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SHORT COMMUNICATION

Entrelaçado, a rare maize race conserved in Southwestern Amazonia

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Abstract Maize (*Zea mays* spp. *mays* L.) is the major domesticated cereal of the Americas and is of great relevance for global food security. For a long time, Amazonia represented an empty space in the racial distribution maps of this species, due to the lack of collections and the idea that locally developed races became extinct during European colonization. However, a native race had been described in Brazilian Amazonia, the *Entrelaçado* race, and a new study placed Amazonia on the map again, with a proposal for a center of diversification in Southwestern Amazonia. We prospected maize in the Brazilian states of Acre and Rondônia (Southwestern Brazilian Amazonia) and found floury landraces belonging to the *Entrelaçado* race, rare in existing collections and often considered extinct in the field. We collected indigenous and local names, general and specific uses for *Entrelaçado*, and characterized these accessions to compare them with other Brazilian floury maize races, based on data from the literature. Floury maize from the Southwest formed a coherent group in the cluster analysis, which grouped with *Entrelaçado* from the literature, confirming its identification and

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demonstrating that this race is conserved in Southwestern Amazonia.

Keywords Landraces · Genetic resources · Conservation · *Zea mays* spp. *mays*

Introduction

The *Zea mays* subspecies *mays* was domesticated in Mexico (Doebley et al. 1990, 1997, 2006) and diversified during its distribution to the extremes of the American continents. New evidence raised hypotheses that the maize domestication process was more complex than originally thought (Vallebueno-Estrada et al. 2016; Ramos-Madrigal et al. 2016) and suggested that maize arrived in Amazonia in a partial state of domestication (Kistler et al. 2018). It arrived in Bolivia's Amazonian lowlands ~ 6800 years BP (Lombardo et al.2020) and in Rondônia, Brazil, ~ 5200 years BP (Hilbert et al. 2017). South America's lowlands have long been considered a secondary center of diversity of maize races (Brieger et al. 1958; Paterniani and Goodman 1977), where different indigenous peoples considered maize important enough to have names that reconstruct linguistically to 4400 years BP (Brown et al. 2014). However, during European conquest and colonization, due to the decimation of indigenous populations (Mann 2005), many of the region's genetic resources became extinct (Clement 1999), possibly the case of Amazonian maize races (Brieger et al. 1958). Data on Amazonian races does not exist in contemporary scientific literature and due to this gap our study prospected native maize races in Southwestern Amazonia.

Maize races are defined as related populations with sufficient morphological characteristics in common to allow their recognition as a group (Anderson and Cutler 1942), which occupy a defined geographic region (Bird and Goodman 1977), and are associated with specific uses. The *Entrelaçado* race is typical of Amazonia, with six sub-races (*Ticuna, Acre, Reyes, Bororó, Tapirapé* and *Chavantes*), but, due to the rarity of collections, a complete characterization was never performed (Brieger et al. 1958). Maize sub-races often have variants in only one racial character, such as endosperm color (Brieger et al. 1958). According to Grobman et al. (1961), the *Entrelaçado* race had the potential to be the most widely distributed race, even though collections in Amazonia were scarce (Brieger et al. 1958; Paterniani and Goodman 1977). This race has the longest ear length among cataloged maize races of the South American lowlands (Brieger et al. 1958). The name *Entrelaçado* was given due to the irregular and interlocked row arrangement of the maize kernels (Fig. 1), the main feature of the race. The interlocked character of the kernels is geographically limited to Amazonia and was mentioned as an ancestral character, which originated in Southwestern Amazonia and was dispersed to Eastern Amazonia (Brieger et al. 1958). In other parts of Amazonia, the race is named *Piricinco* in Peru, and *Pojoso* (Grobman et al. 1961) and *Coroico* (Cutler 1946; Ramirez et al. 1960) in Bolivia. Brieger et al. (1958) and Paterniani and Goodman (1977) classified the *Entrelaçado* race based on 33 and 11 samples, respectively, most of which no longer exist. Brieger et al. (1958) presented a proposal for the geographical distribution of the race and its sub-races in the Amazon Basin, to which we have added the distribution of indigenous language families, demonstrating that many indigenous peoples from Western, Southwestern and Southern Amazonia used this race (Fig. 2). Terms for maize reconstruct among the speakers of the Arawakan, Panoan and Tupian languages up to 4000 years ago, but not for the Ticuna languages, due to lack of data (Brown et al. 2014).

The *Entrelaçado* race has floury endosperm. The protein fractions of the maize grain vary according to the type of endosperm. Floury maize has higher amino acid content and up to 60% more lysine than other types of maize (Mertz et al. 1964). *Entrelaçado*, therefore, may be a source of food with high nutritional value for humans and animals, and has potential to be used in breeding programs aimed at raising the protein quality of cultivars and for the flour market. Improving nutrient content is a major target for future plant breeding in all important crops (Tester and Langridge 2010).

Brieger et al. (1958) regretted the reduced sampling of maize in Amazonia, suspecting that in this area there could be ancient races conserved by indigenous people, but which may already have become extinct before their research team travelled through the region. The *Entrelaçado* was the only native race described for Brazilian Amazonia (Paterniani and Goodman 1977). The most important Brazilian maize

Fig. 1 The name *Entrelaçado* was given due to the irregular and interlocked row arrangement of the maize kernels. Photographic record taken during the collection expedition in Guajará-Mirim, Rondônia. Photograph: Costa, F. M

collection has 4079 accessions conserved in the Germplasm Bank of the Brazilian Agricultural Research Corporation (Embrapa) (platform Allele: http://alelobag.cenargen.embrapa.br/AleloConsultas/Passaporte/detalhesBanco.do?idb=73), duplicated in the International Maize and Wheat Improvement Center (CIMMYT). This collection conserves 38 accessions named *Entrelaçado*, which represent 0.9% of the maize varieties conserved in the collection, most of which have not been renewed recently. The low frequency demonstrates how rare the landraces of this race are in modern collections. In order to recover part of the lost history of this Amazonian maize, the aim of our study was to prospect native maize to characterize the morphology, names and uses of floury races, and identify races currently conserved *on farm* in Southwestern Amazonia.

Materials and methods

Ethnobotanical characterization

Our field expeditions were conducted between August 2017 and April 2019, in the states of Rondônia (RO) and Acre (AC), Brazilian Southwestern Amazonia. A total of 20 farmers participated in the ethnobotanical characterization: (1) 12 informants descended from indigenous peoples and Brazilian migrants, living in the Rio Ouro Preto Extractive Reserve (RESEX ROP), in the municipality of Guajará-Mirim, RO; and (2) eight indigenous people from the Association of the Movement of Indigenous Agroforestry Agents (AMAAIAC), from the municipalities of Jordão, Tarauacá and Feijó, AC. These indigenous people are of the Kaxinawá (self-designated *Huni Kuin*) ethnicity, belonging to the Panoan linguistic group, and live in *Kaxinawá* do Seringal Curralinho (Feijó, AC), *Kaxinawá* do Rio Jordão (Jordão, AC), *Kaxinawá* da Praia do Carapanã (Tarauacá, AC), *Kaxinawá* Seringal Independência (Jordão, AC) and *Katukina/Kaxinawá* (Feijó, AC).

We prospected for floury maize landraces using two strategies: interviews (in RO) and landrace lists (in AC). In RO, a partnership with the National Research Institute of Amazonia included visits with farmers in the Ouro Preto River Extractive Reserve (RESEX ROP). Interviews were conducted individually with 12 farmers, using a semi-structured questionnaire about maize landraces, such as: local maize landrace names, landrace origin, time of cultivation, types of uses, records associated with its cultivation, and the history of maize in the region. In AC, due to cultural differences and authorizations, it was not possible to apply the questionnaire, so we asked them to prepare a list of varieties. The list of landraces was elaborated during the "Races of maize" workshop held at the Pro-Indian Commission (CPI), and contained the names of

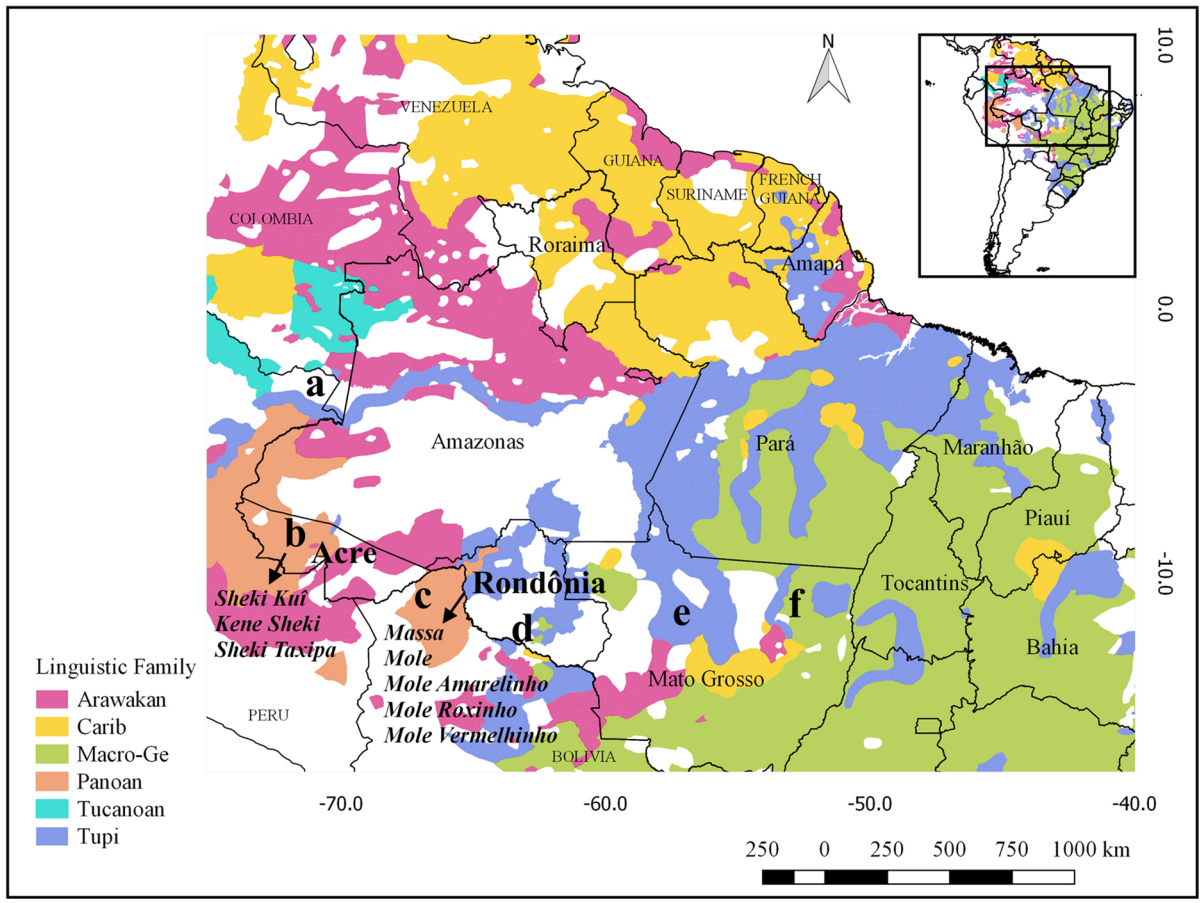

Fig. 2 Geographic distribution of the major Amazonian indigenous language families (Eriksen 2011) and the *Entrelaçado* race and its sub-races in the Amazon Basin: **a** *Ticuna*; **b** *Acre*; **c** *Reyes*; **d** *Bororó*; **e** *Tapirape*; **f** *Chavantes*. The localization of letters is based on the model proposed by Brieger et al. (1958). Survey collections were performed in Acre and Rondônia (highlighted) and the arrows indicate local and indigenous names identified for the *Entrelaçado* race in the ethnobotanical survey. The map was made using QGIS software (http://qgisbrasil.org)

the landraces in Portuguese and in the indigenous language, origin (endogenous or exogenous), their associated uses, as well as the identification of the respondent. This activity was also prepared individually, for each participant, generating a set of eight lists.

The term landraces will be used in this study to refer to local varieties traditionally managed and reproduced by family farmers, which include traditional riverside and indigenous communities. Maize landraces can be used by farmers for different purposes. Therefore, the frequencies of the landraces identified were estimated separately in each of the following categories: family food, animal food, sale and handicrafts (Table 1). Ethnobotanical data were analyzed using descriptive statistics.

Following Brazilian law, this study was approved by the Research Ethics Committee of 'Luiz de Queiroz' College of Agriculture, University of São Paulo (ESALQ/USP), by National Research Ethics Commission (CONEP), through CAAE process n° 60382016.2.0000.5395, National System of Biodiversity Information (SisBio) (registration no 61447-1), and was registered in the National System of Genetic Heritage and Associated Traditional Knowledge Management (SisGen) (registration n° AD2EF0B).

Phenotypic characterization

Phenotypic characterization was performed exclusively for floury maize landraces collected in Brazilian Amazonia, considering that the native races described

Table 1 Local and indigenous uses of maize landraces identified through the ethnobotanical survey in the states of Acre and Rondônia, Brazil

Use of maize landraces	No	%
Family food[a]	15	51.7
Animal food	12	41.4
Sales	1	3.45
Handicraft	1	3.45
Total	29	100

[a]Richness of typical culinary uses of maize: baked sweet cookie, cookie, fried bodó (dumpling), cake, sweet bread, hominy, chicha (fermented drink of indigenous origin), curau (porridge maize), cuscuz (prepared with semolina—incomplete milling—of the maize grain), flour, candied maize (prepared with maize meal), maize roasted in the husk, maize roasted without the husk, maize baked on the fire with honey, maize with meat, maize with sugar, porridge, munguzá—also called chá de burro (porridge made with Brazil nut milk [*Bertholletia excelsa*]), paçoca (roasted maize pounded in the pestle with sugar), pamonha (delicacy prepared with crushed maize, sugar-flavored or salted, then boiled and wrapped in maize husk or banana leaf), maize bread, polenta (cooked maize meal), donut and soup

for the region had this type of endosperm (Brieger et al. 1958). Five floury maize landraces were collected, one from the state of Acre, *Sheki Kuî* (ACF8A) and four from the state of Rondônia, *Massa* (ROF10A), *Mole* (ROF11A), *Mole Amarelinho* (ROF1C), and *Mole Vermelhinho* (ROF1B) (Supplementary Material-1). The collected and characterized samples were those that had unhusked ears (character required for identification, since the classification of the race requires characterization of key ear descriptors) and that the farmers had available to donate at the time of collection. For this reason, the number of landraces identified by the ethnobotanical study (N = 19) was higher than the number of landraces collected and phenotypically characterized (N = 5).

Phenotypic characterization was performed using 17 morphological descriptors considered key for the classification of maize races (Bird and Goodman 1977; Silva et al. 2017). The descriptors are: (1) for the ear [kernel crown color, ear shape, kernel row arrangement, number of rows per ear, number of kernels per row, ear length (cm), ear diameter (cm), cob color, cob diameter (cm) and rachis diameter (cm)]; and (2) for the kernel (grain) [endosperm type (grain), length of kernel (mm), width of kernel (mm), thickness of kernel (mm), shape of upper surface of kernel, pericarp color and endosperm color]. For the qualitative traits, the absolute frequencies of each variable/category within the descriptor were obtained and the highest frequency value (mode) was adopted to characterize the landrace for that descriptor. For the quantitative traits, arithmetic means were calculated.

A cluster analysis was used to associate the Amazonian landraces with known maize races. The analysis considered morphological characteristics of the five maize landraces collected and data available in the literature for the floury maize races described for Brazil, including the *Caingang*, *Entrelaçado*, *Lenha* and *Moroti* indigenous races (Brieger et al. 1958; Paterniani and Goodman 1977). Phenetic distance was estimated using Gower's (1971) genetic similarity index, which combines qualitative and quantitative traits. This analysis aimed to validate the presence of groups and classify the races currently conserved in situ-*on farm* in the region. Multivariate analyzes were performed using Vegan (Oksanen et al. 2016) and Cluster (Maechler et al. 2015) packages in the R platform (R Development Core Team 2015).

Results and discussion

We identified 19 floury landraces in the ethnobotanical survey (8 in AC and 11 in RO) (Supplementary material 2). Farmers reported that the landraces were cultivated by family members in the region for over 100 years, which corresponds to the first rubber boom (1870–1912) (Lacerda 2006). This period was marked by the arrival in Amazonia of a large number of migrants from the Northeast of Brazil to work in the extraction of rubber latex and commercialization of rubber. This migration caused social and cultural transformations in the region and certainly affected the farming system of local family farmers. The Southwest was one of the last regions of the Amazon to suffer the collapse of the indigenous populations during colonization (Mann 2005) and the expansion of the rubber economy accelerated this process (Lacerda 2006). Considering this, the reduction of maize landrace importance in this period may be explained by the following: (1) farmers started to dedicate themselves more to the extraction of rubber and stopped cultivating maize landraces; (2) migrant farmers brought maize seeds from other locations,

which were adopted by local farmers and replaced native landraces in the region; or both reasons altogether.

The diagnosis showed that 79% of the *Entrelaçado* landraces are native to the study region (obtained through family inheritance, indigenous origin, neighbors and exchanges), and 21% are of exogenous origin, introduced from the Amazonian region of Bolivia (Supplementary Material 2). These results show a historical and cultural relationship between maize and humans who inhabit the region, continued by those who live there today, despite the cultural shifts and displacements that occurred in the region. Within this context, the landraces presented different uses, observed by typical preparation and consumption reports (Table 1). We identified 25 human food uses of maize, including traditional and indigenous uses specifically for *Entrelaçado* maize. In addition to current uses, the riverside people reported the historical use of *pão de índio* (*indian bread*, in English) made by indigenous people. According to these farmers, this consists of a rich source of carbohydrates, such as dough made with manioc flour and *Massa* or *Mole* maize of the *Entrelaçado* race. This dough is toasted on the outside, wrapped in banana leaves and buried, which allows its conservation for many years.

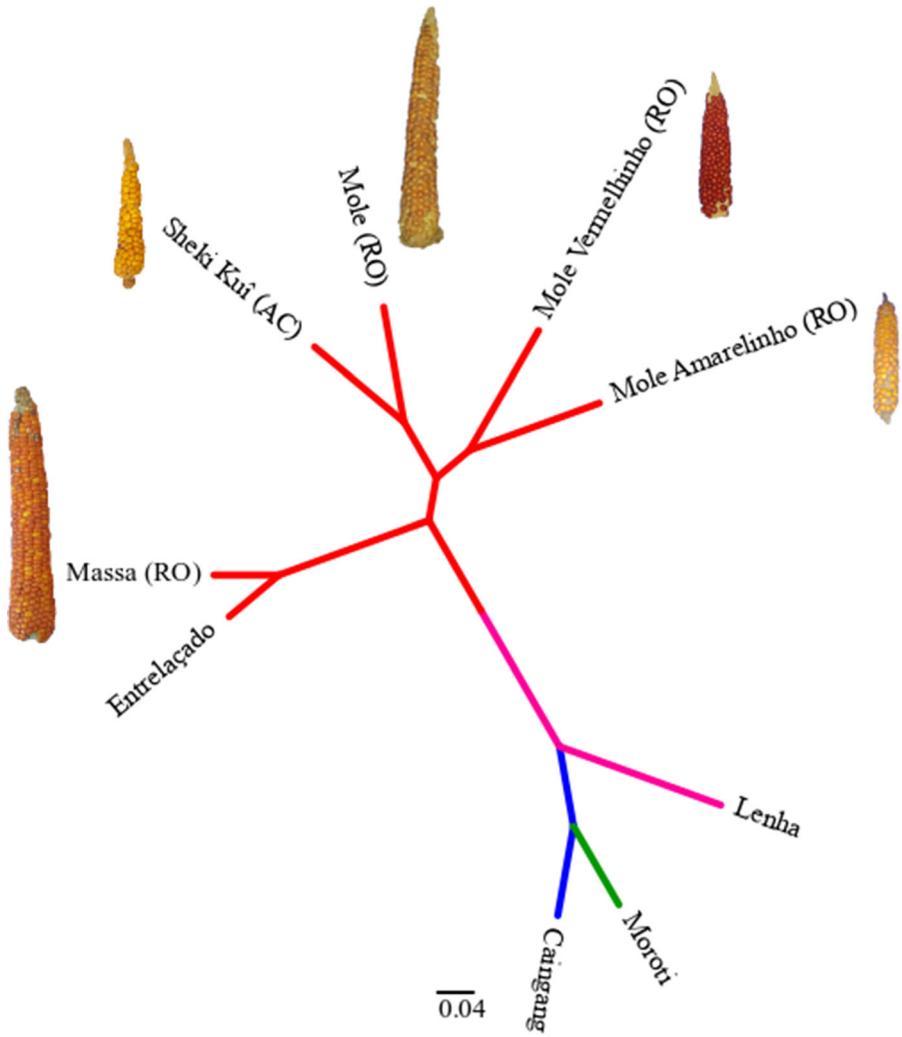

Fig. 3 Ward cluster analysis, based on the Gower Index, of the morphometric characteristics of the landraces characterized in this study—*Sheki Kuî* (Acre), *Massa*, *Mole*, *Mole Amarelinho*, *Mole Vermelhinho* (Rondônia)—and of the floury maize from Brazil described in the literature for the lowlands of South America (Paterniani and Goodman 1977)

Respondents reported that when they find *pão de índio* they still use it as food.

The 19 landraces were tentatively identified as the *Entrelaçado* race with three indigenous names (in AC) and five local names (in RO) (Fig. 2). The names are associated with morphological characteristics, such as color, size and type of endosperm. In AC the names included: *Sheki Kuî* [Maize *Massa*, meaning dough maize] (6 landraces), *Kene Sheki* [Maize *Massa of various colors*] (1) and *Sheki Taxipa* [Maize *Massa Vermelha*, meaning red dough maize] (1), plus two landraces with no names; and in RO: *Massa* [dough(y)] (3 landraces), *Mole* [soft] (5), *Mole Amarelinho* [little yellow soft] (1), *Mole Roxinho* [little purple soft] (1), and *Mole Vermelhinho* [little red soft] (1). No indigenous names for this race were cited by Brieger et al. (1958) or Paterniani and Goodman (1977).

The cluster analysis based on the phenotypic characteristics of five collected landraces and four maize races described in the literature (*Caingang, Entrelaçado, Lenha* and *Moroti*), identified a coherent group composed by the Southwestern Amazonian landraces, Acre (AC) and Rondônia (RO), which grouped with the *Entrelaçado* race (Fig. 3). The landrace *Massa* (RO), cultivated by a farmer with indigenous ancestry in Rondônia, was closer to the *Entrelaçado* race of the literature, and the landraces *Sheki Kuî* (AC), *Mole* (RO), *Mole Vermelhinho* (RO) and *Massa Amarelinho* (RO) were grouped together a little apart. This group of Amazonian maize was isolated from the other floury maize races, which excluded the possibility of belonging to those races. The analysis allowed the classification of the five characterized landraces as belonging to the *Entrelaçado* race.

The identification of the *Entrelaçado* race confirmed the continued existence of this Amazonian race from pre-conquest times to the present day in Southwestern Amazonia, a region proposed as a center for maize diversification, and confirms that the race is not extinct. The race continues to be conserved by traditional farmers and indigenous peoples who inhabit the region, who give local and indigenous names to this race, and have typical culinary uses. We believe it is likely that other traditional communities and indigenous peoples in Amazonia also maintain landraces of the *Entrelaçado* race. Based on recent evidence pointing to the importance of Southwestern Amazonia in the evolutionary process of maize (Kistler et al. 2018), our study emphasizes the importance of Amazonian maize conservation, which may represent one of the oldest races of South America that is still cultivated.

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Author contributions Planning and design of research: FMC, NCAS, RV, CRC and EAV; Collecting data and ethnobotanical characterization: FMC, NCAS, RPA, PCB; Statistical analysis of phenotypic data and classification of maize races: FMC, NCAS and RV; Analysis of ethnobotanical data: FMC and NCAS; Manuscript drafting: FMC, NCAS, EAV and CRC; Manuscript review, support for the interpretation and discussion of the results: FMC, NCAS, RV, CRC, EAV, RPA, PCB, MH and FOF. All authors reviewed and contributed to the final manuscript.

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Data availability The samples of maize from Amazonia, corresponding to the *Entrelaçado* race, collected by this research project are stored in the Genetics Department of the Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, São Paulo, Brazil.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

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