Growth synchrony between leaves and stems during twig development differs among plant functional types of subtropical rainforest woody species

Fengqun Meng¹, Guangfu Zhang², Xincheng Li³, Karl J. Niklas⁴ and Shucun Sun¹,⁵

¹The State Key Laboratory of Pharmaceutical Biotechnology, College of Life Sciences, Nanjing University, Nanjing 210093, China; ²Jiangsu Key Laboratory of Biodiversity and Biotechnology, School of Life Sciences, Nanjing Normal University, Nanjing 210023, China; ³College of Chemistry and Life Sciences, Zhejiang Normal University, Jinhua 321004, China; ⁴Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14850, USA; ⁵Corresponding author (shcs@nju.edu.cn)

Received June 3, 2014; accepted February 11, 2015; published online March 26, 2015; handling Editor Annikki Mäkelä

During the development of woody twigs, the growth in leaf may or may not be proportional to the growth in stem. The presence or absence of a synchronicity between these two phenologies may reflect differences in life history adaptive strategies concerning carbon gain. We hypothesized that sun-adapted species are more likely to be less synchronous between growths in total leaf area (TLA) and stem length compared with shade-adapted species, with a bias in growth in stem length, and that shade-adapted species are more likely to be more synchronous between increases in individual leaf area (ILA) (leaf size) and leaf number (LN) during twig development compared with sun-adapted species, giving priority to growth of leaf size. We tested these two hypotheses by recording the phenologies of leaf emergence, leaf expansion and stem elongation during twig development for 19 evergreen woody species (including five shade-adapted understory species, six sun-adapted understory species and eight sun-adapted canopy species) in a subtropical evergreen broad-leaved forest in eastern China. We constructed indices to characterize the synchronicity between TLA and stem length (\(\alpha_{LS}\)) and between leaf size and leaf number (\(\alpha_{SN}\)) and we derived the \(\alpha\) values from logistic functions taking the general form of \(A = A_{\text{max}}/\left[1 + \exp(\beta - \alpha B)\right]\) (where \(A\) is the TLA or average ILA, \(B\) is the corresponding stem length or LN at a specific time, and \(A_{\text{max}}\) is the maximum TLA or the maximum ILA of a twig; the higher the numerical value of \(\alpha\), the less synchronous the corresponding phenologies). Consistent with our hypotheses, sun-adapted species were higher both in \(\alpha_{LS}\) and \(\alpha_{SN}\), showing less synchronous patterns in the growths of TLA vs stem length and leaf size vs LN during twig development. Moreover, \(\alpha_{LS}\) and \(\alpha_{SN}\) were significantly positively correlated with relative growth rates of LN and leaf size across species, as indicated by both analyses of ordinary regression and phylogenetic generalized least squares. The across-species synchronies during twig development show that the temporal dynamics of the leaf size–twig size spectrum is of adaptive significance in plants. We suggest that temporal dynamics of plant functional traits should be extensively studied to characterize plant life history.

Keywords: leaf size–twig size spectrum, leaf–stem growth synchrony, subtropical evergreen forest, sun- vs shade-adapted species.

Introduction

Plants do not necessarily develop and grow different organs synchronously nor do they always allocate their resources evenly to different structures and functions. Instead, they often optimize their growth synchronies and resource allocation patterns among organs depending on their ontogenetic stage and environmental circumstances (Bloom et al. 1985, Bazzaz et al. 1987, McConnaughay and Coleman 1999, Poorter et al. 2012, Lohier et al. 2014). For example, at the whole-plant level,
numerous studies have observed ontogenetic shifts in growth priorities among organs, as reflected by size or ontogenetic stage-dependent changes in biomass ratios of shoot vs root, leaf vs stem or vegetative vs reproductive organs in response to limiting resources (e.g., light, nutrient and water) or changes in environmental conditions (Bazzaz et al. 1987, McConnaughay and Coleman 1999, Poorter et al. 2012, Lohier et al. 2014). These shifts are often interpreted to reflect adaptive strategies for resource capture and utilization (Poorter et al. 2012, Lohier et al. 2014) that are important to understanding life history evolution and functional plant ecology (Bloom et al. 1985, Bazzaz et al. 1987).

However, despite their potential importance, these kinds of ontogenetic shifts have seldom been examined at a within-plant organ-system level. For example, twigs (e.g., current-year shoots) are one of the most dynamic and important compartments at the whole-plant level because they are usually more physiologically and morphologically plastic in response to changes in water, nutrient and carbohydrate conditions (Westoby et al. 2002) and also perhaps owing to the near absence of secondary tissues. During twig development, leaf growth (including emergence and expansion) and stem elongation occur simultaneously. However, it is not necessarily the case that leaf growth and stem elongation occur in synchrony. Internode elongation can occur before, after or in synchrony with leaf growth, each of which can affect shifts in allocation patterns during twig development. The extent to which the two phenomenologies are in synchrony or not likely affects leaf display in time and space (Nikinmaa et al. 2003, Ishii and Asano 2010) which in turn can affect light-harvesting, water balance and hence carbon gain (Kikuzawa 1995, Preston and Ackerly 2003, Westoby and Wright 2003, Ishii and Asano 2010). For example, plants flushing leaves faster than stem elongation might obtain higher carbon gain per biomass or nutrient investment during the early stage of twig development, whereas the reverse might be true for plants that extend twig internodes faster than the development of leaves.

There are two extreme types of coordination between leaf growth and stem elongation during twig development of woody plants supposing that twigs are equal in length and total leaf area (TLA) (Figure 1). One is where leaves grow (in both size and number) after completing stem elongation. This results in a steeper growth trajectory between increases in stem length and TLA, which results in less synchronicity between the two phenomenologies (Figure 1, curve a). The other extreme is where leaves grow as stems elongate. This results in a shallower growth trajectory between increases in stem length and TLA, which results in a more synchronous growth pattern (Figure 1, curve b). Woody dicots are less likely to develop fully mature leaves before internode elongation, because they generally lack a well-developed intercalary meristem (Zhou 2004). Furthermore, for a given TLA borne by a twig there are also two extreme patterns of synchrony between the expansion of individual leaf area (ILA) (leaf size) and leaf number (LN). Plants may produce leaves as a single flush immediately after bud-break and then begin leaf expansion, which results in a less synchronous pattern between growth in leaf size and LN, or they may produce new leaves as older leaves reach full maturity, which results in a more synchronous pattern between growth in leaf size and LN.

These two extremes present four theoretical possibilities: (i) less synchronous growth in TLA and stem length and less synchronous growth in leaf size and LN (i.e., LN and stem length grow faster than leaf size; Figure 2a), (ii) more synchronous growth in TLA and stem length and less synchronous growth in leaf size and number (i.e., LN grows faster than leaf size and stem length; Figure 2b), (iii) more synchronous growth in TLA and stem length and more synchronous growth in leaf size and number (i.e., LN, leaf size and stem length grow at approximately the same rate; Figure 2c), and (iv) less synchronous growth in TLA and stem length and more synchronous growth in leaf size and LN (i.e., stem length increases faster than LN and leaf size). We would argue that the fourth possibility is unlikely simply because LN must reach its maximum after stem length reaches its maximum.

Consequently, we speculate that there are three biologically reasonable combinations, which are likely to be associated with woody species-groups adapted to different light environments, which is one of the most important external factors influencing shoot growth patterns (Steingraeber et al. 1979, Canham 1988, Suzuki 2003). We speculate therefore that the synchrony between leaf and stem development may reflect an adaptive response in species that are adapted to shaded or sunny conditions,
Although plants may modify various key traits (e.g., canopy, twig and leaf levels) to acclimate to ambient light conditions (Niinemets 2010). For example, during the early stage of twig development in sun-adapted species, juvenile (tender) leaves are directly exposed to high-light intensities in the upper crown and are likely to suffer from photo-inhibition when light intensities exceed light saturation points (Krause et al. 1995, Dodd et al. 1998, Kitao et al. 2000, Bertamini and Nedunchezhian 2003). Thus, very young leaves may have a higher susceptibility to photo-inhibition and experience more severe high-light stress than mature ones (Krause et al. 1995, Bertamini and Nedunchezhian 2003). Moreover, tender expanding leaves may suffer from water deficits during twig development even in wet regions (Reich and Borchert 1984), because high irradiance promotes water loss by increasing transpiration and decreasing leaf water potential (Abram 1986, Valladares et al. 2002) and because water-conducting tissues have not fully developed during leaf emergence and expansion (Lechowicz 1984, Polgar and Primack 2011). Under conditions of high-light and water deficit stress, leaves growing slower than stems (i.e., increased biomass allocation to stems) during the early twig development might be favored provided that older stems provide sufficient water and nutrients (Brouat et al. 1998). Accordingly, we hypothesized that less synchronous growth in TLA and stem length would evolve and thus characterize sun-adapted woody species. Noting that stem growth in length is often positively correlated with LN growth, we further hypothesized that less synchronous growth in ILA and LN might characterize sun-adapted woody species.

Light interception is equally important to plant growth and survival in shade-adapted species (Canham et al. 1990, Valladares 2003). However, plants growing in shaded conditions receive only a small fraction (<3% sometimes) of the light that canopy leaves receive (Chazdon 1988, Rijkers et al. 2000). Therefore, shade-adapted species (and leaves developing deeper within the canopies of sun-adapted species) generally suffer from low-light stress, although they are less likely to be stressed by water deficits. One solution is for leaves to develop faster than stems (provided that leaves growing faster than stems improve light interception efficiency per investment) and for stems to develop horizontally to avoid leaf self-shading. We therefore hypothesized that shade-adapted species might be characterized by more synchronous patterns in their growth of TLA and stem length. Because synchronous growth in leaf size and number can maximize TLA, we further hypothesized that more synchronous patterns in the growth of leaf size and number would characterize shade-adapted species.

To test these hypotheses, we recorded LN, leaf width and length and stem length during twig development, and calculated the relative growth rates for LN and ILA for 19 woody species (five shade-adapted understory species, six sun-adapted understory species and eight sun-adapted canopy species) in a subtropical evergreen broad-leaved forest in eastern China. We constructed indices to estimate the synchronicity between TLA and stem length growth, and the synchronicity between leaf size and number growth during twig development to determine if shade- and sun-adapted species differed.

**Materials and methods**

**Study site**

This study was conducted in an evergreen, broad-leaved subtropical forest in Tiantong National Forest Park of Zhejiang, eastern China (N29°48′, E121°47′), which has been protected for >30 years since it was established in 1981. The mean annual rainfall is ~1600 mm and most precipitation occurs in the summer (from June to August). The mean annual temperature is ~16 °C and is hottest in July at 27.9 °C and coldest in January at 4.1 °C. The soil is forest brown soil (Ding and Song 1999). The tree canopy layer is 12–18 m high and is dominated by Castanopsis carlesii (Hemsli.) Hayata, Castanopsis fargesii Franch, Cyclobalanopsis sessilifolia (Bl.) Schott and Schima superba Gardn. Et Champ. The shrub layer is 2–4 m high and is dominated by Eurya spp., Camellia cuspidata (Kochs) Bean and Symplocos sumuntia Buch.-Ham. ex D. Don.

Light intensities differ significantly between tree canopy and shrub layer. Measurements taken with illuminometers (LX-1330B illuminometers, Tondaj, Shenzhen, China) show that the
canopy layer received an average of 1634 μmol m⁻² s⁻¹ and that the shrub layer received an average of 27 μmol m⁻² s⁻¹ at 10:00–10:30 AM on sunny days during twig development from April 2011 to July 2011 (see Table S1 available as Supplementary Data at Tree Physiology Online). Measurements taken with temperature–humidity automatic recorders once per hour (IL-18, Qingyi EL-TE Co., Ltd, Handan, China) during twig development showed that the average humidity and temperature in the canopy tree layer (at 12 m) were 80.8% and 20.5 °C and that the average humidity and temperature in the understory layer (at 1.5 m) were 87.9% and 19.8 °C, respectively (see Table S2 available as Supplementary Data at Tree Physiology Online).

**Species sampling**

Nineteen evergreen broad-leaved woody species (including five shade-adapted understory species, six sun-adapted understory species and eight sun-adapted canopy species), belonging to 13 genera and 11 families, were selected for study (see Table S3 available as Supplementary Data at Tree Physiology Online). Plant functional types were classified based on species habitats and morphological traits according to Song and Wang (1995); the classification has been demonstrated to be consistent with physiological functional traits (Meng et al. 2013, 2014). Three to five individuals per species were selected for phenological observations on twig development. For canopy species, individuals were sampled from the sides of a firebreak (4 m wide), where branches were fully exposed to the sun and available for measurements. For sun-adapted understory species, individuals were sampled from forest gaps or roadsides; representative branches were fully exposed to sun in the middle of each crown. For shade-adapted understory species, individuals that typically live under the crowns of canopy species were selected and representative branches were sampled from the least shaded part of the understory crown.

Among the species studied, 14 develop twigs in the spring only and complete their twig development in the summer. The remaining five species produce new shoots twice per year: once in the spring (typically beginning in late March and ending in late June), and then again in the autumn (typically beginning in late August ending in early November). A previous study has shown that the second episode of shoot production occurs only in the part of the upper plant crown that is exposed to direct sunlight and that this phenomenology does not contribute much to total leaf growth in any of these five species (Xia et al. 2013). Consequently, we sampled only the twigs produced during the first flush of shoot development for each of these species.

**Phenological observations**

Five branches were sampled before bud-break for each selected individual for each species in early March 2011. One twig (a first-year shoot) per branch was tagged for successive measurements. We recorded LN and measured leaf length and width (for each leaf) and stem length for each tagged twig from bud-break to full leaf expansion of the youngest leaf. Leaves that were 0.5 cm in length were counted to measure LN. Measurements were taken every 2–3 days during the early stages of twig growth, and subsequently once a week until all leaves were fully expanded.

**Data analysis**

**ILA determination** Leaf width (W) and length (L) were measured in the field during twig development to calculate leaf area (A) non-destructively using a regression analysis that could relate LW to A. Specifically, for each species, 200 intact leaves at different developmental stages (from early to full leaf expansion) were sampled from individuals that had not been selected for phenological observations. We measured L, W and A using ImageJ software (National Institutes of Health, Bethesda, MD, USA) and subsequently fitted a regression curve to calculate species-specific leaf area (A) using the formula \( A = aLW \), where \( a \) is species-specific regression constant \( (r^2 > 0.97, P < 0.001) \) for all species; Table S3 available as Supplementary Data at Tree Physiology Online.

**Relative growth rate of ILA (\( \alpha_l \)) and number (\( \alpha_n \))** The data for ILA and LN at any time \( T \) were transformed into percentages of total LN and the maximum ILA at the end of the observation period before determining relative growth rates of LN and ILA (\( \alpha_l \) and \( \alpha_n \), respectively). Percentages were used because the ILA and LN differed significantly among species and among twigs. The transformations used the formula \( L_T = I_T/I_{\text{max}} \) for each twig, where \( L_T \) is the percentage LN or ILA of a twig at time \( T \), \( I_T \) is the corresponding actual LN or average ILA of the twig at time \( T \), and \( I_{\text{max}} \) is the LN or maximum ILA observed after twig development.

We determined the relative growth rates of LN and ILA using the data from all of the tagged twigs from each plant collected during the time interval \( T \). This was accomplished by fitting the data using logistic functions taking the general logistic form \( A = A_{\text{max}}/[1 + \exp(\beta - \alpha a)] \):

\[
LN = \frac{LN_{\text{max}}}{[1 + \exp(\beta - \alpha l T)]} \quad (1)
\]

\[
ILA = \frac{ILA_{\text{max}}}{[1 + \exp(\beta - \alpha n T)]} \quad (2)
\]

where LN is the observed leaf number and ILA is the individual leaf area at time \( T \) (measured as the day of 2011), LN_{\text{max}} is the LN and ILA_{\text{max}} is the ILA at the end of twig development, \( \beta \) is a species-specific constant reflecting the time when the leaves began to grow, and \( \alpha_l \) and \( \alpha_n \) are reflective of the relative growth rate \( (1/\text{day}; \text{intrinsic rate of increase}) \) ofLN and leaf area, respectively. Previous studies have shown that the general logistic function and Eqs (1) and (2) are successful when attempting to fit plant growth trajectories (Kaufmann 1981,
Subsequent regression analyses indicated that these equations fit the data sufficiently well (e.g., Figure 3a and b; see more in Table S4 available as Supplementary Data at Tree Physiology Online).

**Synchronicity between the TLA and stem length growth** ($\alpha_{LS}$) and **synchronicity between ILA and LN growth** ($\alpha_{SN}$) Data on LN, ILA, TLA per twig and twig stem length (SL) were transformed once again into percentages by calculating the percent ratio of actual values at time $T$ with respect to the corresponding values observed at the end of twig development. Individual leaf area was averaged at the twig level before the calculation. Once again, the transformed data were fitted using logistic functions, taking the same general form $A = A_{max}/[1 + \exp(\beta - \alpha B)]$, to determine the growth synchronicity between TLA and stem length ($\alpha_{LS}$) and the growth synchronicity between leaf size and number ($\alpha_{SN}$):

$$\text{TLA} = \frac{T\text{LA}_{max}}{[1 + \exp(\alpha_{S} - \alpha_{S}\text{SL})]}$$

where the $\alpha_{LS}$ and $\alpha_{SN}$ are commensurate with the relative growth rate (i.e., intrinsic rate of increase) of TLA relative to stem length (1/stem length) and of ILA relative to LN (1/leaf number), respectively, and $\beta_{LS}$ and $\beta_{SN}$ are specific constants reflecting the initial value of TLA or ILA. In theory, $\alpha$ and $\beta$ collectively determine the shape of the logistic functions. Statistically significant and positive correlations were observed between $\alpha_{SN}$ and $\beta_{SN}$ and between $\alpha_{LS}$ and $\beta_{LS}$ across all species (both $r^2 > 0.99$, $P < 0.001$; Figure S1 and Table S5 available as Supplementary Data at Tree Physiology Online). Moreover, the greater the $\alpha$ values or $\beta$ values, the less synchrony between TLA and stem length growth or between ILA and LN growth. Therefore, only the numerical values of $\alpha_{SN}$ or $\alpha_{LS}$ could be used to determine growth synchronicities. We used $\alpha_{LS}$ as an index to determine the growth synchronicity between TLA and stem length and $\alpha_{SN}$ to determine the growth synchronicity between leaf size and number. Regression analyses showed that these formulae provided statistically robust fits to the data with...
To determine the differences in the variables of interest among the different functional species groups, we averaged the values of each variable within twigs, within individuals and finally within species, and analyzed the log$_{10}$ transformed data using ANOVA (and post hoc Tukey’s tests when necessary). We also determined the correlation between synchrony indices and the relative growth rates for LN and leaf area ($\alpha_i$ and $\alpha_A$, respectively) to test if the synchronicities are significantly associated with $\alpha_i$ and $\alpha_A$ across species. The relationships between these indices and other traits were determined using linear regression analyses. All the analyses were conducted in JMP 5.0.1 software (SAS Institute 2003).

Phylogenetic regression A correlation among functional traits may result from a phylogenetic bias in a data set (Felsenstein 1985). Therefore, we used phylogenetic generalized least squares (PGLS) protocols to estimate the strength of the phylogenetic signal and phylogenetic correlation ($\lambda$) in our data set (Freckleton et al. 2002) by using the degree to which trait evolution deviated from Brownian motion, i.e., $\lambda = 0.0$ indicates that the relationships among observed traits are phylogeny independent, whereas $\lambda = 1.0$ indicates that the correlations between traits are phylogeny dependent (see White et al. 2009). A phylogeny tree was constructed with program Phylomatic, version 3.0 (http://phylodiversity.net/phylomatic/; Webb et al. 2008); all branches were set equal to one. The PGLS analysis was performed in R version 2.14 (R Development Core Team 2011) using the package ape (Paradis et al. 2004).

Results

Relative growth rates of LN ($\alpha_i$) and ILA ($\alpha_A$)
The three species groups differed significantly in $\alpha_i$ (Figure 4a) and $\alpha_A$ (Figure 4b). The $\alpha_i$ of sun-adapted canopy species was more than twice that of shade-adapted understory species and three times that of shade-adapted understory species. The $\alpha_A$ of sun-adapted canopy species was almost twice that of shade-adapted understory species, whereas the $\alpha_A$ of sun-adapted understory species was intermediate and thus not statistically different from the other two species groups.

Growth synchronicities between the TLA and stem length ($\alpha_{LS}$) and between ILA and number ($\alpha_{SN}$)
The three species groups differed significantly in $\alpha_{LS}$ (Figure 4c) and $\alpha_{SN}$ (Figure 4d). Sun-adapted canopy species and sun-adapted understory species had a larger $\alpha_{LS}$ compared with shade-adapted understory species. The $\alpha_{LS}$ of sun-adapted canopy and understory species was almost three times and twice that of shade-adapted understory species, respectively. The $\alpha_{SN}$ of sun-adapted canopy species was twice that of shade-adapted understory species, whereas the $\alpha_{SN}$ of the sun-adapted understory species was intermediate such that it was not significantly different from the other species groups.

Relationships of synchronicity indices and the relative growth rates for LN and ILA
The $\alpha_S$ was positively correlated with $\alpha_i$ (Table 1; Figure 5a) and $\alpha_A$ (Table 1; Figure 5b), i.e., species with a higher $\alpha_S$ tended to have higher relative growth rates in both leaf emergence and expansion. The $\alpha_{SN}$ was also significantly positively correlated with both $\alpha_i$ (Table 1; Figure 5c) and $\alpha_A$ (Table 1; Figure 5d), indicating that species with a higher $\alpha_{SN}$ tended to have higher leaf emergence and expansion rates. In addition, these relationships were also statistically significant when analyzed using PGLS (Table 1), i.e., no phylogenetic biases were detected.

The foregoing relationships are illuminated further by comparing the two extreme species. Specifically, Lithocarpus glaber had an extremely asynchronous coordination between leaf–stem growth, but was characterized by a high relative growth rate of ILA (see Figure 5e and f, open circles), as indicated by large values of both $\alpha_S$ and $\alpha_A$. In contrast, Eurya rubiginosa var. attenuata had a low relative growth rate of ILA and had an extremely high synchrony between leaf–stem growth (see Figure 5e and f, filled circles), as indicated by small values of both $\alpha_S$ and $\alpha_A$.

Discussion

Previous studies have explored the relationship between leaves and stems within twigs both intraspecifically and interspecifically (e.g., Ackery and Donoghue 1998, Westoby and Wright 2003, Sun et al. 2006, Kleiman and Aarssen 2007, Yang et al. 2008). However, most of these studies have focused on the functional traits of mature leaves and mature twigs at the species level. To the best of our knowledge, our study is the first to explicitly examine the temporal dynamics between maturing leaves and maturing stems over the course of twig development. As predicted, sun-adapted species were found to be less synchronous in the growth of TLA and stem length and to have less synchronous growth in leaf size and number. The data also show that species with less synchronicity between the TLA and twig length growth and between leaf size and number growth characteristically have higher leaf expansion and emergence rates, as indicated by the significantly positive correlation between their synchronicity indices and leaf emergence and expansion rates.

We believe that these differences in synchronicity reflect different strategies for maximizing carbon gain among different species adapted to different light and soil moisture regimes. It is certainly true that physical conditions often differ significantly along the vertical profiles of subtropical and temperate canopies and understory species, and shade-adapted understory species. The three species groups differed significantly in the relative growth rates for LN and leaf area ($\alpha_i$ and $\alpha_A$, respectively). The $\alpha_i$ of sun-adapted canopy species was more than twice that of shade-adapted understory species, whereas the $\alpha_A$ of sun-adapted understory species was intermediate such that it was not significantly different from the other species groups.
tropical closed forests. In our study area, for example, the annual light intensity in the canopy layer (fully exposed to the sun) is 1400 μmol m⁻² s⁻¹, which is almost 30 times greater than that in the shaded understory layer (44 μmol m⁻² s⁻¹; Table S1 available as Supplementary Data at Tree Physiology Online). Likewise, the average temperature in the canopy layer (at 12 m) is between 0.4 and 1.2 °C higher and the average humidity is 5–15% lower than that in the understory layer (at 1.5 m) during the time twigs develop and mature (from April 2011 to July 2011; Table S2 available as Supplementary Data at Tree Physiology Online). In our study area, soil moisture also decreases from March to May during twig development, i.e., soil
moisture is \(~30\%\) in March and \(~20\%\) in May (Shen 2011). These contrasting physical conditions, together with the potential for a spring drought in our study, would favor different synchronicities between leaf and stem growths to maximize carbon gain.

For example, the expanding leaves of sun-adapted species are often exposed to full light and high temperatures that result in water deficit stress especially during twig development because young leaves have a high susceptibility to photo-inhibition compared with mature leaves (Krause et al. 1995, Dodd et al. 1998, Kitao et al. 2000, Bertamini and Nedunchezhian 2003) and because species living in wet regions are generally vulnerable to water deficits during leaf emergence and expansion (Reich and Borchert 1984, Abram 1986, Valladares et al. 2002, Shen 2011). Therefore, growing stems faster than leaves and growing LN faster than leaf size is a reasonable strategy for sun-adapted species to avoid or reduce physiological stresses in part because leaf self-shading (when many leaves are...
The greater synchronicity in the growth of leaves and stems allows shade-adapted species to produce larger photosynthetic leaf areas (both TLA and ILA) per carbon investment during early twig development and to potentially have a faster photosynthetic payback. On the other hand, more synchronous twig development may reduce photosynthetic payback (particularly for the latter emerged leaves) because of slow leaf emergence and expansion rates, thereby decreasing the total annual carbon gain per twig. This drawback might be compensated by the longer leaf lifespans of shade-adapted species compared with sun-adapted species (Reich et al. 1995, 2004, Hikosaka 2005). For example, in our study area, Wang et al. (2000) have shown that the average leaf lifespan of shade-adapted species is 1.84 years, which is significantly longer than the leaf lifespans of sun-adapted understory and sun-adapted canopy species (1.62 and 1.43 years, respectively). We have observed that most of the shade-adapted species in our study area produce leaves in late March and early April (e.g., *E. rubiginosa* var. *attenuata*, a typical shade-adapted species in the understory layer), which is significantly earlier than when sun-adapted species produce their leaves. The earlier emergence of the leaves of shade-adapted species is arguably adaptive, since it allows these species to capture light before canopy closure. For example, in the subtropical forest studied here, understory plants experience significant reductions in light intensity during the growing season. Our measurements show that the monthly average light intensity is 72 μmol m⁻² s⁻¹ from February 2011 to April 2011, much greater than 21 μmol m⁻² s⁻¹, which occurs during May to July 2011 (see Table S1 available as Supplementary Data at Tree Physiology Online). In addition, the more synchronous growth in the leaves and stems of shade-adapted species provides a quick carbon payback, while reducing the loss of leaves during early spring frosts.

In summary, our study has shown for the first time a temporal dynamic coordination between the growth of leaves and stems during twig development. We demonstrate that the synchronicity between leaf and stem growth differs among functional species groups, which can be attributed to differences in environmental conditions, i.e., the temporal dynamic pattern during twig development likely reflects species ecological strategies for light interception and carbon gain. These and other temporal leaf–stem dynamics need to be examined in light of global leaf dimension-abilities (see Westoby et al. 2002) to further our understanding of plant life history strategies.

**Supplementary data**

Supplementary data for this article are available at Tree Physiology Online.

**Authors’ contributions**

S.S. and F.M. designed the experiments; F.M. and X.L. performed the experiments and analyzed the data; F.M., S.S., K.J.N. and G.Z. wrote the manuscript.

**Acknowledgments**

We thank Zhuoyao Dong, Jianqiang Tang and Yangjie Xia for field assistance and the staff of Tiantong National Forest Park for permitting this study to be conducted.

**Conflict of interest**

None declared.

**Funding**

This study was funded by National Science Foundation of China (31170382 and 31325004).

**References**


Moles and Westoby 2000). Our data also show that shade-adapted species tend to be more synchronous in the growth of TLA and stem length, which can maximize light interception efficiency during early twig development. They are also more synchronous in the growth of leaf size and number and present a ‘successive’ leaf emergence pattern, which reduces self-shading (Kikuzawa et al. 1996).

The greater synchronicity in the growth of leaves and stems simultaneously expanding) can reduce light intensity and local temperatures (Kikuzawa et al. 1996).

However, sun-adapted species with less synchronicity during twig development might incur a cost in terms of carbon gain. Less synchronous growth not only decreases total photosynthetic leaf area per investment but also decreases the rate of total carbon gain because twigs sustain many young, small emerging leaves during early twig development (Kursar and Coley 1992, Choiński et al. 2003, Miyazawa et al. 2003), although rapid leaf emergence and expansion rates in less synchronous twigs might compensate by shortening the time tender leaves are exposed to herbivores (Moles and Westoby 2000).

In contrast to sun-adapted species, shade-adapted species receive a comparatively small fraction of light transmitted through the canopy layer. Indeed, the light intensities they experience are often close to their light compensation points and much lower than their light saturation points (Meng et al. 2013, 2014). In response to the constraints on photosynthesis (Canham et al. 1990, Valladares 2003), shade-adapted species typically manifest a suite of traits that maximize light interception at the twig level, e.g., nearly horizontal twig and leaf inclination angles, lower LMA and lower light saturation and light compensation points (Valladares and Niinemets 2008). Our data also show that shade-adapted species tend to be more synchronous in the growth of TLA and stem length, which can maximize light interception efficiency during early twig development. They are also more synchronous in the growth of leaf size and number and present a ‘successive’ leaf emergence pattern, which reduces self-shading (Kikuzawa et al. 1996).

In summary, our study has shown for the first time a temporal dynamic coordination between the growth of leaves and stems during twig development. We demonstrate that the synchronicity between leaf and stem growth differs among functional species groups, which can be attributed to differences in environmental conditions, i.e., the temporal dynamic pattern during twig development likely reflects species ecological strategies for light interception and carbon gain. These and other temporal leaf–stem dynamics need to be examined in light of global leaf dimension-abilities (see Westoby et al. 2002) to further our understanding of plant life history strategies.
Ackerly DD, Donoghue MJ (1998) Leaf size, sapling allometry, and Cor-  
er's rules: phylogeny and correlated evolution in maples (Acer). Am  

Bazzaz FA, Chiariello NR, Coley PD, Petelka LF (1987) Allocating  

Bertamini M, Nedunchezhiyan N (2003) Photoinhibition of photosyn-  
sis in mature and young leaves of grapevine (Vitis vinifera L.). Plant Sci  
164:635–644.

Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants—  

revisited: ontogenetic and interspecific patterns in leaf–stem allometry.  

Canham CD (1988) Growth and canopy architecture of shade-tolerant  

Light regimes beneath closed canopies and tree-fall gaps in temperate  

Chazdon RL (1988) Sunflecks and their importance to forest understo-  


Ding SY, Song YC (1999) The comparison of photosynthesis eco-  
physiology of evergreen broad-leaved forest of Tiantong National For-  
est Park in Zhejiang province, China (in Chinese). Acta Ecol Sin  
19:318–323.

Dodd IC, Critchley C, Woodall GS, Stewart GR (1998) Photoinhibition in  
differently coloured juvenile leaves of Syzygium species. J Exp Bot  


Frecketon RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and  
comparative data: a test and review of evidence. Am Nat 160:  
712–726.

Hikosaka K (2005) Leaf canopy as a dynamic system: ecophysiology  

and photosynthetic activity in promoting complementary use of  
light among coexisting species in temperate forests. Ecol Res  

49:293–299.

Kikuzawa K (1995) Leaf phenology as an optimal strategy for carbon  

for an adaptive linkage between leaf phenology and shoot architecture  

Kitao M, Lei TT, Koike T, Tobita H, Maruyama Y (2000) Susceptibility to  
photooinhibition of three deciduous broadleaf tree species with differ-  
ent successional traits raised under various light regimes. Plant Cell  
Environ 23:81–89.

New Phytol 175:475–479.

Koike T, Ishida H, Kitao M, Maruyama Y (2003) Changes in mesophyll anat-  
omy and sink–source relationships during leaf development in Quercus  
glaucia, an evergreen tree showing delayed leaf greening. Plant Cell  

Koike T, Ishida H, Kitao M, Maruyama Y (2003) Changes in mesophyll anat-  
omy and sink–source relationships during leaf development in Quercus  
glaucia, an evergreen tree showing delayed leaf greening. Plant Cell  

Koike T, Ishida H, Kitao M, Maruyama Y (2003) Changes in mesophyll anat-  
omy and sink–source relationships during leaf development in Quercus  
glaucia, an evergreen tree showing delayed leaf greening. Plant Cell  

Koike T, Ishida H, Kitao M, Maruyama Y (2003) Changes in mesophyll anat-  
omy and sink–source relationships during leaf development in Quercus  
glaucia, an evergreen tree showing delayed leaf greening. Plant Cell  

Koike T, Ishida H, Kitao M, Maruyama Y (2003) Changes in mesophyll anat-  
omy and sink–source relationships during leaf development in Quercus  
glaucia, an evergreen tree showing delayed leaf greening. Plant Cell  

Koike T, Ishida H, Kitao M, Maruyama Y (2003) Changes in mesophyll anat-  
omy and sink–source relationships during leaf development in Quercus  
glaucia, an evergreen tree showing delayed leaf greening. Plant Cell  

Koike T, Ishida H, Kitao M, Maruyama Y (2003) Changes in mesophyll anat-  
omy and sink–source relationships during leaf development in Quercus  
glaucia, an evergreen tree showing delayed leaf greening. Plant Cell  


