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RESEARCH PAPER

Radial growth of *Cinnamomum kanehirae* Hayata displays a larger temperature sensitivity in dominant than codominant trees

Ching-Chu Tsai[1] · Li-Fen Hung[1] · Jeng-Der Chung[2] · Shiang-Jiuun Chen[1,3] · Ching-Te Chien[2] · Wen-Yuan Kao[1] · Ling-Long Kuo-Huang[1,3]

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Abstract

• ***Key message*** **The radial wood growth curves of *Cinnamomum kanehirae* Hayata (an endangered species of subtropical Taiwan) exhibit an S shape. The dominant trees displayed a larger radial growth than the codominant trees, and their growth was more sensitive to air temperature.**

• ***Context*** Knowledge of wood radial growth is important for evaluating the factors that limit tree growth performance. The relevant experiments have mostly been conducted in cold and temperate ecosystems, but rarely in subtropical ecosystems.

• ***Aims*** In this study, we aimed to construct a unified radial growth model for *Cinnamomum kanehirae* Hayata and to identify its sensitivity to temperature.

• ***Methods*** The wood radial increments were quantified for 3 years by either pinning or microcoring. The radial wood growth curves were modelled integratively by semiparametric regression and individually by curve fitting. The effects of tree social class, interannual and environmental factors on radial growth were analysed quantitatively.

• ***Results*** A unified S-shaped growth model for *C. kanehirae* was successfully constructed. By including the social class effect, the model was significantly improved. The maximum radial increment (A) was significantly correlated with the maximum growth rate (μ); both A and μ were significantly higher in dominant than in codominant trees. The time-varying radial growth rate was more sensitive to air temperature in dominant than in codominant trees.

• ***Conclusion*** Semiparametric models revealed an S-shaped growth curve of *C. kanehirae* and confirmed the higher temperature sensitivity of dominant trees compared to codominant trees in humid subtropical areas.

Keywords Wood radial growth · Semiparametric model · Temperature · Tree social classes · Taiwan

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✉ Wen-Yuan Kao
wykao@ntu.edu.tw

✉ Ling-Long Kuo-Huang
linglong@ntu.edu.tw

[1] Institute of Ecology and Evolutional Biology, National Taiwan University, 1, Roosevelt Rd. Sec. 4, Taipei 106, Taiwan

[2] Division of Silviculture, Taiwan Forestry Research Institute, 53 Nanhai Rd, Taipei 10066, Taiwan

[3] Department of Life Science, National Taiwan University, 1, Roosevelt Rd. Sec. 4, Taipei 106, Taiwan

1 Introduction

The formation of wood simultaneously satisfies the requirements for water transport and mechanical support to achieve the remarkable size and age of trees (Tyree et al. 1994; Hung et al. 2016, 2017). Cells in the vascular cambium undergo cell division, cell enlargement and cell wall lignification to become mature xylem cells (Rathgeber et al. 2016). These growth processes are tightly controlled by internal and external factors, shaping characteristic patterns of seasonal radial growth in different ecosystems.

The alternative structure and density profile of tree rings potentially encode environmental signals, such as temperature and precipitation, but to what temporal and spatial dimension is uncertain. To answer this question requires detailed seasonal radial growth patterns in different forest ecosystems. Stangler et al. (2016) utilised phenological information as timestamps to align tracheid diameter profiles of Norway spruce, demonstrating the practical values of tree phenology in tree ring analysis for evaluating tree performance under climate changes (Baas et al. 2016; Rathgeber et al. 2016; Rossi et al. 2016).

The sigmoidal Gompertz function was applied to model the seasonal radial growth in boreal tree species (Deslauriers et al. 2003a, b; Rossi et al. 2003; Thibeault-Martel et al. 2008; Lupi et al. 2014) and was adopted in numerous studies in different terrestrial biomes such as in alpine forests (Rossi et al. 2006; Li et al. 2013), continental and oceanic temperate forests (Rathgeber et al. 2011; Michelot et al. 2012) and Mediterranean forests (Linares et al. 2009; Güney et al. 2016). The studied species were mostly gymnosperms, but Michelot et al. (2012) and Deslauriers et al. (2009) also considered for some angiosperm species. The Gompertz function, however, was not appropriate in fitting bimodal growth patterns in continental Mediterranean climates (Camarero et al. 2010). The bimodal growth curves of *Quercus petraea* (Matt.) Liebl. in lowland temperate forests were successfully fitted by the extended Gompertz function (Michelot et al. 2012). Recently, nonparametric generalised additive modelling revealed more details of cambial phenology, thus allowing researchers to answer mechanistic questions of wood formation (Cuny et al. 2013, 2014, 2015; Balducci et al. 2016). It is common to fit overall growth curves while ignoring the hierarchical structure of longitudinal data (radial increments of the same individual measured repeatedly through the experiment period); however, the repeated measures of radial increment from the same tree may be autocorrelated. In addition, the parameters estimated from fitting individual growth curves of each sample tree can be further analysed to gain biological insights, even though this two-stage analysis is prone to loss of information during parameter extraction (Zuur et al. 2009). In addition to the two-stage analysis, a semiparametric mixed modelling tool including both random components and varying coefficients as fixed components (Zhang 2004) should be included to analyse radial wood growth curves.

In Taiwan, despite high-quality tree ring analysis being conducted in the forests of high latitude (Wright et al. 2015), the study of seasonal radial growth is still in its infancy; only a few assessments being conducted in an interval of four seasons (Chen 2015). Wood growth curves are essential for conservation biology due to their potential in studying the growth performance and the population dynamics of targeted species under climate change scenarios (Morellato et al. 2016). *Cinnamomum kanehirae* Hayata (Lauraceae), an endemic evergreen tree species in Taiwan, is distributed from 200 to 1400 m above sea level (a.s.l.) (Huang et al. 1996). It is of economic importance for its timber and by-product. The quality wood may cost up to 5000 USD per cubic meter. The dead heartwood of *C. kanehirae* is the unique host of Niuchangchih (*Antrodia camphorata* Sheng H. Wu, Ryvarden & T.T. Chang), which is a medicinal fungus with anti-viral, anti-oxidant, anti-cancer and liver-protecting properties (Ao et al. 2009). The high demand for *C. kanehirae*, unfortunately, has led to illegal logging in natural forests. According to the Taiwan Forestry Bureau, the wild population of *C. kanehirae* shrunk from 368,240 m^3 in 1927 to 33,201 m^3 in 1990 and was listed as an endangered species following criterion A1 of the IUCN red list. The natural reproduction of *C. kanehirae* is limited by the seed predation (Huang et al. 1996; Chung et al. 2012) and the low germination rate (Chen and Chien 2012). Therefore, the restoration of the *C. kanehirae* population through management is in urgent demand.

The studies of environmental controls on wood formation are often focused on dominant trees (Fritts 1976; Schweingruber 1996). Nevertheless, trees of other social classes account for a substantial proportion of biomass in a wood stand. The trees of different social classes receive different amounts of solar radiation, resulting in differences in metabolism, development and growth. Thus, the climatic effect on wood formation might differ among trees of different social classes. In this study, we measured the radial increment of *C. kanehirae* planted in a nursery of Taiwan. We aimed to fit the unified radial wood growth curve of the species by using semiparametric mixed models and studied the social class effect and the interannual difference by analysing the growth parameters extracted from fitting individual wood growth curves. We also investigated the effects of temperature and precipitation on the wood growth rate by analysis of covariance.

2 Materials and methods

2.1 Site information, sample trees and climatic data

Established in 1992, the plantation of *Cinnamomum kanehirae* was located in a Xinxian nursery (24° 50′ 27 N, 121° 32′ 02 E, 338 m a.s.l.). The conditions of the plantation, the methods of sapling nursery and the growth performance of the trees were reported by Yu et al. (2012) and are briefly summarised in the supplementary material (M1). Although these trees are of the same age, they can be classified into two social classes: the dominant trees that receive direct sunlight from the top of the canopy as well as from the side, and the codominant trees that receive the sunlight only from the top of the canopy. In this study, we chose three dominant trees (D1, D2 and D3) with diameter at breast height (DBH) of 28.6 ± 2.14 cm and tree height (TH) of 16.25 ± 0.05 m and three codominant trees (C1, C2 and C3) with DBH of 21.7 ± 3.27 cm and TH of 16.05 ± 0.06 m. However, after the serious impact of Typhoon Soulik on the plantation area in 2013, the codominant tree C1 was exposed to an increased solar radiation due to the gap formation. This condition was taken into account when modelling the wood growth curves.

From 2012 to 2014, the hourly air temperature (°C), precipitation (mm) and relative humidity (RH, %) were acquired from the Tonghou auto-weather station (C0A570, 24° 51′0.2″ N, 121° 35′ 22.7″ E, 387 m a.s.l., about 8.5 km from the study sites) of the Central Weather Bureau through the Data Bank for Atmospheric and Hydrologic Research. The hourly data were processed into monthly mean temperature and monthly sums of precipitation with the *xts* Package (Ryan and Ulrich 2017) in R version 3.2.2 (R Core Team 2016). Although the data from the 7th to 30th of December in 2013 are not available due to technical issues, this omission does not seriously affect our interpretation of the phenological data. From 2012 to 2014, the mean monthly temperature was approximately 12.5 °C in winter and 26.5 °C in summer (Fig. 1). The annual precipitation is overall abundant, especially with heavy rains caused by typhoons in summer. For example, the typhoons in 2013 brought about 40% of the total annual precipitation in Tonghou. The overall RH seldom fell below 70%, except in March 2012 (minimum RH of 62%).

2.2 Wood sample preparation and radial increment measurements

Radial increments of the six sample trees were studied by pinning (Yoshimura et al. 1981) in 2012 and by microcoring (Rossi et al. 2006, 2011) in 2013 and 2014. Pinning and microcoring are currently the most reliable methods used to quantify seasonal wood production and were proven to yield similar results (Mäkinen et al. 2008). The sampling intervals varied from 2 to 4 weeks (see the supplementary materials M2 and M3 and Figs. S1 and S2 for the detailed sampling procedure and tissue section preparation).

2.3 Radial wood growth curves modelling and parameter analysis

The wood growth curves were fitted both integratively and individually. To construct a unified growth curve, we applied semiparametric mixed models to deal with the hierarchical data structure, with longitudinal repeated sampling on six trees (specified by the variable Tree) for 3 years (Year), i.e. 18 growth curves (ID). We focused on the active period of cambial growth and removed three zero radial increments in the early growing season (166 DOY of C2-2012, 164 DOY of C2-2013 and 166 DOY of D1-2012) because they were likely caused by random errors, and they led to numerical problems during model-building process. The radial increment was log-transformed to ensure that the model would estimate positive growth increments during the growing season and that the standard deviation envelope would not cover negative values. Furthermore, the log-transformation also improved the residual patterns. Model selection was based on Akaike's information criterion (AIC, Akaike 1973). The lower value of AIC suggests better model performance. The difference between the nested intermediate models was additionally tested by likelihood ratio tests. When a modification did not result in a significant improvement, the model with the least cost of degrees of freedom (*df*) and more satisfactory error structure was retained. We followed the model-building steps suggested by Zuur et al. (2009) and initialised the models by the maximum likelihood method with the package *mgcv* (Wood 2006) (see supplementary material M4 for a brief description of the model-building steps).

To extract parameters from each sampling tree, each of the radial wood growth curves was fitted by both parametric regression based on the Gompertz function (Rossi et al. 2003) and nonparametric cubic smoothing spline with package *grofit* (Kahm et al. 2010) in R software (R Core Team 2016). Please see the supplementary material M5 for a brief summary of the curve-fitting procedure, and also see Kahm et al. (2010) for a detailed workflow of *grofit*. The Gompertz function used in *grofit* follows the parameterisation:

$$y(t) = Ae^{-e^{\left[\frac{\mu e}{A}(\lambda - t) + 1\right]}}$$

where t represents the day of year (DOY), A is the maximum radial growth, μ is the maximum growth rate, and λ is the lag phase between the beginning dates of the experiment to the expected dates of cambial resumption. Here, λ has no biological meaning because the starting dates of the experiment among the study years were chosen arbitrarily and therefore did not provide a consistent basis for comparison. Instead, the beginning dates of the cambial growth were analysed and discussed in this study. For the extracted cambial growth parameters (A and μ) and the investigated phenological parameters (beginning, ending and duration of cambial growth), two-way ANOVA was applied to test the differences between the tree social classes (dominant and codominant) and inter-annual differences (2012, 2013 and 2014). The residuals were inspected with residual plots to check if there were any trends in the residual patterns. The relationship between the parameters was studied by simple linear regression model and

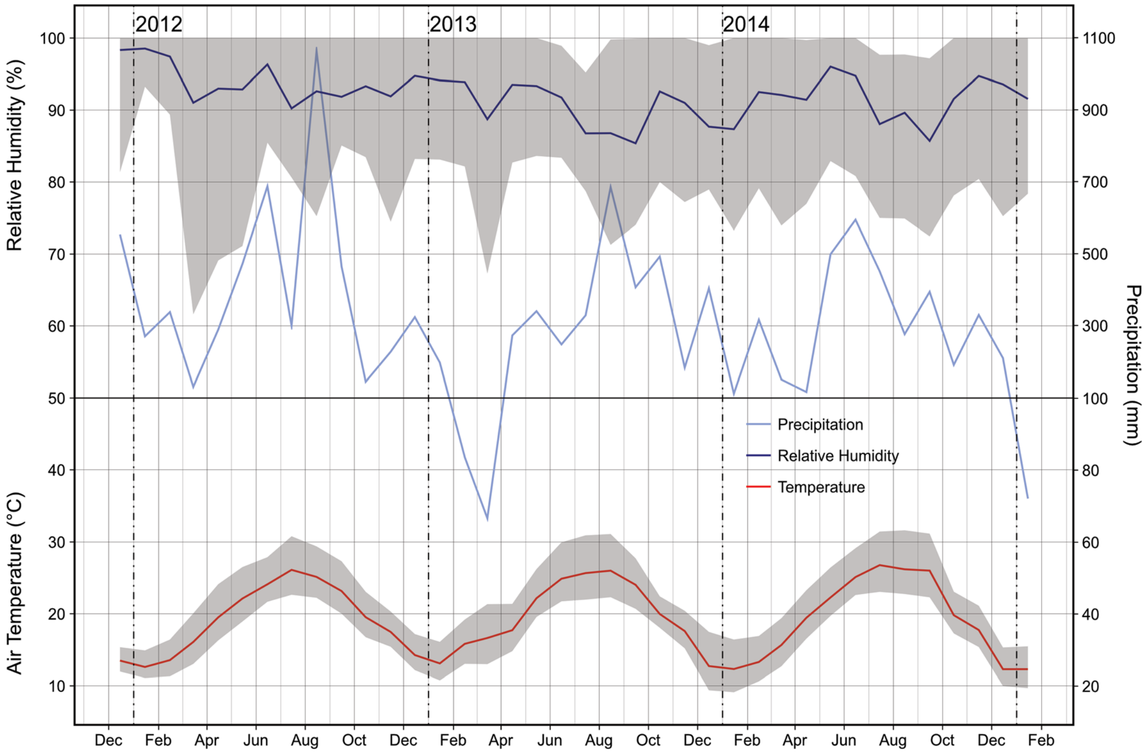

Fig. 1 Climatic information for the study site. Three-year climatic data recorded by Tonghou auto-weather station of Central Weather Bureau. The monthly mean temperature increased from about 12.5 °C in January, peaked at 26.5 °C between July and August and declined back to 12.5 °C in next January. The precipitation was overall abundant and was relatively high in summer due to the heavy rain caused by typhoons. The relative humidity (RH) was high and seldom fell below 70%, except that the minimum RH approaching 62% in March 2012. The grey envelope around the red line indicates the range between the mean monthly maximum and mean monthly minimum temperature. The grey envelope around the dark blue line shows the range between the monthly maximum and minimum RH

Pearson's correlation analyses. The slopes corresponding to different social classes were compared by analysis of covariance (ANCOVA). Four functional relationships were of particular interests: (1) A and μ, (2) A and the duration of cambial growth, (3) the duration and the beginning date and (4) the duration and the ending date.

2.4 Analysing climate influences on wood radial growth

The effects of air temperature and RH on the radial growth rates of *C. kanehirae* were studied. The hourly data of temperature were pre-processed into 3-day mean, 5-day mean and spline smoothed daily mean temperatures to reduce noise while retaining the characteristic seasonal trend. Radial increment data were smoothed by shape constrained additive modelling (SCAM) using the package *scam* (Pya and Wood 2015), which coerce the curves to be monotonically increasing (Fig. S3), thus excluding negative growth rates. The resulting curves were used to compute the growth rate (μ_t) at each time point by the following equation:

$$\mu_t = \frac{g(t) - g(t_{-1})}{t - t_{-1}}$$

where t represents the sampling dates (DOY). t_{-1} represents the sampling date before t, and $g(t)$ and $g(t_{-1})$ indicate the radial increment at time t and t_{-1}, respectively. The influence of social classes of trees on the climate-radial growth relationship was evaluated by ANCOVA. The type III ANOVA table was calculated using the package *car* (Fox and Weisberg 2011).

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

3 Results

3.1 Seasonal dynamics of wood radial growth

The active period of wood production varied considerably among trees within the study years. It commenced between late March and mid-June and ended between mid-August and mid-December. The length of the growing season was 172.3 ± 43.3 days (mean ± SD, $n = 18$) and ranged from 82 to 240 days; no difference was found between dominant and codominant trees ($t = -1.22$, $p = 0.24$).

Table 1 Semiparametric models of the wood radial growth curves of *C. kanehirae*

Models	Fixed variables		Random intercept (sd)	Variance structure (δ)	Correlation structure (ρ)	AIC
	Model formula	adj. r^2				
A	$s(t)$	0.52	ID (0.53)	varPower (− 1.06)	AR1 (0.76)	178
B	$s_{do}(t) + s_{co}(t)$	0.73	–	varPower (− 1.15)	AR1 (0.82)	172
C	$s_{2012}(t) + s_{2013}(t) + s_{2014}(t)$	0.53	ID (0.56)	varPower (− 1.17)	AR1 (0.56)	196

δ the power of the variance, ρ autocorrelation coefficient, *ID* the identification of growth curves, *AIC* Akaike's information criterion

The radial growth curves of *C. kanehirae* were modelled by semiparametric mixed methods (Table 1). All models (models A, B and C) were substantially improved by applying ID as a random intercept, power variance structure and autocorrelation (order 1). In building model B, the random intercept was removed because it became insignificant once the correlation structure was applied. This implied that the random variable might be attributed partly to the fixed component and partly to the autocorrelation structure. Model A represents a unified growth curve for all the sample trees, with an S-shaped curve. The fixed component explained 52% of the total variance. The smoother was significant ($p < 0.001$) with the estimated degrees of freedom (edf) of 4.50, implying that the growth curves were nonlinear.

Model B represents the growth curves concerning the tree social classes. The fixed component explained 72% of the total variance. Both smoothers [$s_{co}(t)$ and $s_{do}(t)$] of Model B were highly significant with edf of 4.02. The fixed effect (class) was significant ($t = 3.49$, $p < 0.001$), suggesting that the growth curves of different social classes exhibited a significant difference in maximum radial increments (Fig. 2). Here, the growth curve of tree C1 in 2014 was treated as a dominant class for the reason described in the 'Materials and methods' section. If the growth curve of tree C1 in 2014 was regarded as a codominant tree, the model would require ID as a random intercept. The resulting model (AIC = 185) underperformed model B (AIC = 172), and the explained fixed component decreased by 6%. We thus treated the growth curve of C1 in 2014 as a dominant class.

Model C represents the growth curves concerning the three study years. The fixed component of model C explained 53% of the total variance. All smoothers were highly significant ($p < 0.001$) with edfs of 3.12, 3.77 and 3.88 for $s_{2012}(t)$, $s_{2013}(t)$ and $s_{2014}(t)$, respectively. The Year effect was not significant ($p = 0.69$), implying that the interannual difference cannot be confirmed using the 3-year data (Fig. 3).

Model B was selected as the best model for three reasons. First, the fixed variables of model B explained more variance than models A and C. Second, model B had the lowest AIC (172). Third, model B had the most satisfactory residual structure (Figs. S4, S5 and S6). Model B can extract the general growth patterns of *C. kanehirae* (Fig. 2) despite the inconsistency among growth curves. These results emphasised the role of social classes in regulating tree radial growth.

Each radial growth curve was fitted with the parametric Gompertz function (Fig. S7) and nonparametric smoothing splines (Fig. S8). The seasonal growth of *C. kanehirae* appeared irregular and therefore could not be fitted appropriately using the Gompertz function, which reduces the confidence in estimating maximum growth rates (μ), particularly in C3-2012, D1-2012, D1-2013, D2-2013 and D3-2012 (Fig. S7). In C1-2014, the Gompertz function estimated a maximum growth (A) that was not actually reached during the study period (Fig. S7, Table S1). Alternatively, a smoothing spline was aptly fitted to the wiggly growth pattern of *C. kanehirae* (Fig. S8). Biologically incoherent decreasing trends were found in D1-2013, D2-2013 and C2-2013, probably due to the heterogeneous radial growth rate over the sampled area.

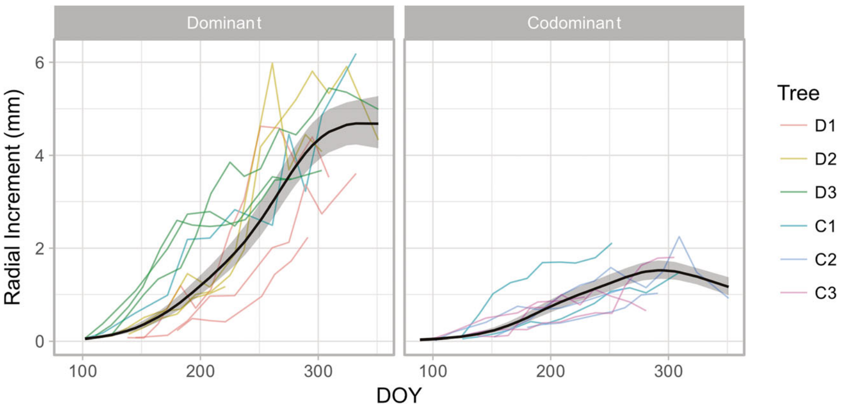

Fig. 2 Estimated radial growth curves (thick line) of *C. kanehirae* by model B considering tree social classes. The grey area indicates the approximate standard errors obtained by the Taylor expansion approach

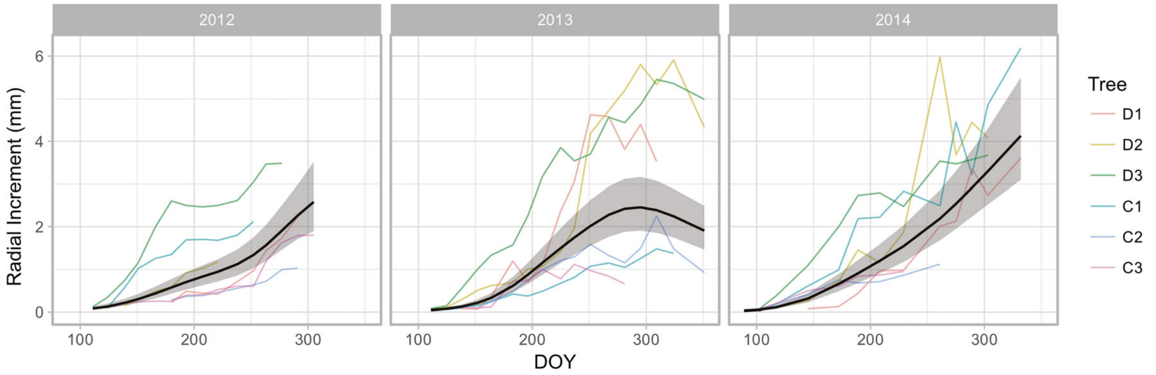

Fig. 3 Estimated radial growth curves (thick line) by model C considering the studied years. The grey area indicates the approximate standard errors obtained by the Taylor expansion approach

However, the *A* and μ estimated by the bootstrap-smoothing spline were not seriously affected and were utilised in the subsequent analysis (Table S2).

The effects of social class and interannual difference on wood growth parameters (*A* and μ) and phenological parameters (the beginning dates, ending dates and the duration of the growing season) were further analysed by linear methods (Tables 2 and 3). For growth parameters, both *A* and μ were significantly higher in dominant trees than in codominant trees ($p < 0.001$, Tables 2 and 3). This result is also supported by model B (Fig. 2). The interannual differences were marginally significant ($0.01 < p < 0.05$). This result must be interpreted with caution because the interactions between Class and Year were significant (Table 3). In addition, model C does not lend support to the significance of the interannual effect (Fig. 3). Between the two tree social classes, no significant difference was detected in phenological parameters. Among the 3 years, the beginning dates cannot be distinguished, while the ending dates and the duration differed significantly. The ending of the growing season of 2013 was significantly later than the other 2 years, and the duration of the growing season in 2013 was the shortest. The interactions between Year and Class were not significant for the beginning date and the duration, and only marginally significant for the ending date (Table 3).

The maximum radial increment (*A*) was controlled by the maximum growth rate (μ) in trees of both classes ($r^2 = 0.87$, $p < 0.01$, Fig. 4). The slopes of dominant and codominant trees were not significantly different from each other (ANCOVA, $p = 0.48$). The relationships between *A* and the growth duration differed between dominant and codominant trees (ANCOVA, $p < 0.01$, Fig. 4). In dominant trees, *A* was positively correlated with the growth duration ($r^2 = 0.91$, $p < 0.01$), but there was no significant correlation in codominant trees ($r^2 = 0.14$, $p = 0.36$). While the correlation between the duration and the beginning date of the growing season was weak ($r^2 = 0.18$, $p = 0.08$), the duration was determined chiefly by the ending dates ($r^2 = 0.74$, $p < 0.01$, Fig. 5).

3.2 Climatic influence on wood radial growth

In our analysis of the correlations between temperature and radial wood growth rate (μ_t), the 3-day mean, 5-day mean and spline smoothed daily mean temperatures led to a similar conclusion. Therefore, only the results of the smooth spline are presented.

The results showed significant interaction between Class and temperature ($p = 0.032$, Table 4), meaning that

Table 2 Mean and standard deviation (SD) of the growth and phenological parameters of the wood radial growth of *C. kanehirae*

	A (mm)		μ (mm/day)		Beginning (DOY)		Ending (DOY)		Duration (day)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Social class										
Dominant	3.86	1.38	0.030	0.011	124.2	21.5	307.0	39.0	182.8	50.6
Codominant	1.37	0.33	0.011	0.004	127.5	24.9	286.8	39.8	159.3	30.3
Year										
2012	1.97	0.95	0.017	0.007	138.3	23.2	272.8	31.1	134.5	35.0
2013	3.18	2.03	0.027	0.018	129.2	16.5	327.8	28.9	198.7	38.2
2014	3.11	1.714	0.021	0.012	109.5	19.5	293.3	40.9	183.8	31.6

A, maximum growth; μ, maximum growth rate. *A* and μ were estimated by the bootstrap-smoothing spline fitting

Table 3 Two-way ANOVA of the effects of the tree social class and the interannual difference on the growth and phenological parameters of the wood radial growth of *C. kanehirae*

	A		μ		Beginning		Ending		Duration	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Class	45.25	0.000	45.0	0.000	0.00	0.972	2.68	0.128	1.97	0.19
Year	2.80	0.030	4.30	0.039	3.22	0.076	6.00	0.016	6.65	0.01
Class × Year	5.59	0.019	6.74	0.011	1.35	0.296	3.90	0.050	2.05	0.17

A, maximum growth; μ, maximum growth rate. *A* and μ were estimated by the bootstrap-smoothing spline fitting

temperature differentially regulated the μ_t values of the dominant and the codominant trees (Figs. 6 and S9). The temperature effect was significant for the dominant trees ($r = 0.32$, $p < 0.001$) but not for the codominant trees ($r = 0.16$, $p = 0.139$); both linear models had heterogeneous residual patterns. For dominant trees, if only the data from the latter part of the growing season (after 260 DOY) were considered, the r increased to 0.64 ($p < 0.001$) with a more satisfactory error structure.

In contrast, no significant correlation could be detected between RH and μ_t among either dominant or codominant trees (Fig. S10, Table 4), while the interaction between Class and RH was significant. There was neither a significant interannual difference nor an interaction between Year and RH (Fig. S11, Table 4)

4 Discussion

4.1 Modelling wood growth curves

In this study, we constructed a unified growth curve for *C. kanehirae* in the humid subtropical area by using an additive mixed model (model A, Table 1). The S-shaped growth curve resembles the curves commonly observed in temperate and boreal forests, despite the large variations among the studied trees. The inclusion of tree social class into our model revealed the importance of this factor in wood radial growth (model B), which will be discussed extensively in section 4.2. Conversely, model C failed to reveal an interannual difference among the 3 years of measurements, probably because the climate during the study period was not extreme enough to substantially affect the tree radial growth or the study period is too short to reveal any climatic trends. Nevertheless, the semiparametric models can potentially be employed to explore temporal trends or to compare the tree radial growth among different regions when the corresponding data are available.

While the wood radial growth was supposed to increase monotonously, model A estimated a negative growth from 300 DOY onward. For our sample trees, an increasing smoothing degree could not completely solve the problem while it also sacrifices characteristic patterns. A recently introduced SCAM was capable of restricting the shape of curves in monotonous increasing (Pya and Wood 2015) and thus produced sensible estimations of growth rates (μ_t) in our analysis of temperature effects. We anticipated that the SCAM could be extended to include random effects, which will be a powerful tool for modelling wood growth curves.

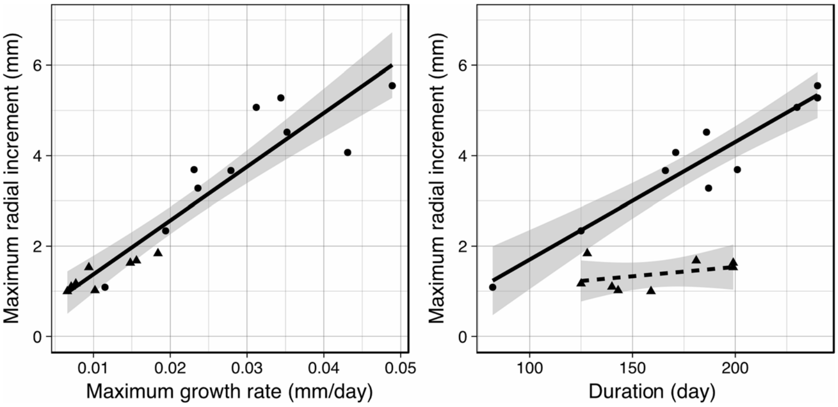

Fig. 4 Relationships between the growth duration, the maximum growth rate (μ) and the maximum radial increment (*A*) of *C. kanehirae.* The *A* of dominant trees is correlated with μ ($r^2 = 0.73$, $p < 0.01$) and the growth duration ($r^2 = 0.91$, $p < 0.01$), while that in codominant trees is only correlated with μ ($r^2 = 0.79$, $p < 0.01$) but not with the duration ($r^2 = 0.14$, $p = 0.36$). Circle: dominant trees ($n = 10$); triangle: codominant trees ($n = 8$)

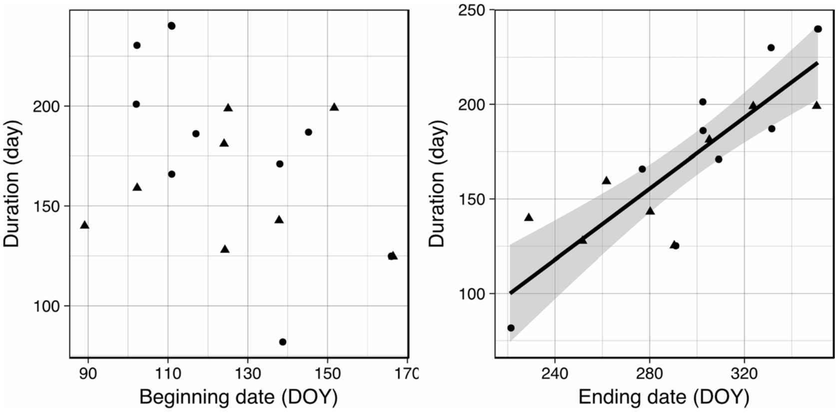

Fig. 5 Relationships between the growth duration and the beginning and ending dates of cambial growth of *C. kanehirae*. For dominant and codominant trees, the growth duration is correlated with the ending date ($r^2 = 0.74$, $p < 0.01$) but not with the beginning date ($r^2 = 0.18$, $p = 0.08$). Circle: dominant trees ($n = 10$); triangle: codominant trees ($n = 8$). Grey envelope: 95% confidence interval. The overlapping data points (D2-2013/D3-2013 and C2-2012/D1-2012) were jittered to avoid overplotting

4.2 Influence of tree social classes on the wood growth curves

Following the result of model B (Fig. 2, Table 1), the difference of tree radial growth between dominant and codominant trees was further explored with two-stage analysis of the parameters. The dominant trees of *C. kanehirae* showed higher maximum growth increments (*A*) and maximum growth rate (μ) than the codominant trees (Fig. 2, Tables 2 and 3), which is similar to the results in silver firs (Rathgeber et al. 2011). The growth duration of *C. kanehirae*, in contrast to the findings in silver firs, was not distinguishable between the two social classes. In dominant trees of *C. kanehirae*, *A* is attributed to both μ and the growth duration, while in codominant trees *A* is attributed mainly to μ (Fig. 4).

In contrast to the stable social organisation in north-eastern France (Rathgeber et al. 2011), the organisation in Taiwan was frequently disturbed by typhoons. Although the typhoon-caused tree fall rate in north Taiwan is only 1.4% of canopy trees, the typhoon-resulted defoliation effectively increased the understorey light level, supporting understorey diversity (Lin et al. 2010). During the strike of Typhon Soulik in 2013, the canopy of tree D2 was partly damaged; a scaffolding was blown away from C1; and the codominant tree C1 was released from the suppression of D2, being exposed to an increased solar radiation. Thus, C1 increased considerably in radial growth in 2014 (Fig. S3) and started to bloom in 2015 (data not shown). This example illustrates the effects of typhoons on understorey light environment and the subsequent tree growth dynamics in the forests of subtropical Taiwan.

4.3 Climatic influences on the wood growth rates

Temperature is a primary factor affecting the secondary growth of trees in boreal, subalpine and temperate forests (Deslauriers and Morin 2005; Michelot et al. 2012; Rossi et al. 2014). The positive relationship between temperature and wood growth rate (μ_t) was also found in dominant *C. kanehirae* trees. However, the relationship was not that apparent in codominant trees (Fig. 6). The results suggest that the relationship is conditioned, probably also depends on other limiting factors such as light availability. In addition, the results also suggest that the radial growth in dominant *C. kanehirae* would be affected more than codominant trees by climate warming if other conditions remain unchanged. Thus, the forest structure could be further differentiated.

Rossi et al. (2016) successfully modelled the effect of annual mean temperature on spring and autumn cambial phenology and the growth duration in cold ecosystems in the Northern Hemisphere. With increasing temperature, the spring cambial phenophases of the conifer species advanced and autumn phenophases delayed linearly, resulting in prolonged duration of xylogenesis. According to the model (Rossi et al. 2016), when the mean temperature was

Table 4 ANCOVA of the climate factors (temperature and relative humidity) on the radial growth rate (μ_t) of *C. kanehirae* considering tree social class (Class) or interannual differences (Year) as a covariate

μ_t – Temperature / Class			μ_t – RH / Class			μ_t – RH / Year		
	F	*p*		*F*	*p*		*F*	*p*
Temperature	0.633	0.427	RH	0.144	0.705	RH	− 0.070	0.792
Class	1.535	0.217	Class	7.530	0.007	Year	− 0.044	0.835
Temp. × Class	4.683	0.032	RH × Class	− 2.206	0.028	RH × Year	0.070	0.792

Class, tree social class; RH, relative humidity

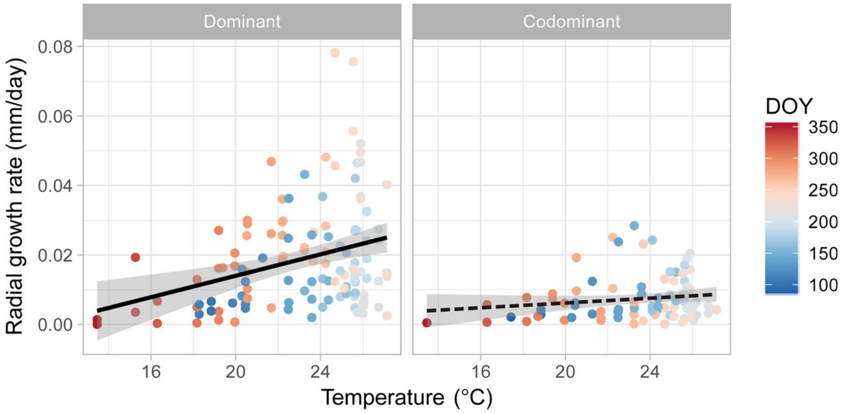

Fig. 6 Relationships between temperature and radial growth rate (μ_t). The radial growth rate of dominant trees was positively correlated to temperature ($r = 0.32$, $p < 0.001$), while codominant trees are less sensitive to temperature ($r = 0.16$, $p = 0.14$). Solid line: regression line; dashed line: regression trend (not significant); grey envelope represents 95% CI. The colours of the circles were mapped to the day of year (DOY). Blue: toward the beginning of the growing season; red: toward the ending of the growing season

tentatively extrapolated to 20 °C for our study site, the expected beginning (of cell wall thickening), ending (of tracheid lignification) and duration of the growing season would be approximately 100 DOY, 305 DOY and 205 days, respectively. However, for *C. kanehirae*, the observed beginning, ending and duration of the growing season were 126 ± 22.4 DOY (mean ± SD), 298 ± 39.6 DOY and 172 ± 43.3 days, respectively. The average beginning date of radial growth was not as early as expected with the model constructed for trees of cold ecosystems. It was even later than the broadleaf species in temperate climates (Michelot et al. 2012). This comparison suggests that factors other than temperature are involved in regulating the commencement of wood production in *C. kanehirae* in the subtropical region.

In response to environmental factors, such as drought or warming, the growth rate and the growth duration compensated each other in regulating wood formation (Balducci et al. 2016): shorter growth period coupled with decreasing growth rate, and vice versa. According to Cuny and Rathgeber (2016), the temperature signal was registered in a tree ring structure in the late growing season when the compensation was absent. In *C. kanehirae*, the positive correlation between the wood growth rate of dominant trees and ambient temperature was greatly improved when only the late growing season data were considered. Though the monitoring of compensation effects in *C. kanehirae* is currently lacking, our results showed a similar trend as the findings of Cuny and Rathgeber (2016).

The tree radial growth of conifers is coordinated by temperature and water availability (Fritts 1966). As indicators of water availability, precipitation and RH are related to the secondary growth of several conifers and broadleaf trees (Deslauriers et al. 2003b) In addition, precipitation is the principal controlling factor of tree ring formation in the tropical dry forest with prominent dry seasons (Reich 1995; Worbes et al. 2003; Rozendaal and Zuidema 2011; Pumijumnong and Buajan 2013). However, in our study area, no apparent relationship was detected between the wood growth rate and rainfall or RH within the study years, suggesting that precipitation was not a limiting factor for *C. kanehirae* (Figs. S10 and S11). This is probably because the precipitation is overall abundant so that drought rarely posed a threat to tree growth. In contrast, the temperature is the only fluctuating climate factor during the year and therefore has a stronger impact on radial growth than RH or precipitation.

5 Conclusion

In this study, we successfully constructed a radial wood growth curve for *Cinnamomum kanehirae* (model A) and investigated the social class differences (model B) and annual variations (model C) of radial increment with semiparametric models. The results confirmed the important role of social class in the growth performance of *C. kanehirae* but failed to reveal the interannual differences. The analysis of individual curves showed that the maximum radial increment correlated significantly with the maximum growth rate in trees of both social classes. However, the sensitivity of maximum radial increment to the growth duration was different between dominant and codominant trees. Also, the variation of growth duration was attributed to the ending rather than the beginning of the growing season for trees of both social classes. Our 3-year study revealed the effects of the climate factors on the wood radial growth of *C. kanehirae* trees of different social classes. The results also suggest that trees of different social classes might respond differently to climate warming.

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Compliance with ethical standards

The Executive Committee of the Executive Yuan, Council of Agriculture, Forestry Bureau granted permissions on Republic of China October 5, 106 to Professor Ling-Long Kuo-Huang, for using endangered species of plant (*Cinnamomum kanehirae*) (No.: 106/010104/02).

Conflicts of interest The authors declare that they have no conflict of interest.

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