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ORIGINAL PAPER

Age and radial growth pattern of four tree species in a subtropical forest of China

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Abstract Subtropical forests are usually composed of many tree species. Knowledge of the age and radial growth variation of the dominant tree species is useful for understanding forest dynamics and community structure and function. The aims of this study are to explore whether there are identifiable annual growth rings in the main tree species and to examine the growth characteristics within and among the species in Mount Gutian subtropical forest of China. The results showed that four out of eight tree species from which samples were collected had visible and cross-datable rings. There were no stable relationships between the age and diameter for these subtropical trees. Significant differences existed in radial growth rate within and among the four species, suggesting a high spatial heterogeneity in the mixed-species subtropical forest. The common pattern in age distribution of multiple species suggests a stand-wide disturbance occurring around the 1960s. It is interesting to note that the growth rate at the same age intervals was different for trees younger than 40 years of age and older than 40 years of age, suggesting a change in climate or forest structure in the two time periods. The results obtained from this study help understand the growth dynamics in other subtropical forests having these tree species.

Keywords Subtropical forests · Tree rings · Growth dynamics · Age interval

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Introduction

Tree species coexisting in a forest have different ecophysiological characteristics and usually show different growth patterns (Stewart 1986). Knowledge about the age and radial growth pattern in dominant tree species is of importance for understanding forest dynamics and structure. In Mount Gutian of eastern China, a 24-ha permanent plot of subtropical broad-leaved forest was established to study the forest dynamics in detail (Ma 2008). Although dendrometers were applied in the permanent plot to monitor the growth rate of dominant tree species, information about the age and long-term growth dynamics is sparse. The lack of data inhibited reliable assessment of the variation in tree growth along the lifespan and among species. Such assessment is essential for forest sustainable management.

Tree-ring analysis is an effective tool to identify the age of trees for evaluating forest dynamics and reconstructing the stand development patterns (Baker et al. 2005; Bergeron 2000; Dang et al. 2010). Tree-ring analysis has been used to obtain insight into canopy disturbance, lifetime growth patterns and historical growth rates of trees in temperate forests (Landis and Peart 2005; Lorimer and Frelich 1989; Lusk and Smith 1998). Seasonal radial growth and annual ring development have been confirmed in some tropical and subtropical tree species (Schongart et al. 2006; Grau et al.

2003; Fichtler et al. 2003; Worbes 1995; Worbes and Junk 1989). To date, most tree-ring research in China focuses on reconstruction of past climate or tree-line dynamics in arid and semiarid areas of western China (Li et al. 2008; Wang et al. 2006; Liu et al. 2004; Zhang et al. 2003), whereas much less studies have been carried out on subtropical trees.

In forestry, there is a general need to estimate the age of trees from their diameter. Such estimation is usually based on empirical relationship between the tree's age and diameter. The age of trees is determined by counting the number of rings in the stem, if the rings are formed annually and clearly visible. Many researchers and managers have used stem diameter as proxy measures of tree age for convenience. The reliability of the estimation depends on the stability of the relationship among individual trees (Burley et al. 2007; Liu and Hong 1999). One of the aims of this study is to examine if there are clearly visible rings in the main tree species in Mount Gutian subtropical forest and if there are stable relationships between the age and diameter. The second aim of this study is to compare growth rates in different size classes and age intervals among the main tree species that have clearly identifiable rings. Such information is useful for understanding the ecological characteristics of the dominant tree species in the subtropical forest and therefore helps to evaluate forest dynamics.

Materials and methods

Study site and sampling

This study was conducted at Mount Gutian National Nature Reserve in Zhejiang Province, eastern China (29°10′19″–29°17′41″N, 118°03′50″–118°11′12″E). The area is characterized by rugged terrain with elevation at the study site ranging from 450 to 750 m above sea level. A total of 1991 vascular plant species, belonging to 244 families and 897 genera, have been recorded within the entire Mount Gutian (Chen and Feng 2002). Within the 24-ha permanent plot, there are 159 tree species which belong to 49 families (Legendre et al. 2009). The dominant vegetation type in the region is subtropical evergreen mixed (broadleaved and coniferous) forest dominated by *Schima superba*, *Castanopsis eyrei*, *Cyclobalanopsis glauca*, *Pinus massoniana* and *Quercus serrata* (Zhu et al. 2008; Yu et al. 2001). The climate is sub-tropical with distinct temperature and precipitation seasonality. According to the meteorological data at the nearby Tunxi weather station from 1953 to 2002, the mean annual number of frost-free days is 250. The mean monthly temperature ranges from 4°C in January to 28°C in July with an annual mean of 16°C and mean annual precipitation of 1723 mm (Fig. 1).

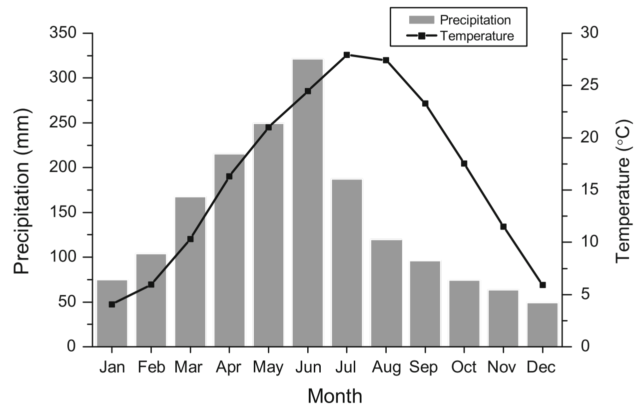

Fig. 1 Monthly rainfall (*gray bars*, *left axis*) and temperature (*black line*, *right axis*) averaged from 1953 to 2002 for Mt. Gutian, China

Increment core samples were collected at breast height from trees that have no sign of obvious rot and damage in the stem. The trees selected for sampling were from eight main species growing in an area adjacent to the 24-ha permanent forest plot. These eight tree species were *P. massoniana*, *S. superba, Cunninghamia lanceolata*, *Q.* serrata*, Daphniphyllum oldhami, C. eyrei, C. fargesii* and *C. tibetana*. The perimeters at breast height of the sampled trees were measured. At least 26 trees of different diameter class from each species were selected for sampling (Table 1).

Tree-ring analysis

In laboratory, the increment core samples were mounted, air dried and sanded with sandpapers of progressively finer grit (up to 600 grits) to make the rings visible. Ring widths of the samples that have clearly visible rings were measured to a precision of 0.001 mm under a stereomicroscope with a Velmex incremental measuring device. The ring-width series were cross-dated and quality checked using the program COFECHA (Holmes 1983) to insure that each ring was assigned to the correct calendar year of its formation. Standard tree-ring chronology of each species was developed from the cross-dated ring-width series using the program ARSTAN (Cook 1985). Negative exponential curves or linear regression lines of negative slope or horizontal lines were used to remove the age-related growth trends (Fritts 1976). Tree-ring samples of less than 20 years old were not included into chronology development, and the early section of each chronology with less than five sample replications was truncated.

The age of the trees was determined by counting the number of rings from the outermost ring to the pith. When the pith was not obtained in the core samples, we estimated the age of the ring closest to the pith according to its shape of curvature (Brienen and Zuidema 2006). It is worth

Table 1 Number of increment core samples of the eight tree species from the Mt. Gutian subtropical forest of China

Species	Total	Diameter classes distribution (cores number)					
		0–10 cm	10–20 cm	20–30 cm	30–40 cm	40–50 cm	50–60 cm
Pinus massoniana	31	6	11	8	4	2	0
Schima superba	30	9	8	7	4	0	2
Cunninghamia lanceolata	30	4	10	9	6	0	1
Quercus serrata	29	11	14	4	0	0	0
Daphniphyllum oldhami	27	6	13	7	1	0	0
Castanopsis eyrei	30	7	10	4	6	3	0
Castanopsis fargesii	26	7	7	5	4	3	0
Castanopsis tibetana	31	7	6	13	5	0	0

noting that the age of the trees obtained thereafter is the age of the stem at the breast height, because the age does not include the time that the trees grow from the ground to the sampling height.

The cumulative radial growth curves of each tree were calculated over its lifetime and averaged to obtain mean growth curves for each species. Multiplying the radial growth values by two, we obtained the cumulative stem diameter of each species which reflect an approximate age–diameter relationship. The size class of different tree species was set to be 10 cm in diameter. The variations in radial growth rates were analyzed for each species by calculating the median, minimum and maximum growth rates for each diameter class. Species were tested for overall differences in growth rates in each size class using Kruskal–Wallis tests and Dunn tests for a posteriori pairwise comparison (Kruskal and Wallis 1952). To examine the growth rate at the same age intervals in young and old trees, we compared the growth rates between trees younger than 40 years and older than 40 years of age in each 10-year age interval. The difference of growth rates between the young (<40 years of age) and old (>40 years) trees was tested by Mann–Whitney test for each age interval (Whitney 1997).

Results

Tree-ring characteristics of the eight tree species

Examination of the tree-ring samples of the eight tree species showed that clearly visible and cross-datable rings were found in four species, i.e., *P. massoniana*, *S. superba, C. lanceolata* and *Q. serrata* (Fig. 2a–d). Tree rings in the rest of the four species were either difficult to distinguish or to cross-date (Fig. 2e–h). For *D. oldhami* and *C. fargesii* trees, the latewood is too narrow and light to be certain if it forms a true ring or is simply a false ring, and this difficulty increases especially in the portion close to the bark. For *C. eyrei* and *C. tibetana* trees, the latewood is too faint to insure if it is the boundary with the earlywood of the following year. Tree-ring widths in the four species that have clearly visible rings were cross-dated for each species and the mean inter-serial correlation coefficients ranged from 0.336 to 0.382, indicating a high quality of cross-dating among the tree-ring series. Tree rings of these species were studied previously in other regions (Song et al. 2011; Shao et al. 2009; Kuang et al. 2008; Fujihara 1996). There have not been any publications on dendrochronological studies of the four species that do not show clearly visible rings.

Tree-ring chronologies for the four species under study are shown in Fig. 3. The correlation coefficients among these chronologies were low, ranging from −0.337 to 0.276 (for the period 1915–2007), suggesting that the habitats in this mixed subtropical forest are heterogeneous. As shown in Table 2, *Cunninghamia* trees showed the highest mean ring width, reflecting its fast radial growth relative to other species. *Schima* exhibited the highest mean sensitivity, suggesting that its ring widths had high inter-annual variability and was sensitive to yearly environmental changes. The first-order autocorrelations ranged from 0.530 to 0.769 for the four chronologies, indicating that the chronologies contained considerable low-frequency variance related with growth condition and tree physiology (Fritts 1976). In common period analyses (1951–2000), the expressed population signal ranged from 0.741 to 0.872 for the four chronologies, indicating that these four species were useful for dendroecological analyses.

Radial growth dynamics within species

The cumulative radial growth in relation to tree's age shows that there is great variation in age for a certain diameter (Fig. 4). For instance, the range of age for a 20-cm DBH tree was 60–112 years for *Pinus*, 35–95 years for *Schima*, 45–110 years for *Cunninghamia* and

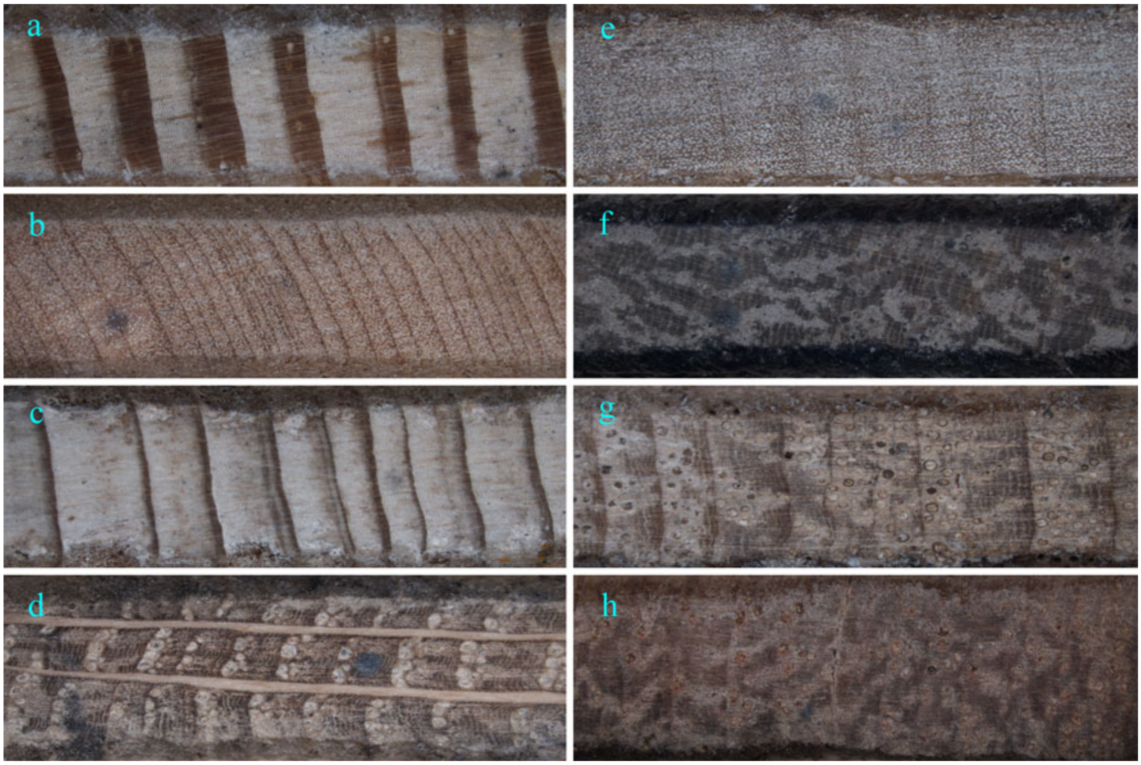

Fig. 2 Photographs of the tree rings of the eight tree species in Mt. Gutian subtropical forest of China. **a** *Pinus massoniana*, **b** *Schima superba*, **c** *Cunninghamia lanceolata*, **d** *Quercus serrata*, **e** *Daphniphyllum oldhami*, **f** *Castanopsis eyrei*, **g** *Castanopsis fargesii*, **h** *Castanopsis tibetana*

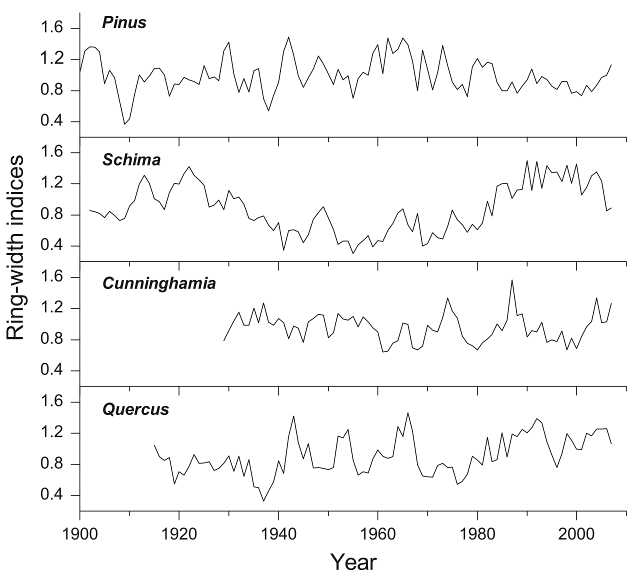

Fig. 3 Ring-width chronologies of the four species in Mt. Gutian subtropical forest of China

40–105 years for *Quercus*. This wide range of age for a given tree size derives from the high variability of individual growth trajectories within the species (Fig. 5). Most *Pinus* and *Cunninghamia* showed fast early growth with decreasing growth rates in larger trees. In contrast, *Quercus* growth trajectories were relatively linear (i.e., constant growth) over the lifetime of the tree. *Schima* had a complex growth pattern. The young trees showed high, linear growth rates, whereas the older trees showed fast early growth, followed by a distinct reduction in growth rate and then a later increase in growth. The dashed lines in Fig. 5 indicate constant diameter growth of 1 mm per year, which is clearly exceeded by most individuals of *Pinus* and *Cunninghamia*.

Radial growth dynamics among species

Species differed strongly in mean age–size relations (Fig. 6). Trees around 5 cm in diameter had comparable mean ages for *Cunninghamia*, *Schima* and *Pinus* trees, but the ages differed strongly among species at larger diameter. For instance, mean ages at 20 cm in diameter varied from 55 years in *Cunninghamia* trees to more than 85 years for *Schima* and *Pinus* trees. The average age–size relations of *Schima* and *Pinus* trees were very similar. *Quercus* trees tended to have slow and constant growth over their entire life span and showed the highest average ages at any diameter. *Cunninghamia* owned the highest average radial growth rate among the four species.

The four species under study showed different patterns in growth rates (Fig. 7). *Schima* had the highest median growth rates of the four species, followed by

Table 2 Statistics for standard tree-ring chronologies of the four species under study in Mt. Gutian subtropical forest of China

Species	*Pinus massoniana*	*Schima superba*	*Cunninghamia lanceolata*	*Quercus serrata*
Mean ring width (mm)	1.02	1.32	1.6	0.88
Mean inter-serial correlation	0.382	0.354	0.336	0.364
Mean sensitivity	0.168	0.181	0.142	0.168
First-order autocorrelation	0.571	0.769	0.530	0.664
Expressed population signal	0.795	0.872	0.741	0.814

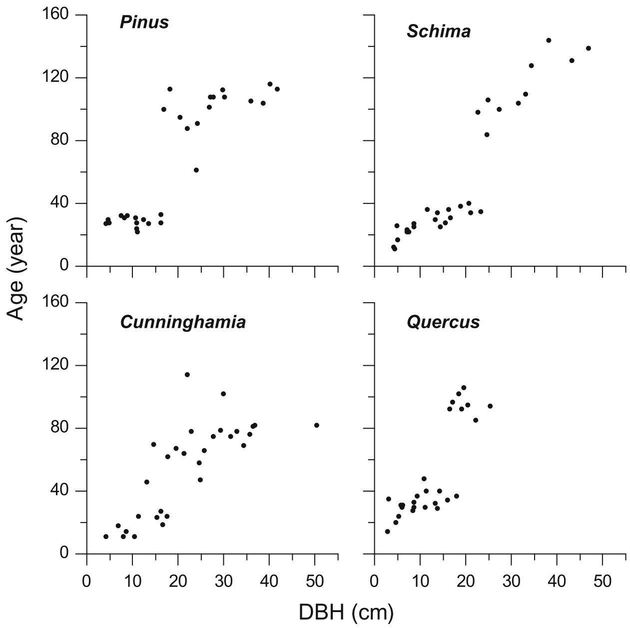

Fig. 4 The relationship between the diameter at breast height (*DBH*) and tree age of the four species in Mt. Gutian subtropical forest of China

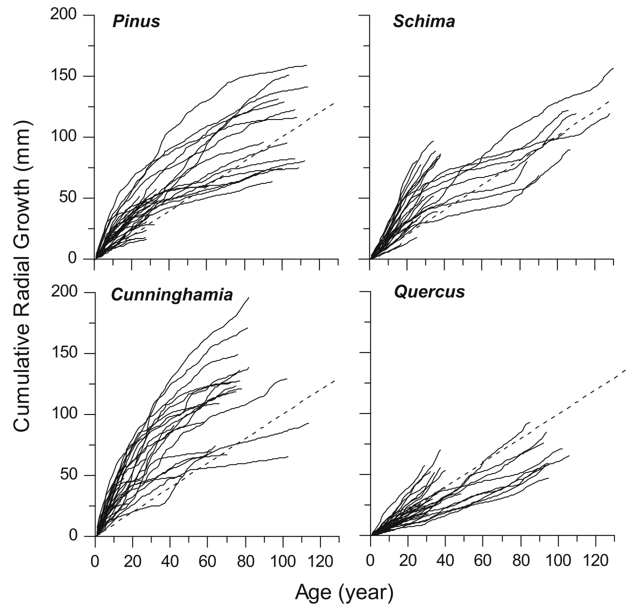

Fig. 5 Cumulative radial growth in relation to tree age for the four species under study in Mt. Gutian subtropical forest of China; each *line* represents one individual tree. The *dashed lines* indicate constant diameter growth of 1 mm per year

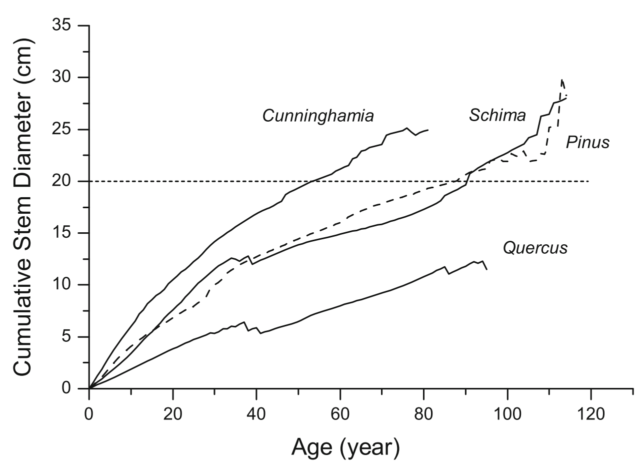

Fig. 6 Mean cumulative stem diameter growth curves for the four species under study in Mt. Gutian subtropical forest of China

Cunninghamia. In *Schima* and *Cunninghamia*, the highest median growth rates were found in the second and first size classes, respectively. Concerning *Pinus* and *Quercus*, the ontogenetic growth pattern was similar, i.e., the growth rate hardly changed with size. The minimum growth rates of the four species were almost about the same values (<0.3 mm/year), but the maximum varied much with different species or size classes. *Cunninghamia* had an especially large gap between the maximum and minimum growth rates.

Radial growth in the same age intervals in young and old trees

Besides the age, there are other factors that affect the radial growth of the four species under study (Fig. 8). For *Quercus*, the growth rate of young trees (<40 years of age) was higher than that of old trees (>40 years of age) in the same age intervals 0–10, 10–20, 20–30 and 30–40 years of age. This pattern was opposite in *Pinus*. The pattern of growth in *Schima* was similar to *Quercus* except the first 10 years. For *Cunninghamia*, the young trees grew more rapidly than the old ones at the initial lifetime, and much

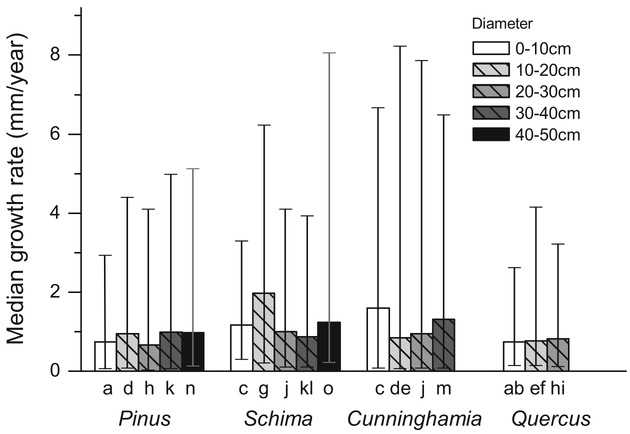

Fig. 7 Diameter growth rates (minimum, median and maximum) of the four species under study in Mt. Gutian subtropical forest of China. Median growth rates differed among species in each of the size categories (Kruskal–Wallis tests, $p < 0.001$). Different superscript letters under the bars indicate significant ($p < 0.05$) differences among species in that size class using the Dunn tests for a posteriori comparison between groups

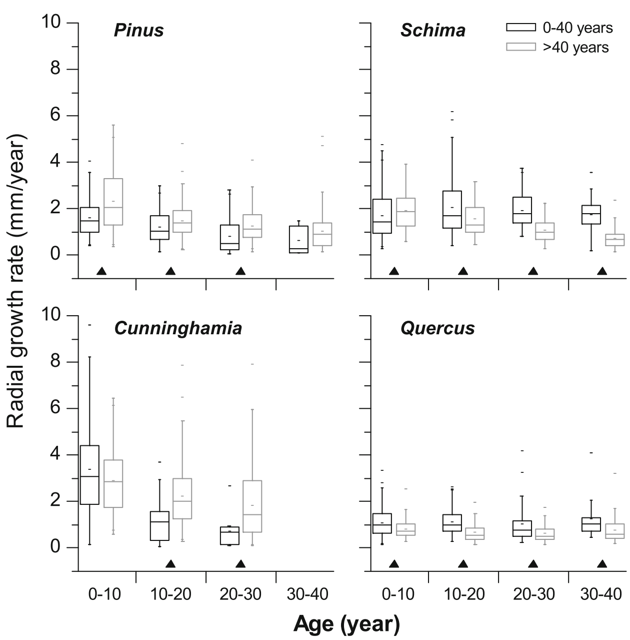

Fig. 8 Radial growth rate (medium, minimum and maximum) for different age intervals in trees younger than 40 years of age and greater than 40 years of age. *Triangles* in the age class axis indicate that the medians of the radial growth rate in young and old trees are significantly different ($p < 0.05$) based on the Mann–Whitney test

slower than the old trees in the age intervals 10–20 and 20–30 years. The Mann–Whitney test showed that there was significant difference ($p < 0.05$) between the medians of the same age interval in young and old trees except the fourth age interval of *Pinus* and the first age interval of *Cunninghamia*.

Discussion and conclusions

The results of our study showed that not all tree species in the Mount Gutian subtropical forest have clearly visible rings. For the four species that have distinct annual growth rings, the age–diameter relationship has a great variation among individuals, suggesting that it is unstable and should be used cautiously. Additional information about the growth condition is needed to obtain a reliable estimation of the tree's age (Baker 2003). This is similar to the results obtained in other studies (Baker and Wilson 2003; Burley et al. 2007; Worbes et al. 2003).

Although our samples were collected from trees of all size classes, the age distribution showed that *P. massoniana*, *S. superba* and *Q. serrata* mainly have two age cohorts, one older than 80 years of age and the other younger than 40 years of age (Fig. 4). This phenomenon suggests that a major disturbance occurred about 40 years ago, i.e., in the 1960s. It was documented that, in order to generate fuel for the local steel industry, many old growth forests in the region experienced various degrees of logging around 1960, before Mount Gutian became a reserve in 1975 (Song et al. 2011; Zhang et al. 2002). The above three are all pioneer tree species, which play an important role in the regeneration process after canopy opening. This disturbance was also evidenced by the growth release in living trees in the mid-1960s (Fig. 3).

The forest might also experience other kinds of disturbances such as typhoon or forest fire. It was reported that the congregation of some *P. massoniana* individuals in approximately 1-ha area of the northern 24-ha permanent plot was a result of a forest fire in the 1920s (Zhu et al. 2008). Information about lifetime growth patterns from a larger number of trees of different species would help in the evaluation of historical disturbances and the acquaintance of community succession (Gutierrez et al. 2004; Splechtna et al. 2005).

Where species richness is particularly high, as in tropical and subtropical mountain ecosystems, diverse tree species with different phenological rhythmicity and different microclimates result in heterogeneities of tree growth for individuals (Hu and Yu 2008; Bräuning et al. 2008). Radial growth patterns of individual trees examined in our study varied within and among species. The differences in radial growth of trees suggest that the habitat of the subtropical forest under study is highly heterogeneous in space and such heterogeneity may contribute to the multi-species coexistence of the forest.

It is interesting to note that the growth rate at 10-year age intervals in trees younger than 40 years of age is different from that at the same age intervals in trees older than 40 years of age. In other words, the age-related growth trend in the early 40 years is different in young trees and old trees. This phenomenon suggests that environmental factors (such as climate) and/or forest structure (such as forest density and canopy structure) might have changed in the recent 40 years. *Quercus* and *Schima* trees showed that the radial growth rates of young trees were faster than that of the initial 40 years of old trees, indicating that the growth conditions in the recent 40 years were more favorable to the growth of young trees than the earlier time. Conversely, the low growth rate in young *Pinus* and *Cunninghamia* trees relative to the same age intervals (except the 1–10 year age interval in *Cunninghamia*) in old trees suggested a poorer condition for the growth of young *Pinus* and *Cunninghamia* trees in the recent 40 years. The changes in growth rates of young trees would alter their progress in basal area coverage and possibly their course reaching the canopy as well, thus eventually affecting the forest structure (Rozendaal et al. 2010; Landis and Peart 2005).

In conclusion, our study demonstrated significant differences in radial growth rate not only within and among tree species, but also among different size classes and age intervals. High variability of radial growth patterns highlights the importance of tree-ring data in studies of habitat heterogeneity and points to uncertainties in diameter-based inference of forest age. Common growth patterns in multiple species could provide information about stand-wide disturbances and such knowledge is essential for forest management. This study further demonstrated that the four tree species growing in this subtropical forest are suitable for dendrochronological studies.

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