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Research Article

Response of imidazolinone-resistant and -susceptible weedy rice populations to imazethapyr and increased atmospheric CO_2

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The authors declare that there is no conflict of interest regarding the publication of this manuscript.

HIGHLIGHTS

- Enhanced CO_2 atmospheric concentration increases weedy rice growth, photosynthesis rates and seed production.
- Enhanced CO_2 atmospheric concentration increases weedy rice spikelet sterility.
- Imidazolinone herbicide application does not affect weedy rice response to CO_2.

ABSTRACT

Background: Weedy rice (*Oryza sativa* L.) is the main weed of rice crop. The high genetic variability of weedy rice contributes to the high phenotypic diversity between biotypes and different responses to environmental stress.
Objective: The present study aimed to evaluate the response of imidazolinone-susceptible and -resistant weedy rice populations to increased atmospheric [CO_2].
Methods: The experiment was arranged in a complete randomized design with six replications. The treatments included two [CO_2] concentration (700 and 400 μmol mol^{-1}) and three treatments: resistant genotype (IMI-resistant) treated with imazethapyr; resistant genotype without imazethapyr, and a susceptible genotype without imazethapyr.
Results: The IMI-resistant and –susceptible weedy rice responded similarly to [CO_2] enrichment. Enhanced [CO_2] increased competitive ability of the weedy rice populations tested, by means of increased plant height. Weedy rice seed production also increased with enhanced [CO_2] by means of increased photosynthesis rate and reduced transpiration (increased water use efficiency). Increased seed production also means increased weed persistence as it increases the soil seedbank size. The application of imazethapyr on IMI-resistant weedy rice did not alter its response to [CO_2]; conversely, increased [CO_2] did not change the resistance level of weedy rice to imazethapyr. High [CO_2] increased spikelet sterility, but this beneficial effect was negated by the overall increase in production of filled grains.
Conclusions: Enhanced [CO_2] concentrations increases weedy rice growth, photosynthesis rates, seed production and spikelet sterility; the imidazolinone application does not affect the response of weedy rice to enhanced [CO_2] affects weedy rice response to imidazolinone herbicide.

1 INTRODUCTION

The atmospheric carbon dioxide concentration [CO_2] reached 400 μmol mol^{-1} in 2017 (NOAA, 2017), representing an increase of over 25% since 1960. The fact that atmospheric CO_2 contributes to plant growth was known since 1890, when Saussure showed, for the first time, that peas exposed to high

[CO_2] grew better than the control plants, which were in ambient air (Kimball, 1983). The amount of CO_2 available to plants affects metabolism, growth, and development, especially when water, light, nutrients, and temperature are favorable (Taiz and Zeiger, 2013; Abdelgawad et al., 2016).

The Intergovernmental Panel on Climate Change (IPCC) estimates that, by the end of the 21st century, global climate changes caused by emission of greenhouse gases will lead to an increase in atmospheric [CO_2] above 700 μmol mol^{-1} (IPCC, 2014). Such condition will cause major changes on the earth's climate, which will then drive changes in agricultural zoning, methods of crop management, and crop yields (Wang et al., 2017). At the plant level, climate change effects modifications in plant physiology, morphology, and biology to enable adaptation to biotic and abiotic stresses. Likewise, the distribution, abundance, and severity of insect pests, diseases, and weeds are projected to change as has already occurred today (Korres et al., 2016). Climate change contributes to the constant adaptation of agriculture (Tokatlidis, 2013). Climate change effects on agricultural production can be positive in some farming systems and regions and adverse in others (Obirih-Opareh and Onumah, 2014). At the plant level, we can observe the interaction effects of increasing [CO_2] and temperature on plant performance. The benefits of elevated atmospheric [CO_2] can be minimized or negated by high temperatures (Korres et al., 2016). Walker et al. (2016) pointed out that with increasing temperature, photorespiration will increase, which could negatively affect yield under future climates despite increases in carbon dioxide.

Weedy rice (*Oryza sativa* L.) is a global weed in rice production, which is most difficult to control because of its high similarity to cultivated rice in genetic, morphological, physiological, and biochemical traits. This hampers its selective chemical control (Sudianto et al., 2016) as it does mechanical and manual weeding. Rice yield losses due to weedy rice infestation can reach 50% in the USA (Shivrain et al., 2010). In their review article on weedy rice, Ziska et al. (2015) reported yield losses between 35 and 100% in direct-seed rice. The Clearfield® rice production system, which uses cultivars resistant to the imidazolinone herbicides, has allowed selective control of weedy rice (Merotto Jr et al., 2016; Sudianto et al., 2016). Imidazolinone herbicides inhibit acetolactate synthase (ALS), which catalyzes the synthesis of branched chain amino acids. The low outcrossing rate between rice and weedy rice and the general inability of farmers to prevent seed production from outcrosses has produced contemporary populations of ALS-inhibitor-resistant weedy rice in the southern USA (Shivrain et al., 2007; Burgos et al., 2008) southern Brazil (Menezes et al., 2009; Roso et al., 2010), Greece (Kaloumenos et al., 2013); Italy (Andres et al., 2014) and other regions where Clearfield™ rice has been adopted (Sudianto et al., 2016). These herbicide-resistant weedy rice populations carry some crop traits and are even more diverse than the historical weedy populations (Burgos et al., 2014), making weedy rice management more challenging.

Although cultivated and weedy rice are the same species, the weedy traits of the former led us to believe that these two types of *Oryza* will respond differently to climate change. Some researchers have explored the behavior of weedy rice in relation to climate change, specifically, increased atmospheric [CO_2] (Ziska and McClung, 2008; Ziska et al., 2014). In a recent study, Refatti et al. (2019) found that increasing atmospheric [CO_2] and temperature may increase the speed of junglerice resistance evolution to herbicides. The combined effect of increased [CO_2] and herbicide application on weeds is an important aspect to address in relation to crop production. This current work aimed to evaluate the response of imidazolinone-resistant and -susceptible weedy rice populations to imazethapyr and increased [CO_2].

2 MATERIAL AND METHODS

Two genotypes of weedy rice (*Oryza sativa* spp. *indica*), similar in morphology and growth cycle, were evaluated. These were collected from the municipality of Dom Pedrito, Mesoregion of Campanha, in Rio Grande do Sul (RS) State (31º02'07" S; 54º52'02" W), in the 2012/2013 crop season from commercial rice fields. To produce relatively homogeneous 'populations' and increase the seed volume, seeds from field-collected accessions were planted for three generations - 1st year in Arroio Grande, RS; 2nd year in Capão do Leão, RS; and 3rd year in Fayetteville, AR, USA). Atypical plants were removed during each cycle. Within this collection, herbicide-resistant (15-189) and -susceptible (15-214) genotypes were chosen based on similarity in morphology and phenology. Genotype 15-189 was confirmed resistant and 15-214 was confirmed susceptible to imidazolinone herbicides in previous resistance screening tests (Menezes et al., 2009).

Using the seeds from the homogenous populations, a growth chamber experiment was conducted in 2016.

The experiment was arranged in a completely randomized design with six replications in a factorial arrangement. Factor A consisted of two environmental conditions (CO_2 levels of 400 and 700 µmol mol^{-1}). Factor B included three weedy rice treatments: IMI-resistant genotype '15-189' treated with imazethapyr; IMI-resistant genotype without herbicide and a susceptible genotype without herbicide. We did not conduct a factorial arrangement of treatments (genotype x herbicide) because the herbicide would kill the susceptible plants.

The experimental units consisted of 7-L pots filled with sieved field soil The soil was Captina silt loam, with the following characteristics: 30.5% sand; 55.5% silt; 14% clay; pH water = 7.3; organic matter content = 2.41%; NO_3 = 32.4 mg kg^{-1}; NH_4 = 16.8 mg kg^{-1}; P = 86 mg kg^{-1}; K = 41 mg kg^{-1}; Ca = 827 mg kg^{-1}; Mg = 827 mg kg^{-1}; S = 10 mg kg^{-1}; Na = 22 mg kg^{-1}; Fe = 671 mg kg^{-1}; Mn = 168 mg kg^{-1}; Zn = 3.6 mg kg^{-1}; Cu = 0.6 mg kg^{-1}; B = 0.2 mg kg^{-1}. Five weedy rice seeds were sown in each pot, which later were thinned to one seedling per pot.

The plants were grown in two growth chambers (Conviron™, model PGW36) with atmospheric [CO_2] of 400 and 700 µmol mol^{-1}, respectively. Both growth chambers were set at 14/10 h photoperiod (day/night), 600 µmol m^{-2} s^{-1} photosynthetic active radiation (PAR), and 34/26 °C (day/night) temperature programmed across a gradient with the peak temperature occurring at mid-day. Starting from the V4 growth stage, the plants were kept in trays with a constant water level to simulate flooding.

Imazethapyr (Newpath™, BASF) was applied at the V3-V4 growth stage at 106 g a.i. ha^{-1} with 1% by volume crop oil concentrate (COC). The herbicide was applied in a spray chamber equipped with a motorized spray boom fitted with two 800067 flat fan nozzles that delivered 187 L ha^{-1} spray volume at 276 KPa. The spray droplets were allowed to dry before returning the plants into the growth chamber.

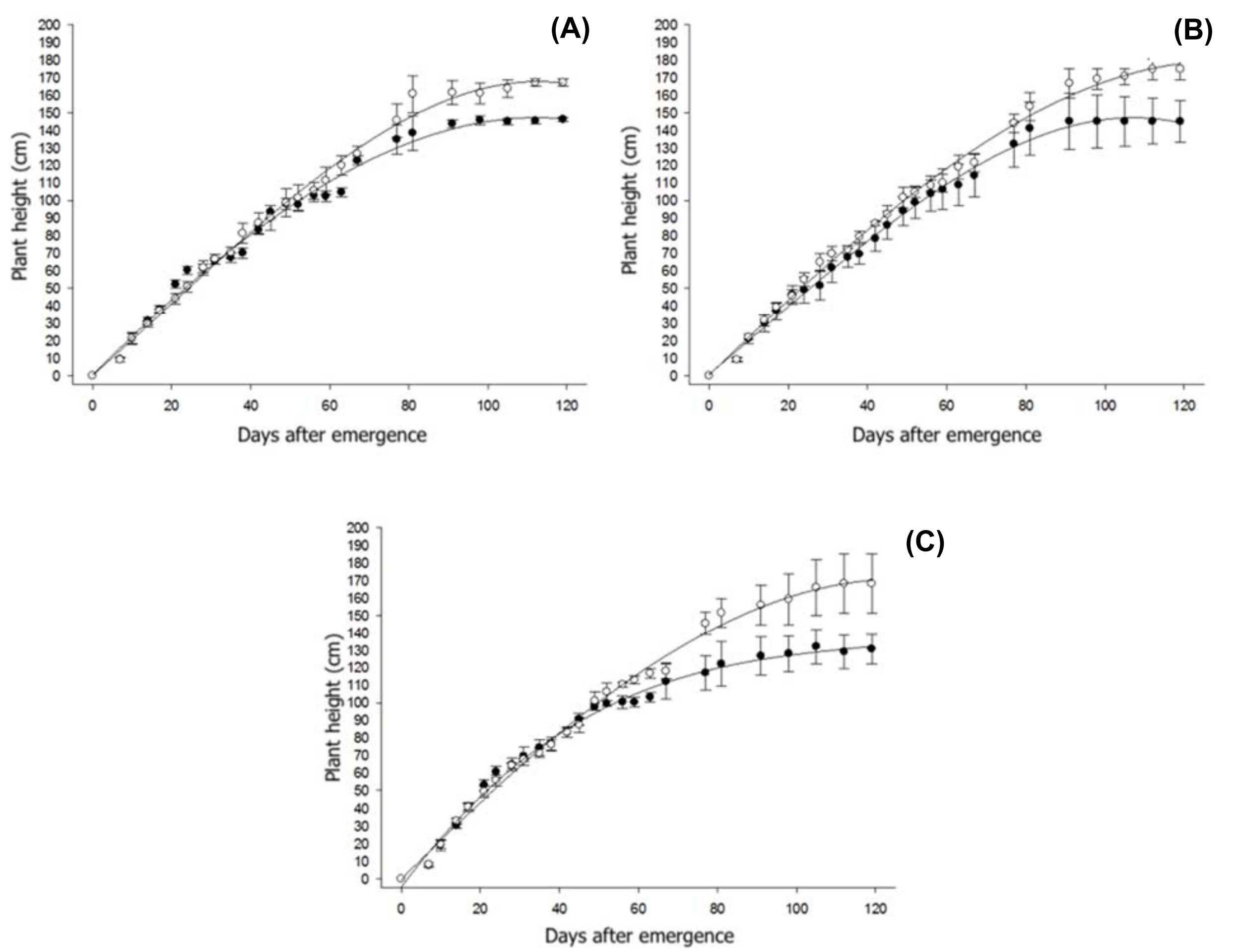
Plant height was measured at 7, 10, 14, 17, 21, 24, 28, 31, 35, 38, 42, 45, 49, 52, 56, 59, 63, 67, 77, 81, 91, 98, 105, 112, and 119 DAE. The number of tillers were counted at 14, 17, 21, 24, 28, 31, 35, 38, 42, 45, 49, 52, 56, 59, 63, and 67 DAE (days after emergence). Photosynthesis parameters were measured at 45 DAE using a LI-COR 6400XT portable photosynthesis meter calibrated at 400 or 700 µmol mol^{-1} of CO_2, 1,000 µmol m^2 s^{-1} light intensity, and between 55 and 60% relative humidity. The response variables evaluated were photosynthesis rate (A), stomatal conductance (Gs), and transpiration rate (E). The chlorophyll content was also measured at 45 DAE using the central-third section of the flag leaf from three tillers per plant, with a SPAD-502 portable chlorophyll meter (Minolta, Japan). The number of panicles per plant was counted at maturity. Spikelet sterility and number of seeds per plant were determined after harvest.

Data were subjected to analysis of variance and when the effect of genotype was significant, the means were compared using the Tukey's test ($p \leq 0.05$). The statistical analysis was conducted using the R Studio program, version 1.0.143. Regression analysis was conducted for plant height and the number of tillers with time. The cubic polynomial model was fitted to the data, based on the coefficient of determination (R^2), the statistical significance (F-test), and goodness-of-fit of the model.

3 Results and Discussion

Plant height was not affected by [CO_2] at the beginning of the growing season but starting at about 80 DAE, the plants were taller under elevated [CO_2] (700 µmol mol^{-1}) compared to those in ambient [CO_2] (400 µmol mol^{-1}) regardless of genotype or herbicide treatment (Figure 1). Further, the susceptible plants grew taller than the resistant ones under elevated [CO_2] later in the season. The regression parameters for plant height with time are presented in Table 1. Although the IMI-resistant and -susceptible genotypes both grew taller under elevated [CO_2], and were of the same height during most of the vegetative stage, the final heights (119 DAE) of the resistant and -susceptible weedy rice were 19.2 and 28.7% greater, respectively, when grown under elevated [CO_2], compared to plants in ambient [CO_2].

The weedy rice growing taller under high [CO_2] has important practical ramifications. First, weedy rice is already generally taller than rice currently (Shivrain et al., 2010). This contributes to the competitiveness of weedy rice with cultivated rice for obvious reasons. Furthermore, weedy rice has weak stalks. In high densities, weedy rice would lodge, taking down the rice crop with it, thereby increasing harvest losses. For weedy rice to grow even taller, or faster, is disastrous to rice production. Second, plant height differential between weedy and cultivated rice could alter the gene flow rate between the weed and the crop. This is highly relevant with respect to the continued use of herbicide-resistant rice technology to manage weedy rice and other weedy species in



Error bars correspond to 95% confidence intervals.

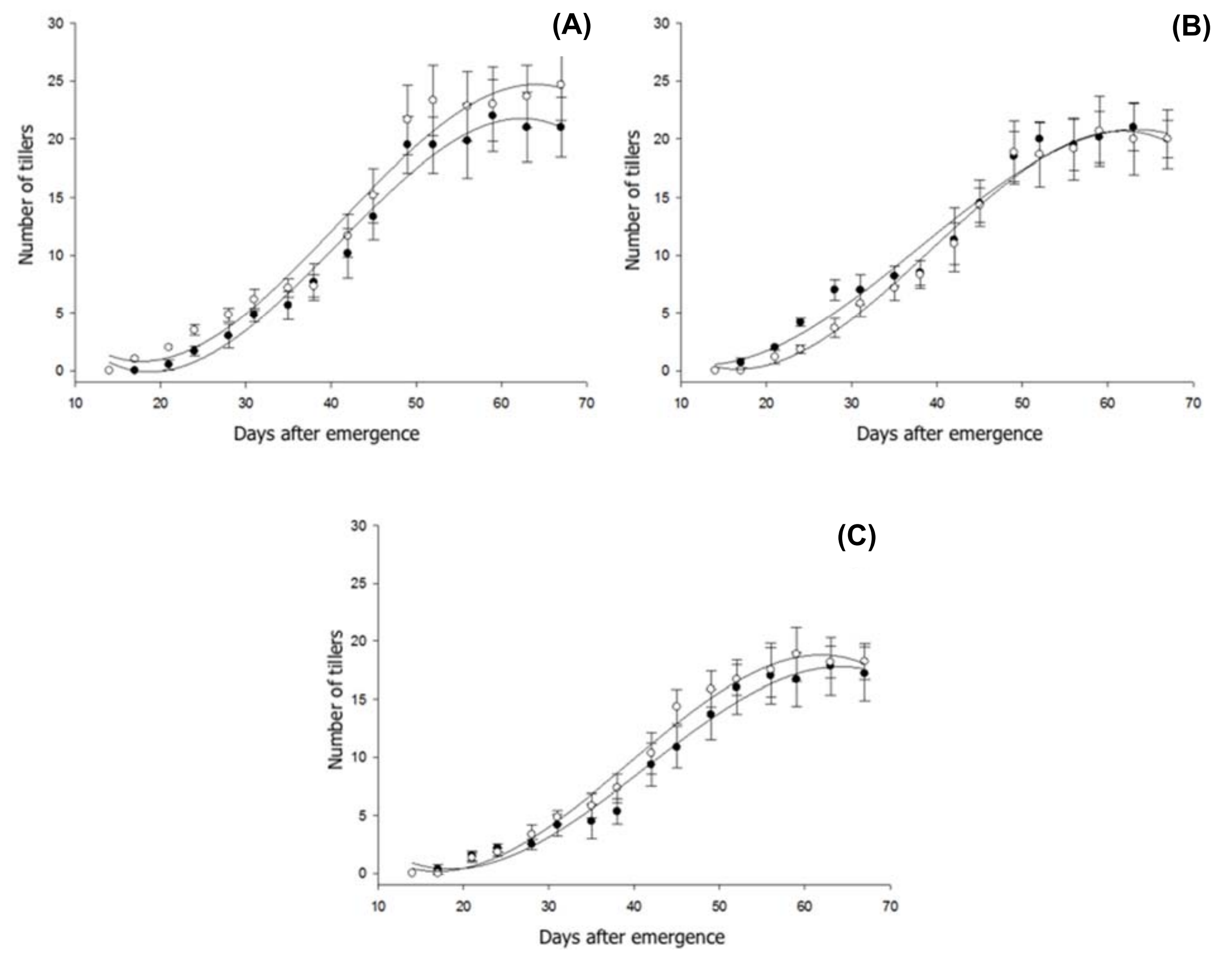
Figure 1 - Effect of atmospheric [CO_2] of 400 (filled circle) and 700 μmol mol^{-1} (empty circle) on plant height recorded over time of weedy rice genotypes with and without imazethapyr application (A = IMI-resistant without imazethapyr application; B = IMI-resistant with imazethapyr application; and C = susceptible biotype without herbicide application).

Table 1 - Parameters of the cubic polynomial equation for plant height and number of tillers of weedy rice genotypes under different atmospheric [CO_2] and as affected by imazethapyr application

Treatment	[CO_2] (μmol mol^{-1})	Regression parameters for plant height				
		y0	a	b	c	R^2
Resistant, without imazethapyr	400	0.2148	2.2753	-0.0056	-0.000036	0.99
	700	0.2595	1.9964	0.0041	-0.000077	0.99
Resistant, with imazethapyr	400	0.8381	1.9143	0.0025	-0.000071	0.99
	700	0.3230	2.1890	-0.0015	-0.000037	0.99
Susceptible, without imazethapyr	400	-4.7338	3.0019	-0.0232	0.000065	0.99
	700	-0.3165	2.2626	-0.0035	-0.000030	0.99
		Regression parameters for number of tillers				
Resistant, without imazethapyr	400	1.5022	-1.8500	0.0641	-0.0005	0.98
	700	14.2021	-1.6577	0.0595	-0.0005	0.97
Resistant, with imazethapyr	400	4.7329	-07310	0.0352	-0.0003	0.98
	700	10.5593	-1.3801	0.0527	-0.0004	0.99
Susceptible, with imazethapyr	400	11.1562	-1.2951	0.0452	-0.0004	0.98
	700	9.9930	-1.2811	0.0483	-0.0004	0.99

rice production and the resulting gene flow from crop to weed (Shivrain et al., 2008, 2009).

Depending on the response of weedy ecotype and cultivated rice, increased [CO_2] may reduce the height differential between the weed and crop, resulting in increased cross-pollination (Gealy et al., 2003). In the same context, Ziska et al. (2012) found that the increase in atmospheric [CO_2] increased the average height of cultivated and weedy rice plants and



Error bars correspond to 95% confidence intervals.

Figure 2 - Effect of atmospheric [CO_2] of 400 (filled circle) and 700 μmol mol^{-1} (empty circle) on the number of tillers per plant recorded over time of weedy rice genotypes with and without imazethapyr application (A = IMI-resistant without imazethapyr application; B = IMI-resistant with imazethapyr application; and C = susceptible biotype without herbicide application).

increased the synchronization of flowering between the weed and crop, resulting in increased gene flow from cultivated rice to weedy rice. Ziska et al. (2012) studied three concentrations of atmospheric CO_2: pre-industrial (300 μmol mol^{-1}), current (400 μmol mol^{-1}) and projected (600 μmol mol^{-1}). The authors recorded higher synchronization of flowering and cross-fertilization between cultivated rice 'CL 161' and weedy rice (StgS) under the highest [CO_2]. In turn, this has increased the number of weedy rice types and the number of herbicide-resistant hybrid weeds. These results, although preliminary, suggest that increased [CO_2] may alter the synchrony of flowering between the crop and some genotypes of the weedy relative and may reduce the effectiveness of herbicides through transfer of herbicide-resistant genes to the weedy relative.

The number of tillers tended to increase under high [CO_2] in both genotypes (Figure 2). The regression parameters for this response variable are presented in Table 1. On average, the IMI-resistant genotype produced 21.5 tillers at 67 DAE while the susceptible had 15.8 tillers. At this time, tiller production had reached its peak. In the field, without competition, strawhull weedy rice (like the ones used in this experiment) can produce an average of 85 tillers per plant (Shivrain et al., 2010). Tillering is crucial for competition (and weediness) because it determines how much space the plant can occupy and crowd-out other plants. It also directly relates to how much nutrients the weed can mine from the soil to support biomass production (Burgos et al., 2006). One reason that weedy rice is highly competitive against cultivated rice is that the former can produce about 3X to 9X more tillers than the latter (Shivrain et al., 2006, 2010). The number of tillers also contributes directly to the number of panicles per plant and, consequently, to seed production.

3.1 Photosynthesis-related responses

The photosynthetic parameters and the chlorophyll meter measurements (SPAD) are shown in Table 2. The SPAD reading is indicative of the chlorophyll

Table 2 - Mean values of photosynthetic rate (A), stomatal conductance (Gs), transpiration (E) and chlorophyll index using a chlorophyll meter (SPAD) for weedy rice genotypes under different atmospheric [CO_2]

Treatment main effect	A	Gs	E	SPAD
Genotype and herbicide effect, averaged across [CO_2]				
Susceptible, without imazethapyr	25.7$^{ns(3)}$	0.27^{ns}	3.4^{ns}	40.3 b$^{(1)}$
Resistant, with imazethapyr	26.0	0.26	3.6	43.8 a
Resistant, without imazethapyr	25.5	0.27	3.6	43.9 a
[CO_2] effect, averaged over genotypes and herbicide treatments				
400 μmol mol^{-1}	23.5*$^{(2)}$	0.29*	3.82*	42.6 $^{ns(4)}$
700 μmol mol^{-1}	28.1	0.24	3.20	42.7

(1) Means followed by different lower-case letters in a column differ by the Tukey's test ($p<0.05$). (2) Means followed by an asterisk* within a column differ by the Student's t-test ($p<0.05$). (3) ns not significant based on Tukey's test ($p<0.05$). (4) ns not significant based Student's t-test ($p<0.05$).

content of the plant. The IMI-resistant genotype had higher chlorophyll content than the susceptible one. These plants are different populations; therefore, we cannot attribute this difference to the resistance trait. However, despite the difference in chlorophyll content, the resistant and susceptible plants did not differ in photosynthesis rate (A), regardless of [CO_2]. This indicates that chlorophyll is not a limiting factor for carbon fixation in this situation. Across genotypes, the photosynthesis rate increased by 16% under high [CO_2] compared to ambient [CO_2].

The genotypes also did not differ in stomatal conductance (G_s), and transpiration rate (E) averaged across [CO_2], but both G_s and E were lower by 21% and 19%, respectively, under high [CO_2] compared to ambient [CO_2]. This indicates that at high [CO_2], weedy rice (a C3 plant) becomes more efficient as it achieves higher photosynthesis rate and increases water use efficiency. [CO_2] is the primary limiting factor for productivity of C3 plants because the RuBisCO enzyme facilitates both carbon fixation and respiration in the mesophyll cells (Hopkins and Hüner, 2009). Since the enzyme affinity for oxygen is higher than for CO_2, respiration is favored under low supply of CO_2 and the plant energy is wasted. Another consequence of this inefficient process is low water use efficiency (Rawson et al., 1977; Morison and Gifford, 1983). When the CO_2 limitation is relieved, photosynthesis rate is expected to increase, and water use efficiency improves as observed in our experiment.

In the long term, it is expected that under higher [CO_2], less stomata are needed for the plant to acquire sufficient CO_2 from the air as can be inferred from decades-old research on stomatal behavior of C3, C3-C4, and C4 species (Huxman and Monson, 2003). Stomates also do not need to stay fully open during the day as [CO_2] is high. Both situations reduce transpiration; therefore, water use efficiency is also expected to increase. All of the above should lead to higher yield of C3 plants such as rice, under high [CO_2].

3.2 Seed production

The susceptible genotype had higher spikelet sterility, fewer panicles, and, consequently, lower seed production per plant than the IMI-resistant genotype averaged across [CO_2] (Table 3). Again, this genotype difference could not be attributed to the resistance trait because these were different populations. The more relevant information pertains to the effect of [CO_2] on the seed production of these weedy rice populations. Averaged across genotypes, increasing the [CO_2] did not increase the number of panicles per plant. This is expected considering that high [CO_2] generally did not increase the number of tillers (Figure 2). On the other hand, high [CO_2] reduced the percentage of sterile spikelets, which partially contributed to increased seed production (Table 3). Under ambient [CO_2], weedy rice produced 1,105 g seed/plant. The number of seeds produced by weedy rice increased by 7% under high [CO_2] compared to ambient [CO_2]. It is important to note that the high number of seeds per plant is due to the fact that the plants were isolated without competition (one plant per pot). Ainsworth (2008) performed a meta-analysis of 71 articles evaluating the behavior of rice in response to the elevation of atmospheric [CO_2] between 1980 and 2007. The authors concluded that high [CO_2] contributes to the 7% increase in grain weight, 17% in the number of panicles, 27% in the number of grains, 9% in biomass, all of which, are consequences of increased photosynthesis. At the same time, increased [CO_2] also decreases stomatal conductance by 25%. This indicates that under high [CO_2] stomates may not stay fully open, or for as long, compared to under ambient [CO_2]. Our experiment produced the same result.

In a study conducted in FACE (free-air carbon dioxide enrichment) system to evaluate the

Table 3 - Mean values of spikelet sterility, number of panicles per plant, and number of seeds per plants of weedy rice as affected by genotypes, herbicide treatments and atmospheric [CO_2]

Treatment main effect	Spikelet sterility (%)	Number of panicles per plant	Number of seeds per plant
Genotype and herbicide effect, averaged across [CO_2]			
Susceptible, without imazethapyr	36.1 a[(1)]	18.0 b	674 b
Resistant, with imazethapyr	11.9 B	21.5 a	1,361 a
Resistant, without imazethapyr	12.6 B	21.5 a	1,395 a
[CO_2] effect, averaged over genotypes and herbicide treatments			
400 μmol mol^{-1}	21.5 *[(2)]	20.4 [ns]	1,105 *
700 μmol mol^{-1}	18.9	20.2	1,181

[(1)] Means followed by different lower-case letters (genotypes) differ by the Tukey test ($p<0.05$). [(2)] Means followed by * differ by the t-test ($p<0.05$). [ns] Not significant by the t-test ($p<0.05$).

interaction of nitrogen fertilizer application and the increase of atmospheric [CO_2] in rice, Liu et al. (2008) found that rice yield increased up to 34% in the enriched environment than in normal environment. Comparing the results of this study to those of Kim et al. (2003) and Yang et al. (2006), we can infer that the yield of *O. sativa* spp. *indica* is more responsive to [CO_2] enrichment than *O. sativa* spp. *japonica* by 13%, when plants are supplied with sufficient nitrogen. In other words, when [CO_2] is no longer limiting, other factors become critical for optimum growth and yield. In these studies, that factor is nitrogen. Therefore, for rice farmers to be able to take advantage of high CO_2 level, for instance, they would need to use more fertilizer. However, the study of Zhu et al. (2008) showed that rice does not respond significantly to high N fertilizer under high [CO_2]; on the contrary, the C4 barnyardgrass (*Echinochloa crus-galli*) does. The optimization of crop production and weed management to keep agriculture sustainable certainly becomes more complex as we experience climate change.

High temperature or low availability of N may lead to limitation of photosynthesis sinks (smaller number of tillers, spikelet sterility, among others), resulting in the reduction of photosynthetic capacity (Kim et al., 2003). Without balancing other growth factors, high [CO_2] or high temperature may have adverse effects on crop productivity. On the other hand, when there is adequate supply of N, and we have climate-resilient varieties, high yield can be realized under various scenarios of climate change (Hasegawa et al., 2013; Shimono and Okada, 2013; Ziska et al., 2014). When evaluating two rice cultivars under high atmospheric [CO_2], the cultivar with higher yield showed higher sink/source ratio, higher gene expression of RuBisCO, as well as higher RuBisCO activity (Zhu et al., 2014). Therefore, crop varieties (not just different weed species or weed genotypes) can respond differentially to climate change factors. Within the *Oryza* genus, there is high diversity in the growth and yield of weedy rice ecotypes or genotypes and rice cultivars in response to high temperature and elevated [CO_2] (Ziska et al., 2014). For this reason, rice improvement programs must include the use of genotypes responsive to increased [CO_2], especially those capable of producing more tillers and, consequently, higher yield.

The efficacy of herbicides may be affected by increasing atmospheric [CO_2] as high [CO_2] could change the plant morphologically, physiologically, and phenologically. These changes could be reflected in leaf morphology; root/shoot ratio; possible reduction in protein content of the leaf (site of action of some herbicides), changes in plant anthesis, or changes in the plant community (Ziska and Bunce, 2006; Ziska et al., 2004; Ziska, 2016). In this context, Ziska and Goins (2006) evaluated the weed seed bank during a growing season and found that the number of C3 grass plants was higher than C4 grass plants, along with other significant changes in the weed population of the area. The efficacy of a herbicide on a particular weed could be reduced as a result of increased root biomass relative to shoots as reported by Ziska et al. (2004) on the reduced efficacy of glyphosate on Canada thistle (*Cirsium arvense*) under elevated [CO_2]. Consequently, weed management approaches need to be adjusted.

4 Conclusions

IMI-resistant and -susceptible weedy rice responds similarly to [CO_2] enrichment. Increased [CO_2] increases competitive ability of the weedy rice populations tested, by means of increased plant height. Weedy rice seed yield also increases with increased [CO_2] by means of increased photosynthesis rate and reduced transpiration (increased water use efficiency). Increased seed production also means increased weed persistence as it increases the soil seedbank size. The application of imazethapyr on IMI-resistant weedy rice did not alter its response to [CO_2]; conversely, increased

[CO_2] does not change the resistance level of weedy rice to imazethapyr. High [CO_2] increases spikelet sterility, but this beneficial effect is negated by the overall increase in production of filled grains.

5 CONTRIBUTIONS

Conceptualization, LBP, NRB, LAA and JAN; Data curation, LBP, CO and JPR; Formal analysis, LBP and LAA; Funding acquisition, LAA, JAN and NRB; Investigation, LBP, JPR, CO and NRB; Supervision, JAN, LAA and NRB; Writing – original draft, LBP and NRB; Writing – review & editing, NRB, LBP, LAA, JAN, JPR and CO.

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