Landscape and Ecological Engineering
https://doi.org/10.1007/s11355-020-00429-4

ORIGINAL PAPER

Long-term structural and functional changes in *Acacia mangium* plantations in subtropical China

Hai Ren[1,6] · **Yiming Fan**[2] · **Zeyuan Zou**[3] · **Dafeng Hui**[4] · **Qinfeng Guo**[5] · **Yao Huang**[1,6]

Received: 15 April 2020 / Revised: 14 September 2020 / Accepted: 17 September 2020

Abstract

Subtropical China has a large area of *Acacia mangium* plantations; however, some key aspects of the structural and functional changes and the associated mechanisms after planting are still not well understood. We established a permanent plot in an *A. mangium* plantation and monitored the plant diversity (i.e., the number of species), biomass, soil physical and chemical properties and light transmittance from 1984 to 2018. Protocols for standard observation and measurement of Chinese Ecological Research Network were adopted. The total number of species in the plantation increased gradually from 3 to 38 during the 34-year period. The biomass in the tree layer initially increased rapidly from 1.60 to 185.01 t/ha within 7 years and then slowly increased to 188.69 t/ha during the following 27 years. The soil fertility of the *A. mangium* plantation improved continuously over the 34-year period. Vegetation restoration had positive effects on soil properties, such as soil moisture, soil bulk density, soil organic matter and soil total nitrogen and available phosphorus contents. The structure (i.e., plant diversity and light transmittance) and function (i.e., biomass and soil fertility) of the *A. mangium* plantation were not restored synchronously after 34 years of development. However, considering that the tree species richness in the natural forests in this region was 134, this plantation has slowly transformed from plantation to a natural forest. Artificial intercropping with native tree species can facilitate succession to a natural forest.

Keywords Plant diversity · Biomass · Soil physical and chemical properties · Light transmittance

Introduction

China has the world's largest area of planted forests, with an area of 69 million ha, which accounts for approximately 33% of its total forest area (State Forestry Administration of China 2015). Compared with natural forests, plantations are often simple in structure with low biodiversity and poor ecosystem services; additionally, they have a slow succession process towards climax that may take hundreds of years (Peng 1996; Kimmins 2004). With social and economic development, forest management in China has shifted from purely industrial/commercial purposes to an emphasis on

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11355-020-00429-4) contains supplementary material, which is available to authorized users.

✉ Hai Ren
renhai@scbg.ac.cn

Yiming Fan
20170240110@fosu.edu.cn

Zeyuan Zou
201715090130@scau.edu.cn

Dafeng Hui
dhui@tnstate.edu

Qinfeng Guo
qinfeng.guo@usda.gov

Yao Huang
huangyao.ok@163.com

[1] Guangdong Provincial Kay Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China

[2] School of Physics and Optoelectronic Engineering, Foshan University, Foshan 528225, China

[3] College of Life Sciences, South China Agricultural University, Guangzhou 510642, China

[4] Department of Biological Sciences, Tennessee State University, Nashville, TN 37209, USA

[5] Eastern Forest Environmental Threat Assessment Center, USDA Forest Service, RTP, NC 27709, USA

[6] College of Advanced Agricultural Sciences, University of Chinese Academy of Sciences, Beijing 100049, China

both industrial/commercial and ecological benefits since the 2000s (Wang et al. 2004). Currently, growing semi-natural forests with industrial/commercial and ecological benefits has gained increasing attention (Ren et al. 2012; Park and Higgs, 2018). It is generally anticipated that native trees can be used to establish semi-natural forests or transform existing plantations into semi-natural forests (Yu and Peng 1996; Ren et al. 2019). Previous studies have shown that the main reason for the poor ecological benefits provided by existing plantations is the lack of native tree species recolonization, this scenario leads to slow succession and the plantation remains in the pioneer community stage for a long time (Li et al. 2001; Wang et al. 2009, 2010; Duan et al. 2010). Understanding the structure and function of fast growing and highly productive plantations would have ecological and economic benefits. Therefore, monitoring and evaluating the structure, function, and dynamics of plantation ecosystems, especially their restoration processes, would help identify effective forest restoration methods and provide a scientific basis for the ecological restoration and reconstruction of degraded ecosystems (Chazdon 2008).

The climax community in subtropical China is the monsoon evergreen broad-leaved forest. Owing to long-term human disturbance, pristine and secondary natural forests are rare in the region. For example, 74% of the forest area of Guangdong Province is planted forests (such as *Pinus massoniana, Eucalyptus citriodora* and *Acacia mangium*) (Yu and Peng 1996; Ren et al. 2019). *A. mangium* is an evergreen leguminous tree native to Australia and Papua New Guinea (Koutika and Richardson 2019). It was introduced in China in 1979 (Pan et al. 1996). Owing to its numerous advantages, such as wide adaptation, tolerance to drought and barrenness, better resistance to pests, soil-improving properties due to nitrogen fixation, fast growth and high yield as well as its economic value, it has been extensively planted in tropical and subtropical regions of China since the 1980s (Ren and Yu 2008). By 2012, its total coverage area was more than 800,000 ha, making it one of the major fast-growing and high-yielding species in the barren hilly areas of South China (Ren et al. 2012).

Numerous studies have been performed on *A. mangium* during the past several decades (Ren et al. 1996; Koutika and Richardson 2019). These studies have mainly focused on its biological and growth characteristics (Ren et al. 1995, 1996; Otsamo 2002), heredity (Atipanumpai 1989), nitrogen fixation and nutrient cycling (Xiong et al. 2008; Paula et al. 2018), biomass and productivity (Xu et al. 1998; Ren and Yu 2008; Hardiyanto and Sadanandan 2014) and effect on the ecological restoration of degraded soil (Otsamo 2000; Norisada et al. 2005). However, most previous studies were restricted to a specific age, especially to early life stage. Those studies showed that the plant diversity in *A. mangium* plantation was low (Duan et al. 2010). The biomass of *A. mangium* plantation increased rapidly in the early stages and continued to grow in the later stages (Xu et al. 1998; Ren and Yu 2008). The soil fertility of *A. mangium* plantation increased rapidly because of N fixation (Xiong et al. 2008). However, few studies on *A. mangium* plantation lasted for more than 12 years and little attention was paid to the overall changes in plant diversity, biomass and soil fertility during development (Koutika and Richardson 2019). Therefore, it is difficult to determine the structural, functional and dynamic trends of *A. mangium* plantations at different age stages based on the previous studies. Here, we report long-term (34 years) research on plant diversity, biomass and soil fertility in an *A. mangium* plantation in subtropical China. We addressed the following four specific questions: (1) Did plant diversity increase with plantation age? (2) How did the biomass of *A. mangium* change with plantation age? (3) Did soil fertility improve with plantation age? (4) What were the structural and functional trends at different ages?

Materials and Methods

Experimental site

This study was conducted at the Heshan National Field Research Station of Forest Ecosystems, one of the members of Chinese Ecological Research Network, which was located in the middle of Guangdong Province (22° 40′ N and 112° 53′ E), subtropical China. The study region is a gently sloping hilly land area, and the highest elevation is approximately 195 m above sea level. The climate of this region is warm and rainy, with a mean annual temperature of 21.7 °C and a mean annual duration of sunshine of 1797.8 h. The annual total rainfall is 1801.1 mm, and it is distributed between the dry (15%, October–April) and wet (85%, May–September) seasons. There are interannual climate fluctuations. During this experiment, there was an extreme drought in 1997. Some plants of this plantation were damaged or killed. When compared with other years, annual mean temperature in 1997 was higher (22.6 °C) but the amount of precipitation was lower (1412.2 mm; Tu et al. 1998; Wang and Wang 2003). The soil is latosolic red soil. The zonal vegetation is monsoon evergreen broad-leaved forest (Fu et al. 2009). Due to human disturbance, most of the original forests in the region have been felled and degraded to subtropical grassland (the main species include *Chaemum indicam*, *Eriache pallesans* and *Baeckea frutescens*). To restore previously degraded grassland and identify the best tree species for ecological restoration, eight types of plantations and a control (grassland) site were established in 1984.

This study focused on the *A. mangium* plantation, which was a monoculture plantation with an area of 3.99 ha. All

1-year-old seedlings (purchased from the Institute of Tropical Forestry, Chinese Academy of Forestry) were planted with a 2.5 m × 2.5 m spacing directly on the degraded grassland without any treatment. The plantation was left to develop naturally without anthropogenic disturbance after planting, except for experiments. We also compared the plant diversity, biomass, soil fertility of the plantation with that of a monsoon evergreen broad-leaved forest (climax in the zone, about 110 km away the plantation) at Dinghushan National Field Research Station of Forest Ecosystems.

Plant diversity monitoring

Representative permanent plots in the plantation were set up in 1984. Applying the neighbouring grid method in each block, we set up four 20 m × 20 m sample plots for the arbour species survey, four 5 m × 5 m sample plots for the shrub species survey and four 1 m × 1 m sample plots for the herbaceous species survey. We searched and marked all *A. mangium* individuals in the plots. The shrub sample plots were located in the lower right corner of one of the tree plots. The herbaceous sample plots were located in the lower right corner of one of the shrub plots. We recorded each tree's height, diameter at breast height and canopy range in the arbour layer, and we measured shrub and grass height, coverage and abundance in the shrub and grass layer (Krebs 1985; Yu and Peng 1996). We investigated the plant plots in June–August in 1984, 1989, 1994, 1997, 2003, 2007, 2013 and 2018. Plant diversity was measured using species richness (i.e., the number of species).

Biomass measurement

We adopted the stratified sampling method to measure the biomass of the plantation (Ren and Yu 2008). The typical standard trees at the periphery of permanent quadrats were selected for measuring the full-harvest biomass of the *A. mangium* plantation. According to the growth curve of *A. mangium*, the biomass accumulation process of this species can be reflected by sampling over 1–14 years (Ren and Yu 2008). The number of plants harvested was 7, 10, 1 and 1 in 1987, 1990, 1994 and 1998, respectively. We used the standard tree data to establish a biomass regression model, i.e., an allometric equation expressed in natural logarithms, for every organ of *A. mangium* (Ren and Yu 2008):

$$\text{Trunk biomass (Ws)}: \ \text{Lg Ws} = -0.221 + 0.609\ \text{Lg}\left(D^2H\right) \quad r = 0.99,$$

$$\text{Branch biomass (Wb)}: \ \text{Lg Wb} = -0.243 + 0.458\ \text{Lg}\left(D^2H\right) \quad r = 0.91,$$

$$\text{Leaf biomass (Wl)}: \ \text{Lg Wl} = -0.424 + 0.561\ \text{Lg}\left(D^2H\right) \quad r = 0.91,$$

$$\text{Total biomass (Wt)}: \ \text{Lg Wt} = 0.154 + 0.568\ \text{Lg}\left(D^2H\right) \quad r = 0.98,$$

where Lg is the logarithm, D is the diameter at breast height and H is the height.

We used tree investigation data in the permanent plot in 1985–1999, 2013 and 2018 to calculate the biomass in the arbour layer. The same biomass estimation model was used for some recolonized non-*A. mangium* trees in the permanent plots (Ren and Yu 2008). We adopted a three 5 m × 5 m quadrat harvesting method to measure the biomass and the existing mass of the shrub layer, herb layer and dead vegetation near the permanent plots and in the same plantation in 1988, 1991, 1995, 1999 and 2013 (Ren et al. 2013).

Determination of physical and chemical properties of soil

Three cores of soil (5 cm diameter × 20 cm deep) were randomly collected and mixed for each tree plot (total of four replicates) in June–August in 1988, 1991, 1995, 1999 and 2013. The soil was ground to pass through a sieve of 2 mm. The soil bulk density and soil water content in the 0–20 cm soil layer were measured following Duan et al. (2010). Soil pH was measured in a 1:5 mixture of soil: deionized water. Soil total nitrogen (TN) and organic matter were measured. The TN concentration was determined by micro-Kjeldahl digestion followed by colorimetric determination on the Lachat FIA (Duan et al. 2010). The soil available phosphorus (P) was extracted with sulfuric acid hydrochloric acid extraction solution and determined by the molybdate blue colorimetric method (Duan et al. 2010). The soil organic matter was determined by the wet combustion method (MEWAM 1986; Pan et al. 2019).

Measurement of light transmittance

Light transmittance was measured using a photometer (ST-III, Beijing Normal University, China) during sunny conditions by measuring light intensity in an open area and in a shaded understory when we surveyed the vegetation in 1988, 1991, 1995, 1999, 2013 and 2018. We randomly selected and measured 15 open spots and 15 shaded understory spots every time. Measurements were taken between 11:00 and 12:00, and the resulting ratio of open and understory light penetration was characterized by an index of the degree of shading (Le Brocque and Buckney 2003).

Data analysis

The experiment was designed as a long-term study. Some measurements for *A. mangium* were missing during 1986–1989 because of a few disruption and we replaced them with the data from the same aged *A. mangium* plantation which was established in 1993 near Heshan Station. At the beginning of planting, the topography, plants and soil of the stand, the height, density and management of the plantation were similar to those of the permanent plots. We had also made similar systematic observations in this neighboured plot as a reference and thus we were able to fill the missing data from this plantation with the same ages. Those included biomass in tree layer from 1986 to 1988, biomass in herb and shrub layer, litter standing crop, physical and chemical properties of soil, and light transmittance in 1988, and plant diversity in 1989. All the data after 1989 in this paper came from the long-term observation of the permanent plots.

We used one-way ANOVA to compare the differences in biomass and soil physical and chemical properties of *A. mangium* plantations at different ages ($P < 0.05$). All statistical tests were performed using SPSS 13.0 for Windows (SPSS, Chicago, IL, USA) (Wang et al. 2009).

Results

Changes in plant diversity

The *A. mangium* monoculture plantation was established and developed from a degraded grassland. The original plant diversity was three (i.e., *Chaemum indicam*, *Eriache pallesans* and *Baeckea frutescens*). Plant diversity in the whole plantation increased gradually to 38 species by 2018 except 1997 in which a rare decline occurred. A total of 13 species once recolonized disappeared from the community during 1984–2018 (Online Appendix Table 1).

The total number of arbour layer species in the plantation increased with time (Fig. 1a), but changes in the species in the arbour layer and the years of replacement were different. Heliophytes including *Ficus simplicissima*, *Toxicodendron vernicifluum* and *Euodia lepta* always appeared in the community. Species that disappeared from this plantation between 1997 and 2003 were other heliophytes such as *Cratoxylon ligustrinum*, *Evodia meliaefolia*, *Ilex triflora* and *Trema tomentosa*. Species that appeared after 2003 were mesophyte and shade tolerant plants including *Cinnamomum burmannii*, *Raphiolepis indica*, *Melia azedarach*, *Syzygium rehderianum* and *Litsea rotundifolia* var. *oblongifolia*.

The total species number in the shrub layer of the plantation fluctuated but generally increased. Within the plantation, heliophytes including *Clerodendrum fortunatum*, *Gardenia jasminoides*, *Ilex asprella*, *Eurya chinensis*, *Myrtus communis* and *Melastoma candidum* existed all the time from the beginning of reforestation to 1994. *Urena* sp. appeared in the early period but disappeared after 1997. Heliophytes species that appeared after 2003 were *Ficus variolosa*, *Glochidion eriocarpum* and *Wikstroemia indica*. The species in the shrub layer changed to some extent. Forests with more heliophyte species were still in the early stage of forest development. Some native mesophytes species were common in zonal forests, such as *Psychotria rubra*, *Ardisia crenata* and *Desmos chinensis,* which emerged in the shrub layer of the plantation.

From 1994 to 2007, the total species number in the herbaceous layer of the plantation showed a similar pattern as that in the shrub layer. Under the canopy, heliophytes including *Dicranopteris dichotoma, Ischaemum ciliare* and *I. capillaire* existed all the time from the beginning of reforestation to 1995. Some species appeared early but then disappeared between 1997 and 2003. These heliophytes species included *Calathodes oxycarpa*, *Polygonum chinense*, *Adiantum flabellulatum*, *Spermacoce latifolia* and *Lophatherum gracile*. Shade tolerant fern species that appeared after 2003 included *Schizoloma heteropyllum* and *Blechenum orientare*. The shade tolerant herbaceous and fern species in the zonal forest, such as *Cyrtococcum patens, Herba loophatheri* and *Blechnum orientale,* had already recolonized the plantation.

Changes in biomass

The changes in biomass in the arbour layer of the A. mangium plantation could be divided into two stages (Fig. 1b): a rapid growth period in which biomass increased from 1.60 t/ha in the 1st year to 185.01 t/ha in the 7th year, and a stable stage in which biomass was stable and fluctuated slightly after the 11th year (from 185.01 to 206.21 t/ha).

The biomass in the shrub layer increased with age from years 4 to 29 (Table 1). Biomass in the herb layer increased from years 4 to 15 and gradually decreased after 15 years. The litter standing crop increased rapidly from years 4 to 5 and then slowly decreased from years 15 to 29 (Table 1).

Variations in soil physical and chemical properties

During the growth period of the *A. mangium* plantation, the soil bulk density and pH value in the upper soil layer (0–20 cm) continued to decline, while the soil organic matter, total N and available P contents increased. The water content in the upper soil layer in July showed fluctuation with an increasing tendency (Table 2).

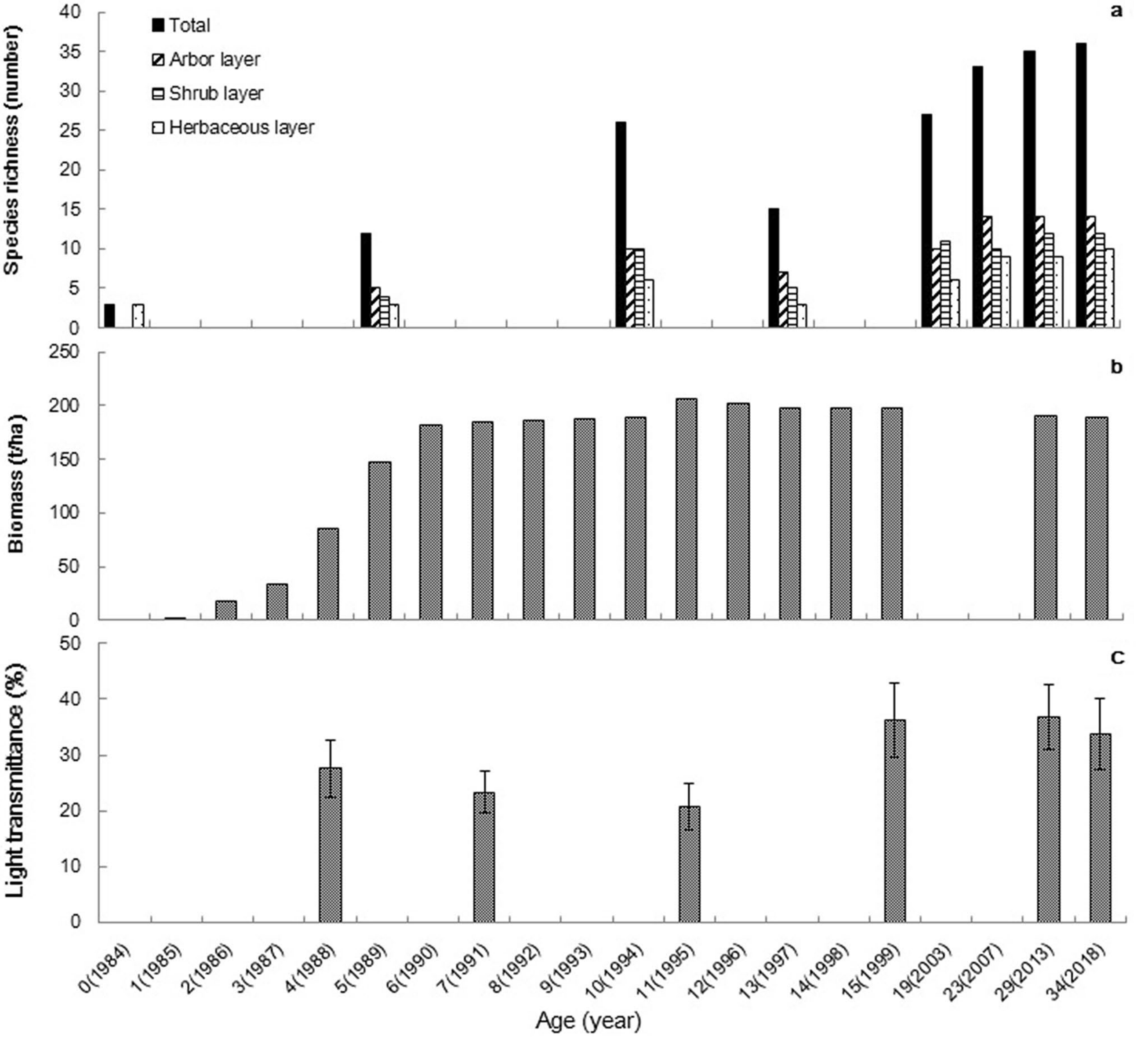

Fig. 1 The structural and functional changes in *Acacia mangium* plantations. **a** Changes in overall number of species and the number of species in the arbour layer, shrub layer and herbaceous layer of the plantation in South China (Numbers are plot-based and time-series data), **b** changes in biomass (the dark line with dots) in the arbour layer of the *A. mangium* plantation in South China, **c** light transmittance in *Acacia mangium* plantations in South China across different ages (The bars indicate standard deviation)

Table 1 Biomass changes in the different layers of the understory of the *Acacia mangium* plantation at different ages

Biomass (t/ha)	Stand age (age/year)				
	4 (1988)	7 (1991)	11 (1995)	15 (1999)	29 (2013)
Shrub layer	2.39 ± 0.32a	4.13 ± 0.25b	4.68 ± 0.53a	5.59 ± 0.49b	5.98 ± 0.18b
Herb layer	2.68 ± 0.14a	3.18 ± 0.66b	1.70 ± 0.21a	1.74 ± 0.39a	1.65 ± 0.11b
Litter standing crop	5.93 ± 1.01a	8.12 ± 1.24b	11.23 ± 1.97a	13.11 ± 1.83b	11.71 ± 2.01a

Values are the mean ± SD. Values within the same row are not significantly different from one another if they share the same letter, while they are different if they bear different letters ($P < 0.05$)

Table 2 The soil physical and chemical properties of the *Acacia mangium* plantation at different ages (mean ± SD)

Soil property	Stand age (year)				
	4 (1988)	7 (1991)	11 (1995)	15 (1999)	29 (2013)
Soil bulk density (g/cm^3)	1.53 ± 2.12a	1.47 ± 0.08b	1.38 ± 0.02a	1.33 ± 0.07a	1.26 ± 0.05b
Water content in upper soil layer in July (%)	18.81 ± 2.31a	17.75 ± 1.98a	20.21 ± 3.21b	25.6 ± 3.97a	23.51 ± 4.58a
pH value	4.39 ± 0.22a	4.33 ± 0.37a	4.16 ± 0.11b	4.12 ± 0.23b	3.88 ± 0.33a
Organic matter (g/kg)	26.38 ± 9.37a	25.03 ± 5.43a	29.87 ± 8.39b	30.58 ± 2.28b	37.55 ± 3.74a
Total N (g/kg)	1.23 ± 0.42a	1.43 ± 0.36b	1.44 ± 0.45b	1.48 ± 0.18a	1.58 ± 0.23b
Available P (mg/kg)	0.94 ± 0.13a	1.02 ± 0.35b	1.01 ± 0.28b	2.25 ± 0.71a	2.62 ± 0.29a

Values are the mean ± SD. Values within the same row are not significantly different from one another if they share the same letter, while they are different if they bear different letters ($P < 0.05$)

Dynamic of light transmittance

The light transmittance of the plantation decreased from 27.6 to 20.7% during year 4–11, increased to 36.3% until year 29, and finally slowly decreased to 33.8% from years 29 to 34 (Fig. 1c).

Discussion

Increased plant diversity with the change of light transmittance

Our results showed a clear increase in plant diversity with plantation age (Fig. 1a, Online Appendix Table 1). The exception was 1997 in which the annual average temperature was 0.9 °C higher than that in 1960–2002, and the annual rainfall was 388.9 mm less. Also, relative to other years, 1997 had a colder early spring, less typhoons in summer, higher temperature, and lower rainfall in winter (Tu et al. 1998; Wang and Wang, 2003). Abnormal climate might have caused a high mortality of some plants and a rare decline in diversity. With the development of *A. mangium* plantation, the increase in overall plant diversity was always accompanied by the decline of heliophytes or pioneer species and the recolonization of mesophyte species in different layers. The number of fern species in the understory increased significantly with time (Online Appendix Table 1).

Light intensity had a great influence on plant diversity of plantation (Fig. 1c). When *A. mangium* plantation was just established, its canopy layer was not closed, so there were some pioneer species or heliophytes to settle down in the stand (Ren et al. 2019). As the canopy of the *A. mangium* plantation grew denser with age, light transmittance decreased from 1988 to 1995. Light capture capacity improved due to leaf biomass accumulation. As the plantation grew slowly with less biomass accumulation after 1995, light transmittance slightly increased. The change or fluctuation in light intensity with the age led to the loss of some early settled heliophytes, while those mesophytes and shade tolerant plants replaced the heliophytes. Those recolonized heliophyte, mesophytes and shade tolerant plants in the plantation led to higher plant diversity. Lin et al. (2003) also reported that microclimatic variables such as surface and soil temperature and air relative humidity in this plantation continued to improve with age, which could have promoted plant diversity.

After 11 years, with the falling dead branches and leaf litter in the mature *A. mangium* plantations (Table 1), the newly opened canopy promoted the rapid growth of understory plants. However, the thicker litter layer on the forest floor hindered the regeneration of the herbaceous layer but had no impact on the shrub layer, which led to different changes in biomass in these layers. As the biomass of the shrub layer continued to increase, understory plants might grow and replace trees with forest development. If there is a natural forest near the plantation, some native species seeds or seedlings can migrate to the plantations, which can facilitate the plantations to reach semi-natural forests or climax conditions (Yuan et al. 2013; Sun et al. 2014). Otherwise, artificial intercropping with native tree species may be needed.

Compared to that 134 tree species (in 10,000 m^2) were reported in the natural monsoon evergreen broad-leaved forest at Dinghushan Mountain in the same region (Sun et al. 2013), the plant diversity of this plantation was still far behind that of natural forest. Although some native species in the shrub and herb layers of zonal vegetation recolonized in the plantation, the dominant species in the tree layer of natural forest, such as *Castanopsis chinensis, Schima superba, Cryptocarya chinensis, C. concinna and Aporosa yunnanensis*, were still missing. It seems that even after 34 years, native tree species still failed to recolonize in the plantation. It may take a much longer time for a plantation to be restored successfully to a natural forest.

Changes in biomass and increases of soil fertility

The biomass of *A. mangium* plantation increased rapidly in the first 11 years and then fluctuated afterwards (Fig. 1b). The pattern of biomass change in the tree layer showed that *A. mangium* was a fast-growing species and suitable for reforestation in subtropical China. Previous studies indicated that *A. mangium* has a strong nitrogen fixation capability and can improve the fertility and biological output of the soil. For example Ding et al. (1989), found that seedlings up to 7-year-old trees of *A. mangium* at this plantation nodulated without inoculation. Ren and Yu (2008) found that the rapid growth period of the biomass (1–7 years) was matched with the period of nodule growth. The possible decline and disappearance of nodule formation with age may be caused by the shrub layer, which occupies a considerable portion of the surface soil and inhibits the development and nodulation of *A. mangium* roots. The biomass data under the tree layer indicated that at the beginning of *A. mangium* planting, the understory vegetation, especially the herb species that were tolerant to barrenness, grew well due to the low stand coverage and moderate barrenness of the soil. Hence, its biomass was relatively large. As the stand coverage became denser due to plant growth and an increase in the litter layer, the growth of the herb layer was inhibited, and its biomass tended to decrease. The shrubs might have adapted to the change and stored more biomass. The nonsynchronous growth of biomass among different layers indicated that species grew at different rates and accumulated different amounts of biomass. Such biomass changes in the understory of the *A. mangium* plantation may be favourable for the development of community composition, biological diversity and soil fertility.

The biomass of natural monsoon evergreen broad-leaved forest at Dinghushan Mountain in the same region was 398.57 t/ha (Peng 1996), much higher than that of the plantation. Our results indicated that the pioneer species *A. mangium* could grow very fast and reach more than half of the biomass of climax in the region within 34 years.

The plantation continuously accumulated soil C, N and P and improved soil physical properties, indicating that afforestation might enhance soil fertility (Table 2). Fu et al. (2009) and Yi et al. (2018) reported that soil microorganisms and nematode communities play a key role in improving soil physical and chemical properties during the growth process. Li et al. (2001) found that this plantation stimulated the nitrification process and converted more ammonium nitrogen into nitrate nitrogen and the nitrification process generally induced soil acidification. This phenomenon and N deposition in the region could explain the soil acidification of the *A. mangium* plantation. In addition, the interaction between plants and soil microorganisms/nematodes promoted the improvement of soil fertility in this plantation (Shi and Fu 2014). The natural development of the plantation could favour the improvement of soil fertility; as a result, it could favour the succession of the plant community from herbaceous species to trees.

The soil bulk density, pH value, organic matter, TN and available P of the natural monsoon evergreen broad-leaved forest stand at Dinghushan Mountain were 0.97 g/cm^3, 3.87, 50.61 g/kg, 2.89 g/kg and 3.80 mg/kg, respectively (Peng 1996). Compared to the soil fertility of the natural forest, the soil fertility of the plantation was at a moderate level. Our results indicated that the pioneer species *A. mangium* could grow quickly to achieve more than half of the biomass and soil fertility of climax forest in the region within 34 years.

Structure and function not synchronized in development

The structure (i.e., plant diversity and light transmittance) and function (i.e., biomass and soil fertility) of the plantation were not synchronized during its growth (Fig. 1a–c). The biomass and soil fertility of the *A. mangium* plantation were restored faster than plant diversity during development. A number of stable ecosystem states were related to ecosystem function and ranged from degraded to intact. There were two principal barriers between degraded and restored ecosystems. The first type was abiotic barriers, which could be a lack of appropriate microclimate, little organic matter and low soil water content. These barriers all required physical modification to bring the ecosystems to a new level of stability associated with improved functioning. The second type was biotic, which might be a result of a lack of appropriate species or interaction between them and abiotic factors. This plantation might cross the first threshold and lead to a new state, which faces biotic recruitment limitations (Bradshaw 1983; Whisenant 1999; Hobbs and Harris 2001).

We also found that the structure of the plantation were far from fully restored to reassemble natural forests over the 34 years and might still be at the early stage of development. However, soil fertility and biomass accumulation improved significantly. This result is similar to the findings of Moreno-Mateos et al. (2017). They analysed 3035 ecological restoration cases worldwide and found that compared to the reference ecosystem level, the recovering ecosystems had values of only 46–51% for organism abundance, 27–33% for species diversity, 32–42% for carbon cycling and 31–41% for nitrogen cycling (Moreno-Mateos et al. 2017). During restoration, the structure and function of the plantation alternately increase. The restoration of damaged ecosystems can only restore certain structures and functions of an ecosystem. Over the long term, ecosystem functions may be gradually or partially restored after the restoration of ecosystem structure.

Conclusions

The plant diversity, biomass and soil fertility of the *A. mangium* plantation improved dramatically over the 34-year period after planting. However, there was a native tree species recruitment limitation and the plantation was still in the early stage of plantation development. The plantation showed non-synchronism between structure and function during development. Plant diversity in plantations increased with age and the pioneer species or heliophytes were replaced by mesophytes and shade species due to change in light transmittance and soil fertility. Plant growth improved soil fertility and soil improvement was conducive to the accumulation of biomass and the increase in biodiversity. During the restoration process from a plantation to a seminatural forest, tree species regeneration should be monitored in the early phase, the structure of vegetation composition needs to be adjusted in the middle period and the structure and function of the plant community must be enhanced in the later period.

Acknowledgements Special thanks to Prof Zuoyue Yu, who founded the Heshan Station and established those plantations. We also thank our colleagues Prof Mingmao Ding, Prof Shaolin Peng, Prof Honglin Cao, Prof Shenglei Fu, Prof Weijun Shen, Mr. Wenqi Zhang, Dr. Xian Cai and Mr Yongbiao Lin at the Heshan National Field Research Station of Forest Ecosystem and Mr Shizhong Liu and Ms Qianmei Zhang at the South China Botanical Garden. This research was funded by the National Natural Science Foundation of China, Grant number 31170493. Dafeng Hui is supported by the US National Science Foundation (NSF) projects. We thank SpringerNature Author Services for editing English. We also thank two anonymous reviewers for their valuable comments. The experiments comply with the current laws in China.

References

Atipanumpai L (1989) *Acacia mangium*: studies on the genetic variation in ecological and physiological characteristics of a fast-growing plantation tree species. Acta Forestalia Fennica 1:206

Bradshaw AD (1983) The reconstruction of ecosystems: presidential address to the British ecological society. J Appl Ecol 20:1–17

Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458–1460

Ding MM, Yi WM, Liao LY (1989) Effects on nodulation and nitrogen fixation of *Acacia mangium* by fertilization. Nitrogen Fixing Tree Res Rep 7:55–56

Duan WJ, Ren H, Fu SL (2010) Community comparison and determinants analysis of understory vegetation in six plantations in South China. Restor Ecol 18:206–214

Fu SL, Lin YB, Rao XQ, Liu SP (2009) Data sets for long term observation and research of forest ecosystems in China: he Shan Station of Guangdong, 1998–2008. Chinese Agriculture Press, Beijing

Hardiyanto EB, Sadanandan NEK (2014) Productivity of successive rotations of *Acacia mangium* plantations in Sumatra, Indonesia: impacts of harvest and inter-rotation site management. New Forest 45:557–575

Hobbs RJ, Harris JA (2001) Restoration ecology: repairing the Earth's damaged ecosystems in the new millennium. Restor Ecol 9:239–246

Kimmins JP (2004) Forest ecology: a foundation for sustainable forest management and environmental ethics in forestry, 3rd edn. Prentice Hall, Upper Saddle River

Koutika LS, Richardson DM (2019) *Acacia mangium* Willd: benefits and threats associated with its increasing use around the world. Forest Ecosyst 6:2

Krebs CJ (1985) Ecology: the experimental analysis of distribution and abundance, 3rd edn. Harper & Row, New York

Le Brocque AF, Buckney RT (2003) Species richness-environment relationships within coastal sclerophyll and mesophyll vegetation in Ku-ring-gai Chase National Park, New South Wales, Australia. Austral Ecol 28:404–412

Li ZA, Peng SL, Rae DJ, Zhou GY (2001) Litter decomposition and nitrogen mineralization of soils in subtropical plantation forests of southern China, with special attention to comparisons between legumes and non-legumes. Plant Soil 229:105–116

Lin YB, Shen WJ, Peng SL, Ren H, Li MH (2003) Comparison of microclimatological effects of three plantations in Heshan of the lower subtropical China. Acta Ecol Sin 23:1657–1666

MEWAM (1986) Methods for the determination of metals in soils, sediments and sewage sludge and plants by hydrochloric-nitric acid digestion. Methods for the examination of waters and associated materials. Her Majesty's Stationary Office, London

Moreno-Mateos D, Barbier BB, Jones PC (2017) Anthropogenic ecosystem disturbance and the recovery debt. Nat Commun 8:14163

Norisada M, Hitsuma G, Kuroda K (2005) *Acacia mangium,* a nurse tree candidate for reforestation on degraded sandy soils in the Malay Peninsula. For Sci 51:498–510

Otsamo R (2000) Early development of three planted indigenous tree species and natural understory vegetation in artificial gaps in an *Acacia mangium* stand on an *imperata cylindrica* grassland site in South Kalimantan, Indonesia. New For 19:51–68

Otsamo A (2002) Early effects of four fast-growing tree species and their planting density on ground vegetation in Imperata grasslands. New For 23:1–17

Pan ZG, Feng S, Lin HS (1996) The introduction, growth and utilization of *Acacia mangium*. Trop For 24:144–152

Pan XZ, Guo ZY, Pan K (2019) Protocols for standard soil observation and measurement in terrestrial ecosystems, 2nd edn. Chinese Environmental Sciences Press, Beijing

Park H, Higgs E (2018) A criteria and indicators monitoring framework for food forestry embedded in the principles of ecological restoration. Environ Monit Assess 190:113

Paula RR, Bouillet JP, Gonçalves JL (2018) Nitrogen fixation rate of *Acacia mangium* Wild at mid rotation in Brazil is higher in mixed plantations with *Eucalyptus grandis* Hill ex Maiden than in monocultures. Ann For Sci 75:14–23

Peng SL (1996) Community dynamic of lower subtropical forests. Science Press, Beijing

Ren H, Yu ZY (2008) Biomass changes of an *Acacia mangium* plantation in southern China. J Trop For Sci 20:105–110

Ren H, Peng SL, Yu ZY (1995) The canopy structure and canopy radiation for *Acacia mangium* communities in different ages. Acta Ecol Sin 15(Supp):58–64

Ren H, Peng SL, Yu ZY (1996) The ecological and biological characteristics of *Acacia mangium*. Chin J Ecol 16:1–5

Ren H, Lu HF, Wang J, Liu N, Guo QF (2012) Forest restoration in China: advances, obstacles, and perspectives. Tree For Sci Biotechnol 6:7–16

Ren H, Chen H, Li L, Li PH, Hou CM, Wan HF, Zhang QM, Zhang PX (2013) Spatial and temporal patterns of carbon storage from 1992 to 2002 in forest ecosystems in Guangdong, Southern China. Plant Soil 363:123–138

Ren H, Liu Q, Li LH, Liu ZF (2019) Introduction to restoration ecology, 3rd edn. Science Press, Beijing

Shi LL, Fu SL (2014) Review of soil biodiversity research: history, current status and future challenges (in Chinese). Chin Sci Bull 59:493–509

State Forestry Administration of China (2015) Forest resource statistics of china 2009–2013: the eighth national forest resource inventory. State Forestry Administration of China, Beijing

Sun ZY, Ren H, Schaefer V, Lu HF, Wang J, Li LJ, Liu N (2013) Quantifying ecological memory during forest succession: a case study from lower subtropical forest ecosystems in South China. Ecol Ind 34:192–203

Sun ZY, Ren H, Schaefer V, Wang J, Guo QF (2014) Using ecological memory as an indicator to monitor the ecological restoration of four forest plantations in subtropical China. Environ Monit Assess 186:8229–8247

Tu YX, Li GP, Dong YC (1998) Abnormal climate phenomena, causes and prevention of agrometeorological disasters in Guangdong Province in 1997. Chin J Agrometeorol 19:39–43

Wang Z, Wang H (2003) Analysis of climate change in Heshan City in recent 40 years. Guangdong Meteorol 3:26–28

Wang S, van Kooten GC, Wilson B (2004) Mosaic of reform: forest policy in post-1978 China. For Policy Econ 6:71–83

Wang J, Ren H, Yang L, Li DY, Guo QF (2009) Establishment and early growth of introduced indigenous tree species in typical plantations and shrubland in South China. For Ecol Manage 258:1293–1300

Wang J, Li DY, Ren H, Yang L (2010) Seed supply and the regeneration potential for plantations and shrubland in southern China. For Ecol Manage 259:2390–2398

Whisenant SG (1999) Repairing damaged wildlands: a process—orientated, landscape scale approach. Cambridge University Press, Cambridge

Xiong Y, Xia H, Li Z (2008) Impacts of litter and understory removal on soil properties in a subtropical *Acacia mangium* plantation in China. Plant Soil 304:179

Xu D, Yang Z, He Q (1998) Above ground biomass production and nutrient cycling of middle-age plantation of *Acacia mangium*. For Res 11:592–598

Yi GT, Wang XL, Liu ZF, Cai XA, Fu SL, Zhou LX (2018) Interannual dynamics of soil microbial biomass carbon under different plantations in subtropical China. Ecol Environ Sci 27:224–231

Yu ZY, Peng SL (1996) Ecological studies on vegetation rehabilitation of tropical and subtropical degraded ecosystems. Guangdong Sciences & Technology Press, Guangzhou

Yuan SF, Ren H, Liu N, Wang J, Guo QF (2013) Can thinning of overstory trees and planting of native tree saplings increase the establishment of native trees in exotic acacia plantations in south china? J Trop For Sci 25:79–95