Rodriguésia 73: e02012019. 2022
*http://rodriguesia.jbrj.gov.br*
DOI: http://dx.doi.org/10.1590/2175-7860202273047

## Original Paper

# Fruiting phenology and dispersal syndromes in a sandy coastal plain in southeastern Brazil

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**Abstract**

Fruits have a wide variety of morphological and phenological characteristics that have been related to environmental conditions and seed dispersal mode. In this paper, we describe the fruit morphology, the fruiting phenology and infer dispersal patterns of 52 species from restinga of Maricá, Rio de Janeiro, in order to understand the richness and temporal variation of these resources in the community. Fleshy, indehiscent, and colored fruits, typical of zoochory, predominate in the restinga (77.8%). Anemochoric fruits represent 13.3%. In 42% of zoochoric species, fruits go through three to five colors until maturity, and different stages of ripeness can be observed on the same plant. A constant supply of zoochoric and anemochoric fruits was observed throughout the year. Unlike flowering, there were no significant correlations between fruiting activity and intensity and abiotic factors. For the community studied, the fruiting pattern observed also contrasts with flowering, due to the lower seasonality, and intensity suggesting that biotic factors, such as seed dispersers (in the case of zoochoric fruits) may have relevance in determining fruit ripening and seed dispersal periods in coastal environments.
**Key words**: reproductive phenology, *Restinga*, seed dispersal, zoochoric fruits.

**Resumo**

Frutos apresentam uma grande variedade de características morfológicas e fenológicas que têm sido relacionadas às condições do ambiente e ao modo de dispersão de sementes. Neste trabalho, descrevemos a morfologia dos frutos, a fenologia de frutificação e inferimos padrões de dispersão de 52 espécies da restinga de Maricá, Rio de Janeiro, no sentido de compreender a riqueza e a variação temporal desses recursos na comunidade. Frutos carnosos, indeiscentes e coloridos, típicos de zoocoria, predominam na restinga (77,8%). Frutos anemocóricos representam 13,3%. Em 42% das espécies zoocóricas, os frutos passam por três a cinco cores até a maturação, e diferentes estádios de maturação podem ser observados na mesma planta. Um fornecimento constante de frutos zoocóricos e anemocóricos foi observado ao longo do ano. Diferentemente da floração, não houve correlações significativas entre percentuais de atividade e de intensidade de frutificação e os fatores abióticos. Para a comunidade estudada, o padrão de frutificação observado também contrasta com o da floração, pela menor sazonalidade e intensidade dos eventos, sugerindo que fatores bióticos, como dispersores de sementes (no caso de frutos zoocóricos) podem ter relevância na determinação dos períodos de maturação dos frutos e de dispersão de sementes em ambientes costeiros.
**Palavras-chave**: fenologia reprodutiva, Restinga, dispersão de sementes, frutos zoocóricos.

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## Introduction

Fruits show a large range of sizes, shapes, number of seeds, colors, odors, ripening phenology, and chemical properties. Many of these features have been related to the environment conditions, mode of seed dispersal, and the animals involved in seed dispersion, being usually gathered to describe dispersal syndromes (van der Pijl 1982; Gautier-Hion *et al.* 1985; Wheelwright & Janson 1985). Color is specially one of the most important cues used by frugivores to find fruits (Lomáscolo & Schaefer 2010). Fruit color convergence in unrelated plants is independent of phylogeny and supports the hypothesis that frugivores play an important role in fruit evolution (Lomáscolo & Schaefer 2010; Valenta *et al*. 2018). Beyond a host of animal species (zoochoric dispersal), diaspores (seeds, fruits, infructescences and other dispersal units) can reach the ground by action of wind (anemochory), water (hydrochory) or by self-dispersal (van der Pijl 1982).

Morphological and phenological characteristics of fruits contribute to the understanding of the temporal variation of these resources and their relationship with seed dispersers (Wheelwright & Janson 1985; Schaik *et al.* 1993). Influence of abiotic (temperature, precipitation, wind, humidity) and biotic factors (primary and secondary dispersers of fruits and seeds, animal predators) results in a most favorable period for seed dispersal (Rathke & Lacey 1985; Opler *et al.* 1976; Schaik *et al.* 1993; Morellato *et al.* 2000). Seasonality in the number of plant species bearing ripe fruits decreases from temperate to tropical forests, largely as a result of the increase in the average duration of the fruiting phenophases (Jordano 2000), resulting in a continuous supply of resources for animals in tropical areas (Morellato *et al.* 2000; Zamith & Scarano 2004; Reys *et al*. 2005; Marchioretto *et al.* 2007). Zoochorous species prevail in tropical environments (van der Pijl 1982; Rathke & Lacey 1985). In the Atlantic Forest, high frequency of animal-dispersed species, specifically bird-dispersed ones, indicate that frugivorous animals are very important for the maintenance of communities (Martins *et al*. 2014). In restinga vegetation (habitat marginal to the Brazilian Atlantic Forest), where conditions are extreme (high temperatures, steady winds, high salinity and sandy soil poor in nutrients), predominance of zoochory was also recorded (Zamith & Scarano 2004; Martins *et al*. 2014).

Here, we described the fruit morphology (size, shape, color and number of seeds) and followed up the fruiting phenology of 52 species from an area of restinga vegetation in southeastern Brazil. These gathered data support us to infer important aspects related to seed dispersion in these areas. It is noteworthy that seed dispersal plays a crucial ecological role in the maintenance of biodiversity and natural regeneration of habitats worldwide (Morellato *et al*. 2016). Despite its great importance, the connection between morphological features, dispersal patterns, and phenology of fruits in restinga ecosystem are unexplored. In this context, we aim in this study: 1- to examine the occurrence and the diversity of seed dispersal syndromes in restinga vegetation; 2- to characterize the distribution throughout the year of the different seed dispersal syndromes; 3- to investigate the relationship between the fruiting periods and climatic factors; 4- to assess the temporal availability of fruit resources for the potential dispersing fauna. In particular, we explore the coloring of the fruits by monitoring of ripeness, the presentation of colors in the plant and the distribution of fruit colors throughout the year. We expect that this study can help incrementing successful restoration and conservation actions for restinga areas, which have been under intense anthropic occupation (Rocha *et al*. 2007; Marques *et al*. 2015).

## Materials and Methods

The study was conducted in restinga (sandy coastal plains) within the Environmental Protection Area of Maricá (APA of Maricá - 496 ha), Rio de Janeiro state, Brazil (22º52'–22º54'S and 42º49'–42º54'W). The climate of the region is Aw tropical humid (Alvares *et al.* 2014), with the weather being wetter between October and March (warm/rainy season). We conducted the study over a 1-year period from April 2010 to March 2011. The mean annual temperature was 23.7 °C (maximum mean in February with 28.5 °C and minimum mean in June with 19.5 °C). The total precipitation was 1,168.7 mm, with 552.6 mm between October and March and 616.1 mm between April and September. We observed a water stress in February (Instituto Nacional de Meteorologia, INMET-RJ).

We carried out fruiting phenological monitoring of 402 individuals of shrubs and trees (all individuals over 50 cm in height). Plants were marked and numbered along a transect of 500 m on the internal sandy ridge (sandy soil where the vegetation grows in thickets interspersed with almost completely clear spaces), divided into 50 plots of 10 m × 10 m. Sampled species represent approximately 80% of woody species in this area (Rodarte 2008). We organized the floristic list according to Flora do Brasil (2020) and The Plant List (2019).

In this paper, we used the botanical term "fruit" in a broad sense to describe types of diaspores irrespective of their origin and structure (*i.e.*, "true" fruit, pseudo-fruit, etc.). We collected ripe fruits from at least five individuals for each species. For each fruit we measured the length (cm) using a caliper, and we counted the number of seeds. We also registered the dehiscence (dehiscent or indehiscent) and the consistency (dry or fleshy). Dehiscent fruits with arillate seeds were regarded as fleshy fruits because they constitute a form of food resource. We classified the colors of ripe fruits of each species by human perception as black, dark brown, brown, red, dark red, yellow, orange, green, and multicolored (color of aril and/or seed contrasting with the outer or inner surfaces of fruit capsules). We followed the color change of the fruits through the course of maturation. We performed inferences about the dispersion syndrome, according to van der Pijl (1982). For eight species we obtained the information about fruit length, seed number, and dispersal syndrome from the literature.

The study involved only the phenophase of fruit set. Two classical methods for the phenological analysis were employed: activity and intensity percentages. Activity method (based in presence or absence of phenophase of the individuals) was used to indicate percentage of individuals in the population that were manifesting fruiting event (Bencke & Morellato 2002). We visually assessed intensity of events using a semi-quantitative scale (Fournier 1974, adapted for four classes), namely: (0) absence of the event; (1) 1 to 33%; (2) 34% to 66% and (3) 67% to 100% of the canopy showing the phenophase. Each individual was evaluated weekly and scored from 0 to 3 for fruiting event during the study period. We plotted the data monthly, using the most representative score for the month. We expressed intensity of events in each month by the formula: % of intensity = $(\Sigma \text{Fournier}/3 \times N) \times 100)$, where: ΣFournier is sum of semi-quantitative data attributed to each individual; 3 is maximum value of categories adopted; and N is total number of plants evaluated (Fournier 1974).

We tested correlation (Spearman *rs* at a significance level of 0.05) between events of fruiting (intensity and activity of fruit set of plant community, and species grouped per syndrome) and some climatic data [precipitation (mm), day length (h), and mean, minimum and maximum temperature ($^o$C) in studied months] (Statsoft 2005). The National Institute of Meteorology INMET/RJ-Maricá Station provided temperature and precipitation data. We calculated day length data according to Pereira *et al.* (2001) and Varejão-Silva (2000).

Voucher specimen were deposited in Herbarium of Museu Nacional (R), Universidade Federal do Rio de Janeiro and Faculdade de Formação de Professores (RFFP) from Universidade do Estado do Rio de Janeiro.

## Results

In the study area, we identified 52 species (30 families), of which 42 produced fruit in the monitoring period (Tabs. 1-2). The most representative family was Myrtaceae (nine species) followed by Leguminosae (five species) (Tab. 2). Fleshy or attractive fruits, featuring zoochoric syndrome, prevailed in species of this study (77.8%); anemochoric fruits represent 13.3% of all fruits (Fig. 1; Tab. 3). Three species (6.7%) showed two types of dispersion (zoochoric and self-dispersion) and one species (4.4%) presented only self-dispersion (Fig. 1; Tab. 3).

Fleshy fruits were recorded in 82% of the species, and indehiscent pattern (71%) was predominant (Tab. 3). *Andira legalis* (Fabaceae) was the only zoochoric species with dry fruit. We observed that 58% of the species studied have fruits with one or two seeds (Tab. 2).

In relation to fruits maturation, we observed that 42% (19) of species, especially the ones whose fruits seems to be dispersed by animals (Fig. 1; Tab. 3), the fruits pass through three or five hues until complete maturation, and different maturation stages (different colors) are present in the same plant (*Calyptranthes brasiliensis*, *Eugenia astringens*, *Myrcia ilheosensis* and *Neomitranthes obscura*). Some species did not change the fruit color during the maturation (e.g., *Andira legalis*) (brown fruits), *Couepia ovalifolia* and *Byrsonima sericea* (both with green fruits).

Considering zoochoric and zoochoric/self-dispersion fruits, there is a predominance of black in ripe fruits, taking up 39.5% of all species, followed by red and multicolored (13.2% each),

**Table 1** – Fruiting period (only ripe fruit) in restinga of Maricá, Rio de Janeiro, Brazil. Intensity: 1 (○), 2 (●), 3 (◊) adapted according to Fournier (1974).

| **Species / months** | a | m | j | j | a | s | o | n | d | j | f | m | a |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Agarista revoluta* | ○ | | | | | ○ | | | ○ | ○ | | | ○ |
| *Alchornea triplinervia* | | ○ | ○ | ○ | | ○ | | ○ | | ○ | ○ | ○ | |
| *Allagoptera arenaria* | | | | | | | ○ | ○ | ○ | | | | |
| *Allophylus edulis* | | | | | | | | | ○ | | | | |
| *Amaioua intermedia* | | | | | | | | | | | | ○ | |
| *Andira legalis* | | | ○ | | | | | | | ○ | ○ | | |
| *Aspidosperma pyricollum* | | ○ | ○ | ○ | | ○ | | | | | | | ○ |
| *Brosimum guianense* | | | | | | | | | ○ | | | ○ | |
| *Byrsonima sericea* | ○ | | | | | | | | | ○ | ○ | ● | |
| *Calyptranthes brasiliensis* | ○ | ● | ○ | | | | | | | | | | |
| *Cathedra rubricaulis* | | | | | | | | | | ○ | | | |
| *Clusia lanceolata* | | | | | | ○ | ○ | ● | ● | ● | ● | ● | ○ |
| *Coccoloba arborescens* | | | | ○ | ○ | ○ | ○ | ○ | ○ | | | | |
| *Couepia ovalifolia* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Cupania emarginata* | | | | | | ○ | | | | | | | ○ |
| *Erythroxylum ovalifolium* | | ○ | ○ | | | | | | | ● | ○ | | |
| *Erythroxylum subsessile* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Eugenia astringens* | ○ | | | | | | | | | | | | |
| *Garcinia brasilensis* | | | | | ○ | ○ | ○ | ○ | ○ | | | | |
| *Gaylussacia brasilensis* | | | ○ | ● | ● | ○ | ○ | | ○ | | | | ○ |
| *Guapira opposita* | | ○ | | | | ○ | ○ | | | ○ | | ○ | |
| *Guapira pernambucensis* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Handroanthus chrysotrichus* | | | | | | | | | | | | | ○ |
| *Jacaranda jasminoides* | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| *Lepidaploa subsquarrosa* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Marcetia taxifolia* | | | ● | ● | | | | | | ● | | | |
| *Monteverdia obtusifolia* | ○ | | | | | | | | ○ | ○ | ○ | ● | |
| *Myrcia racemosa* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Myrcia ilheosensis* | ○ | ● | ○ | | | | | | | | | | |

| **Species / months** | a | m | j | j | a | s | o | n | d | j | f | m | a |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Myrcia multiflora* | | | | | | | | | | | | ○ | |
| *Myrcia vittoriana* | | | | | | | | | | | | ○ | |
| *Myrciaria floribunda* | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | | | ○ |
| *Myrrhinium atropurpureum* | | | | | | | | | | | | ○ | ○ |
| *Myrsine parvifolia* | ○ | | ○ | ○ | ● | ○ | ○ | ○ | ○ | | | | ○ |
| *Neomitranthes obscura* | ○ | | | ○ | | ○ | ○ | | | ○ | | | ○ |
| *Ocotea notata* | ○ | | | | | ○ | | | | | | | ○ |
| *Ormosia arborea* | | | | ○ | | | | | | ○ | ○ | ○ | |
| *Ouratea cuspidata* | | | | | ○ | | ○ | ○ | ● | ○ | ○ | ○ | |
| *Philodendron corcovadense* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Pilosocereus arrabidae* | ○ | | | | | | | | | | | ○ | |
| *Pouteria caimito* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Pleroma gaudichaudianum* | | | | | | | | | | ○ | ● | ● | |
| *Protium brasiliense* | | | | | | | | ○ | ● | ● | | | |
| *Senna appendiculata* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Senna pendula* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Schinus terebinthifolia* | | ○ | | | | | | | | | | | |
| *Swartzia apetala* | ○ | ○ | ○ | ○ | | | | | | | | | ○ |
| *Tapirira guianensis* | | | | | | | | | | ○ | ○ | ○ | ○ |
| *Tocoyena bullata* | | | | | | | | ○ | | | | | |
| *Vitex polygama* | | | | | | | | | | ○ | ● | | |
| *Ximenia americana* | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *Xylopia sericea* | | | | | | | | | | | ○ | ○ | |

yellow (10.5%), orange (7.9%), dark brown and green (5.3% each), brown and dark red (2.6% each) species. All anemochorous species have brown fruits and *Ormosia arborea* (self-dispersion) have multicolored, dry and dehiscent fruit. Multicolored fruits included red, white and orange (*Clusia lanceolata*), black, white and orange (*Swartzia apetala*), brown, red and black (*Ormosia arborea*), red and white (*Monteverdia obtusifolia*), reddish pink and white (*Protium brasiliense*), black and red (*Ouratea cuspidata*).

The set of plants studied showed fruit events throughout the study period (Fig. 2). Lower levels of activity and intensity were recorded in August (2.2% and 1.2%, respectively) and higher levels were recorded in January (12.7% and 6.6%, idem). In relation to zoochoric species, we observed availability and dispersing of fruits throughout the year, with higher rates of intensity and activity in the months of May and September and peaking in January. For anemochoric plants, the highest percentage of dispersal was in February (Fig. 2).

**Table 2** – List of species, length fruit (cm), and number of seeds per fruit in restinga of Maricá, Rio de Janeiro, Brazil. Mean (number of fruits), * = numerous seeds.

| Family | Species | Length Fruit (cm) | Number of seeds |
|---|---|---|---|
| Anacardiaceae | *Tapirira guianensis* Aubl. | 0.96 (25) | 1 (25) |
| | *Schinus terebinthifolia* Raddi | - | 1 (25) |
| Annonaceae | *Xylopia sericea* A.St.-Hil | - | 4.4 (11) |
| Apocynaceae | *Aspidosperma pyricollum* Müll.Arg. [1] | 5 (10) | 6 (10) |
| Araceae | *Philodendron corcovadense* Kunth | - | - |
| Arecaceae | *Allagoptera arenaria* (Gomes) Kuntze | - | 1 (25) |
| Asteraceae | *Lepidaploa subsquarrosa* (DC.) H. Robyns | - | - |
| Bignoniaceae | *Jacaranda jasminoides* (Thunb.) Sandwith | 4.7 (6) | 15 (6) |
| | *Handroanthus chrysotrichus* (Mart. *ex* DC.) Mattos | 9.8 (25) | 15 (25) |
| Burseraceae | *Protium brasiliense* (Spreng.) Engl. | 1.04 (25) | 1.32 (25) |
| Cactaceae | *Pilosocereus arrabidae* (Lem.) Byles & G. D. Rowley | - | * (25) |
| Celastraceae | *Monteverdia obtusifolia* (Mart.) Biral | 1.38 (25) | 1.42 (25) |
| Chrysobalanaceae | *Couepia ovalifolia* (Schott) Benth. *ex* Hook.f. [2] | 4.2 (28) | 1 (28) |
| Clusiaceae | *Clusia lanceolata* Cambess. | 2.5 (15) | 29 (15) |
| | *Garcinia brasiliensis* Mart. [3] | 3.1 (25) | 1.87 (79) |
| Eriaceae | *Agarista revoluta* (Spreng.) Hook. *ex* Nied. | - | * (25) |
| | *Gaylussacia brasiliensis* (Spreng.) Meisn. | - | 10 (5) |
| Erythroxylaceae | *Erythroxylum ovalifolium* Peyr. | 0.76 (25) | 1 (25) |
| | *Erythroxylum subsessile* (Mart.) O.E. Schulz | - | - |
| Euphorbiaceae | *Alchornea triplinervia* (Spreng.) Müll. Arg. | - | 1 (25) |
| Leguminosae | *Andira legalis* (Vell.) Toledo | - | - |
| | *Ormosia arborea* (Vell.) Harms[4] | 6 (30) | 2 (30) |
| | *Senna appendiculata* (Vogel) Wiersema | - | - |
| | *Senna pendula* (Humb. & Bonpl.*ex* Willd.) H.S.Irwin & Barneby | - | - |
| | *Swartzia apetala* Raddi[5] | 2.7 (55) | 1.5 (55) |
| Lauraceae | *Ocotea notata* (Nees & Mart.) Mez | 0.76 (25) | 1 (25) |
| Lamiaceae | *Vitex polygama* Cham. | 0.8 (25) | 1 (25) |
| Malphigiaceae | *Byrsonima sericea* DC. [6] | - | 1 (25) |
| Melastomataceae | *Marcetia taxifolia* (A. St.-Hil.) DC. | - | * (25) |
| | *Pleroma gaudichaudianum* (DC.) A. Gray | 0.8 (25) | * (25) |
| Moraceae | *Brosimum guianense* (Aubl.) Huber | 0.7 (25) | * (25) |
| Myrtaceae | *Calyptranthes brasiliensis* Spreng. | - | 1.3 (25) |
| | *Eugenia astringens* Cambess | - | 1 (4) |
| | *Myrcia racemosa* (O.Berg) Kiaersk. | - | - |
| | *Myrcia ilheosensis* Kiaersk. | - | 2.28 (25) |

| Family | Species | Length Fruit (cm) | Number of seeds |
|---|---|---|---|
| | *Myrcia multiflora* (Lam.) DC. | - | 1 (3) |
| | *Myrcia vittoriana* Kiaersk. | - | 1.6 (25) |
| | *Myrciaria floribunda* (H.West *ex* Willd.) O. Berg. | - | 1 (25) |
| | *Myrrhinium atropurpureum* Schott | - | - |
| | *Neomitranthes obscura* (DC.) N. Silveira | - | 1.4 (25) |
| Nyctaginaceae | *Guapira opposita* (Vell.) Reitz | 0.7 (25) | 1 (25) |
| | *Guapira pernambucensis* (Casar.) Lundell. | - | - |
| Ochnaceae | *Ouratea cuspidata* (A.St.-Hil.) Engl. [7] | 1.15 (25) | 1 (25) |
| Olacaceae | *Cathedra rubricaulis* Miers | - | 1 (25) |
| | *Ximenia americana* L. | - | - |
| Polygonaceae | *Coccoloba arborescens* (Vell.) R.A. Howard | 0.96 (25) | 1 (25) |
| Primulaceae | *Myrsine parvifolia* A. DC. | 0.45 (25) | 1 (25) |
| Rubiaceae | *Amaioua intermedia* Mart. *ex* Schult. & Schult. f. | 1.71 (28) | 13.6 (25) |
| | *Tocoyena bullata* (Vell.) Mart. | - | 1 (25) |
| Sapindaceae | *Allophylus edulis* (A.St.-Hil., A.Juss. & Cambess.) Radlk. | - | 1 (25) |
| | *Cupania emarginata* Cambess. | - | 2 (25) |
| Sapotaceae | *Pouteria caimito* (Ruiz & Pav.) Radlk. [8] | 2.2 (25) | 1 a 2 (25) |

1 = Marques 2003; 2 = Gomes 2002; 3 = Silva 2005; 4,5 = Gonçalves *et al*. 2008; 6 = Rodrigues 2002; 7 = Pinheiro *et al*. 1999; 8 = Gomes 2007.

Spearman correlation coefficients obtained between phenological phases (intensity and activity of fruit set of all species, of anemochoric and zoochoric species) and abiotic factors showed no significant correlation (Tab. 4).

Considering the availability of fruits based in fruit color of zoochoric and self-dispersion species, we observed black and multicolored fruits throughout the year. Black fruits had higher percentages of intensity and activity in May (conspicuously the fruit set of *Calyptranthes brasiliensis*, *Myrcia ilheoensis* and *Vitex polygama*) and September (*Eugenia umbelliflora*, *Guapira opposita* and *Neomitranthes obscura* were the most expressive species). Multicolored fruits showed higher fruiting from October to March. Red and dark red fruits showed higher percentages in January, especially the species *Erythroxylum ovalifolium* and *Alchornea triplinervea*. Yellow fruits were restricted from August to January and April (*Garcinia brasiliensis*, *Cathedra rubricaulis* and *Cupania emarginata*). Green fruits were restricted from January to March (only *Byrsonima sericea*). Orange fruits had higher percentages in December with more expressive fruit set of *Allagoptera arenaria* and *Myrciaria floribunda*. Brown and dark brown fruits were present from June to March, with low percentages (Fig. 3).

## Discussion

Fleshy fruits, indehiscent pattern, and colored, characterizing animal dispersal syndrome, predominate in restinga of Maricá. Zoochoric fruits are the majority in many ecosystems (Jordano 2000), and it is estimated that in tropical forests between 50% and 90% of all trees are zoochorical (Jordano 2000; Fleming 1987). The frequency of 84.5% (77.8% zoochoric and 6.7% zoochoric/self-dispersion) here observed match with the frequency registered for the Atlantic Forest, which varies from 75 to 91% (Zamith & Scarano 2004; Almeida Neto *et al*. 2008; Martins *et al*. 2014).

In restinga areas, animals that feed on fruit comprise resident and migratory birds, small mammals, lizards, and anuras (Cerqueira *et al.* 1993; Fialho *et al*. 2000; Gomes 2006; Silva & Britto-Pereira 2006). In restinga of Jurubatiba (Rio de Janeiro state), Gomes (2006) registered fruits

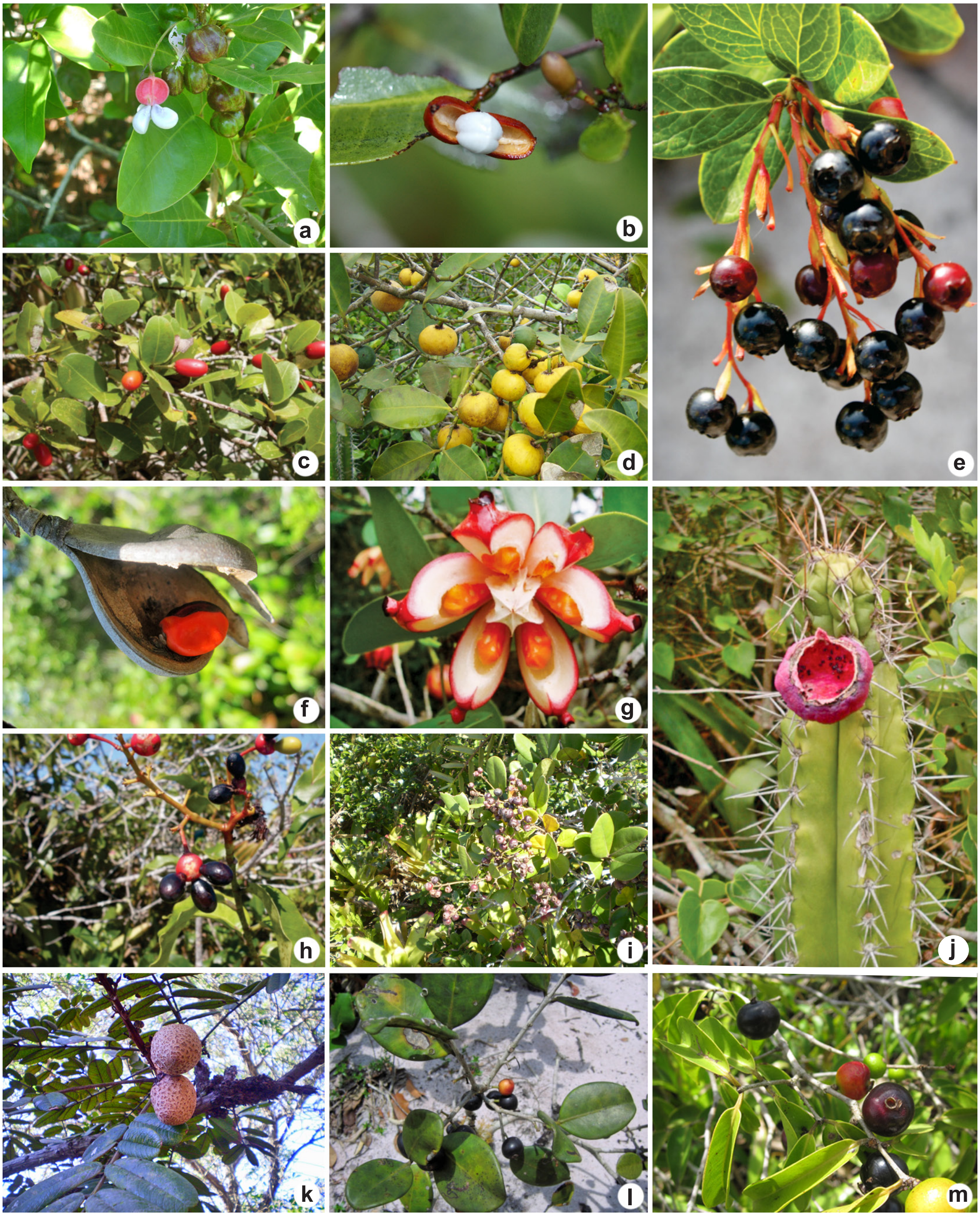

**Figure 1** – a-m. Fruits of the restinga of Maricá, Rio de Janeiro, Brazil – a. *Protium brasiliense*; b. *Monteverdia obtusifolia*; c. *Erythroxylum ovalifolium*; d. *Garcinia brasiliensis*; e. *Gaylussacia brasiliensis*; f. *Ormosia arborea*; g. *Clusia lanceolata*; h. *Ouratea cuspidata*; i. *Myrcia ilheosensis*; j. *Pilosocereus arrabidae*; k. *Andira legalis*; l. *Eugenia astringens*; m. *Neomitranthes obscura*.

**Table 3** – Monitoring the color along the ripening stages of the fruit species studied in APA of Restinga of Maricá, RJ. GR = green; YE = yellow; OR = orange; RE = red; DR = dark red; BR = brown; DB = dark brown; BL = black; MC = multicolor; CF = Colour fruit; Co = Consistency; De = Dehiscence; I = Indehiscent; D = Dehiscent; ZO = Zoochoric; AN = Anemochoric; SD = Self-dispersal.

| Species | GR | YE | OR | RE | DR | BR | DB | BL | MC | CF (ripe) | Co | De | Syndrome |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Agarista revoluta* | x | | | | | x | | | | BR | dry | D | AN |
| *Alchornea triplinervia* | x | | | x | | | | | | RE | fleshy | I | ZO |
| *Allagoptera arenaria* | x | x | x | | | | | | | OR | fleshy | I | ZO |
| *Allophylus edulis* | x | | | | | x | x | x | | BL | fleshy | I | ZO |
| *Amaioua intermedia* | x | | | | | x | x | | | DB | fleshy | I | ZO |
| *Andira legalis* | | | | | | x | | | | BR | fleshy | I | ZO |
| *Aspidosperma pyricollum* [1] | x | | | | | x | | | | BR | dry | D | AN |
| *Brosimum guianense* | x | | | x | | | | | | RE | fleshy | I | ZO |
| *Byrsonima sericea* [2] | x | | | | | | | | | GR | fleshy | I | ZO |
| *Calyptranthes brasiliensis* | x | | | x | x | | | x | | BL | fleshy | I | ZO |
| *Cathedra rubricaulis* | x | x | | | | | | | | YE | fleshy | I | ZO |
| *Clusia lanceolata* | x | | | | x | | | | x | MC | fleshy | D | ZO |
| *Coccoloba arborescens* | x | | | | | | x | | | DB | fleshy | I | ZO |
| *Couepia ovalifolia* [3] | x | | | | | | | | | GR | fleshy | I | SD/ZO |
| *Cupania emarginata* | x | x | | | | | | | | YE | fleshy | D | ZO |
| *Erythroxylum ovalifolium* | x | | | x | | | | | | RE | fleshy | I | ZO |
| *Eugenia astringens* | x | x | | | x | | | x | | BL | fleshy | I | ZO |
| *Garcinia brasilensis* [4] | x | x | | | | | | | | YE | fleshy | I | SD/ZO |
| *Gaylussacia brasilensis* | x | | | | x | | | x | | BL | fleshy | I | ZO |
| *Guapira opposita* | x | | | x | | | | x | | BL | fleshy | I | ZO |
| *Guapira pernambucensis* | x | | | x | | | | x | | BL | fleshy | I | ZO |
| *Handroanthus chrysotrichus* | x | | | | | x | | | | BR | dry | D | AN |
| *Jacaranda jasminoides* | x | | | | | x | | | | BR | dry | D | AN |
| *Marcetia taxifolia* | x | | | | | x | | | | BR | dry | D | AN |
| *Monteverdia obtusifolia* | x | | x | x | | | | | x | MC | fleshy | D | ZO |
| *Myrcia ilheosensis* | x | | | | x | | x | x | | BL | fleshy | I | ZO |
| *Myrcia multiflora* | x | | | | | | | x | | BL | fleshy | I | ZO |
| *Myrcia vittoriana* | x | | x | | | | | | | OR | fleshy | I | ZO |
| *Myrciaria floribunda* | x | | x | | | | | | | OR | fleshy | I | ZO |
| *Myrrhinium atropurpureum* | x | | | | | | x | x | | BL | fleshy | I | ZO |
| *Myrsine parvifolia* | x | | | | | | | x | | BL | fleshy | I | ZO |
| *Neomitranthes obscura* | x | | x | x | x | | | x | | BL | fleshy | I | ZO |
| *Ocotea notata* | x | | | | | | x | x | | BL | fleshy | I | ZO |
| *Ormosia arborea* [5] | x | | | | | x | | | x | MC | dry | D | SD |
| *Ouratea cuspidata* [6] | x | | | x | | | | x | x | MC | fleshy | I | ZO |
| *Pilosocereus arrabidae* | x | | | | x | | | | | DR | fleshy | I | ZO |

| Species | GR | YE | OR | RE | DR | BR | DB | BL | MC | CF (ripe) | Co | De | Syndrome |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pouteria caimito* [7] | x | x | | | | | | | | YE | fleshy | I | ZO |
| *Pleroma gaudichaudianum* | x | | | | | x | | | | BR | dry | D | AN |
| *Protium brasiliense* | x | | | | x | | | | x | MC | fleshy | D | ZO |
| *Schinus terebinthifolia* | x | | | x | | | | | | RE | fleshy | I | ZO |
| *Swartzia apetala* [8] | x | x | x | | | | | | x | MC | dry | D | SD/ZO |
| *Tapirira guianensis* | x | | | | x | | | x | | BL | fleshy | I | ZO |
| *Tocoyena bullata* | x | | | | x | | x | x | | BL | fleshy | I | ZO |
| *Vitex polygama* | x | | | | | | | x | | BL | fleshy | I | ZO |
| *Xylopia sericea* | x | | | x | | | | | | RE | fleshy | D | ZO |

1 = Marques 2003; 2 = Rodrigues 2002; 3 = Gomes 2002; 4 = Silva 2005; 5 = Gonçalves *et al*. 2008; 6 = Pinheiro *et al*. 1999; 7 = Gomes 2007; 8 = Gonçalves *et al*. 2008.

of 35 species which are consumed by birds and concluded that most of the resident and migratory birds of restinga are frugivorous. Among all plant species registered by Gomes (2006), 13 also occur in Maricá (including *O. notata* and *P. arrabidae*), likely also used as food by birds in this area. Cerqueira *et al*. (1994) point out that of the ten species of small mammals studied in restinga of Maricá, eight feed on fruits, particularly the marsupial species *Philander frenatus* (Olfers 1818), which feed on fruits of *Aechmea*, *Erythroxylum*, *Passiflora*, *Paullinia* and *Pilosocereus* (Santori *et al*. 1997). *Erythroxylum ovalifolium* represent 50% of diet of the lizard species *Tropidurus torquatus* (Wied 1820) in restinga of Maricá (Fialho *et al*. 2000). Fruits of *Erythroxylum ovalifolium* and *Monteverdia obtusifolia* are important components of the diet of the threatened Anura species *Xenohyla truncata* (Izecksohn 1959), which inhabits restingas of Rio de Janeiro, including Maricá (Silva & Britto-Pereira 2006). The same authors report that *X. truncata* lives in bromeliads *Neoregelia cruenta* and suggest this species pass seeds through its feces to bromeliads, where *M. obtusifolia* seedlings are easily observed (personal observation).

A variety of colors in ripe fruits was recorded in restinga of Maricá, with a predominance of black, within 39.5% of the species, followed by red and multicolored (13.2% each). Red and black fruits are dominant in many tropical and temperate ecosystems (Wheelwright & Janson 1985; Willson & Whelan 1990; Galetti *et al*. 2011) and, together with multicolored fruits, have been linked to consumption mainly by birds (Schaefer & Schmidt 2004; Galetti 2002; Galetti *et al*. 2011; Valenta *et al*. 2018). According to Schmidt *et al.*

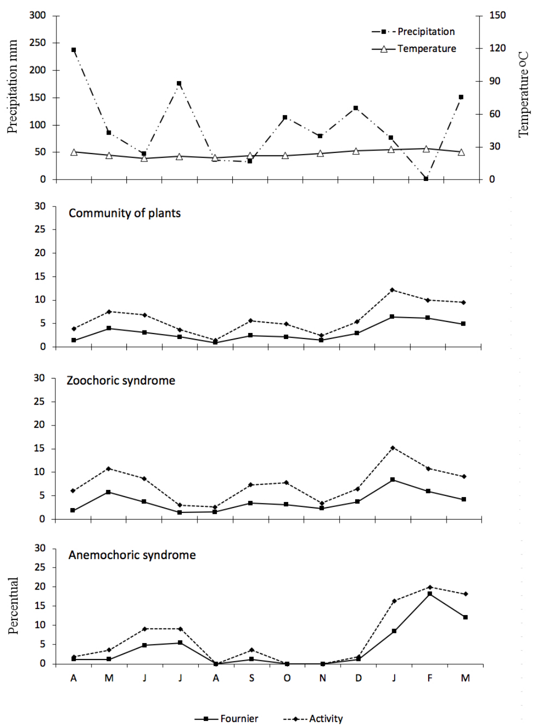


**Figure 2** – Phenological events of fruit set in plant community of the restinga of Maricá, Rio de Janeiro, Brazil – a. mean temperature (ºC) and total precipitation (mm) for the Maricá (The climatic data of temperature and rainfall were provided by the National Institute of Meteorology INMET/RJ); b. percentage of intensity (Fournier 1974) and activity for the fruit set of all species studied; c. percentage of intensity (Fournier 1974) and activity for the fruit set of zoochoric and zoochoric/self-dispersal plants; d. percentage of intensity (Fournier 1974) and activity for fruit set of anemochoric plants.

(2004) the prevalence of black and red colors in plant communities seems to be explained by their greater conspicuity against a natural background (immature fruits of different colors, leaves, bark, petiole, etc.) when compared to other colors, increasing chances of being detected by frugivores, mainly birds.

When we investigated, more specifically, color variation during fruit maturation, we observed that, in 42% of zoochoric species, individual fruits go through three to five hues until complete maturation, and different maturation stages (different colors) can be observed in the same plant. This characteristic was common in some species of Myrtaceae that pass through several colors until complete maturation. In *N. obscura*, for example, plants display fruits of different colors (orange, red, dark red and black), representing the different stages of maturation. Fruits often change color as they mature, and slow and gradual fruit maturation resulting in plants with fruits of different colors may be an important strategy to increase fruit display contrast and influence the detection of these fruits by birds (Willson & Melampy 1983; Wheelwright & Janson 1985). Stiles (1982) suggested plants with immature and ripe colored fruits may function as a pre-ripening fruit flag, a sign that mature fruits will become available over time.

A constant supply of mature fruits was observed in the studied community. The highest percentages were registered in January/February, but they were not much different from the other months. Unlike flowering (Rodarte 2008), there were no significant correlations between fruiting phenophase activity and intensity percentages, and abiotic factors tested (precipitation, temperature and length of day). Morellato *et al*. (2000) also suggested that climatic factors do not limit fruit production in Atlantic forest trees. For the restinga community studied, the fruiting pattern observed also contrasts with flowering due to the lower seasonality and intensity of events (Rodarte 2008). Phenological studies in Atlantic forest habitats have also demonstrated non-seasonal patterns in fruit production (Talora & Morellato 2000; Morellato *et al*. 2000; Medeiros *et al*. 2007). In both the Atlantic rain forest and restinga, flowering is more seasonal, concentrated in the warm/rainy season (October to March) (Morellato *et al.* 2000; Rodarte 2008). These data reinforces the idea that the biotic factors, such as seed dispersers (in the case of zoocoric fruits) may have relevance in determining fruit ripening and seed dispersal periods in coastal environments like Atlantic forest and restinga vegetation (Morellato & Leitão-Filho 1991; Talora & Morellato 2000; Morellato *et al*. 2000).

Zoochoric fruits of different colors are found throughout the year in restinga of Maricá. Black, red and multicolor fruits, commonly associated with dispersion by birds (Willson & Whelan 1990; Valenta *et al*. 2018), were released in fruiting phenophases with higher levels of intensity and activity throughout the year, compared to fruits of the other colors. Gonzaga *et al*. (2000) found significant seasonal variation in composition of the avifauna in restinga of Maricá. Gomes (2006) concluded that constant supply of fruits is important for maintenance of the community of resident and visiting birds in restinga of Jurubatiba. The other colors (mainly yellow and green) are commonly associated with the dispersion of mammals (Willson & Whelan 1990; Valenta *et al*. 2018). Species with fruits of these colors, although they showed less intense fruiting phenophases and a little more restricted availability throughout the year, also constitute an ample supply of edible

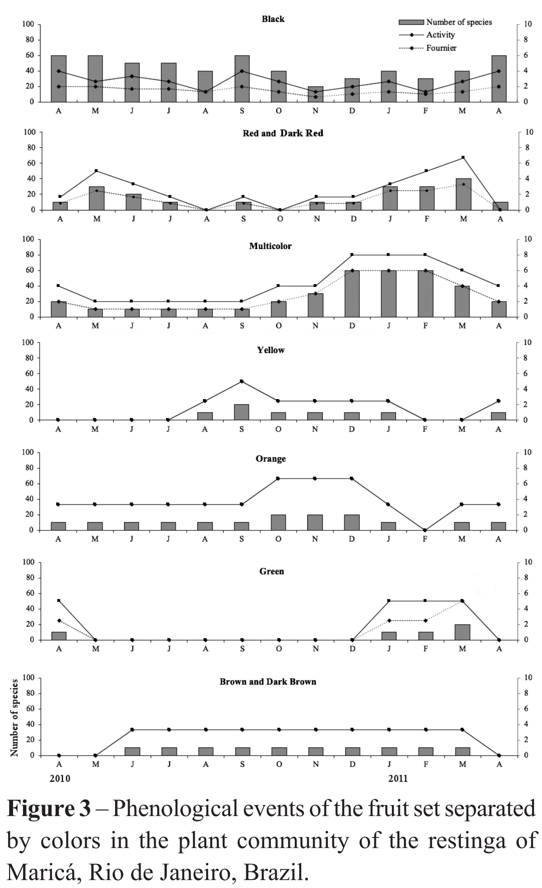


**Figure 3** – Phenological events of the fruit set separated by colors in the plant community of the restinga of Maricá, Rio de Janeiro, Brazil.

**Table 4** – Spearman correlation coefficients ($p < 0.05$), obtained between phenological phases (levels of intensity and activity of fruit set) and abiotic factors [maximum, mean, and minimum temperature (°C), precipitation (mm), and day length measure (h)] in plant community distributed over the internal sand stream of the restinga of Maricá, Rio de Janeiro, Brazil.

| | **Total of fruits** | | **Zoochoric** | | **Anemochoric** | |
|---|---|---|---|---|---|---|
| | **Intensity** | **Activity** | **Intensity** | **Activity** | **Intensity** | **Activity** |
| Temperature | | | | | | |
| Maximum | 0.48 | 0.55 | 0.60 | 0.53 | 0.56 | 0.49 |
| Medium | 0.37 | 0.46 | 0.55 | 0.50 | 0.41 | 0.33 |
| Minimum | -0.1 | -0.05 | 0.13 | 0.07 | -0.23 | -0.28 |
| Precipitation | -0.30 | -0.26 | -0.23 | -0.28 | -0.03 | -0.14 |
| Day length | 0.32 | 0.40 | 0.53 | 0.44 | 0.19 | 0.13 |

fruits. Our results points that vegetation of restinga of Maricá presents fruits very different in colors and these colors are well distributed throughout the seasons, meaning a constant and reliable supply of fruits to the dispersing fauna, especially birds and mammals.

Myrtaceae stands out in this study, since there is always a species of Myrtaceae producing fruits throughout the year. Likewise, in Maricá, Staggemeier *et al*. (2017) also highlighted the family for offering a wide morphological diversity of fruits to different frugivore guilds throughout the year, in an area of restinga vegetation in São Paulo state. According to Rodarte (2008), Myrtaceae is the family with highest species richness and highest value of phytosociological importance (37.2%) in restinga of Maricá. The fruit traits of Myrtaceae species (fleshy, indehiscent, different colors and sizes) highlights the importance of this family as a year round resource for local fauna, especially frugivorous fauna.

The main fruiting peak of anemochoric species occurred in the hottest and rainy season of the year, although no significant correlation with abiotic factors evaluated (precipitation, temperature and day length). The peak in the hot and rainy season displayed by species with wind dispersion owes mainly to the activity and intensity of *Agarista revoluta*, *Pleroma gaudichaudianum* and *Marcetia taxifolia* fruiting. It should be noted that the peak of fruiting of the anemochoric species in the warmest and rainiest season recorded in this study coincides with the blooming peak of species pollinated by the wind, in the same community. *Myrsine parvifolia*, *Alchornea triplinervia* and species of Cyperaceae and Poaceae also bloom in the period from October to March (Rodarte 2008; Albuquerque *et al*. 2013). Winds, low humidity and higher temperatures are constant in the restinga ecosystem, when compared to other habitats of Atlantic Forest (Scarano 2002), mainly in areas closest to the sea (Staggemeier & Morellato 2011). The species analyzed in the present study are frequent in more open physiognomies (open shrub), thus allowing the dispersal of anemochoric seeds throughout the seasons.

We highlight that restinga environments present many key species for the germination of other plants, such as bromeliads (nurse plants). Restingas have relatively low rate of free water available in the soil (Zaluar & Scarano 2000; Scarano 2002) and success in germination and development of seedlings in restinga has been demonstrated to be higher in the microhabitat inside of the bromeliad rather than in the sand around the plant (Fialho 1990; Zaluar 1997). Bromeliads can store a considerable amount of free water (Cogliatti-Carvalho *et al*. 2010), and thus represent a relatively stable microhabitat since tanks tend to remain with water even during periods of drought (Krügel & Richter 1995). In fact, seedlings of various species such as *Monteverdia obtusifolia*, *Guapira opposita*, Myrtaceae, Clusiaceae, among others, are easily found within bromeliads (personal observation). Studies involving recruitment throughout seasons and its relationship with nurse plants and seed dispersers are required in this ecosystem, with flora found in sandy, permeable and nutrient-poor soils.

Our study on the fruiting phenology and the characterization of the fruits of 52 species from an area of restinga vegetation shows a predominance of fruits with zoochoric characteristics, diverse in colors and sizes and available throughout the year for a potentially rich fauna of seed dispersers. In restinga, fruiting events are, however, less seasonal and intense than flowering events and seems to be not limited by climatic factors. Studies on fruiting phenology, dispersion and seeds germination must be incentivated as they can help incrementing successful restoration and conservation actions for restinga areas.

## Acknowledgments

We are grateful to PIBIC-UFRJ, for the scholarship to Patrick de Oliveira.

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Area Editor: Dr. Leandro Freitas
Received in October 25, 2019. Accepted in May 02, 2021.