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Review article

Allelopathic invasive plants as phytoinhibitor bioresource material in weed control: A review

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Abstract

The current status was addressed of chemical pesticides use in raising crop productivity and the judicious utility of natural products from invasive plants which can promote inhibitory activity for noxious weed management. Some allelopathic invasive plants have natural phytoinhibitors which can be used in agricultural crop protection to compensate the drawbacks from chemical pesticide use. The potential allelochemicals attributed to some invasive plants and their modes of action are discussed. In addition, luxuriant invasive plants could provide a rich biomaterial source of inexpensive alternatives for weed control in forging the eco-sustainable development of agriculture.

Involvement of chemical pesticides in crop productivity

The world's population exceeded 7 billion people in 2012 and the burgeoning population growth is forecast to continually swell by 30%, approaching 9.2 billion by 2050 (Popp et al., 2013). To cater for an extra 2.2 billion people in the developing world, and the pressure on the ensuing rise in food demand with better nutrition, broader dietary habits and high-value crops are expected to be increased by 70–100% by 2050 (Godfray et al., 2010). To cope with the disconcerting possibility of a tightening food supply owing to the expanding population, more concerted efforts are needed to search for holistic pest management strategies which are influenced by a wide array of factors such as prolific crop pests, weather and climate changes, soil fertility, labor force shortages, knowledge and technology access, market prices and government policies (Speranza et al., 2008; Campos et al., 2014).

In crop protection practices, pesticide use is widely implemented to eradicate pest outbreaks including weeds, insects and pathogens, in order to minimize crop yield losses. Chemical pesticides were ushered in during the mid-twentieth century, as part of an obligatory need for effective pest control, as exemplified by the 50-fold increase in cumulative pesticide use to substantially improve crop productivity in modern agriculture (Lamberth et al., 2013). The heavy reliance on chemical pesticides by farmers is due to the fact that chemical adoption is the easiest and most cost-effective method to proffer a sizeable increase in crop production using an application rate as low as one gram per hectare with good selectivity for crops. This results in alleviating a farm labor shortage, is less time consuming and lessens tedious work practices inherent with manual weeding and lessens the drudgery in minimizing soil erosion, nutrient and water run-off, greenhouse gas emission and fuel consumption (Gianessi, 2013).

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Weed-inflicted crop yield losses

Considering weed control, crop yield losses caused by weeds (~32%) are significantly greater than those caused by insect pests (18%) and pathogens (15%) (Van Evert et al., 2017). Weed accession in paddy fields is one of the chief impediments to high yield rice production. Rice (*Oryza sativa* L.) is the main staple food source for the majority of the world's population, and about 90% of all rice is produced in Asia (Food and Agriculture Organization, 2014). The insidious spread of weeds which interfere with the rice crop uptake of available resources such as light, space, nutrient and water could impinge on rice yield decline by up to 56% (Rabbani et al., 2011). As a consequence, the scenario of herbicide-based weed management prevails in rice cultivation to safeguard sustainable rice production. Herbicide consumption in Malaysian agriculture, and for rice crops in particular, costs ~USD 10.96 million (1984–2014) (DOS, 2015).

In Asian countries today, the direct-seeded rice (DSR) system has mainly superseded the flooded transplanted rice (FTR) method due to looming water scarcity, rural labor shortages, climbing labor wages and land competition for transplanting rice (Joshi et al., 2013). In the DSR system, rice seeds are sown directly into fields in the absence of standing water and aerobic soil conditions that are highly conducive to weed germination on a monumental scale and concomitantly the emergence in cohorts of the weeds with rice seedlings leads to harsh competition for available resources (Khaliq and Matloob, 2011). More than a thousand weed species have encroached on the global rice fields, with 13 weed species causing the most severe effects, among which includes *Echinochloa colona* (L.) Link (jungle rice) (Holm et al., 1991). The advent of the DSR system has prompted farmers to extensively use chemical herbicides to counteract most weed intervention (Chauhan, 2013).

Chemical pesticide drawbacks

An immediate release of the applied pesticides with more than 90% being lost via spray drift, off-target deposition, degradation and volatilization, results in failure to reach the intended target sites (Wang and Liu, 2007). Moreover, the repeated use of different conventional herbicide formulations with higher doses than the recommended threshold is applied in order to compensate for the losses to non-target sites. The non-judicious and extensive use of chemical pesticides has aggravated the detrimental impacts to the environment with the pesticide remnants jeopardizing a myriad of non-target organisms, with repercussions for pesticide bioaccumulation and food safety apprehensions and human health problems (Popp et al., 2013). The worldwide destruction inflicted by chemical pesticides is predicted to cost USD 100 billion per annum (Alston and Pardey, 2014).

More worrying is the perpetuation of dependence on the use of chemical pesticides which has triggered outbreaks of recalcitrant herbicide-resistant weeds at an increasingly rapid rate (Bhatti et al., 2013). About 250 species of noxious weeds have built up resistance and are able to withstand the known mode of actions (MoAs) by herbicide detoxification worldwide (Heap, 2016). More existing chemical products are vulnerable to weed resistance and cross-resistance. The herbicide-resistant *E. colona* has evolved in plentiful amounts and is becoming less affected by chemical herbicides including ametryn, atrazine, clefoxidym, cyhalofop-butyl, metribuzin, propanil, glyphosate, quinclorac, bispyribac-sodium, imazapyr, triazine and acetyl coenzyme A carboxylase (ACCase) inhibitor (Valverde, 2007; Peerzada et al., 2016). Such dire scourges have wakened researchers to search for new herbicide MoAs to complement the obsolete herbicides. There are about 20 herbicide MoAs in the marketplace and no new herbicide MoAs have been introduced for the last 30 yr (Duke and Dayan, 2015).

Allelopathy for crop protection

In recent years, the agrochemical industry has boosted interest in developing eco-friendly pesticides owing to a steadily growing demand for food safety and stringent restrictions on the use of toxic chemicals (Yusoff et al., 2016). Natural products have gained a recent surge in popularity and could provide a fulgurant array of structural diversity of natural phytotoxins which can act as molecular scaffolds to prepare novel synthetic analogues in developing new herbicide target sites (Sparks et al., 2017). The current paradigm on herbicide-resistant problems can be allayed through advocating natural product use via allelopathy as one weed management option. Plant allelochemicals have multi-site actions which function through the MoAs not owned by commercial herbicides and their use could be suitable in preventing weeds developing resistance (Dayan et al., 2012).

In escalating the involvement of natural products in sustainable weed management, plant emancipated allelochemicals having an interfering effect on recipient plants with non-toxic mechanisms could be used to suppress weeds in agroecosystems (Dayan et al., 2009b). Plants can manufacture a great variety of natural bioactive constituents, thus imparting various kinds of MoAs for different biological activities. Some of the natural phytotoxins synthesized from secondary metabolic pathways have conferred the plants with inducible defenses over their lifetime to debilitate pest attacks (Chandler et al., 2011). Natural phytotoxins are a sustainable feature attributed to new product development with regard to allelopathic approaches including cover crops, mulching, intercropping, green manure and plant extracts (Farooq et al., 2013). The allelopathy concept could offer a green alternative route for the apparent impasse, from the standpoints of crop safety, cost-effectiveness, safer environmental and toxicological profiles.

The concept of allelopathy has garnered interest in exploiting an eye-catching and eco-friendly approach toward identifying new crop protection products as part of a weed control strategy. Allelochemicals are non-nutritive natural products which are elicited by donor living organisms (such as plants, insects and microbes) into the environment with prominent functions to influence the survival, growth and development of receptor organisms through either stimulation or inhibition (Cheng and Cheng, 2015). Many allelochemicals are believed to have emerged over millions of years and they are produced in different parts of plants including the leaves, roots, rhizomes, stem bark, pollen, flowers and fruits (Weir et al., 2004). The allelochemicals could be translocated from decaying plant litter, volatile emissions, leaf leaching and root exudation. The quantity and quality of allelochemicals produced in plants are greatly varied by age, plant parts, genetic factors, biotic and abiotic stresses (Fig. 1) (Belz, 2007; Trezzi et al., 2016).

Allelochemicals are prevalently regarded as safe organic chemicals possessing a short half-life ranging from a few hours to a few months and having less environmental burden for effective weed management (Cheng and Cheng, 2015; Ihsan et al., 2015). In fact, plants have disparate allelochemicals in assorted manners which might act synergistically to confer multiple biological activities, strengthen the capability of inhibition and restrict weed growth and to a greater extent, prevent the development of herbicide-resistant weed biotypes (Duke and Dayan, 2015). The utilization of allelopathy in rice fields has resulted in remarkable weed elimination (Xuan et al., 2005).

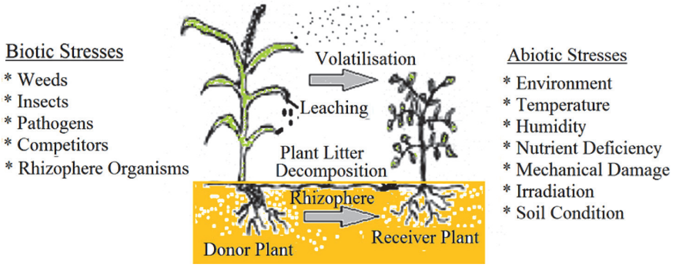


Fig. 1 Schematic diagram showing biotic and abiotic factors which influencing the release of allelochemicals

Allelopathy from invasive plants

In forest ecosystems, invasive plants exude allelochemicals which have been implicated as phytochemical inhibitors to outcompete indigenous species, pests and disease resistance (Pisula and Meiners, 2010). The invasive plants have high fecundity which can be economically invoked for potential use as a weed growth retardant. The exploitation of colonizing plants imposing an allelopathic influences is applicable in a crop protection strategy. Invasive plants exude allelochemicals which serve as chemical defensive and competitive agents which mediate the plant invasion and succession against the indigenous species (Pisula and Meiners, 2010), and act as an insect repellent (Watling et al., 2011) and inhibitor to soil borne pathogens (Mitrovic et al., 2012). In rice cultivation, the mulches of invasive plants *Tephrosia candida* (white hoarypea) and *Bidens pilosa* (blackjack) at 2 t/ha promoted 80% weed reduction along with a 20% increase in rice growth (Hong et al., 2004; Khanh et al., 2005). Other literature has reported on the allelopathic effect of the invasive plant, *Azadirachta indica* A. Juss (neem tree) in controlling the noxious weed, *Echinochloa colona* (L.) Link (junglerice) (Kato-Noguchi et al., 2014).

A broad range of invasive plant species (Fig. 2) has been reported to exhibit a potential allelopathic influence or phytotoxic effect against other organisms. In intercropping with citrus orchards, allelochemical exudates from *Ageratum conyzoides* L. were found to suppress major weeds including *Bidens pilosa* L. (black-jack), *Digitaria sanguinalis* (L.) Scop (hairy crabgrass) and *Cyperus difformis* L. (small-flowered nutsedge) and soil pathogenic fungi (Kong et al., 2004a,b). Furthermore, water extract of the disruptive invader *Clidemia hirta* (L.) D. Don was shown to reduce the seed germination of *Impatiens platypetala* Lindl. (Kinabalu balsam) (Ismaini, 2015).

***Ageratum conyzoides* L.** **(billygoat weed)** ***Asystasia gangetica* (L.) T. Anderson** **(creeping foxglove)**

***Clidemia hirta* (L.) D. Don** **(Koster's curse)** ***Dicranopteris linearis* (Burm.f.) Undrw** **(old world forked fern)**

***Imperata cylindrica* (L.) P. Beauv** **(cogon grass)** ***Melastoma malabathricum* (L.) Smith** **(rhododendron)**

***Mikania micrantha* Kunth ex H.B.K.** **(bittervine)** ***Ottochloa nodosa* (Kunth) Dandy** **(slender panic grass)**

***Pennisetum polystachion* (L.) Schult** **(mission grass)**

Fig. 2 Different invasive plant species showing multiple magnitudes of phytotoxicity of inhibition against *E. colona* reported by Lim et al. (2017)

Yet, the field evidence of allelopathy by *C. hirta* has not been reported.

The allelopathic dominance of the invasive plant *Dicranopteris linearis* (Burm.f.) Underw. results in a tendency to form pure colonies throughout the established region. The frond extract of *D. linearis* exerted a pronounced inhibitory effect on *Echinochloa colonum* (L.) Link (junglerice) and *Avena fatua* L. (wild oat) (Kato-Noguchi et al., 2012). Additionally, allelopathic studies of the invasive plant *Imperata cylindrica* (L.) P. Beauv. have been well documented. The rhizochemical elicited from *I. cylindrica* was found to inhibit *Aristida stricta* Michx. (wiregrass) and *Pinus elliottii* Engelm. (slash pine) (Hagan et al., 2013). The leaf and root extracts of *I. cylindrica* were reported to cause the germination inhibition of *Cynodon dactylon* (L.) and (bermudagrass) *Lolium multiflorum* (Lam.) (ryegrass) (Koger and Bryson, 2003).

The allelopathic influence of the weedy invasive shrub, *Melastoma malabathricum* (L.) Smith was verified to be conducive to cause stunted growth of *Raphanus sativus* L. (radish) and *Echinochloa crus-galli* (L.) P. Beauv. (barnyardgrass) (Faravani et al., 2008). Moreover, the creeping vine *Mikania micrantha* Kunth ex H.B.K. has imparted allelopathic influences by invading nearby native plants (Shao et al., 2003). The *M. micrantha* extracts were found to induce lipid peroxidation on *Coix lacryma-jobi* L. (Job's tears) through peroxidase (POD) and catalase (CAT) activities (Li and Jin 2010). Meanwhile, other invasive plants including *Asystasia gangetica* (L.) T. Anderson, *Ottochloa nodosa* (Kunth) Dandy and *Pennisetum polystachion* (L.) Schult are used as cover crops which smother and displace ground weedy plants in the rubber and oil palm plantations (Lam et al., 1993; Samedani et al., 2012). The phytotoxic effects presented by *A. gangetica*, *O. nodosa* and *P. polystachion* have been reported with mild inhibition on the seed germination and seedling growth of *E. colona* (Lim et al., 2017).

Allelochemical constituents from invasive plants

To enforce the potential applicability of invasive plants, naturally occurring secondary metabolites associated with phytotoxic activity have been a major source of interest for researchers. A great variety of plant phytochemicals are produced in mixtures through various plant biosynthetic pathways (Fig. 3) (Einhellig, 2004; Khanam, 2007) including the phenolics, flavonoids, terpenoids, alkaloids, tannins, saponins, glycosides, amino acids, coumarins, fatty acids and steroids. These diverse phytochemical classes have been reported to be responsible as defensive agents in mediating plant allelopathic activities against pests, pathogen, herbivores and abiotic stresses (Mazid et al., 2011). The plant phenolic compounds which are primarily biosynthesized through the shikimic acid pathway are the most widespread allelochemicals sequestered in the ecosystem to disrupt the physiological processes in the receiver plants (Li et al., 2010; John and Sarada, 2012). The majority of the plant allelochemicals are at least partially to fully water-soluble (Dayan et al., 2009a).

Numerous literature compilations of 21 putative allelochemicals consisting of 12 phenolic acids, 5 non-phenolic acids, 2 flavonoids and 2 phenols (Fig. 4), and their related allelopathic activities or phytotoxic effects have been elaborated. The root extract of *Rumex dentatus* L. (toothed dock) was found to exert allelopathic effect on germination inhibition of *Cicer arietinum* L. (chickpea) and the identified allelochemicals were caffeic acid (3), cinnamic acid (7), ferulic acid (10), gallic acid (11), sinapic acid (18) and vanillic acid (20) (El-Shora and El-Gawad, 2014). More recently, the aqueous leaf extract of *Calotropis procera* (Sodom apple) was identified to suppress the root, shoot and biomass of *Cassia sophera* L. (kasunda) and the main phenolic compounds which mediated the allelopathic behaviour were catechol (5), *p*-coumaric acid (9), gentisic acid (12), *p*-hydroxybenzoic acid (13), resorcinol (17) and syringic acid (19) (Gulzar et al., 2016).

Furthermore, Golisz et al. (2007) reported that the allelopathic attribution of catechin (4), quercetin (16) and chlorogenic acid (6) in the phytotoxic activities of aqueous extracts of *Fagopyrum esculentum* Moench. (buckwheat) stunted *Lactuca sativa* (lettuce) seedling growth. In addition, the exudate of *Cistus ladanifer* L. (gum cistus) was reported to affect the seed germination and root growth of *Rumex crispus* (curled dock) and one of the allelochemicals involved in the phytotoxicity activities was *p*-anisic acid (1) (Chaves et al., 2001). The allelopathic characteristic of cereals was reported to influence the parasitic weed, *Orobanche crenata* (bean broomrape), and one of the metabolites, coumalic acid (8) was responsible for imparting inhibition of root growth of *O. crenata* (Fernández-Aparicio et al., 2013).

Another allelochemical compound, veratric acid (21) was confirmed in the root exudates of *Digitaria sanguinalis* (L.) Scop. (crabgrass) and interfered with the growth of maize, wheat and soybean (Zhou et al., 2013). Amongst the allelochemicals detected in the aqueous leaf extract of *Picea schrenkiana* (Schrenk spruce), *p*-hydroxyphenylacetic acid (14) was found to take part in the inhibition of spruce seed germination and seedling development (Li et al., 2010). In addition, benzohydroxamic acid (2) contains a (2H)-1,4-benzoxazin-3(4H)-one skeleton which has been ascribed to exhibit herbicidal properties (Valle et al., 2011). The appreciable amounts of benzohydroxamic acid and protocatechuic acid (15) were reported to be involved in the allelopathic influence of *Triticum durum* (durum wheat) and *Secale cereale* L. (rye) in controlling weed growth (Niemeyer, 2009; Schulz et al., 2013).

Mechanisms of action of allelochemicals

Plant allelochemicals confer phytotoxic activities which are capable of weed growth suppression. Diverse allelochemicals could exert various mechanisms of action resulting in multiple physiological effects on the target plants. The allelochemicals induce multiple biochemical processes in plants which involve mechanisms of action through photosynthesis, respiration, mitosis, membrane permeability, antioxidant and enzyme activities, phytohormone functions, protein and nucleic acid synthesis and nutrient and water uptake. As a consequence, normal plant growth and development are greatly impacted. In particular, the phenolic acids have shown abundant evidence as phytotoxins having a strong relationship with allelopathic activity. The underlying mechanisms of action of the allelochemicals are outlined below.

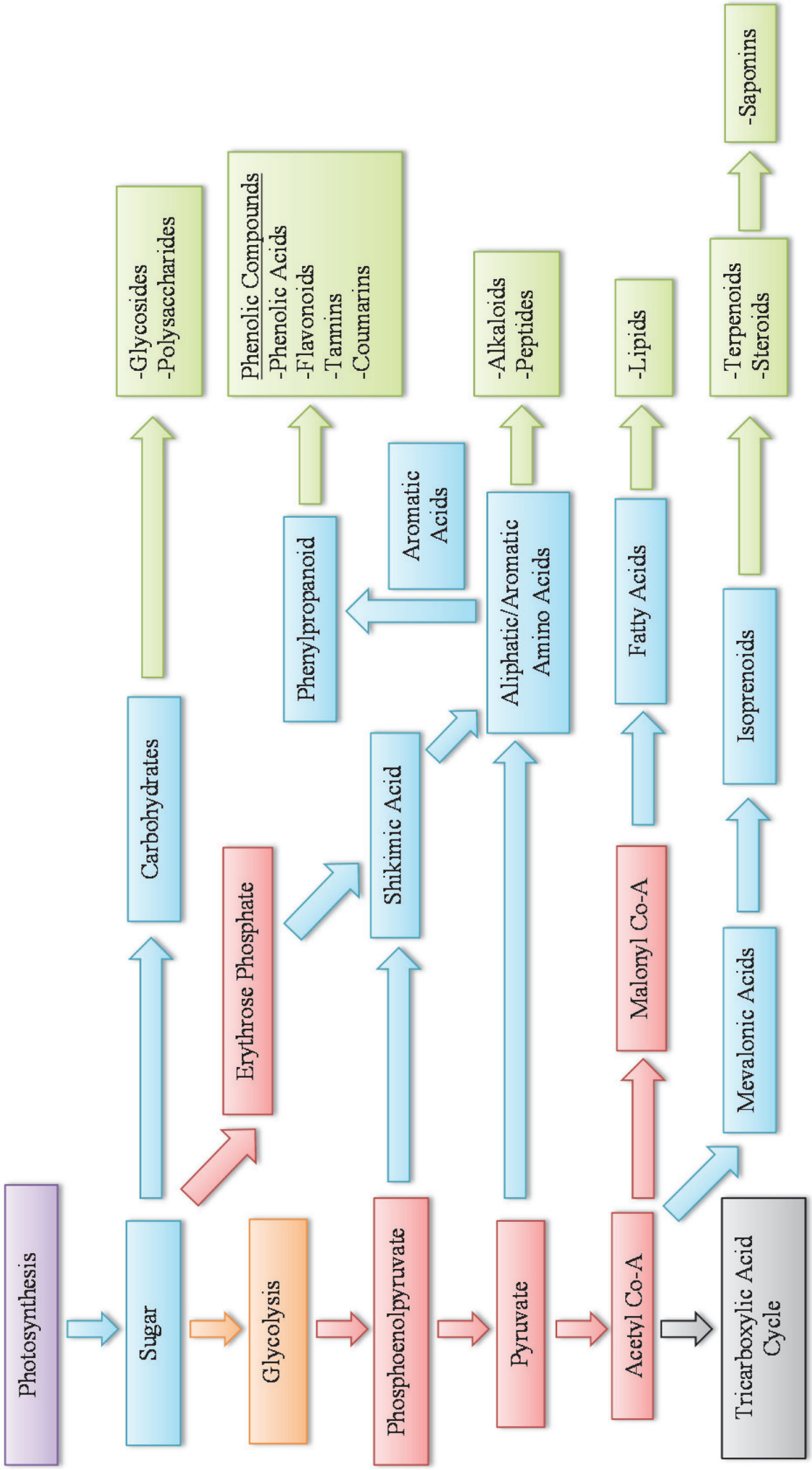
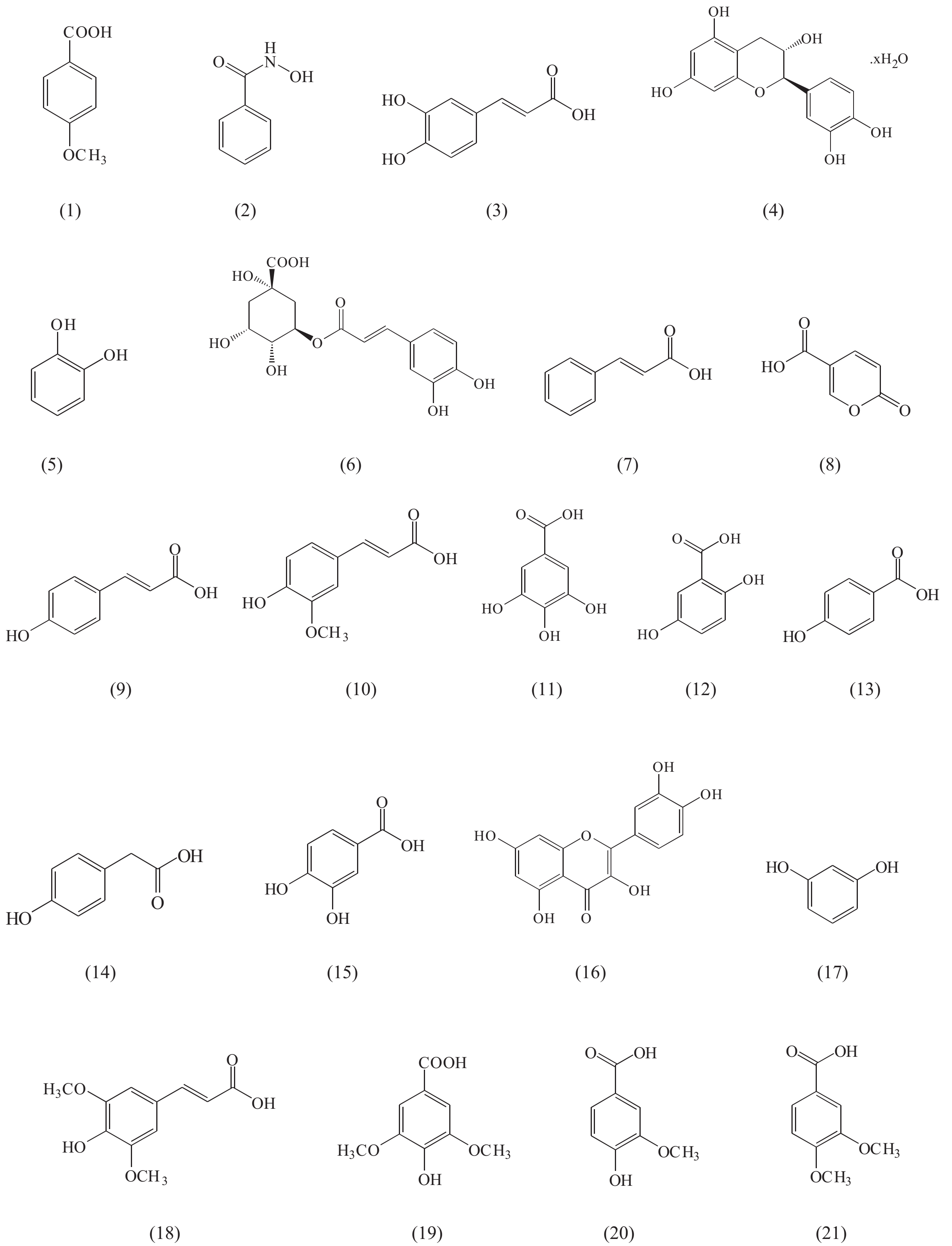


Fig. 3 Schematic overview of plant biosynthetic pathways leading to the formation of secondary metabolites



(1) (2) (3) (4)

(5) (6) (7) (8)

(9) (10) (11) (12) (13)

(14) (15) (16) (17)

(18) (19) (20) (21)

Fig. 4 Chemical structure of phenolic/aromatic allelochemicals

Disturbance of photosynthesis

Allelochemicals could interrupt the function of photosystem II by impairing the plant biosynthesis machinery through blocking the synthesis of adenosine triphosphate (ATP). The reduced stomatal conductance and less energy being supplied to the photosynthetic carbon reduction cycle for dark reaction and thylakoid electron transfer for light reaction result in retardation of the photosynthetic rate and in chlorophyll production (Wu et al., 2004; Yu et al., 2006). A series of allelochemicals including benzoic acid, caffeic acid, cinnamic acid, *p*-coumaric acid, ferulic acid and vanillic acid were reported to severely inhibit the ATP-generating pathway of chloroplasts whereas *p*-anisic acid, chlorogenic acid, gallic acid, gentisic acid, *p*-hydroxybenzoic acid, protocatechuic acid and syringic acid induced the reduction of net photosynthesis in *Lemna minor* L. (common duckweed) (Nyberg, 1986; Scholes, 1987; Moreland and Novitzky, 1987).

Impediments to mitochondrial respiration

Allelochemicals exert capability to weaken oxygen intake capacity which impedes the nicotinamide adenine dinucleotide oxidation, synthesis and formation of ATP in mitochondria and the disruption of oxidative phosphorylation and CO_2 generation, resulting in a decline in mitochondrial respiration activity (Cheng and Cheng, 2015). Phenolic acids including *p*-coumaric, ferulic, gentisic and vanillic were found to reduce the mitochondrial respiration of *Phaseolus aureus* (mung bean) (Koch, 1977). An allelochemical, juglone, from black walnut (*Juglans nigra)* was reported to decrease the oxygen uptake in seedling roots of corn and soybean (Hejl and Koster, 2004). Another allelo-constituent, limonene, was also reported to provoke inhibition of coupled respiration through the ATP and adenine nucleotide translocase activities (Abrahim et al., 2003a; Abrahim et al., 2003b).

Blockages of cell mitotic division and ultrastructure changes

The allelopathic influence of *Calotropis procera* (rooster tree) was reported to impart mitotic aberration of *Cassia sophera* L. (kasunda) (Gulzar et al., 2016). The aqueous leaf extract of *C. procera* was found to induce chromosomal stickiness and clumping and an abrupt decrease in cell numbers for mitotic division in *C. sophera*. Phenolic compounds were spectroscopically identified in the leaf extract comprising caffeic acid, catechol, *p*-coumaric acid, gallic acid, gentisic acid, *p*-hydroxybenzoic acid, resorcinol and syringic acid. Other literature has claimed that an odorine, the potent bisamide allelochemical which was isolated from the ethyl acetate fraction of *Aglaia odorata* Lour (Chinese perfume plant), could suppress growth of the weed of rice fields, *Echinochloa crus-galli* (barnyardgrass). The ethyl acetate portion of the extract was observed to induce abnormal chromatin organization and mitotic spindle damage, thus halting the progression of cell division of *Allium cepa* (onion) roots (Decordier et al., 2008; Teerarak et al., 2012).

Perturbations of cell membrane permeability

Under a stressful environment caused by allelochemicals, impairment in metabolic functions such as the inhibition of antioxidant enzymes increases the free radicals thus leading to depolarization of the cell membrane and lipid peroxidation (Harun et al., 2014; Sunmonu and Van Staden, 2014). The damage to the plasma membrane integrity could encourage electrolyte leakage and increase membrane permeability, ultimately resulting in cellular injury and death (Tanatson et al., 2013; Omezzine et al., 2014). The phenolic allelochemicals ferulic acid and *p*-coumaric acid were reported to increase the malondialdehyde (MDA) content (an indicator of lipid peroxidation) of the treated maize root membrane (Gmerek and Politycka, 2011; Hussain and Reigosa, 2011). A report stated that the presence of cinnamic acid was detected to increase MDA accumulation in the leaves of *Brassica oleracea* var. capitata (cabbage) (Singh et al., 2013).

Suppression of enzyme functions and activities

Allelochemicals could change antioxidant enzyme activities with an increase in free radical production imparting oxidative stress. Batish et al. (2008) reported that caffeic acid generated reactive oxygen species (ROS) in suppressing proteases, POD and polyphenol oxidases activities and thereby retarded the rhizogenesis of *Phaseolus aureus* (mung bean). Other allelochemicals affecting enzyme activities have also been reported, including catechol and chlorogenic acid which were found to exert inhibition on the activities of λ-phosphorylase whereas cinnamic acid was implicated to inactivate ATPase for hydrolytic activities (Rice, 1984; Einhellig, 1995). The phenolic acids *p*-coumaric, *p*-hydroxybenzoic, protocatechuic and vanillic were identified to depress glycolytic enzyme activities (Muscolo et al., 2001). Furthermore, gallic acid and phenol were reported to play a role in retarding phenylalanine ammonia-lyase through regulating the phenylalanine metabolism (Lin et al., 2001).

Alterations of plant growth regulators

The production of ROS induced by allelochemicals causing an oxidative burst leads to changes in plant phytohormone levels (Atwell et al., 1988). Under oxidative stress, the plant hormones abscisic acid (ABA) and ethylene participate in regulating seed germination and dormancy (Barnawal et al., 2012). The allelochemicals could induce imbalances of hormones with an increase in the ABA level and a decrease in the ethylene level; thereby the metabolic activities of 1-aminocyclopropane-1-carboxylic acid synthase (ACS) and 1-aminocyclopropane-1-carboxylic acid oxidase are inhibited, resulting in blocking seed germination and seedling growth (Chae et al., 2003; Poel and Straeten, 2014). Cinnamic and ferulic acids were reported to induce decarboxylation of the plant growth hormone indole-3-acetic acid (IAA) or the accumulation of IAA oxidase, gibberellic acid and cytokinin, thus inhibiting the seedling growth of wheat and soybean (Liu and Hu, 2001; Salvador et al., 2013).

Disruption of protein and nucleic acid synthesis

Plant phenolic allelochemicals could disturb amino acid absorption, binding and transport for synthesizing protein and could diminish the integrity of DNA and RNA (Abenavoli et al., 2003; Li et al., 2010). The rice-produced phenolic constituents including cinnamic acid, ferulic acid and *p*-hydroxybenzoic acid were found to induce changes in gene expression which weaken DNA-repairing ability and damage the genomic DNA, thus preventing mitosis for the growth suppression of *Echinochloa crus-galli* (barnyardgrass) (He et al., 2012; Fang et al., 2015). An invasive plant species *Centaurea maculosa* (spotted knapweed) exuding a phytotoxin catechin initiates the production of ROS which triggers alterations in gene expression, therefore causing root death of the native plants (Bais et al., 2003).

Interference in the water balance and mineral nutrient uptake

Plant growth could be adversely restrained by phenolic allelochemicals through the retention of mineral ions across the cell membrane, thereby causing a decline in the hydraulic conductivity and causing plant water stress (Einhellig, 2004). Phenolic acids (caffeic acid, chlorogenic acid, *p*-coumaric acid and *p*-hydroxybenzoic acid) were reported to decrease leaf osmotic potential due to the loss of turgor which alters the water balance (Barkosky et al., 2000; Barkosky and Einhellig, 2003). Furthermore, the allelochemicals cinnamic acid, *p*-coumaric acid and ferulic acid were reported to inhibit the uptake of NH_4^+, NO_3^- and Cl^- ions and plasma membrane H^+-ATPase activity in corn seedlings (Bergmark et al., 1992; Abenavoli et al., 2010). The allelochemicals cinnamic acid and *p*-hydroxybenzoic acid were affirmed to suppress dehydrogenase, ATPase and nitrate reductase activities, resulting in a reduction in cucumber root uptake of the mineral ions K^+, NO_3^- and $H_2PO_4^-$ (Lv et al., 2002).

Conflict of Interest

The authors declare that there are no conflicts of interest.

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