Elicitation Studies on *Nepeta* spp.: A Review

Kirsten A. Allen[1*], Erik Nunes Gomes[1,2], Or Doni[1], Qingli Wu[1] and James E. Simon[1*]

[1]New Use Agriculture and Natural Plant Products Program, Department of Plant Biology, Rutgers University, 59 Dudley Road, New Brunswick, NJ 08901, USA
[2]EPAGRI – CEDUP Vidal Ramos, Rua Maria Olsen, SN, Marcilio Dias, 89465-250 Canoinhas, SC, Brazil

***Corresponding author:** jimsimon@rutgers.edu

Manuscript received: April 23, 2024

Keywords: Catnip, catmint, elicitors, essential oil, Lamiaceae, nepetalactones, rosmarinic acid

ABSTRACT

Catnip (*Nepeta cataria* L.) and other catmints from the *Nepeta* genus are commonly utilized in ethnomedicine preparations across many geographical regions including South-West and Central Asia, Africa, and North America. Its significance in herbal lore has led researchers to investigate the pharmacological attributes of *Nepeta* spp. in addition to the biological activities of its essential oils and extracts. Nepetalactones are one of the major classes of compounds responsible for catnip bioactivity and the biochemical pathway that produces these iridoid monoterpenes is actively being explored to uncover its regulatory mechanisms on a molecular level. As market trends increase for plant natural products, such as catnip, agronomic tools including elicitation are being implemented to optimize the production of high-value secondary metabolites by stimulating plant stress responses. Therefore, the present review summarizes these key attributes from several *Nepeta* spp. and while also covering the reported literature from the varied abiotic elicitation studies conducted within this genus and others in the Lamiaceae family.

INTRODUCTION

The *Nepeta* genus encompasses many catmint species and is most known for *Nepeta cataria* L., or catnip. It is the most extensively studied species of *Nepeta* despite the genus bearing over 280 species (Salehi et al., 2018). Taxonomically it is positioned under the Lamiales order, the Lamiaceae family, the Nepetoidae subfamily, and the tribe Menthae (ITIS, 2023). The *Nepeta cataria* botanical classification is emblematic of the bioactive capability of catnip to elicit a euphoric response in cats which is attributed to the nepetalactones present in the essential oil of the plant (Bol et al., 2022). As a result, catnip is commonly used by the pet toy industry to manufacture cat-attractant products (Gomes et al., 2020c). Catnip also has a number of traditional uses in herbal preparations and ethnobotanical medicine as later described.

Widely naturalized throughout temperate regions of the world, *Nepeta* is a multi-regional genus distributed mainly in South-west and Central Asia, Europe, Africa, and North America (Hedge, 1986; Dirmenci et al., 2004; Mahr, 2023). Karami et al. (2022) remarks that biodiverse *Nepeta* species can be found across Eurasia including the Irano-Turanian region of southwestern Asia and the western Himalayas. *Nepeta crispa* Willd., a rare and threatened species endemic to western Iran, is extensively used in Iranian traditional medicine (Mahmoodi et al., 2022). The aerial parts of *N. crispa* are prepared as an infusion and beverage with sedative, relaxant, carminative, and restorative properties for nervous and respiratory disorders (Sonboli et al., 2004). *Nepeta nepetella*, native to Algeria, is one of the most reported African species in the genus. Herbalists in the region often apply it externally to treat insect bites and prepare an infusion for its diuretic, febrifuge, spasmolytic and stimulating attributes (Bellahsene, 2017; Gomes et al., 2020b). The Amchis, local medicine men who inhabit the cold, arid zone of the Himalaya known as the Nubra Valley, work with multiple *Nepeta* species to address the public health of tribal communities. Leaf and whole plant preparations are used to treat stomach disorders, cough, and eye conjunctivitis while decoctions of leaves can treat diarrhea, pneumonia, and fever (Kumar et al., 2009). Whereas, in North America, African American herbalists and caregivers have traditionally used catnip (*Nepeta cataria* L.) in the form of a tea to treat infantile colic (Smitherman et al., 2005). These are only a few examples of the multiple ethnopharmacological uses of this genus. Since the list of ethnobotanical uses is extensive, further research utilizing bioassays has also identified promising pharmacological activities in these medicinal plants.

The biological activities of *Nepeta* have been thoroughly investigated via *in vitro* and *in vivo* testing. Essential oils from *N. cataria* L., *N. rtanjensis*, *N. faassenii*, and *N. crispa* have exhibited remarkable antimicrobial activity by inhibiting the growth of bacteria and fungi including *Pseudomonas* spp., *Alternaria* spp., *Escherichia coli*, and *Staphylococcus aureus* (Sonboli et al., 2004; Stojanović et al., 2005; Grbić-Ljaljević et al., 2008; Nedorostova et al., 2009; Formisano et al., 2011; Patel et al., 2023). *Nepeta* essential oils have also been assayed for antioxidant and enzyme inhibitory activity. The essential oils from *N. nuda* subsp. *glandulifera* and *N. cadmea* exhibited radical scavenging and metal chelating activity in addition to inhibitory activity against tyrosinase and α-amylase (Sarikurkcu et al., 2018). Bioherbicidal studies observing the allelochemical effects of essential oils from *Nepeta meyeri* demonstrated inhibitory activity against seed germination and seedling growth of weed species; while *Nepeta cataria* essential oil exhibited phytotoxic activity against the adventitious rooting of several Lamiaceae species (Mutlu et al., 2010; Allen et al., 2023). Though catmint plants are commonly known for their feline-attractant properties, recent studies have explored their insect repellent actions. Catnip essential oils and isolated nepetalactones have been evaluated against mosquitoes (*Aedes aegypti*), bed bugs (*Cimex lectularius* L.), and ticks (*Ixodes scapularis*; *Haemaphysalis longicornis*) showing comparable efficiency to the industry gold standard, N, N-Diethyl-m-toluamide (DEET) (Reichert et al., 2019; González et al., 2022; Patel et al., 2023).

Many of the bioactive characteristics of *Nepeta* species may be attributed to their unique iridoid monoterpenes, nepetalactones and their precursors; however, catmints also produce an array of other secondary metabolites including phenolic acids and their glycosides, flavonoids and their glycosides, other terpenoids, steroids, lignans, and volatile oils (Sharma et al., 2021). Catnip plants produce these bicyclic nepetalactones as a means of chemical defense against pests (Kramer, 2020). To uncover the unique biosynthesis present in *Nepeta* species, Lichman et al. (2019) found that catnip terpenes are formed in a two-enzyme cascade unlike the canonical terpene pathway. The authors reported that one enzyme is responsible for activating 8-oxogeranial and converting it into an enolate intermediate. And a second enzyme, a dehydrogenase, further cyclizes the enolate to form two ring structures. Recent genome analysis work by an international team of researchers has revealed that the ability to produce iridoids was lost in progenitors of catnip, but repeated evolution resulted in catnip regaining the genes for nepetalactone biosynthesis (Max Planck Institute for Chemical Ecology, 2020). Other species in the Nepetoideae subfamily, including well-known herbs such as mint, rosemary, basil, and oregano, do not produce iridoids namely due to the deletion of key pathway genes that encode for iridoid synthases (ISY) (van Hoose, 2020). The discovery of the iridoid synthase genes coupled with further investigation led to the revelation of an additional class of enzymes known as nepetalactol-related short chain dehydrogenases (NEPS) (Lichman, 2021). The genes responsible for producing these enzymes, ISY and NEPS, combined with major latex protein-like genes (MLPL) comprise nepetalactone gene clusters within catmints that then form three different nepetalactone stereoisomers as end products (Figure 1): cis-trans, cis-cis, and trans-cis (Smit and Lichman, 2022).

Due to the numerous studies evidencing biological activities, commercial interest in *Nepeta* species is increasing. Therefore, approaches are needed to produce more bioactive metabolites from the genus. Traditional breeding programs have been developing highly productive, elite cultivars through genetic improvements mainly in *Nepeta cataria* (Reichert et al., 2016). Other research groups have been focusing on strategies to increase the yield of valuable metabolites in catmints. Many agronomic approaches have shown marked potential to improve catnip growth and development while positively impacting the yield of metabolites in *Nepeta* species, including fertilization (Dehsheikh et al., 2021), irrigation (St. Hilaire et al., 2004), harvesting regimes (Gomes et al., 2020a; Gomes et al., 2023), and light treatments (Manukyan, 2013; Marković et al., 2022) among others. But studies are still lacking, especially regarding how these different agronomic approaches affect the accumulation of bioactive compounds at the molecular and transcriptional levels which contribute to the expression of biosynthetic enzymes.

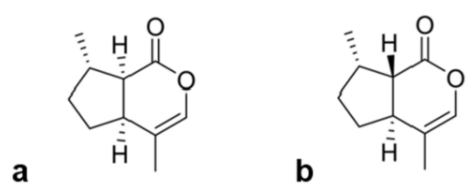

Figure 1. Nepetalactone structures representing the (*cis, trans*) stereoisomer (a) and (*trans, cis*) stereoisomer (b).

A common agronomic approach to increase secondary metabolite production in other Lamiaceae species is elicitation. Elicitation is defined as the stimulation of plant defense responses by stress-inducing factors, known as elicitors, that often trigger the biosynthesis of natural products in plants (Kuzel et al., 2009). Some of the more commonly tested elicitors include salicylic acid, methyl salicylate, jasmonates, and chitosan (Thakur and Sohal, 2013; Guru et al., 2022). The current review aims to discuss the use of elicitors in commercially important plants within the Lamiaceae family while presenting examples of their potential uses and interactions in the molecular pathways of selected species. This work will also comparatively assess the current literature regarding the use of elicitor compounds in *Nepeta* species. The results will discuss existing limitations and recommendations for future work.

2. Elicitation of Medicinal Plants

Medicinal plants display variable responses when exposed to stress induced by elicitors. In some cases, stress may reduce overall growth and development, while positively affecting the yield of therapeutic compounds (Gorelick and Bernstein, 2014). Outside of the mint family, elicitors have been effective at enhancing the quality of medicinal plants valued by the pharmaceutical industry. In Madagascar periwinkle (*Catharanthus roseus* L.), for example, methyl jasmonate in combination with UV-B irradiation increased the accumulation of medically important alkaloids: vinblastine, vincristine, and ajmalicine. The treatments also induced expression of two key synthesis genes: *tryptophan decarboxylase* and *strictosidine synthase* (Rady et al., 2021). An additional medicinal plant of industrial significance is purple foxglove (*Digitalis purpurea* L.), since it is highly regarded for its biosynthesis of cardiac glycosides. Researchers investigating the response of *Digitalis purpurea* L. to polyamines and methyl jasmonate showed that spermidine and methyl jasmonate significantly increased the phenol content, antioxidant activities, cardenolides, and digitoxin content of callus suspension cultures (Rad et al., 2022). Another study involving a foxglove species, *Digitalis trojana* Ivanina, demonstrated the ability of salicylic acid and high temperature treatments to induce cardenolide accumulation while also increasing the levels of proline, total phenolic, and flavonoid content (Cingoz and Gurel, 2016). Abiotic elicitors have been further tested on oriental poppy (*Papaver orientale* L.), a source of morphinan alkaloids. Elicitation with salicylic acid and methyl jasmonate increased the accumulation of morphine and thebaine by upregulating the expression of related pathway genes (Hashemi and Naghavi, 2016).

2.1. Elicitation Effects on Commercially Important Lamiaceae Species

Although the previously cited examples are of particular interest to the pharmaceutical and medicinal industries, elicitor studies have also been conducted on essential oil-bearing plants like those in the Lamiaceae family. These essential oils exhibit potent biological activities that are valuable in natural medicine, pharmacology, cosmetology, and aromatherapy (Sun et al., 2022). A number of studies have tested various elicitors on species in the mint family to assess how these factors might influence metabolite production, gene expression and enzyme activity. Table 1 lists numerous case studies encompassing select species from this family, but there are many more studies represented in the current literature.

Often researchers evaluating the effects of these elicitors will assess a range of physiological and biochemical responses from different species to understand how each species will react differently. Some studies focus on how essential oil yield and composition differ in response to abiotic treatments. Kandoudi et al. (2022) tested both salicylic acid (SA) and methyl jasmonate (MeJa) on four Lamiaceae species: peppermint, basil, hyssop, and marjoram. The authors quantified the essential oil yields and noted any changes to the volatile composition of each species. Their results suggest that Lamiaceae species show different sensitivities to elicitors and the dosages would need to be tailored as such. Some studies determine the effects of elicitor treatment in conjunction with additional abiotic stressors. For example, El-Esawi et al. (2017) assayed how salicylic acid would affect rosemary plants subjected to salinity stress. The authors found that salicylic acid combatted the toxic effects of saline and stimulated the antioxidant enzyme pathway. In a study analyzing the effects of nano-biofertilizer on rosemary during drought stress, the authors observed a 1.57% increase in essential oil percentage despite 30% moisture content (Eskandari et al., 2023). In contrast, Farsi et al. (2019) quantified the growth responses of oregano under limited irrigation conditions and found that treatment with methyl jasmonate led to significant reductions of essential oil yield under mild limited irrigation.

Because a climate change scenario could heavily impact the Mediterranean basin and its surrounding regions, several studies have begun assessing the effects of climate change on economically valuable medicinal and aromatic plant species within the Lamiaceae family due to their wide distribution in the Mediterranean region (Mansinhos et al., 2024b). The Intergovernmental Panel on Climate Change (IPCC) anticipates average temperatures will continue rising along with shifts in precipitation patterns that could reduce soil water availability and increase chances of drought and soil salinity across different ecosystems (IPCC, 2022). As a result, these changes in environmental conditions could directly affect aromatic plant growth and development and secondary metabolism. For example, one study exploring the effects of several abiotic factors on the essential oil (EO) yield, composition, and biological activity on *Lavandula viridis* L'Hér, found that severe heat and high salinity increased the concentration of two most abundant compounds, 1,8-cineol and camphor. Severe heat also improved the enzyme inhibition activity of the EO for butyrylcholinesterase and tyrosinase while drought, salinity, UV-B radiation increased the capacity of the EO to inhibit acetylcholinesterase. Overall, the tested environmental conditions increased the EO yield and altered its antioxidant activity (Mansinhos et al., 2024a).

In addition to drought and salinity, Lamiaceae will likely be affected by pending changes in climate through other environmental stress factors such as temperature, light and heavy metals (Mansinhos et al., 2024b). In a multi-species study comparing the effects of salinity and drought on the essential oil yield of *Mentha spicata* (spearmint), *Origanum dictamnus* (dittany), and *Origanum onites* (oregano), Stefanakis et al. (2024) found that oregano tolerated relatively high saline levels in response to NaCl (100 mM) application in soil. Compared to spearmint, oregano demonstrated significantly lower concentrations of stress markers such as proline and malondialdehyde and exhibited an increased production of essential oil and hydrogen peroxide. Similarly, dittany appeared to maintain its growth and essential oil quality indicators in response to salinity and drought stress. Spearmint, however, exhibited greater oxidative stress and damage compared to the *Origanum* species. Another study focused on *Origanum* explored the effects of light intensity on *Origanum majorana* (sweet marjoram). Hashemifar et al. (2024) assessed how varying the intensity of natural light could influence essential oil content, the expression of monoterpene biosynthesis genes, and other growth parameters. As light intensity increased, both plant dry weight and total sugar content significantly increased. Additionally, the study showed that the essential oil yield of sweet marjoram increased until light intensity reached 70%, but it significantly decreased under full light. The gene expression level of *1-deoxy-D-xylulose 5-phosphate reductoisomerase (DXR)* exhibited a similar pattern suggesting a strong and positive correlation between *DXR* and essential oil synthesis in sweet marjoram. Overall, their study emphasized the importance of maintaining an optimal degree of light intensity to balance both biomass yield and essential oil production.

In addition to analyzing biomass and essential oil yield, many of these studies also evaluate the bioactivity level of enzymes involved in relevant antioxidant pathways or the transcriptional changes of genes involved in the biosynthetic pathways of high-value secondary metabolites. In *Salvia* species, for example, salicylic acid was shown to upregulate phenylalanine ammonia lyase (PAL) expression and increase rosmarinic acid content (Ejtahed et al., 2015). In studies involving both basil and lemon balm, chitosan lactate (ChL) increased antioxidant enzyme activity. Additionally, ChL treatment stimulated the production of rosmarinic acid, anthocyanins, and total phenolic compounds in lemon balm; however, in basil, ChL only increased accumulation of rosmarinic acid (Hawrylak-Nowak et al., 2021). Peppermint has also exhibited variable responses to elicitors. Though chitosan and gibberelic acid downregulated the genes in its menthol biosynthesis pathway, methyl jasmonate upregulated key pathways genes (Soleymani et al., 2017). A non-protein amino acid, β-aminobutyric acid (BABA), could also stimulate the secondary compounds and their associated genes in Lamiaceae plant species. After treating *Mentha suaveolens* × *piperita* (grapefruit mint) with BABA, Akbarzadeh et al. (2023) found that exogenous application of the elicitor effectively mitigated the negative impacts of water deficit stress, improved the essential oil content, and enhanced its essential oil composition by increasing the percentage of linalool and linalool acetate.

Determining which elicitors induce certain biosynthetic genes and enzymes can help us improve the effectiveness of these treatments while furthering our understanding of the molecular "cross-talk" that exists within these signaling pathways. As a result, combinatorial formulations have frequently been tested and evaluated for their elicitation potential. In one study, Stasińska-Jakubas et al. (2023) applied chitosan lactate, selenite, and salicylic acid to lemon balm alone and in combination finding the strongest elicitation effects with chitosan lactate or salicylic acid alone. Another study investigated how the combined application of chitosan nanoparticles and arbuscular mycorrhizal fungi biofertilizer could optimize the physiological characteristics and secondary metabolite production of *Lallemantia iberica* (balangu) under different levels of water deficit stress (Javanmard et al., 2022). The highest essential oil content and yield were achieved under mild water deficit stress (60% field capacity) when treated with a combination of the nanoparticles and biofertilizer. The maximum activity of antioxidant enzymes including superoxide dismutase (SOD), ascorbate peroxidase (APX), and peroxidase (POX) was achieved under the same conditions. The combined treatment of chitosan nanoparticles and fungi biofertilizer not only modulated the response of balangu plants to water deficit, but also optimized the essential oil quantity and quality. Another study investigated how the combined application of salicylic acid and zinc oxide nanoparticles could improve the physiological function of *Salvia virgata* Jacq. under salinity stress. Bozaba and Kuru (2024) found that treated plants exhibited higher levels of photosynthetic pigments and better gas exchange rates compared to untreated stressed plants. The salicylic acid and zinc oxide nanoparticles coapplication significantly increased the activity of key antioxidant enzymes in the leaves of *S. virgata* while also enhancing the content of proline, soluble sugars, and other osmoprotectants.

Because plant species in the Lamiaceae family commonly grow in arid regions subject to changes in climate and environmental conditions, studies should continue simulating the effects of different abiotic factors on plant productivity and phytochemical composition in order to determine the biological properties affected by the climate-related stresses and identify pathways to optimize the production of valuable secondary metabolites (Skrypnik et al., 2024).

2.2. Elicitation in *Nepeta* Species

In contrast to other Lamiaceae, there are much fewer elicitation studies that have been conducted with *Nepeta* spp. Yet, those studies examining the elicitation of secondary products in Nepeta spp are summarized in Table 2.

Most of the elicitation studies in the genus do not attempt to establish a mode of action for the physiological and productive changes observed with the application of different molecules. However, a few studies have pointed out that the elicitors trigger changes in gene expression, inducing resistance to abiotic stresses, changes in essential oil production and composition, and increase production of iridoid compounds (Figure 2).

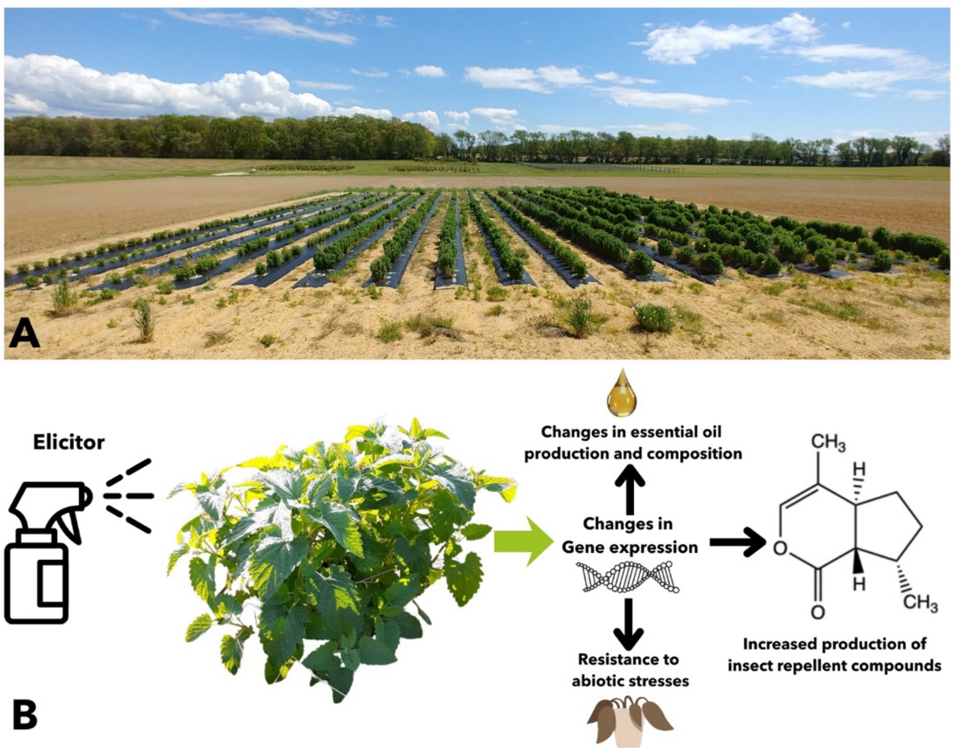

Figure 2. Agronomic studies in *Nepeta* spp. **A:** Experimental field of *Nepeta cataria* at The Rutgers Agricultural Research and Extension Center in Upper Deerfield, NJ, United States, Photo: Teddy Brown. **B** Schematic representation of elicitation studies on *Nepeta species.*

Abiotic Stress and Elicitors

Since a number of *Nepeta* species can be found in arid and semi-arid regions, dehydration stress and water stress studies have been conducted on different chemotypes to understand how these abiotic factors may exert physiological and biochemical changes on the plants. Said-Al Ahl et al. (2016) investigated the effects of three water stress treatments (40, 60, and 80% available soil moisture) and foliar application of salicylic acid (SA) on two *Nepeta* chemotypes: *Nepeta cataria* and *Nepeta cataria* var. *citriodora*. The authors concluded that SA application can improve the growth performance including plant height, number of branches and herb fresh weight in addition to enhancing the accumulation of essential oil marker compounds in *Nepeta* plants under drought stress. Another study explored how changes in water availability are regulated on a molecular level in *N. rtanjensis* and *N. argolica* ssp. *argolica* (Aničić et al., 2020). After the plants were subjected to severe polyethylene glycol (PEG)-induced dehydration stress, transcript abundance decreased in the majority of the 10 nepetalactone (NL) biosynthetic genes that were screened in conjunction with an initial reduction in NL content. The downregulation of related NL biosynthetic genes and transcription factors was well correlated with the metabolic accumulation of NL stereoisomers suggesting that NL biosynthesis is regulated at the transcriptional level. Recently Aničić et al. (2022) assessed the elicitation effects of methyl jasmonate (MeJa) on iridoid biosynthesis in *Nepeta rtanjensis* and *Nepeta nervosa*. Treatment with MeJa elevated the expression of iridoid related biosynthetic genes and increased the accumulation of valuable iridoid monoterpenes in *Nepeta rtanjensis*; however, in *Nepeta nervosa*, fewer genes were upregulated and no iridoids were accumulated post-treatment. In another study, Petrović et al. (2025) demonstrated how waterlogging, hydrogen peroxide elicitation and a combination of both stressors affected specialized metabolism in leaves of *N. nuda* and *N. grandiflora*. Significant changes in the production of volatile compounds upon stress were recorded for both species and the quantify of VOCs significantly increased 48 hours after treatment. The results also revealed significant upregulation of several NEPS genes, key components of iridoid biosynthesis, in both *N. nuda* and *N. grandiflora*. *N. nuda* leaves exhibited greater antioxidant potential than those from *N. grandiflora* which may indicate higher stress tolerance in *N. grandiflora* or superior capacity for *N. nuda* to mitigate oxidative stress.

Another *Nepeta* study compared the influence of different climatic factors on the essential oil content and composition of 20 populations of *N. binaludensis* Jamzad. The essential oil (EO) yield of *N. binaludensis* Jamzad was positively correlated with precipitation and negatively correlated with temperature. The authors also noted that increases in altitude were positively correlated with the EO % of 1,8-cineole and negatively correlated with the EO % of nepetalactone resulting in different chemotypes (Moghaddam et al., 2023). Overall, these results suggest that chemical elicitors and environmental factors such as geographic and climatic variables will influence the *in planta* chemistry and gene regulation of each *Nepeta* species differently. Simulating diverse stress conditions that change the chemical profiles of *Nepeta* species also offers the opportunity for farmers and agronomic stakeholders to create optimal growing conditions that maximize the productions of desired metabolites (Petrović et al., 2025).

Biofertilizers and Phytohormones

The use of biostimulants to influence plant growth and development has also been applied to *Nepeta* spp. Humic substances, such as humic acids, are commonly reported to improve soil physicochemical properties, root nutrient uptake, and lateral root development (Canellas et al., 2015; Albrecht, 2019). In a study using three *Nepeta* species (*Nepeta cataria* [catnip], *Nepeta cataria* var. *citriodora* [lemon catnip], and *Nepeta grandiflora* [giant catmint]), Mohamed et al. (2018) demonstrated that foliar application of potassium humate increased the growth indicators, essential oil yield, and flavonoid content in each species. Optimizing the frequency of potassium humate treatment with successive harvests could enhance the biomass and production of desired essential oil constituents. An additional study utilizing organic and biological stimulants examined how catnip (*Nepeta cataria* L.) responded to combinatorial formulations of chitosan, citric acid, and humic acid (Ozhan et al., 2017). The formulations significantly improved the morpho-physiological traits including plant height and biomass in addition to the biochemical traits, such as the content of nepetalactones, flavonoids, phenols, and sugars.

Though nepetalactones are the major secondary metabolites found in the aerial biomass of catnip, the roots are often cultivated via *in vitro* tissue culture for their production of the phenolic compound, rosmarinic acid (Lee et al., 2010). Yang et al. (2010) investigated the effects of several auxins and polyamines on rosmarinic acid biosynthesis in hairy root cultures of *N. cataria*. Out of the three auxins tested (IAA, IBA, and NAA), IBA was the most effective at inducing hairy roots and producing rosmarinic acid. Similarly, given the three polyamines (putrescine, spermidine, and spermine), putrescine was the most effective at stimulating growth and polyphenol biosynthesis. Since polyamines (PAs) are involved in plant oxidative stress, exogenous application of PAs can produce reactive oxygen species which increase antioxidant activity in plants (Minocha et al., 2014; Chen et al., 2019). In addition to the ability of PAs to improve overall tolerance to oxidative stress, these amine molecules can also adjust the ion balance during osmotic stress. In a salinity stress study, for example, spermidine exerted protective effects on catnip under saline conditions by reducing the accumulation of sodium and chloride ions (Mohammadi et al., 2017).

Synthetic Compounds

Another emerging area in elicitor research is the use of synthetic compounds as agents to stimulate the production of secondary metabolites. Dmitrović et al. (2016) exposed *Nepeta cataria* L. and *N. pannonica* L. plants to DO63 (1,2,4,5-tetraoxane) and DOVF15 (2,5-diphenylthiophene) to examine how these synthetic compounds would affect the production nepetalactone and rosmarinic acid. The authors observed that DO63 only increased the NL content but did not influence the RA levels; whereas DOVF15 decreased RA content in *N. pannonica* and increased RA content in *N. cataria*, however, NL production was not affected. Utilizing these compounds to activate plant defense mechanisms could boost the production of valuable metabolites, however, their application would need to be closely monitored to select the ideal plant development stage as well as the most effective dosage and frequency of treatment (Namdeo, 2007). The application of synthetic compounds would also require environmental risk assessments.

CONCLUSION

Innovative work concerning elicitors is ongoing for Lamiaceae species and other plants with medicinal properties. The different modes of application ranging from foliar spraying and hydroponic cultivation to *in vitro* culture can improve the efficiency of exogenous elicitors depending on the organ of interest. Also defining the timing of application whether during the seedling stage or after flowing should be customized since the ideal conditions will vary for individual species and cultivars. Noting which elicitor treatments produced desirable effects in Lamiaceae may help researchers establish a baseline for other families. Further studies connecting elicitors to their related biochemical mechanisms are needed to understand how these pathways are related on a molecular level.

The use of elicitation to enhance the production of secondary metabolites has also been implemented in an array of *Nepeta* spp. The *Nepeta* genus contains species rich in bioactive metabolites including a unique class of iridoid monoterpenes known as nepetalactones. Catmint plants have been used extensively in ethnobotanical medicine for their restorative and carminative properties. Further research has revealed numerous biological activities in the species from antibacterial and antifungal to bioherbicidal, insect repellant, and feline attractant activity. Recent investigations into the biochemical pathways that produce catmint metabolites have revealed new enzymes and gene clusters that regulate the synthesis of nepetalactone production. Supplementing agronomic cultivation of *Nepeta* species with elicitors and abiotic stresses has the potential to improve the yield of valuable phytochemicals through a targeted approach. This could be a useful method to optimize the secondary metabolite yield in catnip and other medicinal and aromatic plant species.

ACKNOWLEDGEMENTS

The study was funded by the New Jersey Agriculture Experiment Station HATCH project NJ12170 and the New Use Agriculture and Natural Plant Products program.

Table 1. Abiotic elicitation studies conducted with select Lamiaceae spp. and their affected secondary metabolites.

Species	Elicitor (dosage)	Mode of application	Elicitation response	Additional physiological effects	Reference
Mentha piperita	Salicylic acid (0.1 mM and 2 mM); methyl jasmonate (0.1 mM and 2 mM)	Foliar application	2mM SA stimulated essential oil accumulation; reduced pulegone content	SA increased total phenolic content and antioxidant capacity	Kandoudi et al., 2022
***Origanum majorana* L.**			2mM SA stimulated essential oil accumulation; reduced *cis*-sabinene hydrate content. 2mM MeJa elevated volatile production	SA increased total phenolic content and antioxidant capacity	
***Hyssopus officinalis* L.**			0.1 mM SA stimulated essential oil accumulation; increased isopinocamphone content	N/A	
***Ocimum basilicum* L.**			No significant changes to basil EO were detected	SA increased total phenolic content and antioxidant capacity	
Mentha piperita	Chitosan (200 mg/L), gibberellic acid (50 mg/L) and methyl jasmonate (300 µM)	Foliar application	Downregulation of menthol biosynthesis genes in response to chitosan and gibberellic acid; upregulation in response to methyl jasmonate treatment	N/A	Soleymani et al., 2017
***Rosmarinus officinalis* L.**	Salicylic acid (0, 100, 200, and 300 ppm)	Foliar application	Enhanced gene expression within antioxidant enzyme pathway; SA reversed the effects of salinity stress by increasing total phenolic, chlorophyll, carbohydrates, and proline composition of leaves and reducing chloride and sodium salts	Improved vegetative growth traits and stimulated antioxidant pathway	El-Esawi et al., 2017
Origanum majorana L.	Methyl jasmonic acid (100 µM)	Foliar application	MeJa reduced EO% and yield under mild irrigation; reduced content of monoterpene hydrocarbons and increased oxygenated monoterpenes	Improved fresh and dry weight	Farsi et al., 2019
Melissa officinalis L.	Chitosan lactate (100 mg/L and 500 mg/L)	Foliar application	Both concentrations of ChL increased accumulation of rosmarinic acid, anthocyanins, and total phenolic compounds	Increased antioxidant enzyme activity	Hawrylak-Nowak et al., 2021
Ocimum basilicum L.			100 mg/L of ChL increased accumulation of rosmarinic acid	Increased shoot biomass; increased antioxidant enzyme activity	

Rosmarinus officinalis	Riboflavin (25, 50, and 100 mg/L)	Foliar application	50 mg/L riboflavin increased oil yield, nutrient content, and total photosynthetic pigments	Enhanced antioxidant enzyme activity and dry matter yield	Aly et al., 2023
Salvia officinalis	Salicylic acid (250 and 500 µM)	Foliar application	250 µM SA increased rosmarinic acid content	SA upregulated *phenylalanine ammonia lyase* expression	Ejtahed et al., 2015
Salvia virgata			500 µM SA increased rosmarinic acid content	SA upregulated *phenylalanine ammonia lyase* expression	
Salvia officinalis	Methyl jasmonate (50 µM) and silver nitrate (15 µM)	Foliar application	MeJA and Ag+ enhanced the accumulation of rosmarinic acid, caffeic acid, salvianolic acid A, and salvianolic acid B	MeJA and Ag+ affected expression of principal genes in the phenylpropanoid and tyrosine pathways	Pesaraklu et al., 2021
Salvia verticillata			MeJA and Ag+ enhanced the accumulation of rosmarinic acid, caffeic acid, salvianolic acid A, and salvianolic acid B	MeJA and Ag+ affected expression of principal genes in the phenylpropanoid and tyrosine pathways	
***Ocimum basilicum* L.**	Chitosan (0.1 mM), methyl jasmonate (0.1 mM), and methyl salicylate (0.8 mM)	Hydroponic cultivation	Treatments increased total essential oil and methyl chavicol biosynthesis	Induced phenylpropanoid gene expression and chavicol O-methyltransferase enzyme activity	Deschamps et al., 2008
***Satureja hortensis* L.**	Methyl jasmonate (0.1, 1, 10 mM)	Foliar application	MeJa enhanced accumulation of carvacrol; increased accumulation of phenolics, flavonoids, peroxidase, superoxide dismutase, proline and malondialdehyde	Induced expression of *1-deoxy-D-xylulose 5-phosphate reductase* and *β-farnesene synthase*	Kazemi et al., 2024
***Melissa officinalis* L.**	Chitosan lactate (150 mg/L), selenite (10 mg/L), salicylic acid (100 mg/L), a mixture of ChL+Se+SA in the proportion of 1:1:1	Foliar application	Elicitors induced accumulation of rosmarinic acid hexoside	ChL and SA induced oxidative stress and photosynthesis; increased antioxidant activity	Stasińska-Jakubas et al., 2023
***Rosmarinus officinalis* L.**	Drought stress at four levels (30%, 50%, 70%, and 90% plant-available moisture) as a primary factor, and the use of nano-bio fertilizer (Biomic), bio-fertilizer (Nitroxin and Mycorrhiza)	Powder spraying	Nano-biofertilizer increased the essential oil percentage under 30% drought stress	Nano-biofertilizer optimized vegetative growth under stress.	Eskandari et al., 2023

Table 2. Abiotic elicitation studies conducted with different *Nepeta* spp. and their affected secondary metabolites.

Species	Elicitor (dosage)	Mode of application	Secondary metabolite elicited	Mode of action	Additional physiological effects	Reference
N. cataria	Salicylic acid (200 mg/L)	Foliar application	Essential oil majorly composed of geraniol, neral, geranial, nepetalactone and citronellol	N.A.	Counteracted adverse effects of water stress	Said-Al Ahl et al., 2016
N. cataria var. *citriodora*	Salicylic acid (200 mg/L)	Foliar application	Essential oil majorly composed of citronellol, geraniol, neral, geranial, and myristicin	N.A.	Counteracted adverse effects of water stress	
N. rtanjensis	PEG - 8000 (polyethylene glycol)	Added to *in vitro* culture medium	Nepetalactone levels were stable	Changes in gene expression	Stomatal closure, reduced plant aerial biomass, reduced fresh weight, reduced relative water content	Aničić etl al., 2020
N. argolica	PEG - 8000 (polyethylene glycol)	Added to *in vitro* culture medium	Ratio of (*cis, trans*)-nepetalactone to dihydronepetalactone changed	Changes in gene expression	Stomatal closure, reduced plant aerial biomass, reduced fresh weight, reduced relative water content	
N. rtanjensis	250 µM Methyl jasmonate	Added to *in vitro* culture medium	Accumulated (*trans, cis*)-nepetalactones, 5,9-dehydronepetalactone, and 1,5,9,epideoxyloganic acid	Changes in gene expression	Elevated expression of the major biosynthetic genes	Aničić et al., 2022
N. nervosa	250 µM Methyl jasmonate	Added to *in vitro* culture medium	No iridoids were accumulated	Changes in gene expression	Elevated expression of few iridoid-related biosynthetic genes	
N. cataria	Potassium humate (400 ppm)	Foliar application	Essential oil majorly composed of geraniol and nepetalactone	N.A.	Increased plant height, number of branches, fresh weight, and flavonoids	Mohamed et al., 2018
N. cataria var. *citriodora*	Potassium humate (400 ppm)	Foliar application	Essential oil majorly composed of citronellol and geraniol	N.A.	Increased plant height, number of branches, fresh weight, and flavonoids	
N. grandiflora	Potassium humate (400 ppm)	Foliar application	Essential oil majorly composed of o-cymene, c-terpinene, p-cymene and carvacrol	N.A.	Increased plant height, number of branches, fresh weight, and flavonoids	
N. cataria	Combinatorial formulations of citric acid, humic acid, and	Sprayed onto transplanted roots	Accumulated nepetalactone	N.A.	Affected plant height, number of lateral branches, number of	Ozhan et al., 2017

	chitosan at 200, 400, and 800 ppm				leaves, dry weight of leaves, stems, and shoots, content of soluble sugars, phenols, tannins, and flavonoids	
N. cataria	Auxins and polyamines: IAA, IBA, and NAA (0.1 – 1 mg/L); putrescine, spermidine, and spermine (10, 500, and 100 mg/L)	Added to *in vitro* culture medium	Rosmarinic acid accumulated in hairy roots	N.A.	Increased production of hairy root biomass	Yang et al., 2010
N. cataria	Spermidine (0, 100 and 200 ppm)	Foliar application	Increased essential oil (%) under saline conditions and spermidine treatment	Prevents toxicity of Na and Cl ion accumulation, inhibits ionic imbalance	Increased fresh weight, dry weight, and root length	Mohammadi et al., 2017
N. cataria	1,2,4,5-tetraoxane (DO63) and 2,5-diphenylthiophene (DOVF15) (0.1 to 2 mg/L)	Added to *in vitro* culture medium	DO63 only affected nepetalactone content; DOVF15 increased rosmarinic acid content	N.A.	Fresh and dry weights were not affected	Dmitrović et al., 2016
N. pannonica	1,2,4,5-tetraoxane (DO63) and 2,5-diphenylthiophene (DOVF15) (0.1 to 2 mg/L)	Added to *in vitro* culture medium	DO63 only affected nepetalactone content; DOVF15 decreased rosmarinic acid content	N.A.	Fresh and dry weights were not affected	
N. nuda	Waterlogging and/or 100 µM H_2O_2 treatments	Waterlogging via soil-pots; H_2O_2 via foliar spray	VOCs, iridoids and phenolics accumulated after waterlogging and H_2O_2 elicitation	Changes in iridoid biosynthetic gene expression	12-fold increase in nepetalactone content; additional nepetalactone stereoisomer appeared in leaves upon stress; higher antioxidant activity	Petrović et al., 2025
N. grandiflora	Waterlogging and/or 100 µM H_2O_2 treatments	Waterlogging via soil-pots; H_2O_2 via foliar spray	VOCs, iridoids and phenolics accumulated after waterlogging and H_2O_2 elicitation	Changes in iridoid biosynthetic gene expression	1.5-fold increase in 1,5,9-*epi*-deoxyloganic acid (1,5,9-*E*dla)	

N.A.: not applicable

REFERENCES

Akbarzadeh, S., Morshedloo, M. R., Behtash, F., Mumivand, H., and Maggi, F. 2023. Exogenous β-aminobutyric acid (BABA) improves the growth, essential oil content, and composition of grapefruit mint (*Mentha suaveolens* × *piperita*) under water deficit stress conditions. *Horticulturae*, *9*(3), 354.

Albrecht, U. 2019. Plant biostimulants: definition and overview of categories and effects. *EDIS*, *2019*. https://doi.org/10.32473/edis-hs1330-2019

Allen, K., Gomes, E. N., Patel, H., and Simon, J. 2023. Vegetative propagation of *Nepeta cataria* and the inhibitory effects of its essential oil on the adventitious rooting of cultivated Lamiaceae species. *Journal of Medicinally Active Plants*, *12*(2), 18–31. https://doi.org/10.7275/yb2r-tn46

Aly, H., Gharib, F. A., and Ahmed, E. Z. 2023. Response of rosemary (*Rosmarinus officinalis*) plants to riboflavin foliar application: improvement in growth, nutrient content, antioxidant enzyme system, essential oil production, and its antioxidant potential. *Egyptian Journal of Botany*, *0*. https://doi.org/10.21608/ejbo.2023.214502.2359

Aničić, N., Filipović, B., Dmitrović, S., Nestorović Živković, J., Skorić, M., Gašić, U., Milutinović, M., Matekalo, D., Petrović, L., Božunović, J., Banjanac, T., Šiler, B., Todorović, M., Lukić, T., and Mišić, D. 2022. Elicitation effects of methyl jasmonate on iridoid biosynthesis in leaves of *Nepeta rtanjensis* and *Nepeta nervosa*. *Book of Abstracts: 4th International Conference on Plant Biology and 23rd SPPS Meeting;* 2022 Oct 6-8; Belgrade, Serbia, 122.

Aničić, N., Matekalo, D., Skorić, M., Živković, J. N., Petrović, L., Dragićević, M., Dmitrović, S., and Mišić, D. 2020. Alterations in nepetalactone metabolism during polyethylene glycol (PEG)-induced dehydration stress in two *Nepeta* species. *Phytochemistry*, *174*, 112340. https://doi.org/10.1016/j.phytochem.2020.112340

Bellahsene, C. 2017. Examen phytochimique et Pouvoirantimicrobien et Anti-Radicalaire des Extraits de *Nepeta amethystina* (Gouzia) de la Région d'Aïn Sefra (Algérie). Université Abou Bekr Belkaid. http://dspace.univ-tlemcen.dz/handle/112/9552

Bol, S., Scaffidi, A., Bunnik, E. M., and Flematti, G. R. 2022. Behavioral differences among domestic cats in the response to cat-attracting plants and their volatile compounds reveal a potential distinct mechanism of action for actinidine. *BMC Biology*, *20*(1), 192. https://doi.org/10.1186/s12915-022-01369-1

Bozaba, T. O. and Kuru, İ. S. 2024. The effect of the combined application of elicitors to Salvia virgata Jacq. under salinity stress on physiological and antioxidant defense. *BMC Plant Biology*, *24*(1), 788.

Canellas, L. P., Olivares, F. L., Aguiar, N. O., Jones, D. L., Nebbioso, A., Mazzei, P., and Piccolo, A. 2015. Humic and fulvic acids as biostimulants in horticulture. *Scientia Horticulturae*, *196*, 15–27. https://doi.org/10.1016/j.scienta.2015.09.013

Chen, D., Shao, Q., Yin, L., Younis, A., and Zheng, B. 2019. Polyamine function in plants: metabolism, regulation on development, and roles in abiotic stress responses. *Frontiers in Plant Science*, *9*. https://www.frontiersin.org/articles/10.3389/fpls.2018.01945

Cingoz, G. S. and Gurel, E. 2016. Effects of salicylic acid on thermotolerance and cardenolide accumulation under high temperature stress in *Digitalis trojana* Ivanina. *Plant Physiology and Biochemistry: PPB*, *105*, 145–149. https://doi.org/10.1016/j.plaphy.2016.04.023

Dehsheikh, P. B., Sourestani, M. M., Zolfaghari, M., and Enayatizamir, N. 2021. The effects of biological, chemical fertilizers and humic acid on some microbial parameters, elements and oil quantity and quality of catnip (*Nepeta cataria* L.). *Journal of Agroecology*, *13*(1), 73–88.

Deschamps, C., Raskin, I., and Simon, J. E. 2008. Regulation of essential oil accumulation in basil (*Ocimum basilicum* L.) in response to elicitation. *International Journal of Plant Sciences*, *169*(8), 981–986. https://doi.org/10.1086/590454

Dirmenci, T., Yildiz, B., and Tümen, G. 2004. Threatened categories of four *Nepeta* L. (Lamiaceae) species endemic to the East Anatolia. *Turkish Journal of Botany*, *28*(1), 221–226.

Dmitrović, S., Škorić, M., Boljević, J., Aničić, N., Božić, D., Mišić, D., Filipović, V., and Opsenica, D. 2016. Elicitation effects of a synthetic 1,2,4,5-tetraoxane and a 2,5-diphenylthiophene in shoot cultures of two *Nepeta* species. *Journal of the Serbian Chemical Society*, *81*(9), 999–1012. https://doi.org/10.2298/JSC160226054D

El-Esawi, M. A., Elansary, H. O., El-Shanhorey, N. A., Abdel-Hamid, A. M. E., Ali, H. M., and Elshikh, M. S. 2017. Salicylic acid-regulated antioxidant mechanisms and gene expression enhance rosemary performance under saline conditions. *Frontiers in Physiology*, *8*, 716. https://doi.org/10.3389/fphys.2017.00716

Ejtahed, R. Sadat, Radjabian, T., and Hoseini Tafreshi, S. A. 2015. Expression analysis of phenylalanine ammonia lyase gene and rosmarinic acid production in *Salvia officinalis* and *Salvia virgata* shoots under salicylic acid elicitation. *Applied Biochemistry and Biotechnology*, *176*(7), 1846–1858. https://doi.org/10.1007/s12010-015-1682-3

Eskandari, A., Hashemi, M., Sepaskhani, A., Rostami, M., and Shams, Z. 2023. Application of nanobiofertilizer under abiotic stress on the vegetative growth, greenhouse gas emission, and essential oil production of rosemary (*Rosmarinus officinalis* L.). J. *Gene Eng. Bio. Res,* *5*(3), 162-168.

Farsi, M., Abdollahi, F., Salehi, A., and Ghasemi, S. 2019. Growth responses of *Origanum majorana* L. to methyl jasmonic acid under limited irrigation conditions. *Journal of Essential Oil Bearing Plants*, *22*(2), 455–468. https://doi.org/10.1080/0972060X.2019.1602481

Formisano, C., Rigano, D., and Senatore, F. 2011. Chemical constituents and biological activities of *Nepeta* species. *Chemistry and Biodiversity*, *8*(10), 1783–1818. https://doi.org/10.1002/cbdv.201000191

Gomes, E., Allen, K., Jaworski, K., Zorde, M., Lockhart, A., Besancon, T., Brown, T., Reichert, W., Wu, Q., and Simon, J. 2020a. Catnip (*Nepeta cataria* L.): Recent advances in botany, horticulture and production. In *Medicinal and Aromatic Plants of the World* (Vol. 6, pp. 247–284). Springer, Cham. https://doi.org/10.1007/978-3-030-44930-8_11

Gomes, E. N., Allen, K. A., Zorde, M., Wu, Q., and Simon, J. E. 2020b. Ethnobotany, chemistry, and pharmacology of African *Nepeta* species. In *ACS Symposium Series* (Vol. 1361, pp. 219–236). American Chemical Society. https://doi.org/10.1021/bk-2020-1361.ch010

Gomes, E., Reichert, W., Vasilatis, A., Allen, K., Wu, Q., and Simon, J. 2020c. Essential oil yield and aromatic profile of lemon catnip and lemon-scented catnip selections at different harvesting times. *Journal of Medicinally Active Plants*, *9*(1). https://doi.org/10.7275/6v2v-4333

Gomes, E. N., Patel, H., Yuan, B., Lyu, W., Juliani, H. R., Wu, Q., and Simon, J. E. 2023. Successive harvests affect the aromatic and polyphenol profiles of novel catnip (*Nepeta cataria* L.) cultivars in a genotype-dependent manner. *Frontiers in Plant Science*, *14*. https://www.frontiersin.org/articles/10.3389/fpls.2023.1121582

González, J., Lockhart, A., Wu, Q., Simon, J. E., and Toledo, A. 2022. Repellency of novel catnip (*Nepeta cataria*) cultivar extracts against *Ixodes scapularis* and *Haemaphysalis longicornis* (Acari: Ixodida: Ixodidae). *Ticks and Tick-Borne Diseases*, *13*(6), 102046. https://doi.org/10.1016/j.ttbdis.2022.102046

Gorelick, J. and Bernstein, N. 2014. Chapter five - elicitation: an underutilized tool in the development of medicinal plants as a source of therapeutic secondary metabolites. In D. L. Sparks (Ed.), *Advances in Agronomy* (Vol. 124, pp. 201–230). Academic Press. https://doi.org/10.1016/B978-0-12-800138-7.00005-X

Grbić-Ljaljević, M., Stupar, M., Vukojević, J., Soković, M., Mišić, D., Grubišić, D., and Ristić, M. 2008. Antifungal activity of *Nepeta rtanjensis* essential oil. *Journal of the Serbian Chemical Society*, *73*(10), 961–965.

Guru, A., Dwivedi, P., Kaur, P., and Pandey, D. K. 2022. Exploring the role of elicitors in enhancing medicinal values of plants under *in vitro* condition. *South African Journal of Botany*, *149*, 1029–1043. https://doi.org/10.1016/j.sajb.2021.10.014

Hashemi, S. M. and Naghavi, M. R. 2016. Production and gene expression of morphinan alkaloids in hairy root culture of *Papaver orientale* L. using abiotic elicitors. *Plant Cell, Tissue and Organ Culture (PCTOC)*, *125*(1), 31–41. https://doi.org/10.1007/s11240-015-0927-8

Hashemifar, Z., Sanjarian, F., Naghdi Badi, H., and Mehrafarin, A. 2024. Varying levels of natural light intensity affect the phyto-biochemical compounds, antioxidant indices and genes involved in the monoterpene biosynthetic pathway of *Origanum majorana* L. B*MC Plant Biology, 24*(1), 1018.

Hawrylak-Nowak, B., Dresler, S., Rubinowska, K., and Matraszek-Gawron, R. 2021. Eliciting effect of foliar application of chitosan lactate on the phytochemical properties of *Ocimum basilicum* L. and *Melissa officinalis* L. *Food Chemistry*, *342*, 128358. https://doi.org/10.1016/j.foodchem.2020.128358

Hedge, I. C. 1986. Labiatae of South-West Asia: Diversity, distribution and endemism. *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences*, *89*, 23–35. https://doi.org/10.1017/S0269727000008873

IPCC, 2022: Climate Change 2022: Impacts, adaptation, and vulnerability. Contribution of working group II to the sixth assessment report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press. Cambridge University Press, Cambridge, UK and New York, NY, USA, 3056 pp., doi:10.1017/9781009325844.

ITIS. 2023. *Integrated Taxonomic Information System—Report: Nepeta cataria*. https://www.itis.gov/servlet/SingleRpt/SingleRpt?search_topic=TSNandsearch_value=32623#null

Javanmard, A., Ashrafi, M., Morshedloo, M. R., Machiani, M. A., Rasouli, F., and Maggi, F. 2022. Optimizing phytochemical and physiological characteristics of Balangu (*Lallemantia iberica*) by foliar application of chitosan nanoparticles and Myco-Root inoculation under water supply restrictions. *Horticulturae, 8*(8), 695.

Kandoudi, W., Radácsi, P., Gosztola, B., and Zámboriné Németh, É. 2022. Elicitation of medicinal plants *in vivo*—is it a realistic tool? The effect of methyl jasmonate and salicylic acid on Lamiaceae species. *Horticulturae*, *8*(1), 5. https://doi.org/10.3390/horticulturae8010005.

Karami, S., Ejtehadi, H., Moazzeni, H., Vaezi, J., and Behroozian, M. 2022. Minimal climate change impacts on the geographic distribution of *Nepeta glomerulosa*, medicinal species endemic to southwestern and central Asia. *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-24524-8

Kazemi, B., Ranjbar, M., Rezayatmand, Z., Ahadi, A. M., Mahdavi, S. M. E., and Nekonam, M. S. 2024. Exogenous methyl jasmonate affects genes involved in monoterpene biosynthetic pathway, phyto-biochemical accumulation, and enzymatic activity of *Satureja hortensis* L. *Gene*, *892*, 147882. https://doi.org/10.1016/j.gene.2023.147882

Kramer, K. 2020. Weird mechanism behind catnip compound's biosynthesis uncovered. *Chemistry World*. https://www.chemistryworld.com/news/weird-mechanism-behind-catnip-compounds-biosynthesis-uncovered/3009879.article

Kumar G, P., Gupta, S., Murugan, P., and Singh, S. B. 2009. Ethnobotanical studies of Nubra Valley—a cold arid zone of Himalaya. *Ethnobotanical Leaflets*, *2009*(6). https://opensiuc.lib.siu.edu/ebl/vol2009/iss6/9

Kuzel, S., Vydra, J., Triska, J., Vrchotova, N., Hruby, M., and Cigler, P. 2009. Elicitation of pharmacologically active substances in an intact medical plant. *Journal of Agricultural and Food Chemistry*, *57*(17), 7907–7911. https://doi.org/10.1021/jf9011246

Lee, S. Y., Lee, C. Y., Eom, S. H., Kim, Y. K., Park, N., and Park, S. U. 2010. Rosmarinic acid production from transformed root cultures of *Nepeta cataria* L. *Scientific Research and Essays*, *5*(10), 1122–1126.

Lichman, B. R. 2021. How a mint turned into catmint. *The Science Breaker*. https://doi.org/10.25250/thescbr.brk475

Lichman, B. R., Kamileen, M. O., Titchiner, G. R., Saalbach, G., Stevenson, C. E. M., Lawson, D. M., and O'Connor, S. E. 2019. Uncoupled activation and cyclization in catmint reductive terpenoid biosynthesis. *Nature Chemical Biology*, *15*(1), 71–79. https://doi.org/10.1038/s41589-018-0185-2

Mahmoodi, S., Heydari, M., Ahmadi, K., Khwarahm, N. R., Karami, O., Almasieh, K., Naderi, B., Bernard, P., and Mosavi, A. 2022. The current and future potential geographical distribution of *Nepeta crispa* Willd., an endemic, rare and threatened aromatic plant of Iran: Implications for ecological conservation and restoration. *Ecological Indicators*, *137*, 108752. https://doi.org/10.1016/j.ecolind.2022.108752

Mahr, S. 2023. Catnip, *Nepeta cataria*. *Wisconsin Horticulture*. https://hort.extension.wisc.edu/articles/catnip-nepeta-cataria/

Mansinhos, I., Gonçalves, S., Rodríguez-Solana, R., Moreno-Rojas, J. M., and Romano, A. 2024a. Environmental factors related to climate change alter the chemical composition and biological activity of *Lavandula viridis* L'Hér essential oil. *Agriculture, 14*(7), 1067.

Mansinhos, I., Gonçalves, S., and Romano, A. 2024b. How climate change-related abiotic factors affect the production of industrial valuable compounds in Lamiaceae plant species: a review. *Frontiers in Plant Science*, *15*, 1370810.

Manukyan, A. 2013. Effects of PAR and UV-B radiation on herbal yield, bioactive compounds and their antioxidant capacity of some medicinal plants under controlled environmental conditions. *Photochemistry and Photobiology*, *89*(2), 406–414. https://doi.org/10.1111/j.1751-1097.2012.01242.x

Marković, T., Aničić, N., Marković Hadžić, S., Božunović, J., Dmitrović, S., Nestorović Živković, J., Gašić, U., Milutinović, M., Petrović, L., and Mišić, D. 2022. UV-B radiation-elicitated biosynthesis of iridoids in leaves of *in vitro* grown *Nepeta nuda* L.

Book of Abstracts: 4th International Conference on Plant Biology and 23rd SPPS Meeting; 2022 Oct 6-8; Belgrade, Serbia, 85.

Max Planck Institute for Chemical Ecology. 2023. *How a mint became catnip*. ScienceDaily. https://www.sciencedaily.com/releases/2020/05/200513143758.htm

Minocha, R., Majumdar, R., and Minocha, S. C. 2014. Polyamines and abiotic stress in plants: a complex relationship. *Frontiers in Plant Science*, *5,* 175. https://www.frontiersin.org/articles/10.3389/fpls.2014.00175

Moghaddam, H. H., Jafari, A. A., Sefidkon, F., and Jari, S. K. 2023. Influence of climatic factors on essential oil content and composition of 20 populations of *Nepeta binaludensis* Jamzad from Iran. *Applied Biological Chemistry*, *66*(1), 2.

Mohamed, H. F. Y., Mahmoud, A. A., Alatawi, A., Hegazy, M. H., Astatkie, T., and Said-Al Ahl, H. A. H. 2018. Growth and essential oil responses of *Nepeta* species to potassium humate and harvest time. *Acta Physiologiae Plantarum*, *40*(12), 204. https://doi.org/10.1007/s11738-018-2778-5

Mohammadi, S., Saharkhiz, M. J., and Javanmardi, J. 2017. Evaluation of interaction effects of spermidine and salinity on physiological and morphology trait of catnip (*Nepeta cataria* L.). *Zeitschrift Fur Arznei- Und Gewurzpflanzen*, *22*(3), 104–109.

Mutlu, S., Atici, Ö., and Esim, N. 2010. Bioherbicidal effects of essential oils of *Nepeta meyeri* Benth. on weed spp. *Allelopathy Journal*, *26*, 291–300.

Namdeo, A. G. 2007. Plant cell elicitation for production of secondary metabolites: a review. *Pharmacognosy Reviews*, *1*, 69–79.

Nedorostova, L., Kloucek, P., Kokoska, L., Stolcova, M., and Pulkrabek, J. 2009. Antimicrobial properties of selected essential oils in vapour phase against foodborne bacteria. *Food Control*, *20*(2), 157–160. https://doi.org/10.1016/j.foodcont.2008.03.007

Ozhan, N., Goldani, M., Naghdi Badi, H. A., Mehrafarin, A., and Parsa, M. 2017. Changes in nepetalactone content and biochemical traits of catnip (*Nepeta cataria* L.) in response to induction of biostimulants compounds. *Journal of Medicinal Plants*, *16*(64), 32–44.

Patel, H. K., Gomes, E. N., Wu, Q., Patel, N., Kobayashi, D. Y., Wang, C., and Simon, J. E. 2023. Volatile metabolites from new cultivars of catnip and oregano as potential antibacterial and insect repellent agents. *Frontiers in Plant Science*, *14*, 1124305. https://doi.org/10.3389/fpls.2023.1124305

Pesaraklu, A., Radjabian, T., and Salami, S. A. 2021. Methyl jasmonate and Ag+ as effective elicitors for enhancement of phenolic acids contents in *Salvia officinalis* and *Salvia verticillata*, as two traditional medicinal plants. *South African Journal of Botany*, *141*, 105-115.

Petrović, L., Popović, N., Todorović, M., Matekalo, D., Milutinović, M., Nakarada, Đ., and Skorić, M. 2025. Metabolomic and transcriptomic responses to waterlogging stress and hydrogen peroxide elicitation: impact on the production of iridoids and phenolics in leaves of two *Nepeta* species. *Industrial Crops and Products*, *235*, 121762.

Rad, M. M., Abdossi, V., Moradi, P., Rakhshandehroo, F., and Mehrafarin, A. 2022. Phytochemical changes of *Digitalis purpurea* L. in response to polyamines and methyl jasmonate application in callus culture. *Journal of Plant Biochemistry and Biotechnology*, *31*(2), 310–319. https://doi.org/10.1007/s13562-021-00678-w

Rady, M. R., Gierczik, K., Ibrahem, M. M., Matter, M. A., and Galiba, G. 2021. Anticancer compounds production in

Catharanthus roseus by methyl jasmonate and UV-B elicitation. *South African Journal of Botany*, *142*, 34–41. https://doi.org/10.1016/j.sajb.2021.05.024

Reichert, W., Ejercito, J., Guda, T., Dong, X., Wu, Q., Ray, A., and Simon, J. E. 2019. Repellency assessment of *Nepeta cataria* essential oils and isolated nepetalactones on *Aedes aegypti*. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-018-36814-1

Reichert, W., Park, H. C., Juliani, H. R., and Simon, J. E. 2016. 'CR9': A new highly aromatic catnip *Nepeta cataria* L. cultivar rich in Z,E-nepetalactone. *HortScience*, *51*(5), 588–591. https://doi.org/10.21273/HORTSCI.51.5.588

Said-Al Ahl, H., Sabra, A. S., and Hegazy, M. H. 2016. Salicylic acid improves growth and essential oil accumulation in two *Nepeta cataria* chemotypes under water stress conditions. I*talian Journal of Agrometeorology, 21*, 25–36. https://doi.org/10.19199/2016.1.2038-5625.025

Salehi, B., Valussi, M., Jugran, A. K., Martorell, M., Ramírez-Alarcón, K., Stojanović-Radić, Z. Z., Antolak, H., Kręgiel, D., Mileski, K. S., Sharifi-Rad, M., Setzer, W. N., Cádiz-Gurrea, M. de la L., Segura-Carretero, A., Şener, B., and Sharifi-Rad, J. 2018. *Nepeta* species: From farm to food applications and phytotherapy. *Trends in Food Science and Technology*, *80*, 104–122. https://doi.org/10.1016/j.tifs.2018.07.030

Sarikurkcu, C., Ceylan, O., Targan, S., and Ćavar Zeljković, S. 2018. Chemical composition and biological activities of the essential oils of two endemic *Nepeta* species. *Industrial Crops and Products*, *125*, 5–8. https://doi.org/10.1016/j.indcrop.2018.09.001

Sharma, A., Cooper, R., Bhardwaj, G., and Cannoo, D. S. 2021. The genus *Nepeta*: Traditional uses, phytochemicals and pharmacological properties. *Journal of Ethnopharmacology*, *268*, 113679. https://doi.org/10.1016/j.jep.2020.113679

Skrypnik, L., Maslennikov, P., Antipina, M., Katserov, D., and Feduraev, P. 2024. Comparative study on the response of hyssop (*Hyssopus officinalis* L.), salvia (*Salvia officinalis* L.), and oregano (*Origanum vulgare* L.) to drought stress under foliar application of selenium. *Plants*, *13*(21), 2986.

Smit, S. J. and Lichman, B. R. 2022. Plant biosynthetic gene clusters in the context of metabolic evolution. *Natural Product Reports*, *39*(7), 1465-1482.

Smitherman, L. C., Janisse, J., and Mathur, A. 2005. The use of folk remedies among children in an urban Black community: remedies for fever, colic, and teething. *Pediatrics*, *115*(3), e297–e304. https://doi.org/10.1542/peds.2004-1443

Soleymani, F., Taheri, H., and Shafeinia, A. R. 2017. Relative expression of genes of menthol biosynthesis pathway in peppermint (*Mentha piperita* L.) after chitosan, gibberellic acid and methyl jasmonate treatments. *Russian Journal of Plant Physiology*, *64*(1), 59–66. https://doi.org/10.1134/S1021443717010150

Sonboli, A., Salehi, P., and Yousefzadi, M. 2004. Antimicrobial activity and chemical composition of the essential oil of *Nepeta crispa* Willd. from Iran. *Zeitschrift Für Naturforschung C*, *59*(9–10), 653–656. https://doi.org/10.1515/znc-2004-9-1008

St. Hilaire, R., Hockman, A. W., and Chavez, S. M. 2004. Propagation and irrigation regime affect the development of catnip. *Acta Horticulturae*, *629*, 321–327. https://doi.org/10.17660/ActaHortic.2004.629.41

Stasińska-Jakubas, M., Hawrylak-Nowak, B., Dresler, S., Wójciak, M., and Rubinowska, K. 2023. Application of chitosan lactate, selenite, and salicylic acid as an approach to induce biological responses and enhance secondary metabolism in *Melissa officinalis* L. *Industrial Crops and Products*, *205*, 117571.

Stefanakis, M. K., Giannakoula, A. E., Ouzounidou, G., Papaioannou, C., Lianopoulou, V., and Philotheou-Panou, E. 2024. The effect of salinity and drought on the essential oil yield and quality of various plant species of the Lamiaceae family (*Mentha spicata* L., *Origanum dictamnus* L., *Origanum onites* L.). *Horticulturae*, *10*(3), 265.

Stojanović, G., Radulović, N., Lazarević, J., Miladinović, D., and Đoković, D. 2005. Antimicrobial activity of *Nepeta rtanjensis* essential oil. *Journal of Essential Oil Research*, *17*(5), 587–589. https://doi.org/10.1080/10412905.2005.9699004

Sun, J., Sun, P., Kang, C., Zhang, L., Guo, L., and Kou, Y. 2022. Chemical composition and biological activities of essential oils from six Lamiaceae folk medicinal plants. *Frontiers in Plant Science*, *13*. https://www.frontiersin.org/articles/10.3389/fpls.2022.919294

Thakur, M. and Sohal, B. S. 2013. Role of elicitors in inducing resistance in plants against pathogen infection: A Review. *ISRN Biochemistry*, *2013*, 762412. https://doi.org/10.1155/2013/762412

van Hoose, N. 2020, May 13. Catnip's chemical attractant is new twist on old family tradition. *Research News*. https://www.floridamuseum.ufl.edu/science/catnip-twist-on-old-family-tradition/

Yang, Y., Lee, S.-Y., Park, W., Park, N., and Park, S. U. 2010. Exogenous auxins and polyamines enhance growth and rosmarinic acid production in hairy root cultures of *Nepeta cataria* L. *Plant OMICS*, *3*, 190–193.