Deriving Biomass Allocation and Carbon Stocks in Fruit Components of Strychnos Madagascariensis (Poir.) And Strychnos Spinosa (Lam.) In South Africa

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**ABSTRACT**

Fruits contribute to carbon (C) fixation in fruit tree species of savannah woodlands despite that the C fixed in fruits is rapidly turned back to carbon dioxide (CO\textsubscript{2}) when the fruits decompose or are eaten. The aim of this study was to determine biomass allocation between fruit components of Strychnos madagascariensis and Strychnos spinosa and to derive the C stocks sequestered by fruits. A total of 400 ripe fruits were harvested from trees distributed in seven plots across the UMKhanyakude district. Fruit shell and pulp were separated from seeds. Puree and juice of S. spinosa were separated by centrifugation and steam extraction, respectively. Moisture contents of the fruit components were measured. For S. madagascariensis fruits, seeds contributed the most biomass (50.2%), followed by the shell (30.8%), and pulp had the least biomass (16.7%). The loss of material was 2.3%. For S. spinosa, the largest part of fruit biomass was in the shell (41.8%), followed by puree (25.6%), seeds (18.6%), juice (6.2%), and pulp (0.9%). The loss of material was 6.9%. Fruit dry biomass (FDB; in g) and fruit carbon stocks (CB; in g) were both related to fruit diameter ($D$; in cm) for S. madagascariensis ($FDB = 1.022 \times D^2 - 492$; $CB = 0.463 \times D^2 - 535$) and S. spinosa ($FDB = 1.015 \times D^2 - 38$; $CB = 0.198 \times D^2 - 82$). Proportion values and regression techniques were both valid methods to derive biomass and carbon stocks of the fruit and its components.

**KEYWORDS**

Fruit allometry; proportions; moisture content; carbon balance; savannah woodlands

**Introduction**

Fruit trees play a very important role in the dynamics of carbon (C) in savannah woodlands (Wu et al., 2012). Because of their considerable annual production of fruit biomass, which can reach 510 kg ha\textsuperscript{-1} (Campbell et al., 1996), they are major sinks of C fixation in fruit tree species (Pérez-Piqueres et al., 2020). The CO\textsubscript{2} fixed by a mature fruit tree is also distributed to fruits (Sofo et al., 2005). Fruiting trees accumulate more C than non-fruiting trees (Wibbe et al., 1993) because of the high photosynthetic activity during the fruit cell division and expansion. Fruit trees play an important role in the global carbon sequestration (Pérez-Piqueres et al., 2020) despite that some trees with climacteric fruits can produce much ethylene and CO\textsubscript{2} gas during fruit ripening (Rodrigues et al., 2018). In addition to this ecosystem service, fruit trees contribute to food security (Koffi et al., 2020), employment, and income generation (Sulieman and Mariod, 2019). In sub-tropical Africa, fruits are among the main sources of protein, energy, fibers, and minerals (Rodrigues et al., 2018). Fruit tree species belonging to the genus Strychnos are among the most appreciated in rural communities (Nkosi et al., 2020). The species prevalent in Africa include Strychnos spinosa, S. madagascariensis, S. cocculoides, S. lucens,
S. minfiensis, S. mitis, S. pungens, S. innocua, S. potatorum, S. icaia, among others (Delaude et al., 1992). They are commonly called “Monkey Orange” in English (Ngadze et al., 2019; Salmona et al., 2015). They have greatly contributed to the development of traditional medicine (Beaufay et al., 2018; Razzaz et al., 2020) and pharmacology (Mors et al., 2000) thanks to their numerous alkaloids (Arunkumar et al., 2019; Gautam et al., 2020; He et al., 2020; Saya et al., 2019; Semenov et al., 2020).

In South Africa, the district of Umkhanyakude, located in the province of KwaZulu-Natal, is mainly dominated by two species of Strychnos, namely S. spinosa and S. madagascariensis (Boon, 2010). These species are small trees that are indigenous to tropical and subtropical Africa (Sitrit et al., 2003). Strychnos spinosa can grow up to seven meters in height. It bears edible round-shaped fruits that resemble an orange. The fruit has an edible, juicy, and sweet pulp. It also contains many brown seeds (Rodrigues et al., 2018). The fruit of S. madagascariensis is not highly palatable, but its powdered bark produces a useful tonic. Strychnos spinosa is locally called iHlala, Kikwakwa, and Dorignkklapper respectively in isiZulu, Kiswahili, and Afrikaans while S. madagascariensis is known as Umkwakwa in isiZulu. These two species are among the most important multipurpose fruit trees in rural communities of KwaZulu-Natal (Nkosi et al., 2020; Van Rayne et al., 2020). Strychnos spinosa is used as food and medicine (Avakoudjo et al., 2020; Mizrahi et al., 2002; Ngemakwe et al., 2017). Leaf extracts have wound-healing activity (Hassan et al., 2020) and can treat infectious diseases (Isa et al., 2014). Extracts from unripe fruits are used as an antidote against snake bite venom (Mors et al., 2000). Strychnos spinosa has potential as an industrial crop for fruit juice based products (Rodrigues et al., 2018). On the other hand, S. madagascariensis fruit pulp and the seed testa have the potential for food product development (Van Rayne et al., 2020). Although they may contain toxic alkaloids, the fruit pulp and seed testa are processed by some communities in Zimbabwe and South Africa into dried food products that provide nourishment during droughts and famine (Ngadze et al., 2017; Salmona et al., 2015; Shai et al., 2020). However, despite their large production of fruit biomass in the wild, which can reach more than 40 kg per tree (Ngemakwe et al., 2017), S. spinosa and S. madagascariensis are not yet widely commercialized and their fruits remain restricted to domestic consumption (Rodrigues et al., 2018).

Biomass is a term used to refer to the mass of living organisms, including plants, animals, and micro-organisms (Houghton, 2008). In plants, biomass represents the dry weight of all organic matter (Focardi, 2008) that can also be used as fuel (Basu, 2018; Edomah, 2018). Biomass is one of the most fundamental measurements in ecology (Chave et al., 2004; Steinman et al., 2017). It helps to evaluate the contribution of forest ecosystems in C sequestration (Chambers et al., 2001; Pearson and Brown, 2005; Ryan et al., 2011). In savannah woodland trees, approximately 39% of C stocks are sequestered in the roots and 61% in above-ground components (Chen et al., 2003; Dimobe et al., 2018). Biomass is distributed to various components namely the roots, the stem, the branches, the leaves, and the flowers or the fruits (Picard et al., 2012). The sum of the biomass of each compartment generates the total biomass of a tree (Henry et al., 2010; Mugasha et al., 2013). About 50% of measured dry biomass represents the amount of C stored (Chavan and Rasal, 2011; Houghton, 2008; Jana et al., 2009; Paladinić et al., 2009). There exist several methods for measuring the biomass of a tree or a component of a tree (Brown et al., 1989; Carreiras et al., 2013). Direct weighing is the most accurate method and allows the development of allometric equations which can subsequently be used to estimate biomass at a larger scale (Vieilledent et al., 2012). Depending on the tree component whose biomass is estimated, there exist below-ground allometric equations (Kuyah et al., 2012), stem-based equations (Fortier et al., 2017), branch-based equations (Kaitaniemi et al., 2020), foliage-based equations (Lehtonen, 2005; Socha and Wezyk, 2007), and fruit-based equations (Akweni et al., 2020; Akweni, Zharare, et al., 2021; Peters et al., 1988).

Currently, fruit-based allometric equations of S. madagascariensis and S. spinosa are available (Akweni et al., 2020). These equations enable the estimations of fruit biomass production from the wild. However, these fruit-based allometric equations were logically developed to estimate only the fresh fruit biomass, because in rural markets, fruits are sold and eaten fresh (Rodrigues et al., 2018). Therefore, the estimation of dry fruit biomass and C sequestration by fruits are not yet possible at this
stage for *S. madagascariensis* and *S. spinosa* species. In addition, parameters (moisture content and fruit density) that can help to convert fresh fruit biomass into dry biomass are not yet available for these species. Furthermore, their fruit components are different in composition and nature (Ngadze et al., 2017). The shell, pulp, and seeds are found in both fruits, but in addition to these components *S. spinosa* contains juice and puree. It is therefore ideal to investigate moisture content separately. This requires a good understanding of how fresh biomass is distributed between the components of the fruits. This study aims to determine the partitioning of biomass between fruit components of *S. madagascariensis* and *S. spinosa* and to derive the C stocks sequestrated by fruits. The derivation of C stocks in fruits is an essential step toward the establishment of C balance in savannah woodlands. A large amount of C stocks fixed in fruits are rapidly released in the atmosphere as CO₂, CH₄, or C₂H₆ when the fruits are eaten. Marginally, fruits may contribute after decomposition processes to feeding the carbon stocks of the soils.

**Materials and Methods**

**Study Area**

This study was conducted in the UMkhanyakude district, located in the northern coastal region of KwaZulu-Natal province, in South Africa (Figure 1). The district is largely covered by grassland and savannah vegetation (Jewitt, 2018) which are part of the Maputaland coastal thicket biome (Mucina, 2018). The soils of the area are sandy (Botha and Porat, 2007) and the climate is humid with temperatures ranging between 14 and 35°C.

![Figure 1. Location map of harvested plots in the UMkhanyakude district, KwaZulu-Natal province, South Africa.](image-url)
Fruit Sampling and Biomass Measurements

A total of 400 ripe fruits were harvested from seven square plots of 6400 m$^2$ each. The sample plots were identified according to the presence of S. madagascariensis and S. spinosa trees. In each plot, about 58 fruits (29 fruits per species) were collected from all trees found in the plot. From each tree, fruits were collected at random targeting only healthy mature (ripe) fruits still attached to the trees for S. madagascariensis. In the case of S. spinosa, ripe fruits were picked from the ground under the trees. In this species, fruits mostly attached to the trees are unripe. All the harvested fruits were brought to the laboratory where their fresh biomass and diameters were individually measured. The diameter of fruits was measured using diametric tape. After individual measurements, fruits were grouped into eight lots of 50 fruits each, that is to say, four lots for each species. Each lot was composed of 50 fruits to ensure representation of all possible sizes of mature fruits growing in the wild. For each fruit lot of S. madagascariensis (Figure 2A), the shell of each fruit was broken and the pulp was separated from seeds (Figure 2B) after which the shell, pulp, and seeds were weighed fresh (Figure 2C; Figure 2D). For each fruit lot of S. spinosa fruits (Figure 3A; Figure 3B), the shells of the fruits were also broken. Fruit puree and fruit juice were extracted using centrifugation (Figure 3C) and steel steam extraction (Figure 3D), respectively. In the case of fruit juice extraction by steam, the residual pulp was separated from seeds and weighed fresh. Thereafter, shell, pulp, and seeds from all the eight lots were oven-dried at 85°C for 72 hours and their dry biomasses were determined.

Statistical Analysis

For individual fruit data (Dataset 1; in Akweni, Sibanda, et al., 2021), statistical dispersion parameters were calculated. Mean values of fresh biomass and diameter of individual fruits of each species and their respective standard deviations were determined. For grouped fruit data (Dataset 2; in Akweni,
Sibanda, et al., 2021), the mean biomass values of each fruit component, including their standard deviations, were calculated for each species. These mean values were then added together and presented in proportions based on the average total biomass of lots of each species. Thereafter, these proportion values were applied to individual fruit data to generate the fresh biomass of each fruit component. The dry biomasses of the oven-dried fruit components (excluding puree and juice of S. spinosa) were used to calculate their respective moisture contents. The calculated moisture content values of fruit components were then applied to individual fruit data to convert the fresh biomass into dry biomass. Carbon stocks of fruit components were obtained by dividing their dry biomasses by two (Chavan and Rasal, 2011; Jana et al., 2009; Paladinić et al., 2009). The dry biomass and carbon stocks of S. spinosa fruits did not include the puree and juice.

Regression techniques were used as an alternate method to derive dry biomass and carbon stocks of fruit components. A simple linear regression model was fitted to individual fruit data (using the ordinary least squares method) to derive biomass and carbon stocks from fruit diameter. The residual standard error (RSE), the coefficient of determination (R²), and the correlation factor (r) were calculated for each regression. Student T-test was used to compare the values of dry biomass (and carbon stocks) derived by proportions and those derived by regression.

The moisture content (MC; Equation 1), the Student test (T-test; Equation 2), and the standard deviations of mean values (SD; Equation 3) were obtained using the following expressions:

\[
MC = \frac{FB - DB}{FB}
\]  

\[
T = \frac{(FB - DB)}{SD}
\]  

\[
SD = \sqrt{\frac{\sum (FB - DB)^2}{n-1}}
\]
\[ T - test = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{S^2}{n_1} + \frac{1}{n_2}}} \]  

(2)

\[ SD = \sqrt{\frac{\sum(x_i - \bar{x})^2}{n - 1}} \]  

(3)

where FB and DB respectively represent the fresh biomass and the dry biomass of a given fruit component (in g; Equation 1). The terms \( \bar{x}_1 \) and \( \bar{x}_2 \) represent the compared mean values of a given variable of \( \text{S. madagascariensis} \) and \( \text{S. spinosa} \), respectively. The term S is the pooled standard error of the variable of the two species being compared and \( n_1 \) and \( n_2 \) represent the number of fruits for each of the species (Equation 2). The terms \( x_i \), \( \bar{x} \), and \( n \) represent the value (of a given variable) of each fruit (or group of fruits) in the considered data set, the mean value of the considered variable, and the number of fruits (or lots) in the considered data set, respectively (Equation 3). All the statistical analyses were carried out using the R-software (R DEVELOPMENT CORE TEAM, 2014).

**Results**

**Dispersion Parameters of Individual Fruits**

Fresh biomass of individual \( \text{S. madagascariensis} \) fruits varied between 79.8 g and 796.0 g with a mean value of 356.6 g. The fruit diameter ranged from 5.5 cm to 11.4 cm with a mean value of 8.2 cm. For \( \text{S. spinosa} \) fruits, the fresh biomass varied between 154.5 g and 1113.4 g with a mean value of 441.9 g. The fruit diameter ranged from 6.1 cm to 12.5 cm (Table 1). The T-test applied to make a comparison between the mean values of fresh biomass of individual fruits of \( \text{S. madagascariensis} \) and \( \text{S. spinosa} \) gave a significant \( p \)-value (Table 1). The T-test applied to compare the mean values of fruit diameter of \( \text{S. madagascariensis} \) and \( \text{S. spinosa} \) gave a non-significant \( p \)-value (0.1509).

**Fresh Biomass of Fruit Components**

Fresh biomasses of Lot 1, Lot 2, Lot 3, and Lot 4 of \( \text{S. madagascariensis} \) fruits were 18375.9 g, 17717.4 g, 18014.9 g, and 17535.9 g, respectively. This represented on average 17911.1 g for these four lots (Table 2). The mean fresh biomasses of the shell, pulp, and seeds of the four lots (each with 50 fruits) of \( \text{S. madagascariensis} \) fruits were 5511.8 g, 2986.9 g, and 8998.2 g which corresponded to 30.8%, 16.7%, and 50.2%, respectively of the fruit biomass per lot. For \( \text{S. spinosa} \) fruits, fresh biomasses of Lot 5, Lot 6, Lot 7, and Lot 8 were 19770.6 g, 20040.1 g, 20364.1 g, and 21482.1 g, respectively. The mean fresh biomass of these four lots of \( \text{S. spinosa} \) fruits was 20414.2 g. The mean fresh biomass of the shell, pulp, seeds, puree, and juice were 8526.5 g, 189.4 g, 3795.4 g, 5229.3 g, and 1273.7 g which respectively

| Table 1. Dispersion parameters of individually measured fruit variables per species. The standard deviation (SD) and the test of Student (T-test) are provided for the mean values. The measure of the T-test probability (\( p \)-value) is reported at 95% confidence interval where “e” is an exponential factor. |
|-----------------|-----------------|-----------------|-----------------|
| **Dispersion parameters** | **Species** | **Variables** | **Strychnos madagascariensis** | **Strychnos spinosa** | **\( p \)-value (T-test)** |
| **Mean ± SD** | | Fruit biomass (g) | 356.6 ± 123.4 | 441.9 ± 194.1 | 6.507e-06 |
| | | Fruit diameter (cm) | 8.214 ± 0.94 | 8.386 ± 1.2 | 0.1509 |
| **Median** | | Fruit biomass (g) | 346.3 | 417.4 | |
| | | Fruit diameter (cm) | 8.15 | 8.20 | |
| **Minimum** | | Fruit biomass (g) | 79.8 | 154.5 | |
| | | Fruit diameter (cm) | 5.5 | 6.1 | |
| **Maximum** | | Fruit biomass (g) | 796.0 | 1113.4 | |
| | | Fruit diameter (cm) | 11.4 | 12.5 | |
Table 2. Measured fresh biomass (in g) of fruit components of Strychnos madagascariensis and Strychnos spinosa per lot of 50 fruits each. The standard deviation is given for the mean values.

| Lot     | Shell | Pulp | Seeds | Puree | Juice | Loss | Total per Lot |
|---------|-------|------|-------|-------|-------|------|---------------|
|         |       |      |       |       |       |      |               |
| **Strychnos madagascariensis** |       |      |       |       |       |      |               |
| Lot 1   | 5879.6| 2810.5| 9226.0| -     | -     | 459.8| 18375.9      |
| Lot 2   | 5261.9| 3142.1| 8801.3| -     | -     | 511.9| 17717.4      |
| Lot 3   | 5421.5| 3010.9| 8931.4| -     | -     | 651.1| 18014.9      |
| Lot 4   | 5484.3| 2984.0| 9034.1| -     | -     | 33.5 | 17535.9      |
| Mean    | 5511.8| 2986.9| 8998.2| -     | -     | 414.1| 17911.1      |
| ± 262.4 | ± 136.3| ± 179.2|       |       |       | ± 266.2| ± 367.4      |
| **Strychnos spinosa** |       |      |       |       |       |      |               |
| Lot 5   | 8301.1| 179.3| 3816.5| 4970.4| 1387.4| 1115.7| 19770.6      |
| Lot 6   | 8420.0| 187.2| 3919.6| 5743.7| 901.8 | 867.7 | 20040.1      |
| Lot 7   | 8200.4| 203.4| 3751.2| 5241.6| 1212.4| 1754.9| 20364.1      |
| Lot 8   | 9184.6| 187.9| 3694.4| 4961.3| 1593.4| 1860.3| 21482.1      |
| Mean    | 8526.5| 189.4| 3795.4| 5229.3| 1273.7| 1399.6| 20414.2      |
| ± 447.8 | ± 10.0 | ± 96.6| ± 366.7| ± 292.7| ± 483.7| ± 752.0|             |

Figure 4. Fresh biomass proportion chart of fruit components of Strychnos madagascariensis (A) and Strychnos spinosa (B).

represented 41.8%, 0.9%, 18.6%, 25.6%, and 6.2% of the fruit biomass per lot (Figure 4). There was on average 414.1 g and 1399.6 g of loss of materials for fruit lots of S. madagascariensis and S. spinosa, respectively.

There was a linear relationship between fruit diameter and fresh fruit components of S. madagascariensis and S. spinosa. The coefficients of determination of the fitted equations were higher than 0.90 for the regressions that involved fruit fresh biomass (Figure 5A) and seed fresh biomass (Figure 5B) for both species. On the other hand, shell fresh biomass (Figure 5C), pulp fresh biomass (Figure 5D), puree biomass (Figure 5E), and juice biomass regressions (Figure 5F) had coefficients of determination that were lower than 0.90 for both species. The correlation factor between fruit diameter and any of the fresh fruit components of S. madagascariensis was 0.819 whereas the correlation factor between fruit diameter and any of the fresh fruit components of S. spinosa was 0.923.

Moisture Contents of Fruit Components

The moisture contents of the shell, pulp, and seeds of S. madagascariensis were 0.067, 0.771, and 0.539, respectively. For the lots of S. spinosa fruits, the moisture contents of the shell, pulp, and seeds were 0.256, 0.764, and 0.643, respectively (Table 3).
Figure 5. Relationship between fruit diameter and fresh fruit components of Strychnos madagascariensis and Strychnos spinosa. The fitted linear equation (also drawn in red curve), the residual standard error (gray zone surrounding the red curve), the coefficient of determination ($R^2$), and the correlation factor (r) are given for each relationship.

Table 3. Moisture content (MC) and dry biomass (DB) of fruit components of Strychnos madagascariensis and Strychnos spinosa per lot of 50 fruits each. The standard deviation is given for the mean values.

| Lot      | Shell | Pulp | S. madagascariensis | S. spinosa |
|----------|-------|------|---------------------|------------|
|          | DB (g) | MC   | DB (g) | MC | DB (g) | MC |
| Lot 1    | 5215.7 | 0.112 | 655.5 | 0.766 | 4531.3 | 0.508 |
| Lot 2    | 5021.2 | 0.045 | 717.4 | 0.771 | 3851.6 | 0.562 |
| Lot 3    | 5133.5 | 0.053 | 649.2 | 0.784 | 3956.4 | 0.557 |
| Lot 4    | 5186.2 | 0.054 | 706.7 | 0.763 | 4265.2 | 0.527 |
| Mean     | 5139.1 | 0.067 | 682.2 | 0.771 | 4151.1 | 0.539 |
| ± 85.6   | ± 0.03 | ± 34.8 | ±0.009 | ± 308.3 | ±0.03 |
| Lot 5    | 5901.2 | 0.289 | 41.3 | 0.769 | 1408.8 | 0.630 |
| Lot 6    | 6244.1 | 0.258 | 43.5 | 0.767 | 1485.2 | 0.621 |
| Lot 7    | 6310.1 | 0.230 | 48.2 | 0.763 | 1325.2 | 0.646 |
| Lot 8    | 6942.6 | 0.244 | 45.5 | 0.757 | 1201.2 | 0.674 |
| Mean     | 6349.5 | 0.236 | 44.6 | 0.764 | 1355.1 | 0.643 |
| ± 434.1  | ± 0.03 | ± 2.9 | ±0.005 | ± 121.6 | ±0.023 |
Dry Biomass and Carbon Stocks of Fruit Components

The fruit dry biomass (FDB; in g) and the fruit diameter (D; in cm) were related by the following linear expressions FDB = 1.022 x $D^{2.492}$ and FDB = 1.015 x $D^{2.38}$, respectively for S. madagascariensis and S. spinosa, with the highest coefficient of determination ($R^2 = 0.99$; Figure 6A). The fruit carbon biomass (CB; in g) and the fruit diameter were also related by a linear relationship for S. madagascariensis (CB = 0.463 x $D^{2.539}$; $R^2 = 0.659$) and S. spinosa (CB = 0.198 x $D^{2.821}$; $R^2 = 0.85$; Figure 6B). The regressions between the fruit diameter and the seed dry biomass (Figure 6C), shell dry biomass (Figure 6D), or pulp dry biomass (Figure 6E) had the same coefficient of determination per species ($R^2 = 0.659$ for S. madagascariensis; $R^2 = 0.85$ for S. spinosa). The correlation factor between fruit diameter and any of the dry fruit components of S. madagascariensis was 0.819 whereas the correlation factor between fruit diameter and any of the dry fruit components of S. spinosa was 0.923. Table 4 presents all the fitted allometric equations that derive the biomass and carbon stocks of fruit components of S. madagascariensis and S. spinosa.

The Student T-test comparing the mean values of biomass derived by proportion and by regression methods indicated that the parameter $p$-value was higher than 0.05 for fruit dry biomass (Figure 7A), fruit carbon biomass (Figure 7B), and shell dry biomass (Figure 7D), for both species. The same trend

Figure 6. Relationship between fruit diameter and dry fruit components of Strychnos madagascariensis and Strychnos spinosa. The fitted linear equation (drawn in red curve), the residual standard error (gray zone surrounding the red curve), the coefficient of determination ($R^2$), and the correlation factor ($r$) are given for each relationship.
was also observed in the biomasses of juice and puree of S. spinosa (Figure 7F). On the other hand, p-value was lower than 0.05 in the comparison of seed dry biomass (Figure 7C) and pulp dry biomass (Figure 7E) of S. spinosa generated by proportion and by regression methods.
Discussion

Fruit Size and Fruit Biomass

One of the major limitations to the commercialization of *S. madagascariensis* and *S. spinosa* is the scarcity of data on the size of their fruits (Rodrigues et al., 2018) and the relative proportions of the fruit components that can be converted into fruit products. In the present study, there were wide variations in the sizes of the fruits in both species in terms of both their fresh biomass and diameter. In *S. spinosa*, the largest fruit (1113.4 g) was seven times the biomass of the smallest fruit measured, and the diameter of the largest fruit (12.5 cm) was twice that of the smallest fruit. In the case of *S. madagascariensis*, the biomass of the largest fruit (796 g) was 10 times that of the smallest fruit, and the diameter of the largest fruit (11.4 cm) was twice that of the smallest fruit. There was a significant difference in the mean values of fruit fresh biomass between *S. spinosa* and *S. madagascariensis* (*p* < .05; Table 1). This implied that the mean fresh biomass of fruits of *S. spinosa* was statistically higher than that of *S. madagascariensis* at 95% confidence interval. The T-test results showed no significant differences in fruit diameter between *S. spinosa* and *S. madagascariensis* (*p* > .05; Table 1). This result was unexpected, but it means the fruit diameter is a parameter that cannot be used to differentiate between the two species.

Fresh Biomass of Fruit Components

This study showed that for a set of fruits of *S. madagascariensis* species, the fresh biomasses of the shell, pulp, and seeds corresponded on average to 30.8%, 16.7%, and 50.2%, respectively, of the total biomass of the fruit. On the other hand, for *S. spinosa* fruits, the fresh biomasses of shell, puree, seeds, juice, and pulp corresponded to 41.8%, 25.6%, 18.6%, 6.2%, and 0.9%, respectively, of the total biomass of the fruit (Figure 4). As they are proportions, they can therefore be applied to the fresh biomass of fruits regardless of their number. However, material losses must be provisioned as they are inevitable during the process of separating fruit components. This can be due to small wastes during processing or to a gradual loss of moisture from the fruit or its components. As *S. spinosa* fruits contain puree (Figure 3C) and juice (Figure 3D), which naturally possess high amounts of water, it was not surprising to observe a high loss of biomass in *S. spinosa* fruits compared to *S. madagascariensis* fruits. It should be noted that these proportion values of fruit components can vary depending on the methods used for the separation of the fruit components. For example, Rodrigues et al. (2018) reported that the juicy flesh of *S. spinosa* fruits can vary between 30% and 45%. This range is higher than what is reported in this study because the “juicy flesh,” mentioned by Rodrigues et al. (2018), could have been composed of pulp and puree. This study considered them as separate entities. Separation techniques of fruit components are among the constraints to be solved (Ngadze et al., 2017). The separation methods used in this study are not refined industrial methods. They were applied with the intention of reproducing traditional methods used by locals to extract and market fruit juice.

Besides expressing the partitioning of fresh biomass of fruit components of *S. madagascariensis* and *S. spinosa* as proportions, regression is also an option in relating the components of the fruits. This study showed that the fresh biomass of each fruit component of *S. madagascariensis* and *S. spinosa* can also be derived using the linear regression equations that link the biomass of any of the fruit components to the fruit diameter. The quality of the fitted regression equations was good in terms of their coefficients of determination and the correlation factors (Figure 5). Generally, regression models for fruit biomass estimations are developed for specific economic (Akweni et al., 2020) and ecologic purposes. In the context of the current study, the regression models for deriving fruit biomass from fruit diameter provide a nondestructive method of estimating C channeled to fruits in ecological studies. In cases where fruits are harvested from the forest for commercial purpose, the regression models for deriving fruit biomass are useful in estimating none-destructively fresh fruit yield of a forest stand in relation to its commercial value where the fruits are sold and eaten fresh in the
markets (Rodrigues et al., 2018). The regression models for estimating biomass of fruit components also have important applications under commercial production/cultivation should the species be domesticated and commercialized. In this regard, the regression equations deriving seed fresh biomass (Table 4; Figure 5B), shell fresh biomass (Figure 5C), and pulp fresh biomass (Figure 5D) are of interest in estimating waste from processing the fruit for fruit juice and jams (S. spinosa), or food products made from the fruit pulp (S. madagascariensis). The regression equations for deriving fruit fresh biomass (Table 4; Figure 5A), puree (Figure 5E; for S. spinosa), and juice (Figure 5F; for S. spinosa) are important in estimating the amount of specific commercial products that can be made from these fruit parts. In any of these cases above, deriving fruit fresh biomass from fruit diameter is important for the nondestructive determination of biomass of individual fruits. Likewise puree and juice, the derivation of their biomass from fruit diameter is crucial in the quick evaluation of their yield without having to resort to time-consuming processes of extracting them.

**Moisture Contents of Fruit Components**

Fruits are components of trees that are subject to seasonal production. They are therefore elements of reference for the evaluation of carbon (C) dynamics. However, to assess the amount of C sequestered by fruits, it is necessary to know their dry biomass. Dry biomass can also be obtained from fresh biomass by using formulas that involve specific density or moisture content (Alemdag, 1981; Bauwens and Fayolle, 2014; Rondeaux, 1999). Data from the present study revealed that moisture contents of the shell, pulp, and seeds of S. madagascariensis fruits are different with the shell having the least and the pulp the most (Table 3). The same trend was observed for S. spinosa. The differences in moisture content between the shell and the pulp were 0.704 for S. madagascariensis and 0.508 for S. spinosa. This is expected because the hard shell acts as a barrier to water loss by fruit. Surprisingly, the fruit pulp of the two species had almost equal moisture content (Table 3) despite that the fruit pulp of S. spinosa was fully engorged with juice. This can be explained by the procedure that was used to separate the pulp from the juice. In fact, fruit pulp of S. spinosa was obtained after the extraction of juice. It is therefore possible that a significant amount of water in the pulp could have been removed together with the extracted juice.

**Dry Biomass and Carbon Stocks of Fruit Components**

Currently, estimating the amount of biomass and carbon stocks sequestered by forest ecosystems is part of international priorities for the evaluation of their contributions to the purification of the atmosphere (Chave et al., 2004; Ryan et al., 2011). In savannah woodlands, fruit trees contribute to carbon sequestration through their above-ground and below-ground biomass (Mugasha et al., 2013). Unfortunately, the carbon stocks stored in fruits are rarely investigated despite the considerable annual production of fruit biomass by fruit trees. This is because the carbon stocks stored in fruits are rapidly turned back to the atmosphere. Also, methods that derive the fruit dry biomass and carbon stocks have never been developed for most fruit tree species. This study showed that fruit dry biomass is related to fruit diameter by a linear relationship. This implies that the fruit dry biomass of S. madagascariensis and S. spinosa can be derived from their fruit diameter using the regression equations mentioned in Table 4. This also holds for fruit carbon stocks (Figure 6B). It was proven that the dry biomass of each fruit component was positively correlated to the fruit diameter. However, the correlation factor between fruit diameter and dry biomass of any of the fruit components was the same per species. This can be explained by the fact that the dry biomass of each fruit component was obtained from the fresh biomass which was previously derived by proportion values.

From the above, it was necessary to compare both methods used in this study to derive dry biomass and carbon stocks of fruit components. The results of T-test indicated that there was no difference between the mean values of fruit dry biomass (Figure 7A), fruit carbon stocks (Figure 7B), and shell dry biomass (Figure 7D) that were generated by proportion and by regression methods. In other
words, these two methods are valid and can therefore be used to derive dry biomass and carbon stocks of the above-mentioned fruit components of S. madagascariensis and S. spinosa. In addition, the derivation of juice and puree of S. spinosa by both methods was unbiased (Figure 7F; p-value > 0.05). However, there was a significant difference in the mean values of seed dry biomass (Figure 7C; p-value < 0.05) and pulp dry biomass (Figure 7E; p-value < 0.05) of S. spinosa that were calculated by way of proportions and those that were generated via regression. The regression methods significantly underestimated the seed dry biomass and pulp dry biomass of S. spinosa at 95% confidence interval. The differences in the derivation of pulp dry biomass of S. spinosa can simply be explained by the issues of moisture content and separation procedure of pulp that were discussed in the previous section. As for the differences between the two methods in the derivation of seed dry biomass of S. spinosa, this study could not provide a plausible explanation. Further investigations are necessary to determine the variability of moisture content within seeds of S. spinosa.

**Conclusion**

This study established techniques that make it possible to derive biomass allocation and carbon stocks of fruit components of S. madagascariensis and S. spinosa. In the advent of commercializing the fruits of the two species, these findings will be useful in estimating the commercial value of S. madagascariensis and S. spinosa fruits and their products throughout their value chain following harvesting. In addition, the data can be used to assess the contribution of these fruit-bearing species to the carbon dynamics of savannah woodlands.

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**Disclosure Statement**

The authors declare that they have no known competing interest that could have influenced this study.

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