



Disentangling the effects of tree size and light environment on reproductive onset and allocation in three sympatric wild *Acer* species

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Abstract

Key message Flower production in three *Acer* species is primarily determined by individual size, with local light exerting secondary effects depending on species-specific responsiveness.

Abstract Reproductive and growth strategies of long-lived trees depend on both the timing of reproductive onset and the regulation of reproductive allocation, which are shaped by internal and external factors. We investigated how flowering in three *Acer* species—*Acer mono*, *Acer japonicum*, and *Acer amoenum*—is influenced by individual size, light conditions, and position within the crown. Tree height and diameter at breast height (DBH) were measured along with light metrics (relative photosynthetic photon flux density [RPPFD], canopy layer, and gap status), and their effects were evaluated at the individual, branch, and shoot levels. Statistical analyses showed that reproductive onset in *A. mono* and *A. japonicum* was primarily determined by tree size, whereas light conditions additionally influenced *A. amoenum*. Although tree-level flowering intensity was similarly affected by size and light across all species, species-specific trends appeared at the shoot and branch scales. *A. mono*, a light-demanding species, produced more flowers on current-year shoots with greater relative length (RL). No shoot-level trend was evident in *A. japonicum*, a shade-tolerant species. By contrast, *A. amoenum* produced more flowers on relatively short current-year shoots in partially shaded, growth-demanding trees, while flowering was more uniform in isolated trees. A light-manipulation experiment further supported the light-sensitive flowering of *A. amoenum*, highlighting the role of the red-to-far-red (R: FR) ratio, in contrast to the minor response of *A. mono*. Overall, size establishes the threshold for reproductive onset, while light regulates reproductive allocation; flowering patterns reflect species-specific strategies linking growth, reproduction, and light use.

Keywords Reproductive onset · Life history strategy · Phase change · Local light

Introduction

Many organisms transition to the reproductive phase after completing growth phases. This pattern is closely linked to the fundamental life history question of when and to what extent organisms should allocate resources for reproduction (Gadgil and Bossert 1970; Kozłowski 1992). Short-lived herbaceous species invest heavily in late-life reproduction, followed by rapid senescence. In contrast, long-lived trees

undergo an extended period of pre-reproductive growth, and once reproduction commences, their reproductive allocation gradually increases, and growth and reproduction remain balanced throughout their lifetime (Harper and White 1974). The above trends are consistent with those observed across tree taxa; short-lived species concentrate their reproductive investments during the early in life, whereas long-lived species spread such investments over an extended period (Wenk and Falster 2015). Moreover, reproductive onset timing varies considerably among tree species, and this variation has been examined with respect to maximum size, especially maximum tree height (H_{max}) (e.g., Thomas 1996; Davies and Ashton 1999; Wright et al. 2005; Suzuki et al. 2019).

The transition of trees to the reproductive stage is generally constrained by tree size and resource availability (Masaki and Suyama 2011). Delaying reproductive onset

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until reaching a certain size offers three advantages: (1) a reduction in early growth rate due to the cost of reproduction is prevented, (2) individuals have enough time to accumulate sufficient internal resources to support reproductive investment, and (3) by prioritizing size growth, individuals can reach or dominate the canopy earlier, thereby gaining access to more resources and enabling higher reproductive investment. Therefore, delaying reproductive onset can increase lifetime reproductive output if life expectancy is long. In contrast, if life expectancy is short or individuals cannot reach high-light environments, delayed reproduction results in a shortened or lost reproductive period, thereby reducing lifetime reproductive success. Under such conditions, early initiation of continuous seed production will benefit reproductive success if the species is sufficiently shade-tolerant. Early reproduction limits maximum size but can save potential costs in large trees, such as those associated with high cavitation and breakage (Niklas 1994; Koch et al. 2004), and thus benefit lifetime success. To summarize, species can adopt two contrasting strategies: one that delays reproduction until a larger size and high-light conditions are reached, allowing high reproductive investment, and another that initiates reproduction under relatively low-light conditions and maintains low reproductive intensity over a prolonged period (Journé et al. 2024). In fact, within the same forest, shrub and subcanopy species tend to have maturation sizes smaller than those of canopy species (Suzuki et al. 2019), suggesting the contrasting life-history strategies: early reproduction under relatively high mortality risk or shorter life expectancy versus prioritization of growth and delayed reproduction when future resource acquisition is expected.

In reality, in trees, reproductive onset is not entirely controlled by size-related strategies but is also influenced by environmental factors, particularly light. The light environment relevant to tree reproduction is characterized by two distinct aspects. First, light is a critical resource for photosynthesis, and its relationship with reproductive onset has been widely studied. Populations growing in open, high-light conditions tend to flower earlier than those growing in closed forests (Wesselingh et al. 1997; Wright et al. 2005), which suggests that enhanced photosynthetic resource acquisition in high-light environments accelerates reproductive onset. Second, beyond carbon gain, light also acts as a developmental cue for flower development through multiple signaling pathways, including photoperiodic (Li et al. 2020), age-dependent (Wang et al. 2011; Tsuzuki et al. 2019), and light-quality-related mechanisms (Ito et al. 2014; Huber et al. 2021). Thus, light plays a dual role in the transition to the reproductive phase, serving as both an indicator of primary production and a trigger for flowering regulation. The specific wavelengths and intensities of light

that influence flowering vary considerably among species and likely interact in complex ways with individual size and environmental conditions. Previous studies have suggested that the relative contributions of individual size and light environment to lifetime reproductive success differ among species (Uraguchi and Kubo 2005; Berdanier and Clark 2016). However, in forests, light availability generally depends on individual size, particularly tree height, making it challenging to disentangle the effects of these two factors on reproductive onset.

Even after reproduction has begun, trees modulate vegetative and reproductive allocation through the spatial arrangement of reproductive organs among modules. As trees expand their canopies by sequentially adding modular units, the spatial arrangement of vegetative and reproductive modules plays a crucial role in determining overall growth and reproductive output. In mango, a canopy species with high-light requirements, terminal shoots at the outer crown edge exhibit higher flowering and fruiting rates than lateral ones (Normand et al. 2009). In contrast, flowering in understory shrubs like *Eurya japonica* depends on branch order, and flowers are positioned to avoid obstructing crown development (Suzuki 2000, 2001). These examples suggest that the spatial distribution of reproductive modules varies between canopy and understory species and is closely linked to reproductive and growth strategies. Moreover, such patterns of reproductive module allocation may be controlled by resource conditions: whole-tree resource status determines allocation to elongating or flowering shoots, whereas shoot-level resource conditions modulate finer-scale module distribution (top-down and bottom-up control: Obeso 2004). Thus, the spatial arrangement of reproductive organs among modules and their resource dependence are intimately related to tree reproductive and growth strategies.

As discussed above, the timing of reproductive onset and subsequent growth and reproductive allocation are key aspects examined in studies of plant life-history strategies. However, these aspects remain poorly understood in trees due to the complex effects of individual size and light availability and to the hierarchical responses across multiple scales. To disentangle the respective effects of tree size and light environment in forest ecosystems, we conducted model selection analyses on multiyear observational records and performed an experimental light manipulation study on branches of mature trees in three sympatric wild *Acer* species representing contrasting canopy positions. In addition, we examined patterns of flower arrangement on the branches and shoots of each species. Using these approaches, the study aimed to address the following questions: (1) Which factor—size or light environment—is the primary determinant of flowering occurrence and intensity at the individual level? (2) How does light influence

flowering at the tree, branch, and shoot levels? and (3) How does the spatial arrangement of flowers within crowns integrate size- and light-dependent regulation and contribute to interspecific differences?

Materials and methods

Plant species

The *Acer* genus is a monophyletic group comprising four major clades with approximately 200 wild species, which are primarily distributed throughout the temperate regions of the Northern Hemisphere. In this study, we focused on three deciduous *Acer* species—*Acer mono* var. *glabrum*, *Acer amoenum*, and *Acer japonicum* (Table S1)—native to our study site, Tomakomai Experimental Forest (TOEF) of Hokkaido University, which comprised sufficiently large populations for analysis. All three species exhibit andromonic and protandrous reproductive traits (Shibata and Tanaka 2002; Tanaka 2008, Asai 2000; Sato 2002). *A. mono* var. *glabrum* belongs to the Section Platanoidea (Ackerly and Donoghue 1998; Gao et al. 2020) and is classified as a subspecies or variety of *Acer mono* traditionally, thereby placing it within the broader *A. mono* complex. However, recent studies have suggested that some lineages within this complex, including *A. mono* var. *glabrum*, may represent separate species (e.g. Mori et al. 2024). At the study site, this species is a canopy-forming tree that can reach heights of up to 23 m, which is considered a late successional species with moderate shade tolerance (Koike 1988). Largely consistent with other *A. mono* taxa, *A. mono* exhibits a monopodial branching pattern in its vegetative shoots (Sakai 1987). In a reproductive current-year shoot, two lateral buds at the base of the inflorescence elongate after flowering to form a Y-shaped axis (Fig. 1a), as reported for a sister species of *A. mono* by Li et al. (2021). *A. amoenum* var. *amoenum* is a medium-sized tree belonging to the Palmata section (Ackerly and Donoghue 1998). Similar to *A. mono*, this species contributed to the formation of the canopy layer at the study site and reached a maximum height of approximately 21 m. Additionally, *A. amoenum* is categorized as late successional, with seedlings that exhibit greater shade tolerance than those of *A. mono* (Tanaka et al. 2008). According to Uruguchi and Kubo (2005), the lifetime reproductive output of *A. amoenum* remains relatively stable across different light environments, suggesting that this species is less light demanding than *A. mono*. A defining characteristic of the Section Palmata is sympodial branching (Sakai 1987), in which inflorescences are borne terminally between two pseudo-terminal buds on the reproductive shoots (Fig. 1b).

A. japonicum belongs to Section Palmata (Ackerly and Donoghue 1998; Gao et al. 2020) and is a small deciduous tree that reaches up to 16 m at the study site. This species exhibits shade tolerance during juvenile stages. The relative growth rate (RGR) and leaf photosynthetic rate of *A. japonicum* remain relatively stable under varying light conditions (Oguchi et al. 2017). Similar to *A. amoenum*, *A. japonicum* exhibits a sympodial branching pattern characteristic of the Section Palmata (Sakai 1987), with inflorescences positioned between two pseudo-terminal buds (Fig. 1c). Although some reports have noted the occurrence of both males and hermaphrodites (Asai 2000; Sato 2002), nearly all flowering individuals at the study site were hermaphrodites.

Study site

The study was conducted in the Tomakomai Experimental Forest (TOEF), Hokkaido, Japan (42°40' N, 141°36' E; 82 m a.s.l.), which belongs to cool-temperate climate. From 1999 to 2018, the mean annual temperature was 6.9 °C, with monthly averages ranging from −5 °C in January to 20 °C in August. Annual precipitation averaged 1,212 mm, with the highest monthly rainfall (267 mm) occurring in October. Snow accumulates from November to April and reaches a maximum depth of approximately 30 cm. The soil was composed of volcanic ash derived from Mt. Tarumae, which was located approximately 20 km west of the study site and deposited primarily during major eruptions in 1667 and 1739 at a depth of approximately 2 m. The forest predominantly consists of natural stands with mixed compositions, including *Quercus crispula*, *Acer mono*, *Acer amoenum*, *Tilia japonica*, and *Ostrya japonica*.

The study was conducted in three distinct forest stands within TOEF: (1) mature stand in Block 204 (hereafter referred to as the 'Crane Site,' with a stand age of 280 years); (2) secondary forest ranging across Blocks 404, 315, and 310 (stand age: 67 years); and (3) disturbed secondary forest in Blocks 208 and 206 (stand age: 67 years) (Table S2). The Crane Site was established following the eruption of Mt. Tarumae and was equipped with a canopy crane (maximum reach: 30 m in height; 41.5 m arm length). The 67-year-old secondary forest developed after a major disturbance caused by the Toya-maru Typhoon in 1954. In the disturbed site, the uppermost canopy trees were logged in 2018, reducing the maximum canopy height to approximately 15 m at the time of this study. These three stands exhibit distinct vertical light distributions (Matsuo et al. 2022).

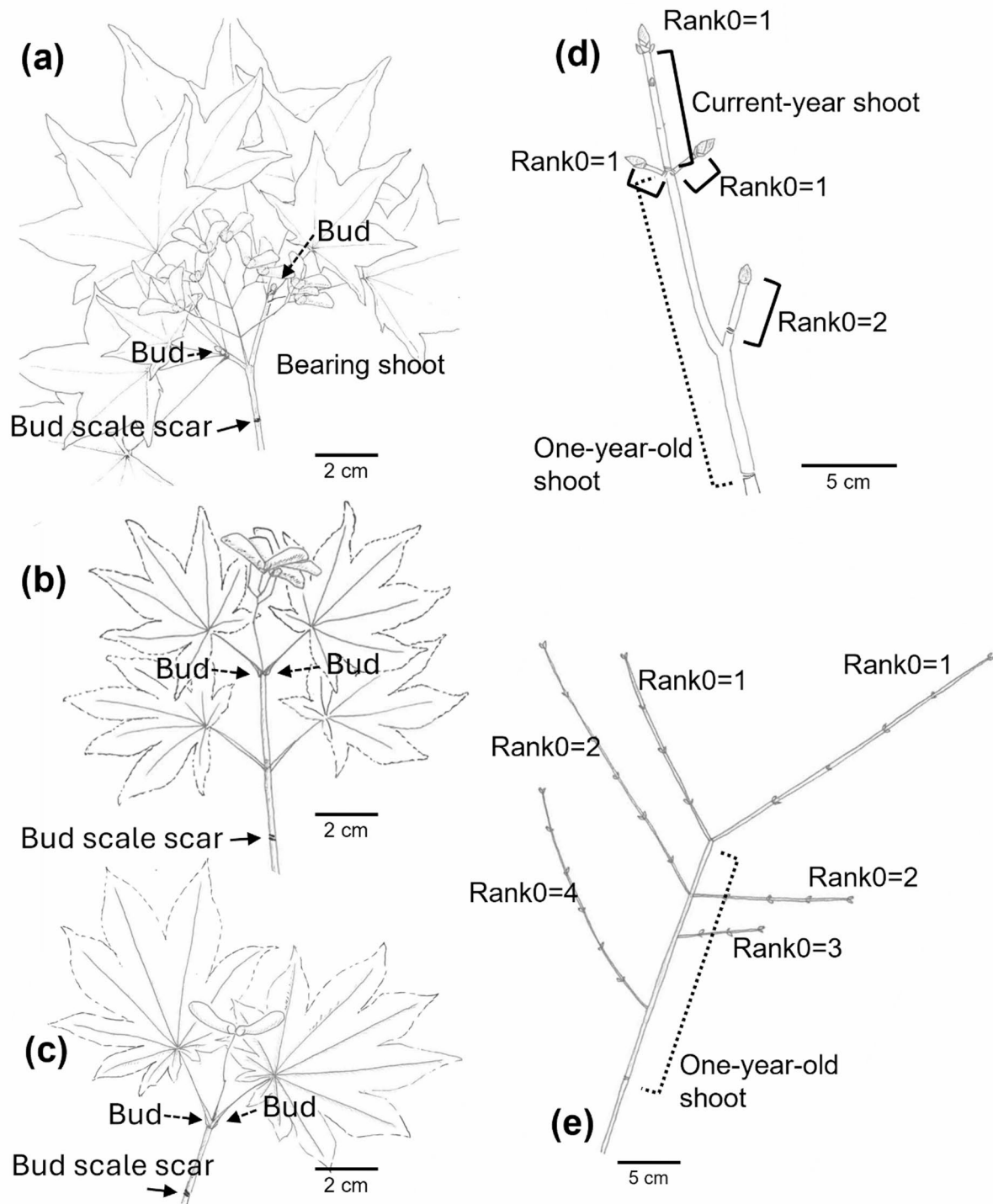


Fig. 1 Morphology and phyllotaxy of current-year and one-year-old shoots. **(a)** *A. mono* reproductive shoot bearing seeds at the top of a Y-shaped current-year shoot. **(b)** *A. amoenum* reproductive shoot. **(c)** *A. japonicum* reproductive shoot **(d and e)** Ranking method. When multiple current-year shoots emerged from the same parent shoot,

ranks were assigned such that shoots from (pseudo-)terminal buds were designated as Rank 1, with ranks increasing toward the basal position. **(d)** shows the *A. mono* monopodial branching case, and **(e)** the sympodial branching pattern of *A. amoenum* and *A. japonicum*

Data collection

Tree size

All individuals of the three *Acer* species with a height of ≥ 1.5 m within each study stand were included in the analysis. In total, 125, 128, and 80 individuals of *A. mono*, *A. amoenum*, *A. japonicum*, respectively, were examined across studied stands (Tables 1a and S2). For each tree, the height (H) and diameter at breast height (DBH) were measured in August 2020, and the light environment was recorded. At the Crane Site, H was measured to the nearest 5 cm using a ballasted measuring tape dropped from the crane for individuals whose uppermost crown had reached the forest canopy. For all other individuals, H was measured from the ground using Vertex IV (Haglöf Sweden AB, Långsele, Sweden).

Light conditions

The light environment of each tree was characterized by two metrics, Layer and Gap Status (GS). Layer was classified into four ordered categories based on the crown's vertical position (Aiba and Kohyama 1997): crown 80%–fully exposed (Layer 1); top exposed but crown partly shaded by other trees (Layer 2); top reaching the canopy layer but not vertically exposed (Layer 3); and top not reaching the canopy (Layer 4). GS was classified into three types according

to the proportion of crown surface receiving direct light: “Gap” (G), $> 90\%$; “Edge” (E), $50\text{--}90\%$; and “Closed-canopy” (C) $< 50\%$. These classifications were visually assessed for all 333 individuals.

As a quantitative indicator of light conditions, photosynthetic photon flux density (PPFD) was measured at a single point directly above the canopy of 122 individuals (Table 1b) using an MQ-200 Quantum Separate Sensor (Apogee Instruments, Logan, USA). Relative PPFD (RPPD; range 0–1) was calculated as the ratio of each measurement to the simultaneously recorded open-sky PPFD. RPPD values were correlated with layer classification, approaching 1 in gaps (G) and slightly higher at gap edges (E) than under continuous canopy cover (C) (Fig. S2, left). In addition, H and RPPD showed little correlation (Fig. S2, right). Thus, at our study site, the light condition perceived by the individual tree was dependent on the Layer and Gap status rather than H. Accordingly, Layer, Gap status, and RPPD were all used as indicators of individual-level light conditions in subsequent analyses.

Individual-level flowering indicators

From 2020 to 2024, flowering intensity—the percentage of flowering shoots in the crown—was visually assessed in 5% increments using binoculars. Trees with $\leq 5\%$ flowering were recorded as “+” and regarded as showing unstable flowering before reproductive maturity. In 2020, assessments were conducted by local technical staff due to COVID-19 travel restrictions. A preliminary survey in autumn 2019 recorded DBH, H, flowering status (based on floral rachis scars), and fruit presence. Flowering occurrence (FO_i) was defined for each tree as 1 if it flowered at least once with $\geq 5\%$ flowering ratio during the five-year observation, or 0 if not. Flowering intensity (FR_i) was averaged over three to five years to minimize effects of annual variation.

Shoot-level flowering indicators

Flowering behavior at the branch and shoot levels was examined from 2019 to 2021 using a subset of flowering individuals. For each selected tree, one–three first-order branches (defined as the terminal branches at the top of the crown with a basal diameter of approximately 1.5 cm) were sampled from the uppermost canopy. The number of current-year shoots per first-order branch ranged from 10 to 50 in *A. mono*, 50–100 in *A. amoenum*, and 10–200 in *A. japonicum*. The presence or absence of flowering was recorded for each current-year shoot (FO_s: 1/0) on the sampled branches. In addition, the lengths of each current-year shoot (L0, mm) and its corresponding parent one-year-old shoot

Table 1 Numbers of measured trees (*N*) with their size range [DBH, cm] (a) and the light condition range [RPPD, %] (b) in the parenthesis

	<i>A. mono</i>	<i>A. amoenum</i>	<i>A. japonicum</i>	Total
(a) <i>N</i> for DBH measurement				
Crane Site	89 [2.4–73.2]	27 [2.4–45.4]	2 [11.6–12.4]	118
Secondary Forest	4 [2.4–3.4]	33 [2.2–32.1]	78 [2.2–29.9]	115
Disturbed Forest	32 [3.2–22.4]	68 [4.0–19.1]	†	100
Total	125	128	80	333
(b) <i>N</i> for RPPD measurement				
Crane Site	42 [2.0–100]	15 [26.2–100]	2 [34.2–48.4]	59 [2.0–100]
Secondary Forest	3 [8.5–12.4]	8 [15.8–25.1]	7 [8.3–48.3]	18 [8.3–48.3]
Disturbed Forest	11 [15.4–100]	34 [3.8–100]	†	45 [3.8–100]
Total	56 [2.0–100]	57 [3.8–100]	9 [8.3–48.4]	122 [2.0–100]

† *A. japonica* trees were not found from the Disturbed Forest stand

(L1, mm) were measured (Fig. 1d, e). Relative current-year shoot length (RL) was calculated as L0 divided by the total length of all sibling current-year shoots emerging from the same one-year-old shoot. RL indicates shoot dominance, approaching 1 for longer shoots and those with fewer siblings. The positional hierarchy was also recorded for each current-year (Rank0) and one-year-old shoot (Rank1), with the terminal shoot assigned rank 1 and progressively higher ranks given to more basal shoots along the branch axis (Fig. 1d, e).

Light manipulation experiment

To separate the effects of light conditions on flowering from those related to tree size, we conducted a light manipulation experiment on *A. mono* and *A. amoenum*. For each species, three individuals with similar tree heights, unobstructed upper canopies, and different levels of competitive pressure from neighboring trees were selected (Table S3). For each tree, nine first-order branches (50–70 cm in length) located in the uppermost canopy with 100% open-sky exposure were selected. These branches were assigned to one of three treatments: (1) three branches covered with shading nets to reducing the RPFd to 50%; (2) three branches covered with MegaCool film (MKV Advance Co., Ltd., Tokyo, Japan) to reduce the RPFd to 50%, while increasing the red: far-red (R: FR) ratio by 120%; (3) three branches left untreated as bright controls. (4) In addition, three first-order branches that were self-shaded by other branches, thereby reducing RPFd to 20%, were selected from the mid-canopy as dark controls. (Fig. 2). In 2022 and 2023, the treatments were applied from the onset of bud formation (late June) to October of the same year. In June of the following year, the flowering presence or absence was recorded for all current-year shoots on each selected branch. Flowering intensity on each branch (FR_b) was calculated as the number of flowering

shoots divided by the total number of current-year shoots on that branch.

Statistical analysis

The influence of tree size and light on multiscale flowering indicators (Table 2) was evaluated using generalized linear mixed models (GLMMs; Brooks et al. 2017) applied to the dataset (Table 3).

First, to examine interspecific differences, we applied GLMMs that incorporated size, light, and species as covariates to the full dataset (Step 1). Three model types were compared (Table 3 and S4): the no-species-effect model, the parallel model including species effect as the intercept of the GLMM, and the interaction model considering species $\times$ size or species $\times$ light effects. In these models, correlated parameter pairs (e.g., H and DBH (Fig. S1), RPFd and Layer (Fig. S2) were not included simultaneously to avoid multicollinearity. A simulation-based quality check (QC) was performed for each model using the DHARMA package in R (Hartig 2025). Among the models that passed this check, data predictability was evaluated using the Bayesian information criterion (BIC). Because information criteria such as BIC presuppose that model assumptions are met, BIC values were interpreted only for models that passed the QC. If the no-species-effect model qualified and showed a smaller BIC value than the parallel or interaction models, interspecific differences were considered neglectable. If the parallel model qualified and had the smallest BIC, each species could differ in flowering indicator values, but their responses to size and light would be consistent. If the interaction model qualified and showed a smaller BIC than both the no-species-effect and parallel models, species-specific responses to size and light were regarded as significant; in this case, the GLMM was applied to the species-wise dataset (Table S4). In some cases, none of the models applied for the pooled dataset passed the QC, suggesting that a single

Fig. 2 Effects of shading treatments on RPFd, R:FR ratio, and blue light. BR refers to bright control., MC: covered with MegaCool, SN: shaded with net, and SS to self-shading (dark controls)

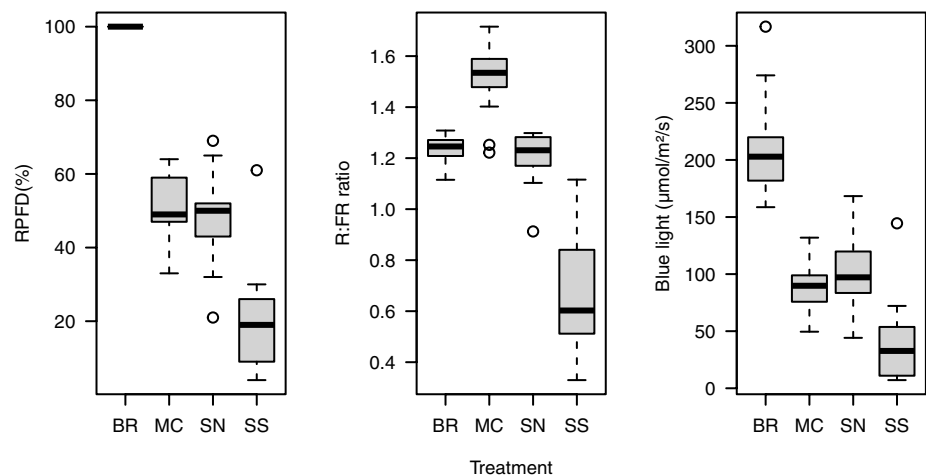


Table 2 Summary of the regression parameters used in statistical models for each level, based on observational (O) or experimental (E) data

Parameter	Descriptions	Individual/Branch/Shoot Level	Observation /Experiment
<i>Light conditions</i>			
Layer	The light condition based on the vertical position of its crown top (1–4)	I	O
GS	Gap status: the lateral light condition (G, E, C)	I	O
RPFD	Relative photon flux density measured at top of the crown (%)	I/B	O/E
R: FR	Red to far-red light ratio measured at top of the crown or branch	I/B	E
<i>Flowering indicators</i>			
FO_i	Flowering occurrence: whether a tree flowered at least once with a flowering ratio $\geq 5\%$ during the five-year observation period (1) or not (0), representative of the transition to reproduction phase	I	O
FR_i	Five-years average flowering intensity (proportion of shoots flowered) (0–100%)	I	O
FR_b	Flowering ratio of a branch: the number of flowering current-year shoots divided by the number of all current year shoots on a target branch (0–100%)	B	E
FO_s	Presence (1) or absence (0) of flowers on a shoot	S	O
<i>Shoot characters (Refer to Fig. 1d, e)</i>			
RL	Relative length of or the dominance indicator of a shoot	S	O
L0	Length of current-year shoot [mm]	S	O
L1	Length of one-year-old shoot [mm]	S	O
Rank0	Rank of the current-year shoot	S	O
Rank1	Rank of the one-year-old shoot	S	O

model was inappropriate for describing the responses across species. In such cases, models were fitted to each species separately, and when they satisfied the QC criteria, they were used for subsequent species-wise analyses.

After assessing species effects, the next step involved stepwise model selection to identify the best parameter sets of tree size and light conditions (Step 2). If the no-species-effect or parallel model had the smallest BIC value in Step 1, stepwise parameter selection was applied to that model. If the interaction model had the smallest BIC in Step 1, stepwise selection was instead performed on the species-specific GLMMs. When none of the models applied for the pooled dataset satisfied the QC criteria in Step 1, stepwise parameter selection was also conducted separately for each species in both forward and backward directions, with QCs applied during model evaluation. The set of evaluated models was then cross-checked for coverage using the MuMIn package in R (Bartoń 2025).

Model structures of the GLMMs are summarized in Table 3. For the model of flowering occurrence on tree individuals (FO_i; 1/0), DBH, H, arcsine-transformed RPFD, Layer (treated as a continuous predictor), and GS were included as explanatory parameters (fixed effects). A binomial error distribution with a logit link function and

a random effect of study stands were assumed. Using this model, maturation size—that is, the tree size at which the predicted flowering probability reached 80%—was calculated for each species by the delta method based on the best model coefficients.

For the model using flowering intensity (FR_i) as the response variable, the distribution was assumed to follow a beta error structure with a logit-link function. DBH, H, Layer, GS, and arcsine-transformed RPFD in the upper canopy were included as fixed effects, with study stand as a random effect.

For flowering occurrence on current-year shoots (FO_s; 1/0), logistic multiple regression was applied. Fixed effects included RL, L0, L1, Rank0, and Rank1, while branch (nested within individual ID), individual ID and Year were incorporated as random effects.

The model for branch-level flowering intensity (FR_b) was based on data from the light manipulation experiment. The response variable, FR_b, was arcsine-transformed for normalization and assumed to follow a Gaussian distribution. Fixed effects included RPFD, R:FR, and Year. Year was modeled as a fixed effect because FR_b of the same branches was measured over two years and showed synchronized interannual variation among individuals. The

Table 3 Statistical model elements explanation. “Sp” denotes species

Level	Response variable	Explanatory parameters	Random effects	Assumed distribution (link function)
<i>Step 1. Examination of species effects</i>				
Individual	FO_i	Sp, DBH, Layer, GS	Stand	Binomial (logit)
Individual	FR_i	Sp, H, Layer, GS	Stand	Beta family (logit)
Shoot	FO_s	Sp, RL, L0, L1, Rank0, Rank1	Branch/ Individual, Individual	Binomial (logit)
Branch	Arcsin(FR_b)	Sp, RPFDF, R:FR, Year	Individual	Gaussian (identity)
<i>Step 2. Selection of explanatory parameters for each species</i>				
Level	Response variable	Explanatory parameters	Random effects	Assumed distribution (link function)
Individual	FO_i	DBH, H, arcsin(RPFD), Layer, GS	Stand	Binomial (logit)
Individual	FR_i	DBH, H, arcsin(RPFD), Layer, GS	Stand	Beta family (logit)
Shoot	FO_s	L0, L1, RL, Rank0, Rank1	Branch/ Individual, Individual, Year	Binomial (logit)
Branch	Arcsin(FR_b)	R: FR, RPFDF, Year	Individual	Gaussian (identity)

modeling of FR_b was conducted separately for each individual, reflecting the individual-specific responses to RPFD and R: FR identified in the FO_i analysis (see **Results**).

For each best model, multicollinearity was evaluated based on VIF values, with thresholds set at > 5. The reliability of parameter estimates was judged according to whether the 95% confidence interval (CI) excluded zero.

Results

Flowering patterns at the study site

Among all individuals examined, the proportion of flowering trees was approximately 50%, 60%, and over 90% for *A. mono*, *A. amoenum*, and *A. japonicum*, respectively (Fig. S3, top row). Although some variation occurred among stands, these percentages remained largely consistent across years within each stand because the flowering status of individual trees was generally stable. *Acer* species are known to exhibit relatively weak masting synchrony among individuals (Shibata et al. 2002). For each species, FR_i remained nearly constant from 2020 to 2022, with minimal

Table 4 Estimated logistic regression model parameters for flowering occurrence at the individual level (FO_i). For each species, the estimated regression coefficients and their 95% confidence intervals [in brackets] are shown for the explanatory variables included in the best models. Bold indicates that the 95% CI did not include zero. NA indicates that the parameter was not included in the best model. See Supplementary Table S5 for model selection results

Species	Fitted parameters		
	Intercept	DBH (cm)	Arcsin(RPFD)
<i>A. mono</i>	-5.10 [-8.00, -2.21]	0.41 [0.17, 0.66]	NA
<i>A. amoenum</i>	-3.99 [-6.40, -1.59]	0.39 [0.14, 0.63]	2.60 [0.15, 5.05]
<i>A. japonicum</i>	-4.87 [-13.7, 3.97]	2.14 [-0.76, 5.05]	NA

interannual variation, but declined in 2023 (Fig. S3, bottom row). In 2024, FR_i values were comparable to or higher than those in 2020–2022. Trees included in the experimental treatment followed this overall trend: 2022 represented an average flowering year, 2023 a poor flowering year, and 2024 a mast year for *A. amoenum* and an average year for *A. mono* (Table S3). Among the three species, *A. amoenum* individuals generally exhibited higher FR_i values than the other two species.

Factors affecting the flowering occurrence at the individual level (FO_i)

Among the three models applied to FO_i for the all-species dataset, the interaction and parallel models exhibited smaller BIC values than the no-species-effect model, suggesting interspecific differences (Table S4). In particular, the interaction model provided the best fit, indicating that the effects of explanatory variables varied among species. Therefore, regression analysis for FO_i was conducted separately for each species.

The model with the lowest BIC value included DBH as the explanatory variable for *A. mono* and *A. japonicum*, and both DBH and RPFD as explanatory variables for *A. amoenum* (Table 4 and S5). For *A. japonicum*, the 95% CI for the DBH coefficient included zero, rendering both the intercept and slope estimates statistically uncertain. If we estimated threshold size for the onset of stable flowering (maturation size; DBH, at which 80% of individuals initiate flowering), it varied between the species. The maturation size was 15.7 ± 1.7 cm (95% CI: 12.4–19.0) for *A. mono*. *A. amoenum* had the smaller maturation size than this, especially in bright environments: 12.6 ± 1.8 cm (9.1–16.1) at an RPFD of 20%, 10.4 ± 1.4 cm (7.7–13.1) at an RPFD of 55%, and 8.7 ± 1.8 cm (5.2–12.2) at an RPFD of 90%. The maturation size for *A. japonicum* was the smallest among species, estimated at 2.3 ± 0.4 cm (1.5–3.1), although this

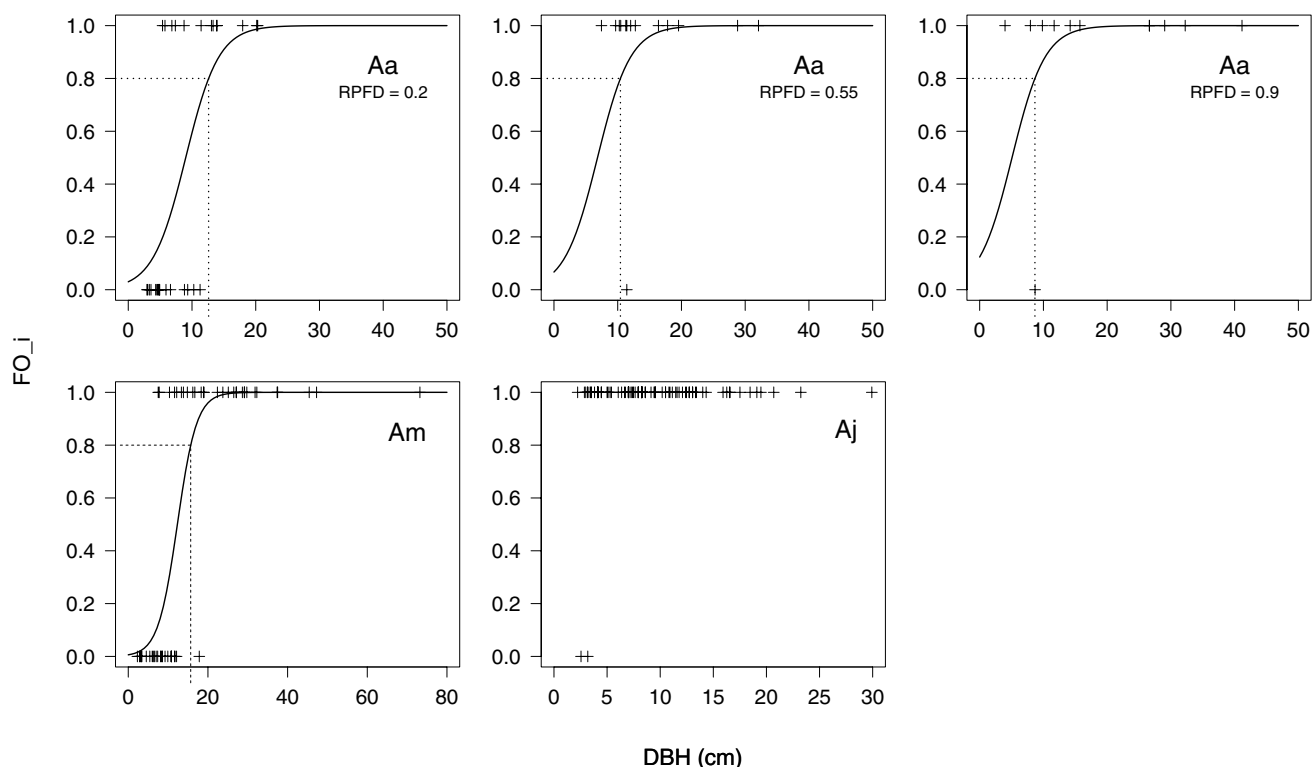


Fig. 3 The influences of DBH on the flowering occurrence in individual trees (FO_i) of three *Acer* species. Logistic regression curves are shown for *A. mono* (Am), *A. amoenum* (Aa), and *A. japonicum* (Aj). For *A. amoenum*, the effect of RPF is represented by three separate panels (RPF=0.2, 0.55, and 0.9). Black crosses indicate individu-

als. Dotted vertical lines denote the estimated threshold DBH at which 80% of individuals initiate flowering (maturation size). Because of this uncertainty, the regression line for *A. japonicum* was undetermined and is therefore not presented (see text)

Table 5 The estimated parameter values of the optimal regression model for flowering intensity (FR_i) are shown. Bold indicates that the 95% CI did not include zero. See Supplementary Table S6 for model selection results

	Estimate	95% CI
<i>Species (Intercept)</i>		
<i>A. mono</i>	-1.41	[-1.71, -1.10]
<i>A. amoenum</i>	-0.83	[-1.45, -0.21]
<i>A. japonicum</i>	0.39	[0.08, 0.69]
<i>Explanatory factors (common to species)</i>		
H (m)	0.13	[0.09, 0.16]
Layer	-0.40	[-0.54, -0.27]

Note: Species effects were parameterized with *A. amoenum* as the baseline. Values for *A. japonicum* and *A. mono* represent deviations relative to *A. amoenum*

value was uncertain due to the scarcity of unflowered individuals (Fig. 3).

Determinants of individual flowering intensity (FR_i)

When comparing the three models for FR_i, the parallel model—which incorporated species differences only in the intercept—yielded the lowest BIC (Table S4). This result

indicated that there were no species-specific differences in the responses of FR_i to tree size and light conditions, and that interspecific differences were limited to the absolute values of FR_i. Consequently, model selection was performed using the parallel model. As a result, FR_i of the three *Acer* species was best explained by H and Layer (Table 5, Table S6, Fig. 4), which likely represented the overall crown light environment more effectively than RPF at the crown top. The estimated intercepts differed among species, being lowest in *A. mono*, intermediate in *A. amoenum*, and highest in *A. japonicum* (Table 5).

Factors affecting presence or absence of flowering on current-year shoots (FO_s)

None of the regression models for FO_s tested with the pooled dataset satisfied the quality criteria, regardless of species effects (Table S4). This was likely due to substantial interspecific variation in shoot-level flowering patterns. Consequently, the pooled dataset was unsuitable for further analysis, and we proceeded with species-wise evaluations to identify the best models separately (Table S7). For *A. amoenum*, the analysis was stratified by canopy layer, with Layer

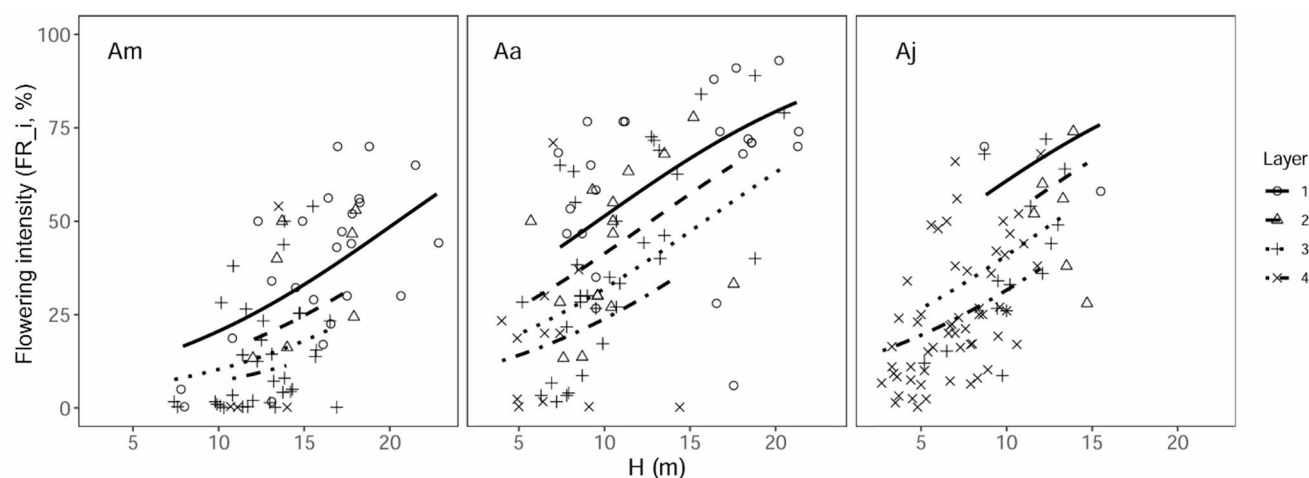


Fig. 4 Flowering intensity (FR_i) in relation to tree height (H, m) and canopy layer (Layer). Am: *Acer mono* (left), Aa: *A. amoenum* (middle), Aj: *A. japonicum* (right)

Table 6 Logistic regression results for the presence/absence of inflorescence on current-year shoots (FO_s) for each *Acer* species. Abbreviations are defined in Table 2. Bold indicates that the 95% CI did not include zero. NA indicates that the parameter was not included in the best model. See Supplementary Table S7 for model selection results

Species	Estimates of fitted parameters		
	Intercept	Fixed effects [95%CI]	Standard deviation of the random effects
<i>A. mono</i>	-5.28 [-6.79, -3.78]	RL: 3.41 [2.07, 4.75]	Tree: 0.00 Tree/Branch: 1.06
<i>A. amoenum</i> (Layer 1 trees)	2.95 [4.71, 5.43]	NA	Tree: 0.50 Tree/Branch: 3.22
<i>A. amoenum</i> (Layer 2 and 3 trees)	0.95 [0.26, 1.64]	L0: -0.015 [-0.021, -0.009] L1: -0.005 [-0.009, -0.001]	Tree: 0.38 Tree/Branch: 0.91
<i>A. japonicum</i>	-3.84 [-4.50, -3.18]	NA	Tree: 0.70 Tree/Branch: 0.61

1 individuals assessed separately from those in Layers 2 and 3, because FO_s varied significantly with the light environment (especially among flowering individuals). In Layer 4, no flowers occurred on first-order branches, leaving no data available.

For *A. mono*, RL was included as a fixed effect in the best-fitted model for FO_s (Table 6; Fig. 5), along with random effects for both individual trees and branches. For *A. amoenum*, the optimal models differed with canopy light exposure. In Layer 1, where crowns were fully illuminated, the best model retained only the intercept and random effects (i.e., no fixed effects; Table S7). In contrast, for individuals in Layers 2 and 3, which received partial direct light, the best model included L0 and L1 as fixed effects (Table 6 and S7; Fig. 5). Several explanatory variables showed negative correlations, for example, between R0 and L0 (Fig. S4). For *A. japonicum*, the lowest-BIC model comprised only

the intercept and random effects, with none of the measured traits (RL, L0, L1, Rank0, or Rank1) selected as predictors of FO_s (Table 6; Table S7).

Manipulation results: light environment affecting flowering on branches (FR_b)

Three pooled-species models for FR_b were tested, but none passed the QC criteria (Table S4). We therefore adopted tree-wise GLMs (Table S8). Except for Aa-I, well-fitted models were obtained for all individuals (Table 7). In the best-fitted model for *A. mono*, either R: FR or RPFDF was selected, but without consistency. Moreover, the 95% CI for the selected coefficient included zero, indicating uncertainty in these effects. By contrast, for *A. amoenum*, the explanatory variable consistently selected was the R: FR ratio. Notably, R: FR showed a positive effect in the isolated tree Aa-I, whereas it had a negative effect in the competing tree Aa-C2 (Fig. 6).

In the legend, 23 and 24 denote the measurement years (2023 and 2024). Regression curves are displayed only when coefficients exclude zero from their 95% CI.

Discussion

Size-dependent regulation of reproductive onset and flowering intensity

Previous studies have shown that the size of reproductive onset correlates with the maximum size of species as well as with the light environment (e.g., Thomas 1996). However, because individual size and light availability are strongly correlated in forests, their effects have rarely been evaluated independently (see Wright et al. 2005). Our results showed

Fig. 5 Relationship between the presence or absence of inflorescence (1/0) of current-year shoots (FO_s) and the explanatory variables included in the best-fitting model. (Top left) *A. mono* (Am). (Bottom left) *A. amoenum* (Aa), Layer 1; (Bottom right) *A. amoenum* (Aa), Layers 2–3. (Top right) *A. japonicum* (Aj). RL: Relative current-year shoot length; L0: length of each current-year shoot (mm)

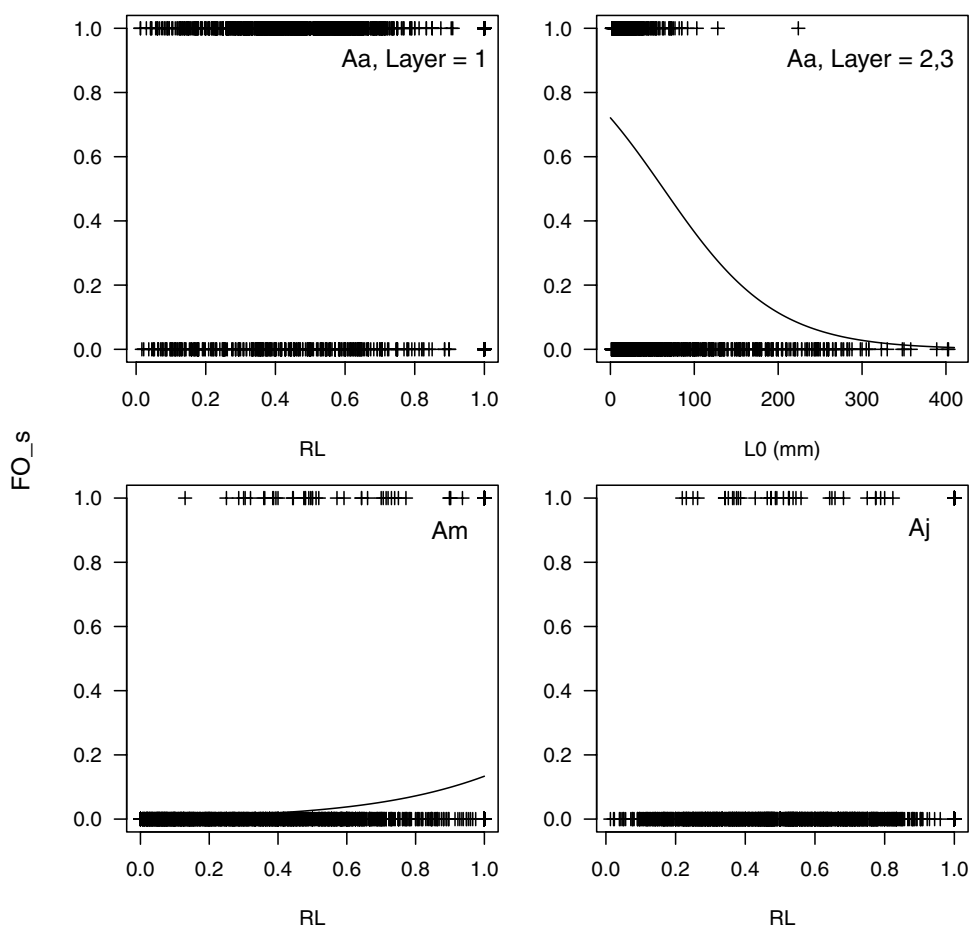


Table 7 Regression results for the effects of R: FR ratio and RPFd on the flowering ratio of first-order branches in *A. mono* and *A. amoenum* (2023 and 2024). Quality check (QC) outcomes are labeled as Pass (P), Fail (F). NA indicates that the parameter was not included in the best model. Bold indicates that the 95% CI did not include zero. See Supplementary Table S8 for model selection results

Tree ID	QC	Fitted parameters [95% CI]			
		Intercept	R: FR Ratio	RPFd	Year
Am-I	P	0.37 [-0.22, 0.96]	-0.23 [-0.66, 0.20]	NA	0.53 [0.32, 0.75]
Am-C1	P	0.06 [-0.13, 0.25]	NA	0.002 [-0.001, 0.004]	0.21 [0.06, 0.37]
Am-C2	P	0.56 [0.25, 0.87]	0.07 [-0.09, 0.24]	NA	0.07 [-0.09, 0.24]
Aa-I	F	-0.12 [-0.23, -0.00]	0.12 [0.03, 0.22]	NA	1.48 [1.41, 1.53]
Aa-C1	P	0.23 [-0.05, 0.51]	-0.15 [-0.39, 0.07]	NA	0.97 [0.78, 1.16]
Aa-C2	P	0.41 [0.16, 0.67]	-0.31 [-0.52, -0.09]	NA	1.22 [1.06, 1.39]

that when the effects of size and light were evaluated independently, reproductive onset (FO_i) was governed primarily by individual size, whereas flowering intensity (FR_i) was regulated by both size and light.

Reproductive onset (FO_i) was strongly size-dependent, particularly on DBH (Table 4), and exhibited interspecific variation in maturation size. Maturation size followed the order *A. japonicum* < *A. amoenum* < *A. mono* (Fig. 3), which is the same order as species' maximum size (Table S1), consistent with the well-documented positive association between maturation size and species' maximum size across a wide range of taxa and forest types (Thomas 1996; Davies and Ashton 1999; Suzuki et al. 2019; Journé et al. 2024), indicating that the observed pattern reflects a general life-history constraint rather than site-specific conditions. In addition to this size-driven pattern, reproductive onset in *A. amoenum* was explained also by RPFd (Table 4). Even though reproductive onset is primarily limited by size, the size threshold for reproductive onset can depend on the actual light environment in some species. Such interspecific differences may be attributable to variation in shade tolerance (Koike 1988) and other species-specific life-history traits (Kozłowski 1992; Obeso 2004) or growth traits (Aiba and Kohyama 1997; Tanaka et al. 2008).

Notably, reproductive onset (FO_i) was most strongly associated with DBH (Table 4), whereas flowering intensity (FR_i) was better explained by tree height (H) and Layer

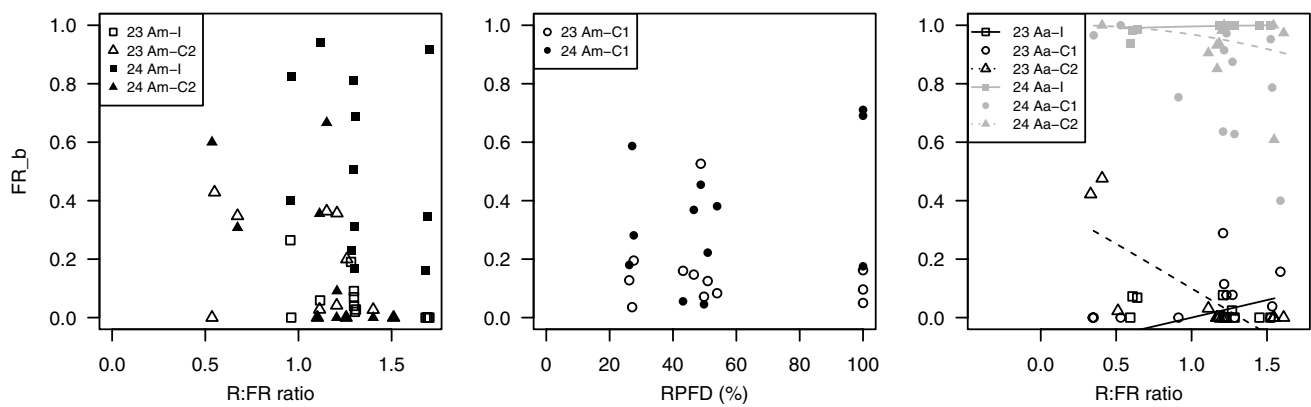


Fig. 6 Results of the light manipulation experiment: relationship between flowering ratio of first-order branches and the light environment (RPFD for Am-C1; R: FR ratio for other individuals)

(Table 5), suggesting distinct regulatory processes for these phenomena. DBH primarily reflects the tree's cumulative structural development, as it is strongly constrained by long-term changes in crown structure rather than instantaneous growth conditions (Sumida et al. 2013). Reproductive onset, or a threshold-type transition from the vegetative to the reproductive phase, may largely depend on the cumulative growth of trees indicated by DBH. In contrast, flowering intensity reflects a continuous allocation process after the transition to the reproductive phase (Obeso 2002); a process that probably depends more on current environmental conditions and is better reflected by H and Layer than by the cumulative growth.

Interaction between size and light environment on reproduction

The GLMM selection results for flowering intensity (FR_i) showed that flowering intensity was influenced jointly by individual size (H) and light conditions (Layer) across all three species (Table 5; Fig. 4). Shared slopes among species suggest a common response to size and crown exposure, whereas differences in intercepts reflect species-specific baselines: highest in *A. japonicum*, intermediate in *A. amoenum*, and lowest in *A. mono*. This baseline ordering of flowering intensity is opposite to the ranking of maturation size, indicating that interspecific differences in flowering intensity cannot be explained simply as a scaled reflection of maturation size. Instead, this reversal in order may partly reflect a trade-off between the timing of reproductive onset and the intensity of reproductive investment (Kozłowski 1992; Wenk and Falster 2015). Although *A. japonicum* trees begin flowering under the canopy and exhibit higher flowering intensity than other species of the same size, they rarely reach the forest canopy. In contrast, *A. amoenum* tends to attain larger size and flowers under brighter conditions, resulting in higher flowering intensity at the population

level than that of *A. japonicum* (Fig. S3). These trends are consistent with predictions of the trade-off theory. However, the comparatively low flowering intensity observed in *A. mono* across the studied species (Fig. S3) contradicts the predictions of trade-off theory. This discrepancy may reflect the limitations of the present analysis, which focuses on flowering intensity and does not necessarily capture reproductive output. Future analyses should incorporate lifetime-integrated evaluations of reproductive output in accordance with light availability (e.g., Uruguchi & Kubo 2005).

The selection of Layer rather than single-point RPFD as an explanatory variable for flowering intensity (FR_i) (Table 5) indicates that flowering intensity was more constrained by whole-individual carbon acquisition under canopy competition than by local light conditions at the canopy top. In deciduous woody plants, flower bud formation occurs early in the preceding growing season (Guédon et al. 2006), when shoots have limited carbon autonomy and when reproductive development depends on whole-plant carbon balance supported by stored reserves and sustained assimilation (Pawar and Rana 2019). Under such conditions, flowering intensity is expected to be regulated by the structural context that determines the stability of carbon supply at the plant level (Imada and Tako 2022), with the effects of short-term fluctuations often being overridden (Peavey et al. 2020). Testing this interpretation will require the direct evaluation of whole-plant carbon and/or nitrogen dynamics using tracer-based approaches (e.g. Han et al. 2016).

Moreover, the shading treatment under light manipulation experiment did not completely suppress flowering at the branch level (Fig. 6), suggesting the control of reproductive onset exerted by whole-plant resource status, probably mediated by sugar signals (Tsuzuki et al. 2019), gibberellin, or age signals (Wang et al. 2011). In addition, we also detected a contribution of local R: FR to branch-level flowering intensity (FR_b) in *A. amoenum* and *A. mono*, with this effect observed only in a few individuals (Table 7;

Fig. 6). Although a previous study suggested that *Acer* saplings respond more strongly to RPD than to the R: FR ratio (Lei and Lechowicz 1990), the R: FR may serve as a more critical cue for flowering in some *Acer* species. The R: FR reflects the local light quality and modulates flowering regulatory pathways (e.g., Ito et al. 2014; Endo et al. 2016; Huber et al. 2021). The RPD correlates with blue light intensity (Fig. 2), a known signal for flowering (e.g., Thomas 2006; Endo et al. 2016), but may be an insensitive cue in high-light environments (Huber et al. 2021). The crosstalk between these internal pathways and light-responsive networks (e.g., Niu et al. 2024) may further integrate environmental and physiological signals to regulate flowering.

Comparison of reproductive strategies in *Acer* species

Our results indicate that reproductive processes in the three *Acer* species examined are governed by a shared hierarchical framework, in which reproductive onset is primarily constrained by whole-tree size, whereas reproductive intensity and local allocation are modulated by light availability at finer scales. This common structure provides a basis for understanding how species-specific reproductive strategies emerge through the differential weighting of size-dependent and light-dependent controls (Obeso 2004). Here, we integrate findings across scales to provide a broader perspective on reproductive strategies.

In the subcanopy species *A. japonicum*, reproductive onset (FO_i) was explained mainly by tree size (Table 4), whereas shoot-level flowering (FO_s) was shaped by individual-level random effects (Table 6); in contrast, flowering intensity (FR_i) also responded to the canopy layer (Table 5). Hence, although the light environment influenced flowering intensity, *A. japonicum* maintained relatively high baseline reproduction even under shaded conditions, consistent with its stable relative growth rate and photosynthetic performance across light regimes (Oguchi et al. 2017). These results indicate that flowering in *A. japonicum* is governed primarily by individual size (a proxy for whole-plant resource status), with local light acting as a secondary factor in a life-history context where individuals typically persist under shaded conditions.

The canopy species *A. mono* with relatively high light requirements (Sakai 1990; Uruguchi and Kubo 2005; Tanaka et al. 2008) has a different strategy. *A. mono* develops Y-shaped branching on its reproductive shoots, thereby allowing simultaneous reproduction and shoot elongation (Fig. 1a). This branching pattern may mitigate the morphological costs of reproduction, such as limitations in bud number (Ishihara and Kikuzawa 2009) and reductions in photosynthetic efficiency (Sterck and Schieving 2007).

In *A. mono*, reproductive onset was determined solely by DBH (Table 4), while shoot-level flowering was linked to shoot dominance (Table 6). Although flowering intensity responded to both size and canopy layer (Table 5), light manipulation experiments did not reveal consistent branch-level effects (Table 7). In *A. mono*, reproductive regulation appears to be largely driven by whole-tree size, while module-level control plays a supplementary role. This species also undergoes a prolonged pre-reproductive growth phase (Fig. 3), postponing flowering until canopy emergence, consistent with a life-history strategy that assumes eventual access to high-light environments (Harper and White 1974). *A. amoenum*, another canopy species, displayed a flexible resource allocation pattern that differed from that of *A. mono*. Although *A. amoenum* has a lower maximum tree height and lower light requirements than *A. mono* (Sakai 1990; Uruguchi and Kubo 2005; Tanaka et al. 2008), its reproductive strategy seemed to be characterized by considerable plasticity in response to local light conditions, in the sense that light-related variables were consistently selected across multiple organizational levels (Tables 4, 5 and 7). In trees competing with neighbors under high-light conditions (e.g. trees at Layers 2 and 3), flowers tended to emerge on shorter, higher ranked shoots closer to the stem (Tables 6 and 7; Figs. 5 and 6), enabling simultaneous reproduction and canopy expansion (Suzuki 2000, 2001). Conversely, in isolated trees with abundant light and minimal competition, flowering occurred without consistent association with shoot rank or length, suggesting that reproductive investment was regulated primarily at the individual-level rather than through shoot-level differentiation. The plasticity observed in *A. amoenum* reflects a life-history strategy that balances growth and reproduction by shifting reproductive regulation across organizational scales. This pattern was revealed by an approach that disentangled size- and light-related effects and integrated reproductive regulation across hierarchical levels.

Conclusion

This study demonstrates that reproductive regulation in the three *Acer* species examined follows a shared hierarchical framework. Reproductive onset was primarily constrained by whole-tree size across species, with light availability playing a supplementary role in two of the three species. Flowering intensity was consistently regulated by both size and light availability across species. Importantly, light effects operated mainly at the whole-canopy scale, being restricted by crown position and intercanopy competition more than by the local light conditions of each shoot and branch. Although these frameworks are shared by the three

species, the relative importance of size- and light-dependent regulations differed between species. *A. japonicum* exhibited almost exclusive size-dependent regulation, *A. mono* showed dominance of size-dependent control with a minor contribution of light conditions, and *A. amoenum* exhibited the strongest weighting toward light-dependent control among the three species. These patterns highlight how species-specific reproductive strategies emerge from different integrations of ontogenetic constraints and forest light environments.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00468-026-02785-4>.

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Data Availability All data are available in the main text or the supplementary materials.

Declarations

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

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