https://doi.org/10.46341/PI2023011
UDC 574.24 + 581.19 : 581.524.13 + 58.006 (477)

RESEARCH ARTICLE

Biochemical and allelopathic features of *Adonis vernalis, Allium ursinum,* and *Leucojum vernum* in the M.M. Gryshko National Botanical Garden of the NAS of Ukraine

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Received: 21.11.2023 | **Accepted**: 07.02.2024 | **Published online**: 17.02.2024

Abstract

The article presents the results of a study on the content and dynamics of the accumulation of biogenic elements and brassinolides in plants of *Adonis vernalis, Allium ursinum*, and *Leucojum vernum* in Kyiv, Ukraine. Data is provided on allelopathic activity, content of macro- and microelements, phenolic compounds, and laccase activity in plants and the rhizosphere soil under the conditions of the M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine (NBG). The plants from the collection of the NBG were used as objects of study in field experiments. The content of biogenic elements in plant tissues and soil was analyzed using an inductively coupled plasma spectrometer. The allelopathic analysis of soil was conducted using a direct bioassay method with *Lepidium sativum* seedlings as the test object. Phenolic compounds were extracted from the soil using the ion exchange (desorption) method. The content of brassinosteroids was measured spectrophotometrically at a wavelength of 450 nm. The content of laccase was measured spectrophotometrically at a wavelength of 530 nm.

The results demonstrate that model plant species employ a wide range of physiological mechanisms throughout the vegetation period to enhance their resistance to abiotic factors. These mechanisms include maintaining potassium and calcium balance and utilizing hormonal compounds. Plants have been proven to have compensatory mechanisms in response to stress factors, substituting one biochemical marker of resistance with another. Both, brassinosteroids and silicon, contribute to the adaptive capacity of organisms.

Keywords: biogenic elements, phenolic compounds, laccase, brassinolides, plant adaptation, phytohormones

Authors' contributions: Nataliia Zaimenko developed the research concept, designed the experiments, wrote, revised and proved the manuscript, analyzed literary sources, and interpreted the experimental data results. Gnatiuk A. and Gritsenko V. grew plants (objects of study), collected and delivered samples for experiments. Zakrasov O., Dziuba O., Pavliuchenko N., Kharytonova I., Didyk N., Yunosheva O., Blum O., Likhanov A., and Holichenko N. were engaged in the preparation and conduct of the analyzes, writing methodological part of the research, interpreted the results and presented the results of experiments, created figures and tables. Zakrasov O. realized statistical data processing. Blum O., Gritsenko V. revised and redacted the text. Gnatiuk A. coordinated the writing of the manuscript, combined experimental data, and prepared the manuscript for publishing. All authors approved the manuscript for publication.

Funding: This research was supported by the target program of scientific research "The Role of Biogenic Elements in Inducing Brassinosteroid Synthesis for Enhancing Plant Resistance to Stress Factors" for 2021–2022.

Competing Interests: Authors declared that they have no conflict of interest.

Introduction

Studying the bioecological characteristics of rare plants has theoretical and practical significance for better understanding the reasons for their disappearance and creating optimal conditions for their conservation. Plant introduction in botanical gardens allows for in-depth studies of biological, ecological, and biochemical features of species with different life forms (Zaimenko & Rakhmetov, 2022).

To overcome adverse environmental factors, plants develop special adaptive systems that enable them to respond appropriately to various ecological influences (Chung et al., 2022). Among the survival and adaptation strategies that plants employ during evolution and in response to changing environmental conditions, they exhibit morphological, physiological, biochemical changes, and molecular reactions. These adaptations are realized through various pathways, including the synthesis of specific phytohormones. Phytohormones play a crucial role in the plant's response to internal and external stimuli, including stressors. In recent decades, the term 'stress phytohormones' has become established in scientific literature. Stress phytohormones, among others, include brassinosteroids (Kolupaev et al., 2016; Kosakivska et al., 2019). Brassinosteroids enhance plant resistance to environmental stress factors, reduce the toxic effects of heavy metals, and strengthen the antioxidant defense system (Kosakivska et al., 2019).

Currently, brassinolide is considered the most active representative of brassinosteroids. Brassinolide is a plant hormone that plays a key role in plant growth and development as it regulates numerous physiological processes, including proton pump activity, cell and shoot growth, leaf architecture, biosynthesis of ethylene and pigments, photosynthesis, stress responses, and more (Golovatskaya & Nikonorova, 2008; Nolan et al., 2020; Ghassemi-Golezani et al., 2020).

Research on the ecology of nutrients has become of enormous importance as it is known that mineral compounds are rarely found in different soils in optimal quantity. At the same time, a balanced ratio is essential for plant growth and development. Plants always compensate for the influence of stress factors through nutrition and subsequent physiological adaptations to the external environment (Zaimenko, 2008). Micro- and macroelements are the most important catalysts of various biochemical processes in plant cells. They regulate photosynthetic activity, participate in biochemical exchanges, and play a significant role in plant resistance to drought, frost, and diseases.

Soils vary in nutrient content, which, in turn, influences the specific chemical composition of plants and determines their growing success. The potential for nutrient uptake depends on the actual need of plants for biogenic elements that support growth functions. On the other hand, different tissues accumulate only a certain amount of nutrients. Research on the absorption of mineral elements and their content in plants shows that these indicators can determine plant adaptation to stress factors (Ivanitska & Zaimenko, 2008). For example, it has been found that potassium deficiency leads to an increase in root diameter, while phosphorus deficiency increases their volume (Zaimenko et al., 2005). Changes in soil pH towards alkaline or acidic reactions reduce the uptake of almost all macro- and micronutrients by plants, except for nitrogen (Ivanitska & Zaimenko, 2008).

Enzymes such as laccases, which can catalyze the oxidation of a wide range of organic and inorganic substrates, also play a vital role in plants' life (Baldrian, 2006). Laccases were found in many species of plants, fungi, and microorganisms (Thurston, 1994). Once in the soil, laccases participate in the transformation of organic matter entering the soil contributing to the formation of humus and other humus-like substances (Zavarzina et al., 2004; Eichlerová et al., 2012).

One of the most significant problems today is the contamination of soils with heavy metals, which negatively affect plant morphological structure (Zhang et al., 2011), plant growth and development (Kosakivska et al., 2019), photosynthesis activity (Mathur et al., 2016), transport of organic and mineral compounds (Zhao et al., 2012), and water exchange (Mukhopadhyay & Mondal, 2015). In this regard, aluminum is essential in providing plants with biogenic elements as it forms stable soluble complexes with natural organic acids. The formation of humic and fulvic complexes of aluminum in the soil is determined mainly by the distribution of natural organic substances in the soil profile (Tyutyunnik et al., 2007). The most phytotoxic effect of aluminum is the inhibition of root growth. The phytotoxicity of aluminum is enhanced in combination with iron ions, aluminum, and manganese, as well as in the absence of phosphorus, calcium, magnesium, and molybdenum in the soil (Kovalevsky, 2011).

Conversely, silicon deserves attention as one of the most abundant chemical elements in the Earth's crust. It is present in clay minerals and silicates. In the soil, silicon in its ionic form acts as a catalyst in the conversion processes of macro- and micronutrient compounds, facilitating their transition from insoluble forms to forms accessible to plants. Under such conditions, the plant's consumption of necessary micronutrients from the soil significantly increases. Silicon plays a positive role in plant development under normal conditions and in response to adverse environmental factors, stimulating mechanisms of stability and plasticity (McGinnity, 2015; Frew et al., 2018). It has been found that under drought and soil salinity conditions, there is active root absorption of silicon from the soil, leading to increased silicon content in leaves (Nedukha, 2019).

It is worth noting that allelopathic activity is inherent in practically all plants and indirectly affects their biochemical composition. Biologically active compounds of above-ground parts (including seeds and fruits) and root exudates determine the level of allelopathic activity. Alkaloids, which are crucial for the chemical defense of plants against phytopathogenic microorganisms, play a significant allelopathic role in root exudates (Wink, 2008). In addition, high content of alkaloids in seeds, fruits, bulbs, and root residues inhibits seed germination and plant growth and development (Rice, 1978; Grodzinsky, 1987; Levchyk et al., 2021). Physiologically active plant exudates influence metabolic processes, resulting in either stimulation or inhibition of growth processes. Among water-soluble compounds adsorbed by the soil, phenolic acids, such as p-coumaric, hydroxycinnamic, vanillic, ferulic, and hydroxybenzoic acids, play a significant role in allelopathic interactions of the plants (Grodzinsky, 1973).

We did not find any data in the literature regarding the content of biogenic elements in tissues of *Adonis vernalis* L. and *Leucojum vernum* L., in particular, with respect to the soil. The available information on such topic for *Allium ursinum* L. (Tymochko & Hrynyk, 2015) requires supplementation. There is no information regarding the content of brassinosteroids in *A. vernalis*, *A. ursinum*, and *L. vernum* plants, and there is no data on the enzymatic activity of the rhizospheric soil. Information on the allelopathic activity of these plants is fragmented (Dragoeva et al., 2015; Kachalova & Dzyuba, 2014; Levchyk et al., 2021).

Adonis vernalis, *A. ursinum*, and *L. vernum* are rare species listed in the Red Book of Ukraine (Didukh, 2009). They are decorative spring-flowering herbaceous perennials of different ecomorphotypes. *Adonis vernalis* is a steppic species with a short rhizome. *Allium ursinum* is a forest species, and *L. vernum* is a forest-meadows species, both with bulbs. In the M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine (NBG), these three species formed stable populations in *ex situ* conditions. Recently, various botanical studies of *A. vernalis* (Gritsenko, 2023) and *L. vernum* (Gnatiuk & Gaponenko, 2023) were implemented, and the study of *A. ursinum* is ongoing at the NBG. Therefore, the investigation of biochemical and allelopathic properties of these species is prioritized.

Hence, this research aimed to investigate the dynamics of accumulation of biogenic elements and brassinosteroids in plants, determine allelopathic activity, phenolic compounds, and laccase activity in the rhizosphere soil of *A. vernalis*, *A. ursinum*, and *L. vernum* in the conditions of the NBG.

Material and methods

The plants of *A. vernalis*, *A. ursinum*, and *L. vernum* from the collection of the Natural Flora Department of the NBG (Fig. 1) were selected for the field experiments.

Adonis vernalis (Ranunculaceae) is a Euro-Siberian forest-steppe species. In Ukraine, it is mainly associated with meadow steppes and is classified as a mesoxerophyte (Didukh, 2009). The plant is ornamental. Its parts, especially the

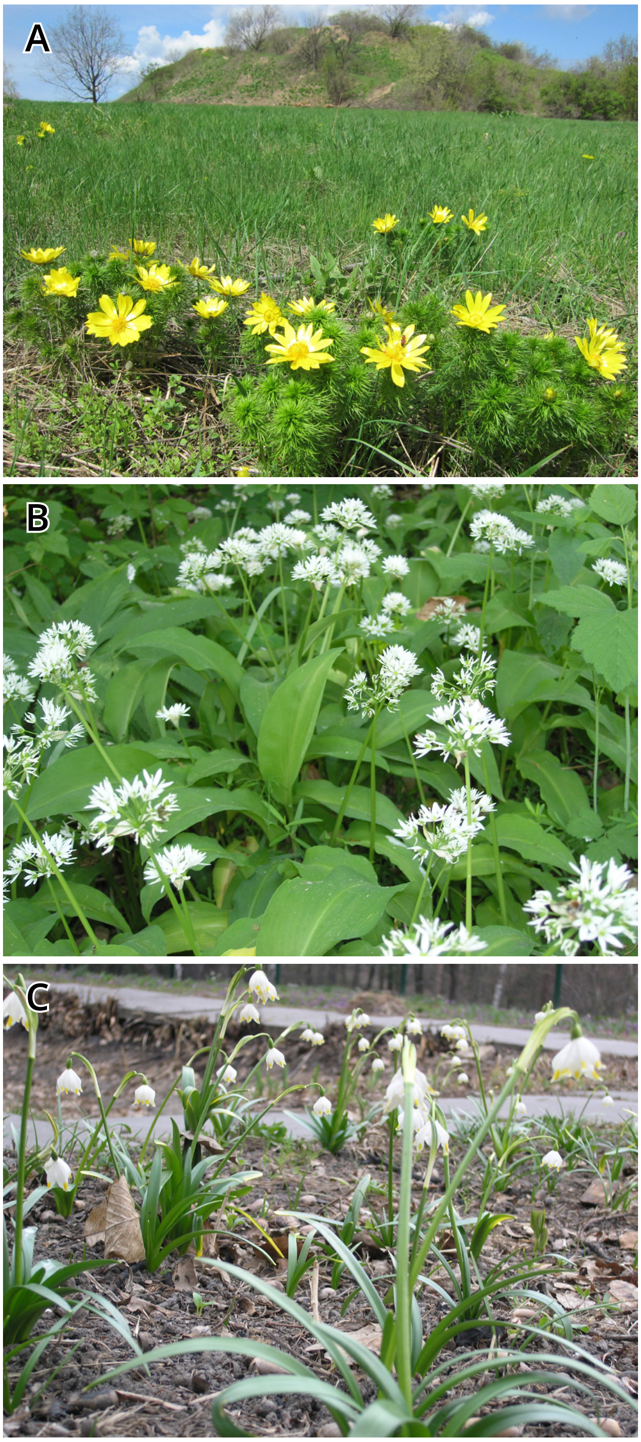

Figure 1. *Adonis vernalis* (**A**), *Allium ursinum* (**B**), and *Leucojum vernum* (**C**), in the M.M. Gryshko National Botanical Garden (Kyiv, Ukraine). Photo credits: **A** – Victoria Gritsenko; **B & C** – Alla Gnatiuk.

above-ground shoots, are used for medicinal purposes (Colalto, 2020). They contain cardiac glycosides, including adonitoxin, cymarin, K-strophanthin-β, acetyladonitoxin, adonitoxol, vernadigine, and others. The herb also contains genins such as β-strophanthidin, strophadogenin, acetyl-strophadogenin, and flavonoids like adonivernit, vitexin, homoadonivernit, phytosterol, adonit alcohol, and others (Grodzinsky, 1989; Shang et al., 2019; Sattari et al., 2020). It demonstrated allelopathic activity (Dragoeva et al., 2015).

Allium ursinum (Alliaceae) is a Central European forest species with a disjunct distribution, geophyte, and mesophyte. In Ukraine, it often acts as a dominant species in natural populations of early spring herbaceous cover in forests (Didukh, 2009). The plant is used as food and applied in folk medicine (Hanelt et al., 1992; Shirataki et al., 2001; Schulz et al., 2003). It contains proteins, carbohydrates, cellulose, organic acids, carotene, vitamins (B group and C), lysozyme, and essential oil. The strong garlic-like aroma is due to the presence of sulfur-containing compounds. It contains steroidal saponins, pregnane glycoside, polysaccharides, lectins, fatty acids, and pigments (Sobolewska et al., 2006, 2015). It is a lectin-containing plant with high hemolytic activity and antibacterial and antifungal properties (Kachalova & Dzyuba, 2014).

Leucojum vernum (Amaryllidaceae) is a Central European species at the eastern edge of its range, geophyte and hygromesophyte. In Ukraine, it is most commonly found in broad-leaved forests of the lower mountain belt (Transcarpathia) and floodplain forests (Ciscarpathia region and plain territories) (Didukh, 2009). This toxic plant is ornamental and applied in folk medicine. It contains alkaloids N-desmethyl galantamine, hippeastrine, 9-O-demethylhomolycorine, 5-α-hydroxyhomolycorine, 11-hydroxyvittatine, lycorine, homolycorine, 2-O-acetyllycorine, leucovernine, acetylleucovernine (Straley & Utech, 2002; Forgo & Hohmann, 2005; Birks, 2006).

The botanical garden (NBG) is located in the Pechersk district, in South-Eastern part of Kyiv city. The area belongs to the Right-Bank Forest Steppe of Ukraine, a temperate climate zone. The gray forest soils with different textures dominate in the NBG. The artificial populations of *A. ursinum* and *L. vernum* are located in the collection plot “Rare species of Ukrainian flora”, having loamy-sandy soil with pH 6.0–6.5. At the same time, the population of *A. vernalis* is located in the botanical-geographical plot “Stepps of Ukraine”, having loamy soil with pH 5.6–6.8.

For analysis, plant samples and rhizosphere soil were collected using a standardized method (Zaimenko, 2021). The term 'rhizosphere soil' refers to the distal fraction of rhizospheric area adjacent to rhizoplan, still under roots' influence but without direct contact with them (Barillot et al., 2013). Plants and their associated soil samples were collected during the plant growing season: in May (during plants' flowering stage), August (for A. *vernalis* plants – fruiting stage; for A. *ursinum* and L. *vernum* plants – shoot senescence stage), and October (for A. *ursinum* and L. *vernum* plants – dormant stage; for A. *vernalis* plants – shoot senescence stage). To avoid damage to the population, the sampling of A. *ursinum* and L. *vernum* was not conducted in October when the plants reached the dormant stage. Soil lumps (ca. 200 cm^3) were collected from the plant root zone at 15–20 cm depth. Plants and soils were immediately transferred in polyethylene bags to avoid excessive desiccation during transportation and stored at 4–6 °C.

The preparation of the soil samples for the analysis of the biogenic elements content was carried out according to the Rinkis & Nolendorf (1982) method. Acid-soluble forms of heavy metals and other chemical elements were extracted using a 1.0 N solution of nitric acid (HNO_3). Preparation of plant samples for analysis was carried out by wet ashing with a solution of nitric acid of high purity using Speedwave Xpert DAP-60X (Berghof, GmbH, Germany), a special system of microwave decomposition of samples. Concentrations of chemical elements in the solution were measured on an ICAP 6300 DUO plasma emission spectrometer (Thermo Fisher Scientific, USA). The content of chemical elements was calculated on the air-dry weight of plant samples and expressed as μg/kg. The relative uncertainty (Ellison & Williams, 2012) ranged from 7 % to 12 % (it was different for different chemical elements). Internal laboratory control of the accuracy of the measurement results was carried out using a standard certified sample of moss M2 (Moss Reference Material M2, *Pleurozium schreberi* – The Finnish Forest Research Institute), using the compatibility criterion.

The allelopathic analysis of soil was conducted using a direct bioassay method with cress seedlings (*Lepidium sativum* L.) as the test object (Zaimenko, 2021). Phenolic compounds were extracted from the soil using the ion exchange (desorption) method, utilizing the ion exchanger KU-2-8 (H^+) as a model of the root system with desorbing and absorbing capacity towards mobile organic compounds (Zaimenko, 2021).

For the analysis of endogenous brassinosteroids, plant samples (leaves of A. *vernalis* and bulbs of A. *ursinum* and L. *vernum*) were transferred to a dark climatic chamber at a temperature of −8 °C. The extraction was carried out in two stages: the first stage with ethyl acetate (three times, 5 ml each) from the aqueous tissue extract (1 g tissue + 5 ml extraction solution). The ethyl acetate fraction was evaporated under vacuum, and the residue was extracted with cyclohexane (5 ml). The second stage of extraction was performed using a mixture of ethanol and water (4 : 1) (three times, 5 ml each) from the phase containing cyclohexane. The ethanol extract was evaporated under vacuum, and the residue was dissolved in a small amount of ethyl acetate. The content of brassinosteroids was measured spectrophotometrically at a wavelength of 450 nm (Kravets et al., 2011) using a spectrophotometer SPECORD 200 (Analytik Jena, Germany, 2003).

Laccase activity was determined by measuring the rate of syringaldazine oxidation in the soil extract. Measurements were conducted on a spectrophotometer at a wavelength of 530 nm (Baldrian, 2009) using a spectrophotometer SPECORD 200 (Analytik Jena, Germany, 2003).

The research results were analyzed using mathematical methods of parametric statistics at a significance level of 95 %. The groups of values were compared using the Mann-Whitney U-test, which is used to evaluate differences between two independent samples and allows detecting differences in parameter values between small samples for $P \leq 0.05$.

The work was carried out at NBG as part of the research project "The role of biogenic elements in inducing brassinosteroid synthesis for enhancing plant resistance to stress factors".

Table 1. The content and dynamics of biogenic elements in the leaves of *Adonis vernalis* and the surrounding rhizosphere soil, mg/kg ± U (*k* = 2, *P* = 0.95).

Chemical element	Soil			Plant		
	May	August	October	May	August	October
Al	11995.0±1032.8	13440.0±41.5	17070.0±1484.9	116.0±11.2	159.0±13.5	231.0±20.4
B	7.08±0.6	7.16±0.6	11.30±1.1	19.33±1.7	23.89±2.1	28.82±2.3
Ca	3104.0±273.5	5771.0±574.9	6254.0±560.1	32335.0±3115.2	27450.0±2559.2	26750.0±2445.2
Cu	15.8±1.2	24.4±2.1	21.5±1.7	9.5±0.8	11.4±1.1	9.9±0.7
Fe	8635.0±397.9	7980.0±1797.6	7496.0±319.0	97.0±4.3	79.2±3.8	168.4±12.7
K	2346.0±159.2	3783.0±451.9	3092.0±197.1	11177.0±1935.9	27410.0±1717.3	9330.0±539.8
Mg	1520.0±99.6	5945.0±358.7	1548.0±112.9	3476.0±201.5	2598.0±237.4	3791.0±236.7
Mn	284.8±17.6	311.1±0.9	336.3±22.8	22.2±1.9	30.1±2.3	45.8±2.3
P	384.0±18.6	323.0±20.3	433.0±27.5	1608.0±128.2	1695.0±103.5	539.2±27.3
S	345.0±31.6	492.0±49.1	405.0±37.7	2238.0±197.7	3818.0±369.2	1039.0±95.4
Si	1438.0±98.4	1062.0±92.3	837.0±33.6	247.0±10.6	568.0±23.2	819.0±49.8
Zn	47.0±2.3	30.0±1.9	46.0±2.5	14.0±0.8	25.0±0.7	12.0±0.6

Results

The analysis of the content of chemical elements in the soil under A. *vernalis* plants (Table 1) revealed significant amounts of Al and Fe at the beginning and end of the vegetation period of plants. The peak values of aluminum content were recorded in October (17070.0 mg/kg in the soil and 231.0 mg/kg in the plant). The highest iron content was observed in May (8635.0 mg/kg in soil) and in October (168.4 mg/kg in plant). *Adonis vernalis* plants demonstrated the highest content of Ca and K. The calcium content in plants (32335.0 mg/ kg) at the beginning of the vegetation period was almost ten times higher than in the soil (3104.0 mg/kg). The maximum concentration of potassium in plants (27410.0 mg/kg) was detected in August, which exceeds its content in the soil (3783.0 mg/kg) in over seven times. From May to October, plants accumulated Mn (its content increased from 22.2 mg/kg to 45.8 mg/kg) and Si (its content increased from 247.0 mg/kg to 819.0 mg/kg).

The distribution of chemical elements in the soil under A. *ursinum* plants also revealed the highest content of Al (8327.0 mg/kg) in May, which gradually decreased by October. The maximum iron content in the soil was observed in May (8016.0 mg/kg). *Alium ursinum* plants had the highest content of K, Ca and S. From May to August, plants actively accumulated Al, K, Mn, and Zn. The plants mainly accumulated K; its content increased from 3299.0 mg/kg in May to 11510.0 mg/kg in August. The calcium content in the plants did not increase so much – from 1860.0 mg/kg in May to 2810.0 mg/kg in August (Table 2).

The rhizosphere soil under L. *vernum* plants had a high content of Ca (10510.0 mg/ kg) and Al (9975.0 mg/kg) in October. In plants, potassium had the leading position; its content in August was the highest and reached 8957.0 mg/kg. From May to August, plants accumulated Al, Cu, Fe, Mn, S, Si, and Zn. The content of these elements had increased in several times (Table 3).

The analysis of chemical elements content in plant tissues (Tables 1–3) of the studied species revealed several general trends. The accumulation of silicon in plants showed a similar pattern until the end of the vegetation period. Compared to the beginning of the vegetation period, the content of Si in plants increased by 3.3 times in A. *vernalis*, by 1.1 times in A. *ursinum*, and by 8.8 times in L. *vernum*. Also, all studied species accumulated Mn during the vegetation season and K from May to August. During this period, the potassium content in plants increased by 2.5 times in A. *vernalis*, by 3.5 times in A. *ursinum*, and by 1.7 times in L. *vernum*.

Table 2. The content and dynamics of biogenic elements in the bulbs of *Allium ursinum* and the surrounding rhizosphere soil, mg/kg ± U (k = 2, P = 0.95).

Chemical element	Soil			Plant	
	May	August	October	May	August
Al	8327.0 ± 403.4	8222.0 ± 452.8	6201.0 ± 301.9	94.0 ± 8.23	342.0 ± 21.3
B	5.4 ± 0.4	6.5 ± 0.5	7.9 ± 0.7	6.8 ± 0.5	9.3 ± 0.8
Ca	3755.0 ± 121.5	2318.0 ± 121.7	16.2 ± 0.9	1860.0 ± 114.1	2810.0 ± 137.4
Cu	19.5 ± 1.7	22.3 ± 1.7	22.4 ± 1.9	9.5 ± 0.9	14.3 ± 1.1
Fe	8016.0 ± 1.3	6426 ± 351.6	3657.0 ± 198.4	59.1 ± 3.6	30.0 ± 7.1
K	1596.0 ± 98.0	1440.0 ± 103.7	1153.0 ± 98.7	3299.0 ± 285.9	11510.0 ± 534.7
Mg	1173.0 ± 85.3	1005.0 ± 78.7	957.0 ± 6.4	588.0 ± 41.2	1068.0 ± 71.3
Mn	246.0 ± 19.3	312.7 ± 21.0	204.5 ± 15.2	7.87 ± 0.3	17.06 ± 1.2
P	255.0 ± 13.9	224.0 ± 12.7	263.0 ± 15.9	1250.0 ± 97.9	1999.0 ± 111.3
S	209.0 ± 12.8	335.0 ± 18.6	281.0 ± 14.3	2518.0 ± 126.4	2539.0 ± 130.3
Si	1217.0 ± 10.8	1452.0 ± 11.7	881.0 ± 14.9	696.0 ± 4.7	730.0 ± 21.4
Zn	73.0 ± 2.9	25.0 ± 1.2	20.0 ± 0.8	7.0 ± 0.3	41.0 ± 1.5

Table 3. The content and dynamics of biogenic elements in the bulbs of *Leucojum vernum* and the surrounding rhizosphere soil, mg/kg ± U (k = 2, P = 0.95).

Chemical element	Soil			Plant	
	May	August	October	May	August
A1	6379.0 ± 59.7	7032.0 ± 64.2	9975.0 ± 93.8	63.0 ± 3.2	491.0 ± 18.3
B	4.3 ± 0.1	7.7 ± 0.3	6.5 ± 0.2	6.8 ± 0.3	6.8 ± 0.2
Ca	2931.0 ± 27.4	8482.0 ± 78.7	10510.0 ± 119.3	819.0 ± 24.3	1558.0 ± 63.8
Cu	27.84 ± 1.2	21.32 ± 1.1	20.08 ± 0.1	8.6 ± 0.4	19.9 ± 1.1
Fe	5475.0 ± 122.9	125.0 ± 4.5	4595.0 ± 218.3	49.0 ± 1.7	399.0 ± 12.8
K	1179.0 ± 49.6	2717.0 ± 84.4	1522.0 ± 52.8	5193.0 ± 176.2	8957.0 ± 98.2
Mg	896.0 ± 37.5	1762.0 ± 65.0	911.0 ± 44.7	618.0 ± 29.5	889.0 ± 39.1
Mn	198.7 ± 8.3	87.34 ± 4.2	238.6 ± 10.6	5.40 ± 0.3	21.03 ± 1.1
P	267.0 ± 11.6	201.0 ± 8.9	209.0 ± 9.1	1499.0 ± 15.6	2049.0 ± 77.8
S	277.0 ± 12.6	337.0 ± 17.4	165.0 ± 7.9	802.0 ± 29.5	5305.0 ± 186.7
Si	2035.0 ± 79.3	1515.0 ± 62.6	653.0 ± 27.4	107.0 ± 5.3	943.0 ± 28.6
Zn	23.0 ± 1.1	23.0 ± 0.9	38.0 ± 1.5	15.0 ± 0.7	35.0 ± 1.4

According to Tables 1–3, for each of the studied species, an increase in magnesium content in plants was observed from May until the completion of the vegetation period. The content of Mg in plant tissues increased by 1.1 times in *A. vernalis*, by 1.8 times in *A. ursinum*, and by 1.4 times in *L. vernum*. Similarly, the copper content in plant tissues of all studied species increased. However, the iron content increased only in *A. vernalis* and *L. vernum* plants, while in *A. ursinum* its content decreased almost in two times.

The obtained results of studying the allelopathic activity of soils under the experimental plant species are presented in Fig. 2. The allelochemicals in the rhizosphere

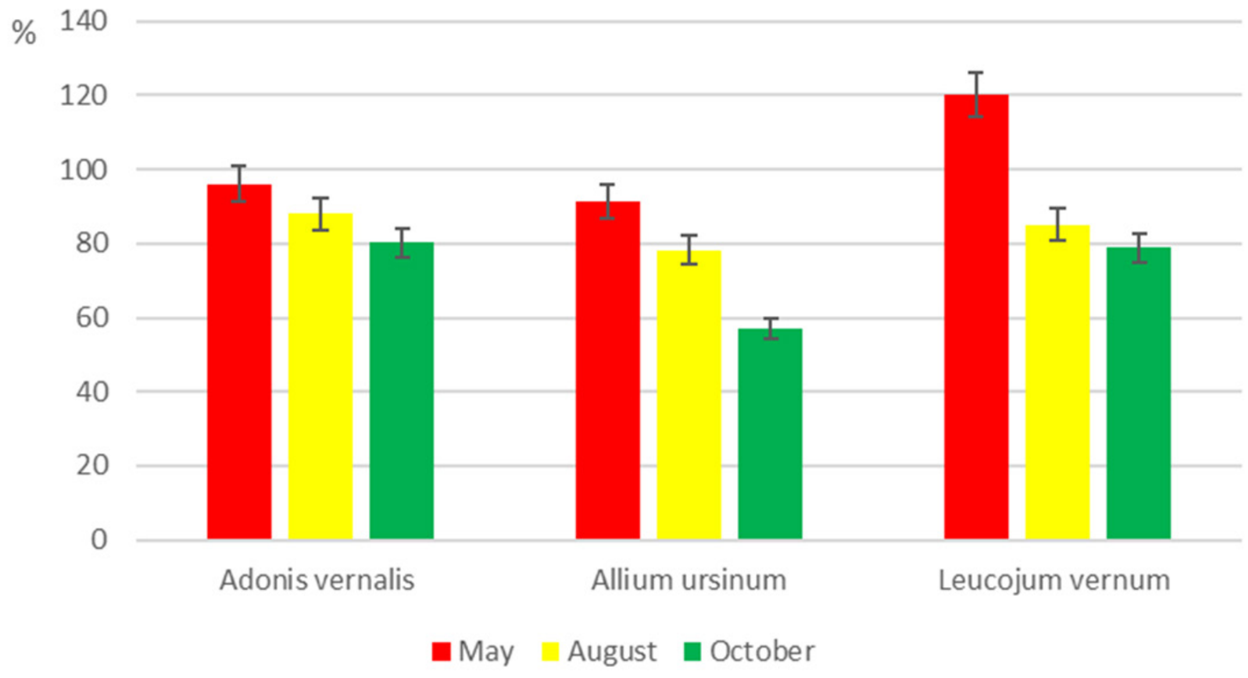

Figure 2. Allelopathic activity of soil under *Allium ursinum, Adonis vernalis*, and *Leucojum vernum* plants (bioassay – growth of *Lepidium sativum* roots). **Whiskers** indicate the standard deviation.

soil of *A. ursinum* exhibited phytotoxic effects at the end of the summer season (inhibited biotest growth by 21.7 % compared to the control), but had the most significant impact in autumn (43.0 % inhibition). During the summer period, the physiologically active compounds in the soil under *A. vernalis* showed a slight allelopathic effect with 11.9 % inhibition of root growth in the receptor plants compared to the control. In autumn, the allelopathic activity of the soil under *A. vernalis* slightly increased (19.8 % phytotoxic effect). There was a growth-stimulating effect (20.3 % compared to the control) of the allelochemicals in the soil under *L. vernum* in May. However, by early autumn, their allelopathic activity shifted towards inhibiting the growth processes of the receptor plants, which intensified towards the end of the vegetation period (14.9 % and 21.1 % inhibition compared to the control).

The dynamics of the accumulation of phenolic compounds in the soil under *A. ursinum* indicates a 1.5-fold increase in their content from spring to the end of the growing season (Fig. 3). Analogous results were obtained for the concentration of phenolic compounds in the soil under *A. vernalis*. The content of phenolic compounds in the soil under *L. vernum* also increased during the growing season. At the same time, their content in autumn was two times higher than in spring.

The maximum soil laccase activity was in spring, with a gradual decrease throughout the entire vegetation season (Fig. 4). It negatively correlated with the content of phenolic compounds in the soil.

The evaluation of brassinosteroid content in different plant organs of the studied species reveals noteworthy findings (Table 4). Certain patterns are observed in the distribution of brassinosteroids in leaves and bulbs. Specifically, a 2.1-fold increase in brassinosteroid content in *A. vernalis* leaves at the end of the vegetation period corresponds to a 3.3-fold increase in silicon concentration. In *A. ursinum* bulbs, a reverse relationship is observed: a 1.2-fold decrease in brassinosteroid concentration and a 7.6-fold increase in silicon concentration. A similar pattern is observed for *L. vernum* bulbs: a 19.0-fold reduction in brassinosteroid content and an 8.8-fold increase in silicon concentration.

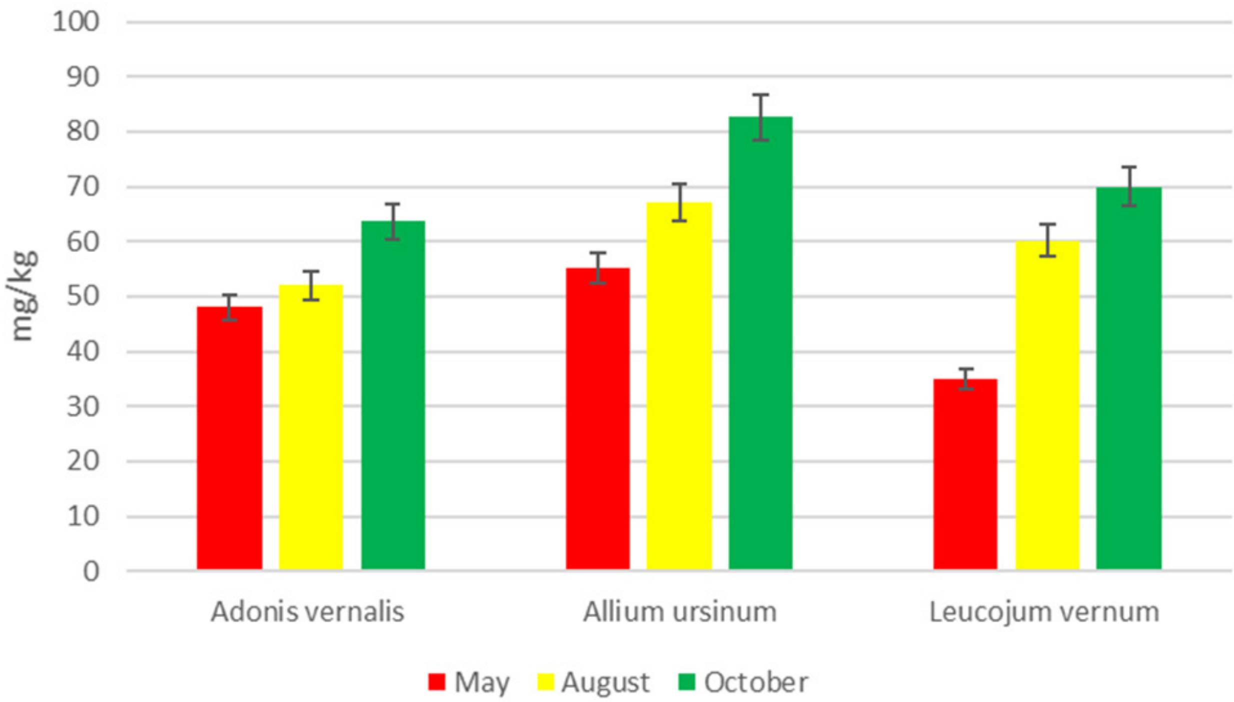

Figure 3. The content of phenolic compounds in the soil under *Allium ursinum, Adonis vernalis*, and *Leucojum vernum* plants. **Whiskers** indicate the standard deviation.

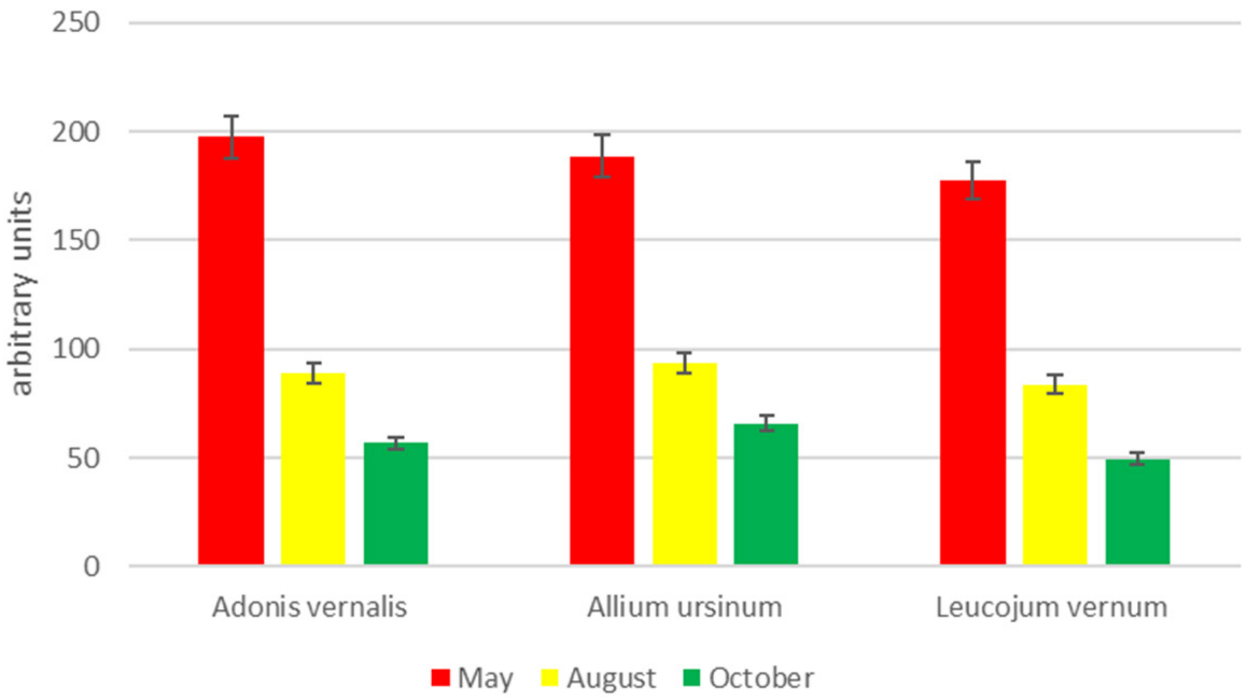

Figure 4. Soil laccase activity under *Allium ursinum, Adonis vernalis*, and *Leucojum vernum plants*. **Whiskers** indicate the standard deviation.

Table 4. The content of brassinosteroids and silicon in different organs of *Adonis vernalis, Allium ursinum,* and *Leucojum vernum*, mg/kg ± U (k = 2, P = 0.95).

Sampling date	Brassinosteroids			Silicon		
	Leaves	Bulbs	Bulbs	Leaves	Bulbs	Bulbs
	A. vernalis	*A. ursinum*	*L. vernum*	*A. vernalis*	*A. ursinum*	*L. vernum*
May	2.5 ± 0.21	2.6 ± 0.21	11.4 ± 0.09	247 ± 20.35	9.6 ± 0.80	107.0 ± 9.50
August	4.1 ± 0.33	2.1 ± 0.17	0.6 ± 0.05	568 ± 51.67	7.3 ± 68.70	943.0 ± 89.80
October	5.3 ± 0.49	-	-	819.0 ± 77.80	-	-

Discussion

The studied plant species differ significantly in their ecomorphotype. Comparative biochemical analysis revealed differences in the distribution of biogenic elements and brassinosteroids in their tissues. For all plants, there is an increase in the concentration of Al, Fe, Si, and Mn. However, bulbs show more pronounced fluctuations in the concentration of these elements than leaves. Notably, bulbs have higher contents of P, K, Ca, and Zn, which can be attributed to assimilation processes involved in plant preparation for dormancy. Calcium is one of the most important signaling molecules in plant cells under stress conditions, controlling processes that contribute to the homeostasis of various macroelements such as potassium, nitrogen, and magnesium, as well as the microelement iron (Wang et al., 2019; Kong et al., 2020; Dong et al., 2021; Liu et al., 2021; Ghosh et al., 2022). The functional role of Ca^{2+} in stress signaling and subsequent activation of tolerance mechanisms has been well established (Sharma et al., 2022). It is known that the perception of the environment and internal signals leads to changes in cytosolic Ca^{2+} signatures, which, in turn, results in gene expression changes and alterations in cellular functions (Wang et al., 2021; Verma et al., 2022).

On the other hand, magnesium is essential for a wide range of physiological and biochemical processes in plants, including chlorophyll synthesis, transport and distribution of photoassimilates, enzyme activation, and protein synthesis (Ishfaq et al., 2022). Potassium regulates the osmotic potential of plants and is crucial for maintaining water balance under stress conditions. Additionally, it plays a vital role in various aspects of plant life, such as photosynthesis, phloem transport, and cellular electrochemistry (Cui & Tcherkez, 2021; Kumari et al., 2021; Li et al., 2021; Lotfi et al., 2022).

Silicon modulates the expression of different genes in plants under stress, regulates the synthesis and accumulation of reactive forms of oxygen and nitrogen, and reduces the negative impact on photosynthesis. Silicon also activates the antioxidant defense system in plants, thereby maintaining cellular redox homeostasis and preventing oxidative damage to cells. It regulates H_2S synthesis or acts synergistically with NO, assuring stress tolerance in plants (Ahire et al., 2021; Basu & Kumar, 2021; Dhiman et al., 2021; Rastogi et al., 2021; Etesami & Jeong, 2023). Based on the abovementioned, the experimentally obtained relationship indicates the high resilience of plants to abiotic and biotic factors, particularly dehydration. Furthermore, the increase in Zn content in bulb tissues provides additional cold tolerance to the plants during winter.

The concept of nutrient availability for plants of different ecomorphotypes should be considered from two independent perspectives. According to the first perspective, in natural soil ecosystems, redistribution of mineral compounds occurs from inaccessible pools to available pools, which supply plants with chemical elements and determine their levels. Habitats significantly differ in the intensity of organic matter decomposition or mineral weathering processes. From the second perspective, the productivity of plants and the entire ecosystem is influenced by inadequate mineral nutrition, which determines the space where productivity decreases due to insufficient doses of nutrients that have been supplied (Zaimenko, 2008; Zaimenko et al., 2022).

Therefore, the concentration of macro- and micronutrients in the plant's tissues is the most reliable indicator of its chemical status. Currently, most hypotheses regarding the uptake of macro- and micronutrients (see Zaimenko, 2008; Zaimenko et al., 2022) are based on ion transport, including thermodynamic forces, characteristics of biological membrane structure and composition, specific chemical properties of elements considering their tendency to form complexes with organic ligands, sensitivity to redox processes, and pH changes.

In light of the mentioned above, research on the allelopathic activity of the soil becomes particularly relevant. All studied plant species exhibit the presence of physiologically active compounds with allelopathic properties in the adjacent rhizosphere soil. Overall, moderate-reductive processes prevail in the rhizosphere soil during the summer under all plants, while intensive-reductive processes dominate in the autumn. This trend is likely associated with the influx of mobile forms of organic compounds into the rhizosphere environment. The accumulation of phenolic compounds in the rhizosphere soil increased throughout the vegetation period, reaching its peak in the autumn, presumably contributing to its phytotoxic properties. It is known that soil phenolic substances encompass various types of compounds, including simple flavonoids, phenolic acids, complex flavonoids, and anthocyanins (Babbar et al., 2014). These compounds are usually associated with plant defense reactions. Polyphenols such as resveratrol, quercetin, butein, fisetin, piceatannol, and curcumin reduce the degree of oxidative stress and restore redox balance (Singh et al., 2023). However, phenolic metabolites also play an essential role in other processes. They serve as attractive substances for pollination acceleration, providing coloration for camouflage and protection against herbivores, as well as demonstrate antibacterial and antifungal effects (Alasalvar et al., 2001; Acamovic & Brooker, 2005; Edreva et al., 2008).

The laccase activity, which catalyzes the transformation of aromatic and non-aromatic substrates with the reduction of molecular oxygen to water, deserves attention. Apart from lignin degradation, differentiation, and fruiting body formation in fungi, laccases are involved in processes such as the adhesion of phytopathogens to host plant cells, organic residue humification, and xenobiotic detoxification (Rivera-Hoyos et al., 2013; Rangelov & Nicell, 2019; Ben Younes et al., 2019).

Conclusions

Our research demonstrated that model species of rare and endangered plants employ a wide range of physiological mechanisms throughout the vegetation period to enhance their resistance to abiotic factors. These mechanisms include maintaining potassium and calcium balance and utilizing hormonal compounds. These plants have been proven to have compensatory mechanisms in response to stress factors, substituting one biochemical marker of resistance with another. Both brassinosteroids and silicon contribute to the adaptive capacity of organisms. Furthermore, *A. ursinum* and *L. vernum* enter a period of dormancy and accumulate silicon in their bulbs during the second half of summer, providing additional resistance to low temperatures. Therefore, further study of the biology and ecology of these rare plant species in the context of conservation and enrichment of biodiversity is promising.

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Біохімічні та алелопатичні особливості *Adonis vernalis, Allium ursinum* та *Leucojum vernum* у Національному ботанічному саду імені М.М. Гришка НАН України

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У статті наведено результати дослідження вмісту та динаміки накопичення біогенних елементів і брасинолідів у рослинах *Adonis vernalis, Allium ursinum* та *Leucojum vernum* у Києві, Україна. Наведено дані щодо алелопатичної активності, розподілу макро- і мікроелементів, фенольних сполук, активності лаккази в ризосферному ґрунті в умовах Національного ботанічного саду імені М.М. Гришка НАН України (НБС). Як об'єкти дослідження в польових дослідах використовувалися рослини з колекції НБС. Вміст біогенних елементів у тканинах рослин і ґрунті аналізували за допомогою спектрометра з індуктивно зв’язаною плазмою. Алелопатичний аналіз ґрунту проводили методом прямого біотестування з використанням проростків *Lepidium sativum* як тест-об’єкта. Фенольні сполуки екстрагували з ґрунту іонообмінним (десорбційним) методом. Вміст брасиностероїдів вимірювали спектрофотометрично при довжині хвилі 450 нм. Вміст лаккази вимірювали спектрофотометрично на довжині хвилі 530 нм.

Результати показали, що модельні види рослин використовують широкий спектр фізіологічних механізмів протягом вегетаційного періоду для підвищення стійкості до абіотичних факторів. Ці механізми включають підтримку балансу калію та кальцію та використання гормональних сполук. Доведено, що рослини мають компенсаторні механізми у відповідь на стресові фактори, замінюючи один біохімічний маркер стійкості іншим. І брасиностероїди, і кремній сприяють адаптаційній здатності організмів.

Ключові слова: біогенні елементи, фенольні сполуки, лакказа, адаптація рослин, фітогормони