Allelopathic Potential of Sorghum (*Sorghum bicolor* (L.) Moench) in Weed Control: A Comprehensive Review

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Contents

Abstract

Weeds constitute the largest biotic threat affecting the yield of cultivated plants. While conventional agriculture relies principally on chemicals for weed control, alternative biological methods may be important tools to reduce weed pressure in

agroecosystems. Furthermore, as the problem of excessive residue of plant protection agents in agroecosystems and the growing number of herbicide resistant biotypes continue to increase, new solutions that have smaller impacts on the environment are becoming increasingly desirable. One promising such method is the use of crops that exert a negative phytotoxic influence on weeds. This natural phenomenon describing the ability of certain plant species to produce compounds that affect the growth of other plants in their surroundings is called allelopathy. Managing weed infestations in cultivated fields by planting allelopathic crops is a sustainable, economic, and environmentally friendly approach that has been strongly articulated in the international arena. Among cultivated crops, sorghum (*Sorghum bicolor* (L.) Moench) has been intensively studied because of demonstrated allelopathic potential.

This report provides a comprehensive literature review of the applications of sorghum allelopathy in agriculture. A critical analysis of the allelopathic properties of sorghum identified the following areas contributing to its ability to reduce weed infestation in agroecosystems:

1. a large number of compounds produced by sorghum have allelopathic properties,
2. allelopathic compounds can be applied in the form of mixed plant extracts or in combination with herbicides,
3. sorghum extracts have a broad spectrum of activity,
4. sorghum may be used to produce bioherbicides.

1. INTRODUCTION

Reducing weeds in crop cultivation leads to an increase in production costs. Weeds have a negative effect on the qualitative and quantitative aspects of yield as they compete for light, water, nutrients, and space with crops (Farooq et al., 2013). In comparison to other biotic factors, weeds cause the highest yield losses. According to estimates, 34% of yield losses are caused by the presence of weeds, while disease (18%) or pests (16%) have a lesser impact (Jabran et al., 2015; Oerke, 2006, Oerke et al., 1999).

Agriculture faces current challenges from various origins. One challenge is the penetration of plant-protection agent residues into soil, groundwater, and the food chain (Beckie and McKercher, 1990). The improper use of herbicides, such as application in unsuitable weather conditions or at the incorrect developmental crop phase, could lead to serious environmental consequences, such as the leaching of active compounds into groundwater or accumulation in the soil (Kruidhof et al., 2008; Walker et al., 2013). The strong selection pressure exerted by herbicides also increases the evolutionary pace of herbicide resistance in weeds (e.g., common windgrass (*Apera spica-venti* (L.), P. Beauv.), cornflower (*Centaurea cyanus* L.),

lambsquarter (*Chenopodium album* L.), redroot pigweed (*Amaranthus retroflexus* L.), rigid ryegrass (*Lolium rigidum* Gaud.), wild oat (*Avena fatua* L.)). There are currently at least 250 herbicide-resistant weed species in the world (International Survey of Herbicide Resistant Weeds, 2016). These species have evolved resistance to 23 of the 26 known herbicide sites of action and to 160 different herbicide active ingredients. Another problem is public lack of acceptance of the use of crop protection agents in agriculture (Dayan et al., 2009a). Indeed, social awareness of environmental threats and the increasing number of customers looking for high-quality agricultural produce are prompting new, safer, and sustainable approaches.

Environmental pollution and the threat to human and animal health caused by incorrect or excessive application of plant-protection agents have driven new searches for alternative methods of weed control (Scarabel et al., 2015; Shaner, 2014; Singh et al., 2003; Sowinski, 2014). Decisions aiming to optimize plant production are made while at the same time respecting the principles of sustainable management. The adoption of safer plant protection methods associated with lower environmental risks, such as biological methods, is gaining popularity. This trend is representative of greener technologies being developed in numerous fields of human activity, such as the development of allelopathic crops in agriculture (Gealy and Yan, 2012, Gealy et al., 2013). The phytotoxic effect of allelochemicals, i.e., biologically active secondary metabolites exuded by higher plants, fungi, or microorganisms, may become a useful way to reduce weed infestation in crop cultivation (Farooq et al., 2011). This report provides a comprehensive literature review of the applications of the allelopathic potential of *Sorghum bicolor* (L.) Moench in agriculture.

2. ALLELOPATHY PHENOMENON

According to Rice (1984), allelopathy is a natural phenomenon involving either direct or indirect effects of one plant (including microorganisms) on another plant through the release of chemical compounds into the environment. The term allelopathy is derived from two Greek words: "allelon," meaning "of each other," and "pathos," meaning "to suffer" (Rizvi et al., 1992). Classical researchers were aware of this concept in the Greek and Roman era (Wills, 2007). Interference between plants was mentioned in the literature for over 2000 years and was formally recognized in 1937 when Austrian plant physiologist, Hans Molisch, named it

allelopathy. Consequently, Molisch is considered the father of allelopathy (Li et al., 2010 quot. Molisch, 1937). A plant with allelopathic potential is called the "donor plant," while the plant affected by allelopathic compounds from the donor plant is called the "acceptor plant" (Muller, 1969).

Allelochemicals can be produced and/or accumulate in nearly all plant parts and tissues, such as leaves, roots, stems, rhizomes, flowers, fruits, and seeds. These bioactive metabolites are released from plants in a number of ways, such as volatilization, foliar leaching, root exudation, or decomposition of residues and leaf litter (Ben-Hammouda et al., 2001; Bonanomi et al., 2006; Kumar et al., 2009; Rice, 1984). When released into the soil, these natural chemicals cause allelopathic effects, which are typically detrimental (inhibitory) or sometimes beneficial (stimulatory) to target organisms (Ghafarbi et al., 2012; Rice, 1984). Effects of allelochemicals can be observed at all levels of organization of a living organism, from physiological responses, through cellular and molecular levels (Rice, 1984). For example, certain allelochemicals can affect germination of surrounding species seed by inhibiting cell division and preventing hydrolysis of nutrient reserves (Balke, 1985; Irshad and Cheemas, 2004). Others inhibit electron transport in photosynthesis and the respiratory chain by altering enzyme activity (Hejl and Koster, 2004; Meazza et al., 2002; Silva et al., 1996). However, the molecular target site of most allelochemicals is poorly understood (Bertin et al., 2007, 2009, Kato-Noguchi and Peters, 2013, Romagni et al., 2000, Toyomasu et al., 2014).

Li et al. (2010) proposed a following classification of allelochemicals according to their different structures and properties: (1) water-soluble organic acids, straight-chain alcohols, aliphatic aldehydes, and ketones; (2) simple lactones; (3) long-chain fatty acids and polyacetylenes; (4) quinones (benzoquinones, anthraquinones, and complex quinones); (5) phenolics; (6) cinnamic acid and its derivatives; (7) coumarins; (8) flavonoids; (9) tannins; (10) steroids; and terpenoids (sesquiterpene lactones, diterpenes, and triterpenoids).

Numerous crops have been reported to show allelopathic effects on associated weeds. Examples include sunflower (Anjum and Bajwa, 2007; Batlang and Shushu, 2007; Khaliq et al., 2012; Mahmood et al., 2010), rice (Jabran et al., 2008; Kayode and Ayeni, 2009; Rehman et al., 2010), brassica (Awan et al., 2012; Khan et al., 2012b; Mahmood et al., 2015a), rapeseed (Mushtaq et al., 2010a), barley (Bertholdsson, 2003; Overland, 1966), wheat (Bertholdsson et al., 2012), and sorghum (Breazeale, 1924; Hozayn et al., 2011; Khan et al., 2015; Khandro et al., 2014; Lehle and Putman, 1983).

3. SORGHUM SPECIES

Sorghum is an annual grass from the *Panicoideae* subfamily most likely descending from the wild species *Sorghum arundinaceum* (Desv.) Stapf (Owuama, 1997). Sorghum originates from Ethiopia, serving as a dietary staple to endogenous populations with the first records of cultivation dating back to 4000 BC. This tropical cereal later migrated from East Africa to other continents (Owuama, 1997; Sène et al., 2001). According to FAOSTAT (2014), sorghum was recently cultivated on 45 million hectares that produced 68.9 million metric tons of grain, making it the fifth most cultivated crop in the global cereal area structure. The United States is the global leader in sorghum production, accounting for more than 22% of world production with an export revenue that exceeds 1.5 billion US dollars.

The *Sorghum* genus includes approximately 25 species that are widely cultivated throughout the world (Hodnett et al., 2005). Over the years, more than 10,000 varieties and genotypes have been cultivated, yet the positions of many of these taxa in taxonomy are ambiguous (Liu et al., 2014). The following subtypes are particularly important among the functional types of *Sorghum bicolor* ssp. *bicolor:* (1) high-stem sweet sorghum, (2) low-stem varieties cultivated for grain, (3) broomcorn (*Sorghum vulgare* var. *technicum*) for technical applications, (4) sudangrass (*Sorghum sudanense* (Piper) Stapf.), and (5) sudex (sorghum:sudangrass hybrid), harvested several times a year (Dahlberg et al., 2011). Sorghum is a species with a wide spectrum of applications, ranging from consumption purposes through the production of animal fodder to technological and construction applications (Sowinski and Szydełko-Rabska, 2013). The importance of this species is increasing worldwide because of the ability to adapt well to changing habitat conditions, particularly increased drought, and a high functional value (Berenji and Dahlberg, 2004; Sowinski, 2009; Sowinski and Liszka-Podkowa, 2008). Another sorghum species, Johnsongrass (*S. halepense* (L.) Pers.), is currently recognized as one of the worst weeds in the world and classified as an invasive species in the United States by the Department of Agriculture (NISIC, 2016).

Within the four past decades, research has documented the allelopathic potential of sorghum and evaluated its extent depending on the part of the plant, age, environmental factors, and species of acceptor plants. This weed suppressive potential is determined by the presence of hydrophilic

Fig. 1 Sorghum allelopathy phenomenon. Allelochemicals are released into the environment from above- and belowground sorghum plant parts.

compounds, phenolic acids, and their aldehyde derivatives, as well as hydrophobic substances, such as sorgoleone and its analogues (Czarnota et al., 2003a; Lehle and Putman, 1983) (Fig. 1).

4. ALLELOCHEMICALS IN SORGHUM

4.1 Phenolic Compounds

Phenolic compounds are important plant products and include several phytotoxins. The basic chemical backbone of phenolic compounds consists of a hydroxy group (–OH) bonded directly to an aromatic ring. They are ubiquitous to the plant kingdom and are released in the soil as plant decomposition products (Li et al., 2010). Phenolic acids and their aldehyde derivatives can also leach from aboveground parts or be exuded from the root system (Funnell-Harris et al., 2008). Sorghum produces many primary phenolic acids that have phytotoxic activity (Al–Tavaha and Odat, 2010; Cheema, 1988; Cheema et al., 2007a) (Fig. 2); however, relative amounts differ between cultivars. For example, Cheema et al. (2007a) reported that *p*–hydroxybenzoic, gallic, syringic, and protocatechuic acids were more abundant than other phytotoxins and were present in all cultivars used in the study. The levels of vanillic, benzoic, *p*-coumaric, and benzoic acids were relatively lower than those mentioned previously and were not present in all cultivars. There was greater phenolic compound diversity between
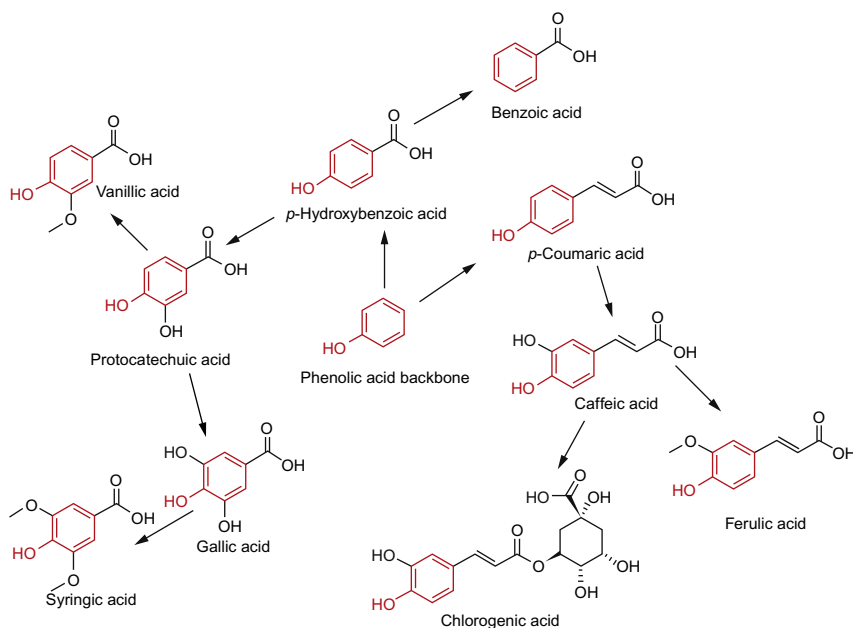
Fig. 2 Phenolic acid backbone (*red*) and its presence in common molecules produced by sorghum.

sorghum hybrids (Cheema et al., 2007a). The JS–263 cultivar had the highest content of total isolated phenolic compounds ($904.6\,\mu g\,g^{-1}$), while extracts of the cultivar Sibbi contained the lowest phenolic content ($51.35\,\mu g\,g^{-1}$). Giza 15 and Giza 115 hybrids accumulated five times more *p*-hydroxybenzoic acid than the Rabeh hybrid (Alsaadawi et al., 2007).

The total content of phenolic acids of sweet sorghum ranges from 2.0% to 2.2% in aboveground dry mass, and 1.1% to 1.6% in roots (Sène et al., 2001). However, phenolic acid levels change during plant development and tend to decrease as plants age (Marchi et al., 2008; Won et al., 2013). These dynamic changes in phenolics may account for some of the variation in overall phytotoxicity of sorghum extracts (Weston et al., 1989).

The literature is replete with such reports on the phenolic contents of sorghum cultivars and hybrids, but their role in allelopathy is overestimated (Cheema et al., 2009; Nicollier et al., 1983; Weston et al., 1989; Won et al., 2013). Indeed, common phenolic acids derived from the shikimate pathway are often cited as potential allelochemicals. However, these compounds are weakly phytotoxic molecules that are ubiquitous to higher plants, making them unlikely to play a role in allelopathy (see review Dayan and Duke, 2009 for more explanations).

4.2 Sorgoleone—The Main Sorghum Allelochemical

4.2.1 Chemical Structure of Sorgoleone and Its Analogues

Sorgoleone, 2-hydroxy-5-methoxy-3-[(Z,Z)-8′,11′,14′-pentadecatriene]–p–benzoquinone, is a lipophilic secondary metabolite consisting of a quinone ring and aliphatic chain (Netzly and Butler, 1986) (Fig. 3). Yet, in literature, this term has also been used to refer to the oily root exudate containing the parent molecule and its congeners (Soltys et al., 2010). Sorgoleone analogues have aliphatic side chains of varying lengths and different degrees of saturation (one to three double bonds). Other analogues may also have an additional methoxy group at the third and fifth atom in the ring (Dayan et al., 2003; Kagan et al., 2003).

Sorgoleone and its 1,4-dihydroxy form (resorcinol) account for 90% of compounds that are present in the root exudates of sorghum (Czarnota et al., 2003a; Fate and Lynn, 1996; Kagan et al., 2003; Rimando et al., 1998). The remaining 10% of root exudate components include sorgoleone analogues originating from the same path of biosynthesis, e.g., 5-ethoxy-sorgoleone (Rimando et al., 1998, 2003), small amounts of protein, and anthocyanins (Dayan and Duke, 2009; Rasmussen et al., 1992). Netzly et al. (1988) identified three other minor p–benzoquinones, similar in chemical structure to sorgoleone. Czarnota et al. (2003b) also noted another minor compound in sorghum root exudates, 2,5-dimethoxysorgoleone, which is closely related to sorgoleone.

4.2.2 Biosynthesis

Sorgoleone is produced exclusively by species in the *Sorghum* genus, upheld by testing of 17 other species from the *Poaceae* family, including closely related *Panicoideae* subfamily members (Baerson et al., 2008). Sorgoleone and its analogues are synthesized specifically in root hair cells (Dayan et al., 2007a), making these specialized cells natural herbicide factories
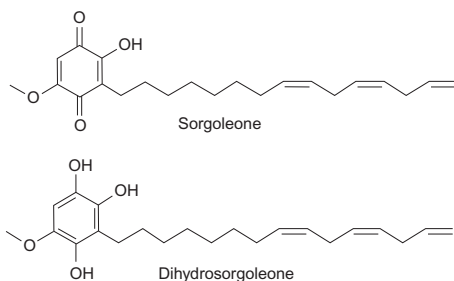

Fig. 3 Structures of sorgoleone and its reduced analogue dihydrosorgoleone.

(Dayan and Duke, 2003). In agreement with this observation, sorghum seedlings grown under conditions where root hairs do not develop have little to no sorgoleone (Yang et al., 2004a). Our group has investigated the bio-synthesis of sorgoleone in great detail, starting with a retrobiosynthetic NMR analysis approach (Dayan et al., 2003) that follows the incorporation of ^{13}C-labeled substrates into the carbon backbone of sorgoleone (Fig. 4). This preliminary study identified key enzymes involved in the biosynthesis of sorgoleone, namely, a specialized fatty acid desaturase that introduces three double bonds in the aliphatic tail, a polyketide synthase that forms the ring, an O-methyltransferase that methylates one or more of the hydroxy groups of the resorcinol intermediate, and a P450 monooxygenase that completes synthesis. The biosynthesis of sorgoleone that takes place with the participation of the endoplasmic reticulum and the Golgi apparatus is constitutive and proportional to the biomass of roots (Czarnota et al., 2003a; Dayan, 2006). A functional genomic approach analyzing an EST library confirmed that the genes encoding enzymes involved in the biosyn-thesis of sorgoleone were enriched in root hair cells (Baerson et al., 2006, 2008). Yang et al. (2004a) identified a fatty acid desaturase gene (SOR1) that

Fig. 4 Sorgoleone biosynthesis as determined from a retrobiosynthetic NMR analysis using ^{13}C-labeled substrates. *Green* = incorporation of 2-^{13}C-glucose, *blue* = incorporation of 2-^{13}C-acetate, and *red* = incorporation of methyl-^{13}C-methionine (Dayan et al., 2003).

was putatively involved in the introduction of some of the double bonds in the aliphatic tail of sorgoleone, but the function of this gene, now called DES1 (Fig. 4), was not confirmed until a later study (Pan et al., 2007). Another study on temporal expression of this gene in several sorghum cultivars found that highest expression occurred within the first 5 days after emergence and subsequently decreased as the plants aged (Dos Santos et al., 2014).

The genes involved in sorgoleone biosynthesis and their functions in isolated *Sorghum bicolor* root hair cells are now fully characterized (Baerson et al., 2008; Cook et al., 2010; Pan et al., 2007) (Fig. 4).

Expression levels of the DES2, DES3, ARS1, ARS2, and OMT3 genes involved in sorgoleone biosynthesis responded positively to the following auxin treatments: indole-3-acetic acid, indole-3-butyric acid, and 1-naphthaleneacetic acid (Uddin et al., 2011). The amount of sorgoleone was highly dependent on exposure time (3, 6, 12, 24, 48, and 72 h after auxin application) and auxin concentration. It was confirmed that, with increased auxin application duration, sorgoleone content also increased. In further studies, Uddin et al. (2013b) found that both methyl jasmonate and jasmonic acid significantly promoted secondary root development, root hair formation, root growth of sorghum, and, as consequence, sorgoleone accumulation. Transcript accumulation was apparent for all genes involved in sorgoleone biosynthesis. The highest increase in expression levels was observed for the *O*-methyltransferase 3 gene. The authors suggested that jasmonates be recognized as potent substances for promoting root hair formation, upregulating expression of genes involved in sorgoleone synthesis, resulting in sorgoleone accumulation in sorghum.

4.2.3 Exudation

The biosynthesis of lipid benzoquinones and resorcinol is a dynamic process. The system that regulates the dynamics of sorgoleone generation and exudation is based on the feedback loop principle (Dayan et al., 2009b). Sorgoleone, deposited in the space between the cell membrane and cell wall, is transported by bulk transport to the top part of root hairs, from which it is then exuded as oily droplets (Czarnota et al., 2003a; Field et al., 2006). The biosynthesis and exudation of sorgoleone can start when root hairs are developed and have reached their final size (Dayan, 2006). According to Dayan et al. (2009b) release of sorgoleone and an associated dimethylated resorcinol analogue is regulated by overall accumulation at root hair tips (Fig. 5).
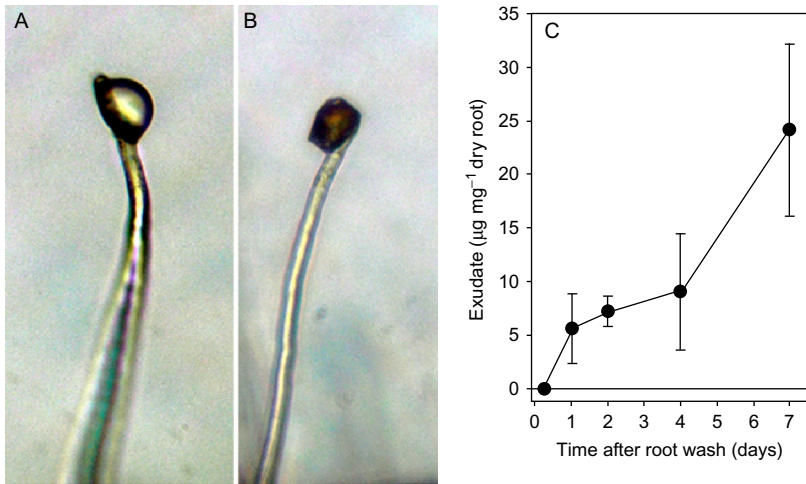
Fig. 5 Droplets of sorgoleone exuded by sorghum root hairs. (A) A droplet, consisting primarily of dihydrosorgoleone, is initially *yellowish* when roots are in a low oxygen environment. (B) When exposed to air, the droplet rapidly turns *dark brown* as its consistency shifts to predominately sorgoleone. (C) Synthesis and exudation of sorgoleone resumes when the oily droplet is removed.

The intensity of sorgoleone production is influenced by a series of environmental factors (Hess et al., 1992). An excessive amount of water impedes growth of root hairs and, as a result, reduces sorgoleone exudation (Dayan, 2006; Hess et al., 1992; Yang et al., 2004b). Temperatures below 25°C or above 35°C and an alkaline pH also have a limiting effect on the intensity of sorgoleone generation (Dayan, 2006). The greatest amount of sorgoleone is secreted at a pH between 4 and 5, suggesting that biosynthesis in acidic soil should be higher than that of alkaline soil. Illumination of sorghum seedlings with blue and red light inhibits sorgoleone synthesis by 50% and 23%, respectively (Dayan, 2006).

The amount of sorgoleone produced varies between and within sorghum species. Certain genotypes may accumulate up to 15 mg of sorgoleone per gram of fresh sorghum biomass (Weston and Czarnota, 2001). The Chalsusu hybrid accumulates 16.5 times more sorgoleone than the Hinsusu hybrid (Uddin et al., 2009). Bertin et al. (2003) found that sorghum, including grain and forage cultivars, typically produces quantities ranging from 1.3 to 1.9 mg of exudate per gram of fresh root biomass. Czarnota et al. (2003b) evaluated chemical composition of root exudates of seven genetically diverse sorghum species. It was demonstrated that Johnsongrass produced the

greatest amount of exudate (14.75 mg per gram of fresh root biomass) compared to other species, which produced only 0.5–1.85 mg per gram of fresh root biomass, although sorgoleone content is generally lower in Johnsongrass than other sorghum biotypes. According to Nimbal et al. (1996a) sorgoleone content may vary from 0.67 to 17.8 mg per gram of fresh root biomass.

4.2.4 Mode of Action

Detailed studies on the phytotoxic activity of sorgoleone demonstrated that its mechanism of action targets the photosynthetic electron transport chain (Czarnota et al., 2001; Rasmussen et al., 1992). Structurally, sorgoleone is similar to plastoquinone (a lipid benzoquinone), resulting in competition with the natural electron acceptor at the plastoquinone binding site on the D1 PSII protein (Fig. 6).

By binding to the D1 protein, sorgoleone is able to block reoxidation of plastoquinone A (Q_{A-}) by plastoquinone B (Q_B) (Gonzalez et al., 1997; Hejl and Koster, 2004). This operating mechanism is identical to that of
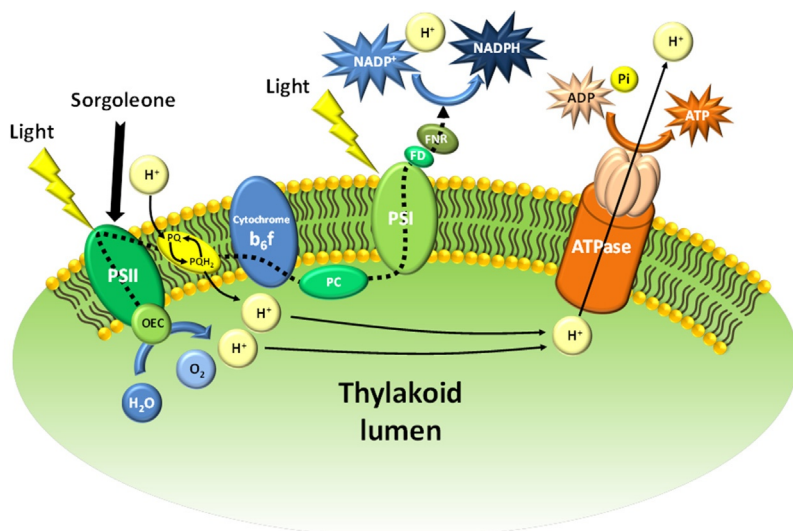

Fig. 6 Schematic of the light reaction of photosynthesis (Z-scheme or Hill reaction) and the location of the binding site of sorgoleone in the D1 protein of photosystem II (PSII). *PC*, plastocyanin; *PQ*, plastoquinone; *PSI*, photosystem I. *Figure adapted from Dayan, F.E., Duke, S.O., 2014. Natural compounds as next-generation herbicides. Plant Physiol. 166 (3) 1090–1105. http://dx.doi.org/10.1104/pp.114.239061.*

atrazine (6–chloro–*N*–ethyl–*N*8–(1-methylethyl)–1,3,5–triazine–2,4–diamine) (Gonzalez et al., 1997; Nimbal et al., 1996b; Streibig et al., 1999). As demonstrated in isolated spinach thylakoids (Nimbal et al., 1996b), sorgoleone is therefore a competitive inhibitor that competes with atrazine for the plastoquinone-binding domain. The authors stated that in the case of atrazine-susceptible redroot pigweed and potato thylakoids, sorgoleone bound to the same Q_B niche of the D1 protein as diuron [3–(3,4-dichlorophenyl)–1,1-dimethylurea] and metribuzin [4–amino–6–(1,1-dimethylethyl)–3–(methylthio)–1,2,4–triazine–5(4*H*)–one]. Nimbal et al. (1996b) did not observe competition for bentazon [3–(methylethyl)–(1*H*)–2,1,3–benzothiadiazin–4(3*H*)–one 2,2–dioxide], another inhibitor of the Hill reaction, which was used as a control. Interestingly, the mutation in the D1 protein imparting resistance to typical triazine inhibitors does not affect the efficacy of sorgoleone on the target site (Dayan et al., 2009c).

An additional mechanism of sorghum phytotoxic activity (Meazza et al., 2002) is the reduction of carotenoid production through inhibition of *p*-hydroxyphenyl pyruvate dioxygenase, a key enzyme in carotenoid synthesis and a target for new herbicide classes. Carotenoid reduction leads to a decreased amount of chlorophyll and subsequent reduced photosynthetic capability. Additionally, sorgoleone lowers the membrane activity of H^+ ATPase, which, in turn, leads to disturbances in water uptake (Hejl and Koster, 2004).

4.2.5 Autotoxicity

In plants that produce phytotoxins, an autotoxicity avoidance mechanism is necessary to prevent internal translocation of potentially toxic root exudates to sensitive parts of the plant (Bertin et al., 2003). Avoidance mechanisms include sequestration, secretion, resistance at the target site, and metabolic inactivation (Dayan and Duke, 2003; Duke et al., 2001). For sorgoleone, rapid, efficient transport and deposition to the outside of root hair cells most likely prevents further transport into more sensitive aboveground plant tissues (Bertin et al., 2003). Furthermore, the high lipophilicity (log*P*) of sorgoleone impedes acropetal translocation via the transpiration stream (Dayan, 2002; Dayan et al., 2009b). Phenolic compounds also necessitate autotoxicity avoidance. To prevent autotoxicity, phenolics are stored in plant cells as inactive esters or glycosides that may be later activated by plant hydrolases (Ben–Hammouda et al., 1995).

5. SCREENING METHODS TO EVALUATE SORGHUM ALLELOPATHIC POTENTIAL

The importance of allelopathy is extremely difficult to test in real eco-systems, causing some authors to question its existence (Hiradate, 2006; Hiradate et al., 2010). Studies on allelopathic properties of plants are poten-tially complicated by interactions including additive, antagonistic, or syner-gistic relationships with other compounds in the soil. Many other factors may also modulate allelopathic potential of a plant, such as growth stage and physiological status, species composition of rhizosphere microorgan-isms, or environmental factors, including moisture, temperature, and pH (Duke, 2015; Inderjit, 2005; Romeo and Weidenhamer, 1999; Wang et al., 2012).

Allelopathy research can be conducted both in field and within con-trolled environments, including laboratory or greenhouse conditions (Falquet et al., 2014). A laboratory bioassay is the first step used to demon-strate the possible existence of allelopathy (Foy, 1999). Preliminary studies should aim to support or refute that a suspected species has allelopathic potential with a rapid, easy to operate, and inexpensive assay (Wu et al., 2001). After preliminary experiments, genotypes with stronger allelopathic potential can be selected for further greenhouse and field studies. This pro-cedure reduces the time, labor, and space needed for an otherwise large screening project.

Another problem in allelopathy research is the extremely challenging task of differentiating the effect of allelopathy from competition for resources (Falquet et al., 2014; He et al., 2012; Inderjit and Del Moral, 1997; Nilsson, 1994; Weidenhamer, 1996). Falquet et al. (2014) instituted a simple, inexpensive allelopathy screening method that provided a means of separating competition for light, nutrients, and water from allelopathic root interactions between a sudex hybrid (donor species) and redroot pigweed (receiver plant). In this method, donor and receiver plants were grown in pots where either roots made contact or were separated by impenetrable bar-riers. The authors also evaluated the effect of shading by the presence or absence of vertical nets between sorghum and redroot pigweed seedlings. With this simple methodology, it was possible to assess the effects of sor-ghum root exudates on acceptor plants regardless of competition. Further-more, activated carbon can be added to the soil to evaluate the contribution of allelochemicals to overall competition between donor and receiver plants.

Activated carbon traps the allelopathic compounds released by donor plants, although it may introduce confounding factors through effects on nutrient availability and plant growth. It is important to consider that the reversal of plant growth inhibition may be a plant response to changes in soil nutrient availability (Lau et al., 2008). Nonetheless, the size of redroot pigweed seedlings grown in the presence of sorghum was dramatically larger when planted in soils amended with activated charcoal than in unamended soils (Fig. 7).

From an ecological standpoint, it is important to select plants species grown in the same ecosystem as the allelopathic plants tested. When conducting a study to evaluate a crop with allelopathic potential for weed control, it is necessary to use relevant weed species as receiver plants (Wu et al., 2000).

5.1 Water Extract From Leaves—Sorgaab

Many studies on sorghum allelopathy have utilized sorgaab water extracts. The term "sorgaab" is the combination of two words: "sorg," derived from "sorghum," and "aab," which means "water" in Urdu (Cheema et al., 2007b). Sorgaab is made from green parts of mature sorghum plants. The extract preparation is easy, inexpensive, and does not require the use of
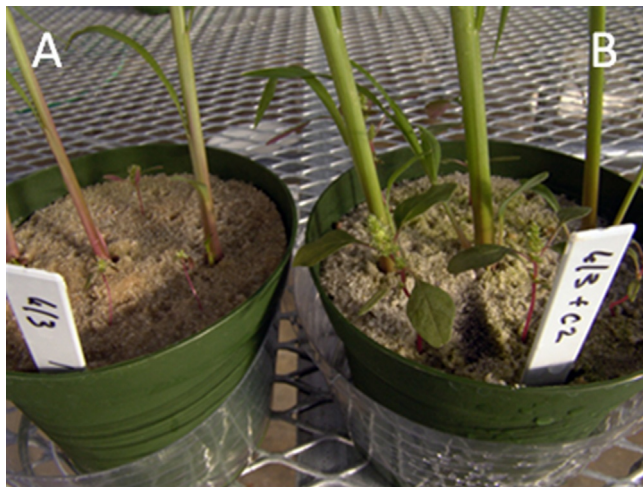

Fig. 7 Effect of activated charcoal on the allelopathic effect of sorghum roots. Notice the difference in size between redroot pigweed seedlings grown in the presence of sorghum (A) in sandy soil and (B) in sandy soils amended with activated carbon.

specialized laboratory equipment. Plant material is first cut into several centimeter-long pieces that are soaked with a specific amount of distilled water for 24 h. After this period, the extract is filtered and then concentrated through boiling. Al-Tavaha and Odat (2010) included a centrifugation step after the first filtration of sorgaab, but this is rarely used in practice.

It should be noted that sorgaab is not likely to contain any sorgoleone since this allelochemical is produced exclusively in roots. This compound is very lipophilic ($\log P = 3.56$) and does not translocate (Dayan et al., 2009b). Therefore, it is unlikely that sorgoleone is present in sorghum leaves and the toxic effect of sorgaab may be associated with the presence of other bioactive secondary metabolites.

The effect of sorgaab on weed species can be assessed under both controlled and field conditions. In the laboratory, the effect of sorghum extract on germination and early phases of weed development can be tested in Petri dishes (Al-Tavaha and Odat, 2010; Randhawa et al., 2002; Yarnia et al., 2009). The experiments can also be carried out in phytotrons or greenhouses, where seed of the receiver plant weeds species is germinated in pots and watered with solutions containing sorgaab (Al-Bedairy et al., 2013; Cheema et al., 2007a). Biometric parameters such as germination, shoot, root and seedling length, and dry mass are measured and compared to a control (i.e., seedlings exposed to water). One of the limitations of this method is the influence of the osmotic potential of sorgaab, since a concentrated extract promotes plant water loss rather than uptake. Seed density and size may also affect the potency of natural phytotoxins (Weidenhamer et al., 1987).

The efficiency of foliar applications of sorgaab to manage weeds in field crops (e.g., corn or wheat) can be evaluated by measuring weed density, fresh and dry mass, and quantitative aspects of crop yield. These results are compared to the level of weed infestation reduction obtained by mechanical weed control or herbicide application. Economic analysis of such studies provides an indication of the potential profitability of sorgaab use.

In another type of study, sorghum residues rather than sorgaab are incorporated into the soil or used as a mulch to evaluate allelopathic effects on weed and crop growth (Correia et al., 2005b; Lahmod and Alsaadawi, 2014). In container experiments, sorghum residues can be mixed into soil in a powder form or as chopped pieces (Ayeni and Kayode, 2013a,b; Khaliq et al., 2011a,b). In field trials, sorghum residues are incorporated into the soil by tilling twice with a disc plow (Alsaadawi et al., 2013). Several

authors have also studied the allelopathic potential of sorghum to control weeds by intercropping sorghum with a main crop (Kandhro et al., 2014; Khalil et al., 2010; Mahmood et al., 2013a).

5.2 Analytical Approaches to Study Allelopathy

As mentioned above, it is difficult to quantify the allelopathic potential of a plant. To validate the role of allelopathy, it is necessary to isolate metabolites from plants tissues and purify the extracts until the structure of a putative allelochemical can be determined. According to Duke (2015), there are two fundamental approaches to detecting allelochemicals: (1) identifying known compounds in crude plant extracts or (2) using bioassay-guided isolation of unknown phytotoxins. The second strategy is scientifically more appropriate. With this method, the tissues or exudates of the potentially allelopathic plant must first be extracted to obtain a crude extract with the highest level of phytotoxic activity. These extracts are then fractionated with solvents of varying polarity. In the case of sorghum, sorgoleone may be extracted with organic solvents such as methanol, chloroform, ethanol (Dayan et al., 2009b; Uddin et al., 2010a) or methylene chloride and 1% acetic acid (Netzly and Butler, 1986). According to Uddin et al. (2010a), methanol provides the greatest sorgoleone recovery. After extraction, the allelopathic potential of separated fractions is evaluated with the use of a rapid bioassay, and finally, active fractions can be further fractionated by additional chromatographic methods (Cheema et al., 2007a; Czarnota et al., 2001; Duke, 2015) and structures can be determined by high-resolution mass spectrometry, proton and carbon NMR, and other advanced methods (Lang et al., 2008; Reid and Sarker, 2012).

Studies at the biochemical level are useful tools for determining the effect of allelochemicals on crucial processes in cells of acceptor plants (Dayan et al., 2000). Such experiments can be conducted using isolated mitochondria and chloroplasts from the etiolated seedlings or leaf discs of receiver plants (Einhellig et al., 1993; Rasmussen et al., 1992; Uddin et al., 2012). A very dynamic, highly promising approach for evaluating allelochemical effects is the combination of molecular and genomic studies, which enables metabolic pathway description through the identification and characterization of all the enzyme-encoding genes involved in biosynthesis (Ju et al., 2014). This approach has successfully been used to study the genes and enzymes involved in the biosynthesis of sorgoleone (Cook et al., 2010).

Detailed cultivar characterization and variability at the molecular level for allelochemical synthesis could contribute to the selection of top, allelopathic lines in breeding programs that may be useful in weed control (Dos Santos et al., 2014; Wu et al., 2001). Before breeding programs can develop sorghum cultivars with increased allelopathic potential, more screening work needs to be accomplished (Wu et al., 2001). Promising results are apparent in rice, where germplasm with higher allelopathic potential than current commercial lines has been developed (Gealy and Yan, 2012; Gealy et al., 2013).

6. APPLICATION OF THE ALLELOPATHIC PROPERTIES OF SORGHUM IN AGRICULTURE

The allelopathic potential of sorghum toward weed species has been extensively studied (Table 1). Although early studies were carried out in laboratory or greenhouse environments, more recent research has been conducted in-field. In-field experiments are particularly valuable, as they shed light on practical allelopathic interactions and their consequences in agroecosystems. Weed repression potential of sorghum has been investigated through (1) foliar application of sorgaab (sorghum water extract), (2) crop rotation systems including sorghum, (3) cultivation of sorghum as cover or intercrops, (4) incorporation of sorghum residues into soil, and (5) development of sorghum-derived alleloherbicides (Alsaadawi and Dayan, 2009; Farooq et al., 2013).

6.1 Sorghum Water Extract

6.1.1 Laboratory Tests of Sorgaab Effectiveness

Allelopathic potential of sorghum extract, sorgaab, varies between developmental stages of both sorghum and weed plants. Typically, sorgaab has the greatest impact on early plant growth stages. For example, extract derived from young, vegetative sorghum plants exhibited greatest growth inhibition on seedlings of redroot pigweed and wild barley (*Hordeum spontaneum* K. Koch) rather than full-grown plants (Al-Tavaha and Odat, 2010; Yarnia et al., 2009). Sorgaab application ($1 \, g/20 \, mL^{-1}$ of distilled water) in another study indicated a 15%–20% germination reduction of desert horse purslane (*Trianthema portulacastrum* L.), a persistent weed that infests cotton (*Gossypium* L.), corn (*Zea mays* L.), and sugar cane (*Saccharum officinarum* L.) in tropical and subtropical regions (Randhawa et al., 2002). Investigations using similar concentrations of sorgaab also revealed shoot length and dry

Table 1 Summary of Weed Species With Growth Inhibition in the Presence of Sorghum or Sorghum-Derived Products

Weed Species	Common Name	Weed Bayer Code	Literature
Abutilon theophrasti Medik.	Velvetleaf	ABUTH	Czarnota et al. (2001), Hoffman et al. (1996)
Aeschynomene indica L.	Indian jointvetch	AESIN	Uddin et al. (2012, 2013a)
Amaranthus hybridus L.	Smooth pigweed	AMACH	Correia et al. (2005b), Hoffman et al. (1996)
Amaranthus palmeri S.Wats.	Palmer amaranth	AMAPA	Burgos and Talbert (1996)
Amaranthus retroflexus L.	Redroot pigweed	AMARE	Alsaadawi et al. (1986), Correia et al. (2005b), Czarnota et al. (2001), Einhellig and Rasmussen (1989), Falquet et al. (2014), Marchi et al. (2008), Uddin et al. (2012), Won et al. (2013), Yarnia et al. (2009)
Amaranthus spinosus L.	Spiny amaranth	AMASP	Correia et al. (2005b), Erasmo et al. (2004)
Ammi majus L.	Bishop's weed	AMIMA	Alsaadawi et al. (2013)
Anagallis arvensis L.	Scarlet pimpernel	ANGAR	Ahmad et al. (1991), Cheema et al. (2004), Ashraf and Akhlaq (2007)
Alternanthera tenella			Correia et al. (2005b)
Avena fatua L.	Wild oat	AVEFA	Alsaadawi et al. (2013), Jamil et al. (2005b, 2009), Mahmood et al. (2015a), Mushtaq et al. (2010b), Sharif et al. (2005)
Beta maritima L.	Sea beet		Alsaadawi et al. (2007)
Beta vulgaris L.	Beet		Alsaadawi et al. (2013)
Bidens pilosa L.	Hairy beggarticks	BIDPI	Trezzi and Vidal (2004)

Continued

Table 1 Summary of Weed Species With Growth Inhibition in the Presence of Sorghum or Sorghum-Derived Products—cont'd

Weed Species	Common Name	Weed Bayer Code	Literature
Brachiaria plantaginea (Link) Hitchc.	Alexander grass		Trezzi and Vidal (2004)
Carthamus oxyacantha Bieb.	Wild safflower	CAUOX	Alsaadawi et al. (2007, 2013)
Cenchrus echinatus L.	Southern sandbur	CCHEC	Dos Santos et al. (2014)
Cercis canadensis L.	Eastern redbud		Geneve and Weston (1988)
Chenopodium album L.	Lambsquarter	CHEAL	Ahmad et al. (1991), Alsaadawi et al. (2007), Cheema et al. (1997, 2004), Czarnota et al. (2001), Hussain et al. (2014), Jabran et al. (2008, 2010a), Mahmood et al. (2015a), Shah et al. (2016), Sharif et al. (2005)
Chromolaena odoratum (L.) King & H.E. Robins.	Siam weed		Ayeni and Kayode (2011)
Commelina benghalensis L.	Benghal dayflower	COMBE	Correia et al. (2005b)
Convolvulus arvensis L.	Field bindweed	CONAR	Ahmad et al. (1991), Awan et al. (2012), Cheema et al. (2000a), Hussain et al. (2014), Khalil et al. (2010), Mahmood et al. (2015b)
Coronopus didymus (L.) Sm.	Lesser swine-cress	COPDI	Ahmad et al. (1991), Bhatti et al. (2000), Cheema et al. (1997, 2004), Jabran et al. (2008, 2010a), Mahmood et al. (2015a), Razzaq et al. (2010, 2012), Shah et al., 2016
Cynodon dactylon (L.) Pers.	Bermudagrass	CYNDA	Dos Santos et al. (2014); Khaliq et al. (1999), Mahmood et al. (2015b)

Table 1 Summary of Weed Species With Growth Inhibition in the Presence of Sorghum or Sorghum-Derived Products—cont'd

Weed Species	Common Name	Weed Bayer Code	Literature
Cyperus eragrostis Lam.	Tall flatsedge	CYER[a]	Rehman et al. (2010)
Cyperus iria L.	Rice flatsedge	CYPIR	Burgos and Talbert (1996), Khaliq et al. (2013a), Rehman et al. (2013)
Cyperus rotundus L.	Purple nutsedge	CYPRO	Ahmad et al. (1991, 1995), Bhatti et al. (2000), Cheema et al. (1997, 2000a, 2005b, 2009), Ihsan et al. (2015), Iqbal et al. (2009), Iqbal and Cheema (2007, 2008), Jabran et al. (2008, 2010a), Khalil et al. (2010), Khaliq et al. (2013a), Mahmood and Cheema, 2004, Mahmood et al. (,2013a, 2015b), Sharif et al. (2005)
Dactyloctenium aegyptium L.	Egyptian crowfootgrass	DTTAE	Mahmood et al. (2015b), Mubeen et al. (2012), Khaliq et al. (1999), Rehman et al. (2010)
Daucus carota L.	Wild carrot	DAUCA	Alsaadawi et al. (2013)
Digitaria sanguinalis L.	Large crabgrass	DIGSA	Nimbal et al. (1996a), Uddin et al. (2012)
Echinochloa colona L.	Junglerice	ECHCO	Cheema et al. (2005b, 2010), Khaliq et al. (2011a, 2013a), Kim et al. (1993), Mahmood et al. (2015b)
Echinochloa crus-galli (L.) P. Beauv.	Barnyardgrass	ECHCG	Cheema et al. (2005b, 2010), Dilipkumar and Chuah (2013), Irshad and Cheema (2005), Khaliq et al. (2013a), Rehman et al. (2010, 2013), Uddin et al. (2012), Weston et al. (1989), Won et al. (2013)

Table 1 Summary of Weed Species With Growth Inhibition in the Presence of Sorghum or Sorghum-Derived Products—cont'd

Weed Species	Common Name	Weed Bayer Code	Literature
Eclipta alba L.	False daisy	ECLAL	Uddin et al. (2012)
Eleusine indica (L.) Gaertn.	Goosegrass	ELEIN	Mahmood et al. (2015b), Mubeen et al. (2012)
Eriochloa acuminata (J. Presl) Kunth.	Southwestern cupgrass	ERBGR	Burgos and Talbert (1996)
Euphorbia dracunculoides Lam	Dragon spurge		Khaliq et al. (2012)
Euphorbia heterophylla L.	Wild poinsettia	EPHHL	Ayeni and Kayode (2013a, b), De Almeida Barbosa et al. (2001)
Fumaria indica L.	Lambsquarter fumitory		Ashraf and Akhlaq (2007), Awan et al. (2012), Hussain et al. (2014), Sharif et al. (2005)
Fumaria parviflora Lam.	Fineleaf fumitory	FUPA[a]	Cheema et al. (1997)
Galium aparine L.	Catchweed bedstraw	GALAP	Cheema et al. (2003a)
Galium spurium L.	False cleavers	GALSP	Uddin et al. (2012, 2013a)
Hordeum spontaneum K. Koch	Wild barley		Al-Tavaha and Odat (2010)
Hyptis lophanta Mart. ex Benth			Erasmo et al. (2004)
Ipomoea grandifolia (Dammer) O'Donell	Pink convolvulus		Correia et al. (2005b)
Leonotis nepetifolia (L.) R.Br.	Klip dagga	LEONE	Correia et al. (2005b)
Lolium rigidum Gaud.	Rigid ryegrass	LOLRI	Alsaadawi et al. (2007)
Lolium temulentum L.	Poison ryegrass	LOLTE	Alsaadawi et al. (2007, 2013)
Malva parviflora L.	Little mallow	MALPA	Alsaadawi et al. (2007)
Melilotus indicus (L.) All.	Indian sweet clover	MEUIN	Alsaadawi et al. (2007)

Table 1 Summary of Weed Species With Growth Inhibition in the Presence of Sorghum or Sorghum-Derived Products—cont'd

Weed Species	Common Name	Weed Bayer Code	Literature
Nicandra physalodes (L.) Gaertn.	Apple–of–Peru	NICPH	Correia et al. (2005b)
Parthenium hysterophorus L.	Congress grass	PTNHY	Javaid et al. (2006)
Phalaris minor Retz.	Littleseed canarygrass	PHAMI	Ahmad et al. (1991), Alsaadawi et al. (2013), Awan et al. (2012), Cheema et al. (1997, 2004), Jamil et al. (2005b, 2009), Mahmood et al. (2015a), Mushtaq et al. (2010b), Razzaq et al. (2010, 2012)
Plantago asiatica L.	Chinese plantain		Uddin et al. (2012, 2014)
Plantago ovata Forssk.	Blond plantain		Alsaadawi et al. (2007)
Polygonum bellardii All.	Narrowleaf knotweed		Cheema et al. (2004)
Polypogon monspeliensis (L.) Desf.	Rabbitfoot polypogon	POHMO	Alsaadawi et al. (2007)
Portulaca oleracea L.	Common purslane	POROL	Cheema et al. (2000a)
Rumex dentatus L.	Toothed dock	RUDE3[a]	Ahmad et al. (1991), Bhatti et al. (2000), Cheema et al. (1997, 2004), Mahmood et al. (2015b)
Rumex japonicus Houtt.			Uddin et al. (2012, 2013a, 2014)
Senecio vulgaris L.	Common groundsel	SENVU	Nimbal et al. (1996a)
Setaria italica (L.) Beauv.	Foxtail millet	SETIT	Weston et al. (1989)
Setaria viridis (L.) P. Beauv.	Green foxtail	SETVI	Bhatti et al. (2000), Hoffman et al. (1996)
Sida rhombifolia L.	Arrowleaf sida	SIDRH	Trezzi and Vidal (2004)

Continued

Table 1 Summary of Weed Species With Growth Inhibition in the Presence of Sorghum or Sorghum-Derived Products—cont'd

Weed Species	Common Name	Weed Bayer Code	Literature
Silybum marianum (L.) Gaertn.	Blessed milkthistle	SLYMA	Alsaadawi et al. (2007)
Sinapis arvensis L.	Wild mustard	SINAR	Urbano et al. (2006)
Solanum nigrum L.	Black nightshade	SOLNI	Czarnota et al. (2001), Nimbal et al. (1996a)
Trianthema portulacastrum L.	Horse purslane	TRTPO	Cheema et al. (2002a, 2003a, 2007a, 2010), Ihsan et al. (2015), Jabran et al. (2008, 2010a), Khalil et al. (2010), Khaliq et al. (2011b, 2013a), Khan et al. (2012a), Mahmood et al. (2010, 2015b), Mubeen et al. (2012), Mushtaq et al. (2010a), Randhawa et al. (2002)
Trifolium repens L.	White clover	TRFRE	Alsaadawi et al. (2007)

[a]US code is used when Bayer Weed Code is not available.

weight suppression of purple nutsedge (*Cyperus rotundus* L.) by 75% over a control (Cheema et al., 2009), as well as congress grass (*Parthenium hysterophorus* L.) and junglerice (*Echinochloa colona* L.) (Javaid et al., 2006; Kim et al., 1993).

In addition to developmental stage, sorgaab allelopathic potential may differ between sorghum cultivars. A survey of water extract allelopathic potential from nine grain sorghum cultivars on desert horse purslane growth reported that J2001 and Kashmor cultivars completely inhibited weed germination, while other cultivars partially inhibited germination (Cheema et al., 2007a). The survey authors speculated that extracts from the J-263 cultivar had the greatest effect on desert horse purslane seedling dry weight (99% reduction over control) due to a higher content of *p*-hydroxybenzoic and *p*-coumaric acids compared to other tested cultivars. Another study implicated that extracts from Jabbal, Hegari, and Sindhar cultivars were most potent to horse purslane. Nonetheless, correlations between sorgaab activity

and the presence of *p*-hydroxybenzoic and *p*-coumaric acids have been demonstrated (Chung et al., 2002).

6.1.2 Field Tests of Sorgaab Effectiveness

Field trials substantiate sorgaab allelopathy manifested in controlled environments. In several trials, two sequential sprays of 10% sorgaab solutions reduced weed populations and biomass while resulting in 21% wheat (*Triticum* L.) yield increases (Anwar et al., 2003; Cheema and Khaliq, 2000; Cheema et al., 2000b). The allelopathic effect of sorgaab was tested on eight plant species: eucalyptus (*Eucalyptus camaldulensis* Dehnh), acacia (*Acacia nilotica* L. Willd. ex Delile), poplar (*Populus deltoides* W. Bartram ex H. Marshall), sheesham (*Dalbergia sissoo* Roxb.), sunflower, tobacco (*Nicotiana tobacum* L.) congress grass, and wheat (Khan et al., 2015). Weed suppression expressed as a reduction of dry biomass (62%) through repeated application of sorgaab. Ashraf and Akhlaq (2007) also highlighted the herbicidal ability of sorgaab in wheat via a decrease in weed density, fresh weight, and dry weight by 29%, 31%, and 27% compared to a control, respectively. Furthermore, double spraying of both sorghum stem and sorghum stem plus leaf extracts led to wheat yield increases by 8% and 19%, yet caused substantial growth inhibition of the following weeds species: pimpernel (*Anagallis arvensis* L.), lambsquarter fumitory (*Fumaria indica* L.), and bur clover (*Medicago polymorpha* L.). In corn, sorgaab foliar sprays reduced weed infestation in one instance by 18%–50% and increased corn yield by 11%–44%, where the most economically effective weed control method was a triple spray with sorgaab (Cheema et al., 2004). Furthermore, a triple spray with sorgaab (at 1:10 volume concentration) applied to rice (*Oryza sativa* L.) reduced weed biomass by 45%–85%, while the application of solely pendimethalin reduced weed biomass by 45% relative to a control (Cheema et al., 2004). Sorgaab application was also reported to increase rice yields (Bhatti et al., 2000). The efficiency of sorgaab to manage weeds in lentil (*Lens culinaris* Medikus) was revealed in another study because of reduced weed dry biomass of 66% and increased lentil yields of 61% (Hozayn et al., 2011).

6.1.3 Effectiveness of Mixtures Containing Extracts From Sorghum and Other Allelopathic Plants

Duke et al. (2000) suggested that mixing two or more water extracts enhances weed control efficacy due to an increased number of allelochemicals. This concept was verified several times with sorgaab mixes

(Khaliq et al., 2012; Mahmood et al., 2010; Mubeen et al., 2012; Mushtaq et al., 2010a). In a corn study, a blend of sorghum and moringa (*Moringa oleifera* Lam.) extracts resulted in a 35% increase in yield associated with greater control of the weed population compared to sorgaab alone (Kamran et al., 2016; Khan et al., 2012b). Similarly, combined application of sunflower and sorghum extract sprayed at $6 \, L \, ha^{-1}$ had the greatest negative impact on wild oat and littleseed canarygrass in wheat field trials (Jamil et al., 2009). Such benefits were also observed in other trials with combinations of sorghum, brassica, and sunflower extracts, where double applications of concentrated extracts of all three species at 45 and 75 days after sowing provided optimum weed control and the greatest wheat yield (Awan et al., 2012). When compared to conventional herbicide treatments (i.e., iodosulfuron plus mesosulfuron), double foliar sprays of sorghum, sunflower, and brassica extract combinations at $18 \, L \, ha^{-1}$ provided economical herbicide alternatives that resulted in 48%–58% weed reduction in a wheat production system (Mahmood et al., 2015a).

6.1.4 Sorghum Extracts Combined With Reduced Doses of Herbicides for Weed Control in Cereal Crops

An interesting potential application of allelopathy is the use of allelopathic plant extracts in combination with reduced doses of conventional herbicides to achieve similar levels of weed control equivalent to full rates of conventional herbicides. This application may enable production cost reductions, yield increases, and agricultural sustainability improvements. Reduced herbicide doses with allelopathic rice species extracts or sorgaab have demonstrated weed control success in cereal crop trials (Gealy and Yan, 2012; Gealy et al., 2013). In one study, the efficacy of a combination of sorgaab ($20 \, L \, ha^{-1}$ each) and a 50% field rate of iodosulfuron plus mesosulfuron was assessed using conventional, reduced, and zero tillage soil management practices for wheat (Khaliq et al., 2013b). The combination weed management approach was very effective, especially in conjunction with zero tillage, providing up to 90% weed suppression and between 52% and 63% yield gains. Similar results were obtained in another study by integrating sorgaab (in ratio 2:10 w/w) with half the recommended dose of cereal herbicides (e.g., bromoxinil + MCPA, fenoxaprop-*p*-ethyl, and carfentrazone-ethyl ester) (Shahid et al., 2007). Further yet, an evaluation of sorghum, sunflower, and mulberry leaf extracts ($18 \, L \, ha^{-1}$ each) in combination with half the recommended field rate of iodosulfuron plus mesosulfuron provided an 86% reduction in weed populations and an 88% reduction in weed dry mass

(Mahmood et al., 2013b), comparable to results of sorghum and sunflower extracts combined with 75% of the recommended field rate of iodosulfuron plus mesosulfuron in another trial (Hussain et al., 2014). There are many more reports in the literature documenting the promising use of allelopathic extracts in combination with reduced rates of conventional herbicides in cereal crops, and readers are encouraged to read the following articles: Cheema et al. (2003a, 2005b, 2010), Elahi et al. (2011), Irshad and Cheema (2005), Jamil et al. (2005a), Mahmood et al. (2015b), Mushtaq et al. (2010b), Razzaq et al. (2010), Rehman et al. (2010, 2013), and Sharif et al. (2005).

6.1.5 Sorghum Extracts Combined With Reduced Doses of Herbicides for Weed Control in Noncereal Crops

Trials applying the same principles as in Section 6.1.4 have been performed in noncereal crops. For rapeseed, sorgaab mixed with pendimethalin (400 and $600 \, g \, ha^{-1}$), sunflower, rapeseed, or rice extract provided better weed control compared to $1200 \, g \, ha^{-1}$ herbicide alone in one field study, particularly for purple nutsedge control (Jabran et al., 2008). Sorgaab combinations have also demonstrated effectiveness for weed control in several cotton studies. Triple spray mixtures of concentrated sorgaab ($12 \, L \, ha^{-1}$) with pendimethalin, S-metolachlor, or trifluralin provided excellent weed control and netted the highest profit in one example (Cheema et al., 2002b). Other cotton studies have shown that the rate of pendimethalin can be reduced by half ($625 \, g \, ha^{-1}$) to maintain weed control if combined with sorgaab ($12 \, L \, ha^{-1}$) (Cheema et al., 2003b, 2005a), and that increasing sorgaab dosage from 12 to $15 \, L \, ha^{-1}$ enables reduction of S-metolachlor application to one-third of the recommended rate while still providing control of weeds such as purple nutsedge (Iqbal and Cheema, 2008). Further research in cotton has also indicated effective, economic weed control using sorgaab in combination with sunflower or rapeseed extract (15 and $18 \, L \, ha^{-1}$) and glyphosate, as well as conventional herbicide reduction of up to 75% to decrease production costs while maintaining satisfactory weed control and crop yield (Iqbal et al., 2009). In sunflower production, three foliar applications of sorgaab ($15 \, L \, ha^{-1}$) combined with one-third the recommended dose of S-metolachlor ($1.6 \, L \, ha^{-1}$) in one trial imparted 93.7% weed suppression and superior sunflower yield compared to extract or herbicide alone (Shah et al., 2016). Research of sorgaab and herbicide mixtures in noncereal crops suggests that allelopathic extracts are able to reduce conventional herbicide load by two-thirds while maintaining effective weed control.

6.2 Sorghum in Crop Rotation Systems

Allelopathic plants can be used directly in various cropping systems, including intercropping, cover cropping, crop rotation, and minimum to no tillage systems. These approaches were suggested decades ago (Hussain and Gadoon, 1981) and supported by early allelopathy research that revealed agroecosystem benefits (Leather, 1983). The interaction between crop plant density and allelopathic potential has also been studied and documented by several investigators (Al-Bedairy et al., 2013; Chunjie et al., 2010; Seal et al., 2004). Sorghum cultivated as a forecrop, follow crop, or intercrop should be considered a highly beneficial, allelopathic element of a crop rotation system. In early research, an accumulation of sorghum allelochemicals in soil following sorghum production appeared to provide residual activity that suppressed weed development (Geneve and Weston, 1988). Crop rotation systems that consisted of sorghum, corn, and soybean (*Glycine max* (L.) Merr.) exhibited reduced weed infestation, whereas soybean and corn rotations excluding sorghum had lower weed suppression (Einhellig and Leather, 1988). Sudex, a sorghum-sudangrass hybrid, has been shown to inhibit the growth of Palmer amaranth (*Amaranthus palmeri* S. Wats.), rice flatsegde, and southwestern cupgrass (*Eriochloa acuminata* (J. Presl) Kunth.) in no-till alfalfa (*Medicago sativa* L.) (Forney et al., 1985) and southern pea studies (Burgos and Talbert, 1996), during which increased sorghum plant density was positively correlated to root exudate concentration and weed suppression. Root exudate potency may vary by cultivar.

6.3 Intercropping With Sorghum

Intercropping is a common practice used by farmers in developing countries since it boosts crop yield while reducing soil erosion (Altieri et al., 1983). Another benefit of this system is the suppression of weeds (Liebman and Dyck, 1993) to achieve integrated weed management (Baumann et al., 2000; Schoofs and Entz, 2000). Sorghum is commonly used in intercropping systems due to allelopathic characteristics (Kondap et al., 1990; Sistachs et al., 1991). When intercropped with corn in one trial, sorghum provided suitable management of purple nutsedge (Mahmood et al., 2013a). In fact, one examination of intercropping systems revealed that sorghum had better weed control performance for purple nutsedge, field bindweed, and desert horse purslane than other systems, including other allelopathic crops, such as sunflower and mung bean (Khalil et al., 2010). Sorghum control of purple nutsedge was also confirmed in an intercropping system with cotton,

resulting in 87%–95% reduction in weed density and 88%–96% reduction in dry biomass (Iqbal and Cheema, 2007). However, sorghum has also been cited to cause a 22% reduction in cottonseed yield, though greater total economic returns were achieved than those of untreated controls. According to Kandhro et al. (2014), intercropping sunflower and sorghum in cotton is an economic, efficient, and environmentally friendly method of weed control that resulted in greater profits than conventional chemical weed control with $2.5\,L\,ha^{-1}$ metolachlor.

6.4 Sorghum as a Cover Crop

The incorporation of cover crops and green manures to field crop cultivation has an overall positive effect in the agroecosystem by reducing soil erosion, enriching soils with organic matter, improving soil moisture retention, and smothering weeds (Altieri et al., 2011; Hartwig, 1988; Hartwig and Ammon, 2002). Consequently, the allelopathic potential of sorghum makes it an effective cover crop. Putnam and DeFrank (1983) identified a negative influence of sweet sorghum, sudangrass, and sudex on the growth of weeds in cherry and apple tree orchards with 40% reduced weed biomass from sorghum planted in fall and 85%–90% reduced weed biomass from spring plantings (Putnam and DeFrank, 1983). A covercropping survey of 10 sorghum genotypes for impacts on lambsquarter, white clover (*Trifolium repens* L.), sea beet (*Beta maritima* L.), and little mallow (*Malva parviflora* L.) determined that 3 genotypes (Giza 15, Giza 115, Enkath) enabled weed biomass reduction and density by 58%–66% and 59%–67%, respectively (Alsaadawi et al., 2007). Sorghum and sudangrass are excellent cover crops for weed management in barley as evidenced by their significant inhibitory effect on weed density and biomass, particularly for wild mustard (*Sinapis arvensis* L.), while sustaining high barley grain yield (Urbano et al., 2006). Similar suppression of Canada thistle (*Cirsium arvense* (L.) Scop.) by sudangrass has also been reported (Bicksler and Masiunas, 2009). Green manure of sorghum hybrid BR304 has been shown to reduce dry biomass of spiny amaranth (*A. spinosus* L.) and *Hyptis lophanta* Mart. ex Benth, an invasive weed common in Central Brazil, as well (Erasmo et al., 2004).

Unfortunately, weed suppression of allelopathic plants may have some drawbacks, specifically crop injury on certain incompatible species. For example, one field study concluded that sudex used as a cover crop negatively affected cabbage (*Brassica oleracea* L. var. *capitata* L.) production (Finney et al., 2009). Nonetheless, under proper conditions and with

compatible species, the incorporation of allelopathic crop mulches or residues into soil may enhance agricultural sustainability by suppressing weed growth and thereby reducing herbicide use (Nagabhushana et al., 2001).

6.5 Sorghum Crop Residues

A portion of allelopathy phenomenon may be the result of plant residue decomposition that gradually releases phytotoxic substances to the environment. In early allelopathy research, Putnam and DeFrank (1983) noted the high efficiency of sorghum mulch in reducing weed infestation. Sorghum residue provides selective weed management through physical presence on the soil surface as well as phytotoxin release (Inderjit and Keating, 1999). As a consequence of $1.3\,t\,ha^{-1}$ sorghum straw application, Trezzi and Vidal (2004) observed 50% reduction of Alexander grass (*Brachiaria plantaginea* (Link) Hitchc.) and arrowleaf sida (*Sida rhombifolia* L.) density. Application of $4\,t\,ha^{-1}$ of sorghum straw reduced Alexander grass, arrowleaf sida, and hairy beggarticks (*Bidens pilosa* L.) infestations by 91%, 96%, and 59%, respectively. In another study, sorghum residues incorporated into soil or used as mulch strongly inhibited purple nutsedge growth, although residue incorporated into soil was most active within the first 20 days and mulch was most active 40 days after mulching (DAM). By 40 DAM, equal application rates of sorghum residue or mulch ($15\,t\,ha^{-1}$) reduced purple nutsedge density and dry mass by 40% and 50% or 45% and 53%, respectively (Mahmood and Cheema, 2004). A study examining the early growth phases of wild poinsettia (*Euphorbia heterophylla* L.) also implicated growth inhibition through powdered sorghum stem residue (Ayeni and Kayode, 2013a,b).

Multiple wheat field trials corroborate sorghum residue weed inhibition studies. In an irrigated wheat crop system, sorghum residues inhibited development of lambsquarter, littleseed canarygrass, purple nutsedge, lesser swinecress, toothed dock (*Rumex dentatus* L.), pimpernel (*Anagallis arvensis* L.), and field bindweed (Ahmad et al., 1991). Similarly, incorporation of $2–6\,t\,ha^{-1}$ mature sorghum plant residue enabled weed infestation reductions of 40%–50% and wheat yield increases of up to 15% in one wheat production system (Cheema and Khaliq, 2000), as well as complete purple nutsedge growth inhibition in another (Cheema et al., 2009). Field trials of crops other than wheat with sorghum residue applications have also been conducted. In a mung bean trial, utilization of 10 and $15\,t\,ha^{-1}$ of sorghum mulch reduced weed infestation by 25% and 27%, respectively, with simultaneous crop yield increases of 19.7% and 13% in comparison to a control

group (Cheema and Khaliq, 2000). Soil incorporation of the same application of chopped mature, sorghum plants reduced weed infestation by 26% and 37% and increased yields by 36% and 40% in a comparable corn field trial (Cheema et al., 2004).

As mentioned in Section 6.1 with sorgaab, combining sorghum residue with other allelopathic crops or reduced doses of conventional herbicides may achieve weed control similar to or better than full rates of conventional herbicides. Khaliq et al. (2011a) indicated growth suppression of junglerice by sorghum residues in a pot study through delayed germination plus decreased root and shoot dry biomass, which was enhanced with combinations of sorghum, sunflower, and brassica allelopathic residues in equal amounts. Similar combination trials were carried out to evaluate the impact of allelopathic residues on germination dynamics and early growth stages of horse purslane seedlings, demonstrating that combined allelopathic crops residues ($6\,g\,kg^{-1}$ of soil; $12\,t\,ha^{-1}$) increased horse purslane seedling suppression (Khaliq et al., 2011b). In field bean (*Vicia faba* L.) cultivation, Alsaadawi et al. (2013) found that the incorporation of $7.6\,t\,ha^{-1}$ of crop residue into soil and the application of half a typical field dose of trifluralin resulted in greater reduction of weed dry mass than a full dose. A subsequent study of the same amount of sorghum residue with a half dose of iodosulfuron and mesosulfuron resulted in phytotoxicity and decreased wheat yield; however, reducing sorghum residue to $3.5\,t\,ha^{-1}$ combined with the same herbicides and application rates provided the greatest wheat yield (Lahmod and Alsaadawi, 2014). The authors suggested that blended methods of weed control (allelopathic crop residue and reduced rates of conventional herbicides) improved both physiochemical and biological properties of soil. Weed population densities of klip dagga (*Leonotis nepetifolia* (L.) R.Br.), *Alternanthera tenella*, pink convolvulus (*Ipomoea grandifolia* (Dammer) O'Donell), Benghal dayflower (*Commelina benghalensis* L.), apple of Peru (*Nicandra physalodes* (L.) Gaertn.), smooth pigweed (*Amaranthus hybridus* L.), redroot pigweed, and spiny amaranth were also reduced by sorghum mulch in combination with reduced rates of imazamox in a soybean field trial (Correia et al., 2005b).

6.6 Sorgoleone as the Precursor for the Development of Alleloherbicide

6.6.1 Efficiency of Sorgoleone in Laboratory Settings

Weeds that produce small seeds tend to be more sensitive to the phytotoxic influence of sorgoleone (De Souza et al., 1999; Einhellig and de Souza,

1992; Peterson et al., 2001). Contrastingly, larger seeded weeds tend to grow faster during early development, enabling their root systems to grow beyond the sorghum rhizosphere and consequently facilitate lower susceptibility to sorghum allelochemicals (Bertin et al., 2003; Leishman et al., 2000). Resistance may also result from lower levels of sorgoleone absorbtion and translocation or faster metabolic degradation (De Almeida Barbosa et al., 2001; Rimando et al., 1998). With ^{14}C-labeled sorgoleone in velvetleaf (*Abutilon theophrasti* Medik.), sorgoleone photosynthesis inhibition was shown to be limited to developing plants in a laboratory environment (Dayan et al., 2009b). Sorgoleone deposition period, decomposition rate, and biotransformation in soil may be applied to evaluate the environmental risks connected with using sorgoleone as an herbicide. In another experiment with ^{14}C-labeled sorgoleone, evaluation of the rate of sorgoleone mineralization in four soil types, including two originating from the United States and two from Denmark, demonstrated that the methoxy group (Fig. 3) decomposed the fastest at a rate of up to 26% during the first 48 h after soil incorporation (Gimsing et al., 2009); other parts of sorgoleone, including the ring and lipophilic tail, degraded slower. The varied rate of functional group decomposition in sorgoleone molecules is recognized as one of the crucial properties for its herbicidal potential. The mineralization of the methoxy group may be associated with reduced allelopathic activity, whereas degradation of the ring or tail renders the molecule inactive. Increased intensity of the mineralization process in soil samples from the United States resulted from the presence of microorganisms that used sorgoleone as a source of energy.

Einhellig and Rasmussen (1989) indicated a higher sensitivity of broadleaf compared to grass weed species to the allelopathic effect of grain sorghum introduced in a crop rotation system. Hydroponic tests suggested that sorgoleone is phytotoxic at concentrations lower than 10 μM, and that grasses are typically more tolerant to this secondary metabolite than broadleaf species (Einhellig and de Souza, 1992; Nimbal et al., 1996a). Further studies indicate that broadleaf seedling growth may be inhibited by as much as 70%–80% (Uddin et al., 2009). These conclusions are supported by more recent greenhouse research examining the application of 150 μg/mL sorgoleone combined with 7.5 mg/mL of tartary buckwheat (*Fagopyrum tataricum* Gaertn.) hairy root extract, where broadleaf weeds exhibited greater growth inhibition than grass weeds for combined rather than individual extracts in particular (Uddin et al., 2013a). Specifically, the mixture of these two natural products inhibited the growth of false cleavers

(*Galium spurium* L.), *Rumex japonicus* Houtt., and Indian jointvetch (*Aeschynomene indica* L.) by 100%, 96%, and 90%, respectively, whereas application of sorgoleone alone led to growth suppression of these weeds species by 81%, 83%, and 75%, respectively.

In laboratory trials, sorgoleone blocked electron transport in mitochondria isolated from etiolated seedlings of corn and soybean (Rasmussen et al., 1992). The target appears to be the step between state III and state IV respiration in both soybean and corn. Sorgoleone is most active as an inhibitor of oxygen evolution in soybean leaf disks and isolated chloroplasts from many species including weeds resistant to conventional PSII inhibitors (Dayan et al., 2009c; Einhellig et al., 1993). Similar investigation have been carried out by Uddin et al. (2012), who studied inhibition of chlorophyll fluorescence and growth by sorgoleone in several weed species under in vivo conditions, including false cleavers, Indian jointvetch, *Rumex japonicus*, Chinese plantain (*Plantago asiatica* L.), redroot pigweed, false Daisy (*Eclipta alba* L.), barnyardgrass, and hairy crabgrass. Significant growth reduction was observed in plants exposed to sorgoleone at 200 μg mL, with the broadleaf weeds (*R. japonicus*, false cleavers, and Indian jointvetch) being most susceptible. Maximum quantum efficiency of PSII (Fv/Fm) was inhibited by 200 μg sorgoleone mL^{-1} 6 h after application.

6.6.2 Development of Alleloherbicide

A promising use of allelopathic plants is to develop the active component as structural scaffolds to develop new herbicide classes, as has been done successfully with the triketone herbicides (Beaudegnies et al., 2009; Dayan et al., 2007b; Gray et al., 1980). The discovery of chemistry with novel modes of action is greatly needed to overcome rising problems associated with evolution of herbicide-resistant weed biotypes to current herbicides (Albuquerque et al., 2011). It should be mentioned that allelochemicals must meet several criteria to become registered herbicides: proved phytotoxic properties between 10^{-5} and 10^{-7} M, described chemical structure, identified mode of action in plants, known time of residence in soil, possible toxic activity on human health, and viability of production on an industrial scale (Soltys et al., 2013 quot. Bhowmik and Inderjit, 2003).

Many studies conducted under laboratory conditions with purified sorgoleone have shown its high efficiency as a broad-spectrum inhibitor of agronomically important weed species (Bertin et al., 2003; Czarnota et al., 2001; Nimbal et al., 1996a; Uddin et al., 2009, 2010b). The phytotoxic activity of sorgoleone combined with its multiple target sites and

relatively long soil half–life are characteristics that could lead to the development of a natural herbicide. Sorgoleone could be developed as a preemergence herbicide, inhibiting photosynthesis in very young weed seedlings (Dayan et al., 2009a). The hydrophobic properties of sorgoleone (Dayan, 2002; Trezzi et al., 2006) enable it to adsorb strongly to soil, especially to organic matter and other hydrophobic molecules. This property is necessary from the point of view of the practical use of the sorgoleone as an herbicide. The herbicide must have defined persistence in the weed (target species) seed germination zone, which implies effective biological activity (Trezzi et al., 2006).

Synthetic analogues of sorgoleone with saturated site chains (hydrogenated sorgoleone and 2-acetoxy-5-methoxy-3-(pent-1-yl)-1,4-benzoquinone) retained their activity against the development roots of cucumber (*Cucumis sativus* L.), lettuce (*Lactuca sativa* L.), *Desmodium tortuosum* (Sw.) DC, pignut (*Hyptis suaveolens* (L.) Poit), and Mexican fireplant (De Almeida Barbosa et al., 2001). The synthetic quinone obtained in this experiment was as active as the natural product. These data are in agreement with another study that demonstrated that the level of unsaturation of the aliphatic tail had no effect on the ability of the benzoquinone to inhibit photosynthesis (Kagan et al., 2003). Therefore, the synthesis of natural products like quinones described by De Almeida Barbosa et al. (2001) can be used to prepare novel quinone herbicides, assuming that these molecules have appropriate toxicologic profiles. Pure sorgoleone remains stable for up to 21 days at $-20\,°C$ (Franco et al., 2011). Similarly, storing roots in a freezer did not alter the quality of sorghum root extracts.

Commercial herbicides are most often formulated with adjuvants to improve their water solubility, increase spreading on leaves and absorption in plants, or prolong their soil stability (Amali et al., 2014). Uddin et al. (2014) developed a wettable powder (WP) formulation of sorgoleone by combining methanol sorgoleone extract with silicon dioxide, kaolinite, calcium carbonate, and polyethylene ether. In Petri dishes, $0.2\,gL^{-1}$ of active ingredient completely inhibited the germination and development of broad–leaved weeds. In greenhouse experiments, the growth of sorrel (*Rumex japonicus* Houtt.) and Chinese plantain (*Plantago asiatica* L.) was also completely inhibited after the application of $0.4\,gL^{-1}$ of the active substance. It was noted that improved weed reduction results may be obtained if the developed bioherbicide is applied after germination.

7. EFFECT OF SORGHUM ON OTHER CROP SPECIES

The deleterious effect of sorghum on the growth of other crop species has been known for a long time (Breazeale, 1924). In laboratory bioassays, aqueous extracts prepared from leaves, stem, and roots of five sorghum hybrids have been shown to inhibit soybean radicle development (Correia et al., 2005a). Sorgoleone alone has also demonstrated phytotoxicity to lettuce, cucumber, and rice (De Almeida Barbosa et al., 2001; Khaliq et al., 2011a; Uddin et al., 2010b). Marchi et al. (2008) observed significant seed germination inhibition as well as reduced radicle and shoot growth of lettuce and tomato treated by a sudex water extract, especially for seedlings after 10 days. Phytotoxicity symptoms, including stunting, leaf necrosis, and color change in tomato, lettuce, and broccoli (*Brassica oleracea var. italica*) following sudex extract application, are indicative of sorghum allelopathic potential, particularly as a cover plant (Summers et al., 2009). To reduce the risk of injury to similarly sensitive crops, it has been suggested that planting be delayed by 6–8 weeks and that crops are not directly planted into sudex residue. According to Roth et al. (2000), the effect of sorghum residue on wheat is highly dependent on the degree of decomposition of the straw before planting wheat. Additionally, tilled sorghum residues do not affect wheat grain yield, though delays in wheat development have been observed. No-till sorghum straw reduces wheat grain yield, perhaps due to slower leaching and degradation of allelochemicals in the soil. Although sorghum has been implicated in a negative effect on yield for peanuts (*Arachis hypogea*) cultivated in tropical areas (Sène et al., 2000 quot. Delafond and Burgos-Leon, 1978), effects may be mitigated by planting peanuts between rows of a previous sorghum crop (Sène et al., 2000). Suppression of germination and early growth in cotton seedlings has been observed after soil application of sorghum powder and aqueous extracts (Kandhro et al., 2016). Mung beans are also sensitive to sorghum aqueous extracts (Moosavi et al., 2011). Consequently, rotations between sorghum and mung bean are not recommended.

In contrast to formerly described observations and studies, one research group has reported that sorgoleone did not have any influence on rice, barley, wheat, corn, tomato (*Solanum lycopersicum* L.), soybean, or Chinese cabbage (*Brassica rapa* L. subsp. *chinensis* (L.) Hanelt) (Uddin et al., 2010b). Other research groups have moreover reported positive, stimulatory effects of

sorghum on major crops. For example, an intercropping of sorghum and cotton was shown to exhibit positive effects such as increased cotton canopy and root mass by 22% and 41%, respectively (Dos Santos et al., 2014). Cheema et al. (2003c) also pointed out a stimulatory effect of foliar applied sorgaab on wheat yield, which is supported by studies conducted by Afzal and Iqbal (2015) that showed increased wheat yield after application of sorghum water extracts. Techniques that capitalize on the benefits of sorghum allelopathy while minimizing negative effects on other crop plants are critical for the implementation of sorghum as a weed control tool (Kandhro et al., 2016). One such technique may be delaying planting following sorghum residue incorporation for at least 1–2 weeks, which was successful in rice (Khaliq et al., 2011a).

8. CONCLUSION

Knowledge of the allelopathic properties of plants is important not only from an academic or scientific point of view but also for its potential impact in agricultural practice (Vyvyan, 2002). Ongoing research in allelopathy should focus on donor plants that produce chemical compounds capable of accumulating to bioactive concentrations (i.e., phytotoxic) that persist within soil long enough to influence the growth of nearby receiver plant species (Chou, 1999; Hiradate, 2006; Hiradate et al., 2010).

The effectiveness of allelopathy under field conditions is often questioned (Cheema et al., 2009), and difficulty in differentiation of allelopathy from plant competition has hindered the development of methods that capitalize on the weed repression potential of allelopathic crops. The production and release of allelochemicals is highly dependent on many external factors including mineral deficiency, light, temperature, and water stress (Kobayashi, 2004). Complex, interlinked physical, chemical, and biological processes occur in the soil and may lead to the modification of properties of exuded allelopathic substances (Tharayil et al., 2008).

The combination of water extracts from sorghum and other plants with lower doses of herbicides may help reduce the overall amount of herbicide introduced into the environment (Einhellig, 1996). Many years of studies on sorgaab demonstrate that the aqueous extract enhances weed control by conventional herbicides, making it an economically viable biological plant protection method (Cheema et al., 2000b; Irshad and Cheema, 2005).

Allelopathy is becoming an increasingly popular alternative for the application of synthetic plant protection agents. It has been projected that

biopreparations will account for approximately 20% of environmentally friendly plant protection agents in the upcoming decades (Li et al., 2003; Turnera et al., 2007). In a broader perspective, new possibilities associated with the use of biotechnology to enhance allelopathy and the synthesis of bioherbicides by crops offer exciting future novel weed management tools. Attempts at genetic manipulation aimed at allelopathy enhancement in donor plants are currently underway. Specifically, overexpression of key enzymes in the sorgoleone biosynthetic pathway may increase the allelopathic potential of sorghum, resulting in greater opportunities for practical applications (Gniazdowska, 2007). Holistic approaches using multi-disciplinary programs will be necessary to carry out the research required for implementation of allelopathy as a useful weed control tool. Molecular research on the genetic control of the synthesis and exudation of allelochemicals as well as the functional characterization of allelochemicals and their fate in soil is necessary.

One should bear in mind that the cost of bioherbicides must be competitive in order to become realistic alternatives to conventional herbicides. Thus, new plant protection methods should be developed in a way that minimizes the cost of crop production. The search and implementation of innovative biological methods of weed control that are competitive with synthetic herbicides and translate into actual economic profits remains challenging in modern agriculture.

It should be noted that, in the last 20 years, agriculture has witnessed a noticeable trend toward the search for new methods to reduce plant production costs, especially with respect to plant protection agents and expenses. The application of allelopathy in agriculture may meet economic needs by reducing costs while at the same time exhibiting a more desirable environmental profile.

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