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HUNGARIAN UNIVERSITY OF AGRICULTURE AND LIFE SCIENCES

PROTECTION AGAINST ABIOTIC STRESS FACTORS DURING POPPY (*PAPAVER SOMNIFERUM* L.) CULTIVATION

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1. BACKGROUND AND OBJECTIVES OF THE WORK

The poppy (*Papaver somniferum* L.) is one of the oldest cultivated plants. One of the purposes of its cultivation is to extract its medicinally valuable alkaloids, the most important of which are morphine, codeine and thebaine. On the other hand, its seeds contain valuable minerals, proteins and oil with a favorable fatty acid composition, making it a popular food, especially in Central and Eastern European countries (Luqman, 2014; Pushpangadan et al., 2012).

In the Hungarian production, the cultivation of autumn confectionary poppy has come to the foreground in the last decade, but for pharmaceutical purposes only spring-type varieties are currently grown here. Poppy cultivation in our country takes place predominantly under non-irrigated conditions, as a result of which its success depends significantly on the amount and distribution of precipitation during the growing season. Since the growing season of spring varieties is short, they are particularly sensitive to the increasingly frequent drought. Autumn varieties are not considered drought-sensitive plants due to their long growing season and more developed root system, but their cultivation carries the risk of frost damage.

The complex climatic changes in the Carpathian Basin make field crop production difficult, therefore, successful poppy cultivation requires the development of new technologies that focus on the most important abiotic stress factors, i.e. protection against frost and drought. In other field crops, such as winter rapeseed or oilseed radish, various synthetic regulators applied on the leaves are already regularly used to protect against the damaging effects of frost. In these crops, as well as in other economic crops, such as wheat, natural-based yield-enhancing preparations (so-called biostimulants) are often used to protect against yield reduction caused by drought (Mihaylov, 2024; Radzikowska-Kujawska et al., 2022). In our work, we examined the effect of such regulator and biostimulant treatments on the poppy plant, taking into account scientific and practical aspects. In addition to open-field experiments, we also tested some selected treatments in a phytotron under controlled conditions. In order to better understand the backgrounds of alkaloid accumulation, we expanded our studies to include the examination of the alkaloid distribution within poppy capsules.

Our goal was to answer the following practice-oriented questions using scientific methods.

1. How do the tested regulators affect the frost tolerance and seed production of autumn culinary poppy and the alkaloid level of the capsules under field conditions?

2. How do the tested biostimulant treatments affect the production of spring industrial poppy in the open field and *in vitro*, and how do the different yield factors (seed yield, capsule yield, alkaloid yield) change as a result of the treatments?

In order to gain a more precise understanding of the effects of the treatments, we also determined additional parameters during our work. With these, we basically wanted to answer the following questions.

3. How do the morphological habit of the poppy plant, the concentration of individual biochemical markers, the concentration of various osmoprotective molecules (glucose, fructose, proline) and the activity of certain characteristic stress enzymes (APX, CAT, GPX, GR, GST) change in the plant under the influence of regulator treatments in the field and *in vitro*, and in the case of biostimulator treatments *in vitro*?

4. How does the size of the capsule affect its alkaloid production (morphine, codeine, thebaine) and in what concentration are the alkaloids present in the individual organelles of the capsule?

5. Our goal was to define new scientific results and also to make suggestions for the applicability of the tested substances in poppy agrotechnology.

2. MATERIALS AND METHODS

The field tests of the spring poppy biostimulator experiment were conducted over three years (2022-2024) on spring sown, high alkaloid containing industrial poppy varieties ('Meara' and 'Morgana'). The test was conducted in the experimental garden and field areas of Sotiva Seed Ltd, which were located in Tiszavasvári, Nemesbikk and Oszlár. The experimental site was characterized by medium-compacted soil with high humus and nutrient content. In 2022, the usual amount of precipitation fell by half, and in the following years the amount of precipitation corresponded to the usual amount. During cultivation, we used fertilizers, and we protected the plants against weeds, various pests and pathogens by spraying with pesticides.

Our studies were carried out on small plots ($5m^2$), with treatments tested in 4 plot replications per variety. During the treatments, ten different substances (Table 1) were applied to poppy plants, in addition to an untreated control. The treatment was carried out by foliar spraying, dissolved in water, twice during the growing season: first at the beginning of stem growth, and secondly at the early green capsule stage, immediately after petal fall. Among the treatments, eight ones were commercially available, approved biostimulants, and two others (MEJA, SALI) were used as natural elicitors.

The height of the plants was measured before harvest. The crop was harvested in full maturity, in the first year per plot and later – in order to a larger number of sample elements and more accurate evaluation – per square meter. The harvested capsule was separated into capsule and poppy seed fractions using a roller sieve, which were weighed separately. Four samples were prepared from the whole capsules per variety and per treatment for the determination of alkaloid content.

Table 1. Characteristics of the applied biostimulatory treatments

Treatment code	Active ingredients	Product name	Manufacturer	Dosage (/m²/time)
KONT	Control (water)	-	-	-
LOMB	20% N, 20% P2O5, 20% K2O, 0,02% B, 0,05% Cu (EDTA chelate), 0,1% Fe (EDTA chelate), 0,05% Mn (EDTA chelate), 0,001% Mo, 0,05% Zn (EDTA chelate)	Kinglife 20-20-20 + micro	Green Has Italia S.p.A., Italy	0,25 g (= 2,5 kg/ha)
HUMU	peat and vermicompost extract, nutrients, water	Kondisol B+S	Huminisz Kft., Hungary	0,5 ml (= 5 l/ha)
FULV	fulvic acid, molasses, macronutrients, water	Fulvic Nature	Adler Agro SL, Spain	0,4 ml (= 4 l/ha)
ANOD	algae (*Ascophyllum nodosum* extract, co-formulants, water	Asco Alga	Techsealab Company, France	0,3 ml (= 3 l/ha)
EMAX	*Ecklonia maxima* algae aqueous extract	Kelpak	Kelp Products (Pty) Ltd, South-Africa	0,3 ml (= 3 l/ha)
MEJA	methyl jasmonate	Methyl jasmonate	Sigma Aldrich/Merck, Germany	0,0282 g (= 282 g/ha) **
SALI	salicylic acid	Szalicilsav	Kévés Béla Kft., Hungary	0,0174 g (=174 g/ha) **
HIPE	potassium hypochlorite, hydrogen peroxide, water*	SteriClean Plant	PANNON-TRADE Kft., Hungary	2 ml (= 20 l/ha)
ASIB	Siberian fir (*Abies sibirica*) needle leaf extract aqueous emulsion	Novosil	Biochimzaschita Co., Russia	0,1 ml (= 1 l/ha)
FLAV	aqueous solution of herbal extract made using cinnamon, rosemary, nettle, lemon, yarrow	Flavo Plant	Permex Vet Kft., Hungary	0,2 ml (= 2 l/ha)

*(a product with high redox potential produced by electrolysis of water and potassium chloride), ** based on pure active ingredient

In the field experiment based on a complex set of criteria, we selected FULV and MEJA treatments for further studies. To explore the physiological and biochemical background of the effect, we also examined them under controlled conditions, in a phytotron, on the ‘Meara’ variety. In one phytotron, we tried to create the most favorable conditions possible for poppy development, therefore, we maintained a soil water capacity (SWC) of 75%, which we will refer to as the “normal chamber” further on. In the other phytotron, we simulated drought (“dry chamber”), in which the soil water capacity was maintained at an average of 50%. During the 136 day growing season, both the temperature and the light cycle were continuously adjusted to the phenophase. During the early development of the poppy, a 10/14 (day/night) hour light cycle was used at a temperature of 13/8°C. The photoperiod was set to 12/12 hours in the rosette stage, then 14/10 hours continuously from the stem growth. The temperature was gradually increased until flowering, then kept at 26/15°C until the end of the experiment. 3 plants were allowed to develop in each pot, which were treated with FULV and MEJA solutions used for the field experiment at a dose of 1 ml solution/plant on the 75th and 110th days. On the 124th day, samples were taken from the uppermost developed leaf of each plant. From these, the concentration of osmoprotectants (glucose, fructose, proline), antioxidant capacity, total polyphenol content, and the activity of the following antioxidant enzymes were determined: ascorbate peroxidase (APX), catalase (CAT), glutathione-S-transferase (GST), glutathione reductase (GR), guaiacol peroxidase (GPX). The fresh and dried weight of the plant parts (root, leafy stem, capsule) were assessed at harvest.

To examine the different sized capsules and the organelles within the capsule, we randomly collected mature main capsules from both varieties from the field poppy growing area in 2023. We measured their height and width, determined the so-called shape index and measured the mass of the capsules. Based on the values obtained, we formed three groups between the extreme values: the group representing the lower third was classified as “small”, the middle as “medium”, and the largest as “large”. We formed 4-4 average samples from each variety from all three size classes to determine the alkaloid content.

To determine the alkaloid content of the organelles within the capsule, we selected capsules from the “medium” group, which after the seeds were removed (since they are inherently free of alkaloids) were further divided into parts: disc, thalamus, placenta, capsule wall. Similarly to capsules of different sizes, we formed 4-4 samples per orgenelle per variety to determine the alkaloid content.

The field tests of the autumn poppy regulator experiment were conducted over three years (2021/22-2023/24) on an autumn sown, low alkaloid containing culinary poppy variety ('Zeno Plus') in the areas of Sotiva Seed Kft. in Nemesbikk.

The first year of this experiment series was also characterized by severe drought, but in the following years, normal precipitation created favorable conditions for the development of the poppy.

During the treatments, regulators containing triazole or triazole + onium type active ingredients were applied once per growing season, tested separately as autumn and spring treatments. The autumn treatments were carried out between November 10-16, depending on the year, when the poppy reached the ideal rosette stage for wintering. The spring treatments were carried out between March 1-10, approaching the end of the rosette stage.

2. táblázat. Characteristics of the applied regulator treatments.

Treatment code	Product name (manufacturer)	Active ingredients and its concentration	Dosage (product ml/ m^2)
KONT	-	-	-
TEBU	Tebu (Sharda Worldwide Exports Pvt. Ltd., India)	250 g/l tebuconazole	0,1 (=1 l/ha)
TEDI	Magnello (Syngenta AG, Switzerland)	250 g/l tebuconazole + 100 g/l difenoconazole	0,08 (=0,8 l/ha)
TEPR	Tilmor (Bayer AG, Germany)	160 g/l tebuconazole + 80 g/l protioconazole	0,12 (=1,2 l/ha)
METK	Metkon 60 (Globachem N.V., Belgium)	60 g/l metconazole	0,1 (=1 l/ha)
MEME	Caramba Turbo (BASF S.E., Germany)	210 g/l mepiquat-chloride + 30 g/l metconazole	0,14 (=1,4 l/ha)
PADI	Respox (Syngenta AG, Switzerland)	250 g/l difenoconazole + 125 g/l pachlobutrazole	0,05 (=0,5 l/ha)

The proportion of frozen plants was determined by visual inspection in the first year and by plant counting in the following years. The height of the plants was measured before harvesting, and the plants were harvested at full maturity. After separating the seeds and capsules, their weight was measured and the capsule samples were ground for the measurement of alkaloid content.

Based on the results in the open field, primarily on frost tolerance, we selected the METK, MEME, PADI treatments for more detailed studies. From these, leaf samples were taken in December 2023 to determine the levels of osmoprotectant sugars and proline, some antioxidant enzymes (APX, CAT), plant hormones (auxin, GA – gibberellic acid, ABA – abscisic acid) and phenolic stress marker molecules. The effect of these three treatments on frost tolerance was also examined in three phytotron series (Table 3). Leaf samples were also taken from these to detect hormones and stress markers. In the first series, the effects of the treatments on the morphological characteristics of the rosette plant were also examined with an automatized phenotyping system.

Table 3. Temperature program of frost tolerance tests performed in the phytotron

First series (Martonvásár) 6-8 leaf plants	Second series (Budapest) 6-8 leaf plants	Third series (Budapest) 8-10 leaf plants
Day 1-2: 2°C	Day 1-2: 2°C	Day 1-2: 2°C
Day 3-4: 0°C	Day 3-4: 0°C	Day 3-4: 0°C
Day 5-6: -2°C	Day 5-7: -2°C	Day 5-7: -2°C
Day 7-10: -4°C	Day 8-10: -6 °C	Day 8-10: -6°C
Day 11-14: 2°C	Day 11-14: 2°C	Day 11-14: 2°C

The alkaloid content of the poppy capsules was determined by UPLC-MS analysis in the laboratories of the Agricultural and Molecular Research Institute of the University of Nyíregyháza. The sugar content of the leaf samples was determined by HPLC-ELSD method in the same laboratory. The total polyphenol content was determined by spectrophotometric analysis, and the antioxidant capacity by FRAP analysis in the Department of Medicinal and Aromatic Plants of the MATE. The activity of antioxidant enzymes and the proline content of the leaves were determined by spectrophotometry and photometry in the Department of Plant Physiology and Metabolomics of the HUN-REN Agricultural Research Institute. The concentrations of plant hormones (auxin, gibberellic acid, abscisic acid) and other stress markers related to them were measured in the same laboratory by UPLC-MS analysis.

For the statistical analysis of the data, one- or two way ANOVA was performed. If the condition of homogeneity of variance (based on Levene's test) was not met, Welch's ANOVA was performed. Kolmogorov-Smirnov and Saphiro-Wilk tests were used to examine normality. In case of significant differences, Tukey HSD, LSD or Games-Howell *post hoc* tests were performed. In all cases, the results were analyzed at $p<0.05$ significance level.

3. RESULTS AND DISCUSSION

The effect of poppy capsule size and structure on yield and alkaloid content

In the examination of poppy capsules of different sizes, in addition to differences in size, we also observed differences in shape between the three groups. In the ‘Meara’ variety, the calculated shape index of small capsules is significantly lower, which in practice means that small capsules are more elongated, while medium or large ones have a rounder shape. This difference can also be observed in the ‘Morgana’ variety, with the difference that in its case a significant difference can only be detected between the small and large groups, the shape index of the medium group forms a transition, not significantly different from either group. The proportion of seeds within the capsule is significantly lower in large capsules.

We also observed differences in the alkaloid content of capsules calibrated according to size. In the ‘Meara’ variety, we observed significant differences in the level of the main alkaloid, morphine, as well as in the total alkaloid content. The average morphine content of small and medium capsules was 2.28%, and the total alkaloid content was 2.36-2.38%. In contrast, we detected significantly lower values in large capsules: morphine was present at a concentration of 0.90%, which, together with minor alkaloids, resulted in a total alkaloid concentration of 0.96%. The 'Morgana' variety did not show significant differences in the total alkaloid content (2.43-2.71%) and morphine content (2.31-2.41%) of capsules of different sizes. However, a significant difference can be observed in the concentration of minor alkaloids. The average thebaine level in large capsules was 0.15%, which is several times higher than the values in the small and medium fractions (0.01-0.02%). The codeine concentration was also higher in large capsules (0.21%) than in the smaller groups (0.07-0.10%). According to our data, the poppy seed ratio, shape, alkaloid concentration and alkaloid profile of different sized capsules may differ. The large capsules of 'Meara' showed a significantly lower alkaloid concentration with an unchanged alkaloid profile. In contrast, in the case of 'Morgana', the total alkaloid levels of the large capsules were not significantly different, but the levels of codeine and thebaine increased significantly.

Significant differences were also observed when examining the alkaloid content of the organelles of the capsule. In the 'Meara' variety, there was no significant difference in the thebaine content of the organelles (0.00-0.02%). The ratio of codeine in the capsule wall was 0.17%, which significantly exceeded the values (0.04-0.08%) measured in the other capsule parts. The concentration of the main alkaloid morphine, gave a statistically different value in each organelle: the lowest accumulation level was measured in the thalamus (0.63%), followed by the disc (0.98%) and the placenta (2.05%). The highest morphine content (2.51%) was detected in the capsule wall. The total alkaloid content followed the trend of morphine. In the 'Morgana', the thebaine content showed significant differences: while the disc contained negligible amounts of thebaine, the thalamus and the wall showed an accumulation level of 0.06-0.09%, with the highest concentration measured in the placenta (0.16%). The level of codeine in the wall and placenta (0.17-0.22%) was significantly higher than the value in the thalamus and disc (0.05-0.07%). The morphine content and the total alkaloid content also moved together in this variety. The morphine content in the thalamus and disc was 0.63-0.86%, and their total alkaloid content was 0.75-0.91%. This was significantly exceeded by the value of the wall (morphine: 2.50%, total alkaloids: 2.76%), which was significantly exceeded by the accumulation level of the placenta (morphine: 3.34%, total alkaloids: 3.71%).

Our results therefore indicate that the location of alkaloids within the capsule is significantly influenced by genotype, and the placenta may play a greater role in alkaloid production than previously reported (Bernáth, 1989; Nash, 1980). The difference between the highest and lowest concentrations inside the capsule is nearly fourfold in the 'Meara' variety, and nearly fivefold in the 'Morgana'.. Our results show that only the main alkaloid, morphine, follows the trend of the total alkaloid content, while the minor alkaloids deviate from it.

<u>Spring poppy biostimulant experiment in open field</u>

The LOMB treatment significantly increased the height of the 'Meara' poppy plants in 2023 (+12%). In the same year, it was also able to significantly increase the yield of seeds and capsules by 20% – it was one of the most successful treatments in terms of capsule yield. However, this effect was not observed in the 'Morgana' variety and in the other two years. In most cases, the LOMB treatment did not significantly affect the alkaloid content and alkaloid composition of the poppy capsules. Only in 2023 did we detect a significantly increased morphine content in the samples of the 'Morgana' variety, but there was no significant difference in the alkaloid yield compared to untreated plants.

In 2023, HUMU treatment significantly increased plant height, capsule yield (+17%) and total alkaloid yield (+22%) in the 'Morgana' variety. In the case of 'Meara', it also increased seed yield (+15%) and morphine concentration. In 2024, HUMU treatment significantly increased the capsule yield in both varieties, as a result of which the alkaloid yield also increased significantly, by about 13-14%.

FULV proved to be very effective in terms of capsule and seed yield. In 2023, the seed yield of the ‘Meara’ variety significantly increased (+16%), and the capsule yield of both varieties increased (+19-31%) compared to the control. Our results are somewhat contradictory regarding the alkaloid content. The treatment resulted in the same alkaloid level as the control in 2022. In 2023, we observed the same in the ‘Morgana’ variety, however, it significantly reduced the morphine content of ‘Meara’. In this case, the alkaloid yield did not significantly exceed the control, since the decrease in the accumulation level shifted the result achieved by increasing capsule production in a negative direction. In 2024, no significant difference in alkaloid content was observed (except for the decrease in thebaine level in ‘Morgana’), however, the alkaloid yield was significantly higher in both varieties (+14-21%). The effect on alkaloid yield was manifested through an increase in the yield of capsules.

The ANOD treatment significantly increased the height of the plants in both varieties in 2023 and 2024 by 3-13%. In 2023, the capsule yield increased significantly in both varieties by 14-17% - however, the seed yield increased only in the ‘Meara’ variety (+21%). Similarly, in 2024, both varieties increased their capsule yield as a result of the treatment (+12-14%), however, in this year the seed yield in neither variety significantly exceeded that of the untreated plants. In 2023, the morphine level in the ‘Morgana’ variety showed a significant increase because of the treatment, as a result of which the alkaloid yield also increased (+25%). The alkaloid yield in 2024 exceeded the control by 16% in both varieties, due to the increase in capsule yield.

Several similarities can be found in the results of the treatment containing algae extract, EMAX, but there are differences in the responses of the varieties. Plant height exceeded the control by 6-10% in both varieties in 2023, and in 2024 in the case of ‘Meara’. The seed yield of ‘Meara’ increased significantly in 2023 (+23%), while that of ‘Morgana’ did not change. There was no significant difference in seed yield in 2024 compared to the control. The capsule yield increased significantly in 2023 in the 'Morgana' variety, and in 2024 in both varieties (+14-17%). Regarding the alkaloid content, we observed a slight decrease in the 'Morgana' variety in 2023, as a result of which the alkaloid yield in this variety did not significantly exceeded the control value, despite the significant increase in capsule production. However, in 'Meara', the alkaloid yield increased by 14% compared to the control. In 2024, only minor changes were observed in the levels of codeine and thebaine due to the treatment, thus,in this year, the alkaloid yield of the varieties increased proportionally to the capsule production.

The MEJA treatment did not affect the height of the plants in 2022 and 2024. However, in 2023, the plants were significantly taller in both varieties compared to the control. In both 2023 and 2024, we observed a particularly large increase both in the capsule yield (+22-38%) and seed yield (+7-49%) in both varieties due to the treatment. We did not detect significant differences in the alkaloid content compared to the control, however, due to the large increase in capsule production, the alkaloid yield also became significantly higher.

As a result of the SALI treatment, the capsule and seed s were statistically the same as the control, and in 2024 the seed yield in the 'Morgana' variety decreased significantly, (-20%). In 2023, the concentration of the morphine, also decreased significantly because of the treatment, as a result of which the alkaloid yield of the 'Meara' variety in this year was also significantly lower (-20%) than that of the control plants. In 2024, the treatment resulted in significantly higher codeine levels in the 'Meara' variety, but did not affect the alkaloid yield, while in the 'Morgana' variety the treatment significantly reduced it (-9%).

As a result of the HIPE treatment, the seed yield in the 'Meara' variety significantly exceeded the control (+28%). The capsule yield in 'Morgana' in 2023 and in both varieties in 2024 exceeded the control (+12-18%). In 2023, as a result of the HIPE, we registered a significant increase in alkaloid yield (+17-28%) in both varieties compared to the control. This was due exclusively to the increase in capsule production in the ’Morgana’ variety, while in the ’Meara’ variety, the significant increase in morphine content also contributed to this. In 2024, only the codeine content of ’Morgana’ increased. At the same time, as a result of the HIPE treatment, the alkaloid yield of both varieties significantly exceeded the control by 14-19% this year.

The ASIB treatment increased the height of the poppy in most cases and most effectively among the treatments (+10-17%). The treatment caused a significant growth in capsule yield in both varieties tested in 2023 and 2024 (+16-21%). In contrast, it had a positive effect on seed yield in only a single case: in the ‘Meara’ variety, in 2023 (+20%). The alkaloid level was not significantly affected by this treatment, significant decrease occurred only in the level of minor alkaloids in some cases. By increasing the capsule yield, it significantly elevated the alkaloid yield in 2023 in ‘Morgana’ and in 2024 in both varieties (+20-24%).

The FLAV treatment resulted in significantly higher plant height in both varieties in 2023 and in 2024 in ‘Morgana’ (+ 8-9%) compared to control. As a result, seed yield also increased: in 2023 both varieties and in 2024 ‘Meara’ significantly exceeded the control yield (13-24%). Similarly, capsule yield in 2023 in ‘Morgana’ and in 2024 in both varieties significantly exceeded the control value (+21-27%). In the second year of the ‘Meara’ variety, the morphine content decreased significantly because of the treatment, while it was not observed in ‘Morgana’. In the following year, only the codeine level of ‘Meara’ decreased. Consequently, the FLAV treatment increased alkaloid yield in both varieties in 2024, while in 2023 only in ‘Morgana’ (+21-31%).

Apart from the two elicitors (MEJA, SALI), the tested biostimulants are marketed in Hungary as yield enhancers. The positive effects observed in our field experiment are therefore in line with our preliminary expectations and those described in other plant species (Alsudays et al., 2024; Rouphael et al., 2017; Villa e Vila et al., 2023). According to the results, these biostimulants may be able to increase the yield of poppy plants under certain conditions, but they do not reliably increase the accumulation level of alkaloids. Our results confirm the findings of Bernáth (1999, 2001), according to which the accumulation level of alkaloids in poppy is primarily regulated by the genotype, but exogenous factors can have a significant effect on the alkaloid yield by influencing capsule production. Since the mode of this effect and its physiological and biochemical backgrounds are not sufficiently clarified, we performed more detailed studies in this direction in a phytotron experiment. We selected the FULV and MEJA treatments for these studies because they produced outstanding results in open field conditions according to our complex evaluation criteria, and their simpler composition enables a more well-founded scientific conclusions.

<u>Spring poppy biostimulant experiment in phytotron</u>

Stem height was significantly affected by water supply, treatment, and the interaction of these two factors. In the normal chamber, plants in the control and FULV treatments grew to 80.5-82.2 cm, which was significantly lower than the value of the MEJA treatment (69.9 cm). In the dry chamber, the average height was 53.1 cm, with no significant difference between the treatments.

Water supply significantly affected all components of plant mass. The treatments significantly affected the fresh and dry weight of the above-ground plant parts, the total fresh plant weight, and the dry matter content of the capsule. The interaction of the two factors had no significant effect on any of the characteristics. In the dry chamber, the average fresh (27.5 g) and dry (8 g) weights per plant were also significantly lower than in the normal chamber (40.2 and 11.2 g).

In the normal chamber, the capsule formation proceeded without disturbance. However, due to drought, the untreated plants were unable to form main capsules. Due to continuous small amounts of water supplementation, they tried to compensate by forming more secondary capsules, which, however, remained small and deformed, and their maturation was delayed. In contrast, the

FULV and MEJA treatments were able to stimulate the plants to form main capsules under dry conditions. It can be assumed that under their influence, the plant directed its energies to the growth of the main capsules, which is supported by the fact that the maturation processes in this cases took place on time, and the water content of these capsules was lower at harvest. Both treatments increased (+22.4-24.3%) the weight ratio of dry capsules within the total plant mass.

The sugar content measured in the leaves did not differ in the normal chamber due to the treatments (glucose + fructose, 13.48-15.34 mg/g) which. was similar to that of untreated plants grown in the dry chamber (11.38 mg/g). However, in the dry chamber, the treatments led to a significant increase in the sugar content of the leaves: in the case of MEJA, the total amount of the two sugars increased doublefold (22.84 mg/g), and in the case of FULV, fivefold (58.80 mg/g). This large increase of the sugar content in the leaves due to the treatments was only expressed under drought stress.

The antioxidant capacity and total polyphenol content measured in leaves were significantly influenced by water supply, treatment and the interaction of these two factors. The antioxidant capacity of leaf samples in the dry chamber was 11% higher than in the normal chamber, which was further increased by the two treatments. In the case of total polyphenol content, the difference between the two chambers was 22%, but only FULV caused a further increase. The proline level measured in leaves was only influenced by water supply. With normal water supply, the proline content was on average 86.52 nmol/gFW, while under dry conditions it was significantly higher, 202.51 nmol/gFW. Dry conditions decreased the average activities of GST and GPX.

Autumn poppy regulator experiment in open field

In most cases, the regulators tested did not have a significant effect on the height of the plants at harvest, either with autumn or spring application. In the year 2022-23, we measured a significantly lower height with TEDI and MEME in autumn treatment, and with TEPR and METK in spring treatment. However, the extent of the decrease (3.4-7.6 cm) is small from a practical point of view. Moreover, in the other two test years, the height of the poppy at harvest was not affected by the treatments.

In our field trials we experienced a significant difference in the extent of frost damage due to the treatments only in the year 2022/23. While we observed 10.9% frost damage in the untreated plots, we found significantly lower values in the PADI and TEBU treatments (7.7-8.8%) and also in the METK and MEME plots (6.5-6.8%). The TEDI and TEPR treatments did not reduce the ratio of frost damage (9.7-10.6%) compared to control. After the spring treatments, no damaging frost effects occurred in any year, and in the year 2023/24, no plant death was measurable during the winter.

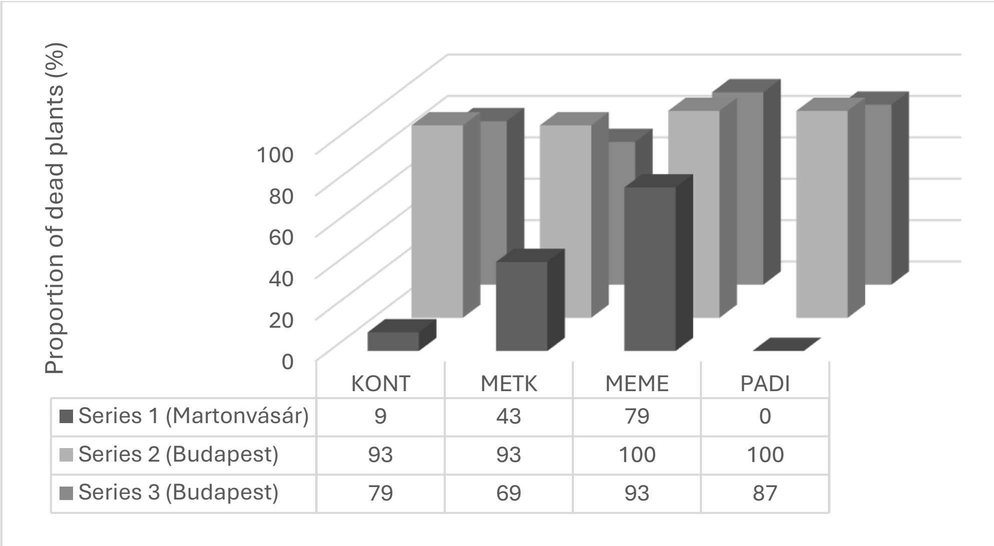
The main effect of treatments significantly affected poppy capsule and seed yield only in 2022/23. Only the PADI treatment, applied in autumn, was able to significantly outperform the control yield: a 19.6% increase in seed yield and a 14.4% in capsule yield were recorded. The regulator treatments did not affect the morphine content of capsules. In our case, the height reduction and yield increase described by Spitzer & Bílovský (2017) occurred rarely and to a lesser extent.

Based on the first results, we selected three treatments for further investigation, the METK, MEME and PADI treatments. By analyzing the leaf samples taken from the field in December 2023, we determined that the amount of osmoprotectants in the leaves did not change due to the treatments. The combined concentration of glucose and fructose was between 207.06-219.38 mg/gDW, while the proline content was between 388.35-536.34 nmol/gFW. There was no detectable difference in the activity of antioxidant enzymes (APX, CAT) measured in the leaf samples of any treatment plots.

Autumn poppy regulator experiment in phytotron

To gain a more precise understanding of the effects of these three selected treatments and to explore the physiological and biochemical background, we also performed three series of phytotron tests. During the phenotyping, the height of the control plants was 75.0 mm, which significantly decreased as a result of the treatments (45.0-63.3 mm). In all three treatments, the area of the rosette plant also decreased (142.3-386.9 mm^2) compared to the control (459.1 mm^2). In both cases, the MEME treatment gave the lowest value, the values of which were also significantly lower than the other treatments. MEME also significantly reduced the so-called roundness index and compactness index. In addition to MEME, PADI also caused a detectable decrease in the plant circumference. According to Dobos et al. (2011), the horizontal leaf position experienced is a characteristic of frost-tolerant poppy.

The treatments in the three different phytotron series gave significantly different results. In the first series, where the minimum temperature applied was -4°C, 9% of the control plants died due to frost. In the METK (43%) and MEME (79%) treatments, much higher frost damage was experienced, while in the PADI treatment there was no death. In the second series, the minimum temperature was lower, -6°C was set. As a result, 93% frost damage was experienced in both the control and METK groups, while all plants died in the MEME and PADI treatments. In the third series, slightly more developed individuals were examined with the same settings. At this time, frost damage was 79% in control, which decreased to 69% due to the METK treatment, and slightly increased in the other two groups (PADI: 87%, MEME: 93%). The results are illustrated in Figure 1.



	KONT	METK	MEME	PADI
Series 1 (Martonvásár)	9	43	79	0
Series 2 (Budapest)	93	93	100	100
Series 3 (Budapest)	79	69	93	87

Figure 1. Effect of treatments on the proportion of frozen plants in phytotron test series (average)

Even though these regulators reduced frost damage in the field experiments, we mostly experienced an increase in frost sensitivity in the phytotron tests. In our field experiment, the tested plant population was less uniform compared to the phytotron tests. In the 2022/23 test, the plants were in 6-14 leaf stage when winter arrived, and according to our observations (not quantified), there, a higher proportion of plants with 12-14 leaves died. Another important difference is that in the field test, the damaging frost effect appeared about 3 months after the treatment, while in the phytotron, we exposed the plants to cold effects 2 weeks after the treatment. It was concluded that the frost tolerance of the variety we tested may be higher at the age of 8-10 leaves than at the generally accepted 4-8 leaf stage (Hornok, 1978; Pappné, 2014). Based on our results, it can be assumed that regulators can influence frost tolerance through their growth-regulating effect, via plant size. Our results support that the effect of these regulators on the frost tolerance of poppy is therefore less predictable.

Leaf samples were taken from the plants of the first phytotron series for laboratory analysis of hormones. Similarly, these tests were also performed on leaf samples previously taken from the field.

In the field samples, no differences were observed in the auxin level (1.77-2.03 ng/g) between the groups. Abscisic acid (ABA) was 6.75 ng/g under MEME and PADI treatments, which was significantly, 20.2% higher than in the control. The concentration of gibberellic acid (GA) in the control was 6.75 ng/g, which did not change significantly under PADI treatment, but increased in METK and MEME treatments (7.73-7.98 ng/g). The levels of plant hormones in the leaf samples from the phytotron experiment differed greatly, as did the responses to the treatments. Auxin was present in significantly different amounts in all four groups, with METK higher than the control value (50.44 ng/g) and MEME and PADI lower. The ABA content was the same both in the control and PADI plants (2.85-2.54 ng/g), and much lower in the METK and MEME treatments (0.15-0.17 ng/g). The level of GA also differed in all four treatments, being lower in PADI (0.54 ng/g), and higher in METK and MEME (1.74-2.54 ng/g) than the control value (1.01 ng/g).

Previously, there was no data available on how triazoles affect plant hormone levels in poppy. In our studies, the hormonal response of poppy to the treatments differed significantly from that described in other plant species (Rademacher, 2016). Contrary to our expectations, the GA concentration in leaves in most cases significantly exceeded the control - a lower value was measured only in the PADI phytotron samples.

Since the treatments stopped the growth of poppy, we assume that blocking of GA synthesis occurred, but this could have been followed by a "rebound effect" (Husiny et al. 2023). Our phytotron results also confirm the ABA-GA antagonism described by Liu & Hou (2018): in the METK and MEME treatments, the concentration of ABA decreased with the increase in GA levels.

However, the results of the samples collected from the field are contradictory: in the MEME treatment, the levels of both ABA and GA increased significantly.

3. CONCLUSIONS AND RECOMMENDATIONS

In our work, we examined how the size of poppy capsules affects the alkaloid content and the proportion of seeds. Within a genotype, small and medium-sized capsules did not differ from each other in any of the tested varieties, but large-sized capsules differed significantly: in the 'Meara' variety, the alkaloid concentration decreased significantly (by 60%), while in the 'Morgana' variety, the concentration of codeine and thebaine increased, while the concentrations of morphine and total alkaloid concentrations remained unchanged. The proportion of seeds in large capsules of this variety decreased significantly. Therefore, larger capsules do not necessarily guarantee proportionally more seeds than smaller ones, this largely depends on the variety and genetic background. In the cultivation of the 'Meara' variety, the highest proportion of small and medium-sized capsules is desirable. In contrast, in the 'Morgana' variety, the formation of large-sized capsules is more advantageous – which can result in higher alkaloid yields.

In both examined varieties, the mass ratio of each organelle within the capsule was similar. The capsule wall accounted for the largest portion of the mass, followed by the placenta. The disc and the thalamus represented a smaller, almost equal to each other parts. Our data demonstrate a higher accumulation level of morphine and total alkaloids in the capsule wall and placenta compared to the disc and thalamus. However, the difference between the capsule wall and the placenta depends on the variety: while the alkaloid concentration of 'Meara' is highest in the wall, 'Morgana' shows a significantly higher accumulation level in the placenta. Morphine follows the trend of total alkaloid levels, but codeine and thebaine often change according to a different trend. In field cultivation, those varieties that accumulate the highest amount of alkaloids in the placenta may be more favorable, since the risk of leaching is lower due to its protected location. More precise knowledge of the accumulation and localization of alkaloids can increase the efficiency of targeted breeding and help in variety selection during field cultivation.

Our results showed that among the biostimulant treatments used, algae extracts and plant extracts may be the most effective in significantly increasing the height of the poppy plant. This effect varies between years and varieties. The greatest increase in height was detected in the ASIB treatment, but significant stimulating effects were also observed in the ANOD (*Ascophyllum nodosum* algae extract) and EMAX (*Ecklonia maxima* algae extract) treatments and in the FLAV treatment containing several plant extracts. The taller spring poppy plants can fight weeds, especially T4 types, more effectively and can be harvested cleaner.

Under field conditions, the biostimulant treatments tested – except for salicylic acid – may also be able to increase poppy yield, but their effects proved to be different for the two yield components, the poppy capsules and poppy seeds. The yield-increasing effect of the tested biostimulant substances varies in each poppy variety, and its appearance can be significantly influenced by the effect of the year. With proper agrotechnics, good soil fertility and nutrient supply, it is supposed that biostimulants generally increase poppy yield more effectively than mineral foliar fertilization (LOMB treatment) that contains solely nutrients. The largest and most frequent yield increase was observed with the treatment containing fulvic acid (FULV) and methyl jasmonate (MEJA), which justified a more detailed investigation of the mechanism of action of these two treatment under controlled conditions.

The concentration of the main alkaloids (morphine, codeine, thebaine) in poppy capsules cannot be reliably increased by biostimulant treatments. Nevertheless, in some cases, certain biostimulant treatments can significantly increase (e.g. HIPE, ANOD, LOMB), or even decrease (e.g. FULV, FLAV) the level of alkaloids in poppy capsules. However, as a result of the treatments, we observed in several cases a significant increase in the alkaloid yield (up to 43.2% compared to the untreated control), which was primarily achieved through an increase in the capsule yield. Based on all this, the use of the approved biostimulants may have a positive effect in the practical cultivation of poppy seeds in Hungarian conditions. However, taking into account the economy, depending on the given conditions and variety use, individual optimization of the agent and the dosage is definitely recommended.

Our phytotron experiment confirmed that foliar treatments with fulvic acid and methyl jasmonate at the beginning of stem initiation and after petal fall promote normal capsule formation under dry conditions. The protective role of these treatments is primarily manifested in the increase in the concentration of simple sugars (glucose and fructose) measurable in the leaves, as well as in the enhancement of antioxidant capacity expressed in ascorbic acid equivalent. The sugar concentration increased approximately doublefold in the MEJA treatment, and fivefold after FULV spraying. Sugar accumulation during drought is an adaptive reaction known from other species, which our work also confirms in the *Papaver somniferum* species. However, the role of proline, also known as an osmoprotectant and signal transducing molecule, is questionable here, as its accumulation level was not influenced by the treatments, but only by the water supply. Under the influence of MEJA, the poppy stem becomes shorter, the mass of the vegetative above-ground plant parts decreases significantly, while the mass of the crop, and the length of the root system does not change demonstrably.

We tested regulators containing different triazole or triazole + onium compounds on autumn-sown confectionary poppy (‘Zeno Plus’ variety) in field and phytotron experiments. Treatments with regulators containing metconazole, metconazole + mepiquat chloride, and paclobutrazol + difenoconazole resulted in the growth of 6-8-leaf, rosette-shaped poppy plants being stunted, and their leaves taking on a spreading position. The size of the plant is reduced in several dimensions: in addition to height, the area and circumference of the rosette plant are also reduced – however, in most cases this does not lead to a reduction in subsequent height. A significant reduction in the height at harvest was only observed in the 2022/23 study, with TEDI and MEME applied in autumn, and TEPR and METK applied in spring. Under field conditions, some regulator treatments (TEBU, METK, MEME, PADI) were able to reduce the proportion of plants that died due to the frost. However, under controlled conditions, this did not occur, or only sporadically, and in most cases the extent of frost damage increased significantly as a result of the treatments. When examining the biochemical background of the phenomenon, we also encountered significant contradictions: the treatments did not increase the concentration of osmoprotectant substances (glucose, fructose, proline) potentially playing a role in frost tolerance, nor did they increase the activity of the antioxidant enzymes APX and CAT.

The tested regulators are also able to significantly influence the levels of plant hormones, but due to the contradictory data it is difficult to draw a clear conclusion: depending on the composition, the treatments may reduce or increase both auxin and ABA and GA levels. It is worth noting that although the tested preparations containing metconazole, mepiquat chloride, paclobutrazol or difenoconazole, according to scientific knowledge, exert their effect by blocking GA synthesis, and thereby inhibiting the growth of the rosette plant. In our studies we nevertheless experienced a significantly increased GA value in almost all cases in the treated groups (14.5-151.5% increase). However, the inhibition of plant growth occurred according to the plant size data, which assumes a GA inhibitory effect. The detected higher GA values may indicate a so-called rebound effect, when the concentration jumps back to a higher value after a temporary decrease. This could possibly be confirmed by regular sampling in the future. In our open field experiment, the damaging frost effect appeared months after the treatment, while in the phytotron we started the freezing program 2 weeks after the treatment. According to our observations, in the 6-14-leaf stand in the open field, mainly large, well-developed plants died, while among the 6-8-leaf plants examined in the phytotron, on the contrary, the smaller ones tolerated the cold poorly. These results allow us to conclude that the effect of the regulators used in poppy depends on the size and development of the plant, the time and extent of the frost effect, and other environmental factors (e.g. soil quality), so their integration into the agrotechnology of poppy involves significant uncertainty.

Based on our results, it can be assumed that regulators affect frost tolerance by influencing growth through the plant's homeostasis and temporarily inhibiting it. However, as mentioned above, their effect can be both negative and positive depending on the timing and environmental conditions. In field cultivation, autumn-sown poppy takes a long time, - often just before the beginning of winter-, to reach the phenophase necessary for overwintering, so growth regulation performed in the autumn period may carry significant risks.

Our three-year results show that the tested regulators do not affect the accumulation level of the main alkaloids in the capsules of the ‘Zeno Plus’ variety, nor do they reliably affect the capsule and seed yield. Based on our data obtained in the experimental areas, the frost damage-reducing effect of triazole or triazole + onium active ingredients in poppy field cultivation could not be proven.

4. NEW SCIENTIFIC RESULTS

1. In the industrial poppy variety 'Meara', large capsules accumulate morphine in lower concentrations than smaller capsules.

2. The placenta of the industrial poppy variety 'Morgana' has a significantly higher alkaloid concentration than the capsule wall, in contrast to other varieties studied so far.

3. According to our results, the use of biostimulants does not affect the alkaloid content of industrial poppy capsules, but increases the capsule and seed yield, and thus the alkaloid yield. Treatment containing methyl jasmonate, fulvic acid[1] and plant extracts with high flavonoid content[2] is highly effective.

4. Under *in vitro* conditions, drought (50% SWC) increases the proline content, the antioxidant capacity and total polyphenol content in the poppy leaves, the activity of the antioxidant enzymes GST and GPX decreases.

5. *In vitro*, foliar spraying with fulvic acid and methyl jasmonate increases the glucose and fructose content of poppy leaves under dry conditions (50% SWC). This effect does not occur under average water supply (75% SWC).

6. Treatment with triazole or triazole + onium type regulators reduces the size of the rosette poppy plant, but according to our data, this is probably not directly related to changes in either GA_1 or auxin levels.

[1] Fulvic Nature product
[2] Flavo Plant product

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