

Stock Density and Fruit Yield of African Walnut in Tropical Lowland Rainforests of Southwest Nigeria

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Abstract

Despite the high socio-economic potentials of African walnut, *Plukenetia conophora* Mull-Arg, there is a dearth of information on stock density and yield studies under different site conditions. Therefore, this study was carried out to investigate the stock density and fruit yields of *P. conophora* in three different habitats (i.e. less disturbed natural forest, recently disturbed natural forest and plantation forest) within Omo Forest Reserve (OFR) and Shasha Forest Reserve (SFR) of Nigeria. Stratified random sampling was used to carry out the inventory survey. Fruit yields were determined by collecting fruit falls through double sampling approach. Both descriptive and inferential statistics were used in analysing the data at $p=0.05$. Stock densities of *P. conophora* were 5.33 ± 1.7 stands/ha, 14.67 ± 2.05 stands/ha and 16.00 ± 2.94 stands/ha in OFR, while they were 7.33 ± 0.47 stands/ha, 14.67 ± 1.25 stands/ha and 10.67 ± 0.47 stands/ha in SFR for recently disturbed forest, less disturbed forest and plantation forest respectively. There were significant differences in number and distribution of species by forest types, but not between forest reserves. The mean yield of *P. conophora* was estimated at 7,800 kg/ha/yr for OFR and 6,534 kg/ha/yr for SFR. Yields from plantation area contributed more in OFR, while yields from less disturbed natural forest area were higher in SFR. Yields from recently disturbed natural forest were consistently lower in the two reserves. These results show that *P. conophora* thrives better in plantation and old re-growth forests. This information is pertinent towards improving the management of the species, increase its productivity and enhance benefits in a more sustainable manner to the rural populace.

Keywords: African walnut; density; yield; tropical lowland rainforests

Introduction

The African walnut, *Plukenetia conophora* Mull-Arg (Syn. *Tetracarpidium conophorum*) is one of the top priority non-timber yielding plant species within the tropical lowland rainforest of southwestern Nigeria (Amusa and Jimoh, 2012). It is a perennial woody climber belonging to the family Euphorbiaceae in the order Malpighiales. It is found mostly in the southern and western regions of Nigeria as well as other West and Central African countries including Sierra-Leone, Benin, Cameroun, Equatorial Guinea and Gabon (Dalziel, 1937). *P. conophora* is widely harvested from natural forests,

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plantations, compound farms and multi strata agroforestry systems. The leaves, bark, root and fruit of the species are considered to have medicinal properties (Samson et al., 2014).

According to Ajaiyeoba and Fadare (2006), the leaves of *P. conophora* are used for the treatment of dysentery and to improve fertility in males. The bark is used in tea as laxative, chewed for toothache, prevent and control high blood pressure and also as a male fertility agent. The root is used for treatment of haemorrhoids, frost bite and varicose ulcers (Samson et al., 2014). The main economic importance of the species lies in the edibility of its oil-rich seeds or nuts, which are consumed by many as a snack and delicacy within its distributional range. It is a soup thickener and an antidote against snake bite. Also, the oil is fast drying and has been used in the formulation of wood varnish, stand oil, vulcanized oil for rubber and leather substitute (Awodoyin et al., 2000; Jiofack et al., 2013).

The importance of *P. conophora* as an indigenous fruit climber is high as it is a multi-purpose crop. Local populations within the West and Central African region exploit the seeds to generate incomes to enhance their social and economic need (Jiofack et al., 2013). Despite the huge socio-economic potentials of this species, information on stock density and yield studies under different site conditions are inadequate. Yet, one of the prerequisite to enhancing the contribution of non-timber forest products to forest conservation and sustainable management is research that provides baseline information and scientific assessment of their potentials. Therefore, this study was carried out to investigate the stock density and fruit yield of *P. conophora* in different habitats within the tropical lowland rainforest of Omo and Shasha Forest Reserves, southwest Nigeria. This is important in order to improve the management of the species, increase its productivity and enhance benefits in a more sustainable manner to the rural populace who are usually smallholder farmers.

2. Methods and Materials

2.1 The Study Area

The study was carried out in Omo and Shasha Forest Reserves (Figure 1) located within the tropical lowland rainforest zone of southwestern Nigeria. Omo Forest Reserve (OFR) is located between Latitudes $6^{\circ} 35' - 7^{\circ} 05'$ N and Longitudes $4^{\circ} 19' - 4^{\circ} 40'$ E in the Ijebu East and North Local Government Areas of Ogun State, Southwestern Nigeria. The Reserve covers an area of about 132,500 ha (Oates et al., 2008) forming common boundaries with Osun, Ago-owu and Shasha Forest Reserves in Osun State and Oluwa Forest Reserve in Ondo State, all of which also share some common natural endowments. The Nigerian Government legally gazetted it a forest reserve in 1918. The government in 1946 established a 460 ha Strict Nature Reserve (SNR) within Omo Forest Reserve. This was upgraded to a Biosphere Reserve (BR) in 1977 by UNESCO (Obioho, 2005). However, going by the UNESCO website's description, the entire OFR could aptly be referred to as a Biosphere Reserve (<http://www.unesco.org/mab/BRs.shtml>). A Biosphere Reserve combines a core protected areas with zones where sustainable development is fostered by local dwellers and enterprises. Still, except in the SNR, all the remaining natural forest in the reserve has been heavily damaged by many years of logging, which continues at a high rate. The vegetation of the reserve is a mixed moist semi-deciduous rainforest. Earlier works reported by Okali and Ola-Adams (1987) distinguished a dry forest in the northern part and a humid forest in the southern part. The plant families with the most abundant individuals include Araceae, Asteraceae, Ebenaceae, Lilliacae, Papilionoideae, Poaceae, Rubiaceae and Violaceae. The most common tree species are *Diospyros spp.*, *Drypetes spp.*, *Strombosia pustulata*, *Rinorea dentata* and *Voacanga africana* (Ojo, 2004). Oates et al., (2008) in a survey coordinated by the Nigerian Conservation Foundation (NCF) revealed that Omo's rainforest contains other important species of trees including: oil palms (*Elaeis guineensis*), bamboo (*Bambusa vulgaris*),

rattans (*Calamus spp*), rubber (*Hevea brasiliensis*) and African mahogany (*Khaya spp*) and possibly still contains the iroko (*Milicia excelsa*). In many parts of the forest there is dense undergrowth and a low density of large trees. The rainy season in OFR usually commences in March. The mean annual rainfall in the area ranges from about 1,600 to 2,000 mm with two annual peaks in June and September, with November and February being the driest months (Isichei, 1995). Temperature ranges from 21.40°C to 32.15°C and a minimum relative humidity of 76.34% (Adebisi, 2004). A large chunk of the forest (94,380 ha) was converted to *Gmelina arborea* monoculture in the early eighties in a programme assisted by loans from the World Bank and the African Development Bank to provide material for a pulp mill at Iwopin (which is now moribund). Oates et al. (2008) estimated total area of remaining natural forest in the reserve at 230 km² (23,000 ha). For effective management, the reserve was sub-divided into areas or sectors called J1, J3, J4 and J6. These sub-divisions were apportioned to people already living in the reserve in isolated villages or camps called enclaves. In addition to these settlements (which have continued to grow), large numbers of migrant farmers have moved into the reserve, some of them encouraged as *taungya* farmers to help create the *Gmelina* plantations. Within the various sectors there are several settlements. Estimated total population in the area is put at between 20,000 and 25,000 people. The communities are farming communities that rely on the forest as a supplementary source of livelihood. Farming, fishing, hunting and collection of Non-timber forest products are the predominant occupations for the majority of the enclaves' population.

On the other hand, Shasha Forest Reserve (SFR) is located between Latitudes 7° 00' - 7° 30' N and Longitudes 4° 00' - 5° 00' E in Ife South Local Government Area of Osun State, Southwestern Nigeria. The Reserve was gazetted in 1925 as part of the Old Shasha Forest Reserve. It shares boundaries with Omo Forest Reserve on the west. The northern and eastern boundaries are with Ife Native Authority Reserve and Oluwa Forest Reserve in Osun and Ondo States respectively. The total area of the Reserve is around 31,000 ha (Balogun, 2007; Oates et al., 2008). Out of this, about 6,920 ha is under plantations of various species such as *Gmelina arborea*, *Tectona grandis*, *Terminalia spp*, *Pinus spp* and *Nauclea diderichii*. The remaining 24,080 ha is currently dominated by pockets of degraded natural forests characterised with broken canopies. The original vegetation structure of the reserve is three storied with scattered emergents (Jimoh, 2002). Plants with the most abundant families include: Sterculiaceae, Ebenaceae, Olacaceae, Euphorbiaceae and Flacaurtiaceae. Currently, the vegetation of the reserve is dominated by pockets of degraded natural forests with broken canopy structure and plantations of exotic forest species as well as few indigenous species. The climate of SFR as described by Kio (1978 cf. Jimoh, 2002) comprises two peaks of rainfall in July and September. The rainy season usually commences from March/April and lasts till November. There is also a short dry spell in August. Total Annual rainfall ranges from 887 mm to 2,180mm. Rainfall also occurs at irregular interval during the dry season with about 10% of the total annual rainfall occurring within the period. The mean annual temperature averages 26.5°C with annual range of between 19.5°C and 32.5°C. The reserve is sub-divided into two major areas viz, Area 4 and Area 5. There are about 40 communities within and around the reserve. They engage in cocoa farming, hunting, forestry works, produce-buying and selling and other menial activities. The population of these communities range from 200 to as many as 2,000 people. The enclaves within the reserve vary in number and size for both Areas 4 and 5. The enclaves are inhabited by people of different ethnic origin who also engage in hunting and Non-timber forest products gathering on seasonal basis. The population of each enclave range from ten to one hundred.

2.2 Methods used

Stratified random sampling was used to carry out inventory survey of *P. conophora* in the study area. Each of the forest reserve was stratified into three viz; less disturbed natural forest (for areas that have been spared of human perturbation for at least ten years); recently disturbed natural forest (for areas that have suffered one form of human perturbation or the other in the last five years); and plantation forest (for areas carrying plantation species). Following a tested methodology for non-timber forest products assessment (Hall and Bawa 1993; Sunderland and Tchouto 1999; Siebert 2004), the inventory consisted of a series of temporary, parallel, 10 m-wide belt transects established along a baseline. In each stratum (as defined above), three belt transects of 500 m×10 m were laid along a predefined compass bearing. Enumeration was done carefully along the belt transect within 5 m on either side of the central line for all individuals of the species. A total of nine transects were inventoried in each reserve.

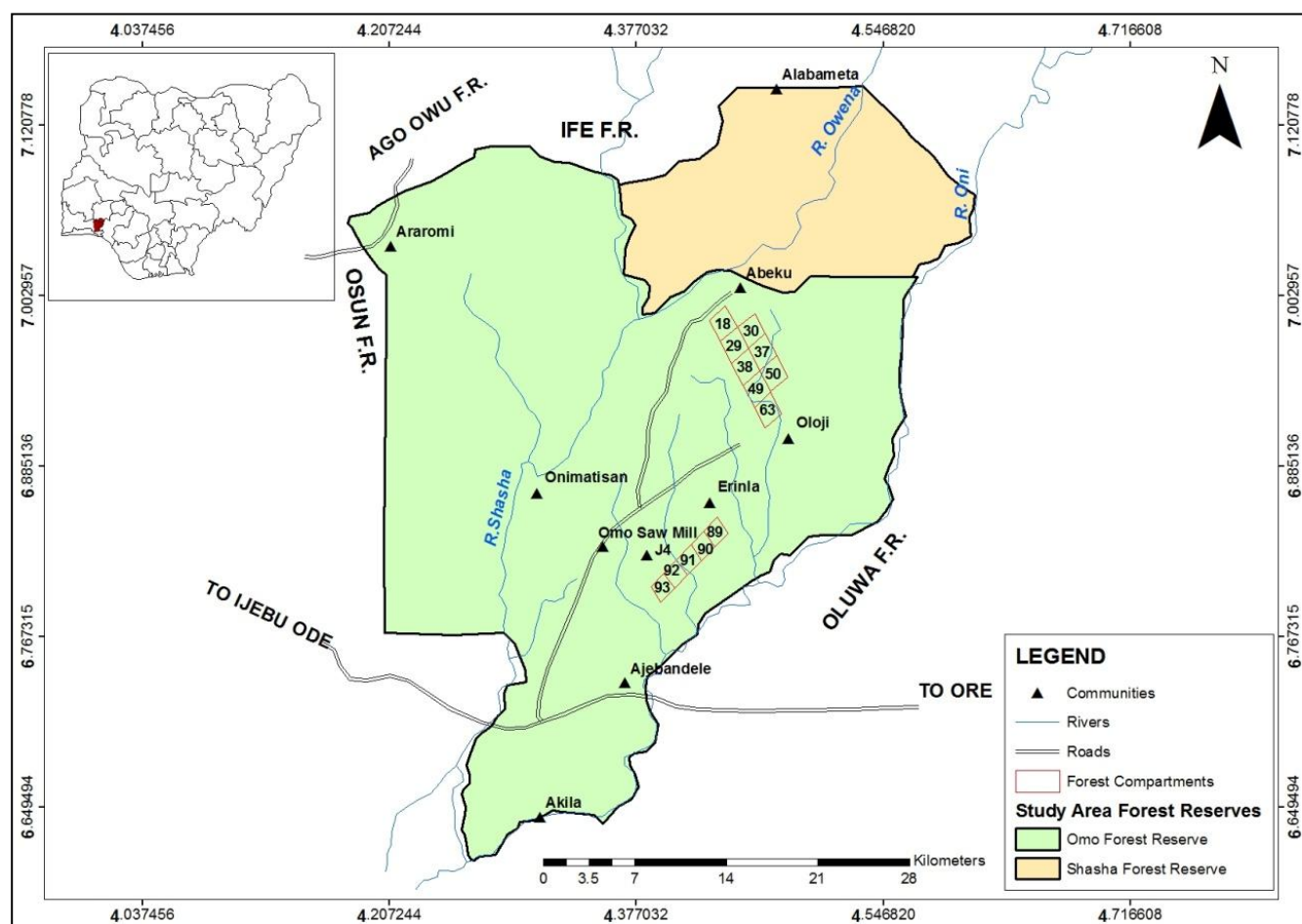


Figure 1: Map of Omo-Shasha Forest Reserve Complex.

In order to determine yield, specific stands of *P. conophora* were randomly selected, marked and monitored within the different forest stratification enumerated earlier. This represents sub-samples from inventory of population, an approach referred to as double sampling by Wong (2000). The yield measurement involved 24 stands, representing 12 stands in each forest reserves and four stands in each forest type. Fruit yield was determined by collecting fruit falls in plots at every 7-10 days interval. Each

collection was weighed and recorded. Values obtained were applied to the inventory of stock densities to give gross product yield of the study area. This was done by deriving a conversion factor. In this case, the mean weights of product per individual plant (kg) multiplied by the estimated total number of individuals in the population was used (Peters 1996; Wong 2000).

The data obtained through inventory survey on *P. conophora* was used in determining the stock density and distribution of the species. The hypothesis that: there is no significant difference in the number and distribution of the species by forest type in the study area was tested using the Kruskal-Wallis test at $p < 0.05$. The Friedman test was further used to analyse for differences in the number and distribution of the species for the two forest reserves. The test was also carried out at $p < 0.05$.

3. Results

P. conophora was fairly prevalent in all forest types sampled for both Omo and Shasha Forest Reserves. More stands of the species were found in the plantation area in OFR. In the Reserve, stock densities of *P. conophora* range from 5.33 ± 1.7 stands/ha in recently disturbed natural forest to 14.67 ± 2.05 stands/ha in less disturbed natural forest and 16.00 ± 2.94 stands/ha in plantation area. In SFR, stock densities were 7.33 ± 0.47 stands/ha in recently disturbed natural forest, 10.67 ± 0.47 stands/ha in plantation area and 14.67 ± 1.25 stands/ha in less disturbed natural forest (Table 1). There were no differences in mean densities of *P. conophora* for all sites in the two reserves. Kruskal-Wallis test, however, showed significant differences in densities and distribution of the species by forest type in both reserves (OFR; Kruskal-Wallis chi-squared=16.2399, df=2, p -value=0.0002975; SFR; Kruskal-Wallis chi-squared=18.4265, df=2, p -value=9.971e-05). The Friedman test showed no significant difference in the density and distribution of the species for the two forest reserves (Friedman chi-squared=0, df=1, p -value=1; Figures 2 and 3). Generally, *P. conophora* seems to be well adapted in all the forest types and grows in association with taller trees.

Table 1: Current population status of *Plukenetia conophora* in Omo and Shasha Forest Reserves.

Site (Forest types)	Forest Reserve			
	OFR		SFR	
	Total number of individuals in each forest types	Mean number of individuals per hectare	Total number of individuals in each forest types	Mean number of individuals per hectare
Plantation Area	24	16.00	16	10.67
Natural Forest (Rested for the past 10 years and above)	22	14.67	22	14.67
Natural Forest (Disturbed within the past 5 years)	8	5.33	11	7.33
Mean (all sites)	18	12	16.33	10.89

The mean yield of product (nuts) produced per hectare per year was estimated at 7,800.00 kg for OFR and 6,534.00 kg for SFR (Table 2). The total yield of product produced per hectare per year was estimated at 23,400.00 kg for OFR and 19,602.00 kg for SFR. Mean yield of product available was estimated at 780,000.00 kg (780.00 tonnes) and 110,745.76 kg (110.75 tonnes) for OFR and SFR respectively. Yields from plantation area contributed more in OFR, while yields from stands in natural

forest area (rested for the past 10 years and above) contributed more to overall estimate in SFR. Yields from disturbed natural forest were consistently lower in the two forest reserves. Extrapolating for the total stock of product (fruit) currently available in the two forest reserves with sampling intensities of 0.010% and 0.034% for OFR and SFR respectively gives estimates of 2,340,000.00 kg (2,340 tonnes) in OFR and 332,237.28 kg (332.28 tonnes) in SFR.

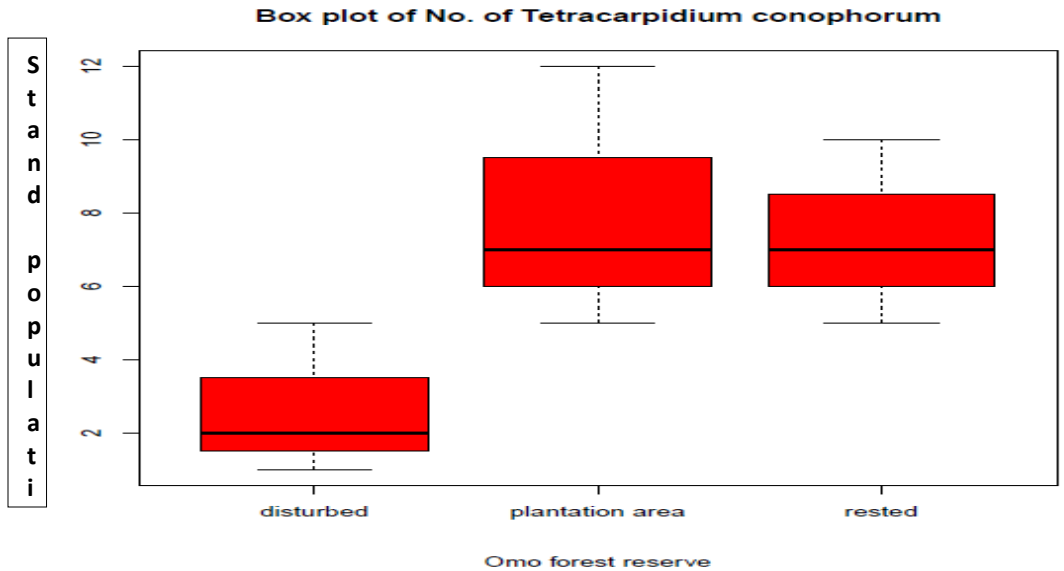


Figure 2: Box plot of number of *Plukenetia conophora* in OFR by forest types.

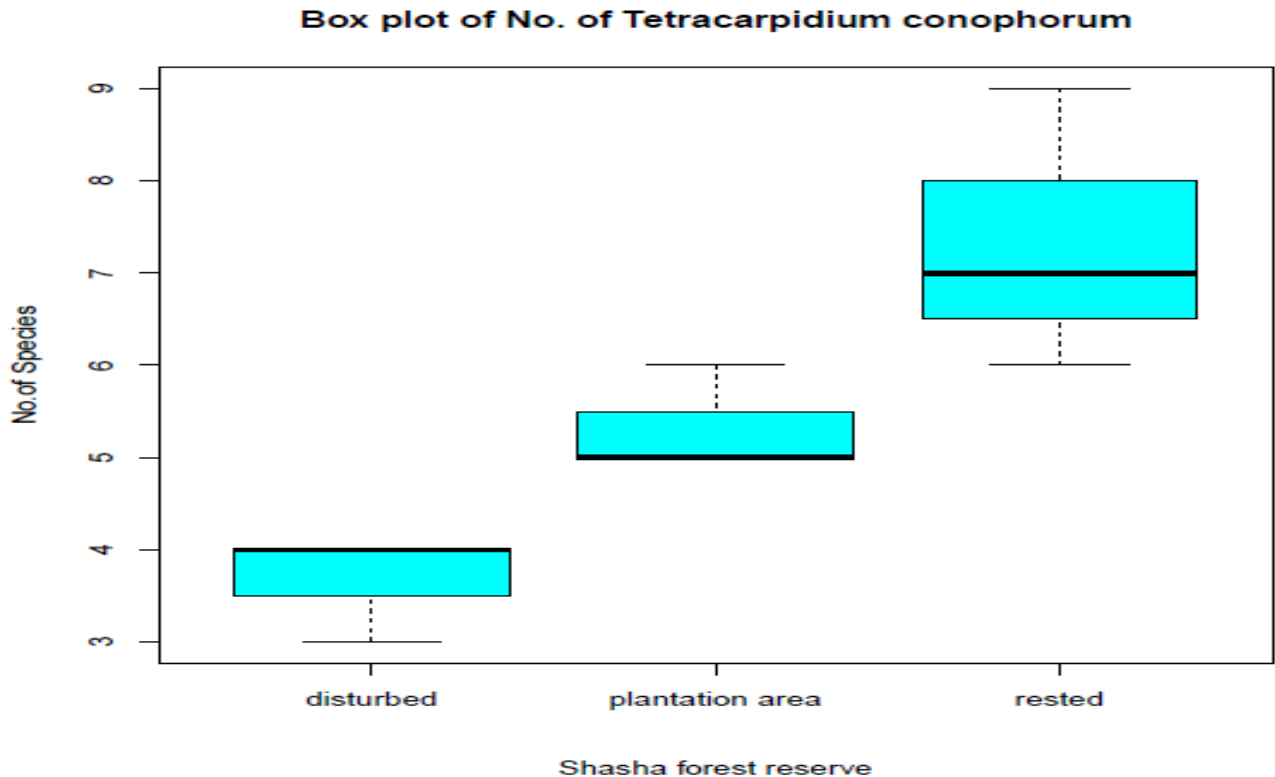


Figure 3: Box Plot of number of *Plukenetia conophora* in SFR by forest types.

Table 2: Yield estimates (kg) of *Plukenetia conophora* nuts in Omo and Shasha Forest Reserves.

Site (Forest types)	Forest reserve			
	OFR		SFR	
	Stock of products per hectare (kg) in each forest types	Stock of products for entire forest reserve (kg)	Stock of products per hectare (kg) in each forest types	Stock of products for entire forest reserve (kg)
Plantation Area	10,400.00	1,040,000	6,402.00	108,508.47
Natural Forest (Rested for 10 years and above)	9,535.50	953,550.00	8,802.00	149,186.44
Natural Forest (Disturbed within the past 5 years)	3,464.50	346,450.00	4,398.00	74,542.37
Total Available Stock (All sites)	23,400.00	2,340,000.00	19,602.00	332,237.28
Mean (All sites)	7,800.00	780,000.00	6,534.00	110,745.76

4. Discussion

The reported stock densities within the different habitat types in this study compared favourably well with the mean value (14 stems/ha) obtained by Jiofack et al., (2013) in their inventory of *P. conophora* within some cocoa-based agroforestry systems in Cameroun central region. Stock densities of *P. conophora* in our study were higher than what was obtained by Udoh et al. (2009) for climber species in their study of life-form and density of valuable non-timber plants in Ukpom Community Forest, Akwa Ibom State, Nigeria. Udoh et al. (2009) had reported climber species population densities of 51.0/ha, 47.0/ha, 10.0/ha, 2.0/ha and 1.0/ha for *Ancistrophyllum secundiflorum*, *Calamus deerratus*, *Gnetum africanum*, *Piper guineense* and *P. conophora* respectively. The authors' reported value for *P. conophora* was attributed to unfavourable micro-climate and paucity of viable seeds to sustain regeneration in the study area. Furthermore, the shading effect of sunlight and the allelopathic nature of some tree plant species were thought of as probable explanation for difficulty of climbers to thrive in the area.

Essentially, stock density and population distribution of plant species are influenced by biotic and abiotic conditions of their habitats. However, it is noteworthy that woody climbers have been reported to be increasing in dominance, relative to trees, in both tropical and temperate forests (Wright et al., 2004; Allen et al., 2007; Swaine and Grace, 2007). This pattern has been related to climate change, although more empirical evidence is needed. Nevertheless, it has been suggested that the dominant climbers in the southern temperate rainforest could be able to cope with land-use change, if forest clearings occur due to human activities. This was attributed to the expression of ecophysiological traits in climbers in relation to light exploitation (Gianoli et al., 2012). Gianoli et al. (2012) established significant association between the dominance of climbing plant species across light environments and changes in ecophysiological traits between forest understory and canopy gaps. This may also underscore the importance of fruit-bearing woody climbers such as *P. conophora* in the livelihoods of forest communities in the light of global change drivers, including land-use change and climate change in the tropics.

Results obtained on fruit yield in this study contrast sharply with the findings of Awodoyin *et al.* (2000) who reported a seed yield of 336.17 kg/plant at six years after planting in a simulated environment within southwest Nigeria. Higher fruit and seed yield reported in our study may be a pointer to the fact that *P. conophora* naturally thrives better in plantation and old re-growth forests. In view of the recent trend in participatory forestry programmes, the socioeconomic contributions of *P. conophora* provide an opportunity to integrate the crop under multiple land-use system within the forest landscape. Estimates of yield of Non-timber forest products such as *P. conophora* would also be of immense practical utility to forest managers and locals. This would allow for the setting of sustainable harvest limit for each product over a given period of time.

5. Conclusion

It is an established fact that deforestation, climate and habitat changes are major drivers of gene pool erosion in many plant species in the tropics. To enhance the conservation of germplasm of species and their contributions to sustainable livelihood in the region, there is need for baseline information and scientific assessment of their potentials. This study has reported considerable population densities for *P. conophora* under the different habitat types investigated. There was an established trend that *P. conophora* thrives better in plantation and old re-growth forests. This information is pertinent towards improving the management of the species, increase its productivity and enhance benefits in a more sustainable manner to the rural populace.

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References

- Adebisi, A.A., 2004. A case study of *Garcinia kola* nut production-to-consumption system in J4 area of Omo forest reserve, south-west Nigeria. *Forest products, livelihoods and conservation: case studies of non-timber forest product systems Africa*, Sunderland, T. and Ndoye, O. Eds. *Centre for International Forestry Research (CIFOR), Bogor, Indonesia*, 2: 115-132.
- Ajaiyeoba, E. O. and Fadare, D. A. 2006. Antimicrobial potential of extracts and fractions of the Africanwalnut. *African Journal of Biotechnology*, 5(22): 2322-2325.
- Awodoyin, R. O., Egunjobi, J. K. and Ladipo, D. O. 2000. Biology, germination and prospects for the domestication of the conophor nut, *Plukenetia conophora* Mull. Arg. [Syn. *Tetracarpidium conophorum* (Mull. Arg.) Hutch. & Dalz.]. *Journal of Tropical Forest Resources*, 16(1): 30-38.
- Bada, S.O, 1999. *Community Participation in the Management of Omo Forest Reserve*. Final Report for FORMECU, Federal Department of Forestry, Abuja, Nigeria, pp.44.
- Balogun, B.O, Salami, A.T. and Oloyede-Kosoko, S.O.A. 2007. Geospatial data application in the assessment of population impact on a tropical lowland rainforest of southwest Nigeria. Paper presented at the UNOOSA/Morocco/ESA International Workshop on the Use of Space Technology for Sustainable Development, Rabat Morocco, 25–27 April, 2007, pp.19
- Dalziel, J. M., 1937. *The useful plants of west Tropical Africa*. Whitefriars Press, London.
- Gianoli, E., Saldana, A. and Jimenez-Castillo, M. 2012. Ecophysiological Traits May Explain the Abundance of Climbing Plant Species across the Light Gradient in a Temperate Rainforest. *PLOS ONE* 7.6:e38831. doi:10.1371/journal.pone.0038831.

- Hall, P., Bawa. 1993. Methods to assess the impact of extraction of non-timber tropical forest product on plant population. *Economic Botany*, 47: 234- 247.
- Isichei, A.O. 1995. Omo Biosphere Reserve, Current Status, Utilization of Biological Resources and Sustainable Management (Nigeria). Working Papers of the South-South Cooperation Programme on Environmentally Sound Socio-Economic Development in the Humid Tropics. UNESCO, Paris, pp.52.
- Jimoh, S.O. 2002. A multiple use planning model for tropical rain forests: The case of Sasha Forest Reserve, Nigeria. Ph.D. Thesis submitted to the Department of Forest Resources Management, University of Ibadan, Nigeria, pp.248.
- Jiofack T., Tchoundjeu, Z., Guedje N.M., Lejoly J., Fokunang C. and Mate, M. 2013. Can the contribution of the African walnut diversifying cocoa agro forests being profitable for local stallholders in Cameroon? *Wudpecker Journal of Agricultural Research*, 2.5: 142 – 150.
- Oates, J.F., Ikemeh, A.R., Ogunesan, A.A. and Bergl, R.A. 2008. A Survey of the Rainforests in Ogun, Ondo and Osun States in South-western Nigeria to Assess Options for Sustainable Conservation. Report prepared for the Nigerian Conservation Foundation. pp.48.
- Obioho, G.I.B. 2005. Ecological ethnobotany and the management of Omo Biosphere Reserve, Nigeria. Proceedings of the 30th Annual Conference of the Forestry Association of Nigeria on Sustainable Forest Management in Nigeria: Lessons and Prospects. 7-11th November, 2005. Popoola, L. Mfon, P. and Oni, P.I. Eds. Kaduna, pp.86-91.
- Ojo, L.O. 2004. The Fate of a Tropical Rainforest in Nigeria: Abeku Sector of Omo Forest Reserve. *Global Nest*, 6(2): 116-130.
- Okali, D.U.U. and Ola-Adams, B.A. 1987. Tree population changes in treated rainforest at Omo Forest Reserve, Nigeria. *Journal of Tropical Ecology*, 3: 291-313.
- Peters, C.M. 1996. The ecology and management of non-timber forest resources. World Bank Technical pp.322. World Bank, Washington, pp.157.
- Samson S. E., Mitsan O., Samuel E. U., Yomi R. A., Alfred F. E. and Comfort B. E. 2014. Antibacterial Activity of Methanolic Leaf Extract of *Plukenetia conophora* Mull. Arg. against Selected Bacteria Isolated from Urinary Tract Infection. *International Journal of Microbiology and Application*, 1(1): 1-10.
- Siebert, S.E. 2004. Demographic effects of collecting Rattan cane and their implications for sustainable harvesting. *Conservation Biology*, 18: 424-431.
- Sunderland, T. C. H. and Tchouto, P. 1999. A Participatory Survey and Inventory of Timber and Non-timber Forest Products of the Mokoko River Forest Reserve, SW Province, Cameroon. Report for USAID/CARPE, pp.43.
- Swaine, M.D. and Grace, J. 2007. Lianas may be favoured by low rainfall: evidence from Ghana. *Plant Ecology*, 192: 271–276.
- Udo, E.S., Olajide, O. and Udoh, E.A., 2009. Life-form and Density of Valuable Non-timber Plants in Ukpom Community Forest, Akwa Ibom State, Nigeria. *African Research Review*, 3(3): 73-80.
- Wong, J.L.G. 2000. The biometrics of non-timber forest product resource assessment: a review of current methodology. Research paper for the European tropical Forest Research Network (ETFRN), Department for International Development (DFID), UK, pp.109.
- Wright, S.J., Caldero´n, O., Herna´ndez, A. and Paton, S. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Barro Colorado Island, Panama´. *Ecology*, 85: 484–489.