

ISSNe 1678-4596 SOIL SCIENCE



# Relationship between root exudation of organic carbon and physiological variables of irrigated rice cultivars

Janielly	Silva Costa	Moscôso1*	📵 Lean	dro Souza	da Sil	va² 👵		
Camila	Peligrinotti	Tarouco <sup>3</sup> 📵	Fernan	do Teixeira	a Nicol	oso³ 🕒		
Fabiane	Figueiredo	Severo <sup>2</sup>	Natália '	Tobin Aita	<sup>2</sup> 📵 L	uís Henrique	Ferreira	Prigol <sup>2</sup> @

**ABSTRACT**: Rhizospheric carbon resulting from root exudation is one of the substrates used by the soil microbiota, and reflects methane  $(CH_{\downarrow})$  emissions in anoxic environments such as irrigated rice cultivation. With the increase of the photosynthetic capacity of the plant in the reproductive period, there is greater accumulation of biomass which, in turn, increases the rate of root exudation. However, genotypic variations in the physiological aspects of rice plants may be related to the amount of root exudates. Ten cultivars of irrigated rice were evaluated for the exudation rate of total organic carbon  $(EXR_{Toc})$ , shoot dry matter (SDM), and physiological variables related to photosynthesis during the full flowering (blooming) period. Two experiments were conducted in the greenhouse of the Department of Soils of the UFSM (University of Santa Maria, Santa Maria, RS, Brazil) in a completely randomized experimental design. The cultivars presented significant differences in  $EXR_{Toc}$  SDM, and all physiological variables as well as positive and significant correlations between  $EXR_{Toc}$  and physiological variables. Early cultivars were more inefficient in the physiological variables reflecting reduced values of  $EXR_{Toc}$  and SDM whereas medium-cycle cultivars were more efficient with larger  $EXR_{Toc}$  and SDM reflections.

**Key words**: Oryza sativa, photosynthesis, exudates, methanogenesis.

# Relação entre exsudação radicular de carbono orgânico e variáveis fisiológicas de cultivares de arroz irrigado

**RESUMO**: O carbono rizosférico resultado da exsudação radicular é um dos substratos utilizados pela microbiota do solo, refletindo-se nas emissões de metano  $(CH_{\downarrow})$  em ambientes anóxicos, como no cultivo de arroz irrigado. Com o aumento da capacidade fotossintética da planta no período reprodutivo, ocorre acúmulo maior de biomassa, que por sua vez, impulsiona aumento na taxa de exsudação radicular. Entretanto, variações genotípicas nos aspectos fisiológicos das plantas de arroz podem se relacionar com a quantidade de exsudatos radiculares. Foram avaliadas dez cultivares de arroz irrigado quanto a taxa de exsudação de carbono orgânico total ( $TEX_{cor}$ ), matéria seca da parte aérea (MSPA) e variáveis fisiológicas relacionadas com a fotossíntese no período de florescimento pleno. Dois experimentos foram conduzidos na casa de vegetação do Departamento de Solos da UFSM em delineamento experimental inteiramente casualizado. As cultivares apresentaram diferenças significativas na  $TEX_{cor}$  na MSPA e em todas as variáveis fisiológicas, bem como, correlações positivas e significantes entre  $TEX_{cor}$  e as variáveis fisiológicas, sendo que as cultivares de ciclo precoce se mostraram mais ineficientes nas variáveis fisiológicas refletindo em valores reduzidos de  $TEX_{cor}$  e MSPA, enquanto que as cultivares de ciclo médio se mostraram mais eficientes com reflexos em maiores  $TEX_{cor}$  e MSPA.

Palavras-chave: Oryza sativa, fotossíntese, exsudatos, metanogênese.

#### INTRODUCTION

Rhizospheric carbon resulting from root exudation is one of the main substrates used by the soil microbiota, reflecting carbon dioxide (CO<sub>2</sub>) emissions in aerobic and methane (CH<sub>4</sub>) in anoxic environments such as irrigated rice cultivation

(GARCIA-ORENES et al., 2010). As a result of the increase in the photosynthetic capacity of the plant during the reproductive period, there is greater accumulation of biomass which, in turn, boosts the increase in rhizodeposition, influencing the rhizospheric carbon dynamics (BATATACHARYYA et al., 2013). Several studies have reported intense

Programa de Pós-graduação em Ciência do Solo, Universidade Federal de Santa Maria (UFSM), 97105-900, Santa Maria, RS, Brasil. E-mail: janiellycosta@hotmail.com. \*Corresponding author.

<sup>&</sup>lt;sup>2</sup>Departamento de Solos, Universidade Federal de Santa Maria (UFSM), Santa Maria, RS, Brasil.

<sup>&</sup>lt;sup>3</sup>Departamento de Biologia, Universidade Federal de Santa Maria (UFSM), Santa Maria, RS, Brasil.

Moscôso et al.

methane emission peaks in areas of irrigated rice cultivation coinciding with plants flowering period. These findings show the contribution of exuded carbon compounds as a substrate for the generation of greenhouse gases (ITOH et al. al., 2011; SU et al., 2015). The microorganisms present in the anoxic environments, mainly the methanogenic bacteria, use carbon from root exudates as final acceptors of electrons in their electron transport chain which result in the production of CH<sub>4</sub>.

The genetic variability found among rice traditional cultivars or among those developed by breeding programs, of medium-cycle (medium duration cultivar) or early-cycle (short duration cultivar), may interfere with the amount of photo-assimilated carbon that is translocated to the plants root and then exuded in the form of organic compounds containing carbon. This variability should be reflected in different physiological variables that are associated with the photosynthetic activity of the plant which should also be closely related to root exudation. The knowledge of this relationship may help in the selection of materials to be cultivated and in rice breeding programs according to the goal of the selection of the materials.

Photosynthesis is the physiological process by which plants capture solar energy of and convert it into chemical energy. This process involves oxidation reactions in which water is oxidized with the release of O<sub>2</sub>, and CO<sub>2</sub> is reduced for carbon fixation and formation of organic compounds (SOUZA, 2016). However, photosynthesis is closely related to transpiration through the stomata. At the same time that the stomata offer resistance to the diffusion of water vapor from the leaf into the atmosphere, these pores also constitute a barrier to CO<sub>2</sub> capture (PEARCY & PTISTISCH, 1991).

Genotypic variations in the photosynthetic metabolism of rice plants such as the rate of  $\rm CO_2$  net assimilation, stomatal conductance, intercellular  $\rm CO_2$  concentration, and transpiratory rate have been reported in the literature (YOSHIDA et al., 1976; GU et al., 2012; LORENÇONI, 2014). Therefore, it is important to understand how the morphophysiological variables of different irrigated rice cultivars may be related to the supply of root exudates that function as a source for the methanogenesis process in rice cultivation under the flood irrigation regime.

The present study aimed to quantify the total organic carbon exudation rate of irrigated rice cultivars during the full flowering period and to correlate this exudation with physiological variables of each cultivar.

### MATERIALS AND METHODS

Two experiments were carried out at the greenhouse of the Department of Soils (DS) of the Universidade Federal de Santa Maria (UFSM), Santa Maria, RS, Brazil. In the first experiment, 10 cultivars of irrigated rice were cultivated in nutrient solution (FURLANI & FURLANI, 1988), 6 early cycle cultivars ('BRS Querência', 'Embrapa 130', 'IRGA 421', 'Koshihikari', 'BRS Pampa' and 'IRGA 430') and 4 medium cycle cultivars ('BRS Taim', 'IAS Formosa', 'IRGA 422', 'IRGA 428'). Vessels with a capacity of 7L containing 6L of nutrient solution were conducted in a completely randomized experimental design with three replicates.

Plants were individually grown until the full flowering period of each cultivar, when the concentrations of total organic carbon (TOC) of root exudates were quantified. In this procedure, which based on the method adapted from AULAKH et al. (2001), roots were washed with distilled water and each plant was placed in glass bottles (containing 600mL of CaSO<sub>4</sub> solution at 0.01mol L<sup>-1</sup> - collection medium) so that the roots of plants remained completely submerged in the collection medium for a period of 2 hours. Immediately after collection, each sample from the collection medium was routed to the TOC-LCPH/CPN total organic carbon analyzer apparatus, discounting any values of the non-plant collection medium functioning as a blank.

The rates of TOC exudation released by roots of rice cultivars were calculated by equation 1:

$$EXR_{Toc} = \frac{C_{exp} - C_C \times 600 \times 24}{PC} (1)$$

In which: EXR<sub>Toc</sub> is the rate of TOC exudation released by roots of irrigated rice cultivars (mg C plant<sup>-1</sup> day<sup>-1</sup>), C<sub>exp</sub> is the exuded carbon per plant (mg mL<sup>-1</sup>), C<sub>c</sub> is the carbon of the control collection medium, 600 is the amount of collection medium used for each plant (mL plant <sup>-1</sup>), 24 is the number of hours of the day, and PC is the collection period of the exudates (2 hours).

The second experiment with the same irrigated rice cultivars was performed in vessels with a capacity of 9L containing 7kg of a typical hydromorphic haplic planosol soil (EMBRAPA, 2013). Soil was sampled in the experimental field of DS of the UFSM, previously air dried, slashed, and sieved in a 4mm mesh with the cultivation of 6 rice plants per vessel in a completely randomized experimental design with three replicates. Vessels remained under continuous flooding until the

maturation stage of the cultivars and were then fertilized according to the recommendations proposed by SOSBAI (2016).

Physiological evaluations were carried out using the "Infra Red Gas Analyzer - IRGA" model LI-6400XP, LI-COR, in two phenological phases, according to the scale published by COUNCE et al. (2000). The first reading was carried out when the early cultivars were in the full bloom stage (anthesis) and the medium-cycle cultivars were in the panicle exsertion phase. The second reading was carried out when the early-cycle cultivars were in the physiological maturation stage and the medium-cycle cultivars were mostly in the anthesis stage. Readings were carried out in two plants per vessel, in the middle third of the fully expanded flag leaf of the stem, with a photosynthetic radiation of 1500µmol m<sup>2</sup> s<sup>-1</sup> and CO<sub>2</sub> concentration of 400µmol mol<sup>1</sup>. We measured the net assimilation rate of CO<sub>2</sub> (A - µmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), the stomatal conductance of water vapors (Gs - mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>), the transpiration rate (E - mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>), the intercellular CO<sub>2</sub> concentration (Ci - μmol m<sup>-2</sup> s<sup>-1</sup>). From these, it was possible to calculate the water use efficiency (WUE - mol CO, mol H,O-1) obtained by the ratio between the amount of CO, fixed by photosynthesis and the amount of transpirated water, and the instantaneous efficiency of carboxylation by Rubisco (A/Ci) obtained by the relation between the amount of CO, fixed by photosynthesis and the intercellular CO<sub>2</sub> concentration. At the end of the experiment, the dry matter of the aerial part of each cultivar was quantified after drying in a greenhouse with forced air ventilation at 65°C.

The means and standard deviation (SD) of the data were calculated, and analysis of variance and F test (P<0.05) were performed with a subsequent Scott-Knot test (P<0.05) as well as phenotypic and genotypic correlations between EXR<sub>Toc</sub> and physiological variables. Phenotypic correlations were estimated by t-test, and the genotypic correlations were estimated by "bootstrap" with 5000 simulations. Correlations were classified according to SHIMAKURA & RIBEIRO JUNIOR (2012) as: 0.0 to 0.19 (very weak), 0.20 to 0.39 (weak), 0.40 to 0.69 (moderate), 0.70 to 0.89 (strong), and 0.90 to 1.00 (very strong). We used the computer program (software) in genetics and statistics Genes in the statistical procedures (CRUZ, 2006).

### RESULTS AND DISCUSSION

The cultivars presented significant differences in the variables evaluated in the two

experiments, carbon exudation rate, shoot dry matter quantification and in all physiological variables in the two readings. The highest rates of carbon exudation were reported in the cultivars BRS Taim, BRS Pampa, and IRGA 428, and among the lowest were the cultivars Koshihikari, IRGA 421 and Embrapa 130 (Table 1). In general, the cultivars of early cycle were those that obtained lower rates of exudation. This is probably due to the fact that these cultivars have a lower development cycle and have lower dry matter production. The longer the cultivars remain in the field, the higher the photosynthetic rates are obtained, resulting in a higher accumulation of biomass, greater translocation of carbon to the root, and greater rhizo deposition of carbon in the soil (BHATTACHARYYA et al., 2013).

The cultivars 'BRS Pampa' and 'IRGA 428' also obtained the highest values of net CO<sub>2</sub> assimilation rate in the 1<sup>st</sup> reading, while the cultivar 'IRGA 421' presented the lowest value. In the 2<sup>nd</sup> reading, the cultivars 'Embrapa 130', 'BRS Taim' and 'BRS Pampa' presented the highest values, whereas the cultivar 'IRGA 421' continued to present the lowest value. These results may be associated with root exudation as cultivars 'BRS Taim' and 'IRGA 428' (both medium cycle cultivars) and 'BRS Pampa' were the ones that had the highest exudation rate, highest rates of assimilation of CO<sub>2</sub>, and highest values of dry matter as well as early-stage 'IRGA 421' which presented the lowest values for these variables (Table 1).

The highest values of stomatal conductance were observed in the cultivars 'IRGA 428' and 'BRS Pampa' (1st and 2nd reading) and the cultivar 'Embrapa 130' (2<sup>nd</sup> reading). The lowest results were observed in the cultivars 'IAS Formosa' and IRGA 421 (both readings) and in the cultivar 'Koshihikari' (2nd reading). High stomatal conductance is possible in situations of abundant water availability as in the case of irrigated rice cultivation. Although, transpiration is elevated under these conditions, it allows a higher rate of CO, absorption ensuring its continuous fixation during photosynthesis (TAIZ et al., 2017). This higher CO<sub>2</sub> fixation may increase the amount of carbon to be translocated to the roots. Considering that the cultivars of rice were being maintained with the same irrigation and were under the same environment, the observed differences are inherent characteristics of each cultivar as in the cultivars 'BRS Pampa' and 'IRGA 428' that presented high stomatal conductance and high net assimilation rates of CO<sub>2</sub> which provides high rates of root exudation.

In general, the cultivars that presented the highest rates of stomatal conductance and liquid CO<sub>2</sub>

Table 1 - Mean values (n = 30) obtained for EXR<sub>Toc</sub> in the full flowering stage (nutrient solution experiment) 1<sup>st</sup> reading (at 78 days after transplant) of the physiological variables (soil experiment) evaluated in 10 cultivars of irrigated rice under greenhouse conditions.

Treatments	A	Gs	Ci	Е	WUE	A/Ci	$EXR_{Toc}$
BRS Querência	24.16d	1.37b	307.8e	11.23b	2.30b	0.08c	54.90c
Embrapa 130	23.63d	0.88d	313.9d	8.74d	2.35b	0.08c	20.72c
IRGA 421	15.19e	0.84d	343.6a	8.36d	2.01c	0.04d	19.80c
Koshihikari	24.08d	1.09c	327.3c	9.97c	2.28b	0.07c	1.56d
BRS Pampa	33.13a	1.41b	323.5c	14.13a	2.35b	0.10a	273.90b
IRGA 430	23.38d	1.22c	329.3c	10.92b	2.08c	0.07c	33.68c
BRS Taim	26.11c	1.27c	334.2b	10.75b	2.12c	0.08c	394.34a
IAS Formosa	26.22c	0.63e	306.6e	9.84c	2.77a	0.09b	54.48c
IRGA 422	28.14b	1.21c	325.0c	11.59b	2.37b	0.09b	29.88c
IRGA 428	28.07b	1.61a	326.7c	12.18b	2.18c	0.09b	252.10b
General mean	25.23	1.15	323.76	10.76	2.28	0.08	126.73
CV (%)	5.01	4.21	0.87	8.65	2.43	3.83	19.47

Mean values (n = 30) obtained for shoot dry matter and  $2^{nd}$  reading (at 93 days after transplant) of the physiological variables (soil experiment) evaluated in 10 cultivars of irrigated rice under greenhouse conditions.

enperment) e talanta in 10 can talo et inigate neo anari givermouse contantons.							
Treatments	A	Gs	Ci	E	WUE	A/Ci	SDM
BRS Querência	16.11d	0.96c	340.80b	7.72d	1.93e	0.04c	63.13c
Embrapa 130	30.54a	1.42b	325.09d	10.78b	2.89c	0.10a	46.23f
IRGA 421	6.80e	0.81d	368.39a	7.11d	1.02g	0.02d	53.56e
Koshihikari	16.07d	0.58e	333.55c	7.29d	2.17d	0.05c	56.85d
BRS Pampa	28.08b	1.91a	335.67c	11.91a	2.23d	0.09a	69.22a
IRGA 430	16.34d	0.97c	313.08e	9.63c	1.64f	0.05c	61.44c
BRS Taim	27.43b	0.83d	314.98e	9.29c	3.01b	0.09a	66.50b
IAS Formosa	16.92d	0.67e	323.90d	7.69d	1.98e	0.05c	59.24c
IRGA 422	20.31c	1.15c	339.64b	7.06d	3.33a	0.06b	60.58c
IRGA 428	21.74c	1.26b	340.03b	9.51c	2.20d	0.06b	65.21b
General mean	20.0	1.06	333.53	8.80	2.24	0.06	60.20
CV (%)	8.11	4.56	0.91	7.48	2.06	4.21	2.94

A = net assimilation rate of CO<sub>2</sub> ( $\mu$ mol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), Gs = stomatal conductance (mol H<sub>2</sub>O m<sup>-2</sup>s<sup>-1</sup>), Ci = concentration of intercellular CO<sub>2</sub> ( $\mu$ mol CO<sub>2</sub> mol<sup>-1</sup>), E = transpiration rate (mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>), WUE = water use efficiency (mol CO<sub>2</sub> mol H<sub>2</sub>O<sup>-1</sup>), A/Ci = instantaneous carboxylation efficiency by Rubisco, EXR<sub>Toc</sub> = total organic carbon exuded from roots (mg C plant<sup>-1</sup> day<sup>-1</sup>), SDM = shoot dry matter of (g<sup>-1</sup> vessel). Means followed by the same letter in the column do not differ from each other by the Scott-Knott test (P <0.05).

assimilation were those with the lowest concentration of intercellular  $\mathrm{CO}_2$  and vice versa (Table 1). Apparently these physiological differences between the cultivars showed the presence of possible variations among the cultivars regarding photosynthetic  $\mathrm{CO}_2$  utilization. This means that the assimilated  $\mathrm{CO}_2$  is being consumed to form the final photosynthesis products such as sucrose or starch or even exudates, thus reducing intercellular  $\mathrm{CO}_2$  concentration values

and indicating a high photosynthetic CO<sub>2</sub> utilization.

With regard to the transpiration rate, the 'BRS Pampa' cultivar presented the highest value in both readings whereas the 'IRGA 421' the lowest one together with the cultivar 'Embrapa 130' in the 1st reading, and the cultivars 'Koshihikari', 'IRGA 422', 'BRS Querência' (early cycle), and 'IAS Formosa' in the 2nd reading. In general, the transpiration rate values are in agreement with the values of stomatal

conductance. Vegetative transpiration, besides being influenced by environmental or external factors, is also influenced by internal factors conditioned by the morphological and physiological characteristics of the plants (PUPATTO, 2003). Reduction in the transpiration rate often results in an increase in water use efficiency since a smaller amount of water is transpired to produce a certain amount of dry matter. This is observed in the cultivar 'BRS Taim' (medium cycle cultivar) that reduced its transpiration, thus increasing the efficiency of water use and stimulating a higher rate of carbon exudation.

Regarding to the values of instantaneous carboxylation efficiency by Rubisco observed in the 1st reading, the highest values were found in the cultivars 'BRS Pampa', 'IRGA 428', 'IRGA 422', and 'IAS Formosa' whereas the cultivar 'IRGA 421' presented the lowest value. Already 2<sup>nd</sup> reading, the cultivar 'BRS Pampa' continued to present one of the highest values for this variable, accompanied by cultivars 'BRS Taim' and 'Embrapa 130' whereas 'IRGA 421' followed with the lowest value obtained. High values of internal CO, concentration associated with low rates of CO, net assimilation indicate a decrease in the instantaneous carboxylation efficiency due to the reduced availability of ATP, NADPH, and substrate to Rubisco resulting in the decrease of the activity of this essential enzyme in the CO, binding process (SILVA et al., 2015). This may explain the low efficiency of Rubisco obtained by 'IRGA 421' which may have influenced the values of exudation rate and shoot dry matter in this early cycle cultivar. In contrast, the cultivars that presented the highest rate of CO, net assimilation were those that obtained the lowest concentration of intercellular CO, and, as a result, higher values of instantaneous efficiency of carboxylation by Rubisco.

As the cultivars had the same condition of luminosity, water availability and mineral nutrition, we may affirm that the obtained differences are actually linked to morphophysiological factors specific to each cultivar.

The physiological variables and the exudation rate, in general, presented genotypic correlations that, if not similar to the phenotypic ones, were higher and of equal sign, indicating that there was no influence of the environment on the expression of the characters and effective experimental precision. This ensures that the correlations and differences presented between the cultivars are expressions linked to morphophysiological factors specific to each cultivar (Table 2).

There was a strong and moderate positive correlation between transpiration rate and exudation rate in the  $1^{st}$  and  $2^{nd}$  readings, respectively, and a

strong correlation between stomatal conductance and exudation rate in the 1st reading. This is the result of strong and very strong positive correlations in the two readings between stomatal conductance and transpiration rate (Table 2). Thus, the cultivars with higher transpiration were those that obtained greater stomatal conductance whereas those with lower transpiration had the lowest values for stomatal conductance therefore influencing exudation rate (see Table 1). Positive correlations were observed between CO, net assimilation rate and moderate exudation rate in the 1st and 2nd readings (Table 2) which reinforces the hypothesis that high photosynthetic rates are directly related to the exuded carbon of the roots of rice cultivars. It is estimated that 30 to 60% of the photosynthetically fixed carbon in the plant would be translocated to the roots, and a considerable proportion of this carbon (up to 70%) could be released into the rhizosphere by means of rhizodeposition (YIQI & ZHOU, 2010).

Significant correlations were also observed in the physiological variables (Table 2). Positive correlations between the net assimilation rate of  $CO_2$  and stomatal conductance under optimal water conditions as in the present study have been observed in rice by KONDO et al. (2000) and LORENÇONI (2014). The strong and very strong positive correlations between  $CO_2$  net assimilation rate and transpiration rate in both readings indicate the effectiveness of the stomatal adjustment mechanism on the transpiration and  $CO_2$  assimilation rates, which are reflected in the water use efficiency and may explain the positive correlations obtained between these variables and the instantaneous efficiency of carboxylation by Rubisco.

For rice, which is a C3 plant, about 400 molecules of water are lost to each carbon molecule fixed by photosynthesis resulting in high water use efficiency for this species. This high value in the C3 plants results from the: concentration gradient governing the water loss which is about 50 times greater than the one that regulates the CO<sub>2</sub> influx. CO<sub>2</sub> diffuses 1.6 times slower by air than water (as the CO<sub>2</sub> molecule is larger than the H<sub>2</sub>O molecule and has a lower diffusion coefficient). CO<sub>2</sub> has to cross the plasma membrane, the cytoplasm and the chloroplast envelope before being assimilated into the chloroplast. These membranes increase the resistance of the CO<sub>2</sub> diffusion pathway (TAIZ et al., 2017).

Based on the results of this study, we were able to detect a response variability among rice cultivars in the use of photosynthetic CO<sub>2</sub> due to the physiological differences that these cultivars present.

Moscôso et al.

Table 2 - Phenotypic (rf) and genotypic (rg) correlations between six physiological variables (soil experiment) at 78 days after transplantation (1st reading) and EXR<sub>Toc</sub> exudate of the roots in the full flowering stage (experiment in nutrient solution), evaluated in ten cultivars of irrigated rice under greenhouse conditions.

Variables	R	Gs	Ci	E	WUE	A/Ci	$EXR_{Toc}$
A	rf	0.53	-0.61	0.88**	0.46	0.98**	0.53
	rg	0.54	-0.60	$0.90^{++}$	0.46	$0.98^{++}$	0.55
gs	rf		0.27	$0.85^{**}$	-0.48	0.40	0.87**
	rg		0.27	0.84**	-0.46	0.42	$0.88^{++}$
ci	rf			-0.19	-0.96**	-0.72*	0.28
	rg			-0.22	-0.96++	$0.71^{*}$	0.28
E	rf				0.01	$0.80^*$	$0.79^{*}$
	rg				0.05	0.83++	$0.80^{+}$
WUE	rf					0.59	-0.41
	rg					0.59	-0.40
A/ci	rf						0.41
	rg						0.43
		At 9	3 days after transp	olantation (2 <sup>nd</sup> read	ding)		
Variables	R	Gs	Ci	Е	WUE	A/Ci	$EXR_{Toc}$
A	rf	0.63*	-0.97**	0.83**	0.83**	$0.99^{**}$	0.68
	rg	0.62	-0.97**	0.83++	0.83+	$0.99^{++}$	$0.68^{+}$
gs	rf		-0.47	$0.90^{**}$	0.21	0.62	0.38
	rg		-0.48	0.91**	0.20	0.61	0.38
ci	rf			-0.75*	-0.86**	-0.97**	-0.71*
	rg			-0.75+	-0.86+	-0.98+	-0.71+
E	rf				0.41	0.83**	$0.67^{*}$
	rg				0.42	0.84++	$0.67^{+}$
WUE	rf					$0.83^{*}$	0.41
	rg					0.83+	0.41
A/ci	rf						$0.70^{*}$
	rg						$0.70^{+}$

A = net assimilation rate of  $CO_2$  (µmol  $CO_2$  m<sup>-2</sup> s<sup>-1</sup>), Gs = stomatal conductance (mol  $H_2O$  m<sup>-2</sup>s<sup>-1</sup>), Ci = concentration of intercellular  $CO_2$  (µmol  $CO_2$  mol<sup>-1</sup>), E = transpiration rate (mmol  $H_2O$  m<sup>-2</sup> s<sup>-1</sup>), E = water use efficiency (mol E0 mol E1), E2 = instantaneous carboxylation efficiency by Rubisco, E1, E2 = total organic carbon exuded from roots (mg E1), E3 and E4 = significant at 1 and 5% probability by the t-test. E4 and E5 = significant at 1 and 5% by the *Bootstrap* method with 5,000 simulations.

Such behavior directly influenced the root exudation rates so that these correlations may help explain the behavior of irrigated rice cultivars in the supply of exudates to the flooded soil for methanogenesis and subsequent CH<sub>4</sub> emission.

The present studies highlighted the importance of quantification and further our knowledge on the exuded carbon ratios of the roots of different rice cultivars with respect to the physiological aspects and future possible  $\mathrm{CH_4}$  emissions by these cultivars. A cultivar may have a good photosynthetic performance that will reflect on its productivity. However, part of that carbon may be translocated to the roots and become available to methanogenic bacteria from the soil. As a result, the most productive cultivar may also be the one that emits more  $\mathrm{CH_4}$  gas into the atmosphere. Finally,

this study elucidated one of the impacts of rice cultivation on the environment and broaden our knowledge of the subject.

#### **CONCLUSION**

Irrigated rice cultivars show differences between each other in terms of carbon exudation, shoot dry matter, and physiological variables linked to photosynthesis. Early cultivars 'IRGA 421', 'Koshihikari', and 'IRGA 430' were more inefficient in variables physiological parameters reflected in reduced values of exudation and dry matter of the aerial part whereas the cultivars of medium-cycle 'BRS Taim' and 'IRGA 428' were more efficient with influence in the rate of exudation and dry matter of the aerial part.

#### ACKNOWLEDGMENTS

The authors gratefully acknowledge Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for granting scholarships and funding for research, and IRGA and EMBRAPA for providing irrigated rice cultivar seeds that were used in this study. This work was carried out with the support of the Coordination of Improvement of Higher Education Personnel - Brazil (CAPES) - Financing Code 001.

## DECLARATION OF CONFLICTING INTERESTS

The authors declare that there is no conflict of interest which could constitute an impediment to the publication of this article.

#### **AUTHORS' CONTRIBUTIONS**

The authors contributed equally to the manuscript.

#### REFERENCES

AULAKH, M. S. et al. Impact of root exudates of different cultivars and plant development stages of rice (*Oryza sativa* L.) on methane production in a paddy soil. **Plant and Soil**, v. 230, p.77-86, 2001. Available from: <a href="https://link.springer.com/article/10.1023/A:1004817212321">https://link.springer.com/article/10.1023/A:1004817212321</a>. Accessed: Apr. 23, 2016. doi: 10.1023/A:1004817212321.

BHATTACHARYYA, P. et al. Influence of elevated carbon dioxide and temperature on belowground carbon allocation and enzyme activities in tropical flooded soil planted with rice. **Environmental Monitoring and Assessment**, v. 185, p. 8659-8671, 2013. Available from: <a href="https://link.springer.com/article/10.1007/s10661-013-3202-7">https://link.springer.com/article/10.1007/s10661-013-3202-7</a>. Accessed: Mar. 15, 2017. doi: 10.1007/s10661-013-3202-7.

COUNCE, P.A. et al. A uniform, objective, and adaptative system for expressing rice development. **Crop Science**, v. 40, p. 436-443, 2000. Available from: <a href="https://pdfs.semanticscholar.org/b054/14c3be8fde57e126b0f3586395a62e9c993e.pdf">https://pdfs.semanticscholar.org/b054/14c3be8fde57e126b0f3586395a62e9c993e.pdf</a>>. Accessed: Jun. 16, 2017. doi: 10.2135/cropsci2000.402436x.

CRUZ, C. D. **Programa Genes**: Análise multivariada e simulações. Viçosa: Universidade Federal de Viçosa (UFV), 2006. Available from: <a href="http://arquivo.ufv.br/dbg/genes/gdown1.htm">http://arquivo.ufv.br/dbg/genes/gdown1.htm</a>>. Accessed: Apr. 14, 2016.

EMBRAPA-Empresa Brasileira de Pesquisa Agropecuária, Centro Nacional de Pesquisa de Solos. **Sistema Brasileiro de Classificação de Solos**. 3º ed. rev. ampl. Brasília, 2013, 353 p.

FURLANI, A.M.C.; FURLANI, P.R. Composição e pH de soluções nutritivas para estudos fisiológicos e seleção de plantas em condições nutricionais adversas. Campinas: Instituto Agronômico, 1988. 34p. (Technical bulletin, 121).

GARCIA-ORENES, F. et al. Soil microbial biomass and activity under different agricultural management systems in a semiarid Mediterranean agroecosystem. Soil & Tillage Research, v. 109, p. 110-115, 2010. Available from: <a href="https://www.sciencedirect.">https://www.sciencedirect.</a>

com/science/article/pii/S0167198710000838>. Accessed: Mar. 05, 2017. doi: 10.1016/j.still.2010.05.005.

GU, J. et al. Physiological basis of genetic variation in leaf photosynthesis among rice (*Oryza sativa* L.) introgression lines under drought and well-watered conditions. **Journal of Experimental Botany**, v. 63, p. 5137-5153, 2012. Available from: <a href="https://academic.oup.com/jxb/article/63/14/5137/536113">https://academic.oup.com/jxb/article/63/14/5137/536113</a>>. Accessed: Mar 18, 2018. doi: 10.1093/jxb/ers170.

ITOH, M. et al. Mitigation of methane emissions from paddy fields by prolonging midseason drainage. **Agriculture, Ecosystems and Environment**, v. 141, p. 359-372, 2011. Available from: <a href="https://www.sciencedirect.com/science/article/pii/S0167880911001034">https://www.sciencedirect.com/science/article/pii/S0167880911001034</a>>. Accessed: Mar. 30, 2018. doi: 10.1016/j.agee.2011.03.019.

KONDO, M. et al. Anatomy of nodal roots in tropical upland and lowland rice varieties. **Plant Production Science**, v. 3, p. 437-445, 2000. Available from: <a href="https://www.tandfonline.com/doi/abs/10.1626/pps.3.437">https://www.tandfonline.com/doi/abs/10.1626/pps.3.437</a>>. Accessed: Mar. 23, 2018. doi: 10.1626/pps.3.437.

LORENÇONI, R. CO<sub>2</sub> assimilation of modern and traditional rice genotypes subjected to water stress. **Brazilian journal of agriculture-Revista de Agricultura**, v. 89, p. 127-140, 2014. Available from: <a href="http://www.fealq.org.br/ojs/index.php/revistadeagricultura/article/view/60">http://www.fealq.org.br/ojs/index.php/revistadeagricultura/article/view/60</a>>. Accessed: Feb. 18, 2018.

PEARCY, R.W.; PFITSCH, W.A. Influence of sunflecks on the  $\delta$  13 C of Adenocaulon bicolor plants occurring in contrasting forest understory microsites. **Oecologia**, v. 86, p. 457-462, 1991. Available from: <a href="https://link.springer.com/article/10.1007/BF00318310">https://link.springer.com/article/10.1007/BF00318310</a>. Accessed: Jun. 18, 2018. doi: 10.1007/BF00318310.

PUPATTO, J.G.C. Trocas gasosas e eficiência de uso da água da cultura do arroz irrigado por aspersão em função da aplicação de silício. 2003. 166 f. Tese (Doutorado em Agronomia) Curso de Pós-graduação em Agronomia, Universidade Estadual Paulista (UNESP). Available from: <a href="https://repositorio.unesp.br/handle/11449/99995">https://repositorio.unesp.br/handle/11449/99995</a>. Accessed: Dec. 03, 2017.

SHIMAKURA, S.E.; RIBEIRO JÚNIOR, P.J. Estatística descritiva: interpretação do coeficiente de correlação. Departamento de Estatística da Universidade Federal do Paraná (UFPR), 2012. Available from: <a href="http://leg.ufpr.br/~/ce003/ce003/node8.html">http://leg.ufpr.br/~/ce003/ce003/node8.html</a> Accessed: Apr.16, 2017.

SILVA, F.G. et al. Gas exchange and chlorophyll fluorescence of eggplant grown under different irrigation depths. **Revista Brasileira de Engenharia Agrícola e Ambiental**, v. 19, p. 946-952, 2015. Available from: <a href="http://www.agriambi.com.br/revista/v19n10/v19n10a06.pdf">http://www.agriambi.com.br/revista/v19n10/v19n10a06.pdf</a>. Accessed: Mar. 25, 2018. doi: 10.1590/1807-1929/agriambi.v19n10p946-952.

SOCIEDADE SUL-BRASILEIRA DE ARROZ IRRIGADO (SOSBAI). Reunião Técnica da Cultura do Arroz Irrigado Arroz irrigado (2016): recomendações técnicas da pesquisa para o Sul do Brasil. Pelotas, RS: SOSBAI, 2016. 200 p.

SOUZA, C.A.V. Mudanças foto-oxidativas em plantas de arroz com reduzida atividade da oxidase do glicolato submetidas ao estresse hídrico combinado ao excesso de luz e calor. 175 f. Dissertação (Mestrado em Produção Vegetal) Curso de Pósgraduação em Produção vegetal, Universidade Federal Rural de Moscôso et al.

8

Pernambuco. Available from: <a href="http://www.tede2.ufrpe.br:8080/tede2/handle/tede2/6854">http://www.tede2.ufrpe.br:8080/tede2/handle/tede2/6854</a> 2016>. Accessed: Dec. 10, 2017.

SU, J et al. Expression of barley SUSIBA2 transcription fator yields high-starch low-methane rice. **Nature**, v. 523, p. 602-620, 2015. Available from: <a href="https://www.nature.com/articles/nature14673">https://www.nature.com/articles/nature14673</a>>. Accessed: May 15, 2017. doi: 10.1038/nature14673.

TAIZ, L. et al. **Fisiologia e desenvolvimento vegetal**. 6. Ed. Porto Alegre: Artmed, 2017. 888 p.

YIQI, L.; ZHOU, X. Soil respiration and the environment. San Diego: Elsevier, 2010. 307p.

YOSHIDA, S. et al. **Laboratory Manual for Physiological Studies of Rice**. Los Baños: IRRI, 1976. 83p.