

# *Entandrophragma*: taxonomy and ecology of a genus of African tree species with economic importance. A review

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This paper is the translation in English of the paper “Le genre *Entandrophragma* (Meliaceae) : taxonomie et écologie d’arbres africains d’intérêt économique (synthèse bibliographique)”, *Biotechnol. Agron. Soc. Environ.*, 2018, 22(2), 113-127.

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**Introduction.** *Entandrophragma* tree species have been the subject of special attention by foresters and scientists for several decades. The purpose of this bibliographic review is to examine the current knowledge acquired on the taxonomy and ecology of this genus in order to identify new research priorities.

**Literature.** The genus *Entandrophragma* has exclusively African species (10 to 12) that are exploited for the quality of their wood. These species are widespread in the Guineo-Congolese region (6 species) and in the Zambezian and Afromontane regions (5 species). The genus is characterized by a taxonomic evolution that has resulted in an important synonymy of species names (36 to 37). Ecological studies have been carried out on some major commercial species (*Entandrophragma angolense*, *Entandrophragma congoense*, *Entandrophragma candollei*, *Entandrophragma cylindricum*, *Entandrophragma palustre* and *Entandrophragma utile*) in their phytogeographic zones, mainly in the Guineo-Congolese region.

**Conclusions.** Taxonomy and ecology of *Entandrophragma* tree species typically occurring in woodlands and savannas have been insufficiently studied in comparison with *Entandrophragma* species occurring in rainforests. Research needs to be developed for the improvement of taxonomic, genetic and ecological knowledge, with a view to formulating appropriate recommendations for the conservation and sustainable management of these species.

**Keywords.** Forest ecology, population genetic, natural range, taxonomy of tree species, tropical forests, Africa.

## **Le genre *Entandrophragma* (Meliaceae) : taxonomie et écologie d’arbres africains d’intérêt économique (synthèse bibliographique)**

**Introduction.** Les espèces d’arbres du genre *Entandrophragma* font l’objet d’une attention toute particulière de la part des exploitants forestiers et des scientifiques depuis plusieurs décennies. Établir un bilan exhaustif actualisé des connaissances acquises sur leur taxonomie et leur écologie afin d’en dégager des pistes de nouvelles recherches est le but de cette synthèse bibliographique.

**Littérature.** Le genre *Entandrophragma* compte des espèces (10 à 12) exclusivement africaines et qui sont exploitées pour la qualité de leur bois. Ces espèces sont répandues dans la région guinéo-congolaise (6 espèces) et dans les régions zambézienne et afromontagnarde (5 espèces). Le genre est caractérisé par une évolution taxonomique qui s’est traduite par une importante synonymie des noms d’espèces (36 à 37). Des études écologiques un peu larges ont été réalisées sur quelques

principales espèces commerciales (*Entandrophragma angolense*, *Entandrophragma congoense*, *Entandrophragma candollei*, *Entandrophragma cylindricum*, *Entandrophragma palustre* et *Entandrophragma utile*) dans leurs zones phytogéographiques comprises principalement dans la région guinéo-congolaise.

**Conclusions.** Les informations sur la taxonomie et l'écologie des espèces d'arbres d'*Entandrophragma* des forêts claires et des savanes sont insuffisantes comparativement à celles des forêts denses humides. Des travaux de recherches devraient être développés pour l'amélioration des connaissances taxonomiques, génétiques et la maîtrise de leur écologie en vue de formuler des recommandations adéquates en matière de préservation et de gestion durable de ces espèces.

**Mots-clés.** Écologie forestière, génétique des populations, distribution géographique, taxonomie des essences forestières, forêt tropicale, Afrique.

## 1. INTRODUCTION

The genus *Entandrophragma* C.DC. comprises according to sources 10 to 12 tree species distributed exclusively in tropical Africa. Belonging to the tribe of Swietenieae A.Juss. and the family Meliaceae, it is related to the genera *Lovoa* Harms, *Khaya* A.Juss., *Pseudoedreia* Harms (Lemmens, 2008) and *Cedrela* P. Browne (Koenen et al., 2015).

Within the family Meliaceae, the genus *Entandrophragma* is the richest in valuable species exploited as timber in Africa (Tailfer, 1989). In addition to its economic importance, this genus is of scientific interest, especially taxonomically, given the multiplicity of genera to which *Entandrophragma* species were initially attached and the number of specific synonymies (36-37; Louis & Fouarge, 1947; Hall, 2008; The Plant List, 2013).

Insufficient information on the ecology of commercial *Entandrophragma* species leads to a lack of knowledge of the basic parameters of their population dynamics and, consequently, to inadequate decision-making by forest managers (Doucet, 2003; FAO, 2011; Biwolé et al., 2012). Moreover, information on the geographical distribution, ecology, taxonomy, genetics and evolution of *Entandrophragma* species is still fragmentary.

The general objective of this study is to review the knowledge acquired on the taxonomy and ecology of all *Entandrophragma* species, with a special focus on the main species exploited in dense moist forests.

The specific objectives are as follows:

- to describe the evolution of their taxonomy and their ecological characteristics;
- to discuss aspects for which knowledge remains insufficient or imprecise in order to suggest avenues for future research in support of improving their sustainable management.

## 2. TAXONOMY OF GENUS

### 2.1. History, synonymy and taxonomical subdivision

**Historical background.** The genus name *Entandrophragma* was proposed in 1894 by Casimir

de Candolle in his “Monographie des Méliacées”. Its etymology alludes to the unique floral particularity of this genus in the Meliaceae family: the existence of a disc under the ovary and ten real “phragma” partitions which form cups at the base of the staminal tube (Tailfer, 1989). Similarities were made with the American genus *Swietenia* Jacq. in 1858 by Welwitsch, then with the Asian genus *Chukrasia* A.Juss. by de Candolle in 1894. The latter genus differs from *Entandrophragma* in the flowers, by a long and narrow staminal tube with no internal partition, and especially by the fruit, which is a multisperm erect capsule (Louis & Fouarge, 1947).

**Synonymy.** The genus *Entandrophragma* is also characterized by an important evolution in the synonymy of the names of the species described by different authors, the census of which leads to a total of 36 to 37 species (**Table 1**). According to Louis & Fouarge (1947), this abundant taxonomic synonymy may be due to the important economic interest of the genus. This interest may have led to renewed attention on the part of systematists who, as a result of the phenotypic variability within species, may have encouraged the sometimes abusive creation of species. Indeed, some of these species were described and named by different authors with insufficient knowledge of the scientific literature of the time. The gradual improvement of scientific knowledge has made it possible to group some of these species into a single species and thus eliminate these synonymies, which are generally old (**Table 1**). Thus, the Conservatoire and the Botanical Garden of the City of Geneva (CJBG, 2012) currently recognizes only 10 species (*E. congoense* [Pierre ex De Wild.] A.Chev. not included) in the entire African area (**Table 1**). Among the species now recognized *E. angolense* (Welw.) C.DC. has a very abundant synonymy, probably due to the relative polymorphism it displays like many large trees with a wide distribution. Relative confusion still persists to this day concerning the synonymy of *E. angolense* and *E. congoense*, supported by Louis & Fouarge (1947) and more recently by Chevallier et al. (2010). On the other hand, Wilks & Issembé (2000) and de Wilde (2015) recognize that *E. angolense* and *E. congoense* are distinct species. This distinction is also made by forest prospectors in Gabon and Cameroon by calling

**Table 1.** Synonymy and subdivision of 10 *Entandrophragma* species recognized in the African Plant Database (*Conservatoire et Jardin Botaniques de la Ville de Genève*). Two additional species are mentioned in ©The Plant List 2013 — *Synonymie et subdivision de 10 espèces d'Entandrophragma reconnues dans la base de données des plantes d'Afrique (Conservatoire et Jardin Botaniques de la Ville de Genève)*. Deux espèces supplémentaires sont répertoriées dans la base de données ©The Plant List 2013.

Section (Louis & Fouarge, 1947)	Specific names currently accepted ( <a href="http://www.villege.ch/musinfo/bd/cjb/africa/">www.villege.ch/musinfo/bd/cjb/africa/</a> , 07/03/2015)	Synonyms according to Louis & Fouarge (1947) and <a href="http://www.villege.ch/musinfo/bd/cjb/africa/">www.villege.ch/musinfo/bd/cjb/africa/</a> , (07/03/2015)
<i>Neoentandrophragma</i> Harms	<i>E. utile</i> (Dawe & Sprague) Sprague (TN: sipo)	<i>E. roburoides</i> Vermeesen (1921) <i>E. thomasi</i> Ledoux (1932) <i>E. macrocarpum</i> A.Chev. (1909) <i>Pseudocedrela utilis</i> Dawe & Sprague (1906)
<i>Pseudoentandrophragma</i> Harms	<i>E. cylindricum</i> (Sprague) Sprague (TN: sapelli)	<i>E. lebrunii</i> Staner (1930) <i>E. angolense</i> Auct. Non C.DC. <i>E. tomentosum</i> A.Chev. ex Hutch. & Dalziel (1928) <i>E. rufum</i> A.Chev. (1909)
<i>Choriandra</i> Harms	<i>E. palustre</i> Staner (TN: -)	<i>Heimodendon tisserantii</i> Sillans <i>Heimodendron tisserantii</i> Sillans (1953)
	<i>E. candollei</i> Harms (TN: kossipo)	<i>E. choriandrum</i> Harms <i>E. ferruginea</i> A.Chev.
<i>Euentandrophragma</i> Harms	<i>E. angolense</i> (Welw.) C.DC. (TN: white tiama)	<i>E. casimiriana</i> De Wild. & Th. Dur. <i>E. candolleianum</i> De Wild. & Th. Dur. (1899) <i>E. gregoireianum</i> Staner (1930) <i>E. congoense</i> (De Wild.) A.Chev. (*) <i>E. platanoides</i> Vermeesen (1921) <i>E. leplaei</i> Vermeesen (1921) <i>E. congoensis</i> (Pierre ex De Wild.) A.Chev. <i>E. macrophyllum</i> A.Chev. (1909) <i>E. pierrei</i> A.Chev. (1909) (*) <i>E. cylindricum</i> Auct. Non (Sprague) Sprague <i>E. rederi</i> Harms (1910) <i>E. septentrionale</i> A.Chev. (1909) <i>Swietenia angolensis</i> Welw. (1859) <i>Leioptux congoensis</i> Pierre ex De Wild.
	<i>E. excelsum</i> (Dawe et Sprague) Sprague (TN: mountain mahogany)	<i>Pseudocedrela excelsa</i> Dawe & Sprague <i>E. speciosum</i> Harms <i>E. gillardini</i> Ledoux <i>E. stolzii</i> Harms (1917) <i>E. deiningeri</i> Harms (1917)
	<i>E. delevoyi</i> De Wild (TN: -)	<i>E. lucens</i> Hoyle (1932)
	<i>Wulforstia</i> (C.DC.) Sprague	<i>E. spicatum</i> (C.DC.) Sprague (TN: mutaco)
	<i>E. caudatum</i> Sprague (TN: -)	<i>Pseudocedrela caudata</i> Sprague (1908)
	<i>E. bussei</i> Harms (TN: -)	-

-.: no information — *pas d'information* ; TN: trade name — *nom commercial*; (\*): species accepted by ©The Plant List 2013 — *espèces acceptées par ©The Plant List 2013*, <http://www.theplantlist.org/tpl1.1/record/kew-2789562>, (20/12/2016); <http://www.theplantlist.org/tpl1.1/record/kew-2789547>, (20/12/2016).

them “white tiama” (*E. angolense*: greyish-white to grey-brown trunk and pink edge with whitish stripes) and “black tiama” (*E. congoense*: brownish-blackish trunk and fairly dark reddish-pink edge; Meunier et al., 2015) respectively. For the rest of this study, we will recognize *E. congoense* and *E. angolense* as two species in their own right according to the “Flore du Gabon” (de Wilde, 2015). Thus, we consider that there are 11 species of *Entandrophragma* and not 10. Furthermore, studies using more advanced molecular genetic approaches and coupled with other botanical criteria notably leaflet symmetry and the number of secondary veins, would be necessary to remove some uncertainties regarding the difference between the two tiamas.

**Subdivision.** With the exception of *E. congoense*, for which doubts remain, *Entandrophragma* species were grouped into five sections (**Table 1**) by Louis & Fouarge (1947). This subdivision is based on fertile characters including the existence of the disc on the ovary, the nature of the ten partitions delimiting the ten cups at the base of the staminal tube and the shape of the capsule. The usefulness of such a subdivision lies in the interspecific links it highlights. However, the study of other characteristics, particularly ecological, anatomical and genetic, would allow a better description of the links/differences between *Entandrophragma* species.

## 2.2. Botanical identification key for *Entandrophragma* species

Different keys for botanical identification of *Entandrophragma* species have been proposed (e.g., Staner, 1943; Wilks & Issembé, 2000; de Wilde, 2015). These keys are based respectively on the description of vegetative and reproductive characteristics (flowers and fruits). However, no flora or field guide proposes an identification key integrating all the *Entandrophragma* species, including *E. spicatum* (C.DC.) Sprague, *E. caudatum* (Sprague) Sprague and *E. bussei* Harms, which are nevertheless partially described. The present review proposes a single key based on the combination of these two main characters (**Box 1**). The identification of large, fertile *Entandrophragma* seems fairly easy, but flowers are not always available.

**Table 2** presents the vegetative criteria for identifying *Entandrophragma* in dense moist forests, including young trees that are not yet fruit bearing (e.g. Wilks & Issembé, 2000; Meunier et al., 2015).

## 3. GEOGRAPHICAL DISTRIBUTION

The genus *Entandrophragma* is exclusively African. The limits of the climatically homogeneous geographical entities generally used (region, sub-region, domain,

etc.) by each author (e.g., Louis & Fouarge, 1947; White, 1986) depend on the degree (spatial dimension) and nature (temporal dimension) of the distributions observed on the basis of available floristic and ecological data. Louis & Fouarge (1947) use the term “domain” (e.g., Zambezi, oriental, etc.) to locate the distribution area of *Entandrophragma*, whereas White (1986) prefers the term “region”, or “sub-region” according to Sépulchre et al., 2008. The present review prefers White’s (1986) concepts since they are the most commonly used and are derived from the classic process of endemism in species conservation that led to the production of the map of the main phytocories of Africa and Madagascar.

The genus *Entandrophragma* has two main geographical distributions (**Figure 1**).

The first group is composed of six species with very wide Guineo-Congolese distributions: *E. angolense* (white tiama), *E. congoense* (black tiama), *E. candollei* (kosipo), *E. cylindricum* (sapelli), *E. palustre* Staner and *E. utile* (sipo). Not including *E. palustre* which is restricted to swamp forests in the Democratic Republic of Congo and the Republic of Congo and probably other parts of Central Africa (Lemmens, 2008), the other species grow in evergreen and semi-deciduous dense rainforests (Meunier et al., 2015) where *E. cylindricum* (Sprague) Sprague and *E. angolense* are locally more abundant than *E. candollei* Harms and *E. utile* (Dawe & Sprague) Sprague (Doumenge et al., 2010). These species extend in a wide band north and south of the equator from the Atlantic coast through the Congo Basin to the western slope of the Kivu Ridge in the east (White, 1986). The one with the most extensive distribution among these four species is *E. angolense* (**Figure 1**). It is certainly confused with its synonym (*E. congoense*) by the CJBG.

The second group comprises five species with “Zambezi” and “Afromontane” distributions (*E. bussei*, *E. caudatum*, *E. delevoiyi*, *E. spicatum* and *E. excelsum*) (Louis & Fouarge, 1947; White, 1986; Malaisse, 1993; Lemmens, 2008). *Entandrophragma excelsum* (Dawe & Sprague) Sprague is a species with both a “Zambezi” and “Afromontane” distribution where it is restricted to mountain forests (Louis & Fouarge, 1947) and occurs in eastern DRC, Rwanda, Burundi, Uganda, Tanzania, Malawi and Zambia (Lemmens, 2008). *Entandrophragma excelsum* (Dawe & Sprague) Sprague is a species with both a “Zambezi” and “Afromontane” distribution where it is restricted to mountain forests (Louis & Fouarge, 1947) and occurs in eastern DRC, Rwanda, Burundi, Uganda, Tanzania, Malawi and Zambia (Lemmens, 2008), *E. caudatum*, *E. delevoiyi* and *E. spicatum*, known as “Zambezi”, are found in dry open or evergreen forests (Louis & Fouarge, 1947; Lemmens, 2008). Only *E. delevoiyi* (with Zambezi and Afromontane distribution) is

1. Terminal bud glabrous or glabrous; petals glabrous on both sides; anthers exerted, elliptical, rounded at the top:
  2. Leaflets hairless, except midrib on underside; petioles 1-6 mm; staminal tube with entire margins, not thickened ..... *E. angolense*
  3. Midrib underneath glabrous on the flanks; network of protruding ribs; sometimes with domatia in the armpit of the ribs; staminal tube 2-3 mm long ..... *E. congoense*
1. Terminal bud tomentose or puberulent; petals at least hairy or puberulent on the outside; anthers exerted or included, elliptical or lanceolate:
  4. Species of eastern mountain forests ..... *E. excelsum*
  4. Hygrophilous forest species:
    5. Leaflets hairless or rarely with fine puberulence on the veins on the face underside without cryptic pubescent domatia; petals refracted with hairy anthesis on both sides:
      6. Stalks 1-5 mm long, pubescent; leaflets 10-18, with 15-22 pairs of lateral veins; petals oblanceolate, narrow at base; anthers exerted, elliptical, rounded at apex ..... *E. candollei*
      6. Stalks 7-10 mm long, hairless; leaflets 6-10 in number, with 10-13 pairs of lateral veins; petals oval-oblong, unshrunk at the base; anthers included, triangular and acute at the apex; swamp forest species ..... *E. palustre*
    5. Leaflets with pubescent cryptic domatia in the armpit of the lateral veins on the underside:
      7. Leaflets with 10-16 very prominent lateral pairs on the underside, not anastomosing in an arc towards the edge; ovary with 6-8 ovules in two sets ..... *E. utile*
      7. Leaflets with 6-9 pairs of lateral ribs not very prominent on the underside, anastomosing in an arc towards the edge; exerted triangular anthers ending in a small point at the apex ..... *E. cylindricum*
  8. Endemic to Tanzania, found in deciduous thickets, open forest and shrubby savannah:
    9. Leaflets oval, asymmetrical, slightly pubescent underneath ..... *E. bussei*
  8. Species of dry open or evergreen:
    10. Leaflets hairless; stalks 15-35 mm; staminal tube with lobed edges, thickened at the top ..... *E. delevoyi*
    11. Leaflets in 3-7 pairs, up to 110 x 70 mm, broadly oblong or obovate-oblong; lower surface densely puberulent, vein forming an apparent network ..... *E. spicatum*
    12. Fruit: a woody capsule, up to 15 cm long, dividing into 5 valves, which bend backwards showing winged seeds attached to a central column ..... *E. caudatum*
  13. Fruits with basilar dehiscence:
    14. Very thin valves, 1-1.5 mm thick, straw yellow columella marbled with dark brown spots ..... *E. delevoyi*
    14. 4-5 mm valves; unmarbled columella:
      15. Mahogany brown columella; 1.5 cm square seeds ..... *E. angolense*
      15. Chocolate-brown columbine; ovoid seeds 2.5 cm long and 1.5 cm wide ..... *E. excelsum*
  13. Fruits with apical dehiscence:
    16. Fruit claviform or ellipsoid, 18-28 cm long, 5-7 cm wide; columella not specified ..... *E. utile*
    16. Fruits not claviform, not exceeding 5 cm wide; columella with hail stipe or 5 cm not stipulated not bearing at the base the remains of the valves:
      17. Fruit not specified at the base, 7-15 cm long and 2.5-3 cm wide; cylindrical columella with winged edges on ½ length ..... *E. cylindricum*
    17. Fruits stipulated at the base:
      18. Fruits 17-23 cm long; columella to stipe 3-5 cm long ..... *E. candollei*
      18. Fruit 22-27 cm long; 8-10 mm long columella with stipe ..... *E. palustre*

**Box 1.** Global simple botanical identification key of the *Entandrophragma* species based on the vegetative and reproductive traits (flowers and fruits) (Staner, 1943; Roux, 2003; Lemmens, 2008; de Wilde et al., 2015; Burrows et al., 2017) — *Clé simple et globale d'identification botanique d'espèces d'Entandrophragma basée sur les caractères végétatifs et reproducteurs (fleurs et fruits) (adapté d'après Staner, 1943 ; Roux, 2003 ; Lemmens, 2008 ; de Wilde et al., 2015 ; Burrows et al., 2017).*

mainly characteristic of dense dry forests (Dikumbwa, 1990; Malaisse, 1993; Malaisse et al., 2000). **Figure 1** shows that its distribution is wider in DRC and Zambia, and restricted in Tanzania. In contrast, *E. caudatum* is distributed in southern Zambia and Malawi, north-eastern South Africa, Zimbabwe, Mozambique and Botswana (Burrows et al., 2017), while *E. spicatum* is confined to southern Angola and northern Namibia (**Figure 1**). In addition, *E. bussei* (Afromontane distribution) is endemic to Tanzania where it occurs in

deciduous thickets, open forest and shrubby savannah (Lemmens, 2008).

## 4. PHYLOGENY AND GENETICS

### 4.1. Phylogeny

For more than a decade, numerous molecular studies have clarified phylogenetic relationships within the

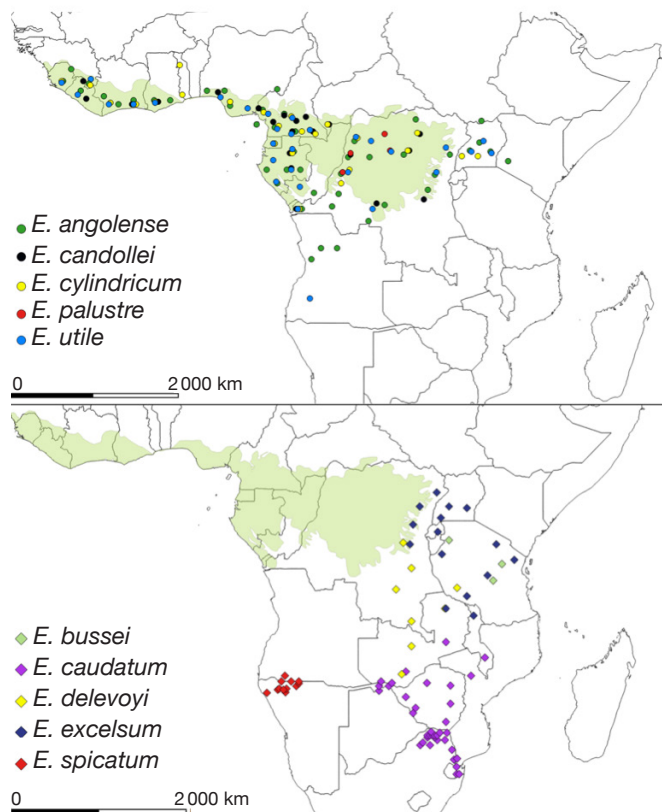
**Table 2.** Botanical differentiation of main *Entandrophragma* rainforest species in Africa (adapted from Wilks & Issembé, 2000; Meunier et al., 2015) — *Différenciation botanique des principales espèces d'Entandrophragma des forêts denses humides en Afrique (adapté de Wilks & Issembé, 2000 ; Meunier et al., 2015).*

Distinctive features	<i>E. angolense</i>	<i>E. congoense</i>	<i>E. candollei</i>	<i>E. cylindricum</i>	<i>E. utile</i>
Tree	up to 50 m high and 1.5 m in diameter, with buttresses or wheelbases at the base	cylindrical or with wheelbases	up to 60 m high and 3 m in diameter, with a powerful crown with large, sinuous branches and rounded buttresses or wheelbases that often extend far from the tree	up to 60 m high and more than 2 m in diameter, with rounded tops. At the base, it has wheelbases or buttresses that are sometimes highly developed	which can exceed 60 m in height and 2 m in diameter, with a powerful hemispherical top. It is equipped with wheelbases or buttresses at the base
Trunk	straight and smooth cylindrical to scaly, is often marked with irregular depressions and lenticels	darker trunk with vertical cracks and elongated scales, normally without buttresses, a more cylindrical base	straight, smooth in young trees, and marked with many deep depressions giving a pitted appearance, with scales, sinuous ridges and scars	straight, grey to brown, is almost smooth in young trees. It is then covered with scales, lenticels and numerous depressions in very old trees, giving it a prickly appearance	straight, silver-grey to yellow-grey, marked with vertical cracks, elongated scales and lenticels
Slice	pink with whitish stripes, it gives off a very slight scent of perfume	pink-red, finely fibrous, turning brown, brittle, E 10-30 mm whitish to orange inner layer	pinkish-red to whitish with orange-yellow granules. Sometimes gum-like lumps are found on old wounds	pinkish-brown and turning very quickly to brown, it has a very strong fragrant smell	pinkish-red, sometimes with white stripes, is not very fragrant. There is a whitish film between the dead and living bark, and the whitish inner layer slowly turns brown
Leaves	grouped together at the end of the branches, are composed of and provided with 4 to 9 pairs of almost opposite wide leaflets, whose acumen has folded edges	acumen often "spoon-shaped" (edge folded up in the shape of a spoon), 8 to 18 pairs of lateral ribs, more elongated shape than the white tiana, L 7-15 cm rachis at 8- the pair of opposite leaflets or nearly so	grouped together at the end of the branches, are composed and provided with 5 to 9 pairs of leaflets with a wavy surface, and traversed by numerous lateral ribs (between 15 and 25 pairs)	grouped together at the end of the branches, composed and provided with 6 to 10 pairs of leaflets, opposite or alternating. They are asymmetrical, marked by a network of protruding ribs on both sides, with the upper side glossy when dry, and sometimes with tufts of hair at the base of the ribs	composed of 6 to 12 pairs of elongated, asymmetrical leaflets with tufts of hair in the armpit of the lateral ribs, the latter also being more or less hairy

**Table 2 (continued).** Botanical differentiation of main *Entandrophragma* rainforest species in Africa (adapted from Wilks & Issembé, 2000; Meunier et al., 2015) — *Différenciation botanique des principales espèces d'Entandrophragma des forêts denses humides en Afrique (adapté de Wilks & Issembé, 2000 ; Meunier et al., 2015).*

Distinctive features	<i>E. angolense</i>	<i>E. congoense</i>	<i>E. candollei</i>	<i>E. cylindricum</i>	<i>E. utile</i>
Flower	greenish and small	-	green-yellow	pale green and small size	yellowish green
Fruit	large, elongated capsules reminiscent of large cigars (up to 22 x 5 cm), with 5 woody valves covered with lenticels, which open at the base and remain fixed at the top	blackish fruits that open late, they are often found whole on the ground	elongated brown capsules reminiscent of large cigars (up to 23 x 5 cm), sometimes with lenticels, with 5 woody valves that open from the top	black on the ground, are elongated capsules that look like big cigars (up to 22 x 4 cm), with 5 valves opening from the top and a relatively smooth surface	large capsules (up to 28 x 7 cm), with very thick valves, with a very warty black-brown surface spreading out from the top and remaining fixed at the base
Seed	flattened and winged	winged	flattened and winged		flat with a long wing

« - » : no information — pas d'information.



**Figure 1.** Geographical distribution of species of the genus *Entandrophragma* (map adapted from the database of the *Conservatoire et Jardin botaniques de la Ville de Genève*), which assimilates *E. congoense* to *E. angolense* — *Répartition géographique des espèces du genre Entandrophragma (carte adaptée d'après la base de données des Conservatoire et Jardin Botaniques de la ville de Genève), qui assimile E. congoense à E. angolense.*

family Meliaceae (Muellner et al., 2006; Muellner et al., 2009; Pennington et al., 2010; Muellner, 2011). Taxonomic revisions have been carried out, particularly for the genera *Carapa* Aubl., *Cedrela* and *Leplaea* (ex-*Guarea*) (Kenfack, 2011; Muellner et al., 2011). According to a recent phylogenetic study on Meliaceae, the genus *Entandrophragma* is considered to be close to the genus *Cedrela* from which it diverged during the Oligocene nearly 30 million years ago (Koenen et al., 2015). Despite these studies, the phylogenetic relationships and the origin of the diversification of species of the *Entandrophragma* genus are still unknown.

#### 4.2. Number of chromosomes and genetic markers

The level of ploidy is fairly homogeneous within the genus *Entandrophragma* ( $2n = 36$ ), although Mangenot & Mangenot (1962) report a duplication of the level of ploidy in *E. angolense*, *E. cylindricum*, and *E. utile* ( $2n = 36$  or  $72$ ). However, the existence of polyploid cytotypes has not been confirmed in *E. cylindricum* by the use of microsatellite markers since their development (Garcia et al., 2004). These genetic markers have opened the way for various studies on the reproductive system and gene dispersal in *E. cylindricum* (Lourmas et al., 2007; Monthe et al., 2017a), as well as on the identification of exploited feet in order to control their trade (Jolivet & Degen, 2012). In particular, they have demonstrated that *E. cylindricum* is mainly allogamous and that pollen and seeds are on average dispersed at more than 600 m (Lourmas et al., 2007; Monthe et al., 2017a). The recent development

of microsatellite markers for other *Entandrophragma* species (e.g., *E. candollei* and *E. utile*) (Monthe et al., 2017b) will most probably improve genetic knowledge of these taxa (e.g., analysis of the impact of exploitation on populations *sensu* Lourmas et al., 2007).

## 5. ECOLOGY AND SILVICULTURE

### 5.1. Climatic niches, edaphic preferences and habitat

**Climatic niches.** No global analysis has ever been carried out on the climatic niches of *Entandrophragma* over their entire range (Doumenge et al., 2010). Using information from herbarium specimens, forest inventories and other field surveys, Doumenge et al. (2010) proposed a climate niche modelling method which they applied to the four most exploited Guinean-Congolese *Entandrophragma* species: *E. angolense*, *E. candollei*, *E. cylindricum* and *E. utile*. Apart from *E. palustre*, which prefers the wettest areas of the Congolese basin, this approach shows that species from dense humid forests seem to be more present in conditions of intermediate humidity, avoiding the most humid climates. A second group consists of species from “drier environments” (*E. bussei*, *E. caudatum*, *E. delevoyi* and *E. spicatum*). These acclimatise best in dry areas and show a clear separation from *E. excelsum*, which is characterized by high altitude climatic preferences, generally between 1,300 m and 2,100 m (Louis & Fouarge, 1947; Lemmens, 2008).

Studies on the characterization of the climatic niches of *Entandrophragma* species remain insufficient and need to be regularly extended to take into account recent and future climate changes over their entire range.

**Edaphic preferences and habitat.** The habitats of the different species of *Entandrophragma* are distinguished by the physico-chemical properties of the soil. According to Hall et al. (2004), in the forests of southwestern Central African Republic (CAR), the presence of the five main *Entandrophragma* species (*E. angolense*, *E. congoense*, *E. candollei*, *E. cylindricum* and *E. utile*) in dense moist forests is correlated with the chemical composition of the soil. For example, only *E. candollei* tolerates very low fertility soils. *Entandrophragma angolense* and *E. cylindricum* are characteristic of soils with atypical pH, whereas *E. candollei* is limited to particularly acidic soils. These analyses should be extended to other species of the genus and to other regions where several species coexist.

In addition, arbuscular and vesicular mycorrhizal associations have been recorded in the main

*Entandrophragma* species exploited by local forestry companies (Onguene & Kuyper, 2001). Mycorrhizal inoculation therefore seems to favor the establishment of *E. utile* seedlings (Mujuni, 2008).

### 5.2. Temperament and silviculture

**Temperament.** The tolerance to shade in the juvenile stage of the most exploited *Entandrophragma* species in dense moist forests (sapelli, sipo, kosipo and white tiama) has been described in different ways according to the authors. These species have been described as sciaphiles (Louis & Fouarge, 1947), shade-tolerant (Hall et al., 2003) or semi-heliophilic (Meunier et al., 2015; Doucet et al., 2016). Although a consensus has emerged from this work in favor of a certain shade tolerance (the semi-heliophilic temperament of these species is currently accepted), there are nevertheless nuances between species (kosipo, sipo, sapelli and white tiama) established by some authors. These nuances in light requirements can also be verified by a more detailed study of woody characteristics by quantifying the diameters of the vessels from pith to bark of the wood of the respective species (Beeckman, 2016). On the other hand, for species of the genus other than those exploited in dense moist forests (*E. bussei*, *E. caudatum*, *E. delevoyi*, *E. excelsum* and *E. spicatum*), temperament is less well known.

**Silviculture.** Insufficient knowledge of the temperament of each *Entandrophragma* species also hinders the implementation of silvicultural techniques, for example to optimize reforestation. Indeed, experiments conducted by Hall (2008) in CAR and by Doucet et al. (2016) in Cameroon show that silvicultural techniques used for regeneration of *Entandrophragma* species are confronted with high mortality rates. Several silvicultural techniques, notably the natural regeneration method by enrichment and single shelter-wood cutting, the layered method and the enrichment method by direct sowing, applied for the renewal of *Entandrophragma* have not given very satisfactory results. Other techniques to improve their regeneration have been tested, such as the creation of small intermediate-sized gaps in logged forests and the supply of seeds to obtain better regeneration (Hall et al., 2003; Makana & Thomas, 2004). Nevertheless, the relevance of these regeneration methods is being questioned by new studies whose results have not been satisfactory with these species (Fayolle et al., 2015; Doucet et al., 2016). All the sapelli observed in Cameroon by Owona Ndongo et al. (2009) presented numerous difficulties due to insect bites during juvenile growth, which would explain in particular their initial delay in growth. According to Eckebil et al. (2017), silviculture of *E. cylindricum* is only just beginning.



Indeed, there is still a need for further silvicultural research on all *Entandrophragma* species throughout their range.

### 5.3. Phenology and fruiting diameter

**Phenology.** In general, studies on phenology have only been carried out on some *Entandrophragma* species (*E. angolense*, *E. candollei*, *E. cylindricum*, *E. utile*, *E. delovoyi* and *E. caudatum*) and more rarely and insufficiently on others (e.g., *E. bussei*, *E. excelsum* and *E. spicatum*).

Indeed, Louis & Fouarge (1947) precise that in the DRC the *Entandrophragma* of dense humid forests (*E. angolense*, *E. candollei*, *E. cylindricum*, *E. palustre* and *E. utile*) are recognized as deciduifolia with the exception of *E. palustre* which is evergreen. The period of leaf removal corresponds approximately to the season of reduced rainfall (beginning of the long dry season). In the forests of West Africa, some phenological studies (Taylor, 1960; Voorhoeve, 1965; Poorter et al., 2004) describe the flowering and fruiting periods of the four main and most exploited species (kosipo, sipo, sapelli and white tiama) (**Table 3**).

The phenology of *Entandrophragma* varies *a priori* according to regions. In Central Africa, and specifically in the Republic of Congo (RC), Gillet et al. (2008) report that the leaf capital of *E. candollei* is reconstituted from September to October after caterpillar attack; flowers are present in December and fruiting takes place in March-April. In *E. cylindricum* (semi-deciduous), leaf renewal takes place in September after the attack of edible caterpillars "*Imbrasia oyemensis*" (Gillet et al., 2008) in August (Eckebil et al., 2017).

In *E. delovoyi* from the dry dense forests of DRC, maximum leaf fall is observed in September and combined fruit and seed fall is generally observed in January (Dikumbwa, 1990). It is also noted that the flowering period in *E. caudatum* is from September to October (Burrows et al., 2017).

**Fruiting diameter.** Quantitative data on minimum fruiting diameter (MFD) and regular fruiting diameter

(RFD) of *Entandrophragma* species in moist dense forests (**Table 4**) are still fragmentary. The MFD is considered to be the threshold at which the first flowering and fruiting starts are observed, which nevertheless result in low diaspora production. This diameter is also called the minimum fertility diameter. The RFD is that from which efficient and regular fructification is observed (Sépulchre et al., 2008). The latter diameter is above all a tool to help determine the minimum exploitable diameter of a species (Menga et al., 2012) because it is indispensable that trees are only exploited (if they are well conformed) if they largely exceed this diameter in order to ensure their regeneration and the sustainability of the species. Although the MFD is determined for some of these species, the RFD is still generally unknown (Durrieu de Madron & Daumerie, 2004; Menga et al., 2012). Minimum legal logging diameters (MLDs) are a fundamental tool for sustainable management that takes into account the diametric structure of tree populations and the need to preserve from felling the fraction of seed trees that must ensure regeneration (Durrieu de Madron et al., 1998; Eckebil et al., 2017). The minimum legal logging (MLD) is then compared to the MFD and RFD when it comes to the rational management of populations of one or more species. Such comparisons should thus be used to revise these exploitation thresholds if necessary.

**Table 4** shows us that the MLDs for the main commercial *Entandrophragma* species have been established on an empirical basis by national forest administrations because they vary greatly from one country to another: for example, between 60 and 110 cm for *E. candolei* between Côte d'Ivoire and Ghana.

### 5.4. Dissemination, natural regeneration and population structure

**Dissemination.** *Entandrophragma* species are all anemochores (Louis & Fouarge, 1947; Medjibe & Hall, 2002; Poorter et al., 2004; Doucet et al., 2016). The capsular fruits of these species show septic dehiscence

**Table 3.** Phenology of *Entandrophragma* species in West Africa (mainly in Côte d'Ivoire, Liberia and Ghana) — *Phénologie des espèces d'Entandrophragma en Afrique de l'ouest (principalement en Côte d'Ivoire, Libéria et Ghana)*.

Species	Trade name	Foliage	Flowering period	Fruiting period	References
<i>E. angolense</i>	White tiama	Deciduous (September- November)	December	July-December	Tylor, 1960 ; Voorhoeve, 1965
<i>E. candollei</i>	Kosipo	Deciduous	November-December	May-August	Voorhoeve, 1965
<i>E. cylindricum</i>	Sapelli	Deciduous	February-March	May-August	Tylor, 1960 ; Voorhoeve, 1965
<i>E. utile</i>	Sipo	Deciduous	January-February	December-March	Voorhoeve, 1965

**Table 4.** Minimum Fruiting Diameter (MFD), Regular Fruiting Diameter (RFD) and Minimum Logging Diameter (MED) of *Entandrophragma* species — *Diamètre minimum de fructification (DMF)*, *diamètre de fructification régulière (DFR)* et *diamètre minimum d'exploitation (DME)* des essences d'*Entandrophragma*

Species	Scientific name	MFD (cm)	RFD (cm)	MED (cm)	Country	Reference
Kosipo	<i>E. candollei</i>	40	85	80	CAR	Yalibanda, 1999
				70	Ouganda	Plumptre, 1995
				110	Ghana	Nyunai, 2008
				90	Liberia	
				60	CI	
				80	Gabon	
					RC Cam DRC	
Sapelli	<i>E. cylindricum</i>	35 55 40	75 85 55	80	CAR	de Madron & Daumeurie, 2004
					Ouganda	Plumptre, 1995
				80	CAR	Petrucci et al., 1995
				80	CAR	Yalibanda, 1999
				90	Gabon	Sépulchre et al., 2008
				60	CI	Palla et al., 2012
				110	Ghana	
				90	Liberia	
				80	RC	
				100	Cam	
80	DRC					
Sipo	<i>E. utile</i>	85	85	90	Gabon	Sépulchre et al., 2008
				110	Ghana	Mujuni, 2008
				100	Cam	
				90	Liberia	
				60	CI	
				80	RC	
				80	DRC	
				80	CAR	
White tiama	<i>E. angolense</i>	55 50	85	80	CAR	Petrucci et al., 1995
				80	CAR	Yalibanda, 1999
					Ouganda	Plumptre, 1995
				110	Ghana	Tchinda, 2008
				90	Liberia	
				60	CI	
				80	Gabon	
				80	RC	
				80	Cam	
				80	DRC	

« - »: no information — *pas d'information*; RC: Republic of Congo — *République du Congo*; Cam: Cameroon — *Cameroun*; DRC: Democratic Republic of Congo — *République Démocratique du Congo*; CAR: Central African Republic — *République centrafricaine*; CI: Côte d'Ivoire.

in five woody valves. These fruits contain single-winged seeds that disperse by swirling in the wind (Louis & Fouarge, 1947). Almost all seeds of the fruits are of the “heavy glider” type and usually fall in the immediate vicinity of the seed trees (Medjibe & Hall, 2002). However, the dispersal of *Entandrophragma* samaras should be checked by additional dispersal measures (identification of installed seedlings). Indeed, a recent study based on molecular methods shows that wind dispersal of these samaras is greater than previously thought ( $\pm 600$  m) (Monthe et al., 2017a). This study also shows that samaras that are close to the mother foot due to low dispersion may be subject to higher predation. The latter is caused by annoying insects, e.g. *Hypsipyla* (de la Mensbrughe, 1966; Poorter et al., 2004), rodents and/or ungulates (Poorter et al., 2004) attracted by the high oil content of *Entandrophragma* seeds (Louis & Fouarge, 1947).

**Natural regeneration.** The low germination capacity of *Entandrophragma* seeds (de la Mensbrughe, 1966), their predation (Louis & Fouarge, 1947; de la Mensbrughe, 1966), a somewhat unpredictable fruiting time in a year (Hall, 2011), a flowering that seems rhythmically supra-annual with years of better fruiting (Gillet et al., 2008) are all reasons why it is rare to encounter abundant natural regeneration of *Entandrophragma*. This rarity of natural regeneration varies from one *Entandrophragma* species to another, but is almost general to all species of the genus (Lemmens, 2008).

**Population structure.** The distribution curve of the population by diameter class is an indicator of the population structure and the level of regeneration. Population structure with a decreasing exponential curve indicates good regeneration, while a bell curve indicates poor regeneration. Between these two extremes, there are many intermediate curves whose interpretation is often delicate, notably due to the history of the forest and the accuracy of the inventory (Dainou & Doucet, 2010). Several preparatory studies for the drafting of management plans (FRM, 2007; FRM, 2009; Nature+, 2011) show that the structure of *Entandrophragma* species populations varies according to the degree of natural regeneration, the density, numbers and volumes of stems inventoried and the ecological conditions of each species. The structure of sapelli populations, for example, is generally an exponential decreasing curve or a linear decreasing curve, with a peak in the intermediate classes where young stems are better represented (generally in the undergrowth waiting for the canopy to open up so that they can develop). Regeneration is therefore not in deficit (FRM, 2007; FRM, 2009; Ekebil et al., 2017). In order to stabilize the exploitable population of this

species, it would be necessary to limit sampling rates or extend the rotation period (Karsenty & Gourlet-Fleury, 2006; Ekebil et al., 2017). The population structure of kosipo, sipo and white tiama is variable and their distribution curves are generally not characteristic. Thus, the exploitation of each of these species requires particular attention. Many measures must be taken (major recommendations) in order to guarantee their maintenance. These measures include increasing the minimum management diameter (MMD) or limiting exploitation coefficients, providing regeneration aid and even prohibiting their exploitation in certain plots or management series (Dainou & Doucet, 2010).

## 6. CONCLUSIONS AND OUTLOOK

The present review shows that the taxonomy of the genus *Entandrophragma* has undergone a major evolution since this generic name was proposed in 1894 by Casimir de Candolle. Nevertheless, some uncertainties remain about the delimitation of the species, in particular *E. congoense* which has been made synonymous with *E. angolense* by some authors, whereas it is recognized as a species in its own right by others. This problem could be solved, in particular using molecular genetic tools. Knowledge of the ecology and genetics of *Entandrophragma* species remains equally insufficient and deserves to be deepened. Thus, future research could focus in particular on:

- updating the geographical distribution of each species;
- molecular phylogeny likely to understand the distribution patterns of species within the genus;
- detailed knowledge of the temperament of each species by quantifying the diameters of the vessels from the marrow to the bark of the wood;
- detailed knowledge of the phenology of each species, taking into account the diversity of habitats and climate variations throughout the genus’ range;
- the improvement of techniques to promote natural regeneration;
- the improvement of knowledge on the dissemination and fruiting of the species.

These new scientific investigations will contribute to improving the sustainability of *Entandrophragma* species.

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