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Seasonal Changes in Photosynthesis of Four Understory Herbs in Deciduous Forests

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Seasonal patterns of photosynthesis and respiration of single leaves of four understory perennial herbs in deciduous forests were investigated in relation to their leaf growth and light conditions on the forest floor. *Anemone flaccida* shows rapid growth of leaf area and high rates of gross photosynthesis at light saturation (*Psat*) in its early stage of development. Its photosynthetic activity is restricted to a brief period of high light intensity before the closure of overstory canopies. *Disporum smilacinum* possesses light-photosynthesis curves of the shade-leaf type throughout its whole growing period. A shading experiment has shown that this plant is low-light adapted and can utilize weak light efficiently. The light-photosynthesis curve of *Syneilesis palmata* shifts from the sun-leaf type to the shade-leaf type in response to the seasonal change of light regime on the forest floor. Evergreen leaves of *Pyrola japonica* have three year longevity, and light-photosynthesis curves of the shade-leaf type. They maintain some photosynthetic activity even in late autumn and winter.

Key words: Leaf growth—Light condition—Photosynthesis—Respiration—Understory herb.

In the deciduous forest, the light reaching the forest floor varies seasonally with the development of forest canopy (Anderson, 1964). After the closure of the overstory canopy, light intensities often drop to 3-6% of the full sunlight. From a viewpoint of matter production, the survival of an understory species under changing light conditions may depend largely on its ability to make effective use of reduced light for photosynthesis.

The understory herbs differ from each other in phenology and in response to the seasonal shift of light intensity. Sparling (1964, 1967) investigated the phenology and photosynthetic characteristics of woodland herbs in relation to light intensity in a deciduous forest in Canada. He (1967) distinguished three different groups, i.e. 'shade tolerant', 'shade intolerant' and 'semi-shade tolerant', and suggested a strong relationship between the light intensity in which young leaves expanded, and their subsequent photosynthetic characteristics. Taylor and Pearcy (1976) also showed a correlation between the phenology and the seasonal trends of photosynthetic characteristics based on their investigation of six North American woodland herbs. For understory herbs

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in deciduous forests in Japan, however, information on their phenology and seasonal behavior of photosynthetic characteristics is very limited, except in the case of a spring herb, *Maianthemum dilatatum* (Koyama and Kawano, 1973).

The purpose of the present study is three-fold; first to describe the seasonal changes of photosynthetic characteristics of four understory perennial herbs in deciduous forests; second to investigate the response of two summergreen understory herbs to shade treatment; and third to discuss the different strategies of the four species in adapting to the changing light environments of temperate deciduous forests.

Materials and Methods

The selected species were *Anemone flaccida* Fr. Schm., *Syneilesis palmata* Maxim., *Disporum smilacinum* A. Gray and *Pyrola japonica* Klenze. They grow in deciduous forests and have different phenological characteristics (Fig. 1); *A. flaccida* is a spring herb, *S. palmata* and *D. smilacinum* are summergreen perennial herbs, and *P. japonica* is an evergreen perennial herb.

A. flaccida (Ranunculaceae) is distributed in Japan, China and Sakhalin (Ohwi, 1965), growing under deciduous trees. The plants were collected from a deciduous forest in Nikko Botanical Garden, the University of Tokyo, in Tochigi Prefecture (lat. 36°45′N, long. 139°35′E). The forest is composed of *Quercus serrata* Thunb., *Q. acutissima* Carruth. and *Carpinus tschonoskii* Maxim. In *A. flaccida* the aerial parts, few radical leaves and one or two stems, start to develop from rhizome early in spring, bear two or three white flowers and wither before the full closure of overstory canopy,

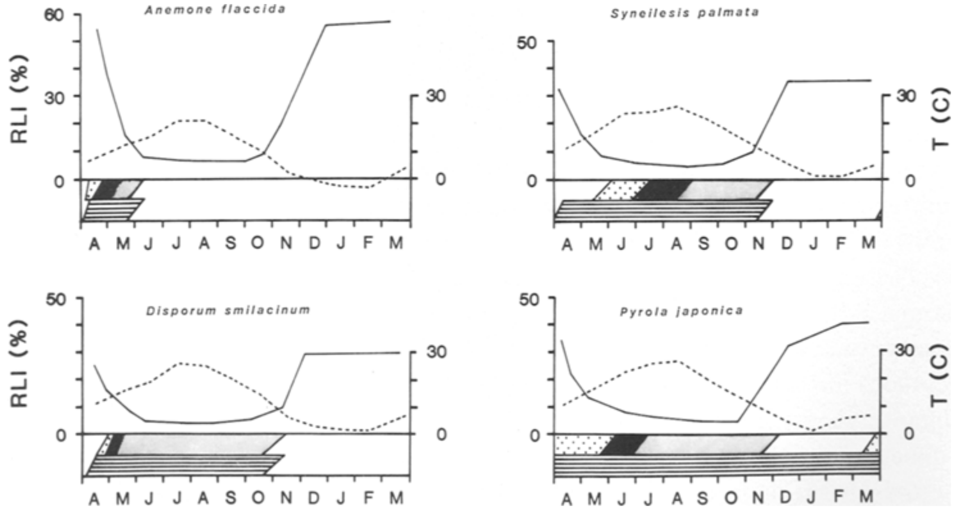

Fig. 1. Phenological diagrams of four understory species: *Anemone flaccida* in Nikko, Tochigi Prefecture; *Syneilesis palmata* and *Disporum smilacinum* in Honjo, Saitama Prefecture; *Pyrola japonica* in Kiyosumi, Chiba Prefecture. ▤, growing season (the foliated period); ▒, flower buds bearing; ■, flowering period; ░, fruits and seeds scattering. Solid lines show the relative light intensities (*RLI*) on the forest floors and dotted lines the monthly mean air temperatures (*T*) in the habitats.

and the growing period is about two months. The sample plants of *A. flaccida* were transplanted into pots and brought immediately back to the laboratory of Waseda University in Tokyo for measurement of photosynthetic rates. The measurements were made at intervals of about a week from April to May of 1981.

S. palmata (Compositae) is distributed in central and southern Japan, Korea and China (Numata and Asano, 1970). The plant is found both on forest floors and at the edge of forests. The aerial parts, a stem and one or two peltate palmate leaves, begin to develop in early spring, bear a great number of tubulous flowers in summer, and wither in autumn. An elongating winter bud is separated from the withered mother plant in winter. A total of more than 200 plants of *S. palmata* were collected from a deciduous forest dominated by *Q. serrata* in association with Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) on the Honjo campus of Waseda University in Saitama Prefecture (lat. 36°13′N, long. 139°11′E), and were transplanted into pots at the end of February in 1979, when they were dormant. A quarter of the potted plants were put back in their natural habitats. The other three quarters were grown in an experimental field in Honjo under artificially reduced sunlight (25, 6 and 3%) obtained by using black nylon screening supported by wooden frames. Measurements of the photosynthetic rates of these plants were made at intervals of about one month from April to November of 1979.

D. smilacinum (Liliaceae) is distributed in Japan, the Kuriles, Sakhalin and Korea (Horikawa, 1972), growing on a shaded or half-shaded forest floor. The plant develops a stem 15-40 cm long with several elliptic leaves and bears single or double, cup-shaped white terminal flowers in spring, and produces ramets in autumn. The plants were collected in February, 1981 from a deciduous forest mixed with Japanese red pine in Honjo, adjacent to the site for *S. palmata*, and were transplanted into pots and grown both in their natural habitats and in an experimental field under artificially reduced sunlight (50, 10, 6 and 3%). Photosynthetic rates were measured at intervals of about one month from April to October, 1981.

P. japonica (Pyrolaceae) is distributed widely in Japan, Korea, China and Formosa (Numata and Asano, 1970), growing mainly on the forest floors. The plant has a few creeping rhizomes forming a dense population. New aerial parts begin to grow in April, develop a scape among the several round evergreen leaves with long petioles and bear white flowers in June. New subterranean parts grow in autumn. The life span of the leaves extends to three years. The plants were collected from a deciduous forest dominated by *Q. serrata* in association with *Q. acutissima*, *Castanea crenata* Sieb. et Zucc. and *Albizia julibrissin* Durazz., in the Chiba Experimental Forest of the University of Tokyo in Kiyosumi, Chiba Prefecture (lat. 35°12′N, long. 140°08′E). They were transplanted into pots in September, 1976 and grown in their natural habitat for two years. Photosynthesis of the potted plants was measured at intervals of about one month from April of 1978 to March of 1979.

In *A. flaccida*, *S. palmata* and *D. smilacinum*, photosynthesis was measured with an intact leaf of the potted plant. Measurements were repeated using four or five potted plants for each species. The assimilation chamber was connected to an

Table 1. Air temperature in the chamber during the measurement (T)[1], and dark respiration (R)[3] and the light compensation points (LCP)[4] for

	Anemone flaccida	Apr. 20	Apr. 25	Apr. 30	May 6
	T	10	16	16	17
	Psat	8.2	12.7	14.3	9.0
	R	2.3	1.8	1.3	0.9
	LCP	22.1	14.0	10.0	8.5
	Syneilesis palmata	Apr. 6	Apr. 13	May 2	May 31
	T	12	14	16	20
	Psat	9.9	11.5	9.3	8.6
	R	1.1	1.3	0.9	0.6
	LCP	19.5	16.5	8.0	4.0
	Disporum smilacinum	Apr. 18	Apr. 29	May 27	Jun. 13
	T	15	17	20	21
	Psat	7.7	9.8	6.5	5.4
	R	1.0	1.3	0.7	0.6
	LCP	7.2	8.3	3.1	4.1
	Pyrola japonica	Apr. 26	May 8	Jun. 24	Jul. 22
0-year-old leaves	*T*	13	19	24	28
	Psat	2.7	3.5	4.1	4.3
	R	0.7	0.5	0.4	0.2
	LCP	9.1	4.0	2.3	1.3
1-year-old leaves	*Psat*	3.0	2.9	2.8	2.6
	R	0.4	0.3	0.2	0.2
	LCP	2.8	1.8	1.2	1.2
2-year-old leaves	*Psat*		1.3		0.9
	R		0.3		0.2
	LCP		2.0		1.8

[1] Corresponding to the mean air temperature of the natural habitat, °C.
[2] $\mathrm{mgCO_2dm^{-2}hr^{-1}}$.
[3] $\mathrm{mgCO_2dm^{-2}hr^{-1}}$.
[4] $\mu\mathrm{E\ m^{-2}sec^{-1}}$.

open-flow infrared gas analyzer (Horiba, VIA-300). A 300 or 500 W incandescent lamp (Toshiba spot photoreflector lamp) was used as the light source. Leaves in the chamber were preilluminated at 300-400 $\mu\mathrm{Em^{-2}sec^{-1}}$ for about 30 min to make the stomata open. The incident quantum flux on the leaf surface was varied by altering the distance of the lamp from the assimilation chamber. Nylon screening was also used to obtain lower levels of quantum flux. Incident quantum flux on the leaf seasonal changes in the rates of gross photosynthesis at light saturation (*Psat*)2), four understory species

May 16					
15					
7.3					
0.8					
7.4					
Jul. 3	Aug. 7	Aug. 29	Oct. 8	Nov. 11	
26	29	25	20	13	
7.1	4.9	4.7	4.2	3.7	
0.5	0.4	0.3	0.3	0.3	
3.0	2.6	1.8	1.7	1.8	
Jul. 16.	Sep. 1	Oct. 10			
28	22	17			
4.9	4.5	3.7			
0.6	0.5	0.6			
3.6	3.0	3.6			
Aug. 25	Sep. 20	Oct. 24	Dec. 15	Feb. 13	Mar. 17
29	22	17	8	6	9
3.7	3.3	2.9	2.8	2.3	2.3
0.2	0.2	0.2	0.2	0.1	0.1
1.3	1.2	1.2	1.2	1.2	1.2
2.3	2.1	1.4	1.1	1.2	1.1
0.2	0.2	0.2	0.2	0.2	0.2
1.1	1.1	1.4	1.2	1.1	1.1
	0.7				
	0.2				
	1.5				

surface was measured with a light meter equipped with a quantum sensor (Lambda Instruments, model LI-190S). Air flow rate was about 4 *l* min^{-1}. The chamber was placed beneath a water-heat filter, in which cooled or warmed water was circulated. Air temperature in the chamber was regulated to maintain a daily mean air temperature recorded at the collection site during five or ten days before the measurement (Table 1). The photosynthetic rates thus obtained were corrected to those under 0.03

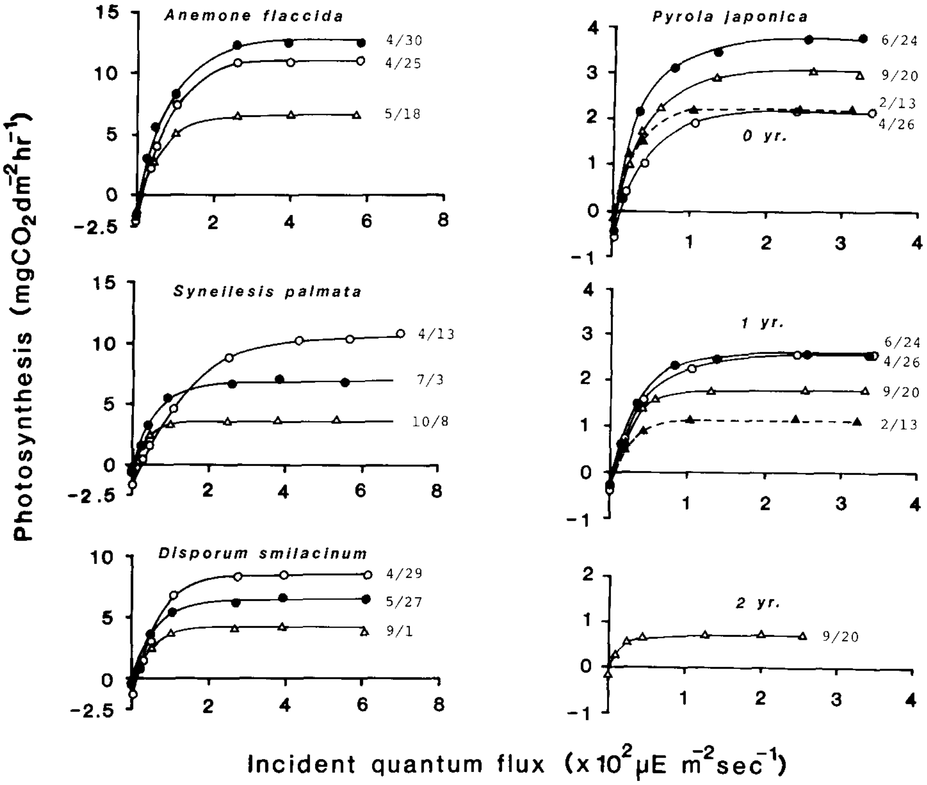

Fig. 2. Light-photosynthesis curves of leaves of understory species, *Anemone flaccida* (1981), *Syneilesis palmata* (1979), *Disporum smilacinum* (1981) and *Pyrola japonica* (1978-1979) at various times during the growing period. In *P. japonica*, the leaves consist of three age classes; 0-year-old (April to the next March), 1-year-old and 2-year-old leaves. See also Table 1.

vol % CO_2.

Photosynthetic rates of *P. japonica* were measured with detached leaves, after separating them into three age classes. The leaves were placed on wet filter paper in the chamber immersed in water 15 cm deep maintained at a constant temperature. Other procedures for photosynthesis measurement were the same as those described above.

Rates of the dark respiration of leaves were measured after the determination of light dependence of CO_2 uptake.

Results

Anemone flaccida

The light-photosynthesis curves observed in late April had the light-saturation point at high quantum flux and high rates of photosynthesis and respiration (Fig. 2). The light-compensation point (*LCP*) at that time was 22.1 μEm^{-2}sec^{-1}.

The leaves fully unfolded about two weeks after emergence. The gross photosynthetic rate at light saturation (*Psat*) values during the leaf-expansion period increased in parallel with the increase of the leaf area (Fig. 3). The photosynthetic rate attained its maximum on April 30, when the leaf-expansion was almost completed. The first sign of yellowing of the leaves was observed on May 6, about one month before the full closure of the overstory tree canopy. As the leaf yellowed, the rates of photosynthesis and pespiration (*R*) decreased remarkably. As the leaf matured and aged, its *LCP* value decreased with decreasing of the respiration rate (Table 1).

Syneilesis palmata

The leaves began to expand from early April and matured by mid July. The light-photosynthesis curve on April 13 had a high *Psat* value and a relatively high *LCP* value (Fig. 2). The curves observed with matured leaves on July 3 and October 8, on the other hand, had lower *Psat* and lower *LCP* values. The seasonal shift of the photosynthetic characteristics might be correlated with the change of light regime on the forest floor (Fig. 1).

The seasonal peak of the *Psat* value was observed on April 13, more than two months before the maturation of the leaves (Fig. 3). From mid April to late August, the values of *Psat* and *R* of the leaves decreased markedly (Table 1). The *LCP* value declined greatly from early April to late August.

With the *S. palmata* plants grown under the artificially reduced sunlight, the seasonal changes of

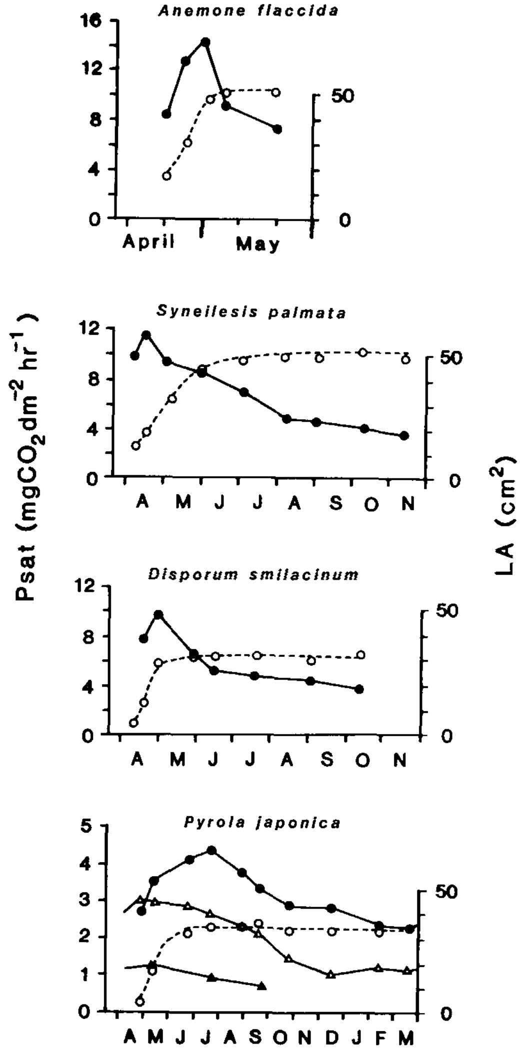

Fig. 3. Seasonal changes in light-saturated gross photosynthetic rate (*Psat* : solid line) and leaf area (*LA* : dotted line) of an individual plant of for understory species, *Anemone flaccida*, *Syneilesis palmata*, *Disporum smilacinum* and *Pyrola japonica*. In *P. japonica*, closed circles and open and closed triangles represent the 0-year-old, 1-year-old and 2-year-old leaves, respectively. Seasonal changes in *LA* of the 1-year-old and 2-year-old leaves are omitted for simplicity.

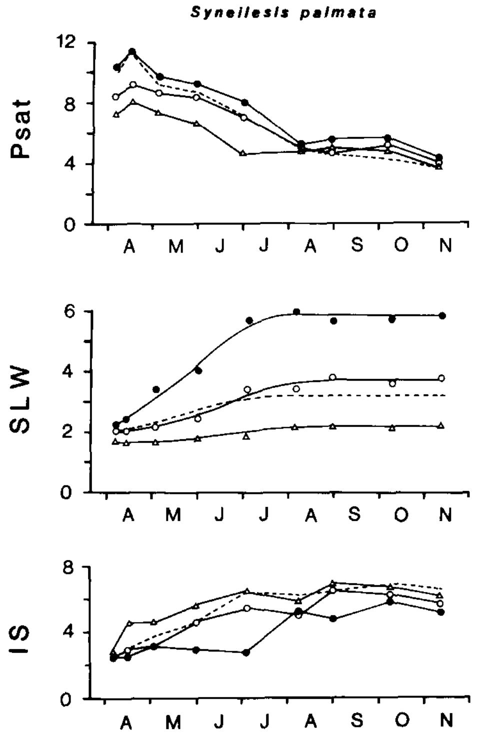

Fig. 4. Seasonal changes in the *Psat* (mg CO_2 dm^{-2} hr^{-1}), *SLW* (specific leaf weight, mg d.w. cm^{-2}) and *IS* (initial slope of light-photosynthesis curves, mg CO_2 μE^{-1}) of *Syneilesis palmata* grown at experimentally reduced light levels (●, 25%; ○, 6%; △, 3% light) and in the natural habitat (dotted line).

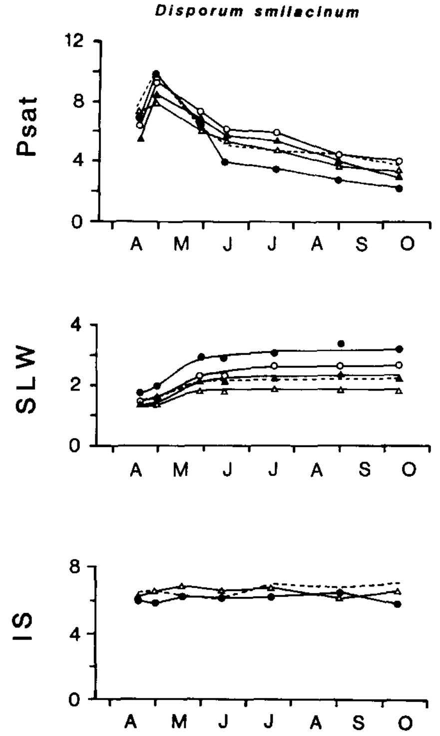

Fig. 5. Seasonal changes in the *Psat* (mg CO_2 dm^{-2} hr^{-1}), *SLW* (mg d.w. cm^{-2}) and *IS* (mg CO_2 μE^{-1}) of *Disporum smilacinum* grown at experimentally reduced light levels (●, 50%; ○, 10%; ▲, 6%; △, 3% light) and in the natural habitat (dotted line). The *IS* values for 10% and 6% light levels are omitted for simplicity.

Psat, *SLW* (specific leaf weight) and *IS* (initial slope of light-photosynthesis curves) were followed (Fig. 4). The seasonal trends of *Psat* value in this series were similar to those of the plants grown in their natural habitat. During the period from April to July, higher values of *Psat* were found in the plants which received higher light intensities. From August to November, however, there was little difference in the *Psat* values among plants grown under various light conditions. The *SLW* value under each light condition increased from April to July when the leaves were expanding, and then became constant. The higher were the light intensities, the higher the *SLW* values were. Higher *IS* values, on the other hand, were found under lower light intensities, during the period from April to July. Thereafter, there was little difference in the *IS* value among shade treatments.

Disporum smilacinum

The leaves began to emerge in early April and fully expanded in mid May, one and a half months after the emergence. Light-photosynthesis curves of the leaves had lower values of *Psat* and *LCP* (Fig. 2). Seasonal change in the rate of gross photosynthesis of *D. smilacinum* was similar to that of *S. palmata* (Fig. 3). The *Psat* values during leaf expansion were relatively high as compared with those in later stages. The maximum value of *Psat* was reached at the end of April, about two weeks before the leaves fully expanded. The *Psat* values then declined rapidly until June, as relative light intensity on the forest floor decreased with the development of the overstory canopy. The values of *LCP* and *R* also decreased in parallel with the value of *Psat* (Table 1). The *IS*s were almost constant throughout the growing period.

Seasonal changes in the *Psat*, *SLW* and *IS* values were also pursued in *D. smilacinum* grown under the artificially reduced sunlight (Fig. 5). The *Psat* value under each light condition showed a similar seasonal trend to that in the natural habitat. There was no clear relationship between the *Psat* value and the light intensity received. The *SLW* values under various light conditions increased from April to May when the leaves were expanding, and then maintained nearly constant values. Higher values of *SLW* were found in the plants grown at higher light intensities, although the difference was not so large compared with the case of *S. palmata*. There was no clear relationship between the *IS* value and light intensity received. The *IS* values were high throughout the whole growing period.

Pyrola japonica

Leaves of this evergreen perennial herb consist of three age classes; 0-year-old (April to the next March), 1-year-old and 2-year-old leaves (Table 1). New leaves emerged in April and fully expanded in July. Senescence of the leaves began in the autumn of the current year, but most of the emerged leaves survived through the first year. In the second year, however, more than half of the 1-year-old leaves died. In the third year, all of the 2-year-old leaves fell by the beginning of winter.

The light-photosynthesis curves for these three age classes had low *Psat* and *LCP* values (Fig. 2; Table 1).

Seasonal changes in *Psat* values for *P. japonica* are presented in Fig. 3. During the expansion of the leaves, the *Psat* value of the 0-year-old leaves increased and reached a maximum at the end of July, after the leaves had fully expanded. The photosynthetic activity decreased from July until October, and then increased slightly. This increase may be caused by the improved light condition on the forest floor due to leaf fall of overstory canopies. The leaves maintained some photosynthetic activity even in winter. Photosynthetic activities of the 1-year-old leaves were lower than those of the 0-year-old leaves, throughout the year except in April (Fig. 2). The *Psat* values of the 1-year-old leaves showed a seasonal trend similar to those of the 0-year-old. The 2-year-old leaves showed a low *Psat* value of about 1.0 mg CO_2 dm^{-2} hr^{-1} in spring and died by the end of October. The *LCP* and *R* values for leaves of each age class were relatively high in spring, but they became lower after the closure of the overstory tree canopy (Table 1). The *IS* was less steep in new leaves than in those in later stages.

Table 2. Summary of phenology and photosynthetic

Species	Growing period (months)	Period of *LA* growth (days)	Period from leaf emergence to the maximum value of *Psat* (days)
Anemone flaccida	2	10 - 14	10 - 14
Syneilesis palmata	8	90-100	15 - 20
Disporum smilacinum	7	40 - 45	25 - 30
Pyrola japonica	12	60 - 70	90-100

[1] *LA*, leaf area of an individual plant; *Psat*, gross photosynthesis at *LAmax*, the maximul leaf area of an individual plant.

Discussion

Phenological and photosynthetic characteristics of the four understory perennial herbs grown on deciduous forest floors are summarized in Table 2. They differ in the manner of adaptation to reduced light intensities under the canopy of deciduous trees.

They belong to different types in their photosynthetic characteristics: *Anemone flaccida*, sun-leaf type (Lundegårdh, 1921) with high *Psat* values, high light-saturation points, high *LCP*s and high respiration rates; *Disporum smilacinum* and *Pyrola japonica*, shade-leaf type (Lundegårdh, 1921) with low *Psat* values, low light-saturation points, low *LCP*s and low respiration rates; *Syneilesis palmata*, sun-leaf/shade-leaf type showing seasonal shift of light response curve of photosynthesis.

Light-photosynthesis curves of *A. flaccida* indicate that this plant belongs to the "shade intolerant" group as designated by Sparling (1967), and it appears to be a high-light adapted species similar to such understory plants as *Erythronium americanum* and *Allium tricoccum* (Taylor and Pearcy, 1976). The high activity of photosynthesis in *A. flaccida* is restricted to a brief period before the closure of the overstory canopy. As a typical spring herb in a deciduous forest, *A. flaccida* is characterized by rapid growth of leaf area and high *Psat* values in the early stage of development. As shown in Table 2, the time of the maximum *Psat* value was coincident with the time of the maximal leaf area of an individual plant (*LAmax*). Light intensities in the habitat observed at the time of *LAmax* were more than 30% of full daylight. These may be of great advantage for matter production of *A. flaccida*, growth of which is restricted to a brief period in early spring.

Both *S. palmata* and *D. smilacinum* are summergreen perennial herbs and have a similar growing period (7 to 8 months). The maximum *Psat* values of these species were found in the early stage of plant development. However, they differ with respect to the period of growth in total leaf area of the plant and the type of light response curve of photosynthesis (Table 2).

*characteristics of the four understory species*1)

The maximum value of *Psat* ($mgCO_2dm^{-2}hr^{-1}$)	*RLI* at the maximum value of *Psat* (%)	*RLI* at *LAmax* (%)	Shape of the light-curves
14.3	*32*	*33*	*Sun-leaf type*
11.5	*25*	*5*	*Sun-leaf / shade-leaf type*
9.8	*18*	*11*	*Shade-leaf type*
4.3	*6*	*10*	*Shade-leaf type*

light saturation ; *RLI*, relative light intensity in the natural habitat;

D. smilacinum in the natural habitat possesses light-photosynthesis curves of the shade-leaf type even in the early stages of plant development, with lower values of *Psat* and *LCP* as compared with those of *S. palmata*. The *IS* was relatively high throughout the whole growing season, indicating that *D. smilacinum* can make an efficient use of weak light for photosynthesis.

It is widely noted that there is a strong relationship between the light regime during expansion period of young leaves and their subsequent photosynthetic characteristics (Sparling, 1967; Nobel *et al.*, 1975; Chabot, 1978; Young and Smith, 1980). However, the shading experiment using *D. smilacinum* showed no evidence of such relationship. This plant exhibited much less modification of photosynthetic characteristic in response to light intensity received, showing light-curves of shade-leaf type at 50% daylight. The *IS*s were high, independent of degree of shading (Fig. 5). Moreover, the *Psat* values of the matured leaves grown at 50% daylight were lower than those grown at lower light intensities. These facts suggest that *D. smilacinum* is a low-light adapted species, with a small extent of phenotypic response to light intensity.

Photosynthetic characteristics of a leaf of *S. palmata* was very flexible, since the shape of the light-photosynthesis curve shifted from sun-leaf type to shade-leaf type with the change of light condition on the forest floor (Fig. 2). The *IS* was low but became steeper after closure of the forest canopy. Such eco-physiological modification in response to light intensity must be of great advantage for matter production and survival of this herb in changing light environments.

Morphological and eco-physiological plasticity of *S. palmata* in response to light intensity was also shown by the shading experiments. Shape of light-photosynthesis curves, observed during the period from April to July, at 25% daylight was of a sun-leaf type, whereas that at 3% daylight was of a shade-leaf type. The *IS* was much steeper at 3% daylight than at 25% daylight except for early April (Fig. 4). Various shade treatments brought about a great difference in *SLW*, as a measure of leaf thickness. The *SLW* values increased rapidly during the period of leaf expansion from April to July, and the final value at 25% daylight was about three times as large as that at 3% daylight (Fig. 4), indicating a great morphological plasticity of this plant. As shown in Table 2, period of leaf area growth of *S. palmata* is twice as long as that of *D. smilacinum* (90-100 days vs. 40-45 days). It is possible, therefore, that greater morphological plasticity of *S. palmata*, as compared with *D. smilacinum*, is related to much longer period of leaf area growth.

The shape of the light-photosynthesis curves of *P. japonica*, an evergreen herb, is of the shade-leaf type (Fig. 2). This plant belongs to the "shade-tolerant" group (Sparling, 1967). Unlike the above-mentioned three species, its *Psat* value was low, and the maximum *Psat* value of the 0-year-old leaves was observed after the time of *LAmax* of the leaves (Table 2). Much time is needed to expand young leaves and to attain high *Psat* value. These characteristics would be disadvantageous for matter production. However, this disadvantage may be compensated for by photosynthesis of the 1-year-old and 2-year-old leaves, which maintain some photosynthetic activity even in late autumn and winter.

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