Forest Ecology and Management 399 (2017) 235–246

Contents lists available at ScienceDirect

Forest Ecology and Management

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

New insights on above ground biomass and forest attributes in tropical montane forests

Aida Cuni-Sanchez [a,*], Marion Pfeifer [b], Rob Marchant [c], Kim Calders [d,e], Cathrine L. Sørensen [a], Patrícia V. Pompeu [f], Simon L. Lewis [d,g], Neil D. Burgess [a,h]

[a] Center for Macroecology, Evolution and Climate, University of Copenhagen, Universitetsparken 15, Copenhagen DK-2100, Denmark
[b] School of Biology, Newcastle University, Ridley Building 2, Newcastle Upon Tyne NE1 7RU, UK
[c] York Institute for Tropical Ecosystems, Environment Department, University of York, Heslington, York YO10 5NG, UK
[d] Department of Geography, University College London, Gower Street, London WC1E 6BT, UK
[e] Earth Observation, Climate and Optical Group, National Physical Laboratory, Hampton Road, Teddington, Middlesex TW11 0LW, UK
[f] Department of Forestry, Federal University of Lavras, PO Box 3037, Lavras, Brazil
[g] School of Geography, University of Leeds, Leeds LS2 9JT, UK
[h] United Nations Environment Programme World Conservation Monitoring Center, 219 Huntingdon Road, Cambridge, UK

ARTICLE INFO

Article history:
Received 5 November 2016
Received in revised form 15 May 2017
Accepted 16 May 2017

Keywords:
Africa
Forest structure
Tree diversity
Height-diameter allometry

ABSTRACT

Despite the potential of tropical montane forests to store and sequester substantial amounts of carbon, little is known about the above ground biomass (AGB) and the factors affecting it in these ecosystems, especially in Africa. We investigated the height-diameter allometry, AGB, and related differences in AGB to taxonomic and structural forest attributes in three distinct forest types (dry, mixed species and elfin) in three mountains of northern Kenya. We established 24 permanent plots (20 m × 100 m) and sampled all trees ≥10 cm diameter following standard Rainfor protocols.

We identified that different height-diameter allometric models could be used for different forests types, with the exception of the Michaelis–Menten model. In our study area, model choice had little effects on AGB estimates.

In general, mixed forests had greater AGB than other forest types: in Mt Nyiro AGB estimates were 611, 408 and 241 Mg ha^{-1} for mixed, elfin and dry forests respectively. Forests in Mt Nyiro, the highest mountain had greater AGB than in the other mountains. In our study area, differences in AGB were related to forest structure attributes, with little influence of taxonomic attributes. The mixed and elfin forests in Mt Nyiro, dominated by *Podocarpus latifolius* and *Faurea saligna* contained comparable AGB to lowland rainforests, highlighting the importance of tropical montane forests as large carbon stock, which could be released if converted to another land cover type.

1. Introduction

A considerable amount of data on above-ground biomass (AGB) stored in live trees in lowland tropical forests, and the factors affecting it, have become available in the past few years (e.g. Malhi et al., 2006; Slik et al., 2010; Quesada et al., 2012; Lewis et al., 2013; Poorter et al., 2015; Fayolle et al., 2016). Far less information is available on patterns of AGB in tropical montane forests, although their potential to store and sequester substantial amounts of carbon has been emphasised (Spracklen and Righelato, 2014). Tropical montane forests (TMFs), defined here as forests between 23.5°N and 23.5°S above 1000 m.a.s.l., make up 8% of the world's tropical forests (Spracklen and Righelato, 2014). They are of importance, not only because they have high levels of biodiversity and endemism, but also because they provide water to tens of millions of people (Mittermeier et al., 2004; Bruijnzeel et al., 2011).

Most studies of AGB along elevational transects have found a declining relationship with elevation (e.g. Girardin et al., 2010, 2014; Leuschner et al., 2013), which has been linked to associated declines in tree height (reviewed in Girardin et al., 2014). Individual tree height does not correlate with diameter in a simple manner (Nagendra, 2012) but instead the height-diameter allometry is related to species, precipitation, temperature and region (Feldpausch et al., 2011; Banin et al., 2012; Fayolle et al. 2016), and usually decreases with elevation (Girardin et al., 2014).

* Corresponding author.
E-mail address: aidacuni@hotmail.com (A. Cuni-Sanchez).

http://dx.doi.org/10.1016/j.foreco.2017.05.030

In fact, there has been a historical debate on the shape of the height-diameter allometry for tropical trees. Some authors argued in favour of a truly asymptotic model (Lewis et al., 2009; Rutishauser et al., 2013), or a second order polynomial of the log-log data (Chave et al., 2014) mimicking the saturation of tree height with tree diameter, while others argued in favour of the power law model (Djomo et al., 2010; Feldpausch et al., 2011) such as predicted by the metabolic theory of ecology (West et al., 1997, 1999) (see Fayolle et al., 2016 for further details). It has been highlighted that the power law model is unrealistic biologically because of the basic assumption of factors limiting tree growth in height but not in diameters (Molto et al., 2014), and most recent studies have chosen a truly asymptotic model. Among the asymptotic models, Feldpausch et al. (2012) found that the Weibull model was the most appropriate for biomass prediction, as it reduces error in small-diameter trees. This is important because of the skewed distribution of stand-level biomass found in smaller-diameter trees in many forests (Feldpausch et al. 2012). However, Banin et al. (2012) and Kearsley et al. (2013) found that a nonlinear 3-parameter exponential model was the most appropriate for biomass prediction. Two recent studies, which considered an asymptotic model Michaelis-Menten (Molto et al., 2014; Fayolle et al., 2016), not included in previous studies, preferred this later one, arguing that not only it outperformed Weibull but also that it was easier to manipulate than Weibull and its exponential function. All these studies focused on lowland rainforest types, and to our knowledge, the shape of the height-diameter allometry for tropical has not been studied in depth for TMFs, which tend to have shorter trees for a given diameter.

Declining AGB with increasing elevation has also been related to changes in other characteristics of forest structure affecting AGB, such as stem density and stand basal area.

In general, stem density and stand basal area have been shown to increase with altitude in Hawaii (US), Mt Kinabalu (Malaysia), Udzungwa Mountains (Tanzania) and the Andes (Herbert and Fownes, 1999; Takyu et al., 2002; Lovett et al., 2006; Girardin et al., 2014). However, some studies demonstrate a decrease in stem density with increasing altitude (e.g. Mt Elgon in Kenya-Uganda, Hamilton and Perrott, 1981) or no trend between stand basal area and altitude (e.g. Andes: Girardin et al., 2014). Because biomass increases exponentially with tree diameter, average tree diameter, large tree density and stand basal area tend to be better predictors of AGB than overall tree density (Slik et al., 2010; Lewis et al., 2013; Poorter et al., 2015).

Changes in AGB with increasing elevation have also been related to changes in tree species richness. Higher species richness enhances the variation in species traits found in the community, leading to niche complementarity, a higher resource capture, more efficient resource use and higher productivity (Poorter et al., 2015). Higher species richness may also enhance facilitation (e.g. a nitrogen-fixing species enhances soil fertility, and therefore the productivity of the other species); and it might also increase the chance of a selection effect (selecting highly productive or large species). Generally, there is a decline in tree species richness with increasing altitude (e.g. Dossa et al., 2013; Sassen and Sheil, 2013; Girardin et al., 2014), because of a greater role of environmental filtering at higher elevations (e.g. cooler temperatures, fog, reduced light incidence and higher relative humidity). Nevertheless, this was not observed on, for example, the Udzungwa Mountains in Tanzania (Lovett et al., 2006). In the Andes, several elevation gradients showed mid-elevational peaks in numbers of families, genera and species, at the base or below the cloud base, highlighting the importance of the cloud formation as a driver of species composition (Girardin et al., 2014). Apart from tree species richness, tree species evenness can also affects AGB. A recent study on TMFs in Tanzania described a unimodal relationship between AGB and tree species evenness (Shirima et al., 2016). These authors suggested that forests at higher altitudes with a high number of multi-stemmed individuals may contribute to the unimodal pattern in the AGB-richness relationship, because multi-stem dominated plots comprise less biomass than plots dominated by large single-stem trees and low tree species richness.

In this study, we estimated AGB in different TMFs located at different altitudes and mountains and we investigated the relationship between AGB and forest structural and taxonomic attributes, including height-diameter allometry. We address three major questions: are there significant differences in height-diameter allometry between different types of TMFs? Does AGB differ significantly between different types of TMFs? And, are differences in AGB related to differences in forest structure, tree species composition or both?

2. Materials and methods

2.1. Study area

This study focused on the forests present on three prominent mountains in northern Kenya: Mt Nyiro (2752 m), Mt Kulal (2285 m) and Mt Marsabit (1707 m) (see Appendix A). While Mt Nyiro consists of old crystalline Precambrian basement rocks, mainly extremely durable gneisses and granites, Mt Kulal and Mt Marsabit are Quaternary volcanic peaks. Soils are generally attributed to Regosols and Cambisols in Mt Nyiro (higher to lower altitudes respectively), Andosols and Cambisols in Mt Kulal (higher to lower altitudes respectively) and Andosols and Nitisols in Mt Marsabit (higher to lower altitudes respectively) (Sombroek and Pauw, 1980). Annual rainfall ranges between 800 and 1400 mm (semi-humid area, zone III Sombroek et al., 1982). Rainfall is concentrated in two wet seasons, from March to May and from October to December, but great inter-annual variation occurs, with some years having one or no rainy season. Fog presence is common at higher altitudes and is known to be an important source of water for these montane forests (Bussmann, 2002).

These mountains support similar vegetation types (Bussmann, 2002). From low to high altitudes, these comprise: (i) dense thorny bushland (*Commiphora*, *Grewia* and partly *Acacia*), (ii) 'dry montane forest' (*Croton megalocarpus-Olea europaea* subsp. *africana* forest association in Mt Marsabit or *O. europaea-Juniperus procera* forest association in Mt Kulal and Mt Nyiro), (iii) 'mixed species forest' (with abundant *Cassipourea malosana* and *Olea capensis* in all mountains), and (iv) 'elfin-like forest' (with similar composition to mixed species forest but at least 15% shorter trees with twisted stems and many epiphytes on their branches) (see Bussmann, 2002). This study focuses on the last three types thereafter called dry, mixed and elfin. These forest types occur at different altitudes in the mountains studied (see Fig. 1), because of (i) mountain distance to the ocean (the further, the drier, see Fig. A1 in Appendix A) and (ii) the mass-elevation or telescopic effect (larger mountains are better at warming the atmosphere above them and are warmer at a given altitude, Jarvis and Mulligan, 2011).

The forests studied provide key services to surrounding communities, including water, firewood, medicine resources and fodder (Cuni-Sanchez et al., 2016). Mt Marsabit is an important elephant habitat in northern Kenya (Ngene et al., 2009), but there are no elephants on Mt Kulal or Mt Nyiro. While commercial logging never occurred on Mt Kulal or Mt Nyiro, because of the steep terrain and remoteness of the area, local communities around Mt Marsabit reported small-scale 'illegal' selective logging in some parts of the forest during the 1960s (Cuni-Sanchez, pers. obs.). For the purpose of this study, we assume that the forests are largely pristine and that currently observed forests' structure and