


The ecology of *Maesopsis eminii* Engl. in tropical Africa

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Abstract

Maesopsis eminii is referred to as one of the most widely distributed African tree species. However, its occurrence in Africa has never been mapped and little is known as to how this species can sustain in different environments. To gain insight into *Maesopsis*' ecology, we (i) made a synthesis of its functional trait data from the literature, (ii) investigated phenological patterns using data on four *M. eminii* trees from Yangambi, DR Congo, (iii) assessed an empirical provenance trial from Uganda on 600 *Maesopsis* trees and (iv) synthesized geo-referenced point location maps of *Maesopsis* entailing WorldClim precipitation and temperature and FAO soils, rainfall and ecological zones for Africa. We found *M. eminii* to straddle the equator equidistantly in terms of latitude (10.97°N and 10.98°S) covering five forest types where twenty soil types and variable rainfall regimes support complex plant biodiversity. *Maesopsis eminii* was, however, largely concentrated in the tropical rainforest ecosystem which contains fertile Orthic Ferralsol soils. More than 97% of the point locations were found where annual precipitation was >1000 mm, and 82% occurred where average annual temperature was 22–28°C. Its functional traits, phenology and provenance trial findings explained its occurrence in Africa.

Key words: climate, equatorial, functional traits, pioneers

Résumé

Maesopsis eminii est connu comme une des espèces d'arbres les plus largement répandues d'Afrique. Mais sa présence n'a jamais été cartographiée et l'on sait peu de choses sur

la façon dont cette espèce supporte différents environnements. Pour avoir un aperçu de l'écologie de *Maesopsis*, nous avons (i) fait une synthèse de données sur ses caractéristiques fonctionnelles trouvées dans la littérature, (ii) étudié les schémas phénologiques en utilisant les données provenant de quatre *M. eminii* de Yangambi, RD Congo, (iii) évalué un test de provenance empirique d'Ouganda portant sur 600 *Maesopsis* et (iv) synthétisé des cartes avec les points géoréférencés de *Maesopsis* comprenant les précipitations et la température de WorldClim et les sols, les chutes de pluie et les zones écologiques en Afrique selon la FAO. Nous avons trouvé que *M. eminii* chevauche l'Équateur de façon égale en termes de latitude (10.97°N–10.98°S), présent dans cinq types forestiers où vingt types de sols et des régimes de pluviosité variables soutiennent une biodiversité végétale complexe. *Maesopsis eminii* était cependant fortement concentré dans l'écosystème de forêt pluviale tropicale qui contient des ferralsols orthiques fertiles. Plus de 97% des points de localisation se trouvaient là où la température annuelle moyenne est comprise entre 22–28°C. Ses caractéristiques fonctionnelles, sa phénologie et les tests de provenance expliquaient sa présence en Afrique.

Introduction

Maesopsis eminii Engl. is an angiosperm that belongs to the Rhamnaceae family, which includes many extremely drought-tolerant species. *Maesopsis* is considered to be a complex of four subspecies: *berchemioides*, *eminii*, *stuhlmannii* and *tessmannii* native to tropical Africa (Hall, 1995; CABI, 2016; www.theplantlist.org). The subspecies *berchemioides* occurs from Sierra Leone to Congo Republic, while from the Democratic Republic of Congo (DR Congo)

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through Central African Republic further east and south to Angola and Zambia the subspecies *emini* dominates (Hall, 1995). Little is known about the specific distribution of subspecies *stuhlmannii* and *tessmannii*. The subspecies *tessmannii* is even indicated as a 'doubtful' species in the GBIF database (www.gbif.org). We will therefore not focus on the individual subspecies. At the species level, *M. eminii* is typically regarded as a Guineo-Congolian species (Hall, 1995).

Naturally, *M. eminii* grows in rainforests, riverine forests (Schabel & Latiff, 1997), mixed swamp forests (Eggeling, 1947; Jenkin *et al.*, 1977), shrub-dominated transition zones that separate forests from grasslands (Hall, 1995), between high forests and savannah (Orwa *et al.*, 2009), and lowland and submontane forests (Binggeli & Hamilton, 1993; Dawson, Burslem & Hulme, 2011). In its natural occurrence, *M. eminii* has been characterized as a subclimax forest species (Eggeling, 1947; Hall, 1995), being a long-lived pioneer species that can live for more than 150 years (Binggeli & Hamilton, 1993). It tolerates drought for up to 2–6 months (Hall, 1995; Jøker, 2000; Ani & Aminah, 2006). Commenting on soil type, Orwa *et al.* (2009) said that *M. eminii* tolerates a wide range of site conditions but grows best on deep, moist and fertile sandy loam soils with a neutral to acid pH. *Maesopsis eminii* is, however, quite susceptible to attacks by species of butterflies of the Lepidoptera order: *Hesperiidea* (e.g. *Eagris decastigma*) and *Nymphalidae* (e.g. *Charaxes achaemenes* and *Charaxes lactetinctus*) (Ferrer-Paris *et al.*, 2014), beetles (*Monohammus scabiosus*), fungi (*Fusarium solani*, *Volutella* spp.), browsing animals (Orwa *et al.*, 2009) such as elephants (Eggeling, 1947), termites (Isoptera) (Eggeling, 1947; Orwa *et al.*, 2009) and spider mites (personal observation).

Maesopsis eminii provides excellent timber and crop shade services and is often grown for these purposes (Engler, 1906; Eggeling, 1947; Struhsaker, 1987; Binggeli & Hamilton, 1993; Plumptre, 1996; Owunji & Plumptre, 1998; Jøker, 2000; Ani & Aminah, 2006; Orwa *et al.*, 2009; Buchholz, Tennigkeit & Weinreich, 2010a; Hall, 2010). It has been reported to grow well on a range of altitudes and topographical ranges. Even though naturally it does not occur on steep slopes, when planted on such terrain, it grows well (Eggeling, 1947; Binggeli & Hamilton, 1993; Hall, 1995; Jøker, 2000). Human introduction of *M. eminii*, for example in East Africa during the early 20th century for reforestation purposes (Binggeli *et al.*, 1989; Hall, 1995; Bosu, Apetorgbor & Refera, 2009), has

brought *M. eminii* outside of its natural range. *Maesopsis eminii* has also been reported as a human-introduced species outside of Africa, namely in Australia, Philippines, Bangladesh, Brazil, Costa Rica, Fiji, India, Malaysia, Samoa, Solomon Islands, Hawaii, Puerto Rico and Indonesia (Buchholz, Tennigkeit & Weinreich, 2010a; Hall, 2010; Slik *et al.*, 2015; CABI, 2016). Nevertheless, in this study, we focus on the African continent. Through introduction of *M. eminii* in new regions within Africa, it has become invasive in several areas: in disturbed forests (Binggeli & Hamilton, 1993; Hall, 1995; Cordeiro *et al.*, 2004; Bosu, Apetorgbor & Refera, 2009; Dawson, Burslem & Hulme, 2011, 2015) with large gaps and with a high litter turnover rate (Hall, 1995) and in areas where climate has shifted for example in the case of the East Usambara, Tanzania, where occurring forest type changed from submontane to a more lowland type (Binggeli & Hamilton, 1993). Humair *et al.* (2014) defines such non-native invaders as species that spread spontaneously and rapidly, exerting negative impact on native species, ecosystem processes, the economy or human health. Indeed, *M. eminii* in the East Usambara forest possesses these characteristics (see Binggeli & Hamilton, 1993; Hall, 1995). *Maesopsis eminii* has been recorded as invasive in East Africa, for example Tanzania and Rwanda since the late 1970s (Binggeli & Hamilton, 1993; Binggeli *et al.*, 1989; Bosu, Apetorgbor & Refera, 2009; CABI, 2016; Cordeiro *et al.*, 2004; Dawson, Burslem & Hulme, 2011, 2015).

Hall (1995), Orwa *et al.* (2009) and others state that *M. eminii* is one of the most widespread tree species in Africa's tropical forests. However, they do not provide a spatially explicit description of its distribution over Africa. This is what we attempt to address in this article. We have in our study not considered the natural and introduced *M. eminii* populations separately, but rather have sought to understand its general ecology through a functional description of this species by synthesizing published and unpublished data sets. Next to the literature, we specifically used unpublished empirical data from a historical provenance trial in Uganda and a phenological study from the forest population of Yangambi, DR Congo. Lastly, we gathered occurrence data of *M. eminii* from multiple databases and linked these occurrences to the prevailing environmental conditions (i.e. climate and soil). The main objective of this analysis is to increase our insight into the ecology and specifically the spatial distribution of *M. eminii* over the African continent.

Materials and methods

Data sets used

Maesopsis eminii's functional traits and trait attributes were synthesized from reviewed published and unpublished data on the species. Unpublished data on its (i) phenology were extracted from a legacy data set of the National Institute for Agronomy in Belgian Congo (INEAC; 1939–1956) in the DR Congo, and (ii) provenance trials in Uganda (1964–1976) were obtained from the archives of the Forest Department, Government of Uganda (1968). The 209 geo-referenced occurrence points (i.e. natural and introduced populations, as distinction is not possible due to a lack of specification in the used data) of *M. eminii* were obtained from previous studies and data portals (Table S1).

Original map sheets of Africa's monthly precipitation (1961–1990 climatological normals; raster; spatial resolution (SR) 10 arc min; coordinate reference system (CRS): WGS84), soil type (FAO-UNESCO, 1971–81; vector; CRS: WGS84) and ecological zones (vector; CRS: WGS84) were obtained from FAO (<http://www.fao.org/geonetwork/srv/en/main.home> on the 6th of April 2015). Data of Africa's long-term current (1960–1990), annual mean temperature, and precipitation (SR: 30 arc min) used to establish *M. eminii*'s ecological niche were obtained from the WorldClim (version 1.4) data portal (www.worldclim.org accessed on the 28th of November 2016; Hijmans *et al.*, 2005).

Phenology of *M. eminii*

Data were extracted from a phenological study conducted between 1938 and 1957 on more than 2000 individual trees of over 500 species (including eight individuals of *M. eminii*) in the rainforest reserve of Yangambi, DR Congo. The Yangambi reserve covers an area of 6297 km² and is located just north above the Congo River about 100 km west of Kisangani, DR Congo. The region has an Af-type tropical rainforest climate and receives up to 1762 ± 295 mm of precipitation per year. Temperatures are high and constant throughout the year with a minimum of $24.4 \pm 0.4^\circ\text{C}$ in July and a maximum of $25.5 \pm 0.6^\circ\text{C}$ in March. Soils on the Yangambi plateau are Ferralsols. Vegetation in the reserve is characterized by moist semi-deciduous rainforest, with fragments of moist evergreen rainforest, transition forest, agricultural land, fallow land and swamp forest (Kearsley *et al.*, 2013). From

this historical phenological study, annual patterns of fruit/seed dispersal, leaf shedding/defoliation, fruiting and flowering of eight *M. eminii* trees were scored as present (1) or absent (0), as in Couralet *et al.* (2013). Data collection occurred approximately every 10 days. Information on how phenological stages were determined or how observations of crowns were made is not available in the INEAC archives. But according to Couralet *et al.* (2013), INEAC's sampling was random based on the local tree species composition.

For our study, however, four *M. eminii* trees were selected based on the fact that they were simultaneously and continuously followed for 9 years (1948–1956). Averages and standard deviations of the observed phenological frequencies were determined. These phenological data were also linked with climatological data from the same period (1948–1956) retrieved from the local meteorological station at Yangambi, also operated by INEAC. Details on the available observation years for each individual tree can be obtained from Table S2.

Provenance trials

We synthesized unpublished data from a historical provenance trial that was conducted between 1964 and 1976 in the Kibale rainforest reserve, Uganda (altitude: 1280–1494 m a.s.l.; soils: Humic Nitosols and annual rainfall of 1346–1524 mm per annum). Trial seeds were sourced from two different locations in Uganda: Kalinzu located 1463 m a.s.l, with annual rainfall of 795–1124 mm and Mollic Andosol soil, and Busiro at 1158 m a.s.l, annual rainfall of 1124–1499 mm and Orthic Ferralsol soil. The Kibale rainforest reserve is, respectively, ~236 km from Busiro and ~116 km from Kalinzu. The distance between Busiro and Kalinzu is ~289 km. Seeds were sown in pots after which their seedlings were planted in 1965 in 0.1-acre plots replicated twelve times in randomized blocks. Each plot contained 25 trees planted at 20 × 20 m link spacing giving a total of 600 experimental trees. Throughout the study period, annual assessments for survival, height, yearly height increment, diameter at breast height (DBH) and yearly diameter increment were made. Yearly means and standard deviations for the provenances were calculated.

Maps

Thematic maps were generated through mapping geo-referenced *M. eminii* occurrence point locations onto

FAO's soil, precipitation and forest ecosystem map sheets using Arc-GIS 10.3 software (ESRI, Redlands, CA, USA). The intersect function of Arc-GIS 10.3 was used to determine in which soils and ecosystems *M. eminii* occurred. Zonal statistics were used to determine the mean annual rainfall at the individually mapped occurrence points. *Maesopsis eminii*'s ecological niche was determined by plotting annual precipitation as a function of the mean annual temperature.

Results

Functional traits

Based on our literature review on the functional traits of *M. eminii* (summarized in Table 1), we can state that it is a fast-growing and light-demanding pioneer tree species. Depending on the growth conditions and the geographical area, *M. eminii* can grow to various heights (up to 40 m) and has wood with relatively low density ($0.56 \pm 0.27 \text{ g cm}^{-3}$).

After an age of 10 years or less, *M. eminii* trees produce conspicuous flowers to attract insect pollinators which result into production of fleshy fruits. When these fruits ripen, they attract arboreal animal dispersers (birds and mammals) that disperse the seeds to strategic niches to begin the cycle of tree life. The rapidly dispersed seeds have various useful attributes (Table 1) and can stay dormant for up to 200 days. Furthermore, *M. eminii* that is known to be naturally semi-deciduous turns drought-deciduous under severe drought conditions. *Maesopsis eminii* possesses a tap root combined with lateral roots allowing both horizontal and vertical resource uptake.

Phenology

From the onset, it is important to point out that capturing tree phenological data within the tropics is quite difficult. Tree crown visualization can namely be impeded by the sometimes dense canopy and tall trees. Particularly for this study, the 10-days window period for data collection presented a bias in that flowering that usually occurs for only 3 days might have been missed (explaining the pattern in Fig. 1 discussed below). That said, of the four *Maesopsis* trees observed at Yangambi forest reserve, the average annual patterns in defoliation, flowering, fruiting and seed dispersal are found related to the seasonal precipitation pattern (Fig. 1). Defoliation occurs at the

start of the largest wet season (Aug-Sept), but only with low frequencies (<10% of the observations), suggesting that *M. eminii* is not deciduous in Yangambi. Flowering increases from October during the large wet season and peaks in January during the large dry season where more than 40% of the observed trees had flowered (Fig. 1). The flowering period was followed by a fruiting period, although higher frequencies of fruiting were observed. This piggybacks to the earlier mentioned difficulty in observing flowering, in addition to our 10-days frequency data collection window implying that the observers might have unintentionally missed *M. eminii* flowering that usually occurs for only 3 days. Nonetheless, fruiting is shown to increase from January, peaking in April (>80% of the observations) towards the end of the short rainy season. Seed dispersal peaked more or less at the same time as fruiting (March-April).

Provenance trials

All the 600 test seedlings of the provenances survived the first year in Humic Nitosol soil condition of Kibale. However, survival sharply declined to ~50% after a year and declined steadily to about 40% at the age of 12 years (Fig. 2a). Survival rates were low as a result of breakage of tops in Kibale due to arboricide-treated trees falling on planted trees, animal browsing (e.g. bush bucks, elephants), neglected tending, line opening and climber cutting. Morphological characteristic differences of the Busiro and Kalinzu provenances were not evident in sizes of leaves, crown sizes or in type of branching. Thus, on average, tree growth performances for the two provenances were remarkably similar throughout the trial period as statistics graphed in Fig. 2 show. The DBH (Fig. 2b) and the vertical height (Fig. 2d) of both provenances indicated an increasing pattern. Yearly increments in DBH (Fig. 2c) and height (Fig. 2e) illustrated a decreased incremental trend beyond 1973. This was attributed to poor overwood treatment that caused shading and might have affected growth.

M. eminii's ecological niche

The 209 geo-referenced occurrence point locations of *M. eminii* within several rainfall regimes (Fig. 3), ecological zones (Fig. 4) and soils of 19 African countries (Table S1; Fig. S1) are composed of both natural and introduced populations. Equidistantly, the distribution of

Table 1 Reviewed functional traits for the African tree species *Maesopsis eminii*

Functional traits	Trait attributes
Reproductive traits	
Flower colour	Yellowish-green ¹
Flowering age	4–6 years (plantation); 10 years (natural regeneration) ^{1,2,3}
Reproductive mode	Hermaphrodite and protogynous ¹
Pollination	Insects ¹
Fruit colour	Purplish-black (mature) ^{1,4,5,6} Green to yellow (immature) ^{1,4,5,6}
Fruit type	Soft fleshy exocarp ^{1,3,4,5,6}
Fruit length (cm)	2–3 ³
Fruit ripening	2–4 months after flowering ^{7,16}
Seed dispersal	Birds (<i>Tauraco fischeri</i>), hornbills (<i>Bycanistes bucinator</i> , <i>B. brevis</i> , <i>Ceratogymna brevis</i>), fruit bats (<i>Eidolon helvum</i>), blue monkey (<i>Cercopithecus mitis</i>) and chimpanzees ^{3,22}
Seed traits	
Seed setting	1–2 seeds per endocarp ^{1,5,6}
Seed length (mm)	20–35 ^{1,5,6}
Seed width (mm)	10–18 ^{1,5,6}
Seed viability (%)	40–60 ^{1,5,6}
Seed dormancy (days)	90–200 ^{1,5,6}
Seed germination (days)	30 ²⁰ (seeds contained in a sisal bag were soaked in a basin of water at room temperature until roots broke through the seed wall, they were then immediately sown in pots in the greenhouse where eventually the first pair of leaves emerged)
Seed colour	Black ¹
Photosynthetic traits	
Leaf aging	Semi-deciduous (deciduous during severe drought) ⁴
Leaf display	Dorsiventral, hypostomatic and dentate simple alternate ^{1,9}
Leaf blade (cm)	6–15 × 2–5 (elliptic-lanceolate) ¹
Leaf sizes (cm ²)	Small (2.25–20.25) and medium (20.25–182.25) ^{4,10}
Leaf stomata distribution	Irregular shaped stomata ⁹ , usually surrounded by four or more subsidiaries, variable in position, shape and size ²¹ .
Leaf carbon storage (%)	42.0±0.8 ⁸
Leaf dry matter (%)	35 ¹
Wood traits	
Branch apparent modulus of elasticity (MPa)	15 ⁸
Wood density (g cm ⁻³)	0.37–0.75 ^{1,11,19}
Wood anatomy	Growth rings indistinct or absent, wood is diffuse porous, intervessel pits alternate and are of medium size: 7–10 µm, mean tangential diameter of vessel of vessel lumina is ≥200 µm, <5 vessels per square mm, mean vessel element length: 350–800 µm, contains different paratracheal axial parenchyma (e.g. vasicentric, aliform, lozenge-aliform, winged aliform and confluent) ¹⁹
Site-specificity traits	
Diameter at breast height (mature, cm)	50–180 ^{3,4,7,12,13,14,15}
Height (at maturity, m)	40 [Uganda and Tanzania (<i>eminii</i>)] ¹⁶ 35 [Democratic Republic of Congo (<i>eminii</i>)] ¹⁶ 25–30 [Angola (<i>eminii</i>) westwards (<i>berchemioides</i>)] ¹⁶ 10–35 ^{1,3,4,7,12,13,14,15}
Branch aging (self-pruning, m)	Unbuttressed ^{4,17}
Rooting traits	Lateral and deep tap roots ¹⁸
Ecological strategy	Shade intolerant from 1 year ^{3,5,6} Fast growing light demanding pioneer ^{4,17}

¹Orwa *et al.* (2009); ²Mugasha (1981); ³Binggeli & Hamilton (1993); ⁴Eggeling (1947); ⁵Binggeli (1989); ⁶Binggeli & Hamilton (1990); ⁷CABI (2016); ⁸Epila *et al.* (2017a); ⁹Tihurua (2012); ¹⁰Raunkier (1934); ¹¹Chave *et al.* (2009); ¹²Ani & Aminah (2006); ¹³Buchholz *et al.* (2010a); ¹⁴Buchholz *et al.* (2010b); ¹⁵Hall (2010); ¹⁶Hall (1995); ¹⁷Bulafu *et al.* (2013); ¹⁸Taylor (1989); ¹⁹www.insidewood.lib.ncsu.edu; ²⁰Personal observation; ²¹Prabhakar (2004); ²²Cordeiro *et al.* (2004).

M. eminii straddles the equator to 10.97°N, 3.14°W in Burkina Faso and 10.98°S, 26.73°E in Likasi, DR Congo (Figs 3 and 4 and Fig. S1). Based on synthesized occurrence and rainfall data (Table S1), ~97% of the geo-referenced sites with *M. eminii* occur in areas with rainfall exceeding a yearly mean of 1000 mm (Fig. 3; Table S1). The intersect query between occurrence data and the ecological zones map indicated that *M. eminii* concentrates mainly in tropical (evergreen and semi-deciduous) rainforest of Uganda, DR Congo through to western coast of Africa. Nevertheless, it is also observed to occur in tropical shrubland of Burkina Faso and Tanzania, tropical moist deciduous forest in Angola, DR Congo, Zambia and Sudan, tropical mountain ecosystems in Cameroon, DR Congo, Uganda and Kenya, and in Burkina Faso and Tanzania in the tropical dry forest (Fig. 4). The occurrences therein, however, cannot be distinguished (native or planted) due to lack of available information in the data that were used. Extracted information on *M. eminii*'s preferred precipitation and temperature regimes defined its ecological niche (Fig. 5) as one requiring ample precipitation (1000–2000 mm year⁻¹; 97% of geo-referenced occurrence sites) and moderate temperatures (22–28°C; 82% of occurrences).

Soils

A similar intersect query was run for soils to generate Fig. S1. However, as the attribute table born from the intersection between the soil map and the *M. eminii* occurrence points had country as one of the listed attributes, we made an overview per country of the soils *M. eminii* thrived in (Table S1). Based on the Land and Water Department Division, FAO soil codes, *M. eminii* has been found to grow on twenty different dominant soil types that constitute nine soil groups with differing physical and chemical qualities. The approximate per cent breakdown of soil preference is, in order of importance: Orthic Ferralsols (Fo; 26%), Xanthic Ferralsols (Fx; 8%), Lithosols (I; 7%), Ferric Luvisols (Lf; 7%), Eutric Nitosols (Ne; 6%), Humic Nitosols (Nh; 6%), Ferralic Arenosols (Qf; 6%), Orthic Acrisols (Ao; 5%), Ferralic Cambisols (Bf; 5%), Dystric Nitosols (Nd; 5%), Ferric Acrisols (Af; 4%), Humic Gleysols (Gh; 4%), Humic Ferralsols (Fh; 2%), Dystric Gleysols (Gd; 2%), Pellic Vertisols (Vp; 2%), Eutric Cambisols (Be; 1%), Humic Cambisols (Bh; 1%), Calcic Cambisols (Bk; 1%), Rhodic Ferralsols (Fr; 1%) and Calcaric Gleysols (Ge; 1%; Fig. S1; Table S1).

Discussion

Our study objective was to enhance our understanding of the ecology and specifically the distribution of *M. eminii* in Africa. We achieved this by combining information from *M. eminii*: (i) functional trait attributes (Table 1), (ii) site-specific studies of tree phenology and growth (Figs 1 and 2) and (iii) occurrence at sites with different precipitation regimes (Fig. 3), different forest types (Fig. 4) and soils (Fig. S1). This resulted in the establishment of *M. eminii*'s ecological niche (Fig. 5), which was described by plotting yearly precipitation as function of mean annual temperature.

Firstly, it is clear that our mapping has improved our understanding of *M. eminii*'s ecology and occurrence distribution over Africa, and preferred ecological niche (based on presence data). We show that this tree species associates with growth conditions prevailing under several rainfall regimes, variable ecological conditions in several forest types and numerous soil types (Figs 3 and 4, Fig. S1). Our observation of *M. eminii*'s high occurrence in the rainforest region (Fig. 4) supports Hall's (1995) technical report that states that *M. eminii*'s distribution range corresponds merely to the African rainforest zone. Observed *M. eminii* stands in forests outside this realm, especially within Tanzania's tropical dry and shrubland forest, are as a result of planting. We also illustrate that *M. eminii* occurs – at least scantily – at the centre of the Congo Basin (Figs 3 and 4, Fig. S1), not previously observed by Hepper (1979), and where Hall (1995) attributed the absence of the species to swampy condition. Furthermore, we show that *M. eminii*, based on its ecological niche (Fig. 5), is unlikely to occur in very cool (<19°C) temperature environments (82% of the occurrences were within an average annual temperature range of 22–28°C). *Maesopsis eminii*'s ecological strategy (Table 1) and our provenance trials (Fig. 2) support its nonpreference of cool environments as overwood shading was observed to affect growth of the Ugandan provenances. Canopy-induced shading has been observed by de Frenne *et al.* (2013) to lower understory microclimate. Nevertheless, such hump-shaped growth curves (Fig. 2c and e) can also be linked to ontogenetic variation in growth rate (Herault *et al.*, 2011).

The maps further depict *M. eminii* to occur most often on Orthic Ferralsols (Fig. S1; Table S1). Hall (1995) notes that in localities with an extended (5–6 months) dry season where *M. eminii* occurs, fertile soils such as Rhodic

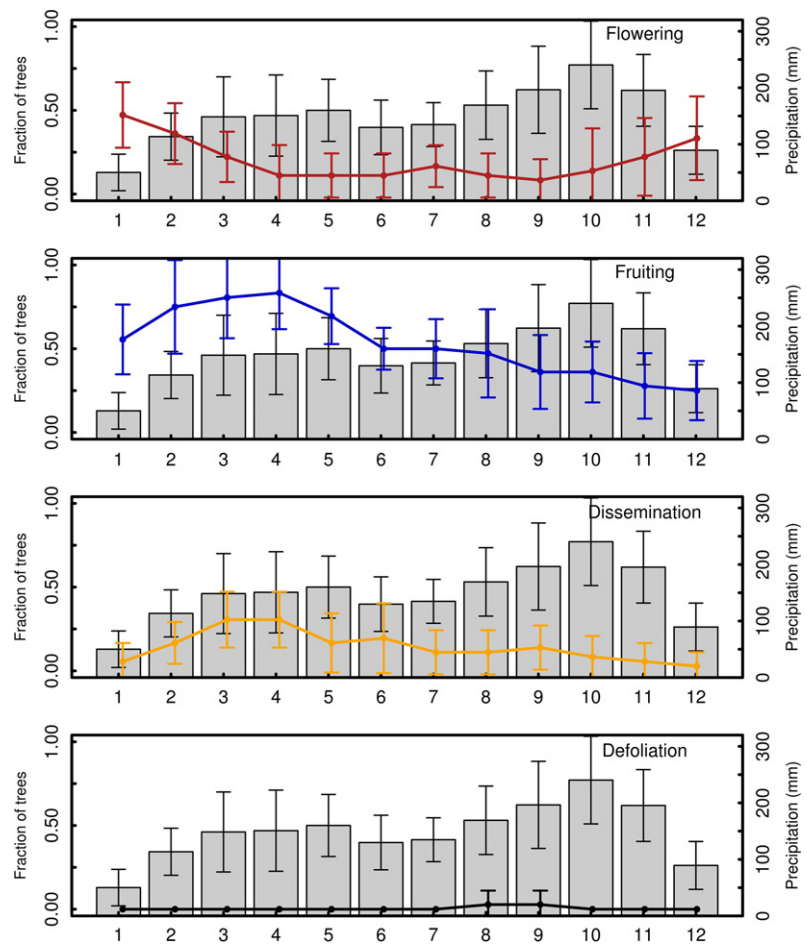


Fig 1 Phenology of four *Maesopsis eminii* trees in Yangambi, Democratic Republic of Congo, followed for 9 years. The plot contains the mean frequencies and standard deviations of observed phenology of the four trees. The high observed fruiting and low flowering show how difficult it is to observe phenological changes in dense tropical forests

Ferralsols in DR Congo, Eutric Nitisols and Ferric Luvisols of Tanzania and Sudan are present. Eggeling (1947) and Mugasha (1981) also attached great significance to soil quality in the establishment and growth of *M. eminii*. However, our empirical data from the provenance trial in Uganda (Fig. 2; although the provenance only covers a narrow habitat range) suggest that soil fertility is not a prerequisite for *M. eminii*'s establishment. Indeed, the pioneer *M. eminii*, within its preferred ecological niche (Fig. 5), thrives under numerous soil types (Fig. S1; Table S1) provided there is continuous soil moisture supply (657–3217 mm year⁻¹; Fig. 3; Table S1). This supports the notions that *M. eminii* on the one hand has broad ecological amplitude (Binggeli & Hamilton, 1993), but on the other hand does not favour soils prone to drought stress (Hall, 1995). Water-limiting forces might

thus explain why the existing latitudinal expansion of *M. eminii* is less extensive within the tropical deciduous forest ecosystems and beyond where soil moisture is limiting (Figs 3 and 4).

Another explanation for *M. eminii*'s presence latitudinal band could be linked to its arboreal dispersers that live in trees (Table 1). Furthermore, *M. eminii* does not invade and establish inside the fire-prone dense grass communities (Hall, 1995; Hafashimana, pers. comm.), suggesting that *M. eminii*'s presence is probably abated by nonconductive environments for both the species *M. eminii* and its arboreal seed dispersers.

Functional traits determine plant growth, survival and reproductive success and as such play important roles in shaping species distribution pattern along environmental gradients (Maharjan *et al.*, 2011). In introduced non-

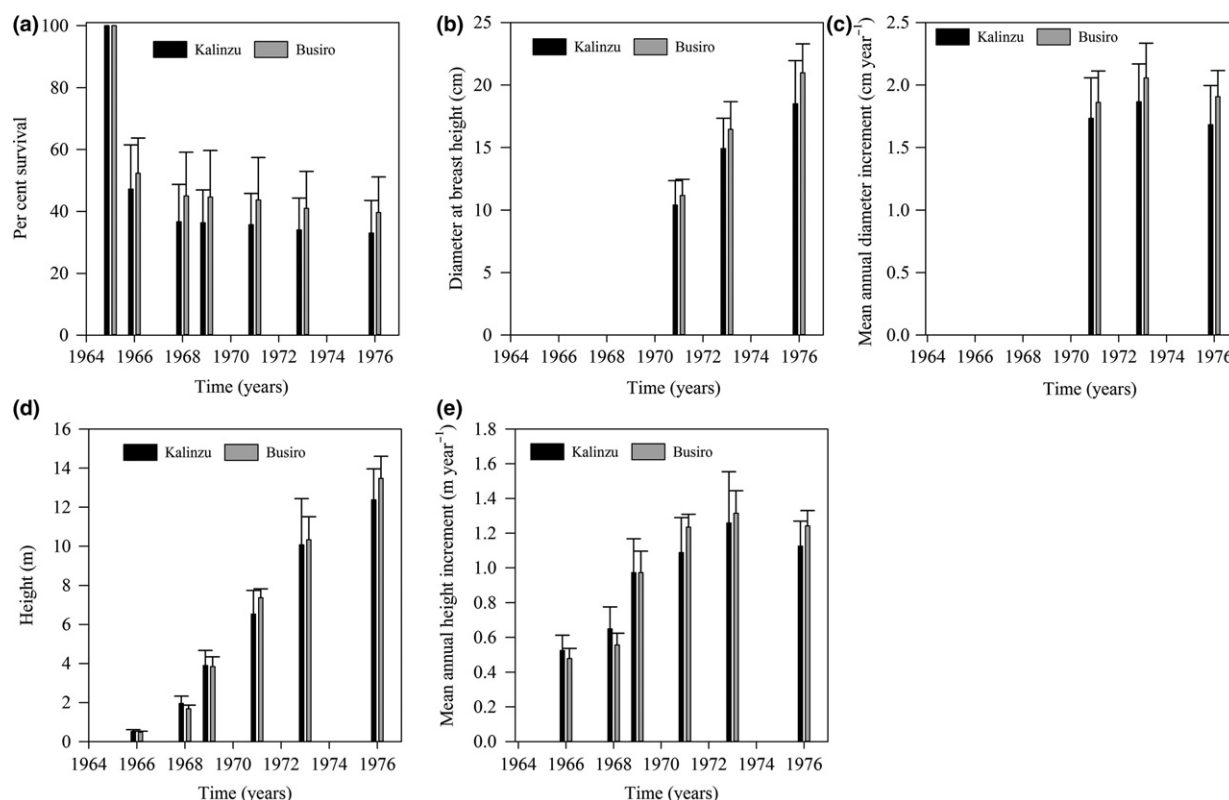


Fig 2 Performance variables for the two Ugandan provenances from Busiro and Kalinzu: per cent survival (a), diameter at breast height (DBH) (b), yearly increment of DBH (c), height (d) and yearly height increment (e) with their respective standard deviations followed during provenance trials in Kibale forest, Toro. Blank years portray situations where data were not collected or are missing

native parts like Tanzania (Figs 3 and 4, Fig. S1), the invasion ecology of *M. eminii* can be related to its functional traits (Table 1). Firstly, *M. eminii*'s reproductive biology as indicated by our phenology data (Fig. 1) shows an all year-round seed production (Table 1; Fig. 1). Indeed, other studies report that seeds are produced frequently and copiously (e.g. Hall (1995), Cordeiro *et al.* (2004) and Dawson, Burslem & Hulme (2015)). Furthermore, high germination rates are found as long as large gaps (due to disturbance, forest edges) exist, soil moisture is sufficient and arboreal seed dispersers are present, aiding in *M. eminii*'s invasion (Dawson, Burslem & Hulme, 2011). A typical example of the invasion of *M. eminii* is the Amani, Tanzania case. Here, massive fruiting of *M. eminii* occurred in the Kwamkoro plantation which was readily dispersed by hornbills to Amani's natural forest leading to *Maesopsis*' invasion of Amani (see Hall, 1995). Cordeiro *et al.* (2004) also suggest that the enhanced expansive *Maesopsis* invasion in the East Usambara is linked to the

presence of an effective dispersal agent, the silvery-cheeked hornbill (*Ceratogymna brevis*; Table 1) that may transport seeds over tens of kilometres. Additionally, as a fast-growing pioneer species, *M. eminii* possesses a trait ensemble favouring resource acquisition and growth (e.g. wide long vessels with medium sized intervessel pits to facilitate efficient water movement; Table 1) that increases its invasive potential once established, given that drought is not pronounced as *M. eminii*'s hydraulic architecture might confer it vulnerable to drought-induced cavitation (Epila *et al.*, 2017a).

We stated above that water availability is a limiting factor for the occurrence of *M. eminii*. Indeed, 97% of the mapped *M. eminii* occurs in sites receiving an annual mean of more than 1000 mm of rain. However, we also observe that the species appears under a very wide range of rainfall regimes in terms of total annual rainfall (657–3217 mm year⁻¹) and seasonality which is varying with latitude. As the cosmopolitan family to which *M. eminii*

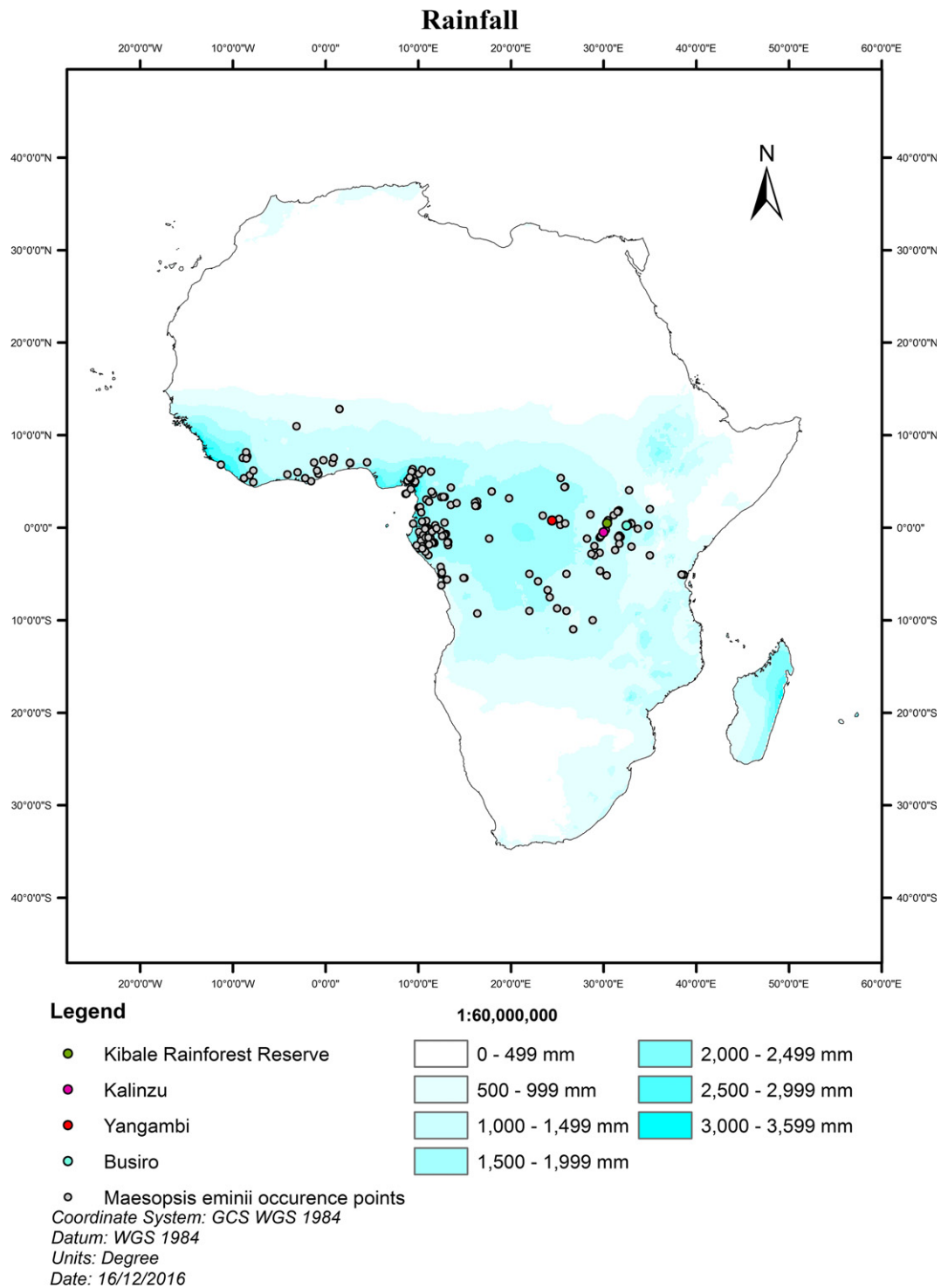


Fig 3 Map of Africa showing the geo-referenced occurrence positions of *Maesopsis eminii* under the different rainfall regimes based on available data sets. The different colour dots illustrate where more detailed studies on *M. eminii* (i.e. phenology and provenances) were performed. The original map sheet was sourced from FAO

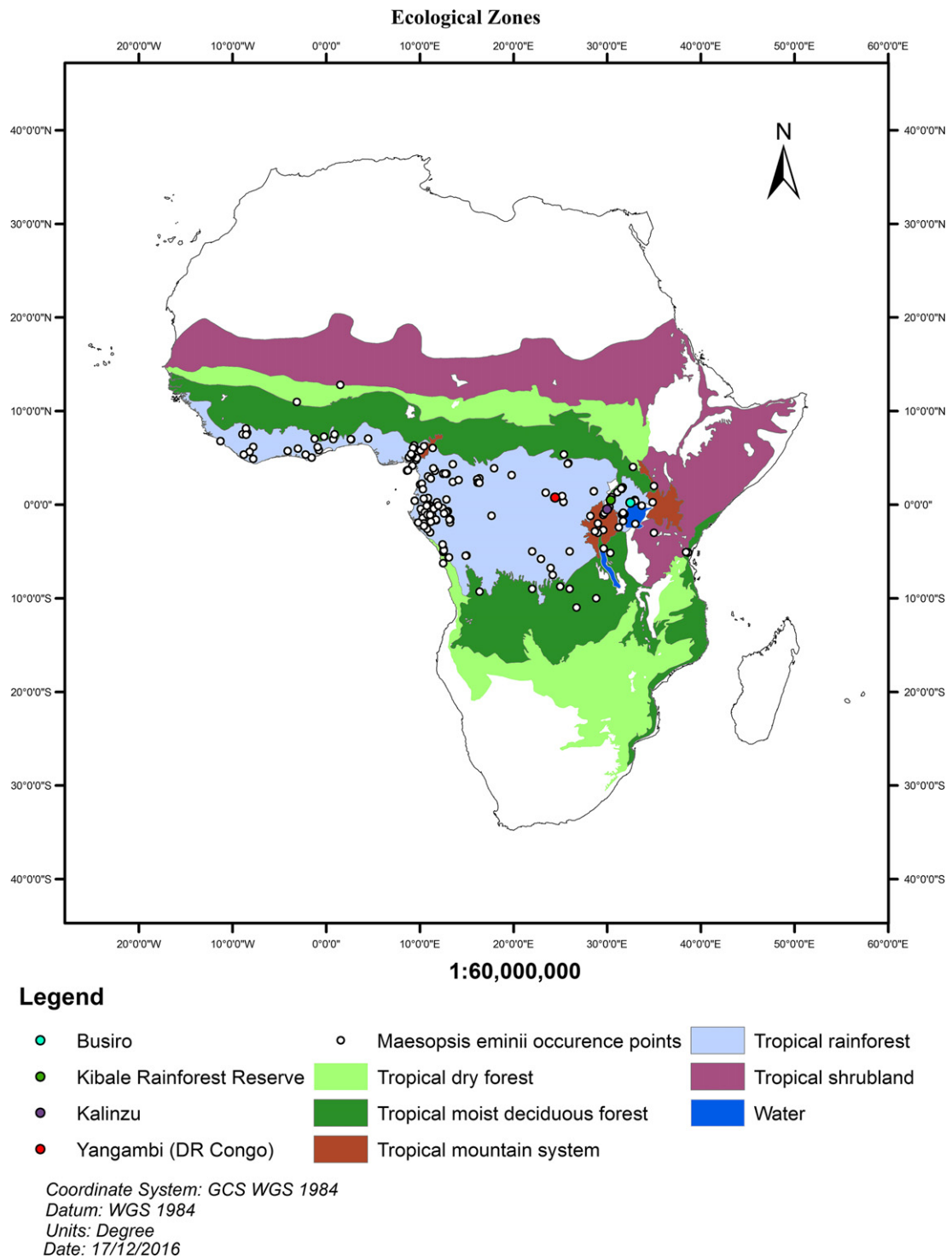


Fig 4 Map of Africa showing the geo-referenced occurrence positions of *Maesopsis eminii* within different ecological zones based on available data sets. The different colour dots illustrate where more detailed studies on *M. eminii* (i.e. phenology and provenances) were performed. The original map sheet was sourced from FAO

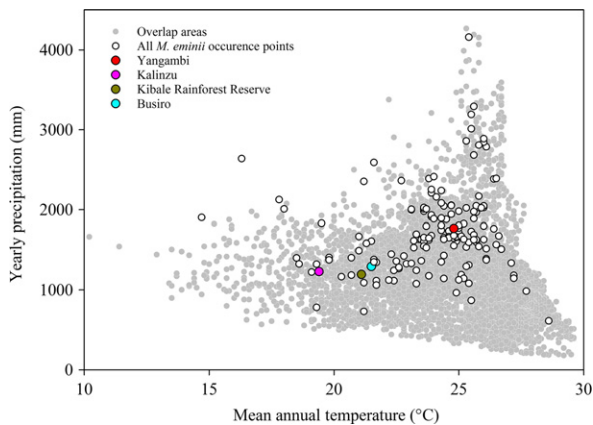


Fig 5 Plot of precipitation as a function of temperature gives an idea of *Maesopsis eminii*'s ecological niche based on occurrence data. Climate information was extracted from land comprised between 20°W (Atlantic Ocean) and 50°E (Indian Ocean) and 20°N (Sahara Desert) and 20°S (Kalahari Desert) so as to capture the region of *M. eminii* occurrence. RStudio Team, 2015 was used to perform the analysis. The grey shaded region therefore signifies the temperature and precipitation value within the latitudinal band that *M. eminii* is observed to occur in Africa. The different colour dots illustrate where more detailed studies on *M. eminii* (i.e. phenology and provenances) were performed

belongs has been noted by Richardson *et al.* (2004) to have a tendency towards xeromorphism, with preference for dry habitats, *M. eminii* might be drought tolerant. Consequently, its occurrence in several relatively dry sites (Table S1), plus the ability to survive and grow well in a new environment (provenance trials, Fig. 2), indicates that *M. eminii*'s functional traits (Epila *et al.*, 2017a,b; Table 1) allow the species to establish in more marginal environments too. Borchert (1994) classifies trees with similar functional traits as *M. eminii* for example deciduousness and low wood density (Table 1), as species that have high stem water storage, allowing them to grow in moderately dry sites. This is true for *M. eminii* with elastic cell walls based on its low modulus of elasticity value (Epila *et al.*, 2017a; Table 1), a value which based on Bartlett, Scoffoni & Sack (2012) and others' range of 5–80 MPa implies elastic cell walls. Epila *et al.* (2017a) found *M. eminii* seedlings to have a substantial hydraulic capacitance [C ; C_{elastic} ($319 \pm 20 \text{ kg m}^{-3} \text{ MPa}^{-1}$), $C_{\text{inelastic}}$ ($655 \pm 56 \text{ kg m}^{-3} \text{ MPa}^{-1}$) and pooled C ($518 \pm 38 \text{ kg m}^{-3} \text{ MPa}^{-1}$)] and vessel-associated parenchyma localized around their hydraulic vessels, both indicating substantial stem water storage. Another strategy to cope with dry events might be related to leaf phenology.

Although our phenological data (Fig. 1) indicate that leaf defoliation was not really influenced by the dry–wet season cycles in DR Congo, we know that complete leaf shedding helps *M. eminii* in some cases to survive severe drought (Eggeling, 1947). In addition, we can also mention that *M. eminii*'s long period of seed dormancy (Table 1) ensures that the seed can germinate when the rains return after a long dry period.

Finally, the root functional traits probably play an essential role in allowing *M. eminii* to grow under a wide range of site conditions. *Maesopsis eminii* has both deep tap roots and an intricate mat of lateral roots (Table 1) that permeate the subsoil, allowing the species to explore resources (nutrients and water) from both shallow and deep soil layers supporting its fast-growing and competitive habit.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Map of Africa showing the geo-referenced occurrence positions of *Maesopsis eminii* and soil types therein based on available data sets. The different colour dots illustrate where more detailed studies on *Maesopsis eminii* (i.e. phenology and provenances) were performed. The original map sheet was sourced from FAO.

Table S1. Geo-referenced occurrence point locations of *Maesopsis eminii* with their respective presence points, obtained from the different databases and datasets.

Table S2. Unpublished historical data of seasonal phenology of eight *Maesopsis eminii* trees thriving in a semi-deciduous forest in Yangambi DR. Congo (1939–1956).