

## Reproductive ecology of *Coula edulis* Baill., source of a valuable non-timber forest product

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**Abstract:** The reproductive ecology of *Coula edulis* (Olacaceae), source of a highly valuable non-timber product for African populations, has been investigated on a large tree sample size in a Gabonese forest for a 3-year period, in order to propose options for its domestication. Reproduction is annual and the minimum tree diameter for flowering was 10.6 cm while the diameter for regular fructification was 23 cm. The annual diameter increment (ADI; mean = 0.22 cm year<sup>-1</sup>) was affected by crown exposure, but not by initial tree diameter or fruit production. Tree diameter influenced fruiting frequency and fruit production. There was a strong correlation between fruit production of 2011 and 2012 (Pearson's  $r = 0.85$ ;  $P < 0.001$ ), suggesting a high heritability of that trait. Phenotypical selection should be performed prior to any propagation activity. Moreover, as most of *C. edulis* fruits were sterile (64 %), we propose that silvicultural strategies should be based on vegetative propagation.

**Resumen:** La ecología reproductiva de *Coula edulis* (Olacaceae), fuente de un producto no maderable con gran valor para poblaciones africanas, fue investigada en una muestra grande de este árbol en un bosque de Gabón durante un período de tres años, con el fin de proponer opciones para su domesticación. La reproducción es anual y el diámetro mínimo del árbol para la floración fue de 10.6 cm, mientras que el diámetro para la fructificación regular fue de 23 cm. El incremento anual en diámetro (IAD, con una media = 0.22 cm año<sup>-1</sup>) se vio afectado por la exposición de la copa, pero no por el diámetro inicial del árbol o de la producción de frutos. El diámetro del árbol tuvo un efecto en la frecuencia de fructificación y la producción de frutos. Hubo una correlación fuerte entre la producción de frutos de 2011 y 2012 ( $r$  de Pearson = 0.85,  $P < 0.001$ ), lo que sugiere una alta heredabilidad de ese rasgo. La selección fenotípica debe ser realizada antes de cualquier actividad de propagación. Además, como la mayoría de los frutos de *C. edulis* fueron estériles (64 %), proponemos que las estrategias silvícolas deben basarse en la propagación vegetativa.

**Resumo:** A ecologia reprodutiva de *Coula edulis* (Olacaceae), fonte de um produto não-

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lenhoso de alto valor para as populações africanas, foi investigada numa grande amostra de árvores numa floresta do Gabão, por um período de 3 anos, a fim de propor alternativas para a sua domesticação. A reprodução é anual eo diâmetro mínimo da árvore para a floração foi 10,6 cm, enquanto o diâmetro para frutificação normal era de 23 cm. O incremento anual de diâmetro (ADI; média = 0,22 cm ano<sup>-1</sup>) foi afetado pela exposição da copa, mas não pelo diâmetro inicial da árvore ou pela produção de frutos. O diâmetro da árvore influenciou a frequência da frutificação e a produção de frutos. Encontrou-se uma forte correlação entre a produção de frutos de 2011 e 2012 ( $r$  de Pearson = 0,85,  $P < 0,001$ ), o que sugere uma alta heritabilidade dessa característica. A seleção fenotípica deve ser realizada antes de qualquer atividade de propagação. Além disso, como a maioria dos frutos da *C. edulis* foram estéreis (64 %), propõe-se que as estratégias silvícolas devem ser baseadas na propagação vegetativa.

**Key words:** Diameter growth, fruit production, phenology, NTFP, tropical rainforest.

## Introduction

For centuries, non-timber forest products (NTFPs) have played a considerable role for rural people inhabiting tropical rainforest zones, by providing them with food and trade products (FAO 2010; Hill *et al.* 2007; Moupela *et al.* 2011). Despite their importance, NTFPs have received little attention by ecologists as they are economically less important than timber products (Aiyelaagbe *et al.* 1998; Anebeh *et al.* 2003; Atangana *et al.* 2001; Debroux 1998; Guariguata *et al.* 2010; Guedje *et al.* 2003). As a result, there is a real risk of loss of certain NTFPs due to unsustainable harvesting, especially taxa with a small or restricted spatial range. Domestication initiatives can prevent such a loss as they aim to integrate NTFPs into farming systems; thus reducing the pressure on natural forests (Atangana *et al.* 2001; Kanten & Beer 2005; Leakey & Simons 1998). While providing food and a diverse range of other products to farmers, agroforestry practices can also generate substantial cash for households. As domestication requires a perfect command of the propagation mechanisms of the target species, prior knowledge of its natural reproductive system is essential (Simons & Leakey 2004). If efficient, the natural regeneration process may simply be encouraged for establishing artificial plantations in crop lands.

In the African rainforest, plant taxa with NTFP value that have been studied are generally those with a high commercial potential internationally, such as *Baillonella toxisperma* Pierre, *Garcinia lucida* Vesque, *Dacryodes edulis* Lam., *Irvingia gabonensis* Baill. and *Prunus africana* Hook. In contrast, the African walnut, *Coula edulis* Baill., may appear less interesting

since its harvestable non-timber products are generally marketed only at a national scale, and it has a limited distribution range. It occurs only in the Guineo-Congolian evergreen rainforests in West and Central Africa (Tchiegang *et al.* 1998). However, *C. edulis* is undoubtedly very important for Central and West African populations, as the seeds are much appreciated by local people (Moupela *et al.* 2011).

Despite the regional importance, *C. edulis* is still considered as a wild tree species, and only scarce information is available about its reproductive ecology and population dynamics (reviewed by Moupela *et al.* 2011). Specifically, documented topics comprise botanical descriptions (Adam 1971; Adriaens 1951; Aubréville 1959; Louis & Léonard 1948; Villiers 1973; Vivien & Faure 2011), some propagation methods (Bonnéhin 2000; De La Mensbrugge 1966; Miquel 1987) and its use by local populations (Ekop & Eddy 2005; Fort *et al.* 2000; Van Neer & Clist 1991). The topics that have not received attention so far regarding this taxon and relevant aspects for domestication processes include characterization of its natural reproductive ecology, its fruit production potential and the factors, which determine fruiting characteristics.

The present work aimed to characterize the natural reproductive patterns and fruit production potential in *C. edulis* in an evergreen forest of Gabon. Specifically, the study aimed to: (1) describe the reproductive phenology of the focal species, (2) record fruit and seed characteristics and fruit production over two years, and (3) assess relationships between dendrometric tree traits (tree growth and crown exposure), reproductive phenology and fruit production.

## Material and methods

### *Study species*

*Coula edulis* (Olacaceae) is commonly called African walnut or Gabon nut. Its distribution extends from Sierra Leone to the Democratic Republic of Congo (Vivien & Faure 2011). It displays a dependence on the evergreen forest zone (Vivien & Faure 2011), prefers clayey soils (Sosef *et al.* 2004) and can be found in the forest understorey as well as in the top canopy, with an average adult diameter of 100 cm and a height of 30 m.

The African walnut plays an important role in the local economy (Bonnéhin 2000; Bukola & Kola 2008; Johnson & Johnson 1976; Schnell 1957); its wood is renowned for resistance to termites and is used locally in construction; its seeds contain a sweet and odorless yellow oil with a high nutritive value (Adraïens 1951; Busson 1965; Louis & Léonard 1948; Tchiegang *et al.* 1998); and its bark is used in traditional medicine as a purgative and for treatment of back pain (Tamokou *et al.* 2011; Walker & Sillans 1995). Cirad (2008) suggested that the wood of *C. edulis* could be of economic interest in the future.

### *Study site*

The study was conducted in the forest concession managed by the logging company Precious Woods Gabon, located near Lastourville, southeastern Gabon, between 0° 30′–1° 00′ S and 12° 30′–14° 0′ E (Fig. 1). The vegetation is a typical evergreen forest dominated by Caesalpiniaceae and Burseraceae (White 1986). The climate is equatorial, with two high-rain seasons (March–May and September–December; thereafter called “wet” seasons) and two seasons with less rainfall (June–August and January/February; hereafter called “dry” seasons). Annual rainfall is 1,700 mm and average annual temperature is around 26 °C, with peaks from February to April and minimum temperatures in July/August.

The dominant soil-type is a yellow lateritic derived from a hydrolyzed substratum in which most of the bases are exported. These soils display a low chemical level of fundamental components, but physical properties are suitable when the clay content is high enough (Martin *et al.* 1981).

### *Phenological monitoring and assessment of diameter growth*

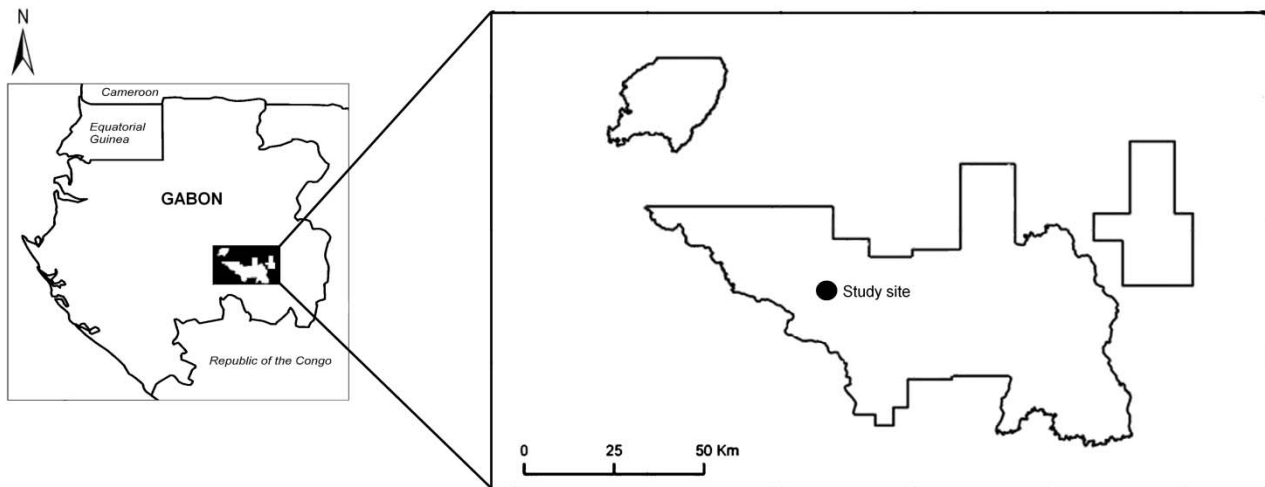
A total of 150 trees with a diameter at breast height (dbh)  $\geq$  5 cm were monitored. Phenological

observations were recorded once per month from March 2009 to July 2012 (40 months). Each month, a team of three local technicians used a semi-quantitative method to estimate the intensity of phenophases, using binoculars to observe the percentage of the crown covered by each organ type: leaves, flowers and fruits (e.g. Bentos *et al.* 2008; Bourland *et al.* 2012; Engel & Martins 2005; Tesfaye *et al.* 2011). For each organ, values provided by the three observers were averaged to obtain the estimate of phenophase intensity. In addition, to minimize inter-observer variance, the same team of technicians conducted all phenological observations throughout the 3-year study period.

Annual diameter measurements were obtained for a subsample of 130 trees (Table 1). We excluded 20 trees from the 150 individuals sampled for phenological observations since their trunks had major defects. Diameter was consistently measured by the same technician, using the same diameter tape. The measurement line on the tree trunk was delimited by two painted bands. The annual increment in stem growth was estimated by the difference in diameter of the last and the first measurements (cm) divided by time (years). In order to assess the impact of crown position (*sensu* Dawkins 1958) on growth, the method suggested by Moravie *et al.* (1999) was used. This method is based on the codification proposed by Dawkins (1958) and Synnott (1979). The value assigned to a tree depends on its exposure to sunlight. Moravie *et al.* (1999) and Gourlet-Fleury (1998) demonstrated the reliability of this codification (analogous to crown illumination index) in estimating the quantity of light received by a target tree crown.

### *Fruits of Coula edulis and their characteristics*

The total fruit biomass of *C. edulis* individuals was assessed for two consecutive fruiting seasons (2011 and 2012), from December to April (corresponding to the yearly period of fruit production), based on a sample of 25 adult trees of different diameters. These met all the following criteria: (i) the trees were isolated and selected from 130 individuals monitored for diametric growth and (ii) the adult trees did not occur in areas accessible to local populations. Each of these sampled trees was far enough away from other conspecific trees (minimum 30 m) that fruits found beneath a target crown were sure to have come from that focal tree. A plastic circular collector as large as the crown



**Fig. 1.** Location of the study site in a logging concession, Gabon.

**Table 1.** Diameter structure of sampled trees and parameters of mean fruit production (standard error).

Diameter class	Number of trees (N)		Number of mother trees sampled		Fruit mass (kg tree <sup>-1</sup> )		Number of fruits tree <sup>-1</sup>	
	Phenology	Growth diameter	2011	2012	2011	2012	2011	2012
[5-10 cm]	23	22	0	0	0	0	0	0
[10-20 cm]	29	28	6	6	1.8 (0.8)	4.3 (1.6)	62 (31)	135 (48)
[20-30 cm]	27	26	7	7	19.2 (4.7)	20.6 (4.9)	578 (160)	600 (161)
[30-40 cm]	25	21	6	6	60.1 (13.4)	48 (7.3)	2048 (492)	1544 (292)
≥ 40 cm	46	33	6	6	92.4 (51.2)	67.4 (31.1)	3207 (1808)	2810 (1209)
Total	150	130	25	25	42.2 (13.3)	36 (8.8)	1438 (470)	1246 (335)

surface was installed about 1 m above the ground, to avoid predation from terrestrial animals. The following data were gathered every week for each collector: (1) the total number and weight of all fruits, (2) the total weight of fresh and intact fruits, (3) the proportion of fruits without kernel (sterile fruits), based on a random subsample of 50 fruits/tree (a total of 1,250 fruits), and (4) the proportion of fruits displaying insect damage, based on a random subsample of 10 fruits/tree (250 fruits in total). Points (3) and (4) were conducted only in 2011.

Finally, we selected 10 intact fruits from each of 14 mother trees for a detailed characterization of fruit physical traits. For each fruit and its nut and kernel (the latter being dried before characterization), we recorded: (1) mass, using a precision scale, (2) length and width (median diameter), measured with a caliper.

### *Data analysis*

Following the description of each phenological phase, the different diameter thresholds for the onset of fertility (sexual maturity of trees) and fructification were determined. The minimum diameters for fertility (MDFe) and fructification (MDFr) correspond to the minimum stem diameters for which flowers and fruits were observed, respectively. The relationship between stem diameter and probability of fruiting, at least, once over a three-year period was established using a binary logistic regression. The relationship between diameter and frequency of fruiting was tested with a Kruskal-Wallis non-parametric analysis of variance (ANOVA), to compare the average diameter of four expected productive groups (trees with dbh > MDFr): (1) those that did not bear fruit, *T0*; (2) those that produced fruit once in three years,

*T1*; (3) those that bore fruit twice in three years, *T2*; and finally (4) those that bore fruit three times in three years, *T3*. A pairwise comparison of groups was then performed using the Mann-Whitney test.

For each tree, the mean annual diameter increment (ADI), over three years, was calculated, and the influence of initial diameter and crown exposure on ADI was tested by performing a linear regression and analysis of covariance (ANCOVA), respectively, assuming that diameter is the covariate of the crown exposure parameter for the latter. Variation in ADI between years was tested using an ANCOVA with repeated measures. To verify a possible impact of fruiting frequency on stem growth, ADI of the different fruiting groups (*T0*, *T1*, *T2* and *T3*) was compared. For that, we performed an ANCOVA and specified tree diameter as the covariate of fruiting frequency. Along the same lines, we performed a linear regression between individual ADI and fruit production for testing the hypothesis that with more resources allocated to reproduction tree growth will be less.

A biometric characterization of the diaspore traits (fruits, kernels and nuts) was carried out. We then presented a correlation matrix illustrating at which extent a given organ can be estimated from the others.

The statistical analyses were carried out with the STATISTICA version 6.0 program. Mean values of different parameters were provided with their standard errors.

## Results

### *Phenological spectrum and reproductive demography*

As the African walnut is an evergreen species, leaves are abundantly present in the crown regardless of climatic season. The renewal of older leaves is continuous, though more pronounced during the long dry season (June-August). Leaf cover peaks during the wet seasons.

Flowering and fruiting are regular and annual in *C. edulis* (Fig. 2). At individual level, these two reproductive phases last on average  $46 \pm 34$  days and  $76 \pm 47$  days, respectively. Flowering peaks in November or December, but total flowering time can encompass a 6-month period, from July to January. The end of the dry season from February to March corresponds with the period of greatest fruit production.

Flowering was observed in individuals with a minimum diameter of 10.5 cm (MDFe). However,

mature fruits were observed only on individuals of at least 12.3 cm diameter (MDFr). The probability of an individual being able to produce ripe fruits can be estimated from Fig. 3; this suggests dbh  $\approx$  23 cm is the most probable minimum size for bearing ripe fruits (with a probability  $> 95\%$ ), at least once during three years (Fig. 3). Therefore, dbh of 23 cm may be considered a reliable estimate of the diameter for regular fructification.

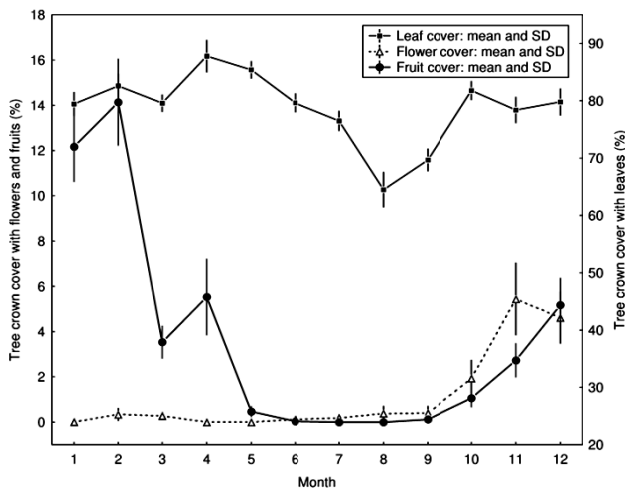
Fruiting frequency was affected by tree diameter (ANOVA K-W,  $H = 30.24$ ,  $P < 0.0001$ ). A pairwise comparison showed that there is no significant difference between the three first categories (*T0*, *T1* and *T2*). Trees that produced fruit every year had significantly greater diameters than the other trees: dbh =  $38.9 \pm 15.2$  cm versus  $19.9 \pm 7.0$  cm.

### *Diameter growth and interaction with other tree traits*

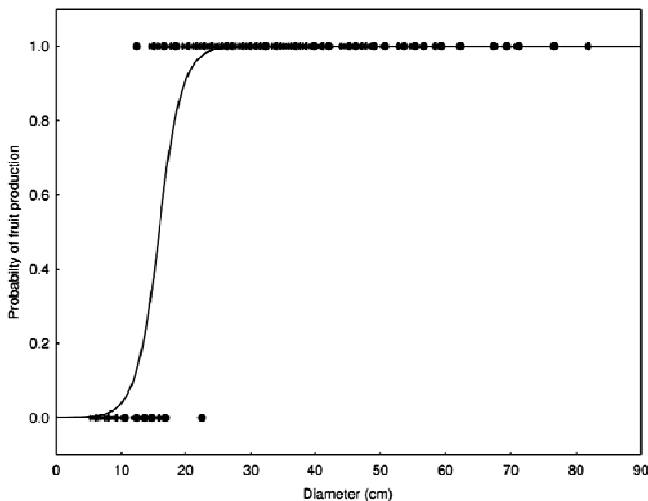
Overall, the mean ADI (130 individuals, 3-year measurement period) was  $0.22 \pm 0.2$  cm<sup>2</sup> year<sup>-1</sup>. Pearson's correlation revealed no significant relationship between initial tree diameter and ADI ( $r = 0.149$  and  $P = 0.097$ ). However, crown exposure influenced diameter growth (ANCOVA,  $F_{5,117} = 3.63$ ,  $P = 0.004$ ). The pairwise comparison highlighted a significant difference between categories 2c (least exposed) and 2b (grouping of highly exposed individuals) (Fig. 4). ADI significantly varied from one year to another (repeated ANOVA;  $F_{3,120} = 55.78$  and  $P < 0.001$ ). Repeated Student's *t* test showed that growth in year 2 was significantly different from the two other years. Finally, fruiting frequency did not affect annual diameter increment (ANCOVA;  $F_{3,77} = 0.96$  and  $P = 0.415$ ).

### *Fruit production and interaction with tree size parameters*

Mean fruit cover ranged from 21 % in 2012 to 38 % in 2011. As expected, fruit production followed the same trend, with  $36.0 \pm 8.8$  kg tree<sup>-1</sup> in 2012 versus  $42.0 \pm 13.3$  kg tree<sup>-1</sup> in 2011. The yearly number of fruits per tree also varied from 1246 to 1438 on average (Table 1). Fruit production significantly correlated with tree diameter, with Pearson's correlation coefficients ranging from 0.70 to 0.75 (Fig. 5). In addition, there was a significant correlation between yearly fruit production at an individual level: trees that gave the lowest amount of fruit in 2011 did similarly in 2012, while the best producers in 2011 maintained their status in 2012 (Pearson's  $r = 0.85$ ;  $P < 0.001$ ). But there was



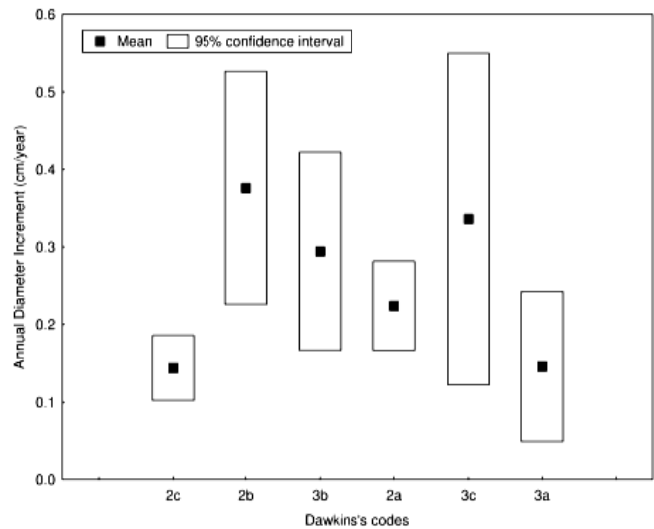
**Fig. 2.** Phenology dynamics. Months: 1 = January; 2 = February; etc.



**Fig. 3.** Probability of fructification according to diameter. Logistic regression:  $y = e^{(-8.62 + 0.54x)} / (1 + e^{(-8.62 + 0.54x)})$ ; where  $y$  = probability of fructification, and  $x$  = diameter of the tree (cm).

no relationship between diameter increment and average fruit production over the two years (Pearson's  $r = 0.34$ ;  $P = 0.098$ ).

Thorough measurements of 140 fruits revealed a mean mass of  $38.5 \pm 7.7$  g with a mean length of  $4.0 \pm 0.3$  cm and diameter  $3.8 \pm 0.2$  cm. Each kernel weighed  $21.3 \pm 3.7$  g on average with a length of  $3.6 \pm 0.2$  cm and diameter  $3.0 \pm 0.2$  cm. The nuts presented a mean individual weight of  $7.4 \pm 1.5$  g with length  $2.0 \pm 0.13$  cm and diameter  $1.8 \pm 0.12$  cm. Simple correlation between these characters showed that all are significantly correlated (an example of the mass of the different organs was given in Table 2). We also noted that



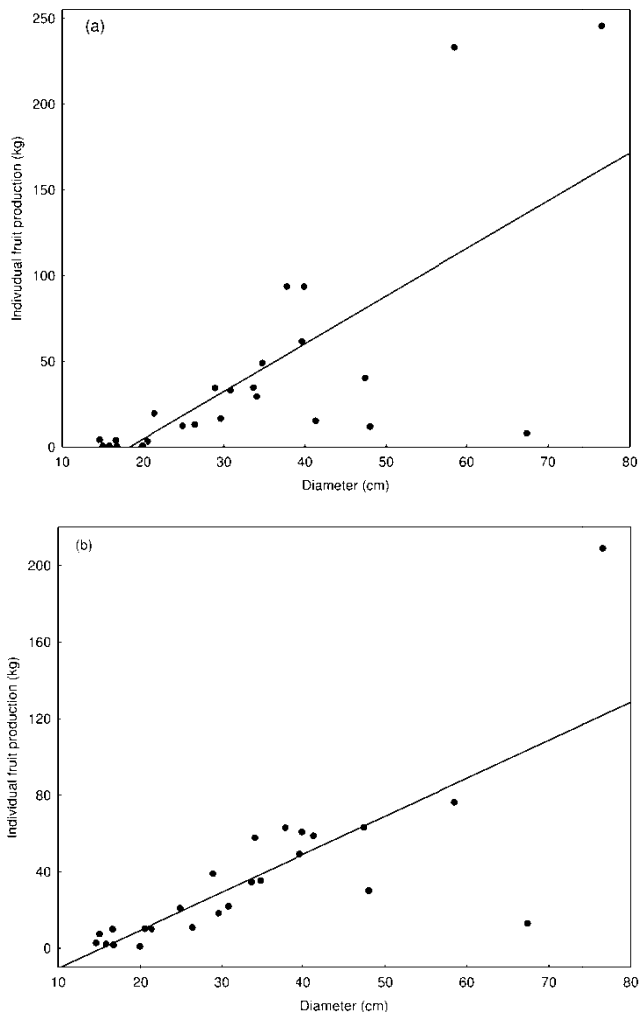
**Fig. 4.** Growth following the Dawkins code (adapted from Moravie *et al.* 1999). The arrangement of the codes follows a gradient of exposure of the crowns to sunlight.

tree diameter did not influence the average individual mass of fruit, kernel and nut (Table 3).

A notable proportion of *Coula* fruits were attacked by insects (56%), resulting in many holes in the kernel. In some cases, the kernel was entirely destroyed, and became mealy. There was no significant correlation between tree size and occurrence of damaged fruits (Pearson's  $r = -0.19$ ;  $P = 0.339$ ). We also observed that pollination does not appear to be efficient in the study population: 64% of non-damaged fruits sampled appeared to be sterile, as the kernel was lacking. The proportion of "empty" fruits was significantly greater in trees with higher values of dbh (Pearson's  $r = 0.42$  and  $P = 0.037$ ).

## Discussion

This is the first description of its type for *Coula edulis*, an important NTFP-producing tree species for West and Central African human populations. Ideally, studies of phenology, diameter growth or fruit production require mid- to long-term observation periods in order to take into account influences of climate. However, long-term investigations are challenging in tropical rainforest conditions, and only a small proportion of studies are able to provide such data. The present work, based on data collected over a 3-year period and comprising a large sample size, is, therefore, highly valuable.



**Fig. 5.** Relationship between biomass of fruit produced and diameter of the adult tree (a) in the year 2011 ( $r^2 = 0.49$ ;  $P = 0.001$ ) and (b) in the year 2012 ( $r^2 = 0.58$ ;  $P < 0.001$ ).

#### Phenology of *C. edulis*

Hecketsweiler (1992) was the first to describe the phenology of *C. edulis* in the Impassa forest of Gabon. His results were based on 15 trees with a dbh  $\geq 19$  cm. Hecketsweiler (1992) observed that a partial leaf-shedding occurs during the longest dry season (June to August). The results of the present study confirm this, and also show that previous studies using small sample sizes with a high diameter threshold were inadequate for understanding the reproductive ecology of the African walnut. *Coula edulis* regularly bears ripe fruits from 23 cm of dbh, but fruit production can occur in smaller trees, to dbh of 12 cm. This information is essential for farmers interested in planting this tree species in crop land. One may

note that although *C. edulis* is a typical plant of evergreen forests, the peaks of flowering and fruiting appear to be sensitive to some climatic inductions because they match climatic seasons or transition periods: the end of a wet season for flowering (November/December), and the end of a dry season for the fruiting peak (February/March). A number of authors have documented the possible influence of various climatic factors on flowering and fruiting rates in the tropical equatorial zone. In Gabon, Hecketsweiler (1992) reported that 63–71 % of tree species in our study region have reproductive timing similar to that of *C. edulis*. In the southern part of Cameroon, Mbarga *et al.* (1999) also noted that fruit ripening of tree species presents two peaks, with one in March. This trend was confirmed in other species-specific studies [e.g. Kouadio (2009) for *Mansonia altissima* Chev., Dainou *et al.* (2012) for *Milicia excelsa* Berg].

Reproductive phenophases depend on climate and intrinsic physiological cues. However, the exact climatic factors under the onset of those phenomena remain obscure (Debroux 1998). Khan *et al.* (1999) suggested changes in rainfall or temperature to be the main factors influencing fruiting. Others (Anderson *et al.* 2005; Bollen & Donati 2005; David *et al.* 2012; Rojas-Robles & Stiles 2009; White 1994) have proposed that relative humidity, day length and solar radiation may constitute the triggers of initiation of flowering and fruiting. The difficulties incurred in disentangling the role of each factor may be because most of these studies only considered some of the potential influencing factors for their specific analyses. In addition, several climatic variables inter-correlate, meaning that testing the determinants of reproductive phenology requires unbiased and powerful methods of analysis. In our case, we were not able to determine the climatic cue, which may explain flowering or fruiting initiation in *C. edulis*. We had monthly rainfall data for the study area, but because phenophases are annual in *C. edulis*, many years of monitoring would be necessary for testing relationships between changes in rainfall and the start of phenophases.

Knowledge of the duration of reproductive phenophases and associated plant requirements is important for the development of agroforestry strategies, in order to schedule diaspore collection and to plan crop rotation. Fruiting in *C. edulis* can last up to six months; similar to other animal seed-dispersed plant species from the same region (e.g. see Debroux 1998). Theoretically, the selective

**Table 2.** Correlation coefficients ( $r$ ) between three fruit components: mass of the entire fruit, the kernel and the nut \*\* and \*\*\* indicate significant correlations (Pearson's  $r$ ).

	Fruit mass	Kernel mass	Nut mass
Fruit mass	-	0.516***	0.321***
Kernel mass	-	-	0.245**

**Table 3.** Correlation coefficient ( $r$ ) between tree diameter and mean weight of the entire fruit, the kernel and the nut.

Parameters	$r$	$P$ -value
Fruit mass	-0.006	0.945
Kernel mass	0.017	0.841
Nut mass	-0.086	0.327

pressure against individuals to reproduce at peak moments has been proposed as an explanation for long flowering and fruiting periods in plants (Ollerton & Lack 1992). This theory could apply to the case of *C. edulis*: although we did not record the temporal dynamics of predation incidence, it is likely that fruit predation or dispersal will mostly occur at the peak of fruiting, as is the case for the majority of animal-dispersed plant species (Aizen 2003; Howe & Smallwood 1982; Tadwalkar *et al.* 2012). As most frugivorous animals interested in *C. edulis* fruits act as predators rather than dispersers (Moupela, submitted), diaspores produced at fruiting peak may not be selectively favored, leading to the persistence of a large variance in flowering and fruiting times, as described for other species (Nyiramana *et al.* 2011; Beaune *et al.* 2012).

*Annual diameter increment (ADI):  
determinants and interactions with tree  
characteristics*

The annual diameter increment of *C. edulis* was low (0.22 cm year<sup>-1</sup>), as is that of *Garcinia lucida* (0.1 cm year<sup>-1</sup>, Guedje *et al.* 2003), which is also an understorey NTFP-producing tree species of tropical forests. In general, shade-bearing woody plants have a slower growth rate than canopy tree species (mostly light-demanders). In the case of *C. edulis*, diameter growth was not influenced by either initial tree diameter or fruit production. The former result concurs with the findings of Gourlet-Fleury (1998) who demonstrated that in general, initial diameter be used to predict diameter incre-

ment. However, the latter result was surprising: as Fenner (1998) showed, efficient reproduction generally occurs to the detriment of diameter growth. It should be emphasized that for the purpose of the present study, we considered fruit production to reflect reproductive effort, and stress that flowering effort should also be included. Even in cases where flower cover could represent reproduction, in the global equation to quantify individual reproductive effort, the relative importance of flowering and fruiting is unknown. We acknowledge and stress that fruiting effort is not always analogous to reproductive effort. On the other hand, we found that ADI was influenced by crown exposure of the tree: the least exposed trees displayed the lowest growth values. While this result was in accordance with several other studies (e.g. Dyer *et al.* 2010; King *et al.* 2005), it highlighted uncertainties regarding light requirements of *C. edulis* reported by Doucet (2003): a shade-bearing tree species typical of mature evergreen forest should present greater growth at understory stage than at canopy level.

Based on an ADI of 0.22 cm year<sup>-1</sup>, it would take approximately 104 years for an individual to reach the regular diameter for fructification (23 cm) in natural conditions. Assuming that this natural growth pattern would not significantly change in a farming environment, vegetative propagation techniques (stem cutting, grafting, layering, etc.) for domestication are recommended, as they generally accelerate both vegetative and sexual maturity processes (Meunier *et al.* 2008).

*Fruit production: perspectives for agroforestry*

This study was the first to extensively characterize fruit production and fruit traits of *C. edulis*.

Fruit production significantly varied between individuals and between years. We note that our estimates could have been biased by fruit consumption from arboreal rodents before diaspores fell beneath mother trees. Fruit production is also under genetic influence, and more than flowering for example (Nanson 2004), and this is evident here as the correlation coefficient between years was high and significant (Pearson's  $r = 0.85$ ). This assertion requires further investigation, in order to determine the heritability of the trait; but we assume fruiting parameters to be highly heritable in *C. edulis* as they are in most of plant species (McCarthy & Quinn 1990). Therefore, for agroforestry purposes, trees



should be selected on the basis of favorable fruiting characteristics compared to other individuals from the same population. Ideally, candidate trees should have similar diameters to prevent a biased selection work due to the significant correlation between tree diameter and fruit production (see also Anderson *et al.* 2005; Takenoshita *et al.* 2008; Zardo & Henriques 2011) (otherwise, the majority of selected individuals would be simply the larger ones).

Unlike the observations of Hecketsweiler (1992) and Loung (1996), *C. edulis* seems to be a highly productive species with a regular fruiting rate in Gabon. Nevertheless, a significant proportion of diaspores are subject to insect attack which can reduce their economic value. Moreover, more than 60 % of the fruits appeared to be sterile. This is likely to be the main difficulty for mass production of *C. edulis* by sowing in agroforestry systems. Undoubtedly, vegetative propagation is necessary to domesticate the African walnut.

The average sizes of fruits, kernels and nuts observed in Gabon were similar to those indicated for other African countries (Aubréville 1959; Villiers 1973; Vivien & Faure 2011). Although tree diameter determined the total fruit production per individual, it did not influence the average mass of each fruit. Similar observations have been made for *Irvingia gabonensis* Baill. in Cameroon (Atangana *et al.* 2001).

## Conclusions

The African walnut is an important resource for people in Central and West Africa, making it a valuable candidate for domestication. Our study constituted the first overview of the reproductive ecology of *C. edulis*, with a special emphasis on aspects pertaining to agroforestry. We revealed that, as with most rainforest tree species, *C. edulis* can become sexually mature at small diameters. But this might be due to a low annual diameter growth, meaning that the youngest flowering *C. edulis* trees are as old as those of other taxa, which display greater diameter increments. We also found interactions between phenology, tree size parameters, diameter growth and fruit production. For example, it should be borne in mind that the number of fruits produced per tree seems to be highly heritable, but this suggestion requires further investigation. For agroforestry purposes, vegetative propagation methods should be tested in the future, since sowing is not likely to provide good results and the majority of seeds are

naturally sterile. In addition, vegetative propagation maintains tree characteristics while accelerating flowering and fruit production.

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