



Individual tree size inequality enhances aboveground biomass in homegarden agroforestry systems in the dry zone of Sri Lanka



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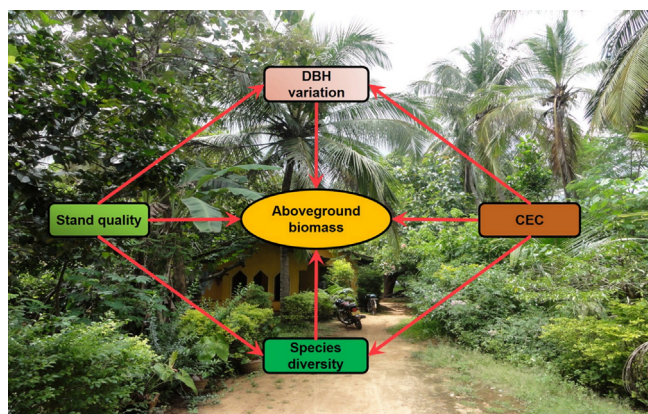
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HIGHLIGHTS

- Tree size variation had the strongest positive direct effect on aboveground biomass.
- Stand structure is a main determinant for the variation in aboveground biomass.
- Dominance of certain productive species may enhance aboveground biomass.
- Above ground biomass can be enhanced through different management practices.

GRAPHICAL ABSTRACT



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ABSTRACT

Individual tree size variation, which is generally quantified by variances in tree diameter at breast height (DBH) and height in isolation or conjunction, plays a central role in ecosystem functioning in both controlled and natural environments, including forests. However, none of the studies have been conducted in homegarden agroforestry systems. In this study, aboveground biomass, stand quality, cation exchange capacity (CEC), DBH variation, and species diversity were determined across 45 homegardens in the dry zone of Sri Lanka. We employed structural equation modeling (SEM) to test for the direct and indirect effects of stand quality and CEC, via tree size inequality and species diversity, on aboveground biomass. The SEM accounted for 26, 8, and 1% of the variation in aboveground biomass, species diversity and DBH variation, respectively. DBH variation had the strongest positive direct effect on aboveground biomass ($\beta = 0.49$), followed by the non-significant direct effect of species diversity ($\beta = 0.17$), stand quality ($\beta = 0.17$) and CEC ($\beta = -0.05$). There were non-significant direct effects of CEC and stand quality on DBH variation and species diversity. Stand quality and CEC had also non-significant indirect effects, via DBH variation and species diversity, on aboveground biomass. Our study revealed that aboveground biomass substantially increased with individual tree size variation only, which supports the niche complementarity mechanism. However, aboveground biomass was not considerably increased with species diversity, stand quality and soil fertility, which might be attributable to the adaptation of certain productive species to the local site conditions. Stand structure shaped by few productive species or independent of species diversity is a main determinant

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for the variation in aboveground biomass in the studied homegardens. Maintaining stand structure through management practices could be an effective approach for enhancing aboveground biomass in these dry zone homegarden agroforestry systems.

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1. Introduction

Homegarden agroforestry systems in the tropics often have a multi-level structure and its canopy resemblance to forests incur that they store carbon and conserve biodiversity (Kumar, 2006; Kumar and Nair, 2004). Agroforestry systems are important for ecosystem functioning, and hence store more carbon than previously thought, probably associated to their multifunctional role in providing income, food and ecosystem services while reducing pressure on natural forests (Mattsson et al., 2015; Mohri et al., 2013; Schroth et al., 2015). However, we still lack a complete understanding of the determinants (mechanisms) whether tree size inequality and species diversity increase aboveground biomass in homegarden agroforestry systems. Generally, species diversity is considered as a component of stand structure, but variances in tree diameter at breast height (DBH) and height in isolation or conjunction is typically defined as individual tree size variation (Brassard et al., 2008). In natural forests, it is well known that species diversity and stand structural diversity promoted aboveground biomass (Ali et al., 2016b; Dănescu et al., 2016; Wang et al., 2011). Moreover, variability in tree size inequality and species diversity depends to a large extent on soil fertility (Poorter et al., 2015; Zhang and Chen, 2015), and may also depend on stand quality (Schroth et al., 2015). However, the influence of tree size inequality and species diversity on aboveground biomass remains debated, in part because a well-documented coupling factor such as stand quality (i.e., good, medium and low), which represents the biophysical characteristics of a stand, has not often been explicitly considered.

Understanding the relationship between biodiversity and ecosystem functioning has been a central pursuit in ecology for more than four decades (Ali et al., 2016a; Grime, 1973). It is becoming increasingly known that aboveground biomass is significantly affected by species diversity in forest ecosystems (Poorter et al., 2015; Zhang and Chen, 2015). However, the question is whether tree size inequality within and among component species (Clark, 2010), which represent different niches, may enhance aboveground biomass in forest ecosystems. It is theoretically plausible that different tree species have relatively different growth patterns and dimensions leading to different aboveground stratification and biomass productivity in complex forests (e.g., Lei et al., 2009; Liang et al., 2007; Poorter et al., 2016). For instance, some studies have reported that the direct relationship between species diversity and aboveground biomass was either positive (Dayamba et al., 2016; Wang et al., 2011; Zhang and Chen, 2015), negative (Ali et al., 2016b; Szwagrzyk and Gazda, 2007), or non-significant (Vilà et al., 2003). In addition, the effects of soil fertility and stand quality cannot be overlooked due to its fundamental role in the species diversity, stand structure, aboveground biomass and productivity (Poorter et al., 2015; Schroth et al., 2015; Zhang and Chen, 2015). The effects of stand quality and soil fertility on aboveground biomass may be direct or indirect, via tree size inequality and/or species diversity.

Multi-layered stand structure may be theorized to enhance light capture and increase light use efficiency in forest ecosystems (Yachi and Loreau, 2007). Recent studies have indicated that tree size inequality or stand structural diversity links forest diversity and aboveground biomass in multilayered stand structures (Ali et al., 2016b; Zhang and Chen, 2015), due to the efficient utilization of light in natural forests (Yachi and Loreau, 2007). Moreover, species diversity increases tree size inequality, and as a consequence, enhances the aboveground biomass (Ali et al., 2016b; Zhang and Chen, 2015). Alternately, the tree

size inequality is critical to species diversity (Clark, 2010), and in turn impart a positive indirect effect on the aboveground biomass (Ali et al., 2016b; Zhang and Chen, 2015). Also, species diversity and tree size inequality provide positive feedback to each other, and hence increases aboveground biomass in natural forests (Ali et al., 2016b). In this study, we treated tree size inequality and species diversity as independent predictors for aboveground biomass, which has rarely been tested in the previous studies. Consequently, we hypothesized that tree size inequality and species diversity have positive direct effects, after considering for the effects of stand quality and soil fertility, on aboveground biomass in homegarden agroforestry systems.

We have previously reported a vast heterogeneity of carbon stock and tree species diversity within the less studied dry zone homegardens; results that contribute to more knowledge of their expansion potential as well as climate change mitigation and adaptation potential (Mattsson et al., 2015). In this study, we aim to investigate the effects of tree size inequality and species diversity on aboveground biomass, while accounting for the effects of stand quality and soil fertility. We employed structural equation model (SEM; Malaeb et al., 2000) to analyze data from 45 dry zone homegardens in Sri Lanka. Specifically, we tested the following hypotheses, represented by SEM paths: 1) the effects of stand quality and soil fertility on aboveground biomass, tree size inequality and species diversity; 2) the indirect effect of stand quality and soil fertility on aboveground biomass via tree size inequality and species diversity, and 3) the direct effects of tree size inequality and species diversity on aboveground biomass.

2. Materials and methods

2.1. Study area and homegardens

The study was conducted in the neighboring villages of Padikapuhela (6°21'30"N–6°22'30"N and 81°14'30"E–81°15'10"E) and Pilimihela (6°21'00"N–6°21'60"N and 81°15'20"E–81°15'60"E), located in Thanamalwila Division in the most southern part of Moneragala district in the south-eastern part of Sri Lanka. The topography is undulating lying between 50 and 70 m above sea level. The villages are located within the driest agroecological zone in Sri Lanka where the soils are predominately alfisols (Panagos et al., 2011). Major forest types in the area are dry mixed evergreen forests and tropical thorn scrub forests while the dominant land use is subsistence agriculture from paddy rice, banana, homegardens and shifting cultivation. This region has a dry tropical climate with a distinct dry season between May and September. The mean annual temperature is 27 °C and the mean annual rainfall is 1050 mm, most of which falls between October and January (Mattsson et al., 2015).

Forty-five homegardens were randomly sampled in March 2013. To cover the wide variations in the distribution of aboveground biomass and forest diversity of the individual homegardens in the villages, the total area of all homegardens were sampled which resulted in a total sample area of 30 ha. All sampled homegardens were between 20 and 30 years old and the size of homegardens ranged from 0.2 to 1.2 ha where a majority of homegardens were rectangular in shape.

All stems ≥ 3 cm DBH were individually tagged and measured for DBH using a diameter tape and identified to species-level. A total of 4278 stems were recorded belonging to 70 species, 55 genera and 30 families across 45 homegardens. The total tree height for each tree was measured with a telescopic pole for heights of up to 15 m, and

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