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FORESTRY SCIENCE

Population structure, aggregation, and dispersal of *Euterpe edulis* Mart. at two sites of interior atlantic forest

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Abstract: Habitat destruction and fragmentation can change environmental conditions and disrupt mutualistic interactions, leading to impacts on natural populations. Here we checked how plant population structure responds to environmental degradation by quantifying effective seed dispersal and patterns of population distribution for the animal-dispersed palm Euterpe edulis Mart. (Arecaceae). Thus, we assessed E. edulis population structure at two locations with different degrees of fragmentation in the Interior Atlantic Forest (west of the State of Paraná, Brazil), where we registered the density of saplings at increasing distances from adults palms and from large trees in the vicinity (perch-trees). We found differences between locations, with aggregated saplings and highest densities at the most fragmented site, although in this site Immature individuals were almost absent. We also identified patches of saplings under perch-trees canopies, in a way which suggests these individuals originate from dispersal events. In both sites, the abundance of Immature saplings was similar either nearby adult palms or perch-trees, pointing to perch-trees being relevant to *E. edulis* population dynamics. Thus, while conservation of E. edulis in the Interior Atlantic Forest can benefit from such new data, it is still necessary to check whether our findings are recurring and consistently found elsewhere.

Key words: Animal-plant interactions, fragmentation, perch trees, perturbance.

INTRODUCTION

Forest conversion or exploitation can change ecosystems in ways that range from habitat degradation following fragmentation and isolation of forest remnants, and the loss of species and ecological interactions, to habitat destruction. Currently limited mostly to a set of small fragments (Ribeiro et al. 2009), the Atlantic Forest is an ecoregion under both direct and indirect effects of forest destruction. Atlantic Forest fragments are mostly under some level of degradation associated with edge-effects and improved access by invasive exotic species, hunters, fire, diseases, and timber and nontimber illegal harvesters (de Lima et al. 2020). For plants, fragmented landscapes favor pioneer species (Tabarelli et al. 2004), increase tree mortality (Laurance et al. 2002), and decreases fertility, growth, and regeneration of populations (Bruna et al. 2009, García & Chacoff 2007). Once it that can be mediated by biotic interactions, plant regeneration can be impacted by defaunation because animals act as pollinators, dispersers, predators or important herbivores of many species (Cordeiro & Howe 2001, Cramer et al. 2007, Farwig & Berens 2012), pointing to a complex interaction between plants and animals for the integrity of natural ecosystems.

Even though habitat degradation tends to have idiosyncratic effects on individual species, at least some forms of degradation have ecosystem-wide consequences, especially when affecting populations of keystone species. Euterpe edulis Mart. (Arecaceae), or juçara-palm, is a typical palm found in the Atlantic Forest. This palm species depends on high levels of habitat conservation because it develops well under shade and under wet soils (Braz et al. 2014, Paulilo 2000, R.C.Q. Portela, unpublished data), being classified as late-successional species (Carpanezzi & Carpanezzi 2006). Besides being negatively affected by habitat loss and fragmentation, E. edulis has been subjected to illegal exploitation for decades (Galetti & Fernandez 1998, Tabarelli et al. 2004), leading to local extinction and listed as vulnerable in the endangered flora of Brazil (CNC FLORA 2012). Contrasting with its concerning conservation status, *E. edulis* is considered a keystone species (Galetti et al. 1999, Reis et al. 1996) because it bears fruits for long intervals - even though the onset and end of fruiting varies between regions - that are consumed by more than 50 animal species (Castro et al. 2007, Galetti et al. 1999, da Silva & dos Reis 2019). In turn, the presence of dispersers, along with suitable abiotic conditions, seems to be key to the maintenance of juçara-palm populations (Galetti et al. 2015, Pizo et al. 2006, Portela & Dirzo 2020). Because animals either swallow or manipulate E. edulis fruits, many species end up dispersing its seeds, which can benefit palm populations by lowering intraspecific competition, finding or repopulating suitable habitats, and maintaining gene flow among populations (de Barros Leite et al. 2012, Seoane et al. 2005, Soares et al. 2019). Given such relevance of seed dispersal, the absence of effective dispersers may hence compromise the proper functioning of *E. edulis* populations.

Separating actual dispersal from seed predation is a difficult task. Quickly quantifying the actual consequences of absent or reduced

dispersal rates is equally difficult for plant populations. Large birds are probably among the most important dispersers of *E. edulis*, both for carrying seeds over long distances and for doing so mostly without causing damage to the seed embryo (da Silva & dos Reis 2019, Galetti et al. 2015). Many of those birds use large trees as perches (hereafter "perch-trees"), where they manipulate fruits or defecate the seeds, generating a "seed rain" (Mikich & da Silva Possette 2007, Howe & Smallwood 1982). Thus, to quickly access whether dispersal is occurring, interrupted, or recently reset, we propose here to contrast population size structure of E. edulis under perch-trees with that under adult juçara-palms.

Typical population size structure of E. edulis has a high number of saplings in the initial developing stages, forming seedling banks (Matos et al. 1999, Reis et al. 1996), and a few individuals in the advanced developing stages, leading to a concave or reverse J-shaped population structure (Portela & dos Santos 2014, Reis et al. 1996, Rother et al. 2016). Nevertheless, E. edulis is found along a wide range of latitudes (CNC Flora 2012) and, thus, under many distinct environmental conditions, so that population parameters are still somewhat uncertain (Melito et al. 2014), especially in the transitional region of the Interior Atlantic Forest. In addition, population parameters are likely directly and indirectly affected by fragmentation and degradation. Direct effects may arise on overall population size and population size structure because of abiotic changes and of exploitation history. Indirect effects, in turn, can arise under reduced dispersal, indicated by aggregated saplings underneath and nearby adult-palms and by a steep decay in sapling abundance with increasing distances from adult-palms - even though such patterns can arise either because of aggregated resources (see Ricklefs 2010) or differences in the degree of fragmentation and degradation between areas.

Here we described and contrasted populations of Euterpe edulis in two sites of Interior Atlantic Forest and assessed how its population structure can be affected by either environmental degradation or differences in effective dispersal. We contrasted a most pristine site that we are aware of in the region (taken here as the reference site and for which we have a reference population), with another under fragmentation and habitat degradation. Given the ecological requirements of *E. edulis*, we expected to observe more plants (saplings and adults) and a less aggregated spatial distribution of saplings due to the effective activity of dispersers at the reference site. Assuming that the reference site harbors more effective dispersers and that each site was internally homogeneous in terms of environmental conditions, we predicted the following patterns: first, in the reference site, there should be a flatter decay curve for the number of saplings with increasing distances from reproductive jucara-palms, indicating high rates of fruit and seed removal. Second, seedlings and saplings of E. edulis should be more common under perch-trees in the reference site, pointing to effective dispersal mediated by seed-disperser birds. Third, clustering of saplings should be lowest for the smallest development stages in the reference site because of higher rates of fruit or seed removal. To describe such patterns and check our predictions, we quantified the population size structure, counted and categorized saplings of *E. edulis* by size at different distances from adult-palms and from perch-trees, and calculated indices of spatial distribution for both sites.

MATERIALS AND METHODS

Study region

Samplings were carried out in the Iguaçu National Park and in the Suely Marcondes de Moura Festugatto Environmental Education Center, both located in the western region of the State of Paraná (Brazil; Figure 1), between April and November 2018. The two sites belong to the transitional area of Interior Atlantic Forests (Tabarelli et al. 2010), with forests classified as a mix of Semideciduous Seasonal Forest and of Mixed Ombrophylous Forest. The study region has a subtropical climate (Cfa following Köppen 1948), with an average annual precipitation of 1,800 - 2,000 mm and no dry season (Nitsche et al. 2019).

In the Iguaçu National Park, data were collected in Céu Azul municipality, along the Information and Control Post Ecological Trail (coordinates 25°08'38"S and 53°48'42"W). The Iguaçu National Park hosts one of the largest remnants of Interior Atlantic Forests in the country (185,262.5 ha) and is the closest to a pristine forest for the region. Samplings were located on the north portion of the Park, at an elevation of c.d. 650 m.a.s.l., where plant composition is mostly typical of Semideciduous Seasonal Forest (Souza et al. 2017). Given the proximity to the control post, this region of the Park underwent little illegal hunting and palm heart extraction. Because of its dimensions. protection, and its high degree of conservation, this site will be identified by "reference" (for both conservation status and *E. edulis* population).

The remaining data were collected at the Suely Marcondes de Moura Festugatto Environmental Education Center, a municipalitylevel protected area located nearby the BR-277 highway (km 573 to km 571), in Cascavel municipality (central geographic coordinates 25°0'5"S 53°17'21"W). This site harbors a small



Figure 1. Range map of *Euterpe edulis* Mart. throughout the Brazilian Atlantic Forest, highlighting the location of the sampling sites in the municipalities of Cascavel (fragment) and Céu Azul (reference site) in western Paraná State, Brazil.

to medium sized forest fragment (135 ha), at an elevation of c.d. 800 m.a.s.l., where plant composition is a transition between species from Mixed Ombrophylous Forests and Semideciduous Seasonal Forests (Castella & de Britez 2004). The fragment underwent selective logging before it was turned into a protected area in 1998 (Brocardo & Cândido Júnior 2012). Here, this site was considered degraded given the small size and the strong past and ongoing human uses (hereafter "forest fragment" or just "fragment").

Study species

The juçara-palm *Euterpe edulis* Martius (Arecaceae) is a typical palm found in the Atlantic Forest. *Euterpe edulis* ranges along most of the Brazilian Atlantic Forest and some parts of Cerrado biome, being found also in Argentina and Paraguay (de Souza & Prevedello 2019). The species grows well under shade and under wet soils (Braz et al. 2014, Paulilo 2000), has a single stipe, which is unable to regrowth after cut, and has slow growth, taking at least 10 years to reach maturity (CNC FLORA 2012). Besides its role as a climax species (Carpanezzi & Carpanezzi 2006), E. edulis is also well-known for its ecological relevance (Muler et al. 2014). It grows rounded, fleshy fruits that are purplish and with c.d. 13 mm when ripe (Pizo et al. 2006). The fruits are displayed for long intervals, with ripe fruits available from the fall to the ending of winter, when fruit abundance of other plants tends to be low (Galetti et al. 1999, Castro et al. 2007). In our study region, ripe fruits were available from April to July.

Populational data

The first procedure was to count *E. edulis* adults in both sites. In the forest fragment, given the low local abundance of the species, all adults sighted near trails were sampled, totaling a sampling area of c.d. 1 ha. In the reference site, all adults sighted in a 0.5 ha plot were sampled. All adult individuals were tagged and georeferenced (GPS Garmin Gpsmap 64). For each adult palm, a transect was delimited considering the selected adult as the starting point and following in a direction to avoid other nearby adults; if there were no nearby adults, the direction of the transect was established at a random direction. The slope of the terrain was measured for each transect. This information was later included in the analysis to assess whether any relationship existed between slope and dispersal distance. Along the transect, saplings were counted in circular plots (1 m radius) placed at every 2 m. The transect was sampled for at least 10 m long and up to a distance where no saplings were found anymore in two subsequent plots (Figure

2), thus transect size ranged from 10 m to 22m long.

To estimate the effect of animal dispersal of E. edulis seeds, we selected trees likely to be used as perch by birds. Given that perch-trees had to be located at least 15 m away from any reproductive adult of jucara-palms, sampling area added up to c.d. 2 ha at each site. Perchtrees were identified based on the presence of a "patch" of jucara-palm younglings under their canopy, being tagged and georeferenced as previously described for E. edulis adults. For each perch-tree, diameter at breast height (CBH) and height was recorded, but we were unable to get each tree species identity. For each perchtree, saplings of *E. edulis* were sampled using a transect and circular plots as described for adult juçara-palms (Fig. 2b): by delimiting the transects considering the selected perch-tree as the starting point and following in a direction to avoid other nearby adult jucara-palms but also other perch-trees.

In transects starting at either adult juçarapalms or perch-trees, saplings of *E. edulis* were



Figure 2. Summary of the sampling design, depicting transects starting from either a) *Euterpe edulis* adults or b) perch-trees. Each transect (2) had several plots (1) were saplings were counted at distinct development stages. Illustration by Gabriel Barreto. counted and categorized into five development stages (adapted from Reis et al. 1996): Seedling (saplings with up to two open leaves), Juvenile I (saplings with at least three leaves or with a height of 30 cm from the ground to the insertion of the youngest leaf), Juvenile II (saplings with >30 cm but lacking a woody stipe), Immature I (individuals with woody stipe, but shorter than 1.3 m), Immature II (plants with woody stipe, ≥ 1.3 m tall, but lacking any trace of reproductive structures). Adult palms were identified by traces of or existing reproductive structures.

Data analysis

To assess differences in the population structure of Euterpe edulis between sampled sites, a χ^2 test of independence was calculated, followed by the adjusted residuals test. Next, the abundance and distribution of saplings by stage and across plots was modeled as a function of the sampling site (forest fragment or reference site), type of source (whether adult juçara-palm or perch-tree), distance from the source, and slope of the terrain. To fit such relationships, a generalized linear mixed model (GLMM) was calculated, where the abovementioned variables were included as fixed effects and transects kept as a random effect. A negative binomial distribution (with quadratic parameterization – "nbinom2") was assumed for the count data, with a logarithmic link function. The structure of the full model was:

number of saplings in stage ~ source + distance + site + slope + (1 | transect)

Finally, the spatial distribution was tested for the aggregation of younglings using the Morisita dispersion index (standardized to the interval –1 to +1 and adjusted to a confidence interval between –0.5 to +0.5; Smith-Gill 1975). According to this index, values from -1 to -0.5 indicate individuals dispersed regularly, -0.49 to +0.49 indicates individuals dispersed randomly, and values from +0.5 to +1 indicate aggregated individuals.

All analyses were run in R (R Core Team 2021) using package "glmmTMB" for GLMMs (Brooks et al. 2017), "DHARMa" for validation of modeling strategy by assessing homoscedasticity, normality, and extreme values in model residuals (Hartig 2021), and "vegan" (Oksanen et al. 2020) for Morisita index calculations.

RESULTS

We found 26 adults of Euterpe edulis, half along the trails in the fragment, and half in the reference site. The estimated density of saplings for the fragment was 16,372 ind.ha⁻¹, and 6,061 ind.ha⁻¹ in the reference site. The distribution of saplings along development stages followed a reverse J pattern on both sites (Figure 3, left panel), although the proportion of younglings at each stage differed between sites (χ^2 = 238.6, df = 4; P < 0.001). In the fragment, Seedling and Juvenile I stages accounted for 86% of all younglings, with the Juvenile I stage (54%) being even proportionally more abundant than Seedling (32%). Still in the fragment, we found no Immature II individuals nearby adults (Figure 3 - top-right), with only a few of such individuals being recorded away from any adult juçara-palm in our whole sample.

Within transects, the greatest distance found between an adult-palm and saplings was 22 m in the fragment and 12 m in the reference site. For perch-tree transects, saplings of *E. edulis* were found up to 48 m away from the nearest adult-palm in the fragment and up to 57 m in the reference site. An exponential decay in the total abundance of saplings was found with increasing distances from adult juçara-palms (GLMM, Z = -9.014; P < 0.001; Figure 4a, Supplementary Material - Table SI), a pattern expected when gravity is the main dispersal agent. Such decay



Figure 3. Population structure of *Euterpe edulis* as the distribution of saplings at distinct development stages in the reference site and in the fragment (left panel) and details of the structure nearby the adult-palms and perchtrees in the fragment (top-right) and in the reference site (bottom-right). To aid visualization, *E. edulis* abundances were log-transformed (LN).

was found at both the fragment and the reference site, although a steeper decay was found in the fragment (Figure 4a). For perch-trees, a distancedecay relationship was also observed, but with a smaller decay due to a lower abundance of saplings than for adult-palms (GLMM, Z = -2.625; P = 0.009; Figure 4d). Palms at later development stages had flatter to no distance-decay patterns, resulting, for instance, in little explanation for the abundance of Immatures (GLMM, Z = 0.828; P = 0.408; Also see Figure 4). Terrain slope was uncorrelated with the abundance of *E. edulis* saplings (GLMM, Z = -0.967; P = 0.333) and was left out of the above-mentioned models.

Overall, 145 saplings of *E. edulis* were found near perch-trees in the fragment, whereas 57 were found near the perch-trees in the reference site. Although the CBH of perch-trees was similar at both sites (average CBH of 2.0 m), it varied less in the reference site (standard deviation of the mean, SD = 0.50) than in the fragment (SD = 0.94). The abundance of saplings peaked at 2 and 6 m away from the perch-tree trunks (Figure 4d), matching the most suitable location for dispersers to land on given the size of the trees and the arrangement of their branches. In comparison to the perch-trees, the peak in saplings of *E. edulis* found near adult-palms had a higher slope (Figure 4a), an expected pattern due to the higher abundance of propagules nearby adult-trees. However, such differences in abundance near the different origins faded when considering only saplings from latter stages (Immature I and II; Z = -0.427; P = 0.67; Figure 4c, f).

Dispersal seems to be effective at both sites because of a low to no clustering of saplings for most stages (11 out of 18 Morisita index-values in the interval between –0.5 and +0.5; Figure 5), especially for saplings of *E. edulis* in the reference site, which were distributed mostly randomly all over the site. For the fragment, in turn, the distribution was mostly clustered – both away from adult-palms and from perchtrees. The random distribution of saplings near perch-trees in the reference site might result from the higher density of large trees suitable



Figure 4. Abundance of *Euterpe edulis* saplings with increasing distances from adult-palms (left column) or perchtree (right column), for the pooled data of all saplings (a and d), for pooled data of Seedlings and Juveniles (b and e) or for Immatures only (c and f). Solid and dashed lines indicate fitted distance-decay relationships (GLMM).

as perches, and therefore the availability of perches at this site.

DISCUSSION

Our expectation – that the population structure and distribution of *E. edulis* would change following direct and indirect effects of

fragmentation and anthropogenic disturbance – was corroborated, even though our predictions were only partially supported. As predicted, we found a decay in the abundance of saplings farther from adult juçara-palms, a pattern that was repeated nearby perch-trees. Also, as predicted, we found a spatial distribution of saplings in the reference site that was less



Figure 5. Spatial dispersion of *Euterpe edulis* saplings by development stage nearby either adult-palms (a) or perch-trees (b) and for either the fragment or reference site. Spatial dispersion is represented by the standardized version of the Morisita index, where interpretation is as follows: -1 to -0.5 (regular); -0.49 to +0.49 (random); +0.5 to +1 (aggregated).

aggregated than at the forest fragment. On the other hand, we found significantly more juveniles of *E. edulis* in the fragment compared to the reference site, contradicting our initial expectation.

We observed that *E. edulis* populations at both sites followed a reverse J population structure, as expected and described by other authors (Rother et al. 2016, Souza Milanesi et al. 2021, Reis et al. 1996). Likewise, the numbers of saplings found here (16,372 and 6,061 ind. ha⁻¹) were consistent with that found by other authors, given a similarly wide variation has been reported elsewhere, *e.g.*, 17,315 and 11,517 ind. ha⁻¹ in the State of São Paulo (Fantini & Guries 2007); 12,565 ind. ha⁻¹ in the State of Santa Catarina, (Reis et al. 1996); 1,290 ind. ha⁻¹ in the State of Paraná (E.L. Tonetti, unpublished data). It seems that the species tends to show high densities of adults in well-conserved sites (c.d. 300 ind. ha⁻¹; Rother et al. 2016), which had been reported in the Iguaçu National Park in a phytosociological study (370 ind. ha⁻¹; Souza et al. 2017).

The decline in the abundance of E. edulis seedlings with increasing distance from adult palms was expected. Such a pattern can result from a high production of fruits and high rates of dispersal by barochory (no other means than by gravity alone) or by primary dispersal agents (Reis & Kageyama 2000). A similar pattern was found for perch-trees, although saplings were in a lower abundance and concentrated c.d. 4-6 m away from the tree trunk. The concentration at these distances suggests the seeds were carried there by birds (da Silva & dos Reis 2019), although the role of other dispersal agents remains unknown. Similarly, the higher number of individuals found near the adult-palms compared to perch-trees was expected, being explained by the higher number of seeds coming from the adult itself. However, this difference vanishes in later developmental stages of E. edulis (Juvenile II and Immatures), suggesting dispersers and seed dispersal are beneficial by driving the seeds to greater distances, where there is a greater chance of survival because of a release from density-dependent restrictions to population growth. Thus, our results suggest perch trees are important and dispersers are being effective at both sites.

The forest fragment had more saplings than be directly lowered by predation by capuchin reference site. Larger rates of regeneration monkeys (Portela & Dirzo 2020), we found no

the reference site. Larger rates of regeneration in sites under disturbance were found elsewhere (Marcos & Matos 2012. Melito et al. 2014, Portela et al. 2010, Fantini & Guries 2007). The large number of *E. edulis* saplings observed in the fragment can be explained by several factors, directly or indirectly associated with fragmentation. First, reduced fruit removal can increase seed germination near adult-palms (Cramer et al. 2007). Second, reduced rates of seed attack by pathogens and predatory insects can result from a less-specialized predatory community in the fragment than at the reference site (Ricklefs 2010). Third, a process of density compensation can be ongoing, in which E. edulis is filling the place left by species with a lower tolerance to environmental changes that follow fragmentation and edge-effects. This can be the case because, notwithstanding E. edulis being considered typical of well-conserved sites, its seeds have a wide germination niche (Braz et al. 2014) and are likely to recruit under indirect sunlight, as in either gaps, forest edges, or riverbanks (Paulilo 2000, Sanchez 1999).

The proportion of plants in different stages of development varied between sites. The high abundance of *E. edulis* saplings at the fragment is mainly because of a high number of plants in the earlier stages of development, with few to no plants in the later stages, close to maturity. The low number of Immatures in the fragment might be due to a much lower intra-specific competition in the reference site or distinct ages of the populations studied. At the reference site, a high mortality in the early life stages of *E. edulis* – due to either seed predation or pathogen attack - might reduce the negative effects of density dependence, favoring survival to later stages such as Immature and adult stages, thus maintaining the population. Besides, although Immature abundance can

monkeys (Portela & Dirzo 2020), we found no signs of such predation here. The age of the populations studied differs since the fragment population is very young (c.d. 20 years old; Brocardo CR, personal communication), likely explaining the low abundance of individuals in later stages therein. However, plants near to maturity were observed away from the adultpalms, corroborating the hypothesis of negative density-dependent effects.

Saplings of *E. edulis* were aggregated in the fragment, contrasting with a more random distribution in the reference site. This difference is likely related to direct and indirect effects of fragmentation. First, sites under lower rates of anthropogenic disturbance (e.g., conserved environments such as our reference site) can be environmentally more even and favor a random distribution of organisms (Ricklefs 2010). Second, a lack of or a low number of animal dispersal agents can be a limiting factor and result in an aggregated spatial distribution of saplings nearby adult plants in fragments (da Silva & dos Reis 2019, Galetti et al. 2013). In contrast, the aggregated distributions observed near both perch-trees and adult-palms in the fragment likely result from distinct processes. Near adults, the pattern is likely due to many nondispersed and non-predated seeds that end up germinating. Near perch-trees, the aggregated pattern might suggest that the low abundance of large trees ends up increasing their usage as perches by animals (Oliveira et al. 2008).

In short, differences between sites is likely the output of different *Euterpe edulis* population dynamics. While saplings were aggregated and under high densities in the fragment, the reference population has a lower density and plants at all developmental stages that we considered here, differences that we suggest are associated with fragmentation. Perch-trees seem to be relevant for *E. edulis* population dynamics and pointed to active dispersal on both sites, since we found several saplings under their canopies and far away from adultpalms. Because saplings were common under perch-trees, we suggest dispersers, especially birds, are dispersing *E. edulis* seeds, so that mutualistic interactions, key to the maintenance of *E. edulis* populations, still exist even in the most degraded site. Yet, to fully address the conservation of E. edulis on Interior Atlantic Forests fragments, it is still necessary to further investigate if patterns found here are observed across fragments in the region. In future studies, aspects such as the role of changes to biotic (such as defaunation) and abiotic factors on E. edulis population dynamics should be further investigated, thus aiding in better strategies for maintenance of the species in the region. Finally, even though we provided new data for E. edulis populations, indicating that even the population at a degraded site seems sustainable at this point, monitoring them to check whether the population in the fragment is under longterm risk and whether similar risks apply to other isolated populations of juçara-palm in the Interior Atlantic Forests are still open questions.

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SUPPLEMENTARY MATERIAL

Table SI.

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K. A. Baggio designed the study, collected and analyzed data and wrote the first draft of the manuscript. E. L. H. Giehl analyzed data. J. F. Cândido Jr. designed the study. All authors contributed to writing and reviewing the submitted version of the manuscript.

