

Allelopathy Researches in the former USSR: 1960-2010

Y.H. Tsytsiura^{*}, D.A. Sampietro¹ and S.S. Narwal²

Faculty of Agronomy and Forestry, Vinnytsia National Agrarian University,
21008, Soniachna street, 3, Vinnytsia, Ukraine.

E-Mail: yaroslavtsytsyura@ukr.net, yaroslav301974@gmail.com,
dasampietro2006@yahoo.com.ar, allelopathy2021@gmail.com

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^{*}Correspondence author, ¹LABIFITO. Universidad Nacional de Tucumán, Ayacucho 471 (4000). San Miguel de Tucumán, Argentina, ²Department of Agronomy, Haryana Agricultural University Hisar-125004, India.

ABSTRACT

Research on the biochemical interactions among plants started in the former USSR and in Germany in late 1920s. Boris Tokin, a Russian embryologist, reported in 1930 that plant excretions contains substances which possess antimicrobial activity and termed them as *Phytoncides*. Later, Molish in 1937 published the first book on allelopathy and concluded that chemicals released by plants take part in plant interactions. Numerous scientists of the former USSR worked in allelopathy during 1960-90. This review summarises their most outstanding researches done in the world-renowned Soviet Scientific Schools lead by Boris Tokin, Andrei Grodzinsky and Valentina Roschina. The topics covered include investigations on Plant excretions, Biocenology, Ecology, Plant physiology, Biochemistry, Immunology, Pharmacology and Agronomy.

Keywords: Allelochemicals, Allelopathy, Antifungals, Bioactivity, Biosphere, Excretions, Phytocenosis,

1. INTRODUCTION

Modern vision of plant communities is linked to the direct and indirect chemical interactions among plants, between plants and other organisms. These interactions are investigated by a sub-discipline of chemical ecology named 'Allelopathy', in the framework of cellular, rhizosphere and physiological processes that occur during plant growth and development. Allelopathic research unravels basic laws of species coexistence in the biosphere, also known as biocenosis, with important biological, ecological and agricultural implications. It has provided knowledge currently applied in several areas of sustainable agriculture such as integrated plant protection, pesticidal use and agricultural practices. The former USSR played a prominent role in the generation of this knowledge during the period 1960-1990, with prominent scientists leading various research groups. This review analyses the main achievements in allelopathic research achieved by the USSR scientists, during 1960-1990, during this period > 5000 scientific papers and 20 Monographs were published in USSR (125). Many of these publications not only established fundamentals of Allelopathy but also defined its applied aspects. During this time, allelopathic research in USSR was conducted in following areas (16,125): (i) Biospheric role of plant excretions, (ii) Allelopathical interactions in cultivated and natural phytocenosis, identification of allelopathically tolerant phytocenosis, (iii) Identification of allelochemicals in plant excretions and their cellular mechanisms and actions.

2. ALLELOPATHY IN CULTIVATED AND NATURAL PHYTOCENOSIS

I. Cultivated phytocenosis

(i). **Soil Sickness:** Allelopathic research began long before 1960 in USSR (33,36). Soil fatigue due to crop secretions were investigated at the end of 19th and beginning of 20th century. Aqueous exudates effects in the rhizosphere were tested on plant growth and development. The tests done with donor and receptor plants of same crop species, proved autotoxicity, it is one of the causes of soil fatigue and highlighted the need of crop rotation to prevent it (51,95). Allelopathic research also continued during the 30s and 50s of the 20th century, when the principles to study plant communities (phytocoenology) were formulated (35,138), including plant community patterns,

classifications of plants based on their life history (104) and the phytocoenotic stratification (104,139,140-144). These concepts lead to the hypothesis of chemical interactions among terrestrial plants through the soil by plant excretions (101,134,135,143). Allelopathic studies related to plant ecology continued in the early 60s, by Academician A.M. Grodzinsky (1926-1988) and his Scientific School of Allelopathy, in Central Republican Botanical Garden, Academy of Sciences of the Ukrainian SSR, Kiev (133). This School began research in 1965 and in 1983 received official status in the USSR. During 1965-1990, the Grodzinsky's school actively worked in the following areas: (i). Soil fatigue and substrate fatigue; (ii) Effects of volatile compounds with antimicrobial activity (phytoncides); (iii). Allelopathic features of certain plant species; (iv). Physiological and biochemical bases of plant-plant and plant-microorganisms interactions (87). Four doctoral and 30 undergraduate Dissertations on allelopathy were submitted under Grodzinsky's leadership, 16-Monographs and 17-collections were also published (3,14,105,159,160). Grodzinsky was the first to generalize 15-ecological mechanisms of chemical interactions between organisms (58) which served as the basis for the modern concept of allelopathy. He investigated the main features of phytocenoses formation involved in monocropping. The morphological analysis of plant development in sick soil led him to propose phyto-indicators of this phenomenon (55). Grodzinsky and his followers formulated the principles of growing different crops in crop rotation and intercropping, depending on the soil fertility (52,55,59,62,103,168), flowering plants (175) and fruit plantations (92,93,171). Over 30-years Grodzinsky's School, allelopathy research was related to soil fatigue in >30 crops (14,15,20,21,22,24,30,38,55,58,103,105,166,167,173), 10 fruit trees (58,93,94,171), various ornamental woody and floral species (6,98,161,172,175) and aromatic plants (160,168).

(ii). Agrophytocenosis Research: Professor P.A. Moroz (1938-2016) did allelopathy Research on fruit trees in agrophytocenoses (93). He was student of Prof. Grodzinsky, he did allelopathy research in orchards, analyzing the effects of allelopathic interactions of fruit crops during joint growth to increase the species diversity and productivity of gardens. He proposed ways to overcome soil fatigue in orchards, recommended schedules for the rational alternation of crops in horticulture and in nursery crop rotation, developed the concept for greening gardening and modern ideas about the importance of biodiversity in the formation of ecosystems (94).

II. Natural phytocenosis

Grodzinsky's School in managed and natural ecosystems, introduced the phytodesign concept in agriculture and recommendations for landscape design based on the compatibility or incompatibility of plant species. These recommendations are used in landscape design to establish Botanical gardens and Arboretums (61,83,87). They provided optimal inclusion ratios for plant species in the vegetation layers in the plant landscape, defining herbaceous and flowering plants at the bottom, ornamental bushes and semi-shrubs (181,182) in the middle and tree and lianas at the top (61). Methods were developed to measure the allelopathic phenomena considering the structure, stability and productivity of natural and man-made phytocenoses (53,56). The chemical influence among plants was shown through the release of root exudates and volatile compounds

(68). The role of volatile compounds released in the phytocenoses was main research of Tokin (154,155). Air purification properties of the phytoncides in the biosphere were studied (51,55,61,68,125,126). Tokin proposed the growth of phytonciding plant species for air quality maintenance in closed environments such as space flights. The supply of phytoncides in the indoor air disinfects the atmosphere, increases human immunity to diseases and provides relaxation to over worked or stressed organisms. Grodzinsky even investigated phytoncides, root exudates and other plant excretions in terrestrial plant interactions, in the formation of the cenosis and in relation to the effects of the cosmic cyclical environment on the plant rhythms (61,68). Through the study of allelopathic relationships in the phytocenosis, Soviet scientists established principles for developing binary crops, varietal and species blends, emphasizing the principles of vitality of species in natural cenoses (30,38,62,65,87). Allelopathically active substances released into the environment were identified from several plant species, and the presence of these compounds was related to the dominance of their plant producers in managed or natural ecosystems (58). Chemical composition analyses of the plant excretions showed that they are continuously released by some plant species (53,58,62,64,69). Grodzinsky's findings further contributed to breeding for high allelopathic crop varieties or cultivars to control weeds and their dominance in agrocenoses (65).

III. Weeds Phytocenology: The scientific school of Grodzinsky investigated the role of weeds allelopathy in the formation of phytocenosis structure. They investigated the physiological processes involved in weeds growth (52,53,64,65), methods for biological and allelopathic weed control (52,58,59,65-68,89), the interactive growth and development of weeds and cultivated plants in complex phytocenotic systems (23,51,52,65,68), the role of allelopathy in prevention of weed growth, and important aspects of the mechanisms of allelopathic interactions between specific weed-crop combinations (125). He investigated weediness level in USSR agroecosystems. Grodzinsky conceived several concepts currently used in modern weed science including the occurrence and dominance of some weed species associated to the cultivation of specific crops and the critical periods of weed interference in crop plants (52,53,54,64,66,67).

Grodzinsky and his followers laid the foundations and practice of creating allelopathically balanced phytocenoses, based on a proven biotesting system (59,86), phytosanitary approaches and principles for designing agrophytocenoses (61,83), diagnosing allelopathic relationships in natural and managed ecosystems (62,68,165). Main differences were found between the allelopathic relationships in the multispecific natural plant communities (i.e. in forest, forest-steppe, steppe and mountain vegetation and those in annual and perennial crops (38,39,43,52,57,61).

3. BIOSPHERIC ROLE OF PLANT EXCRETIONS

I. Nikolay Grigorievich Kholodny (1888-1953): Kholodny, Tokin and Chornobrivenko were the founders of Allelopathy research in USSR. Nikolay Grigorievich Kholodny (1882-1953) Ukraine authored more than 200 research papers on various aspects of Soil Science, Microbiology, Plant Physiology, Anatomy and Ecology. Based on long-term research (1938-1952), he developed the theory of air nutrition with phytogenic volatile substances and postulated their role on plant growth in the cenosis (76,80). He formulated

the idea of mutual chemical plant interactions (77,78) and developed biotests to determine the volatile emissions of seeds, soil and other natural materials (79,80). Kholodny presented plant interactions as the circulation of volatile substances, such as unsaturated hydrocarbons, formed in the soil by microorganisms from excreted plant products (80). These compounds move from soil to the atmosphere, where they exert their effects on plants. The higher plants always produce highly active volatile substances, which he called atmovitaminams - respiratory vitamins. In 1943, he showed the release of volatile organic compounds from living plants (germinating pea seedlings, leaves, flowers, and fruits of apple-tree) and their assimilation by the soil microbes (79,80). Leaves of *Artemisia absinthium* L. and *Mentha longifolia* L., flowers of *Solidago canadensis* L. and branches of *Pinus sylvestris* L. also released the active volatiles. Unlike other plants releasing the odorous substances, which control many microbes, however, the flowers of the non-odorous Crassulacian plant *Sedum oppositifolium* L. induced abundant growth of actinomycetes. The leaf excretions of *Solidago oppositifolium* L. stimulated the growth of ectomycorrhizal fungi. In 1957, Kholodny published the results of his work on the volatile excretions of plants and soil microorganisms, which greatly helped in the development of allelopathy (80). The original experiments on air nutrition of plants and microorganisms with volatile organic products became the basis for the concept of the mutual chemical influence among plants. Kholodny's ideas were further explored by Sanadze (129-132) and Porutskiy *et al.* (99,100). These scientists analyzed the chemical transformation of plant volatile and gutational excretions and their roles in the soil-plant-air-soil system.

II. Boris Petrovich Tokin (1900-1984): He developed the phytoncide theory (148,149) and defined phytoncides as compounds with defensive role participating in the interaction of higher plants and animals, lower and higher plants, and microorganisms (149). Tokin proposed the practical use of phytoncides in biological plant protection, disinfection of substrates and environments, treatment of wounds, ulcers and a number of diseases, ensuring the induction of acquired plant immunity (150-152). He described for the first time, many patterns of biospheric allelopathic interactions in terms of the phytoncide research and demonstrated the theory of the regulatory effects of plant extracts on growth and development of other plants (151,153). Tokin's ideas were similar to the studies of Grummer (72). He was first to show the importance of phytoncides in ecology and in the life of biocenosis related to allelopathy (154,155). Hence, phytoncides became an interesting field of research for Physicians, Pharmacologists, Immunologists, Ecologists, Agronomists and Foresters (151,156,157). Phytoncides had bactericidal, fungicidal and pesticidal activities (156). Tokin published 6-Monographs on phytoncides (81,82,150-153,156) explaining the characteristics of plants excretions. For 40 years, he organized the All-Union Conferences on phytoncides and edited their proceedings in Book form. Phytoncides were considered as natural factors of plant immunity (158), they kill or control microorganisms and other parasites (156,157,180) when applied at high concentrations but at low concentrations serve as nutrients for microorganisms (2,19,77). Tokin's ideas were expanded by the Soviet scientist Chaylakhyan (7), he proved that phytoncides can act not only as inhibitory substances but also as growth stimulants. Chasovennaya (8-9) and Golomedova (27,28) investigated the stimulatory effects of phytoncidal substances on the plant growth processes and their impact on plant morphogenesis.

III. Sergei Ivanovich Chornobrivenko (1899-1967): He modelled allelopathic interactions not only in laboratory assays but also in field experiments. He was the first to generalize the effects of plant secretions in the soil-rhizosphere-plant system. In a Monograph (11), he presented a valuable summary of his results on chemical plant interactions obtained during the period 1934-1955. He classified plant species according to their allelopathic influence as mutually or unilaterally promoting growth or suppressing it, as well as indifferent. He referred the plant allelopathic substances as plant secretions. Chornobrivenko's ideas were developed in depth by Shandi (136,137), who related the plant-plant interactions to species composition and the multiple influences in plant communities.

IV. Andrei Mikhailovich Grodzinsky (1926-1988): He was the first to formulate allelopathy as a cycle of physiologically active substances in the biogeocenosis (10,52,83). He defined methods to assess the allelopathy taking into account the cenotic structure of plant communities (10,53). Grodzinsky conceived the scheme of donor-acceptor plants with the participation of root exudates, volatiles (phytoncids) and products of soil biochemical activity (54,55). This scheme today is part of the fundamentals of allelopathy and used to describe allelopathic phenomenon. He elucidated the role of allelopathy in the formation, structure, stability and productivity of plant communities in natural and managed ecosystems (56). He did long-term study of the role of allelopathy in agrophytocenology, specially in the weed-crop interactions (58,59). Grodzinsky established clearly the goals for the allelopathic science (60) including: (i) Disclosing the mechanism of soil fatigue (57), Selection of plant species in mixed crops (61,69,73), Bio-electromagnetic field and allelopathy (61,68), Selection of suitable bioassays (59), Principles of plant protection based on natural products applied to agroecosystems (61), Methodological basis to investigate allelopathic activity in phytocenoses (62,68), Assessing the biochemical and allelopathic activity of soils (63), Assessing allelochemical uptake by plants (52,58). His research also concerned the contribution of plant residues, forest litter and green manure in soil allelopathy and the level of weediness in the fields (64,70,71). The scientist actively investigated the stimulatory properties of weeds (52,53,64,65), methods for biological and allelopathic control of weeds (52,65-68), growth and development of weeds and cultivated plants in plant communities (51,52,65,68). His concept of allelopathy as a circulation of physiologically active substances established that these compounds regulate the internal and external relationships in the biogenesis and are responsible for the balance, stability and changes observed in plant communities (60,61,63,68). Grodzinsky proposed the following in-depth Allelopathy research areas (125): (i) Mechanisms of soil autotoxication (exhaustion)/soil sickness after various crops, (ii) Compatibility of crop species in mixtures, and (iii) Relationship between biologically active light emission (Gurvich rays stimulatory to plant growth) and allelopathy. Grodzinsky (60) was the first scientist formulating the signalling role of allelochemicals, which was discovered during investigations on seed germination of orchids and parasitic plants. These studies were successfully continued by a Grodzinsky's student, the Academician Matveev who did his research at Samara State University. He postulated that allelochemicals exert an allelopathic action, when they overcome a specific threshold that can be measured and was named the allelopathic threshold of sensitivity. He developed methods to study it and published the first research on this issue (90,128).

V. Moroz, Yurchak: Moroz, Yurchak (1937-2010) and Golovko (1937-2005) were students of Grodzinsky. They worked from 1970 to 1990 and identified allelochemicals isolated from > 200 plant species. Allelopathic methods were developed to investigate soil processes during long-term monocropping (20-22,50,66,105) and in mixed crops (21,24). Their researches about root exudates and allelopathic pressure during mixed cropping of forage and grain crops are particularly interesting (161,162,165-167). They elucidated the chemical structure of allelochemicals secreted from various plant species and their relationships with mycorrhizal growth, microbiological activity in soil, the levels of mobility of the organic soil matter and mobile forms of the main nutrients, the effect of non-humified organic matter produced by donor plants on the biochemical soil processes, as well as on growth, development and productivity of acceptor plants (85). The chemical composition of secretions and extracts from aromatic plant species (98,168), the role of green manures in soil allelopathy and the release of green-manure allelochemicals in crops rotations were also investigated (64,68,70,71,176). They also studied the release of phytotoxic and growth promoting allelochemicals from decomposing residues and their effect on soil microflora (68,70,71,102,161,163,164,172-174) and the increase in crop yields and the stability of agrophytocenoses (165,173,174). The effects of root exudates on plant nutrients uptake was also investigated in both field (25,70,71) and hydroponic cultivation (26). Works dealing with similar issues appeared 15 years later in the West. Allelopathic properties of woody Ukraine forest-forming species were clarified (4). The stimulatory or inhibitory effects of volatile excretions from the flowers of *Philadelphus* L., *Catalpa* Scop., *Robinia pseudoacacia* L., *Aesculus hippocastanum* L., *Syringa vulgaris* L. and other plant species, were reported on pollen germination and fruit development (84).

Interactions between aromatic plants and microorganisms were investigated. These researches considered the stage of growth and development of aromatic plants and established the effects of fungal allelochemicals on plant growth (168). Biotests were designed to determine the aromatic emissions from many medicinal plants (172). Varieties were selected for crop rotation based on low autotoxicity and their allelopathic effects on preceding and subsequent crops involved in the cropping sequence. Investigations were also devoted to the allelopathic effect of crop residues (i.e. crop stubbles, straws) and how plant nutrition and mineral fertilization affect crop allelopathy (172). The scientific foundations for agrophytocenoses of aromatic plants were established for the first time, including the analysis of their allelopathic effects and the chemical nature of their root exudates (168). These pioneer researches in agroecology were first steps needed to implement the sustainable agriculture (170).

VI. Erast Golovko (1937-2005): He investigated the impact of plant root exudates on rhizosphere and soil microbiota as a whole, obtained qualitative and quantitative data on soil microbial species from crop fields (29,30), answering several questions regarding the participation of allelopathy in soil fatigue and providing microbial indicators useful to design stable and highly productive agroecosystems (31,32,34). Size variations in soil microbial populations with important ecological or trophic participation were monitored during the living cycle of several crops. The structure of the soil microbial community was quantitatively characterized by using the coefficients of mineralization-immobilization, pedrotrophy, oligotrophy and humification during monocropping and associated to

residues remaining on fields after harvest such as stubbles, straws, among others. These described how soil microbiota act either in degrading or restoring soil fertility and the involvement of allelopathy in soil fatigue. Fungi were identified as an important source of phytotoxins which accumulates in the soil and negatively affect crops (30,39-41). The allelochemicals produced by higher plants and microorganisms had a herbicidal potential for weed control (38).

Golovko studied allelopathic properties of vegetable and aromatic plants in closed ecosystems (37,38). He proved that volatile plant secretions increases competition between plants growing in a limited habitat (38). New technologies were developed for growing vegetables with high vitamins contents and to study plant interactions mediated by volatile compounds and their concentrations in headspace (43). He identified compounds affecting the plant growth, which were isolated from higher plants, exotic species (e.g. genus *Allium* L., *Rhododendron* L., *Echinacea* Moemch., *Tagetes* L. and *Syringa* L.), and proposed the use of these compounds as natural phyto regulators (37,42). New knowledge was obtained on microbial diversity in crop fields and how it is affected by plant excretions (39-41). He isolated phytotoxins produced by plants and microorganisms and analyzed the taxonomic structure of rhizosphere microbiocenoses of steppe plants with subsequent identification of the microbial biodiversity, which created a gene bank of microbial-allelochemical producers with more than 500 strains (41). The allelopathic activity of 27 dominant steppe plant species was determined (43). He developed methods to isolate and identify physiologically active substances that simulate the absorbing activity of root systems and tested microbial and plant systems (41). He published 200 scientific publications including Monographs and Articles, where he highlighted the formation of steppe plant associations, the principles of donor-acceptor interactions of plants through root exudates, phytoncides and microbial waste products (96,97).

VII. Russian School of Allelopathy (Vasilii Ivanov, Givi Sanadze, Alexander Tambiev, Mikhail Telitchenko, Petr Yurin, Vsevolod Dadykin, Mikhail Kolesnichenko, Ivan Rakhteenko and Nikolai Matveev): The Russian School of Allelopathy was developed in parallel with the Ukrainian's School. Good allelopathy researches were done by Professors Vasilii Ivanov, Institute of Plant Physiology, Moscow and Mikhail Kolesnichenko, Voronezh Agricultural Institute (125,126). Ivanov (74) for the first time traced the release of plant allelochemicals from roots of herbaceous plants using radioactive isotopes. Kolesnichenko research on biochemical interactions in forest phytocenosis was published in two monographs (75,82). He recommended the use of phytoncides and allelopathic characteristics of woody plants in forest plantings in urban and rural areas. He showed the effects of both volatile and water-soluble allelochemicals and phytoncides released from the roots on CO₂ assimilation in leaf photosynthesis and P-assimilation during the plant growth in mixed plantings. He also identified sensitive tree species using different technologies in their cultivation. Professor Ivan N. Rakhteenko from Byelorussia (Institute of Experimental Botany was NAN Byelorussia, Minsk) was the first to investigate allelopathic interactions in root systems (106), the phenomenon of mutual stimulation of pollen germination in mixtures of some grasses in field experiments (44-49).

4. BIOACTIVITY OF ALLELOCHEMICALS IN PLANT EXCRETIONS

The isolation and identification of allelochemicals is fundamental to understand the allelopathic interactions at plant-plant and plant-phytocenosis-biogeocenosis levels. More allelochemicals were identified thanks to the progress in chemical, chromatographic and mass-spectrometric methods. Hydrocyanic acid (17), molecular hydrogen (129,130) and isoprene (132) were reported at the beginning among the volatile substances released from the plant leaves. Later, a large number of aldehydes, alcohols and ketones were identified in the vapours released from leaves and shoots (12,99,109,110). Gas chromatography (110,117,119) and microspectrofluorometry (117,119) were used for the first time in allelopathic studies on plant excretions. Laboratory experiments with decomposed leaves of woody plants showed that their volatile excretions inhibited seed germination of radish. However, very long exposures showed inhibitory effects due to CO₂ and methane (112). Use of gas chromatography to study the allelochemicals and phytoncides allowed detection of hydrocarbons aldehydes and ketones in leaves and shoots vapours (13,100,107,111,131,179). In general, volatile plant excretions contains small concentrations of gaseous substances viz., ethylene, propylene, butylene and isobutylene (e.g. flowers of *Yurinea* (L.) Rchb. and *Linum* sp. (L.) ethylene or propylene (e.g. spikelets and chloroplasts from wheat caryopsis) (100). The application of radioactive phosphorus in wheat increased the gas chromatogram peak of isobutylene in spikelets, but not in chloroplasts.

I. Volatile excretions

Volatile and liquid plant excretions showed significant biological activity (125). The volatiles from plants of the Rosaceae family contains high concentrations of ethylene and propylene and showed a strong biological activity. Pear volatiles are an exception in this family because they are mainly contains propylene, which had low phytonciding activity (100). Volatiles from Solanaceae plants are rich in butylene and showed low phytonciding activity. An exception is the *Physalis* genus with volatiles saturated with ethylene. The Gramineae and Malvaceae species mainly released ethylene and were biologically active as phytoncides and growth regulators. These findings indicated that the biological activity of ethylene was stronger than that of propylene and butylene. Prof. Dadykin *et al.* (13) studied volatile excretions from vegetables growing in closed systems suitable for space trips. He identified the best combinations of crop species to be grown in such conditions, including cucumbers, tomatoes, spicy leafy crops, onions and parsley. Prof. Drabkin (18) and Dr. Chasovennaya (8,9) were the first to investigate the physiological effects of allelochemicals on plant and animal cells. Under short exposure to volatile phytoncides, the plant cells suffered disturbances such as the decomposition of chloroplasts, cytoplasm coagulation and apoptosis. The cells or organisms exposed to phytoncides and allelochemicals showed following: (a) Decreased respiration and respiratory enzymes in helminths of *Lumbricus* sp. L. (18), (b) Exoosmosis of *Triticum aestivum* L. wheat metabolites on other cereal plants (91), (c) Changes of chloroplasts movement in cytoplasmic streaming of *Elodea canadensis* L. and *Elodea densa* L. (108,111), (d)

Changes in the membrane permeability of *Beta vulgaris* var. *rubra* (127), (e) Changes in cytoplasm viscosity of *Allium cepa* L. (108), (f) Photochemical reactions of chloroplasts of *Pisum sativum* L. (107), (g) Bio-luminescence of a DOPA artificial system (145,179), (h) Redox changes of electron carriers in photosynthesis of *Pisum sativum* L. (114), (i) Cholinesterase activity of chloroplasts and leaves of *Pisum sativum* L. (121). A model system based on L-DOPA (dioxypheylalanine) oxidation showed a high oxidative activity of root excretions from rye (*Secale cereale* L.), wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), pea (*Pisum sativum* L.), jointweed (*Polygonum* sp.) and white mustard (*Sinapis alba* L.) (145,146,177,178). Electron paramagnetic resonance spectroscopy of the excretions demonstrated that the free radicals formed in this system are correlated with the allelopathic activity (145). The volatile excretions of 25 species were studied with the help of the L-DOPA-model. Extracts of *Chelidonium album*, *Equisetum compestre*, *Tanacetum vulgare* L. and *Vicia faba* L. showed both high oxidative and allelopathic activity. Cellular bioassays done by the Russian scientists (147) developed new biochemical and biophysical methods useful to investigate the effects of plant excretions on other organisms.

II. Phytoncides and allelochemicals

The impact of phytoncides and other allelochemicals was also investigated at cellular level (100,107,108,113,127,131,132,152,156,179). Cellular processes investigated were oxidative and energetic changes (107,111,113,127,128), shifts in membrane permeability (113,127), enzymatic activities (115,116) and light emission or autofluorescence of intact cells (118,120). Some new concepts of cell-cell contacts in allelopathic interactions were reported. Substances known as neurotransmitters in animal cell-cholinic ester acetyl choline and biogenic amines (dopamine, noradrenaline, adrenaline, serotonin, histamine) were found in plant cells and their excretions (115,116,124) and thus, the concept of chemoreception was added to allelopathic interactions (113,116,124). It was reported that plant excretions called antizonants (volatile and other forms of excretions) react with ozone and their reaction products may be active in biocenosis (116).

III. Valentina Dionis'evna Roshchina (1922-2019)

She was Professor and Head, Department of Botany, Pedagogical Institute of Voronezh. During 1965-1975, she investigated the woody plant excretions and mechanisms of their action at cellular level. She showed the sensitivity of some cellular processes to the excretions and water infusions from 30 woody plant species. New cellular biotests were recommended for the allelopathic studies viz., movement of chloroplasts in the cytoplasmic streaming, the cytoplasmic viscosity (74,107), permeability of cell membranes (e.g. plasmalemma, chloroplasts and tonoplast) (107,108,109,110,113,117, 119,123,127), and the Hill reaction in isolated chloroplasts (107,111). Prof. Roshchina applied gas chromatography in allelopathic studies of woody plants at the end of 1960s. She found volatile alcohols, aldehydes, ketones, aliphatic compounds and phenolic compounds in transpiration water and water infusions of these plants. Some excretions were allelopathically active. Prof. Roshchina and Dr. Tambiev introduced the term 'Exometabolite' to designate an extracellular compound involved in allelopathy during the First USSR Conference on Allelopathy in 1966 (74) and later this term was used

frequently (111,145). In the 1970's, Prof. Roschina summarized the cellular action of water infusions/leachates and exometabolites released during plant transpiration (107,109, 110,124,127,147,179). In 1974, she received Doctor of Science degree for the Dissertation 'The Exometabolites of Woody Plants and Mechanisms of Their Actions' from the Institute of Plant Physiology, Ukraine Academy of Sciences, Kiev. She wrote > 70 research papers. Her monograph *Excretory Functions of Higher Plants* was published in 1989 in Russian language by Nauka Publishing House, Moscow. It included modern views on the plant excretory functions as a whole and the chemical Interactions in biocenosis. In 1993, its English edition was published by Springer-Verlag, Berlin, Germany.

IV. Victoria Vladimirovna Roshchina (1949-2025)

She is daughter of Prof. V.D. Roschina, conducted researches on allelopathy till now. Her first research paper "The mechanisms of action of the woody plants extracts on plant membranes", was published in 1970 (127). From 1977 to 1990, she was scientist, Institute of Soil Science and Photosynthesis, Pushchino and worked on regulation of photosynthesis by natural biological regulators, including phytoncides and other allelochemicals. Thereafter, she studied the action mechanisms of the natural growth regulators, including neurotransmitters, and their occurrence and functions in plants (108,109,110,111,113,122-124,175). She identified insecticidal metabolites released from the toxic plant *Scuta virosa* L. and *Capsicum annuum* L. These compounds were also powerful modulators of photosynthetic functions viz., chloroplasts movement and permeability (115,116,118, 120,124). Besides, the neurotransmitters acetylcholine, catecholamines, serotonin, histamine found in plant excretions were also identified in chloroplasts. In 1989, Victoria and her mother authored the monograph 'The Excretory Function of Higher Plants' in Russian language by Nauka Publishing House, Moscow. Its English Edition was published in 1993 by Springer-Verlag, Berlin, Germany. In 1990, she moved to Russian Academy of Science, Institute of Cell Biophysics, Pushchino. In 1991, she received the highest degree Doctor of Biology for the research work 'Biomediators in Chloroplasts', dealing with the new concept of the action of neurotransmitters on plant cell. In the same year, her monograph 'Biomediators in Plants: Acetylcholine and Biogenic Amines' was published in Russian language by Biological Centre, USSR Publishing House, Pushchino.

The research achievements of Grodzinsky's School were based on significant analytical laboratory and field research. Till 1990, the allelopathic properties of over 900 plant species (including over 200 weed species) were analyzed and over 30,000 plant samples and over 20,000 soil samples were chemically analyzed (87). The allelopathy research done in USSR, from 1967 to 1987, were systematized (54). The physiological effects of allelopathic substances documented on laboratory and field studies were summarized in more than 1000 scientific publications.

5. CONCLUSIONS

This review highlighted the most important literature on allelopathic research in the former USSR, focussed mainly on 1960-1990 period. More than 300 scientists worked in Allelopathy, despite the restricted access to financial support and laboratory equipments for chemical analyses. Investigations comprised: (i) Isolation, identification

and bioassay of allelochemicals, (ii) Modelling of the allelopathic relationships, (iii) Design of drugs with allelopathic-phytoncidal activity, (iv) Weed control in crops, (v) Stimulation in post-Soviet Era. We hope that the scientific legacy described here will contribute to a renewed interest in Allelopathy research by research communities in all countries.

DECLARATION OF COMPETING INTERESTS

The authors declare that they have no competing financial interests related to the publication of this manuscript. The research was conducted independently, free from any conflicts of interest that could have biased the findings.

AUTHORS' CONTRIBUTIONS

All authors approved and finally draft of manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest. All authors agree to publish it.

ETHICAL STATEMENT

This is to inform you that in this study, we have not been involved in any animal and human studies.

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