

Article

How Tightly Linked Are *Pericopsis elata* (Fabaceae) Patches to Anthropogenic Disturbances in Southeastern Cameroon?

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Abstract: While most past studies have emphasized the relationships between specific forest stands and edaphic factors, recent observations in Central African moist forests suggested that an increase of slash-and-burn agriculture since 3000–2000 BP (Before Present) could be

the main driver of the persistence of light-demanding tree species. In order to examine anthropogenic factors in the persistence of such populations, our study focused on *Pericopsis elata*, an endangered clustered timber species. We used a multidisciplinary approach comprised of botanical, anthracological and archaeobotanical investigations to compare *P. elata* patches with surrounding stands of mixed forest vegetation (“out-zones”). Charcoal samples were found in both zones, but were significantly more abundant in the soils of patches. Eleven groups of taxa were identified from the charcoals, most of them also present in the current vegetation. Potsherds were detected only inside *P. elata* patches and at different soil depths, suggesting a long human presence from at least 2150 to 195 BP, as revealed by our charcoal radiocarbon dating. We conclude that current *P. elata* patches most likely result from shifting cultivation that occurred *ca.* two centuries ago. The implications of our findings for the dynamics and management of light-demanding tree species are discussed.

Keywords: Afrormosia; Assamela; Central Africa; tropical rain forest; autecology; forest history; shifting cultivation; past human disturbances; charcoal

1. Introduction

While tropical moist forests have long been viewed by the general public as pristine and stable ecosystems, the last three decades have seen a radical change in this preconception. The growing hypothesis is that the tropical rainforests of Central Africa have changed quite dramatically, both in terms of extension and composition, during the last 20,000 years [1]. It is argued that climate has been the main driver of this phenomenon [2]. While this hypothesis is probably true at large spatial scales over long time spans (10,000 years or more), humans may have strengthened the effects of climate variation on vegetation composition, mainly during the last 2000 years [3–5]. This hypothesis is based on the current abundance of light-demanding tree species in most Central African moist forests; an unexpected outcome if we consider only the paleoclimate. In those forests, climax vegetation is normally mainly composed of shade bearers. Since the last maximum glacial period dated to *ca.* 15,000 BP, light-demanders should be less represented nowadays. As this is not the case, many authors have invoked the role of large gaps created by Bantu populations who penetrated the forest from 3000 to 2000 BP together with a sharp climatic change that reduced the forest cover [6]. Slash-and-burn agriculture practiced by those Bantu speakers originated gaps much larger than those generated by natural tree falls. Therefore, openings and fires of anthropogenic origin may have resulted in a gradual and substantial increase of light-demanding species densities in the Congo Basin forests [7–9].

Light-demanding species now contribute to improving plant richness and represent the major part of timber production in Central Africa [10,11]. However, their regeneration rates are low [12], and some authors have argued that this may be due to the current absence of gap conditions needed for their development, since Bantu populations are now settled on roadsides [13].

How human land use intensification has affected the composition of the forest vegetation is of great interest for tropical ecologists and managers in order to assess the past and future dynamics of this

ecosystem. However, addressing such topics in tropical moist forest zones is challenging, as archaeological artefacts are scarce, partially due to the acidity of soils and the warm and humid conditions that prevent their conservation [14]. Nevertheless, charred materials from wood or hard-coated seeds found in these humid regions can be viewed as evidence of human activity, because natural fires very rarely occur in the humid tropics [15–17].

In recent years, the assumption that the opening of rainforests by climatic changes around 3000–2000 BP favored forest settlers (e.g., [9]) has been tested. Those studies revealed mainly indirect evidence of the relationships between past human activities and the establishment of light-demanding tree species. By contrast, [18] pointed out a direct influence of human disturbance on the development of mahogany (*Entandrophragma* spp.) forests in Nigeria. In the context of moist forest resources depletion [19,20], understanding the drivers of timber species distribution has become a crucial issue for forest managers in order to implement, e.g., efficient planting methods [21].

This paper focuses on a high-value timber species of African moist forests, *Pericopsis elata* (Harms) Meeuwen, to provide insights into the patterns that may have shaped the distribution of light-demanding species. *P. elata* was chosen because: (1) it is a light-demanding species with an evident lack of regeneration in closed canopy forests; (2) its populations form aggregated and well-delimited groups; a fact that may facilitate the comparison of habitats dominated by this species and the surrounding zones of mixed forest stands; (3) it is considered as “Endangered A1cd” by the International Union for Conservation of Nature (IUCN) and is listed on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix II; and (4) it is logged and of high commercial value, so that its dynamics is of particular interest to both conservationists and forest managers.

Our study aimed to understand the aggregated distribution of *P. elata* with respect to past human influences. The research questions addressed in this manuscript are: (1) are *P. elata* patches different from the surrounding vegetation; (2) was the past vegetation composition different from the current one; and (3) is *P. elata* linked to past human activities? First, we performed floristic inventories to characterize the differences between *P. elata* patches and the surrounding vegetation and to compare the past vegetation reconstructed from charcoals with that of the extant forest. Second, we looked for past human activities through anthracological investigations. Then, the implications for forest management and silvicultural treatments are discussed.

2. Experimental Section

2.1. Study Species

P. elata (Fabaceae) is a tall tree of almost 150 cm in diameter at breast height (dbh) and a total height of about 40 m. Seeds are dispersed by wind to a maximal distance of about 100 m; the species tends to occur in clumped forest stands [22]. Its natural range extends from West to Central Africa (Cameroon, Congo and the DRC; [23]) and is characteristic of mainland semi-evergreen forests [24]. It is either classified as a pioneer or a non-pioneer light-demanding species [23,25,26]. The population structure generally presents a bell-shaped curve depicting a lack of regeneration [23]. In Cameroon, the diameter increment was estimated to be 0.31 ± 0.05 cm [27].

2.2. Study Sites

The study was conducted in a logging concession located on the Cameroonian southern plateau between 3°01'–3°25' N and 14°05'–14°31' E (Figure 1). Elevations range between 600 and 700 m above sea level. Mean annual rainfall is *ca.* 1625 mm. Soils are derived from metamorphic rocks and mostly range from ferrallitic red to typical yellow [28]. The vegetation belongs to the Congolese mixed moist semi-evergreen forest [29]. Study sites are located on well-drained soils, far away from the zones proposed to be the main Pleistocene and Holocene forest refugia [30,31]. The average density of *P. elata* was locally estimated at 107 ± 11 trees km^{-2} (dbh ≥ 20 cm; [12]).

Three study sites were selected (Sites 1 to 3) and included a well-delimited area dominated by *P. elata*, thereafter called a “patch”. A continuous line connecting edges of outer *P. elata* tree canopies defined the boundary of each patch. The surrounding forest where the species was absent was called “the out-zone”. The estimated patch area and density (dbh ≥ 10 cm) of *P. elata* for Sites 1–3 were 14.7, 3.3 and 9.5 ha and 132, 63 and 105 stems, respectively. The minimum and maximum recorded dbh were 13 and 101 cm for *P. elata*. The shortest distance between two adjacent sites was 7.5 km.

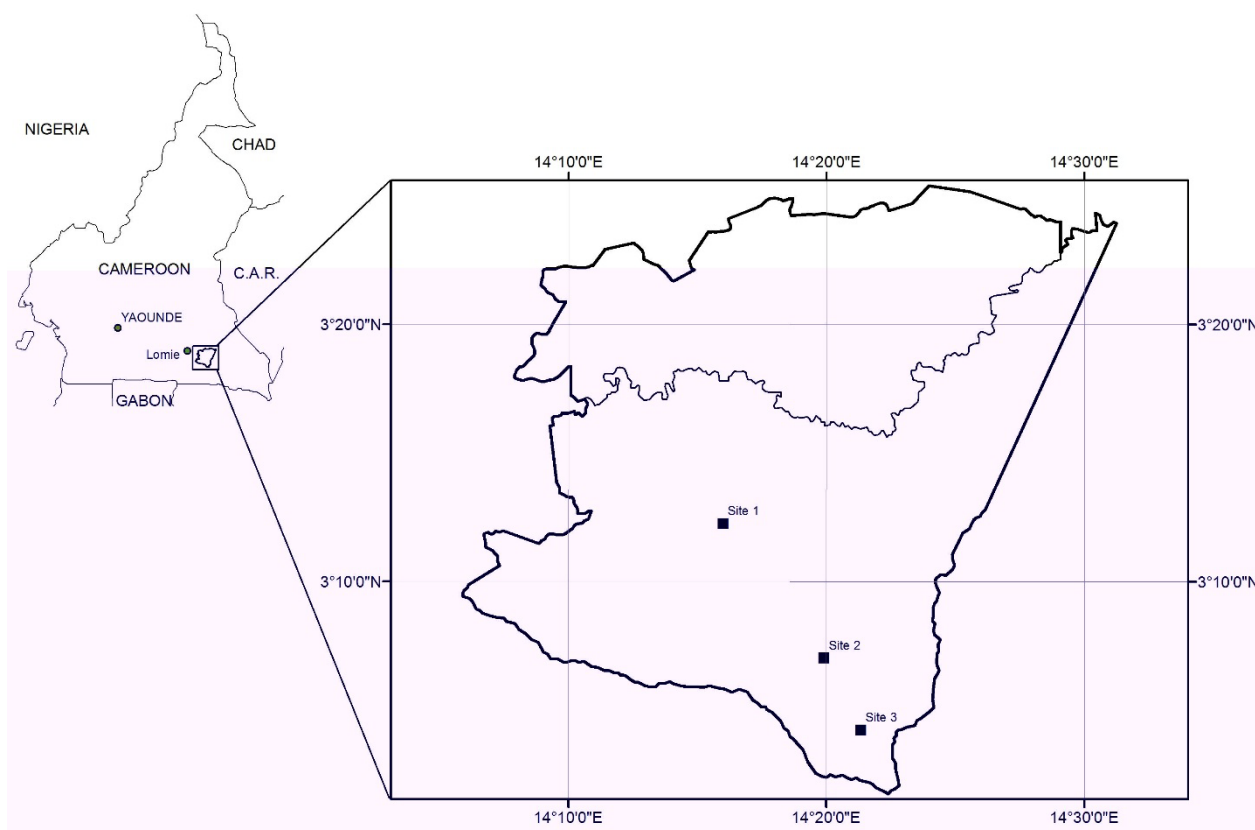


Figure 1. Location of the study area, a forest concession in Cameroon of 118,052 ha. The geographical positions of the study sites are represented by black squares. The Boumba River flows westbound across the study area (shown on the map).

2.3. Data Collection

All investigations were performed on transects established for the purpose of the study. Each transect was located alongside the toposequence (*i.e.*, at right angles to contour lines), starting in the patch and protruding in the out-zone of each site. The total transect lengths were 1215, 705 and 840 m for Sites 1–3, respectively. For each site, transect lengths were more or less equally distributed in the two compared zones.

2.4. Botanical Surveys

Individuals of tree species with dbh ≥ 10 cm were surveyed in adjacent rectangular plots of 30×15 m along the toposequence (each plot covered 0.045 ha). Seedlings and saplings (dbh < 10 cm; minimum 0.50 m tall) of *P. elata* were inventoried in each sampling plot to assess the regeneration rate of the species in the present context of forest management. A total of 3.65 (81 plots), 2.12 (47 plots) and 2.52 ha (56 plots) was surveyed at Sites 1–3, respectively. Considering the plots located within patches, the sampling rates were 14%, 33% and 13% for the patches of Sites 1–3, respectively.

2.5. Charcoal Collection and Identification

Charcoal is a chemically inert material that is little affected by weathering and can persist in soils for thousands of years [32]. Charcoal has two other characteristics that make it useful for this study. First, large samples can enable the identification of the burnt vegetation, since carbonization preserves most of the wood structure. Second, charcoal samples can be dated by radiocarbon (^{14}C) methods. Investigations to detect charcoal and past human evidence were carried out along transects through hand auger sampling and pits. Auger sampling was performed at a maximal depth of 120 cm: a check for human evidence was done for each 20 cm step. This sampling was done at each visual change in the vegetation, topography and/or soil depth (*e.g.*, rock outcrop). A total of 37 auger samples were collected: 16 (half in each zone), 8 (half in each zone) and 13 (6 inside the patch, 7 outside) at Sites 1–3, respectively.

Based on the auger sampling findings, pits were dug where the charcoal content was high. Pits were $1.5 \times 1 \times 2$ m in length, width and depth, respectively. Six pits were dug, at the rate of one pit per zone (patch and out-zone) in each of the three sites. The pit in each out-zone was at least 100 m away from the patch boundary. In each pit, a row of contiguous squares of 20×20 cm was drawn on the pit wall along a line going straight from the surface level to the maximum depth. A 1.5-liter soil volume was then excavated within each of the squares for further charcoal investigation purposes. Charcoal abundance was assigned following the rating system proposed by [33]: from “rare” (one or two flecks of small fragments, diameters < 2 mm) to “abundant” (many large pieces, diameters > 10 mm).

Taxonomical identification of a selection of charcoal fragments of at least 0.1 cm^3 was carried out at the Service of Wood Biology of the Royal Museum for Central Africa (Belgium) following a specific protocol [34].

Radiocarbon dating was conducted on four burnt fragments collected from all sites (1, 1 and 2 fragments from Site 1–3, respectively). This selection was based on: (1) the requirement of a minimum of one dating to be performed per site; (2) the finding of a piece of charred palm nut

(*Elaeis guineensis*) in Site 1; (3) the presence of a charcoal fragment in direct contact with a pottery element in Site 3, which makes it possible to estimate the age of the ceramic. Selected burnt elements were pre-treated and then analyzed following the accelerator mass spectrometry method [35]. Dating radiocarbon calibration was done using the OxCal 4.2 program (Oxford Radiocarbon Accelerator Unit: oxford, UK) [36].

2.6. Data Analysis

In order to assess floristic similarity and differences between patches and the surrounding forests, we computed the Morisita–Horn index, which gives a nearly unbiased measure of similarity when the sample size is small compared to the actual community size [37]. The computation of this index was done using BiodivR 1.2 (Evolutionary Biology & Ecology: Brussels, Belgium) [38]. For these analyses, *P. elata* individuals were removed from the dataset so as not to introduce a bias due to the potential overabundance of the species within the patches.

Tree density and mean basal area (= “basal area of the average tree” *sensu* [39]; MBA) were computed in each site (1, 2 or 3) and zone (patch or out-zone) and extrapolated to 1 ha of forest. All species were considered for those computations. For the MBA, after assumptions of normality and homoscedasticity were verified, the differences were investigated with a general linear model (GLM) analysis using the type III adjusted sum of squares and considering “site” (1–3) and “zone” (patch and out-zone) as fixed factors. For vegetation analysis, the units of replication were the trees.

After verification of the assumptions of normality and homoscedasticity, differences in subsurface charcoal abundance between soils inside and outside patches were investigated using three-way ANOVA. Site, zone and depth of collection were considered as fixed factors. For the analysis of charcoal abundance, units of replication were the plots in which auger samples were collected.

Statistical analyses were performed using Minitab software (2000–2006 Minitab Inc., State College, PA, USA).

3. Results and Discussion

3.1. Floristic Inventory

A total of 45 families were identified over a total surveyed area of 8.28 ha (all sites and zones included). Some 173 different taxa were identified (Table 1). The seven most represented families and species counted for *ca.* 50% and 30% of the 3004 inventoried trees, respectively. No seedling or sapling of *P. elata* was recorded during the floristic survey.

Statistical analysis revealed no influence of “site” on the MBA, but a significant effect of “zone” (GLM; $F_{2,2998} = 1.24$, $p = 0.290$; $F_{1,2998} = 19.73$, $p < 0.0001$), the MBA being higher in the patches. Forests surrounding the patches showed similar pools of prevalent species (Table 1 and Supplementary Table S1). The Morisita–Horn indices were 0.77, 0.76 and 0.69 for Sites 1–3, respectively, suggesting floristic similarity between the patches (all species considered, apart from *P. elata*) and the out-zones of the three sites (Table 1).

Table 1. Some characteristics of the standing vegetation (trees with dbh ≥ 10 cm) in the study sites (1–3). TD, tree density; MBA, mean basal area; MDBH, mean diameter at breast height. Means are computed over all recorded stems per site and zone (the standard deviation (SD) is given between brackets). Tree density is reduced per ha taking into account the surveyed area in the given site and zone. No regeneration (dbh < 10 cm) was detected for *P. elata*.

| Characteristic | Species | Inside Patches | | | Outside Patches | | |
|--|-----------------|------------------|------------------|------------------|------------------|------------------|------------------|
| Site (surveyed area in ha) | | Site 1 (2.12) | Site 2 (1.08) | Site 3 (1.26) | Site 1 (1.49) | Site 2 (0.99) | Site 3 (1.22) |
| TD in n/ha | | 287 | 342 | 405 | 395 | 416 | 423 |
| MBA in m ² (SD in m ²) | All species | 0.10 (0.01) | 0.08 (0.01) | 0.10 (0.01) | 0.06 (0.01) | 0.07 (0.01) | 0.07 (0.01) |
| | <i>P. elata</i> | 0.43 | 0.39 | 0.35 | / | / | / |
| | individuals | (0.17) | (0.25) | (0.27) | | | |
| MDBH in cm (SD in cm) | All species | 27.9 (1.7) | 25.7 (1.9) | 28.4 (1.8) | 22.8 (1.3) | 23.8 (1.7) | 24.7 (1.5) |
| | <i>P. elata</i> | 71.6 | 66.2 | 61.4 | / | / | / |
| | individuals | (18.0) | (24.8) | (27.2) | | | |

3.2. Anthracological Findings

Fifty-four fragments of charcoal were collected, among which four were used for ¹⁴C dating. Fifty-six percent of fragments were suitable for taxonomic identification. Charcoal elements were collected during soil excavations in 56% and 54% of the pits and auger sampling, respectively. On average, we found more charcoal in auger samplings in Sites 1 and 3 (Figure 2), but this result has to be interpreted with care, as only a few auger samples were taken in Site 2 due to its restricted area.

The factor “site” did not influence the amount of collected subsurface charcoal ($F_{2,35} = 2.41$; $p = 0.109$), but the abundance of charcoal was higher inside patches than outside ($F_{1,35} = 7.74$; $p = 0.010$). In addition, soil depth had a significant impact on charcoal abundance ($F_{5,36} = 2.79$; $p = 0.037$), with abundance decreasing with depth (Figures 2 and 3).

Taxonomic identification of the charcoal led to the determination of 11 types, possibly corresponding to 30 taxa. The taxa with the highest probabilities of correct identification are those also encountered in the extant vegetation of our study area: *Duboscia macrocarpa*, *Lepidobotrys staudtii*, *Polyalthia suaveolens* and *Stemonocoleus micranthus*. Even when we considered identifications with lower probabilities, no charred fragment appeared to be to *P. elata* (Supplementary Table S2).

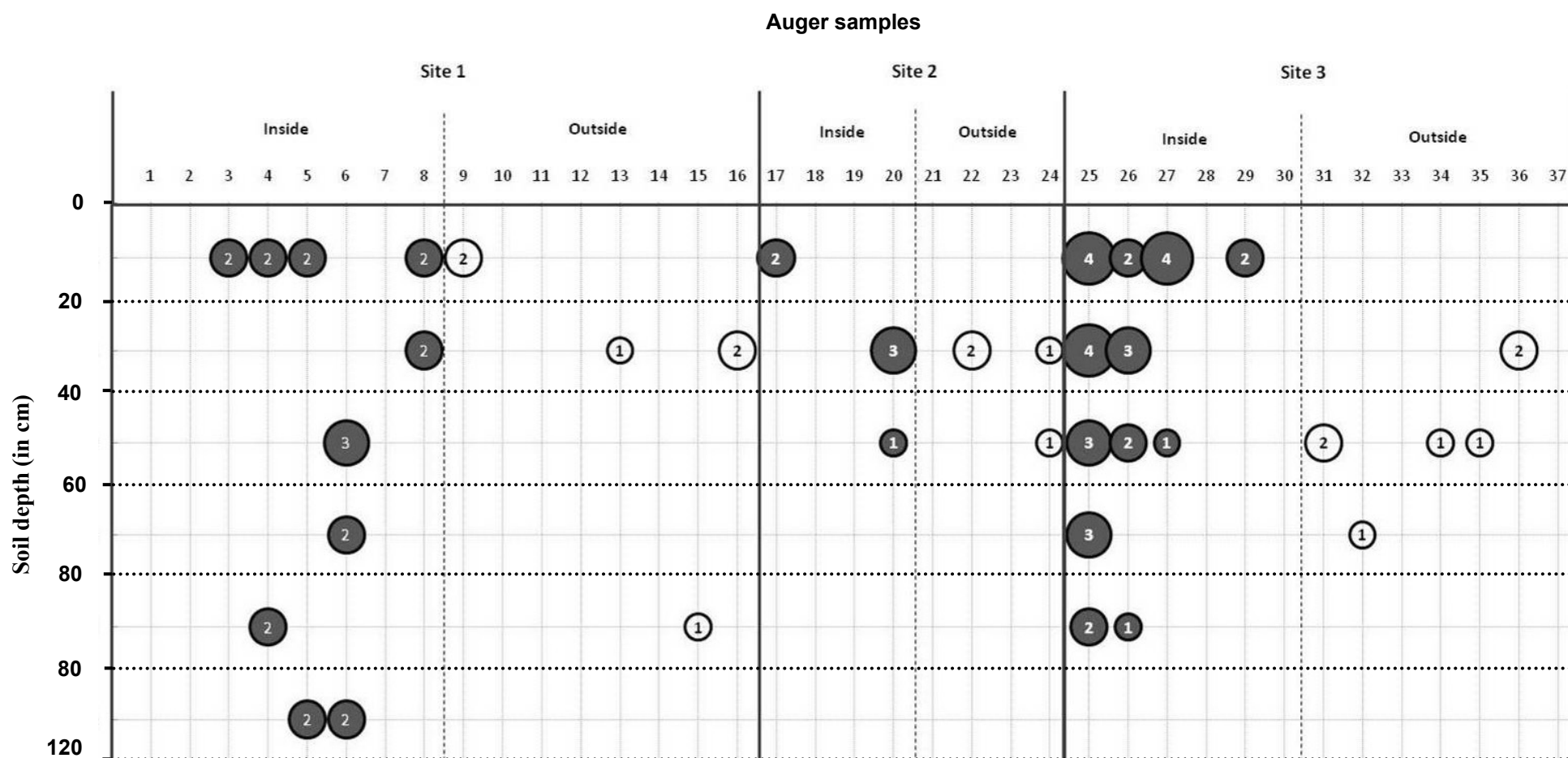


Figure 2. Abundance of the subsurface charcoal discovered in each of the 37 (identified by a number from 1 to 37) auger samples collected from the study area (southeastern Cameroon). Abundance rate 1 = rare, 2 = occasional, 3 = frequent, 4 = common, 5 = abundant. See [33] for further details on how these rates were assigned. Abundances inside and outside *P. elata* patches are represented by shaded and open dots, respectively. The diameter of each dot is proportional to the abundance rate. Dotted lines represent the limit between the patch and its surrounding vegetation (in columns) and the limit between two layers of soil (in rows).

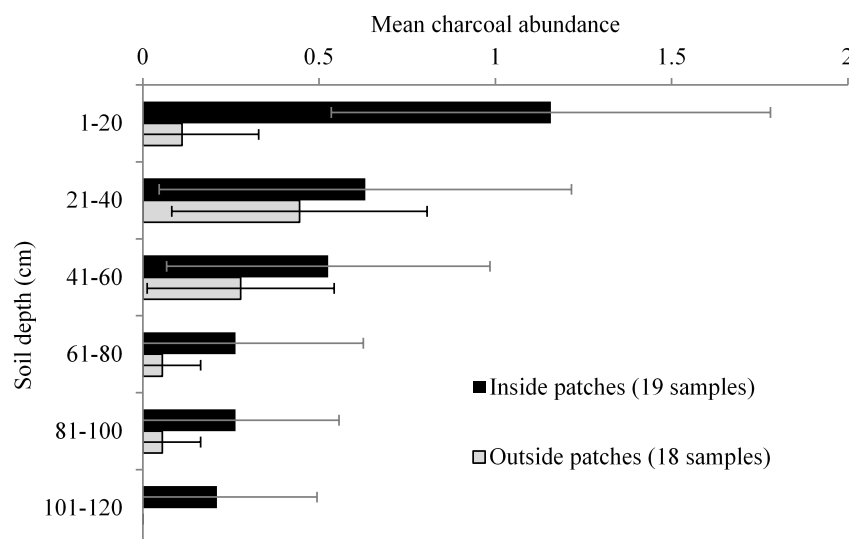


Figure 3. Mean abundance of subsurface charcoal by soil depth and whether belonging to *P. elata* patches or not. Data collected from 37 auger samples taken in Sites 1–3 (118,052 ha study area, southeastern Cameroon). Means with 95% CI are computed on abundance rates, as defined by [33].

The radiocarbon ages of selected burnt elements varied from 195 ± 30 to 2150 ± 45 BP (Table 2).

Table 2. Radiocarbon dating of a selection of four subsurface burnt woody elements collected in the study sites (southeastern Cameroon). Uncalibrated dates (BP) are provided with the standard deviation. The origin is defined as “seed” or “charcoal” for a carbonized seed of *Elaeis guineensis* or a carbonized woody part of the tree/shrub (root, trunk or branch), respectively.

| Site | Type of Sampling | Depth (cm) | Origin | Age ^{14}C (BP) | Radiocarbon Laboratory Number |
|------|------------------|------------|----------|--|-------------------------------|
| 1 | Auger | 41–60 | Seed | 1795 ± 40 (68.2%: 1632–1810 cal BP; 95.4%: 1609–1825 cal BP) * | KIA-38933 Z1S1 40–60 |
| 2 | Auger | 0–20 | Charcoal | 2150 ± 45 (68.2%: 2060–2301 cal BP; 95.4%: 2004–2308 cal BP) * | KIA-38938 L3S1 0–20 |
| 3 | Pit | 0–20 | Charcoal | 205 ± 30 (68.2%: 11–296 cal BP; 95.4%: 24–305 cal BP) * | KIA-38934 CAM. MIN 1.2 |
| 3 | Pit | 0–20 | Charcoal | 195 ± 30 (68.2%: 13–289 cal BP; 95.4%: 25–302 cal BP) * | KIA-38942 F4 200–220 |

* Radiocarbon calibration was done using the OxCal 4.2 program [36]. Cal BP: “Calibrated years Before Present”.

KIA–Leibniz Laboratory for Radiometric Dating and Stable Isotope Research: Kiel, Germany.

3.3. Archaeological Findings

Potsherds were collected opportunistically in the pits dug within patches of Sites 2 and 3 (no potsherds were found in Site 1). Discovered artefacts were counted; a total of 132 fragments of pottery were found in Site 2; unfortunately, all of them were spatially scattered and of small or medium sizes (ca. $6 \times 6 \times 4$ cm, for the largest fragment). Even if shapes and sizes could not be reconstructed for many

items, the *peigne gouge* decoration technique was identified on some fragments, as well as on the remains of a beaker (Site 2). Fragments were collected at depths of between 16 and 50 cm, and in the case of Site 3, all potsherds were found between 16 and 30 cm depths. In Site 3, the wooden *roulette* decoration technique was identified on some artefacts. When considering both sites, *ca.* two-thirds of all fragments were collected between 26 and 40 cm. No fragments were collected in Site 1 or in outside patches.

3.4. Autecology of *P. elata*

Our results confirmed that *P. elata* is a clustering species, occurring in patches with easily identified boundaries. This tendency to establish clustered stands is shared with other light-demanding wind-dispersed timber trees, such as *Triplochiton scleroxylon* [40].

Some authors estimated that the average logging gap area in this forest concession was *ca.* 265 m² [28]. We assumed that the average natural tree fall gap area would be in the same order of magnitude in the study sites, which appears insufficient for regeneration given the minimum gap size of 1000 m² to fulfil the species requirements according to [41]. This would explain why no seedlings or saplings of *P. elata* were detected during our fieldwork. It also confirms the absence of regeneration in other study sites (Figure 4) and its high light requirements at early stages of growth. In Cameroon, contemporary slash-and-burn agriculture gap sizes vary between 6500 and 7300 m² [42]. This cultivation method, assuming historic practices were similar, could have created openings large enough to favor the regeneration of *P. elata*.

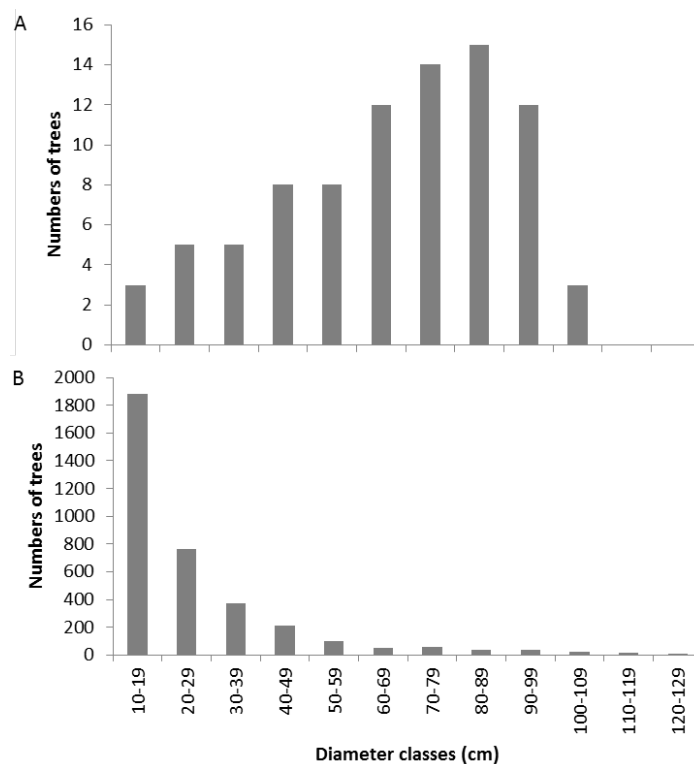


Figure 4. Population structure of *P. elata* (A) and all of the species (B) individuals recorded in the botanical sampling plots installed in all sites and zones. The absolute number of trees is given by diameter class.

3.5. Anthracology and Archaeology Outcomes: The Likely Human-Induced Origin of *P. elata* Populations

The presence of pottery in multiple layers indicates a long succession of human activity over centuries or thousands of years, rather than an event that occurred in a relatively restricted period of time. This suggestion is confirmed by the results of dating showing *ca.* 2000 years separating the youngest and oldest fire events. Even if the topographical situation of Site 3 is consistent with a possible settlement of a village (hilltop, close to a river; [43]), neither iron furnaces nor old rubbish pits were discovered in our study. As stated in other works [44], such a discovery would have corroborated the likely presence of a village in an area where elements of a beaker and other pottery fragments were located along with abundant pieces of charcoal. Contrary to the findings of [18], our collections of both charcoal and potsherds were not restricted to a single layer of soil. In similar tropical forests, some authors observed that subsurface charcoal was relatively widespread [45].

The radiocarbon dating of Sites 1 and 2 suggests potential human-induced disturbances around 2000 BP. The decoration technique identified on some fragments of Site 2 is the *peigne gouge*. As pointed out by [46], this coincides with the Early Iron Age, a period during which [47] noticed a demographic explosion of metallurgists in West Congo Basin forests. Compared to Site 3, where most of the potsherds were discovered close to current ground level, the soil of Site 2 showed a much more scattered and deeper distribution of artefacts. This may reflect that Site 2 hosted human activities in the remote past and over a long period of time.

In Site 3, where two charcoal fragments were collected, dated to 195 ± 30 and 205 ± 30 BP, *P. elata* individuals: (1) had a mean diameter of *ca.* 60 cm; (2) had a mean annual diameter increment of 0.31 cm ([27]; same study area); and (3) had similar diameters. Therefore, we assigned the mean age of this patch to *ca.* 200 years (see also the results of the study led on *Microberlinia bisulcata* in Korup National Park, Cameroon [48]). This corresponds to the age of the charcoal collected in the same site (*ca.* 200 BP; the end of the Late Iron Age). In addition, the *roulette* decorating technique observed on one of the collected pottery fragments (patch of Site 3) is known to have been used in this region from 1000 years ago to the present time [49].

Our findings suggest that anthropogenic activities occurred in southeastern Cameroon during both the Early and Late Iron Ages, the latter being very likely the origin of current *P. elata* patches.

All taxa identified with a high degree of probability from the charcoal fragments correspond to species presently growing in the studied forests, some of them even being prevalent (*P. suaveolens* and *D. macrocarpa*). While some caution is required when interpreting these results, we noticed that no charcoal of *P. elata* was identified. If we make the assumption that the studied forests have not undergone significant changes in tree species composition, the absence of *P. elata* in charcoal fragments appears contradictory to the high abundance of this species in extant vegetation. However, because they are characterized by a high wood density, mature *P. elata* trees are extremely difficult to fell without a chain saw; therefore, some may have been left standing in traditional shifting cultivation fields [50]. In addition, the species is described as resistant to fire [51], leading one to infer that some seed trees might have survived close to croplands. According to [22], the average weight of wind-dispersed fruits is 1.32 ± 0.10 g, meaning the indehiscent pods would be dispersed in the vicinity of the mother tree. Thus, we suggest that human-disturbed zones subsequently left to regenerate may have presented

favorable conditions for *P. elata* regeneration and growth. Nevertheless, the soil characteristics could also influence the survival and development of *P. elata* seedlings and saplings [41]. It is also important to mention that not all patches of African light-demanding tall trees are caused by human-induced disturbances (*i.e.*, the lack of recruitment may be indicating transient dominance *sensu* [48]).

3.6. Important Issues Regarding the Methodology

The cornerstone of the methodology is the way in which patches and out-zones were defined: the presence/absence of *P. elata* individuals in a restricted geographical area. A direct implication is that the results of floristic comparisons between in- and out-zones must be interpreted with caution. This is especially important when using incidence-based richness estimators, such as Chao [52], as it may induce potential bias. On the other hand, this innovative approach allows reliable investigations, which appear not to be relevant at different perception levels. Having worked in the same study area, but at larger scales, contrary to our findings (see Figure 3), some authors could not detect correlations between the local distribution of light-demanding species and soil charcoal abundance [53].

To allow pedological investigations, we recommend taking auger and composite samples as described in the methodology: alongside the toposequence each time vegetation and/or topography changes. Additional samples can be taken following contour lines as an option for narrowing down the investigation. If charcoal is widespread in forests around the globe [53–55], the one located in the superficial soil layers does not always reflect recent human disturbance. The upper soil layer (0–25 cm) contains a mixture of both recent and ancient charcoal [53]. We thus recommend as many ¹⁴C datings as funding permits of charcoal collected within the upper soil layer. Even if the short residence times of rain forests coarse woody debris is commonly recognized, preference shall be given to charred short-lived plant materials (*e.g.*, charred nuts), so as to limit the inbuilt-age error [56,57]. In our study, the oldest charcoal was found in the soil of Site 2 (2150 BP; Table 2), but this result must nevertheless be interpreted with caution for the reason noted above. The Suess effect may also further complicate the dating for biological samples formed between 1640 and 1950 [58–60], but its amount and geographical spread is uncertain and any Suess correction heavily remains reliant on theoretical modelling (see *e.g.*, [61]).

In the specific case of *P. elata* for which annual tree-ring formation is confirmed [62], stem coring can be useful to crosscheck the average/modal age of the patch. This may apply, or have been done, for the study of other tall African tree clustered species, like *Gilbertiodendron dewevrei* [63,64], *Brachystegia laurentii* [65] or *M. bisulcata* [48].

Working in a forest concession is another innovative aspect of the methodology (but, see [53,66]). Large-scale forest management inventories have already been carried out by logging companies in Central African forests, providing a unique opportunity to identify in advance the best spots to investigate (*e.g.*, high density of light-demanding tall trees).

4. Conclusions

Some studies concluded that some timber tree species currently abundant in Central African moist forests were established in response to previous human disturbances [40,41]. Several of these species currently suffer from poor recruitment, especially *P. elata* in the southeast of Cameroon. In this region, it

occurs in patches together with other long-lived light-demanding species. Our study found that charcoal is widespread and abundant in the soils of these forests, mostly inside patches. We also uncovered numerous potsherds; evidence of past human activities. Furthermore, we showed that the average age of *P. elata* individuals coincides with fire events in a region where fires rarely occur naturally. There is no evidence that modern disturbances, such as selective logging, substantially encourage the regeneration of *P. elata*. The knowledge of historic disturbance regimes and subsequent *P. elata* regeneration and growth is crucial to the identification and development of strategies for ensuring sustainable resource management and the maintenance of ecological services for both local populations and the forestry sector.

In Central Africa, timber species can only be logged when they have greater than species and country-specific diameters. For *P. elata*, this diameter ranges from 60 to 90 cm, depending on the country. The short-term impacts on the recovery rate after a cutting cycle (25 or 30 years, depending on the country) are thus highly variable [27]. However, considering the population structure, the decline from one harvest to the next is expected to be dramatic [67]. In this context, silvicultural interventions, specifically creating larger canopy gaps, are needed. Thinning will probably have little effect on *P. elata* individuals already reaching the canopy. Creating large gaps around seed trees, just after fructification, could enhance reproduction [68], but the implementation of such a technique is not permitted by current forest legislations. In this context, enrichment plantings with desired, gap-dependent species in logging gaps or degraded forests are probably the best way to regenerate the light-demanding timber species associated with historic human land uses and associated ecological disturbances [21].

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Author Contributions

Nils Bourland, Alexandre Livingstone Smith, Jean-Louis Doucet and François Cerisier conceived of and designed the experiments. François Cerisier, Nils Bourland, Eric Ntoudé Tiba, Fousséni R. Fétéké and Philippe Lejeune facilitated or performed field research. François Cerisier, Yves Brostaux, Wannes Hubau, Alexandre Livingstone Smith, Hans Beeckman, Adeline Fayolle and Nils Bourland analyzed the data. Adeline Fayolle, Wannes Hubau, Hans Beeckman and Joris Van Acker contributed analysis tools and/or commented on the data analysis. Jean-Louis Doucet and Jean-François Gillet controlled the botanical identifications. Nils Bourland, François Cerisier, Julie Morin-Rivat and Achille Bernard Biwolé contributed to the literature search. Nils Bourland, François Cerisier, Jean-Louis Doucet and Kasso Daïnou wrote the paper. Alexandre Livingstone Smith, Achille Bernard Biwolé, Julie Morin-Rivat and Jean-François Gillet commented on the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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