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Physiological and agronomic responses to the application of post-emergence herbicides on sweet potato cultivar selected for its potential as biofuel feedstock

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Abstract

Sweet potato exhibits a prostrate growth habit, which makes weed management to be manually performed or conducted through the application of selective herbicides. Considering the absence of registered herbicides for the selective control of broad leaf weeds on the sweet potato crop, we investigated the physiological and agronomic responses of the sweet potato cultivar Duda, selected for its great potential in biofuel production, to different post-emergence herbicides. Two experiments, one conducted under field conditions and the other under controlled (potted plants) conditions, were performed under a randomized complete block design, with four replicates each. Four different herbicides, atrazine and S-metolachlor (3,5 L.ha⁻¹), carfentrazone-ethyl (0,75 L.ha⁻¹), fomesafen and fluazifop-P-butyl (1,8 L.ha⁻¹) and nicosulfuron (1,25 L.ha⁻¹), were used and the experiments were composed by five treatments with the control (no herbicide application) treatment,. Physiological indicators, including carbon assimilation, stomatal conductance, leaf transpiration rate, internal CO₂ concentration, and water-use efficiency were monitored at 24 h, 48 h and 15 d after herbicides application, while agronomic evaluations were performed at 30 and 152 days from herbicide application. Application of atrazine (inhibitor of photosystem II) together with S-metolachlor (inhibitor of cell division/elongation) led to reductions on the physiological indices soon after treatment imposition but it had no effect on dry matter accumulation in the shoot, nor on the roots, not affecting the starch content, storage root productivity, and estimated ethanol production as well. In contrast, application of carfentrazone-ethyl, a protoporphyrinogen oxidase inhibitor, exerted significant negative physiological and agronomic effects, decreasing root productivity and estimated ethanol yield. We conclude that the use of atrazine in a mixture with S-metolachlor represents a suitable selective approach for the control of broad leaf weeds in sweet potato crops.

Keywords: ethanol yield; Ipomoea batata, plant physiology, selectivity, storage roots.

Introduction

The growing pollution level generated by the use of fossil fuels has raised awareness regarding their harmful effects on human health and to the environment (EPA, 2019). For this reason, many countries have introduced different recommendations to control greenhouse gas emissions while others have attempted to achieve energy independence (ÚNICA, 2014; IEA, 2018). The search for short- to medium-term solutions to this problem has directed attention to the use of plant biomass as a renewable source of energy.

Ethanol is a highly energetic fuel derived from starch- and sucrose-rich plants and is considered an important ally in pollution control (EIA, 2019). Considering the environmental and energetic importance of ethanol, By virtue of the environmental and energetic importance of ethanol, more than 60 countries have adopted its obligatory blending with fossil fuels, resulting in a worldwide consumption of approximately 100 billion L of this biofuel in 2017 (ÚNICA, 2014; IEA, 2018). It is also estimated that, under favorable market and policy conditions, annual ethanol production could reach 145 billion Lin 2023 (IEA, 2018).

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Sweet potato [*Ipomoea batatas* (L.) Lam. (Convolvulaceae)] is an attractive feedstock for ethanol production due to its high starch contents. Moreover, it is the second most produced tuberous root crop in the world after cassava, being cultivated in more than 100 countries, with the Asia continent accounting for 70.5% (equivalent to 79.6 million tons) of the total production of sweet potato in 2017 (Ray and Ravi, 2005; FAO, 2017). The production of ethanol from sweet potato storage roots has gained particular interest since the introduction of new cultivars, both of which enabled storage root productivity to be increased to 40 t ha⁻¹ and starch content to 18 - 30%, greatly improving its use for biofuel production (Silveira et al., 2014).

One of the main problems associated with sweet potato management on a small, medium or large scale is weed control. Invasive plants compete with the crop for space, water, light and mineral nutrients, and it can also facilitate the introduction of insect pests, nematodes and diseases. Moreover, weed infestation can cause losses of 40 to 85% depending on the weed species, the degree of invasion, and edaphoclimatic conditions (Karam and Cruz, 2004; Oliveira Junior et al., 2011; Lorenzi, 2014). Sweet potato exhibits a prostrate growth habit with a vine system expanding horizontally on the ground. Thus, the control of invasive species is basically performed by manual weeding, which is both expensive and time consuming (Glaze and Hall, 1990). Mechanical weeding techniques do not provide an appropriate alternative, since they can damage the plants and remove soil from the planting beds. Post-emergence control of narrow-leaf weeds can be performed using acetyl CoA carboxylase (ACC) inhibitor fluazifop-P-butyl, which eliminates annual and perennial grassy weeds. However, there are no selective herbicides against broad leaf weeds registered for use in sweet potato plantations, and this represents a true bottleneck in the cultivation of this species (Miranda et al., 1987).

Given that the mode of action is key to understanding why some plants are affected by herbicides and others are not, we aimed to investigate the physiological and agronomic responses to four different post-emergence herbicides on sweet potato plants from the Duda cultivar, selected for its potential as a biofuel feedstock, grown under field and greenhouse conditions.

Results

Physiological responses of potted plants to post-emergence herbicides

Significant differences ($P \le 0.05$), among treatments and evaluation times, were detected in all of the photosynthetic parameters studied, with the exception of *LT* (Figure 1).

At 24 HAA, stomatal conductance was significantly lower in treatments T4 and T5 ($g_s = 0.26$ and 0.11 mol m⁻¹ s⁻¹, respectively) involving protoporphyrinogen oxidase (PROTOX) inhibitors compared with the control T1 (0.92 mol m⁻¹ s⁻¹), whereas g_s values for T2 and T3 ($g_s = 0.54$ and 0.74 mol m⁻¹ s⁻¹, respectively) were similar to that of the control treatment T1 (Figure 1a). At 48 HAA, only T5 showed reduced g_s levels (0.01 mol m⁻¹ s⁻¹) when compared to T1 ($g_s = 0.59$ mol m⁻¹ s⁻¹), while at 15 DAA no differences were observed in g_s values among treatments..

In relation to leaf transpiration rates (*E*), no significant differences were detected among treatments T2, T3, T4 and T1 (Figure 1b). However, *E* values for T5 at 24 and 48 HAA exhibited significant reductions (up to 96%) when compared to T1. After 15 days from herbicide application, *E* values were similar among all treatments, similar to the pattern observed for g_s .

Water-use efficiency (*WUE*)significantly reduced for all herbicide treatments at 24 and 48 HAA, except for T3 at 24 HAA (Figure 1c). At 48 HAA, for example, *WUE* for T2, T3, T4, and T5 reached levels of -0.33, 0.83, 0.73, and -2.90 μ mol CO₂ μ mol H₂O⁻¹, respectively, which corresponds to reductions of 110.5, 74, 77 and 192%, respectively, indicating that all herbicides negatively affected leaf gas exchange of sweet potato plants. T5 was the most detrimental treatment, since it reduced *WUE* by 88.6% on average during the first 48 hours, when compared to T1.

Regarding carbon₂ assimilation, all herbicide treatments significantly reduced the photosynthetic rate of sweet potato plants at 24 and 48 HAA (Figure 1d). At 24 HAA, the increasing order of damage was T3 < T4 < T5 < T2 (A = 9.96, 3.33, -1.65, and -4.94 µmol m⁻² s⁻¹, respectively), corresponding to reductions in A values of approximately 40, 80, 110 and 130% in comparison with T1. At 48 HAA, A values of T3, T4, T5 and T2 were, respectively, 46, 86, 107 and 116% lower than that of T1. Nevertheless, A values in all herbicide treatments returned to levels similar to that observed for T1 at 15 DAA.

At 24 and 48 HAA, the internal $CO_2(C_i)$ concentrations for T2 to T5 were significantly higher than T1 (Figure 1e). In particular, C_i levels of T2, T4 and T5 (433, 326.6 and 567.3 µmol.mol⁻¹, respectively) at 48 HAA increased by 75, 32 and 129%, respectively, in relation to T1 (C_i = 248 µmol mol⁻¹). Although treatments T2 and T5 presented the highest C_i values, such improvement did not result in enhanced photosynthetic rates, as shown in figure X. There was an inverse relationship between the *A* and g_s levels and C_i . Thus, while T1 presented high *A* and g_s values and low levels of C_i at the different evaluation times, the opposite pattern was observed for herbicide treatments.

In relation to instantaneous carboxylation efficiency (*iCE*), when compared to the control treatment T1, T2 and T5 showed reductions of 120 and 107% at 24 HAA, with these reduced levels being also present at 48 HAA (Figure 1f). On the other hand, T3 presented a similar *iCE* value to that of T1 at 24 HAA and a reduction of only 61% at 48 HAA. At 15 DAA, *iCE* values from all herbicide treatments returned to levels similar to that of T1.

Leaf temperature was not altered by herbicide treatment at any of the evaluation times (Figure 1g).

Agronomic responses of potted plants to post-emergence herbicides

At 30 DAA, significant differences were observed among treatments for leaf DW, vine, and total plant biomass. In treatments T2 and T3, the respective mean DWs of leaves (3.37 and 4.79 g; Figure 2a), vines (4.51 and 5.53 g; Figure 2b), and total biomass (16.39 and 20.47 g; Figure 2d) were similar to those observed for plants from the control treatment (T1). In contrast, in treatments T4 and T5, which comprised PROTOX inhibitors, the respective mean DWs of leaves (2.38 and 2.53 g; Figure 2a), vines (3.23 and 3.25 g; Figure 2b) and total biomass (10.26 and 11.08 g; Figure 2d) were significantly ($P \le 0.05$) lower than plants from T1. In relation to roots, no significant differences were observed among herbicide treatments and the control treatment (Figure 2c).

Comparing *A* (Figure 1d) and total biomass DW (Figure 2d) for potted plants, it was possible to observe that photosynthetic capacity was most affected in T2 soon after herbicide application, although it considerably recovered at 15 DAA. This improvement in photosynthetic rates may have contributed to the enhancement of total DW biomass in T2. In contrast, total DW biomass from T4 and T5 were significantly lower than that of T1, despite the improvement in photosynthetic rates recorded at 15 DAA.

Agronomic responses of field plants to post-emergence herbicides

At 152 DAA, the SDW values of field grown plants that from treatments T2, T3 and T4 (33.7, 21.2 and 29.3t ha^{-1} , respectively) were similar to that of control T1 (Figure 3a).

However, SDW from T5 (15.6 t ha⁻¹) was significantly reduced, thereby demonstrating the toxicity of carfentrazone-ethyl, which promoted defoliation. The SRDW values of field grown plants were similar among the different treatments (Figure 3b).

The productivity of SR from T5 plants under field conditions was significantly ($P \le 0.05$) lower than that of T1 plants (H = 23.6 and 72.2 t ha⁻¹, respectively), whereas the SR productivities from T2 and T4 plants (H = 70.1 and 56.5 t ha⁻¹, respectively) were similar to that of the control plants (Figure 3c). Although SDW and SR productivity from T5 plants were reduced by 50 and 67% in comparison with controls plants, respectively, new leaves were observed at 15 DAA and this recovery may have contributed to the improvement observed in physiological parameters (Figure 1). New leaves were also observed in T2 and T4 at 15 DAA, and this was sufficient to ensure relatively high SDW values and SR productivities at the end of the plant cycle (152 DAA). This was clearly not the case, however, for T5 plants.

Regarding treatment with nicosulfuron (T3), although the physiological parameters from these plants were similar to or higher than those observed for the other herbicide treatments, SDW (21.2 t ha⁻¹) and SR productivity (39.5 ton ha⁻¹) were significantly ($P \le 0.05$) lower in comparison with T1. Such reductions were likely caused by leaf chlorosis and, consequently, decreased photosynthetic rates, and this effect persisting for up to three months. Furthermore, plants from T3 a relatively higher growth of the shoot exhibited excess shooting, and this may have negatively influenced SR productivity, since it negatively affected root development.

The starch contents of SRs were similar in all treatments (Figure 4a), while estimated ethanol yields from T2 and T4 plants were similar T1 (Fig. 4b). In contrast, estimated ethanol yields were significantly ($P \le 0.05$) lower for T3 and T5 when compared to T1, and this can be explained by the observed reduction in SR productivity.

Discussion

Physiological evaluation for herbicide selection

The use of herbicides to control invasive plants may induce physical and physiological reactions that trigger deleterious effects in susceptible crops. However, damage caused by herbicides may not always be visible and, for this reason, the measurement of physiological parameters is important in selecting appropriate herbicides for specific cultures (Torres, 2012).

Stomatal conductance

Determination of g_s is particularly important since it can directly interfere on photosynthesis-related parameters such as *A*, *C_i* and *E* (Paiva et al., 2005). Herbicide application on sweet potato promoted modification on gs levels, which consequently altered gas exchange rates. The reason for this is associated to the fact that herbicide application may induce the production of reactive oxygen species (ROS). These molecules act as secondary messengers, promoting the opening of ligand-gated Ca²⁺ channels and releasing Ca²⁺ cations from intracellular compartments into the cytoplasm. Alterations in this intracellular signal transduction pathway results in stomatal closure (Taiz and Zeiger, 2017) and reduction of gas exchange rates, affecting mainly, but not exclusively, herbicide-susceptible plants.

Transpiration and water use efficiency (WUE)

Leaf transpiration rate (*E*) is directly influence by g_s , and it drives the process of mass flow, through which oscillations in leaf temperature are minimized (Kerbaury, 2008). In addition, it can directly affect WUE. Under normal conditions, WUE in C3 plants such as sweet potato vary ranges from 1 to 3 µmol CO₂ / 1 µmol H₂O (Silveira, 2012). Herbicide application on sweet potato plants reduced WUE to less than1 µmol CO₂ µmol / 1 µmol H₂O. Reductions in *WUE* can be caused by exposure to biotic and abiotic stresses, including the application of herbicides that induce stomatal closure, resulting in the reduction of water uptake (Paiva et al., 2005; Kerbaruy, 2008).

Carbon assimilation rate (A)

Herbicide-susceptible plants exhibit reduced A rates within few hours after application (Lorenzi, 2014). Moreover, A rates are often limited by the availability of water, CO_2 and light, and these factors are highly interconnected (Kerbaury, 2008). In the present study, however, the sweet potato plants were not exposed to water deficit and/or insufficient light, and so A rates obtained here can be attributed exclusively to herbicide treatment.

Internal carbon dioxide concentration (C_i)

The higher the photosynthetic rate, the faster is the consumption of CO_2 and lower is its concentration within the leaves, implying that C_i is inversely proportional to A. Under stress conditions A is generally reduced while C_i is increased (Galon et al., 2009). Accordingly, sweet potato plants submitted to herbicide application showed reduced A levels, but increased C_i when compared to control. According to, Increased C_i levels in C3 plants under stress conditions may be caused by impaired fixation of the CO_2 reaching the mesophyll cells, possibly resulted from metabolic restrictions in the Calvin cycle, thus reducing the photosynthetic rates (Larcher (2004)).

Agronomic evaluations for herbicide selection Dry weight (DW)

Plant DW is an important agronomic indicator of the health and biomass accumulation from the time of germination until the end of the plant life cycle (Galon et al., 2009). In this study, most herbicides (T2, T3, and T4) led to a reduction on the shoot DW of sweet potato plants when compared to plants from the control treatment. Reductions in shoot biomass is associated with a decrease in the photosynthetic area which in turn reduces carbohydrates accumulation of in roots with consequent effects on crop productivity Viana et al., (2001).

In sweet potato plants, the shoot is potentially useful for the production of ethanol fuel, which can augment the yield of ethanol per hectare, and may also serve as animal fodder in fresh form or as silage (Barreira, 1986; Costa, 2018). Our study revealed that the shoot dry weight values of sweet potato treated with the mixture of atrazine and *S*-metolachlor (T2) or fomesafen and fluazifop-P-butyl (T4) were similar to those of control plants (T1).

In this study, we observed that carfentrazone-ethyl caused defoliation in sweet potato plants, effects that were similar



Fig 1. Physiological parameters of sweet potato potted plants treated with different post-emergence herbicides: T1 - control plants (no herbicide); T2 – atrazine and *S*-metolachlor mixture; T3 - nicosulfuron; T4 - fomesafen and fluazifop-P-butyl mixture; and T5 – carfentrazone-ethyl. Evaluation times were performed at 24 HAA: 48 h HAA and 15 DAA. Stomatal conductance (A); Leaf transpiration rate (B); Water-use efficiency (C); Carbon assimilation rate (D); Internal CO₂ concentration (E); Instantaneous carboxylation efficiency (F); and Leaf temperature (G). Bars bearing dissimilar lower (upper) case letters indicate statistically significant differences between treatments (evaluation times) according to ANOVA and Tukey test (P < 0.05). Abbreviations: HAA, hours after application; DAA, days after application



Fig 2. Dry weight (DW) of potted of sweet potato plants treated with different post-emergence herbicides (T1 - control plants (no herbicide); T2 – atrazine and S-metolachlor mixture; T3 - nicosulfuron; T4 - fomesafen and fluazifop-P-butyl mixture; and T5 – carfentrazone-ethyl) and evaluated after 30 days from herbicide application. a) leaves; b) vines; c) roots; and d) total biomass. Bars bearing dissimilar upper case letters indicate statistically significant differences between treatments according to ANOVA and Tukey test (P < 0.05).



Fig 3. Agronomic analysis of field grown sweet potato plants treated with different post-emergence herbicides (T1 - control plants (no herbicide); T2 – atrazine and S-metolachlor mixture; T3 - nicosulfuron; T4 - fomesafen and fluazifop-P-butyl mixture; and T5 – carfentrazone-ethyl) and evaluated after 152 days from herbicide application. a) Shoot dry weight (SDW); b) dry weight of storage roots (SRDW); and c) storage root productivity. Bars bearing dissimilar uppercase letters indicate statistically significant differences between treatments according to ANOVA and Tukey test (P < 0.05).



Fig 4. Agronomic analysis of field grown sweet potato plants treated with different post-emergence herbicides (T1 - control plants (no herbicide); T2 – atrazine and S-metolachlor mixture; T3 - nicosulfuron; T4 - fomesafen and fluazifop-P-butyl mixture; and T5 – carfentrazone-ethyl) and evaluated after 152 days from herbicide application. a) Starch content in storage roots; b) estimated ethanol yield. Bars bearing dissimilar upper case letters indicate statistically significant differences between treatments according to ANOVA and Tukey test (P < 0.05).

to those produced by flumioxazin, another PROTOX inhibitor (Stephen et al., 2014). According to Bertoncello et al., (2011), defoliation drastically reduces productivity by interfering with the distribution of photoassimilates within the plant, and recovery depends on the extent of defoliation and the degree of development of the crop at the time of exposure to the herbicide. Although PROTOX inhibitors have reduced crop selectivity when sprayed during leaf emergence (Oliveira Junior et al., 2011), they do not damage new leaves that.

Our results showed that application of a mixture of atrazine and *S*-metolachlor (treatment T2) to sweet potato at doses of up to 3.5 L ha⁻¹ had little effect on most of the agronomic parameters, which remained similar to those of the control treatment (T1), thus demonstrating the potential of this mixture for post-emergence control of broad leaf weeds. However, a dose-dependent effect of this mixture has been observed on sweet potato, such that productivity after herbicide application (1.5 kg a.i. ha⁻¹) remained similar to the one observed in control plants (39. 2 t ha⁻¹) but decreased to 25.1 t ha⁻¹ as the herbicide dose increased to 3.5 kg a.i. ha⁻¹ (Korieocha et al., (2011).

Starch levels

Starch may act as an alternative substrate for the production of ethanol fuel, considering its great capacity for conversion

into fermentable sugars. The starch content (18.8%) of the sweet potato Duda cultivar observed here was 23% lower than levels previously reported for the same cultivar (Silveira, 2014). This discrepancy may be explained by genotype x environment interaction, since in contrast to the earlier study, our experiments were carried out during the dry season, where temperatures and photorespiration rates are higher and photosynthetic rates are lower than those encountered during the rainy season. This explanation can be better understood by considering the relationship between sink organs (tubers, seeds and roots), which are photosynthetically inactive and importers of resources, and source organs (leaves), which are photosynthetically active and responsible for the acquisition of carbon resources. Spatial and temporal variations occur in the use of reserve carbohydrates, in that plants accumulate carbohydrates in storage sinks during periods of excess and deplete them when the rate of utilization exceeds the rate of production, hence a sink may be turned into an internal source under certain environmental conditions (Taiz and Zeiger, 2017). According to Silveira et al., (2014), ethanol yield of the Duda cultivar can reach 10,467 L ha⁻¹, but in the present study estimated yields, even those of control plants, were considerably lower, mainly due to the lower starch contents observed here.

Materials and methods

Site of study and experimental design

The experiments were performed in the campus of the Federal University of Tocantins (UFT), Palmas, TO, Brazil (10°10' S, 48°21'W; 220 m altitude). During the experimental period, the mean temperature and relative humidity were 27.8°C and 65.4%, respectively. There was basically no precipitation (0.6 mm) during this period and overall solar radiation was 1445.3 kJ/m² (INMET, 2018).

Two different experiments were performed, one carried out with potted plants and one under field conditions, with both of them following a randomized complete block design with four replicates. Both experiments comprised five different treatments, a control (T1), no herbicide application, and the application of four different herbicides, atrazine and Smetolachlor (3,5 L ha⁻¹) (T2), Nicosulfuron 5 L ha⁻¹ (T3), Fomesafen and Fluazifop-P-butyl (1,8 L ha⁻¹) (T4), and Carfentrazone-ethyl (0,75 L ha⁻¹) (T5). All plants were exposed to natural climatic conditions. Physiological analyses of potted plants were carried out at three evaluation times, 24h, 48 h after application (24 and 48 HAA) and 15 days after application (15 DAA), whereas agronomic analyses were performed at 30 and 152 DAA. All analyses were performed in the Laboratório de Sistemas de Produção de Energia a partir de Fontes Renováveis (LASPER) at UFT.

Soil preparation

The area delineated for the field experiment was prepared by plowing, harrowing, and lifting 30 cm planting beds. Planting and cover fertilization were performed, as necessary, based on the results of soil analysis carried out in accordance with the recommendations of the Brazilian Agricultural Research Corporation (Embrapa, 1995). Each experimental plot comprised two planting beds (70 x 210 cm), spaced 70 cm apart, each containing seven plants in 30 cm intervals. Soil for plants cultivated in pots was obtained from the experimental field area after fertilization, as described above.

Plant material

Both experiments were performed with sweet potato plants from the Duda cultivar, which was developed for the purpose of ethanol fuel production, by the plant breeding program at UFT. These are main characteristics of this cultivar: harvesting after 180 days from planting, mean productivity of 65.0 t ha⁻¹, dry matter content of 40.4%, and ethanol yield of up to 161.04 Lt⁻¹ from storage roots (Silveira et al., 2014).

Experimental planting were carried out on April 12, 2017 by transferring the upper-third portions (15-20 cm long) of sweet potato vines, containing three to five internodes, to field planting beds or to 4.5 L pots containing substrate. Post-emergence herbicides were applied to potted and field grown plants after 28 days from planting by means of a backpack sprayer with a built-in pressure gauge that had been adjusted to dispense a regular dose of 200 L ha⁻¹. Manual weeding was performed in the planting of control plants (T1).

Physiological and agronomic evaluations on potted plants Dry weight (DW) of leaves, vines, and roots of potted plants were evaluated at 30 DAA by drying the fresh plant material in a forced air oven at 65° C for 72 h, with a periodic weighing of the heated powder until constant weight, as determined using a digital analytical balance with 0.0001g accuracy (Embrapa, 2012). Dry weight of the total biomass was calculated as the addition of the three types of plant material.

In order to establish photosynthetic performance, gas exchange rates, i.e. carbon assimilation rate (A; µmol m⁻² s⁻¹), leaf transpiration rate (E; mol H₂O m⁻² s⁻¹), and stomatal conductance (g_s ; mol m⁻¹ s⁻¹), along with internal carbon dioxide concentration (C_i ; µmol mol⁻¹) and leaf temperature (LT; °C) a LCpro-SD portable photosynthesis system (ADC Bioscientific, Hoddesdon, UK) was used, with these parameter being evaluated at 24 HAA, 48 HAA and 15 DAA. Readings (one per plot) were performed on a fully expanded leaves, selected from the middle-third portion of the vine, from 9:00 to 12:00 am of sunny cloudless days. Water-use efficiency (WUE; µmol CO₂ µmol H₂O⁻¹) was calculated from the A/E ratio, and instantaneous carboxylation efficiency (*iCE*; µmol m⁻² s⁻¹) was established from the A/C_i ratio.

Agronomic evaluations and ethanol yield from field grown plants

All evaluations were performed at 152 DAA. Shoot DW was determined as previously described for potted plants and expressed in t ha⁻¹. Storage root DW (SRDW) was determined by drying a fresh sample of separated root material (5 g) on a glass Petri dish in a forced air oven at 105°C for 8 h, followed by periodic (every hour) weighing of the heated powder until constant weight (Silveira et al., 2014). SRDW values were calculated according to equation 1.

SRDW(%) =

(weight of Petry dish with dry sample-weight of empty Petry dish)x100 weight of fresh sample

Total productivity of sweet potato storage roots per hectare (H; t ha⁻¹) was measured by weighing the roots from each plot (14 plants) and calculated according to equation 2.

Productivity of storage roots $(tha^{-1}) = 10,000m^2 xplot productivity$

area of the plot(m|2)

Starch content (%) was established by near infrared reflectance spectroscopy (NIRS), using a NIR 900 PLS spectrophotometer (FEMTO, São Paulo, SP, Brazil) and the FemWin900 software. Briefly, sweet potato storage roots were washed, skinned, and sliced using a manual grater. The slices were pre-dried at room temperature and subsequently placed on a tray and dried in an air circulation oven at 55°C for 72 h. Starch flour was obtained by grinding the dehydrated material in a knife mill through a 20 mm mesh screen (Savelli et al., 1995), and stored in sealed containers until required for NIRS analysis. Diffuse reflectance spectra were acquired at 5 nm intervals in the 1100 - 2500 nm region, and each sample was scanned in triplicate. The wet weight of starch in a sample (% WW) was determined according to equation 3 (Mapa, 2014).

 $Starch(\%WW) = \frac{(100xDWstarch) - (moisturexDWstarch)}{100}$

Ethanol yield (L ha⁻¹) was estimated on the basis of the starch content and productivity of sweet potato storage roots per hectare (H) according to Camargo et al., (2016), equation 4.

 $E than olyield (Lha^{-1}) = (10.349 x starch \% WW - 89.349) H$

Data analysis

Differences between treatments were determined by oneway ANOVA. When ANOVA was significant, means were discriminated using Tukey's multiple comparison test at P \leq 0.05. All statistical analyses were performed by the Sisvar software version 5.6 (Ferreira, 2011). Analysis of variance (ANOVA – See Supplementary Material) and the *F* test were employed to assess the equality of means, while the Tukey test was used to compare mean values.

Conclusions

Most physiological parameters (i.e. gs, E, A, Ci and WUE) reduced in sweet potato plants in the first 48 h of exposure to post-emergence herbicides, but the magnitude of the effect was dependent on the type of herbicide. A mixture of atrazine (photosystem II inhibitor) and S-metolachlor (inhibitor of cell division/elongation) reduced physiological indices (photosynthetic rates) immediately after application, but had little effect on agronomic traits such as dry mass accumulation in the shoot and storage roots, productivity, starch content of storage roots, and estimated yield of ethanol. In contrast, the PPO inhibitor carfentrazone-ethyl exerted harmful physiological and agronomic effects with significant reductions on root productivity and estimated ethanol yield. Our work is important for two main reasons: (i) this is the first study to assess the impact of post-emergence herbicides on the sweet potato cultivar Duda, a variety specially developed for ethanol production, and (ii) we have demonstrated that the use of a mixture of atrazine and Smetolachlor represents a suitable selective approach for the control of broad leaf weeds in sweet potato crops. However, further studies are required to investigate the best time of application and dose, and potential interactions between pre- and post-emergence herbicides.

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