Variability and estimating in fruiting of shea tree (*Vitellaria paradoxa* C.F. Gaertn) associated to climatic conditions in West Africa: implications for sustainable management and development

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ABSTRACT
Shea tree (*Vitellaria paradoxa*) is one of the main native oil plants with high economic value in Africa. Its fruits are used for food, medicinal, cultural and exportation purposes. However, the lack of efficient tools to assess annual fruit production of the species limits the sustainable management of its resources. Therefore, production statistics are useful to organize the activities of the shea sector. This study aimed to (i) assess the interannual variation in fruit production along a climatic gradient in Burkina Faso, (ii) examine fruit production patterns according to climatic zones and tree size, (iii) assess the contribution of high-yielding trees in the annual potential production and (iv) develop allometric equations for estimating fruit yields of the species. The yield of 212 trees distributed across three climatic zones was monitored over four successive years. Within each climatic zone, fruit production was significantly different among years. Fruit production was positively and significantly correlated with tree size. The interannual variation in fruit production at tree individual level was higher in drier climatic conditions. The mean interindividual synchrony was less than 50% in each zone, suggesting a large range in fruit production patterns of the species. Annually, more than 55% of the total fruit production was supported by high-yielding trees. The best regression models for estimating fruit yields had $R^2$ values of 69–73% with prediction errors ranging from –7% to 4%. Our findings are useful tools for the planning of rational exploitation of shea tree's resources and its sustainable management.

Introduction
The exploitation of nontimber forest products (NTFPs) is an important source of incomes for local people in sub-Saharan Africa countries where economic resources are limited (Tchatat & Ndoye, 2006). Specifically, the shea tree (*Vitellaria paradoxa*) plays an important role in Africa due to the high economic value of its fruits with huge industrial and domestic uses of its butter (Yeboah, Lowor, Amoah, & Owusu-Ansah, 2011). The species also plays an important ecological role in the agroforestry parklands by improving microclimate, fertility and protection of the soils against water erosion for associated crops (Bayala, Teklehaimanot, & Ouédraogo, 2002; Yeboah et al., 2011). Lastly, the shea tree makes a significant contribution to the local climate regulation through its important potential in carbon sequestration (Dimobe et al., 2018; Sanogo et al., 2016). A monoecious species belonging to the Sapotaceae family, the shea tree is listed among the most important useful tree species for local populations in West Africa (Van der Stege, Prehsler, Hartl, & Vogl, 2011). The peak of its production period coincides with that of food shortage, when cereal granaries are almost empty, but labor requirements are the highest for cropping activities. The pulp of its fruit becomes an important source of food for farmers (Boffa, 2015). The butter extracted from the dry kernels has various local uses: food, medicinal, cosmetic and cultural uses (Ouédraogo, Lykke, Lankoandé, & Korbéogo, 2013). The marketing of dry kernels and shea butter contributes to 12% of the total income of the poorest households in Burkina Faso (Pouliot, 2012). The use of shea butter in food and cosmetic industries in developed countries created a high demand in international markets and therefore, the export of shea kernels and butter makes a significant contribution to the economy of producing countries (Bup, Mohagir, Kapseu, & Mouloungui, 2014; Rousseau, Gautier, & Wardell, 2015). Despite its socioeconomic importance, the recent studies indicated that *Vitellaria paradoxa* is listed among the most vulnerable food species with ‘severe threat levels’ which are mainly caused by human pressure (overexploitation, cotton production, bush fires, grasing pressure, uncontrolled tree cutting for firewood and charcoal production) and climate change (Boffa, 2015; Gaisberger et al., 2017; Ouédraogo et al., 2017). These...
different threats compromise the conservation and sustainable management of the species as well the economy of the shea sector (Boffa, 2015; Venturini, Haworth, Coudel, Alonso, & Simonet, 2016). Therefore, it is urgent to develop resilience practices adapted to the context to secure the sustainable management of the species’ resources. For this purpose, some authors recommended that the initiatives and shea parkland conservation programs must enlist the cooperation of local farmers whose endogenous knowledge of the species’ ecology, management and particular challenges are essential for the success of the strategies of the management and conservation of the shea tree (Boffa, 2015; Diarassoboua, Koffii, N’Guessan, Van Damme, & Sangare, 2008; Elias, 2015). However, the lack of reliable scientific tools to assess accurately the annual potential of the fruit production at local and national level is a major constraint to the shea tree sector in view of optimizing the exploitation for sustainable and more profitable uses. In Burkina Faso, the annual potential of the shea kernel production is estimated at 70,000–300,000 tons (Bup et al., 2014) and at more than 800,000 tons (Government of Burkina Faso, 2015; Nfon Dibié, Francois, & Danthonny, 2012). These national statistics generally based on export data are imprecise and not reliable because the national statistical monitoring systems fail to deliver comprehensive data on the export by road (Rousseau et al., 2015). In addition, the previous studies indicated that in some major West African producing countries, such as Burkina Faso, about half of the total available potential shea production is uncollected in the fields (Boffa, Yaméogo, Nikiéma, & Knudson, 1996; Lovett, 2004). An important part of the nuts collected, estimated between 41% and 55% (Lovett, 2004; Reynolds, 2010), is also locally consumed and therefore, escapes to the trade statistics. To provide reliable statistics on the potential of shea production, a regional model based on a range of environmental parameters was developed to predict the potential shea distribution and production in sub-Saharan Africa (Naughton, Lovett, & Mihelcic, 2015). This model indicates a huge variation in potential of shea kernel production, ranging from 2.44 million tons to more than 20.1 million tons across sub-Saharan Africa depending on which tree densities and kernel yields are used in the model. Therefore, the authors recommended that each country invests in this research to obtain detailed data, including shea yields and tree densities in order to provide better estimates. In sub-Saharan Africa, allometric equations are frequently developed and used as models for estimating tree biomass (Henry et al., 2011). However, to develop reliable allometric equations, the sampling design needs to integrate environmental factors and tree morphological parameters that are suspected to affect biomass production (Bognounou et al., 2013; Mbow, Verstraete, Sambou, Diaw, & Neufeldt, 2013). Climatic gradient, land use and soil types were found as important factors affecting the performance in fruit production of shea tree (Aleza, Villamor, Nyarko, Wala, & Akpagana, 2018; Glèle Kakai et al., 2011; Lamien, Ouédraogo, Diaéro, & Guin, 2004). Moreover, fruit production of shea tree is generally marked by significant interannual variations (Boffa et al., 1996; Soro, Koffii, & Soro, 2011). In Burkina Faso, the allometric models developed to estimate fruit yield of the species were based on 1-year data collected in local sites (Lamien, Tigabu, Guinko, & Oden, 2007a). Because of high interannual variation in fruit production in sub-Saharan Africa woody species, data for the estimation of annual fruit production need to be collected over a period of 3–5 years (Kouyaté, Nacoumla, Lykke, & Thiombiano, 2016). Therefore, multi-years data distributed in different climatic zones, are needed to develop accurate allometric models for estimating the fruit production of the shea tree.

This study aimed to contribute to the sustainable management of shea tree resources in West African parklands. The specific objectives were to (i) assess the interannual variation in fruit production along a climatic gradient; (ii) examine the fruit production patterns according to climatic zones and tree size; (iii) assess the contribution of high-producing trees in the annual potential of shea tree production; (iv) develop allometric equations for estimating annual fruit yield of the species. The following hypotheses are posited: (i) the climatic zone with high annual rainfall exhibits the best performances in fruit production of shea tree, (ii) the higher variability in fruiting is associated to drier climatic conditions and (iii) the annual potential of fruit production strongly depends on high-yielding trees.

Materials and methods

Study sites

Our study covers the three climatic zones of Burkina Faso namely the Sahelian zone, the Sudano-Sahelian zone and the Sudanian zone (Dipama, 2010) where the shea tree is widely distributed. To account for the influence of climatic gradient on fruit production, 12 study sites, distributed in the three climatic zones were selected (Figure 1). Four (04) shea tree populations located in four sites and exclusively managed in parklands were selected in each climatic zone. In each site, the selected populations were distant of at least 15 km to account for genetic diversity that could exist between them. Climate data (rainfall and temperature) from the nearest meteorological stations to the study sites were used to characterize the climatic conditions of each zone (Table 1).
Tree sampling

The adult trees which can produce fruits were selected in 2014 during the full fruiting period of shea trees (April–May). To account for the variability of tree size which is essential in the tree biomass estimation (Mbow et al., 2013), the sample trees were randomly selected and grouped into six diameter classes (stem diameter at 1.30 m aboveground [DBH]) of 5–15, 15–25, 25–35, 35–45, 45–55 and >55 cm. These classes were defined based on the diameter of the smallest productive tree (DBH = 9.55 cm) observed in the field. At least 18 trees were selected per population with a minimum of three individuals per diameter size class. However, in the Sahelian zone, 15 trees were selected per population because the productive trees with a diameter less than 15 cm were not found. Within each population, a minimum distance of 100 m was observed between sampled trees to avoid selection of closely related individuals and to ensure the independence of the observations. The observations on sampled trees were collected during four consecutive years from 2014 to 2017. For this purpose, individual trees were marked with paint and their geographical coordinates were recorded. For each sample tree the following dendrometric parameters were measured: stem diameter at 1.3 m aboveground (DBH), the total height (H) and the mean crown diameter (Mcd).

Table 1. Rainfall and temperature values of the three climatic zones for the period 2014–2016.

| Year | Sahelian zone Rainfall (mm) | Temperature (°C) | Sudano-Sahelian zone Rainfall (mm) | Temperature (°C) | Sudanian zone Rainfall (mm) | Temperature (°C) |
|------|-----------------------------|------------------|-----------------------------------|------------------|-----------------------------|------------------|
| 2014 | 766.6                       | 29.65            | 797.7                             | 29.44            | 1278.3                      | 28.05            |
| 2015 | 915.3                       | 29.36            | 1149.2                            | 29.18            | 1173.1                      | 28.15            |
| 2016 | 920.8                       | 29.91            | 808                                | 29.83            | 1190.6                      | 28.41            |
| Mean | **867.56**                   | **29.64**        | **918.3**                         | **29.48**        | **1214**                    | **28.20**        |
the study with 80 trees in the Sudanian zone, 72 in the Sudano-Sahelian zone and 60 in the Sahelian zone.

Monitoring of annual fruit production

Fruit production of the same trees was assessed over the four consecutive years from 2014 to 2017. The fruit production was visually measured by counting the number of fruits on the fruiting branches. To assess fruit production per tree, the method of branches used by Bondé et al. (2018) in the foliage biomass estimation of *Tamarindus indica* L. was adopted to count the number of fruits. Thus, the diameter of all fruiting branches of each tree was initially measured and then ranked into seven branch size classes (in cm): ≤5, 5–8, 8–11, 11–14, 14–17, 17–20 and 20–23 cm. For each branch class, the following sample branches were selected based on the total number of fruiting branches to count fruits:

- two sample branches, when the number of fruiting branches is less than or equal to 5;
- three sample branches, when the number of fruiting branches is between 5 and 10;
- and four branches, when the number of fruiting branches is more than 10.

The number of fruits of these sample branches was then counted. The total number of fruits of a given branch size class was obtained by multiplying the average number of fruits of the sample branches with the number of fruiting branches. The total number of fruits of the tree derives from the summation of the number of fruits of its different branch size classes. Before adopting this method, the error of estimation was tested on a sample of 10 trees by performing consecutively on each tree the partial counting of fruits based on the method of branches and the integral counting of fruits. Since the local people directly gather the ripe fruits of the shea tree when they fall, the counting of fruits was done before their maturity (May–June according to climatic zones). This allows to avoid an under-estimation of the fruit production due to the harvest of ripe fruits. The data on fruit biomass were collected in the maturity period of the fruits which approximatively corresponds to the fruits falling period (June–August). To determine the fresh weights of fruits and pulp and the dry weight of kernels per tree, 20 ripe fruits were randomly selected from each tree. The fresh weight of these fruits was immediately determined after collection in the field by using an electronic balance (weight 0–5 kg, with precision 1 g). The fruits were depulped after taking their weight and their pulp was also weighted. The fruit nuts were dried in an oven at 105°C at the laboratory until obtaining constant dry weight. Dry nuts were shelled and their kernels were weighed.

Data analysis

The total fresh weight of fruits (FWF), fresh weight of pulp (FWP) and dry weight of kernels (DWK) per tree were assessed using the sample of 20 fruits harvested on each tree according to the following Eqs. (1)–(3):

\[
FWF = \text{Total number of fruits} \times \text{Fresh weight of 20 fruits}/20;
\]

\[
FWP = \text{Total number of fruits} \times \text{Fresh weight of pulp of 20 fruits}/20;
\]

\[
DWK = \text{Total number of fruits} \times \text{Dry weight of 20 kernels}/20
\]

The correlations between all tree dendrometric parameters (DBH, H and Mcd) on the one hand and between production variables (number of fruits, fruit biomass, pulp biomass and dry kernels biomass) on the other hand were performed using Pearson correlation tests. The estimation error of the method adopted to assess fruit production per tree was calculated using the equation adopted by Bondé et al. (2018).

Variation in fruit production

Variation in fruit production was assessed by using generalized linear models (GLMs) with Poisson distribution (log link function). GLM with Poisson distribution were used to account for the non-normal errors and the increasing variances with increasing mean that is associated with count data (Crawley, 2007). Climatic zones and years were treated as fixed factors, production variables as response variables and DBH was used as a covariate to adjust the effect of tree size. When significant effects (p value < 5%) were detected, pair-wise comparison was conducted using the Wilcoxon test. Regarding the effect of tree size, the comparisons of production variables were done between tree diameter classes.

Fruit production patterns

Variability in fruit production at tree individual level was measured by calculating the coefficients of variation (CV). The coefficients of variation were calculated as the ratio of the standard deviation to the mean fruit production for each tree multiplied by 100 for the 4-year (2014–2017) time series (Rosenstock, Hastings, Koenig, Lyles, & Brown, 2011). Trees with CV > 1 were
considered as trees with high variability in fruit production.

To test whether interannual fruiting ability was synchronized among the trees, the level of synchrony of fruit production among the trees from one year to another was determined for each climatic zone. For this, the fruit production patterns of all possible pairs of individual trees were analyzed with Spearman’s rank correlation (Zywiec, Holeksa, & Ledwo, 2012). In this study, synchrony of fruit production is considered as the simultaneous occurrence of annual fruiting ability (measured in terms of fruit biomass) among shea trees. We estimated the mean interindividual synchrony (Rs) as the mean of all pairwise correlations of Spearman between individuals. In addition, the level of synchrony between heavy and low crop years was assessed according to the method adopted by Zywiec et al. (2012). Heavy crop years were defined as years when the fruit production is higher than the 4-year mean and low crop years as those when the fruit production was lower than this mean. For each year, the proportions of trees that had fruit production above and below their 4-year mean were computed. Then, these proportions were considered as the level of synchrony for the heavy and low crop years respectively.

Within each climatic zone, the high-yielding trees were selected using quantile analysis and their contribution to the annual total fruit biomass was calculated. The data points above the 75th percentile in fruit biomass were selected as representing the high-yielding trees (Snook, Camara-Cabralesb, & Kelty, 2005). The proportions of nonbearing trees (production < 1 fruit) were also calculated for each year.

Allometric equations
Specific climatic zone models were fitted using linear, polynomial and power models for exploring the best correlations. Tree dendrometric parameters (DBH, H and Mcd) were considered as explanatory variables (X) and fruit biomass as response variable (Y). For each sample tree, the average fruit biomass of the 4 years was used for models fitting. In order to develop allometric models that are more objective in terms of prediction, the data of each climatic zone were explored following the protocol described by Zuur, Ieno, and Elphick (2010). Then, the outliers were identified and reexamined. These outliers corresponded to trees with exceptional productions (4-year mean) rarely observed in the field. Therefore, we decided to drop the outliers in the model fitting because this approach improves the prediction ability of the models in relation to the fruit production commonly observed in the shea tree in the fields. Finally, 185 trees were used to fit allometric models with 65 trees in the Sudanian zone, 65 trees in the Sudano-Sahelian zone and 55 trees in the Sahelian zone. For each zone, 80% of sample trees were randomly selected to fit models and 20% were used for the validation of models (Zhao et al., 2013). Tree selected for fitting and validating the models were distributed across all diameter classes. Multiple and simple regressions using the transformation of variables (Y and/or X) were performed. Regarding linear models, three important assumptions were tested on the residuals: normality, homoscedasticity and independence of residuals (Makunywa et al., 2013). The Shapiro–Wilks test, Breush–Pagan test and Durbin–Watson test were applied to check these assumptions, respectively (Picard, Saint-André, & Henry, 2012). The Furnival’s index (I) was calculated (Eq. (4)) to evaluate the goodness-of-fit and used for selecting the best fitted models because our models had different response variables (Parresol, 1999). Models with lowest index value were considered as the best fitted models. To assess the prediction ability of these best fitted models a validation step was performed by comparing the predicted biomasses with independent biomasses of those used for fitting the models (Picard et al., 2012). The correction factor (CF), as indicated in Eq. (5), was used for correction of the logarithmic bias that occurs when log biomass is back-transformed to arithmetic units. Thus, CF was applied to the predicted values of biomass in cases the response variables had been log-transformed (Mwakalukwa, Meilby, & Treve, 2014). The coefficient of determination (R²), Akaike’s information criterion (AIC) and prediction error (PE) were used to select the best prediction models. PE was calculated using Eq. (6).

\[
I = RMSE \times |f'(Y)|^{-1} \tag{4}
\]

\[
CF = \exp\left(\frac{RSE^2}{2}\right) \tag{5}
\]

\[
PE = \left(\frac{\text{predicted biomass} - \text{observed biomass}}{\text{observed biomass}} \right) \times 100 \tag{6}
\]

Where \( f'(Y) \) is the derivative of the dependent variable with respect to biomass, the square brackets signify the geometric mean, and RMSE is the root mean square error of the fitted equation. RSE is the residual standard error of the model.
error obtained from the model regression and PE is the predicting error.

Since fruit production varied greatly between years, the equations for estimating fruit biomass in the years of lowest and highest production were developed to calculate the uncertainties related to the equations based on 4-year mean. Here, the uncertainties were considered in terms of prediction errors based on interannual variation in fruit production. Thus, for both year categories, the prediction errors in comparison with average estimates (stem from 4-year mean equations) were calculated using Eq. (6).

Results

Variation in fruit production of shea tree based on climatic zones and years

The production variables assessed per tree were the number of fruits, fresh fruit biomass, fresh pulp biomass and dry kernel biomass. The statistical analysis indicated that the climatic zone had a significant effect on all these production variables (Table 2). Furthermore, significant correlations were observed between fruit biomass and the other production variables ($\rho > 0.93$; $p$ value $< 0.0001$, in each climatic zone). Hence, fruit biomass was considered as a measure of fruit production. The 4-year mean of fruit biomass per tree was 12.77 kg ($CV = 152.25\%$) in the Sahelian zone, 10.57 kg ($CV = 117.78\%$) in the Sudano-Sahelian zone and 18.59 kg ($CV = 130.46\%$) in the Sudanian zone. Interannual variation in fruit production was globally significant over the 4 years in each climatic zone (Table 2). In the Sahelian zone, the highest fruit biomass was recorded in 2016 with an average of 20.73 kg ($CV = 92.19\%$) per tree.

Fruit production patterns based on climatic zones and tree size

The results showed that the interannual variability in fruit production at tree individual level was higher in the Sahelian zone as compared to the two other zones (Table 3). The proportions of trees with high variability ($CV > 100\%$) were 61.02\% in the Sahelian zone, 20.83\% in the Sudano-Sahelian zone and 22.50\% in the Sudanian zone. Variability was not significantly correlated with tree size ($p > 0.05$). Annually, 16\% of trees in the Sahelian zone, 3\% in the Sudano-Sahelian zone and 5\% in the Sudanian zone did not bear fruits. The mean interindividual synchrony for the 4 years was less than 50\% in each climatic zone (Table 3). However, the level of synchrony was higher in the low crop years compared to the heavy crop years (Table 3). The results showed that, whatever the year, the high-yielding trees which represent about 25\% of sample trees

| Table 2. Results of GLM presenting the effects of climatic zone, year and tree size on fruit yield of Vitellaria paradoxa in Burkina Faso, West Africa. |
|-----------------|-----------------|-----------------|-----------------|
|                  | Number of fruits |                  |                  |
|                  | Estimate         | Standard error  | $Z$ value        | $Pr (>|Z|)$   |
| Intercept        | 5.26E + 00       | 6.29E - 03      | 836.2            | <0.0001      |
| Climatic zone    | 3.18E - 01       | 1.76E - 03      | 180.9            | <0.0001      |
| Year             | -1.76E - 01      | 1.22E - 03      | -143.6           | <0.0001      |
| DBH              | 2.28E - 02       | 7.126E - 05     | 320.7            | <0.0001      |
| Fruit biomass    |                 |                  |                  |              |
| Intercept        | 1.351            | 0.042           | 31.88            | <0.0001      |
| Climatic zone    | 0.313            | 0.011           | 26.55            | <0.0001      |
| Year             | -0.143           | 0.008           | -17.49           | <0.0001      |
| DBH              | 0.024            | 0.0005          | 49.54            | <0.0001      |
| Biomass of fresh pulp |             |                  |                  |              |
| Intercept        | 0.873            | 0.055           | 15.874           | <0.0001      |
| Climatic zone    | 0.243            | 0.015           | 15.914           | <0.0001      |
| Year             | -0.104           | 0.011           | -9.749           | <0.0001      |
| DBH              | 0.024            | 0.0006          | 37.951           | <0.0001      |
| Biomass of dry kernel |             |                  |                  |              |
| Intercept        | -1.125           | 0.125           | -9.013           | <0.0001      |
| Climatic zone    | -0.184           | 0.023           | -7.956           | <0.0001      |
| Year             | 0.024            | 0.001           | 17.838           | <0.0001      |
contributed to more than 55% of the total fruit biomass produced in each zone (Figure 3).

**Variation in fruit production based on tree size**

High correlations were detected between DBH and the others tree dendrometric parameters (\(r > 0.79; p \text{ value} < 0.0001\), in each climatic zone). Thus, DBH was considered as a measure of the shea tree’s size. Tree size had significant effect on fruit production in each climatic zone (Table 2). In general, fruit production increased proportionately with tree size. The relationship between tree diameter and fruit biomass was visualized by the regression curves resulting of GLM analysis (Figure 4). The analysis of fruit production according to tree diameter size classes (Figure 5) showed that in the Sahelian zone, the highest 4-year mean in fruit biomass estimated at 19.26 kg (\(CV = 134.53\)) per tree was observed in trees with \(DBH\) ranging from 45 to 55 cm. In the Sudano-Sahelian zone, trees with \(DBH > 55\) cm recorded the highest mean estimated at 19.74 kg (\(CV = 81.91\)) per tree while in the Sudanian zone the highest production estimated at 28.03 kg (\(CV = 122.96\)) of fruits per tree was observed in trees with \(DBH\) ranged from 35 to 45 cm. The number of fruits, pulp biomass and kernels biomass per tree according to tree size and climatic zones are presented in Table 4.

**Allometric equations for the prediction of fruit biomass**

The linear, polynomial and power models were fitted in this study. Among these models, the regression parameters of linear models were significant (\(p < 0.05\)). The linear models that satisfied the conditions of linear regressions (especially the normality, homoscedasticity and independence of residuals) were selected and presented in Table 5. In the whole three climatic zones, the
models using square root functions exhibited the best regressions. The two best fitted models (models with the lowest $I$ values) were: $SZ_2 (R^2 = 0.72; I = 0.53)$ and $SZ_3 (R^2 = 0.72; I = 0.52)$ for Sudanian zone; $SSZ_1 (R^2 = 0.73; I = 0.56)$ and $SSZ_2 (R^2 = 0.73; I = 0.56)$ for Sudano-Sahelian zone; $SaZ_1 (R^2 = 0.72; I = 0.56)$ and $SaZ_4 (R^2 = 0.69; I = 0.85)$ for Sahelian zone. The prediction ability of these models was evaluated through a validation step where the final best prediction models that had the lowest $AIC$ and $PE$ values were selected (Table 6).

Among the models, $SZ_2$ (in the Sudanian zone), $SSZ_1$ (in the Sudano-Sahelian zone) and $SaZ_1$ (in the Sahelian zone) with prediction errors of $-7.26\%$, $-7.05\%$ and $4.54\%$ were the best prediction models, respectively. The uncertainties allowing to estimate fruit biomass in the years of lowest and highest production were presented in Table 6. The relationship between fruit biomasses estimated by the models based on 4-year mean and models for year categories was plotted in Figure 6.

Allometric equations were developed on the basis of fruit biomass and the proportions of pulp and dry kernel were calculated to estimate their production. The results showed that in 1 kg of fruits, the pulp represented $62.56\%$ in the Sahelian zone, $59.26\%$ in the Sudano-Sahelian zone and $55.30\%$ in the Sudanian. The dry kernel accounted for $10.55\%$ of the fruit biomass in the Sahelian zone, $10.86\%$ and $14.62\%$, respectively in Sudano-Sahelian and Sudanian zones. These proportions can be applied to the fruit biomasses predicted by the

Figure 3. Contribution of high-yielding trees to the total fruit yield of *Vitellaria paradoxa* across climatic zones in Burkina Faso, West Africa. (a) = Sahelian zone, (b) = Sudano-Sahelian zone and (c) = Sudanian zone.
equations to estimate the annual production of pulp and kernels.

**Discussion**

*Variation in fruit production of shea tree based on climatic zones and years*

The results of this study showed that the climatic zone had a significant effect on the shea tree performance in fruit production. The fruit biomass produced per tree (4-year mean) in the Sudanian zone was higher than those in Sudano-Sahelian and Sahelian zones. In Benin, the highest fruit production of shea tree was also observed in the Sudanian zone (Glèlé Kakaï et al., 2011). This suggests that the Sudanian zone (with annual rainfall ≥ 1100 mm) offers the most favorable climatic conditions for the fruit production of shea tree in the West African parklands. The average fruit biomass

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**Figure 4.** Relationship between fruit yield of *Vitellaria paradoxa* and tree size across climatic zones in Burkina Faso, West Africa. (a) = Sahelian zone, (b) = Sudano-Sahelian zone and (c) = Sudanian zone.
recorded in the Sudanian zone during the period of this study was estimated at 18.59 ± 24.25 kg per tree. Previous studies carried out in the same zone over a few years on shea tree production found similar fruit biomasses: 18.8 kg per tree in Burkina Faso (Boffa et al., 1996) and 17.4 ± 11.7 kg per tree in Bénin (Aleza et al., 2018).

In general, fruit production of shea tree was highly variable from year to year in each climatic zone. A significant interannual variation in fruit production of the species was locally observed by Boffa et al. (1996), Serpantié (1996) and Soro et al. (2011). Variation in fruit production from year to year is a common characteristic in many woody species. Indeed, a wide interannual variation in fruit production was also observed in *Sclerocarya birrea* (Shackleton, 2002) and *Detarium microcarpum* (Kouyaté, Van Damme, & Diawara, 2006). Interannual variation in fruit production could be related to alternating cycles which can be regularly maintained over several years or be interfered with by climatic or pathological factors (Boffa, 2015). The existence of an alternative production

Table 4. Production variables of *Vitellaria paradoxa* (4-year mean) based on climatic zones and tree size in Burkina Faso, West Africa. CV = coefficient of variation.

| Number of fruits | Pulp biomass | Kernels biomass |
|------------------|--------------|-----------------|
|                  | Mean (kg)    | CV (%)          | Mean (kg)    | CV (%)          | Mean (kg)    | CV (%)          |
| Sahelian zone    |              |                 |              |                 |              |                 |
| 5–15             | 541.5        | 150.99          | 7.99         | 155.94          | 1.35         | 160.74          |
| 15–25            | 153.31a      | 155.71          | 2.43a        | 193.31          | 0.316a       | 181.10          |
| 25–35            | 394.37b      | 162.08          | 5.20b        | 136.39          | 0.90a        | 142.70          |
| 35–45            | 631.84c      | 127.80          | 8.03bc       | 133.82          | 1.48bc       | 144.99          |
| 45–55            | 815.81d      | 139.02          | 11.66c       | 138.61          | 2.08c        | 142.25          |
| >55 cm           | 689.84c      | 119.6824        | 12.28c       | 130.98          | 1.88c        | 130.85          |
| Sudano-Sahelian zone | 525.31      | 114.62          | 6.27         | 121.53          | 1.15         | 118.26          |
| 5–15             | 114.97a      | 122.51          | 1.51a        | 143.07          | 0.27a        | 122.57          |
| 15–25            | 341.59b      | 86.44           | 3.65b        | 81.30           | 0.72a        | 94.65           |
| 25–35            | 431.50bc     | 109.31          | 4.69b        | 102.74          | 0.96ab       | 115.54          |
| 35–45            | 684.23c      | 86.23           | 8.82c        | 106.37          | 1.52b        | 99.87           |
| 45–55            | 612.96c      | 105.19          | 7.59c        | 96.25           | 1.27b        | 104.01          |
| >55 cm           | 966.56d      | 84.81           | 11.31d       | 92.38           | 2.13c        | 85.20           |
| Sudanian zone    | 822.1        | 138.81          | 10.28        | 123.93          | 2.72         | 154.78          |
| 5–15             | 247.70a      | 100.23          | 2.90a        | 98.43           | 0.83a        | 102.29          |
| 15–25            | 314.49a      | 146.85          | 3.41a        | 143.96          | 1.00a        | 130.08          |
| 25–35            | 718.83b      | 85.94           | 11.98b       | 105.07          | 2.34b        | 89.85           |
| 35–45            | 1235.93c     | 137.60          | 15.00c       | 109.73          | 4.13c        | 153.68          |
| 45–55            | 1023.70d     | 104.82          | 12.57bc      | 96.52           | 3.08bc       | 94.25           |
| >55 cm           | 1261.43c     | 107.46          | 14.23c       | 98.00           | 4.46c        | 131.96          |

Notes: Different letters between diameter classes of the same climatic zone indicate significant differences according to the test of Wilcoxon at 5% level.
cycle in woody plants such as the shea tree is controversial, but the consensus denotes that under the influence of external factors (climatic conditions or pathological events), a significant decrease in carbohydrate is commonly observed in woody plants during the years of high production, creating a carbohydrate deficit in plant organs which leads to low production during the following year (Lamien, 2006). In this study, the results showed that the years of high production are generally followed by the years of low production. The climatic conditions can indirectly or directly affect the annual fruit production. It states that plants allocate a fraction of assimilated carbon to the reproduction each year (Burns, 2012). The author indicates that, the years with favorable climatic conditions that promoting high rates of carbon assimilation result in greater seed production while in years with poor climatic conditions, plants fix less carbon and produce fewer seeds. Climatic conditions can directly affect the level of fruit yield by causing a premature fall of flowers and young fruits (Serpentié, 1996). For the year with stressfull climatic conditions (low rainfall, high temperature and high speed of wind), the author observed a low yielding in shea tree due to the strong abortion of flowers. In some species such as Acacia mellifera, significant and positive correlation was found between its seed production and rainfall of the preceding rainy season, suggesting that rainfall affects interannual

Table 5. Fitted allometric equations for predicting fruit biomass of Vitellaria paradoxa in the three climatic zones in Burkina Faso, West Africa: No. = model number, $Y = $fruit biomass, $D = $DBH, $McD = $mean crown diameter, $H = $tree height, $\beta_0$ and $\beta_1$ = model coefficients, $I =$ Furnival's index, $CF =$ correction factor, $n =$ number of trees used in the fit of models (significance: *$p < 0.01$, **$p < 0.001$, ***$p < 0.0001$).

| No. | Allometric equations | $\beta_0$ (SE) | $\beta_1$ (SE) | $R^2$ | $I$ | $CF$ |
|-----|----------------------|----------------|----------------|-------|-----|-----|
| **Sudanian zone (n = 52)** | | | | | | |
| SZ1 | $Y = \beta_0 + \beta_1 \ln(D)$ | $-51.37$ (6.99) *** | $19.53$ (2.03) *** | $0.65$*** | $7.18$ | $-$ |
| SZ2 | $\sqrt{Y} = \beta_0 + \beta_1 \sqrt{D}$ | $-2$ (0.51) *** | $0.98$ (0.09) *** | $0.72$*** | $0.53$ | $-$ |
| SZ3 | $\sqrt{Y} = \beta_0 + \beta_1 \sqrt{D}$ | $0.66$ (0.28)* | $0.09$ (0.007) *** | $0.72$*** | $0.52$ | $-$ |
| SZ4 | $\sqrt{Y} = \beta_0 + \beta_1 \sqrt{McD}$ | $-2.75$ (0.73) *** | $2.32$ (0.26) *** | $0.61$*** | $0.62$ | $-$ |
| SZ5 | $\ln(Y) = \beta_0 + \beta_1 \ln(Mcd)$ | $-1.4$ (0.45) ** | $1.89$ (0.22) *** | $0.59$*** | $6.61$ | $1.23$ |
| **Sudano-Sahelian zone (n = 52)** | | | | | | |
| SSZ1 | $\sqrt{Y} = \beta_0 + \beta_1 \sqrt{D}$ | $-1.19$ (0.35) ** | $0.69$ (0.06) *** | $0.73$*** | $0.56$ | $-$ |
| SSZ2 | $\sqrt{Y} = \beta_0 + \beta_1 \sqrt{D}$ | $0.79$ (0.20) *** | $0.66$ (0.005) *** | $0.72$*** | $0.56$ | $-$ |
| SSZ3 | $\ln(Y) = \beta_0 + \beta_1 \ln(Mcd)$ | $-1.42$ (0.38) *** | $1.68$ (0.19) *** | $0.60$*** | $4.21$ | $1.28$ |
| SSZ4 | $\ln(Y) = \beta_0 + \beta_1 \ln(H)$ | $-1.71$ (0.56) ** | $1.57$ (0.22)* ** | $0.45$*** | $4.93$ | $1.40$ |
| **Sahelian zone (n = 44)** | | | | | | |
| SaZ1 | $\sqrt{Y} = \beta_0 + \beta_1 \sqrt{D}$ | $-3.44$ (0.64) *** | $1.06$ (0.10) *** | $0.72$*** | $0.56$ | $-$ |
| SaZ2 | $Y = \beta_0 + \beta_1 \ln(D)$ | $-60.62$ (8.23) *** | $20.04$ (2.28) *** | $0.65$*** | $5.62$ | $-$ |
| SaZ3 | $\ln(Y) = \beta_0 + \beta_1 \ln(Mcd)$ | $-3$ (0.49) *** | $2.46$ (0.24) *** | $0.72$*** | $4.22$ | $1.17$ |
| SaZ4 | $\sqrt{Y} = \beta_0 + \beta_1 \sqrt{McD}$ | $-3.62$ (0.70) *** | $2.39$ (0.24) *** | $0.69$*** | $0.58$ | $-$ |
| SaZ5 | $\ln(Y) = \beta_0 + \beta_1 \ln(H)$ | $-2.69$ (0.73) *** | $2.04$ (0.31) *** | $0.50$*** | $5.6$ | $1.33$ |
| SaZ6 | $\sqrt{Y} = \beta_0 + \beta_1 \sqrt{H}$ | $-2.59$ (0.84) ** | $1.76$ (0.26) *** | $0.52$*** | $0.72$ | $-$ |

Figure 6. Relationship between fruit biomasses of Vitellaria paradoxa estimated by 4-year mean model and year category models in three climatic zones in Burkina Faso, West Africa.
production of the species (Joubert, Smit, & Hoffman, 2013). In the present study the highest fruit production of the shea tree was generally recorded in the years with high rainfall in each climatic zone. However, an analysis with detailed climatic data derived from the 12 sites is needed in the future to clarify the real role of climatic parameters in the interannual variation in fruit production of shea tree. The effects of pollinator and predator insects could also have contributed to interannual variation in fruit production of the species. The activities of entomophilous pollinators play an important role in the fruiting of shea trees. Lamien, Diallo, Ouédraogo, and Guinko (2007b) found in the shea tree that the protected inflorescences against pollinators’ action experienced the lowest fruiting rates compared to unprotected inflorescences. Therefore, it is probable that the influence of human or natural disturbances on the populations and the activities of these insects from one year to another can affect the performance in fruit production of the species. An important spatiotemporal variation of the pollinator populations related to the influence of climatic conditions was noted in Elaeis guineensis with a direct consequence on its production (Mariau, Houssou, Lecoustre, & Ndigu, 1991). Moreover, a premature abscission of flowers and fruits was observed on shea trees infested by the predator insects of genus Salebria (Lamien, Tigabu, Dabiré, Guinko, & Oden, 2008). This suggests that years with high infestation would experience low fruit yields.

### Fruit production patterns based on climatic zones and tree size

The interannual variation in fruit production at tree individual level and the proportion of tree with high variability were higher in the Sahelian zone. This climatic zone is the most arid zone of the country and therefore, these results suggest that drier climatic conditions stimulate high individual variability in fruit production of the species. However, this variability was not correlated with tree size, suggesting it is a common characteristic in individual trees of the species. During the 4 years, the synchrony of fruit production among shea trees was relatively low with a mean interindividuals less than 50% in each climatic zone. This indicates the existence of a large range of production patterns between shea trees that is probably related to the environmental influences on fruit production or a large genetic diversity among individual trees of the species. In West Africa, a wide range of genetic diversity was observed in shea trees (Lovett & Haq, 2000; Ugese, Baijeri, & Mbah, 2010). The low level of synchrony among shea trees offers enormous possibilities to select the trees with desirable production patterns. Taking years into consideration, we found that the level of synchrony among shea trees was higher in the years of low fruit production than in the years of heavy crop within each climatic zone. This result reveals that, in each year category, the shea tree populations of each zone are dominated by the trees having an individual production lower than their 4-year mean. This suggests that the annual potential of shea nut production in a given zone is strongly dependent on a small number of trees. The results obtained confirmed this suggestion because they showed that, whatever the year, the high-yielding trees (which represent about 25% of sample trees) contributed to more than 55% of the total fruit biomass produced in each zone. By analyzing the relationship between the size of high-yielding trees and their fruit yields, positive and significant correlations were found in each zone but not for all years. This indicates that the shea tree has some potentialities of production, regardless of tree size, which could be related to the sol types or genetic variation among trees in terms of the allocation to reproduction (Davi et al., 2016). In the southern part of Burkina Faso, Boffa et al. (1996) also found that 59% of the total production of shea tree was produced by high-yielding trees.
**Tree size effect on fruit production**

Fruit production of shea tree generally increased with tree’s size in each climatic zone, independently of the year. A positive correlation between fruit production and tree size was also reported in some other tree species such as *Lannea microcarpa*, *Afzelia africana*, *Adansonia digitata* and *Sclerocarya birrea* (Haarmeyer et al., 2013; Nacoulma, Lykke, Traoré, Sinsin, & Thiombiano, 2016; Schumann, Wittig, Thiombiano, Becker, & Hahn, 2010; Shackleton, 2002).

Plants allocate their surplus energy for the reproductive allocation which generally increase with plant size (Natio et al., 2008; Wenk et al., 2015). For deciduous species as the shea tree, the initiation of flowers and growth of buds totally depends on reserve metabolites such as starch, for example which is the main reserve of carbohydrates (Lamien, 2006). Indeed, during this period, the elaboration of new carbohydrates would be highly limited because the species does not have its photosynthesis organs (i.e. its leaves). During this crucial stage, the small trees invest these carbohydrates of reserve for both vegetative growth and reproduction attributes and are therefore expected to be less productive than large trees. In addition, access to resources is essential for greater reproductive investment (Rosa, Barbosa, & Koptur, 2014). The highest fruit production observed in large trees is probably related to their greater capacity to capture sunlight (crown volume) and a correspondingly larger root biomass, which allow these trees to have access to ground water and therefore, to reduce the moisture stress (Snook et al., 2005).

**Allometric equations for estimating fruit production**

Specific climatic zone equations based on 4 years data were developed in this study to account for interannual variation in fruit production and the effect of climatic gradient. Among the tree morphological parameters measured in the field, DBH was the best predictor variable for estimating the fruit biomass of shea trees. DBH was also found as the best predictor variable for fruit number of *Adansonia digitata* and calyx weight of *Bombax costatum* (Muchiri et al., 2003; Ouédraogo, Nacoulma, Ouédraogo, Hahn, & Thiombiano, 2014). On the opposite, crown diameter and total tree height exhibited the strongest relationship with fruit yield from *Vitex payos* (Kimondo et al., 2011). This suggests the best predictor variables for estimating fruit production highly depend on species and tree architecture (shrubs, small trees and large trees). Moreover, the precision of the measurement of predictor variables is very significant in the development of allometric equations (Picard et al., 2012). In many tree species such as shea tree, the measurement of DBH is more accurate than height and crown diameter because their measurement can be subject to operator errors and therefore, they may not be the appropriate predictor variables (Kuyah et al., 2015). Equations with DBH have two advantages: DBH equations give satisfactory estimates of individual tree biomass and DBH is easily and accurately measured in the field with low time investment i.e. it is not time consuming (Zhang, Peng, Guo-Sheng Huang, & Zeng, 2016). The best predicting models were based on DBH and therefore are simple tools, easy to use in the field.

The $R^2$ values of the best predicting models in this study ranged from 69% to 73%. Lankoandé, Ouédraogo, Boussim, and Lykke (2017) who monitored fruit production from *Carapa procera* over three consecutive years in the Sudanian zone of Burkina Faso also found a $R^2$ value relatively high for the allometric equation for estimating its seed biomass ($R^2 = 70\%$ with DBH as predictor variable). These different $R^2$ values are low compared to those of species-specific aboveground biomass equations developed in many studies (Bayen, Bognounou, Lykke, Ouédraogo, & Thiombiano, 2015; Ranaivoson, Brinkmann, Rakouth, & Buerkert, 2015). In general, the relationship between fruit production and tree diameter is relatively strong. This can be explained by the influence of ecological factors on fruit production, especially pathological events (predation of fruits) and climatic conditions which can lead to the premature abscission of flowers and young fruits. Therefore, to reduce the effect of environmental factors on the performance of allometric models, the use of specific zone equations is recommended. The equations developed are valid for parkland trees with diameter ranged from 10.50 to 65.89 cm for the Sudanian zone, 10.50 to 92.93 cm for the Sudano-Sahelian zone and 16.23 to 96.13 m for the Sahelian zone. Given that the proportions of fresh pulp and dry kernel for 1 kg of fresh fruits were evaluated, these equations give the possibility to estimate simultaneously the fresh weight of pulp and the dry weight of kernels per tree.

**Conclusion**

This monitoring study of the fruit production of shea tree over four consecutive years aimed to assess the interannual variation in fruit production and understand the production patterns of the species. The combined effects of internal factors (genotype, elaboration and use of carbohydrate) and external factors (climatic conditions, predator and pollinator actions) are responsible for the interannual variation in fruit production of
shea tree. As the effects of these factors were not directly tested in this study, specific investigations are needed in the future to identify the determining factors of this interannual variation. However, the study showed that variability in tree individual level was associated to drier climatic conditions. The results revealed a low interindividual synchrony in shea trees, suggesting the existence of a relative large range of production patterns, which offers the possibility to select the trees with desirable production patterns.

For each zone considered in this study, the annual potential of fruit production of the species was strongly depending on high-yielding trees which represent about 25% of sample trees. The allometric equations developed with uncertainties of prediction are efficient tools to estimate average fruit biomass of shea tree as well as those in the years of lowest and highest production. These equations are valid for parklands and specific climatic zones. The actors of the shea industry involved in the production can use these tools to assess the annual potential of NTFPs of shea trees available in their parklands in order to optimize the production and assess associated income. This will directly encourage more active parkland management, maintenance and enrichment. Moreover, the findings of this study could be used as the basis in the formulation of strategies for the sustainable management of shea trees in West Africa and can serve to improve regional models. At national level, study on the shea tree population stands is advisable to have detailed information concerning tree density and tree dendrometric parameters to assess the national potential of fruit production on the basis of reliable field data.

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