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Population Ecology in Natural *Syneilesis palmata* Stands: I. Relationship between Flowering and Plant Size

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In this study, the relationship was explored between flowering potential and plant size in a population of *Syneilesis palmata* (THUNB.) MAX., Usannamul. For this perennial shade-tolerant herb, the flowering rate, plant size, and changes that occurred in the next year after flowering were monitored in two different types of natural stands: moderately shaded (MS; for 11 years) and severely shaded (SS; 7 years). The correlation coefficients (CC) between inflorescence number and other factors, i.e., widths of the first leaf, second leaf, or total leaf breadth, were significant at the 1% level in both stands. In particular, the CC was >0.9 between the number of inflorescences and total leaf breadth. Although the mean flowering rates averaged 6.8% in MS and 8.6% in SS, those values varied widely, ranging from 0 to 53% among years. These rates were not related to petiole length but did increase in proportion to the width of the leaf blade. Flowering began when plants moved beyond the medium size class; the rate in the MS environment was 100% for the largest-sized plants. For plants in the SS, however, the highest rate was 35%. Over the 11 years, 62.8% of all plants in the MS never flowered, while another 30.8% bloomed only once. In comparison, plants observed for 7 years in the SS showed a non-flowering rate of 78.1% and a one-time-only rate of 19.2%. In the next year after flowering, 57.6% of the MS plants exhibited reduced growth while 25.8% of those individuals each split into two plants. In the SS, 37.8% had decreased development the following year, and a mortality rate of 37.8%.

Keywords: closed canopy, flowering rate, leaf blade, plant size, *Syneilesis palmata*

Many perennial plants have three options for energy allocation: toward maintenance growth, vegetative propagation, or sexual reproduction (Worley and Harder, 1996). For example, when energy is limited in clonal plants, sexual reproduction and vegetative propagation must compete for resources (Cook, 1983). Two strategies can be utilized -- survival of the plant itself (i.e., only essential growth processes) versus population growth, which, in perennial species, entails simultaneous vegetative propagation and sexual reproduction in order to increase the number of plants. Thus, the quantity or size of ramets vegetatively reproduced affects population dynamics. However, because those ramets are physiologically connected to the mother plant, the amount of energy invested toward them cannot be measured separately.

In contrast, seed production is related to plant age or size, as well to environmental factors. Except for plants with annual rings in their corms or rhizomes, the age of perennial herbs cannot be estimated, so the only reliable dating system involves recording all the individuals found within permanent quadrats over a long time period (Holland, 1981). Therefore, studies of the potential for seed production must be based on plant size rather than age. Fortunately, size and reproductive output are strongly and positively correlated (Silvertown, 1982; Klinkhamer et al., 1992). Generally, a minimum size, which can vary by species and even by growing conditions within a species Verburg et al. (1996), is required for the onset of flowering. This is why the optimal age or size at maturity is determined by a balance between the benefits of starting to reproduce early and the costs entailed for future survival and production (Wesselingh et al., 1997). However, there is a large overlap in plant size at flowering (i.e., the threshold size) among vegetative individuals (Wesselingh et al., 1993, 1997). Inghe and Tamm (1985) have classified flowering-plant size according to stage within the life cycle. Although many and diverse hypotheses have been proposed, the minimum threshold size varies with species or environmental factors within the same species. Inghe and Tamm (1985) have investigated the population dynamics for a species growing in various environments, but no studies have yet fully considered the effect of plant size or status after flowering. Generally, monocarpic species die after they produce flowers, but polycarpic plants show diverse patterns according to their species or environment (Tamm, 1972; Clauss and Aarssen, 1994). For example, *Heloniopsis orientalis* (Min, 2000) continuously flowers at a minimum plant size whereas *Arisaema* changes its sex after the female blooms (Bierzychudek, 1982; Min and You, 1998). In the latter species, one may interpret this to mean that the energy investment toward the vegetative organs is too little to sustain the female.

The aim of the research described here was to clarify the relationship between flowering time and plant size, and to monitor changes in plant status after flowering in two natural stands of *Syneilesis palmata* that differed in their regimes of incipient light.

MATERIALS AND METHODS

The study area was located on a natural deciduous forest at Suha-ri, Doam-myeon, Pyeongchang-gun, Kangwon Province (37°3710N, 128°4241E), Korea (Fig. 1). Permanent quadrats (4 × 5 m each) were chosen in two stands of *Syneilesis palmata* (THUNB.) MAX., Usannamul. One had a semi-closed canopy (moderately shaded; MS) while the other had a completely closed canopy (severely shaded; SS). Both had westerly aspects. The stands were 30 m apart,

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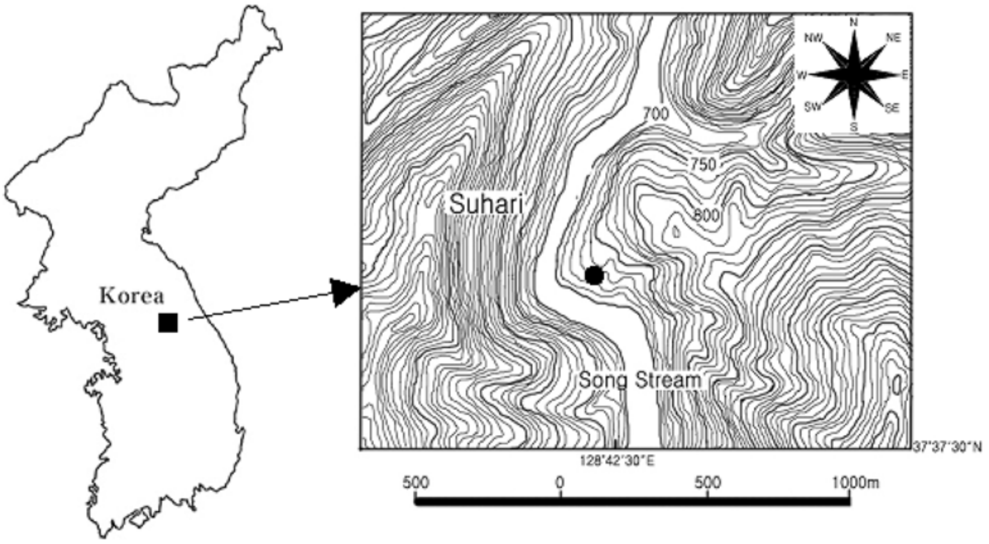

Figure 1. Map of study sites.

Table 1. Coverage and height of each layer at two stands (moderately shaded MS and severely shaded SS) on each survey date.

Layer	Properties	MS		SS	
		1992. 7. 24	2002. 8. 2	1992. 7. 24	1998. 8. 3
Tree	Height (m)	12	15	17	18
	Coverage (%)	70	80	95	95
	Dominant species	*Quercus serrata*	*Quercus serrata*	*Quercus Mongolica*	*Quercus mongolica*
Subtree	Height (m)	6	6	5	6
	Coverage (%)	40	30	30	30
	Dominant species	*Quercus serrata*	*Quercus serrata*	*Acer pseudo-sieboldianum*	*Quercus serrata*
Shrub	Height (m)	1.3	1.5	1	1
	Coverage (%)	10	20	30	20
	Dominant species	*Stephanandra incisa*	*Quercus serrata*	*Tripterygium regelii*	*Tripterygium regelii*
Herb	Height (m)	0.3	0.2	0.1	0.3
	Coverage (%)	20	10	10	20
	Dominant species	*Carex siderosticta*	*Carex lanceolata*	*Viola albida*	*Carex lanceolata*

and they differed in elevation by 5 m. The MS had a 5° slope; the SS, a 15° slope. On 24 July 1992, MS had 70% tree coverage, where heights averaged 12 m. This tree layer comprised *Quercus serrata*, *Q. mongolica*, and *Pinus densiflora*. The coverage and height of the sub-tree layer were 40% and 6 m, respectively. In that layer grew *Q. serrata*, *Prunus leveilleana,* and *Lindera obtusiloba*. The shrub layer had a 10% cover and was composed of *Stephanandra incisa*, *Rhododendron mucronulatum*, and *Tripterygium regelii*. Its herb layer, containing *Carex siderosticta*, *C. lanceolata*, *Atractylodes japonica*, *Codonopsis lanceolata*, *Euphorbia sieboldiana*, *Viola variegata*, and *Syneilesis palmata* (the focus of this project) covered less than 20% of the area. The litter layer was 5 cm deep. Although coverage in the tree layer had increased to about 80% by the end of this survey (2 August 2002), the coverage and species composition in the other layers remained relatively constant over its 11-year span (Table 1). In SS at the start of the survey, tree-layer coverage and height were 95% and 17 m, respectively. This layer mainly contained *Populus davidiana*, *Q. mongolica*, *Q. serrata*, *P. leveilleana*, and *Betula davurica*. Coverage and height of the sub-tree layer were 30% and 5 m, which included *Acer pseudo-sieboldianum*, *Q. serrata*, *Tilia rufa*, and *L. obtusiloba*. The shrub height had 30% coverage and an average height of 1 m. Its main species were *Tripterygium regelii*, *R. mucronulatum*, and *R. yedoense* var. *poukhanense*. Herb species *V. albida*, *V. acuminata*, *V. variegata*, *C. lanceolata*, *E. sieboldiana*, *Ainsliaea acerifolia*, and *Pyrola japonica* covered 20% of that layer, and the litter was 10 cm deep. During this evaluation period, the mean annual precipitation and air temperature at these sites were 1,581 mm and 6.3°C, respectively (Korea Meteorological Administration, 1991). Two permanent quadrats were set up on 24 July 24 1992. Each *Syneilesis palmata* plant within them was numbered with a fomex bar, with the total ranging from 135 in MS to 190 in SS. Field surveys were carried out between late July and early August over 11 years in MS and over 7 years in SS. Once per year, the *S. palmata* petiole lengths, leaf breadth, leaflet number of the first and second leaves, number of inflorescences, and peduncle lengths were mea-

Table 2. Soil properties at two stands (moderately shaded MS and severely shaded SS) on 24 July 1992.

Stand	Depth of A layer (cm)	Depth of litter layer (cm)	Organic matter (%)	Total T (mg g^{-1})	Available P (mg kg^{-1})	K (mg g^{-1})
MS	5	22	10.1	5.4	8.9	1.88
SS	10	57	21.4	11.4	23.6	2.54

sured. Data for all flowering plants were used to analyze the relationships between each pairing of factors, so that, in all, 68 were considered in MS and 37 in SS. The flowering rate was calculated as the number of flowering plants per total population. To analyze their correlations with flowering events, plant dimensions were grouped into 10 size classes, based on petiole length, leaf breadth, and leaflet number of the first leaf. Changes in plant status after flowering were estimated by finding the ratio of current leaf breadth to that measured the previous year. Depths of the litter and A layers were measured, and the soil was sampled at 10 cm deep on 24 July 1992. After the samples were air-dried, organic matter content was determined by the method of loss on ignition, run at 550°C for 4 h. Micro-Kjeldahl and stannous-reduced molybdophosphoric blue-color techniques were used to measure total nitrogen and available phosphorus. Potassium was extracted with a 1 N ammonium acetate solution and was measured in a flame photometer (Coleman 51).

RESULTS

The MS litter and A layers were thinner than those of SS (Table 2). Moreover, soil in the former had lower contents of organic matter, total nitrogen, and potassium, suggesting that its physical environment for plant growth also was better. However, because canopy coverage was denser in SS than in MS, *S. palmata* received less sunlight in the former stand.

All the plants that flowered had two leaves while those that never bloomed had only one. The ranges in leaflet

Table 3. Size range for flowering plants from 1992 to 2002 in moderately shaded stand (MS), and from 1992 to 1998 in severely shaded stand (SS). (F, first leaf; S, second leaf; L, length; B, breadth; N, number; f, flower; l, leaf; pt, petiole; pc, peduncle. TBl = F-Bl + S-Bl)

Properties	Stand	
	MS (*n*=68)	SS (*n*=37)
F-Lpt (cm)	14-40	22-58
F-Bl (cm)	13-29	12-24
F-Nl	7-10	6-9
S-Lpt (cm)	6-37	2-23
S-Bl (cm)	8-24	11-20
S-Nl	3-7	3-7
Lpc (cm)	16-52	33-55
TBl	20-53	23-48
Nf	0-40	2-59

Table 4. Correlation coefficients between property pairings from flowering plants. (F, first leaf; S, second leaf; L, length; B, breadth; N, number; f, flower; l, leaf; pt, petiole; pc, peduncle. TBl = F-Bl + S-Bl).

Moderately shaded stand (MS), (*n*=68)

	F-Bl	F-Nl	S-Lpt	S-Bl	S-Nl	Lpc	Nf
F-Lpt	0.565**	0.070	0.133	0.522**	0.119	0.312*	0.315*
F-Bl		0.204	-0.076	0.628**	0.227	0.469**	0.387**
F-Nl			-0.097	0.059	0.304*	0.228	0.343**
S-Lpt				-0.166	0.254*	0.148	0.084
S-Bl					0.126	0.409**	0.372**
S-Nl						0.153	0.247
Lpc							0.765**
TBl							0.923**

Severely shaded stand (SS), (*n*=37)

	F-Bl	F-Nl	S-Lpt	S-Bl	S-Nl	Lpc	Nf
F-Lpt	-0.227	-0.057	0.446**	0.021	-0.137	-0.093	-0.162
F-Bl		0.210	-0.150	0.683**	-0.052	0.539**	0.488**
F-Nl			0.311	0.352*	0.236	0.019	0.180
S-Lpt				-0.095	0.055	-0.164	-0.250
S-Bl					0.139	0.464**	0.627**
S-Nl						0.080	0.242
Lpc							0.675**
TBl							0.958**

**, 1% level; *, 5% level.

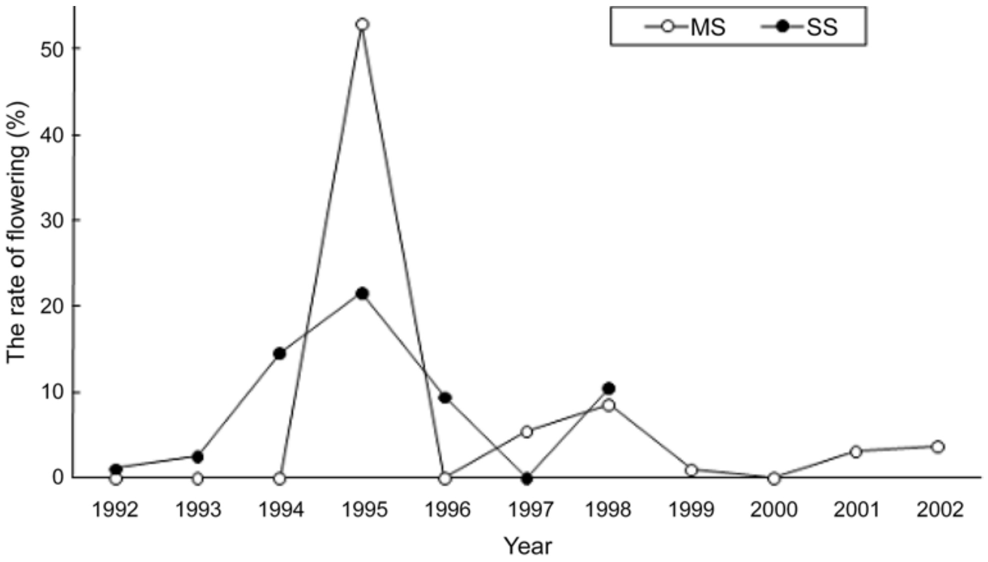

Figure 2. Changes in flowering rates for *S. palmata* over 11 years in moderately shaded stand (MS) and 7 years in severely shaded stand (SS).

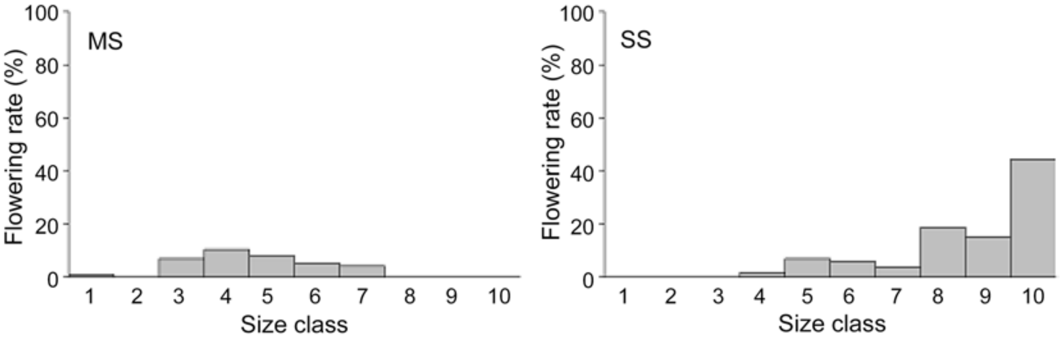

Figure 3. Flowering rate as function of size class for petiole length (in cm). 1, <10; 2, 10-15; 3, 15-20; 4, 20-25; 5, 25-30; 6, 30-35; 7, 35-40; 8, 40-45; 9, 45-50; 10, 50.

number (Nl) for first and second leaves were narrow between MS and SS (Table 3). In comparison, wide variations were found in petiole length (Lpt), leaf breadth (Bl), peduncle length (Lpc), and inflorescence number (Nf). For example, values for Nf ran from 0 to 40 in MS and from 2 to 50 in SS. The lack of inflorescences on peduncles was thought to be the result of plants either being too small to flower or else having been attacked by an animal.

Correlation coefficient values (CC) between two factors -- Lpts of the first and the second leaf, Bls of the first and the second leaf, Nls of the first and the second leaf, or Lpc, Nf, and Bl of the first leaf plus the second one (TBl) -- were calculated separately for MS and SS (Table 4), but no significant or consistent trends were noted between the two stands. CCs between Lpt and Bl of the first leaf also showed a reverse trend from MS and SS. However, CCs for pairings between Nf and Bl (first and second leaf), Nf and Lpc, Nf and TBl, the two Bl parameters, or Lpc and Bl were significant at the 1% level in both stands. The CC between Nf and TBl was the highest of all the correlations here -- 0.923 in MS and 0.958 in SS.

Flowering rates in these stands showed extreme annual fluctuations (Fig. 2), but averaged 6.8% in MS and 8.6% in SS. For example, except for 1995 (when the rate in MS was 52.9%), the frequency of flowering in that stand was always <10% over the entire 10-year survey. In fact, for both stands, flowering rates were the highest in 1995 and also relatively high in 1998, and each stand had identical peaks. One might conclude, therefore, that macroclimate rather than microclimate affected the flowering of *S. palmata*; such factors will need further examination.

Flowering rate as a function of petiole length classes in MS was dissimilar to that in SS (Fig. 3); in the former, the rate was highest from plants in the medium size class, i.e., 20 to 25 cm, and no flowering was observed from plants with petioles longer than 40 cm. By contrast, the rate in SS appeared to increase with Lpe values, suggesting that parameter may be a suitable criterion for predicting flowering potential as well as leaf number when one is investigating severely shaded areas but not those that are only moderately shaded. Under the latter type of canopy coverage, *S. palmata* probably invests it energy supply toward organs other than the petiole. Likewise, in heavily shaded stands, the petioles may receive more energy in order to capture the maximum amount of available sunlight.

Flowering rates as a function of leaf breadth classes were positively correlated and very similar between MS and SS (Fig. 4). In MS, the minimum size for the onset of flowering

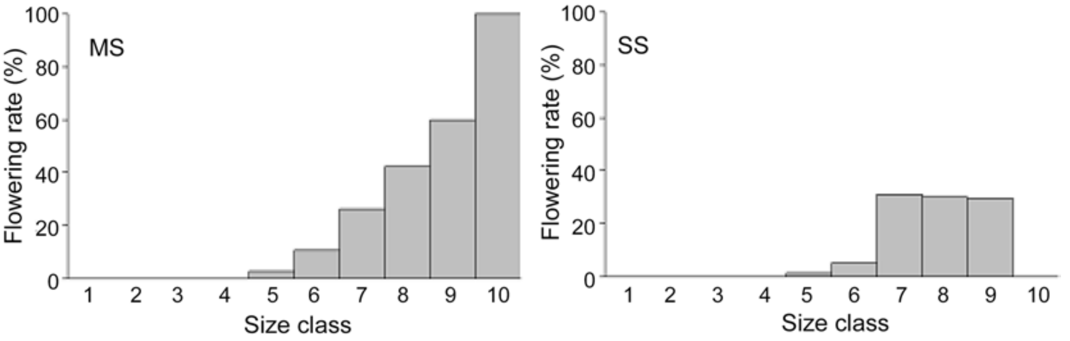

Figure 4. Flowering rate as function of size class for leaf width (in mm). 1, <30; 2, 30-60; 3, 60-90; 4, 90-120; 5, 120-150; 6, 150-180; 7, 180-210; 8, 210-240; 9, 240-270; 10, 270.

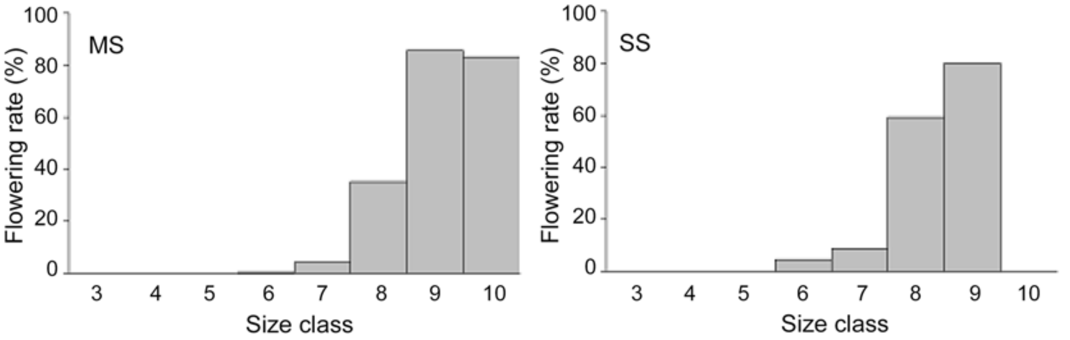

Figure 5. Flowering rate as function of leaflet number for first leaf.

was associated with the 12- to 15-cm class, and all plants taller than 27 cm flowered. In SS, that minimum was the same, but the flowering rate was constant and only about 30% when leaves were wider that 18 cm, regardless of overall plant size. Likewise, patterns for flowering rate as a function of the leaflet number of the first leaf were similar in MS and SS (Fig. 5). Plants required at least six leaflets in order to begin flowering, and that rate increased with leaflet number.

Nevertheless, during this field survey, most plants never flowered at all (Table 5). In fact, non-flowering rates were 62.8% in MS (11 years) and 78.1% in SS (7 years), perhaps a reflection of the high mortality found over those study periods. In MS, plants that flowered only once were 30.8% of the total, compared with 19.2% in SS. Only a few plants bloomed more than three times.

After flowering occurred, changes in plant status also were recorded. These were based on petiole length and leaf breadth the following year, and were divided into five categories (Table 6). Within individual stands, petiole length and leaf breadth showed similar patterns over time, but those between stands were somewhat different. Of the five categories used for comparison, the greatest change in plant behavior in the year after flowering was noted as a decrease in either petiole length or leaf breadth. Following those, the next most common responses were seen in the division of one plant into two (MS; 25.8%) and higher mortality (SS; 37.8%).

Table 5. Number of times individual plants flowered over 11 years in moderately shaded stand (MS) and 7 years in severely shaded stand (SS).

Times	Stand	
	MS (*n*=68)	SS (*n*=37)
Zero	98 (62.8)	118 (78.1)
One	48 (30.8)	29 (19.2)
Two	9 (5.8)	4 (2.6)
Three	1 (0.6)	
Total	156 (100.0)	151 (100.0)

Table 6. Changes in physiological properties of *S. palmata* plants after flowering in moderately shaded stand (MS) and severely shaded stand (SS).

Category	Petiole length		Leaf breadth	
	MS	SS	MS	SS
Decreased size	29 (42.6)	15 (40.5)	38 (55.9)	14 (37.8)
Increased size	11 (16.2)	4 (10.8)	4 (5.9)	5 (13.6)
Division into two plants	17 (25.0)	1 (2.7)	17 (25.0)	1 (2.7)
Death of plant	9 (13.2)	14 (37.8)	9 (13.2)	14 (37.8)
No changes in size	2 (2.9)	3 (8.1)	0 (0.0)	3 (8.1)
Total	66	34	68	37

DISCUSSION

For both stands, ranges in most growth parameters were similar, although values for first-leaf Lpt were larger in SS plants. This may have occurred because the petioles of *S. palmata* were more elongated when plants were grown in the shade. However, the greater the increase in leaf area in that species, the more Nf that was produced. Generally, the amount of seed produced coincides with overall plant size (Silvertown, 1982) because the leaf is a photosynthetic organ and photosynthate is proportional to leaf area when all other conditions are equal. However, this positive correlation between Nf and Lpc requires further study. For example, when peduncles are taller, the potential increases for seeds to be dispersed over longer distances, perhaps to avoid their dense aggregation (Min, 2000).

As flowering rates increased with plant size, leaflet number was the best indicator for estimating flowering potential. Leaf breadth and petiole length were not as reliable, especially under the moderately shaded conditions found in MS. Other researchers also have reported that plant size is a good predictor of flowering, as long as all members are the same within a population (Hirose and Kachi, 1982; Samson and Werk, 1986; Iwasa and Cohen, 1989; Thompson et al., 1991; Klinkhamer et al., 1992; Schmid and Weiner, 1993). Wesselingh et al. (1997) have also shown a large overlap in size between flowering plants and those that are in a vegetative (non-flowering) phase (Wesselingh et al., 1997). A similar overlap was observed for the *S. palmata* plants examined here.

Because *S. palmata* plants had low flowering rates, i.e., blooming only a few times during the project, this species is considered iteroparous because it invests just a small amount of energy toward sexual reproduction. In such cases, therefore, the optimal age or size at maturity is determined by the balance between the benefits of starting to reproduce early and the costs this may have for future survival and reproduction (Wesselingh et al., 1997). For example, flowering frequencies vary widely in populations of *Hepatica nobilis* and *Sanicula europaea* (Inghe and Tamm, 1985), and a flowering event generally lowers the probability of repeat blooming in the next year. In addition, juveniles or weakened, mature ramets may persist for decades without flowering at all (Inghe and Tamm, 1985). Finally, shade-tolerant, temperate-forest herbs devote less energy to sexual reproduction than do grassland herbs (Bierzychudek, 1982). This iteroparous strategy was seen in the *S. palmata* studied here in the shaded area. However, more research is necessary on the annual production of fertile seeds as well as the biomass of the underground portions of *S. palmata*.

Based on observations of plant status changes after flowering, one might conclude that *S. palmata* invested more energy toward vegetative organ development in MS than in SS. Reproductive output is maximized by an instantaneous switch, from a purely vegetative period to a reproductive phase (Cohen, 1971). Flowering also increases the risk of mortality (Svensson et al., 1993), which may explain why *S. palmata* in SS had higher death rates when more energy was channeled to its sexual organs. For the SS, plant density varied from year to year, making it necessary for that population to maintain itself via the recruitment of seed.

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