



Intra- and inter-specific differences in crown architecture in Chinese subtropical mixed-species forests



Rubén Guisasola^a, Xiaolu Tang^b, Jürgen Bauhus^a, David I. Forrester^{a,*}

^aChair of Silviculture, Faculty of Environment and Natural Resources, Freiburg University, Tennenbacherstr. 4, 79108 Freiburg, Germany

^bChair of Forest Inventory and Remote Sensing, Georg-August-Universität Göttingen, Büsgenweg 5, 37077 Göttingen, Germany

ARTICLE INFO

Article history:

Received 6 March 2015

Received in revised form 16 May 2015

Accepted 22 May 2015

Available online 6 June 2015

Keywords:

Intra-specific variability

Inter-specific variability

Crown architecture

Leaf-area density

ABSTRACT

Absorption of photosynthetically active radiation (APAR) is fundamental for tree growth and is strongly influenced by crown architecture. The aim of this study was to quantify the intra- and inter-specific variability in crown architecture in monospecific and mixed-species subtropical Chinese forests. A total of 68 trees, including *Castanopsis eyrei*, *Castanopsis sclerophylla*, *Cunninghamia lanceolata*, *Cyclobalanopsis glauca* and *Liquidambar formosana* were destructively sampled and their crown architectures were quantified in terms of the vertical distribution of live branch diameter, individual branch leaf area, leaf area and leaf-area density. The vertical distributions were fitted by a two-parameter right truncated Weibull distribution. Inter-specific variability was assessed using ANCOVA and post hoc Tukey tests and intra-specific variability was assessed by fitting linear and linear mixed effect models. The peak in the vertical distribution of leaf area was highest for the least shade tolerant species, *L. formosana* (relative depth into the crown of 0.5), intermediate for *C. sclerophylla* (0.55), *C. glauca* (0.55) and *C. lanceolata* (0.6) and lowest for *C. eyrei* (0.75). For all species, the vertical distribution of leaf area was influenced by tree size except for *C. glauca*. For *L. formosana* and *C. lanceolata*, the distribution of leaf area or branch sizes shifted upwards as tree diameter increased, possibly to overtop neighbouring trees. In contrast, as *C. eyrei* stem diameter increased, the vertical distribution of mean branch diameter shifted downwards, indicating that larger *C. eyrei* trees invested a higher proportion of their crown growth into their lower crown when compared to smaller trees. The vertical distribution of leaf-area density varied between species but not within a given species. Crown architectures were not influenced by stand density (basal area) or the species composition of the plot. This intra-specific consistency is useful for modelling light in forests. This study shows that there is a significant inter-specific variability in the crown architectures of the co-occurring species in these subtropical forests. There is also significant intra-specific variability related to tree size and this relationship varies between species. This crown architectural variability and its effect on stand structure are likely to influence the light absorption of these stands.

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1. Introduction

The absorption of photosynthetically active radiation (APAR) is fundamental for tree growth. Tree-level APAR is influenced by crown size, in terms of leaf area and its distribution (Niinemets, 2007, 2010). The vertical distribution of the leaf area within a crown not only influences APAR (Vose et al., 1995; Vose and Swank, 1990) and growth (Niinemets, 1996) but also the radial profile of sap flux density (Fiore and Cescatti, 2008; Forrester et al., 2012), stem taper by influencing diameter increment

(Kershaw and Maguire, 2000), and wood quality by influencing the size, frequency and distribution of knots originating from branches (Medhurst and Beadle, 2001; Forrester et al., 2012). Therefore intra- and inter-specific differences in leaf area distribution can be used to examine or model within-crown spatial distributions of light availability, foliar nutrition, gas exchange and other physiological processes (Duursma and Medlyn, 2012) as well as wood quality (Clatterbuck and Hodges, 1988; Forrester et al., 2012). The intra- and inter-specific variability in leaf area and leaf mass distributions has received little attention in subtropical or tropical forests and was the focus of this study.

The vertical distribution of leaf area for a given species can be influenced by tree size (Maguire and Bennett, 1996), age (Kantola and Mäkelä, 2004), stand density (Xu and Harrington, 1998), inter-specific competition (Garber and Maguire, 2005; Binkley,

* Corresponding author.

E-mail addresses: ruben.guisasola@outlook.com (R. Guisasola), xtang@gwdg.de (X. Tang), juergen.bauhus@waldbau.uni-freiburg.de (J. Bauhus), david.forrester@waldbau.uni-freiburg.de (D.I. Forrester).

1992), tree dominance class (Maguire and Bennett, 1996; Xu and Harrington, 1998; Šrámek and Čermák, 2012), and shade tolerance. For example, stand density had a greater influence on the vertical leaf area distributions of less shade tolerant species (Garber and Maguire, 2005).

Shade tolerance is often quantified relative to other species, rather than as an absolute value (Valladares and Niinemets, 2008), which makes it difficult to compare species, sites and ages from different studies. Nevertheless, it has been suggested that for a given stand density, shade-intolerant species tend to have mono-layered, condensed crown structures that might be skewed upwards because the lower branches do not survive under low light conditions (Horn, 1971). In contrast, the crown structure of shade-tolerant species in even-aged stands tends to be more evenly distributed along the height profile as a result of their ability to maintain foliated branches at lower light intensities (Horn, 1971). Stand density and thinning can also influence the crown architecture, such that under high light availabilities (e.g., open grown or dominant trees) it can shift downwards because lower leaves and branches are maintained for longer to increase the surface exposed to direct sunlight and therefore, the APAR of these trees will also increase (Garber and Maguire, 2005; Forrester et al., 2012).

Garber and Maguire (2005) and Binkley (1992) showed that inter-specific competition in mixed-species stands can influence vertical leaf area distributions. However, most studies have been done in monocultures and for conifers in temperate or boreal regions (Maguire and Bennett, 1996; Xu and Harrington, 1998; Mäkelä and Vanninen, 2001), whereas very little is known about tropical or subtropical species, or for different species growing together in mixed-species forests. The subtropical forests of south-eastern China are known for their high biodiversity, with wide ranges in growth rates and shade tolerance (Shen et al., 2007; Ni, 2011). Competition for light is likely to be an important determinant of growth but there is very little information about intra- and inter-specific variability in the vertical leaf area distributions.

The aim of this study was to quantify the inter- and intra-specific variability in vertical distributions of leaf area, leaf-area density and branch sizes within crowns and to determine which factors influence it, including tree size, stand density, and species composition. We hypothesised that:

- (1) the leaf area or leaf-area density of more shade tolerant species is concentrated lower within the crown than in less shade tolerant species,
- (2) leaf area or leaf-area density is also lower within the crowns of larger and more dominant trees (of a given species and stand) than suppressed trees, and
- (3) these differences are exacerbated at higher stand densities.

These hypotheses were examined in mixed-species forests dominated by *Castanopsis eyrei*, *Castanopsis sclerophylla*, *Cunninghamia lanceolata*, *Cyclobalanopsis glauca*, *Liquidambar formosana* and adjacent monospecific plantations of *Cunninghamia lanceolata*.

2. Methods

2.1. Study area

Crown architecture was examined in forests located across Shitai County (29°59'–30°24'N, 117°12'–117°59'E), Anhui Province, China. The mean annual rainfall is 1176 mm. The

monthly mean maximum and minimum temperatures in July and January are 32.6 °C and 0.1 °C, respectively (NOAA, 2013).

The forests of the study area can be classified into two main types: relatively young plantations (15- to 25-years-old) of *C. lanceolata* scattered among tea plantations and natural stands on relatively accessible terrain. The second type of forest is natural mixed-species stands (15- to 49-year-old) of broadleaved species dominated by *C. sclerophylla* in the upper canopy with *C. eyrei* and *C. glauca* in the lower canopy. Scattered *C. lanceolata* individuals originating from natural regeneration also occur in the mixed stands. *L. formosana* is also present, usually as scattered groups of dominant trees. The canopy structure is typically multi-layered due to inter-specific differences in growth rates and differing tree ages that result from coppicing individual trees. The leaf area index of the plots ranged from about <1 to 9.8, and the basal areas from 4 to 34 m² ha⁻¹ (Guisasola, 2014; Forrester et al., 2014). Differences in stand density were observed between mixed-stands and *C. lanceolata* monocultures. The mean was 710 ± 680 trees ha⁻¹ (range from 88 to 2829) for mixed stands and 1980 ± 700 trees ha⁻¹ (range from 1400 to 2500) for monocultures. The tree ages were about 20–31 years for *C. eyrei*, 16–49 years for *C. sclerophylla*, 15–25 years for *C. lanceolata*, 20 years for *C. glauca* and 16–36 years for *L. formosana* (Guisasola, 2014; Forrester et al., 2014).

2.2. Field measurements

The crown architectures were measured for 68 destructively sampled trees from 17 circular plots with radii of 10 m. The main attributes of the sampled trees are given in Table 1. One dominant, one co-dominant and one suppressed tree were sampled in each plot for each tree species. The selected trees were randomly sampled after dividing the trees by species, dominance class and excluding trees that had been damaged (e.g. missing tops).

Branch and leaf angles (from horizontal) of about three trees per species (18 sampling trees) were estimated at the base, middle and at the top of the crown while the trees were still standing. After felling the trees, the diameter and height of all branches were measured up to the height where diameter over bark (DOB) of the stem was <2 cm. The part of the tree above this point was defined as the “top branch”. The DOB of each branch was measured at 2–3 cm from the insertion point to the stem to avoid the basal swelling. Additional measurements for each branch included the status (live, dead or senescing) and aspect (north, east, west, and south). Three living branches per tree from different parts of the canopy were randomly sampled to develop allometric equations for branch leaf areas and branch lengths.

2.3. Laboratory measurements

For the broadleaved species, all leaves were cut off each sample branch. However, due to the small size and high number of *C. lanceolata* leaves, it was not practical to remove all of the leaves from all sample branches. A subsample of the *C. lanceolata* sample branches was used because it was found that there was a good linear relationship between the leaf mass and the length (Eq. (1)) of all branch segments for that branch. This relationship was used to calculate the leaf mass and hence leaf area of each *C. lanceolata* sample branch, and was developed using 25 branches and top branches. To develop Eq. (1), each of these *C. lanceolata* branches was divided into two categories: branch segments with a diameter larger and smaller than 1 cm. For branch segments >1 cm in diameter, Eq. (1) is not appropriate and it was necessary to cut all leaves off all of those segments for drying and weighing. For branch segments <1 cm in diameter, branches were divided into simpler segments, each of which did not contain any secondary branches.

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