

Allelopathy Research in Continuous Cropping Problem of *Panax ginseng*

C.P. Xiao, J. Yang, J. Sun, Y.X. Jiang, L.M. Yang¹, L.L. Weng* and Z.D. Qiu*
Key Laboratory of Quality Resources, Identification of Chinese Medicine,
School of Pharmaceutical Sciences, Changchun University of Chinese Medicine,
Changchun 130117, China
E-mail: btxnw@163.com , qzdczy@163.com , 735110462@qq.com

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*Correspondence author, ¹College of Chinese medicinal materials, Jilin Agricultural University, Changchun, 130118, China

ABSTRACT

Panax ginseng is traditional Chinese herb, which is continuously cultivated on the same land, hence, its yield and quality is decreased. Thus, overcoming the problems of soil sickness in Ginseng in continuous cropping is key issue. The autotoxicity of Ginseng is one of the critical factors in continuous cropping problems. We have reviewed the current research status of continuous cropping problems in ginseng and role of ginseng allelopathy are summarised. Based on the relationships between the allelochemicals and continuous cropping problems in *P. ginseng*, future research areas are suggested.

Key words: Allelochemicals, allelopathy autotoxicity, continuous cropping problem, *Panax ginseng*, root exudates

1. INTRODUCTION

With an ever increasing demand for Chinese medicinal materials in the international and domestic markets, the medicinal plants production needs to be increased. In long-term medicinal plants cultivation, is adversely affected by retarded growth, serious diseases and insect pests infestation which reduces the crop yield and quality. The Chinese medicinal Plants are mainly grown in continuous cropping, hence face the problem of soil sickness (68,102). The continuous cropping soil sickness adversely affects the yield and quality of Chinese medicinal materials, hence, it needs to be studied and solved. Researches have shown a close relationship between the continuous cropping problem and allelochemicals in the medicinal plants. Thus allelopathy plays major role in continuous cropping problem of medicinal plants (85,109).

In Allelopathy, chemicals released by one plant species directly or indirectly affects another plant species or even on itself as well as microorganisms (60). Allelopathy is plants mechanism to compete for growth resources (plant nutrients, soil moisture, space) (45,98), and occurs through the release of secondary metabolites (allelochemicals,) into the environment. Autotoxicity is a form of allelopathy widely occurs in nature and affects the plant growth and development (26,110). About 60 % medicinal plants cannot grow in continuous cropping due to the soil sickness problem, especially in ginseng species [*Panax ginseng*, *P. quinquefolius* L. and *P. notoginseng*, etc (2,7,23,42,54,56,57,65,100,107)] distributed in some provinces of China (Table 1) (Fig. 1).

Ginseng Morphology: The main components of ginseng plants are: root and rhizome, which contains the chemicals with medicinal properties.

(i). ***P. ginseng*** : *P. ginseng* is mainly grown in China, South Korea and North Korea (Fig. 2). Its plant consists of main root (fleshy, cylindrical or fusiform) and rhizome [short, hyperplasia of one section per year, on which adventitious roots grow (known as Ding)]. Leaves are compound with 5-lobules. The apex gradually becomes acuminate, blade edge is serrated, umbel is single and grows on the stem apex, and globose drupe has shape similar to berry, which turns red at maturity (Fig. 3).



Figure 1. Ginseng growing areas in China

Note: ■ *P. ginseng* and *P. quinquefolium* growing areas, ■ *P. ginseng* growing areas, ■ *P. quinquefolium* growing areas, ■ *P. notoginseng* growing areas, ■ *P. japonicus* growing areas

(ii). *P. quinquefolius* (American ginseng) : Its morphological characters are similar to *P. ginseng*, and the only difference is in contour of lobules, with acuminate leaf apex. The main medicinal parts root and the rhizome have same efficacy to *P. ginseng* (Fig. 3). It is mainly grown in China and Canada.

(iii). *P. notoginseng* (Sanqi): The differences from the *P. ginseng* are the shape of main root, the number of lobules are 3~7, with bristles on both sides of the leaf vein. It is mainly grown in Southwest China, Yunnan province (Fig. 3).

(iv). *P. japonicus* : Its rhizome is horizontal, bamboo-whip-shaped, with indented stem scars between nodules. It is the most widely distributed species of *Panax*. It originates from east Japan, west Nepal, South Sikkim, and in China [Shaanxi, Gansu, Anhui, Zhejiang, Jiangxi, Fujian, Henan, Hunan, Hubei, Guangxi, etc (Fig. 3)].

(v). *P. vietnamensis* : It is grown in Kon Tun Province of Vietnam. The difference between *P. vietnamensis* and *P. ginseng* are the size of the main root and rhizome are reversed, with small root adhering to the tail of rhizome (Fig. 3).

Table 1. Ginseng plant species of *Panax* (Family *Araliaceae*)

Allelochemicals released	Research aspect studied	Economic uses	References
<i>Panax ginseng</i> C.A. Mey/ Ren Shen			
Alkanes, Organic acids and esters, Pyran, Alkane derivatives, Phenolic acids, Saponins, etc. Butanedioic acid diisobutyl ester, Palmitic acid, Benzoic acid, Stigmasterol, Glycerol, 3-Hydroxybutyric acid, Cholesterol, ginsenosides, etc.	Cultivation technique, Continuous cropping problems and mechanism, New resource development, Metabolic and metabonomic studies, Chemical composition, Biosynthetic pathway of ginsenoside, Pharmacological action, Clinical application, etc.	i. Improved brain function ii. Pain-relieving effects iii. Preventive effects against tumors as well as anti-tumor activity iv. Enhanced immune system function v. Anti-diabetic effects vi. Enhanced liver function vii. Adjusted blood pressure viii. Anti-fatigue and anti-stress effects ix. Improved climacteric disorder and sexual functions x. Anti-oxidative and anti-aging effects	7,23,56,65
<i>Panax quinquefolius</i> L./Xi Yanshen			
Fatty acid, Organic acids and esters, Phenolic acids, Cinnamyllic acid and the derivatives, Coumarins, Terpenes and steroids, etc. Oxalic Acid, Syringic acid, Ferulic acid, Coumaric acid, Vanillin alcohol, p-coumaric acid, etc.	Cultivation technique, Continuous cropping problems and mechanism, Chemical composition, Pharmacological action, Structure–function relationship, Clinical application, etc.	i. Effects on the central nervous system ii. Cardiovascular system, iii. Antidiabetic effects iv. Cancer chemoprevention v. Endocrine system and immune system	2,57,107
<i>Panax notoginseng</i> (Burk) F.H.Chen /San Qi			
Alkanes, Organic acids and esters, Palmitic acid, Benzoic acid, Phenolic acids, Terpenes, etc. Such as p-hydroxybenzoic acid, vanillic acid, syringic acid, p-coumaric acid, ferulic acid, Benzoic acid, <i>Panax notoginseng</i> saponins	Cultivation technique, Continuous cropping problems and mechanism, Chemical composition, Pharmacological action, Clinical application, etc.	i. A protective effect on acute hepatic injury ii. Effect on the kidneys iii. Hypoglycaemic activity and effect on early diabetic nephropathy and diabetic macroangiopathy iv. Enhanced immune system function v. Immunological adjuvant activity and immunostimulatory action vi. Anti-inflammatory and analgesic activity vii. Antioxidant activity and effect on plasma lipid level viii. Anti-tumour activity ix. Effect on sperm motility and estrogen-like activity x. Hemostatic activity and effect on haemorrhagic shock xi. Effect on platelet aggregation and anti-atherosclerotic activity, etc	42,54,100

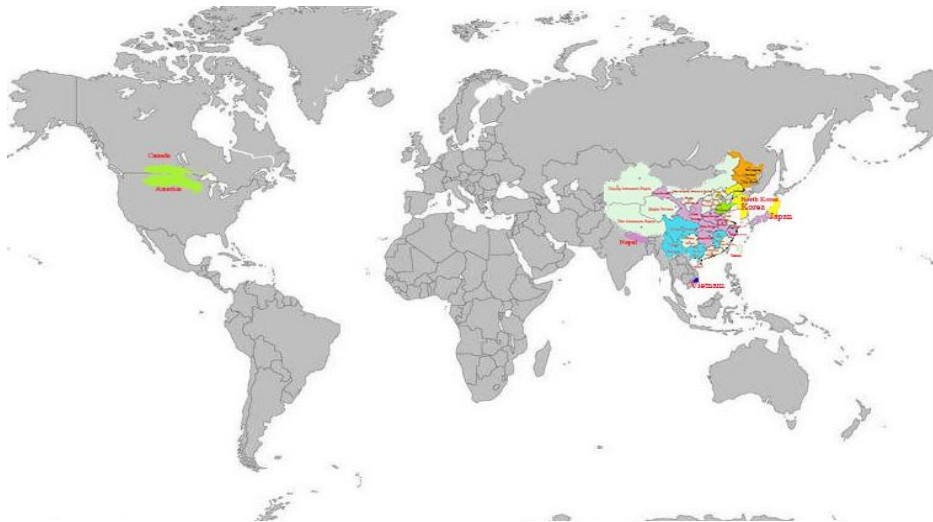


Figure 2. The Ginseng cultivation areas in World

Note: ■ *P. ginseng* and *P. quinquefolium* growing areas, ■ *P. ginseng* growing areas,
■ *P. quinquefolium* growing areas, ■ *P. notoginseng* growing areas,
■ *P. japonicus* growing areas, ■ *P. vietnamensis* growing areas,

Panax ginseng

Compared to other *Panax* species, it is traditional Chinese medicinal material with very high medicinal and economic value. It is grown between 40-45° North Latitude and 117.5-134° East longitude is, i.e. Eastern Liaoning, Jilin and Helongjiang province (100). Its main growing areas are in Changbai mountains, eastern Jilin Province in China (89) (Fig.3). It has the largest cultivated area and produces > 70 % of the world's ginseng production. Other species of *Panax* are also grown in America, Canada, Korea, Vietnam and Japan (Tab. 2) (Fig. 1).

With the rapid development of ginseng industry, the area under ginseng cultivation has increased significantly. However, the yield is severely hindered by the continuous cropping problem. *P. ginseng* cannot be cultivated on the same field consecutively for several years due to development of soil sickness (72). In continuous

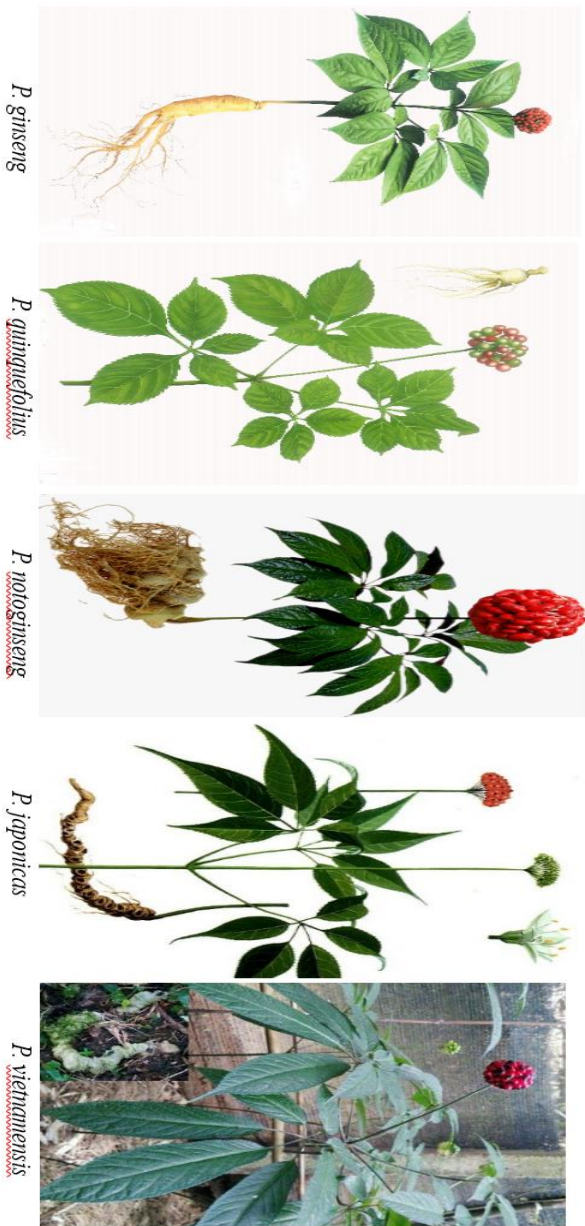


Figure 3. The cultivated ginseng (*Panax*) Species

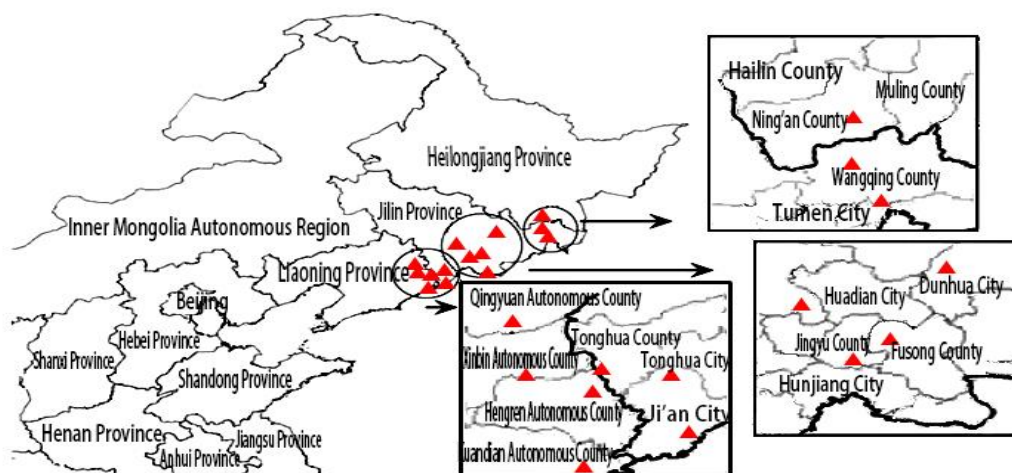


Figure 4. Ginseng growing areas in Jilin province, China

Table 2. The Ginseng growing Areas in various Countries

S. No	Ginseng spp.	Country	Growing Regions	Area (Million ha)*	Rating
1	<i>P. ginseng</i>	China	Heilongjiang, Jilin, Liaoning Province, etc.	15.6 (China)	I
3	<i>P. notoginseng</i>	China	Yunnan, Guangxi, Jiangxi, Sichuan Province, etc.	13.2 (China)	II
2	<i>P. quinquefolium</i>	China, Canada, America	Heilongjiang, Jilin, Shandong Province and Beijing City, etc.	0.98 (China)	III
4	<i>P. japonicus</i>	China, Japan, Nepal	From Japan in the east to Nepal in the west, from Gansu and Shanxi in the north to Sikkim in the South. In China, it is growing in Shanxi, Gansu, Hebei, Henan, Hubei, Hunan, Zhejiang, Anhui Province, etc.	0.02 (China)	IV
5	<i>P. vietnamensis</i>	Vietnam	Kontum Province, etc.	0.012 (Vietnam)	V

*The area for other countries not available

cropping, ginseng roots turn rusty and rot due to soilborne diseases. Generally, the seed germination in the second year is reduced < 30%, and about 70% fibrous roots become red and diseased (28). The continuous cropping problems also exists, in the new forest soil resulting in poor growth, reduced yield and quality. In continuous cropping problem, the plant nutrients became unbalanced and pH is reduced (82).

2. RESEARCH STATUS

Ginseng continuous cropping problem is very complicated. There are 4-main factors in ginseng continuous cropping (86), viz., (i). Increase in numbers of soil pathogenic microorganisms, (ii). Imbalanced soil microbial community, (iii). Changes in

soil physico-chemical properties leading to decreased soil fertility and (iv). Ginseng autotoxicity. The hypotheses that the interactions among the allelochemicals deteriorates the cultivated soil and soil pathogenic microorganisms are main factors in ginseng continuous cropping problem (101). Owing to recent advances in science and development of precision analytical instruments, researches on allelopathic effects have progressed to better understand the problems in ginseng cultivation.

Why and under what conditions do Ginseng plants release allelochemicals? What are the allelochemicals? And do they interact with each other? Is the ginseng plants growth affected directly or indirectly by ginseng allelochemicals? What role does ginseng allelopathy play in its continuous cropping disorder? These are many questions and their answers are of great value in understanding the nature of allelopathy and the causes of continuous cropping problems in Ginseng. Therefore, an in-depth study of the role of ginseng allelopathy in continuous cropping problems is of strategic value in the sustainable development of ginseng industry.

3. CAUSES OF SOIL SICKNESS IN GINSENG

Plants cannot escape or change the environment, hence for survival, they adapt to the environment (94). Under stress conditions, the plants ability to overcome stress is greatly reduced as they have also to compete with other organisms (30). One of the most important pathways to survive under stress is the generation and release of allelopathic substances, which affects the seed germination and plant growth of the same or different plants, distribution of microorganisms, nutrients availability and increased plant resistance to toxicity.

3. 1. Perennial plant with Long-growth cycle: Owing to shortage of land, multiple and high-density cultivation of ginseng is done in the same plot of land, this further deteriorates the soil (91). The long term ginseng cultivation aims to increase the secondary metabolites contents in roots. Ginseng is long duration crop (several years or even decades), hence, more susceptible to allelopathic effects. With the increase in cultivation years, ginseng secondary metabolites are continuously released into the soil and get accumulated. Besides, the allelochemicals released from ginseng plant residues and root system are allelopathic to normal growth of ginseng plants.

3.2 Similarity between ginseng allelochemicals and active ingredients: Allelochemicals are derived from the secondary plant metabolites (77). The physiologically active substances, specific to ginseng, are also secondary metabolites (saponins, organic acids, phenolic acids etc.) (34). In ginseng cultivation, these are released into the environment, making the ginseng plant susceptible to their allelopathic effects (74) and this aggravates the problem of soil sickness in continuous cropping.

4. ALLELOPATHIC EFFECTS OF GINSENG

4.1 Autotoxic Allelochemicals of *P. ginseng*

4.1.1 Sources: Allelochemicals are released as volatiles into the air, plants roots exudates, leachates or decomposition of plant material, these promote or inhibit the growth of surrounding plants and microorganisms. The root exudates play main role in soil sickness. Even small amount of allelochemicals affects the plants growth and the microorganisms of plant rhizosphere (25). The ginseng allelochemicals characteristics are: (i) Ginseng is interacting host as well as the guest in reaction and (ii) allelochemicals affect the growth and development of ginseng (19,30). The ginseng allelochemicals are mainly derived from the root exudates and decaying plant residues (69). During the growth of ginseng, the root exudates and the substances of decomposing plant residues are distributed in the plant rhizosphere soil. When these substances reach a critical concentration, the plant itself is poisoned and this is called autotoxic effect.

Table 3. Autotoxic allelochemicals of *P. ginseng*

Allelochemicals in Root exudates	References
Allelochemicals in soil growing <i>P. ginseng</i>	
DL-Lactic acid, Glycolic acid, 3-Hydroxybutyric acid, 3,4-Dihydroxybutanoic acid g-lactone, Benzoic acid, 4-Hydroxybutanoic acid, 3-hydroxyvaleric acid, Glycerol, 2,3-dihydroxy-Propanoic acid, 3,4-Dihydroxybutanoic acid g-lactone, DL-Pyroglutamic acid, L-threonic acid, g-lactone (6CI), 4-Hydroxybenzoic acid, arabinofuranose, D-Ribose, 2,3-O-Isopropylidene-D-Ribonic gamma-lactone, Arabinose, 3,4,5-Trihydroxypentanoic acid, D-Xylonic acid, D-Arabino-Hexonic acid, 3-deoxy-2,6-Dimethylcyclohexanol, Diisobutyl phthalate, D-Fructose, l-Methionine, n-Pentadecanoic acid, Pentadecanoic acid, a-L-mannopyranoside, methyl-16-deoxy-β-D-Glucopyranose, D-(+)-Xylose, L-Talose, D-Mannitol, Galactose, Hexadecanoic acid, Inositol, cis-9-Hexadecenoic acid, Glucopyranose, D-Glucose, Gluconic acid, Heptadecanoic acid, (Z,Z)-9,12-Octadecadienoic acid, Linolenic acid, trans-9-Octadecenoic acid, cis-13-Octadecenoic acid, cis-9-Octadecenoic acid, cis-6-Octadecenoic acid, Octadecanoic acid, cis-10-Nonadecenoic acid, Isopimaric acid, Dehydroabietic acid, Eicosanoic acid, Phthalic acid, mono-(2-ethylhexyl) ester, Behenyl alcohol, Behenic acid, Docosane, Heptacosane, Heneicosanoic acid, Lignoceric alcohol, 1-Octacosanol, Tetracosanoic acid, Heptadecane, Pentacosanoic acid, Hexacosanol, D-γ-tocopherol, 1,2-Epoxyoctadecane, Hexacosanoic acid, Campesterol(6CI), Stigmastan-3-ol(3b)-, β-Sitosterol, Stigmast-4-en-3-one, p-coumaric acid, Cinnamic acid, etc.	53,39,67,71
Allelochemicals in soil less cultivation of <i>P. ginseng</i>	
Stigmasterol, DL-Lactic acid, 3-Hydroxybutyric acid, Hexadecane, Glycerol, 1,2-dihydroxy Propanoic acid, Butanedioic acid diisobutyl ester, 1,2,3,4-butanetetrol, Benzenepropanoic acid, 2,3,4,5-Tetrahydroxypentanoic acid, Cinnamic acid, Hexanedioic acid bis (2-methylpropyl) ester, Pentadecane, Ribitol, D-Fructose, 1,2-Benzenedicarboxylic acid, bis2-methylpropylester, Nonadecane, 1,2-Benzenedicarboxylic acid, butyl2-methylpropylester, 1,2-Benzenedicarboxylic acid, Dibutyl phthalate, D-Mannopyranose, D-Mannitol, Eicosane, Hexadecanoic acid, 3-Bromo-5-ethoxy-4-hydroxybenzaldehyde, Glucopyranose, (Z,Z)-9,12-Octadecadienoic acid, Docosane, trans-9-Octadecenoic acid, cis,6-Octadecenoic acid, Oleic acid, Octadecanoic acid, Tris(1,3-dichloroisopropyl)phosphate, Tricosane, Bis(2-ethylhexyl) adipate, Tetracosane, Eicosanoic acid, Phthalic acid, mono-(2-ethylhexyl) ester, cis-10-Nonadecenoic acid, Hexacosane, Docosanoic acid, Heptacosane, α-D-Glucopyranoside, Lignoceric alcohol, α-Cyperone, Tetracosanoic acid, Octacosane, Oxirane, heptadecyl, Cholesterol, β-Sitosterol, 7-ethyl-eicosane, 1,3-dioxolan-4-methyl, 4-ethyl-4-pentadecanoic, Citric acid ethyl, Dodecane, 1-cyclopentyl-4-(3-cyclopentylpropyl), 3,4-diethyl,1,1'-biphenyl, Myristate, Ethyl palmitate, 9-helinski-heptadecanoyl, 2-pentadecanone,6,10,14-trimethyl, n-hexadecane acid, Tert-hexadecanethiol, Heneicosanoic, Ethyl stearate, Four-tetradecane, Pentacosane, E-11,13-dien-14-alcohols, Ethyl citrate, 2-methyl-n-hexadecane (n)mercaptan, Bis (2-methylpropyl)-1,2 terephthalate, Palmitic acid, 1,2-benzenedicarboxylic acid bis(2-methylpropyl), Butyl citric acid, Mono (2-ethylhexyl) phthalate, Azoxystrobin, etc.	99

4.1.2 Types: Allelochemicals are the secondary metabolites of plants (52). Rice (60) has broadly classifies these into 15 types: simple water-soluble organic acids, alcohol, fatty alcohols, fatty aldehydes and ketones, fatty acids and polyacetylene, phenol, benzoic acid and cinnamic acid and its derivatives, coumarin, tannin, terpenoid and steroid, amino acid and peptides, alkaloid and cyanohydrin, simple unsaturated lactone, quinones, flavonoids, purine and nucleosides and other compounds. These allelochemicals are produced in plant roots, leaves, fruits, stems, etc. The main autotoxic allelochemicals of *P. ginseng* are: organic acids, alcohols, esters, alkanes, phenols, terpenes as well as its derivatives are (Table.3). (5,10,27,39,43,67,71,76,99).

During the growth of ginseng, the root system not only absorbs nutrients and water from the environment, but also secretes the proteins, ions and organic matter into the soil. The autotoxic allelochemicals of *P. ginseng* are mainly found in root exudates. Since the first identification of ginseng root exudates by Chen (5) in 2006, more than 100 components of ginseng root exudates have been reported (37) (Table.3). Liu (47) collected the root exudates of *P. ginseng* from the soil free culture medium, and detected more than 50 compounds including 2-hydroxypropionic acid and cinnamic acid, while 78 compounds were detected in the ginseng soil extracts. Nico (55) found ginsenoside, a specific chemical released during the growth of *P. ginseng* plants. Zhang (97) detected 20 compounds including 1,3-dioxolane and ethyl citric acid from the root exudates of ginseng, among which alkanes were dominant followed by organic acids, esters and phenolic acids. In addition, di-n-butyl phthalate was also detected from the ginseng root exudates (5,40).

4.1.3 Characteristics: In general, low concentrations of allelochemicals promote the physiological and biochemical metabolism and growth of plants, while high concentrations were inhibitory. The decomposing materials of ginseng roots are inhibitory to seeds germination of Cruciferae plants, but the seedlings growth was promoted at low concentrations and inhibited at high concentrations (87). Huang (21) found that benzoic acid and DIBP (diisobutyl phthalate) at high concentrations significantly reduced the content of ginsenosides. The palmitic acid also reduced the ginsenoside content. The DIBP reduced the content of ginsenoside at higher concentrations but increased at low concentrations. Allelopathy is the result of combination of multiple allelochemicals. The ginseng root exudates were tested against seeds germination of 4-medicinal plants (*Rheum officinale*, *Silybum marianum*, *Arctium lappa* and *Melilotus albus*), the root exudates had variable effects on 4-plants seeds germination. The aqueous extracts at low concentrations, inhibited the germination of *Rheum officinale* and *Silybum marianum*, but promoted that *Melilotus alba* (36). The allelopathic effects of ginsenosides on the root development of common cultivated crops also differed (103). Ginsenosides were very inhibitory to wheat growth and cucumber roots, but did not affect the adventitious root development in cucumber and mung bean (103).

The allelochemicals that interact in nature, comes from more than one plant and microbes, forming the complex mechanism of action (63). In natural ecosystem, allelopathy is the result of interactions of various kinds of allelochemicals, which together

inhibits or promotes the receptor plants (31). When the combined effects of allelochemicals are higher than expected, it is a synergistic effect. If equal to the expected value, it is additive effect, and if lower than expected value it is antagonistic effect (13). Ginseng root exudates are complex mixture of active ingredients (mostly low molecular organic acids and phenols) (47). The interactions between the lactic acid and benzoic acid, gluconic acid and phthalic acid in the root exudates of ginseng are mainly antagonistic i.e., the mixture of two reduces the allelopathic activity of ginseng (90). These results showed that the allelopathic autotoxicity of ginseng was not only related to monomeric substances with allelopathic potential, but also to the interactions between various substances and was an important factor in plant allelopathy. Besides, He (18) showed that the synergistic effects of phenolic acids or antagonistic interactions were related to the allelochemicals concentration levels. The allelochemicals such as Vanillic acid and Cinnamic acid had synergistic effects depending on their concentration.

4.2 Allelopathic effects of Ginseng allelochemicals

4.2.1 Seed germination : The ginseng rhizosphere soil had strongest allelopathic effects on ginseng seeds germination (40), while the soil extract from continuous cropped soil significantly affected both the seeds germination and root elongation of *P. ginseng*. The rhizosphere soil extract also inhibited the amylase activity in the germinating ginseng seeds. The allelochemicals (anilines, phenolic acids and their derivatives present in soil extracts), inhibited the ginseng seeds germination at higher concentrations but were stimulatory at lower concentrations. The higher concentrations inhibited the growth of both radicle and hypocotyl of germinating ginseng seeds. Phenolic acids also had variable effects on the morphology of root tips and the growth of root hairs (4,20,49,80). The autotoxic allelochemicals are present in various parts of the plant and in the rhizosphere soil of *P. ginseng*, they inhibit the seeds germination and development of the radicle and hypocotyl, in concentration dependent manner.

4.2.2 Plants Growth: The ginseng allelochemicals are toxic to the growth of its own seedlings (21) and also affects their yield and quality. The autotoxicity of ginseng rhizosphere soil inhibits the growth of ginseng, abnormal bud growth, blackening or necrotic root tip and fibrous roots (4) to different degrees. The starch granules at internal root tip tissues show varying degrees of vacuolization and are gradually dissolved, the nuclear membrane and nucleolus disappear and normal life activities are not completed (88). The effects of exogenous ginsenosides on the growth of ginseng seedlings were also studied, and it was found that the growth and fresh weight of ginseng roots was inhibited with different concentrations of exogenous ginsenosides and the degree of inhibition was concentration dependent (95). The toxic ginseng chemicals are inhibitory to the growth of ginseng plants and also showed "concentration effect". Further, allelopathic effects also exist in ginseng root residues (87), which can inhibit the growth and development of other plants.

4.2.3 Chemotaxis in ginseng rhizosphere microorganisms: The in-depth research about the interactions among the ginseng and microorganisms in soil, found that the ginseng root

exudates had selective effects on the rhizosphere microbial community structure (9,58,84). Root exudates acted as selective medium to select the populations that were suitable for certain root exudates, and prompting the microorganism to form specific community structures (38). The root exudates are rich in sugars and amino acids, to provide abundant carbon and nitrogen to microorganisms, prompting some soil microorganisms to display chemotactic response and move to these substances instinctively and colonize around the roots. However, root exudates also provide nutrients for the survival and reproduction of pathogenic bacteria and fungi and increasing their numbers causing the plant diseases. The changes in plant-microbe interactions mediated by root exudates, play important role in plant growth and development (15,50). Our research team has been working on the biological characteristics of ginseng rhizosphere for many years (Unpublished). The autotoxicity and its occurrence in continuous cropping of *P. ginseng* resulted from the interactions of plants and specific microorganisms mediated by root exudates (9,35,82,83,84,100). The increase in cultivation years, led to significant changes in the microbial community structure of ginseng rhizosphere soil, a reduction of beneficial microbial groups such as Alcaligenaceae, and the increase in pathogenic fungi such as *Cryptococcus* (108). Phenolic acids promote the spores germination and growth of *Cylindrocarpon destructans*, thereby aggravating the ginseng disease (44). Sugars and amino acids in plant exudates are very chemotactic to *Alternaria panax* (96). Ginsenosides regulates the chemokines in ginseng metabolism and microbial populations (33,93) and had inhibitory effects on ginseng pathogens, and strongly inhibited the non-ginseng pathogenic fungi (106). The low and medium concentration of ginseng saponins stimulated the chemotropism of *Fusarium sapropelis* and also influenced the *Cylindrocarpon destructans* (8). Thus the ginseng allelochemicals in root exudates had variable effects on the ginseng pathogens, depending on kind of chemical and its concentrations, affecting both spore germination and colony growth of rhizosphere microorganisms.

4.3 Effects of allelochemicals on Ginseng plants

4.3.1 Destruction of cell structure: The cell membranes are the original sites of plant allelopathy. Most allelochemicals affects the absorption of ions by affecting the cell membrane potential, changing the membrane permeability and inhibiting H⁺-ATPase activity of root plasma membrane and tonoplasts (51). Ginseng rhizosphere soil extracts containing phenols, phenolic acids and their derivatives and anilines, were recognized as allelochemicals (47). Treatment with Ginseng root exudates damages the cell membrane of ginseng root callus and the nucleus gradually disintegrates and disappears. This hinders the cell division, growth and inhibits the growth of root callus (12,64). Allelochemicals also cause peroxidation of cell membrane by reducing the amount of sulfhydryl groups in the cell membrane, thereby destroying the cell membrane structure and functional integrity, resulting in decreased nutrients uptake by plant root cells and infiltration of extracellular material (11).

4.3.2 Metabolism of reactive oxygen species (ROS): ROS are important signaling molecules in plants, essential for plant growth and development, but as by-product of

cellular aerobic metabolism, these also causes cell damage (53). The stress causes the oxidative damage of cell membranes due to decrease in *in-vivo* oxidase activity, which is responsible for continuous cropping problem (78). In continuous cropping, the allelochemicals inhibited the activities of catalase and superoxide dismutase in the same plants, causing the accumulation of reactive oxygen species leading to membrane peroxidation and cell membrane damage (46). Zhang (95) showed that different concentrations of exogenous ginsenosides could increase the content of malondialdehyde in roots of ginseng seedlings, affecting the superoxide dismutase, catalase and peroxidase activities. The enzyme activity changed to varying degrees, making it difficult to balance the system of production and elimination of reactive oxygen species in the ginseng cells. Such cells are unable to perform normal physiological functions, thereby inhibiting the growth of ginseng. The changes in CAT, POD and PAL activities in roots of ginseng seedlings were significantly correlated with the types and concentration of allelochemicals (22). The increase in enzyme activities in the roots of ginseng seedlings may be a stress mechanism initiated by allelopathic stress induced by the oxidative stress in ginseng roots. However, this adaptive response only worked within certain degree of damage. When the peroxidation products in the cells accumulated to a certain level (0.01~1.00 mg/L), various enzymes could not function normally.

4.3.3 Gene expression and protein synthesis: The influence of allelochemicals on nucleic acids and protein metabolism is an important action of plant allelochemicals. When a specific gene responds to allelopathic stress, it activates other genes with lower expression levels and some genes that are normally expressed are turned off (16,32). It is helpful to elucidate the molecular mechanism of ginseng allelopathic autotoxicity from the perspective of molecular biology by screening and researching the response of ginseng genes under allelopathic stress, and elucidating the biological functions of its expression products. A transcriptome database was constructed from miRNA of ginseng roots, stems, leaves and flowers using high-throughput sequencing technology and numerous miRNAs related to environmental stress were analyzed (81). Antioxidant genes were selected and labeled in the ginseng ETS database, while a transcriptome database was prepared after the abiotic stress treatment and the role of these genes was described in plant resistance regulation mechanisms (62). It was shown that phenolic acids and alkaloid allelochemicals could affect the nucleic acids and protein metabolism. The transcriptome analysis was done with ginseng adventitious roots treated with methyl jasmonate, and the stress-related genes and ginsenosides synthesis pathway-related genes of ginseng were screened under methyl jasmonate stress (66). Benzoic acid was identified as one of the ginseng allelopathic substance. A high-throughput sequencing technology was used to study the differential expression of ginseng functional genes under benzoic acid autotoxicity stress at the transcriptome level. It showed the signalling pathways and expression regulation modes of differentially expressed genes, and transcriptome databases were prepared for ginseng in response to benzoic acid stress at different times (48,75).

Allelochemicals could also affect the plant growth by inhibiting the amino acid transport and protein synthesis. Phenolic acids (cinnamic acid, benzoic acid, ferulic acid,

coumaric acid and p-hydroxybenzoic acid) inhibit the binding of P to DNA and RNA (29). Furthermore, the incorporation of methionine into protein may be inhibited by some phenolic acids, thereby affecting the protein synthesis.

4.3.4 Hormone metabolism: Plant hormones are physiologically active substances that play an important role in plant growth, development and stress resistance. Common plant hormones are: auxins (IAA), cytokinins (CTK), gibberellic acid (GA), abscisic acid (ABA), ethylene (ETH), and jasmonic acid (JA), etc. (61,70). Of these, IAA, CTK and GA mainly regulates the plant growth and development, while the ABA, ETH and JA are related to plant stress (79). IAA is an important hormone that regulates the growth and development of plants. Many phenolic acids-like substances (henbane, chlorogenic acid, cinnamic acid and benzoic acid), affects the plant growth and development by regulating the content of IAA (31). The soil extract of ginseng rhizosphere significantly decreases the IAA content in callus, thereby inhibiting its growth and development (6,7). The application of mixture of ginsenoside to forest soil, decreased the IAA and GA content and increased the ABA content in ginseng seedlings (104). As a stress hormone, ABA increase the resistance of plants to stress. The allelopathic autotoxicity of ginseng induced by ABA accumulation in plants, activates the stress response genes and enhances its resistance to allelopathic effects. Hence, autotoxic allelochemicals could break the balance between the hormones and inhibits the normal growth and development of plants.

4.4 Ginseng allelochemicals in soil

The rhizosphere microenvironment of plants is an important place for the accumulation of allelochemicals and it is prerequisite for allelopathic effects and whether it could accumulate to certain active concentration in the soil. This is not only related to the nature of allelochemicals, but is also closely related to some factors (adsorption and desorption, retention and degradation in the soil), which are important part of allelopathic research.

4.4.1 Mobility: Water transports the root exudates in soil and the movement depends on soil type. In loam soil (due to the large soil pores and particle size, pore formation is difficult) the transport of allelochemicals is restricted. In sandy soil (the soil water holding capacity is poor, and the organic matter content is low), hence the transport rate of allelochemicals is highest (73). Thus, the transport of allelochemicals in the same soil is affected by soil texture, structure and organic matter content. The order of migration/transport of 5-ginseng allelochemicals same concentration, in one soil followed the order : saponins > vanillic acid > ferulic acid > syringic acid > coumaric acid (slowest) (14). The various Rf values of different concentrations of allelochemicals in the soil indicates that the structural properties and allelochemicals solubility in water is affected their mobility (14). The Rf value of benzoic acid (extracted from the root exudates of ginseng in the new forest land), was lower than old ginseng soil (59). Compared with the new forest soil, the old ginseng soil had strong adsorption, weak desorption and low bearing capacity.

4.4.2 Adsorption-desorption: The adsorption-desorption determines the behavior of allelochemicals in the soil, directly affecting the magnitude of allelopathic effects. Lower the adsorption coefficient, the greater is the mobility in soil. Allelochemicals could be adsorbed in the soil by electrostatic adsorption, ion exchange adsorption, van der Waals adsorption, hydrophobic binding and hydrogen bonding between the organics, ligand exchange, etc.(1). The adsorption mechanism differs due to soil and the type of allelopathic substances. The isotope labeling technique was used to study the adsorption-desorption process of five phenolic acids in soil (3). It was found that desorption behavior of phenolic acid exhibited a deferral or hysteresis phenomenon, which might be directly related to the adsorption irreversibility. The adsorption-desorption of allelochemicals in soil depends on the soil characteristics (soil particle structure, acidity and alkalinity and organic matter content), the adsorption kinetic mechanism is very complicated and cannot be judged from the above single characteristic of soil. Adsorption kinetics experiments to investigate the adsorption and desorption behavior of benzoic acid in ginseng soil by Ren (59) showed that the adsorption capacity of benzoic acid in soil was very strong. The nature of adsorption was physical and high concentration of benzoic acid molecules were in the bound state on the soil particles. Further in-depth study of the adsorption-desorption mechanism of ginseng allelochemicals could help to elucidate the main reasons for the deterioration of soil physico-chemical properties.

4.4.3 Transformation : The transformation of allelochemicals in the soil has attracted more attention. Both biotic and abiotic factors affect the transformation of allelochemicals in the soil. The allelopathic activity of m-tyrosine in root exudates was significantly reduced by soil microbes (17). Phenolic acids could lose their allelopathic effects due to polyphenolization reactions in the soil to form polyphenolic substances (24).

There were significant differences between the two components (Table 3), compared with the ginseng root exudates and ginseng soil extracts collected under aseptic condition (47,59). All above findings suggest that once the allelochemicals enter the soil, chemical transformation occurs through various means leading to the formation of polymers degraded to form smaller molecular substances and lose the allelopathic activity. The transformation of allelochemicals is extremely complicated in soil, hence, the transformation of soil allelochemicals in the environment and the effective allelochemicals must be analysed and identified.

4.4.4 Retention and degradation : Allelochemicals secreted by plant roots cannot remain stable in the soil for long time and are easily transformed into three forms, by soil adsorption (i). free form, (ii). reversible bound state and (iii). fully bound state (68). Allelopathic activity exists only in free state, while the reversible bound state reduces the concentration of biologically active allelochemicals in the soil. In addition, degradation by soil microorganisms converts the allelochemicals into other non-allelopathic substances by the process of soil self-detoxification. The degrading bacteria effectively decompose the self-toxic active substances in the soil, thereby reducing the damage caused to plants. Li (41) used selected allelopathic self-degrading bacteria to verify the buffering effect on the self-toxicity of ginseng and the results showed that the inoculated degrading bacteria could

significantly increase the growth of ginseng seedlings and had no adverse effect on ginseng root growth. The residual dynamics of phenolic acids (p-hydroxybenzoic acid, vanillic acid, vanillin, phenolic acids) in the soil has been studied (105) and found that these are easily adsorbed in the soil or converted into other substances by the microorganisms. The residues of phenolic acid were only 25%~17.5% and most of the phenolic acids were decomposed or consumed by the microorganisms within one week. The retention of allelochemicals is restricted by many factors in soil and the allelopathic effect was the final result based on the ability of plant roots to secrete far beyond the soil adsorption capacity and degradation ability of microbes.

5. SUGGESTED FUTURE RESEARCHES

In the past 10- years, the method of ginseng planting has changed from cultivating in the cut forests to planting in the farmland. To solve the continuous cropping problems in *P. ginseng*, future suggested research areas are:

(i). **Allelochemicals identification:** The identification of allelochemicals after microbial action is very critical, hence, determine the transformation mechanism of allelochemicals by soil microbes in the soil.

(ii). **Appropriate bioassays:** In present bioassays, the role of osmotic potential is ignored. It not only affected the inhibitory or promoting effects of allelochemicals in bioassay results, but also changed the results. In all bioassay, the influence of osmotic potential must be studied to eliminate the detection error caused by non-allelopathic substances.

(iii). **Interaction among plant, microorganism and soil:** The continuous cropping problem is not due to a single factor, but the auxiliary or synergistic effects of multiple factors. Thus study: (i) How the autotoxic allelochemicals affects the physico-chemical properties of ginseng soil, (ii) How these changes affect the microbial community.

(iii) **Microbial community:** The effects of changed soil microbial community on the transport and transformation of allelochemicals in the soil. Study the effects of ginseng root exudates on interactions among the plant, microorganism and soil, to elucidate the development of ginseng continuous cropping problem.

(iv). **Allelopathy autotoxicity:** In future research, use the molecular biology and proteomics to understand the mechanism of ginseng allelopathy autotoxicity.

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