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# Population Ecology in a Natural *Syneilesis palmata* Stand: II. Vegetative Growth and Population Structure

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**Vegetative growth and changes within populations of *Syneilesis palmata* (THUNB>) MAX. Usannamul were monitored in two natural stands with different levels of incoming light. This perennial, shade-tolerant herb was measured for its plant size, petiole length, leaf breadth, and leaflet number over 11 years in a moderately shaded (MS) stand and over 7 years in a severely shaded (SS) stand. At the end of each growing season, a shoot primordium developed at the center of the root system. Correlation coefficients were mostly high between pairings of two properties -- total weight, petiole length, petiole weight, leaf breadth, leaf blade weight, leaf area, specific leaf area, and leaflet number. Mean annual mortality of this species was higher in SS (22.97%) than in MS (8.85%), but great fluctuations were seen from year by year. Mortality was lowest for medium-sized plants. Regarding petiole length, differences in mean annual growth rates were conspicuous, i.e., 2.6% in MS and 8.4% in SS, while growth rates for leaf breadth were 3.1% in MS and 24.2% in SS. Changes in plant frequency within individual size classes roughly showed a normal distribution curve. However, the mode varied year by year, and such changes were more remarkable in SS than in MS. Under severe shading, *S. palmata* had a higher growth rate and but also greater mortality than did plants under moderate shade. Therefore, one can conclude that the population structure in SS was unstable over time.**

*Keywords:* frequency distribution, growth rate, mortality, plant size, shaded stand, *Syneilesis palmata*

Population ecology is a specialized branch of plant science dealing with the numerical impact of interactions on a special set of individuals, as they occur within a defined geographical area (Silvertown, 1982). The structure of a population is determined by growth rates, mortality, and the influx of seedlings. For annuals and biennials, new plants are recruited via seed germination, while perennial species are increased through germination as well as vegetative reproduction (Harper, 1977). Ramets that become isolated from the mother plant form new plants; the number or size of this increase varies by species, the dimensions of the mother, and the ramet type (i.e., source organ). For example, stolons and rhizomes attached to the mother plant can produce new shoots and roots on their nodes, and those shoots also can be isolated, resulting in a potentially large number of new plants that can appear all at once or over an entire growing season (Silvertown, 1982). Because the age of individual plants cannot be estimated in this process, such population must be studied for a long time (Tamm, 1972a, b; Inghe and Tamm, 1985). Therefore, for most herbaceous plants, the only reliable dating system involves the recording of all individuals within permanent quadrats over several years (Holland, 1981). Because time is a limiting factor in most scientific research, investigations of this type are few (Bierzychudek, 1982). However, when ramets become isolated due to the death of an underground plant organ, e.g., the rhizome or stolon from a pseudo-annual, their evaluation is simple and clear (Kawano, 1985; Verburg et al., 1996; Dong et al., 1997; Verburg and During, 1998). Although ramets can also originate from a tuber, bulb or root, few have been studied in natural populations, except for crop plants (Kawano and Nagai, 1975; Holland, 1981).

Because herbaceous species growing under 100% canopy coverage do not receive sunlight that is sufficient for sustaining year-round development, these spring ephemerals must either finish their life cycles before the canopy closes or else have a shade-tolerant strategy. Although they may multiply partly by seed production, their germination rates are too low to result in many seedlings by that means. Therefore, these plants are increased largely by their vegetative organs, stolons, or rhizomes. Shade-intolerant grasses may produce many ramets from their rhizomes over a short period, but species that grow individually and in patches under a closed canopy usually are non-flowering, and produce 0 to 2 ramets per year. These ramets develop at the tips of elongated stolons, which become disconnected from the parent ramet at the end of the growing season (Wijesinghe and Whigham, 1997). Such asexually produced ramets do not have an aerial shoot during the year they are formed, so their initial growth depends entirely on resources supplied by the parent ramet (Kudoh et al., 1999). When that mother plant dies, the remaining ramets must rely on resources within the population structure (Verburg et al., 1996).

The patterns of flowering and the changes that occur in those plants afterward have already been reported for a *Syneilesis palmata* population (Min, submitted). Therefore, the aim of the study described here was to clarify the relationship between plant growth and population structure over several years in two natural *S. palmata* stands that differed in their canopy cover.

## MATERIALS AND METHODS

The study sites, survey period, and monitoring method were the same as described previously (Min, submitted). The two stands included one that was under a semi-closed canopy (MS; moderately shaded) while the other was under

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a completely closed canopy (SS; severely shaded). To examine the relationships among organs from *S. palmata* (THUNB.) MAX., Usannamul, 65 plants from MS and 14 from SS were sampled at the periphery of two permanent quadrats on 24 July 1992. These materials were divided into root, petiole, and leaf blade portions, and were oven-dried at 85°C for 48 h. Afterward, they were measured for length and area, then weighed. The correlation coefficients were calculated between pairs of properties, i.e., petiole length, petiole weight, leaf breadth, leaf blade weight, leaf area, specific leaf area (SLA), and leaflet number. To confirm the existence of new ramets, five plants were sampled at the periphery of the MS plot on 10 November 1993. Based on their petiole lengths and leaf breadths, all plants were divided into 10 size classes, and their frequency was determined within each class. The rate of annual increase in size was calculated by dividing current dimensions by those in the previous year.

## RESULTS

After a *S. palmata* shoot had withered at the end of a particular growing season, a new primordium developed at the center of the old root system (Fig. 1). These roots remained until a new shoot formed and a leaf unfolded for photosynthesis. When no old primordium existed, that plant died and no new primordium emerged the following year.

Plants were somewhat larger in SS (severe shading) than in MS (moderate shading) (Table 1). However, those differences were not significant because of the wide range in all size parameters, except leaflet number. Specific leaf area (SLA) was higher in MS than in SS.

The correlation coefficients (CC) between property pairs were mostly significant at the 1% level in MS and SS (Table 2). Because of the strong relationship between total weight and other properties, it was assumed that plant size could be estimated based on petiole length and leaf breadth, so that the plants did not have to be destructively sampled. CC values between SLA and other properties were negative but all CCs among other properties were positive. Moreover, the CCs between SLA and leaf area were significant at the 1% level, –0.646 in MS and –0.691 in SS.

The number of plants declined slowly in MS from 1992 to 2002 (from 135 to 66, for a survival rate of 49.8%) but decreased abruptly in SS from 1992 to 1998 (190 vs. 38; 20% survival; Fig. 2). In fact, the population in MS was larger in 1996 than in 1995, a result of one plant dividing into two.

Mortality was extremely varied from one year to another in both MS and SS (Fig. 3). For example, except for 1997,

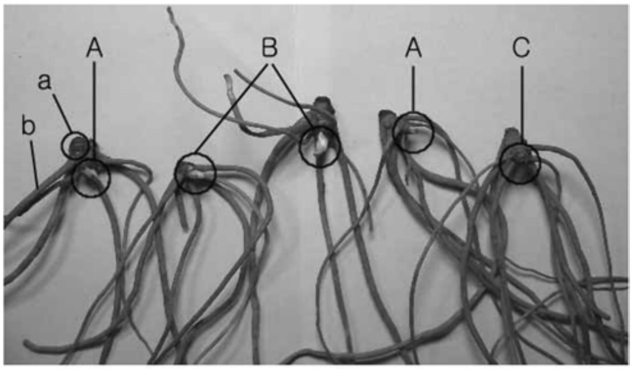

**Figure 1**. New primordium of *S. palmata* at end of growing season is located at center of maternal plant root system, and grows in reverse direction of old shoot. (**A**) Unfaithful primordium. (**B**) Faithful primordium. (**C**) No primordium. a, scar where shoot was cut off; b, root.

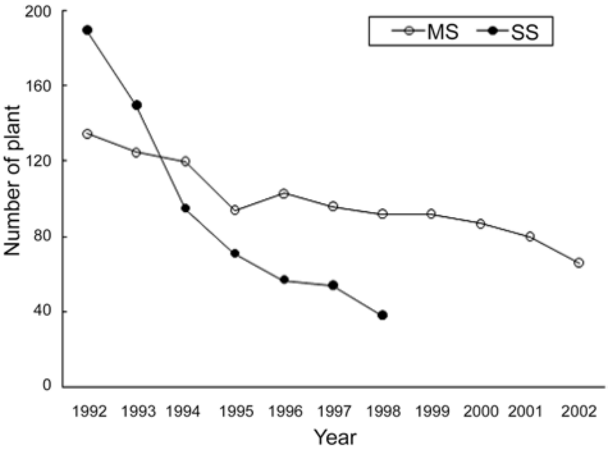

**Figure 2**. Number of surviving *S. palmata* plants during 11 years in MS (moderate shading) or 7 years in SS (severe shading).

**Table 1.** *S. palmata* properties for moderately shaded (MS) stand and severely shaded (SS) stand on 24 July 1992. (W, weight; N, number; L, length; A, area; B, breadth; SLA, specific leaf area; t, total; pe, petiole; lb, leaf blade; ll, leaflet)

| Property | Stand | | | |
|---|---|---|---|---|
| | MS ($n$=65) | | SS ($n$=14) | |
| | Mean ± SD | Range | Mean ± SD | Range |
| Wt (mg) | 1793 ± 1468 | 79-6982 | 3515 ± 2686 | 95-7773 |
| Lpe (cm) | 25.8 ± 8.0 | 12.0-43.6 | 29.0 ± 10.0 | 10.5-42.0 |
| Wpe (mg) | 403 ± 350 | 16-754 | 863 ± 717 | 20-2210 |
| Blb (cm) | 13.4 ± 3.6 | 4.0-18.0 | 14.1 ± 6.1 | 4.0-22.0 |
| Alb (cm$^2$) | 189.8 ± 122.3 | 12.0-471.8 | 325.6 ± 231.5 | 17.0-637.6 |
| Wlb (mg) | 712 ± 540 | 30-2,411 | 1396 ± 1019 | 39-2641 |
| SLA (cm$^2$/g) | 303 ± 57 | 196-462 | 261 ± 58 | 217-436 |
| Nll | 5.9 ± 0.7 | 5-7 | 6.3 ± 1.1 | 5-8 |

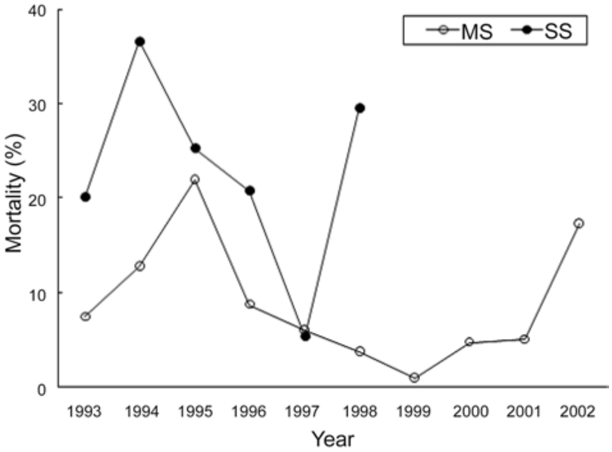

**Figure 3**. Mortality of *S. palmata* during 11 years in MS (moderate shading) or 7 years in SS (severe shading).

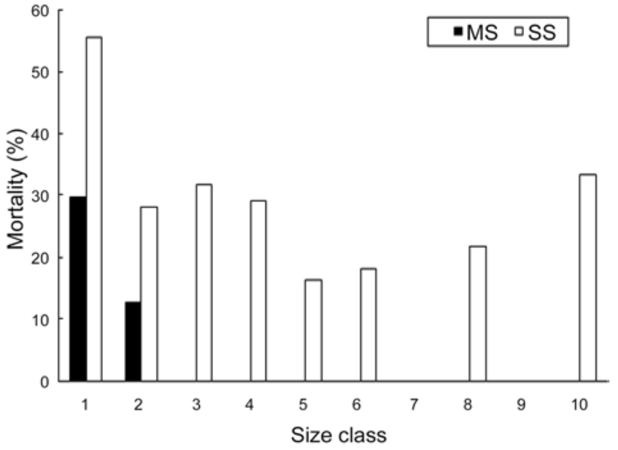

**Figure 4**. Mortality of *S. palmata* along size class, based on petiole length (cm). 1, <10; 2, 10-15; 3, 15-20; 4, 20-25; 5, 25-30; 6, 30-35; 7, 35-40; 8, 40-45; 9, 45-50; 10, 50.

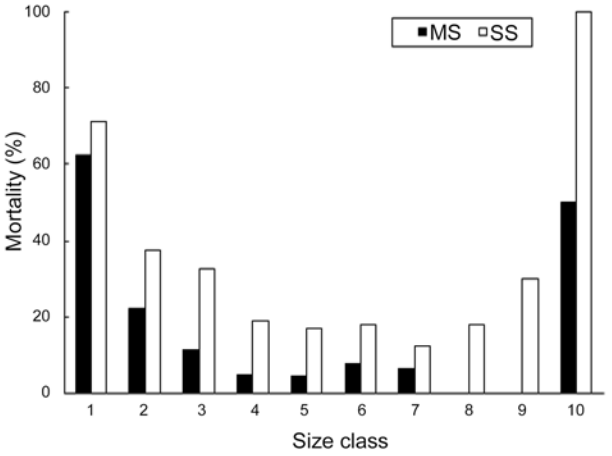

**Figure 5**. Mortality of *S. palmata* along size class, based on leaf breadth (mm). 1, <30; 2, 30-60; 3, 60-90; 4, 90-120; 5, 120-150; 6, 150-180; 7, 180-210; 8, 210-240; 9, 240-270; 10, 270.

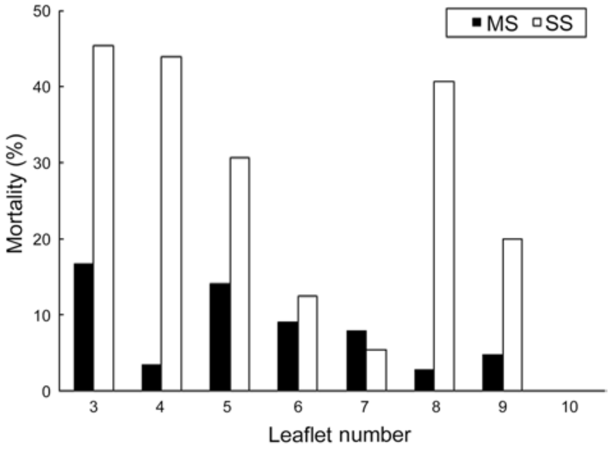

**Figure 6**. Mortality of *S. palmata* along size class, based on leaflet number.

the rate in SS was always >20%. In contrast, except for 1995 and 2002, the rate in MS was always <20%. Mean annual mortalities were 8.9% for MS and 22.8% for SS. The highest mortality rates occurred in 1995 (22.0%) for MS and in 1996 (36.7%) for SS, while the lowest were in 1999 (0.9%) for MS and in 1997 (5.3%) for SS.

When comparisons were based on petiole length, only MS plants within the two smallest size classes (<15 cm) were susceptible to death each year. In particular, the greatest mortality (29.6%) for MS was found in plants smaller than 10 cm (Fig. 4). In contrast, SS plants of almost any size were susceptible. For example, although the smallest class had the highest rate, that of the largest size also was relatively high, at 33.3%. Therefore, no relationship was found between mortality and plant size in SS.

In contrast, when determinations were based on leaf breadth, patterns of mortality were similar between MS and SS (Fig. 5), decreasing to the middle-sized class, then rising with plant size. The highest rates were 62.5% in MS and 100.0% in SS; the lowest, 0.0% in MS and 12.5% in SS. When leaflet number was the factor for comparison, SS averaged 3 to 9 while MS had 10, and mortality decreased with higher numbers (Fig. 6). However, mortalities again varied by size class, and patterns were dissimilar between MS (0.0% to 16.7%) and SS (5.4% to 45.4%).

In 1998, the rate of petiole growth was not calculated for SS because that stand had too few plants (38). Nevertheless, the mean annual growth rate for that organ was 2.6% in MS and 8.4% in SS (Fig. 7). The standard deviations for those differences within a stand were conspicuous whereas those between stands were not significant. The highest rate was +16.2% (116.2%) in 1998 for MS and +32.1% (132.1%) in 1996 for SS. The lowest rate of increase in petiole length was –14.4% (85.6%) in 1999 for MS and –9.7% (90.3%) in 1997 for SS. Therefore, the times of maximum and minimum growth did not coincided for these two stands.

With regard to leaf breadth, mean rates of increase were +3.1% (103.1%) in MS and +24.2% (124.2%) in SS (Fig. 8); those differences between stands were more apparent compared with petiole length. However, the ranges (or standard deviation) between MS and SS fairly overlapped. The highest annual rate of increase was +29.0% (129.0%) in 1995 for MS and +62.9% (162.9%) in 1996 for SS. The lowest rates were –16.4% (83.6%) in 2001 for MS and –4.2%

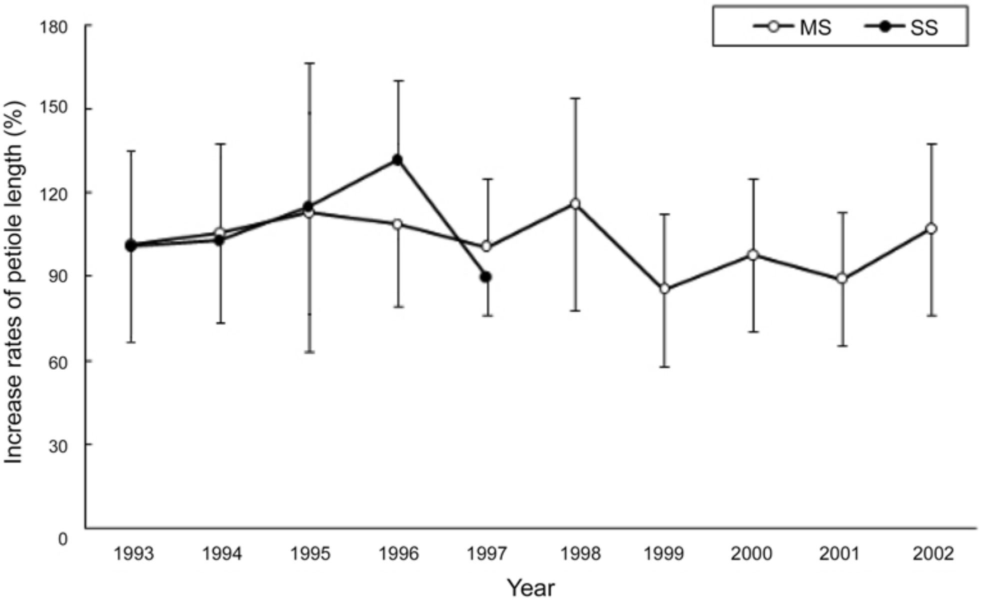

**Figure 7**. Change in growth rate of *S. palmata* for petiole length in MS (moderate shading) over 10 years and in SS (severe shading) over 6 years.

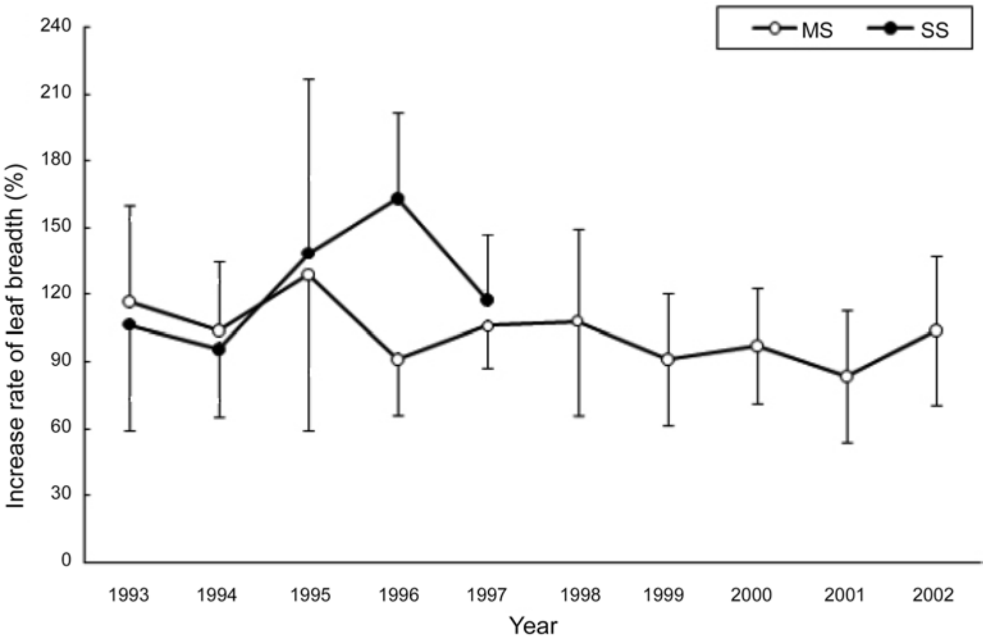

**Figure 8**. Change in growth rate of *S. palmata* for leaf breadth in MS (moderate shading) over 10 years and in SS (severe shading) over 6 years.

(95.8%) in 1994 for SS. Therefore, these results, based on two properties, did not coincide but did have similar patterns.

Frequencies for each size class based on leaf breadth fluctuated over time (Fig. 9). For MS, plants showed nearly normal distribution curves, with the medium-sized class being conspicuously larger than the others. Thus, population structures were more or less constant. However, in SS, the frequency for that medium-sized class was not always higher, and differences among classes were small. Moreover, frequencies for each size class changed considerable from year to year.

## DISCUSSION

The emerging shoot primordium of *S. palmata* is important to plant continuity and population structure in the following growing season, but its existence depends upon the amount of energy available in the root system. This type of reproduction, where the mother plant dies in the current year, contrasts with that of *Heloniopsis orientalis*, in which the original shoots and roots remain alive throughout the winter and the new primordia easily develop in the next year (Min, 2000a, b).

Here, the leaves of *S. palmata* were thinner in the semi-

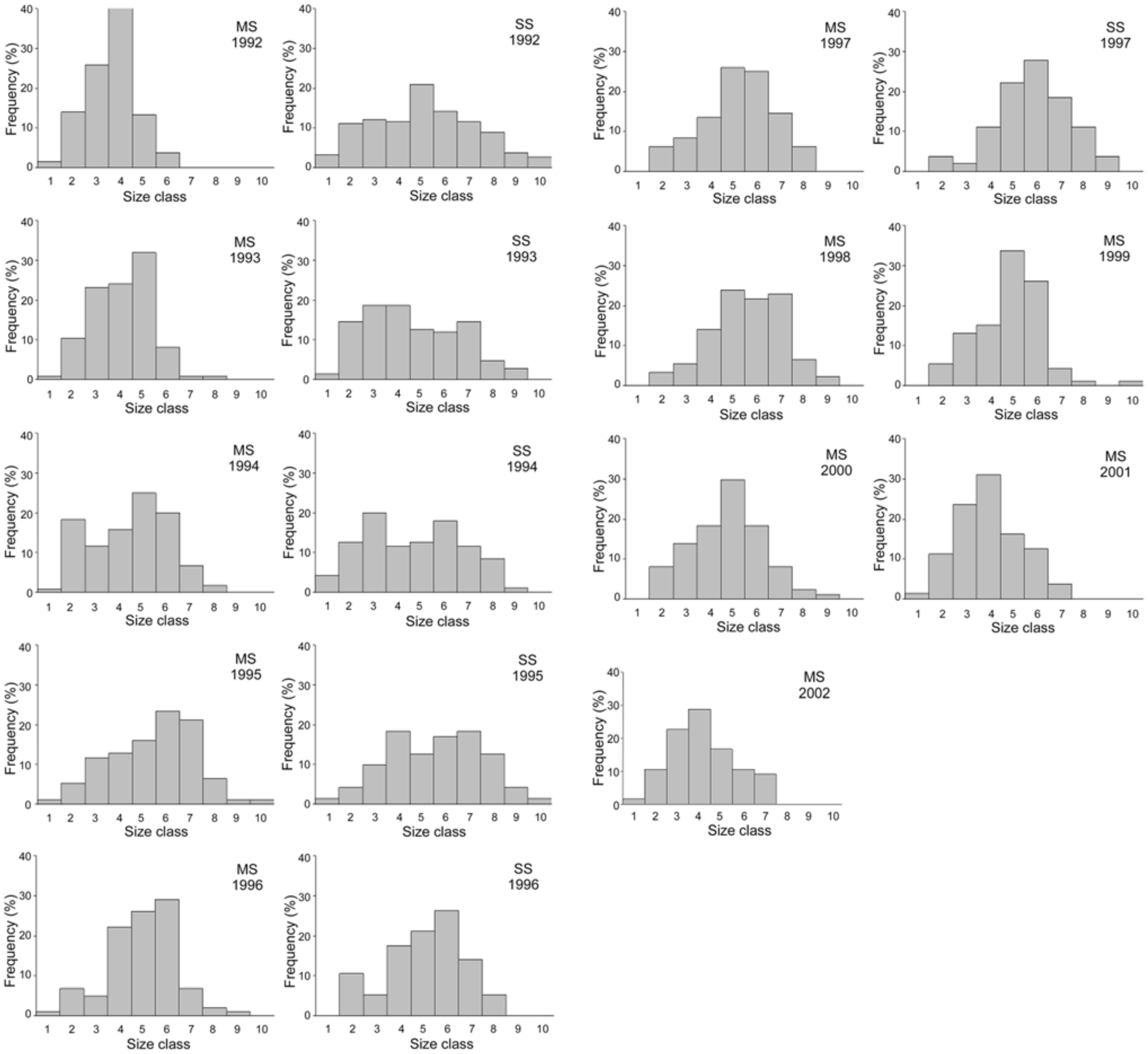

**Figure 9**. Frequency distributions in *S. palmata* population along size class, based on leaf breadth in MS (moderate shading) from 1992 to 2002, and in SS (severe shading) from 1992 to 1998. Classes are as described for Figure 4.

closed canopy than under 100% cover. Generally, SLA values are higher for shaded plants than for those grown in an open area (Grubb et al., 1996; Mitchell, 1998; Robinson and McCarthy, 1999; Casella and Ceulemans, 2002; Simioni et al., 2004; Ali and Kikuzawa, 2005). *Glehnia littoralis* shows a similar growth pattern (Min, 2006). Therefore, more study is needed concerning the response of *S. palmata* leaves to various intensities of sunlight.

In *S. palmata*, leaf thickness decreased as leaf area increased; this behavior was not related to the intensity of light the plants received. However, because other species tend to have thicker leaves when intensities are greater, one might conclude that the leaves of *S. palmata* are better adapted to low-light conditions. Nevertheless, further research should clarify how those leaves respond when exposed to direct light. The author has recently reported (Min, 2007) that the petioles and peduncles in this species are shorter on plants grown under moderate shade than in full shading. This suggests that its patterns of adaptation to light intensity differ among its organs.

Mortality in *S. palmata* is thought to be affected by microclimate rather than macroclimate but, as previously reported (Min, 2007), the soil environment was actually more favorable for plant growth in SS, implying that other factors were more important to plant survival. For example, the light regime may have been limiting under extreme shade; however, plants in that habitat tended to be larger than in MS. Moreover, the mortality rates for typical shade-tolerant species, e.g., *Arisaema triphyllum*, *Erythronium japonicum*, *Fritillaria japonica*, *Lilium cordatum*, *Trillium tschonoskii*, and *Anemone hepatica*, are no more than 10% (Bierzychudek, 1982). Therefore, the main factors, e.g., animal herbivory or

**Table 2.** Correlation coefficients among properties of *S. palmata* in moderately shaded (MS) stand and severely shaded (SS) stand on 24 July 1992. (W, weight; N, number; L, length; A, area; B, breadth; SLA, specific leaf area; t, total; pe, petiole; lb, leaf blade; ll, leaflet) MS ($n$=65)

| | Wt | Lpe | Wpe | Alb | Blb | Wlb | SLA |
|---|---|---|---|---|---|---|---|
| Lpe | 0.252* | | | | | | |
| Wpe | 0.972** | 0.891** | | | | | |
| Alb | 0.909** | 0.880** | 0.918** | | | | |
| Blb | 0.784** | 0.876** | 0.838** | 0.912** | | | |
| Wlb | 0.967** | 0.880** | 0.974** | 0.970** | 0.843** | | |
| SLA | -0.724** | -0.645** | -0.706** | -0.646** | -0.075 | -0.730** | |
| Nll | 0.398** | 0.480** | 0.485** | 0.466** | 0.462** | 0.441** | -0.173 |

SS ($n$=14)

| | Wt | Lpe | Wpe | Alb | Blb | Wlb | SLA |
|---|---|---|---|---|---|---|---|
| Lpe | 0.861** | | | | | | |
| Wpe | 0.933** | 0.785** | | | | | |
| Alb | 0.953** | 0.913** | 0.912** | | | | |
| Blb | 0.983** | 0.886** | 0.905** | 0.966** | | | |
| Wlb | 0.980** | 0.907** | 0.894** | 0.960** | 0.997** | | |
| SLA | -0.628* | -0.795** | -0.576* | -0.691** | -0.640* | -0.665** | |
| Nll | 0.945** | 0.821** | 0.967** | 0.926** | 0.929** | 0.924** | -0.628* |

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

attacks by microorganisms, that might cause this degree of mortality in *S. palmata* must be examined further. For example, if the condition of the new primordium in the root system at the end of one growing season is important to future growth, then serious damage by soil organisms could inhibit plant development the following year.

Here, the relationship between survival and size differed among three measured plant properties -- petiole length, leaf breadth, and leaflet number. If total plant weight was the representative trait, then the most reliable criterion for estimating plant size was leaf breadth in MS and SS. In fact, CCs values for total plant weight and leaf breadth were the highest of the three comparisons (Table 2). Based on that, one could have concluded that the population structures of those two stands would be constant and the frequencies of the medium-sized class would remain high for many years. Almost universally, small or young plants tend to have higher mortality rates than do larger or adult plants (Harper, 1977). However, in the third or fourth year of growth, the seedlings of contractile-root plants show less survival because of insect attack. Therefore, the relationship between mortality and plant size differs by species or population (Bierzychudek, 1982).

As mentioned here and previously (Min, 2007), petiole growth of *S. palmata* was influenced by light intensity, but the expansion of leaf breadth or specific leaf area (SLA) was not. However, petiole growth seemed to be affected by microenvironment, e.g., the depth of the litter layer or competition from peripheral plants.

Generally, the stability of the population structure for a shade-tolerant herb species under a closed canopy in a temperate deciduous forest depends upon its environment (Tamm, 1956). For example, when growing conditions are constant and favorable, *Primula veris* can survive for long periods without great changes in plant numbers, compensating for dying plants through vegetative propagation via branching. When environmental changes are slow, many years may elapse before a plant eventually dies (Tamm, 1972b). In contrast, the structure of an *Arisaema triphyllum* population is unstable, with density rising or falling annually, even in a consistent, ideal environment (Bierzychudek, 1982). In the current study, the population structure of *S. palmata* was considered stable under moderate shading, but was seriously impacted by low light intensity.

In summary, plants of *S. palmata* generally produce one new primordium each, an organ that is thought to be labile to extrinsic factors. Because its SLA does not increase when light intensity is diminished, one can conclude that its leaves are not well-adapted to heavy shading, which is disadvantageous for plant growth, even when the soil environment is more favorable. Hence, the mortality rate in this species is high, and shows wide annual fluctuations, leading to changes in population structure each year. Moreover, if one does not consider the influx of seedlings into a population, then only a relatively short period might elapse before plants die. For example, in the severely shaded stand studied here, plant numbers declined from 190 to 38 over 7 years. Based on this trend, one might predict that the *S. palmata* population under such conditions could disappear in less than 10 years.

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