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Research Article

Influence of geographic provenance on phenotypic variation in seed and kernel traits of the African oil tree from southern Benin and implications for species breeding

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Abstract

Knowledge of oilseeds plants' traits and features is fundamental to understanding the natural selection process and improving conservation programs through species selection. As a forest oilseed, *Ricinodendron heudelotii* is the object of growing interest among value chain actors, who are increasingly interested in its intrinsic characteristics. To date, there is a lack of information on plant morphological traits for the selection of the best genotype, especially as far as seed and kernel traits are concerned. The aim of this study was to make a typology and establish the relationship between seed and kernel traits of *Ricinodendron heudelotii*, depending on provenances represented by wild populations of trees in southern Benin. We sampled the provenances constituted equally and per tree, ten random samples each of fruits, seeds, kernels, and shells were collected for measurement. Hierarchical classification, common component analysis, Pearson's, and Chi-square association tests were performed for statistical analysis. Substantial variation between seed and kernel traits was observed between and within provenances. High coefficients of variation for the quantitative descriptors (length, width, and mass) of seeds and kernels appear to be the essential traits that discriminate the plant into two morphotypes. Furthermore, seed and kernel characteristics show a significant positive correlation with these discrimination criteria. The upper morphotype contains accessions from three provenances with huge seeds and kernels but few seeds per fruit, while the lower morphotype includes the other provenances with tiny seeds and kernels. The results of the study provided essential information that could be an avenue for improvement with further biochemical and molecular characterization studies.

Keywords: accessions; domestication; forest products; maps; mass; multipurpose tree; provenances

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Introduction

The conservation of the diversity of genetic resources for food and their sustainable use for food security and well-being of present and future generations is a global priority (Pilling *et al.*, 2020; FAO 2022). Phenotypic diversity is the result of the expression of a genotype in interaction with environmental factors. Phenotypic variation is used by farmers to identify preference traits in individuals of a priority wild species in the domestication process (Weltzien *et al.*, 2019; Nakyewa *et al.*, 2021) and is essential for natural selection and the evolution of plant communities. Morphological traits of seeds are valuable tools for quantifying diversity (Rimlinger *et al.*, 2020; Di Santo *et al.*, 2021) and are also used in the life history and restoration of forest species (Wang *et al.*, 2014; Barak *et al.*, 2018; Lovas-Kiss *et al.*, 2020). In addition, seeds are among the reproductive, highly heritable traits that are valuable in selecting parent plants (Bawa, 2016). Therefore, the study of these traits is a priority for establishing breeding programs and conserving the genetic diversity of forest species.

Ricinodendron heudelotii (Baill) Pierre & Ex. Heckel (Euphorbiaceae) is a dioecious forest oilseed species, endemic to central and western Africa and Madagascar (Plenderleith, 1997). Still called the African wood-oil nut tree, there are two geographically different variants, *R. heudelotii* subspecies *heudelotii* occurs in West Africa from Ghana to Benin, and subspecies *africanum* occurs from Nigeria, Uganda, Sudan, Tanzania, Angola, Mozambique, and Madagascar through Cameroon, Gabon, Equatorial Guinea, the Central African Republic, Congo, the Democratic Republic of the Congo, and Zambia (Tchoundjeu and Atangana, 2006; Pax and Hoffman 1911; Leonard, 1961). Morphologically, the *africanum* subspecies has two fully mature seeds, while the *heudelotii* subspecies has three seeds per fruit, with one immature seed (Leonard 1961). Seeds contains kernels used as spices in sauces; kernels are rich in oil (43.1-67%), carbs (6.11-8.83%), and protein (49.9-65.2%) [(Manga *et al.*, 2000; Coulibaly *et al.*, 2018; Yirankinyuki *et al.*, 2018; Kinge et al., 2019); Sharapov, 1959)]. Kernel's oil has high nutritional value (Kouame *et al.*, 2008; Vroh *et al.*, 2014; Ouattara *et al.*, 2016, therapeutic and antihypertensive properties (Olasehinde *et al.*, 2016; Sut *et al.*, 2020). It is also used in the coating industry (Assanvo *et al.*, 2015; Yirankinyuki *et al.*, 2018; Edja *et al.*, 2015); or in the manufacture of soap and varnishes (Ekam, 2003). The production and marketing of kernels is growing, for example, between 2013 and 2015, 13.17 t of the 65.8 t produced in South West Cameroon were sold on local markets and in Nigeria for €33,511 (Tabuna *et al.*, 1999; Cosyns *et al.*, 2011; Ndumbe *et al.*, 2018). Therefore, kernels are very important and constitute the main organ of economic interest in *Ricinodendron heudelotii*.

In Benin, *Ricinodendron heudelotii* is an important plant genetic resource, occupying the 2nd place among priority oilseed trees (Hounsou-Dindin *et al.*, 2022). It is restricted to two phytogeographic zones, Pobè and Borgou-Nord (Akoègninou *et al.*, 2006), and is the most abundant (77.6%) in the tree stratum of the semi-deciduous forest of Pobè (Sokpon 1995). It has been reported that between 2005 and 2015, the rate of disappearance of natural formations in Benin estimated at 2.2% each year (Mama *et al.*, 2020). Currently, several studies have reported that the species is subject to serious threats linked to the massive exploitation of the trunk in the manufacture of Guèlèdè masks (Boko-Haya *et al.*, 2017; Moussa *et al.*, 2020). These constraints have meant that the species very rare in open woods, and its exploitation has already reached protected forests at the request of the royal authority (A. Badou, CRAPP, personal communication, September 2018). This human-induced habitat degradation and disturbance has a detrimental effect on the genetic diversity of species, with the possibility of extinction in small populations (Holsinger 2000; Helm *et al.*, 2009; Schlaepfer *et al.*, 2018; Dudley and Alexander, 2017; Jiang *et al.*, 2018). To avoid the genetic extinction of *R. heudelotii*, knowledge of the phenotypic variability available within populations of this threatened species is a fundamental step in establishing effective breeding and conservation programs.

Previous work has revealed that the number of seeds per fruit varies from one to five (Fondoun *et al.*, 1999; Mpeck *et al.*, 2003; Eyog Matig *et al.,* 2006), with significant variation in fruit and seed mass (Nehemiah *et al.*, 2007). As a result, the relationship between phenotypic characteristics of fruits and seeds is tenuous

(Mpeck *et al.*, 2003; Tchoundjeu and Atangana 2006), which is a handicap in predicting seed production from fruit morphological traits in farmers (Ayuk *et al.*, 1999; Franzel *et al.*, 2007). Due to its woody endocarp being very hard and adherent to the kernel, and therefore very difficult to extract intact, information on the intrinsic quality characteristics of the kernels and on the seed-kernel relationship is lacking. Kernel quality is of paramount importance in the production and marketing of nut fruits. In a collection of *R. heudelotii* seeds, farmers and breeders are interested in morphometric characteristics and the seed-kernel relationship, while consumers are interested in kernel colour because of the importance of these traits in the value chain. For example, the size, colour, and shape of shea kernels are important criteria for purchasing, processing, and treatment equipment designs but also priority criteria in plant breeding programs (Honfo *et al.*, 2012; Nde *et al.*, 2016; Agúndez *et al.*, 2020). Therefore, it is important for farmers, buyers, and processors to know the intrinsic characteristics of the seeds and kernels for better valorization of the species.

Knowledge of the morphological characteristics of the seeds and kernels is a priority for conservation and improvement of the resource; it can help understand phenotypic variation within populations of different provenances. Inter- and intra-provenance variation in edible fruit tree traits are prerequisites for cultivar development and plus tree identification. Variation in kernel colour is influenced by site (Sakar *et al.*, 2021) and kernel mass can vary from tree to tree (Bai *et al.*, 2021). Furthermore, between populations within the same agro-ecological zone, seed mass shows inter- and intra-specific variation (Tsobeng *et al.*, 2020). Therefore, it is likely that the morphological characteristics of *Ricinodendron heudelotii* seeds and kernels are influenced by their provenances. To date, no studies have been undertaken to assess the seed and kernel characteristics of local populations of the African oil tree and how these traits can be used as indicators in the improvement of *Ricinodendron heudelotii*.

This study assessed the morphological characteristics of the 'African oil tree' populations in the south-eastern region of Benin, described the natural variation traits of the seeds and kernels that can be used as tools for discriminating between populations by value chain actors, and investigated the links between these traits in order to guide growers and breeders in the choice of the best plant material for production and domestication strategies in a context of increasing demand for almonds. We hypothesized that (i) seed and kernel provenance influence the morphological characteristics of different populations of *R. heudelotii* and (ii) a strong correlation exists between the morphological variation of the seeds and their kernel.

Materials and Methods

Study site

The study was carried out in the phytogeography of southern Benin (6°25'E to 7°30'N), under a Guinean-Congolese climate with an annual rainfall varying from 900 to 1300 mm with hydromorphic, ferralitic soils without concretions (Adomou *et al.*, 2006). Three boundaries of the Plateau phytodistrict characterized by dense semi-deciduous forests were considered: the western plateau west of the Ouémé valley with the Agrimey and Massi provenances located on hydromorphic soil and a rainfall of 1100-1300 mm; the southern border of the Eastern Plateau with Pobe with the provenances Akouho, Itchede, and CRAPP located on a ferralitic soil without concretions and a rainfall of 1100-1300 mm; and the northern border of the Eastern Plateau with Zou with the provenances Adaka, Ilagbe, Idena, Ilikimou, and Woroko located on a red ferralitic soil without concretions and a rainfall of 900-1300 mm. The majority of these provenances are located in south-eastern Benin, near the Nigerian border (Figure 1). The main geographical factors that influence the ecological conditions for plant growth are presented in Figure 2. The population around these phytogeographical zones is mainly made up of the Nago and Yoruba ethnic groups, heirs to endogenous knowledge of Guèlèdè mask making from *R. heudelotii* wood (Boko-Haya *et al.*, 2017; Fagbohoun *et al.*, 2019; Akpovo and Fandohan, 2021).

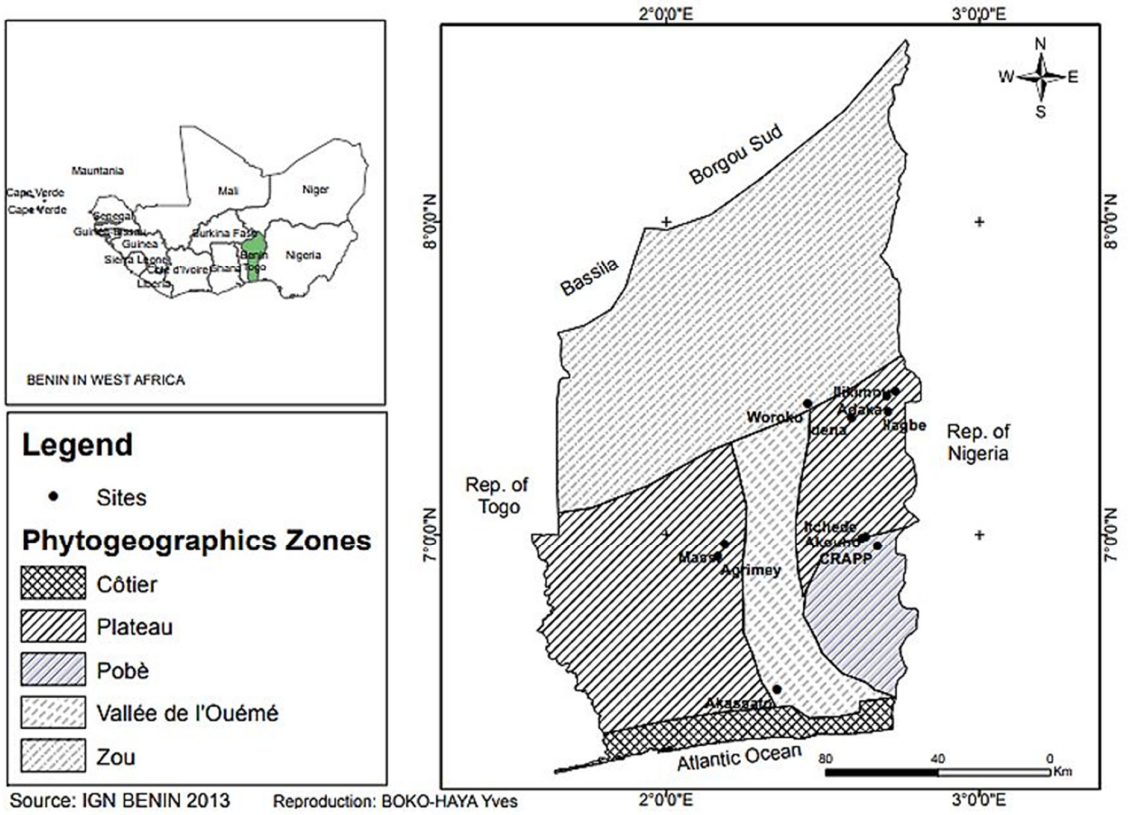


Figure 1. Sample sites in Benin

Sampling

A preliminary survey with the help of key informants (carvers, forest reserve rangers, and endogenous cult leaders) identified through snowball sampling identified provenances and trees that produced fruit. Between July and October of the 2018 season, the period of maximum productivity and free-fall of fruit, ten newly fallen ripe fruits (Figure 3a) were collected at random, below the total leaf area of each tree. Trees were at least 100 m apart to avoid collecting information on related individuals (Nevill *et al.*, 2010; Amirchakhmaghi *et al.*, 2018; Lloyd *et al.* 2020) and provenances were at least 10 km apart; therefore, trees from all provenances were considered as different populations (Te Beest *et al.*, 2009). The total number of trees sampled was 56 equitably (n= 5 at least) to the provenances and the total number of fruits was 560.

To extract the seeds associated with each fruit and tree, an adapted protocol was tested. Fruits from each tree (Figure 4), were fermented separately in small labeled bags for about one month in a trench below ground to allow decomposition of the mesocarp and weakening of the sclerotized endocarp (Figure 3b). The number of seeds per fruit was counted, and these freshly extracted seeds from each fruit were rinsed with tap water and the whole constitutes the seed collection for this tree. Then, in Akassato (2°20'58.382 "E, 6°30'25.207 "N), at an average temperature of 27 °C, these collections were dried alternately in the shade and in the sun for about six months in order to cause the natural detachment of the kernel from the shell wall and to facilitate the extraction of the intact kernels after a very light hammering of the extremely hard shell. From each specified seed collection, ten seeds were randomly selected and crushed to obtain the kernels. In the event that a seed was found to be kernelless, it was replaced by another seed from the corresponding collection. Thus, 560 seeds and 560 local kernels were obtained. Samples from Lobaye forest (3°52'4.11"E, 17°59'21.22"N, Central African Republic) belong geographically to *R. africanum* subspecies, used as control.

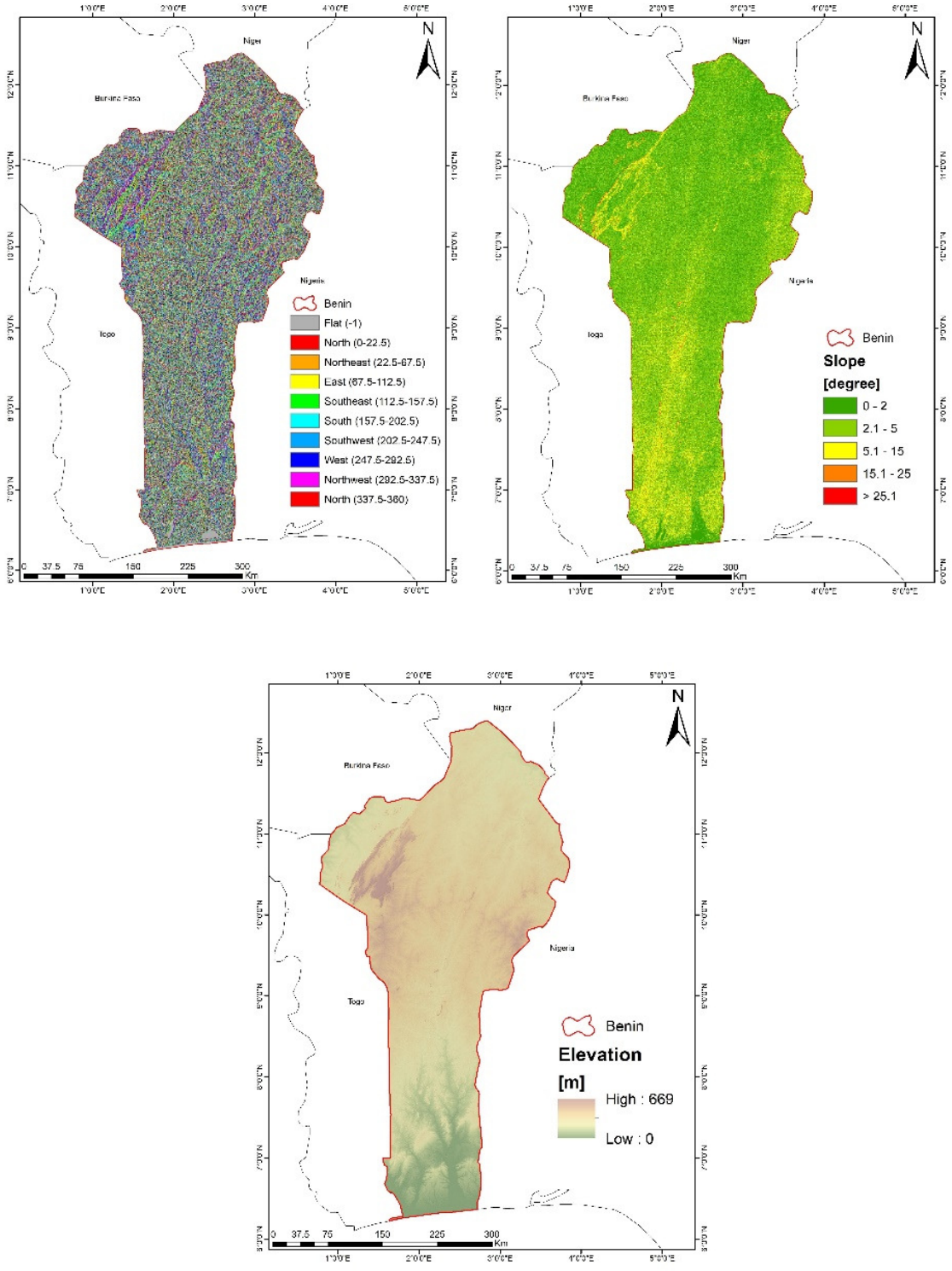


Figure 2. The main geographical factors that influence the ecological conditions of plants

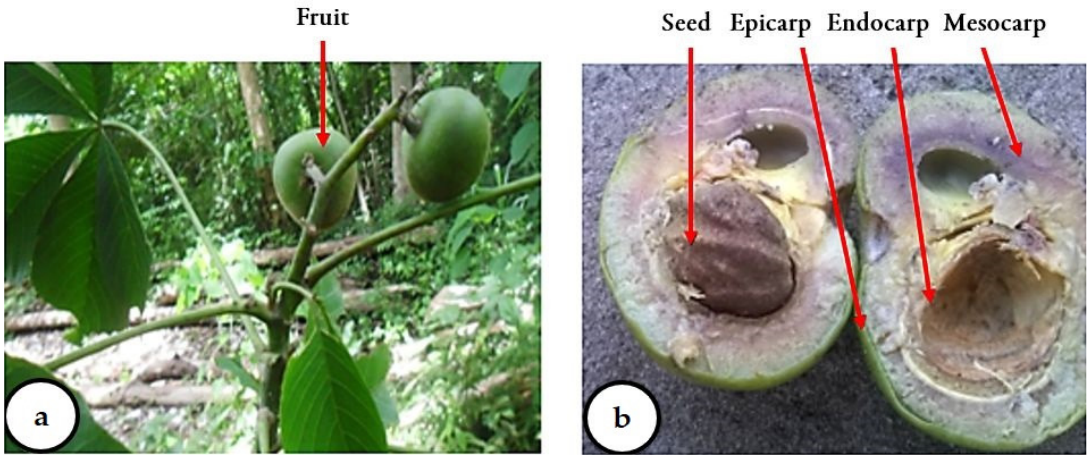


Figure 3. Fruit-bearing leafy shoot (a) and internal fruit structure (b)

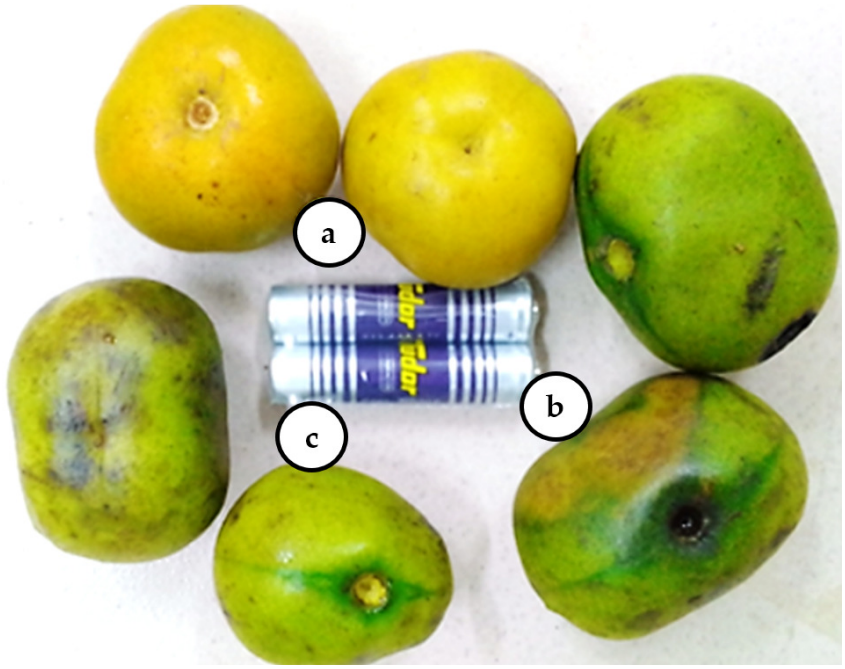


Figure 4. Fresh fruit with 3 lobes with 3 seeds (a), 2 lobes with 2 seeds (b), and 2 lobes with one seed (c) in *Ricinodendron heudelotii*

Collection of morphological data

Quantitative data were collected based on the survey and collection guide for local crop varieties (Marchenay and Lagarde, 1986) and the descriptors selected by IPGRI for other fruit species (shea, citrus, and date palm). So, length, width and thickness were measure using a calliper with a precision level of 0.01 mm (Figure 5). Seed mass were collected using a 0.01 g precision balance. In addition, the number of seeds per fruit, the number of striae and hilum-micropyle distance were recorded.

Qualitative data were also collected, seed colour and appearance (Figure 6), seed apex shape (Figure 7) and kernel colour (Figure 8) and other characters and modalities detailed in Table 1. All these data were used to phenotypically differentiate seeds and kernels from different provenances.

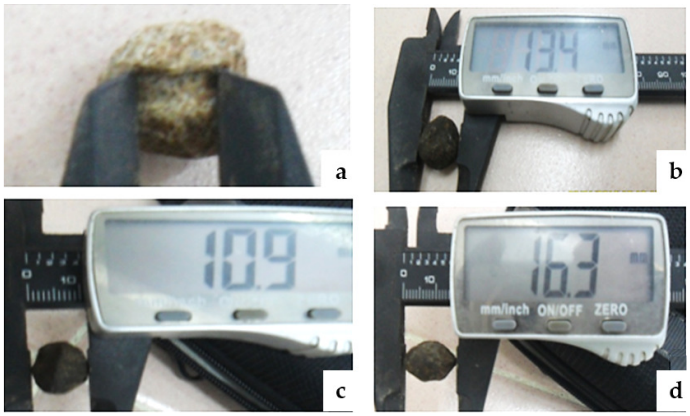


Figure 5. Measurements of ventral groove length (a), width (b), thickness (c), and seed length (d)



Figure 6. Aspect of seeds: smooth (a), rough (b), eruptive (c)

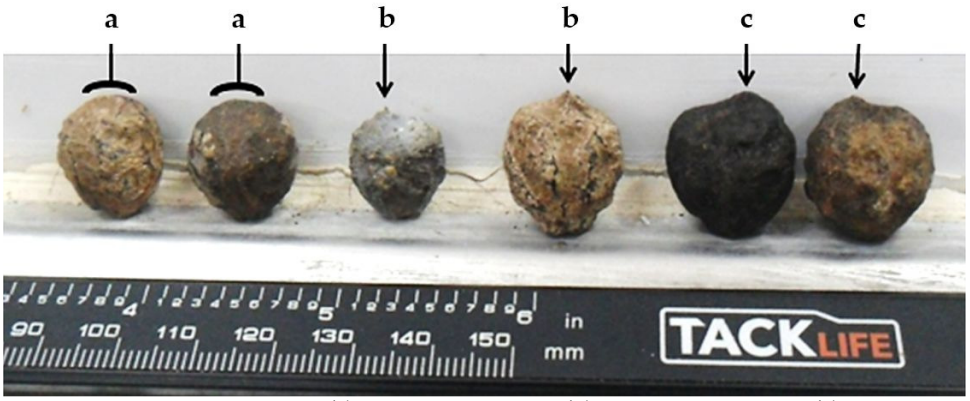


Figure 7. Seeds apex: wide rounded (a), symmetrical pointed (b), asymmetrical pointed (c)



Figure 8. Aspect of kernels: smooth (a), rough (b), eruptive (c)

Table 1. Qualitative traits and modalities

Descriptors	Modalities
Seed colour	Khaki; Khaki spotted black; Brown; Black; Gray; Black-brown; Black-brown
Seed aspect	Rough; Smooth; Rough hooked
Seed shape	Elliptical; Obovate; Cordiform.
Dorsal aspect of the seed	Grooved; Reticulated; Grooved and Reticulated
Seed apex aspect	Convex; Symmetrically pointed; Asymmetrically pointed; Round and wide
Kernel colour	White; Yellowish; Black
Kernel aspect	Oily Rough; Ashen Rough; Rough; Smooth

Data analysis

We performed a common component analysis of variance to determine the source of variability in seed and kernel morphological traits using the lme4 (Bates *et al.*, 2015) and lmerTest (Kuznetsova *et al.*, 2017) packages. In this model, provenance and mother tree were respectively considered as fixed and nested factors. Besides, hierarchical principal component classification (HCPC) ward realized on the matrix of seed and kernel morphological characteristics by using Minitab 18 software. Also, due to the non-normality of the residuals shown by the Shapiro-Wilks test and the inequality of variances, generalized least squares models were used to test the difference of means for each fruit descriptor between the groups. Elsewhere, we performed Pearson's correlation test to describe the linearity relationship between morphological characteristics and the chi-square test to determine the relationship between the clusters and seed and kernel qualitative traits. All analyses were performed using R software, version 4.0.2 (R Core Team, 2022).

Results

Variation in phenotypic traits between and within provenances

Significant variation ($p<0.01$) was observed between provenances for all morphological traits, with the exception of seed, kernel, and shell thickness (Table 2). Similarly, common component analysis of variation revealed considerable heterogeneity both between and within provenances (Table 3).

Overall, heterogeneity in organ functional characteristics was noted between provenances. This variance was greater than 50% for several of the characteristics assessed. Thus, between provenances, 80.41% and 61.88% of the variance in seed length (SdL) and width (SdW) was detected respectively, as well as 59% and 58.77% of the variation in ventral groove length (VGL) and width (VGW). Similarly, between provenances, 60.08% and 79.58% of the variance in the number of dorsal striae (SrN) and the distance between the micropyle and hilum (DHM) were detected. When kernels were included, the results were similar to those found with seeds, i.e., 70% and 74.38% of the variance in kernel length (AlL) and width (AlW), respectively, were observed between provenances. Provenance affected the seed and kernel length growth of *R. heudelotii*.

Within provenances, 52.00% and 87.30% of the differences in seed thickness (SdT) and kernel shell thickness (ShT), respectively, and 63.55% of the differences in kernel thickness (AlT), were identified. The mean seed, kernel, and shell thickness varied widely between mother trees of the same provenance.

Identification of morphotypes

Using principal component analysis, hierarchical clustering produced two large groups (Figure 9) that are statistically distinct ($p<0.005$). The first group encompasses 63.63% of the provenances (Akouho, Massi, Agrimey, Ilikimou, CRAPP, Woroko, and Adaka) and has over 37.5% similarity. Akouho forms one monophyletic group within this first group, while the other provenances form the other monophyletic group. Provenances of Woroko, Adaka, Agrimey and Massi, were quite close. Such, relationship can be understood by their shared ecological circumstances (or morphometric characters). On the other hand, the proximity of the

Ilikimou and CRAPP provenances, which do not share similar ecological conditions, may be related to similarity in morphometric characteristics. Table 3 shows that this first group is characterized by seeds and kernels with means and coefficients of variation (CV) of length (1.46 cm, CV = 07.08 and 1.07, CV = 09.77), width (1.38 cm, CV = 07.15 and 0.93 cm, CV = 23.35), thickness (1.08 cm, CV = 10.98 and 0.72 cm, CV = 15.70), and distance between hilum and micropyle (1.24 cm, CV = 9.80). Similarly, at the fruit level, the respective means and coefficients of variation of the length (3.92 cm, CV = 10.73) and mass (26.38 g, CV = 21.53) of this first group are lower and significantly different (P<0.001) from those of the second group, except for the number of seeds per fruit (2.92, CV = 9.70), while the width of the fruits (3.31 cm) of the first group is not significantly different from that of the second group (3.37 cm).

Table 2. Results of the common component analysis performed on the variables for each organ (var: variances and var in %: percentages of variation)

Variance components	Var/%	Seed							
		SdL	SdW	SdT	VgL	VgW	DHM	ShT	SN
Provenance	Var	0.012	0.007	0.005	0.009	0.003	0.009	0.001	0.592
	%	**(80.41)**	**(61.88)**	(48.00)	**(59.00)**	**(58.77)**	**(60.08)**	(12.70)	**(79.58)**
Provenance: Mother tree	Var	0.003	0.004	0.005	0.007	0.002	0.006	0.005	0.152
	%	(19.59)	(38.12)	**(52.00)**	(41.00)	(41.23)	(39.92)	**(87.30)**	(20.42)
Variance components	**Var/%**	**Kernel**			**Fruit**				
		AlT	AlL	AlW	FrL	FrW	FWg	SdN	
Provenance	Var	0.004	0.007	0.008	0.070	0.086	21.841	0.138	
	%	(36.45)	**(70.00)**	**(74.38)**	**(50.17)**	**(99.00)**	**(92.71)**	**(90.18)**	
Provenance: Mother tree	Var	0.007	0.003	0.003	0.070	0.000	1.718	0.015	
	%	**(63.55)**	(30.00)	(25.62)	(49.83)	(1.00)	(7.29)	(9.82)	

Seed – SdL: seed length, SdW: seed width, SdT: seed thickness, VgL: ventral groove length, VgW: ventral groove width, DHM: distance hilium-micropyle, ShT: shell thickness, SN: striae number | Kernel – AlT: kernel thickness, AlL: kernel length, AlW: kernel width | Fruit – FrL: fruit length, FrW: fruit width, FWg: fruit weight, SdN: seed number | Var: variance value, %: %age/proportion.
Bold values correspond to proportions associated with the variance components which explain the variability of the measured parameters among the factors for each organ.

The second group includes 36.36% of provenances with less than 37.5% similarity (Lobaye, Itchede, Ilagbe, and Idena). Within this group, two distinct subgroups exist: Beninese and Central Africans. Illagbe, Idena, and Itchede constitute the Beninese sub-group. The seeds and kernels of Ilagbe and Idena are quite similar to those of Itchede in this Beninese subgroup. This similarity can be explained by their common agro-ecological zone which is Kétou, where the geographical gradient and ecological circumstances are more homogeneous than in the agro-ecological zone of Pobè, which includes Itchede. In contrast, the Central African subgroup is composed entirely of Lobaye, i.e., seeds and kernels indigenous to Central Africa, where the climatic and soil circumstances are different from those in Benin (West Africa). This second group is defined by seeds and kernels, with mean values and coefficients of variation for length (1.75 cm, CV = 06.25 and 1.29 cm, CV = 07.46), width (1.63 cm, CV = 08.29 and 1.12 cm, CV = 14.77), thickness (1.29 cm, CV = 07.97 and 0.90 cm, CV = 13.28), and number of dorsal striae (2.95, CV = 55.50) (Table 3). Similarly, the means and coefficients of variation for length (4.55 cm, CV = 6.24) and mass (30.36 g, CV = 14.62) of this second group are higher and significantly different (P< 0.001) from those of the first group, except for the number of seeds per fruit (1.86, CV = 21.75). The second group contains trees with large seeds and large kernels but few seeds per fruit, while the first group contains trees with more seeds and kernels but smaller sizes.

Table 3. Descriptive statistics (ME: mean, CV: coefficient of variation) of fruits, seed, and kernel morphological traits according to characteristics

Traits	Groupe 1		Groupe 2		Global		Statistics	
	ME	CV	ME	CV	ME	CV	Value F	Prob.
Fruits								
FrL	3.92	10.73	4.55	6.24	3.98	11.25	104.85	<0.001
FrW	3.31	34.17	3.37	4.67	3.31	32.58	0.18	0.675
Fwg	26.38	21.53	30.36	14.62	26.74	21.28	23.11	0.001
SdN	2.92	9.70	1.86	21.75	2.83	14.98	585.77	<0.001
Seeds								
SdL	1.46	(07.08)	1.75	(06.25)	1.49	(09.21)	20.54	<0.001
SdW	1.38	(07.15)	1.63	(08.29)	1.41	(09.02)	17.08	<0.001
SdT	1.08	(10.98)	1.29	(07.97)	1.10	(12.01)	12.59	<0.001
VgL	0.72	(22.28)	0.95	(16.12)	0.74	(23.57)	10.85	<0.001
VgW	0.30	(32.90)	0.42	(36.11)	0.31	(35.55)	07.95	<0.001
DHM	1.24	(09.80)	1.51	(10.80)	1.27	(11.93)	15.62	<0.001
ShT	0.18	(315.99)	0.18	(23.78)	0.18	(298.66)	00.03	0.979
SrN	4.44	(23.72)	2.95	(55.50)	4.28	(28.44)	-09.65	<0.001
Kernels								
AlT	0.72	(15.70)	0.90	(13.28)	0.74	(17.14)	11.67	<0.001
AlL	1.07	(09.77)	1.29	(07.46)	1.09	(11.33)	15.60	<0.001
AlW	0.93	(23.35)	1.12	(14.77)	0.95	(23.19)	06.60	<0.001

Fr: Fruit; Sd: Seed; Sh: Shell; Al: kernel; DHM: Distance hilium-micropyle; VG; Ventral groove; L: Length; W: Width; T: Thickness and SrN: Striae number.

Comparing seed and kernel masses of *R. heudelotii* by groups, we observe that the generalized least squares results suggest that groups have a substantial influence on seed ($F = 64.99$, $p<0.001$) and kernel ($F = 15.48$, $p<0.001$) masses of *R. heudelotii*. The seed and kernel masses of group 1 (12.94 g ± 0.35) and 5.08 g ± 0.14) were significantly different from those of group 2 (21.43 g ± 0.58) and 6.71 g ± 0.35). Seeds and kernels in group 2 are also heavier than those in group 1.

With the exception of the kernel, shell thickness (ShT), all seed and kernel characteristics are statistically extremely different ($p<0.001$) between the two groups or morphotypes (Table 4). The two morphotypes differed mainly in seed and kernel length, width, thickness, and mass, but also in the number of dorsal striae.

For the qualitative traits, the independent chi-square test (Table 4) reveals a significant difference ($p<0.001$) between the groups in terms of colour, seed appearance, dorsal aspect, and apex shape on the one hand, and seed appearance on the other. The relative frequency (%) of each of these characteristics at the group level shows that, seeds in group 2 are black (68.33%) or brown (20%), while those in group 1 are grey (32.15%) or khaki (27.25%); seeds in group 1 are rough (97.45%), while those in group 2 are rough (68. 33%) or hooked rough (26.66%); group 1 seeds are symmetrically pointed (54.70%) or round (28.62%), while group 2 seeds are mainly symmetrically pointed (80%). The shape of seeds in group 2 is obovate (83.33%) or elliptical (16.66%), compared to the shape of seeds in group 1 (62.74% and 18.23%, respectively), where the cordate shape also exists (17.84%); the dorsal aspect of seeds is grooved (97.05%) in cluster 1 compared to cluster 2 (80%), where 20% are also grooved and reticulated; the colour of the kernels was white (91.66%) in cluster 2, and white (74.70%) or yellowish (16.47%) in cluster 1; the appearance of the kernels was smooth (81.56%) in cluster 1 compared to rough (38.33%) or ashy rough (33.33%) in cluster 2.

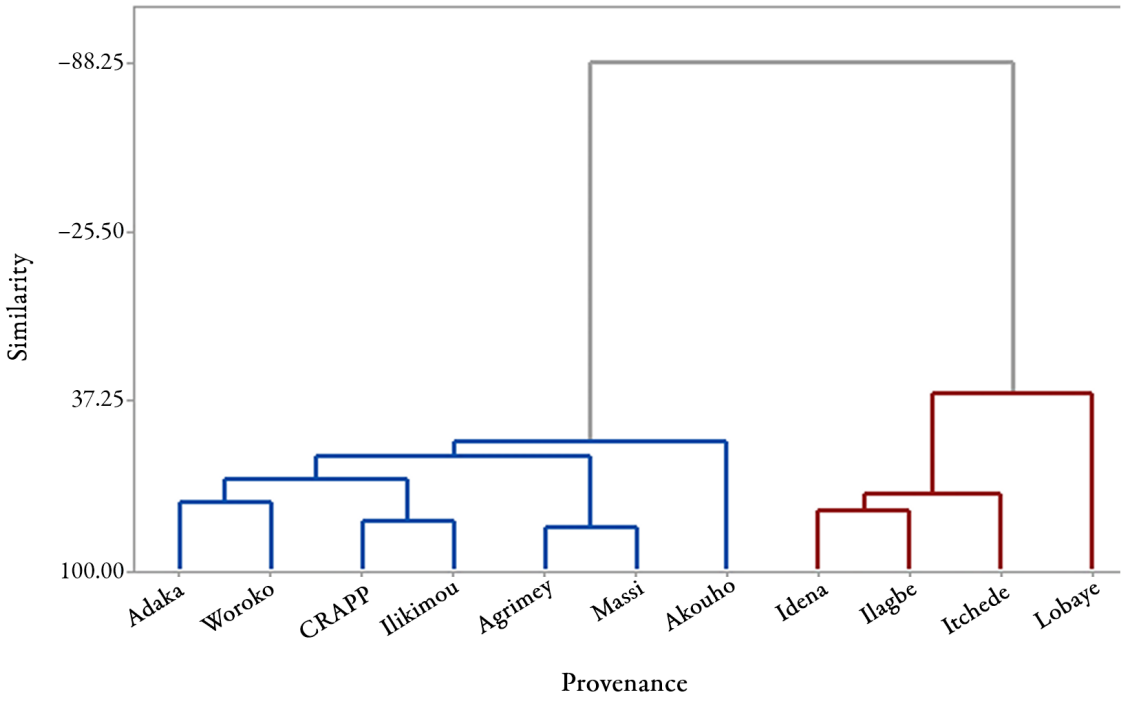


Figure 9. Hierarchical classification on multivariate analysis (mixed data factor analysis) of the morphological traits of the kernel and seed

Table 4. Results of chi-Deux independent test measuring the degree of association between clusters and organs traits

Organs	Chi-square	df	Prob.
Kernel			
Colour	9.28	3	0.026
Aspect	222.44	3	<0.001
Seed			
Colour	62.21	5	<0.001
Aspect	141.97	2	<0.001
Shape	14.99	3	0.002
Dorsal aspect	39.15	2	<0.001
Shape apex	61.15	4	<0.001

R. heudelotii was identified as having two morphotypes: morphotype 2, located in Ilagbe, Itchede, and Idena, has black or brown seeds that are obovate or elliptical in shape, rough and/or hooked at the apical end, and have longitudinal striae (3-4) or are reticulated on the dorsal side; morphotype 1 has grey or khaki (yellow-brown) seeds that are obovate with 4-7 longitudinal striae. In morphotype 2, the kernels are white, rough, and sometimes ashy, whereas in morphotype 1, they are white or yellowish to yellow with a smooth appearance. In general, the kernels have the same shape as the seed from which they are derived.

Relationships between descriptors of R. heudelotii

Pearson's correlation coefficient indicated that many of the attributes examined had substantial positive associations ($p<0.001$) (Table 5). The correlations between seed length and width ($r = 0.77$), seed thickness ($r = 0.57$), distance between hilum and micropyle ($r = 0.68$), and kernel length ($r = 0.62$) were all positive.

Table 5. Correlation matrix between seed and kernel morphological traits

Traits	Statistics	Traits									
		SdL	SdW	SdT	VGL	VGW	DHM	ShT	SrN	AlT	AlL
SdW	r	**0.77**									
	p	0.000									
SdT	r	**0.57**	**0.69**								
	p	0.000	0.000								
VGL	r	0.43	0.49	0.34							
	p	0.000	0.000	0.000							
VGW	r	0.43	0.39	0.26	0.28						
	p	0.000	0.000	0.000	0.000						
DHM	r	**0.68**	**0.62**	**0.51**	0.32	0.37					
	p	0.000	0.000	0.000	0.000	0.000					
ShT	r	-0.02	0.01	-0.28	0.00	0.29	-0.06				
	p	0.601	0.751	0.000	0.936	0.000	0.142				
SrN	r	-0.32	-0.17	-0.15	-0.07	-0.25	-0.28	0.02			
	p	0.000	0.000	0.000	0.094	0.000	0.000	0.674			
AlT	r	0.35	0.27	0.14	0.28	-0.01	0.22	-0.03	-0.18		
	p	0.000	0.000	0.001	0.000	0.811	0.000	0.456	0.000		
AlL	r	**0.62**	0.41	0.35	0.21	0.28	0.46	-0.02	-0.38	0.34	
	p	0.000	0.000	0.000	0.000	0.000	0.000	0.585	0.000	0.000	
AlW	r	0.32	0.30	-0.05	0.18	0.36	0.20	**0.79**	-0.14	0.25	0.31
	p	0.000	0.000	0.259	0.000	0.000	0.000	0.000	0.001	0.000	0.000

Sd: Seed; Sh: Shell; Al: kernel; DHM: Distance hilium-micropyle; VG; Ventral groove; L: Length; W: Width; T: Thickness and SrN: Striae number. Statistics abbreviations: r = correlation coefficient; p = the calculated value of p.

Kernel width was found to be favourably related to kernel thickness (r = 0.69) and distance from the hilum to the micropyle (r = 0.62). Similarly, the distance between the hilum and the micropyle was favourably related to the thickness of the seed (r = 0.51). In addition, there was a strong and positive correlation between shell thickness and kernel width (r = 0.79).

Discussion

Due to the significant correlation between seed thickness and length (r = 0.58), long seeds are also large. In contrast, the association between kernel thickness and length was very weak (r = 0.34); as long kernels do not necessarily have a large thickness, this discrepancy is due to kernels that are not filled in the shell. Furthermore, Pearson's correlation test revealed a substantial association between seed mass and kernel mass (Coef = 0.79, Pr = 0.001). Seeds with a high mass also have a high kernel mass.

Phenotypic traits show great variation

Planning sustainable domestication and plant breeding strategies requires knowledge of population variability. We examined the phenotypic variability of *R. heudelotii* seeds and kernels from wild populations to identify the most useful traits for breeding and conservation. In *R. heudelotii*, seed and kernel length, width, and mass, as well as the number of dorsal striae and the distance between the micropyle and the hilum, showed high inter-provenance variation, but seed, shell, and kernel thickness showed high intra-provenance variation. Cluster analysis confirmed the phenotypic diversity, grouping the provenances into two major groups (morphotypes).

This study emphasizes the hypothesis that provenances have a significant effect on seed and kernel dimensions. Previous studies showed that seed length and mass, seed width, colour, and texture of *Jatropha curcas* were found to be key characters for identification and discrimination of morphotypes between phytodistricts in Benin (Padonou *et al.*, 2013). Many forest species have shown inter-provenance variation in seed length and width, including *Faidherbia albida* (Delile) A. Chev. (Fredrick *et al.*, 2015), *Pinus roxbrughii* (Ghildiyal *et al.*, 2009), *Celtis australis* (Singh *et al.*, 2006), *Argania spinosa* (Belcadi Haloui *et al.*, 2017), and *Pterocarpus erinaceus* Poir (Johnson *et al.*, 2020), suggesting that seed length and width are strongly influenced by geographical origins (Harel *et al.*, 2011; Singh and Thapliyal, 2012; Madjelia and Kadidiatou, 2015; Belcadi Haloui *et al.*, 2017; Louati *et al.*, 2019). Geographical origin is under the influence of climatic and soil factors, which are responsible for the overall variation in plant traits (Joswig *et al.*, 2022). In the current study, all origins belong to the same climatic zone, the Guinean-Congolian zone, which suggests that the observed variations are not potentially climate-related. However, slight differences in rainfall, latitudinal, or physical and chemical soil properties are responsible for variations in morphological traits (Jongschaap *et al.*, 2007; Abasse *et al.*, 2011; Grozeva *et al.*, 2016; Sama *et al.*, 2022). In addition to soil conditions, the observed intra-provenance variation in thickness (seeds, hulls, and kernels) highlights a likely influence of the mother tree. Therefore, phenotypic variation in seeds and kernels may originate from soil conditions, maternal traits, or a combination of both (Kołodziejek, 2017). However, the cohabitation of both morphotypes at the CRAPP site, seems to support the hypothesis of a genetic difference between the two morphotypes.

Experiments in common gardens will be necessary to better elucidate the origin of this genetic difference. The high variation obtained means that the traits are heterogeneous and offer opportunities for selection of desirable traits to be maintained (Adler *et al.*, 2013). In addition to these new traits, the two morphotypes were distinguished by variations in seed and kernel colour, dorsal aspect of the seeds, and number of striae. The colour of the kernels is an important quality characteristic that defines the visual acceptance of consumers and the preferences of agro-industrialists and is also a criterion for discriminating between cultivars of *Prunus dulcis* (Mill.) D.A. Webb. Also, according to Barthlott (1981), cuticular striations, inclusions, and thickenings of the visible outer walls of the seeds are among the surface characters used in taxonomy; for example, in most *Leiothrix* species, the striated seed coat is a distinctive ornamentation of the seeds that also increases the germination rate (Silva Mascarenhas and Scatena, 2021). For example, to avoid granivores, seeds take on the colour of the soil in which they grow to avoid detection (Porter, 2013).

The information on these new discriminating characters is valuable and complements the knowledge of the morphological description of the species. In the present study, the Central African accessions from Lobaye, phylogenetically closer to those from Ilagbe, Itchede, and Idena, and having an average of two seeds, would therefore be *R. heudelotii* var. *africanum*, whereas the accessions from Massi, Akouho, Woroko, and Agrimey with three perfectly mature seeds would *be R. heudelotii* var. *heudelotii*. Group 2, comprising Itchede, the best morphotype in our survey, could be considered for valorization in Benin given that the large seeds are large-kernel and potentially have nutrient reserves responsible for good germination and seedling growth (Boko-Haya *et al.*, 2021; Hounsou-Dindin *et al.*, 2022). Future research should investigate this morphological differentiation using biochemical and molecular genetic markers to show the potential of the two morphotypes.

The extend of correlations between morphometric traits

The study shows a linear correlation between the productive traits of seeds and kernels. Intriguing correlations were found between most of the productive traits. The strong positive correlation ($r = 0.58$) between seed thickness and seed length, between seed thickness and kernel length ($r = 0.34$), and between seed length and kernel length ($r = 0.62$) indicates that large and long seeds also have large and long kernels. This newly discovered relationship is extremely interesting in the selection of productive traits; that is the same for mass, where seeds with high mass also have high kernel mass; this relationship is very beneficial for the productivity of the species. Similar observations have been made in *Pentaclethra macrophylla* Benth (Tsobeng

et al., 2015), *Phoenix dactylifera* L. (Gros-Balthazard *et al.*, 2016), *Juglans regia* (Orman *et al.*, 2020) and *Juglans mandshurica* (Zhang *et al.*, 2021).

These positive correlations between productive seed traits and kernels of *R. heudelotii* provide a useful indicator for predicting kernel yield of the species, a crucial challenge for farmers who may now consider large seeds as a key criterion for improving kernel yields. Thus, the study partly demonstrates a linear correlation between productive seed traits and kernels; these traits can predict each other (Talhouk *et al.*, 2000) and an improvement in one quantitative trait can lead to changes in the other (Loha *et al.*, 2006; Čolić *et al.*, 2012). It is desirable that *plus trees* 'selection for yield could be based on qualities that show substantial correlations with the target attribute as criteria (Khadivi-Khub and Etemadi-Khah, 2015). So, do the differences in kernel colour and appearance clearly noted in this study reflect differences in the oil quality of *R. heudelotii*?

Conclusion

Among the Benin accessions of *R. heudelotii*, two morphotypes were clearly distinguished based on the length, width, thickness, and mass of the seeds and kernels, as well as the number of dorsal striae on the seeds and kernels. Former descriptions of *R. heudelotii* used fruit to differentiate populations, but as seeds cannot be predicted from fruit, the results of the present study complement the former description by assessing seed and kernel morphology. Heavy seeds have heavy kernels, thus establishing a significant positive association between seed mass and kernel mass, which is crucial to the yield attribute of the species, which was a key concern of farmers. *R. heudelotii* has a high phenotypic diversity in nature and various correlated traits, which could be valuable for domestication and genetic improvement. Three provenances (Itchede, Illagbe, and Idena) were recommended for the selection of the best morphotype. The future application of genetic molecular markers to accessions from different provenances could help to elucidate this finding concerning phylogenetic relationship.

Authors' Contributions

Field work and drafting of the manuscript: BYY. Statistical analysis: AYY. Critical revision of the manuscript and supervising of the work: OAINC, and AC.

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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