Original article

Geographical distribution, tree density and fruit production of *Tamarindus indica* L. (Fabaceae) across three ecological regions in Benin

Belarmain Fandohan*, Achille Ephrem Assogbadjo, Romain Glèlè Kakaï, Brice Sinsin

Lab. Appl. Ecol., Fac. Agron.
Sci., Univ. Abomey-Calavi,
01 BP 526, Cotonou, Benin,
bfandohan@gmail.com

* *Correspondence and reprints*

Received 19 February 2009
Accepted 3 June 2009

Fruits, 2011, vol. 66, p. 65–78

DOI: 10.1051/fruits/2010043
www.fruits-journal.org

***Resumen Español**, p. 78*

Geographical distribution, tree density and fruit production of *Tamarindus indica* L. (Fabaceae) across three ecological regions in Benin.

Abstract — **Introduction**. There has been increasing interest in the domestication potential of indigenous fruit trees. Nevertheless, our understanding of how these species' abundance and yield of fruit is altered by ecological conditions, which is critical to foresee realistic sustainable management plans, is limited. **Materials and methods**. We used local ecological knowledge, presence / absence data and quantitative methods to examine the effect of ecological conditions on the distribution, abundance and yields of tamarind trees (*T. indica*) across three ecological regions in Benin, West Africa. **Results and discussion**. Rural communities' knowledge on the species' ecological range was congruent with scientific findings. The natural distribution of tamarind individuals was limited to the Sudanian and the Sudano-Guinean regions and their density declined with increasing moisture, being highest (2 trees·km^{-2}) in the Sudanian region and lowest in the Guineo-Congolian region (scarce). On the other hand, fruit and pulp mass and number of seeds per fruit varied significantly, being higher in the Guineo-Congolian wetter region. However, no significant variation occurred among ecological regions for estimated overall fruit yields per tree. This might indicate that tamarind trees tend to invest in a small number of very large fruits under wetter conditions and a very large number of small fruits under dryer conditions. **Conclusion.** The results showed that semi-arid lands would best suit *T. indica* domestication. Nevertheless, its productivity could be higher under wetter conditions. Because of its affinity for gallery forests, we recommend thorough studies on its capacity to survive the increasing drought in its current ecological range.

Benin / *Tamarindus indica* / population distribution / population density / fruiting / indigenous knowledge

---

Répartition géographique, densité des arbres et production de fruits de *Tamarindus indica* L. (Fabaceae) dans trois régions écologiques au Bénin.

Résumé — **Introduction**. Le potentiel de domestication des arbres fruitiers indigènes a suscité un intérêt croissant. Néanmoins, la façon dont l'abondance de ces espèces et leur rendement en fruits sont affectés par les conditions écologiques, élément essentiel pour prévoir des plans de gestion durable réalistes, est peu documentée. **Matériel et méthodes**. Nous avons utilisé des connaissances écologiques locales, des données de présence / absence et des méthodes quantitatives pour étudier l'effet des conditions écologiques sur la répartition, l'abondance et les rendements des tamariniers (*T. indica*) dans trois régions écologiques du Bénin, en Afrique de l'Ouest. **Résultats et discussion**. La connaissance de l'aire de répartition écologique par les communautés rurales a été en accord avec les résultats scientifiques. La répartition naturelle des tamariniers a été limitée aux régions soudanaise et soudano-guinéenne et leur densité a diminué avec l'accroissement du taux d'humidité ; la densité a été la plus élevée (2 arbres·km^{-2}) dans la région soudanaise et la plus basse dans la région guinéo-congolaise (présence rare). D'autre part, la masse de pulpe et de fruits ainsi que le nombre de graines par fruit ont sensiblement varié ; ces caractères ont été les plus élevés dans la région humide guinéo-congolaise. Cependant, aucune variation significative n'est apparue d'une région écologique à l'autre en ce qui concerne les rendements globaux de fruits par arbre. Cela pourrait indiquer que les tamariniers tendent à produire un petit nombre de gros fruits en milieu plus humides et un grand nombre de petits fruits en milieu plus sec. **Conclusion**. Nos résultats pourraient suggérer que les zones semi-arides pourraient mieux convenir à la domestication de *T. indica*. Néanmoins, la productivité de l'espèce pourrait être plus élevée en conditions plus humides. Sur la base de son affinité pour les forêts-galeries, nous recommandons des études approfondies sur la capacité de l'espèce *T. indica* à survivre à des stress hydriques croissants dans son environnement écologique actuel.

Bénin / *Tamarindus indica* / distribution des populations / densité de population / fructification / connaissance indigène

1. Introduction

Until recently, little interest has been shown in indigenous multipurpose tree species compared with their industrial timber counterparts. Available information generally lacks adequate quantitative analysis for the development of economic opportunities based on local resources as an alternative to excessive import of exotic products. Thus, initiatives in agroforestry seek to integrate indigenous trees whose products have traditionally been gathered from natural forests into tropical farming systems [1]. This is also to provide marketable products from farms that will generate income for resource-poor rural households. As such, it has led to an increasing interest in the domestication potential of some traditionally valued agroforestry trees in Africa, *i.e.*, *Detarium microcarpum* Harms [2], *Irvingia gabonensis* (Aubry Lecomte ex O'Rorke) Baill. [3] and *Sclerocarya birrea* (A.Rich.) Hochst.) subsp. *caffra* (Sond.) [4], to cite just a few.

The growing number of studies on the domestication potential of indigenous trees have provided information about morphological and genetic diversity [5, 6], potential productivity [7] and nutritional and medicinal properties [8]. However, as local environmental conditions influence variation in plants [9], domestication programs should also consider the impact of ecological factors on distribution, abundance and fruiting potential of the targeted species. Such aspects are poorly explored but critical for identification of priority sites for planting and genetic improvement. In addition, such information may highlight the extent to which natural populations could supply market demand with products (*i.e.*, fresh fruit and pulp) depending on ecological conditions. Although a number of studies have demonstrated that the distribution, abundance and fruiting potential of indigenous multipurpose trees depend on environmental conditions [7, 10], the effect of environmental conditions may vary with plant species. In addition, the accuracy of abundance estimation may be strongly dependent on the method used and robust statistical methods should be used whenever possible.

T-Square sampling [11] is a distance-based sampling method which has been used in ecology to estimate sizes and densities of many plant populations [12]. It is a robust method that can provide informative results even if no prior information exists about the randomness or the uniformity of the spatial pattern of the species studied, and is especially suited to large-scale population studies [13]. *T*-square sampling can therefore be used to evaluate the abundance of indigenous fruit trees or multipurpose trees nationwide or regionwide. In addition, recent ethnoecological studies advocate an integration of local ecological knowledge and ecological studies to advance our understanding of ecological processes and develop better plans for sustainable resource use [14]. To enable such integration, it is important to evaluate the congruence of local ecological knowledge with available scientific findings [14].

Tamarindus indica L. is a semi-evergreen tree widespread in the tropics (Africa, Asia, Madagascar, South America), featuring prominently in riparian habitats [15]. In efforts to enhance the species' genetic resource conservation and utilization, it has recently been identified as one of the top ten agroforestry tree species to be prioritized for future crop diversification programs and development in sub-Saharan Africa [16]. There has been extensive interest in tamarind's biochemical, medicinal and nutritional properties, reproductive biology, morphology, cultivation and genetics [17]. Studies on the species in Asia, Africa and Latin America have documented its domestication potential in terms of sociocultural and nutritional values, and aptitude for seed and vegetative propagation [17]. Tamarind's global distribution map has given strong evidence of its plasticity in the tropics [18]. Studies on the species' native populations in Africa have provided data on biochemical analysis of its fruits [19], genetic diversity, phenology, reproductive biology including pollinators, biometrical characters of seeds and seedlings [20–23], and impact of habitat type on its conservation status [24]. However, little scientific information is available on how ecological conditions locally influence its distribution, abundance and productivity in Africa. In this study, we used LEK and ecological studies to examine the distribution and productivity of tamarind trees in Benin as a case study. The following questions were addressed: (1) What is the distribution range and abundance of *T. indica* in relation to the ecological conditions it lives in? (2) How do ecological and tree-level factors alter its productivity of fresh fruits, pulp and seeds?

2. Materials and methods

2.1. Study area

Our study was conducted in Benin (West Africa). Ongoing work on the ecological niche of *T. indica* in Benin has confirmed the presence of tamarind individuals in the three ecological regions of the country (the Sudanian, Sudano-Guinean and sub-humid Guineo-Congolian regions [25]). Thus, this study was conducted nationwide (114 673 km^2) [26].

In the Sudanian region (9°45'–12°25' N), rainfall is unimodal. Mean annual rainfall is often less than 1000 mm, the relative humidity varies between 18% and 99% (highest in August) and temperature varies between 24 °C and 31 °C. The Sudanian region has hydromorphic soils, well-drained soils and lithosols.

In the Sudano-Guinean region (7°30'–9°45' N), rainfall is unimodal, from May to October, and lasts for about 113 days with an annual total rainfall varying between 900 mm and 1110 mm. Mean annual temperature ranges from 25 °C to 29 °C, and the relative humidity from 31% to 98%. The soils in this zone are ferruginous.

In the Guineo-Congolian region (6°25'–7°30' N), rainfall is bimodal with a mean annual rainfall of 1200 mm. Mean annual temperature varies between 25 °C and 29 °C and the relative humidity varies between 69% and 97%. The soils are either deep ferrallitic or rich in clay.

The principal ethnic groups are the Dendi, Bariba, Fulani, Waama and Gourmantché in the Sudanian region; the Fon, Tchabè, Nago, Agnin and Idatcha in the Sudano-Guinean region; and the Yoruba, Adja, Tori, Holi, Péda and Xwla in the Guineo-Congolian region. We focused on these 16 aforementioned ethnic groups during this study because they were the most ancient in their locations throughout the study area.

2.2. Ethnoecological survey

Our survey aimed at documenting local perceptions about the distribution of tamarind trees in Benin. We applied semi-structured individual interviews to five traditional hunters / healers and five Fulani herders randomly sampled within each of the 77 state districts of Benin (770 respondents). The sampling was limited to persons of at least fifty, so that only experienced informants were questioned. We targeted Fulani herders because they are culturally associated with the species and usually keep the fruits during migrations (personal field observation). The healers and hunters were chosen because of their local reputations in plant knowledge. These socio-professional groups are more likely to hold very informative knowledge about the past and present distribution of the species. The following questions were asked: (i) As an indicator of its presence in earlier times, we asked whether tamarind had a local name in the language of the most ancient indigenous ethnic groups of each district; (ii) Is the species currently found in the natural vegetation? If yes, in which habitats? (iii) Was the species present in the native vegetation in earlier times? If it was present in earlier times but is not currently present, then why has it disappeared?

2.3. Characterization of the distribution patterns and density of tamarind

In each of the 77 state districts, we made a visual confirmation of the species' presence/absence within protected areas, forests and farmlands, following unfixed transect lines across natural vegetation, with the help of transhumants or hunters recommended by local leaders.

Then, we performed a sampling plan for tamarind density estimation based on the ten phytogeographical subdivisions of the three ecological regions [27]. We randomly selected one to two sites (protected areas and surrounding farmlands) within each phytogeographical district where tamarind natural populations were observed (*table I*). The density of the species was estimated using the *T*-Square sampling method. Each phytogeographical district was represented by 45–90 sampled points for density estimation (overall 630 points for 112,622 km²), following a protocol already published [28]. To address any underlying heterogeneity in tamarind trees' pattern, a stratification of the vegetation and a systematic sampling approach were performed. Thus, each selected site was first stratified into three habitats: forest, savannah and farmland. We established 15 points in each habitat. The 15 points were distributed on five azimuth transects of 15 km, so that each transect was divided into three equally spaced marks (5 km) (S_i); then, from each marked point, the distance (x_i) to the nearest tamarind individual (T_1) was measured using a global positioning system (GPS Garmin 76). Next, the distance (y_i) between T_1 and its nearest neighbor (T_2) situated in the 'half-plane' excluding S_i was measured [29] (*figure 1*). We used a GPS instead of a tape measure or a decameter since "*x*" and "*y*" distances were often over 500 m, except in gallery forests.

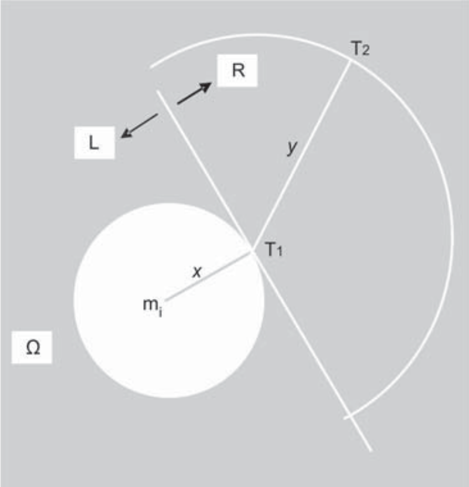

Figure 1.
T-Square sampling method [tamarind trees (T); sampling point (m_i); distances labeled *x* and *y*; planes labeled L and R; region of interest (Ω,)] (adapted from Diggle [29]).

2.4. Estimating average yield of fresh fruit, pulp and seeds

Data were collected on a total of 65 trees sampled among the trees that we located when estimating tree density. Thirty trees were sampled in both the Sudanian and Sudano-Guinean regions while only five trees were selected in the Guineo-Congolian

Table I.
Sampling plan for assessing geographical distribution, tree density and fruit production of *Tamarindus indica* L. in three ecological regions of Benin.

N°	Ecological regions	Phytogeographical district	State district	Study site	Coordinates	
					Lat. E	Long. N
1	Sudanian	Atacora Chain	Tanguiéta	Pendjari National Park	1° 44'	11° 07'
2		Mekrou-Pendjari	Karimama	W National Park	2° 54'	12° 06'
3		Mekrou-Pendjari	Tanguiéta	Pendjari National Park	1° 30'	11° 25'
4		Borgou North	Banikoara	W National Park	2° 40'	11° 55'
5		Borgou North	Pehunco	Upper Alibori Forest	2° 17'	10° 59'
6	Sudano-Guinean	Borgou South	Tchaourou	Monts Kouffé Forest	2° 08'	9° 00'
7		Borgou South	Kalalé	Three Rivers Forest	3° 19'	10° 50'
8		Bassila	Bassila	Penessoulou Forest	1° 64'	9° 21'
9		Zou	Djidja	Gbadagba Forest	2° 01'	7° 57'
10	Guineo-Congolian	Oueme Valley	Zogbodomey	Locoly Swamp Forest	2° 36'	7° 10'
11		Plain	Kétou	Kétou-Dogo Forest	2° 60'	7° 73'
12		Plain	Houéyogbé	Houéyogbé Forest	1° 85'	6° 50'
13		Pobè	Pobè	Pobè Forest	2° 68'	7° 07'
14		Coast	Ouidah	Ahozon Forest	2° 16'	6° 37'

region. The lower number in the latter region was due to the scarcity of tamarind trees in that region. For consistency and to make realistic comparisons, sampling was limited to trees with a diameter at 1.3 m above ground (D_{130}) of at least 20 cm. Sampled trees were measured for D_{130}, total height and crown diameter. Crown areas were computed according to a method published elsewhere [30]. For each fruit-bearing tree, fruits were harvested and weighed together.

To estimate fruit and pulp mass and number of seeds per fruit, 30 fruits were sampled per fruit-bearing tree as described elsewhere [31]. After weighing, fruits were oven-dried at 65 °C for 48 h to obtain dry mass. Dried fruits were broken and the content extracted (pulp + seeds + fibers). Pulp was removed by soaking in water. The remainder (seeds and fibers) was oven-dried at 65 °C for 48 h and weighed. Pulp mass was computed as: dry mass of the fruit minus dry mass of the remainder. Finally, the number of seeds per fruit was also counted.

Climatic data for over 30 years (1978–2008) were obtained for each sampling site within ecological regions from the Worldclim data [32].

2.5. Data analysis

For ethnoecological data, we computed a response rate per question using the following formula [33]: $F = [100 \times (S / N)]$, where S is the number of responses to a particular question and N is the total number of persons interviewed.

The density of *T. indica* in each phytogeographical district was calculated according to the following formula [29]:

$$\lambda = \frac{m}{\pi} \times \frac{1}{\sqrt{\sum_{i=1}^{m} x_1^2 \times \frac{1}{2} \sum_{i=1}^{m} y_1^2}}$$

, where: λ is the estimate of the number of adult trees ($D_{130} \geq 10$ cm) per km², m is the number of sampling points, x_i is the distance from the i^{th} point to the nearest tamarind (T_1) tree, y_i is the distance between T_1 and its closest neighbor (T_2) in the opposite plane which does not contain the i^{th} sampling point, and π is approximately equal to 3.14.

The distribution and abundance of *T. indica* were then mapped using Arcview software.

The mass of the pulp content (wp) in each fruit was computed using the following formula: $wp = wP_i - wR_i$, where wp is the pulp content of a fruit for a given tree; wP_i is the total dry mass of the fruit (i); and wR_i is the total dry mass of seeds, fibers and husk of the fruit (i). Overall yield of pulp and number of seeds of the sampled trees were estimated based on total yield of fresh fruits and mean values obtained for fresh mass and dry mass of fruit.

The climatic index of Mangenot (I_M), which is a measure of water availability [27], was computed for each sampled site as follows:

$$I_M = \frac{\frac{P}{100} + M_S + \bar{U}_X}{nS + \frac{500}{\bar{U}n}}$$

, where P is the mean annual rainfall (mm); M_S is the mean rainfall of dry months (rainfall less than 50 mm); nS is the number of dry months; Ux is the maximum of annual relative humidity (%) ; and Un is the minimum of annual relative humidity (%). This index provides a better quantitative assessment of climatic conditions than any single climatic variable and was used here as the indicator of the environmental conditions in each ecological region [27].

Because productivity of fresh fruits and, pulp and seed values were not normally distributed (Ryan-Joiner test of normality) [34], the non-parametric test of Kruskal-Wallis was applied to describe and compare the three ecological regions. To investigate the correlation between ecological conditions, tree characteristics (D_{130}, height, crown area) and differences in tamarind productivity, a Standardized Principal Component Analysis (PCA) was first performed on the productivity traits of the species (pulp mass, number of seeds per fruit, overall yield of fruits and pulp, and number of seeds per tree). The principal components obtained from the PCA were then correlated with D_{130}, height, crown area of tamarind trees and the climatic index of Mangenot using Pearson's correlation coefficient. This method was used to avoid evident correlation between the productivity traits of the species that could bias the estimation of the degree of link they have with the dendrometric and ecological parameters.

3. Results

3.1. Local perception on past and present distribution of tamarind

All the respondents knew the species because of their profession. From this survey, it appeared that, except for the Yoruba ethnic group, tamarind had no local name within the Guineo-Congolian region (*table II*). According to the respondents from the Sudano-Guinean and Guineo-Congolian regions and all questioned Fulani herders (78% of respondents), the current distribution of the species is limited in the south by the Sudano-Guinean region. However, the species was said to have totally disappeared or to be fading out of some locations where it used to be abundant due to tree felling for urban construction and agricultural purposes in that region (near its borders with the Guineo-Congolian region). Other human practices (debarking for medicine, pruning for fodder and fruit harvest) were also mentioned as threats to the species. In state districts within the Sudano-Guinean region, local ethnic groups generally associated tamarind trees with Fulani people. Furthermore, in this region, Fulani people still have the tendency to appropriate the harvest from any tamarind, even if trees are on farmers' land. Tamarind fruits are important for the Fulani as a laxative during transhumance trips.

Table II.
Tamarind local names according to ethnic groups in Benin.

Ecological region	Ethnic group	Names
Sudanian	Bariba	Môkôssô - Môhôhô
	Dendi	Bobosséi - Bosséi
	Fulani	Djêtami
	Gourmantché	Bu pugubu
	Waama	Pusika
Sudanian-Guinean	Agnin	Gougnémou
	Fon	Djêvivi
	Idatcha	Arinran
	Nago	Kaïma
	Tchabè	Adjagbon
Guineo-Congolian	Adja	–
	Holi	–
	Ouémè	–
	Péda	–
	Xwla	–
	Yoruba	Adjagbon

3.2. Characterization of the distribution patterns and abundance of tamarind

Tamarind is widespread in Benin (*figure 2*). It was identified in all state districts except those in the phytogeographical district of Oueme-valley. However, as suggested by the survey on local ecological knowledge, tamarind trees are extremely rare in the native vegetation within the Guineo-Congolian region. Observed trees were reported to have been planted 20-60 years ago. On the other hand, in the Sudanian and Sudano-Guinean regions, tamarind stands (with gregarious patterns of trees) were only found along water courses in gallery forests. Beyond gallery forests, the species was observed as isolated individuals and was sometimes shrub-shaped in open savannah ecosystems.

Density of tamarind adult trees declined from the Sudanian region (approximately 2 trees per km²) to the Guineo-Congolian region (totally absent) (*figure 2*). Based on the densities obtained, estimation of tamarind adult tree abundance per phytogeographical district was estimated (*table III*). The overall number of tamarind adult trees in Benin was estimated at 68,114 trees, meaning approximately an average of 0.6 trees per km² for the whole country.

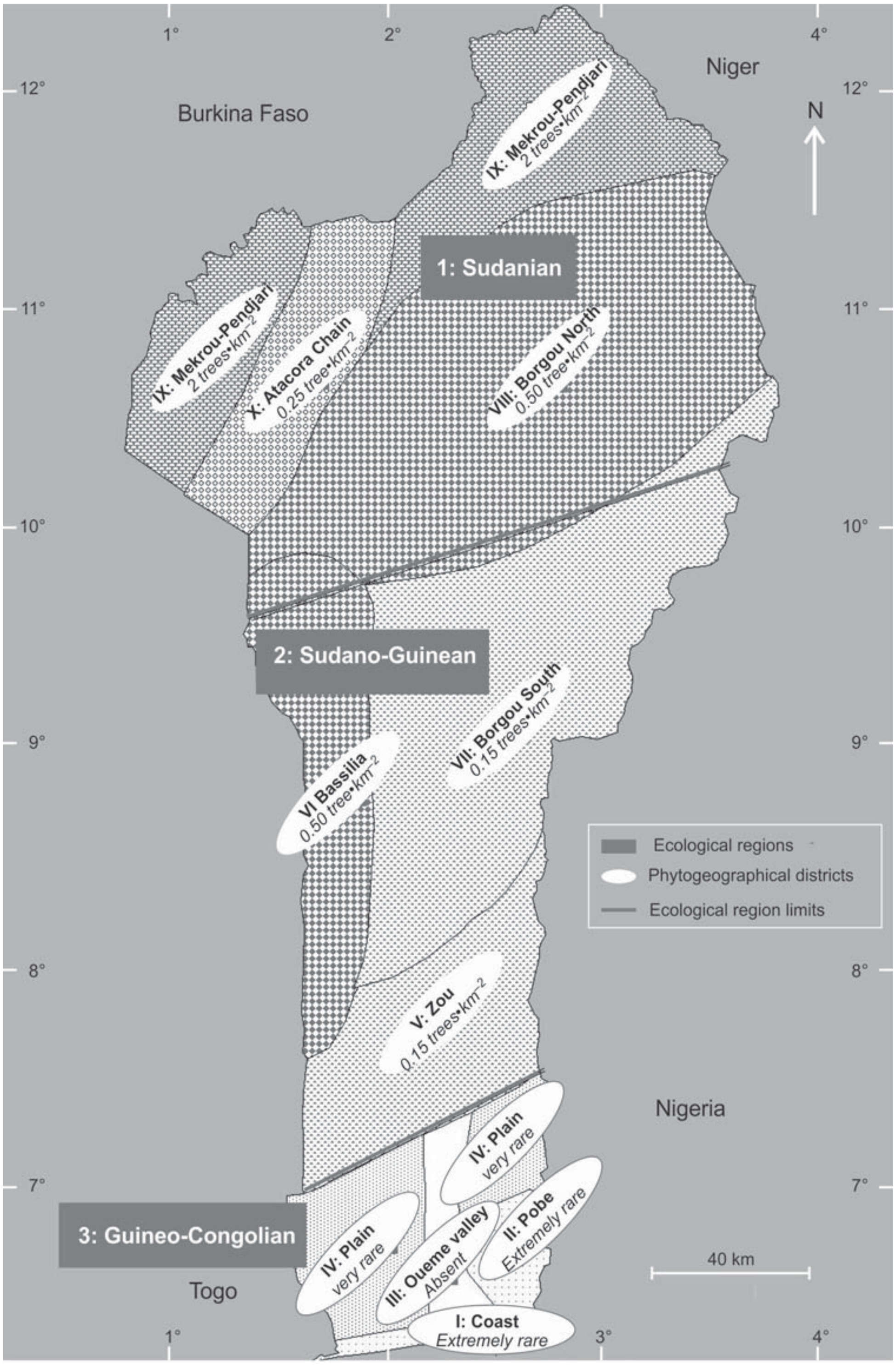

Figure 2.
Distribution patterns and density of tamarind according to the phytogeographical subdivision of the three ecological regions of Benin.

Table III.
Abundance of tamarind according to the phytogeographical districts within three ecological regions of Benin.

Ecological region	Phytogeographical district	Area (km^2)	Density (trees·km^{-2})	Abundance[1] (trees)
Sudanian	Atacora Chain	6,905.46021	0.25	1,726.365
	Mekrou-Pendjari East	10,579.0816	2.04	21,581.326
	Mekrou-Pendjari West	6,261.25419	2.04	12,772.959
	Borgou North	32,676.6419	0.51	16,665.087
Sudano-Guinean	Borgou South	9,599.48146	0.15	1,439.922
	Bassila	24,726.4271	0.50	12,363.214
	Zou	10,431.6667	0.15	1,564.750
Guineo-Congolian	Plain-East	2,071.22318	Very rare	–
	Plain-West	5,098.4805	Very rare	–
	Coast	686.07915	Extremely rare	–
	Pobé	1,613.20103	Extremely rare	–
	Oueme Valley	1,973.0031	Absent	–

[1] Abundance = area × density.

Table IV.
Mean and coefficient of variation of yields of fruits, pulp and seeds of tamarind according to their location in one of the three ecological regions in Benin.

Ecological region	Fruit mass		Pulp mass per fruit		Number of seeds per fruit		Fruit yield per tree		Pulp yield per tree		Seed yield per tree	
	Mean (g)	Coefficient of variation (%)	Mean (g)	Coefficient of variation (%)	Mean	Coefficient of variation (%)	Mean (kg)	Coefficient of variation (%)	Mean (kg)	Coefficient of variation (%)	Mean	Coefficient of variation (%)
Sudanian	11.29	40.57	4.10	51.22	8.12	28.20	34.42	46.19	12.39	40.07	24758	45.18
Sudano-Guinean	17.54	37.69	5.51	45.55	7.68	31.51	39.07	125.75	12.89	105.62	20550	125.76
Guineo-Congolian	48.85	26.64	14.59	30.23	9.73	20.76	74.73	94.53	22.42	91.16	14889	89.01
Significance[1]	< 0.0001		< 0.0001		< 0.0001		0.41		0.26		0.049	

[1] According to the Kruskal-Wallis non-parametric test.

3.3. Estimating tamarind productivity of fresh fruit, pulp and seeds according to ecological regions

Significant differences were observed among ecological regions for individual fruit and pulp mass, and number of seeds per fruit ($p < 0.001$; H = 314.96; H = 216.99 and H = 35.57, respectively; *table IV*). Fruits from the Guineo-Congolian region had the highest values for fruit and pulp mass and number of seeds per fruit. In contrast, no significant differences were found between ecological regions regarding overall yields in fruits, pulp and number of seeds per tree ($p = 0.05$; H = 1.79; H = 3.55; H = 2.57, respectively). However, the coefficients of variation (cv) suggested considerable tree-to-tree variation for the majority of the investigated variables (*table IV*).

The Principal Component Analysis (PCA) performed on productivity characteristics showed that the first two axes explained 85.83% of the observed variations in fruit and pulp mass and number of seeds (*table V*). The first axis is the productivity axis; it shows a positive relationship with and between all the productivity characteristics. The correlation between this axis and the dendrometric and ecological parameters shows a relatively significant and positive correlation between I_M (the climatic index of Mangenot, which is a measure of water availability) and productivity characteristics. This means that fruit and pulp mass, number of seeds per fruit, and overall yield of fruits, pulp and number of seeds per tree increased with higher I_M values (*i.e.*, wetter regions). Correlation between the first axis component of the PCA and D_{130}, height and crown area were not significant ($P > 0.05$) and cannot be used here to explain the observed variations. The second axis did not take into account productivity traits of *T. indica* species and was not used to assess and describe the link between productivity of the species and the dendrometric and ecological parameters.

4. Discussion

Our findings provide insight into the effect of ecological conditions on the distribution, abundance and productivity of tamarind. They also reflect the effect of human disturbance on its distribution. The nonexistence of local names for the species in some ethnic groups suggests a very recent contact with the species and thus its very late migration to their locations. This matches the hypothesis which assumes the species to have a dry ecosystem origin and suggests its very late introduction into humid regions. By contrast, the affinity of the species for water courses (gallery forests) suggests that habitats with less arid conditions better suit its establishment and expansion. The precise origin of *T .indica* is still under debate. Remnants of orchards dating back from 400 BC are known from Egypt [35], but Buddhist scriptures refer to it as 650 BC [21]. What is broadly accepted is that the species have a tropical African, Madagascarian and Asian origin [22]. Considering biogeographical regions in Africa, tamarind is most common in the Sahelian and the Sudanian ecological regions [25]. Nonetheless, it is established in

Table V.
Correlation between productivity characteristics, tree-level and ecological parameters of tamarind trees in Benin, and the axes 1 and 2 of Principal Component Analysis factors (in brackets is the proportion of variation explained by each axis, expressed in percentage).

Characteristics	Axis 1 (73.93%)	Axis 2 (11.9%)
Fruit yield per tree	0.954	-0.243
Pulp yield per tree	0.937	-0.322
Seed yield per tree	0.686	-0.409
Fruit mass	0.745	0.320
Pulp mass per fruit	0.669	0.23
Number of seeds per fruit	0.544	0.139
Diameter at 1.3 m above ground (D_{130})	0.023	-0.400*
Height	0.257	-0.307
Crown area	0.318	-0.367
Climatic index of Mangenot (I_M)	0.534**	0.531**

"*,**" : $p < 0.005$ and $p < 0.01$, respectively.

more humid zones and in coastal regions [36]. Hypotheses have assumed that the climatic variation observed from 20,000 to 10,000 Before Present and from 2,800 to 2,000 Before Present [37], and the subsequent replacement of dense forests of Equatorial Africa by savannah landscapes might have allowed the natural establishment of some savannah tree species (*i.e., Adansonia digita* L., *Vitellaria paradoxa* C.F. Gaertn., *Borassus aethiopum* Mart.) within zones of higher rainfall [7]. The latter authors have also suggested that high density of these species within the highest rainfall zone of Benin may have to do with the Dahomey Gap phenomenon which dried the humid green forest block. But tamarind might have colonized these regions before those climate change periods. During the last two decades, scientific interest has increased in the Holocene vegetational history of West Africa [38–40], and the Dahomey gap in Benin more specifically [41]. However, none of these studies, including studies in areas where tamarind is currently found, have mentioned *T. indica*, suggesting a very late migration of the species. This overlaps with our results on local ecological knowledge. However, the absence of *T. indica* from paleobotanical findings might be linked to its erratic occurrence at very low frequencies, which might result in a large under-representation compared with other taxa. In addition, considering that tropical trees are often ecologically highly plastic (at least within the tropics), their natural distribution may rather be strongly correlated to their natural dispersion strategies than local variation in environmental conditions. The correlation between spatial patterns of plant species and their dispersion strategies has been highlighted [42]. Since tamarind is a zoochorous species (monkeys and humans are its natural dispersal agents), its distribution out of its native areas might be linked to monkey and human migrations. It has been illustrated that gene flow related to Fulani migrations might explain the low inter-population genetic diversity noticed within tamarind populations in West Africa [21]. The prevalence of some economically important tree species in the savannahs of Africa north of the equator, combined with paleobotanical and historical evidence, are strong indicators of human involvement in tree dispersal [43]. However, Fulani herders' passings (*i.e.*, transhumance) are very recent in some Sudano-Guinean localities where natural and very old tamarind trees were observed, and thus transhumance cannot explain the presence of these trees (Sinsin, pers. commun.). The contribution of human migrations to the distribution of *T. indica* may be addressed through the study of the pattern of lineages among the species' populations across the main migration corridors, using chloroplastic DNA analyses [21]. With regard to the observed gregarious pattern of tamarind trees along water courses (*i.e.*, gallery forests), two questions may need to be further addressed: which are the factors or events underlying the affinity of a species typical of arid lands for wetter habitats (*e.g.*, gallery forests)? Was the paleo-climate, which favored the establishment of the species, wetter than the current climate it is facing? And, in the case of a positive answer, how far could the adaptability of the species allow its persistence in arid ecosystems?

The findings from this study confirmed the species' erratic distribution in Benin. The marked reduction of tamarind tree density between phytogeographical districts within the Sudanian and the Sudano-Guinian regions might be due to tree felling and mortality of natural regeneration caused by field burning for agricultural purposes. The natural range of the species (especially in the phytogeographical districts of Borgou North and Borgou South, as well as Zou) is characterized by extensive agriculture such as cotton (*Gossypium* spp.) production. In addition, according to our field surveys, in Borgou South and Zou the species is less important to the people except for the Fulani tribes. Thus, tamarind trees were not spared when land was cleaned for agricultural purposes. Though it is frequently observed on hillsides, tamarind was found in low density in landscapes dominated by hills and mountains such as the phytogeographical districts of the Atacora chain and partly that of Zou. This observation contrasts with findings on baobab trees [7] and may be linked to the preference of tamarind for well-drained and deep soils [17]. Three reasons may explain the presence of tamarind on hillsides: (i) tamarind seeds might have been disseminated by monkeys; and/or (ii) when dry periods start, hillsides have plentiful grass plants and are ideal pasture lands for cattle, so Fulani herders might have disseminated tamarind seeds while roaming with their cattle; (iii) cattle might also have contributed to the species' dispersion since they also feed on its fruits.

Productivity (fruit and pulp mass, and number of seeds per fruit) of tamarind trees significantly varied with ecological conditions. This is consistent with other studies that have shown that environmental variables can affect fruit size and shape, and kernel mass [7, 38]. However, estimated overall fruit yields per tree did not significantly differ across ecological regions, suggesting that tamarind trees may tend to invest in a small number of very large fruits under wetter conditions and a very large number of small fruits under dryer conditions.

Fresh fruit yield per tamarind tree in this study was 3 to 6 times lower than the figure in East Africa [(150 to 300) kg] [36]. Productivity, including overall fruit yield per tree, was weakly correlated to tree-level factors (diameter, height and crown area) and the results did not show a linear increase in productivity with tree size, in contrast with other studies [44, 45]. However, a positive correlation was observed with the climatic index of Mangenot (I_M), suggesting productivity to be relatively higher under more humid conditions. Successful fruiting in one year is often followed at the cost of vegetative growth and some woody plants alternate supra-annual schedules of low and high production years [46]. This may explain the high tree-to-tree variation revealed by the coefficients of variation (cv). It can also explain why some trees with greater diameter or crown area showed very low fruit yield. This also provides strong evidence that ecological conditions which are much less variable than production itself are not the only determinants of variation in tamarind productivity [47]. For example, disease, herbivores, adverse weather such as high-speed winds, particularly during key phenological events such as pollination or fruit development, seasonal fire [48], and severe pruning can reduce yield [49]. Variation in productivity may also reflect genetic differences [50]. In addition, because tree productivity may greatly fluctuate with time, a single census study can hardly provide an accurate estimation. Besides, the results on seed production irrespective of ecological regions indicate that the often observed lack of regeneration in the species' populations is not driven by lack of seed production. Other factors such as insect feeding pressure on seeds and soil degradation and vegetation fire could be involved.

5. Conclusion

Our study has highlighted the difficulty in understanding the current distribution of tamarind and the need for greater research on this topic. It has also provided useful preliminary information on the variation in fruit yield in tamarind. Savannah landscapes where natural populations of the species exist (*i.e.*, the phytogeographical districts within the Sudanian and the Sudano-Guinean regions) are obviously suitable for tamarind plantation. However, the affinity of the species for gallery forests elicits further interest in its capacity to survive the increasing drought stress in its current ecological range. Multi-year census studies are needed to consistently model the impact of environmental characteristics (including soil characteristics), dendrometric characters, genetic variation and human harvesting pressure (pruning) on the inter-annual variation in fruit yield in order to understand the species’ productivity better.

Acknowledgments

This study was supported by Domestication and Development of Baobab and Tamarind (EU-DADOBAT project). We especially thank Patrick Van Damme for comments on an earlier version of the manuscript. We are very grateful to the Fulani herders, local hunters and healers for their help during the field survey and the anonymous reviewers for their useful comments on improving the manuscript.

References

[1] Leakey R.R.B., Simons A.J., The domestication and commercialization of indigenous trees in agroforestry for the alleviation of poverty, Agrofor. Syst. 38 (1998) 165–176.

[2] Kouyaté A.M., Van Damme P., Caractères morphologiques de *Detarium microcarpum* Guill. et Perr. au sud du Mali, Fruits 57 (2002) 231–238.

[3] Atangana A.R., Ukafor V., Anegbeh P., Asaah E., Tchoundjeu Z., Fondoun J-M., Ndoumbe M., Leakey R.R.B., Domestication of *Irvingia gabonensis*: 2. The selection of multiple traits for potential cultivars from Cameroon and Nigeria, Agrofor. Syst. 55 (2002) 221–229.

[4] Leakey R.R.B., Shackleton S., du Plessis P., Domestication potential of marula (*Sclerocarya birrea* subsp. caffra) in South Africa and Namibia: 1. Phenotypic variation in fruit traits, Agrofor. Syst. 64 (2005) 25–35.

[5] Bouvet J-M, Kelly B., Sanou H., Allal F., Comparison of marker- and pedigree-based methods for estimating heritability in an agroforestry population of *Vitellaria paradoxa* C.F. Gaertn. (shea tree), Genet. Resour. Crop Evol. 55 (2008) 1291–1301.

[6] Ekué M.R.M., Gailing O., Finkeldey R., Transferability of Simple Sequence Repeat (SSR) Markers developed in *Litchi chinensis* to *Blighia sapida* (Sapindaceae), Plant. Mol. Biol. Rep. 27 (2009) 570–574.

[8] Leakey R., Fuller S., Treloar T., Stevenson L., Hunter D., Nevenimo T., Binifa J., Moxon J., Characterization of tree-to-tree variation in morphological, nutritional and medicinal properties of *Canarium indicum* nuts, Agrofor. Syst. 73 (2008) 77–87.

[7] Assogbadjo A.E., Sinsin B., Codjia J.T.C., Van Damme P., Ecological diversity and pulp, seed and kernel production of the baobab (*Adansonia digitata*) in Benin, Belg. J. Bot. 138 (1) (2005) 47–56.

[9] Schlichting C.D., Pigliucci M., Phenotypic evolution: a reaction norm perspective, Sinauer Assoc., Sunderland, Mass., U.S.A., 1998.

[10] Gaoue O.G., Ticktin T., Impacts of bark and foliage harvest on *Khaya senegalensis* (Meliaceae) reproductive performance in Benin, J. Appl. Ecol. 28 (2008) 34–40.

[11] Diggle P.J., Robust density estimation using distance methods, Biometrika 62 (1) (1975) 39–48.

[12] Young L.J., Young, H., Statistical ecology: a population perspective, Kluwer Acad. Publ., Boston, U.S.A., 1998.

[13] Diggle P.J., Besag J., Gleaves J.T., Statistical analysis of spatial point by means of distance methods, Biometrics 32 (1976) 659–667.

[14] Gaoue O.G., Ticktin T., Fulani knowledge of the ecological impacts of *Khaya senegalensis* (Meliaceae) foliage harvest in Benin and its implications for sustainable harvest, Econ. Bot. 63 (3) (2009) 256–270.

[15] Maundu P.M., Ngugi G.W., Kabuye C.H.S., Traditional food plants of Kenya, Natl. Mus. Kenya, Nairobi, Kenya, 1999.

[16] Eyog Matig O., Gaoué O.G., Dossou B., Réseaux "Espèces Ligneuses Alimentaire", C. R. Prem. Réun. Réseau, 11–13 déc. 2000, CNSF, Ouagadougou, Burkina Faso, Inst. Int. Ressour. Phytogénét., 2002.

[17] El-Siddig K., Gunasena H.P.M, Prasad B.A. Pushpakumara D.K.N.G., Ramana K.V.R., Vijayanand P., Williams J.T., Tamarind, *Tamarindus indica* L., Southampt., Cent. Underutil. Crops, Southampt., U.K., 2006.

[18] Bowe C., Haq N., Quantifying the global environmental niche of an underutilized tropical fruit tree (*Tamarindus indica*) using herbarium records, Agric. Ecosyst. Environ. 139 (1–2) (2010) 51–58.

[19] Soloviev P., Niang T.D., Gaye A., Totte A., Variabilité des caractères physico-chimiques des fruits de trois espèces ligneuses de cueillette récoltés au Sénégal : *Adansonia digitata*, *Balanites aegyptiaca* et *Tamarindus indica*, Fruits 59 (2004) 109–119.

[20] Diallo B.O., Biologie de la reproduction et évaluation de la diversité génétique chez une légumineuse : *Tamarindus indica* L. (Caesalpinioideae), Univ. Montp. II, Sci. Tech. Languedoc, Thèse, Montp., France, 2001.

[21] Diallo B.O., Joly H.I., Mckey D., Hossaert-Mckey M., Chevallier M.H., Genetic diversity of *Tamarindus indica* populations: Any clues on the origin from its current distribution?, Afr. J. Biotechnol. 6 (7) (2007) 853–860.

[22] Diallo B.O., Mckey D., Chevallier M-H., Joly H.I., Hossaert-Mckey M., Breeding system and pollination biology of the semi-domesticated fruit tree, *Tamarindus indica* L. (Leguminosae: Caesalpinioideae): Implications for fruit production, selective breeding, and conservation of genetic resources, Afr. J. Biotechnol. 7 (22) (2008) 4068–4075.

[23] Diallo B.O., Joly H.I., McKey D., Hossaert-McKey, M., Chevallier M.H., Variation des caractères biométriques des graines et des plantules de neuf provenances de *Tamarindus indica* L. (Caesalpinioideae), Fruits 65 (3) (2010) 153–167.

[24] Fandohan B., Assogbadjo A.E., Glèlè Kakaï, R., Sinsin, B., Van Damme P., Impact of habitat type on the conservation status of tamarind (*Tamarindus indica* L.) populations in the W National Park of Benin, Fruits 65 (1) (2010) 11–19.

[25] White F., The vegetation of Africa, UNESCO Paris, France, Nat. Resour. Res. 20 (1983) 1–356.

[26] Anon., Troisième recensement général de la population et de l'habitation (RGPH-3), Résultats définitifs : Caractéristiques générales de la population, Inst. Natl. Stat. Appl. Econ. (INSAE), Cotonou, Bénin, 2003.

[27] Adomou C.A, Sinsin B., van der Maesen L.J.G., Phytosociological and chorological approaches to phytogeography: a meso-scale study in Benin, Syst. Geogr. Plants 76 (2006) 155–178.

[28] Grais R.F., Coulombier D., Ampuero J., Lucas M.E.S., Barretto A.T., Jacquier G., Diaz F., Balandine S., Mahoudeau C., Brown V., Are rapid population estimates accurate? A field trial of two different assessment methods, Disasters 30 (3) (2006) 364–376.

[29] Diggle P.J., Statistical analysis of spatial point processes, Second ed., Arnold, Lond., U.K., 2003.

[30] Lamien N., Tigabu M., Guinko S., Oden P.C., Variations in dendrometric and fruiting characters of *Vitellaria paradoxa* populations and multivariate models for estimation of fruit yield, Agrofor. Syst. (2007) DOI 10.1007/s10457-006-9013-x.

[31] Leakey R.R.B., Fondoun J.-M., Atangana A., Tchoundjeu Z., Quantitative descriptors of variation in the fruits and seeds of *Irvingia gabonensis*, Agrofor. Syst. 50 (2000) 47–58.

[32] Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A., The WorldClim interpolated global terrestrial climate surfaces, Vers. 1.3., http://biogeo.berkeley.edu/, 2004.

[33] Kouyaté A.M., Aspects ethnobotaniques et étude de la variabilité morphologique, biochimique et phénologique de *Detarium microcarpum* Guill et Perr. au Mali, Univ. Ghent, Thèse, Ghent, Belg., 2005.

[34] Ryan T.A., Joiner B.L., Normal probability plots and tests for normality: technical report, Univ. Park, Stat. Dep., Pa. State Univ., State Coll., Pennsylvania, U.S.A., 1976.

[35] Aubréville A., Flore forestière soudano-guinéenne, AOF-Cameroun-AEF, Soc. Ed. , Marit. Colon., Paris, France, 1950.

[36] Jama B.A., Mohamed A.M., Mulatya J., Njui A.N., Comparing the “Big Five”: A framework for the sustainable management of indigenous fruit trees in the drylands of East and Central Africa, Ecol. Indic. 8 (2) (2008) 170–179.

[37] Maley J., Brenac P., Vegetation dynamics, palaeoenvironments and climatic changes in the forests of West Cameroon during the last 28,000 years, Rev. Palaeobot. Palynol. 99 (1998) 157–188.

[38] Salzmann U., Waller M., The Holocene vegetational history of the Nigerian Sahel based on multiple pollen profiles, Rev. Palaeobot. Palynol. 100 (1998) 39–72.

[39] Salzmann U., Are savannas degraded forests? A Holocene pollen record from the Sudanian zone of NE Nigeria, Veg. Hist. Archaeobot. 9 (2000) 1–15.

[40] Salzmann U., Hoelzmann P., Morczineck I., Late Quaternary climate and vegetation of the Sudanian zone of NE Nigeria, Quat. Res. 58 (2002) 73–83.

[41] Salzmann U., Hoelzmann P., The Dahomey gap: An abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene, Holocene 15 (2) (2005) 190–199.

[42] Collinet F., Essai de regroupement des principales espèces structurantes d’une forêt dense humide d’après l’analyse de leur répartition spatiale (Forêt de Paracou-Guyane), Lab. Biom., Génét. Biol. Popul., UMR CNRS 5558, Group. Intérêt Sci. Sylvolab, Guyane, France, 1997.

[43] Maranz S., Wiesman Z., Evidence for indigenous selection and distribution of the shea tree, *Vitellaria paradoxa*, and its potential significance to prevailing parkland savanna tree patterns in sub-Saharan Africa, north of the equator, J. Biogeogr. 30 (2003) 1505–1516.

[44] Wadt L.H.O., Kainer K.A., Gomes-Silva D.A.P., Population structure and nut yield of *Bertholletia excelsa* stand in southwestern Amazonia, For. Ecol. Manag. 211 (2005) 371–384.

[45] Zuidema P.A., Boot R.G.A., Demography of the Brazil nut tree (*Bertholletia excelsa*) in the

Bolivian Amazon: Impact of seed extraction on recruitment and population dynamics, J. Trop. Ecol. 18 (2002) 1–31.

[46] Kelly D., Sork V.L., Mast seeding in perennial plants: why, how, where?, Annu. Rev. Ecol. Evol. Syst. 33 (2002) 427–447.

[47] Koenig W.D., Knops J.M.H., Patterns of annual seed production by Northern Hemisphere trees: a global perspective, Am. Nat. 155 (2000) 59–69.

[48] Stephenson A.G., Flower and fruit abortion: Proximate causes and ultimate functions, Annu. Rev. Ecol. Evol. Syst. 12 (1981) 253–279.

[49] Ghosh S.N., Bera B., Kundu A., Roy S., Dutta Ray S.K., Fruit production and quality improvement in aonla (*Emblica Officinalis* Gaertn.) through canopy management, J. Agric. Technol. 3 (8) ser. n°21 (2009) 40–43.

[50] Assogbadjo A.E., Kyndt T., Sinsin B., Gheysen G., Van Damme, P., Patterns of genetic and morphometric diversity in Baobab (*Adansonia digitata*) populations across different climatic zones of Benin (West Africa), Ann. Bot. 97 (2006) 819–830.

Reparto geográfico, densidad de los árboles y producción de los frutos de *Tamarindus indica* L. (Fabaceae) en tres regiones ecológicas en Benín.

Resumen — **Introducción**. El potencial de domesticación de los árboles frutales indígenas suscitó un creciente interés. Sin embargo no hay muchos documentos sobre la forma en la que las condiciones ecológicas afectan la abundancia de estas especies y su rendimiento en frutos, lo que es un elemento esencial para prever planes de gestión sostenible realistas. **Material y métodos**. Para estudiar el efecto de las condiciones ecológicas en el reparto, la abundancia y los rendimientos de los tamarindos (*T. indica*) en tres regiones ecológicas de Benín, en África del Oeste, empleamos los conocimientos ecológicos locales, datos de presencia/ausencia y métodos cuantitativos. **Resultados y discusión**. El conocimiento del área de reparto ecológico por las comunidades rurales concordó con los resultados científicos. El reparto natural de los tamarindos se limitó a las regiones sudanesas y sudano-guineanas y su densidad disminuyó con el aumento del índice de humedad; la densidad más alta (2 árboles·km^{-2}) fue en la región sudanesa y la más baja en la región guineo-congolesa (presencia escasa). Por otra parte, la masa de pulpa y de frutos, así como el número de semillas por fruto variaron notablemente; estos rasgos fueron más frecuentes en la región húmeda guineo-congolesa. No obstante, no apareció ninguna variación significativa entre una región ecológica y otra, en cuanto a los rendimientos generales de frutos por árbol. Esto podría indicar que los tamarindos tienden a producir un número bajo de frutos grandes en un medio más húmedo y un número elevado de frutos pequeños en un medio más seco. **Conclusión**. Nuestros resultados pueden sugerir que las zonas semi-áridas convienen mejor a la domesticación de *T. indica*. Sin embargo la productividad de la especie podría ser más alta en condiciones más húmedas. En base a su afinidad por los bosques de galería, recomendamos más estudios profundizados sobre su capacidad de sobrevivir a crecientes estreses hídricos en su entorno ecológico actual.

Benin / *Tamarindus indica* / distribución de la población / densidad de la población / ructificación/ conocimiento indígena