



Life history, uses, trade and management of *Diospyros crassiflora* Hiern, the ebony tree of the Central African forests: A state of knowledge

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ABSTRACT

The Central African forest ebony, *Diospyros crassiflora* Hiern, is a small tree native to the moist forests of the Congo Basin. Its appealing black heartwood was one of the first products to be exported from the Gulf of Guinea in the 17th century and is today one of the main sources of ebony globally. Like for other ebony species, its commercial exploitation raises serious questions about the long-term sustainability of its trade and the viability of its populations, but the dots are yet to be joined. An examination of the interface between biology, trade, and ecology is crucial to identify the interrelated factors that could influence the potential success of its conservation. This paper reviews scientific and grey literature, forest inventories, herbarium and trade data to provide a critical assessment of the main threats to *D. crassiflora* populations and gaps in the current state of knowledge. It is shown here that the species is widespread but never abundant. In the longer term the species is threatened by forest conversion to agriculture and widespread hunting of large mammals on which the species rely for seed dispersal. It is currently selectively logged principally to make musical instruments and for the hongmu Chinese market, for which only one alternative black wood, the near-threatened *Dalbergia melanoxylon* Guill. et Perr., is commercially available. Trade statistics suggest that exports from source countries where the species is cut under the forest concession system are relatively low compared to countries like Cameroon which has seen a recent increase in exports, and where ebony is exploited without forest management plans. Logging remains a concern where the exploitation and trade of *D. crassiflora* are managed in response to demand rather than informed by current stock levels, growth rate and the particular reproductive biology of this species. The recent successes of private sector initiatives to ensure the long-term supply of ebony in Cameroon are promising, but would require long-term and large-scale commitments involving direct and indirect stakeholders to develop programs for the plantation and policies for the sustainable management of the species.

1. Introduction

Ebony, as the name is used in commerce, refers to a homogeneously black or streaked wood that is dense enough to sink in water. This fine-grained wood can be polished to a high sheen (Normand et al., 1960; Gérard et al., 2011) making it greatly prized for ornamental use. Considered a precious wood, its value can attain up to USD 18,000 per m³ (Jenkins et al., 2002). Evidence of long distance trade in ebony dates back to antiquity and the word ebony itself can be traced back to the Old Kingdom of ancient Egypt (c. 2700–2200 BCE) (Erman and Grapow, 1971). Despite millennia of exploitation and trade however, our

knowledge of the basic biological characteristics of the tree species that produce this emblematic wood is at best rudimentary.

We do know that most species yielding ebony are slow-growing tropical trees belonging to the *Diospyros* genus in the Ebenaceae family. The conjunction of a slow growth rate and sustained market demand for ebony wood have today given rise to sustainability issues, with many species being harvested to near-extinction. In tropical regions where they grow, basic information on the spatial distribution of most tree species and the causes of population decline is often lacking. Ignorance of basic ecology, and how tree survival, regeneration and genetic diversity might be impacted by deforestation, selective logging and over-

Abbreviations: CAR, Central African Republic; DBH, Diameter at Breast Height; DRC, Democratic Republic of the Congo; EG, Equatorial Guinea; RoC, Republic of Congo.

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hunting, could severely hinder efforts to formulate policy for conservation and sustainable use. The situation is further compounded by taxonomic confusion in many groups, and the fact that few common names used in forestry surveys and trade are unique to a single taxonomic species (Guitet et al., 2014). The use of trade names, such as for example ‘ebony’ hinders regulation, enforcement, tracking and reporting of *Diospyros* species in timber trade. In other words, biology, trade, harvest regulation, and ecology are overlapping spheres of knowledge that together contribute to inform the state of the conservation of commercially important tree species.

With more than 700 species known worldwide, *Diospyros* is the 30th most species-rich genus of flowering plants (Frodin, 2004). Despite this diversity only ca. 30 species of *Diospyros* are known to produce black wood in various proportions (Hillis and Soenardi, 1994) and only a handful of them, from Asia, Madagascar and Africa, produce the coveted homogeneously black wood. These have long been the focus of intense trade, and now, of conservation concern. In Asia, after millennia of destructive felling, little remained of *Diospyros ebenum* J. Koenig ex Retz. for the British to exploit when they came to power in India. Of the plentiful stocks in Sri Lanka at that time, only pockets of relict populations remain (Schmerbeck and Naudiyal, 2018). Currently, *D. ebenum* is classified as nationally endangered in Sri Lanka (IUCN-SL and MENR-SL, 2007) and export, other than as handicraft with a license, is banned (Sri Lanka Export Development Board, 2014). In 2010 Madagascar prohibited the exploitation of all its *Diospyros* species, including the near-threatened endemic *Diospyros perrieri* Jum (Ke and Zhi, 2017; Faranirina et al., 2019), due to habitat destruction from selective logging, agriculture and fires. *Diospyros tessellaria* Poir., was overexploited in Mauritius from the early 17th, becoming rare by the end of the 19th century, and it is now listed as vulnerable (Lamusse, 1990; Page, 1998).

In Africa, although not a *Diospyros* species, black wood was historically sourced from the species that the ancient Egyptians referred to, *Dalbergia melanoxylon* Guill. et Perr. (Dixon, 1961). The species is listed as near-threatened on the IUCN Red List (WCMC, 1998). The large volumes harvested in semi-arid East Africa have exhausted the merchantable trees locally (Jenkins et al., 2002). Finally, the ebony of the moist tropical forests of Central Africa, *Diospyros crassiflora* Hiern, the focal species of this study, often regarded as the true ebony of Africa, has become one of the main sources of ebony wood globally. Ebony appeared in accounts of the trade in the Gulf of Guinea as early as the 17th century (Eachard, 1691) and it was among the first commodities to be exported in bulk beginning from the mid-18th century (Chamberlin, 1977). Recently, it was the subject of an IUCN Red List evaluation which identified the destruction of its natural habitat, the Central African forest, as a bigger threat to its survival than logging after considering its distribution and probable abundance, the size of the ebony market and the plantation program in Cameroon. The evaluation concluded that the species category is vulnerable and emphasized the need to document the life history, population size, distribution and the harvest level trends to further assess the state of the conservation (Schatz et al., 2019).

The development of informed conservation strategies is particularly crucial in Central Africa which has recognized biodiversity hotspots, and from where increasing volumes of wood are exported to China (CITES, 2016). However, information about *D. crassiflora* is currently limited, being mostly anecdotal and scattered through scientific journals, historical and grey literature, appearing in various languages and usually not recent, and has thus been largely overlooked by most researchers. Given the tragic fate the other species yielding jet-black ebony and the long and uninterrupted history of exploitation of *D. crassiflora* till date, it is critical to systematically review the current state of knowledge to assess the present conservation status, better inform policy makers and stakeholders, and guide future research.

The aim of the present paper is two-fold: i) to identify and synthesize the scientific and grey literature and various archived and available data and, based on the compiled information, ii) to provide a critical assessment of main threats to population sustainability and important

knowledge gaps regarding *D. crassiflora*. The three parts of this paper correspond to three overlapping spheres of knowledge that could influence the potential success of the conservation of *D. crassiflora* viz. biology, trade and management, and finally ecology. We start with 1) an overview of the biology of *D. crassiflora* where the known geographic distribution and abundance of the species is presented followed by a description of the morphological characteristics. The discussion on the taxonomical confusion around this species and physical characteristics of its wood are linked to 2) its use, trade and management which is the focus of the following section. Here the actual and potential uses of the species are analysed to interpret trends in permitted harvesting and international trade. Existing regulations are assessed in terms of their impacts on logging and stock management. Finally, 3) the ecological traits, pollination and seed dispersers of *D. crassiflora* are reviewed to understand the sensitivity of populations to logging and hunting pressures, which are linked to both trade and basic knowledge of its reproductive biology.

2. Methods

In order to assess threats to the sustainability of and gaps in the knowledge related to *D. crassiflora* I a) reviewed the scientific and grey literature available online, b) compiled and computed the species abundance from large-scale published forest inventories, c) consulted *D. crassiflora* collections in 12 herbaria as well as the datasets of small-scale scientific and private sector forest inventories to obtain observed geographic occurrences of the species, and lastly d) collated trade data from both source and destination countries statistics. The methods used for each are detailed below. Although the search of data was not aimed to focus on any one country, overall, little information was found for Democratic Republic of the Congo (DRC), Equatorial Guinea (EG) and Nigeria. The collated dataset in c) provide greater details for Cameroon and Gabon than for other countries because private sector data were available from these two countries only, and because of the spatial bias in sampling effort of herbarium specimens (Sosef et al., 2017). The trade data from source countries collected in d) was only available for Cameroon thanks to the special legislation for ebony in this country. Some data on the trade of the other source countries was found in a).

a) General literature was identified by searching the keyword (*Diospyros* OR ebony) AND (country names OR Africa OR trade) in publicly available databases. Given the paucity of recent literature written in English on the subject, the search was broadened to include databases focusing on French literature and historical accounts: Google Scholar (<http://scholar.google.com>); Google Books (<http://books.google.com>), HathiTrust Digital Library (<http://www.hathitrust.org>), Internet Archive (<http://archive.org>), Biodiversity Heritage Library (<http://www.biodiversitylibrary.org>), Gallica (<http://gallica.bnf.fr>) and Persee (<https://www.persee.fr>). The same query was repeated in French and German, the current and former official languages of most countries where the species is found. Original studies reporting findings relevant to *D. crassiflora* biology, taxonomy, use, trade, management, and ecology were identified and cited in the present review.

b) Data from published forest inventories, identified using the same methods as outlined above for the literature search, were used to compute the abundance of *D. crassiflora* in undisturbed forests. For this, the numbers of trees ≥ 10 cm in DBH in a given surface were extracted from the systematic floristic inventories examined. Counts were converted to trees ha⁻¹. Given the low abundance of the species, inventories covering a surface less than 3 ha were deemed to be too small in scale and not considered for abundance computation.

c) To map the geographic range of *D. crassiflora*, the geographic coordinates of localities as recorded in herbarium sheets and small-scale scientific and private sector forest inventories were extracted and compiled. The occurrences were collated from (i) 212 dried herbarium collections examined at BR, BRLU, LBV, MA, MO, FHI, K, L, P, U, WAG and YA herbaria (acronyms following the Index Herbariorum of Thiers)

and the Global Plants database (<http://plants.jstor.org>); (ii) 1352 ebony trees cut by Crelicam S.A.R.L. Ebony mill in Cameroon from 2014 to 2018, 157 of which were associated with a dried leaf sample examined during this study; (iii) 248 unique occurrences of *D. crassiflora* recorded in inventories conducted post-2005 in logging concessions in Gabon collected by Sylvafrica; (iv) 16 collections of dried plant samples kept at the Université Libre de Bruxelles extracted from the RAINBIO dataset (Dauby et al. 2016); and (v) 155 unique occurrences of the species in inventory data from old-growth forests collated by Gilles Dauby and Ferry Slik (Slik et al., 2015). An earlier version of this dataset was published in Schatz et al. (2019). In the present study, occurrences were classified as verified or unverified according to the availability of dried vegetal material to ascertain the identification of the species during this study. When not specified on the herbarium label, the geographical coordinates of the locality found on the herbarium samples were searched for on 1/200,000 IGN maps for Cameroon and www.openstreetmap.org for other countries. The data collected in (i) are available as Supplementary Material linked to this paper. After removing duplicated coordinates across and within datasets, 1884 unique occurrences remained.

d) In addition to the published statistics from source countries found during the review conducted according to methods outlined in a), custom statistics of destination countries were searched for in the UN Comtrade international database (<https://comtrade.un.org>), Eurostat (<http://epp.eurostat.ec.europa.eu>) for the European Union and USITC DataWeb (<https://dataweb.usitc.gov>) for the United States of America (USA). In addition, the statistics of ebony trade from the port of Douala in Cameroon was obtained from the COMCAM (Commercialisation Forestière du Cameroun) database available at <http://www.apvca.meroun.cm> (MINFOF, 2019). When tonnage summed across destination did not match the tonnage summed across exporters in the COMCAM dataset, the highest value was retained. Annual exploitation quota for ebony were retrieved from the literature (Ingram and Schure, 2010) and from the Ministry of Forestry and Wildlife, Cameroon (MINFOF, 2008–2019). The quantities and source of annual data are provided in Supplementary Material S1.

3. Biology

3.1. Distribution and abundance

The distribution of *D. crassiflora* had initially been assessed by White (1978) and Letouzey (1985). They found that it is a relatively widespread species across the Lower Guinean and Congolian lowland forests of Africa which extends between the Dahomey gap and the Albertine Rift. In the Congo Basin it was found in a relatively narrow band between the equator and ca. 4°N up to the eastern rim of the Congo Basin. The species occupied evergreen forests and islands of evergreen forests within dry semi-evergreen forests below 1,000 m a.s.l. (White, 1978; Letouzey, 1985).

Occurrence points compiled during this study from herbaria and forest inventories are shown in Fig. 1. They point to a substantially larger distribution than reported in the maps of Letouzey and White (1970a) (Supplementary Material S2), with occurrences found in the evergreen forest of north-eastern Gabon and southern Cameroon. The species westward limit is the Omo Forest Reserve in South West Nigeria (Ojo, 2004). More to the east, it is found in the forests of Cameroon, Central African Republic (CAR), DRC, EG, Gabon and Republic of Congo (RoC). The lack of known occurrences in the coastal forests of Gabon and the absence of the species from an exhaustive inventory of all tree with a DBH above one cm in 25-ha of forest at Rabi (Memiaghe et al., 2016) points to the absence of the species in this ecoregion.

Reported abundance of *D. crassiflora* stems larger than 10 cm in DBH in published forest inventories is presented in Table 1. The abundances are indicative of local abundance where the species was found and identified and cannot be directly extrapolated over larger area.

Throughout its range, the abundance of *D. crassiflora* varies by more than one order of magnitude. In every account except the Omo forest, the species was neither reported as one of the ten most frequent nor among those having the largest basal area.

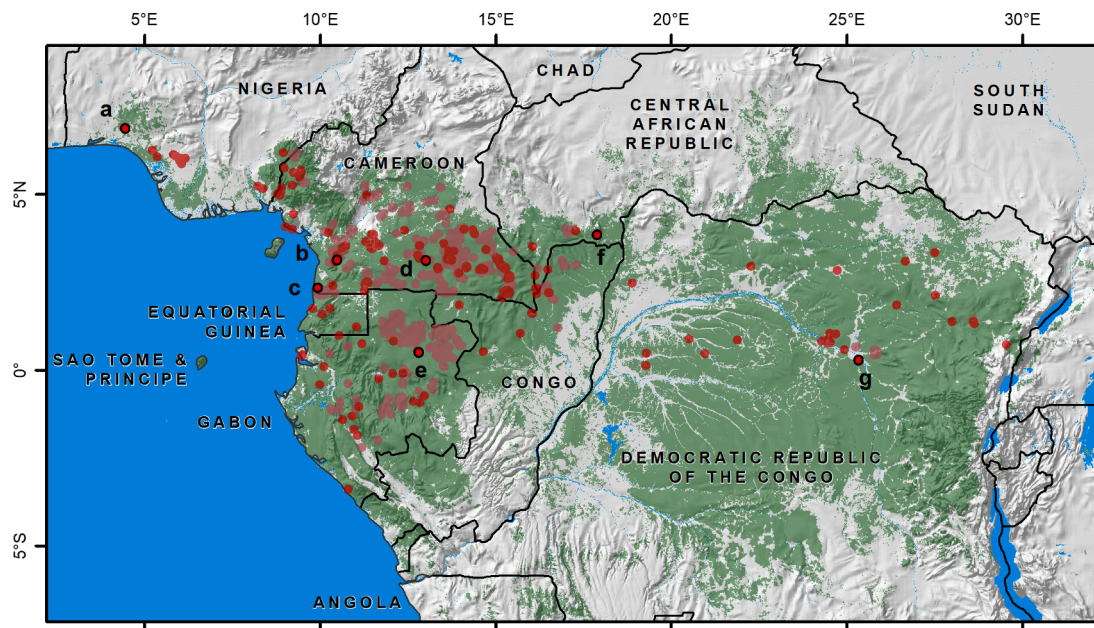


Fig. 1. Geographical distribution of known occurrences of *D. crassiflora*. Vegetal samples whose identifications were confirmed during this study are shown as bright-red dots. Lighter-red dots correspond to occurrences reported in databases, scientific inventory and logging industry data that cannot be verified. The forest inventories mentioned in the text are shown as red dots encircled in black: a, Omo (Nigeria); b, Ngovayang; c, Campo and d, Dja (Cameroon); e, Ipasa (Gabon); f, M'Baïki (CAR); g, Yoko (DRC). The current distributions of tropical terra firme broadleaved closed forests (green area) and water bodies (blue area) is adapted from the 2015 land cover map v2.0.7 provided by ESA (2017). Hillshade are derived from GMTED2010 data (Danielson and Gesch, 2011). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1Abundance of *Diospyros crassiflora* in forest inventories of trees ≥ 10 cm in DBH. Geographical distribution of the inventories is shown in Fig. 1.

Country	Locality	Vegetation type	Surface (ha)	Nbr. trees ha ⁻¹	Basal area (m ² ha ⁻¹)	Source
Nigeria	Omo	SE	16	0.31	NA	Ojo (2004)
Cameroon	Dja	EG	22.5	0.58	0.066	Sonke and Couvreur (2014)
	Campo	EG	3	5.3	0.207	Sunderland et al. (1997)
	Ngovayang	EG	5	2.9	NA	Gonmadje et al. (2011)
Gabon	Ipassa	EG	14	6.1	NA	Rosin and Poulsen (2018)
CAR	M'Baiki	SE	40	4.4	0.3	Bedel et al. (1998)
DRC	Yoko	SE	4	4.0	0.064	Lokonda (2018)

SE, semi evergreen forest; EG evergreen forest; NA, not available.

3.2. Morphology and wood characteristics

D. crassiflora is a small tree up to 25 m tall and 1.2 m in DBH. It bears large fleshy fruits 10×6.5 cm which contain up to 10 seeds $5 \times 2 \times 1.5$ cm (White, 1987). The tree is easily identified by its

macromorphological features (Fig. 2). Like for most Ebenaceae, its growth architecture consists of successive whorls of horizontal branches on the main stem according to Massart's model with regular reiterations of the model (Hallé et al., 1978). Immature leaves have a characteristic reddish colour. Black spots, often found on the lower surface of leaves,

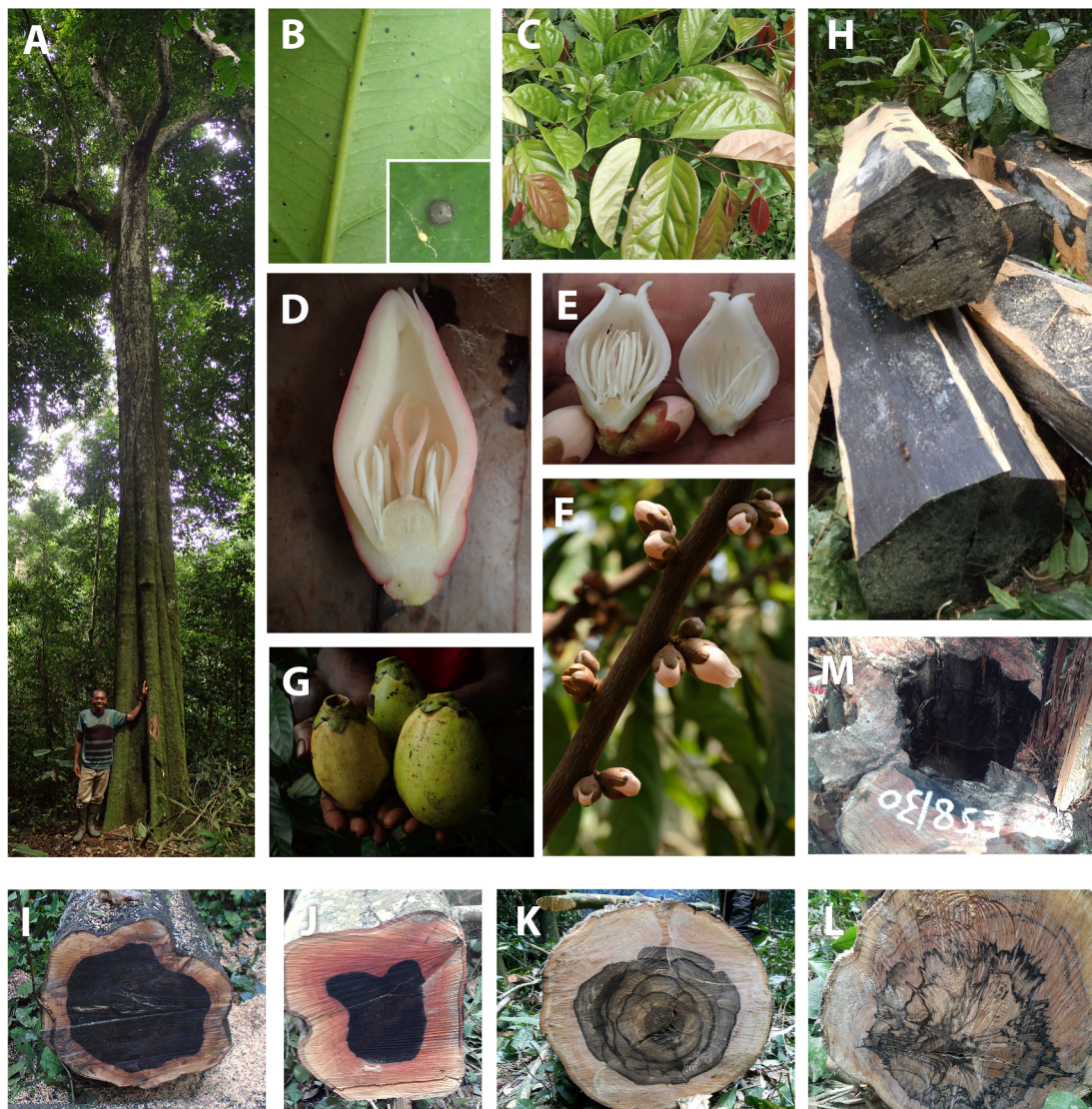


Fig. 2. Principal characteristic features of *Diospyros crassiflora*. (A) a large tree, 105 cm in diameter with typical fluted base; (B) the extrafloral nectaries on the abaxial surfaces of leaves, enlargement in the inset; (C) the growth architecture follows Massart's model and young leaves have a characteristic reddish colour, the branches are verticillate in whorls of five, with much reduced leaves on the main stem; (D) a section of a pistillate flower, with the ovary, 3 stigma (2 removed) and staminodes visible; (E) a section of staminate flowers showing numerous fertile stamens; (F) an inflorescences with pistillate flower; (G) the ripe fruits are obovate in shape and yellowish green to reddish in colour; (H) a square logs with sapwood removed at the felling site; (I, J) sections of the trunk of two different trees, ca. 60 cm in diameter, showing variable jet-black heartwood to sapwood ratio; (K, L) sections of the trunk of two different trees, ca. 60 cm in diameter, showing marble or streaked ebony pattern; (M) a freshly cut stump with hollow centre with a thin margin of black heartwood. Photo credits A—G, V. Deblauwe; H—M, Crelicam. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and usually reported as “glands” in taxonomic treatments are extrafloral nectaries (Contreras and Lersten, 1984).

With increasing age and size, the heartwood at the centre of the trunk and main branches turns black. The column of black wood is irregular and asymmetric in shape, both radially and longitudinally, usually sharp in outline and with increments not always conforming to annual growth (Hillis and Soenardi, 1994). Homogeneous black wood is the exception rather than the rule. The heartwood comes in a variety of colours, from whitish to jet black, sometimes alternating in a streaked, variegated or marbled pattern (Fig. 2I–L). When the trunk exceeds roughly 60 cm in DBH, heart rot frequently sets in, leaving a hollow pith bordered with black wood (Fig. 2M). These hollow trees are regarded as being past maturity by tree fellers and usually abandoned in the forest (Smith, 1948). The nature of the coloured substance and the mechanisms of accumulation in wood tissues have been discussed for *D. ebenum* by Wright (1904) and for 27 *Diospyros* species by Hillis and Soenardi (1994). According to the authors, the common occurrence of streaks of different intensities of black in the heartwood indicates that their formation follows a different mechanism than for normal heartwood. Ebonized zones are often associated with knots, branch stubs, decay, insect holes or injury. Hillis and Soenardi (1994) suggested that chemicals imparting the black colouring are deposited in the lumina of the cells as a distant response to infection by fungi or microorganisms after injury. The absence of black wood in some large trees could be due to the absence of invasion of appropriate pathogens. The environmental control on wood coloration is also suggested by the higher proportion of black wood in trees growing on poor rocky soils reported independently for ebony species in Indonesia (Lemmens et al., 1995), Madagascar (Perrier de la Bathie, 1950) and Sri Lanka (Wright, 1904). The genetic and environmental determinants of wood quality require further investigation as plantation programs are developed.

3.3. Taxonomic confusion in commercial ebony

A great deal of confusion surrounds the taxonomy of ebony producing species of Africa in the literature. Their botanical identity was poorly understood before the 1930s and no taxonomic revision or phylogenetic work has been done recently. Ebony exploited in the natural range of *D. crassiflora* was commercially identified by its provenance: Benin ebony after the Edo-speaking nation in Nigeria, Old Calabar, Cameroon or Cameroons, Kribi, Gabon or Gaboon ebony. Usage of these common names persist till date. ‘African blackwood’, the common name for *Dalbergia melanoxylon* wood, is sometimes erroneously used for *D. crassiflora*, which also shares the names ‘African ebony’ and ‘West African ebony’ with a variety of other African *Diospyros* (Obeng, 2012). Because the commercial names either refer to an actual or supposed source region, or to an ambiguous identification, the historical accounts of ebony trade and use must be taken with caution and interpreted in relation to current knowledge of the species distribution and uses.

Throughout its range, *D. crassiflora* is the object of a large variety of common names that sometimes refer to multiple ebony producing species: abokpo (Edo) in Nigeria; epindé-pindé (Douala), lembé (Baka), mevini (Ewondo) in Cameroon; evila (Mpongwé, Fang) in Gabon; bingo (Issongo), ngoubou (G’baya) in CAR; and Mopini in RoC, among others (Normand et al., 1960; Bouquet, 1969; Ben-Amos, 1979; Raponda-Walker and Sillans, 1995).

The scientific names used before the 1930s for species which were the source of ebony wood in Central Africa should be interpreted with caution as well. Until the end of the 19th century, the species exported from Central Africa was often erroneously identified as *D. ebenum*, a species endemic to India and Sri Lanka. It was also commonly assumed to be *D. dendo* Welwitsch ex Hiern (Chevalier, 1916). The botanical identity of the source trees has long remained controversial because of the scarcity of fertile herbarium specimens and the diversity of black wood-producing species in moist forests of Africa. For instance, *D. dendo*

(up to 30 cm in DBH), *D. gracilescens* Gürke (1 m), *D. hoyleana* F. White (25 cm), *D. iturensis* (Gürke) R. Let. & F. White (50 cm, syn. *D. insculpta* Hutch. & Dalziel), *D. preussii* Gürke (30 cm) and *D. viridicans* Hiern (40 cm) have been reported to produce ebony wood; *D. suaveolens* Gürke (50 cm, syn. *D. confertiflora* Gürke ex J. D. Kenn.), *D. zenkeri* (Gürke) F. White (30 cm) and *D. bipindensis* Gürke are known to produce grey or streaked wood which was probably used to craft small objects. Due to their rarity, small trunk sizes, or the imperfection of their wood, contemporary observers of tree felling in Cameroon and botanists concur that the wood of these above species could not have constituted a substantial part of exports from the continent (Smith, 1948; Letouzey and White, 1970a; Paquis and Normand, 1976).

Pellegrin (1934), Chevalier (1934) and Normand et al. (1960) in their respective studies of the origin of commercial ebony, concluded that all the ebony exported from the coast between Congo and Niger rivers was *D. crassiflora*. In Nigeria, an additional species yielding ebony has been exploited, *D. dendo* (syn. *D. atropurpurea*). It is a small tree from the forests of Central Africa with black heartwood and a geographical distribution similar to that of *D. crassiflora*, although extending further westward and not as far eastward. In the Cross River Basin, close to the Niger Delta, Smith (1948) made the observation that *D. crassiflora* and *D. dendo* (syn. *D. atropurpurea*) were both exploited, though most wood came from the former. In the Benin City area to the west, *D. crassiflora* still gives the bulk of ebony wood (Ben-Amos, 1979). West of this point the abundance and commercial importance of *D. crassiflora* seems to decrease relative to *D. dendo*. In the Abeokuta city area in Nigeria, *D. dendo* is said to constitute the main ebony species of commerce, where it is sold as “Lagos ebony”. The abundance of *D. dendo* was shown to be more than 40 times higher than *D. crassiflora* in the area (Ojo, 2004).

Based on an extensive sampling of fertile herbarium specimens, Letouzey and White (Letouzey and White, 1970a,b; White, 1978, 1980, 1988), established the current conception of *D. crassiflora*, which includes the synonyms *D. incarnata* Gürke ex De Wild., *D. ampullacea* Gürke and *D. evila* Pierre ex A. Chev. They recognized that the names *D. atropurpurea* Gürke and *D. flavescens* Gürke, are in fact both synonyms of *D. dendo*. They also concluded that an ebony wood producing species that Chevalier erroneously named *D. flavescens* (Chevalier, 1916), was in fact *D. crassiflora*.

Additional taxonomic confusion was created by the publication in 1952 of a homonym, *D. crassiflora* H. Perrier (non Hiern), by Henry Perrier de la Bathie for a distinct shrubby species endemic to Madagascar (Perrier de la Bathie, 1952). This name is illegitimate since the combination *D. crassiflora* had already been validly published in 1873 by W.P. Hiern in reference to the Central African ebony that is the focus of this paper. The confusion between these two distinct taxa began to have ramifications in 2011 when the CITES attempted to ban the trade of a list of ebony species from Madagascar (CITES, 2011). The CITES notification created ambiguity over the identity of the species targeted by mentioning “*Diospyros crassiflorides* (*Diospyros crassiflora*)”, inadvertently creating a new name, and making *D. crassiflora*, without the author’s name, synonym. Although this inclusion was intended to cover the species present in Madagascar only, authors of technical and scientific reports began to consider *D. crassiflora* Hiern, the Central African species, as being listed in the CITES Appendix while it is not. The confusion was clarified the following year (CITES, 2012) by listing instead the name *D. mcphersonii* G.E. Schatz & Lowry, which has just been published as a valid replacement name for *D. crassiflora* H. Perrier (Schatz and Lowry, 2011). Later, the Conference of the Parties agreed to move the Malagasy species from Appendix III to II, this time including all Malagasy specimens from the genera *Dalbergia* and *Diospyros* without reference to specific epithets (CITES, 2013). However, the confusion between the two species remain as some authors still erroneously consider *D. crassiflora* Hiern as a synonym of *D. mcphersonii*. Hereafter, the name *D. crassiflora* stated without an author name refers to *D. crassiflora* Hiern.

4. Trade and management

4.1. Domestic and export uses

Various traditional medicinal uses of leaves, bark and seeds have been observed across the range of the species. In RoC, a bark decoction of *D. crassiflora* is drunk or used as a wash to treat ovarian problems, and the bark powder is applied to heal wounds. The leaf sap is applied as eye drops for the treatment of purulent ophthalmia (Bouquet, 1969). In Cameroon, the Baka people use the powdered bark to treat abscesses, delivery pain, stomach aches and, as an enema, for abortion. They chew the seeds as an aphrodisiac (Brisson, 2011). In Gabon, the bark powder is mixed with a powder of the wood of *Pterocarpus soyauxii* Taub. to treat yaws (Raponda-Walker and Sillans, 1995).

Pharmacological research has confirmed the antifungal and antibacterial properties of stem bark extracts in vitro (Dzoyem et al., 2006; Tangmou et al., 2006; Dzoyem et al., 2007). The authors provide evidence that the presence of a naphthoquinone derivative (crassiflorone), a coumarin glycoside (gerberinol) and low concentration of plumbagin in the bark are responsible for the antimicrobial activity. The latter is a compound present in other *Diospyros* species (Rauf et al., 2017) that has been reported to have various medicinal attributes including antibacterial, antifungal, anticancer, antimalarial, antimutagenic and antioxidant. However, side effects include being a potent DNA damaging agent at high doses (Demma et al., 2009; Sumsakul et al., 2014). Crassiflorone, plumbagin and crude extract from *D. crassiflora* were later shown to be effective in vitro against gonorrhoea and tuberculosis (Kueté et al., 2009). No evidence was found in literature that these supposed and proven medicinal properties resulted in local or international trade.

The wood of *D. crassiflora* is traditionally used for the crafting of small objects like pipes, mortars or arrowheads (Bernardin, 1877; Raponda-Walker and Sillans, 1995). Recently the bulk of ebony carving was either bought locally by tourists or directly exported abroad. For instance, the ebony-carvers of Benin City in Nigeria are famous for the small sculptures they make out of *D. crassiflora* harvested for this purpose. This is a relatively recent use for this wood, ebony being a clear departure from materials traditionally used for carving (Ben-Amos, 1979). Estimates of the quantities of ebony sold on the local markets or used by local carvers and the relative importance of the species in use are not available. Outside of Nigeria, where *D. dendo* wood serves as an alternative, the lack of an acceptable substitute might give incentive for the regional market to take a wider view of harvestable quality and to continue the harvesting where export-grade timber have been locally exhausted, as observed in the case of *Dalbergia melanoxylon* (Jenkins et al., 2002). I was able to personally observe ebony carvings currently sold in tourist markets of Lagos, Douala and Yaoundé. A large portion of the wood used in Cameroon for this purpose appears to be rejected wood from local ebony sawmills that possess exploitation permits. The wood is received by carvers in the form of offcuts and rejected semi-finished pieces (blanks) prepared for the musical instrument industry. The wood for the largest pieces of art, which cannot have been carved out of these small blanks, might be sourced illegally. Therefore, the permitted quantities in Cameroon account for at least a part of the carving industry. Apart from this occasional inclusion, the wood exploited for local carvers is not recorded in any official trade statistics of source and destination countries. Further investigations into the quantities used, region exploited, value chain and possible regional trade is therefore urgently needed.

Because of its tendency to crack when dried, ebony wood is not suitable as primary material for large pieces of furniture, but can be incorporated as inlays or decorative elements or to make small objects (Ke and Zhi, 2017). In 19th century France, the bulk of ebony wood was used to make table knife handles and various instruments (Pagé, 1896). Around 1910, data from wood-using industries in 22 states of the USA showed that 1095 m³ of ebony wood was used over the period of one year to make billiard cues (41% of total ebony quantity), various handles

(31%), interior decoration (11%), organs and pianos (12%) and finally string musical instruments (0.36%) (Supplementary Material S3). Fingerboards and bridges of string instruments are traditionally made from three “tonewoods”: maple, rosewood and ebony, in particular from *D. crassiflora* (Bennett, 2016). However, it is only recently that the bulk of *D. crassiflora* exports has been used in the making of high-end guitars and bowed instruments (Verbelen, 1999; Taylor, 2012). This change is well illustrated by the purchase in 2011 of the largest ebony mill in Cameroon by Taylor Guitars and tonewood distributor Madinter to source ebony for fingerboards (Gibson and Warren, 2016). Ebony presents tonal and physical properties such as good workability, abrasion resistance, low damping, high dimensional stability, rigidity and density, as well as presenting an attractive colour and polish that makes it particularly desirable for the making of fingerboards (Bennett, 2016; Sproßmann et al., 2017). Interestingly guitar makers have started using streaked ebony, in which black and white colour intermingle in heartwood, for fingerboards as it has equivalent tonal characteristics than the more prized jet-black type (Paul, 2018).

According to the China's 2000 National Standard GB/T 18,107 revised in 2017, *D. crassiflora* is one of the 29 timber species whose heartwood meets quality requirements for being categorized as *hongmu* in Chinese pinyin (红木, literally meaning “red wood”) (中国国家标准化管理委员会, 2017). *Hongmu* is mostly used for the production of antique looking furniture reproducing the style and wood characteristics of the Ming and Qing Dynasties (Ke and Zhi, 2017) but also for musical instruments, inlays and various carvings. The special category for jet-black ebony species (乌木, wūmù) includes only *D. crassiflora* and *D. ebenum*. *Dalbergia melanoxylum* is included in a separate category. *Hongmu* furniture production has benefited from government incentives and is one of the fastest growing sectors of the Chinese timber industry. Given the growing demand from collectors on the one hand and the diminishing supply on the other, these woods are subject to speculation by investors (CITES, 2016; Ke and Zhi, 2017). The COMCAM database in Cameroon shows that the volume of ebony wood exported to China increased from 2007 to 2012 from 59 to 344 metric tonnes and decreased to 148 tonnes in 2018 (Fig. 3). Due to the scarcity of quantitative studies on the share and trends in ebony usage by different manufacturing sectors, the nature of the growing demand, whether musical industry, *hongmu* market or other uses, remains for the most part unclear.

4.2. Regulation

Beginning in 1905 in Nigeria, special protection was given to ebony trees, allowing only license holders to exploit them. This policy was meant to discourage local populations from cutting the trees but it failed to prevent the forest from being cut for agriculture (Egboh, 1985). Since 1926 in Cameroon the harvesting and transport of ebony wood without prior acquisition of special exploitation permits has been forbidden. The permits are valid for one person and for one year for harvesting a limited quantity anywhere in the country except in areas where a cutting permit has been granted for other species. The additional cost and procedures associated with the permit restricted the access of local traders to the commercial exploitation of this wood. The same year, a minimum diameter of exploitation of 40 cm was legally imposed for ebony trees (Commissariat de la République Française au Cameroun, 1927).

In the 1990 s to the mid-2000 s, important changes occurred in the regulatory frameworks of most forested countries of Central Africa, in order to foster sustainable management of the forest resources and to increase transparency and co-benefits from the use of such resources. Cameroon, CAR, DRC, EG, Gabon and RoC adopted new forest codes during the period. Under these codes, a company was to produce, at its own expense, a management inventory of all timber species and a management plan of the concession. These inventories serve to assess the dynamic of renewal of the various species and to set the management Minimum Harvesting Diameter (MHD), which in turn determine the

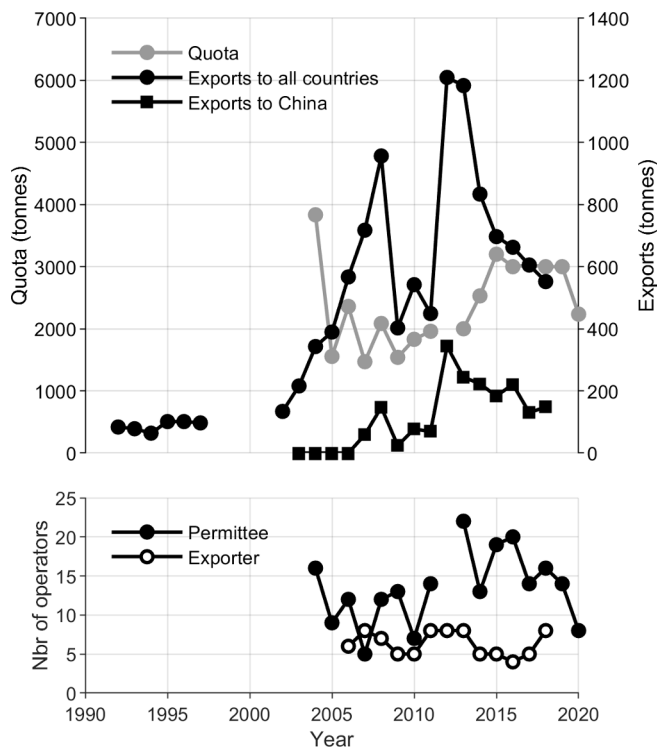


Fig. 3. Inter-annual fluctuation in ebony exploitation and export in Cameroon. Trend in ebony annual quota and exports are shown on top panel. The wood is first extracted under quota (left scale) from the forest as square logs. It is then processed in standardized blanks before being exported overseas (right scale). Both vertical scales are chosen so to show that the expected exported quantity is a fifth of the quota because of the 80% loss of wood during processing of squared logs into blanks. Trend in the number of permittee and exporters is shown on the bottom panel. Gaps in the time series represent missing data.

land surface and timber volume of Annual Allowable Cut. The plan establishes a rotation system of 25 to 30-year between annual harvesting lots within the concession. The management MHD is selected to ensure regeneration rates from 50% to 75% of the stumpage volume at the end of the fallow period (Karsenty and Ferron, 2017). It is set at or above an administrative MHD value which, for *D. crassiflora*, is 50 cm in DRC, 40 cm in CAR, RoC and Gabon (Présidence de la République Centrafricaine, 1990; MEFEPEPN, 2004; Sepulchre et al., 2008). Presently, however, in these countries only a portion of concessions have a management plan and their actual implementation and the sustainability of harvests without silvicultural operations are questioned (Karsenty and Ferron, 2017).

In the Cameroon forest law of 1994, the minimum harvesting diameter of *D. crassiflora* was increased to 60 cm. The exploitation of ebony remained the subject of a special exploitation permit, keeping the species separated from the concession system and the obligation of management plans (République du Cameroun, 1994). The logging companies annually apply for a permit corresponding to an ebony quota from the Ministry of Forests and pay a regeneration tax. The 2017 finance law increased the tax for ebony from 10 to 100 XAF per kg (Karsenty et al., 2006; République du Cameroun, 2016). The permits allow the holders to exploit ebony in non-permanent forest estates only, and some years also exclude community forests (MINFOF, 2008–2019). Ebony is thus supposed to be cut in forest lands that may later be converted to uses other than for forestry and exploitation is not allowed in Cameroon's logging concessions, as they are considered permanent forest estates. This considerably limits the exploitable area as the permanent forest estate accounts for more than a third of Cameroon's land surface and comprises mostly dense forest (WRI, 2012). This limitation is not part of the forest code, however, and one case of concession

owners having received ebony exploitation permit has been reported (Betti, 2007a). From 2013 to 2019, the number of private companies which were granted an exploitation permit for ebony fluctuated between 13 and 22. During the same period, 4 to 8 of them exported ebony (Fig. 3). The quantity of ebony and other special products transported from the forest by each permit holder is recorded at the local Forestry Control Post. The system of exchange of information from waybills, Control Posts, regional MINFOF delegations and the major customs controls at ports and border posts that feed into the COMCAM system is insufficient to verify the correspondence between permitted, transported and exported quantities (Ingram and Schure, 2010). Finally, although the current system of quotas could serve as a legal instrument to limit the exploitation of ebony trees, the total annual quantity permitted is based on the request of the private sector and not on quantitative forest inventories, exploited volume or regeneration time that would prevent overexploitation. Currently, it is the logging companies who decide where they will source their quota, and therefore when the same permit is granted to several operators, they compete to exploit the same trees (Casey et al., 2017).

4.3. International trade

Methods used to locate *D. crassiflora* trees and transport them to the nearest route have changed little since the early days of exploitation. The trees are selectively logged by specialized traders. When the diameter of the black wood is deemed insufficient or when it is mostly hollow, the felled trees are left in the forest, resulting in considerable waste. Sapwood is removed and heartwood is cut into ca. 1 by 0.1–0.4 m squared logs (Fig. 2H) weighting up to 40 kg at the felling site before it is transported. The delay between the felling and transport of wood often results in unnecessary exposure of logs in the forest for extended periods and increases degradation (Casey et al., 2017). The wood is not floated, as it will sink, nor hauled, but carried by porters to the nearest transport route: river, railway or road (Normand et al., 1960; Smith, 1948; Service des Affaires économiques, 1913). In present times, square logs of *D. crassiflora* are processed before export into blanks that are purchased by makers of musical instruments. According to ebony mill workers, during this conversion around 80% of the wood is lost as sawdust or discarded because of its lack of merchantable value (Casey et al., 2017), a number that compares well with the 80–95% loss that occurs during the processing of *Dalbergia melanoxylon* blackwood, a smaller tree with frequent knots and defects (Jenkins et al., 2002).

Quantitative information on imports of *D. crassiflora* was not found in official statistics of importing countries. As with many other speciality timbers, ebony wood is included under general customs codes for tropical hardwoods. Reference to ebony wood in the statistics of the source countries have been scarce in the recent decades. It has been reported that the main exporter is currently DRC (WCMC, 1991) but information regarding the quantities exported was not publicly available. CAR reported exports of 14.7 tonnes of raw ebony wood in 2004 (D.S.E.E., 2005). On average, 183 m³ (ca. 200 tonnes) of ebony was exploited annually in North RoC in 2010, 2012 and 2013 (PPECF and MEFDDE, 2016). The relatively small volumes in CAR and RoC and the absence of ebony in the recent export statistics of Gabon suggests that concession owners are more likely to focus on highest return timber species, which appears not to be ebony.

Contrarily to the previous countries, the state of Cameroon has developed and maintained a dedicated database to systematize the acquisition and recording of forest product trade data. Developed from 2001, the COMCAM database collects information on exporter, origin, destination and quantities of timber and special forest products exported from the port of Douala. The quantities are underestimated as COMCAM does not include undeclared merchandises, those exported from the smaller ports of Bota (Limbé), Tiko, Idenau, Campo, Kousséri, and Kribi, or illegally exported to Nigeria by other routes (Betti, 2007b). Despite these inconsistencies, this database provides an indication of the extent

and trends in ebony trade from Cameroon. Given the 20% recovery rates at the sawmill, and assuming that all the wood is processed into blanks before export, it is expected that exports would amount to a fifth of the exploitation quota. Cameroon's annual export statistics and quota are shown in Fig. 3. Exports have increased over the last two decades, from about 134 tonnes of blanks in 2002 to 1209 tonnes in 2012 and 552 tonnes in 2018. Possible causes of this increase are the growth of the musical instrument industry and the Chinese *hongmu* market. Further, since trade of the more highly prized ebony wood from Sri-Lanka, India and Madagascar have either been banned or more strictly regulated, the international market might be shifting towards sourcing its ebony in Africa. Reported annual exports are of a similar order of magnitude to the quantity expected given the permitted quota. However, before 2015, annual exports often substantially exceeded quota. Discrepancies might partly be due to the carrying-over of granted quotas to subsequent years until a permit is issued and to the possible time lag between exploitation and export. For instance, in 2004, 3835 tonnes of ebony were granted for exploitation to the logging industry, but most of the permits were not issued that year because the signature was subjected on the payment of tax arrears and the validity of this relatively large permitted quantity was extended to 2005 and 2006 (Betti, 2007a). The difference between quota and exports from 2012 to 2014 remain however unexplained.

Assessing the sustainability of current exploitation level in Cameroon is complicated by the lack of a baseline of extensive forest inventories in places where the trees are being cut. Furthermore, as the illegal logging of wood is estimated to exceed legal trade in the Congo Basin countries (Jianbang et al., 2016), further investigation into possible gaps between allocated quota, declared exploited quantities and exports are needed to assess the actual extents of legal and fraudulent trade.

The regulation applied to exploitation and trade does not only affect the quantity of wood cut and the redistribution of the benefits; it also has an impact on the structure and functioning of tree populations in the forest. The following section will attempt to identify the ecological traits of the species that are related to its sensitivity to the most common human-induced disturbances, viz. logging and hunting.

5. Ecology

5.1. Environmental requirements and functional traits

The distribution of DBH at population level shows that *Diospyros crassiflora* is a shade-tolerant species, found under shade conditions both as young and older plants, and has a good regeneration rate in both semi-evergreen and evergreen forests (Bedel et al., 1998; Sepulchre et al., 2008). The species displays the characteristic traits of shade-tolerant species with a "conservative" strategy: relatively low specific leaf area, leaf nitrogen content and stomata density on one hand and high leaf dry matter content, stem density and fibre wall thickness on the other hand (Akinsulire et al., 2018; Mirabel et al., 2019). As expected for a shade tolerant species, it was shown experimentally that recruitment of *D. crassiflora* in forest gap increases with the forest gap age (Bongjoh and Nsangou, 2001).

As commonly seen with tropical trees, it is difficult to estimate the age of mature *D. crassiflora* trees at harvest as they lack distinct growth rings (Obeng, 2012). In Cameroon, the three largest ebony trees in a 50-year old monoculture plot were 40 cm in DBH on average, i.e. an average annual increment rate of 0.8 cm yr⁻¹ (Owona Ndongo 2009). However, most trees in forest display slower growth rates. In a native forest at Mbaïki, CAR, the annual diameter growth rate of trees above 10 cm in DBH was estimated to be 0.64 cm yr⁻¹ at most (95th percentile) (Gourlet-Fleury et al., 2011; Fayolle et al., 2012) and, on average, 0.17 and 0.33 cm yr⁻¹ in unexploited forests and exploited-thinned forests respectively (Bedel et al., 1998). This makes it one of the slowest growing species found in Congo Basin forests (Owona Ndongo 2009; Fayolle et al., 2012). Furthermore it was found that the rate of recruitment of *Diospyros crassiflora* was relatively low, as the number of trees

above 10 cm in DBH only increased by 0.3% annually (Bedel et al., 1998). This slow growth and regeneration indicate that populations would be slow to recover after exploitation.

The oven-dry wood density of *D. crassiflora* as measured in 5 different studies is 0.86 g cm⁻³ on average (Zanne et al., 2009) which is higher than most other species from the same habitat. For instance, in the Dja Biosphere Reserve, Cameroon, the average oven-dry density of standing wood is 0.60 g cm⁻³ (Djuikou et al., 2010). Both low nutrient and low water availability may favour species with high wood density (Fayolle et al., 2012). However, it is not known whether *D. crassiflora* tends to be associated with relatively poorer soils or more xeric conditions within its habitat.

The minimum diameters for exploitation (40 to 60 cm depending on countries, see above) were deemed reasonable because they are substantially larger than 22 cm, the diameter at which trees have been observed to start reproducing (Sepulchre et al., 2008). The relative reproductive contribution of the large mature trees that are selectively logged is unknown, and therefore it is not possible to assess the impact of cutting them on regeneration.

5.2. Flowering and pollen dispersal

A nine-year phenological study conducted in the Lopé Reserve, Gabon, suggests that the flowering of *Diospyros* species is triggered by minimum temperatures of 19 °C or lower in the dry season (Tutin and Fernandez, 1993; Tutin and White, 1998). From 1955 to 2006, in Central Africa, the minimum day and night temperature have significantly increased. The frequencies of both coldest night and day have decreased at a faster rate than the global average during the same period (Aguilar et al., 2009) and according to IPCC (2012) there is a high confidence that they will continue to decrease during this century due to global warming. Inter-annual differences in minimum temperatures are small in lowland forests, and a small shift upwards in minimum temperatures could therefore have dramatic consequences; not only would these species regeneration rates be reduced, but the quantity of food available to frugivores that depend on them would also be affected.

A wide range of pollinating species have been reported for Ebenaceae species: bees, beetles, butterflies, flies, moths, wasps, sunbirds (Wallnöfer, 2001). However, the pollinator species and pollen dispersal distance of *D. crassiflora* have not been reported till date.

5.3. Seed dispersal

The seeds of *Diospyros* species are dispersed by a range of mammals and birds (Wallnöfer, 2001) and even reptiles (Griffiths et al., 2011). Given the large size of fruits and seeds one would expect that only the largest mammals would disperse *D. crassiflora* seeds.

Remains of *D. crassiflora* fruits were found in forest elephant dung (*Loxodonta africana cyclotis*, vulnerable according to IUCN) in northern RoC (Blake, 2002). In the same area, remains of fruit flesh was found in the stomach content of two duiker species, *Cephalophus callipygus* and *C. dorsalis* (near threatened according to IUCN) (Feer, 1989). The largest duiker species, *C. sylvicultor* (near threatened according to IUCN), have been observed ingesting various seeds up to 4.7 cm long, and so could potentially be a dispersal agent that ingests and spits out viable seeds after some time in the rumen, a process referred to as spit dispersal (Feer, 1995).

Western lowland gorillas (*Gorilla gorilla* ssp. *gorilla*, critically endangered according to IUCN) have been reported to consume *D. crassiflora* fruits in CAR and RoC (Nishihara, 1995; Doran et al., 2002; Fuh, 2013; Masi et al., 2015; Luef et al., 2016). The pulp and seeds of ripe fruits of *D. mannii* are eaten by gorillas. Intact seeds have been found both at gorilla's feeding sites and in their faeces (Tutin et al., 1996). The fruits and seeds of *D. mannii* are of comparable size to *D. crassiflora* and the geographic distributions overlap (Letouzey and White, 1970a), which suggest that gorillas can disperse *D. crassiflora* seeds.

Chimpanzees (*Pan troglodytes*, endangered according to IUCN) consumption of *D. crassiflora* fruits have been reported in Gabon and RoC (Hladik, 1973; Morgan and Sanz, 2006). They however might have a smaller swallowing threshold than gorillas as the maximal seed size reported to have been ingested intact was 2.7 cm long in a study of dung in Uganda (Wrangham et al., 1994). Chimpanzees have been observed eating the flesh of *D. manni* fruit but only fragments of seeds have been found in their faeces (Tutin et al., 1996).

Mandrill (*Mandrillus sphinx*) in Makokou region, Gabon, eat the flesh of the fruits but do not swallow the seeds (Lahm, 1986). *Diospyros crassiflora* does not have repellent hairs on its fruits like *D. mannii*, and primates are therefore possible predators of immature seeds as reported for other *Diospyros* species (Williamson et al., 1990). Immature seeds of all *Diospyros* fruit are vulnerable to predation as the testa is initially soft, and only hardens progressively during seed development. Within the genus, the potential vulnerability to predation increases with seed size (Tutin et al., 1996).

The removal of *D. crassiflora* seed by unidentified rodents have been reported (Rosin and Poulsen, 2018). Large rodents, such as, Emin's pouched rat (*Cricetomys emini*) and the African brush-tailed porcupine (*Atherurus africanus*) have been shown to cache and eat large seeds of other tree species and may act as both seed predators and short distance dispersers (Rosin and Poulsen, 2017).

Overall, published observations suggest that *D. crassiflora* is dispersed by large-bodied mammals that are all categorized as threatened to various degrees in the IUCN Red List. Large-bodied species are subject to higher hunting pressures as they are often favoured by hunters and are less resilient to hunting due to their slower reproductive rates (Abernethy et al., 2013). The decline of elephant, lowland gorilla, chimpanzee and yellow-backed duiker populations have already been reported in the Congo Basin (Laurance et al., 2006; Haurez et al., 2013; Poulsen et al., 2017; Kamgaing et al., 2019). In the absence of the large mammals, seed dispersal would be limited to barochory and possible short distance caching by rodents thus becoming a gregarious species as reported for other *Diospyros* species (Griffiths et al., 2011). The absence of effective dispersers is known to lead to important plant population declines due to competition, distance- and density-dependant mortality at both the seed and seedling stage (Comita et al., 2014; Terborgh et al., 2008).

6. Discussion and conclusion

The present study has examined the interface between biology, trade and ecology to elucidate the conservation status of *D. crassiflora* and identify factors that could influence the potential success of its conservation. Based on a combined reading of the contribution of these different but interlinked domains, a clearer picture is emerging of the current situation and the gaps in the knowledge.

It was shown here that *D. crassiflora* has a widespread distribution over much of the evergreen and semi-evergreen forest domain of Central Africa where it is the largest ebony producing species. This species accounts for the bulk of black wood exported from the coast of south-east Nigeria to south Gabon since the mid-18th century until today. Its abundance is relatively low and only a small proportion of felled trees provide the quality of wood that is suitable for export, hence the concerns about the sustainability of its exploitation. Moreover, the trade in ebony from the other regions of the world have either been banned or more strictly regulated, possibly increasing the demand for the African ebony, *D. crassiflora* and the African blackwood, *Dalbergia melanoxylon*.

Traditional uses are limited to medicinal treatments and wood carving. The latter might be substantial locally, as reported from south-east Nigeria, and pose significant threat to species survival because substitute woods are scarce or do not exist. Harvested quantities, origin of the wood and connection with international trade are undocumented and should be investigated.

Diospyros crassiflora is a shade tolerant species that will not

regenerate in fallows or in degraded forests unless intentionally planted. In a recent global assessment, deforestation was identified as a bigger threat to its survival than logging because the estimated harvesting rate was deemed small relative to its distribution and abundance (Schatz et al., 2019). The annual net deforestation and degradation rates of the Congo Basin humid forests from 2000 to 2005 were 0.17% and 0.09%, respectively (Ernst et al., 2013). Though these rates are smaller than what was observed in the Amazon Basin and Southeast Asia, the Congo Basin forests destruction is mostly driven by subsistence agriculture and it has been estimated that under the assumption of a fivefold human population growth all of DRC's primary forests will have been cleared by 2100 (Tyukavina et al., 2018). Given the particularities of each country in terms of forest clearing, ebony exploitation rate and regulation, it would be important to assess the species at the national levels. Confident country-wise assessment is however hindered by the lack of extensive inventory data and the fragmented information on regeneration rates, annual increment of harvestable timber, proportion of trees left in the forest after felling due to perceived wood defects, legal and possible illegal logging.

It is tempting to consider as positive the large gap between the minimum diameter for flowering on one hand and the diameter at which the heartwood starts to turn black and at which exploitation is allowed on the other. However, the relative contribution to regeneration of populations of these large trees that are cut is unknown.

Most source countries exploit ebony within the forest concession system in which the logging companies lease forest lands and develop a forest management plan in exchange for a monopoly over its exploitation. A notable exception to this is Cameroon where *D. crassiflora* harvesting is usually not permitted in forest concessions (though one exception was reported), but rather left to be exploited in the non-permanent forest estate. Trade statistics suggest that Cameroon is presently the main country of export. Exploitation levels in Cameroon are limited by quotas and the obligation to acquire annual permits. However, the permitted quantities are not guided by an estimation of the existing stock. The permits do not specify a precise area of harvesting and several companies can receive a permit for the same administrative region. Possible consequences of this competitive exploitation is a case worth exploring, in particular the incentive it creates for each company to harvest trees regardless of size and quality ahead of the other operators where the resource is easily accessible (Casey et al., 2017). Common-property competitive exploitation and private-property maximization of profits are indeed known to be two social conditions of overexploitation (Clark, 1973).

The recent increase of exports from Cameroon gives cause for concern. The musical instrument and the Chinese *hongmu* industries are the two main users identified in this study and warrant being closely followed. Of further concern is the scarcity of substitute woods for these uses. *Dalbergia melanoxylon*, mainly used for the making of woodwind instruments, is the single alternative homogeneous black wood that is still commercially available but is under unsustainable exploitation pressure locally (Jenkins et al., 2002). It meets the *hongmu* standards and was reported to be a potential alternative wood for fingerboards (Sproßmann et al., 2017) though no evidence was found during this review that it constitutes a sound commercial alternative. In the absence of alternative wood available in large quantities, the global ebony market would have to accept price increases related to higher exploitation costs if the resource become scarce. Fast-growing alternative timber species with equivalent wood characteristics are being explored by instrument manufacturers and wood scientists (Bennett, 2016; Sproßmann et al., 2017; Liu et al., 2020) but wood workability, tonal properties and consumer choice would ultimately limit the range of replacement woods.

The importance of considering the population size, reproductive biology and growth rate of a species into account when designing forest management strategies to ensure that genetic diversity and evolutionary processes are maintained have been recognized (Ratnam et al., 2014). In

this regard, the combination of low abundance, slow growth, slow regeneration and dioecy in *D. crassiflora* make the species potentially sensitive to selective logging pressures. This would warrant an in-depth study of mating system, gene flow and inbreeding depression. In particular, information is needed on the pollinators, flowering phenology and synchrony.

Tree populations may be threatened even in the absence of logging or forest conversion. Observations of animal consumers of *D. crassiflora* fruits show that the large mammals probably responsible for seed dispersal are near threatened to critically endangered. The consequences of removing the dispersal agent, including the possible replacement of this function by smaller mammals, and the possible effect on dispersal distance, recruitment, seed and seedling mortality and genetic diversity and structure need to be investigated.

In conclusion, *D. crassiflora* is threatened over the long term by the clearing of forests and by hunting-induced defaunation. Data show that selective logging for export is substantial in Cameroon and probably lower elsewhere. The exact consequences of the current logging practices are unclear and require further investigation. To ensure the sustainable production in Cameroon, quotas for export of the species should be based on knowledge of the distribution and abundance of the species in the areas of harvesting. In this regard, the acquisition of extensive forest inventory data is an urgent priority. Mechanisms should subsequently be put in place to ensure effective compliance with the permitted quota and harvestable area.

7. Way forward

Despite successful monospecific cultivation (Owona Ndongo 2009) and vegetative multiplication trials (Tsoheng et al., 2011) few efforts at large scale plantations of *D. crassiflora* have been attempted. In the absence of extensive plantation programs held by the government, the responsibility of developing a sustainable model of exploitation is left to the initiative of the private sector. An indicator of the growing demand for good practice and sustainable yield of *D. crassiflora* is the increase in the number of forestry concessions that list the species in their management plans and are certified as sustainably managed by the Forest Stewardship Council from one in 2010 to five in 2020 (from 0.5 to 3.0 10⁶ ha, all in RoC) (FSC, 2020). The musical instrument industry, responsible for most of the demand for this wood, has recently launched initiatives to ensure the long-term supply of tropical hardwood, the transparency of provenance and the capacity to demonstrate compliance and environmental stewardship responsibilities (Gibson and Warren, 2016). In the case of *D. crassiflora*, such efforts have resulted in an increased interest in models of integrated agroforestry (see review by Pelletier and Dudley, 2015) and the development of in vitro multiplication techniques to provide plant material for large scale restoration efforts (Tchouga et al., 2020).

In Cameroon, certification by third party agencies is currently impossible because ebony logging companies do not manage a surface of forest. Cultivation programs provide a credible option to achieve sustainable harvesting and maintain ebony population size and genetic diversity in the absence of forest management. A recent partnership between the state of Cameroon, public sector and local communities, have incorporated *D. crassiflora* in existing agroforestry systems within rural communities' land ownership system while improving ecological services (Deblauwe et al., 2019).

Finally, to further inform policy makers seeking to ensure a sustainable trade in ebony, a global value chain approach should be undertaken to identify key direct (loggers, mills, carvers, exporters, woodworkers, consumers) and indirect (local communities, governments and non-governmental organisations) stakeholders, their conflicting objectives and the multiple uses of what is one of the last commercially available ebony trees of the world.

Declaration of Competing Interest

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118655>. The occurrences collected in herbaria to generate Figure 1 are available as a table from <https://zenodo.org/record/4084978>. DOI: [10.5281/zenodo.4084978](https://doi.org/10.5281/zenodo.4084978).

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