Article

Redeployment of Shoots into Better-Lit Positions within the Crowns of Saplings of Five Species with Different Growth Patterns

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Abstract: Research Highlights: We demonstrate the first quantitative evidence that the shoot shedding of fast-growing species growing in a high-light environment is part of the process of shoot redeployment into better-lit outer parts of the crown. Background and Objectives: Light foraging by redeploying organs from shaded regions of a tree crown into better-lit regions is considered to apply to both leaves and shoots. To date, however, this hypothesis has never been tested for shoots. Materials and Methods: We investigated the shoot dynamics of saplings of five deciduous woody species. We included fast-growing and slow-growing species (*Alnus sieboldiana* Matsum., *Castanea crenata* Siebold & Zucc., *Betula ermanii* Cham., *Acer distylum* Siebold & Zucc., and *Fagus crenata* Blume). Results: Shoots in the shaded regions of the crowns of the fast-growing trees showed higher mortality rates than those at better-lit positions. Because of the selective shedding of the shaded shoots, at the end of the growth period the light environment experienced by the shoots that survived until the following spring was similar to that at the early stage of the same growth period. By contrast, the slow-growing trees displayed slow and determinate growth, with a very low mortality rate of shoots at all positions in the crown. Conclusions: The rapid shoot turnover of the fast-growing species resulted in the redeployment of shoots into better-lit positions within the tree crown in a manner similar to the redeployment of leaves.

Keywords: branch lifespan; shoot lifespan; stem lifespan; branch shedding; shoot shedding; stem shedding; canopy; crown development; tree architecture; light foraging

1. Introduction

A plant canopy is a dynamically changing system due to the continuous production, growth, and death of leaves and shoots [1–15]. The light environment within a canopy therefore changes temporally during plant growth [1,9,10,14,16]. Although studies on static plant form and function, such as allometric scaling approaches [17–24], are useful for analyzing time-averaged plant characteristics, investigations of plant organ dynamics are essential to understanding the development of individual plants and stands.

The dynamics of the aboveground parts of plants are driven by three processes: the production, growth, and death of leaves and shoots. Plants in different light environments differ in their shoot dynamics. In low-light environments (e.g., forest understories), plants may accelerate the shedding of their shaded, lower-positioned leaves or shoots because of their negative carbon balances [1]

(but see [6]). For plants in open habitats, the continuous production of leaves into better-lit, higher positions in a canopy is an essential strategy to outcompete neighbors [25–27]. New leaves in the higher or outer positions of a canopy shade the leaves in the lower or inner part of the canopy [14,28–30]. Senescence and death of the shaded leaves of plants in high-light environments are a part of organ redeployment into better-lit positions [9,27,28,31–39]. Light foraging by organ redeployment from shaded regions into better-lit regions of a tree crown is considered to apply to shoots in addition to leaves [40,41]. To the best of our knowledge, however, no empirical study has tested the applicability of this hypothesis to shoots.

The temporal changes of a crown are determined by two-way interactions between the light environment and the dynamics of the leaves and shoots; light affects the dynamics (i.e., production, growth, and death) of organs, and the dynamics of organs affect the environment [1,4,5,8,10,14,42]. Shoot production rates are higher and shoot mortality rates are lower in better-lit, outer parts than in shaded, inner parts of the crown [13,40,43]. Furthermore, shoot growth and death depend on whether the shoots are shaded relative to other shoots throughout the entire crown, a phenomenon known as correlative inhibition [41,44–47]. Although these previous studies have successfully elucidated how the light environment affects shoot dynamics, they have clarified only the one-way effects of environmental factors on shoot dynamics. By contrast, only a few empirical studies (e.g., [6]) have quantified the effect of shoot dynamics on light environments, despite the importance of these effects having long been recognized in theoretical studies [1,4,5,8]. Therefore, further empirical studies of this two-way interaction are needed.

In this study, we investigated the two-way interactions between the within-crown light environment and shoot dynamics of saplings of five temperate, winter-deciduous woody plants that included fast- and slow-growing species grown in open, well-lit places. We tested the hypothesis that light foraging by organ redeployment from shaded regions into better-lit regions of a canopy, an idea well supported for leaves, also applies to shoots. We also expected that the interaction between shoot dynamics and light environments would be greater for fast-growing species than for slow-growing species because of their difference in shoot production and survival rates.

2. Materials and Methods

2.1. Study Species

We investigated saplings of five temperate, winter-deciduous tree species, all of which are native to Japan. The alder (*Alnus sieboldiana* Matsum.) is a nitrogen-fixing [48] pioneer species that grows in open habitats after disturbances [49]. Its higher photosynthetic rates than those of typical slow-growing species [50] indicate that this is a fast-growing species because the photosynthetic rates of leaves and whole-tree growth rates are positively correlated [51–53]. The Japanese chestnut (*Castanea crenata* Siebold & Zucc.) is an early-successional species that regenerates in sunny places [54]. In this study, we classified *A. sieboldiana* and *C. crenata* as fast-growing species based on their growth rates (see Results). The Russian rock birch (*Betula ermanii* Cham.) is an early-successional species, and its leaves have higher photosynthetic rates than those of typical late-successional species [55]. Thus, we classified *B. ermanii* as a medium-growth-rate species. *Acer distylum* Siebold & Zucc. is a shade-tolerant sub-canopy species [56] found in climax beech forests [57]. Although it can tolerate a shaded understory, this species also can grow rapidly in gaps [58]. Siebold's beech (*Fagus crenata* Blume) is a shade-tolerant [59] and late-successional [55] species that dominates in cool-temperate climax forests in Japan [60]. The leaves of this species have lower photosynthetic rates than those of typical early-successional species [55,61–64]. *A. distylum* and *F. crenata* were classified herein as slow-growing species.

2.2. Study Sites and Sample Trees

The current study was conducted from 2002 to 2003 at two study sites in Japan. To ensure that the number of current-year shoots measured for each species exceeded 300, which we believed to be sufficient to describe species-specific patterns, we examined three to six saplings of each species (Table 1). Saplings of *A. sieboldiana*, *C. crenata*, and *F. crenata* were investigated at the experimental garden of, or a plantation adjacent to, the Center for Ecological Research (CER), Kyoto University (34°58′ N, 135°57′ E, 150 m asl). The mean annual temperature and precipitation at this location are 14.6 °C and 1618 mm, respectively (years 2006–2010; data from CER). Saplings of *B. ermanii* and *A. distylum* were investigated in a nursery at the Kamigamo Experimental Forest Station (KEFS), Kyoto University (35°04′ N, 135°46′ E, 140 m asl), which is approximately 21 km from CER. The mean annual temperature and precipitation at KEFS are 14.6 °C and 1580 mm, respectively (years 1971–2000; data from KEFS). Therefore, the two study sites had very similar temperatures and precipitation. All of the saplings investigated in the study were grown in open, well-lit places.

Table 1. Sample sizes of current-year shoots from the saplings of different species of trees.

	Alnus sieboldiana	*Castanea crenata*	*Betula ermanii*	*Acer distylum*	*Fagus crenata*
No. of saplings	3	3	3	6	4
Tree height (m)	0.81–1.03	0.95–1.13	0.61–0.81	0.86–1.72	0.81–1.02
No. of shoots for the shoot census [1]	581	425	318	325	343
No. of shoots for the leaf census [1]	189	251	259	288	339

[1] Total number of current-year shoots from all saplings of each species that we investigated.

2.3. Shoot Census

For each sapling, we identified and periodically investigated all the current-year shoots that appeared in 2002 (Table 1, Figure 1). In 2002, we measured the length of each shoot after it had completely elongated. Shoot lengths (i.e., the annual shoot elongation) and the number of vegetative buds (i.e., the production of daughter shoots) were used as indices of the growth rates of each shoot. For *A. sieboldiana*, *C. crenata*, and *A. distylum*, we observed sylleptic shoots: lateral buds that grew from current-year shoots within the same year. All of these were regarded as part of their parent (proleptic) shoots, and the lengths and numbers of vegetative buds of the sylleptic shoots were summed with those of their parent to calculate the annual shoot elongation and bud production of the parent shoot. In April 2003, we evaluated the survival of each shoot. A shoot was defined as alive if it had at least one living bud (vegetative or flower bud). A shoot was defined as dead if it had been shed before April 2003 or if it lacked any living bud in April 2003.
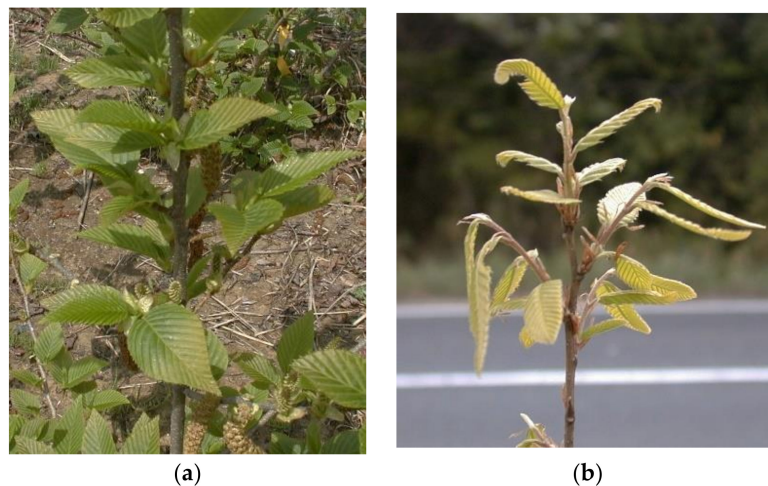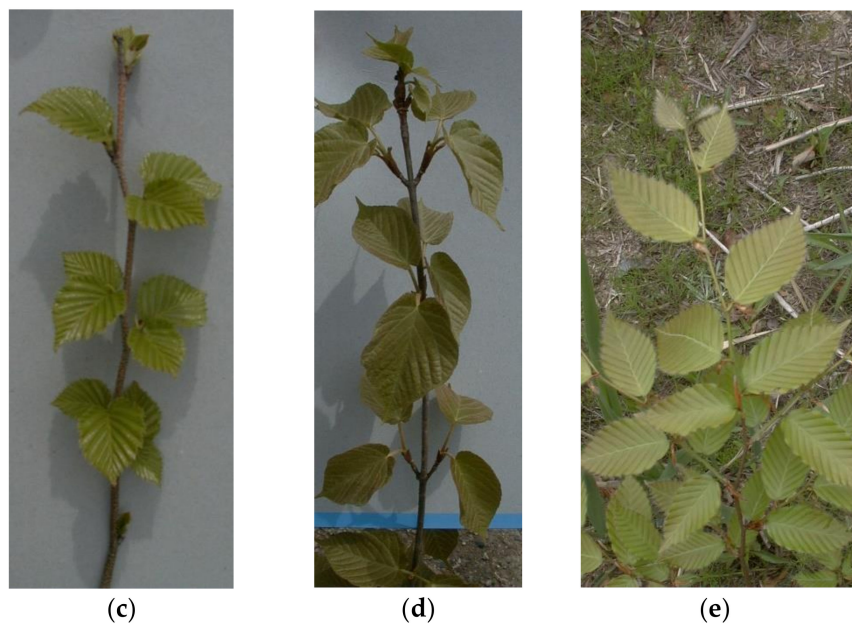

(a)   (b)

Figure 1. *Cont.*

Figure 1. Young shoots of (**a**) *Alnus sieboldiana*, (**b**) *Castanea crenata*, (**c**) *Betula ermanii*, (**d**) *Acer distylum*, and (**e**) *Fagus crenata* (photographs captured in April 2002 by Hiroyuki Shirakawa).

2.4. Leaf Census

From bud break (late March 2002) to completion of leaf fall (late January 2003), we periodically investigated all leaves of the selected shoots of each species (Table 1) and recorded the numbers of leaves that appeared from these shoots every one or two weeks. The date of leaf emergence was postulated to be the midpoint between the date of a previous observation and the date that a new leaf was observed [65]. For each shoot, we calculated the shoot elongation period as the time between the emergence of the first and last leaf (i.e., the leaf emergence period calculated for each shoot). All leaves on the monitored shoots of *F. crenata* emerged as a flush within seven days between two successive census days (8 and 15 April 2002). The shoot elongation period of *F. crenata* was therefore estimated at 3.5 days.

2.5. Measurement of Light Environments

We measured the light environment within each crown for all the current-year shoots of the studied saplings. For the two fast-growing species (*A. sieboldiana* and *C. crenata*), which had indeterminate growth patterns, we investigated seasonal changes of the light environment within each canopy by conducting the same measurements twice during the same growth period in 2002 for all the shoots. The first measurement was taken in June or July, when almost all of the current-year proleptic shoots had emerged, but their elongation (including elongation of their sylleptic shoots) was not yet complete. The second measurement was conducted in September, when the elongation of almost all of the shoots was either complete or nearly so. For the other three medium- or slow-growing species, the measurements were conducted once, between June and September, when the elongation of most of the shoots was complete or nearly so (the dates of the measurements for each species are shown in the Results). We conducted the measurements from 11:00 to 13:00 local time on overcast days. On each measurement day, we used two quantum sensors (IKSX-7/101; Koito Manufacturing, Tokyo, Japan) to measure the photosynthetic photon flux density (PPFD) simultaneously. One sensor was fixed horizontally to a pole at the top of each tree. Light conditions at the tops of the trees in the open experimental gardens were nearly the same as those in the open full-lit location. Another sensor was fixed horizontally at the top of each shoot [46,66] with a hand-held measuring bar, as described in Muraoka et al. [67,68] (Figure 2). The investigators took care so as to not shade the sensor. We calculated the relative PPFD (rPPFD) as the ratio of the PPFD at the tip of each shoot to the PPFD at the top of the

tree [46]. A previous study demonstrated that rPPFD measured on the horizontal surface at the tip of a branch represents the average light environment of that branch because it is highly correlated with the mean rPPFD of distal-to-proximal secondary shoots on that branch [46]. Therefore, we used the rPPFD at the tip of each shoot as a representative value for the average light environment of that shoot.
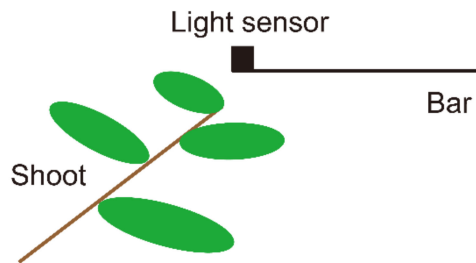

Figure 2. A schematic diagram demonstrating the measurement of light environments of different shoots in this study. A sensor was fixed horizontally with a hand-held measuring bar. (Illustration by Kohei Koyama).

Some sylleptic shoots emerged after the first measurements (June–July) and were considered part of their parent proleptic shoots. Therefore, if a proleptic shoot had sylleptic shoots, the continuum of proleptic–sylleptic shoots of the same age (i.e., those shoots that emerged within the same growth period) was considered as one current-year shoot. In that case, the top of that current-year shoot was measured in the second measurement. In the case of a shoot that had been shed prior to the second measurements, we measured the PPFD at the approximate prior position of the shoot tip (estimated from its length).

We analyzed the effect of rPPFD that was obtained at the first measurement on each shoot for each species on the subsequent survival of that shoot in April 2003 using a generalized linear mixed model (GLMM) with the function *glmer* (binomial (link = "logit")) [69] and R software v4.0.3 (Vienna, Austria) [70]:

$$\ln\left(\frac{y}{1-y}\right) = a + bx + r \Leftrightarrow y = \frac{\exp(a + bx + r)}{1 + \exp(a + bx + r)} \Leftrightarrow y = \frac{1}{1 + \exp(-a - bx - r)}, \tag{1}$$

where y is the survival of that shoot in April 2003 (0 = dead, 1 = survived), x is the fixed effect (rPPFD), a and b are the coefficients estimated by the *glmer*, and r is the random intercept (individual tree). The significance of the fixed effect of rPPFD (coefficient b) was tested by a likelihood ratio test with the R function *anova* (test = "Chisq") by comparing Equation (1) with the null model with no rPPFD dependence ($b = 0$).

As mentioned, for the two fast-growing species, we conducted the PPFD measurements twice (i.e., the early (June or July) and the late (September) stages) in 2002 for the same set of shoots. The survival of the shoots was monitored until April 2003. The shoots were then assigned to one of two groups: (1) survivor group, those that survived until April 2003, or (2) dead group, those that had died by April 2003. We performed two types of comparisons (A and B) as follows. (A) Using all of the shoots from the survivor and dead groups, we compared the early versus late environments within the same growth period in 2002 within each tree crown. We expected that because of the rapid and indeterminate growth of the fast-growing species, the later-stage shoots would experience an inferior light environment compared with the early-stage shoots. This expected result would indicate that rapid growth causes an increment of self-shading. (B) We compared all the shoots at the early stage with the rPPFD of the survivor group shoots at the late stage. The survivor group shoots at the late stage were considered to be the shoots for the next year. Finally, we compared the difference in the results between (A) and (B). We hypothesized that any difference between (A) and (B) would indicate an effect of shoot shedding on the within-crown light environment. We expected that shoot deaths would counter the development of self-shading by the selective shedding of shaded shoots. For these

two types of comparisons, we tested the differences in the two distributions of rPPFD (early versus late) with two-sample Kolmogorov–Smirnov tests using R software. All of the datasets used in this article are available online as Supplementary Materials.

3. Results

3.1. Growth Rate and Pattern

Table 2 summarizes the results of the growth and survival rates of the shoots. The shoot elongation period was longest for the fastest-growing species (*A. sieboldiana*), which showed typical indeterminate growth and successive emergence of leaves (Figure 3). By contrast, the elongation period was shortest for the slowest-growing species (*F. crenata*), which displayed typical determinate growth and a flush of leaf emergence during a very short time. The remaining species showed intermediate patterns. *C. crenata* experienced three flushes of leaf emergence, while *B. ermanii* and *A. distylum* showed one flush of emergence of early leaves and the successive emergence of late leaves.

Table 2. Growth and survival rates of the shoots.

	A. sieboldiana	*C. crenata*	*B. ermanii*	*A. distylum*	*F. crenata*
Species category	Fast	Fast	Medium	Slow	Slow
Annual shoot elongation [1,2] (cm year^{-1})	26.9	8.0	4.4	1.5	2.2
Shoot elongation period (days) [1]	156	33	18	8	3.5
Number of daughter buds per shoot [1,2,3]	5.1	2.7	1.9	1.1	1.1
Shoot survival rate	0.54	0.78	0.88	0.93	0.98

[1] Mean values for each species. [2] The lengths of sylleptic shoots and the number of their vegetative buds were summed with those of their parent proleptic shoots. [3] Shoots without vegetative buds were not included.
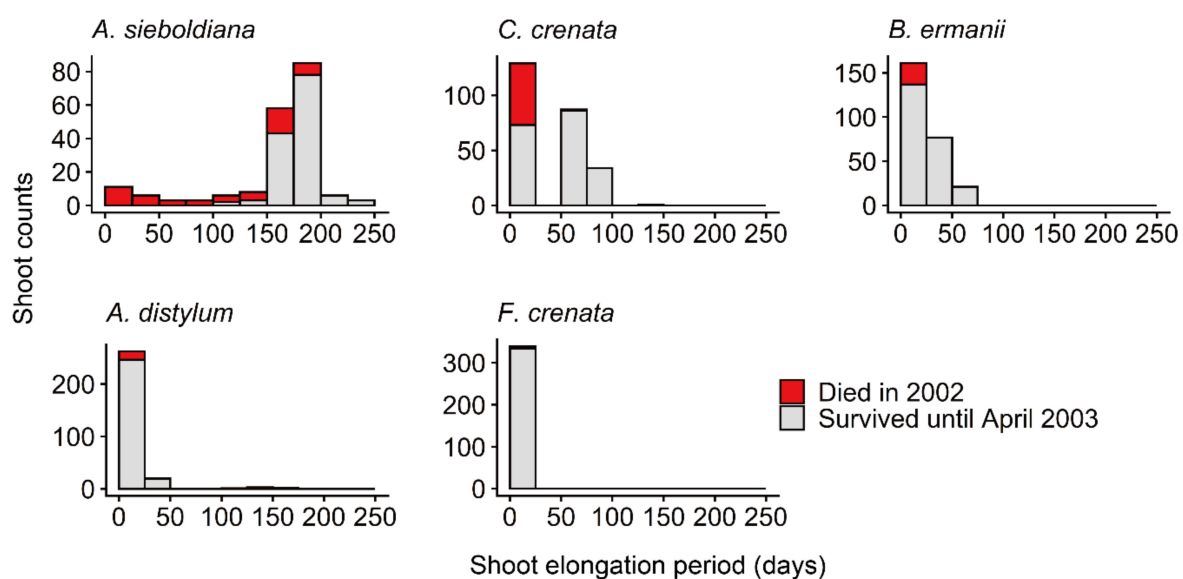

Figure 3. Histogram of shoot elongation period. The shoot elongation period is defined as the time interval between the emergence of the first and last leaves.

3.2. Shoot Survival

The shoot survival rate was lower for the fast-growing species than for the slow-growing species (Table 2). The shoots in the shaded part of the canopy of the two fast-growing species (*A. sieboldiana* and *C. crenata*) experienced a high mortality rate (Figure 4, Table 2). By contrast, the shoots of the slow-growing species (*A. distylum* and *F. crenata*) experienced a low mortality rate at all positions within the canopy, regardless of the light environment (Figure 4, Table 2). The mortality rate of the shoots of the medium-growth-rate species (*B. ermanii*) was intermediate between these two extremes (Figure 4, Table 2). Logistic regression analysis demonstrated that those shoots located in a low-rPPFD

environment were significantly less likely to survive than shoots located in a high-rPPFD environment in fast-growing (*A. sieboldiana* and *C. crenata*, $p < 0.001$) and medium-growth-rate species (*B. ermanii*, $p < 0.001$), but not in slow-growing species (*A. distylum*, $p = 0.54$; *F. crenata*, $p = 0.45$).
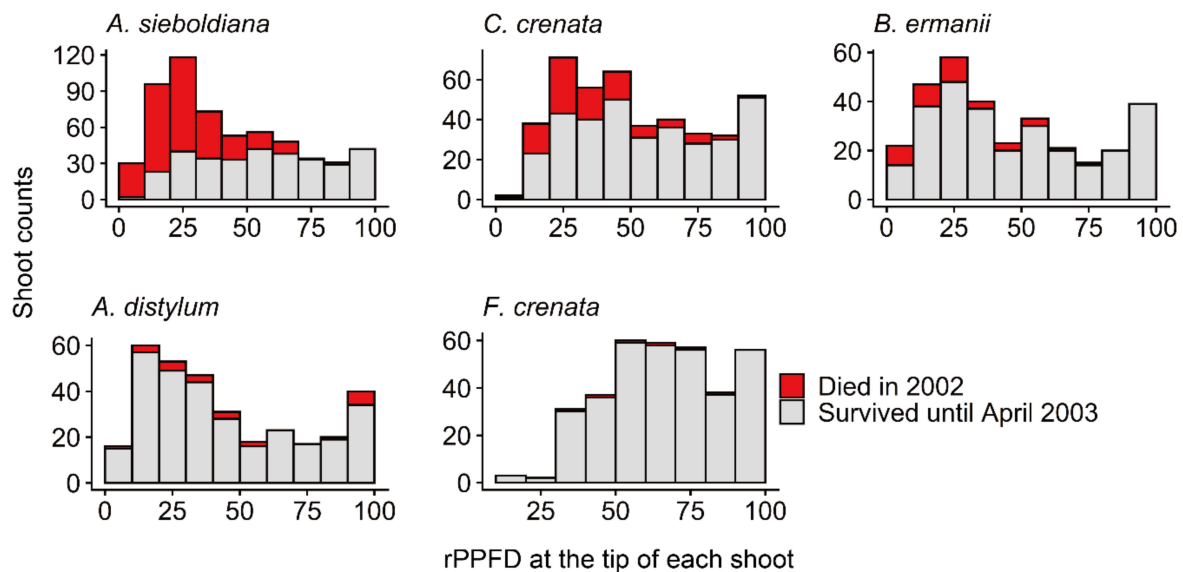

Figure 4. Relative photosynthetic photon flux density (rPPFD) at the shoot tips in summer and autumn in 2002 and number of surviving or dead shoots in April 2003. Dates of rPPFD measurements in 2002 are as follows: *A. sieboldiana*, 15–24 June; *C. crenata*, 19 July; *B. ermanii*, 17 June; *A. distylum*, 4 August–1 September; *F. crenata*, 27 August–26 September.

3.3. Light Environment

The long shoot elongation periods observed for the two fast-growing species caused the development of self-shading during a single growth period. Shoots of the two fast-growing species (*A. sieboldiana* and *C. crenata*) experienced significantly more self-shading in the late stage than the early stage of the same growth period ($p < 0.001$; Figure 5a). Nonetheless, the light environment in the later stage of growth experienced by the shoots that survived until April 2003 (i.e., the shoots for the next year) was similar to the one experienced by all the shoots in the early stage (Figure 5b). For both of the fast-growing species, the light distributions during the two stages did not differ significantly (*A. sieboldiana*, $p = 0.48$; *C. crenata*, $p = 0.10$; Figure 5b).
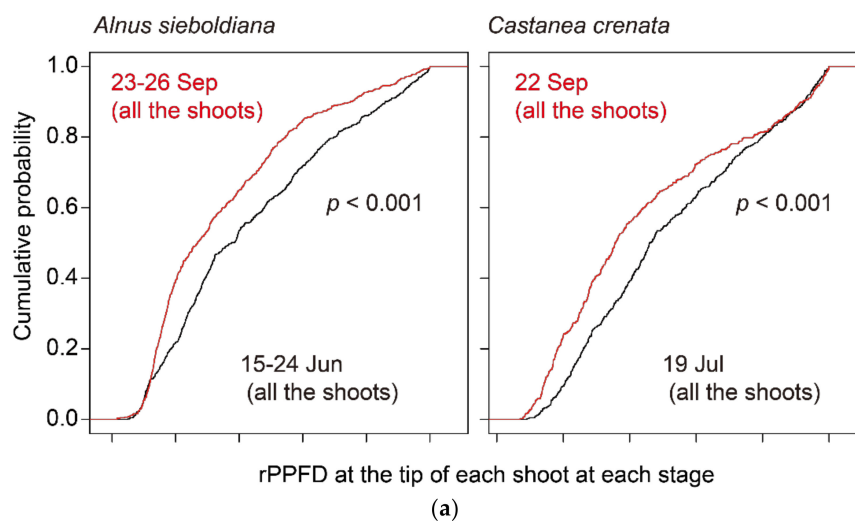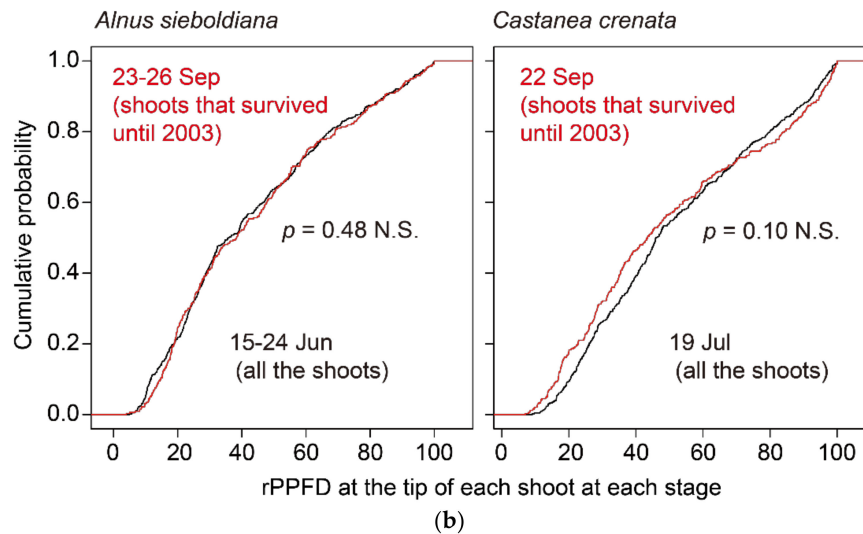

(**a**)

Figure 5. *Cont.*

Figure 5. Comparison of the light environments between the first (early stage of the growth period, black curves) and the second (late stage, red curves) measurements illustrated by empirical cumulative distribution functions. (**a**) All the shoots were analyzed for both stages. (**b**) All the shoots were analyzed for the early stage, and only the shoots that survived until April 2003 were analyzed for the late stage. *p*-values are the results of two-sample Kolmogorov–Smirnov tests, which were used to determine whether the difference between each pair of distributions (early vs. late) was significant. N.S., not significant.

4. Discussion

The high metabolic activities of plant organs are generally associated with their fast turnover rates and short lifespans [71]. We observed that the shoot growth and mortality rates were higher for the fast-growing species than for the slow-growing species. Recent advances in plant ecophysiology have led to the concept of a "plant economics spectrum," a covariation of a suite of traits that can be largely explained by a position on the single axis of fast versus slow strategies [71]. The core relationships in the economics spectrum are the negative correlations between trait values associated with productivity (e.g., higher growth rate, higher leaf photosynthetic rate) and those associated with persistence (e.g., slow turnover rate, mechanical stability, longer lifespan). This growth–persistence trade-off has been reported both at the organ level (e.g., "leaf economics spectrum" [72], "wood economics spectrum" [73], "root economics spectrum" [74]) and at the whole-plant level (fast vs. slow strategies or "plant economics spectrum") [51,71,75–77], based on the rationale that more active organs afford individuals with better whole-plant growth rates at the expense of lower survival rates [1,51,73,75,78,79]. Such trade-offs have been found across different taxa, including different vascular plant groups [51,71–78], ferns [80], and mosses [81]. Similar trade-offs have also been observed in interspecific comparisons globally [72,73,82] and locally [55,83–85]. Analogous trade-offs have been quantified at intraspecific levels as well [86].

Two major theories have been proposed to explain the negative correlation between growth and survival rates. The first is the physiological constraints theory, which states that an organ or an individual cannot attain both high productivity and high persistence [87,88]. Such a trade-off may arise because of the selective investment of resources between traits related to high activity and those related to persistence [71,75,89]. For example, an investment of nutrients into the photosynthetic apparatus enhances photosynthetic rates [90] at the expense of investment in defense chemicals that reduce herbivory [75] or into mechanical toughness [91]. Likewise, stems comprising dense wood with narrow conduits are durable but may be less effective at transport [88] (but see [73]). Thus far, the physiological constraints underlying growth–persistence trade-offs have been intensively studied both theoretically [92] and empirically [73,91,93]. The second explanation for the negative correlation between growth and survival rates is the theory of optimal longevity (TOL): an organ should be replaced

at an optimal time to maximize whole-plant carbon gain [9,29,31,38–40,94–96]. The key idea is that plant organs should be continuously moved into more productive environments [9,29,31,39,40,71,97] because a plant generally competes with its neighbors for light [25,26,71]. The production and deployment of new leaves and shoots into better-lit positions cause self-shading of the shaded inner part of the plant canopy [1,28,36] resulting in the death of the shaded leaves or shoots [1,3,9,29,30,39,97]. Such organ redeployment would be faster if the plants or shoots were growing faster [3,9,14,31,36,65,97]. TOL predicts that a higher growth rate is one of the reasons for a shorter organ lifespan. The two theories are not mutually exclusive, and the difference between them is a difference between proximate and ultimate or evolutionary factors [98].

Previous studies of shoots, however, have focused primarily on testing physiological constraints (i.e., causes of short organ lifespan), whereas few studies [13,40] have directly investigated the consequences of a shortened organ lifespan. Specifically, although the concept of the economics spectrum may apply to any organ [71], quantitative assessment of the TOL is limited to leaves [39,99] or fine roots [100]. It has been suggested that TOL can also be applied to shoots [40,101]; however, those studies did not quantitatively evaluate the effects of shoot shedding on light environments within crowns. Our results quantitatively demonstrated a consequence of rapid shoot shedding; i.e., redeployment of shoots into better-lit positions within a tree crown. The present results are consistent with the predictions of TOL, which, to date, have been thoroughly tested with leaves but not with shoots.

Based on the wood economics spectrum theory [73], we analyzed the wood density of four of the five species from the published literature and reconfirmed the predicted relationship [73] that the shoot survival rate is higher for species with higher wood density (Figure 6). A recent study [102] further proposed that a variation in crown structure (e.g., those maximizing light capture vs. those maximizing vertical growth) can be considered a new trait trade-off continuum: the structural economics spectrum [102]. This spectrum can be integrated with the previously described concepts of the leaf and wood economics spectra [102], in which the turnover rate of organs (i.e., leaf lifespan) plays a central role as an indicator of plant strategy [71–73]. Quantitative results regarding the consequence of organ turnover on the crown structure and light environment, such as those presented in this study, would be useful for investigating the suggested linkage among those economics spectra in future studies.
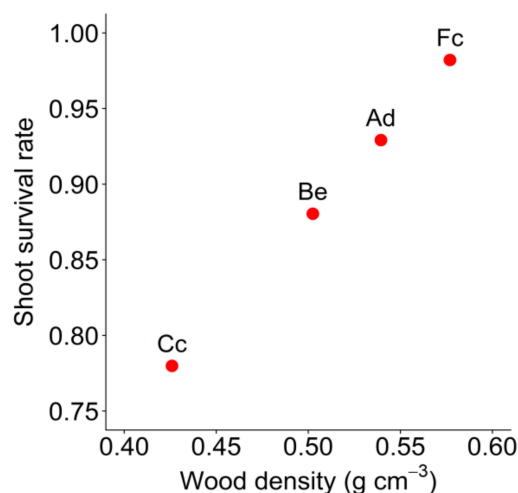

Figure 6. Shoot survival rates in relation to wood density. Fc: *Fagus crenata* (data from [24]); the original publication contained a typographical error (the same numbers were expressed in the wrong units [kg m^{-3}], and therefore the correct units [g cm^{-3}] have been used here, based on personal communication with the first author of [24]). Ad: *Acer distylum* (calculated from values in [103]), Be: *Betula ermanii* (data from [104]), and Cc: *Castanea crenata* (data from [24]). The wood density of *A. sieboldiana* was not found in our literature survey.

A simulation that was based on a dynamic functional-structural model [1] suggests that the death of shade shoots among shaded understory saplings is merely a passive response to the negative carbon balance of shaded shoots. Later, Laurans and Vincent [6] conducted an empirical study to test that suggestion. Their results showed that shoot shedding was not accelerated, whereas shoot production was suppressed for saplings in more heavily shaded understories than the conspecific individuals in less-shaded gaps. Laurans and Vincent [6] intentionally excluded pioneers that grew only in open habitats from their experimental design because their objective was to clarify how the suppression of shoot production in the shade and the long lifespan of the branches of shade-tolerant species determined crown morphological variation as a mechanism of shade tolerance. However, neither of those previous studies [1,6] clarified the consequences of shoot shedding on the within-crown light environment of vigorously growing trees in open, well-lit places. In the present study, we focused on plants in high-light environments, in which the continuous production and growth of shoots are expected. Our results, therefore, cannot be directly compared with those of these previous studies. In contrast to the cases of trees, there have been many results from experiments on herbaceous species grown in well-lit places that clarified the consequences of leaf shedding on the within-canopy light environment (e.g., [9,28–30,39]). These studies reported the function of the redeployment of leaves from shaded into well-lit places. Thus, our results of the shoot redeployment process observed in open, well-lit experimental gardens are more similar to the results of herbaceous species in open places than to the results of woody species in shaded understories.

Our study had several limitations. First, we monitored the trees for only a short time. The shoot mortality rate of the slow-growing trees was very low during the single growth period investigated in this study. It has been reported that late-successional old trees maintain their within-canopy structure by continuously replacing branches [105]. The implication may therefore be that fast- and slow-growing species maintain their within-crown light environments by replacing shoots rapidly and slowly, respectively. Further studies that monitor trees for more extended periods of time are therefore needed. Second, competition with neighbors was excluded in our experiment, which involved growing each sapling in an isolated condition. Nonetheless, the development of a tree crown in a real stand is also affected by competition with neighboring trees [102,106,107] and shading by a surrounding forest canopy [1,4,6,8]. Further studies are therefore needed before the present results can be generalized to real forest conditions.

5. Conclusions

We demonstrated the first empirical evidence that production and shedding of shoots for the saplings of fast-growing woody plants in high-light environments are part of a process of the redeployment of shoots into better-lit parts of the crown, similar to the redeployment of leaves. By contrast, the slow-growing trees displayed slow and determinate growth, with a low mortality rate of the shoots at all positions in the crown. These results indicate that fast- and slow-growing species maintain their within-crown light environments by replacing shoots rapidly and slowly, respectively.

Data Availability Statement: The data presented in this study are available in the Supplementary Materials.

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