Forest Ecology and Management 313 (2014) 55–62

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Diagnosing the demographic balance of two light-demanding tree species populations in central Africa from their diameter distribution

Nestor Laurier Engone Obiang [a], Alfred Ngomanda [a], Oliver Hymas [b,c], Éric Chézeauxl [d], Nicolas Picard [a,e,*]

[a] IRET, BP 13354 Libreville, Gabon
[b] University College London, London, UK
[c] Zoological Society of London, London, UK
[d] Rougier-Gabon, ZI Oloumi, BP 130 Libreville, Gabon
[e] CIRAD, UPR Bsef, 34398 Montpellier Cedex 5, France

ARTICLE INFO

Article history:
Received 15 April 2013
Received in revised form 25 October 2013
Accepted 29 October 2013
Available online 26 November 2013

Keywords:
Aucoumea klaineana
Diameter distribution
Gabon
Lophira alata
Natural forest
Population dynamics

ABSTRACT

The diameter distribution of a tree species population in a natural forest reflects its demographic dynamics and the impact of past disturbances. A modal diameter distribution can be the mark of a demographic imbalance or it can be the consequence of a particular growth pattern. By comparing the observed diameter distribution with the one that follows from a reference growth model under the hypothesis of demographic balance, we diagnosed demographic balance. In a forest concession in Gabon before logging, an unbalanced diameter distribution was found for *Aucoumea klaineana*, a long-lived pioneer species and also a valuable commercial species. The *Aucoumea klaineana* population consisted of old trees without meaningful recruitment, thus indicating an ageing, declining population. In contrast, in the same concession, a balanced diameter distribution was found for *Lophira alata*, a pioneer to moderate light-demanding species. The history of this forest concession, once heavily populated and subsequently depleted from human perturbation (shifting cultivation), can be used to interpret these demographic statuses. These results reinforce the view of a forest that is constantly changing and shaped by past human perturbations, with the implication for its conservation that some kind of perturbation should be maintained.

1. Introduction

A major proportion of the tropical rain forests of central Africa currently have a dedicated use, such as productive forests or protected areas (Wasseige et al., 2009). Maintaining this use on the long term through sustainable management or conservation requires to understand the drivers of forest dynamics. In central Africa, the vision of a mature pristine forest in a steady state in accordance with the mosaic cycle concept (Remmert, 1991) has been somewhat challenged by the vision of a forest constantly changing in response to climate or human disturbance (van Gemerden et al., 2003). Across millennia, it is now clearly evidenced that the tropical rain forests of central Africa have undergone deep environmental changes (Bonnefille, 2011). Palaeoecology (Brncic et al., 2009; Lejju, 2009; Ngomanda et al., 2005; Vincens et al., 1999), tree species genetics (Daïnou et al., 2010), and archaeology (Oslisly, 2001; Wotzka, 2006) jointly concur to show in a consistent manner that the major part of the current forest block of the Congo basin was once covered with savannah during the last ice age, and that the transitions between forest and savannah during the Quaternary responded to climate changes (Leal, 2004; Ngomanda et al., 2009).

Even on a shorter term, the question "are central African undisturbed mature forests at steady state?" has no definite answer (van Gemerden et al., 2003; Lewis et al., 2009). In many undisturbed tropical African rain forests, an apparent decline of some tree species populations is locally observed (Forni, 1997; Kalema and Kasenene, 2007; Thomas et al., 2005). These populations typically have a modal diameter distribution, with either an accumulation of large individuals and a deficit of small ones, or a hump in a globally decreasing distribution (Fournier and Sasson, 1983; Rollet, 1974). Most of the species that are concerned by this phenomenon are light-demanding fast growing species that are also, for a majority of them, commercial species (Ouédraogo et al., 2011).

There are two main hypotheses to explain this modal distribution. The first one is that it corresponds indeed to a demographic imbalance, with a past peak of recruitment and a current deficit of regeneration (Condit et al., 1998; Goodburn and Lorimer, 1999; Lykke, 1998; Wang et al., 2009). Strictly light-demanding species such as pioneers often present peaks of recruitment

* Corresponding author. Address: CIRAD, BP 2572 Yaounde, Cameroon. Tel.: +237 90 92 62 90.

E-mail addresses: engonobiang@yahoo.fr (N.L. Engone Obiang), ngomanda@yahoo.fr (A. Ngomanda), ohymas@onetel.com (O. Hymas), chezeaux@groupe-rougier.com (É. Chézeauxl), nicolas.picard@cirad.fr (N. Picard).

0378-1127/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2013.10.045

associated with disturbances. Cohorts of individuals issuing for the same disturbance event then age together and form humps in the diameter distribution. According to this hypothesis, the modal diameter distribution results from inherently transient population dynamics. Because hurricane, river and volcanic disturbances are rare in central Africa, human disturbance (such as shifting cultivation or fire) is most often advocated as the driving process of this dynamics (van Gemerden et al., 2003). The second hypothesis is that this modal distribution follows from a particular dependence of growth and mortality on diameter (Palla et al., 2002b; Zavala et al., 2007): a diameter growth that increases beyond a given diameter x combined with an almost null mortality above x can indeed result at steady state in a mode of the diameter distribution at x. This second hypothesis is thus compatible with a demographic balance of the population. This particular dependence of growth and mortality on diameter is hypothesized for non-pioneer light-demanding species that do not necessitate full light to reproduce but require light at critical stages of their life. Diameters x that correspond to humps in the diameter distribution would then mark these critical stages. The critical life stage that is the most often advocated for non-pioneer light-demanding species is the access to the canopy.

Discriminating these two explanative hypotheses has important implications for the conservation and sustainable management of these populations. If the population is in demographic imbalance and declining, it would naturally vanish if the current conditions maintain in the future. Preserving the undisturbed forest in its current condition may then not be the best option for conservation. On the contrary, if the population is in demographic balance, it can maintain under the current conditions. The present study aims at diagnosing the demographic balance of tree species populations based on their diameter distribution and a reference model for diameter growth. Two contrasting tree species populations in a tropical rain forest in central Africa were investigated: one population of okoume (*Aucoumea klaineana* Pierre, Burseraceae), that is a strict light-demanding species, and one population of azobe (*Lophira alata* Banks ex C.F.Gaertn., Ochnaceae) that is, depending on authors, a pioneer to moderate light-demanding species.

2. Materials and methods

2.1. Study site

The study site is the Haut Abanga forest concession under sustainable management in Gabon, where a concession in central Africa designates a state-owned forest area granted to a logging company for a given time. This concession that covers 288,627 ha is located in northwestern Gabon, at the eastern piedmont of the Monts de Cristal mountain range, between longitudes 10°30′ and 11°30′W and latitudes 0°15′ and 0°50′N (Bayol, 2002; Tancré, 2001). The forest concession is divided into nine forest management units. It is crossed from North to South by the Abanga river (Fig. 1). The relief consists of hills with a gradient of slopes from the East-Centre (gentle slopes) to the West (steep slopes). Altitudes range between 250 and 1022 m. Climate is equatorial, with an annual rainfall that varies between 1800 and 2000 mm depending on slope aspect, and a mean annual temperature between 24 and 26 °C. The geological formation consist of an Archean basement with metamorphic and granitic rocks. Soils are ferralitic sandy-clayey or clayey soils. Vegetation is dominated by Burseraceae (18% of the basal area), Myristicaceae (15%), Cesalpiniaceae (15%) and Euphorbiaceae (9%). The Abanga river was once a communication corridor between northern and central Gabon, and lost this role when the modern road network was set up. Maps of human occupation show that this area, and in particular the Abanga river banks, were populated till the 1940s (Fig. 1; Peyrot, 2008). Human populations then moved close to the roads and, by 1950, the Haut Abanga concession was empty of any human settlement (Bayol, 2002).

A forest inventory was conducted in the Haut Abanga concession in 1998–1999. The minimum dbh for inventory was 10 cm, and dbh classes were 10 cm wide, except the last class that gathered all trees greater than 160 cm dbh. The sampling design was systematic using 0.5-ha sampling plots, with a planned sampling rate of 1% for trees with diameter at breast height (dbh) $\geqslant$ 20 cm and of 0.2% for trees with 10 cm $\leqslant$dbh $<$ 20 cm, and an achieved rate of 1.2% for the former (Bayol, 2002). This inventory gave the number of trees in 16 diameter classes for 313 species and for each forest management unit, with an estimation error <10%.

2.2. Focus species

Two light-demanding species were selected for this study: *Aucoumea klaineana* Pierre (Burseraceae), or okoume as it is commonly called in Gabon, and *Lophira alata* Banks ex C.F.Gaertn. (Ochnaceae) or azobe. These two species are the two most important timber species in Gabon, with a volume entering mills of 931,473 m^3 for okoume and of 37,700 m^3 for azobe in 2007 (82% and 3% of the total timber production of Gabon, respectively) (Wasseige et al., 2009, chapter 3). Although these species are abundant in Gabon, they have been classified as vulnerable in the IUCN red list because of logging. Additionally, okoume has a natural range that is restricted to western and central Gabon and areas of Equatorial Guinea, Republic of Congo and Cameroon (Fig. 1). Azobe is in Gabon and Democratic Republic of Congo at the southern limit of its natural range that extends till Casamance in Senegal (Biwolé et al., 2012). Okoume and azobe have different light dependency (Mapaga et al., 2002; Palla et al., 2002a). Whereas okoume is a strict light-demanding species that requires light to regenerates, azobe seedlings can settle under the forest cover and need light when they become saplings (Biwolé et al., 2012; Doucet, 2003). Like a pioneer species, okoume is able to colonize open spaces (Brunck et al., 1990), and is also able to form monodominant stands (Peh et al., 2011). Azobe is sometimes found as a companion species of okoume in forest regrowth on savannah (White et al., 2000). Its ecological behaviour ranges from pioneer to moderate light-demanding depending on the authors (Biwolé et al., 2012; Doucet, 2003; Fayolle et al., 2012). Both okoume and azobe are wind-dispersed species. Like most light-demanding species, okoume is fast growing with a light wood (wood specific gravity of 0.378 g cm^{-3} on average; Zanne et al., 2009), whereas azobe has paradoxically a heavy wood (0.897 g cm^{-3}). Tree density across the whole concession was 8.00 stems ha^{-1} for okoume and 1.53 stems ha^{-1} for azobe.

2.3. Statistical analyses

2.3.1. Characterizing the species within the forest stand

Two correspondence analysis (CA) were conducted to identify the relationships between the two focus species and the forest stand structure. One CA was based on the 313×9 contingency table that cross-tabulated tree abundances depending on species and forest units, and aimed at identifying the position of okoume and azobe among the forest units. The other CA was based on the 313×16 contingency table that cross-tabulated tree abundances depending on species and diameter classes, and aimed at identifying the position of okoume and azobe within the diameter structure of the Haut Abanga forest.