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Allelopathic Plants. 17. Sugarcane (*Saccharum officinarum* L.)

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ABSTRACT

Sugarcane is crop of tropical and subtropical regions mainly cultivated for sugar production. It has been cultivated for thousands of years, hence, its morphology, biology and ecology are well known. It is source of sucrose and several of its bioactive compounds and possess pharmaceutical and plant defence properties. Intra and interspecific allelopathy have been described for sugarcane. In this review, sugarcane is presented as source of several allelopathic compounds, as evident from laboratory, pot and field studies.

Keywords: Allelopathy, autotoxicity, residues, sugarcane, weed control, yield decline.

1. INTRODUCTION

Sugarcane is a monocotyledonous crop plant cultivated in the tropical and subtropical world regions for its ability to store high concentrations of sugar (sucrose) in its stem internodes (6). Noble canes or high sucrose producer genotypes belonging to *Saccharum officinarum* L., have no known wild forms (37). Its origin was hypothesized to be in Polynesia, from there it was transported through south east Asia and Irian Jaya (Indonesia), where most specimens from *Saccharum* genus were collected in early nineteen century for taxonomical analysis (10). First domesticated genotypes appeared as

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early as 2500 BC (10). Sugarcane was introduced by spaniards in the New World during sixteenth century, where its cultivation was rapidly extended and acquired economical importance. Nowadays, sugarcane is cultivated in more than 72 countries contributing to 60 % of the world´s sugar production (6). Modern sugarcane varieties are complex interspecific hybrids obtained after making crosses between the *S. officinarum* L. and *S. spontaneum* L. (9). In fact, modern sugarcane hybrids resembles the natural intermediate forms which slowly led to selection of *Saccharum officinarum* L., it is complex product from *S. spontaneum*, *Erianthus arundinaceous* and *Miscanthus sinensis*. It is also hypothesized that *S. officinarum* is selection from *S. robustum*, from wet tropics (10).

2. THE SUGARCANE PLANT

Sugarcane is large tropical perennial grass, which produces stems consisting of many nodes and internodes (23). After germination, the terminal bud of each shoot develops several nodes, each with a dormant bud and one or more rows of root primordia below a growth ring known as intercalary meristem (Fig 1A). The internodes stores sucrose in its parenchyma cells and vascular tissue.

As the stem develops, one leaf emerges per node, attached at the base of the node. The leaves grow alternately on opposite sides of the cane stalk. Mature stalks have an apical meristem at the top, followed by many short internodes with their respective expanding leaves. A fully grown stalk have about dozen expanded leaves and many senescent leaves. Mature plant has more dead than green leaves (Fig. 1B). The base of each leaf is attached to the stem at node, but during growth it wraps the stem to form a sheath that loosely encloses the internode to which the node subtends. Internode length can reach over 30 cm, depending on growth conditions and stems can reach 2 to 3 m in normal growing season (5).

Sugarcane has fibrous and shallow roots (Fig. 1C). However, the plant also develops buttress roots that serve to anchor into soil and some deeply penetrating roots that grown downwards up to 5-7 m to adsorb water (36).

It is propagated vegetatively by planting pieces of recently harvested stems, called setts, each containing two or more buds (24, 40). Germination leads to growth of primary shoots (consisting of a number of short, under ground internodes), afterwards, stems emerged above ground elongate and become stalks. Each node on stem/stalk, develops in to bud and root primordia, which successively give rise to secondary and tertiary shoots and roots. This process is known as sugarcane tillering (5). Sugarcane yield is expressed by number of stalks and weight of each stalk. Stalks gradually accumulate sucrose and its concentration increases with age.

Sugarcane stalks are harvested in 9 to 20 months after planting, depending on the climatic conditions, where it is grown (28). First sugarcane growth from roots and shoots arising from the setts is called the 'plant' crop. The subsequent crops after the first harvest are known as 'ratoon' crops and develop from buds on the basal portion of the plant left in the soil after harvest (24, 40). The duration of the crop cycle is variable. In the tropics up to 20 ratoon crops are taken, while, shorter periods of 3 (Louisiana, USA,) and 4 years (Australia and Argentina) are also found (2,3,11,28).

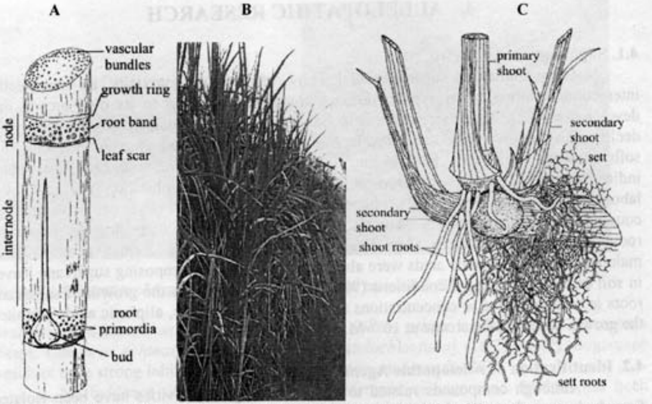

Figure 1. (A) Stem of sugarcane, (B) sugarcane plants near maturity, (C) shoots and roots grown from a sugarcane sett (22).

3. METABOLITES IDENTIFIED IN SUGARCANE

The metabolite with highest economical importance extracted from sugarcane is sucrose. Traditional medicinal properties like diuretic and tonic activities and the use of the plant to treat anaemia, inflammations and ulcers are often attributed to this carbohydrate (31). However, other bioactive metabolites have also been indentified (Table 1).

Table 1. Bioactive metabolites identified in sugarcane plant

Metabolite	Chemical nature	Biological activity	Reference(s)
Glycolic acid	α-hydroxyacid	Used for peeling (cosmetic) and as photoprotective and anti-inflammatory	25, 27
1-Octanosol (C28), 1-Triacontanol (C30)	Long chain aliphatic alcohols (in sugarcane waxes)	Hypercholesterolemic activity in animals and humans	1
Luteolinidin, apigeninidin and Caffeic ester of 5-*o*-Arabinosyl apigeninidin	Phenolic compounds	Phytoalexins active against red rot (*Colletotrichum falcatum* Went).	12,38
Flavonoid glycosides	Phenolic compounds	Active in resistance against smut (*Ustilago scitaminea* Sydow).	16
Piceatannol	Stilbene	Phytoalexin active against red rot	4
Polyamines conjugated to phenolic acids	Miscellaneous compounds	Increase suceptibility against smut.	26

4. ALLELOPATHIC RESEARCH

4.1. Sugarcane autotoxicity

Early studies on sugarcane allelopathy referred to autotoxicity, an intraspecific interaction occuring when a plant releases compounds harmful to its own growth and development (22). Autotoxicity seems to be an important component in sugarcane yield decline observed in several countries. In Australia, filter sterilized aqueous leachates from soils showing sugarcane yield decline, inhibited the growth of sugarcane test plants, indicating that phytotoxins are responsible for sugarcane growth inhibition (19). In Taiwan laboratory and field experiments, phenolic acids (ferulic, *p*-hydroxybenzoic, vanillic, *p*-coumaric, and syringic acids) were identified from the soil decomposing the sugarcane roots as possible autotoxins (39). Besides, the aliphatic acids, formic, acetic, oxalic, malonic, tartaric and malic acids were also identified in the decomposing sugarcane leaves in soil under water logged conditions (7). Phenolic acids inhibits the growth of sugarcane roots in water cultures at concentrations as low as 50 ppm, while, aliphatic acids inhibited the growth of ratoon sugarcane at 10^{-3} M.

4.2. Identification of Allelopathic Agents

Although compounds related to specific biological activities have been isolated from sugarcane, but phytotoxins have rarely been identified. Early works suggested the presence of phytotoxins in apical (13) and root tissues (8), but the chemical nature of these compounds was not elucidated. Further studies showed that leachates from senesced sugarcane leaves reduced the germination of lettuce (*Lactuca sativa* L.) seeds more than green leaves (14). Recently, 2,4-dihydroxy-1,4-benzoxazin-3-one and 2-benzoxazolinone have been isolated from sugarcane leaves (35). At 0.45 mM to 1.25 mM concentrations, these two compounds reduced the root growth of lentil (*Lens culinaris* Medik.) seedlings, but seed germination was not affected. Ferulic, vanillic and syringic acids have also been identified as phytotoxins in sugarcane straw (30, 31). Ferulic and vanillic acids assayed separately, affected root growth of lettuce and weed species in laboratory conditions at concentrations found in sugarcane straw leachates (32). The identified phenolic acids modified the permeability of root cell membranes, depressed energy metabolism, leading to inhibition in cell division in root tips. These substances also affected both normal density of root hairs and root branching (31).

4.3. Sugarcane Residues

Air pollution and soil degradation resulting from the burning of sugarcane before or after crop harvest in South American countries have increased public concern for more sustainable harvest practices. Thus retention of sugarcane residues (straw plus tops) on the soil surface has became a major practice in Argentina and Brazil etc. (Figure 2).

Retention of sugarcane residues on the soil implies 15-20 t/ha of dry matter, leads to both inter and intraspecific allelopathic interactions (18). It is detrimental to sugarcane ratoon growth in heavy or poor drainage soils, where anaerobic conditions favour accumulation of phytotoxins, similar to Taiwan soils (7). Nevertheless, retention of postharvest sugarcane residues has no effect on sugarcane yields but suppresses the broad

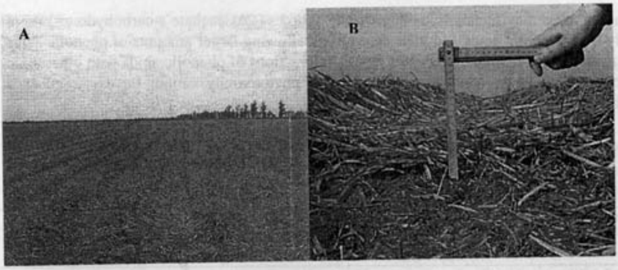

Figure 2. (A) Retention of sugarcane straw on soil surface after harvest and (B) its thickness (5-10 cm).

leaf weeds [*Amaranthus deflexus* L., *Sida* spp., *Bidens pilosa* L., *Brachiaria decumbens* Stapf, *Cenchrus echinatus* L. and *Ipomoea aristolochiaefolia*] (16,21,34,42). Sugarcane residues have strong inhibitory effects on seed propagated weeds (20).

No evidence of mechanism(s) of interference of sugarcane residues has been reported. Similar to other crops, sugarcane straw may inhibit plant growth through changes in soil microbial activity, physical hindrance or allelochemicals in top soil, where most weed seeds are located. Furthermore, leachates from sugarcane straw may inhibit weed growth through release of organic and/or inorganic compounds which may act directly or indirectly onto receptor plants (15). To answer some of these concerns, greenhouse experiments were conducted, evaluating the effect of soils amended with burned and unburned sugarcane straw leachates on growth of the *Bidens subalternans* L. weed and *Brassica campestris* L. (29).

Inhibition of root elongation was the primary effect of straw leachate on weed growth. Addition of straw leachates into soil previously amended with activated charcoal (adsorbent often used to scavenge organic molecules), attenuated inhibitory effects on root growth suggesting a direct participation of organic molecules. Inorganic straw constituents did not inhibit root growth, while microbial activity increased leachate phytotoxicity (Table 2). Soil chemical analysis also suggested a direct action of organic molecules in leachate phytotoxicity rather than variations in soil macro and micronutrients or nutrient microbial immobilization. Among evaluated soil properties, only increase in total phenolic contents was highly correlated to phytotoxic activity of straw leachates. Further studies led to isolation of vanillic, ferulic and syringic acids as possible allelopathic agents released from sugarcane straw (31, 32). However, these phenolic acids separately assayed on weed and crop plants could not completely explain the strong biological activity of straw leachate. Both phenolic acids and straw leachate stimulated the growth of certain plant species at low concentrations suggesting that in certain field situations they may have hormetic effects (30). Soil microorganisms increased phytotoxic activity of straw leachate, but reduced that of phenolic acids (Tables 2 and 3). This suggests that microbial byproducts arising from leached phenolic acids were not responsible for the increased activity observed in straw leachates. Nevertheless, as sugarcane straw leachate is a complex mixture of toxic and non-toxic compounds, it was hypothesized that soil microorganisms may metabolize other carbon sources (i.e. leachate´s carbohydrates) more readily than phenolic acids and their derivatives, allowing larger amounts of phenolic acids to be available for uptake by receptor plants. Interactions of phenolic acids with other toxic molecules from straw leachate contributing to phytotoxicity cannot be discarded as a possible explanation.

Table 2. Concentration of sugarcane straw leachate needed to reduce 25% root elongation (EC_{25}) of weed species grown in unsterile soil, sterile soil and unsterile soil plus activated charcoal (29,30)

Treatment	EC_{25} (g l^{-1})			
	Sida rhombifolia L.	*Bidens subalternans* L.	*Amaranthus quitensis* L.	*Brassica campestris* L.
Unsterile soil	12 ± 4	17 ± 4	20 ± 4	18 ± 3
Sterile soil	20 ± 6	29 ± 6	25 ± 5	25 ± 5
Unsterile soil + activated charcoal	16 ± 1	23 ± 2	21 ± 2	22 ± 4

The EC_{25} values are expressed as mean ± SD (95 % confidence interval).

Table 3. Concentrations of ferulic, syringic and vanillic acids needed to reduce 25% root growth (EC_{25}) of the weed species grown in unsterile soil and sterile soil (30)

Treatment	EC_{25} (g l^{-1})			
	Sida rhombifolia L.	*Bidens subalternans* L.	*Amaranthus quitensis* L.	*Brassica campestris* L.
Vanillic acid				
Unsterile soil	350±10	155±8	275±10	140±6
Sterile soil	75±5	60±3	100±7	45±3
Ferulic acid				
Unsterile soil	374±20	400±10	600±21	200±14
Sterile soil	200±16	91±5	116±10	93±13
Syringic acid				
Unsterile soil	761±31	476±45	650±52	176±15
Sterile soil	415±40	226±24	200±15	65±18

The EC_{25} values are expressed as mean ± SD (95 % confidence interval).

Direct physiological effects of straw leachates were evaluated on weed growth in soil conditions (29,33). Experimental evidence indicated that sugarcane straw leachates increased leaf proline contents in *B. pilosa* and *B. campestris*. Proline accumulation was regarded as a direct effect of organic molecules released from straw leachates. The same result was observed on *Sida rhombifolia* suggesting that proline accumulation is stress response induced by sugarcane allelochemicals (33). These substances also induced proline accumulation in both roots and shoots of *S. rhombifolia*. However, induction of proline accumulation in roots seem to be a consequence of an oxidative stress while water stress seems to be the main cause of high proline content in the cotyledons. Although the observed responses could be due to phenolic compounds, the involvement of organic molecules with other chemical nature cannot be excluded (29,33).

5. FUTURE LINES OF RESEARCH

Further research is needed on sugarcane allelopathy to clearly elucidate the following aspects.

(i) Identification of allelochemicals released from roots and decomposing straw residues.

(ii) Comprehension of microbial activity in these processes through assay of mixtures of toxic as well as non toxic molecules released by sugarcane plants. Activity of sugarcane allelochemicals requires assays of their mixtures in the presence and absence of soil microbial activity.

(iii) Extensive screening of sugarcane varieties for allelopathic activity. Rational screening should be possible through identification of toxic and non-toxic compounds related to sugarcane allelopathy, genes involved in their synthesis, and quantitative trait loci (QTL) analysis.

(iv) Reasons for plant population and yield decline in sugarcane ratoons.

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