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Temporal expression of the *sor1* gene and inhibitory effects of *Sorghum bicolor* L. Moench on three weed species

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ABSTRACT

The temporal expression of gene *sor1* and the inhibitory effect of *Sorghum bicolor* L. Moench against weeds were studied by semiquantitative polymerase chain reaction and intercropping management, respectively. To quantify *sor1* expression, seeds were sown in pots and RNA was collected from the roots at 5, 10, 15, 20 and 30 days after emergence (DAE). In the inhibition assay, cotton and three weeds were evaluated during single cropping and during intercropping with *S. bicolor*. The assay was completely randomized, with eight replications. We found early expression of *sor1* in most *S. bicolor* accessions by 5 DAE, and a gradual reduction thereafter. Only one of the accessions showed *sor1* expression up to 30 DAE. In the inhibition assay, the most significant effects were related to the dry matter production (shoots and roots) of the weeds *Cenchrus echinatus* and *Cynodon dactylon*. The intercropping of cotton and *S. bicolor* had no apparent deleterious effects.

Key words: Allelopathy, semiquantitative PCR, sorgoleone, weeds

Introduction

Weeds are a serious problem in all kinds of crops, because they affect the development cycle and yield, especially in herbaceous species before flowering. Although various control methods are available, the most effective is the use of synthetic herbicides, which unfortunately have high costs in terms of management, as well as posing risks to human health and the environment (Bolonhezi *et al.* 2005; Cheema *et al.* 2003). The use of such herbicides in a single-cropping system can also lead to further selection of herbicide-resistant weeds (Neves 2005).

Despite the numerous benefits that classical breeding has brought to crop yields, it is still limited in its capacity to generate weed-resistant cultivars. In contrast, the current techniques, which are based on the use of biotechnology-derived herbicide-resistant crops, have contributed to minimizing the use of herbicides, thereby providing greater crop protection and productivity (Parker *et al.* 2005; Correia & Durigan 2007; Imura *et al.* 2011). However, the management of such crops can still require the use of chemical herbicides.

Weed control through the use of natural defensive agents obtained from other plants is an agroecological alternative often adopted by farmers of small plots of land (less than 10 ha). In general, a solution containing extracts from several herbicide species is sprayed weekly between rows of short-cycle crops, such as beans, corn, cotton and peanuts (Melo *et al.* 2013). In the literature, several studies have demonstrated the potential of allelopathic herbicides, at low concentration, to control monocot and dicot weeds (Bertin *et al.* 2003; Weston & Duke 2003; Albuquerque *et al.* 2010). This practice is beneficial to the environment and offers the potential for biorational weed control. It can also minimize the cost of management, given that many of the herbicide species are widely distributed on croplands.

According to Souza Filho *et al.* (2006), allelochemicals produced by plants affect local vegetation and the succession of others plants, as well as playing a role in the induction of dormancy and seed preservation. Such chemicals therefore constitute an important mediator of population dynamics because they determine the pattern and density of vegetation, in natural and crop systems alike. Numerous plants have been reported to be allelopathic, including lichens, alfalfa, cucumber, rye, barley, wheat, rice, soybeans, and sorghum (Singh *et al.* 2003; Belz 2007; Albuquerque *et al.* 2010).

Sorghum bicolor L. Moench is an important food crop for farmers working land within semi-arid environments. It is also an allelopathic species that represses the growth

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of numerous weeds, mainly the small-seeded species, due to exudates released by its roots, those exudates consisting mainly of sorgoleone, a biologically active lipid benzoquinone (Forney & Foy 1985; Netzly & Butler 1986; Meazza *et al.* 2002; Dayan *et al.* 2007; Marchi *et al.* 2008; Albuquerque *et al.* 2010). Sorgoleone (2-hydroxy-5-methoxy-3-[(8'*Z*,11'*Z*)-8',11',14'-pentadecatriene]-*p*-benzoquinone) is highly phytotoxic to broad-leaf and grass weeds at concentrations as low as 10 μM, affecting shoot growth with little or no effect on root growth (Einhellig & Souza 1992; Nimbal *et al.* 1996; Czarnota *et al.* 2001). The most active ingredients of sorgoleone reside in the 1,4-hydroquinone portion, which constitutively releases ~80-95% of the molecule (Dayan *et al.* 2007; Albuquerque *et al.* 2010). Depending on the genotype, the expression of sorgoleone will have a greater or lesser potential to inhibit germination of the surrounding plants, particularly broad-leaf and grass weeds, at low concentrations (Yang *et al.* 2004).

According Meazza *et al.* (2002) and Hejl & Koster (2004), the role of sorgoleone as a natural herbicide is due to its effect on electron transport in the chloroplasts, whereby it inhibits the production of *p*-hydroxyphenylpyruvate dioxygenase (HPPD) in a manner similar to that of synthetic herbicides. Inhibition of HPPD disrupts the biosynthesis of carotenoids and results in the bleaching of leaves, due to a loss of chlorophyll. In the field, sorgoleone has an inhibitory effect on the growth of several species, including beans, wheat, and soy, although its greatest effect has been shown to be on the growth of weeds (Roth *et al.* 2000; Souza Filho *et al.* 2006). Sorgoleone is biosynthesized, during early seedling establishment, by root hairs, which possess the entire metabolic machinery (Dayan 2006; Baerson *et al.* 2008a, 2008b). According to Marchi *et al.* (2008), sorgoleone is rapidly degraded in soil and is mainly produced in younger plants, its production peaking by 10 days after emergence (DAE). However, other authors have reported that sorgoleone has a long half-life in the soil, with long-term effects on many cellular targets (Dayan *et al.* 2007; Baerson *et al.* 2008a, 2008b; Barbosa *et al.* 2010).

Molecular studies have described the metabolic pathway of sorgoleone, and a number of genes involved in the event cascade have been identified and characterized (Buchanan *et al.* 2000; Dayan *et al.* 2003; Pan *et al.* 2007; Baerson *et al.* 2008a, 2008b). According to Dayan *et al.* (2003), the gene *sor1*, which encodes a membrane desaturase, is the main precursor of sorgoleone synthesis.

Although the cellular localization and the steps of the biosynthetic pathway of sorgoleone have been determined (Dayan *et al.* 2003; Pan *et al.* 2007; Baerson *et al.* 2008a, 2008b), there is a lack of studies investigating its differential expression among genotypes and its bioactivity *in vivo*. Therefore, the evaluation of accessions that show variability for sorgoleone synthesis could contribute to the selection of the top lines in breeding programs for food production, as well as for weed control, in farming systems.

In the present study, we evaluated the temporal expression of *sor1* in *Sorghum* accessions. We also quantified its inhibitory effect in an intercropping system with three herbaceous weeds.

Material and methods

Experimental procedure and RNA extraction

Seeds of five *Sorghum bicolor* accessions, one each of the cultivars IPA 467-4-2, IPA 7301011, IPA 4202, CNB 9040, and Sudan, were sown in the greenhouse of the Department of Agronomy of the Federal Rural University of Pernambuco, in 5-L pots containing commercial substrate (Plantmax; Eucatex, São Paulo, Brazil). At 5, 10, 15, 20, 30 and 50 DAE, rootlets were collected for RNA extraction (Plant RNA Mini-Spin Invisorb kit; Invitec, Berlin, Germany) from fresh tissue samples (100 mg), in accordance with the manufacturer's recommendations. The concentration and purity of the RNA were estimated with a spectrophotometer (BioPhotometer Plus; Eppendorf, Hamburg, Germany).

cDNA synthesis and semiquantitative polymerase chain reaction

We synthesized cDNA using a Super SMART PCR cDNA Synthesis Kit (Clontech, Palo Alto, CA, USA), in accordance with the manufacturer's recommendations, using 1 μg of RNA from each accession, at different root ages. Specific *sor1* primers (Genbank, EF206348.1) were used in order to perform a 25-μl reverse-transcriptase polymerase chain reaction (RT-PCR), as follows: 1 μl of each cDNA; 2.5 μl (2 mM) of each forward primer (5' TGCCTCCTCGCGCAAAGAAG 3') and reverse primer (5' GGTATAACAACAATGCTCCT 3'); 0.2 μl of Taq polymerase (5 U/μl); 0.5 μl (10 mM) of a deoxynucleoside triphosphate set; 2.0 μl (25 mM) of $MgCl_2$; and 2.5 μl of 10X buffer. The thermal conditions, achieved with a thermal cycler (Mastercycler Gradient; Eppendorf), were as follows: pre-denaturation at 95°C for 5 min; 35 cycles of denaturation at 95°C for 60 s; annealing at 56°C for 60 s; and extension at 72°C for 60 s. A final extension step, at 72°C for 10 min, was added. The products of the reactions (690 bp) were analyzed on an agarose gel (0.8%) with a 1-kb DNA ladder (Plus DNA Ladder; Invitrogen, Carlsbad, CA, USA). As a constitutive control, another reaction was performed with β-actin primers (forward: 5' GATCTGGCATCACACCTTC 3'; and reverse: 5' AGGAAGCTCGTAGCTCTT 3', 570 bp).

In vivo *effect of* Sorghum bicolor *density on the growth of weeds and cotton*

We performed the *in vivo* inhibition assay in a greenhouse, using the *Sorghum bicolor* accession that showed the highest *sor1* expression in the semiquantitative RT-PCR.

We first evaluated the effect of *S. bicolor* on the weeds *Cyperus rotundus*, *Cynodon dactylon*, and *Cenchrus echinatus*. Plastic pots (17 cm in diameter) were filled with organic substrate (Plantmax; Eucatex), plus N:P_2O_5:K_2O fertilizer (20:10:20). On the basis of the work carried out by Trezzi & Vidal (2004), we planted a total of nine plants in each pot, at the following weed-*S. bicolor* ratios: 9:0, 5:4 and 0:9. To investigate the possible allelopathic effect of *S. bicolor* on cotton, we added an arrangement of *S. bicolor* and cotton (*Gossypium hirsutum* L., cv. CNPA 8H), in pots filled with the same substrate plus N:P2O5:K2O-fertilizer (60:60:60), at sorghum-cotton plant ratios of 9:0, 7:2, and 0:2. The experimental design adopted was totally randomized, with eight replications. Pots were watered daily. Each individual plant height (cm) and dry biomass (g) were measured at 56 days. Statistical analysis were performed with the GENES program (Cruz 2006).

Results and discussion

The semiquantitative expressions of *sor1* and β-actin in *Sorghum bicolor* accessions are shown in Fig. 1. The expression profile of *sor1* differed among accessions, as well as among roots of different ages. In general, the expression of *sor1* was highest during the first 20 DAE, varying among accessions and trending downward. We observed *sor1* expression as early as 5 DAE, except in the IPA 4202 cultivar (Fig. 1), from which the gene was absent at that stage.

The best *sor1* expression was seen in the Sudan and IPA 7301011 cultivars, the latter distinguished by expression that was more uniform and prolonged, being detectable at up to 30 DAE (Fig. 1). This result is interesting because the longer duration of the *sor1* activity might translate to more effective control of the surrounding weeds, especially in denser cropping. Another aspect is that, in a *Sorghum bicolor* improvement program, hybridization between the Sudan and IPA 7301011 cultivars could result in high-sorgoleone progenies, prolonging the effects and consequently improving protection against various weeds. Because *sor1* expression was observed at 30 DAE in the Sudan and IPA 4202 cultivars, we also investigated *sor1* expression in both at 50 DAE; however, no activity was found. On the basis of those results, the Sudan cultivar was selected for the *in vivo* assay involving *S. bicolor* density with weeds and cotton. We found that *S. bicolor* had no major effect on the plant height of the cotton or the weeds (Fig. 2). However, it did have an effect on the dry masses of shoots and roots in *Cenchrus echinatus* and *Cynodon dactylon* (Fig. 3).

In the cotton and *Sorghum bicolor* treatment, we found no phytotoxic effect on dry mass. Instead, we observed increases of 122% and 141% in the mass of cotton canopy and roots, respectively. Cheema *et al.* (2003) also reported a beneficial effect of intercropping *S. bicolor* with wheat. The authors carried out a study involving the control of weeds and wheat competition by foliar application of *S. bicolor* water extract (12 L ha^{-1} at 30 and 40 days after sowing) and observed a 33-53% reduction in weed biomass, together with a 7-14% increase in wheat yield. These results seem to be associated with the density of *S. bicolor* in management with other cultures. Hallak *et al.* (1999) found anatomical changes in beans (*Phaseolus vulgaris* L.) grown in the presence of root exudates of *S. bicolor* at 0.10 and 0.15 mM. The authors observed a reduction in the number of cell layers, thickening of the cellulose portions of the collenchyma, and deformation of vessel elements. In a similar study, Souza *et al.* (1999) found sorgoleone to be phytotoxic to wheat, beans, soy, and pigweed, even resulting in death, at 0.10 mM.

Although *Sorghum bicolor* is considered to be a highly allelopathic species, its toxic effect is not the same for other crops, because it depends on many factors, such as genotype concentration, plant density, fertility, and soil moisture (Rice, 1984; Kruse *et al.* 2000; Yang *et al.* 2004). However, the efficacy of control against some weeds might not occur immediately, as does that of commercial herbicides, but could build over time, as with most natural products (Belz 2007). Netzley *et al.* (1988) reported that the concentration of sorgoleone exuded into the soil from *S. bicolor* roots can reach 10-100 μM. According to Czarnota *et al.* (2001), the post-emergence application of sorgoleone inhibits the

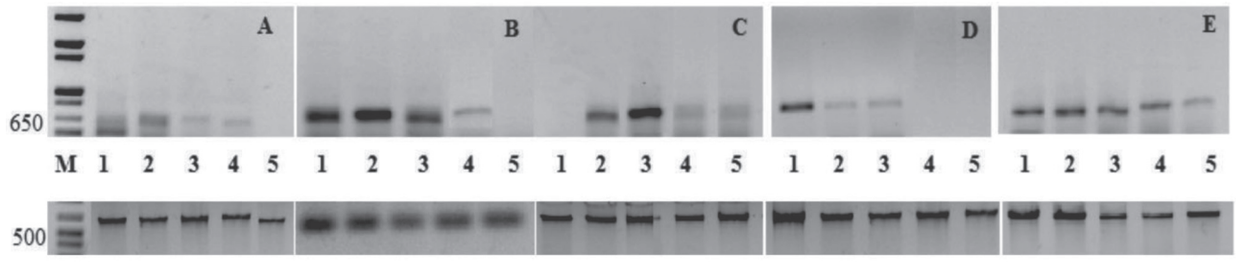

Figure 1. Temporal expression in *Sorghum bicolor* accessions: of the *sor1* gene (upper gel); and of β-actin (lower gel).

A – cultivar IPA 467-4-2; B – cultivar IPA 7301011; C – cultivar IPA 4202; D – cultivar CNB 9040; E – cultivar Sudan; M – molecular weight marker (1-kb DNA ladder); 1, 2, 3, 4, and 5 – rootlets collected at 5, 10, 15, 20, and 30 days after emergence, respectively.
Values on the left indicate the number of base pairs.

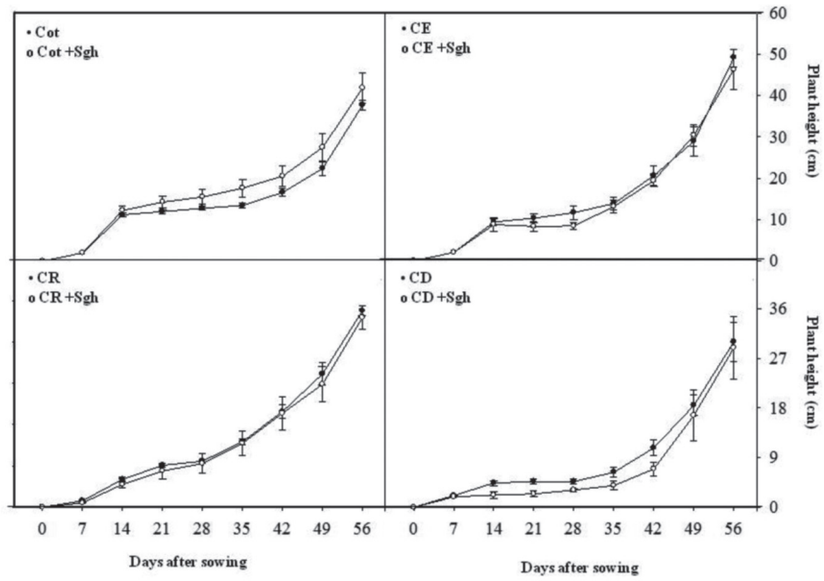

Figure 2. Plant heights of *Sorghum bicolor*, cotton and three weeds in single-cropping and intercropping treatments.

Cot – cotton; CE – *Cenchrus echinatus*; CR – *Cyperus rotundus*; CD – *Cynodon dactylon*; Sgh – *Sorghum*.

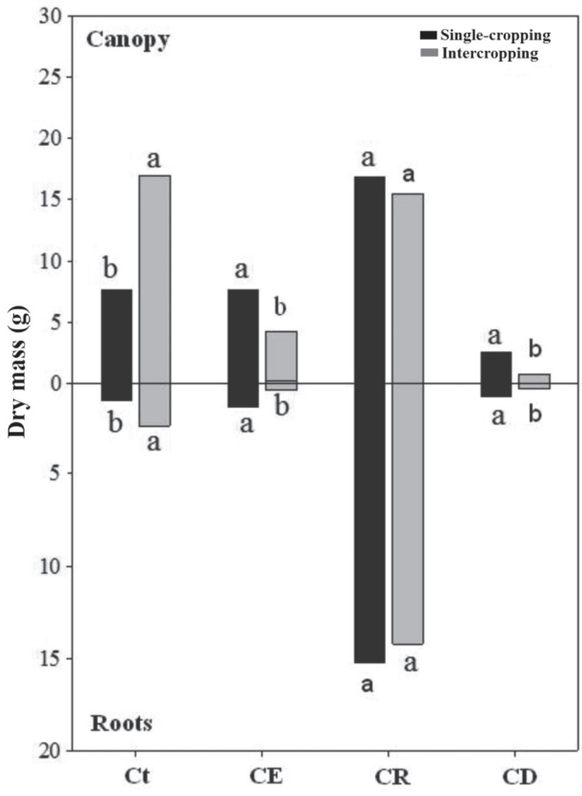

Figure 3. Dry biomass of *Sorghum bicolor*, cotton and three weeds in single--cropping and intercropping treatments.

Cot – cotton; CE – *Cenchrus echinatus*; CR – *Cyperus rotundus*; CD – *Cynodon dactylon*.
Different letters indicate significant differences at $p<0.05$ (Tukey's test).

growth of various weeds, especially broad-leaf weeds, at the same concentration as the synthetic herbicide atrazine (0.6 kg a.i. ha^{-1}). Weston & Czarnota (2001) also showed *S. bicolor* toxicity in pre-emergent small-seeded weeds.

The results of the present study confirm the findings of Wu *et al.* (1999), who showed that there is genetic variability in sorgoleone production among *Sorghum* accessions at the intraspecific and interspecific levels. At the molecular level, Yang *et al.* (2004) demonstrated such variability from the amino acid sequence of the SOR1 protein among species of tomato, potato, tobacco, sesame, beans, rice, and sorghum. These findings open a range of opportunities for genetic improvement of the germplasm containing this gene, in order to select crops with high allelopathic ability. Despite the great benefit of crops with allelopathic properties for the agroecological management of weeds, scientists emphasize the need to understand the genetic control of allelopathy (Baerson *et al.* 2008b; Albuquerque *et al.* 2010).

On the basis of our results, not only those related to the *sor1* expression in the roots of the different *Sorghum bicolor* accessions but also those related to the inhibitory effect of the Sudan cultivar on the biomass production of two major weeds, we suggest a pyramid breeding scheme involving the Sudan and IPA 7301011 cultivars with other high-yield top lines, in order to generate progenies for further use in single cropping or intercropping agroecological management. It should be borne in mind that, prior to intercropping management, the absence of an allelopathic effect on the other main crop should be verified, in order to ensure that *S. bicolor* will be phytotoxic only to the weeds.

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