

Size-dependent leaf emergence and expansion pattern in a perennial understory herb *Arisaema serratum* (Araceae)

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Fumiko Yamashiro¹ and Naoya Wada²: Size-dependent leaf emergence and expansion pattern in a perennial understory herb *Arisaema serratum* (Araceae)

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Abstract

We observed the onset date of leaf emergence and the completion date of leaf expansion in a perennial herbaceous understory plant *Arisaema serratum* (Thunb.) Schott, growing in a secondary forest of Toyama Prefecture, central Japan, with reference to plant size. Basal diameter, plant height, and the number of leaflets were significantly correlated with biomass. Light intensity on the forest floor decreased from spring to early summer. *Arisaema serratum* emerged and completed the leaf expansion prior to canopy closure. Smaller sized individuals showed earlier leaf emergence and expansion than larger sized ones within a population. The onset date of leaf emergence as well as the date of leaf expansion was found to be significantly correlated with plant size. We discuss the earlier leaf emergence and faster expansion in smaller sized individuals in relation to the light availability in spring and the size-related growth pattern of *A. serratum*.

Key words : *Arisaema*, leaf phenology, light availability, plant size, understory plant.

Introduction

In temperate deciduous forests, the light conditions for understory plants change remarkably through time (Kawano and Nagai 1975 ; Uemura 1994 ; Oshima et al. 1997 ; Seiwa 1998). Especially from spring to early summer, light availability on the forest floor drastically decreases during the leaf development stage of canopy trees (Kawano et al. 1978 ; Oshima et al. 1997 ; Seiwa 1998). In such a condition, earlier leaf emergence and faster expansion may enable understory plants to acquire a large amount of light resources and photosynthetic carbon gain prior to canopy closure (Routhier and Lapointe 2002). In current-year seedlings of *Acer mono*, for instance, 61% to 79% of annual dry mass gain was obtained within two months of germination until closure of the canopy foliage (Seiwa 1998). Thus, for plants living at the understory, individuals having earlier leaf emergence and faster expansion are more advantageous for resource acquisition of light on the forest floor prior to canopy closure.

In forest ecosystems, the spatial as well as the

temporal heterogeneity of foliage may cause great variations in light availability for understory plants. Light availability vertically decreases from the canopy to the forest floor (Kira et al. 1969) and even from the top of the herbaceous layer to the ground (Oshima et al. 1997). Therefore, smaller sized individuals are always more compelled under lower light availability conditions than larger sized ones, even within the same species. In this case, smaller individuals might escape from their lower light availability conditions by changing the leaf performances, i.e., earlier leaf emergence and faster expansion (Seiwa 1999 a, 1999 b). Thus, we hypothesize that leaf emergence and expansion may be related to plant size, and smaller sized individuals should emerge and expand their leaves earlier than larger sized ones in a population.

Arisaema serratum (Thunb.) Schott, well known as a reversible sex plant species depending on plant size (Kinoshita 1986, 1987 ; Kinoshita and Harada 1990), is a perennial herbaceous understory plant, which blooms in the middle spring in temperate forests. This plant

has a quite simple structure: the plant body consists of four major parts; root, corm, leaf (including pseudostem), and reproductive structure (see Kinoshita 1986). A single shoot covered by cataphylls emerges above the ground in early spring and one or two leaf-lamina are flush at the top of the shoot in middle spring (Fig. 1). These structural and developmental characteristics of a shoot and its leaves facilitate our measuring the leaf phenology in relation to the individual plant size (i.e. basal diameter and plant height). In a previous study on *A. japonicum*, Kinoshita (1986) found that flowering occurred earlier in males (i.e. smaller sized individuals) than females (i.e. larger sized ones), suggesting that size-related phenological variations may occur in *Arisaema* species. However, there is little information concerning size-related leaf phenology both in juvenile and reproductive individuals co-examined for aspects of their light-acquisition behaviors (but see Seiwa (1999 a, 1999 b) in tree species). If smaller individuals may have a lower number of leaflets within the smaller leaf area, earlier leaf emergence and faster expansion will be more facilitative as compared to larger individuals.

In this study, we tested the hypothesis that smaller sized individuals will emerge and expand their leaves earlier than larger sized ones within a population of *A. serratum*. We observed leaf phenology and seasonal changes in light intensity, and examined the relationships between the timing of leaf emergence, expansion, and plant size of *A. serratum* in relation to the light

availability and size-related growth pattern.

Materials and methods

Arisaema serratum is a perennial herbaceous plant, commonly distributed on the forest floors of temperate regions, from the Kuril Islands, to northeastern China, Korea, and the Japanese archipelago (Ohashi 1982). The sex expression of this species is closely related to corm weight, biomass, and plant size (pseudostem diameter): sex expression changes from male to female as the plant grows larger (Kinoshita 1986, 1987). Small sized individuals (<ca. 3 mm in diameter) have no inflorescence (spadix and spathe) and scape, and males range from ca. 3 mm to 16 mm and females from ca. 7 mm to 50 mm in diameter (Kinoshita 1987).

We carried out this study in a secondary deciduous forest of the Sarukura-Yama Forest Park, Ohsawano, Toyama Prefecture, central Japan (36°33' N, 137°14' E). In this forest, the canopy layer was composed of *Quercus serrata* Thunb., *Castanea crenata* Sieb. et Zucc., *Carpinus tschonoskii* Maxim. and *Mallotus japonicus* (Thunb. ex Murray) Muell. The shrub layer was dominated by *Lindera umbellata* var. *membranacea* (Maxim.) Momiyama and *Acer palmatum* var. *matsumurae* Makino. In April of 2000, a 10 m×20 m quadrat was established, and 50 individuals of *A. serratum* at the pre-leaving stage (Fig. 1 A) were randomly selected and tagged: 12 (asexual) juveniles, 32 males and 6 females, which were not aggregated but scattered in the quadrat. For each individual, we re-

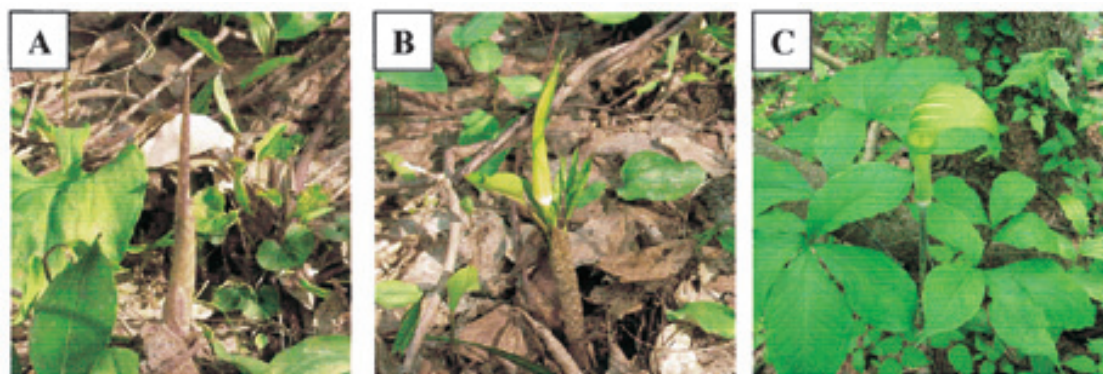


Fig. 1. Pictures of *Arisaema serratum* from shoot emergence above the ground to leaf expansion finished.

A, a shoot emerged in early April; B, a phase of "leaf emergence"; C, a phase of "leaf expansion".

corded the date of leaf emergence and leaf expansion every one- to two day interval from mid-April of 2000. We defined "leaf emergence" as the leaf lamina emerging from the cataphyll covers (Fig. 1 B) and "leaf expansion" as leaflets horizontally expanding completely (Fig. 1 C). We measured the pseudostem diameter, plant height, and the number of leaflets for each individual at mid-May when height growth of *A. serratum* appeared to reach a plateau.

We measured the light intensity at 50 cm above the ground around the quadrat at 1-hr intervals from 1 April to 31 May in 1999, by using a light intensity logger (StowAway LI, Onset Computer Co. Ltd., MA, USA). In 2000, we set up eight light intensity loggers arranged on a 2 × 4 grid having 2-m spacings within the quadrat and measured light intensity at 50 cm above the ground at 1-hr intervals from 5 May to 31 May. Then we calculated the daily mean light intensity measured from 4:00 to 18:00 each day ($n = 14$ measurements / d) during the periods.

Furthermore, we examined the relationships between plant size (basal diameter of pseudostem and plant height), the number of leaflets per plant, and biomass. We measured "plant height" as the height at the top layer of leaf lamina for each plant (inflorescence was not included in reproductive individuals). We sampled 13 juveniles, 9 males, and 7 females outside the quadrat on 12 May 2000. After the plant size and the number of leaflets per plant were measured, we carefully dug out the corm and root and extracted the whole plant in each sampling. Those samples were washed and dissected into leaflets, pseudostem, corm, roots, and reproductive organs (in males and females). Each part was dried at 80°C for 48 hrs and weighed. We then analyzed the relationships between the biomass and the pseudostem diameter, plant height and number of leaflets per plant.

Results and discussion

Temporal changes in light intensity at the understory are shown in Fig. 2. In 1999, a 7-day moving average clearly indicated that light intensity decreased from early April to late May, in spite of a large daily fluctuation (Fig. 2 A). In 2000, the intensity was apparently higher in

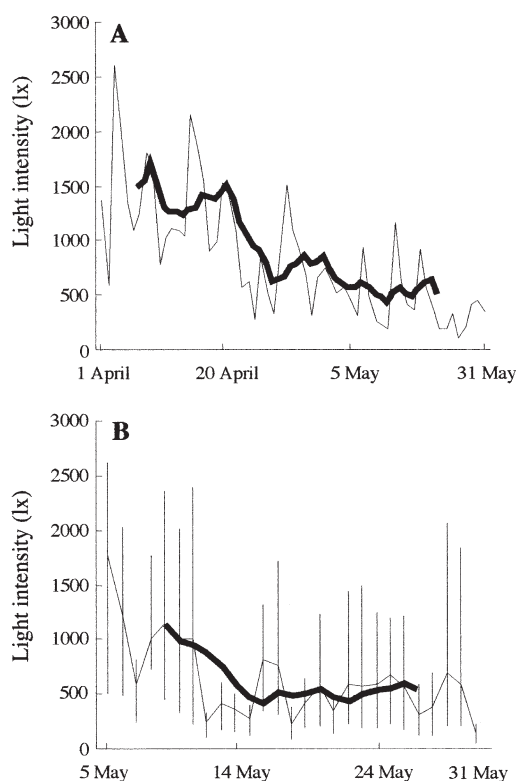


Fig. 2. Temporal changes in light intensity (lx) at the understory in 1999 (A) and in 2000 (B). A bold line is a 7-day (A) or a 5-day moving average of the intensity (B). In 2000, daily mean value of the eight sensors is shown with maximum intensity (positive vertical line) and minimum one (negative line), respectively.

early May than in mid- or late May (Fig. 2 B). A 5-day moving average showed that the intensity decreased until mid-May and it was relatively constant after that time (Fig. 2 B). In both years, leaf flushing of the small trees was observed in mid-April, and leaves emerged from the canopy trees in late April to early May, resulting in a constant low light intensity on the forest floor after mid-May. Thus, it appears that leaf emergence before mid-May might be essential for *A. serratum* to acquire a large amount of light prior to canopy closure at this site.

The allometric relationships between total dry mass and pseudostem diameter, plant height, and the number of leaflets are shown in Fig. 3. Significant positive correlations were found between biomass and pseudostem diameter ($r^2 = 0.990$, $n = 29$, $P < 0.0001$; Fig. 3 A) and plant height ($r^2 = 0.968$, $n = 29$, $P < 0.0001$; Fig. 3 B).

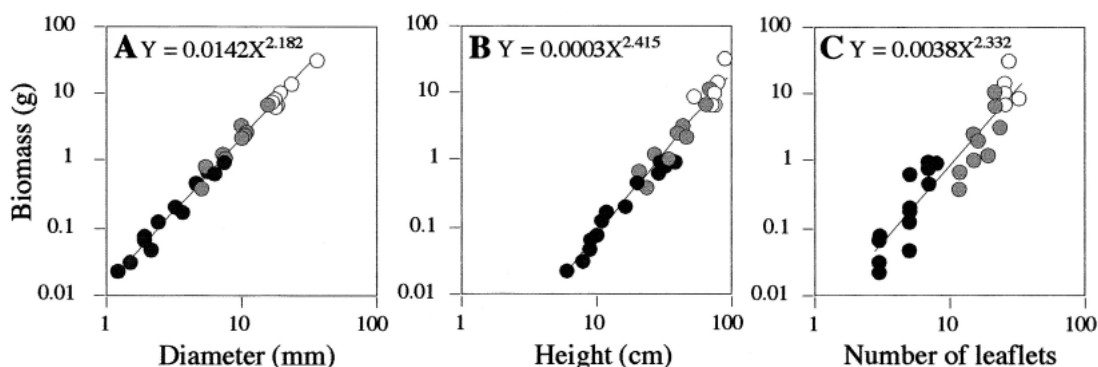


Fig. 3. Allometric relationships between biomass and pseudostem diameter (A: $r^2 = 0.990$, $P < 0.0001$), plant height (B: $r^2 = 0.968$, $P < 0.0001$), and the number of leaflets per plant (C: $r^2 = 0.884$, $P < 0.0001$) in *Arisaema serratum*. Symbols: closed circles, juveniles; gray-shaded circles, males; open circles, females. Sample size (n) is 29.

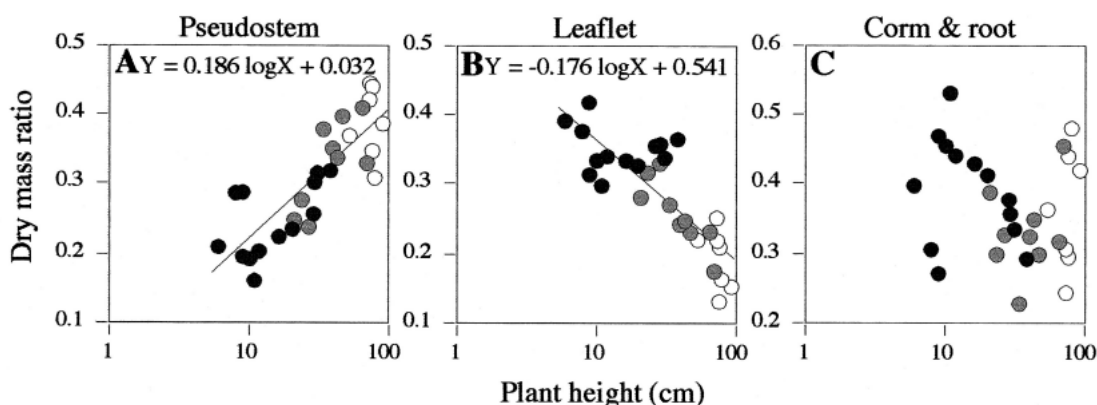


Fig. 4. Dry mass allocation to pseudostem (A: $r^2 = 0.667$, $P < 0.0001$), total leaflets (B: $r^2 = 0.675$, $P < 0.0001$), and corm and root (C: $r^2 = 0.052$, $P > 0.1$) with reference to plant height in *Arisaema serratum* ($n = 29$). Symbols: closed circles, juveniles; gray-shaded circles, males; open circles, females.

The number of leaflets per plant was also correlated significantly with biomass ($r^2 = 0.884$, $n = 29$, $P < 0.0001$; Fig. 3 C). As plant height increased, *A. serratum* tended to allocate more dry mass into the pseudostem, i.e., the support organ (Fig. 4 A). Whereas, allocation to leaflets, i.e., an assimilation organ, decreased with increases of the plant height (Fig. 4 B), there was no significant correlation between the storage organ (corm and roots) and the plant height (Fig. 4 C). This suggests that a greater investment in the pseudostem with increasing plant size might greatly contribute to arranging the leaf lamina at a vertically higher position in order to capture more light resources at the understory.

Plant size, the number of leaflets, and leaf phenology in juveniles, male, and female indi-

viduals, are summarized in Table 1. Leaf emergence occurred earlier in juveniles (25.3 ± 0.9 (SD) days from 1 April of 2000, $n = 12$) than in males (26.2 ± 2.5 days, $n = 32$) and females (27.5 ± 3.0 days, $n = 6$). All tagged individuals finished their leaf expansion by 7 May (37 days from April 1), i.e., a range of 27 to 37 days. The onset date of leaf emergence was positively correlated with the plant size and the number of leaflets per plant (Table 2), thus, indicating a size-dependency. The leaf expansion completion date was also positively correlated with the plant size and the number of leaflets (Table 2). The duration from the onset of leaf emergence to the completion of leaf expansion was significantly correlated with the basal diameter and the number of leaflets per individual: however,

Table 1. Basal diameter (D), plant height (Height), the number of leaflets per plant (Leaflet No.), and leaf phenologies (LED, leaf emergence date; LXD, leaf expansion date; DU, duration between LED and LXD) in juvenile ($n = 12$), male ($n = 32$) and female individuals ($n = 6$) of *Arisaema serratum*. Means \pm standard deviations are shown with their ranges in parentheses

	D (mm)	Height (cm)	Leaflet No.	LED (days*)	LXD (days*)	DU (days)
Juveniles	4.9 \pm 1.4 (3.2–8.2)	23.8 \pm 6.7 (15–38)	5.4 \pm 0.8 (5–7)	25.3 \pm 0.9 (24–27)	29.6 \pm 1.7 (27–32)	4.3 \pm 1.5 (2–7)
Males	10.8 \pm 3.6 (6.3–17.0)	44.3 \pm 13.6 (24–73)	18.2 \pm 4.7 (12–28)	26.1 \pm 2.5 (24–32)	32.2 \pm 2.8 (27–37)	6.1 \pm 1.4 (3–9)
Females	19.5 \pm 2.4 (15.3–22.0)	69.3 \pm 5.8 (61–75)	24.5 \pm 4.1 (19–31)	27.5 \pm 3.0 (24–32)	32.8 \pm 2.7 (30–37)	5.3 \pm 0.5 (5–6)

*Days from 1 April.

Table 2. Kendall rank correlation coefficients (τ) between plant size (diameter and height), the number of leaflets, and leaf phenologies (LED, onset date of leaf emergence; LXD, date of leaf expansion; DU, duration from emergence to expansion) in *Arisaema serratum* ($n = 50$)

	Diameter	Height	Leaflet No.
LED	0.304**	0.311**	0.274**
LXD	0.494***	0.440***	0.506***
DU	0.222*	0.148 ^{ns}	0.284**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ^{ns}, non-significant.

there was no correlation with the plant height (Table 2). Because larger sized individuals tended to have many leaflets (Fig. 3 C) having larger leaf areas (Kinoshita 1986), it appears to take more time for them to emerge and expand their leaves than smaller sized ones.

Our results support the hypothesis that smaller sized individuals emerge and expand their leaves earlier than larger sized ones. This could be explained by an “ontogenetic constraint” in the larger individuals compelling them to grow many leaflets having larger leaf areas on only one shoot, in addition to the reproductive organs (spadix, spathe, and scape), as they mature in the reproductive stage. Although larger sized individuals expand their leaves later, size-related dry mass allocation to pseudostem (Fig. 4 A) might enable the plants to acquire more light resources at vertically higher positions, resulting in compensation of the delayed leaf phe-

nology.

In this study, however, we did not present any direct evidence of what portions earlier leaf emergence and faster expansion contribute to gain carbons or dry mass in *A. serratum*. In a spring-flowering understory plant *Trillium erectum* (Liliaceae), Routhier and Lapointe (2002) showed that the annual growth rate decreased with the shortened duration of the high light period in early spring prior to canopy closure along a latitudinal gradient, suggesting a higher advantage in individuals having earlier leaf emergence. Although interspecific variations in leaf phenology among tall and small trees have been studied as a “strategy” for light acquisition in forest stratification (e.g. Kikuzawa 1983, 1984), only a few studies so far have reported intraspecific variations in leaf emergence within a population in relation to plant size (e.g. Seiwa 1999 a, 1999 b). Earlier leaf emergence and

faster leaf expansion in smaller sized individuals at the earlier growth stage seems to be an essential behavior for temperate understory plants to gain carbons prior to canopy closure. Further quantitative investigations of the temporal patterns of carbon gain and the relationships between leaf phenology and dry-mass production are necessary to evaluate the ecological and evolutionary significance of size-related leaf emergence in *A. serratum*.

Acknowledgments

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- (Received August 31, 2002; accepted September 25, 2002)
- 山城富美子¹・和田直也²：多年生林床草本植物マムシグサにおけるサイズに依存した葉の展開様式
- 多年生林床草本植物マムシグサについて、展葉開始日と展葉完了日を植物体のサイズに着目して富山県の二次林で調査した。根際直径、草高および個体当たりの小葉数は個体バイオマスと有意な正の相関関係を示した。林床上の光強度は春から初夏にかけて減少したが、マムシグサは林冠が閉鎖する前に葉を出し展葉を完了していた。調査した個体群では、

より小さなサイズの個体の方がより葉の展葉開始日が早くかつ展葉完了日も早かった。展葉開始日と展葉完了日は植物体のサイズと有意な正の相関関係を示した。より小さな個体ほど展葉開始日と展葉完了日がより早いという結果を、春先の光資源の利用と

サイズに依存したマムシグサの成長様式の観点から考察を行った。

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