

Article

Optimization of Clonal Micropropagation Stages of *Lilium pensylvanicum* Using Crezacin: In Vitro Rooting and Ex Vitro Acclimatization

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Abstract

The current challenges associated with the conservation and restoration of plant biodiversity make it necessary to test new biotechnological approaches. Optimizing the stages of clonal micropropagation using synthetic growth biostimulants—protatranes (1,2,3)—enables the targeted modification of physiological processes in plants. This increases their stress resistance, stimulates development, and reduces the cost of the final product. In this paper, the stimulating effect of the protatran (1), which we have named “crezacin”, on the processes of in vitro rooting and acclimatization to ex vitro conditions in microplants of the rare wild species *Lilium pensylvanicum* Ker Gawl was studied. No effect of crezacin and α -naphthylacetic acid on the development and growth of the microbulb during the rooting stage was detected. Crezacin at a concentration of 1.0 mg/L inhibited root elongation, but did not affect root number. Using α -naphthylacetic acid at a concentration of 0.93 mg/L was ineffective in inducing in vitro rhizogenesis. The survival rate of regenerated plants cultivated on media supplemented with crezacin was found to be 100%. The positive effect of crezacin on the content of photosynthetic pigments in the leaves of regenerated plants was also demonstrated. The addition of ultra-low concentrations (0.001–0.1 mg/L) of crezacin increased pigment content by up to 1.5 times ($p < 0.05$) compared to the control group. The increase in chlorophyll and carotenoid levels upon the addition of crezacin to the culture medium significantly facilitated the transition from a heterotrophic to an autotrophic mode of nutrition when microplants were transplanted into a soil substrate. Further research on clonal micropropagation of rare plant species and horticultural crops will be conducted using protatranes 2 and 3.



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1. Introduction

Biodiversity conservation of plants is a fundamental challenge of our time, and the future of humanity is closely intertwined with addressing this issue. However, due to various biological, geographical, and socioeconomic factors, as well as the impact of human activities, many rare plants are still at risk of extinction.

It is evident that the efforts of conservation organizations, international agencies (the International Union for Conservation of Nature [1], the United Nations Environment Programme [2], and the Convention on Biological Diversity [3]), and national governments have collectively contributed to the expansion of the areas dedicated to plant conservation in both natural (in situ) and artificial habitats (ex situ). However, despite these efforts, the number of species on the brink of extinction continues to increase [4,5].

Current challenges in plant biodiversity conservation require new strategies and methodological approaches to be developed and tested. In this regard, plant conservation biotechnology is a promising area that has been actively developing in recent decades [6–10].

Thanks to its effectiveness and wide range of applications, clonal micropropagation (CMP) plays a key role in plant biotechnology. This method of vegetative propagation enables the rapid production of pathogen-free, true-to-type plantlets of the donor plant under sterile laboratory conditions [11,12].

Rooting (rhizogenesis) is the most critical stage in both conventional cuttings and CMP. The survival, viability, and subsequent development of the plants depend on the success of this process. The composition of the culture medium is therefore of paramount importance at this stage, particularly when working with rare species, since the selection of the optimal combinations and concentrations of growth regulators directly influences the success of in vitro cultivation [8,10,13,14]. This stage is pivotal in determining the degree of preparation of the plants for non-sterile ex vitro conditions.

“Atranes”, which were developed at the Irkutsk Institute of Organic Chemistry SB RAS (Irkutsk, Russia) (Figure 1), are an extremely promising class of synthetic biologically active compounds that can be used as growth regulators and in the preparation of culture media [15–17].

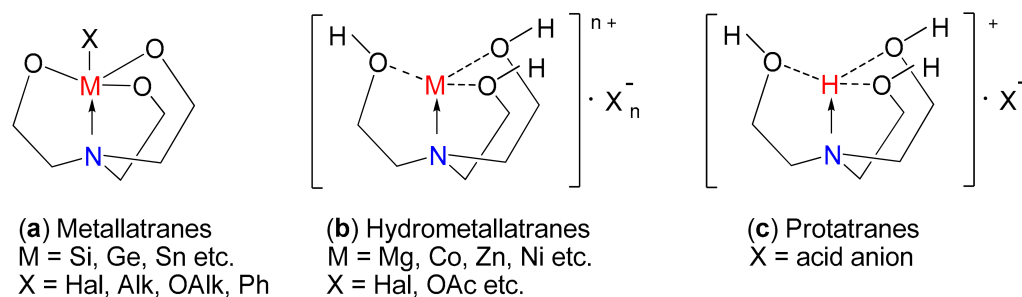


Figure 1. Atranes: (a) metallatranes, (b) hydrometallatranes, (c) protatranes.

Atranes include metallatranes (a), hydrometallatranes (b), and protatranes (c). For example, protatranes (1–3), with the general formula $\text{ArXCH}_2\text{COO}^-\text{H}^+\text{N}(\text{CH}_2\text{CH}_2\text{OH})_3$ (Figure 2), typically consist of an anion derived from biologically active arylchalcogenylacetic acids, $\text{ArXCH}_2\text{COOH}$ (where Ar = aryl; X = O, S, SO_2) [18,19] and a cation of the biogenic (involved in biological processes) amino alcohol, triethanolamine, $\text{N}(\text{CH}_2\text{CH}_2\text{OH})_3$ [20].

The unique tricyclic structure of atranes, particularly protatranes, is responsible for their exceptional physical and chemical properties, as well as their high and diverse biological (physiological and pharmacological) activity.

For example, effective anticancer and protective agents (adaptogens), immunomodulators, and biostimulants have been identified among protatranes. These significantly enhance the development and growth of cells, while increasing their resilience [21–23]. A distinctive feature of protatranes is their ability to exhibit biological activity at micro- and even nanoconcentrations (10^{-4} – 10^{-10} mass. %). Furthermore, protatranes are non-toxic and virtually harmless even at doses exceeding 1 g/kg (LD_{50} 3000–6000 mg/kg) [17,21].

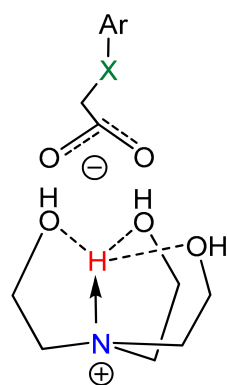


Figure 2. Structure of protatranes 1–3. Ar = 2-Me-C₆H₄, X = O (1); Ar = *p*-Cl-C₆H₄, X = S (2); Ar = *p*-Cl-C₆H₄, X = SO₂ (3).

The mechanism of the biological action of atranes (protatranes) remains unclear. However, some data suggest that they are readily adsorbed onto the surfaces of cellular (biological) membranes through hydrogen bonds and dipole–dipole interactions with the polar groups of proteins and lipids (Figure 3a). After adsorption, protatrane “pushes apart” these polar groups, thereby “thinning” the membrane (Figure 3b). Protatrane then penetrates the cell and begins to exert its active effect [23].

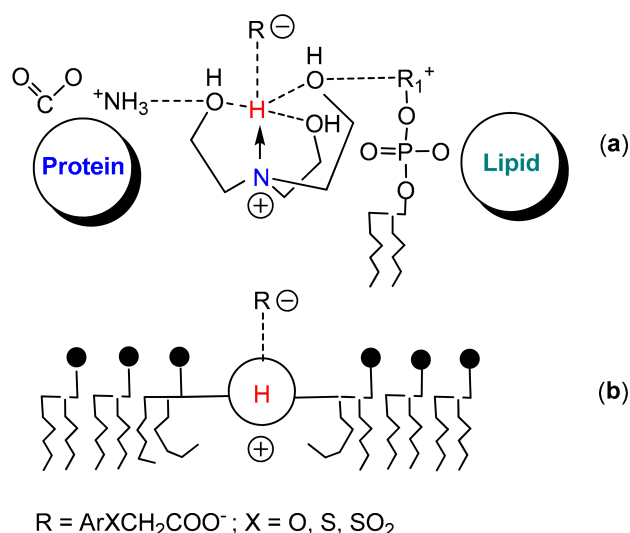


Figure 3. Hypothetical mechanism of biological action of silatranes. (a)—proposed interaction of protatrane with polar groups of proteins and lipids of biological membranes, (b)—orientation of adsorbed protatrane molecules in the lipid monolayer of biological membranes.

In light of the above, we synthesized the triethanolammonium salt of oxygen-containing cresoxyacetic acid, which we have named “crezacin” (1) and abbreviated as CR, as well as salts of sulfur-containing acids (2, 3) (Figure 2) [17,21].

The use of new synthetic stimulants of types 1–3 modifies physiological processes in plants, such as the intensity of photosynthesis and respiration, as well as enzyme activity. These compounds stimulate growth and development, increase resistance to stress factors, and reduce the production costs. Consequently, the study and application of such stimulants is becoming a priority area in modern crop production, particularly in plant biotechnology. Several experimental studies have confirmed that CR is an effective stimulant for cultivating agricultural plants and for increasing their yield [24,25].

The *in vitro* propagation of rare wild species of the genus *Lilium* Tourn. ex L. (family Liliaceae Juss.) is of significant scientific and practical interest due to the need to conserve

genetic resources [26–28], as well as to their ornamental [29–32] and medicinal value [33,34]. At the same time, CMP technologies for lilies are distinguished by the high genetic stability of microclones [26], which is a notable advantage when producing planting material for ornamental crops [35].

The literature contains numerous accounts of successful biotechnological propagation of vulnerable *Lilium* spp. that require special protection. Among these are *L. brownii* Poit. [36], *L. caucasicum* (Misch.) Grossh. [37], *L. chalcedonicum* L. [38], *L. pensylvanicum* Ker. Gawl. [9,39], etc. Nevertheless, the development of standard regeneration schemes for *Lilium* species does not eliminate the need to modernize classical protocols. Today, this field requires the implementation of cutting-edge technological solutions, mainly innovative growth regulators to ensure high stability in plant development. In particular, the transition of regenerants to autotrophic existence remains a critical stage. It is known that the addition of growth stimulants before acclimatization to ex vitro conditions can significantly increase survival rates and improve key biometric indicators of regenerants [37–41]. In this regard, one of the most promising areas of contemporary research in the field of clonal micropropagation of rare and medicinal geophytes is the search for effective, economically accessible and environmentally safe compounds with a broad spectrum of action that are capable of inducing endogenous defense mechanisms and increasing resistance to abiotic stress during the adaptation phase [35,42,43].

Lilium pensylvanicum, which is native to East Asia (Figure 4), is a species with significant conservation and plant breeding potential. It is classified as rare across much of its range, where population sizes are steadily declining [44–48]. At the same time, *L. pensylvanicum* is one of the best parent species for breeding new lily varieties that are highly resistant to cold, heat, and drought [49,50].

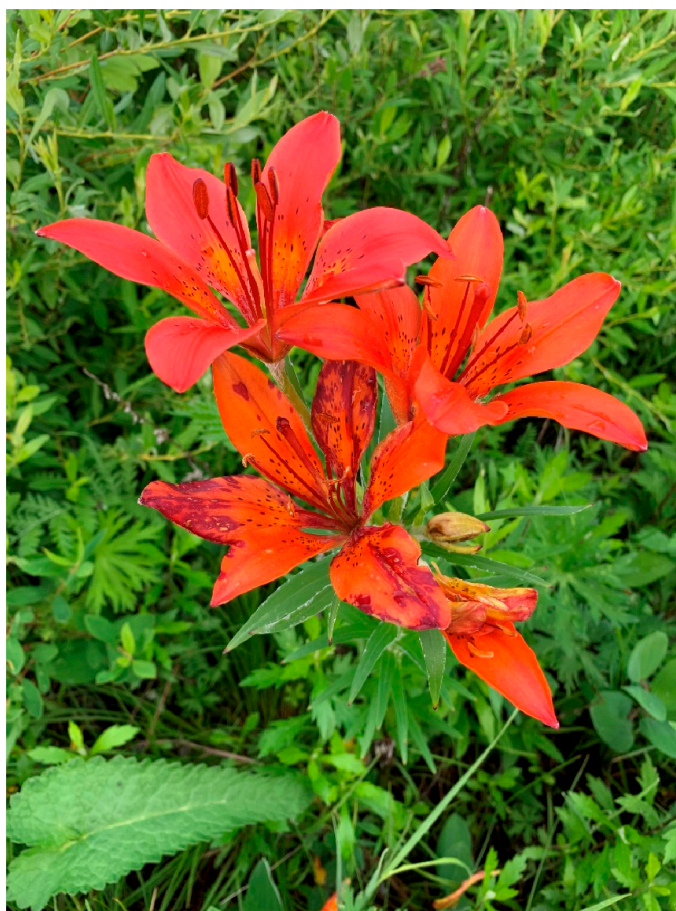


Figure 4. *Lilium pensylvanicum* in a natural forest community (Irkutsk Region, 29 June 2019).

The aim of this work is to study the effect of protatranes, specifically crezacin (**1**), on the in vitro rooting and ex vitro acclimatization of *L. pensylvanicum* microplants.

2. Materials and Methods

2.1. In Vitro Rooting

The intact plants (bulbs) of *L. pensylvanicum* were collected at the site of its natural habitat in Russia, Trans-Baikal Territory, Mogocha district, in the vicinity of Mogocha town in 29 May 2025. Before studying the effect of the growth stimulators on in vitro rhizogenesis, microbulbs were cultured for four passages on solid Murashige–Skoog basal salt medium (MS) [51]; the passage duration was 5 weeks.

Individual microbulbs without roots were rooted on solidified MS medium (0.6% agar; Dia-m, Moscow, Russia) supplemented with 30.0 g/L sucrose (LenReactiv, Saint-Petersburg, Russia). pH was adjusted to 5.7 before autoclaving the medium at 121 °C for 20 min. The in vitro rhizogenesis in microbulbs was stimulated by the addition of auxin α -naphthylacetic acid (NAA; Sigma-Aldrich, St. Louis, MO, USA) and/or the growth stimulator crezacin (CR) to the nutrient medium. NAA was added to the medium at a concentration of 0.93 mg/L, and CR was added at concentrations of 0.001, 0.01, 0.1, and 1.0 mg/L. The combination of 0.93 mg/L NAA and 0.01, 0.1, and 1.0 mg/L CR were tested. A hormone-free MS medium served as the control. CR (**1**) and salts of sulfur-containing acids (**2**, **3**) were synthesized by the methods described in [17,21].

When working with CR, a stock solution with a concentration of 0.1% was preliminarily prepared. The required working concentrations were then obtained by diluting this stock solution in a liquid culture medium. After autoclaving, substances that stimulate growth and development were added to the culture medium.

During the in vitro rooting stage, the cultures were incubated at 23 ± 2 °C under a cool white fluorescent lamp ($30 \mu\text{mol m}^{-2} \text{s}^{-1}$) with a 16 h photoperiod. The duration of passages was 5 weeks.

2.2. Ex Vitro Acclimatization

Regenerated plants (the entire cluster of formed microbulbs) with well-developed root systems (no less than 3 roots per cluster) and foliage (at least 1 leaf per microbulb) were adapted to non-sterile conditions ex vitro. For each treatment, twenty plants were planted in a soil mixture of peat, coconut fiber, and sand (1:1:1). High humidity was maintained for the first two weeks by covering the container with polyethylene film and misting the plants. After this period, the film was gradually removed to reduce humidity levels. Acclimatization took place in a greenhouse under natural light. The effectiveness of acclimatization to ex vitro conditions (survival rate, %) was assessed by the proportion of plants that developed new leaves from the total number of planted bulb clusters 45 days after their planting in the soil substrate.

The following parameters were recorded at the end of the passage: rooting frequency (%); survival rate (%); and biometric parameters describing the development of the root and shoot systems, such as bulb size (mm), bulb scale number per bulb (pcs.), number of roots per bulb cluster (pcs.), root length (cm), number of leaves per bulb (pcs.), and leaf length (cm). Rooting frequency and survival rate were calculated per cluster; bulb size, length of root and leaf were evaluated individually; bulb size and root length were measured at the end of both rooting and acclimatization stages.

2.3. Determination of Photosynthetic Pigment Concentrations

The effect of CR was assessed by determining the photosynthetic pigment content (chlorophyll a, b, and carotenoids) in the leaves of regenerated plants using a spectrophoto-

metric method [40,52]. Pigment content was evaluated twice: 1. at the in vitro stage—at the end of in vitro rooting stage immediately before planting in the soil substrate; and 2. at the ex vitro stage—at the end of ex vitro acclimatization stages, after two months of growing in soil substrate. The fresh leaves (30–35 mg) were ground with 95% ethanol (1.5 mL). The homogenate was then centrifuged for 10 min at 8 000 rpm, and 1.5 mL of 95% ethanol was added to the supernatant. The optical density was measured at wavelengths of 470, 649, and 664 nm; 95% ethanol served as the control. The optical density of the extracts was determined using a UNICO 2100 UV spectrophotometer (UNICO, Princeton, NJ, USA). The concentration of photosynthetic pigments was calculated using the formulas proposed by H.K. Lichtenthaler and C. Buschmann [52]:

$$C_a = (13.36 \times A_{664} - 5.19 \times A_{649});$$

$$C_b = (27.43 \times A_{649} - 8.12 \times A_{664});$$

$$C_c = (1000 \times A_{470} - 2.13 \times C_a - 97.64 \times C_b)/209,$$

where C_a , C_b , and C_c are the concentrations of chlorophylls a, b and carotenoids (mg/mL) in the ethanol extract; A_{470} , A_{649} , and A_{664} are the optical densities of the extract at wavelengths of 470, 649, and 664 nm, respectively.

The concentration of photosynthetic pigments (C_p) in leaf tissues was calculated and expressed in mg/g of fresh weight using the following formula [40]:

$$C_p = C \times V / (1000 \times n),$$

where C is the pigment concentration in the ethanol extract (mg/mL), V is the extract volume (mL), and n is the fresh weight of the sample (g).

2.4. Statistical Analysis

All the experiments were set up in triplicate per treatment and a minimum of 15 microplants were used for each treatment. The values presented in the tables and graphs are arithmetic means with confidence intervals. To identify statistically significant differences, a one-way analysis of variance (ANOVA) was performed, followed by Tukey's HSD test. Two-way ANOVA was used to analyze the effect of the CR and NAA on photosynthetic pigment concentrations. This study discusses differences that are statistically significant at the 95% level. The data were analyzed using Microsoft Office Excel 2007 (Microsoft Corp., Redmond, WA, USA) and STATISTICA 10 (Statsoft Inc., Tulsa, OK, USA).

3. Results

3.1. In Vitro Rooting

All nutrient media used ensured a high rooting frequency, but root system quality varied significantly (Table 1). Regardless of the nutrient medium composition for in vitro rhizogenesis induction, the microbulbs doubled in size by the end of the passage. A comparison between CR and NAA at the in vitro rooting stage revealed that CR had a greater effect on root development (the number and length of roots), whereas NAA affected leaf development (the number and length of leaves) (Table 1). Moreover, CR causes a dose-dependent inhibition of root length: the shortest roots were observed at a concentration of 1.0 mg/L, while low and medium concentrations (0.001–0.1 mg/L) of CR gave results comparable to the control.

NAA at a concentration of 0.93 mg/L was ineffective in inducing in vitro rhizogenesis of *L. pensylvanicum*. Despite 100% rooting, significantly fewer roots were formed and their

length was shorter (by 34.4% and 33.3%, respectively) compared to the control variant. The combined use of NAA and CR enhanced this effect.

Table 1. Effect of nutrient medium (MS) components on the growth and development of *Lilium pensylvanicum* bulbs at the in vitro rooting stage.

Growth Regulator, mg/L	Rooting Frequency, %	Bulb Scale Number per Bulb	Bulb Size, mm	Root Number per Bulbs Cluster	Root Length, cm	Leaf Number per Bulb	Leaf Length, cm
Control	100.0	3.3 ± 0.2 ^a	4.5 ± 0.4 ^a	9.6 ± 1.8 ^a	1.8 ± 0.2 ^a	2.4 ± 0.2 ^{abc}	6.5 ± 0.4 ^a
CR 0.001	89.5	3.8 ± 0.4 ^a	4.2 ± 0.4 ^a	8.7 ± 0.9 ^{abc}	2.0 ± 0.2 ^a	1.7 ± 0.2 ^c	4.3 ± 0.4 ^c
CR 0.01	87.5	3.6 ± 0.4 ^a	4.1 ± 0.3 ^a	8.8 ± 1.5 ^{ab}	1.8 ± 0.2 ^{ab}	2.1 ± 0.5 ^{abc}	3.6 ± 0.7 ^{bc}
CR 0.1	94.4	3.5 ± 0.3 ^a	4.1 ± 0.4 ^a	8.7 ± 1.5 ^{abc}	1.7 ± 0.2 ^{abc}	2.8 ± 0.3 ^{ab}	6.3 ± 1.0 ^{ab}
CR 1.0	92.0	3.3 ± 0.2 ^a	4.1 ± 0.3 ^a	8.7 ± 1.2 ^{abc}	1.4 ± 0.1 ^{bcd}	2.0 ± 0.2 ^{bc}	4.7 ± 0.5 ^c
NAA 0.93	100.0	3.8 ± 0.4 ^a	4.3 ± 0.6 ^a	6.3 ± 1.5 ^{bcd}	1.2 ± 0.1 ^{cd}	3.1 ± 0.4 ^a	7.0 ± 0.8 ^a
CR 0.01 + NAA 0.93	100.0	3.7 ± 0.3 ^a	4.3 ± 0.5 ^a	4.5 ± 1.5 ^{cd}	0.9 ± 0.1 ^d	1.7 ± 0.5 ^c	5.0 ± 0.6 ^{bc}
CR 0.1 + NAA 0.93	92.3	3.4 ± 0.5 ^a	4.1 ± 0.7 ^a	3.2 ± 1.3 ^d	1.0 ± 0.2 ^d	2.1 ± 0.3 ^{bc}	4.7 ± 0.6 ^{bc}
CR 1.0 + NAA 0.93	92.3	3.5 ± 0.5 ^a	4.0 ± 0.6 ^a	5.1 ± 1.4 ^{bcd}	1.1 ± 0.2 ^d	2.3 ± 0.8 ^{abc}	4.3 ± 0.7 ^c

Means followed by different letters in the same column are significantly different ($p \leq 0.05$) according to Tukey's HSD test.

L. pensylvanicum is characterized by a high regenerative potential, as evidenced by the 100% in vitro rhizogenesis on the control medium, as well as on media containing NAA 0.93 mg/L and CR 0.01 mg/L + NAA 0.93 mg/L. The rate never fell below 87.5% (CR 0.01 mg/L). This is also confirmed by the multiplication of microbulbs on media intended to induce rooting. The number of microbulbs developed per explant ranged from 2.5 ± 0.9 (NAA 0.93 mg/L) to 4.9 ± 1.3 (CR 0.01 mg/L).

In some cases, the use of NAA 0.93 mg/L resulted in the formation of atypical roots that were thickened and brittle and lacked root hairs. On media containing CR, the developing roots were flexible and densely covered with root hairs (Figure 5c). Overall, NAA was found to inhibit root system development compared to the control. Furthermore, no clear stimulatory effect of CR on rhizogenesis in *L. pensylvanicum* was observed.

3.2. Ex Vitro Acclimatization

The resulting cluster of shoots, which had developed during the in vitro rhizogenesis stage, was transferred to a soil substrate. Cultivation on a medium containing 0.001 mg/L CR ensured a 100% survival rate of microbulbs; a further increase in the concentration reduced this figure (Figure 6). Plants grown on CR-containing media adapted to non-sterile conditions more quickly. The leaf blade area of leaves formed in vitro increased and new leaves grew. The root system continued to develop after planting in the substrate, and new roots formed. The root system of plants treated with CR increased significantly: each bulb in the cluster formed 3–4 true roots, and root length had increased 3–5-fold at 45 days after the start of acclimatization (Figure 5d). No new metameric nodes were formed, but the size of the bulbs increased by an average of 20%. Plant biometric parameters after rooting on CR-supplemented media after 45 days of acclimatization were comparable to control values. The exception was root length in acclimatized plants rooted on a medium containing CR: control— 6.3 ± 1.0 cm; CR 1.0 mg/L— 4.4 ± 0.5 cm.

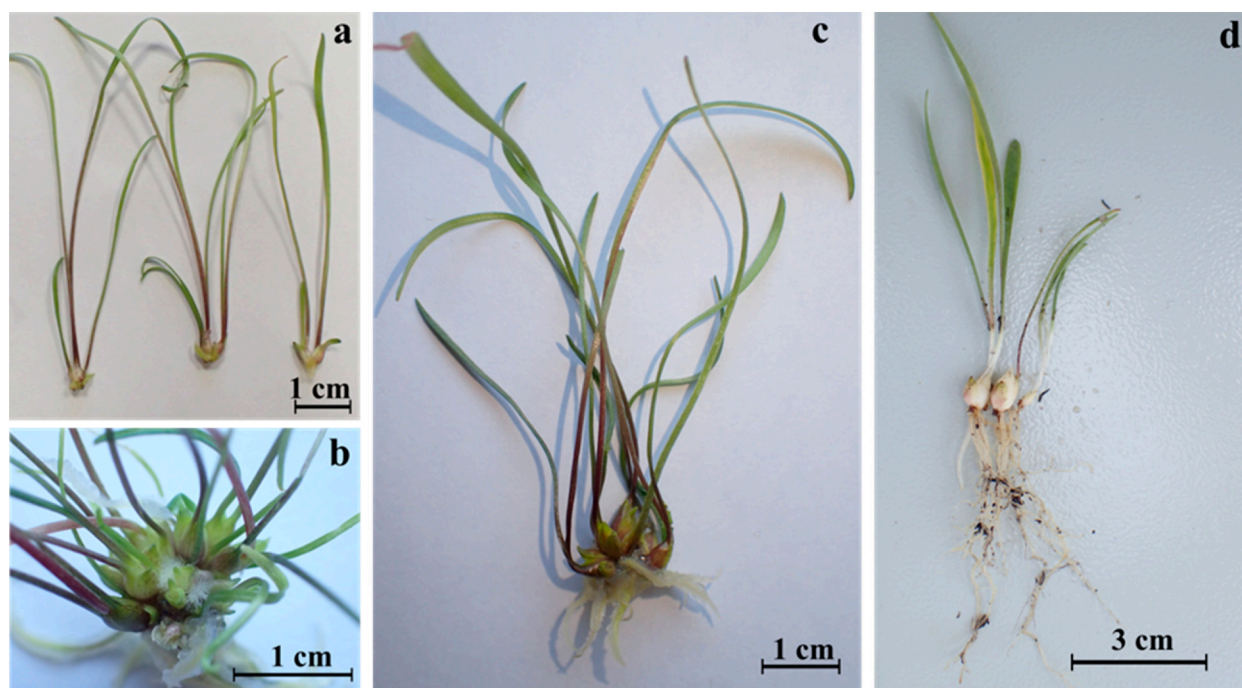


Figure 5. In vitro rooting and ex vitro acclimatization stages of *Lilium pensylvanicum* microbulbs: (a)—bulblets at the beginning of the rooting stage, MS; (b)—microbulb multiplication, MS + CR 1.0 mg/L; (c)—bulblet cluster at the end of the in vitro rooting stage, MS + CR 0.001 mg/L; (d)—plants acclimatized to ex vitro conditions, a peat: coconut fiber: sand (1:1:1) substrate.

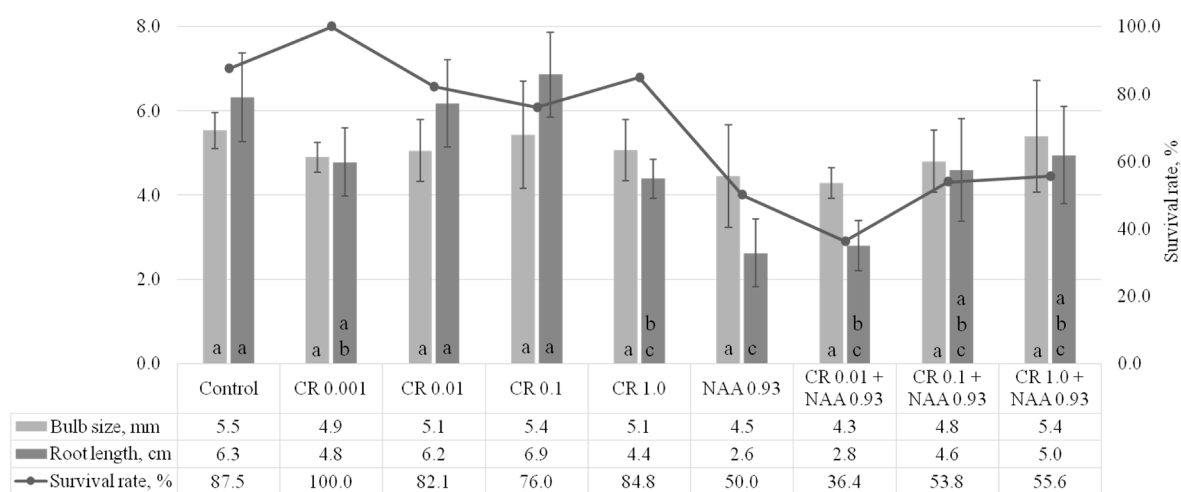


Figure 6. Survival rate and growth parameters of *Lilium pensylvanicum* plantlets after 45 days of ex vitro acclimatization. Means followed by different letters between treatments are significantly different ($p \leq 0.05$) according to Tukey's HSD test.

A severe decrease of up to 2.7 times in the proportion of plants acclimatized to non-sterile conditions was observed following rooting in media containing NAA (with and without CR). Plant survival after cultivation in the presence of NAA did not exceed 56%. NAA was found to negatively affect root length, which was almost 2.4 times shorter than the control on media supplemented with NAA 0.93 mg/L or CR 0.01 mg/L + NAA 0.93 mg/L. The combination of NAA and CR (0.1 and 1.0 mg/L) partially neutralized the inhibitory effect of NAA on root growth and survival rate in ex vitro conditions (Figure 6). In all treatments, the leaves formed in vitro died off, and new leaves developed poorly when plants were grown in the soil mixture.

3.3. Determination of Photosynthetic Pigment Concentrations at the In Vitro and Ex Vitro Stages

When assessing chlorophyll a and b, as well as carotenoid content at the end of rooting (in vitro stage), the following patterns were identified: (a) the concentration of pigments remained consistently high regardless of CR concentration in the medium; and (b) a decrease in pigment content when NAA was added to the culture medium, bringing levels back to control values (Table 2). The addition of ultra-low concentrations of CR (0.001–0.1 mg/L) increased pigment content by up to 1.5 times ($p < 0.05$) compared to the control. The chlorophyll a/b ratio at level 2.8 on a medium supplemented with 0.1 mg/L CR and 0.93 mg/L NAA was the lowest for *L. pensylvanicum* leaves at the in vitro stage. This treatment also demonstrated the lowest carotenoid content at the in vitro stage. In all other treatments analyzed, the chlorophyll a/b ratio ranged from 3.1 to 3.3, which is optimal.

Table 2. Effects of CR and NAA on photosynthetic pigment concentrations in leaves of *Lilium pensylvanicum* plants at the end of the in vitro rooting and ex vitro acclimatization stages.

Growth Regulator, mg/L	In Vitro				Ex Vitro			
	Concentration, mg/g			Chl a/b Ratio	Concentration, mg/g			Chl a/b Ratio
	Chl a	Chl b	Crt		Chl a	Chl b	Crt	
Control	0.57 ± 0.06 cd	0.18 ± 0.02 bc	0.16 ± 0.01 cd	3.2	0.82 ± 0.04 ab	0.21 ± 0.02 abc	0.23 ± 0.01 ab	3.9
CR 0.001	0.86 ± 0.07 a	0.27 ± 0.02 a	0.23 ± 0.02 a	3.2	0.87 ± 0.01 a	0.23 ± 0.01 ab	0.25 ± 0.00 a	3.8
CR 0.01	0.84 ± 0.10 a	0.26 ± 0.04 a	0.23 ± 0.02 a	3.2	0.79 ± 0.03 ab	0.21 ± 0.00 abc	0.24 ± 0.00 a	3.8
CR 0.1	0.80 ± 0.06 ab	0.24 ± 0.04 a	0.22 ± 0.01 ab	3.3	0.69 ± 0.05 b	0.19 ± 0.02 c	0.20 ± 0.01 b	3.6
CR 1.0	0.72 ± 0.08 abc	0.23 ± 0.02 ab	0.20 ± 0.02 abc	3.1	0.86 ± 0.07 a	0.24 ± 0.02 a	0.24 ± 0.02 a	3.6
NAA 0.93	0.47 ± 0.09 d	0.14 ± 0.02 c	0.13 ± 0.02 d	3.4	0.90 ± 0.04 a	0.22 ± 0.01 abc	0.24 ± 0.01 a	4.1
CR 0.1 + NAA 0.93	0.53 ± 0.06 cd	0.19 ± 0.02 abc	0.14 ± 0.02 cd	2.8	0.83 ± 0.07 a	0.21 ± 0.02 abc	0.23 ± 0.02 ab	4
CR 1.0 + NAA 0.93	0.63 ± 0.04 bcd	0.20 ± 0.02 abc	0.17 ± 0.01 bcd	3.2	0.74 ± 0.11 ab	0.19 ± 0.03 bc	0.21 ± 0.03 ab	3.9
Two-way ANOVA results for examining the effect of each factor and their interactions								
Factor				F	p			
Growth regulator				4.61	0.00			
Stage				83.94	0.00			
Growth regulator × Stage				5.64	0.00			

Notes: Chl—chlorophyll, Crt—carotenoids. Means followed by different letters in the same group are significantly different ($p \leq 0.05$) according to Tukey's HSD test.

The most significant differences in the concentration of photosynthetic pigments and the chlorophyll a/b ratio at the ex vitro stage were observed in the hormone-free control medium and NAA-supplemented media (Table 2). The levels of chlorophyll and carotenoid in the leaves of plants grown on media containing only CR did not fluctuate significantly after being planted in soil. Therefore, CR at ultra-low concentrations (0.001–0.01 mg/L) acted as a stimulant, increasing the pigment content and affecting the ratio between them.

For all analyzed treatments, the chlorophyll a/b ratio at the ex vitro stage approached a value of 4:1. The shift in the chlorophylls' ratio was most noticeable upon completion of the acclimatization stage under natural light for plants cultivated in NAA-supplemented media (Table 2).

Thus, an assessment of the effect of CR on the rhizogenesis and acclimatization of *L. pensylvanicum* microbulbs revealed that CR has a positive impact on the biometric

parameters and survival rate of regenerated plants under ex vitro conditions compared to the impact of NAA.

4. Discussion

A well-developed root system enables microplants to adapt to ex vitro cultivation. Auxins are traditionally used as root-inducing agents in in vitro culture. However, some protocols do not include growth regulators during the rooting stage, instead applying new growth stimulants. It is known that when regenerated plants are transferred to ex vitro conditions, they experience several physiological stresses due to the morpho-anatomical characteristics of their development in in vitro culture: low photosynthetic activity, underdeveloped leaf mesophyll and cuticle, impaired transpiration, inadequate root system function, etc. [37,41]. The addition of growth stimulants before acclimatization to ex vitro conditions can significantly increase survival rates and improve key biometric indicators of regenerants [37,40,41]. Therefore, the search for effective, environmentally safe compounds with a broad spectrum of action that enhance resistance to abiotic stress during the acclimatization phase is a promising area of research in the development of protocols for clonal micropropagation. Protatrane crezacin (CR) is a non-toxic (LD_{50} 6300 mg/kg) biologically active compound with great potential for use in plant tissue culture. It positively affects the acclimatization of grape regenerants to ex vitro conditions, improving their survival and development [41]. Its main advantages include high efficacy even at ultra-low concentrations (which is economically beneficial and environmentally safe), as well as its multifunctional action. CR accelerates seed germination, while increasing plant height, aboveground and root system mass, and productive bushiness. It also enhances plant resistance to adverse environmental factors and infections, and improves the accumulation of metabolites. CR can simultaneously stimulate rhizogenesis, callus formation, and morphogenesis, as well as enhance stress tolerance [25,53,54].

The investigations into the effects of CR have primarily focused on agricultural crops. Treating oat seeds with CR has been found to increase the accumulation of proline, phenolic compounds, flavonoids, and low-molecular-weight fructose in naked oat seedlings [54]. Pre-sowing treatment of amaranth seeds with a 10^{-7} M CR solution did not enhance the concentration of chlorophyll in the leaves of seedlings. However, it increased the rate of photosynthetic phosphorylation and the cellular energy pool. At the same time, enhanced root system growth and increased biomass were observed while shoot height remained unchanged [53]. According to the results obtained by Singh et al. [55], treating wheat seeds with silatrane (a type of Si-atrane) enhances root and shoot growth in a dose-dependent manner and increases the content of photosynthetic pigments in seedlings. Another group of plant growth biostimulants consists of silicon chelates.

Treatment of the roots of regenerating strawberry plants with silicon chelate stimulated the growth and biomass of the shoots and roots under in vitro conditions. It also activated the antioxidant defense system. However, it did not affect the chlorophyll and carotenoid content in the leaves [40].

The most extensively studied application of CR in tissue culture is the induction of root formation. Studies on interspecific hybrids of the Hasansky and Agat Donskoy grape cultivars have demonstrated the high effectiveness of adding CR to the culture medium [24,41]. When cultured on media containing CR and indolylbutyric acid, 75% of plants were adapted, whereas 84% of plants were adapted when cultured on media containing only CR [41]. There are no reports describing the results of CR application during the clonal micropropagation of bulbous geophytes. However, the effect of other growth stimulants on the development of regenerated plants, particularly lilies, has been examined. Malyarovskaya and Samarina [37] have noted that the use of biological preparations (NV-

101, Zircon, Epin, Plant) during the acclimatization stage of *L. caucasicum* bulbs (watering the substrate with an aqueous solution) to ex vitro conditions stimulates the root and foliage development and increases the percentage of rooted plants.

This study revealed the adaptogenic effect of ultra-low concentrations (0.001 mg/L) of CR when microplants were transferred to ex vitro conditions. Given that the content of photosynthetic pigments reflects a plant's ability to adapt to environmental conditions, it is reasonable to assume that regenerated plants that were rooted in media containing CR would be better adapted to non-sterile ex vitro conditions.

It was found that CR positively affects the concentration of photosynthetic pigments (chlorophylls and carotenoids). This is likely explained by the good development of the root system, the high content of photosynthetic pigments, and the optimal ratio of chlorophyll a/b under the influence of CR and, as a consequence, more active growth at the adaptation stage. The survival rate of plants after cultivation in the presence of NAA did not exceed 55.6%, whereas it was 100% in the presence of CR (0.001 mg/L). In general, NAA at a concentration of 0.93 mg/L has a negative effect on in vitro rhizogenesis. In this case, weak root development affects the effectiveness of acclimatization to ex vitro conditions.

Auxins are known to regulate chlorophyll metabolism in plants, with both endogenous and exogenous auxins acting as regulators of chlorophyll accumulation [56]. Although minimal, the observed decrease in the chlorophyll a/b ratio to 2.8 in a medium supplemented with 0.1 mg/L CR and 0.93 mg/L NAA at the in vitro stage is within the normal range. However, this may suggest a slight hypertrophy of the light-harvesting complexes (LHC), resulting from an increased proportion of chlorophyll b. In turn, a shift in the chlorophyll a/b ratio at the ex vitro stage to 4:1 indicates adaptation to high levels of natural light when transferred to greenhouse conditions and does not indicate changes to the photosynthetic apparatus in response to stress. A ratio value greater than 5 would be significant, indicating nitrogen deficiency or senescence. It can be hypothesized that NAA enhances the response to light stress: plants grown in a soil substrate at the ex vitro stage reduce the number of LHC rich in chlorophyll b and increase the proportion of reaction centers composed of chlorophyll a. CR, in turn, ensures a high content of photosynthetic pigments while maintaining an optimal chlorophyll a/b ratio. Given that the content of photosynthetic pigments reflects a plant's ability to adapt to environmental conditions, it is reasonable to assume that regenerated plants that were rooted in media containing CR are likely to be better adapted to non-sterile ex vitro conditions.

Thus, CR enhances the adaptive potential of plants cultivated in vitro, facilitating acclimatization to ex vitro conditions, and thereby increasing the efficiency of the clonal micropropagation process of this rare and ornamental lily. The high biological activity observed at low doses suggests that this compound exhibits hormone-like properties [53]. In this regard, the in vitro system is a useful model for studying the effects of protatranes, particularly CR, on various physiological and biochemical processes of plants.

5. Conclusions

In summary, in this work, biostimulants, protatranes (1–3), were synthesized.

The stimulatory effect of protatran (1), crezacin (CR), on the in vitro rooting and ex vitro acclimatization of *L. pensylvanicum* microplants was examined for the first time. The survival rate of regenerated plants cultivated on CR-supplemented media reached 100%. The positive effect of CR on the photosynthetic pigment content in the leaves of regenerated plants was demonstrated. Thus, the addition of ultra-low concentrations of CR (0.001–0.1 mg/L) increased pigment content by up to 1.5 times ($p < 0.05$) compared to the control. The increase in chlorophyll and carotenoid levels resulting from the addition of

CR to the culture medium significantly facilitated the transition from a heterotrophic to an autotrophic mode of nutrition when the microplants were transplanted into a soil substrate.

Previous research has shown that the synthesized sulfur-containing protatranes (2) and (3) exhibit higher biological activity than oxygen-containing protatrane 1 in some cases. Therefore, research into the clonal micropropagation of rare plants and garden crops will continue.

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