



Growth, leaf gas exchange and mycorrhizal colonization of three medicinal species submitted to different irradiance levels

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ABSTRACT: This study evaluated growth, leaf gas exchange and arbuscular mycorrhizal fungi root colonization in three medicinal plant species under different irradiance intensities. *Fridericia chica* (Bonpl.) L.G.Lohmann, *Mikania laevigata* Sch.Bip. ex Baker and *Varronia curassavica* Jacq. were propagated by cutting and cultivated for 120 days in artificially shaded environments using black shade-type screens, obtaining four irradiance levels: 100%, 70%, 50% and 30%. The experimental design was completely randomized in a 3 x 4 factorial scheme (three plant species and four irradiation levels) with seven replicates. The three medicinal species showed higher liquid assimilation, mass growth and arbuscular mycorrhizal fungi root colonization rates when exposed to environments with 70% light availability. In relation to physiological responses, *V. curassavica* presented higher photosynthetic rate, stomatal conductance and transpiration when submitted to 70% irradiance, being able to be cultivated in more open environments with higher irradiation levels. Conversely *F. chica* and *M. laevigata* presented shade tolerance characteristics. At the initial growth phase, the results obtained can be used as indicators to recommend the ideal cultivation environment for these species in agroforestry systems.

Key words: light availability, biomass allocation, gas exchange, arbuscular mycorrhizal fungi.

Crescimento, trocas gasosas foliares e colonização micorrizica de três espécies de plantas medicinais submetidas a diferentes níveis de irradiância

RESUMO: O objetivo deste trabalho foi avaliar o crescimento, as trocas gasosas foliares e a colonização por fungos micorrízicos arbusculares em três espécies de plantas medicinais, sob diferentes intensidades de irradiância. *Fridericia chica* (Bonpl.) L.G. Ohmmann, *Mikania laevigata* Sch.Bip. ex Baker e *Varronia curassavica* Jacq. foram propagadas por estaquia e cultivadas por 120 dias em ambientes artificialmente sombreados, utilizando telas do tipo sombrite, em quatro níveis de irradiância, 100%, 70%, 50% e 30%. O delineamento experimental foi inteiramente casualizado, em esquema fatorial 3 x 4 (três espécies de plantas e quatro níveis de irradiação) com sete repetições. As três espécies medicinais avaliadas apresentaram maiores taxas de assimilação líquida, crescimento em massa e colonização radicular por fungos micorrízicos arbusculares quando expostas a ambientes com 70% de disponibilidade de luz. Em relação às respostas fisiológicas, *V. curassavica* apresentou maior taxa fotossintética, condutância estomática e transpiração quando submetidas a 70% de irradiância, podendo ser cultivada em ambientes mais abertos e com maiores níveis de radiação. Por outro lado, *F. chica* e *M. laevigata* apresentaram características de plantas tolerantes à sombra. Os resultados obtidos na fase inicial de crescimento podem ser utilizados como um indicador para recomendar o ambiente de plantio dessas três espécies medicinais em sistemas agroflorestais.

Palavras-chave: disponibilidade de luz, alocação de biomassa, trocas gasosas, fungos micorrízicos arbusculares.

INTRODUCTION

Fridericia chica (Bignoniaceae), *Mikania laevigata* (Asteraceae) and *Varronia curassavica* (Boraginaceae) are medicinal plants native to Brazil, with economic importance due to their active ingredients (LIMA et al. 2020). *F. chica*, popularly known as ‘pariri’, is used as anti-inflammatory (LIMA et al. 2020), healing and anti-anemic agent, and is also used to treat intestinal colic, hemorrhage,

diarrhea and leukemia (BEHRENS et al., 2012). *M. laevigata*, commonly known as ‘guaco’, has leaves rich in coumarin and are used in the treatment of respiratory disorders, having anti-inflammatory action (DELLA PASQUA et al. 2019). *V. curassavica*, known as ‘erva-baleeira’, has anti-inflammatory activity (OLIVEIRA et al., 2020a) and is used as raw material for the first herbal medicine fully developed in Brazil, Acheflan[®], which is based on the essential oil from this species (LIMA et al. 2020).

In addition to medicinal properties, some studies have demonstrated various biological activities for the species, such as repellent for the control of urban ant *Dorymyrmex thoracicus* (OLIVEIRA et al. 2019), as well as antibacterial (RODRIGUES et al. 2012), anti-allergic (PASSOS et al., 2007), antifungal, and antiprotozoal action (NIZIO et al. 2018).

The quality of the raw material of medicinal plants is determined by the content of bioactive compounds, mainly resulting from the influence of the environment in which plants are grown. Biotic, abiotic and genetic factors influence the chemical composition of medicinal oils (BOARO et al, 2019). For example, for *V. curassavica*, changes in the content of bioactive compounds were observed due to changes in the light availability (SILVA et al. 2017), also depending on the time of year (MARQUES, et al. (2019) and the access used for collection (OLIVEIRA et al. (2020b). Studies carried out with the species have shown that in protected environments with 50% solar radiation incidence, it is possible to obtain higher levels of bioactive compounds such as trans-caryophyllene, α -humulene, germacrene D and α -zingiberene (SILVA, 2017).

Similarly to what is observed for species of the genus *Varronia*, for species of the genus *Mikania*, TORMES (2019) demonstrated that plants grown in 50% full sun condition have higher coumarin levels, one of the main active principles of this genus. Therefore, understanding the ability of medicinal species to adapt to different light availability conditions allows determining the ideal cultivation conditions to achieve higher levels of biomass and active principles of economic and pharmacological interest.

Plants exposed to changes in irradiance levels have the ability to acclimate to a greater or lesser degree to the new condition. Acclimatization maximizes total carbon gain, which can occur through changes in leaf assimilation properties, physiological adjustments and changes in leaf characteristics related to photosynthesis or changes in the biomass allocation pattern in favor of the vegetative part more affected by light changes. The nature of the morphogenic response can vary considerably among *F. chica*, *M. laevigata* and *V. Curassavica* species according to the acclimatization capacity and dependence on the quantity or light quality (LIMA et al., 2008).

The ability of species to morphologically and physiologically acclimatize to variations in nutrient availability and to associate with arbuscular mycorrhizal fungi (AMF) favors the establishment of plants in environments with limited water and light availability. By establishing a symbiotic mutual

association with the roots of most plant species, AMF promote an increase in the absorption of nutrients such as N, P, Zn, Mg and Ca (MATSUBARA et al. 2009, ZUBECK et al. 2015), increase in the levels of photosynthetic pigments in leaves (PEDONE-BONFIM, et al. 2015) and higher production of primary metabolites, which are precursors of secondary metabolism pathways (MANOHARAN et al. 2010 and PEDONE-BONFIM, et al. 2015). Zengh et al. (2013) conducted a survey of studies with 49 different medicinal plants species and reported values from 6.42% to 765.56% higher of secondary compounds in plants that have associations with MFA, when compared to control plants.

This research evaluated the behavior of three medicinal species regarding growth, leaf gas exchange and arbuscular mycorrhizal fungi colonization submitted to different irradiance levels.

MATERIALS AND METHODS

The experiment was carried out at the State University of Santa Cruz (UESC), Ilhéus, BA from September 2017 to January 2018. *F. chica*, *M. laevigata* and *V. curassavica* plants obtained by cutting were transplanted into plastic pots with capacity of 10 L containing a mixture of soil and sand at proportion of 2:1 (v/v). Initially, seedlings were rustified (submitted to rustication) in natural shade for a period of 30 days, and then submitted to treatments corresponding to four irradiance levels obtained by coverage with black screens corresponding to 100%, 70%, 50% and 30% in relation to full sun. Within shade treatments, distance of 30 cm between plants was maintained, and plants were daily irrigated. No supplementary fertilization was carried out in the experimental period. Seedlings remained in treatments for a period of 120 days.

Leaf gas exchange, growth, chlorophyll index, and mycorrhizal colonization evaluations were carried out (described below). All material collection was carried out in a single day between 08:00 am and noon. Mycorrhizal colonization evaluation was carried out at laboratory as described below.

Light availability assessment

Photosynthetic active radiation (PAR) values were measured at the top of plants using BQM quantum sensor (Apogee Instruments USA). Evaluations were performed on 18 consecutive days from 07:00 am to 06:00 pm. The average PAR value observed at 100% irradiance was 34.2 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, followed by treatments of 26.0, 22.0 and 12.0

$\mu\text{mol photons m}^{-2} \text{s}^{-1}$, corresponding to 70%, 50% and 30% irradiance, respectively.

Gas exchange evaluation

Leaf gas exchange measurements were performed at the end of the experiment in two completely expanded and mature leaves of each individual per replicate. Net photosynthesis rates (Pn), stomatal conductance to water vapor (gs), and transpiration (E) were measured using portable photosynthesis system (LI-6400, LI-COR Bioscience, Lincoln, NE, USA), equipped with 6400-02B RedBlue artificial light source. Measurements were performed with equipment providing $1,000 \mu\text{mol photons m}^{-2}\text{s}^{-1}$, and chamber adjusted at $26 \text{ }^{\circ}\text{C}$, and ambient CO_2 concentration ($\pm 380 \mu\text{mol}$).

Growth assessment

At the beginning and end of the experiment, height and diameter of eight plants were measured using millimeter ruler and digital caliper, respectively, being collected from roots, stem and leaves. After measuring the total leaf area per plant, plants were stored and arranged to dry in forced air circulation oven at $75 \text{ }^{\circ}\text{C}$ until reaching constant mass. Root dry mass (RDM), stem dry mass (SDM) leaf dry mass (LDM) and total dry mass (TDM) were determined. Leaf area (LA) was determined using LI-3100 leaf area meter (Li-Cor, Nebraska, USA).

From dry mass and leaf area data, specific leaf area (SLA), mean relative growth rate in mass (RGRm), diameter (RGRd) and height (RGRh), net assimilation (TAL), stem (SMF), leaf (LMR), and root (RMF) mass rates were calculated according to HUNT (1990).

Chlorophyll Index

At 120 days SPAD, chlorophyll index (ISPAD) was determined using portable SPAD chlorophyll meter (Minolta model SPAD-502). Two readings were made in fully expanded and mature leaves in four plants per treatment.

Mycorrhizal colonization

At the end of the experiment, the mycorrhizal colonization percentage in roots of three plants of each treatment was evaluated. Roots were cut and packed in plastic vials containing 100 mL of 70% ethanol, clarified and stained according to PHILLIPS & HAYMAN (1970) method. Mycorrhizal colonization rate (COL), internal hyphal (HI), external hyphal (HE), vesicles (VES) and spores (ES) were evaluated by the intersection method of MCGONIGLE et al. (1990).

Data analysis

The experimental design was completely randomized (DIC) in a 3 x 4 factorial scheme (three species and four irradiance levels) with eight replicates. Results were submitted to analysis of variance (ANOVA), and when significant differences were observed, they were submitted to the Tukey test at 5% probability using the Sisvar[®] software (FERREIRA, 2011).

RESULTS AND DISCUSSION

Variables RGRd, Pn, gs, E and spore percentage (ES) were influenced by one of the factors: species (Sp) or light (L). RGRh, RGRd, as well NAR, LMR, RMR, SLA, ISPAD, and variables related to mycorrhizal colonization (COL, HI, HE, and VES) were influenced by the species x light interaction (Table 1). The growth variables of species under study were influenced in different ways by light availability. The high RGRh, LMR and SLA values were observed with decreased radiation, while RGRm, NAR, SMR (except for *F. chica*) and RMR showed higher values with increased light availability (Table 2).

Higher RGRh value presented by plants under shade occurs in response to faster growth promoted by greater investment in cell stretching (MOTA et al., 2012), consisting of an important adaptation mechanism and an escape strategy at low luminosity conditions (YANG et al. 2013; AMISSAH et al. 2015). Associated with this fact, the increase in SLA and ISPAD in environments with low light availability indicates greater carbon investment to capture light (TANG et al. 2015, COSTA et al. 2019), as an acclimatization strategy to this condition. The increase in chlorophyll content (ISPAD) under low light conditions has already been reported by other authors (FAVARETTO et al. 2011, CERQUEIRA et al. 2017) and aims to increase the light radiation assimilation efficiency (GONÇALVES et al. 2001). Conversely, the increase in RMR (root mass ratio) under conditions of greater light availability increases the water absorption by roots (POORTER, 2012). Under conditions of high irradiance, the demand for water increases and the greater carbon allocation to roots (higher RMR) ensures a balance between absorption and transpiration rates (COSTA et al. 2019).

Gas exchange variables (net photosynthesis (Pn), stomatal conductance to water vapor (gs), and transpiration (E)) showed isolated effects of species and light regimes (Table 1). *V. curassavicas* presented higher Pn, gs and E values when compared to the other species (Table 1), and

Table 1 - Summary of the analysis of variance (ANOVA) for: RGRh - Relative growth rate in height ($\text{mg g}^{-1}\text{day}^{-1}$); RGR - Relative growth rate in mass ($\text{mg g}^{-1}\text{day}^{-1}$); NAR- Net assimilation rate ($\text{g cm}^{-2}\text{day}^{-1}$); LMR - leaf mass ratio; SMR - stem mass ratio; RMR - root mass ratio; SLA - specific leaf area (cm g^{-1}); Pn - net photosynthetic rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$); gs - stomatal conductance to water vapor ($\mu\text{mol m}^{-2}\text{s}^{-1}$); E - transpiration ratio ($\text{mol m}^{-2}\text{s}^{-1}$); ISPAD - SPAD Index; COL - Mycorrhizal colonization rate; HI - internal hypha; HE - external hyphal; VES - vesicles e ES - spores for *Fridericia chica* (FC), *Mikania laevigata* (ML), *Varronia curassavica* (VC) growth at four levels of irradiance. (Sp: Species; L: Light; Sp x L: Species x Light).

	-----Species-----			-----Levels of Irradiance (%)-----				-----ANOVA-----		
	FC	ML	VC	30	50	70	100	Sp	L	Sp x L
RGRh	5.70	7.13	4.83	7.18	5.54	5.60	5.23	**	**	**
RGRm	25.24	22.38	24.27	22.14	22.70	26.68	24.27	*	**	*
NAR	2.21	1.32	2.58	1.68	1.68	2.78	2.01	**	**	*
LMR	0.19	0.52	0.16	0.32	0.31	0.26	0.27	**	**	**
SMR	0.32	0.34	0.62	0.44	0.40	0.45	0.42	**	*	*
RMR	0.48	0.22	0.21	0.23	0.29	0.27	0.31	**	**	*
SLA	130.40	109.90	150.10	195.40	128.90	102.30	94.00	**	**	*
Pn	9.45	8.06	12.68	9.29	9.19	11.05	10.74	**	**	ns
gs	0.18	0.12	0.33	0.18	0.20	0.23	0.22	**	*	ns
E	3.45b	2.66c	5.73a	3.94	3.90	4.28	3.66	**	*	ns
ISPAD	37.90	37.60	22.20	37.30	30.10	30.8	32.10	**	**	**
COL	56.30	66.30	72.90	57.30	59.50	75.00	68.50	**	**	**
HI	34.70	36.60	46.10	28.90	38.60	46.90	42.00	**	**	**
HE	22.40	23.90	23.40	21.00	21.10	25.50	25.50	ns	**	**
VES	32.30	23.50	33.00	25.00	23.40	34.80	35.40	**	**	**
ES	2.40b	0.60b	9.70a	2.60	4.30	3.80	6.70	**	ns	ns

(*) $P > 0.05$ e (**) $P > 0.01$ e (ns) not significant.

Lowercase letters indicate values that differ only between species.

higher values were observed in treatments of 70% and 100% irradiance. These high Pn, gs and E values demonstrated the ability of plants to physiologically acclimate to high irradiance conditions, corroborating its classification as heliophilous (SMITH, 1970). The increase in Pn values occurs at the expense of higher gas exchange and E values when greater light availability (DALMOLIN et al. 2015) and low irradiance environments have greater stomatal control and; consequently, higher water use efficiency (KARATASSIOU & NOITSAKIS 2010).

In relation to mycorrhizal colonization, the highest radiation levels promote greater mycorrhizal colonization rate (COL), internal hyphal (HI), external hyphal (HE) (except for *M. laevigata*) and vesicles (VES) values (except for *F. chica*) (Table 3). Among these three species, *V. curassavica* presented the highest COL, HI and VES values. Arbuscular mycorrhizal fungi (AMF) have symbiotic relationships with plants, constituting a specific type of ecological relation, mutualism, in which both components benefit from the interaction (SMITH & SMITH 2011). The irradiance levels significantly influence AMF colonization, presenting better results in environments

with higher irradiance levels. In environments with low irradiance levels, *F. chica*, *M. laevigata* and *V. curassavica* species presented low colonization and low RMR, and the lower the proportion of roots, the lower the AMF colonization. This is probably due to lower carbon translocation to roots, which implies lower amount of exudate for AMF maintenance, requiring photosynthesis products from the host plant (GEHRING, 2013).

Mycorrhiza increase the uptake of water and nutrients from soil to plants by means of two absorption paths. One by root epidermis and root trichomes, the other by AMF extraradicular hypha and symbiotic cortical arbuscule cell interface (SMITH & SMITH 2011). In fact, for *F. chica* and *V. curassavica* species, higher EH percentage (extraradicular hyphae) was observed for higher irradiance environment, where biomass partition for roots was higher.

CONCLUSION

Young *F. chica*, *M. laevigata* and *V. curassavica* plants showed morpho-physiological

Table 2 - Mean values (\pm se) for relative growth rate in height (RGRh, cm cm⁻¹ day⁻¹), relative growth rate in mass (RGRm, mg g⁻¹ day⁻¹), net assimilation rate (NAR, g cm² day⁻¹) leaf mass ratio (LMR), stem mass ratio (SMR), root mass ratio (RMR), specific leaf area (SLA, cm² gr⁻¹) and SPAD Index (SPAD) of *Fridericia chica* (FC), *Mikania laevigata* (ML), *Varronia curassavica* (VC) growth at four levels of irradiance.

Variables	Species	-----Irradiance (%)-----			
		30	50	70	100
RGRh	FC	5.38 \pm 2.04 Ba	5.94 \pm 0.74 Aa	5.49 \pm 1.65Aa	6.09 \pm 1.00Aa
	ML	8.67 \pm 0.99 Aa	7.48 \pm 0.74 Aab	6.45 \pm 0.98Ab	5.92 \pm 0.75Ab
	VC	7.49 \pm 0.96 Aa	3.19 \pm 1.53 Bb	4.83 \pm 1.65Ab	3.78 \pm 0.93 Bb
RGRm	FC	22.08 \pm 2.75 Ab	25.45 \pm 2.70 Aa	26.42 \pm 1.39Aa	27.01 \pm 1.72 Aa
	ML	21.30 \pm 1.75 Ab	20.89 \pm 2.91 Bb	26.27 \pm 2.40 Aa	21.03 \pm 2.88 Bb
	VC	23.04 \pm 2.14 Ab	21.97 \pm 2.15 Bb	27.35 \pm 2.54 Aa	24.73 \pm 1.56 Aab
NAR	FC	1.56 \pm 0.54 Bb	2.21 \pm 0.54 Aab	2.50 \pm 0.63 Ba	2.58 \pm 0.70 Aa
	ML	1.15 \pm 0.32 Bb	1.02 \pm 0.22 Bb	2.08 \pm 0.18 Ba	1.03 \pm 0.46 Bb
	VC	2.33 \pm 0.52 Ab	1.82 \pm 0.59 Ab	3.76 \pm 0.48 Aa	2.42 \pm 0.55 Ab
SMR	FC	0.37 \pm 0.03 Ba	0.32 \pm 0.03 Bab	0.33 \pm 0.05 Bab	0.28 \pm 0.04 Cb
	ML	0.32 \pm 0.02 Bb	0.32 \pm 0.04 Bab	0.37 \pm 0.02 Bab	0.38 \pm 0.03 Ba
	VC	0.64 \pm 0.04 Aab	0.57 \pm 0.10 Ac	0.67 \pm 0.03 Aa	0.60 \pm 0.02 Abc
RMR	FC	0.42 \pm 0.03 Ac	0.49 \pm 0.05 Ab	0.45 \pm 0.07 Abc	0.57 \pm 0.05 Aa
	ML	0.10 \pm 0.03 Cc	0.12 \pm 0.02 Cab	0.16 \pm 0.03 Ba	0.13 \pm 0.03 Cab
	VC	0.17 \pm 0.04 Bc	0.25 \pm 0.08 Ba	0.21 \pm 0.02 Bab	0.22 \pm 0.02 Bab
SLA	FC	225.70 \pm 56.3 Aa	115.30 \pm 16.0 Bb	88.70 \pm 25.9 Bb	91.90 \pm 5.1 Ab
	ML	161.20 \pm 19.5 Ba	109.30 \pm 6.4 Bb	84.60 \pm 39.1 Bb	84.60 \pm 6.6 Ab
	VC	199.30 \pm 16.5 Aa	162.20 \pm 17.5 Ab	133.40 \pm 15.5 Abc	105.60 \pm 8.5 Ac
ISPAD	FC	47.40 \pm 0.7 Aa	32.00 \pm 2.5 Bc	36.30 \pm 4.5Ab	36.30 \pm 1.8 Ab
	ML	40.60 \pm 3.9 Ba	38.40 \pm 3.7Aa	32.00 \pm 4.5 Bb	39.40 \pm 2.3 Aa
	VC	24.00 \pm 3.1 Ca	20.10 \pm 1.1 Ca	24.00 \pm 3.8 Ca	20.70 \pm 2.2 Ba

Means followed by the same capital letter do not differ between species, and means followed by the same lowercase letters do not differ between light environments. Tukey test ($P > 0.05$). Mean values of five replicates (\pm SD).

Table 3 - Mean values (\pm se) for mycorrhizal colonization rate (COL), internal hypha (HI), external hyphal (HE) and vesicle (VES) of roots of *Fridericia chica* (FC), *Mikania laevigata* (ML), *Varronia curassavica* (VC) growth at four levels of irradiance.

Variable	Species	-----Irradiance (%)-----			
		30	50	70	100
(%)					
COL	FC	45.0 \pm 4.0 Cc	51.78 \pm 1.7 Bb	72.0 \pm 2.0 Ba	56.5 \pm 3.0 Cb
	ML	57.6 \pm 0.9 Bb	55.1 \pm 3.2 Bb	73.9 \pm 2.5 Aba	78.8 \pm 3.8 Aa
	VC	69.5 \pm 1.7 Ab	71.8 \pm 2.2 Ab	79.1 \pm 2.9 Aa	71.0 \pm 2.7 Bb
HI	FC	17.4 \pm 1.0 Cc	32.9 \pm 2.2 Bb	46.0 \pm 1.0 Ba	42.5 \pm 1.8 Aa
	ML	29.9 \pm 3.3 Bc	34.8 \pm 1.5 Bbc	42.5 \pm 1.7 Ba	39.2 \pm 3.7 Aab
	VC	39.5 \pm 2.3Ac	48.3 \pm 2.9 Aab	52.1 \pm 1.8Aa	44.5 \pm 2.0 Abc
HE	FC	15.1 \pm 3.3 Cc	19.0 \pm 0.6 Bb	29.3 \pm 1.8 Aa	26.4 \pm 1.2 Aa
	ML	26.3 \pm 2.6 Aab	27.0 \pm 0.6 Aa	19.9 \pm 1.1 Bc	22.6 \pm 1.4 Bbc
	VC	21.4 \pm 1.9 Bb	17.4 \pm 1.0 Bc	27.3 \pm 2.1 Aa	27.6 \pm 1.0 Aa
VES	FC	26.8 \pm 3.8 Ab	24.5 \pm 3.0 Ab	34.6 \pm 4.4 Bb	43.2 \pm 3.0 Aa
	ML	17.0 \pm 1.2 Bb	24.1 \pm 3.3 Aa	28.7 \pm 1.4 Ca	24.2 \pm 4.7Ba
	VC	31.1 \pm 2.3 Ab	21.5 \pm 0.5 Ac	41.1 \pm 1.9 Aa	38.6 \pm 1.5 Aa

Means followed by the same capital letter do not differ between species, and means followed by the same lowercase letters do not differ between light environments. Tukey test ($P > 0.05$). Mean values of five replicates (\pm SD).

changes that enable them to survive under different irradiance levels. The three medicinal species evaluated showed higher liquid assimilation rate, higher mass growth rate and greater mycorrhizal fungi colonization when exposed to environments with 70% light availability. However, *V. curassavica* seems to be more acclimatized in environments with greater light availability, while *F. chica* and *M. laevigata* can be grown in more shaded environments.

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DECLARATION OF CONFLICT OF INTEREST

We have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

All authors equally contributed to the design and writing of the manuscript. All authors critically reviewed the manuscript and approved the final version.

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