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Leaf gas exchange in cowpea and CO_2 efflux in soil irrigated with saline water

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ABSTRACT
Leaf gas exchanges in plants and soil respiration are important tools for assessing the effects of salinity on the soil-plant system. An experiment was conducted with cowpea irrigated with saline water (0, 2.5, 5.0, 7.5, 10.0 and 12.5 dS m^{-1}) prepared with two sources: NaCl and a mixture of Ca, Mg, Na, K and Cl ions in a randomized block design and a 6 x 2 factorial scheme, with four replicates, totaling 48 experimental plots. At 20 days after planting (DAP), plants were evaluated for net photosynthesis (A), stomatal conductance (gs) and transpiration (E) using the Infra-Red Gas Analyzer (Model XT6400- LICOR), and water use efficiency, intrinsic water use efficiency and instantaneous efficiency of carboxylation were calculated. At 60 DAP, the soil CO_2 efflux (soil respiration) was determined with a camera (Model 6400-09- LICOR). Salinity caused reductions in A, gs and E. However, the salt source did not have significant effect on these variables. Soil CO_2 efflux was reduced with the increase in the electrical conductivity, especially in the mixture of ions.

Palavras-chave:
fotossíntese
salinidade
estresse salino
respiração do solo

Trocas gasosas em feijão-caupi e efluxo de CO_2 do solo irrigado com água salina

RESUMO
As trocas gasosas em plantas e a respiração do solo são ferramentas importantes para avaliar os efeitos da salinidade no sistema solo-planta. Com este propósito conduziu-se um experimento com feijão-caupi irrigado com seis níveis de condutividade elétrica (0; 2,5; 5,0; 7,5; 10,0 e 12,5 dS m^{-1}) elaborados com duas fontes: NaCl e uma mistura de íons de Ca, Mg, Na, K e Cl, em blocos ao acaso e arranjo fatorial 6 x 2, com 4 repetições totalizando 48 parcelas; aos 20 dias após o plantio (DAP) foram determinadas fotossíntese líquida (A), condutância estomática (gs) e transpiração (E) com o Infra-Red Gas Analyzer (Modelo XT6400- Licor) e se calcularam a eficiência do uso da água, a eficiência intrínseca do uso da água e a eficiência instantânea de carboxilação; aos 60 DAP determinou-se o efluxo de CO_2 (respiração do solo) com uma câmara de solo (Modelo 6400-09- LICOR). Observaram-se reduções de A, gs e E com o aumento da salinidade; entretanto, a fonte de sal não apresentou efeito significativo para tais variáveis; já para a respiração do solo ocorreu redução com o aumento da condutividade elétrica da água de irrigação sendo mais pronunciado quando se utilizou somente a mistura de sais.

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Introduction

Soil salinity is one of the main abiotic stresses and is characterized by the presence of high concentrations of salts in the soil solution, with wide occurrence in the world, especially in regions of arid and semi-arid climate. It is a research topic that deserves attention, since it decreases the yield of crops through the reduction of water availability in the soil and also through the toxicity of chemical elements, especially sodium and chlorine (Souza et al., 2012; 2014). The evaluation of agricultural crops that are cultivated in regions prone to salinization is of great relevance. The cowpea crop stands out, for being a staple food in family farming and widely cultivated in the semi-arid region of the Northeast, with economic and social importance (Fernandes et al., 2015).

The effect of toxicity induced by salinity causes damages to the photosynthesis due to the alterations in the gas exchanges (Silva et al., 2015). Silva et al. (2013) and Soares et al. (2013) observed that the increase in the saline concentration of the water reduces the photosynthesis and stomatal conductance of the cowpea crop.

Soil carbon efflux quantification provides the actual CO_2 emission of the soil and this information can be used, for instance, to calculate the carbon sequestration of the ecosystem (Pinto Júnior et al., 2009) and also to evaluate soil biological quality. The CO_2 efflux in the soil is composed of two steps. The first one is the production of CO_2 in the soil through the respiration of roots and microorganisms; the second one is the transport of CO_2 to the atmosphere.

The increase in soil salinity decreases root growth and microbial activity, causing a lower release of CO_2 from the process of respiration, i.e., the determination of CO_2 efflux can be used to verify the impact of salinity on the soil. The CO_2 efflux from the soil started to be called "soil respiration" in the 1920s, by the Swedish researcher Henrik Lundegärdh, responsible for the first measurements using "static closed chamber" (Kutsch et al., 2010).

This study aimed to evaluate the gas exchanges in cowpea irrigated with solutions of increasing salinity levels and prepared with different ionic concentrations, as well as quantify the CO_2 efflux of the soil at the end of the cultivation.

Material and Methods

The soil used in the experiment was collected in the municipality of Pesqueira, PE, Brazil, in the layer of 0-30 cm, and classified as Fluvic Neosol (EMBRAPA, 2013), free from salinity and sodicity problems. Then, the soil was air-dried, pounded to break up clods, homogenized and sieved through a 4-mm mesh.

For soil chemical characterization, the air-dried fine earth (ADFE) was analyzed for the exchangeable cations Ca^{2+}, Mg^{2+}, Na^+ and K^+ (Thomas, 1982). The saturation extract was obtained through the preparation of the saturation paste (Richards, 1954), which was analyzed for electrical conductivity, the soluble bases (Ca^{2+}, Mg^{2+}, K^+ and Na^+) and the chloride ion (EMBRAPA, 1997). The results of the exchange complex were used to calculate the values of sum of bases (SB) and exchangeable sodium percentage (ESP).

The soil has, in the saturation extract, Ca^{2+} (1.00 $mmol_c$ L^{-1}), Mg^{2+} (1.04 $mmol_c$ L^{-1}), Na^+ (5.34 $mmol_c$ L^{-1}), K^+ (1.12 $mmol_c$ L^{-1}) and Cl (6.80 $mmol_c$ L^{-1}), EC (0.99 dS m^{-1}) and $pH_{(1:2.5)}$ 8.71. The sorption complex has Ca^{2+} (5.53 $cmol_c$ kg^{-1}), Mg^{2+} (2.22 $cmol_c$ kg^{-1}), Na^+ (0.26 $cmol_c$ kg^{-1}), K^+ (0.5 $cmol_c$ kg^{-1}), SB (8.51 $cmol_c$ kg^{-1}), ESP (3%) and $pH_{(1:2.5)}$ 7.7.

Physical characterization was performed using the methodology of EMBRAPA (1997). The soil showed 312 g kg^{-1} of fine sand, 117 g kg^{-1} of coarse sand, 422 g kg^{-1} of silt and 149 g kg^{-1} of clay. The soil showed clay dispersed in water of 102 g kg^{-1}, bulk density of 1.24 g cm^{-3}, particle density of 2.52 g cm^{-3} and total porosity of 50.79%. The water contents at field capacity and permanent wilting point, at tensions of 0.10 and 15 atm, respectively, were equal to 0.24 g g^{-1} and 0.05 g kg^{-1}.

The experiment was carried out in a greenhouse of the Federal Rural University of Pernambuco (UFRPE), located at the coordinates 08º 00' 59.9" S and 34º 56' 38.6" W from March to May 2014.

Cowpea plants, cultivar IPA 206, were cultivated in pots with capacity for 6 L, filled with soil. Before planting the cowpea seeds, the pot was irrigated to increase soil moisture to 80% of field capacity, in order to better estimate what occurs under field conditions, in which the water content, most of the time, remains below the field capacity. Each plot consisted of a pot with soil and two plants.

In order to meet the nutritional requirements of the crop, fertilization was applied according to the Manual of Recommendation of Fertilization of the Agronomic Institute of Pernambuco (IPA, 2008).

The soil was irrigated using water with electrical conductivity (EC) values of 0, 2.5, 5, 7.5, 10 and 12.5 dS m^{-1} elaborated through the addition of two sources of salts: NaCl and a mixture of $CaCl_2$, $MgCl_2$, NaCl, and KCl, simulating the mean ionic composition found in wells of the region of Pesqueira, PE (Table 1).

Irrigation was performed always at the end of the day, by replacing the water lost through evapotranspiration measured through weighings on a digital scale.

Table 1. Salt concentrations (g L^{-1}) required to obtain the values of electrical conductivity (EC) used for the irrigation water of both salt sources and the osmotic potential of the solutions (MPa)

EC dS m^{-1}	Sources of water							
	Sodium chloride		Mixture of salts					
	NaCl	Ψ_o	NaCl	KCl	$MgCl_2$	$CaCl_2$	Total	Ψ_o
0	0	0	0	0	0	0	0	0
2.5	1.360	-0.104	1.051	0.005	0.306	0.244	1.606	-0.117
5.0	2.906	-0.223	1.990	0.013	0.556	0.443	3.002	-0.233
7.5	4.669	-0.358	3.201	0.016	0.886	0.693	4.796	-0.346
10.0	6.650	-0.510	4.650	0.027	1.297	1.006	6.980	-0.538
12.5	8.826	-0.676	6.501	0.040	1.823	1.409	9.773	-0.706

During the first seven days, distilled water was used and, from the eighth day on, the saline water was gradually applied until all treatments showed the established level of salinity, in order to avoid a possible osmotic shock (increasing 2.5 by 2.5 dS m^{-1} every two days up to 12.5 dS m^{-1}). All pots were equilibrated with the EC values corresponding to the treatments at 16 days after planting (DAP).

At 20 DAP, plants were evaluated for net photosynthesis (A), transpiration (E) and stomatal conductance (gs), using the Infra-Red Gas Analyzer (IRGA - Model LICOR XT6400) to verify whether there was damage to the plant caused by salinity. Even in the beginning of plant development, the readings were performed from 9 to 11 a.m., while the mean temperature and relative humidity at the time of reading were equal to 44.9 °C and 30.4%, respectively.

An air flow of 500 mL min^{-1} was used and the readings were performed when the photosynthetically active radiation reached more than 1000 μmol m² s^{-1} with mean value of 1350 μmol m² s^{-1}, and ambient CO_2 concentration of 400 μmol m² s^{-1}. The readings were performed on a leaf from the middle section of the plant.

The IRGA data were used to calculate the water use efficiency (WUE) (Eq. 1), the intrinsic water use efficiency (IWUE) (Eq. 2) and the instantaneous carboxylation efficiency (EiC) (Eq. 3).

$$WUE = \frac{A}{E} \tag{1}$$

$$IWUE = \frac{A}{gs} \tag{2}$$

$$EiC = \frac{A}{Ci} \tag{3}$$

where:

Ci - internal CO_2 concentration.

At 60 DAP, after harvesting the experiment and removing the shoots, the CO_2 efflux was quantified using a soil chamber (Model 6400-09- LICOR) installed directly on the soil surface and adapted to the IRGA for data acquisition. Soil respiration was determined at the end of the experiment to verify its effects on the soil after one crop cycle. The analysis was performed from 4 to 6 p.m. Then, root dry matter was determined after drying in a forced-air oven.

The experiment was conducted in randomized blocks with a 6 x 2 factorial scheme, corresponding to six levels of electrical conductivity and two sources of salt, with 4 replicates, totaling 48 experimental plots. Regression models were fitted to the salinity levels.

Results and Discussion

According to the analysis of variance, there was no significant difference ($P > 0.05$) between the types of salts used in the elaboration of the EC levels for the variables A, E, Ci, WUE, IWUE, EiC; however, for all of these variables, there was significant difference ($P < 0.05$) regarding the electrical conductivity, allowing the fit of regression equations (Figure 1).

For stomatal conductance, there was significant reduction between the EC values (Figure 1A). The EC of 2.5 dS m^{-1} led to reduction of 34% in relation to the control; for the EC values of 5, 7.5, 10 and 12.5 dS m^{-1}, the reductions were equal to 57, 72, 81 and 87%, respectively. One of the primary mechanisms for the reduction of water loss in plants under salt stress is the reduction of stomatal opening (Lima et al., 2014). With the increase in saline concentration and, consequently, greater difficulty of the plant to absorb water from the soil, the plant needs to reduce the water loss, resulting in the decrease of stomatal conductance. With the decrease in stomatal conductance and consequent stomatal closure, other parameters such as net photosynthesis and water use efficiency suffer alterations.

Corroborating the results found in the present study, Wilson et al. (2006) observed reduction in stomatal conductance in four cowpea cultivars with the increase in irrigation water salinity. Such decrease is a response to the increase in irrigation water salinity due to the osmotic effect caused by the accumulation of soluble salts in the soil and in the plant.

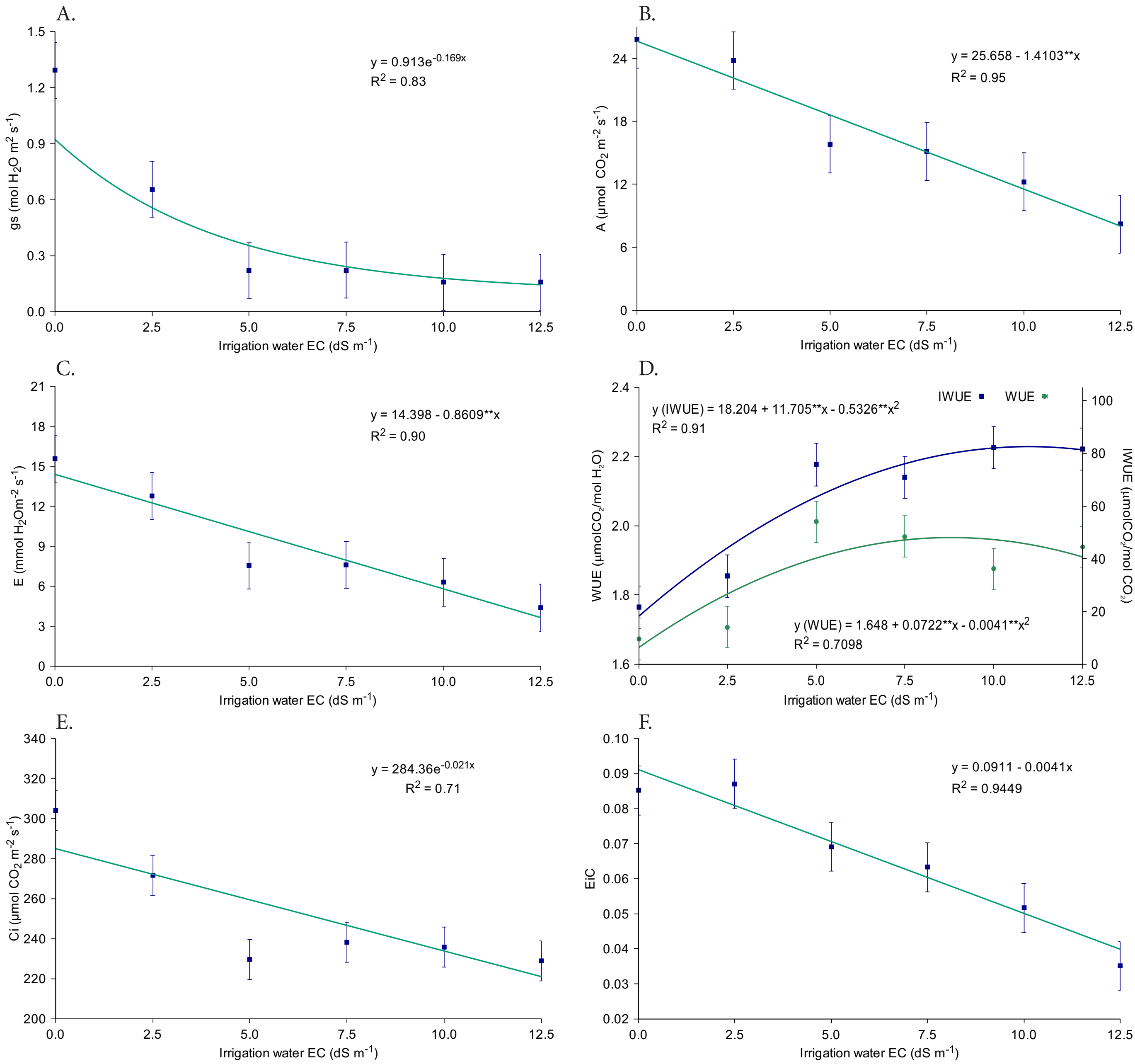
Net photosynthesis (Figure 1B) and transpiration (Figure 1C) decreased linearly with the increase in the electrical conductivity. The net photosynthesis is a very useful tool to evaluate the salt stress (Hatamnia et al., 2013). Similarly, Praxedes et al. (2010) found reduction in net photosynthesis evaluating the cowpea crop under salt stress. The decrease in net photosynthesis is related to the lower entry of CO_2 in the leaf, caused by the decrease in stomatal conductance and consequent reduction of the internal CO_2 concentration. The same was found by Hirich et al. (2014), working with quinoa plants irrigated with saline water.

The reduction in transpiration is also caused by the decrease in stomatal conductance, resulting in a lower water loss by the plant, which has difficulty to absorb it due to the reduction in the soil water potential.

This reflex of the decrease in transpiration and stomatal conductance can be observed in WUE and IWUE. There was a significant increase in WUE and IWUE (Figure 1D). Azizian & Sepaskhah (2014) observed increment in the values of intrinsic water use efficiency cultivating maize with saline water. Ashraf (2003), working with *Panicum antidotale* under flooding and saline conditions, observed the highest values of intrinsic water use efficiency for the conditions of salinity. Ashraf (2001), investigating various species of Brassicas, found higher values of water use efficiency and intrinsic water use efficiency in the species more tolerant to salinity.

As observed, the increase in salinity caused decrease in plant transpiration and photosynthesis due to the closure of the stomata; however, the effect of salinity caused greater reductions in transpiration than in the net photosynthesis, which resulted in higher WUE values. A similar mechanism occurred with IWUE, whose decrease in stomatal conductance was higher than that caused in net photosynthesis, favoring the increase in IWUE values with the increase in salinity.

For the instantaneous carboxylation efficiency, there was a linear reduction with the increase in irrigation water EC



Bars indicate the standard error of the mean

Figure 1. (A) Stomatal conductance (gs); (B) net photosynthesis; (C) Transpiration (D); water use efficiency and intrinsic water use efficiency; (E) Internal CO_2 concentration (Ci); (F) Instantaneous carboxylation efficiency (EiC) in cowpea as a function of the electrical conductivity of the irrigation water (EC) 20 days after planting

(Figure 1F). The instantaneous carboxylation efficiency is closely related to stomatal opening and closure. The reduction in stomatal conductance resulted in decrease of photosynthesis; the stomatal closure also causes a lower CO_2 diffusion to the substomatal chamber and, as a consequence, lower internal CO_2 concentration (Figure 1E). Although there was a decrease in both variables, the reduction in the internal CO_2 concentration was smaller than that in net photosynthesis, which explains the decrease in EiC.

Corroborating the results of the present study, Soares et al. (2013) and Furtado et al. (2013) observed a reduction in the instantaneous carboxylation efficiency in cowpea plants under salt stress. Rodrigues et al. (2014) observed reduction in the instantaneous carboxylation efficiency with the increase of the saline concentration in castor bean plants.

Despite the reductions in transpiration, stomatal conductance and internal CO_2 concentration, which are denominators in the determination of WUE, IWUE and EiC, respectively, these variables behaved differently. The WUE and IWUE use, as denominators, variables related to the passing of water through the leaf. The EiC has, as denominator, a variable related to the CO_2 flow. This occurs because the gradient of concentration between the plant and the atmosphere is much stronger for the water than for the CO_2, and the CO_2 diffuses more slowly because it finds higher resistance in the plant, causing the variables related to the water to suffer greater reductions compared with that related to the CO_2. The CO_2 efflux in the soil (soil respiration) showed significant difference between the types of salts ($P < 0.05$) and between the EC levels of the irrigation water ($P < 0.05$). In general, there was a reduction in the CO_2 efflux with the increase in EC elaborated with two sources of salts: NaCl and Mixture (Figure 2).

It is interesting to point out that the reduction of soil respiration was more pronounced under irrigation with water elaborated with a mixture of salts, indicating greater effect on the reduction in the microbial activity and/or root development. The reduction in soil respiration followed the decrease in root dry matter.

There was a substantial decrease in root dry matter between the control and the other treatments. The treatment with EC of 2.5 dS m^{-1} caused a reduction of 56% in the roots. This reduction was equal to 85% for the treatment with EC of 12.5 dS m^{-1}, both in relation to the control.

Plants cultivated under salt stress exhibit reduction in the photosynthetic capacity and consequent reduction of total biomass, including that corresponding to the roots. The reduction in the mass of roots causes a decrease in the respiration, which consequently causes a reduction in the release of CO_2 in the soil.

The soil microbiota also suffers the negative interference of high values of electrical conductivity. Adviento-Borbe et al. (2006), analyzing the effect of four levels of soil electrical conductivity (ECs) - 0.5, 1.0, 1.5 and 2.0 dS m^{-1} - on soil microbial respiration, observed that this variable was reduced with the increase in electrical conductivity, mainly because of the osmotic stress. Yuan et al. (2007), studying eleven soils with EC varying from 0.32 to 23.05 dS m^{-1}, aiming to account for the effects of salinity on the size, activity and structure of the community of soil microorganisms in arid soils in a Chinese province, observed a negative exponential relationship between the EC and the carbon of the microbial biomass, nitrogen of the microbial biomass and basal respiration of the soil.

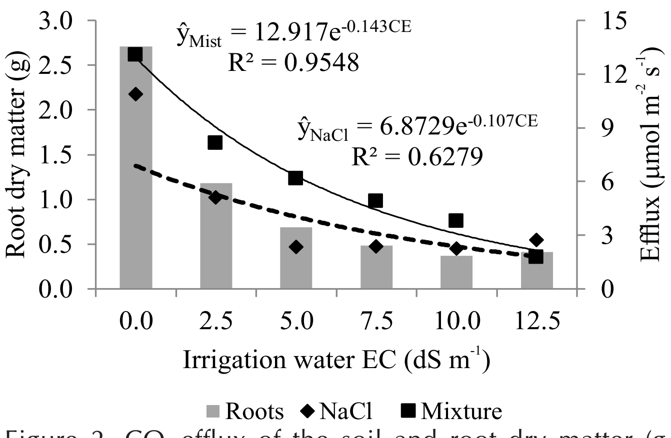


Figure 2. CO_2 efflux of the soil and root dry matter (g $plant^{-1}$) of cowpea plants cultivated under different levels of electrical conductivity in the irrigation water (EC) and types of salts 60 days after planting

Conclusions

1. The salt source did not have significant effect on the variables related to leaf gas exchanges.

2. There were reductions in net photosynthesis, stomatal conductance, transpiration and internal CO_2 concentration with the increase in the electrical conductivity of the irrigation water from 2.5 dS m^{-1} on.

3. The increase in salinity caused increase in water use efficiency and intrinsic water use efficiency and reduced the instantaneous carboxylation efficiency.

4. There was a reduction in the CO_2 efflux of the soil with the increase in the electrical conductivity of the irrigation water and it was more pronounced when the mixture of salts was used.

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