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Plant Autotoxicity: A Review (Part IV). Families: Poaceae to Zingiberaceae

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ABSTRACT

Autotoxicity, one of the major causes of soil sickness in plants, can inhibit plant growth, lead some soil diseases, and result in negative soil environment and economic loss. In this paper, 46 plant species from 37 genera in 16families were briefly reviewed on their autotoxicity to give some hints to deal with the soil sickness for agricultural crops or medicinal plants, or the regeneration problems for forest plant species. The 19 families reviewed here are as the following: Poaceae, Polygonaceae, Proteaceae, Ranunculaceae, Rosaceae, Rubiaceae, Rutaceae, Salicaceae, Scrophulariaceae, Solanaceae, Taxodiaceae, Theaceae, Typhaceae, Verbenaceae, Vitaceae and Zingiberaceae.

Key words: Autotoxicity, autotoxins, crops, forest plants, medicinal plants, Poaceae, soil sickness, weeds, Zingiberaceae

1. INTRODUCTION

Autotoxicity is an intraspecific allelopathy that occurs when a plant releases chemicals that inhibit or delay germination and growth of the same plant species (63). It causes a strong decline in the yield and performance of several crops, such as orchards and perennial forages (13), and perennials plants (coniferous trees, orchards) (63). Autotoxicity studies cover a wide range of taxonomically distant species (51). The extracts of *Dactylis glomerata* L., *Lolium rigidum* Gaud, *Oryza sativa* L., *Saccharum officinarum* and *Rehmannia glutinosa* Libosch. (17,25,29,42,56,70) and root exudates of *Hordeum vulgare* L. ssp. *vulgare, Triticum aestivum* L., *Coptis chinensis* Franch, *Fragaria ananassa* Duch. and *Nicotiana tabacum* L., etc. have been observed to have autotoxic potentials (8,10,22,36,75,79,80,91).

In this paper, autotoxicity of plants from 16 families were briefly reviewed. The 16 families are as following: Poaceae, Polygonaceae, Proteaceae, Ranunculaceae, Rosaceae, Rubiaceae, Rutaceae, Salicaceae, Scrophulariaceae, Solanaceae, Taxodiaceae, Theaceae, Typhaceae, Verbenaceae, Vitaceae and Zingiberaceae.

2. POACEAE

Poaceae, formerly called Gramineae, grass family of monocotyledonous flowering plants. The Poaceae are the world's single most important source of food. They rank among the top five families of flowering plants in terms of the number of species. Plants from 14 genera in this family had autotoxic effect. Such as *Anthoxanthu*, *Dactylis*, *Digitaria*, *Festuca*, *Hordeum*, *Lolium*, *Oryza*, *Pennisetum*, *Saccharum*, *Setaria*, *Sorghum*, *Spartina*, *Triticum* and *Zea*.

2.1. *Anthoxanthu*

The leachate of *Anthoxanthu odoratum* Linn. was inhibitory to shoot dry weight of three months old *A. odoratum*. The dry weight declined 7-15 % with the control (51).

2.2. *Dactylis*

Aqueous extracts of *Dactylis glomerata* L. restrained its own germination, root and shoot growth. The aerial extracts of the plants was more inhibitory than root extracts (29).

2.3. *Digitaria*

Crabgrass (*Digitaria sanguinails* (L.). Scop) was autotoxic to seed germination and seedling growth of *D. sanguinails*. The germination rate of *D. sanguinails* was 17 % in 1:5 ratio of nutrient solution to plant extract, while the water treatment was 34 %. Chlorogenic acid, isochlorogenic acid, and sulfosalicylic acid were identified in the plant extracts (53).

2.4. *Festuca*

Decomposition of tall fescue (*Festuca arundinacea* Schreb) residue is the vital reason leading the lawn degrades yearly. When treated with 0.06 g/mL decomposed liquid, the germination rate, root length, seedling height, single plant weight, germination energy, germination index and vigor index were reduced by 58.64 %, 37.86 %, 41.13 % , 30.43 %, 81.68 %, 73.34 % and 81.63 %, respectively. The CAT activity first increased and then decreased in the 0.06 g/mL decomposed liquid treatment, and the MAD content increased, while soluble protein content was reduced (76).

2.5. *Hordeum*

Barley (*Hordeum vulgare* L. ssp. *vulgare*) is well known for its allelopathic compounds. Seeds (43), residues (30) or root exudates of this species (8) have been examined for their allelopathic potential against some crop species or weeds. Barley was also found to be autotoxic (6) what decreased its own seed germination or seedling development. The autotoxic activity of barley root exudates was also studied by a “seed-after-seed” protocol. In this protocol, the donor and the receiver species of water-soluble allelochemicals are grown one after the other in the same dishes, in conditions reducing resource competition between both species. Growth of the receiver was inhibited in a dose-dependent manner, when using increasing barley seed densities (0, 8, 19 and 25 seeds per Petri dish). Furthermore, the autotoxicity of the allelochemicals increased after their release by roots, between day 0 and day 6 (10).Further researches revealed that the inhibition of barley radicle growth was positively correlated with total phenolics (p-hydroxybenzoic, syringic and p-coumaric acids) content of barley (52).

2.6. *Lolium*

2.6.1. *Lolium perenne*

Autotoxicity affect the respiration and yield of GL66 (fast-respiring population) and GL72 (slow-respiring population), two populations of perennial ryegrass (*Lolium perenne* L. cv. S23). The slow-respiring population, GL72, suffered from autotoxicity only when long-term accumulation was allowed (monoculture, growth in replenished nutrient solution). The predominant autotoxic effect was dependent on dry matter percentage and dry weight of leaf sheaths (37).

2.6.2. *Lolium rigidum*

Lolium rigidum Gaud is an annual, self-incompatible grass very frequent in Mediterranean environments. It is commonly cultivated as a crop, as the main component of self-regenerating pastures (25).

The aqueous extracts of adult tissues of *L. rigidum* produced significant effects on the germination and seedling growth of conspecific individuals. Aqueous extracts reduced the final percentage of germination and inhibited radicle length, which in turn affected biomass allocation. Seedling growth was more sensitive to autotoxins than germination, and extracts of above-ground organs displayed the strongest effects (13).

2.7. *Oryza*

Autotoxicity is also a common problem in continuous monocropping of rice (*Oryza sativa* L.) because decomposing rice straw is left in fallow fields. Different cultivars showed different autotoxicity capability. It was reported that 2 rice cultivars showed higher autotoxic effect than other rice cultivars (47).

Various phenolic acids like p-coumaric, p-hydroxybenzoic, syringic, vanillic, ferulic and o-hydroxyphenylacetic acids have been isolated from the decomposing residues in the soil (18,62). Besides, a few flavones and terpenoids (5), are also potent autotoxins. At 25 mg/L, o-hydroxyphenylacetic acid revealed significant inhibition on the radicle growth of rice (18). Chi (14) reported that ferulic acid may have a significant role for rice to inhibit rice root elongation through modulating ethylene and jasmonic acid hormone homeostasis. FA-induced gene expression of AA/AP (amino acid/auxin permease) transporters may contribute to detoxicification of the autotoxin.

Adding rice straw into rice crop soil significantly decreased both rice growth and the available nitrogen and the soil cations, Zn^{2+}, Cu^{2+}, Ca^{2+}, Mn^{2+} and Na^{+}. The phytotoxicity of aqueous extracts of soil treatments was higher than that of rice straw, which indicated that rice residues may decompose in soil and produce phytotoxicity (17). Meanwhile, the study showed that incorporated rice residue not only inhibits the germination and growth of weed species, but also inhibits the germination and growth of a subsequent rice crop (65). Interestingly, autotoxicity in rice provides an adaptive strategy to the plants because they are grown in sufficiently water-logged soils deficient in oxygen and thus develop a negative redox potential in soil due to decomposing rice residues. This leads to inhibition of root growth of rice plants accompanied by swelling of root cells in order to capture more oxygen (16).

2.8. *Pennisetum*

Saxena (61) investigated the root and shoot aqueous extracts of pearl millet (*Pennisetum glaucum* (L.) R. Br.), at the concentration of 20, 40, 60 and 80 g/L (dry weight basis), on pearl millet germination and the growth of early seedling. The root and shoot extracts obviously retarded the seed germination, at the highest concentration (80 g/L), the germination rate of seed declined by 60 % and 40 %, respectively.

2.9. *Saccharum*

For many years, evidence has indicated that “sugarcane soil sickness” led to a reduction in the crop yield. It is most possible that sugarcane (*Saccharum officinarum*) allelochemicals was transformed to more phytotoxic products by microorganism (60). Sugarcane residue contained triterpenoids, steroids, flavonoids, pungent bitter essential oils and phenols, which may cause negative impacts, such as millable cane height, number of internodes, number of canes per stool and cane weight (33).

2.10. *Setaria*

In 1967, Lee *et al*. demonstrated that the soil sick phenomena of *Setaria italica* (L.) Beauv. was related to its autotoxicity (40).

2.11. *Sorghum*

Decaying Johnson grass (*Sorghum halepense* L.) rhizome and leaf mixed with soil, inhibited seed germination and seedling dry weight itself. The phytotoxins chlorogenic acid, p-coumaric acid and p-hydroxybenzaldehyde were the main plant inhibitors present in the leaf and rhizome extracts (1).

2.12. *Spartina*

The invasive smooth cordgrass (*Spartina alterniflora* Loisel) was a salt-resistant plant with an ecologically important role. Recent, researches showed that *S. alterniflora* had autotoxic effect. The aqueous extracts of the rizhosphere soil of smooth cordgrass restrained its own seed germination and seedling growth at high concentration ($>$0.3 g/mL). The aqueous extracts and the methanol extracts of smooth cordgrass soil, plant residue, root exudates contained autotoxic long-chain fatty acid, such as palmitic acid, oleic acid and stearic acid. The SOD, POD and CAT activities of smooth cordgrass decreased treated at 0.5 g/mL (57).

2.13. *Triticum*

The wheat (*Triticum aestivum* L.) residues left in the field adversely affect the germination, growth, and subsequent yield of the wheat itself (63). Extracts of wheat straw residues were inhibitory to wheat germination and seedling emergence (63,84). Wu (79) suggested that plant extract and root exudates of wheat inhibited wheat germination, radicle growth and coleoptile growth. Interestingly, aqueous extract of wheat differed in varietal autotoxicity, inhibiting wheat germination by 2-21 %, radicle growth by 15-30 %, and coleoptile growth by 5-20 %, depending on the combination of the receiver and donor. Meanwhile, the root exudates also differed in varietal autotoxicity. These results suggested that careful selection of suitable wheat varieties is necessary in a continuous cropping system in order to minimize the negative impacts of varietal autotoxicity. Straw residues were found to contain chemicals such as ferulic, p-coumaric, p-hydroxybenzoic, syringic and vanillic acids (45), which may act as autotoxins.

2.14. *Zea*

In the case of corn (*Zea mays* L.) the continuous monoculture cropping results in lower yields in the subsequent years (20,69,82). This is more detrimental in the tillage farming practices where corn residues are left in the fields for decomposition. Yakle and Cruse (1983) demonstrated in a series of experiments that fresh as well as partially decomposed residues of corn left in the field have an adverse effect on germination and growth of corn and the effect varied with the age and placement of the residues in the soil. The aqueous extracts of its residues inhibited the germination and seedling growth of corn (47,82). Corn root residues that remain in the field after harvesting are a source of water-soluble compounds, which can inhibit growth of succeeding corn crops through autotoxicity. The 0.15 % (w/v) root extract treatment decreased root biomass and increased guaiacol peroxidase (G-POD) activity and concentrations of the major water-soluble compound benzoxazinone 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) in roots of corn seedlings (24). Turco et al. (69) pointed that corn residues left in the soil for decomposition alter the microorganisms in the rhizosphere soil, which in turn are inhibitory to the corn growth. Dzafic (24) confirmed that arbuscular mycorrhizal fungi (AMF) can alleviate the negative effects induced in maize seedlings by water-soluble compounds from maize roots and show potential importance of AMF in extensive agricultural practice.

3. POLYGONACEAE

3.1. *Rumex*

In 1975, Newman (51) reported that the growth of the red sorrel (*Rumex acetosa* L.) reduced by its own and the shoot dry weight of receiver species was 1.23 g/pot but the control was 1.45 g/pot.

4. PROTEACEAE

4.1. *Grevillea*

*Grevillea robusta*is a timber species of subtropical rain forest. However, monocultures of this tree grow poorly in South Queensland where the tree occurs naturally.

In *G. robusta* plantations *G. robust*a does not regenerate. In plantations of *G. robusta* the tips of the leaves of seedlings of this species become characteristically blackened and the seedlings die. That *G. robusta* fails to regenerate in *G. robusta* plantations was because of some water-transferable factor associated with the rhizosphere of this species (77).

5. RANUNCULACEAE

5.1. *Copits*

Coptis chinensis Franch is a most widely used medicinal plant in Traditional Chinese Medicine (TCM). Its rhizomes are harvested 3-5 years after planting and are used in TCM as source for isoquinoline alkaloids (berberine, epiberberine, palmatine jatrorrhizine, coptisine etc.). However, many studies have revealed that the aqueous extracts of different parts of *C. chinensis* inhibits its own growth and the release of plant chemicals into the soil is one of the reasons for autotoxicity leading to the continuous cropping obstacle. After the harvest of *C. chinensis*, soil is not suitable for replanting for usually over 2 years and the growth of new plants is affected. Isoquinoline alkaloids are released into soil through root exudates, leaching of above-ground parts and from litter decomposition. Among the released chemicals, the highest amount is berberine (5-8 %) which can inhibit plant root growth (80), followed by coptisine, worenine, palmatine, jatrorrhizine, columbamine, obakunone, obakulactone and magnoflorine, etc. In the root exudates, the amount of berberine is the highest (1.4-2.8 %) and it is also present in leaves (4.83-5.48 %) of *C. chinensis*, along with other chemicals (38).

6. ROSACEAE

The Rosaceae is a large family of approximately 122 genera and 3,370 species of trees, shrubs and herbs of worldwide distribution, with its maximum development in north temperate regions (23). Plants from 3 genera in this family had autotoxic effect, including *Amygdalus*, *Fragaria* and *Malus*.

6.1. *Amygdalus*

The bark of old peach (*Amygdalus persica* L.) roots was found to be very toxic to young growing peach plants (55). In the 2-year-old peach in field, autotoxins such as gallic acid, catechins, syringic acid, chlorogenicacid, benzoic acid, p-hydroxybenzoic acid, coumarin, ferulic acid, cinnamic acid, vanillin, cumaric acid and amygdalin have been identified. The content of the aforementioned autotoxins were 0.11, 2.35, 5.08, 0.5, 3.7, 0.96, 0.02, 0.09, 0.14, 1.27, 1.21 and 17240 μg/g, respectively (88). Among these chemicals, amygdalin, is a cyanogenic compound isolated from the root bark (54). After release, amygdalin is broken down in the soil by microorganisms into toxic cyanide substances, causing injury to young peach seedlings. The intensity of effect was directly co-related to the amount of roots present in soil. The presence of nematodes in the soil plays an important role in releasing and hydrolyzing amygdalin (49).The content of phenolic acids and amygdalin in soil obviously increased the content of seedlings chlorophyll, and decreased the net photosynthesis rate (86).

6.2. *Fragaria*

The root exudates of strawberry (*Fragaria ananassa* Duch.) could inhibit the seedling growth (91).Lactic, benzoic, succinic, adipic and p-hydroxybenzoic acids were detected in the root exudates of strawberry. The fresh weight and the dry weight of strawberries shoots, the dry weight of roots and the maximum root length in hydroponic culture were significantly inhibited by benzoic acid (36). The activities of 2, 3, 5-tripheyl tetrazolium chloride (TTC) and SOD decreased significantly by the root exudates, while root relative conductivity and malondialdelyde (MDA) contents increased by the root exudates (91).

6.3. *Malus*

In 1959, for the first time Borner (3) reported replant problem in apple (*Malus prunifolia* Borkh.) orchards even after 1 or 2 years of cultivation. The apple trees grown in the old orchards have retarded growth with shorter internodes. The radicle length of apple seed was restrained by apple root exudates and root leachate, containing autotoxic substances phthalic acid, butylated hydroxytoluene and palmitic acid. The chemical compounds like phlorizin, phloretin, p-hydroxy hydrocinnamic acid, p-hydroxybenzoic acid, and phloroglucinol was found in root bark and was released into the orchard soil after microbial decomposition of fallen root bark (7). Besides, a number of phenolic acids and flavonoids in the leaves, bark, and fruit of apples were also responsible for the replant problems (78). The autotoxins caused reactive oxygen species (ROS) accumulating, the production rate of superoxide anion and hydrogen peroxide (H_2O_2) content increasing, root activity decreasing and MDA content increasing (3).

7. RUBIACEAE

7.1. *Coffea*

Coffee (*Coffea arabica*) plantations are cultivated extensively in many parts of the world. Several allelochemicals, such as caffeine, theophylline, theobromine, paraxanthin, scopoletin, caffeic acid, coumaric acid, ferulic acid, p-hydroxy benzoic acid, vanillic acid and chlorogenic acid, have been identified from the plantations as well as the floor soil (19). Caffeine is, however, the most potent allelo-chemical and is found in maximum amount (1.5 ± 3 %) in fruits (71). It plays an important ecological role rather than merely a source of nitrogen (67,71). The germinating seedlings of coffee are highly susceptible to caffeine when applied exogenously thereby showing the autotoxic effects (26). The effect is even pronounced at the lower concentrations. Interestingly, it has been seen that coffee seeds are able to germinate despite the high amount of the endogenous caffeine. Waller et al. (1986) and Waller (1989) have shown that coffee seeds have effectively developed a mechanism to avoid autotoxicity.

8. RUTACEAE

8.1. *Citrus*

In the Citrus orchards too the replant problem has been observed, particularly in the orchards of *Citrus aurantium* L. and *Citrus jambiri*. Autotoxicity in the old citrus orchards has been demonstrated due to the release of toxic substances from the dead and decaying roots left in the soil (63). Burger and Small (12) demonstrated that ether extractable substances like homovanillic acid, seselin, and xanthyletin, etc. present in the *C. jambiri* roots caused severe toxicity to the young plants. The inhibitors stopped root cell elongation and caused root swelling. Gog *et al*. (27) investigated the autotoxicity of endogenous essential oil of *C. jambiri* by slicing through containment structures (glands or tubes). Significant toxicity, manifested by reduced photosynthetic activity, was observed. The most toxic constituents of the essential oil were monoterpenes. Further, in the case of sour range (*C. aurantium*), Hassan et al. (34) demonstrated that extracts of orchard soil and decaying roots reduce the growth of young plants, whereas non-citrus soils are nontoxic. Thus, autotoxicity plays an important role in these orchards.

9. SALICACEAE

9.1. *Balsam*

Balsam poplar (*Populus balsamifera* L.) dormant bud extracts (5 % w/v) completely prevented the oxidation of ammonium. The same extracts (2 % w/v) still prevented the oxidation of ammonium to nitrate to a large extent (68). It may interfere with the germination, growth, and establishment of young seedlings.

10. SCROPHULARIACEAE

10.1. *Rehmannia*

Rehmannia is medicinal plants in China. Autotoxicity has been reported to be one of the major problems hindering the consecutive monoculture of Rehmannia. Qi (56) suggested that the ethyl acetate, methanol and aqueous extracts the rizhosphere soil of rehmannia (*R. glutinosa*), at concentration of 5 g/mL, inhibited the radicle growth of rehmannia seed, and their RI was -0.17, -0.73 and -0.67, respectively. The results revealed that the autotoxicity of the three extracts decreased as the followed: methanol extract＞aqueous extract ＞ethyl acetate extract. Seven phenolic compounds were isolated from aqueous extracts of the fibrous roots and demonstrated as the autotoxic compounds. These seven phenolic compounds significantly reduced radicle growth in a concentration-dependent manner. The autotoxic compounds were also found in the top soil of the commercially cultivated rehmannia fields. It appears that a close link exists between the autotoxic effects on the seedlings and the compounds extracted from fibrous roots of rehmannia (42).

11. SOLANACEAE

Plants from 4 genera in this family had autotoxic effect including *Capsicum*, *Datura*, *Nicotiana* and *Solanum*.

11.1. *Capsicum*

The root leachates of hot pepper (*Capsicum annuum* L.) had autotoxicity against the seed germination and radicle length and the autotoxic effects showed positive correlation with concentration. The leaf extract and root leachates had greater autotoxic effect than that of root and stem extracts (66,74). The extract of rizhosphere soil of hot pepper possessed autotoxicity too and the extract decreased the stem diameter, plant height, leaf length, leaf width, leaf number, fresh and dry weight of pepper seedling (87).Zhang (87) isolated the autotoxin, (1,2-benzenedicarboxylicacid, bis (2-methy-lpropyl)ester), in rizhosphere soil extracts of 1-3-year-old pepper.

After the treatment of the rizhosphere soil extracts, chlorophyll content, chlorophyll a/b, Fv/Fm (maximal PSII efficiency at open centers in the absence of NPQ), Pn (net photosynthetic rate), qP (photosynthetic active fluorescence quenching), ΦPSⅡ(actual PS Ⅱefficiency) and Gs (stomatal conductance) decreased significant; the activity of SOD, POD, CAT and dehydroascorbate (DHA) content decreased while ascorbic acid (AsA), proline (Pro), soluble protein, malondialdehyde (MDA) content increased. It was noteworthy that the exogenous NO and ABA could promote the increase of indexes, including Gs, qP, Fv/Fm, ΦPSⅡ, SOD, POD, CAT, Pro and soluble protein, under autotoxicity stress (87).

11.2. *Datura*

Mubarak and Hussain (50) reported that *Datura innoxia* Mill. had autotoxic effect. *D. innoxia* seed exudates significantly inhibited the radicle growth. Aqueous extract from seed coat and cotyledon of *D. innoxia* slightly reduce seed germination, therefore, the germination of *D. innoxia* seeds was autotoxic by the phytotoxins present in the seed coat and cotyledon of the seeds.

11.3. *Nicotiana*

Wang (75) demonstrated that four extracts (plant leachates, root exudates, root rhizosphere extracts and root residue decomposition) of three tobacco (*Nicotiana tabacum* L.) varieties (Yunyan87, Yunyan97, k326) had autotoxic effect on seed germination, seedling radicle and seedling growth. Specifically, when the concentration of plant leachates, root exudates, root rhizosphere extracts and root residue decomposition reached 0.1, 0.05, 0.2 and 0.2 g/mL, the inhibition rate on seed germination of variety k326 were 85.67 %, 82.33 %, 85 % and 84 %, respectively. The inhibition rates of root exudates on plant height, the maximum leaf length and leaf width were the best compared with those of the other three extracts.

In the root exudates of the variety Burley at two, four, and six-leaf stages, the content of autotoxins phthalate esters(PAEs) were 7.6 %、0.3 % and 0, respectively, while in the variety K326, they were 35.6 %, 51.3 % and 2.2 %, respectively. Di-sec-butyl phthalate ester (DBP) and bis (2-ethylhexyl) phthalate ester (DIOP) were identified as the main PAEs in tobacco root exudates (21). Ren (58) also reported that the autotoxins in the variety Flue-Cured Tobacco were β-cembrenediol (terpenoids), di-n-hexyl phthalate and bis (2-propylheptyl) phthalate (phthalate derivatives). Tobacco root and stem lengths were significantly reduced by 60.26 % and 42.31 % with 200 μg/mL β-cembrenediol, and by 45.45 % and 39.8 % with 200 μg/mL di-n-hexyl phthalate. Further, the autotoxins dibutyl phthalate, dioctyl phthalate, and di-isooctyl phthalate were identified in tobacco root exudates. When the concentrations of these compounds were more than 0.5 mmol/L, the seed germination and seedling growth of tobacco were restrained (22).The activities of superoxide dismutase and catalase first increased, then decreased with increasing DBP and DIOP concentration, and reached the highest at 0.5 mmol/L, while MDA contents increased gradually. PAEs at 0.5 mmol/L decreased the antioxidant capacity of the root system, finally led to autotoxicity effects (21). It is rather remarkable that the photosynthetic capacity of *Nicotiana sylvestris* and *Nicotiana glauca* producing nicotine in a 1 mM nicotine-containing hydroponic solution was decreased significantly (4).

11.4. *Solanum*

11.4.1. *Solanum lycopersicum* Mill.

Un-decomposed tomato (*Solanum lycopersicum* Mill.) residues had a negative effect on the growth of tomato in laboratory by causing the wilting disease. Leaves residues are more autotoxic than roots residues (9). The growth of tomato seedlings was affected by high concentration of tomato root extracts (41). The germination was inhibited by moderate concentration of root leachate. Especially, the autotoxic effect of root leachates on root growth was greater than that of stem and leaf (64). Mechanism studies demonstrated that the root leachates reduced chlorophyll a, chlorophyll b and total chlorophyll contents, and the inhibition increased with concentration. Activity of SOD and POD was also inhibited while CAT activity was stimulated (64). Similarly, after the treatment of the root extract, SOD, POD and CAT activity first increased, then decreased (41).

11.4.2. *Solanum melongena* L.

At 0.015 g/mL, the aqueous extract of the stem and leaf of eggplant (*Solanum melongena* L.) significantly inhibited the radicle growth. At 0.075 g/mL, the seedling growth was also inhibited. The chemicals of the aqueous extract caused autotoxicity by the inhibition of the absorption of NO_3^-, PO_4^{3-}, K^+, Mg^{2+} and Ca^{2+} (73).

11.4.3. *Solanum tuberosum* L.

The aqueous extract of potato (*Solanum tuberosum* L.) inhibited the seed germination, germination rate and root growth and plant height (44). The autotoxicity of the aqueous extract of root was the better than those of stem and leaf. Particularly, the root extract was inhibitory to the number of branches and stem diameter, and their RI values were -0.11 and -0.13, respectively. The RI values of the root surface area, root tip number and branch number were -0.25, -0.32 and -0.32, respectively, in the treatment of root extract. The POD and CAT activity and chlorophyll contents decreased whereas MDA contents increased by the root extract (72).

12. TAXODIACEAE

12.1. *Cunninghamia*

Replant problem was existed in the Chinese-fir (*Cunninghamia lanceolata* (Lamb.) Hook.) and *Cryptomeria fortune* Hooibrenk ex Otto. The aqueous extract of root, fresh leaves and litter of the Chinese-fir at the concentration of 10 % (w/v) and the aqueous extract of root at the concentration of 1 % (w/v) were inhibitory to the seed germination and the seedling growth (35). Extracts of soils collected from replant woodlands significantly reduced the growth of Chinese-fir seedlings. Extracts and decomposing root residues also significantly inhibited the growth of Chinese-fir seedlings (89). HPLC analysis revealed that the nine autotoxic phenolic compounds were syringic, gallic, protocatechuic, o-coumaric, m-coumaric, p-coumaric, p-hydroxybenzoic, vanillic and ferulic acids (35). Further, a cyclic dipeptide (6-hydroxy-1,3-dimethyl-8-nonadecyl-[1,4]-diazocane-2,5-diketone) released by the roots was demonstrated as another autotoxin. When the content of the cyclic dipeptide in the root exudates reached 9.43 μg/g, it was sufficiently inhibitory to the seedling growth (81).

12.2. *Cryptomeria*

The high concentration 1:10 (the extract: distilled water, v/v) of the aqueous extract of litter and the rizhosphere soil of *Cryptomeria fortune* Hooibrenk ex Otto inhibited the seed germination and the inhibition increased with the increase of concentration. The inhibition capability sequence of different parts was as the following: un-decomposed litter ＞semi-decomposed litter＞soil. The autotoxins in the aqueous extract of litter and the rizhosphere soil were identified as ferulic acid, cinnamic acid and β-hydroxybenzoic acid (85).

13. THEACEAE

13.1. *Camellia*

The soil of consecutively cultured tea (*Camellia sinensis* (L.) O. Ktze.) plantations resulted in significant autotoxicity which negatively affected tea seedling growth, metabolism, yield, and quality. For example, seedlings grown in the 30-year-tea-plantation soil had 20 % lower growth rates, 17 % less soluble sugar, 28 % less soluble protein, 37 % less polyphenol, 34 % less theanine, 25 % less amino acid, 37 % less caffeine, and 40 % less of eight catechols than tea seedlings grown in new soil with no history of tea production (83). Caffeine and theobromine present in the inner seed coat of tea seeds inhibit the growth of embryonic tissues (shoot as well as root) of its own germinating seeds (67).

14. TYPHACEAE

14.1. *Typha*

Regulation of population due to autotoxicity has also been seen in case of typha (*Typha latifolia* L.) where extracts of leaves and soil in which it grows and even water from the typha marshes prevent germination and seedling growth of typha itself (48).Grace (28) confirmed that typha had autotoxicity. Only more than or equal to 3 % typha (dry weight to volume) in liquid cultures restrained seed germination of typha, and the autotoxicity effects of water extracts increased with the development of water molds, addition of the soil to nutrient solution culturing typha can strengthen the inhibition of extracts on seed germination rate.

15. VERBENACEAE

15.1. *Lantana*

Lantana camara L. (Verbenaceae), a wild luxuriantly growing plant has encroached upon large areas of pasture and forests in tropical and subtropical parts of the world. In nature, it propagates sexually. However, its seeds either do not germinate or fail to establish seedlings in the area of its colonization, probably due to autotoxic properties.

In 1991, Kumar demonstrated that *Lantana* oil had enormous autotoxic potential. The vapours of *Lantana* oil impaired the germination of its own seeds. Among those of germinated seeds, the lengths of radicle or plumule were drastically shortened compared to those grown under controlled conditions (without oil vapours of *Lantana*). The leaves of mature *Lantana* plants showed less content of total chlorophyll and water in comparison to the respective parts of the plant used as control (39).

Arora and Kohli (2) also confirmed the effect of crude volatile oils extracted from the young leaves of *Lantana camara* var. *camara* on the parent plant itself. It was found that the contents of water and chlorophyll, of leaves apart from seed germination, seed vigour and length of seedlings of the parent plant were adversely affected with increasing concentration of the *Lantana* oils; this indicated autotoxic potential of the oil.

Lantana oil is rich in *p*-cymene, α-phellandrene, α-pinene, dipentene, γ-terpinene, caryophyllene, cardinene, cineole, linalool, geraniol, α-terpinol, phelandral and citral components (59).

16. VITACEAE

In this family, *Tetrastigma formosanum* (Hemsl.) Gagnep., *Tetrastigma hemsleyanum* Diels et Gilg and grape (*Vitis rupestris* Scheele, *Viti sriparia* Michx. And *Vitis vinifera* L.) had autotoxic effect.

16.1. *Tetrastigma*

The aqueous extract of the leaves and stem of 3-year-old *T. formosanum* was inhibitory to the seedling height, root length and fresh weight (15). At the concentration of 0.1 g/mL, 40 d after the treatment, the aqueous extract of the tuber of *T. hemsleyanum* reduced root length, the height and fresh weight of seedling by 55.3 %, 52.8 % and 46.06 %, respectively. However, at the same concentration, the extract of leaf and extract of stem were not significantly inhibitory to the seedling height (92).

16.2. *Vitis*

The replant problem has been observed in grape (*Vitis rupestris* Scheele, *Vitis riparia* Michx. and *Vitis vinifera* L.) nurseries too. The cuttings do not grow well in the same vineyard after 2 to 3 years of repeated growing. The symptoms appear in the form of brown and stunted roots. This problem is not reversed by fumigation, fertilization, and cover crops, and pathogens were also not found to be involved. Brinker and Creasy (11) attributed this to the autotoxic effects of grape where old roots start decaying in the orchard soil. They found the orchard soil to be very toxic when compared with the non-orchard soil. The extracts of this soil reduced phenyl alanine ammonia lyase activity. Further, some toxic substances were also isolated from the roots of grapes.

The chloroform extraction phase of the root exudates of grape (*V. vinifera*) contained hydrocarbon, amides, benzene, indoles, luorenone and acridine. Among these compounds, the content of alkanes is the highest and followed by amide. At 0.5 mmol/L, the main autotoxin hexamethyl-cyclotrisiloxane reduced the fresh weight of the above-ground and the fresh weight of the under-ground by 49.73 % and 57.05 %, respectively (31). The root exudates of grape (*V. vinifera*) inhibited the growth and development of grape plants. The fresh weight of shoot and root, plant height, root activity, the chlorophyll content, the photosynthetic rate and the SOD activity were reduced (31).

17. ZINGIBERACEAE

17.1. *Zingiber officinale* Rosc.

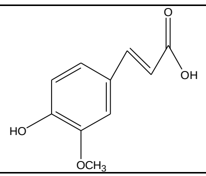
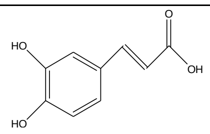
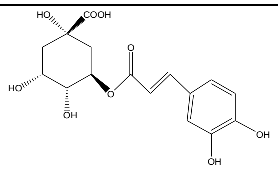
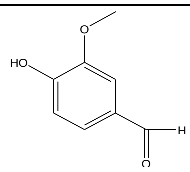
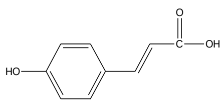
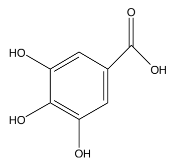
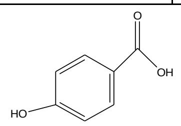
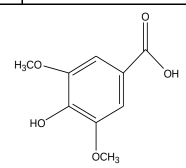
Ginger (*Zingiber officinale* Rosc.) was reported to possess autotoxicity. Higher concentrations (80 g/L) of the aqueous extracts of ginger rhizomes significantly inhibited the shoot height, underground (i.e. rhizome yield), total biomass of ginger seedlings and decreased the total chlorophyll content but increased the lipid peroxidation and membrane permeability. The increased concentrations (10, 20, 40 or 80 g/L) of stem and leaf extracts decreased the activities of major antioxidant enzymes (superoxide dismutase, peroxidase, catalase and ascorbate peroxidase) in leaves of ginger seedlings. The autotoxicity of extract at same concentrations followed the order of decreasing inhibition: stem > leaf > rhizome (32).

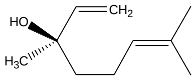
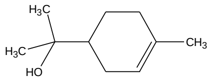
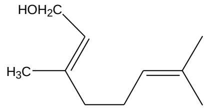
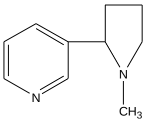
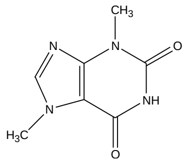
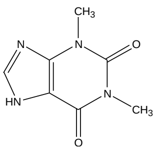
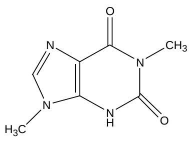
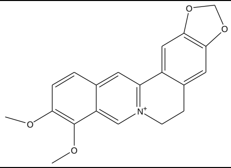
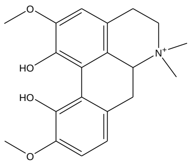
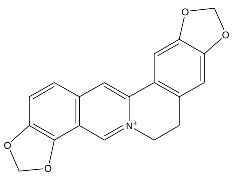
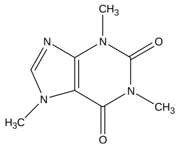
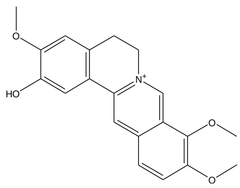
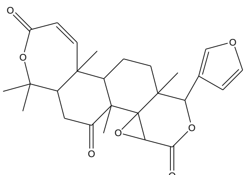
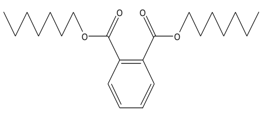
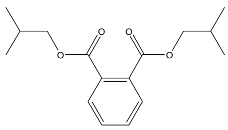
Table 1. Autotoxic plants and their autotoxins

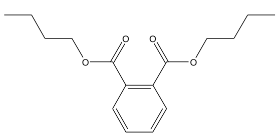
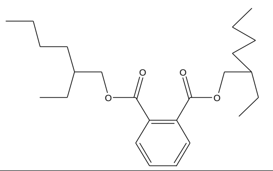
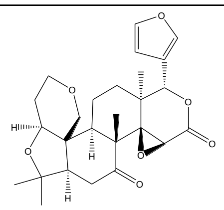
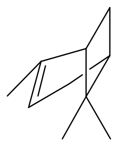
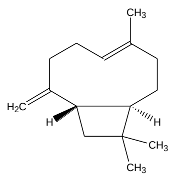
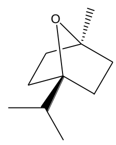
Family	Genus	Plant	Autotoxins	Refer-ence
Poaceae	*Digitaria*	*D. sanguinails*	Chlorogenic, isochlorogenic acid, and sulfosalicylic acid	53
	Hordeum	*H. vulgare*	p-hydroxybenzoic, syringic and p-coumaric acids	52
	Oryza	*O. sativa*	p-coumaric, p-hydroxybenzoic, syringic, vanillic, ferulic and o-hydroxyphenylacetic acids	18,62
	Sorghum	*S. halepense*	chlorogenic and p-coumaric acids, p-hydroxybenzaldehyde	1
	Spartina	*S. alterniflora*	palmitic acid, oleic acid and stearic acid	57
	Triticum	*T. aestivum*	ferulic, p-coumaric, p-hydroxybenzoic, syringic, vanillic acids	45
	Zea	*Z. mays*	2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one	24
Ranuncula ceae	*Coptis*	*C. chinensis*	berberine, epiberberine, palmatinejatrorrhizine, coptisine, worenine, columbamine, obakunone, obakulactone and magnoflorine	38,80
Rosaceae	*Amygdalus*	*A. persica*	gallic, syringic, chlorogenic,benzoic, p-hydroxybenzoic, ferulic, cinnamic, cumaric acids and amygdalin, catechins, coumarin, vanillin	88
	Fragaria	*F. ananassa*	lactic, benzoic, succinic, adipic and p-hydroxybenzoic acids	36
	Malus	*M. prunifolia*	phthalic acid, butylated hydroxytoluene and palmitic acid, phlorizin, phloretin, p-hydroxyhydrocinnamic acid, p-hydroxybenzoic acid, and phloroglucinol	3,7
Rubiaceae	*Coffea*	*C. arabica*	caffeine, theophylline, theobromine, paraxanthin, scopoletin, caffeic, coumaric, ferulic, p-hydroxybenzoic, vanillic and chlorogenic acids	19
Rutaceae	*Citrus*	*C. jambiri*	homovanillic acid, seselin, and xanthyletin	12
Solanaceae	*Capsicum*	*C. annuum*	1,2-benzenedicarboxylic acid, bis(2-methy-lpropyl)ester	87
	Nicotiana	*N. tabacum*	Di-sec-butyl phthalate ester and bis(2-ethylhexyl)	21,22

			phthalate ester, dibutyl phthalate, dioctyl phthalate, and di-isooctyl phthalate	
		N. sylvestris *N. glauca*	nicotine	4
		N. tabacum	β-cembrenediol (terpenoids), di-n-hexyl phthalate and bis(2-propylheptyl) phthalate	58
Taxodiaceae	*Cunninghamia*	*C. lanceolata*	syringic, gallic, protocatechuic, o-coumaric, m-coumaric, p-coumaric, p-hydroxybenzoic, vanillic, and ferulic acids, 6-hydroxy-1,3-dimethyl-8-nonadecyl-[1,4]-diazocane -2,5-diketone	35,81
	Cryptomeria	*C. fortune*	ferulic acid, cinnamic acid and β-hydroxybenzoic acid	85
Theaceae	*Camellia*	*C. sinensis*	Caffeine and theobromine	67
Verbenaceae	*Lantana*	*L. camara*	p-cymene, α-phellandrene, α-pinene, dipentene, γ-terpinene, caryophyllene, cardinene, cineole, linalool, geraniol, α-terpinol, phelandral and citral	59
Vitaceae	*Vitis*	*V. vinifera*	hexamethyl-cyclotrisiloxane	31

Table 2. Chemical structures of autotoxins

Phenolic compounds		
		
Ferulic acid 18,19,35,45,62,85,88	Caffeic acid 19	Chlorogenic acid 1,19,53,88
		
Vanillin 88	p-coumaric acid 1,18,52,45,62	Gallic acid 35,88
		
p-hydroxybenzoic acid 7,18,19,35,36,45,52,62,88,	Syringic acid 18,35,45,52,62,88,	

Diols		
		
Linalool 59	α-terpinol 59	Geraniol 59
Alkaloids		
		
Nicotine 4	Theobromine 67	Theophylline 19
		
Paraxanthin 19	Berberine 38	Magnoflorine 80
		
Coptisine 80	Caffeine 67	Columbamine 80
Esters		
		
obakunone	bis(2-propylheptyl) phthalate	diisobutyl phthalate,

80	58	bis(2-methy-lpropyl)ester 87
		
dibutyl phthalate 22	bis(2-ethylhexyl)phthalate ester 21	Obakulactone 80
Terpenoids		
		
α-pinene 59	Caryophyllene 59	Cineole 59

18. CONCLUSIONS

Autotoxicity is the main reason causing continuous cropping obstacle in the plantation of some important agricultural crops and medicinal plants. In this review, autotoxicity of 46 species from 16 families were summarized. Most of these species were crops (such as *Hordeum vulgare*, *Oryza sativa*, *Saccharum officinarum*, *Triticum aestivum*, *Nicotiana tabacum*, *Zea mays*, etc.) or medicinal plants (*Coptis chinensis*, etc.). Only a few of them were notorious invasive weed species (such as *Spartina alterniflora*).

In general, the self-toxic effects of crops and medicinal plants can cause great economic losses for people, but it is non negligible for some high-level plants autotoxicity, which are closely related to intraspecific competition and ecosystem stability. Such as *Nyssa yunanenesis* and *Picea mariana*, etc. Autotoxicity is known to regulate density-dependent intraspecific competition in plants, but at the same time due to the effects on regeneration and hence population size, it may have implications for conservation (90).

The autotoxin isolation and identification studies showed that phenolic acids were the main autotoxin type contributed to autotoxicity of crop species (Table 1). More structure types of autotoxins were found in crops, medicinal plants and tree species (Table 2). The elucidation of autotoxins were not only important in solving the problem of continuous cropping obstacle, but also meaningful in the finding of new herbicidal chemicals. Therefore, the elucidation of autotoxins from more medicinal plants and invasive weed species deserves more attention.

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