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Full Length Article

Climate Change Scenarios Increase the Growth and Resistance of Barnyardgrass to Imazethapyr

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Abstract

The effects of CO_2 concentration and temperature on growth and control of barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.] susceptible and resistant to imazethapyr were evaluated. The treatments were doses of imazethapyr (zero to 848 g ha^{-1}) applied in imidazolinone-susceptible (SUSSP01 and MOSTS01) and -resistant (ARRGR01 and PALMS01) biotypes, grown at ambient and elevated temperature (24/20°C or 30/26°C (day/night)) and CO_2 concentrations (400 or 700 ppm). The herbicide effect on resistant biotypes was lower with the increase of CO_2 concentration and temperature. Temperature increase from 24/20°C to 30/26°C enhanced the resistance factor (RF) in plants grown under 400 ppm from 3.58 to 31.73 in the biotype ARRGR01 and from 3.87 to 11.07 in the biotype PALMS01. When grown at 700 ppm, the increase in the RF was from 6.85 to 12.67 (ARRGR01) and from 7.95 to 27.11 (PALMS01) in response to increasing the temperature. The greater resistance in climate change scenarios can be explained by physiological and growth parameters. Plants cultivated at higher temperatures and CO_2 concentration had a higher number of tillers per plant, shoot and root dry mass. The relative chlorophyll content was lower under high temperature, as a consequence of increased growth and demand for nutrients. The electron transport rate was severely reduced by increasing the CO_2 concentration in plants grown at a temperature of 24/20°C. In summary, increases in CO^2 concentration and temperature make resistant barnyardgrass even more insensitive to imazethapyr.

Keywords: Global warming; Carbon dioxide; Weed resistance; Imidazolinone; ALS

Introduction

At the same time CO_2 and temperature are among the main factors essential for plant growth and development, and main components of global climate change (Sheppard and Stanley 2014). Along with variations in the magnitude of these two factors, changes in agricultural systems including weeds response to climate change have been described (Peters *et al.* 2014; Kathiresan and Gualberti 2016).

Weed competition has been conducted in order to characterize the effects of temperature and CO_2 concentrations increases on the physiology and growth of plant species (McDonald *et al.* 2009; Wang *et al.* 2011). From the adaptive and dispersal point of view of species, the impact of weeds is expected to increase with the climate change scenario (Thuiller *et al.* 2006). On the other hand, from the competition point of view, research points to the decrease of weed interference on crops (Davis and Ainsworth 2012). This is explained by the fact that most cultivated plants have C3 photosynthetic metabolism. For being more efficient photosynthetically, C4 plants respond less to CO_2 increases (Ziska and McConnell 2016), since the saturation point of 360 ppm is lower than the concentration present in the atmosphere, which is currently around 410.60 ppm (NOAA 2019), compared to 700 ppm needed by C3 plants (IPCC 2014).

However, the positive effect of the increase in CO_2 concentration on plant growth can be inhibited by increasing the temperature, especially in C3 plants, since C4 species are more photosynthetically efficient than C3 plants under higher temperatures (Peters *et al.* 2014). In addition, enzymatic processes related to performance and resistance of weeds to herbicides is related to temperature and may lead to changes in plant intoxication (Mahan *et al.* 2004).

Barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.] is one of the main weeds of irrigated rice worldwide. It is C4 specie and presents biotypes resistant to various herbicides, including imidazolinones (Heap 2019). Imidazolinone herbicides inhibit the acetolactate synthase (ALS) enzyme, responsible for the synthesis of the essential branched-chain amino acids valine, leucine and isoleucine (Powles and Yu 2010). In some biotypes herbicide

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enhanced metabolism by cytochrome P450 monooxygenase (P450) and glutathione S-transferases (GST) enzymes is involved in the mechanism of resistance (Matzenbacher *et al*. 2015; Dalazen *et al.* 2018a). Therefore, the effect of climatic changes can affect the activity of these enzymes and, consequently, the resistance magnitude to herbicides.

Some studies indicate the higher accumulation of biomass and anticipation of the barnyardgrass flowering under high temperatures (Peters and Gerowitt 2014). However, there is no information about interaction of temperature with the CO_2 concentration on the growth and control of this species with herbicides. The aims of this study were to evaluate the effect of CO_2 concentration and temperature on barnyardgrass resistance to imazethapyr, whose mechanism of resistance is due to degradation enhancement, and to determine the effect of these variations on the growth and physiological parameters of plants of this species.

Materials and Methods

Plant material

Barnyardgrass resistant biotypes were from Arroio Grande-RS (ARRGR01) and Palmares do Sul-RS (PALMS01), collected from paddy fields of South Brazil, selected based on the historic use of Clearfield®-rice cultivars. Previous studies have indicated that degradation enhancement is related with the mechanism of resistance to imazethapyr in these populations (Matzenbacher *et al*. 2015; Dalazen *et al*. 2018a). Susceptible biotypes were from Engenheiro Coelho, SP (SUSSP01) and Mostardas do Sul, RS (MOSTS01), both in Brazil. The susceptible biotype SUSSP01 was originally from an area where no herbicides had been applied and efficient control had been obtained during previous studies using imazethapyr.

Seedlings were transplanted individually into 200 mL pots. Pots were filled with a mixture of acrisol and organic compound, in the ratio of 10:1, plus mineral fertilizer (05-20-20 NPK) at 2.5 g kg^{-1} of substrate. The plants were grown in growth chambers model Conviron ATC 40, which is able to regulate temperature and CO_2 concentration. The photoperiod used was 12/12 h (day/night) and light intensity of 240 μmol m^{-2} s^{-1}.

Barnyardgrass control with imazethapyr

The experiments were arranged in a factorial split-plot design with four replicates, where the main plots (factor A) were the growth chambers at temperatures of 24/20°C and 30/26°C (day/night) in combination with 400 ppm or 700 ppm of CO_2 (factor B). Factor C was four barnyardgrass biotypes: two susceptible (SUSSP01 and MOSTS01) and two resistants (ARRGR01 and PALMS01) to imazethapyr. Factor D was doses of imazethapyr (Imazetapir Plus Nortox, 106 g a.i. L^{-1}, Nortox S.A.) determined from previous studies. For the susceptible populations, the doses used were 0; 6.625; 13.25; 26.5; 53; 106 and 212 g ha^{-1}. In the resistant ones, the doses used were 0; 26.5; 53; 106; 212; 424 and 848 g ha^{-1}. In all herbicide treatments the adjuvant Dash HC (5% of oleic acid, 22.5% of polyoxyalkylene fatty alcohol phosphate esters, 37.5% of fatty acid methyl esters, Basf S.A.) was added at 0.5% (v/v).

Spraying of the treatments was performed when the plants had three leaves. Plants grown at 24/20°C and 30/26°C reached the herbicide spraying stage at 8 and 7 days after transplanting, respectively. Spraying of the herbicide was carried out in an automated spray chamber (Greenhouse Spray Chamber, model Generation III), using a TJ8002E spray nozzle, with a constant pressure of 42 lb. pol^{-2} and speed of 1.16 m s^{-1}, resulting in a spray release of 200 L ha^{-1}.

The evaluation of herbicide efficiency was assessed at 7 and 14 days after the treatment (DAT) by a visual scale, where zero means no symptoms and 100 correspond to plant death. The shoot dry mass (SDM) was measured at 14 DAT, after drying the plants in a dryer (60°C) until they reached a constant mass.

Growth and physiological parameters of barnyardgrass

Additional plants of the four barnyardgrass biotypes were grown together with the experiment described above under the same temperature conditions (24/20°C and 30/26°C day/night) and CO_2 concentration (400 ppm and 700 ppm). Four replicates were used per treatment.

At 28 days after transplanting, the number of tillers per plant (NTP), relative chlorophyll content (RCC), electron transport rate (ETR), shoot dry mass (SDM), root dry mass (RDM) and shoot/root ratio (S/R) were evaluated. The relative chlorophyll content was measured with SPAD 502 and electron transport rate was measured with the OS1-FL Chlorophyll Fluorometer (Opti-sciences). Both evaluations were performed on the last expanded leaf of each plant.

Statistical analysis

The data were submitted to the analysis of the variance, followed by Tukey's HSD ($P < 0.05$) comparison of means, using the software RStudio. Non-linear regressions were fitted to quantify the relationships between variables using SigmaPlot 12.0. Data were adjusted by the logistic model $y = a / [1 + (x / x_0)^b]$, where a is the distance between maximum and minimum asymptotes, x_0 is the inflection point of the curve, which corresponds to the ED_{50} or GR_{50} (dose of the herbicide that causes 50% control or reduction in growth, respectively); and the parameter b describes the slope of the curve around the ED_{50} or GR_{50}.

Results

Barnyardgrass control with imazethapyr

In the first evaluation, at 7 DAT, there was interaction among the studied factors. In the susceptible biotypes, the control was higher in plants grown at the highest temperature (30/26°C day/night) regardless of CO_2 concentration (Fig. 1). For the SUSSP01 population at the recommended dose of imazethapyr (106 g ha^{-1}), the controls were 80 and 90% at concentrations of 400 ppm and 700 ppm of CO_2, respectively, at 24/20°C (Fig. 1A). However, the plants cultivated at 30/26°C showed control of 97.5 and 100%. In susceptible biotype MOSTS01, at these same conditions, the increase in control was even higher, by approximately 20% with the increase of temperature, in both CO_2 concentrations (Fig. 1B). In these populations, for most of the evaluated doses of imazethapyr, CO_2 concentration had no significant effect on the barnyardgrass control.

Resistant biotypes (Fig. 1C and 1D) were better controlled at lower temperature (24/20°C), especially at doses of imazethapyr below recommended levels (106 g ha^{-1}). At the dose of 26.5 g ha^{-1}, in the PALMS01 biotype (Fig. 1D), the controls were 52.5 and 71.25% at 30/26°C and 24/20°C, respectively, regardless CO_2 concentration. In the ARRG01 biotype (Fig. 1C), there was also a reduction in the control in response to temperature increase, however, in lower proportion than in the PALMS01 biotype.

The ED_{50} and the resistance factor (RF) at 7 DAT also varied according to CO_2 concentration and temperature, especially in resistant biotypes (Table 1). The highest values of ED_{50} and RF were observed in the treatments which combined the highest temperature with the highest CO_2 concentration. In PALMS01 biotype, the ED_{50} was 8.75 g ha^{-1} of imazethapyr when the plants were grown at 400 ppm of CO_2 and temperature of 24/20°C. At the same CO_2 concentration, the ED_{50} rise to 19.36 g ha^{-1} of imazethapyr with increasing temperature, resulting in an increase in the RF from 2.48 to 5.48 in relation to the SUSSP01 susceptible biotype. At the concentration of 700 ppm of CO_2, the ED_{50} increased from 8.61 g ha^{-1} to 21.97 g ha^{-1} of imazethapyr, resulting in an increase in the RF from 2.44 to 6.22. In the ARRGR01 biotype, the response was similar, with an increase in the ED_{50} and RF values with the increase in CO_2 concentration and temperature.

The greater increases in ED_{50} and RF values were observed in response to temperature, since the increase in CO_2 concentration caused less effect. In the ARRGR01 biotype, the increase of CO_2 concentration generated an increase of approximately 10 and 15% in the RFs at temperatures 24/20°C and 30/26°C, respectively. Nevertheless, the increase in temperature generated an increase in the RF in the order of 64.5 and 54% in the concentrations of 400 and 700 ppm of CO_2, respectively. In the PALMS01 biotype, the effect of the temperature on the RF was even higher, reaching 154% in the concentration of 700 ppm of CO_2.

At 14 DAT, at lower evaluated doses of imazethapyr, the control of susceptible biotype SUSSP01 was greater at 30/26°C (Fig. 2A), similar to that observed at 7 DAT.

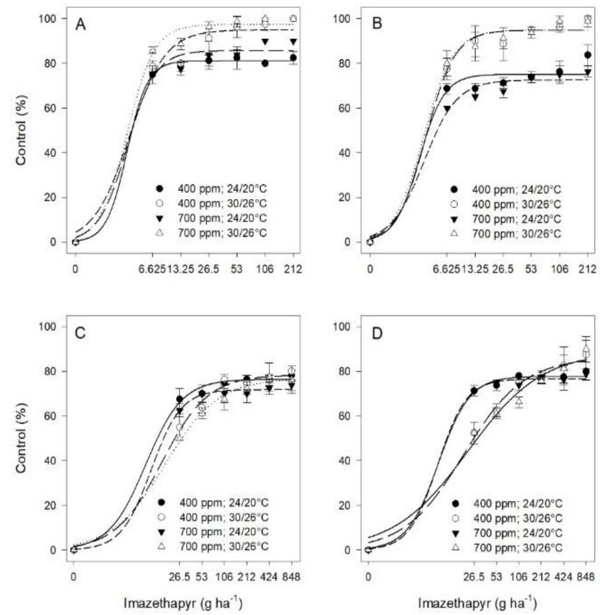

Fig. 1: Control (%) of barnyardgrass susceptible [SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [ARRGR01 (**C**) and PALMS01 (**D**)] in response to imazethapyr, CO_2 concentration (400 ppm and 700 ppm) and temperature (24/20°C and 30/26°C day/night) at 7 days after application of the treatments. Vertical bars indicate the confidence interval

However, in the resistant biotypes (Fig. 2C and 2D) the control was lower at higher temperature (30/26°C) and CO_2 concentration (700 ppm). The greater differences were obtained in doses less than 106 g ha^{-1}. At the dose of 26.5 g ha^{-1} of imazethapyr, plants of the resistant biotype ARRGR01 (Fig. 2C), cultivated at 400 ppm of CO_2 showed controls of 62.5 and 42.5% at 24/20°C and 30/26°C, respectively, resulting in a 20% reduction in the control. For the concentration of 700 ppm of CO_2, the controls were reduced to 53.75 and 36.25% at temperatures of 24/20°C and 30/26°C, respectively. In the PALMS01 biotype (Fig. 2D), at 106 g ha^{-1}, the lowest control was observed when the highest CO_2 concentration was combined with the highest temperature, with a reduction of up to 25% in the control compared to the other treatments.

The ED_{50} and RF at 14 DAT reflected the observed control data, in which plants cultivated at higher CO_2 concentration and temperature were more resistant to imazethapyr (Table 1). In the resistant biotype ARRGR01, the ED_{50} values at 400 ppm of CO_2 were 13.42 and 119 g ha^{-1} of imazethapyr at 24/20°C and 30/26°C, respectively. When the CO_2 was raised to 700 ppm, the ED_{50} were 26.68 and 47.54 g ha^{-1} of imazethapyr at 24/20°C and 30/26°C, respectively. These values generated RFs of 3.58 and 31.73 for the concentration of 400 ppm of CO_2 at temperatures of 24/20°C and 30/26°C, respectively. At 700 ppm, the RF increased from 6.85 to 12.67 as the temperature increased. In the PALMS01 biotype, the values of ED_{50} at 400 ppm rose from 14.52 to 41.50 g ha^{-1} of imazethapyr with the

Table 1: ED_{50}, GR_{50} and resistance factor (RF) for the barnyardgrass control at 7 and 14 days after the treatment (DAT) and shoot dry mass (SDM), in response to imazethapyr, CO_2 concentration (400 and 700 ppm) and temperature (24/20°C and 30/26°C day/night)

Treatment		7 DAT†		14 DAT		SDM φ	
		ED_{50}‡ (CI§)	RF¶	ED_{50} (CI)	RF	GR_{50}‡ (CI)	RF
SUSSP01	400 ppm; 24/20°C	3.53 (0.78)	1.00	3.75 (0.63)	1.00	0.49 (1.86)	1.00
(susceptible)	400 ppm; 30/26°C	3.76 (0.88)	1.06	3.51 (0.70)	0.94	1.74 (0.78)	3.55
	700 ppm; 24/20°C	3.55 (0.93)	1.01	4.27 (0.59)	1.14	1.27 (1.46)	2.59
	700 ppm; 30/26°C	3.55 (0.77)	1.01	3.77 (0.27)	1.01	2.74 (0.84)	5.59
MOSTS01	400 ppm; 24/20°C	3.36 (1.55)	0.94	3.52 (0.68)	0.94	2.03 (1.51)	4.14
(susceptible)	400 ppm; 30/26°C	3.96 (0.78)	1.12	3.74 (0.53)	1.00	1.47 (1.60)	3.00
	700 ppm; 24/20°C	3.78 (0.82)	1.07	3.71 (0.56)	0.99	0.37 (1.71)	0.75
	700 ppm; 30/26°C	3.75 (0.73)	1.06	3.34 (0.85)	0.89	1.89 (1.67)	3.86
ARRGR01	400 ppm; 24/20°C	9.25 (2.35)	2.62	13.42 (6.66)	3.58	18.69 (4.40)	38.14
(resistant)	400 ppm; 30/26°C	15.21 (2.55)	4.31	119.00 (12.14)	31.73	20.05 (2.93)	40.91
	700 ppm; 24/20°C	10.95 (3.54)	3.10	25.68 (10.10)	6.85	17.94 (3.35)	36.61
	700 ppm; 30/26°C	16.84 (1.89)	4.77	47.54 (10.20)	12.67	19.36 (3.67)	39.51
PALMS01	400 ppm; 24/20 °C	8.75 (2.80)	2.48	14.52 (3.37)	3.87	14.30 (2.42)	29.18
(resistant)	400 ppm; 30/26°C	19.36 (2.70)	5.48	41.50 (5.70)	11.07	17.36 (1.80)	35.42
	700 ppm; 24/20°C	8.61 (3.73)	2.44	29.80 (5.65)	7.95	13.01 (1.46)	26.55
	700 ppm; 30/26°C	21.97 (5.64)	6.22	101.68 (67.20)	27.11	15.25 (4.57)	31.12

† days after the treatment; φ Shoot dry mass; ‡ ED_{50} and GR_{50}: dose causing 50% of control and reduction of plant growth, respectively; § confidence interval of parameter x_0 (α = 0.05); ¶ resistance factor in relation to biotype SUSSP01 at 400 ppm and 24/20°C

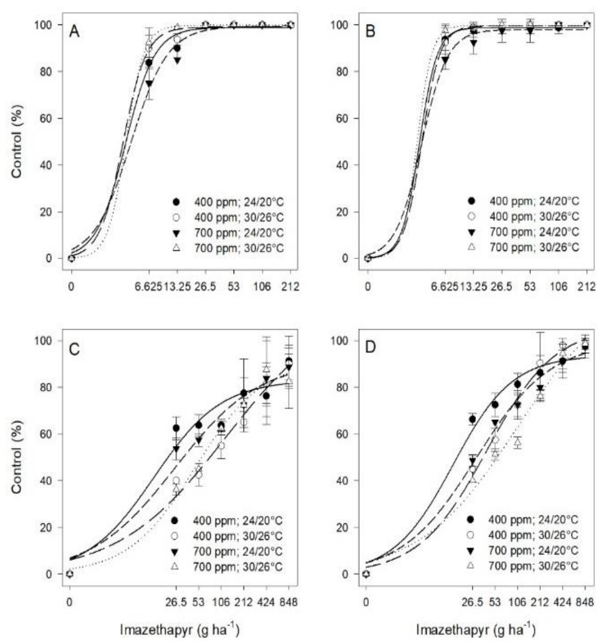

Fig. 2: Control (%) of barnyardgrass susceptible [SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [ARRGR01 (**C**) and PALMS01 (**D**)] in response to imazethapyr, CO_2 concentration (400 and 700 ppm) and temperature (24/20°C and 30/26°C day/night) at 14 days after application of the treatments. Vertical bars indicate the confidence interval

temperature rise. At 700 ppm, ED_{50} were 29.80 and 101.68 g ha^{-1} of imazethapyr at temperatures of 24/20°C to 30/26°C, respectively. The RF at 400 ppm of CO_2 rose from 3.87 to 11.07 with the increase in temperature. When grown at 700 ppm of CO_2, the RF increased from 7.95 to 27.11 with temperature increasing from 24/20°C to 30/26°C, respectively. As at 7 DAT, at 14 DAT the increase in temperature was more important than the increase in CO_2 concentration for both resistant ARRGR01 and PALMS01 biotypes. In the susceptible biotypes, there was no variation of these values in response to CO_2 concentration and temperature.

In all biotypes, the SDM in treatments without herbicide application were higher than in treatments which combined high temperature and CO_2 concentration (Fig. 3). Nevertheless, in the susceptible biotypes (Fig. 3A and 3B), in treatments with imazethapyr spraying at doses of 13.25 g ha^{-1}, there was no difference between climatic change scenarios on accumulation of SDM due to the high control provided by the herbicide.

In resistant biotypes (Fig. 3C and 3D), the highest SDM accumulation was observed in plants cultivated at 30/26°C, regardless of CO_2 concentration, or at 24/20°C combined with 700 ppm of CO_2. In both resistant biotypes, differences in SDM were observed in doses equal to or lower than 212 g ha^{-1} of imazethapyr (twice the recommended dose). At the dose of 106 g ha^{-1} of imazethapyr in the ARRGR01 biotype, at 400 ppm of CO_2, SDM accumulation was 0.04 and 0.27 g $plant^{-1}$ at 24/20°C and 30/26°C, respectively. This corresponds to 85% increase in the accumulation of SDM at high evaluated temperature. For the concentration of 700 ppm of CO_2 at the same dose, the SDM increased from 0.08 to 0.27 g $plant^{-1}$ with the increase in temperature, corresponding to 70% increase. Similarly, in the PALMS01 biotype, at 400 ppm of CO_2, there was higher accumulation of SDM with the increase in temperature. At the concentration of 700 ppm, temperature increase caused a 91% SDM gain at 106 g ha^{-1} of imazethapyr. The values of ED_{50} and RF for SDM, as well as for the control data, were higher at 30/26°C, with little or no effect due to the increase in CO_2 concentration (Table 1). The highest RF was observed in the ARRGR01 biotype, with values close to 40 when the barnyardgrass was grown at 30/26°C.

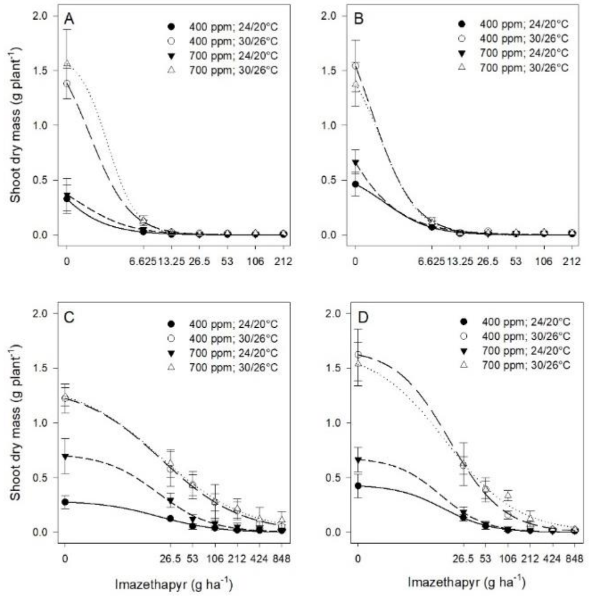

Fig. 3: Shoot dry mass (SDM) of barnyardgrass susceptible [SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [ARRGR01 (**C**) and PALMS01 (**D**)] in response to imazethapyr, CO_2 concentration (400 and 700 ppm) and temperature (24/20°C and 30/26°C day/night). Vertical bars indicate the confidence interval

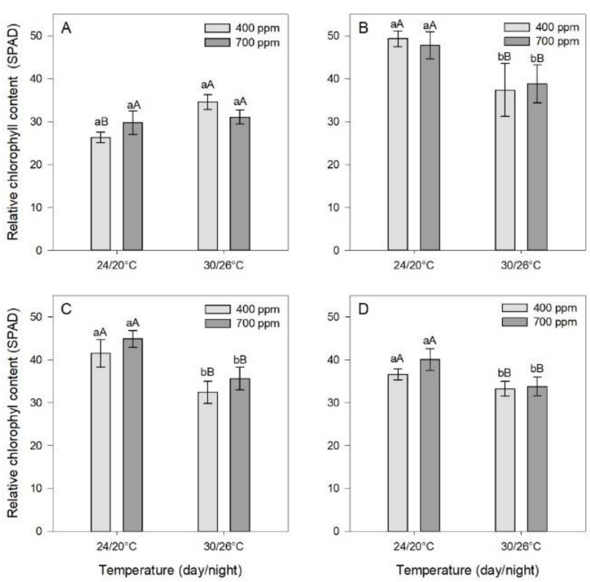

Fig. 4: Relative chlorophyll content (RCC) of barnyardgrass susceptible [SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [ARRG01 (**C**) and PALMS01 (**D**)] to imazethapyr in response to CO_2 concentration (400 and 700 ppm) and temperature (24/20°C and 30/26°C day/night). Lowercase letters indicate statistical significance ($P < 0.05$) between CO_2 concentrations within each temperature. Capital letters indicate statistical significance between the temperatures within each CO_2 concentration. Vertical bars indicate the confidence interval

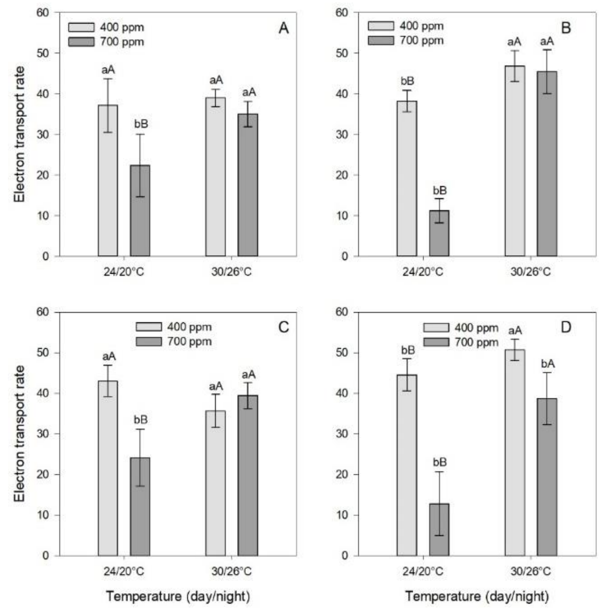

Fig. 5: Electron transport rate (ETR) of barnyardgrass susceptible [SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [ARRG01 (**C**) and PALMS01 (**D**)] to imazethapyr in response to CO_2 concentration (400 and 700 ppm) and temperature (24/20°C and 30/26°C day/night). Lowercase letters indicate statistical significance ($P < 0.05$) between CO_2 concentrations within each temperature. Capital letters indicate statistical significance between the temperatures within each CO_2 concentration. Vertical bars indicate the confidence interval

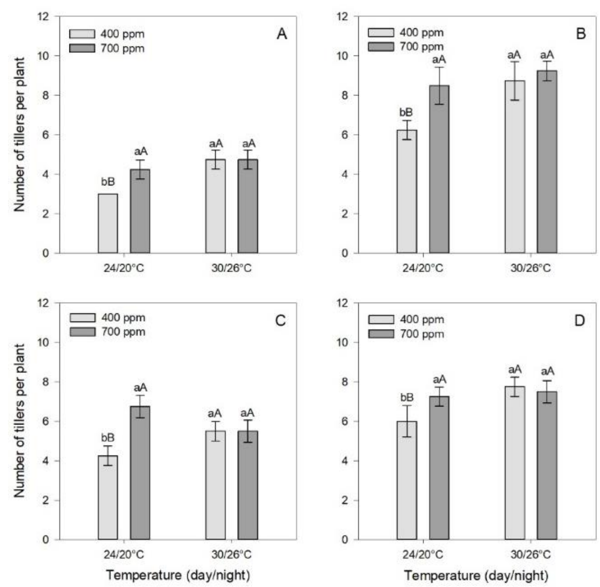

Fig. 6: Number of tillers per plant (NTP) of barnyardgrass susceptible [SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [ARRG01 (**C**) and PALMS01 (**D**)] to imazethapyr in response to CO_2 concentration (400 and 700 ppm) and temperature (24/20°C and 30/26°C day/night). Lowercase letters indicate statistical significance ($P < 0.05$) between CO_2 concentrations within each temperature. Capital letters indicate statistical significance between the temperatures within each CO_2 concentration. Vertical bars indicate the confidence interval

Growth and physiological parameters

The relative chlorophyll content (RCC) was higher in plants cultivated at 24/20°C (Fig. 4), except in the SUSSP01 biotype (Fig. 4A), regardless CO_2 concentration. The largest differences due to temperature were observed in MOSTS01

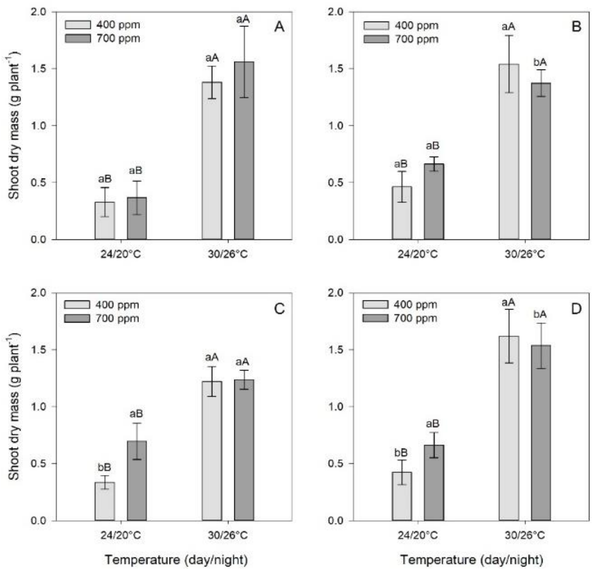

Fig. 7: Shoot dry mass (SDM) of barnyardgrass susceptible [SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [ARRG01 (**C**) and PALMS01 (**D**)] to imazethapyr in response to CO_2 concentration (400 and 700 ppm) and temperature (24/20°C and 30/26°C day/night). Lowercase letters indicate statistical significance (P < 0.05) between CO_2 concentrations within each temperature. Capital letters indicate statistical significance between the temperatures within each CO_2 concentration. Vertical bars indicate the confidence interval

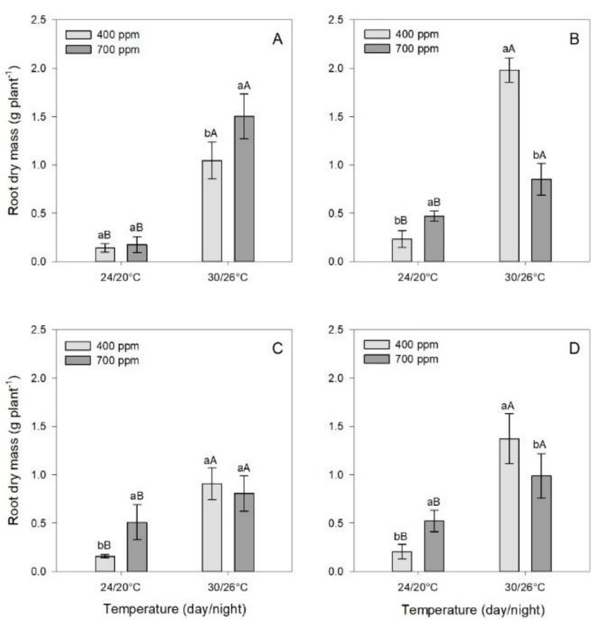

Fig. 8: Root dry mass (RDM) of barnyardgrass susceptible [SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [ARRG01 (**C**) and PALMS01 (**D**)] to imazethapyr in response to CO_2 concentration (400 and 700 ppm) and temperature (24/20°C and 30/26°C day/night). Lowercase letters indicate statistical significance (P < 0.05) between CO_2 concentrations within each temperature. Capital letters indicate statistical significance between the temperatures within each CO_2 concentration. Vertical bars indicate the confidence interval

(Fig. 4B) and ARRGR01 (Fig. 4C). In these biotypes, the RCCs were approximately 21% lower in plants grown at 30/26°C. In PALMS01 biotype (Fig. 4D), the reduction of RCC with increasing temperature was 12.5%. The highest values were observed in the MOSTS01 biotype, with 48.57 at the temperature of 24/20°C.

In all evaluated biotypes, the electron transport rate (ETR) was lower when the temperature of 24/20°C was combined with 700 ppm CO_2 (Fig. 5). In the susceptible biotypes (Fig. 5A and 5B), the reductions in the ETR with the increase of the CO_2 concentration at 24/20°C were 39.78 and 70.56%, respectively. For the resistant biotypes (Fig. 5C and 5D), the reduction in the ETR was 43.78 and 71.24%, respectively. The PALMS01 biotype, in addition to having the highest reduction in the ETR at 24/20°C, was the only one in which there was also a reduction in the ETR at 30/26°C with the increase in CO_2 concentration. At this temperature, the ETR was 50.70 and 38.75 at concentrations of 400 ppm and 700 ppm, respectively.

For the number of tillers per plant (NTP), at 30/26°C there was no difference between CO_2 concentrations (Fig. 6). However, at 24/20°C the supplementation with CO_2 caused an increase in the NTP in all the evaluated biotypes. The highest NTP was observed in the MOSTS01 biotype (Fig. 6B), with values higher than nine tillers per plant. Therefore, both the increase in CO_2 concentration and temperature generates more tillered plants.

The accumulation of SDM was higher in plants grown under the temperature of 30/26°C, regardless the biotype and CO_2 concentration (Fig. 7). At this temperature plants had a SDM of two to three times greater than at 24/20°C. However, at the temperature of 24/20°C, higher SDM was observed in imazethapyr-resistant biotypes at higher CO_2 concentration (Fig. 7). Considering the main factors, CO_2 concentration levels did not cause difference on SDM. Nevertheless, for the temperature factor, plants accumulated, on average, 67% more SDM when grown at 30/26°C.

The effect of the treatments in relation to the accumulation of root dry mass (RDM) was similar to that observed for the SDM. Root growth was higher in plants grown at 30/26°C (Fig. 8). However, at this temperature, the highest CO_2 concentration (700 ppm) caused a reduction in the accumulation of RDM in the biotypes MOSTS01 and PALMS01 (Fig. 8B and 8D). At the temperature of 24/20°C, as well as for the SDM, except for the SUSSP01 biotype, the increase in CO_2 concentration generated higher root growth.

The shoot/root ratio (S/R) indicates that in plants cultivated at a temperature of 24/20°C, except for the SUSSP01 biotype, the highest CO_2 concentration (700 ppm) resulted in a lower S/R ratio (Fig. 9). These results are due to the higher root growth of the barnyardgrass cultivated at 700 ppm of CO_2 (Fig. 7). Although at 24/20°C the increase in CO_2 concentration caused a higher accumulation of SDM, the proportion in the increase of the accumulation of RDM was higher. In the mean of the three biotypes in

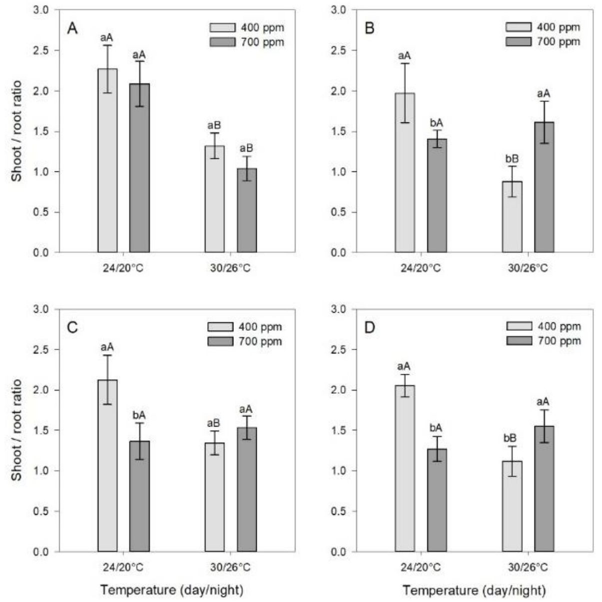

Fig. 9: Shoot/root ratio (S/R) of barnyardgrass susceptible [SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [(ARRG01 (**C**) and PALMS01 (**D**)] to imazethapyr in response to CO_2 concentration (400 and 700 ppm) and temperature (24/20°C and 30/26°C day/night). Lowercase letters indicate statistical significance ($P < 0.05$) between CO_2 concentrations within each temperature. Capital letters indicate statistical significance between the temperatures within each CO_2 concentration. Vertical bars indicate the confidence interval

which CO_2 concentration had effect, the accumulation of SDM was 44.39% higher in plants grown at 700 ppm. However, the accumulation of RDM in this scenario was 62.55% higher, explaining the lower S/R ratio observed. In Fig. 10 it is possible to observe the effect of the temperature and CO_2 concentration on the growth of shoot and roots of the plants.

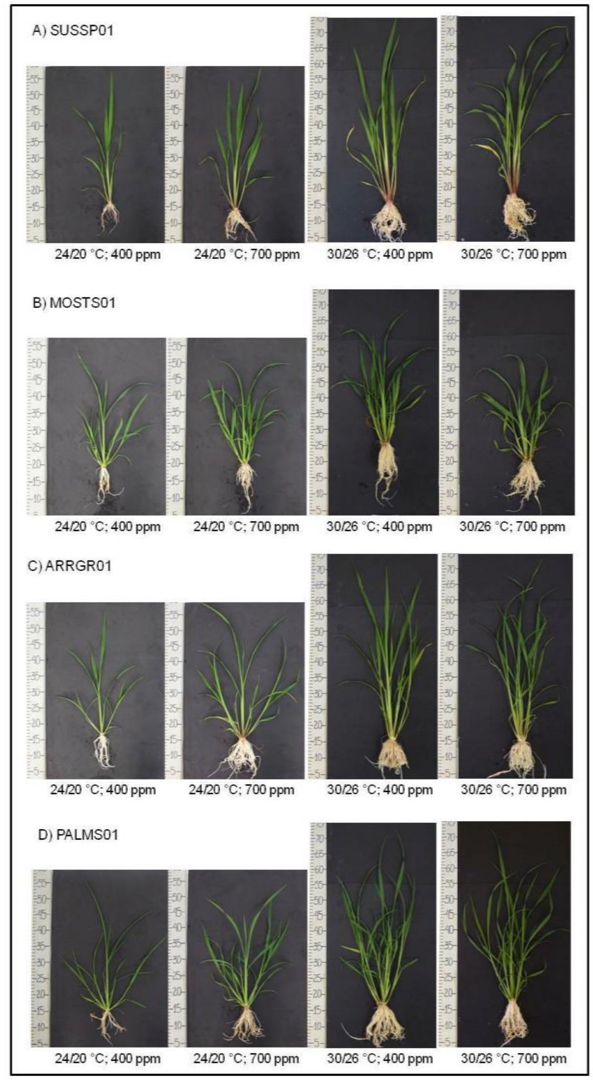

Fig. 10: Effect of temperature (24/20°C and 30/26°C day/night) and CO_2 concentration (400 and 700 ppm) on the growth of barnyardgrass susceptible [(SUSSP01 (**A**) and MOSTS01 (**B**)] and resistant [(ARRG01 (**C**) and PALMS01 (**D**)] to imazethapyr

Discussion

In susceptible biotypes, the greater initial control (Fig. 1A and 1B) observed at higher temperatures may be related to the higher absorption and translocation of the herbicide at 30/26°C. The greater herbicide absorption under high temperature conditions may occur due to the greater permeability of the plasma membrane under these conditions (Los and Murata 2004). The highest translocation of systemic herbicides at high temperatures occurs because these conditions are similar to the conditions in which C4 plants, such as barnyardgrass, present the highest photosynthetic activity. Thus, unlike resistant biotypes, since susceptible do not have enough detoxifying enzymes for herbicide metabolism to occur, susceptible plants are even more sensitive to the imazethapyr herbicide at higher temperatures.

In resistant biotypes, the simulated climate change scenario increased plant tolerance to imazethapyr, mainly for PALMS01 biotype (Fig. 1D and 2D and Table 1). This biotype has detoxification by P450 enzymes as a mechanism of resistance to the herbicide imazethapyr, due to the greater expression of *CYP* genes (Matzenbacher *et al*. 2015; Dalazen *et al*. 2018a, 2018b). Studies have shown that plant intoxication by herbicides is lower under high temperatures, since the detoxifying activity of P450 enzymes is favored. In palm amaranth [*Amaranthus palmeri* (S.) Watson] the rate of metabolization of mesotrione by detoxifying enzymes were higher at elevated temperatures (Godar *et al*. 2015). Similarly, grass species presented 56 and 68% metabolization of amicarbazone at 25/20°C and 40/35°C (day/night), respectively (Yu *et al*. 2015). In corn, temperatures between 25–30°C provided maximum selectivity to the herbicide rimsulfuron, which was not observed at 10°C (Koeppe *et al*. 2000).

Some physiological and phytometric parameters were affected by the increase in temperature and/or CO_2 concentration. ETR is a real-time measure of the photochemical activity of photosystems, being the photosynthetic variable more sensitive to environmental variations (Pimentel *et al*. 2011). The ETR reduction in response to increase of CO_2 concentration in all barnyardgrass biotypes in present research (Fig. 5) has already been observed in other species (Hüner *et al*. 2014; Long *et al*. 2004). The cultivation of plants under conditions of high CO_2 concentration may lead to the inhibition of photosynthesis due to the accumulation of carbohydrates in the cytosol (Stitt and Quick 1989). The accumulation of carbohydrates occurs because the regulation of other processes alters plant growth patterns and demands for photoassimilates due to environmental limitations, such as temperature (Ainsworth *et al*. 2004). Thus, as observed in this study, when combining low temperature (24/20°C) and high CO_2 concentration (700 ppm), a reduction in the ETR occurs, resulting in accumulation of photoassimilates and inhibition of the photosynthesis process.

The highest NTP observed in plants grown in the treatments that combined high temperature (30/26°C) with high CO_2 concentration (700 ppm), or high CO_2 concentration (700 ppm) with lower temperature (24/20°C), coincides with the treatments that provided a higher accumulation of SDM (Fig. 7). This may be explained by the fact that the NTP is the main component of SDM production (Sugiyama 1995). The tillering process is regulated by genetic and environmental factors (Kim *et al*. 2010). Both the increase in the CO_2 concentration and temperature may cause an increase in the tillering of poaceae (Morison and Lawlor 1999). In these conditions, the highest accumulation of photoassimilates occurs, which is one of the main factors that stimulate the emission of new tillers (Kim *et al*. 2010).

The accumulation of SDM (Fig. 7) was inversely proportional to the relative chlorophyll content (RCC) (Fig. 4). Under higher temperature conditions (30/26°C), the accumulation of SDM was higher and the RCC was lower. Chlorophyll content is directly linked to the availability of nitrogen (N), since this element is one of the main components of the chlorophyll molecule. With the increase of the photosynthetic rate and the higher accumulations of photoassimilates and SDM, the demand for N increases, causing N deficiency in the leaves and consequentially lower RCC (Kim *et al*. 2011). Thus, it may be inferred that the demand for N by barnyardgrass will be higher at high temperature and CO_2 concentration conditions, increasing competition with crops.

The higher root growth observed in the scenarios of high temperatures and/or CO_2 concentration increases the competitive capacity of the barnyardgrass. With a more robust root system, the volume of explored soil is large, resulting in greater competiveness with crops for water and nutrients. Irrigated rice, one of the main crops infested by barnyardgrass, is a C3 plant, which would benefit from increasing atmospheric CO_2 concentration. Nevertheless, the increase in temperature may cancel the positive effect of CO_2 supplementation on C3 plants, since the optimal temperature for photosynthesis in C3 plants is approximately 20–25°C. However, in C4 plants, the temperature range at which the photosynthetic activity is the highest is between 30 and 40°C (Yamori *et al*. 2014).

Although the results demonstrate that the effect of the increase in temperature was more significant than the increase in CO_2 concentration, it is important to note that one of the main consequences of increasing the concentration of this gas in the atmosphere is precisely the increase in temperature (Tubiello *et al*. 2007). Hence, with the increase in the atmospheric CO_2 concentration, in addition to the fertilization caused by the gas, C4 plants may also be affected by the increase in temperature. Projections indicate that by the end of the century, CO_2 concentration should be between 730 and 1,020 ppm and the temperature could rise from 1.1 to 6.4°C, depending on the scenario set in the next few years (IPCC 2014).

Because of this climate change scenario, based on the results of this study, the management of barnyardgrass will become more difficult from the point of view of herbicide efficiency in resistant populations whose mechanism of resistance is due to enhanced metabolism. This may happen for two reasons: firstly, herbicide efficiency will decrease due to higher activity of detoxifying enzymes, which are more active at higher temperatures (Puchkaev *et al*. 2002); secondly, the increased growth of plants undergoing climate change scenarios will make the plants more vigorous and therefore more tolerant to herbicides (Maun and Bennett 1986). Furthermore, the high growth of these plants will probably shorten the ideal application period, since the plants will reach the ideal application stage (three leaves) faster (Šoštarčić *et al*. 2019). This will also imply a faster reinfestation of the areas, which leads to an increase in the number of herbicide applications, favoring weed resistance selection.

Conclusion

The simulated climate change scenario in this study indicate that the control of barnyardgrass with imazethapyr may be favored in areas with herbicide-susceptible plants. However, in resistant biotypes involving detoxification enzymes (P450), the control was lower under conditions of high temperature (30/26°C) or high CO_2 concentration (700 ppm). The increase in temperature had a more pronounced influence on the sensibility of barnyardgrass to imazethapyr compared to the increase in CO_2 concentration. The higher CO_2 concentration had a greater effect when combined with the lower evaluated temperature (24/20°C). With the increase in temperature from 24/20°C to 30/26°C, the resistance factor (RF) of plants grown under 400 ppm increased by 72 and 55% for the resistant biotypes ARRGR01 and PALMS01, respectively. When grown at 700 ppm, the increase in the RF was 43% (ARRGR01) and 46.5% (PALMS01) in response to the increase in temperature. In addition to possibly favoring the higher activity of detoxifying enzymes, the increase in temperature caused a greater accumulation of shoot dry mass (SDM), making the plants more vigorous. Plants cultivated at 700 ppm of CO_2 and 30/26°C showed greater tillering, favoring the accumulation of SDM. In addition to higher shoot growth, climate change scenarios also favored root growth of plants and root dry mass (RDM) accumulation, which may increase the effect of interspecific competition, especially with C3 crops infested with barnyardgrass.

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Author Contributions

Giliardi Dalazen, Luis Antonio de Avila, and Aldo Merotto Jr. designed the experiments. Giliardi Dalazen and Alexandre Pisoni performed the experiments. Giliardi Dalazen, Aldo Merotto Jr., and Christian Bredemeir analyzed the data. Giliardi Dalazen and Aldo Merotto Jr. wrote the manuscript. Giliardi Dalazen, Alexandre Pisoni, Christian Bredemeier, Luis Antonio de Avila, and Aldo Merotto Jr. discussed the results and revised the manuscript.

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