



Regulation of tree crown phenology and fruit set of *Cinnamomum kanehirae* Hayata, an endangered evergreen tree in Taiwan

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ABSTRACT: Phenological pattern of forest trees reveals climatic controls on phenophases and fruit development, hence providing key information for managing endangered species. We aimed to investigate tree crown phenology and fruit development of even-aged, dominant and codominant trees and to integrate the results with our study of wood radial growth of *Cinnamomum kanehirae* (Tsai *et al.*, 2018). We conducted a 3-year ground-based observation of leaf, flower and fruit phenology. The fruit set and development were compared among 3 comparison groups: leafless inflorescence, leafy inflorescence and defoliated leafy inflorescence. The reproductive growth of *C. kanehirae* was present only in dominant trees. Dominant trees saw leaf flushes twice a year, while codominant trees once or twice. The overlapped spans of reproductive and vegetative growth implied resource competitions between these two phenophases and might cause fruitlet self-thinning in March and premature abortion in Autumn. Fruit development was correlated to the number of nearby ordinary leaves instead of inflorescence leaves. Reduced sunshine hours in autumn, 2011 may lead to the delayed flowering and truncated wood growing season of dominant trees in 2012. The different reproductive ability between tree social classes and the response of floral phenology to sunshine hours suggest important roles of light availability in fruit nursery.

KEY WORDS: *Cinnamomum kanehirae*, fruit development, leafy inflorescence, resource allocation, tree social class.

INTRODUCTION

Phenological pattern of a tree species result from interactions among genetic control, resources availability and climatic factors. Trees tract climatic cues in arranging crown phenology and wood radial growth (Yáñez-Espinosa *et al.*, 2006). By doing so, they grow and reproduce in optimal climatic conditions, increasing their abundance in the community. Thus, phenology of leaf and cambium were commonly synchronized within the warm season in temperature-limited forests (Čufar *et al.*, 2008; Rossi *et al.*, 2009; Michelot *et al.*, 2012; Delpierre *et al.*, 2015; Urban *et al.*, 2015), while within the rainy season in water-limited forests (Rao and Rajput, 2001; Worbes, 2002; Lisi *et al.*, 2008; Patel *et al.*, 2014). However, the development of many plant organs and tissues in a short time course would demand considerable amount of energy and nutrients. Therefore, resource availability and trees' ability to assimilate and allocate the resources coordinate the timing of tree crown phenophases and wood radial growth (Ratheke and Lacey, 1985; Rao and Rajput, 2001; Yáñez-Espinosa *et al.*, 2006; Čufar *et al.*, 2008; Patel *et al.*, 2014; Pérez-de-Lis *et al.*, 2017; Puchałka *et al.*, 2017).

Understanding the timing and drivers of phenological events are essential for the conservation of endangered species. For example, phenology calendars for seed collection helped in situ or ex situ conservation of rare plant species (Ali and Trivedi, 2011). *Cinnamomum kanehirae* has been listed as an

endangered species in the IUCN red list because the total timber volume in Taiwan reduced 90.2% from 1927 to 1990 due to excessive logging (Chung *et al.*, 2012). The natural regeneration of this species relied heavily on stump re-sprouting rather than seed reproduction (Huang *et al.*, 1996). The Taiwan Forest Research Institute collected the clones of *C. kanehirae* and successfully regenerate the population using root cutting (Kao and Huang, 1997a; b; Yu and Horng, 1997). Also, the Forestry Bureau of Taiwan set up reserve-seed tree forests (natural tree populations or plantations reserved for seed production) in 1975 and built a seed orchard in 1980 with clones collected from natural tree populations to maintain genetic diversity. Unfortunately, the seed production in these stands cannot meet the reforestation demand (Chung *et al.*, 2012). The low production rate was related to the low heterozygosity caused by inbreeding (Lin *et al.*, 1997); however, cross-pollination did not improve seed production (Chung *et al.* unpublished data). The causes of the low seed production remain unknown. In the efforts toward conserving *C. kanehirae*, phenological studies may provide evidence to identify the factors limiting fruit production, such as resource competition among vegetative and reproductive growth, climatic disturbance, and mismatch of phenophases (Morellato *et al.*, 2016).

Phenological surveys of *C. kanehirae* were reported (Lee and Jiang, 2011); however, the proximate drivers of the phenological events of this species have not been identified. Our previous study revealed sigmoidal



growth curves of *C. kanehirae* in relation to air temperature, and confirmed more temperature sensitivity of dominant trees than codominant ones (Tsai *et al.*, 2018). Trees of different social classes receive different amounts of solar radiation, leading to differences in metabolism, development and growth. Accordingly, among trees of different social classes, tree crown phenology might also differ in response to internal and external factors. In addition, tentative extrapolation using a model of cold ecosystems (Rossi *et al.*, 2016) predicts a much earlier date of wood radial growth (100 DOY) than the mean date (126 DOY) observed for *C. kanehirae* (Tsai *et al.*, 2018).

In the present study, we compared the crown phenology of the dominant and codominant trees including flower, fruit, and leaf phenophases. *C. kanehirae* produced inflorescence bearing both flowers and inflorescence leaves (IL). To improve our knowledge of fruit development of *C. kanehirae*, we compared fruit set and fruit growth on reproductive shoots with and without IL and conducted a manipulated experiment to quantitatively assess the impact of IL on fruit set and development. The number of ordinary leaves (OL) on 1-year-old branchlet bearing inflorescence was also analyzed. Compiling the results of this study and our previous study (Tsai *et al.*, 2018), we discussed the relationship among crown phenophases and the coordination between crown phenology and wood radial growth in terms of resource allocation theory.

MATERIALS AND METHODS

Site information, sampling trees and climatic data

The study site, Xinxian nursery (24°50'27"N, 121°32'02"E, 338 m a.s.l.) in northern Taiwan, is near the northernmost distribution limit of *C. kanehirae*. The condition of the plantation was detailed in Yu *et al.* (2012). At the beginning of the study (2012), the average tree height (TH) of 64 trees in the plantation was 12.1 ± 3.0 m (mean ± sd), while the diameter at breast height (DBH) was 23.9 ± 8.5 cm. Following our previous study, the same dominant trees (D1, D2, D3, TH: 16.25 ± 4.51 m, DBH: 28.6 ± 2.14 cm) and codominant trees (C1, C2, C3, TH: 16.05 ± 6.43 m, DBH: 21.7 ± 3.27 cm) were surveyed. The dominant trees receive direct sunlight from the top of the canopy as well as from the side, and the codominant trees receive the sunlight only from the top of the canopy. Notably, the C1 was grouped into the dominant class (Tsai *et al.*, 2018) after the visit of Typhoon Soulik in 2013.

Climatic data including air temperature (°C), precipitation (mm) and relative humidity (RH, %), recorded by the Tonghou auto-weather station (24°50'54"N, 121°35'52.7"E, 360 m a.s.l. about 8.5 km from the study sites) of the Central Weather Bureau

(CWB), were acquired through the Data Bank for Atmospheric and Hydrologic Research. The hourly data were processed into monthly mean temperature and monthly sums of precipitation (see Fig. S1 and Tsai *et al.* 2018). From 2012 to 2014, monthly mean temperature was approximately 12.5°C in winter and 26.5°C in summer. The annual precipitation was overall abundant, especially with heavy rains brought by typhoons in summer. The overall RH in each month was >70%, except in March 2012 (minimum RH of 62%). The temperature data from 7th to 30th December 2103 were not available due to technical problems; this deficiency did not seriously affect our interpretation of phenological data.

Crown phenology

To gain access to the tree crown of *C. kanehirae*, a scaffolding of 15.3 m height was built in the plantation (Fig. 1A). From 2012 to 2014, the major phenophases including leaf flush and leaf coloring, flower bloom and senescence, and fruit set were observed at a 2-week interval (occasionally 3 or 4 weeks) and recorded by digital cameras (Nikon D5100 and D7100 with Nikon Nikkor 70-300 mm VR). *C. kanehirae* produces perfect flowers arranging in thyrse with cymes attaching to an indeterminate main axis. The phenophases including inflorescence bud burst (Fig. 1B, C), bloom (Fig. 1D), flower senescence and fruit set (ovary diameter > 1 mm, Fig. 1E) were recorded when the event could be observed on more than 50% of tree crowns. Since *C. kanehirae* is evergreen, the leaf phenophases were recognized by the changes of leaf color: young leaves appeared pink to light green and relatively transparent (Fig. 1D-J), mature leaves dark green and leathery, and senescent leaves orange-red to brown-red and stark (Fig. 1K). Relative coverage of young mature and senescent leaves of tree crown was also evaluated semi-quantitatively by 2 observers who discussed and recorded the percentage leaf coverage with respect to leaf colors. The results can reflect the annual pattern of leaf coverage on a tree basis and is corroborated by the quantitative data of leaf demography.

Leaf demography

In 2012, a total of 267 scale buds of the dominant tree D2 around the scaffolding were randomly selected and tagged before budburst; these buds subsequently developed into inflorescences or vegetative shoots. After leaves fully expanded (Fig. 1J, F), the number of leaves on each shoot was recorded biweekly until the leaves fell. Leaf-like hypsophylls (Fig. 1L) shed within 2–4 weeks are excluded. The leaves on a shoot often changed color concomitantly (Fig. 1K) and thus was considered as an observational unit in estimating leaf lifespan. Accordingly, the dates when half-number of the leaves expanded or shed were recorded. Leaf loss due to extrinsic causes (*e.g.*,

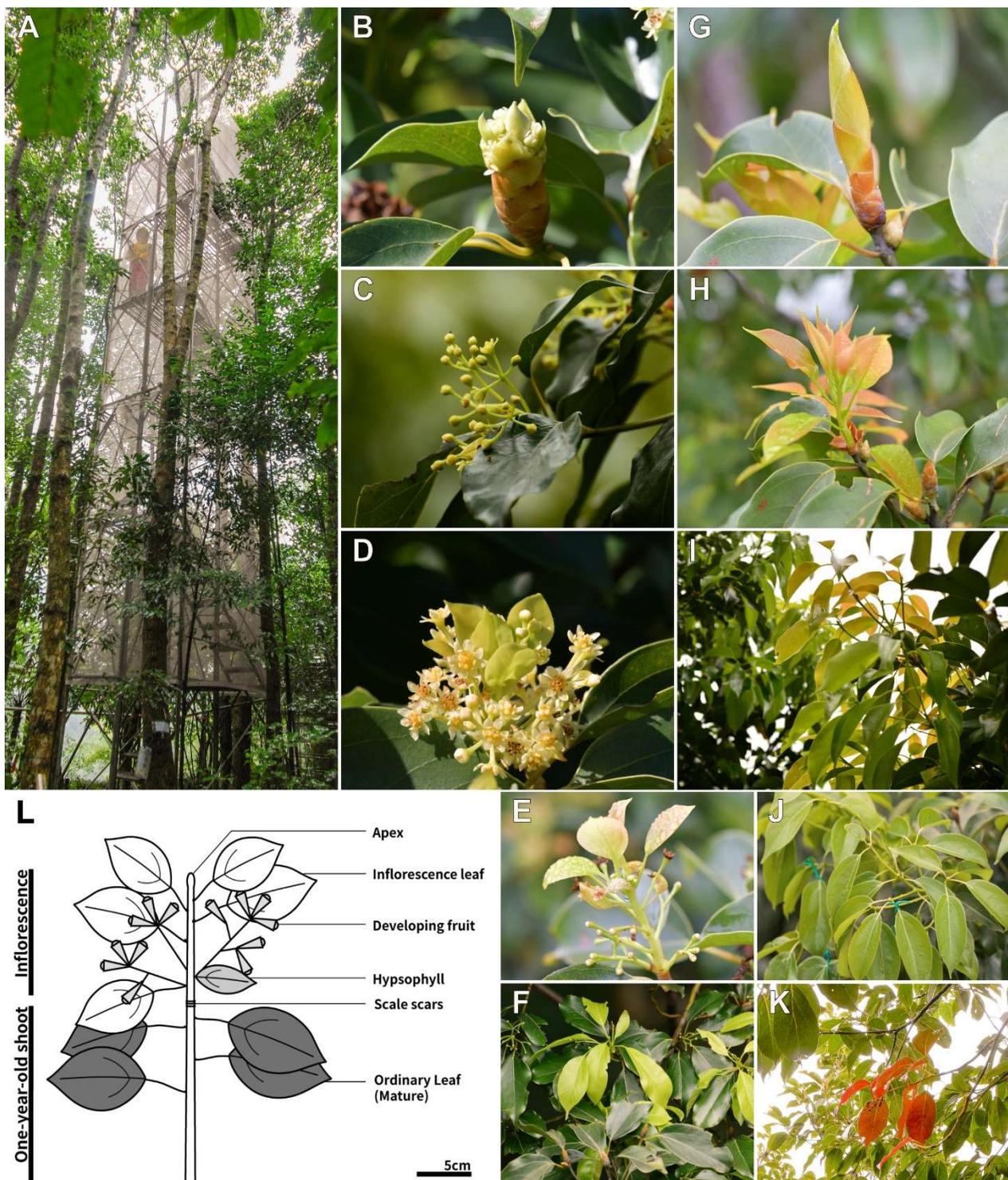


Fig. 1. Phenological observation of tree crowns of *Cinnamomum kanehirae*. (A) The scaffolding to assess the tree crowns. (B) Budburst of a reproductive shoot. (C) Flower buds yet to open in a leafless inflorescence. (D) Full bloom in a leafy inflorescence. (E) Ovary swelling (> 1 mm in diameter). (F) Inflorescence leaves reaching full size. (G) Vegetative bud exposing its green tip. (H) Pink, young leaves on a vegetative shoot. (I) Light green, young leaves in contrast to dark green, leathery mature leaves. (J) Ordinary leaves reaching full size. (K) Red, leathery senescent leaves (L) Illustration of a part of a fruit-bearing branchlet.



typhoon) was censored. The leaf lifespan was estimated as a restricted mean survival time that measures the average survival from day 0 to a specific day, which corresponds to the area under the Kaplan-Meier (K-M) survival curves. The K-M survival curves of leaves were constructed with *survival* package (Therneau and Grambsch, 2000) in R (R Core Team, 2016). The difference between the survival curves of the 2 leaf types was tested by Mantel-Haenszel (log-rank) and Peto and Peto modification of the Gehan-Wilcoxon test. The latter method is more sensitive as the hazard rate is low at the later stage (Kalbfleisch and Prentice, 2002).

Fruit development in relation to inflorescence leaves

To observe the fruit development and to evaluate the effects of IL on fruit growth, a survey of inflorescence (reproductive shoots) and a manipulated experiment were conducted in 2017 on the dominant tree D3. Buds were marked randomly on 4th March when inflorescences just emerged. We counted fruit numbers on 3 comparison groups of reproductive shoots: Group I, leafless inflorescence, inflorescence bearing only flowers; Group II, leafy inflorescence, inflorescence bearing both flowers and leaves; and Group III, leafy inflorescence with leaves being removed on 4th or 19th March when leaves just emerged (Fig. S2). A total of 115 inflorescences were surveyed from 4th March to 27th July. For each of 8 surveys, 5 or 6 inflorescences of each comparison group were collected. The fruits yet to develop during the first survey was thus excluded from the analysis. We recorded fruit number on each inflorescence and the maximum diameter of each fruit after its diameter reached 1 mm (Fig. 1E) and counted the mature OL (Fig. 1L) on the branchlet carrying the inflorescence. Self-thinning of immature fruits was observed from 19th March to 19th April. Thus, the rate of fruit set, i.e., the proportion of flowers setting fruits, was calculated as the fruit number in each inflorescence measured on 19th March divided by that on 19th April (Fig. S3).

For analyzing the influence of IL on the fruit count in the inflorescence, the zero-inflated models were considered because the natural thinning during the early fruit development (Fig. S3) resulted in a considerable amount of zero values in data. The zero-inflated negative binomial (ZINB) model was chosen over the zero-inflated Poisson model (ZIP) because the data exhibit over-dispersion (the variance significantly larger than the mean). In addition, the ZINB outperformed the ZIP (Akaike information criterion: -1122 vs. -1289, $p < 0.001$ for likelihood ratio test). Based on ZINB, the analysis was considered in 2 periods, i.e., before and after natural thinning. We further evaluated the main effects (the difference between comparison groups and the number of OL), and the interactions. Insignificant effects were removed based on AIC and likelihood ratio

tests ($p > 0.05$). The reduced model was used to analyze the fruit numbers among the comparison groups. The rate of fruit set was analyzed by analysis of variance. In the pre-test, the number of ordinary leaves showed no significant effects on the rate of fruit set (likelihood ratio test, $p = 0.067$) and was thus excluded from the analysis. The means of comparison groups were compared pairwise by Tukey's honestly significant difference.

When analyzing the fruit size development, we tried 4 different approaches: polynomial regression, a non-linear model with Gompertz function (NLS-Gompertz), a non-linear model with logistic function (NLS-logistic), and generalized additive model (GAM, Fig. S4). The GAM (effective degrees of freedom = 5.98, AIC = 1269) outperforms the other methods (df = 5, AIC = 1383 for polynomial regression; df = 4, AIC = 1753 for NLS-Gompertz; df = 4, AIC = 1606 for NLS-logistic) in fitting fruit growth curves of *C. kanehirae* (likelihood ratio test, $p < 0.001$). Other than the smooth term of DOY, the fixed effect included the effects of inflorescence leaves (the 3 comparison groups) and the number of ordinary leaves. Furthermore, in the experiments we randomly sampled the branchlets (infructescence) and measured the diameter of each attached fruits. The fruits of the same branchlet likely shared similar growth condition and might thus be intercorrelated. This hierarchical structure (several fruits on a branchlet) can be handled easily by assigning random intercept (branchlets) in the mixed effect model. Therefore, the GAM was expanded to include random effects of branchlets and thus became a GAMM. The model was further improved to consider heterogeneous variance among each censoring date and autocorrelation structure order 1 (AR1).

RESULTS

Tree crown phenology

Almost all observed fresh shoots of *C. kanehirae* were developed from preformed buds, whereas neo-formed shoots were occasionally observed, especially when the terminal buds were accidentally damaged, e.g., Lammas shoots caused by the gust of typhoon. *C. kanehirae* produces 3 types of buds: inflorescence buds that produce leafless inflorescence (Fig. 1C), mixed buds that produce leafy inflorescence (Fig. 1D–E) and leaf buds (Fig. 1G–J). During the 3-year (2012–2014) survey, reproductive shoots were only observed in the 3 dominant trees, but not in the 3 codominant trees.

The inflorescence buds and mixed buds burst between 31st January and 11th February in 2012 and between 9th and 22nd January in 2013 and 2014 (Fig. 2). One to 2 weeks after the budburst, the flowers opened and lasted for about 2 weeks. The overall blooming period lasted for about 3 weeks.

In mixed buds, the inflorescence leaves flushed as the flowers opened (Fig. 1D). The fruitlets were visible

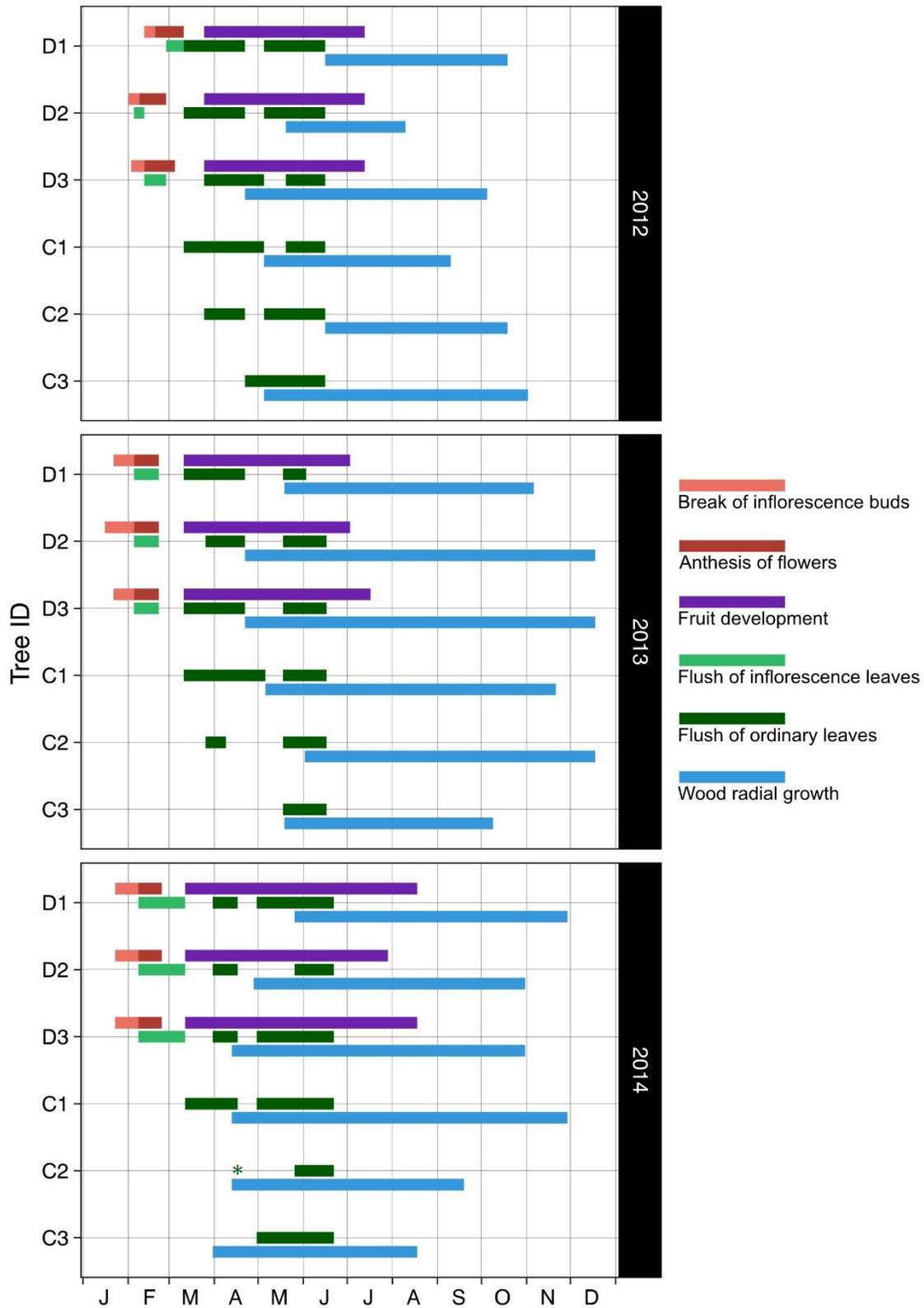


Fig. 2. Timing and duration of reproductive events, leaf flushing and radial growth of *Cinnamomum kanehirae*. See main text for description. The radial growth data were taken from Tsai *et al.* (2018). Note that in 2014, the spring flush in C2 was only observed on 16th April and thus was expressed as *.



between late February and early March (Fig. 1E). The diameter of fruitlets increased to about 15 mm until June or August; however, no ripened fruits were observed during the survey.

C. kanehirae has intermittent shoot growth pattern, *i.e.*, young shoots are produced in a short period of a year. In addition to the flush of IL, the dominant trees generally had 2 major leaf flushes (Figs. 2 and 3). The first one occurred between mid-March and early May (spring flush), and the second one between early May and late June (summer flush). No significant trend was observed in the relative amount of new leaves produced by the 2 flushes. The codominant trees (C1, C2, C3) flushed once or twice a year. In C1, the spring flush occurred between mid-March and early May, and the summer flush between early May and late June. The relative leaf coverage of the 2 flushes were comparable. C2 also flushed twice. The duration of spring flush varied among years. The relative coverage of spring flush was remarkably less than that of the summer flush. C3 exhibited only summer flush between late April and mid-June. Lammas shoots were observed in September for C2 in 2013 and D2, C1, C3 in 2014. Leaf senescence (Figs. 1K and 3) was observed most frequently from February to June and from October to November, when new leaves expanded rapidly or just achieved full size. The leaf coverage did not fluctuate dramatically so their crown appeared evergreen.

Leaf demography

The inflorescence leaves (IL) formed in February, reached full size in March and gradually abscised from September to October. Its lifespan was 184.4 days (SE = 13.2, $n = 96$). The old ordinary leaves (OL) shed until new OL fully expanded. Its lifespan was more than 1 year ($393.4 \pm \text{SE } 11.3$ days, $n = 55$). The survival curves were significantly different between IL and OL (Fig. S5, $\chi^2 = 45.8$, $p < 0.001$ for the Mantel-Haenszel test; $\chi^2 = 49.9$, $p < 0.001$ for the modified Gehan-Wilcoxon test), suggesting that for dominant trees, the 2 major leaf falls observed in Feb-June and Oct-Nov (Fig. 3) may correspond to OL and IL, respectively.

Fruit development in relation to inflorescence and ordinary leaves

On 19th March 2017, the numbers of fruits and OL on branchlets were not significantly different among the 3 comparison groups (for fruits, $F = 1.26$, $p = 0.29$; for OL, $F = 0.79$, $p = 0.46$, Table S1). Similarly, the number of IL did not differ between Group II and III ($t = -0.78$, $p = 0.44$). The fruit number (ca. 12 per inflorescence) decreased significantly after self-thinning (< 1 per inflorescence, Table S2).

The ZINB model showed that the fruit number differed among group ($p = 0.038$, Table S3) and differed before and after thinning ($p < 0.001$). However, both

among-group and temporal differences were compounded by the interactions (Comparison group \times Fruit set stage and Number of OL \times Fruit set stage, Table S3). The fruit number of each inflorescence was positively related to the number of OL for Group III before thinning and for all groups after thinning (Fig. 4). After thinning, the slope of fruit-OL relationship was larger in leafless (Group I) than in leafy inflorescences (Group II, Fig. 4). The ZINB model (Fig. 5) predicted that before thinning Group I and II had comparable fruit numbers, and that Group III had slightly larger number than the other groups, while after thinning the Group II had slightly fewer fruits than the other groups. The rate of fruit set was significantly different ($p = 0.039$) among comparison groups. The value of Group I is marginally greater than those the other groups, while Group III (defoliation) did not show difference with Group II (Tukey's HSD test with 90% confident level, Fig. S6). Fitting growth curves of fruits revealed similar a pattern of fruit development among groups and also showed that fruits of Group I are slightly but significantly larger than those of the other groups (differences between Groups I and II: 0.17 mm, $p = 0.002$; I and III: 0.14 mm, $p = 0.011$). Removing IL from leafy inflorescence did not impact the fruit size (Groups II and III, Fig. 6), neither did the number of ordinary leaves ($p = 0.76$).

DISCUSSION

Differences in the phenophases of tree crown were found between dominant and codominant trees, and among the 3-year survey of *C. kanehirae*. The observed pattern may be resulted from climatic variations and resources limitation. No mature fruits were collected in our survey because of self-thinning of fruitlets and abortion of premature fruits. The possible causes are discussed as follows.

Difference between dominant and codominant trees

Plant size can influence the acquisition of resources, such as incident radiation and soil nutrients (Berntson and Wayne, 2000), and hence affect growth rate and reproductive and vegetative phenology. Our previous study of *C. kanehirae* revealed differential wood radial growth between dominant and codominant trees (Tsai *et al.*, 2018). In this study, we found differentiation in reproductive growth and in number and relative coverage of leaf flushes between the 2 social classes. In the even-aged plantation, reproductive shoots were found only in dominant trees. Plants start to bloom only after they reached reproductive maturity or a specific size level (Rathcke and Lacey, 1985). Dominant trees of *C. kanehirae* possibly intercepted more solar radiation and thus developed faster to maturity than codominant trees. In addition, light can stimulate stem conductance and increase potassium ion concentration in xylem sap

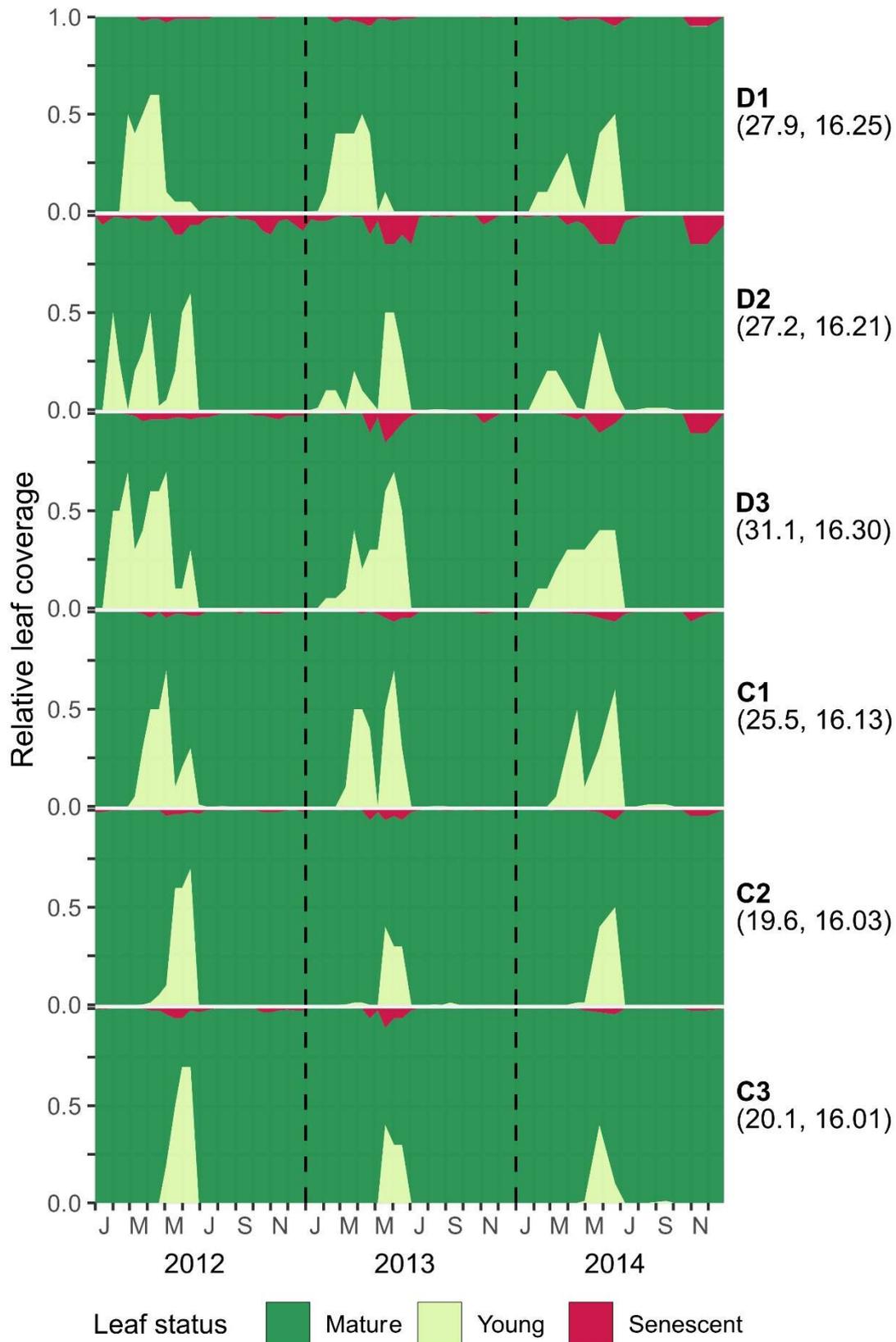


Fig.3. Annual variation of relative leaf coverage in tree crowns of *Cinnamomum kanehirae*. The diameter at breast height (cm) and tree height (m) of dominant (D1, D2, D3) and codominant (C1, C2, C3) trees are listed in parentheses.

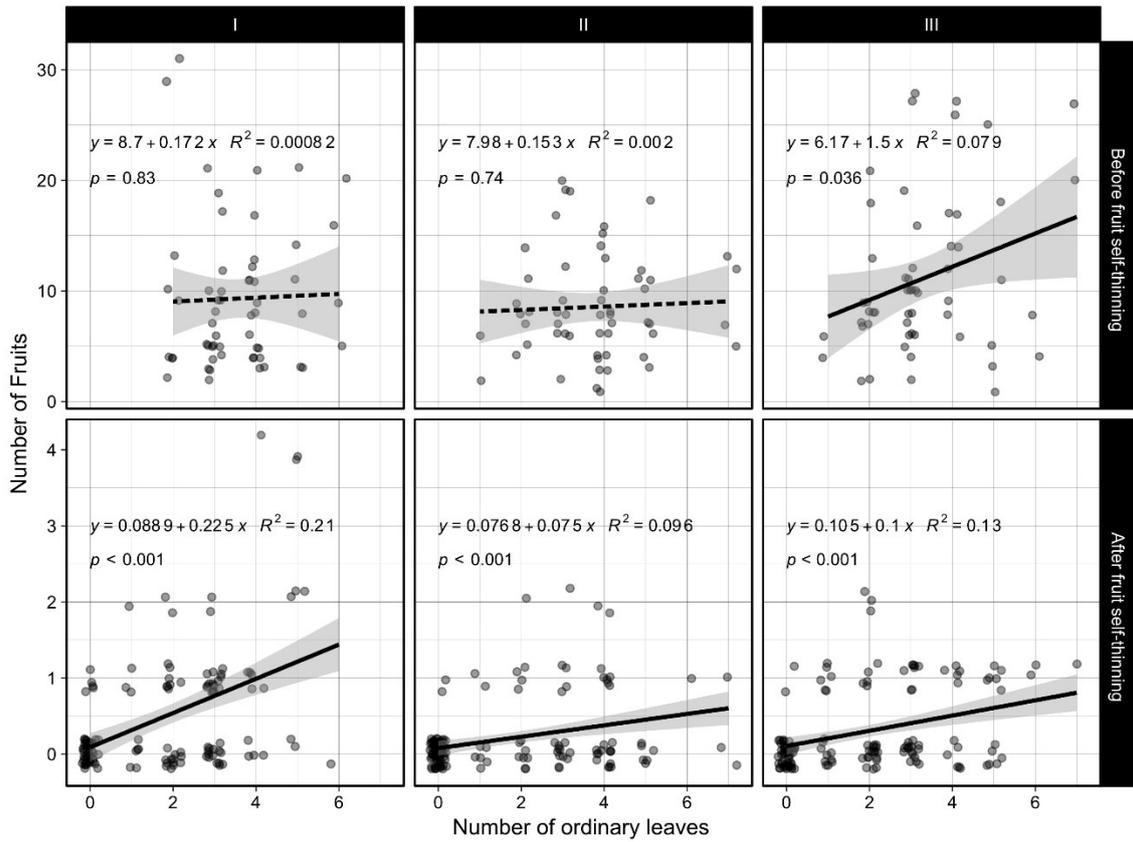


Fig. 4. Relationship between numbers of ordinary leaves and fruits on fruit-bearing branchlets. (I) Leafless inflorescence, (II) leafy inflorescence, (III) leafy inflorescence with IL removed. Points were jittered to avoid over-plotting.

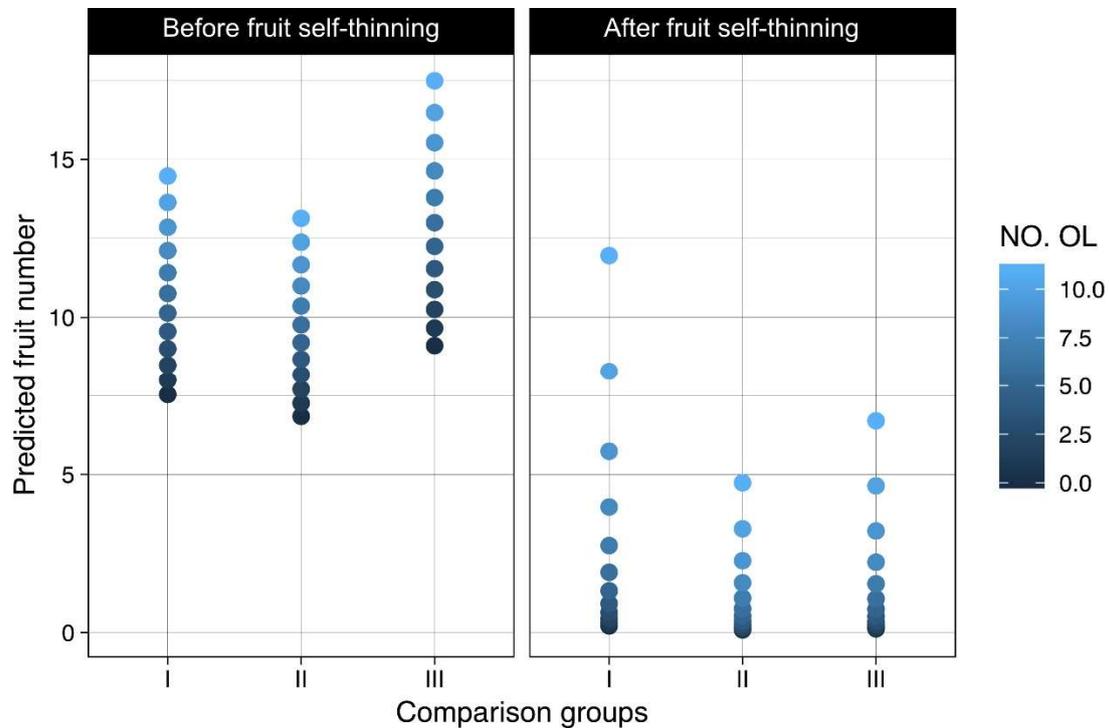


Fig.5. Prediction of fruit number on fruit-bearing branchlets of *Cinnamomum kanehirae* with the zero-inflated negative binomial model (ZINB). (I) Leafless inflorescence, (II) leafy inflorescence, (III) leafy inflorescence with IL removed. The results suggested that IL provides no advantage in fruit set. In contrast, removing IL slightly increased fruit number of group III. OL: ordinary leaves.

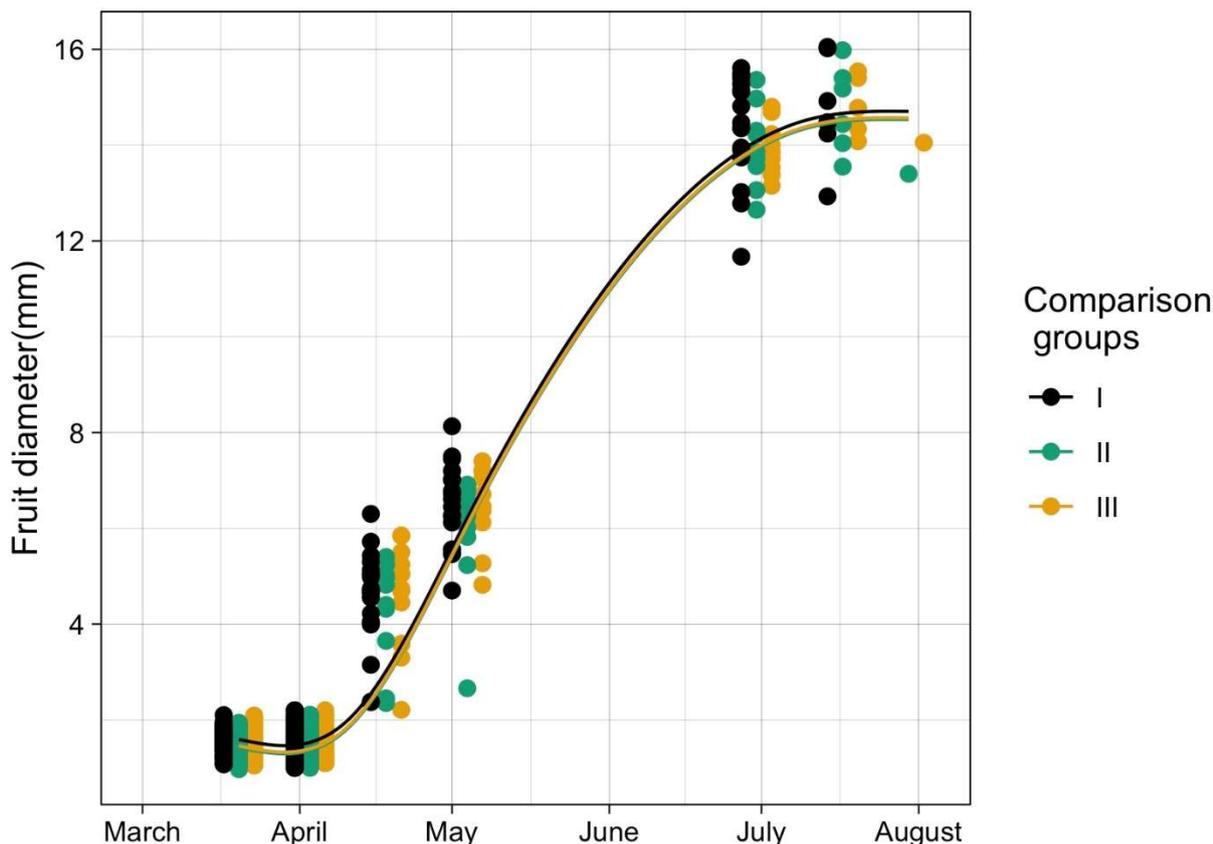


Fig.6. Fruit growth curves of *Cinnamomum kanehirae*. (I) Leafless inflorescence, (II) leafy inflorescence, (III) leafy inflorescence with IL removed. IL has little impact on fruit diameter. On the contrary, the fruits of leafless inflorescence (I) are slightly but significantly larger than those of the other groups (II and III). Points of different groups were juxtaposed to avoid over-plotting.

(Meinzer *et al.*, 1997; Sellin *et al.*, 2010) which is important for reproduction (Erel *et al.*, 2016). Accordingly, more light acquisition by dominant *C. kanehirae* may lead to higher nutrients unloaded onto crown shoots, consequently triggering reproductive process. The number and relative coverage of leaf flushes in codominant *C. kanehirae* is likely limited by tree size and light availability which was shown to regulate the flush number in *Eurya japonica* (Nitta and Ohsawa, 1997).

Influences of external factors on phenology of C. kanehirae

Weather conditions, such as light availability and precipitation, of both previous and current year can influence shoot growth and wood radial growth (Welander and Ottosson, 1998; Löf and Welander, 2000; Kagawa *et al.*, 2006; Kuster *et al.*, 2014). Poor photosynthetic yield may hinder bud formation, reduce carbon reserves in stem tissues and consequently arrest the whole plant growth in the following growing season (Kagawa *et al.*, 2006; Kuster *et al.*, 2014). In dominant *C. kanehirae*, inflorescence budburst was delayed (Fig.

2) and wood growing season was shortened in 2012 than in 2013 and 2014 (Tsai *et al.*, 2018). These phenomenon might be related to the exceptionally high rainfall and less sunshine hours in 2011 (Table S4, data recorded by Taipei climate station, CWB, 25°02'15" N 121°30'54" E, 5 m a.s.l.). The reduced light availability could impede photosynthesis of *C. kanehirae*, subsequently arrest bud formation, truncate the starch storage, and thus delay bud break and cambial reactivation, leading to the short growing season and narrow growth ring in 2012. This putative carry-over effect demands further evidence from long-term phenological observation, manipulated experiments and tree-ring analysis. The results will help evaluate the performance of *C. kanehirae* under the changing environment.

Internal regulation of phenophases and the fruit sets

Overlapping of flowering, fruiting and vegetative growth would consume considerable amount of energy and nutrients. On the other hand, decoupling of the phenophases may reduce resource competition among plant organs. However, the durations of fruit development, leaf flush and wood radial growth



overlapped in dominant trees of *C. kanehirae* (Fig 2). These overlapping implies resource competition among organs. The internal competition in dominant trees may result in fruit abortion, delayed radial growth and lower radial growth rate at early growing season (Tsai *et al.*, 2018).

The ecological roles of OL and IL with different lifespans (Fig. S5) in *C. kanehirae* are still unclear. However, the lifespan of IL is just long enough to cover the span of fruit development, which motivated the investigation to the role of IL in fruit set and fruit development. The impacts of IL on fruit differ among plant species. In *Citrus*, IL improved fruit set and fruit development by increasing sink strength of the inflorescence (Moss *et al.*, 1972; Erner and Bravdo, 1983; Saidha *et al.*, 1985; Erner and Shomer, 1996). Conversely, in apples, vegetative growth competes with reproductive growth for photoassimilates when light is limited (Bepete and Lakso, 1998). The fruit-bearing branchlets were assumed carbon autonomous (Sprugel *et al.*, 1991; Hasegawa *et al.*, 2003), some tree species draw photoassimilates from nearby branchlets when resource became limited (Hoch, 2005). In *C. kanehirae*, the absence of IL had no negative impact on both fruit set and fruit development (Figs. 4, 5, 6 and S6). Furthermore, based on that the rate of fruit set is higher and the fruit size is slightly larger in leafless inflorescence and that the fruit number is the lowest in leafy inflorescence, the young IL may compete with developing fruits for resources. The results tend to support IL as an evolutionary relict rather than a specialized organ for supporting fruit growth. Practically, the inflorescences of *C. kanehirae* were bagged with IL partially removed to avoid seed predatory. The effect of defoliation on fruit development was not evaluated before. Our study suggests that cutting IL during fruit bagging do not have severe negative effects on fruit harvests in the nursery. In contrast to IL, the number of OL on the same branchlet was positively correlated to fruit number after thinning, especially in the leafless inflorescence (Fig. 4). This suggests that fruit sets and fruit growth were limited by photosynthate from OL of *C. kanehirae*.

Internal resource competition may impact number, size and quality of fruits (Ferree *et al.*, 2001). The large fruits (15 mm in diameter) and enclosing seeds of *C. kanehirae* takes 4 to 6 months to develop, which overlapped entirely with spring and summer leaf flushes and partially with stem growth. Imai and Ogawa (2009) found that in *C. camphora*, fruit-based CO₂ exchange rate peaked twice during fruit development, corresponding to dry mass increments of fruit pulp and embryo. The fruit development of *C. kanehirae* may share similar features with the 2-stage process of *C. camphora*. At the early stage, the fruitlets probably competed with unfolding spring leaves for photoassimilates, resulting in fruit self-thinning in

March. On the other hand, at the late stage, developing fruits competed with summer flush and wood radial growth, which may impede embryo development and thus leads to premature abortion in autumn. This explained the well-developed fruit pulp but an ill-developed embryo observed in aborted fruits of *C. kanehirae* (Chung *et al.*, 2012).

Crown phenology is an important factor influencing the activity of vascular cambium (Callado *et al.*, 2001) because leaves provide photosynthates energizing all metabolic processes. At the early growing season, old OL likely produced limited carbohydrate which was preferably transported to the developing flowers, leaves and shoots (higher sink priority), and later to the vascular cambium (lower sink priority) (Dickson and Isebrands, 1991). The allocation pattern would result in the temporal order of budburst and wood radial growth and also the lower wood growth rate at the early growing season (Tsai *et al.*, 2018).

The resource competition induced by phenophase overlapping would become prominent when resources are limited, *e.g.*, photosynthesis is significantly reduced in closed forests due to mutual shading of leaves. The planting density of *C. kanehirae* is higher in the Xinxian nursery (2 m × 2 m, Yu and Horng 1997) than the other plantations, such as the seed orchard in the Sanmin nursery in eastern Taiwan (6 m × 6 m) where the seed production increased year by year except for the years impacted by typhoons (Lin, 1997) and the one in the Chuyunsan nursery (middle Taiwan) where healthy seeds were steadily produced since 2013 (circa 4 m × 5 m, personal communication). Whether increasing the planting distance could release internal competitions and thus increase the fruit productivity of *C. kanehirae* in northern Taiwan is a practical issue demanding more investigation.

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