Seasonal pattern of leaf production and its effects on assimilation in giant summer-green herbs in deciduous forests in northern Japan

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Abstract: Understory vegetation of northern deciduous forests in far eastern Asia is characterized by giant summer-green herbs. We examined the patterns of height growth, leaf accumulation, photosynthetic characteristics, daily net assimilation, and dry matter allocation within aboveground parts of six giant summer-green herbs with reference to light conditions in deciduous forests. Plant height, leaf number, and total leaf area per plant increased with progressing tree-canopy closure in five species (*Cacalia hastata* L. subsp. *orientalis* Kitam., *Cirsium kamtschaticum* Ledeb., *Filipendula kamtschatica* (Pall.) Maxim. f. *kamtschatica*, *Senecio cannabifolius* Less., and *Urtica platyphylla* Wedd.) that had continuous leaf production throughout the growing season, whereas one species (*Veratrum album* L. subsp. *oxysepalum* Hulten) with early leaf production, completed leaf production mostly before the beginning of tree-canopy closure. Maximum photosynthetic and dark respiration rates decreased seasonally in all species. Species with continuous leaf emergence accumulated leaves acclimatized to shade conditions, which offset the decreasing photosynthesis of individual leaves with progressing tree-canopy closure, resulting in stable carbon gain even under decreasing light availability. In contrast, *V. album* assimilated vigorously during the short period of high irradiance before tree-canopy closure, and decreased its assimilation rate continuously thereafter.

Key words: continuous leaf production, early leaf production, giant summer-green herb, net assimilation rate, photosynthetic rate, tree-canopy closure.

Résumé : La végétation de sous bois des forêts nordiques décidues de l'Asie orientale est caractérisée par de grandes herbacées vertes en été. Les auteurs ont examiné les patrons de la croissance en hauteur, l'accumulation des feuilles, les propriétés photosynthétiques, l'assimilation quotidienne nette, et l'allocation de la matière sèche dans les parties épigées de six grandes herbacées vertes en été, en relation avec les conditions de lumière en forêts décidues. La hauteur des plantes, le nombre de feuilles, et la surface foliaire totale par plante augmentent avec une fermeture progressive de la canopée arborée, chez cinq espèces (*Cacalia hastata* L. subsp. *orientalis* Kitam., *Cirsium kamtschaticum* Ledeb., *Filipendula kamtschatica* (Pall.) Maxim. f. *kamtschatica*, *Senecio cannabifolius* Less., et *Urtica platyphylla* Wedd.). Ces espèces possèdent une production foliaire continue et complètent leur production foliaire tout au long de la saison de croissance. Cependant, le *Veratrum album* L. subsp. *oxysepalum* Hulten, ayant une production foliaire précoce, complète sa production de feuilles avant le début de la fermeture de la canopée arborée. Les taux maximums de photosynthèse et de respiration à l'obscurité diminuent saisonnièrement chez toutes les espèces. Les espèces à émergence foliaire continue accumulent des feuilles adaptées aux conditions ombragées, ce qui compense pour la diminution de la photosynthèse des feuilles individuelles, à mesure que la canopée arborée se ferme; ceci conduit à un gain en carbone constant, même sous des conditions de moindre disponibilité de la lumière. Au contraire, le *V. album* assimile activement au cours de la courte période de fort éclairement précédant la fermeture de la canopée arborée, et diminue continuellement son taux d'assimilation, par la suite.

Mots clés : production continue de feuilles, production précoce des feuilles, grandes herbacées vertes en été, taux net d'assimilation, taux de photosynthèse, fermeture de la canopée arborée.

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Introduction

Summer-green herbs inhabiting temperate deciduous forests often start to grow before the leaf flush of canopy trees and retain their leaves after tree-canopy closure. This indicates that they utilize both the short light-abundant season of early spring and the light-limited season under the closed tree-canopy of summer (Hicks and Chabot 1985). These summer-green herbs show high maximum photosynthetic rates in early spring that decrease with progressing tree-canopy closure from spring to summer (Taylor and Pearcy 1976; Koizumi and Oshima 1985; Yoshie and Yoshida 1987; Graves 1990; Rothstein and Zak 2001). Thus, it might be beneficial for these herbs to concentrate their carbon production during the short period of abundant light in early spring (Rothstein and Zak 2001), as do spring ephemeral plants (Taylor and Pearcy 1976; Mahall and Bormann 1978; Hicks and Chabot 1985; Lapointe 2001).

Many summer-green herbs inhabiting temperate deciduous forests have a relatively small aboveground structure (50–60 cm in height, Kawarasaki and Hori 2001). However, some summer-green herbs growing in northern deciduous forests in far eastern Asia have large aboveground structures, sometimes reaching above 2 m. Because the construction and maintenance of tall plant structures requires large carbon investments, it is possible that these giant summer-green herbs undergo longer periods of efficient carbon gain than small summer-green herbs.

Plant productivity depends not only on the photosynthetic rate per unit leaf area but also on the cumulative leaf area per plant (Björkman 1981). Thus, we predict that if giant summer-green herbs are able to accumulate a large vertical leaf area, a positive carbon balance might be maintained under light-limited conditions within a closed tree-canopy, even though the actual photosynthetic rate per unit leaf area decreases. However, the effectiveness of leaf accumulation might depend on the patterns of leaf production and photosynthetic acclimation to dark conditions because lower leaves are shaded by upper leaves of own and other plants (Jurik and Chabot 1986; Sakai 1991; Kikuzawa et al. 1996; Yamada et al. 2000; Kikuzawa 2003).

To test this hypothesis, we studied six giant herb species with early or continuous leaf production. First, patterns of height growth and leaf accumulation per plant were examined with reference to changes in seasonal light availability on the floor of deciduous forests in northern Japan. In addition to the light conditions under the tree-canopy layer, we also assessed the light distribution within herb layers. Second, seasonal changes in photosynthetic characteristics were measured along vertical foliage stratifications of individual plants, then seasonal transitions in net assimilation rates of individual plants were estimated. We then combined the seasonal dynamics of light conditions and leaf development processes into a simulation of carbon gain per plant. This has been attempted only rarely in the past, although the carbon gain of wild plants has been simulated in several studies (Botkin 1969; Mooney 1972; Cunningham et al. 1974; Tenhunen et al. 1980; Young and Smith 1982; Gross 1986; Jurik and Chabot 1986; Graves 1990). Because the points of interest of this study were patterns of leaf accumulation and production processes during the height growth period, the growth census was conducted only until plants achieved their maximum heights.

Since the construction of tall structures is likely to be costly with regard to support organs (stems and petioles), at the expense of allocation to assimilatory organs (leaves) (Givnish 1982, 1987; Sakai 1994), we also predict that giant summer-green herbs are able to reduce the cost of support organs. Therefore, we also determined the relationship between the dry weight allocation of assimilatory and non-assimilatory organs to evaluate the cost of constructing tall structures.

Materials and methods

Study sites and plant materials

The study was conducted in two lowland deciduous forests in Nopporo Forest Park (NFP; 43°2′N, 141°31′E, 80 m elevation) and Tomakomai Experimental Forest of Hokkaido University (TOEF; 42°41′N, 141°36′E, 30 m elevation), Hokkaido, northern Japan. Dominant trees were *Fraxinus mandshurica* var. *japonica* and *Ulmus davidiana* var. *japonica*, and *Acer mono* and *Quercus crispula*, respectively, and predominant understory species were *Veratrum album* and *Polystichum tripteron*, and *Dryopteris crassirhizoma* and *Pachysandra terminalis*, respectively. Snow usually disappears around 10 April in both areas.

Six species of giant summer-green herbs were studied: *Cacalia hastata* L. subsp. *orientalis* Kitam. (Asteraceae), *Cirsium kamtschaticum* Ledeb. (Asteraceae), *Filipendula kamtschatica* (Pall.) Maxim. f. *kamtschatica* (Rosaceae), *Senecio cannabifolius* Less. (Asteraceae), *Urtica platyphylla* Wedd. (Urticaceae), and *Veratrum album* L. subsp. *oxysepalum* Hulten (Liliaceae). Leaf production of *V. album* occurs simultaneously early in the growing season, whereas production in the remaining five species is continuous. *F. kamtschatica* was observed in NFP in 2002, *C. kamtschaticum* and *V. album* were observed in NFP in 2003, *S. cannabifolius* and *U. platyphylla* were observed in TOEF in 2003, and *C. hastata* was observed in TOEF in 2004. All species commonly grow in deciduous forests, and have a vertical stem and numerous leaves at different heights. Aboveground parts emerge in spring soon after snowmelt, and flowering occurs in mid summer. *V. album* is sometimes classified as a spring ephemeral because of its relatively short leaf longevity compared with typical summer-green herbs (see Results). Non-flowering plants of this species have pseudo-stems composed of transformed petiole bases.

Light

Hourly cumulative solar radiation was measured in each plot during the stem extension period at the top of the herb layer, 200 cm above the soil surface, using a quantum sensor (PCM-01L, Prede, Tokyo, Japan) connected to a data logger (KADEC-UP, Kona System, Sapporo, Japan). Measurements were conducted from 1 May to 20 July 2002 and 26 April to 4 July 2003 in NFP, and from 3 May to 5 July 2003 and 21 April to 15 July 2004 in TOEF. Seasonal changes in radiation were fitted to a logistic curve with four parameters for each plot and each year, in which the radiation on day x can be written as:

$$\text{Radiation}(x) = \text{Rad}_{\max} + K/(1 + e^{\frac{C-x}{r}})$$

where $\text{Rad}_{\max}$ is the average daily mean solar radiation for the first 5 d, K is a negative value indicating the difference between the asymptotic minimum and maximum irradiance, C represents the day at the inflection point of the curve, and r is a numeric scale parameter on the x axis. Based on the fitted curves, initiation and completion of tree-canopy closure were defined as the days on which the radiation decreased to 95% and 5% of the maximum value, respectively. We defined the "tree-canopy closing period" as the number of days from the beginning to completion of tree-canopy closure.

Relative light intensity within the herb layer, i.e., at a height of 0–200 cm, was estimated based on hemispherical whole-canopy (total foliage of tree-canopy and herb layer) photographs taken at randomly selected four points per plot

at 25 cm intervals from 25 to 200 cm above the ground using a digital camera (Coolpix950, Nikon, Tokyo, Japan) with a fish-eye lens (FC-E8, Nikon, Tokyo, Japan). Photographic points were randomly selected at the first measurement in each plot, and the same points were used throughout. Photographs were taken 11–15 times at 5–8 d intervals from 28 April to 29 July 2000 in NFP, and from 29 April to 30 July 2000 in TOEF; all were taken during daytime (10:00–14:00) on cloudy days or in the evening just before sunset on sunny days. Digital images of the whole-canopy hemisphere were analyzed using PC software (Gap Light Analyzer, Simon Fraser University, Burnaby, British Columbia, Canada and Institute of Ecosystem Studies, Millbrook, New York, USA) to calculate the degree of whole-canopy openness.

Patterns of height growth and leaf expansion

Plant height, numbers of living leaves, and the sum of living leaf lengths per plant were measured in three randomly selected plants per species. Measurements were conducted from 3 May to 16 June 2002 for *F. kamtschatica*, from 16 May to 2 July 2003 for *U. platyphylla* and *S. cannabifolius*, from 18 May to 26 June 2003 for *V. album* and *C. kamtschaticum*, and from 10 May to 21 June 2004 for *C. hastata*. Because it took 2–3 weeks for complete leaf expansion from first leaf emergence in these species, measurements were started at the time of full expansion of first leaves. Measurements were made at 7–15 d intervals for all species. All sampled plants of the five species with continuous leaf production set flowers. In contrast, no plants of *V. album* set flowers in the observation year although they grew taller than 80 cm, corresponding to the adult size in this population. Undeveloped leaves yet to fully expand were included in the height measurements but excluded from the counts of leaf number and measurements of leaf lengths. Cumulative leaf area per plant was calculated based on the allometric relationships between the leaf length (*L*, cm) and leaf area (*A*, cm^2) of individual leaves, which were preliminarily examined using 18–30 leaves from 6–10 plants of each species in mid-June 2001. The following allometric relationships were observed using quadratic regression passing through the origin: $A = 0.462L^2$, $N = 18$, $R^2 = 0.97$ for *C. hastata*; $A = 0.326L^2$, $N = 30$, $R^2 = 0.97$ for *C. kamtschaticum*; $A = 0.929L^2$, $N = 18$, $R^2 = 0.96$ for *F. kamtschatica*; $A = 0.263L^2$, $N = 30$, $R^2 = 0.92$ for *S. cannabifolius*; $A = 0.318L^2$, $N = 28$, $R^2 = 0.91$ for *U. platyphylla*; and $A = 0.414L^2$, $N = 18$, $R^2 = 0.98$ for *V. album*.

Measurements of light-response photosynthetic curves

Photosynthetic CO_2 gas exchange of individual species was measured on the same days and with the same three plants as the census of height and leaf development using a LI-6400 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA). The number of leaves used to measure photosynthesis increased from one to three per plant (taken from lower, middle, and upper parts of the plants) with height growth of species with continuous leaf production, while for the species with early leaf production, *V. album*, photosynthetic rates were measured using three leaves per plant (from lower, middle, and upper parts) throughout the

growing season. Light-response curves of photosynthetic rates were generated for each leaf under a selected temperature (20 °C). In a preliminarily measurement in 2000, the daily mean maximum temperatures during a week around 10 May and 30 June, corresponding to the first and last measurement dates of photosynthesis, were 18.2 °C and 20.5 °C in NFP and 17.3 °C and 20.1 °C in TOEF, respectively. Nine intensities of photosynthetically active radiation (PAR) (1500, 1000, 500, 250, 100, 50, 20, 10, and 0 μmol·m^{-2}·s^{-1}) were provided in 2002 and 2004, and seven (1500, 500, 300, 100, 50, 20, 0 μmol·m^{-2}·s^{-1}) in 2003, using a red-blue LED light source. Ambient CO_2 concentrations were kept constant at 350 μmol·mol^{-1} while controlling the humidity of incoming air at 1.1 vapor pressure deficit (VPD, hPa). The data obtained for each leaf were fitted to a non-rectangular hyperbola equation by a procedure of non-linear least squares regression to estimate the photosynthetic parameters using *R* (http://www.r-project.org/) as follows:

$$P = \frac{fI + P_{\max} - \sqrt{(fI + P_{\max})^2 - 4fIqP_{\max}}}{2q} - R$$

where *P*, $P_{\max}$, *f*, *I*, *q*, and *R* indicate the net photosynthetic rate (μmol·m^{-2}·s^{-1}), light-saturated rate of photosynthesis (μmol·m^{-2}·s^{-1}), initial slope of the light-response curve, intensity of PAR (μmol·m^{-2}·s^{-1}), curvature of the line, and dark respiration rate (μmol·m^{-2}·s^{-1}), respectively (see Lambers et al. 1998).

Simulation of plant productivity

Daily net assimilation rates were simulated for the three plants per species sampled throughout the height-growth period. Simulations were conducted on each photosynthesis measurement day plus two days before and two days after this under the assumption that photosynthetic rates were constant over this five-day period. Mean net assimilation during this period was then calculated. On each simulation day, daily net assimilation rates of individual plants were assessed as follows.

First, the light levels at each leaf were estimated for all selected plants. The one-hour cumulative solar radiation at 200 cm above the soil surface (described above) was then converted to the cumulative PAR per hour in accordance with the regression equation whereby 1 W·m^{-2} = 4.24 μmol photons·m^{-2}·s^{-1} (McCree 1972), where irradiance is assumed to be constant. To estimate the vertical light reduction rate of a focal leaf at *h'* cm above the ground on a certain day, we used the openness values of the closest date and the nearest measurement point to the target plant in each plot. Although openness and photosynthesis were measured in different years, we assumed identical vegetation structures between years. If *h'* is located between two openness measurement heights, h_i and h_{i+1}, the openness at *h'* (*o'*) is calculated using the following proportional equation:

$$\frac{(o' - o_i)}{(o_{i+1} - o')} = \frac{(h' - h_i)}{(h_{i+1} - h')}$$

where o_i and o_{i+1} are the openness at h_i and h_{i+1}, respectively. The light level (PAR) at *h'* was calculated by multi-

Fig. 1. Seasonal variation in daily cumulative solar radiation at the top of the herb layer (200 cm above the soil surface) in 2002 and 2003 (NFP), and 2003 and 2004 (TOEF) (solid lines). Moving averages of five-day values are shown by broken sigmoidal curves. Shaded areas indicate the tree-canopy closing period (for details, see text).
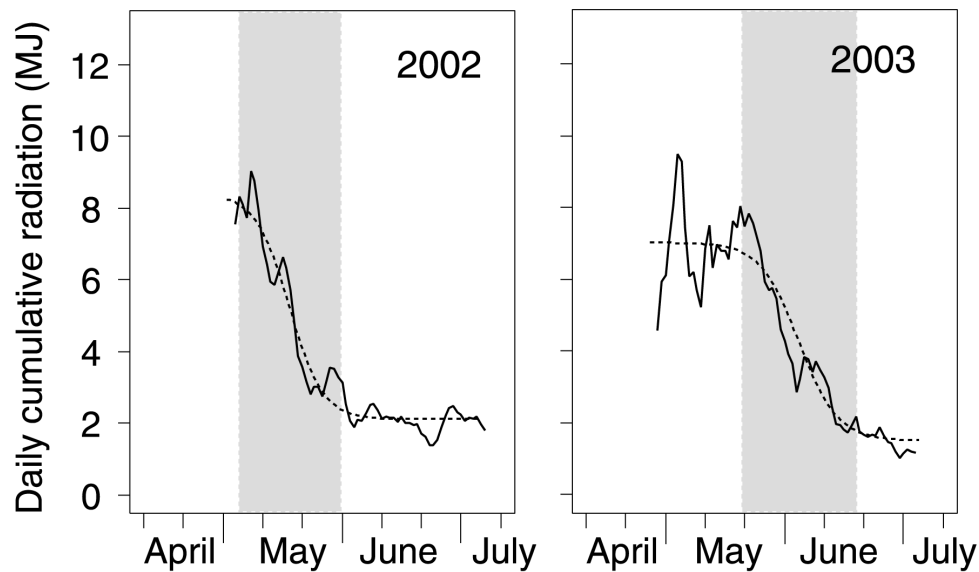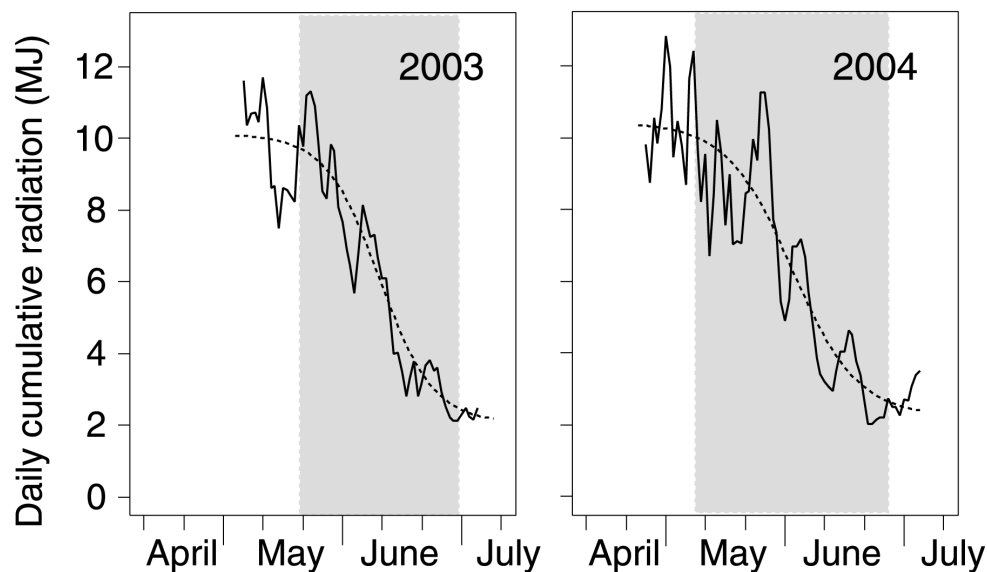
plying PAR at 200 cm and relative openness at h' to the openness at 200 cm.

Second, we estimated photosynthetic rates of all leaves on all selected plants. Because we did not measure the light responses of photosynthetic rates of all leaves within a plant, we assumed that non-measured leaves showed the same light response as the nearest measured leaf. Using the PAR, photosynthetic rates, and leaf areas estimated for all leaves, net assimilation rates per hour were calculated for all leaves from each sampled plant on each simulated day. By sum-

ming up the results, daily net assimilation per plant per day was then calculated.

Measurement of aboveground mass

A total of 25–30 randomly selected plants were harvested for *F. kamtschatica* (18 June 2002), *V. album* and *C. kamtschaticum* (11 June 2003) from NFP, and *U. platyphylla*, *S. cannabifolius*, and *C. hastata* (5 and 27 July 2003, and 16 Jun 2004, respectively) from TOEF. Harvested plants were washed and divided into leaf blades,

Fig. 2. Seasonal changes in the vertical transition of whole-canopy openness (including tree-canopy and herb layer) within herb layers in both plots in 2000, at 25 cm intervals. Numbers in figures show the measurement height. Mean values of four measurement points are shown.
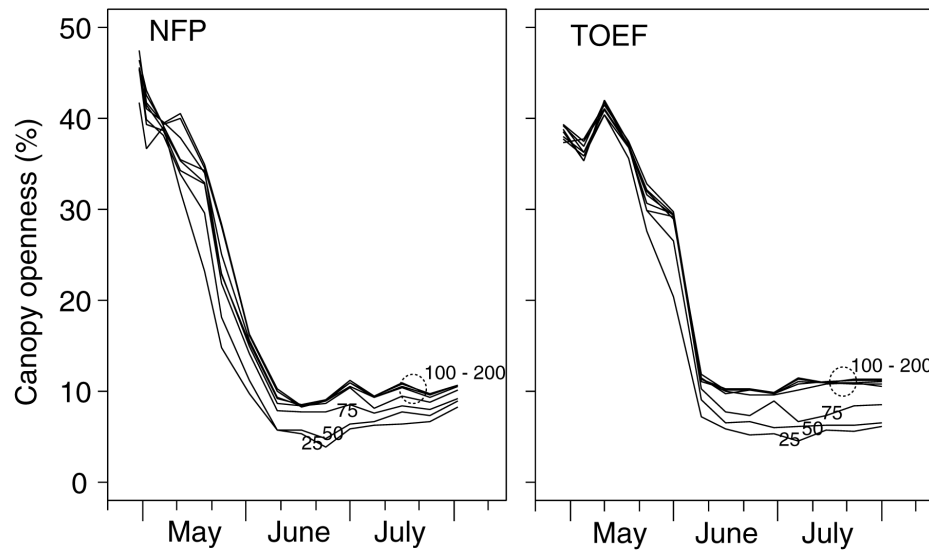
stems, petioles, and reproductive organs if present then each organ was weighed after drying at 80 °C for 3–4 d. The relationship between assimilatory (leaf blades) and non-assimilatory organs (stems, petioles, and flowers) was then analyzed based on their dry weights using major axis linear regression.

Results

Light

Light levels decreased to 20%–25% after tree-canopy closure compared with those in early spring in both plots (Fig. 1). The tree-canopy closing period varied between years and plots (4–29 May in 2002, 19 May – 17 June in 2003 in NFP; 19 May – 28 June in 2003, 8 May – 25 June in 2004 in TOEF).

Seasonal minimum values of openness were 3.9% in NFP and 4.6% in TOEF, both of which were observed at 25 cm above the soil surface (Fig. 2). Differences in openness 25–200 cm above the soil surface were less than 7% in NFP and 5% in TOEF after tree-canopy closure. Light level was similar between 100 cm and 200 cm in the herb layer in both plots. These results indicate that vertical light depression within the herb layer was much smaller than the seasonal light depression at the top of the herb layer, reflecting relatively sparse herbaceous vegetation in site.

Height growth and leaf expansion

Plant height, numbers of living leaves, and cumulative leaf area per plant increased synchronously from spring to early summer (Fig. 3), especially during the tree-canopy closing period, in all species with continuous leaf production, but not *V. album*. Patterns of height growth were similar among individual plants of all species, but leaf number or leaf area varied among individual plants of *C. hastata*, *U. platyphylla*, and *F. kamtschatica*. Leaf senescence scarcely occurred during the height growth period of species with continuous leaf production, but it gradually occurred

after flowering in August followed by complete leaf shedding by mid- or late November (data not shown).

In the species with early leaf production, *V. album*, height growth and leaf expansion occurred rapidly after the first leaf emergence and were almost completed before the beginning of tree-canopy closure. Leaf senescence occurred intensively from early or mid-June, and aboveground parts completely shed by the end of June.

Light response of photosynthetic rates

Before tree-canopy closure (at the first measurement), early-emerged leaves located at the lower position of species with continuous leaf production, and all leaves of *V. album* showed high P_{max} and dark respiration rates (Fig. 4). Rates decreased rapidly with progressing tree-canopy closure in all species. Lower leaves of *U. platyphylla* and *V. album* had senesced by the time of the last measurements. In parallel with the seasonal decrease in P_{max} and dark respiration rates, vertical gradients of these parameters also formed within individual plants of all species from upper to lower leaves. Mid and upper leaves that developed during the tree-canopy closing period on species with continuous leaf production, except *C. kamtschaticum*, showed an initially lower P_{max} than leaves that emerged earlier (lower leaves). However, this trend was not observed with dark respiration rates, which were consistently high at a young stage irrespective of emergence timing.

In contrast, seasonal trends for the initial slopes and curvature of the light-response curves of all species were unclear (data not shown). Both parameters showed large variance among individual plants at all leaf heights in all species.

Daily net assimilation at the whole plant level

In the five species with continuous leaf production, net assimilation rates per plant increased and reached a peak within the tree-canopy closing period (Fig. 5) despite a linear decrease in light levels during this period (Fig. 1). Fol-

Fig. 3. Seasonal changes in plant height (A), numbers of living leaves (B), and cumulative living leaf area per plant (C) in all species from first leaf emergence to completion of height growth. Arrows in (A) indicate the date of first leaf emergence. Different symbols represent different plants (*n* = 3 per species). Shaded areas indicate the tree-canopy closing period (see Fig. 1).
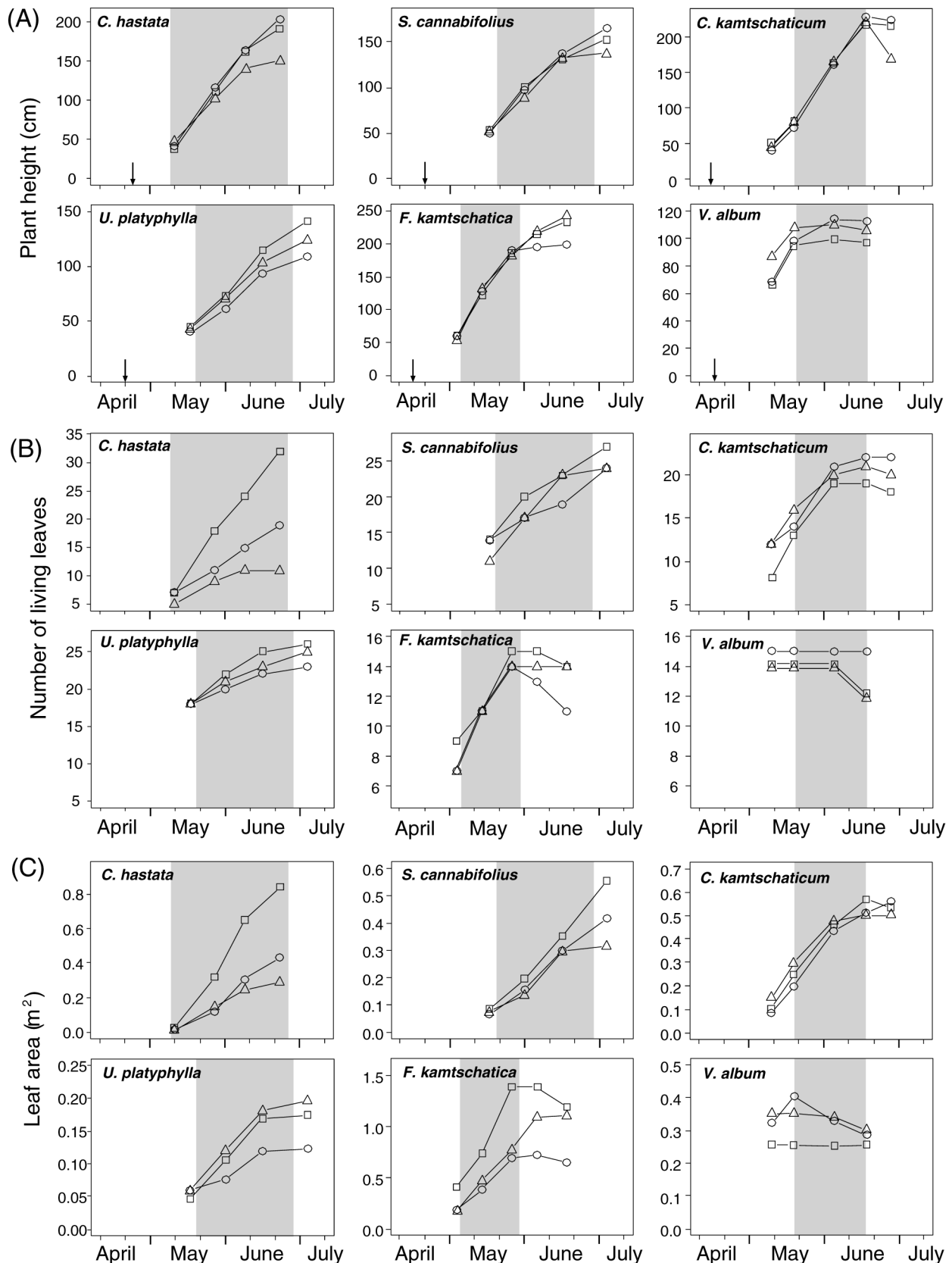
Fig. 4. Seasonal changes in maximum photosynthesis, P_{max} (A) and dark respiration rates (B) in all species with reference to leaf position. Three leaves per plant representing different positions (lower, middle, and upper) and emergence time were repeatedly measured using the same individuals included in the census of height growth and leaf development (Fig. 3). Values represent means ± SE of three plants. ○, lower leaves; △, middle leaves; □, upper leaves. Shaded areas indicate the tree-canopy closing period (see Fig. 1).
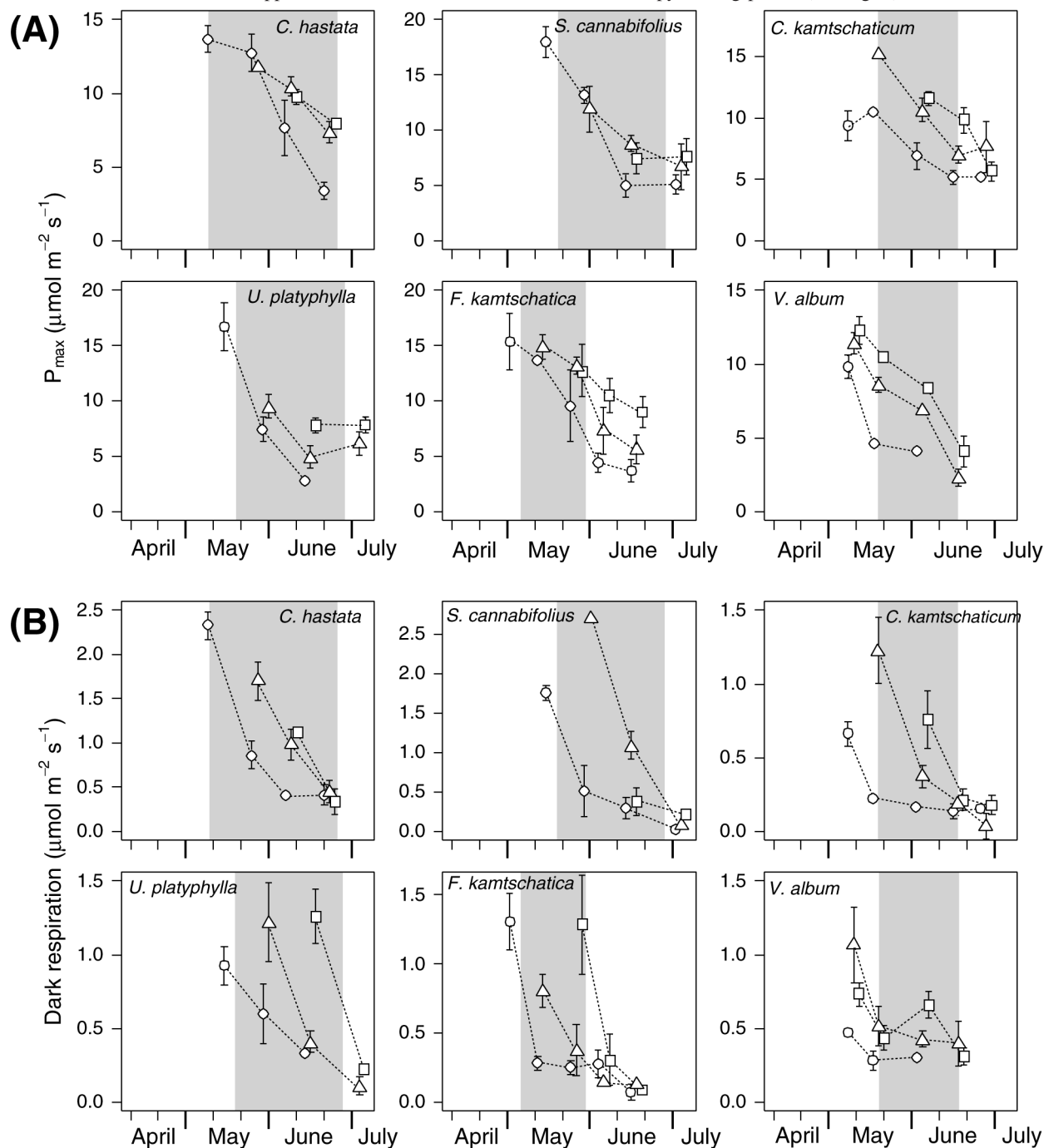

lowing this, rates declined or were maintained. Although seasonal changes in plant height were similar among target plants within species, net assimilation rates per plant varied among individual plants, especially in *C. hastata* and *F. kamtschatica*. In contrast, daily net assimilation rates of *V. album* were highest just before the tree-canopy closing period, continuously decreasing thereafter with the decreasing light levels.

Allocation to aboveground parts

Dry weights of non-assimilatory organs (stems, petioles, and flowers) increased proportionally with leaf blade weight (Fig. 6), indicating that the unit mass of assimilatory organs is supported by a constant non-assimilatory organ mass, irrespective of plant size (height), in each species. All species had hollow stems and the dry weight of non-assimilatory organs was not beyond twofold of the leaf blade mass.

Fig. 5. Estimations of seasonal changes in daily net assimilation rates at the whole plant level for all species. Simulations were conducted using the three plants per species used for measurements of photosynthetic rate, plant height, leaf number, and leaf size. Daily mean net assimilation rates were calculated on each photosynthesis measurement day plus two days before and two days after; averaged values (±SE) of these five days are shown. Shaded areas indicate the tree-canopy closing period (see Fig. 1). Refer to Fig. 3 for symbols.
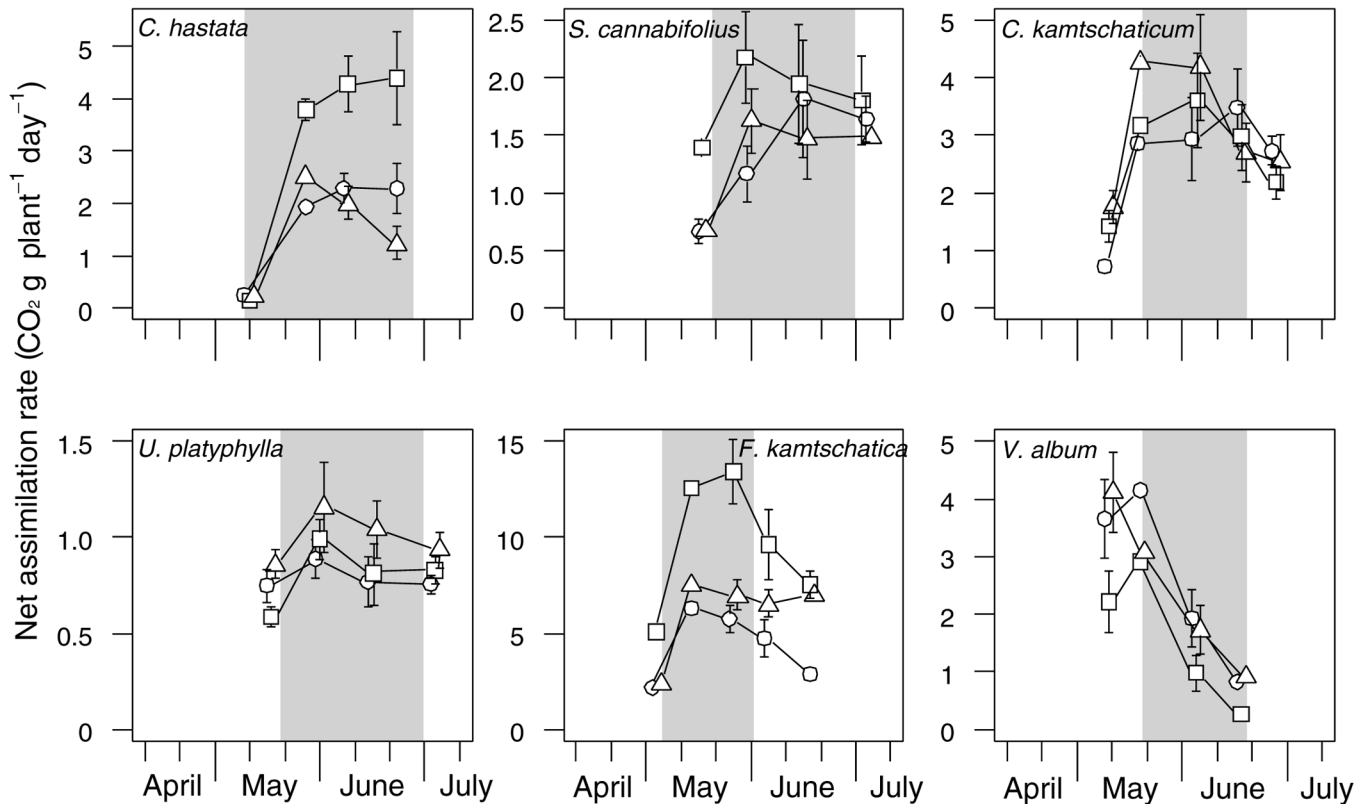
Discussion

Light availability and aboveground construction

As predicted, leaf accumulation and height growth of understory herbs with continuous leaf production progressed during the tree-canopy closing season as a result of retention of old leaves (Fig. 3). In contrast, plants inhabiting dense open habitats often exchange leaves rapidly during the growing season, because effective carbon gain can be achieved by unshaded young leaves with high photosynthetic activity under high irradiance (Jurik and Chabot 1986; Kikuzawa 1988, 2003). Due to this rapid leaf turnover, leaf distribution is usually concentrated in the upper stems of tall herbs growing in open habitats. Although lower-positioned old leaves are shaded by upper-positioned young leaves, most old leaves were maintained in the understory herbs. The analysis of whole-canopy openness (Fig. 2), indicated that the vertical gradient of light conditions was gentle within the herb layer, probably because of predominant diffused light in understory. Because of this mild light gradient, the lower-positioned old leaves of these herbs would maintain a positive carbon balance while overcoming the negative effects of self-shading.

The species with early leaf production *V. album* constructed its aboveground structure rapidly under bright conditions (Fig. 3) and shed its leaves soon after tree-canopy closing, earlier than the species with continuous leaf production. Therefore, the majority of assimilation activity in this species is concentrated in the short leafless season of canopy trees, as seen in spring ephemerals (Sparling 1967; Taylor and Pearcy 1976; Kawano et al. 1982; Hicks and Chabot 1985). In contrast, species with early leaf production inhabiting open habitat usually have longer leaf longevity than species with continuous leaf production (Kikuzawa 1983, 1988). This contrast might reflect the length of the high irradiance season in each habitat. These findings show that patterns of aboveground construction in giant herbs inhabiting the forest floor completely differ from those of tall herbs inhabiting open habitats.

Patterns of photosynthesis

P_{max} and dark respiration rates of individual leaves decreased with progressing tree-canopy closure (Fig. 4). Despite the different leafing phenologies, seasonal declines in P_{max} were commonly observed in species with both continuous and early leaf production. Because P_{max} and dark respiration rates of leaves often decline with aging (Mooney and Ehleringer 1997), discrimination between light acclimation and the aging effect is sometimes difficult (Hikosaka et al. 1994; Hikosaka 1996). However, in this study, late emerging (mid and upper) leaves of most species with continuous leaf production had an initially low P_{max}, suggesting that light acclimation of photosynthesis does occur, at least in these

Fig. 6. Relationship between the weight of assimilatory (leaf blades) and non-assimilatory organs (stems, petioles, and flowers) in each species. Regression lines and equations are shown.
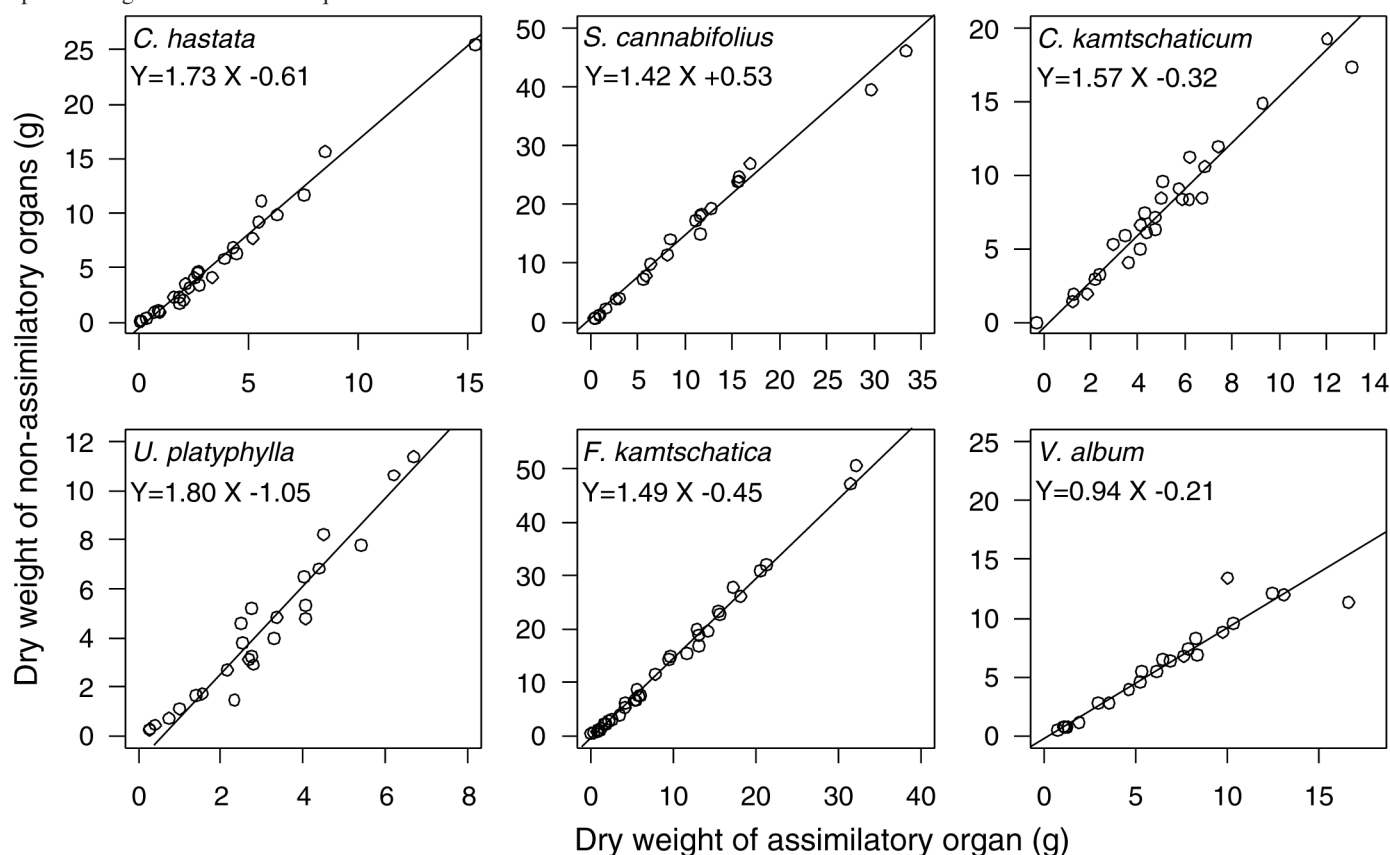
leaves. Acclimation of the photosynthetic characteristics of individual leaves to micro light conditions means that understory species are able to maintain a positive carbon balance under seasonally fluctuating light conditions (Boardman 1977; Björkman 1981; Hicks and Chabot 1985; Rothstein and Zak 2001).

In addition to the seasonal trends, P_{max} and dark respiration rates also decreased from the top to bottom of individual plants (Fig. 4). These vertical photosynthetic gradients are often explained as a consequence of nitrogen allocation within plants in which nitrogen is predominantly translocated to leaves with higher light availability (Mooney et al. 1981; Field 1983; Field and Mooney 1983; Hirose and Werger 1987). It is possible, therefore, that regulation of nitrogen re-allocation might also occur along a vertical light gradient in giant forest herbs.

In contrast to the P_{max} and dark respiration rates, the initial slopes and curvature of the light response curves did not show clear seasonal trends. Björkman and Holmgren (1963) reported that the initial slope of photosynthetic light response curves is similar between shaded and non-shaded leaves. These facts suggest that the slope and curvature of light response curves are insensitive to changes in the physiological and light conditions of leaves.

In this study, photosynthetic rates were measured under a controlled temperature condition (20 °C); however, actual photosynthetic rates might be influenced by the fluctuating

ambient temperature. Some studies have reported, however, that photosynthetic rates are not so sensitive to temperature (Stoy 1965; Cooper and Tainton 1968; Jeffers and Shibles 1969). Thus, the results obtained here seem to reflect actual seasonal trends in the assimilative process.

Daily net assimilation

In our simulation, a positive carbon balance was maintained under decreasing light availability in species with continuous leaf production (Fig. 5). This result supports the initial prediction that leaf accumulation within a plant can offset the reduced carbon gain per unit leaf area during the tree-canopy closing period. At the individual plant level within species, plants with a large leaf area (Fig. 3C) showed a higher level of carbon assimilation (Fig. 5), despite similar height growth rates among plants (Fig. 3A). Thus, leaf accumulation under decreasing light conditions seems to be important for these species.

The species with early leaf production showed a different assimilatory pattern (Fig. 5). By simultaneous expansion of its leaf area, *V. album* concentrates its effective assimilation to the light availability period of early spring. A similar assimilatory pattern is observed in the summer-green species *Viola pubescens* (Rothstein and Zak 2001). Considering that seasonal changes in the photosynthetic light responses of leaves were similar among species with continuous and early leaf production, this difference in assimilatory patterns

is likely to have been caused by the patterns of leaf area accumulation within individual plants.

Kikuzawa (1988, 2003) suggested that the habit of continuous leaf production is more efficient in constantly bright environments than is simultaneous leaf production early in the growing season. For summer-green herbs inhabiting forest floors, we can therefore conclude that the habit of continuous leaf production might be beneficial under seasonally fluctuating light-limited conditions.

In our calculation, we did not take into account the net assimilation during the period from the leaf emergence in late April to the first measurement in early May. Although plants receive full sunlight in this season, small-sized immature leaves may not contribute for net assimilation so much due to large respiration rate (Larcher 2003).

The mean PAR per second was calculated by averaging the hourly cumulative PAR without considering the effect of sunflecks (i.e., short-time direct irradiance). However, several studies have demonstrated that sunflecks often contribute to a large proportion of the daily assimilation products in understory plants (Gross 1982; Pearcy and Calkin 1983; Weber et al. 1985; Gross 1986; Chazdon and Pearcy 1991; Hull 2002). The calculation of net carbon gain per plant based on the constant light level using mean PAR values may overestimate the actual value in comparison with the calculations that sunflecks are taken into account (Gross 1986). If the frequency and intensity of sunflecks vary seasonally or vertically across leaf layer in the understory, consideration of spatiotemporal variation in sunflecks should be important for the accurate estimation of net assimilation.

In this study, we did not consider factors other than light condition, such as midday depression in photosynthesis. The midday depression is caused by stomatal closure and photoinhibitory damage under high temperature and water deficit conditions in midday, and it is usually reported in plants growing in dry climates or in canopy leaves exposed to strong radiation (Schulze et al. 1980; Tenhunen et al. 1981; Ishida et al. 1996; Valladares and Pearcy 1997). If the midday depression exists, our calculation of net assimilation rate per plant might be somewhat overestimated in early spring under full sunlight. However, the midday depression effect might not occur after tree-canopy closure because of the shaded and humid conditions of our forest floors.

Allocation to aboveground parts

We found that species with early and continuous leaf production are able to construct and maintain their tall plant structures by accumulating their leaf area before and after the beginning of tree-canopy closure.

If the carbon investment in support organs increases more than proportional to the increase in plant height (Iwasa et al. 1984; Kume and Ino 2000), the mass ratio of assimilatory to non-assimilatory organs must decrease with height growth (Givnish 1982; Jurik 1991). However, all target species in this study showed almost proportional allocation between leaf blades and non-assimilatory organs irrespective of plant height (Fig. 6). Hollow stems lightened the weight and decreased the construction cost of stems, which consequently increased the allocation to leaf blades in these species. This supports our prediction that giant herbs reduce the cost of support organs to increase their allocation to leaves in light-

limited deciduous forests. In addition, the cost of support organs might be reduced more sufficiently in the species with early leaf production *V. album* than in other species due to the pseudo-stems.

Leaves of our target species are arranged at regular intervals on the stem to form multilayer crowns. Such a leaf arrangement may have a mechanical advantage by reducing the construction cost of stems compared with plants with the umbrellalike leaf arrangement that is more common form in summer-green herbs (Givnish 1987). Although the multilayer crown structure may result in a self-shading (Givnish 1987), the effect of self-shading seems to be small in our plants as mentioned before. As another mechanism for reducing the cost of stem production, Andrews et al. (2005) reported that a giant herb, *Impatiens glandulifera*, supports aboveground structures by accumulating the nitrate and potassium in stems to generate osmolarity in place of costly organic molecule production. Such a physiological mechanism may be important for giant herbs showing rapid height growth.

Conclusions

The herbs with continuous and early leaf production in this study showed different patterns of light utilization, carbon acquisition, and leaf longevity. However, the growth strategies of both seemed to be efficient in the seasonally fluctuating light conditions beneath deciduous forest canopies. The species with early leaf production assimilated intensively during the short leafless season of canopy trees in early spring. A number of reports have demonstrated that forest-floor herbs with various leaf habits commonly exploit the light abundant period in early spring or late autumn for growth (Kimura 1970*a*, 1970*b*; Taylor and Pearcy 1976; Hicks and Chabot 1985; Kawano 1985; Yoshie and Kawano 1986; Uemura 1994; Tissue et al. 1995; Rothstein and Zak 2001). However, in this study, giant herbs with continuous leaf production effectively used decreasing light conditions during the tree-canopy closing period. These findings contribute to our further understanding of the diverse adaptive strategies of forest floor herbs in cool-temperate deciduous forests.

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