: PCR Analysis Results for Potato Virus X Identification in Potato Plants. M – marker; 1,2 – Ulan variety plant; 3,4 – Tokhtar variety plant; 5,6 – Babayev variety plant; 7,8 – Aliyans variety plant; 9,10 – Narli variety plant.

At 3 days post inoculation, amplification of a PVM-specific fragment of approximately 755 bp was successfully obtained in all analyzed samples. The electrophoretic profiles showed clear bands of the expected size without nonspecific amplification products, indicating high reaction specificity. Comparable band intensities among all samples suggest uniform infection efficiency across varieties under *in vitro* conditions. The confirmed and homogeneous infection status of all plant samples provides a reliable experimental basis for subsequent analyses of antioxidant enzyme activity, as it minimizes variability related to differences in viral load and allows observed biochemical responses to be attributed to genotype-specific reactions to PVM infection.

Antioxidant Enzyme Activity in Potato Plants

In the five studied potato cultivars, changes in peroxidase (POD) activity were evaluated in leaf explants at 3, 5, and 7 days after treatment. Fig. 3 presents the mean values and standard deviations of the activities of three key antioxidant enzymes – peroxidase (POD, units) (Fig. 4A), catalase (CAT, units) (Fig. 4B) and superoxide dismutase (SOD, units) (Fig. 4C).

The analysis of enzymatic activity presented in Fig. 4 reveals pronounced cultivar-specific differences in the functioning of the potato antioxidant system under viral infection (PVM), water deficit, and their combined effects. Peroxidase (POD) activity (Fig. 4A) exhibited the highest variability and served as the primary indicator of early oxidative stress. At 3 days post-inoculation (dpi), a multiple increase in POD activity was observed in all cultivars. In Aliyans, POD activity increased by +472% under PVM, +338% under drought, and +238% under combined stress. In Ulan, the corresponding increases were +220%, +266%, and +220%; in Narli, +194%, +220%, and +123%; and in Babayev, +263%, +189%, and +181%. The most pronounced response was recorded in Tokhtar, where POD activity increased by +483%, +639%, and +402% under PVM, drought, and combined stress, respectively (Table A1). At 5 dpi, POD activity declined across all treatments, reflecting attenuation of the acute oxidative response; however, the magnitude of reduction differed among cultivars. In Aliyans, POD activity decreased by -61% under PVM, whereas drought-induced reduction was less pronounced (-20%), a pattern also observed in Ulan (-20% under PVM and stable levels under drought), Narli (-47% and -18%), and Tokhtar (-29% and -19%). By 7 dpi, enzymatic activity stabilized while maintaining cultivar-specific characteristics: under PVM, values approached control levels (e.g., +12% in Aliyans), whereas drought and combined stress sustained elevated POD activity, reaching +134-221% in most cultivars (Table A1).

Catalase (CAT) activity showed a similar but more moderate response pattern (Fig. 4B). At 3 dpi, CAT activity increased significantly in all cultivars, particularly under PVM: +157% in Aliyans, +231% in Ulan, +184% in Narli, +45% in Babayev, and +102% in Tokhtar. Drought stress also stimulated CAT activity at early stages (+109% in Aliyans, +245% in Ulan, +169% in Narli). At 5 dpi, CAT activity partially declined but remained above control levels, especially under drought conditions, where a sustained increase (+23-221%) was observed in most cultivars, indicating the prolonged nature of water stress. At 7 dpi, partial recovery of CAT activity was noted; however, drought and PVM+D continued to induce elevated levels, whereas the response to PVM alone became moderate (Table A1).

Table A1: Comparative antioxidants activity in five potato cultivars exposed to control, PVM, drought, and combined PVM+D stress at 3, 5, and 7 dpi

Variety	3dpi				5 dpi				7 dpi			
	Contr	PVM	Drought	PVM+D	Contr	PVM	Drought	PVM+D	Contr	PVM	Drought	PVM+D
						Peroxidase						
Aliyans	2.9±0.5	16,6±0.6	12,7±0.4	9,8±0.3	2.7± 0.3	6.4 ± 0.6**	10.2±0.5	8.8±0.4	3.24±0.14	5.2±0.7*	9.3±0.4	9±0.2
Ulan	3.5±0.5	11.2±0.5	12.8±0.2	11.2±0.2	2.6±0.2	9 ± 0.3	12.9±0.2	10.50.4	3.5±0.2	6.03±0.5*	10.3±0.5	9.7±0.4
Narli	3.5±0.4	10.3±0.5	11.2±0.2	7.8±0.2	3.4±0.2	5.5±0.4**	9.1±0.2	8.1±0.1	3.3±0.2	5.6±0.4**	8.8±0.1	7.4±0.1
Babayev	2.7±0.6	9.8±0.4	7.8±0.3	7.6±0.5	2.6±0.2	6.6±0.4**	7.03±0.2	6.6±0.3	2.9±0.1	5.5±0.5*	6.8±0.3	5.8±0.3
Tokhtar	1.8±0.4	10.5±0.5	13.3±0.1	9.03±0.2	2.5±0.1	7.5±0.6	10.8±0.3	8.3±0.3	2.9±0.2	4.8±0.7*	9.3±0.1	7.3±0.4
						Catalyse						
Aliyans	357.1±4.2	919.3±4.7	745.1±16.7	647.9±4.4	352.9±5.4	478.7±7.9	473.1±3.8	387.3±6.9**	339.9±1.4	434±5.5	459.4±0.5	389.4±4.7
Ulan	158±2.8	522.9±2.1	544.9±10.4	486±8.1	163.6±2.1	365.4±4.4	526.3±7.4	372±9.8	162.5±1.6	231.9±8.7	415.7±5.1	397.3±2.9
Narli	192.7±1.6	546.9±11.9	519.5±7.6	472.4±3.8	194.4±2.04	528.7±3.2	346.1±3.9	319.4±4.4	192.7±1.6	413.7±4.5	228.9±1.6	257.7±3.6
Babayev	419.4±5.2	608.7±4.1	800.1±3.0	717.2±2.1	419.9±6.3	506.2±8.3	516.9±5.02	591.5±3.2	427.9±1.9	429.9±3.6^{ns}	431.4±3.6^{ns}	509.6±2.5
Tokhtar	396.8±4.7	802.6±3.6	614.8±9.1	514.4±3.6	397.1±8.4	515.9±4.4	483.9±3.3	469.2±2.2	373.2±4.2	420.2±7.4^{ns}	435.5±9.7*	373.2±5.6^{ns}
						SOD						
Aliyans	214.6±	280.0±3.7	293.2±5.6	291.5±4.1	212.3±2.2	233.9±2.8	249.5±1.5	234.5±1.7	206.9±2.9	207.9±2.5^{ns}	206.9±2.9^{ns}	224.5±3.01**
Ulan	206.5±1.8	281.62.2	381.7±1.6	311.9±1.7**	205.9±3.9	255.02±2.1	294.4±0.9	285.4±3.6	186.8±5.2	222.6±1.8	222.1±2.1^{ns}	273.6±2.7
Narli	236±1.5	292.2±3.1	271.1±4.1	298.9±1.2	231.7±1.6	247.4±2.8^{ns}	249.6±1.96**	262.1±1.6	230.9±2.9	226.5±1.5**	225.2±2.5^{ns}	253.8±2.8
Babayev	249.02±1.9	301.06±1.5	293.8±3.9	272.9±2.5	250.6±1.2	277.12±4.4**	274.4±2.9**	213.5±1.97	243.9±2.7	242.9±1.9^{ns}	243.9±2.7^{ns}	210.7±1.95
Tokhtar	223.9±	278.4±0.8	275.5±6.5	254.4±3.1	219.4±1.15	266.2±3.7	255.9±1.7**	244.9±7.3	207.2±1.5	233.9±2.6^{ns}	224.8±1.3*	225.4±1.3

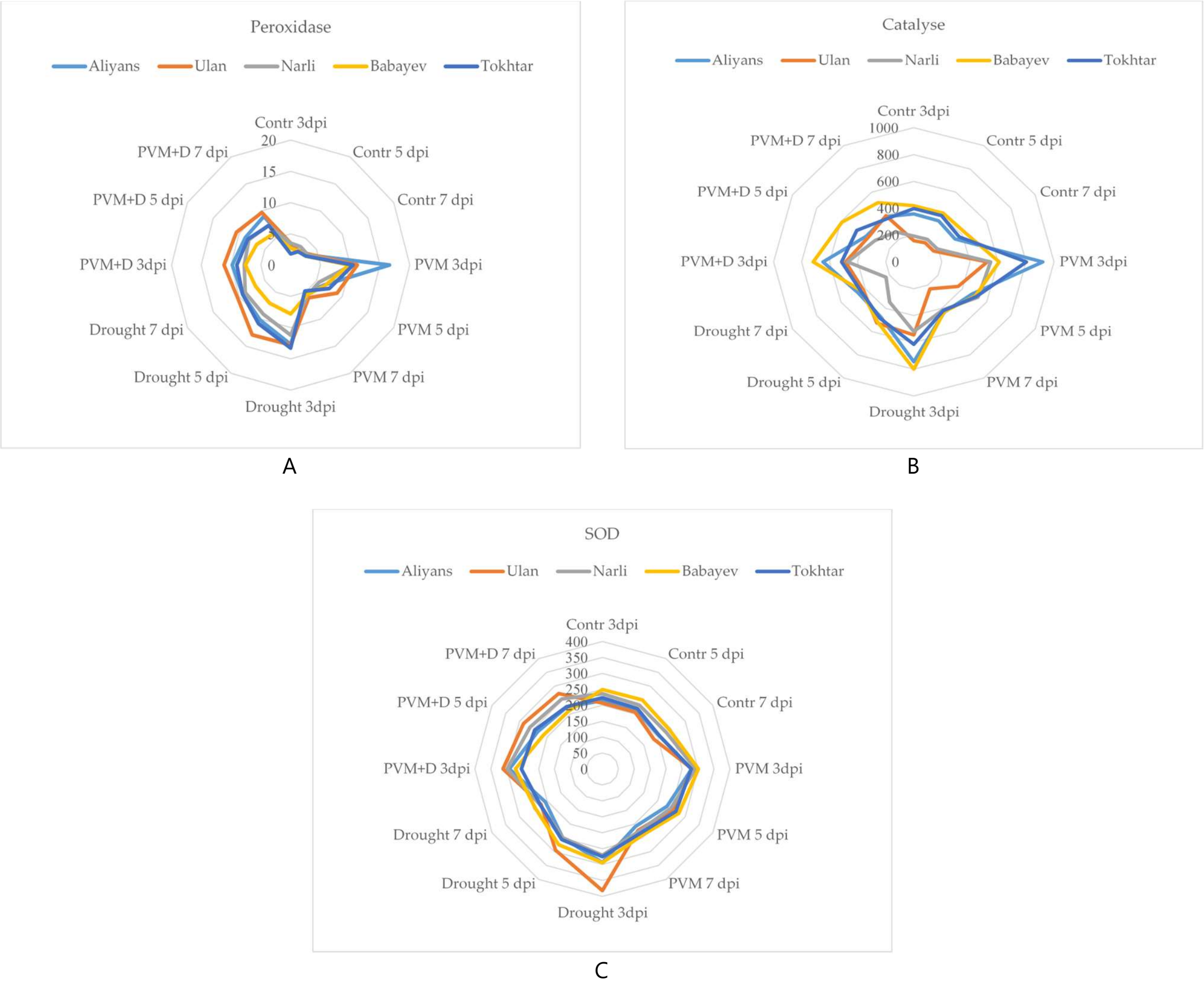

Fig. 4: Peroxidase (POD) (A), Catalyse (CAT) (B), Superoxide dismutase (SOD) (C) activity profiles in five barley cultivars under control, PVM infection, drought stress, and combined PVM+Drought treatment at 3, 5, and 7 dpi.

Superoxide dismutase (SOD) activity exhibited a lower amplitude of variation compared with POD and CAT but showed a more stable response (Fig. 4C). At 3 dpi, a moderate increase in SOD activity was detected in most cultivars, reaching +30-37% in Aliyans and +36-85% in Ulan, while changes in Narli, Babayev, and Tokhtar were less pronounced (+20-30%). At 5 dpi, SOD activity remained moderately elevated under drought and combined stress (+6-43%). By 7 dpi, responses stabilized, with minimal deviations from control values, except under combined stress in Aliyans and Ulan, where increases of +13-17% were observed (Table A1).

Overall, the dynamics of enzymatic responses indicate that drought represents the most intense and prolonged stress factor, inducing sustained activation of peroxidase, catalase, and superoxide dismutase across all cultivars. PVM infection caused a sharp but transient increase in antioxidant activity, most evident for POD and CAT at 3 dpi. Combined stress resulted in an intermediate response pattern without evidence of synergistic enhancement. Based on the magnitude and persistence of enzymatic deviations, Tokhtar and Ulan can be classified as the most sensitive cultivars; Aliyans and Narli exhibited moderate responses, whereas Babayev was characterized by the lowest amplitude of enzymatic changes.

Photosynthetic Activity

During viral pathogenesis, substantial alterations in metabolic processes occur in infected plant tissues. In addition to systemic disturbances in plant physiology, phytopathogenic viruses often induce physical deformations such as leaf wrinkling, curling, and mosaic patterns, thereby reducing the effective photosynthetic surface area of the leaf apparatus (Bahar et al., 2020; Shonazarova et al., 2025). These morphological and physiological changes lead to a reduction in photosynthetic intensity, one of the most critical determinants of plant productivity (Cheaib & Killiny, 2025).

The heatmap presents the contents of chlorophyll a, chlorophyll b, and total chlorophyll (a+b) in the leaf tissues of five potato cultivars in response to PVM infection, osmotic stress, and their combined effects at 3, 5, and 7 days after treatment. The obtained data reflect the dynamics of photosynthetic stability among cultivars and enable identification of differences in their responses to biotic and abiotic stresses (Fig. 5).

Analysis of chlorophyll a, chlorophyll b, and total chlorophyll (a+b) contents in the leaves of five potato cultivars revealed a pronounced dependence of pigment responses on stress type and exposure duration. A common trend observed across all cultivars was a substantial reduction in photosynthetic pigment levels at the early stage (3 dpi) under both PVM infection and drought stress, with the most severe suppression induced by combined stress (PVM+D). This decline persisted or intensified at 5 dpi, and only partial stabilization was observed by 7 dpi, without full recovery to control levels.

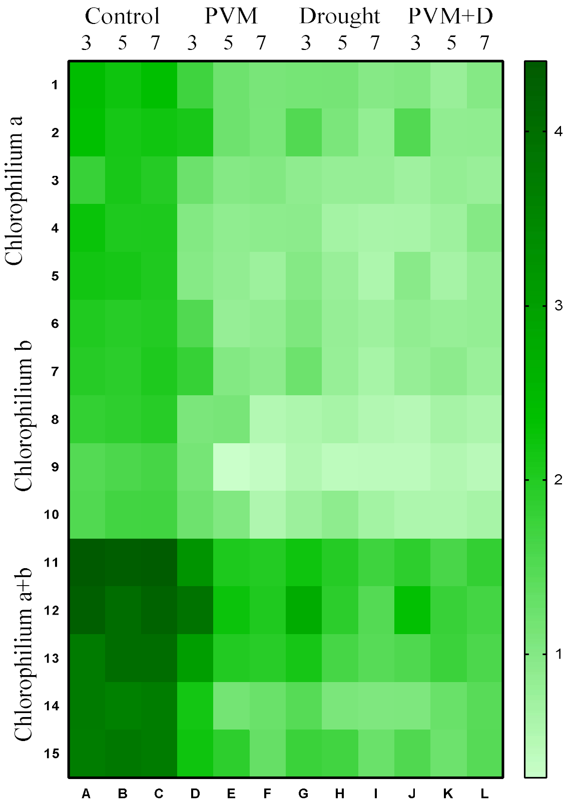

Fig. 5: Heat map of chlorofile profile (a, b, a+b) in five potato cultivars. (Samples 1, 6, and 11 – Aliyans; 2, 7, and 12 – Ulan; 3, 8, and 13 – Narli; 4, 9, and 14 – Babayev; 5, 10, and 15 – Tokhtar).

In the cultivar Aliyans, chlorophyll a content at 3 dpi decreased by 29% under PVM, by 52% under drought, and by 57% under combined stress. A similar response was observed for chlorophyll b, which declined by 24%, 47%, and 57%, respectively. At 5 dpi, pigment suppression intensified, particularly under PVM and PVM+D, and remained pronounced at 7 dpi, with chlorophyll levels 53-58% below the control. Total chlorophyll (a+b) followed a comparable pattern, decreasing by 27-57% at 3 dpi and remaining strongly suppressed at 5 and 7 dpi.

In the cultivar Ulan, viral infection caused a relatively mild early reduction in chlorophyll a and b (10% and 9%, respectively), whereas drought and combined stress resulted in marked declines of 35-58%. At 5 dpi, pigment levels continued to decrease, especially under drought (up to -59% for chlorophyll a). By 7 dpi, chlorophyll a, b, and a+b remained substantially reduced relative to the control (-49-68%), indicating a prolonged effect of water deficit.

The cultivar Narli proved to be among the most sensitive. At 3 dpi, chlorophyll a content declined by 30-59%, chlorophyll b by 40-73%, and total chlorophyll by 19-59%. At 5 dpi, suppression intensified (up to -61-77%) and persisted at 7 dpi (-52-73%), reflecting high vulnerability of the photosynthetic apparatus. The cultivar Babayev exhibited the most pronounced pigment depletion among all genotypes. At 3 dpi, chlorophyll a decreased by 55-72%, chlorophyll b by 23-71%, and total chlorophyll by 42-72%. At 5 dpi, pigment loss reached a maximum (up to -82% for chlorophyll b), and at 7 dpi pigment levels remained extremely low, indicating an absence of compensatory recovery.

Similarly, Tokhtar showed high sensitivity to stress exposure: at 3 dpi, chlorophyll a decreased by 54-56%, chlorophyll b by 20-62%, and total chlorophyll by 40-58%. At 5 dpi, suppression ranged from 50-67% and persisted at 7 dpi, remaining 60-67% below control values (Table A2).

Overall, the data demonstrate that all studied potato cultivars experience substantial reductions in photosynthetic pigment content under stress conditions, although the degree of sensitivity varies markedly. The most severe and persistent pigment suppression was observed in Babayev, Tokhtar, and Narli, whereas Aliyans and Ulan exhibited more moderate responses. Drought and combined stress exerted a stronger negative impact on the photosynthetic pigment system than PVM infection alone, highlighting the dominant role of abiotic stress in suppressing photosynthetic activity.

Gene Expression Dynamic in Potato Plants

The expression level of the transcription factor *StDREB2* (Dehydration-Responsive Element Binding), which regulates genes involved in dehydration stress responses, was assessed in leaf tissues of the studied potato cultivars using quantitative reverse transcription PCR (qRT-PCR). Relative gene expression was calculated using the ΔΔCt method with normalization to the housekeeping gene StActin. Levels of statistical significance relative to the control are indicated in the graph (Fig. 6).

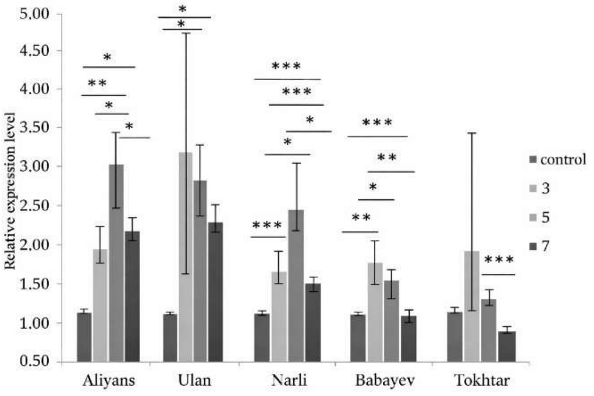

Fig. 6: Expression levels of the drought-tolerance gene *StDREB2* in five potato cultivars. (Note: * P<0.05; ** P<0.01; *** P<0.001).

Analysis of the relative expression of *StDREB2* revealed a pronounced cultivar-specific and temporally structured response, indicating differential activation of dehydration-responsive regulatory pathways among potato genotypes.

Table A2: Photosynthetic Activity of Potato Plants under PVM Infection, Drought, and Combined Stress Conditions

Variety	3dpi				5 dpi				7 dpi			
	Contr	PVM	Drought	PVM+D	Contr	PVM	Drought	PVM+D	Contr	PVM	Drought	PVM+D
						Chlorophilium a						
Aliyans	2.39±0.04	1.697±0.08	1.141±0.07	1.018±0.03	2.197±0.06	1.221±0.03	1.145±0.09	0.791±0.06	2.36±0.06	1.113±0.04^{ns}	0.983±0.04	0.986±0.08
Ulan	2.34±0.07	2.1±0.04**	1.512±0.1	1.509±0.05**	2.117±0.01	1.22±0.07	1.091±0.08	0.864±0.06	2.184±0.08	1.107±0.07	0.847±0.05	0.878±0.03
Narli	1.77±0.12	1.24±0.04**	0.89±0.03**	0.722±0.07**	2.1±0.09	0.986±0.03	0.818±0.08	0.834±0.08	1.97±0.05	1.02±0.09	0.817±0.09	0.79±0.08
Babayev	2.25±0.07	1.01±0.04	0.92±0.04	0.63±0.03	2.041±0.05	0.874±0.04	0.679±0.03	0.74±0.06	2.049±0.05	0.904±0.04	0.62±0.03	0.99±0.03
Tokhtar	2.16±0.1	0.977±0.04	0.99±0.04	0.95±0.03	2.12±0.07	0.854±0.03	0.7833±0.03	0.6554±0.03	2.03±0.03	0.746±0.04	0.586±0.03	0.825±0.01
						Chlorophilium b						
Aliyans	2.013±0.05	1.522±0.08	1.058±0.07	0.871±0.03	1.943±0.08	0.822±0.9	0.817±0.03	0.81±0.04	1.983±0.06	0.871±0.1**	0.731±0.1	0.842±0.05
Ulan	1.959±0.06	1.79±0.1^{ns}	1.231±0.06	0.817±0.06	1.902±0.07	1.009±0.02	0.808±0.07	0.913±0.03	2.033±0.02	0.919±0.05	0.639±0.07	0.776±0.05
Narli	1.819±0.1	1.09±0.05*	0.578±0.05**	0.493±0.07**	1.87±0.1	1.124±0.03**	0.649±0.05	0.657±0.07	1.944±0.2	0.517±0.07**	0.535±0.04**	0.597±0.04**
Babayev	1.488±0.01	1.14±0.01	0.544±0.04	0.434±0.03	1.569±0.1	0.293±0.09**	0.417±0.02	0.531±0.04	1.631±0.09	0.361±0.07	0.428±0.06	0.458±0.05
Tokhtar	1.523±0.07	1.226±0.01*	0.758±0.05	0.584±0.02	1.667±0.1	1.031±0.1**	0.899±0.03	0.575±0.03	1.685±0.03	0.562±0.04	0.68±0.1	0.647±0.2**
						Chlorophilium a+b						
Aliyans	4.403±0.05	3.219±0.08	2.199±0.07	1.889±0.03**	4.303±0.07	2.043±0.4	1.962±0.06	1.601±0.05	4.343±0.06	1.984±0.07	1.714±0.07	1.828±0.07
Ulan	4.299±0.06	3.89±0.07	2.743±0.08	2.326±0.05*	4.019±0.04	2.229±0.05	1.899±0.08	1.777±0.04	4.217±0.05	2.026±0.01	1.486±0.06	1.654±0.04
Narli	3.729±0.11	3.03±0.05**	2.121±0.04	1.539±0.07	4.002±0.08	1.995±0.03	1.626±0.08	1.747±0.08	4.003±0.1	1.939±0.08	1.456±0.07	1.566±0.04
Babayev	3.738±0.04	2.15±0.03**	1.464±0.04	1.064±0.03	3.61±0.07	1.167±0.07	1.096±0.03	1.271±0.05	3.68±0.07	1.265±0.05	1.048±0.05	1.448±0.04
Tokhtar	3.683±0.09	2.203±0.03**	1.748±0.04	1.534±0.03	3.787±0.04	1.885±0.07	1.6823±0.03	1.2304±0.03	3.715±0.03	1.308±0.04	1.266±0.07	1.472±0.1

At the early stage of stress exposure, the strongest and most rapid induction of *StDREB2* was detected in the cultivars Ulan and Aliyans, suggesting a highly efficient early stress-sensing and signal transduction capacity. In Ulan, transcript abundance increased to approximately threefold relative to the control, accompanied by substantial variability, as reflected by large standard deviations, indicative of dynamic transcriptional regulation. Aliyans similarly exhibited a robust upregulation of StDREB2 expression, reaching approximately 2.5-2.8-fold above control levels.

In contrast, the cultivars Narli and Babayev displayed a delayed transcriptional response, with maximal *StDREB2* induction occurring at later time points. In Narli, peak expression was observed at 5 dpi, reaching approximately a twofold increase, while Babayev showed a moderate induction during the 3-5 dpi interval followed by partial attenuation by 7 dpi. This delayed activation pattern likely reflects reduced responsiveness of upstream signaling components or slower engagement of dehydration-related transcriptional networks. The cultivar Tokhtar exhibited the weakest *StDREB2* response, characterized by a low-amplitude and transient induction that did not exceed 1.2-1.4-fold relative to the control, suggestin g Limited involvement of DREB-mediated pathways in its stress response strategy.

Across all cultivars, *StDREB2* expression declined by 7 dpi compared with peak levels, indicating attenuation of the acute stress response phase. Nevertheless, in Ulan and Narli, residual expression remained significantly elevated relative to the control, implying sustained engagement of dehydration-responsive regulatory mechanisms. The statistical significance of most expression peaks further supports the biological relevance of these transcriptional changes.

The expression dynamics of the virus-resistance gene *Rm* were also investigated to assess its contribution to stress adaptation. Transcript profiling revealed stress-induced activation of *Rm*, reflecting its involvement in antiviral defense responses. Variations in the magnitude and duration of *Rm* induction among cultivars highlight differences in the efficiency of virus perception and immune signaling, thereby enabling discrimination between genotypes with contrastin g Levels of virus resistance (Fig. 7).

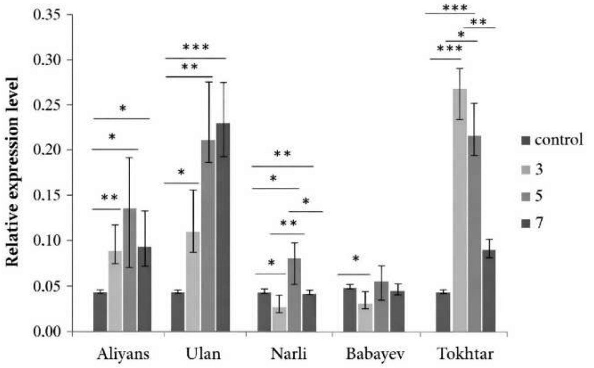

Fig. 7: Expression levels of the virus-resistance gene *Rm* in five potato cultivars. (Note: * P<0.05; ** P<0.01; *** P<0.001).

The obtained data reveal a pronounced cultivar- and time-dependent specificity of *Rm* gene expression, indicating substantial differences among potato genotypes in the activation of virus-resistance mechanisms. The strongest induction of *Rm* was observed in the cultivars Tokhtar and Ulan, suggesting a rapid and efficient engagement of antiviral defense pathways. Tokhtar exhibited a sharp early transcriptional response, with peak relative expression at 3 and 5 dpi (approximately 0.27 and 0.21, respectively), followed by a marked decline to ~0.09 by 7 dpi, indicative of a fast but transient activation of resistance signaling. In Ulan, elevated *Rm* expression was maintained across all time points, reaching maximal levels of approximately 0.20-0.23 at 5-7 dpi and remaining significantly higher than the control even at the late stage, which points to a more sustained antiviral response.

The cultivar Aliyans showed a moderate yet stable increase in *Rm* expression throughout the experiment (approximately 0.08-0.13), with statistically significant differences from the control at selected time points, suggesting an intermediate resistance strategy characterized by steady but less intense gene activation. In contrast, Narli and Babayev displayed consistently low basal and inducible *Rm* expression. In Narli, relative transcript levels remained within the range of ~0.03-0.07, while in Babayev they varied between ~0.04 and 0.06, with only sporadic statistically significant deviations from the control, indicating limited involvement of *Rm*-mediated antiviral defense.

Across all cultivars, peak *Rm* activation generally occurred during the early to mid-stages (3-5 dpi), followed by attenuation at 7 dpi. However, the persistence of elevated expression in Ulan underscores genotype-specific differences in the duration and effectiveness of antiviral responses. Overall, these results demonstrate that *Rm* exhibits strong and rapid induction in Tokhtar and Ulan, moderate activation in Aliyans, and weak responsiveness in Narli and Babayev, supporting the utility of *Rm* expression intensity and dynamics as an informative molecular marker of cultivar-specific viral resistance.

Genotype-Phenotype Correlation

Correlation analysis revealed that the drought-tolerance gene *StDREB2* is substantially more tightly associated with biochemical and photosynthetic traits than the virus-resistance gene *Rm* (Fig. 8).

Under drought and combined stress conditions, *StDREB2* expression exhibited a strong positive relationship with antioxidant enzyme activity. Increasing transcript levels of *StDREB2* were accompanied by elevated activities of peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD). In the correlation plots, data points clustered along positively sloped regression lines, indicating coordinated activation of both the enzymatic antioxidant defense system and DREB-dependent signaling pathways. The association between *StDREB2* expression and POD activity was particularly pronounced, whereas correlations with CAT and SOD showed greater dispersion but maintained an overall positive trend. These patterns suggest that higher *StDREB2* expression is linked to more effective enzymatic control of reactive oxygen species (ROS) under water deficit and PVM infection.

A similar relationship was observed between *StDREB2* expression and photosynthetic characteristics. Under drought, viral, and combined stress treatments, higher *StDREB2* transcript levels were associated with increased contents of chlorophyll a, chlorophyll b, and total chlorophyll (a+b). In the corresponding correlation plots, regression lines displayed positive slopes, and data points were predominantly distributed toward higher chlorophyll values at elevated *StDREB2* expression levels. This indicates that activation of *StDREB2* is associated not only with induction of antioxidant defense mechanisms but also with improved preservation of the photosynthetic apparatus under stress conditions, reflecting enhanced functional stability of leaf tissues.

In contrast to *StDREB2*, the correlation profile of the *Rm* gene was fundamentally different. For most combinations of *Rm* expression with antioxidant enzyme activities, data points were distributed nearly randomly around regression lines with minimal slopes, indicating the absence of a strong relationship between *Rm* transcript levels and the activities of POD, CAT, and SOD. Only in isolated cases was a weak tendency toward increased peroxidase activity observed at higher *Rm* expression levels; however, this trend was inconsistent and was not reproduced for the other enzymatic parameters.

A similar pattern was observed for the relationship between *Rm* expression and photosynthetic traits. In the "*Rm*-chlorophyll" correlation plots, regression lines were nearly horizontal, and data points were widely scattered along the pigment-content axis, indicating no clear association between *Rm* expression and the maintenance of the chlorophyll-containing photosynthetic apparatus under stress conditions. Only for total chlorophyll did some treatments show a slight positive inclination; however, this effect was markedly weaker than that observed for *StDREB2*.

Taken together, the correlation analysis highlights a clear functional divergence between the two genes. *StDREB2* is tightly linked to activation of the antioxidant defense system and preservation of photosynthetic activity under drought and combined stress, reflecting its role as an integrative regulator of general stress adaptation. In contrast, *Rm* appears to operate primarily within specific antiviral defense pathways, showin g Limited association with variation in biochemical and photosynthetic parameters across the studied cultivars. This distinction supports the use of *StDREB2* as a marker of broad stress tolerance, whereas *Rm* more accurately reflects genotype-specific viral resistance.

DISCUSSION

Potato is affected by more than 50 different viruses, and their impact on plant physiology remains one of the key challenges facing the global potato industry. Verchot (2022) emphasized that viruses, as obligate parasites, deeply interfere with plant metabolism by disrupting photosynthesis, carbohydrate metabolism, and antioxidant defense systems, ultimately leading to substantial yield losses and deterioration of tuber quality. These conclusions are supported by the findings of Ospankulova et al. (2023), who demonstrated that PVY, PVS, and PVM infections reduce dry matter and starch content and alter starch granule structure, including decreases in granule size, crystallinity, and changes in the amylose-to-amylopectin ratio. Collectively, these results indicate that viral infections exert complex effects, leading not only to reduced plant biomass but also to compromised nutritional and technological quality of potato tubers (Weber et al., 2021; Manasseh et al., 2023). Our results are consistent with these observations, as PVM-infected plants exhibited a pronounced reduction in photosynthetic pigment content, indicating impaired photosynthetic function. All cultivars showed decreased levels of chlorophyll a, chlorophyll b, and total chlorophyll (a+b), with the most pronounced declines recorded in the Narli and Babayev cultivars, reflecting their high sensitivity to viral stress. Similar effects have been reported for PVY, where viral infection caused chloroplast degradation, a reduction in thylakoid number, and decreased Rubisco activity, further confirming the link between viral stress and photosynthetic deterioration (Kalatskaja et al., 2023). An increasingly important aspect of modern crop production is the simultaneous exposure of plants to multiple stress factors. Although interactions between viral infections and abiotic stresses remain insufficiently explored, accumulating evidence suggests that combined stress conditions elicit distinct physiological responses that differ from those induced by individual

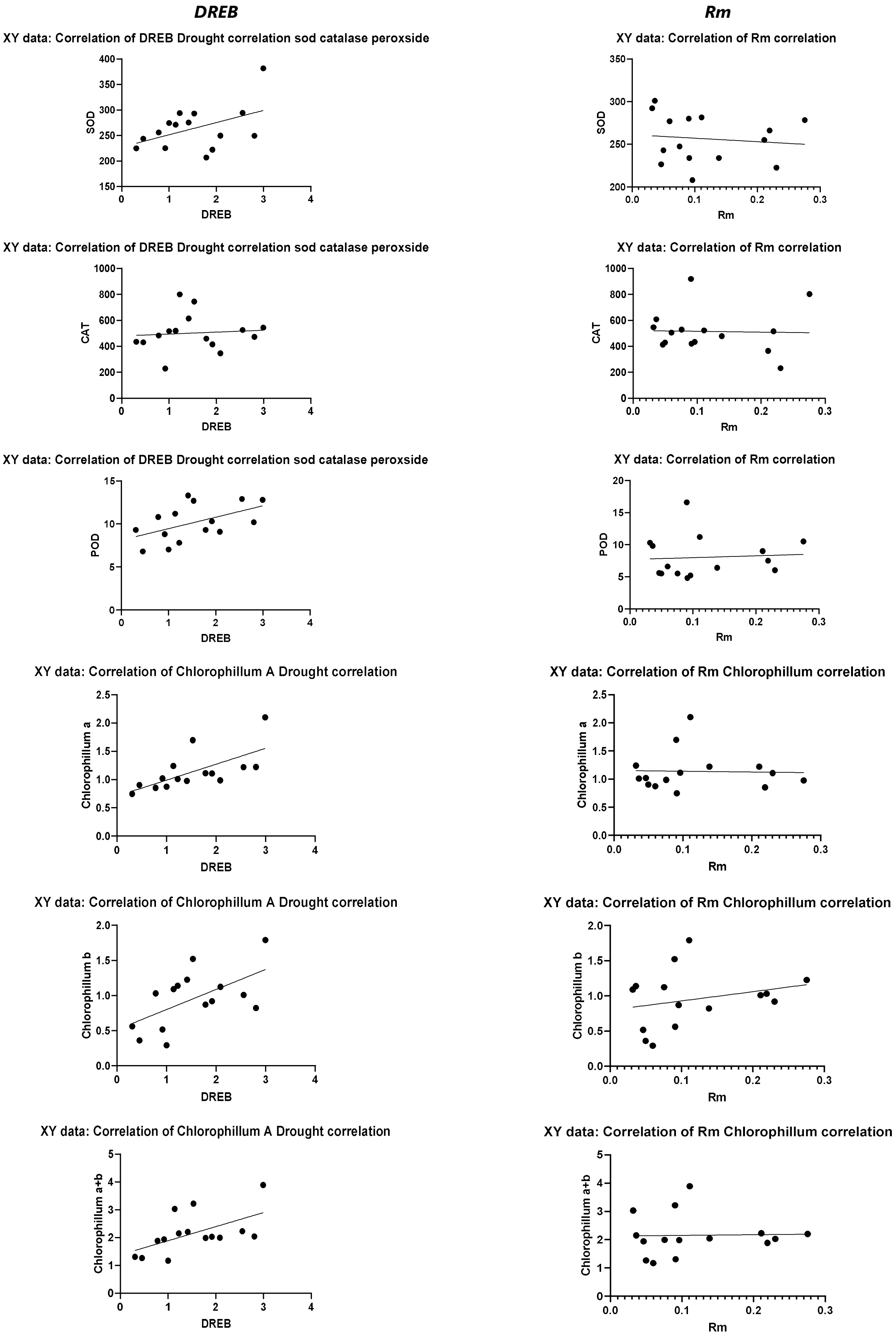

Fig. 8: Comparative correlation of *StDREB2* and *Rm* expression with physiological stress indicators.

stressors (Abd Elhady et al., 2021; Al-Selwey et al., 2023; Cohen et al., 2023; Bi et al., 2024). Kalatskaja et al. (2023) further demonstrated that under combined PVY infection and drought stress, potato plants exhibit enhanced accumulation of antioxidants and a marked increase in antioxidant enzyme activities. Notably, hydrogen peroxide levels in leaves declined more strongly under combined stress than under individual stresses, which the authors attributed to the activation of protective mechanisms aimed at mitigating oxidative cellular damage.

Our data are consistent with these observations: the antioxidant enzymes POD, CAT, and SOD in potato exhibited a characteristic phase-dependent dynamic pattern, with a sharp increase in activity at early stages (3 dpi), followed by a decline at 5 dpi and stabilization at cultivar-specific levels by 7 dpi. The most pronounced changes were observed under single viral stress and, in particular, under combined PVM + drought stress, whereas drought stress alone often elicited a less intense response. Similar patterns have been reported in studies examining the effects of PVY and PVX on tomato and tobacco, where early induction of POD and CAT activity represents a typical response to viral replication and ROS accumulation in infected tissues. Our results indicate that this mechanism is also characteristic of PVM infection, while cultivar-specific differences – most notably the strong responses observed in Aliyans, Ulan, and Tokhtar – may reflect variation in the efficiency of enzymatic ROS scavenging.

Interestingly, viral infection may not only exacerbate the negative effects of drought but can also activate molecular pathways that enhance plant tolerance to water deficit (Uraji et al., 2012; Finkelstein, 2013; Barbaglia et al., 2016; Heidari et al., 2023). Lin et al. (2025) demonstrated that infection by +RNA viruses, including PVY, activates ABA signaling and enhances phosphatidic acid production via PLDα1. Subsequent inhibition of PLDα1 suppressed virus-induced drought tolerance, indicating a direct involvement of viral components in drought-response regulation. Similarly, Prakash et al. (2024) showed that viral infection can improve plant tolerance to water deficit through enhanced expression of stress-adaptive genes. Our study further supports the involvement of viral factors in stress-response regulation. Expression of *StDREB2*, a key regulator of dehydration-related signaling cascades, was strongly induced at early stages in the Ulan and Aliyans cultivars, suggesting more efficient activation of adaptive responses. In contrast, Narli and Babayev exhibited delayed expression peaks, which may explain their increased sensitivity in physiological assays. Similar differences in *StDREB2* dynamics between drought-tolerant and drought-sensitive potato genotypes have been reported by El-Esawi & Alayafi (2019) and Mushtaq et al. (2021), where *StDREB2* served as a marker of stress-adaptation activation.

Equally important was the observed modulation of the virus-resistance gene *Rm*. The highest *Rm* transcription levels were detected in Tokhtar and Ulan, in agreement with their strong antioxidant enzymatic responses. Elevated *Rm* expression may indicate the establishment of an early immune response to PVM. Similar patterns have been reported for potato resistance to PVY, where R-type genes showed rapid induction during hypersensitive response development (Baebler et al., 2020). In contrast, Narli and Babayev displayed minimal *Rm* activation, which may explain their heightened susceptibility to both viral and combined stress (Zaki & Radwan, 2022; Saleem et al., 2022; Sun et al., 2022; Li et al., 2025).

The correlation analysis performed in this study demonstrates that *StDREB2* gene expression is tightly associated with the enzymatic component of the antioxidant system and the functional state of the photosynthetic apparatus. Positive correlations between *StDREB2* transcript levels and the activities of POD, CAT, and SOD, as well as with chlorophyll a, chlorophyll b, and total chlorophyll content, indicate that activation of this transcription factor constitutes part of an integrated adaptive response to water deficit and viral infection. Similar patterns have been reported across multiple crop species, where overexpression of *DREB* factors enhances antioxidant enzyme activity and improves drought tolerance in potato, cotton, poplar, and other plants, concomitantly reducing ROS accumulation and preserving photosynthetic performance (El-Esawi & Alayafi, 2019; Geng et al., 2023; Ul Ain-Ali et al., 2024).

In potato specifically, drought-tolerant genotypes are characterized by earlier and stronger induction of DREB-like genes, coupled with increased antioxidant enzyme activity and smaller reductions in chlorophyll content compared with drought-sensitive cultivars (Yang et al., 2019; Zaki & Radwan, 2022; Kanat et al., 2024). Against this background, the positive correlations observed here between *StDREB2*, enzymatic antioxidant activity, and pigment levels provide strong evidence for the central role of DREB-dependent pathways in shaping complex tolerance to drought and combined PVM + drought stress. Notably, cultivars with higher *StDREB2* expression also exhibited stronger activation of antioxidant enzymes and better preservation of the photosynthetic apparatus, fully consistent with the current concept that *DREB* factors coordinate the expression of genes involved in osmotic protection, ROS detoxification, and stabilization of photosynthetic structures (Sadau et al., 2024; Gaoua, 2025).

In contrast, the weak and mostly statistically insignificant correlations between *Rm* gene expression and antioxidant enzyme activity or chlorophyll content reflect a more specialized function of this gene, primarily associated with the activation of specific antiviral defense rather than general physiological adaptation to multifactorial stress. It is well established that R-type genes, including *Rm*, encode NLR receptor proteins that trigger hypersensitive responses and local restriction of infection, and their expression does not necessarily correlate directly with global physiological traits (Liu et al., 2021; Zhu et al., 2025). Recent comparative transcriptomic analyses of R genes in tomato and potato further showed that only a small subset of R genes is differentially expressed during viral and other infections, with changes often being tissue-specific and weakly linked to overall photosynthetic performance or antioxidant status (von Dahlen et al., 2023). Similarly, studies of resistance to PVM and other potato viruses indicate that the presence or activation of specific R genes (including *Rm*) reliably predicts hypersensitive response development and restriction of viral replication but does not necessarily determine enzymatic activity levels or pigment content under prolonged stress (Tatarowska et al., 2020; Ross et al., 2022).

In this context, the correlations identified in our study can be logically interpreted as evidence of functional divergence between two marker groups: *StDREB2* acts as an integrative regulator of multifactorial stress tolerance, whereas *Rm* primarily reflects a component of specific viral resistance that is weakly associated with variation in biochemical and photosynthetic parameters at the whole-plant level. Thus, our data indicate that potato tolerance under PVM infection and drought stress is determined by a multilevel interaction among the antioxidant defense system, the photosynthetic apparatus, and stress-regulatory transcription factors. Viral infection enhances oxidative stress and disrupts photosynthetic processes, while drought alone causes damage to cellular structures; however, when combined with viral infection, drought can elicit complex and sometimes contrasting physiological responses, ranging from enhanced defense activation to severe growth inhibition in susceptible cultivars.

These findings expand current understanding of the interplay between viral and abiotic stresses and highlight the necessity of an integrated assessment of potato cultivars using biochemical and molecular markers of stress tolerance. Furthermore, the results point to the potential applicability of *StDREB2* and *Rm* genes as indicators of stress resilience in breeding programs aimed at developing potato cultivars capable of withstanding multifactorial stress conditions.

Conclusion

The present study provides an integrated physiological, biochemical, and molecular assessment of potato responses to Potato virus M (PVM) infection, drought stress, and their combined effects. The results demonstrate that plant stress tolerance is not determined by a single protective mechanism but is instead shaped by coordinated regulation of the antioxidant defense system, maintenance of photosynthetic functionality, and activation of stress-induced transcriptional cascades. Among the examined factors, drought emerged as the most persistent and system-wide stress, whereas viral infection predominantly triggered rapid and transient responses. Combined stress produced intermediate response patterns, reflecting partial convergence of biotic and abiotic stress signaling pathways. The pronounced cultivar-specific variability observed highlights the high plasticity of adaptive strategies in potato and underscores the decisive role of the timing and intensity of regulatory responses in determining stress tolerance. From both scientific and practical perspectives, these findings emphasize the necessity of multidimensional stress phenotyping that integrates molecular markers with physiological and biochemical traits. Future studies should extend this framework by examining additional regulatory pathways, including abscisic acid signaling, ROS-lipid interactions, and hormonal crosstalk, by increasing the duration of stress exposure, and by validating the results under field conditions. The integration of transcriptomic, metabolomic, and phenomics data will enable deeper insight into the interactions between biotic and abiotic stresses and improve the accuracy of predicting potato productivity under changing climate conditions.

DECLARATIONS

Funding: This study did not get any financial support from any organization/agency.

Acknowledgement: The authors express their sincere gratitude to Bekbolat B. Khassenov, Head of the Laboratory of Genetics and Biochemistry of Microorganisms, National Center for Biotechnology (NCB, Astana, Kazakhstan), for providing access to laboratory facilities and for his support in conducting biochemical analyses, as well as for methodological assistance during the experimental work; Vladimir S. Kiyan, Head of the Laboratory of Biodiversity and Genetic Resources, National Center for Biotechnology (NCB), for providing the laboratory facilities of the Research Platform for Agricultural Biotechnology used for electrophoretic and biochemical analyses of antioxidant enzymes; Almagul A. Kakimzhanova, Head of the Laboratory of Plant Biotechnology and Breeding, National Center for Biotechnology (NCB), for providing the opportunity to conduct research on the production of virus-free potato material in her laboratory.

Conflict of Interest: The authors declare no conflicts of interest.

Data Availability: All data generated or analyzed during this study are included in this published article, and the data are available from the corresponding author on reasonable request.

Ethics Statement: Not applicable.

Author's Contribution: Conceptualization, A.G.; methodology, R.T. and D.S.; software, A.Z.; validation, D.S. and I.K.; formal analysis, A.S., G.I. and G.B.; investigation, A.G.; data curation, I.K.; writing – original draft preparation, A.G.; writing – review and editing, A.G. and F.Z.; visualization, N.G.; supervision, R.O. All authors have read and agreed to the published version of the manuscript.

Generative AI Statement: The authors declare that no Gen AI/DeepSeek was used in the writing/creation of this manuscript.

REFERENCES

Abd Elhady, S.A., El-Gawad, H.G.A., Ibrahim, M.F.M., Mukherjee, S., Elkelish, A., Azab, E., Gobouri, A.A., Farag, R., Ibrahim, H.A. & El-Azm, N.A. (2021). Hydrogen Peroxide Supplementation in Irrigation Water Alleviates Drought Stress and Boosts Growth and Productivity of Potato Plants. *Sustainability*, *13*(2), 899. https://doi.org/10.3390/su13020899

Al-Selwey, W.A., El-Sayed, A.R., Hassan, M.M., El-Sheery, N.M., El-Hady, E.M.A., Al-Huqail, A.A., Al-Malki, A.L., Abdallah, A.M. & Shehata, A.A. (2023). Morphological and Biochemical Responses of Potato to ZnO and SiO_2 Nanoparticles under Water Deficit Conditions. *Horticulturae*, *9*(8), 883. https://doi.org/10.3390/horticulturae9080883

Argynbayeva, A., Daurov, D., Sapakhova, Z., Zhambakin, K.Z. & Shamekova, M. (2023). Potato Viruses in Kazakhstan and Methods for Obtaining Virus-Free Seed Material. *BULLETIN of L.N. Gumilyov Eurasian National University. Bioscience Series*, *143*, 54-68. https://bulbio.enu.kz/index.php/main/article/view/310

Baebler, Š., Coll, A. & Gruden, K. (2020). Plant Molecular Responses to Potato Virus Y. *Viruses*, *12*, 217. https://doi.org/10.3390/v12020217

Bahar, T., Qureshi, A., Qurashi, F., Abid, M., Zahra, M.B. & Haider, M. (2020). Changes in Phytochemical Status upon Viral Infections in Plants. *Phyton*, *90*, 1-14. https://doi.org/10.32604/phyton.2020.010597

Barbaglia, A.M., Hoffmann-Benning, S., Clark, D.G. & Jones, A.M. (2016). Phloem Proteomics Reveals New Lipid-Binding Proteins with a Putative Role in Lipid-Mediated Signaling. *Frontiers in Plant Science*, *7*, 563. https://doi.org/10.3389/fpls.2016.00563

Bi, Z., Wang, J., Liu, Y., Li, X., Zhang, Q., Chen, X., Zhou, H., Li, W. & Xu, Y. (2024). Overexpression of *StCDPK13* Enhances Tolerance to Drought Stress in Potato. *International Journal of Molecular Sciences*, *25*, 12620. https://doi.org/10.3390/ijms252312620

Cheaib, A. & Killiny, N. (2025). Photosynthesis Responses to Infection with Plant Pathogens. *Molecular plant-microbe interactions: MPMI*, *38*(1), 9-29. https://doi.org/10.1094/MPMI-05-24-0052-CR

Cohen, A., Basu, S. & Crowder, D.W. (2023). Drought Stress Affects Potato-Vector-Pathogen Interactions. *FEMS Microbiology Ecology*, *99*, fiac142. https://doi.org/10.1093/femsec/fiac142

Corrales-Gutierrez, M., Medina-Puche, L., Yu, Y., Wang, L., Ding, X., Luna, A.P., Bejarano, E.R., Castillo, A.G., & Lozano-Duran, R. (2020). The C4 protein from the geminivirus Tomato yellow leaf curl virus confers drought tolerance in Arabidopsis through an ABA-independent mechanism. *Plant Biotechnology Journal*, *18*(5), 1121-1123. https://doi.org/10.1111/pbi.13280

Devaux, A., Goffart, J.-P., Kromann, P., Andrade-Piedra, J., Polar, V. & Hareau, G. (2021). The Potato of the Future: Opportunities and Challenges in Sustainable Agri-Food Systems. *Potato Research*, *64*, 681-720. https://doi.org/10.1007/s11540-021-09501-4

El-Esawi, M. & Alayafi, A. (2019). Overexpression of StDREB2 Enhances Drought Tolerance. *Genes*, 10, 142. https://doi.org/10.3390/genes10020142

Finkelstein, R. (2013). Abscisic Acid Synthesis and Response. *Arabidopsis Book*, *11*, e0166. https://doi.org/10.1199/tab.0166

Gajimuradova, A.M., Kirgizova, I.V., Silayev, D.V., Turpanova, R.M., Ismukanova, G.Z. & Shvidchenko, V.K. (2023). *In vitro* potato variability and its effect on tuber nutritional properties. *Herald of science of S. Seifullin Kazakh agrotechnical university: Multidisciplinary*, *2*(117), 69-78. https://doi.org/10.51452/kazatu.2023.2(117).1417

Gaoua, O. (2025). Integrating Physiological, Biochemical, and Molecular Mechanisms Reveals Insights into Drought Tolerance in Sugar Beet (*Beta vulgaris* L.). *Discover Plants*, *2*, 325. https://doi.org/10.1007/s44372-025-00416-9

Geng, L., Ren, J., Ji, X., Yan, S. & Song, X.S. (2023). Over-expression of DREB46 enhances drought tolerance in *Populus trichocarpa*. *Journal of Plant Physiology*, *281*, 153923. https://doi.org/10.1016/j.jplph.2023.153923

Gervais, T., Creelman, A., Li, X.-Q., Bizimungu, B., De Koeyer, D. & Dahal, K. (2021). Potato Response to Drought Stress: Physiological and Growth Basis. *Frontiers in Plant Science*, *12*, 698060. https://doi.org/10.3389/fpls.2021.698060

Heidari, P., Pessarakli, M., Ebrahimi, M., Firoozabadi, A.H. & Amini, S. (2023). Comparative Analysis of Phospholipase D (PLD) Gene Family in *Camelina sativa* and *Brassica napus* and Its Responses in *Camelina* Seedlings under Salt Stress. *Agronomy*, *13*, 2616. https://doi.org/10.3390/agronomy13102616

Hu, X., Jiang, H., Liu, Z., Gao, M., Liu, G., Tian, S. & Zeng, F. (2025). The Global Potato-Processing Industry: A Review of Production, Products, Quality and Sustainability. *Foods*, *14*, 1758. https://doi.org/10.3390/foods14101758

Kalatskaja, J.N., Baliuk, N.V., Rybinskaya, K.I., Herasimovich, K.M., Yalouskaya, N.A., Yarullina, L.G. & Tsvetkov, V.O. (2023). Increasing Potato Sustainability to PVY under Water Deficiency by Bacillus Bacteria with Salicylic Acid and Methyl Jasmonate. *International Journal of Plant Biology, 14*, 312-328. https://doi.org/10.3390/ijpb14010026

Kanat, R., Shamekova, M., Sapakhova, Z., Toishimanov, M., Daurov, D., Raissova, N., Abilda, Z., Daurova, A. & Zhambakin, K. (2024). Gene Expression Analysis for Drought Tolerance in Early Stage of Potato Plant Development. *Biology*, *13*(11), 857. https://doi.org/10.3390/biology13110857

Kumar, A., Katiyar, A., Jailani, A., Chakraborty, A. & Mandal, B. (2023). Genetic Diversity of Potato Virus M in the Indo-Gangetic Plain and Characterization of a Distinct Strain. *Frontiers in Microbiology*, *14*, 1265653. https://doi.org/10.3389/fmicb.2023.1265653

Kumar, R., Kaundal, P., Arjunan, J., Sharma, S. & Chakrabarti, S.K. (2020). Visual Detection of Potato Virus S by RT-LAMP. 3 *Biotech*, *10*, 1-8. https://doi:10.1007/s13205-020-02214-4

Lal, M.K., Tiwari, R.K., Kumar, R., Naga, K.C., Kumar, A., Singh, B., Raigond, P., Dutt, S., Chourasia, K.N., Kumar, D., Parmar, V. & Changan, S.S. (2021). Effect of potato apical leaf curl disease on glycemic index and resistant starch of potato (*Solanum tuberosum* L.) tubers. *Food Chemistry*, *359*, 129939. https://doi.org/10.1016/j.foodchem.2021.129939

Li, X., Luo, L., Shi, X., Li, L., Li, D., Li, F. & Shigui, L. (2025). Screening Drought Tolerance in Potato Germplasm Resources in the Northwestern Region of China. *BMC Plant Biology, 25*, 777. https://doi.org/10.1186/s12870-025-06716-2

Lin, J., Wang, S., Zhang, W., Du, L., Xiao, L., Zhang, H., Shi, Y., Li, H., Sun, B., & Sun, H. (2025). +RNA Viruses Enhance Plant Drought Tolerance through Modulation of Phospholipase Dα1 (PLDα1)-Derived Phosphatidic Acid (PA). *Plant, Cell & Environment*, *48*(9), 6552-6567. https://doi.org/10.1111/pce.15637

Lindqvist-Kreuze, H., Bonierbale, M., Grüneberg, W. J., Mendes, T., De Boeck, B., & Campos, H. (2023). Potato and sweetpotato breeding at the international potato center: approaches, outcomes and the way forward. *TAG. Theoretical and applied genetics. Theoretische und Angewandte Genetik*, *137*(1), 12. https://doi.org/10.1007/s00122-023-04515-7

Liu, J., Liu, Y., Fang, Y., Zhang, L., Yu, K., Wu, X., & Cheng, X. (2021). Evaluation of potato virus X resistance in potato cultivars and identification of an innate immunity-independent resistance phenotype. *Phytopathology Research*, *3*(1), 21. https://doi.org/10.1186/s42483-021-00099-6

Manasseh, R., Berim, A., Kappagantu, M., Moyo, L., Gang, D.R. & Pappu, H.R. (2023). Pathogen-Triggered Metabolic Adjustments to Potato Virus Y Infection in Potato. *Frontiers in Plant Science*, *13*, 1031629. https://doi.org/10.3389/fpls.2022.1031629

Masoud, H.M.M., Abdel-Monsef, M.M., Helmy, M.S., Esa, S.S. & Darwish, D.A. (2025). Isolation and Characterization of Peroxidase from Potato Leaves. *Journal of Genetic Engineering and Biotechnology*, *23*, 100584. https://doi.org/10.1016/j.jgeb.2025.100584

Ministry of Agriculture of the Republic of Kazakhstan (2024). Potato Stocks Sufficient to Fully Cover Domestic Demand. Official Information Source of the Prime Minister of the Republic of Kazakhstan. Available online: https://primeminister.kz/en/news/ministry-of-agriculture-potato-stocks-sufficient-to-fully-cover-domestic-demand-29586

Murtaza, A., Khan, A.H., Imtiaz, M., Ali, L., Noor, L., Shahid, M.A., & Alim, M. (2026). Integrated genetic and disease management strategies in fruit and vegetable crops. *Medicinal Plant Letters*, *2*, 1–14. https://doi.org/10.65822/j.mpl/2026.001

Mushtaq, N., Younas, A., Qaisar, U., Jabeen, Z., Shahzad, A., Rashid, M., Khan, M.A., Zafar, S. & Khan, A.A. (2021). Genome-Wide Analysis, Identification, Evolution and Genomic Organization of the Dehydration-Responsive Element-Binding (DREB) Gene Family in *Solanum tuberosum*. *PeerJ.*, *9*, e11647. https://doi.org/10.7717/peerj.11647

Nasir, M. & Toth, Z. (2022). Effect of Drought Stress on Potato Production: A Review. *Agronomy*, *12*, 635. https://doi.org/10.3390/agronomy12030635

Ospankulova, G., Khassanov, V., Kamanova, S., Toimbayeva, D., Saduakhasova, S., Bulashev, B., Aidarkhanova, G., Yermekov, Y., Murat, L., Shaimenova, B., Muratkhan, M. & Li, W. (2023). Effect of Infection of Potato Plants by Potato Virus Y (PVY), Potato Virus S (PVS), and Potato Virus M (PVM) on Content and Physicochemical Properties of Tuber Starch. *Food Science & Nutrition*, *11*(7), 4002-4009. https://doi.org/10.1002/fsn3.3386

Pagliarani, C., Moine, A., Chitarra, W., Nerva, L., Catoni, M., Tavazza, R., Matić, S., Vallino, M., Secchi, F., & Noris, E. (2022). The C4 protein of tomato yellow leaf curl Sardinia virus primes drought tolerance in tomato through morphological adjustments. *Horticulture Research*, *9*, uhac164. https://doi.org/10.1093/hr/uhac164

Prakash, V., Sharma, V., Devendran, R., Prajapati, R., Ahmad, B. & Kumar, R. (2024). A transition from enemies to allies: how viruses improve drought resilience in plants. *Stress Biology, 4*(1), 33. https://doi.org/10.1007/s44154-024-00172-y

Rakesh, V., Rajesh, V., Jeevalatha, A. & Ghosh, A. (2024). Relationship of Potato Viruses with Aphid and Whitefly Vectors. In Approaches for Potato Crop Improvement and Stress Management; *Springer*: Singapore; pp. 249-287. https://doi.org/10.1007/978-981-97-1223-6_9

Riseh, R.S., Fathi, F., Vatankhah, M. & Kennedy, J.F. (2024). Catalase-Associated Immune Responses in Plant-Microbe Interactions. *International Journal of Biological Macromolecules*, 280, 135859. https://doi.org/10.1016/j.ijbiomac.2024.135859

Ross, B.T., Zidack, N., McDonald, R. & Flenniken, M.L. (2022). Transcriptome and Small RNA Profiling of Potato Virus Y Infected Potato Cultivars, Including Systemically Infected Russet Burbank. *Viruses*, *14*, 523. https://doi.org/10.3390/v14030523

Sacco Botto, C., Matić, S., Moine, A., Chitarra, W., Nerva, L., D'Errico, C., Pagliarani, C., & Noris, E. (2023). Tomato Yellow Leaf Curl Sardinia Virus Increases Drought Tolerance of Tomato. *International Journal of Molecular Sciences*, 24(3), 2893. https://doi.org/10.3390/ijms24032893

Sadau, S.B., Liu, Z., Ninkuu, V., Guan, L. & Sun, X. (2024). DREB Transcription Factors Are Crucial Regulators of Abiotic Stress Responses in *Gossypium* spp. *Plant Stress*, *11*, 100350. https://doi.org/10.1016/j.stress.2024.100350

Saleem, M.H., Wang, X., Parveen, A., Perveen, S., Mehmood, S., Fiaz, S., Ali, S., Hussain, S., Adnan, M., Iqbal, N., Alatawi, A. & Ali, S. (2022). Alleviation of drought stress by root-applied thiourea is related to elevated photosynthetic pigments, osmoprotectants, antioxidant enzymes, and tubers yield and suppressed oxidative stress in potatoes cultivars. *PeerJ, 10*, e13121. https://doi.org/10.7717/peerj.13121

Shonazarova, N.I., Eshboev, F.B. & Fayziev, V.B. (2025). Identification of Symptoms of Potato Virus Y in Indicator Plants. *Modern Biology and Genetics*, *2*(12), 29-38. https://cyberleninka.ru/article/n/identification-of-symptoms-of-potato-virus-y-pvy-in-indicator-plants

Sinton, S.M., Falloon, R.E., Jamieson, P.D., Meenken, E.D., Shah, F.A., Brown, H.E., Dellow, S.J., Michel, A.J. & Fletcher, J.D. (2022). Yield Depression in New Zealand Potato Crops Associated with Soil Compaction and Soil-Borne Diseases. *American Journal of Potato Research*, *99*, 160-173. https://doi.org/10.1007/s12230-022-09864-5

Sun, C., Liang, W., Yan, K., Xu, D., Qin, T., Fiaz, S., Kear, P., Bi, Z., Liu, Y., Liu, Z., Zhang, J. & Bai, J. (2022). Expression of Potato StDRO1 in Arabidopsis Alters Root Architecture and Drought Tolerance. *Frontiers in Plant Science, 13*, 836063. https://doi.org/10.3389/fpls.2022.836063

Tatarowska, B., Plich, J., Milczarek, D. & Flis, B. (2020). Temperature-Dependent Resistance to Potato Virus M in Potato (*Solanum tuberosum*). *Plant Pathology*, *69(8)*, 1445-1452. https://doi.org/10.1111/ppa.13245

Ul Ain-Ali, Q., Ali, M., Hussain, S., Khan, M.A., Shahzad, A. & Khan, A.A. (2024). Cloning and Overexpression of the *DREB30* Gene Enhances Drought and Osmotic Stress Tolerance in Transgenic Potato. *Journal of Plant Interactions, 19*(1), 2364656. https://doi.org/10.1080/17429145.2024.2364656

Uraji, M., Katagiri, T., Okuma, E., Ye, W., Hossain, M.A., Masuda, C., Miura, A., Nakamura, Y., Mori, I.C., Shinozaki, K. & Murata, Y. (2012). Cooperative Function of PLDδ and PLDα1 in Abscisic Acid-Induced Stomatal Closure in *Arabidopsis*. *Plant Physiology, 159*(1), 450-460. https://doi.org/10.1104/pp.112.195578

Verchot, J. (2022). Potato Virus X: A Global Potato-Infecting Virus and Type Member of the Potexvirus Genus. *Molecular Plant Pathology*, *23*, 315-320. https://doi.org/10.1111/mpp.13163

Von Dahlen, J.K., Schulz, K., Nicolai, J. & Rose, L.E. (2023). Global Expression Patterns of R-Genes in Tomato and Potato. *Frontiers in Plant Science, 14*, 1216795. https://doi.org/10.3389/fpls.2023.1216795

Weber, E.L., Busse, J.S. & Bethke, P.C. (2021). Current-Season Infection with Ordinary and Recombinant Strains of Potato virus Y Has Detrimental Effects on Chipping Potato Yield and Tuber Quality. *Plant Disease*, *105*(2), 450-455. https://doi.org/10.1094/PDIS-06-20-1281-RE

Xu, H., D'Aubin, J. & Nie, J. (2010). Genomic variability in potato virus M and the development of RT-PCR and RFLP procedures for the detection of this virus in seed potatoes. *Virology Journal*, *7*, 25. https://doi.org/10.1186/1743-422X-7-25

Yang, X., Liu, J., Xu, J., Duan, S., Wang, Q., Li, G. & Jin, L. (2019). Transcriptome Profiling Reveals Effects of Drought Stress on Gene Expression in Diploid Potato Genotype P3-198. *International Journal of Molecular Sciences*, *20*(4), 852. https://doi.org/10.3390/ijms20040852

Yusubakhmedov, A.A., Fayziev, V.B., Adilov, B., Makhmudov, T.Kh., Abduvaliev, B.A., Kurganov, S.K., Bekmatova, E.E., Temirov, A.A., Erdanaeva, S.P. & Atabaeva, D.T. (2024). Molecular Identification of Potato Virus M Isolate PVM-UZay1 with Coat Protein (CP) Gene and Phylogenetic Analysis. *SABRAO Journal of Breeding and Genetics*, *56*(5), 1769-1777. https://doi.org/10.54910/sabrao2024.56.5.2

Zaki, H.E.M. & Radwan, K.S.A. (2022). Response of Potato Cultivars to Drought Stress under *In Vitro* and Field Conditions. *Chemical and Biological Technologies in Agriculture, 9*, 1. https://doi.org/10.1186/s40538-021-00266-z

Zhao, W., Wang, L., Liu, M., Zhang, D., Andika, I.B., Zhu, Y. & Sun, L. (2022). A Reduced Starch Level in Plants at Early Stages of Infection by Viruses Can Be Considered a Broad-Range Indicator of Virus Presence. *Viruses*, *14*(6), 1176. https://doi.org/10.3390/v14061176

Zhou, H., Zhao, L., Song, Y., Du, X., Huo, J., Mei, W., Wang, X., Feng, N., Zheng, D., & Wu, Z. (2025). Changes in Antioxidant and Photosynthetic Capacity in Rice under Different Substrates. *Biology*, *14*(1), 34. https://doi.org/10.3390/biology14010034

Zhu, M., Feng, M., & Tao, X. (2025). NLR-mediated antiviral immunity in plants. *Journal of integrative plant biology*, *67*(3), 786-800. https://doi.org/10.1111/jipb.13821