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Relationship between the sexual and the vegetative organs in a *Polygonatum humile* (Liliaceae) population in a temperate forest gap

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Abstract

Background: The aim of this study was to clarify the relationship between the sexual reproduction and the resource allocation in a natural *Polygonatum humile* population grown in a temperate mixed forest gap. For this aim, the plant size, the node which flower was formed, the fruiting rate, and the dry weight of each organ were monitored from June 2014 to August 2015.

Results: Firstly, in 3–13-leaf plants, plants with leaves ≤ 8 did not have flowers and in plants with over 9 leaves the flowering rate increased with the number of leaves. Among plants with the same number of leaves, the total leaf area and dry weight of flowering plants were larger than those of non-flowering plants. The minimum leaf area and dry weight of flowering plants were 100 cm^2 and 200 mg, respectively. Secondary, the flowers were formed at the 3rd~8th nodes, and the flowering rate was highest at the 5th node. Thirdly, cumulative values of leaf properties from the last leaf (the top leaf on a stem) to the same leaf rank were greater in a plant with a reproductive organ than in a plant without a reproductive organ. Fourthly, fruit set was 6.1% and faithful fruit was 2.6% of total flowers. Biomasses of new rhizomes produced per milligram dry weight of leaf were 0.397 ± 190 mg in plants that set fruit and 0.520 ± 0.263 mg in plants that did not, and the difference between the 2 plant groups was significant at the 0.1% level.

Conclusions: *P. humile* showed that the 1st flower formed on the 3rd node from the shoot's base. And *P. humile* showed the minimum plant size needed in fruiting, and fruiting restricted the growth of new rhizomes. However, the fruiting rate was very low. Thus, it was thought that the low fruiting rate caused more energy to invest in the rhizomes, leading to a longer rhizome. A longer rhizome was thought to be more advantageous than a short one to avoid the shading.

Keywords: Flowering rate, Fruiting, Leaf area, Leaf dry weight, *Polygonatum humile*, Rhizome

Background

In temperate deciduous forests, understory herbaceous plants grow under insufficient irradiance after canopy closure (Emborg 1998, Augusto et al. 2003). These plants use diverse strategies to adapt to the low-light environment. Spring ephemerals complete life cycles before canopy closure, and shade-tolerant plants slowly grow (Schemske et al. 1978, Houle 2002, Legner et al.

2013). In any case, photosynthetic substances produced during the growing season are limited, and understory plants use the pertinent energy strategy to ensure their survival and reproduction. In particular, a young perennial herbaceous plant invests energy in growth or survival rather than in reproduction until its size is to a certain extent (Silvertown 1982, Hartnett 1990). These plant species reproduce asexually and sexually. Asexual reproduction is closely related to growth, and generally, reproductive potential is evaluated by the sexual one. Reproductive potential of perennial herbaceous species

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depends on plant size rather than on its age (Klinkhamer et al. 1992). When clonal plants reach the reproductive stage, sexual reproduction and vegetative propagation may compete for resources in the plant (Cook 1983). In perennial herbaceous plants, resource allocation to asexual and sexual reproduction is an indicator of adaptive plasticity and a strategy for survival, and this topic has been addressed many times in population ecology (Jerling 1988, de Kroon and Schieving 1991). Moreover, information on reproduction strategies is essential to predict for population dynamics in the future (Silvertown 1982). In other words, in clonal perennial herbaceous plants, energy budget strategies for asexual and sexual reproduction determine the entire life cycle, and the plant's response resulting from these strategies is the basis for interpreting environmental adaptation or genetic output (Stephenson 1981). Microenvironmental adaptation to insufficient sunlight is transiently reflected by morphological and physiological diversity. However, the energy budget in a plant cannot be precisely divided into that for asexual and sexual reproduction because of methodological and physiological difficulties (Klinkhamer et al. 1990). Putting aside respiration during seed production, total net production by a plant does not remain at its disposal, since photosynthetates are lost because of organ death, herbivore predation, and physical damage. Thus, to estimate the energy used for sexual reproduction, an indirect method has been used: sexual organs are removed and weighed, and biomasses are compared for flowering and non-flowering plants (Klinkhamer et al. 1990, Ehrlén and van Groendael 2001). This method has been tested in diverse settings by many researchers (Samon and Werk 1986, Reekie and Bazzaz 1987, Verburg et al. 1996). They used the term "reproductive efforts" with respect to the plant's reproductive investment. Reproductive efforts are the rate of the overall resources (biomass or nutrients) used for reproductive organs or seeds.

Polygonatum humile (Liliaceae) is generally distributed in grasslands or at the periphery of a shrub in Korea (Choung 1991, Jang 2002) or in grasslands and sand dunes in Japan (Hasegawa and Kudo 2005). Thus, this species needs full sunlight. And *P. humile* is a clonal perennial herb, which reproduces asexually by rhizomes and sexually by seeds (Choung 1991, Hasegawa and Kudo 2005). Unlike other species of genus *Polygonatum*, the shoots of *P. humile* are erect and its rhizomes are long (Jang 2002, Hasegawa and Kudo 2005). The total length of the rhizome which grows for about 3.3 years and is connected in 1 line is 47.6 ± 25.6 cm a shoot, and rhizomes grow at a rate of 15.5 ± 4.4 cm a year (Hasegawa and Kudo 2005). Each plant has 2 rhizomes (Choung 1991, Jang et al. 1998) or 1~4 rhizomes (Jang 2002). The

flower germinates from the axilla of the leaf (node). The number of flowers is 19.0 (Jang et al. 1998) or 2.7 ± 1.1 (Hasegawa and Kudo 2005) per stem and 2~6 (Jang et al. 1998) or 1 (Jang 2002) or 1~2 (Lee 2003) per node. The reported number of seeds per fruit is 6.1 ± 2.71 (Hasegawa and Kudo 2005) or many (Jang 2002). Thus, the number of flowers produced by *P. humile* varied according to the reports. Besides the studies mentioned above, there are few ecological studies on *P. humile*. Moreover, there are much fewer pharmaceutical and agricultural studies for *P. humile* than for other *Polygonatum* species (Seo et al. 2011).

The aim of this study was to clarify the relationship between the sexual reproduction and the resource allocation in a natural *P. humile* population grown in a temperate mixed forest gap. For this aim, the plant size, the node which flower was formed, the fruiting rate, and the dry weight of each organ were monitored from June 2014 to August 2015. The properties of plant sizes were the leaf area, the dry weight of leaf, root and rhizome, and the length of stem and rhizome.

Methods

The study area was located at Yeongheung-ri, Yeongwal-eup, Yeongwal-gun, Gangwon province (37° 11′ 35.7″ N, 128° 28′ 04.0″ E). The study site was 385 m a.s.l. (slope, 5°; direction, 175°). Annual mean air temperature and precipitation in an average year were 10.8 °C and 1224.1 mm, respectively, and those in 2015 were 12.5 °C and 676 mm, respectively, on Yeongwal Meteorological Station. *P. humile* grew in a gap created to move a grave to another place (radius, 10 m) and was momentarily shaded by trees in the south. *P. humile*'s patch was about a 5 m × 6 m circle. Except for *P. humile*, the herb layer was 5% in coverage and composed of *Aster scaber, Carex lanceolata, Festuca ovina*, and *Zoysia japonica*. The surrounding forest had 4 layers of vegetation. The tree layer was composed of *Pinus densiflora, Quercus mongolica*, and *Quercus dentata* and had 90% coverage. There were *P. densiflora, Quercus serrata, Prunus sargentii*, and *Euonymus sieboldiana* and 40% coverage in the subtree layer. There were *Exochorda serratifolia, Pourthiaea villosa*, and *Rhododendron mucronulatum* in the shrub layer and *C. lanceolata, Leibnitzia anandria*, and *A. scaber* in the herb one. The coverage was 10% in the former and 1% in the latter. The litter layer was 10-cm deep and a layer of soil was 10-cm deep. However, the soil of the study area where the *P. humile* population was distributed had been disturbed by the work in relocating the grave but had settled by the time of the study. A field survey was carried out for 2 purposes. One was to check the changes in the sexual organ. A quadrat of 2 × 2 m was chosen on April 25, 2015. Each flowering plant of *P. humile* was numbered by using a plastic rod,

and the phenological stages of the sexual organ were checked every week till June 27, 2015. The phenological stages were based on Hasegawa and Kudo (2005). At the end of August 2015, all numbered plants were dug out. The other was to conform the difference between flowering plants and non-flowering ones, so that all plants of *P. humile* were divided into 2 groups and the properties of the plant organ analyzed. In the lab, the plants were divided into the root and shoot systems. The roots were separated according to the age of the rhizome, and the rhizomes were numbered R_0 (this year's rhizome), R_1 (the last year's rhizome), and R_2 (2-years-ago rhizome). The leaf ranks on a stem were numbered from the lowest (the leaf closest to the soil surface) or the 1st leaf on a stem (L_1) to the highest (the last leaf on a stem). The position of the leaf was coincided with a node, so that the leaf rank on a stem was the same as the node one. And flowers germinated in the axilla of leaf (node). Thus, L_1 was the same as the 1st node. The number of leaves on a stem was from 3 to 13. However, 13-leaf plants (13-L) were not sufficiently sampled and were excluded from the analysis. Length, width, and/or area of the rhizomes, leaves, and stems were measured, followed by oven-drying at 85 °C for 48 h and weighing on a Hansung Analytical & Precision Balance, Model MARK M (1-mg unit), and Model YMJ-C Digital Leaf Area Meter (0.0001-cm^2 unit). The total leaf area, total leaf dry weight, and specific leaf area of a plant were divided into the 10 classes. That was, the total leaf area, the total leaf dry weight, and the specific leaf area were divided by 20 cm^2 (range of 59–260 cm^2), 100 mg (range of 99–1252 mg), and 30 cm^2 g^{-1} (range of 203–511 cm^2 g^{-1}), respectively. The cumulative values of leaf properties of a stem were calculated for the following reasons and methods. In this study, I made 2 assumptions for the resource allocation during the main growth season. Firstly, the photosynthetic substance produced in the leaf moved from the last leaf to the new rhizome (R_0). Secondary, the resource provided to the reproductive organ (flower or fruit) was synthesized in posterior leaves (the last leaf rank direction) rather than in the anterior ones (L_1 direction), based on the reproductive organ. Thus, it was thought that leaves in the posterior nodes based on the reproductive organ had a profound effect on seed production. Cumulative values of leaf properties were summed for the

flowering plants from the last leaf to the closest leaf rank having a reproductive organ (L_R). Types of L_R were L_3, L_4, L_5, L_6, L_7, and L_8, but L_3 was excluded in the analysis. To compare, the cumulative values of leaf properties for the non-flowering plants were summed from the last leaf to the leaf which its rank was the same as L_R but did not have a reproductive organ. This time, the specific leaf area (SLA) was not cumulative but mean values. Significance of the differences was verified by Student's *t* test, and correlation coefficients (CCs) between the 2 factors were calculated by using Pearson's equation ($y = ax + b$).

Results and discussion

Relationship between the sexual organ and the plant size

The flower bud of *P. humile* appeared at the same time as the leafing on April 20, 2015, and the last petal was attached until May 30, 2015. And the fruit was 1st observed on May 21, 2015, and remained on the node at the end time of the field survey (September 10, 2015). Two thirds of *P. humile*'s shoots have sprouted, and small flower buds at the nodes were observed by April 25, 2015. The 1st fruit was firstly observed on May 20, 2015, and all corollas fell down by May 27, 2015 (Table 1). Thus, corollas attached at the nodes were observed during 37 days in this *P. humile* population. After June 2, 2015, the peduncle (after flower fall) or fruit was observed. However, because the 3 stages (flower budding, flowering, and flower withering) could not be easily distinguished, it was determined whether a white corolla was attached at the node or not. In Japan, *P. humile*'s shoots sprouted in mid-May, and it flowers from June 5 to June 22 at high latitude (42° 39′ N) (Hasegawa and Kudo 2005). Thus, the flowering time of *P. humile* is very diverse on the habitat. The fruit set was 6.1% of the total flowers, and 2.6% of those were over 110 mg (the fruit where the diameter was over 8 mm, faithful fruit) and the remainder (the fruit where the diameter was about below 5 mm, 3.5%) below 64 mg (Table 1). The criterion of whether the fruit was faithful followed Lee (1996). By Lee (1996), *P. humile*'s fruit is 8–9 mm in diameter. However, the fruit set was 49–61% (Hasegawa and Kudo 2005) or 75.9% (Jang et al. 1998). Thus, the fruit set of *P. humile* was much lower in this study than in the other 2 studies, likely because the plants
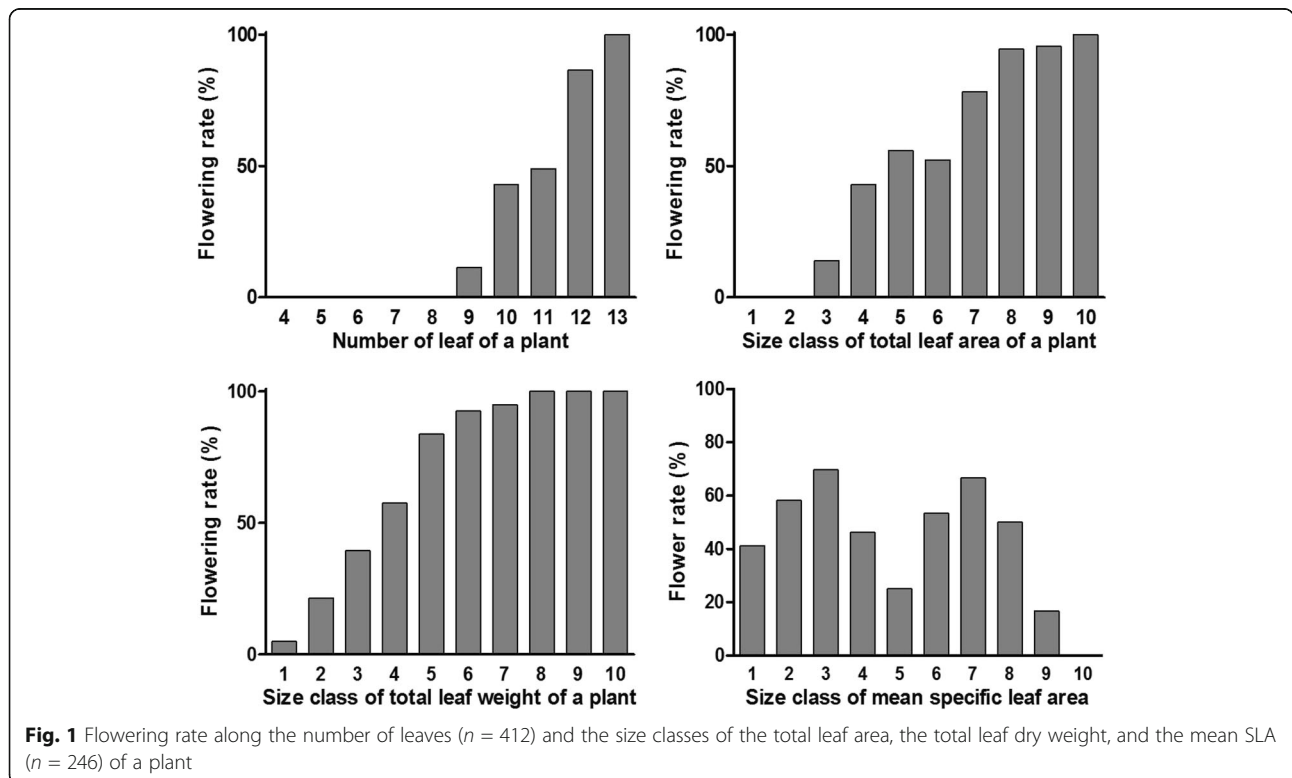
Table 1 Fruit set in the *P. humile* population 2014 and 2015 (size of fruit)

Date	No. of flower	Size of fruit (rate)		
		Over 110 mg (faithful)	Under 64 mg (unfaithful)	Total
Aug. 22, 2014	148	5 (3.5%)	7 (4.7%)	12 (8.1%)
Aug. 26, 2015	196	4 (2.5%)	5 (2.6%)	9 (4.1%)
Total (rate)	344	9 (2.6%)	12 (3.5%)	21 (6.1%)

examined in this study grew in a forest gap, where sunlight was insufficient, whereas plants examined in the other 2 studies grew in full sunlight. Although sexual reproduction could be limited, the study site was over 5 cm in the litter layer and soil water was not in shortage by shading. Thus, because of insufficient sunlight, *P. humile* growing in a forest gap might prefer asexual reproduction rather than the sexual one. The number and the largest length of rhizome per shoot were 1~3 and 25.5 cm, respectively, as the previous report.

The minimum number of leaves needed for flowering (at least 1 flower per stem) was 9 (Fig. 1). The flowering rate increased with the number of leaves, and that of 13-leaf plants was 100%. There were no flowering plants with a total leaf area per plant below 100 cm^2. The flowering rate increased with leaf area, and plants with leaf area over 240 cm^2 had 100% flowering rate. The flowering rate increased with leaf dry weight and was 5% at 200 mg and 100% at > 800 mg. However, the flowering rate showed 2 peaks with an increase of SLA and was almost not affected by SLA values. As a result, the flowering rate of *P. humile* increased with leaf size. For the same number of leaves, each organ of the flowering plants was larger than that of the non-flowering plants, but SLA was not. Moreover, of the 11 properties, the differences between the 2 groups were significant at the 0.1~5% level in 6 properties in 9-leaf plants, in 10 in 10-leaf plants, and in 6 in 11-leaf plants (Fig. 2). Leaf area

and dry weight significantly differed between the 2 groups at the 0.1~5% level regardless of the number of leaves. However, SLA and rhizome size significantly differed between the 2 groups at the 0.1~5% level for 10-leaf plants only. The differences in stem length and dry weight between the 2 groups were significant at the 0.1~1% level in the 9- and 10-leaf plants. According to these results, the *P. humile* population showed the following properties. Generally, a minimum plant size is required before sexual reproduction occurs (Hirose and Kachi 1982, Schmid and Weiner 1993). Plant flowering in the field was positively correlated with shoot size (Verburg et al. 1996). However, the relationship between plant size and vegetative reproductive effort has received little attention and data are scarce, and methodological and physiological difficulties remained (as mentioned above). First, *P. humile* required a minimum number of leaves for sexual reproduction. And the number of leaves might be an indicator of plant size. However, the number of leaves was not an appropriate indicator because the flowering rate was not 100% even in 12-leaf plants which almost reached maximum size. Moreover, if the number of leaves and flower buds had been determined before the shoot sprouting, the flowering plants might have already invested more energy from the rhizome into shoot growth than the non-flowering plants regardless of the fruit set. In other words, plants that formed
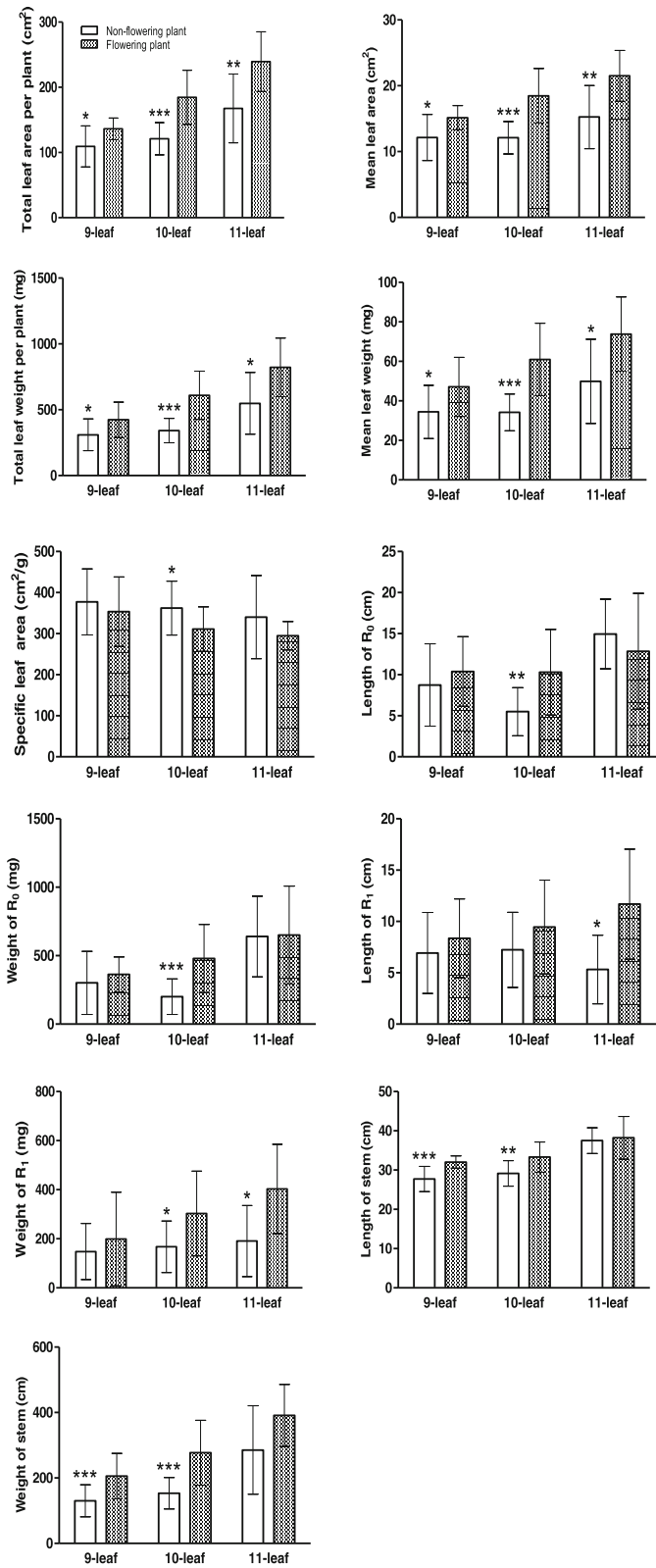

Fig. 1 Flowering rate along the number of leaves (*n* = 412) and the size classes of the total leaf area, the total leaf dry weight, and the mean SLA (*n* = 246) of a plant

Fig. 2 Comparison of organ sizes between the flowering and the non-flowering plants which had the same number of leaves on June 28, 2014. *, **, and *** indicate the significant level at 5, 1, and 0.1%, respectively

flower buds probably invested energy into other organs rather than only in the increase in the number of leaves. Second, stem length in plants that had ≥ 11 leaves was maximal, whether the plants flowered or not. Unlikely other species in genus *Polygonum*, *P. humile* shoot erects. Third, the flowering rate increased with the total leaf area but was 100% at the largest class only. Thus, stem length and total leaf area were not good indicators of flowering plants. Fourth, the increase of total leaf dry weight was proportioned to the flowering rate. Thus, total leaf dry weight was thought to be the most proper indicator of the relationship between the plant size and flowering.

Leaf ranks (or nodes) with flower

Each leaf rank (node) had a flower or not. And the flower was from the 3rd node (or L_3) to the 6th node (or L_6) in 9-leaf plants and from L_3 to L_8 in 10~12-leaf plants. Thus, there was no flower at 2 nodes from the bottom and at 2~4 nodes from the top. The flowering rate was highest at the L_5 in 9~12-leaf plants and decreased toward the bottom (in the direction of the L_1) and to the top (in the direction of the last leaf) (Fig. 3). The resource provided to reproductive organ (flower or fruit) was synthesized in posterior leaves (the last leaf direction) rather than in the anterior ones (the L_1 direction), based on a reproductive organ. Cumulative values of leaf properties were summed for the flowering plants from the last leaf to the closest leaf rank having a reproductive organ (L_R). To compare, cumulative values of leaf properties for the non-flowering plants were summed from the last leaf to the leaf where its rank was the same as L_R but did not have a reproductive organ. At each leaf rank, the cumulative values of leaf area and leaf dry weight were larger in the flowering plants (L_R plants) than in the non-flowering plants (non-L_R plants) (Fig. 4), and the differences between the 2 groups were almost significant at the 5% level. In particular, the cumulative values of leaf properties from the L_{12} to the L_8 in 12-L were larger in plants with L_R at the L_8 than in plants without a reproductive organ to the L_8. On the fact that the flowers were mainly in the middle of the stem, it was thought that flowers secured 2~4 leaves supplying photosynthetic substances for fruit setting, whereas the 2 or 3 leaves at the bottom might have provided energy to the root system (rhizome and root) regardless of the fruit set. However, if photosynthetic substances are transported both up and down, sexual reproduction and rhizome growth might compete for resources. Generally, in clonal plants, sexual reproduction and vegetative propagation may compete for resources within the plant (Cook 1983), and *P. humile* is a clonal plant. Energy used for flower bud germination can be
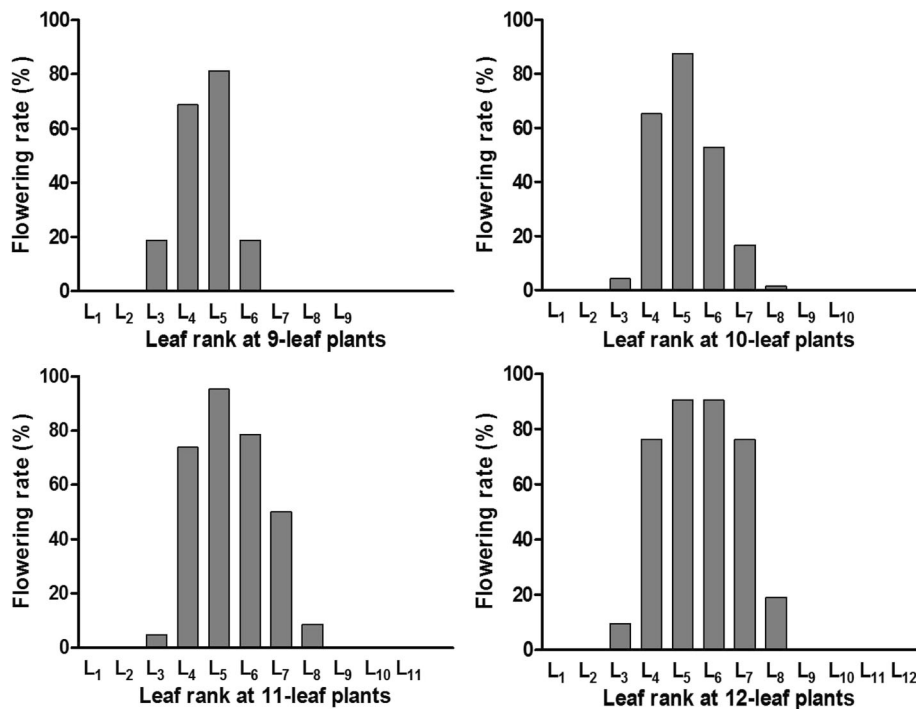

Fig. 3 Of the flowering plants (plants which had 1 or more flowers), flowering rate along the leaf rank (or node) in each number of leaves (9-L, 10-L, 11-L, and 12-L) of a plant
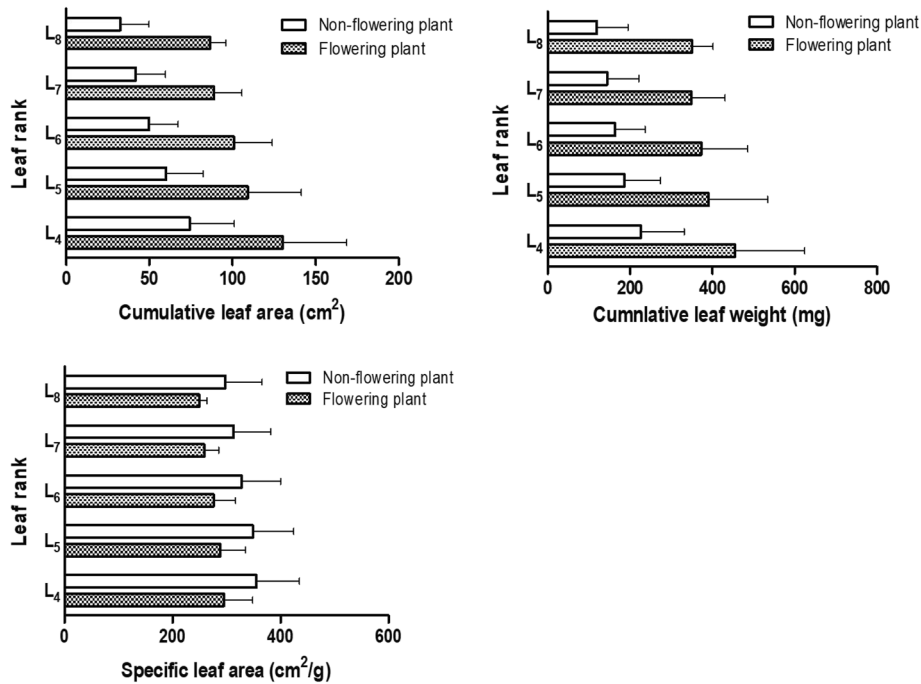
Fig. 4 Mean SLA, cumulative values of the leaf area, and the leaf dry weight in flowering and non-flowering plants. Flowering plants: plants which had a reproductive organ at each leaf rank (LR); non-flowering plants: plants which had no reproductive organ from the last leaf to the leaf rank equal to LR. LR was the closest leaf rank to the last one and had a reproductive organ

brought from the last year's rhizome, but energy for the fruit set must be transported from the nearest leaves (Stephenson 1981). Jang (2002) reported that *P. humile* produced 2~4 rhizomes. Production of ramets decreases the risk of genet mortality. Sexual reproduction varied negatively with both growth and vegetative propagation (Worley and Harder 1996). Shade-tolerant temperate forest herbs devote energy to sexual reproduction to a lesser extent than grassland herbs (Bierzychudek 1982). Thus, *P. humile* in a forest gap might keep at least 2~3 leaves for asexual reproduction by rhizome growth.

Resource budget of new rhizome and fruit

The dry weight of new rhizome per milligram of leaf was 0.397 ± 0.190 mg in plants that set fruit and

0.500 ± 0.263 mg in plants that did not (Fig. 5). Difference between the 2 groups was significant at the 0.1% level, although standard deviation was large. The sum of dry weight of new rhizome and fruit per milligram of leaf was 0.520 ± 0.177 mg in plants that set fruit. The dry weight of new rhizome per square centimeter of leaf was 1.289 ± 0.596 mg in plants that set fruit and 1.689 ± 1.003 mg in plants that did not. The difference between the 2 groups was significant at the 0.1% level. The dry weight sum of new rhizome and fruit per square centimeter of leaf was 1.683 ± 0.579 mg in plants that set fruit. This value was similar to that of plants that did not set fruit. Thus, the productivity of leaves was the same in both plant groups, and sexual reproduction suppressed rhizome growth in this *P. humile* population. If
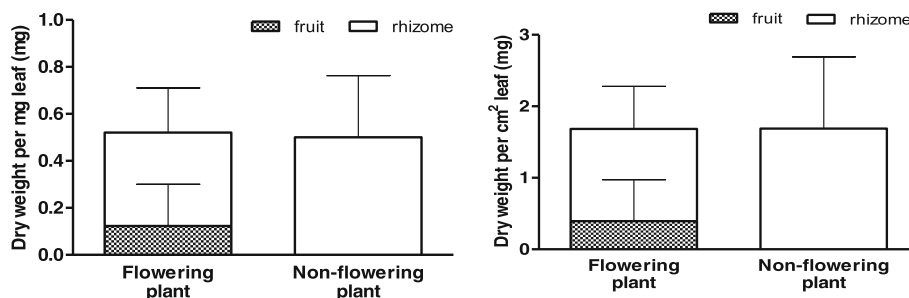

Fig. 5 Dry weight (mg) of fruit and/or new rhizome per milligram leaf dry weight (*left*) or per square centimeter leaf area (*right*) in fruit plants and non-fruit plants

rhizome and seed reproduction are not clearly temporally separated processes, a trade-off between both reproductive modes might be expected, especially when plants grow under severe resource limitation (Stears 1989). As mentioned above, this *P. humile* population growing in a forest gap did not have sufficient sunlight and probably invested the resources in asexual rather than sexual reproduction. As a result, the fruit set was very low below 10%. Generally, the proximate factor that limits fruit and seed production is the energy supply from leaf photosynthesis (Stephenson 1981). Thus, it was thought that the low fruiting rate caused more energy to be invested in the rhizomes, leading to a longer rhizome. A longer rhizome was thought to be more advantageous than a short one to avoid the shading.

Conclusions

Relationship between the sexual organ and the plant size

The minimum sizes the plant needed for flowering (at least 1 flower a stem) were 9 in leaf number, 100 cm^2 in total leaf area, and 200 mg in total leaf dry weight, and the flowering rate increased with the plant sizes. Of the 3 size factors, total leaf dry weight was thought to be the most proper indicator of the relationship between the plant size and flowering.

Leaf ranks (or nodes) with flower

There was no flower at 2 nodes (to L_2) from the bottom and at 2~4 nodes from the top in all plants. And flowering rate was highest at the L_5 in 9~12-leaf plants and decreased toward the bottom (in the direction of the L_1) and to the top (in the direction of the last leaf). Thus, the sex organ and new rhizome might be assured of resources from the several leaves at the end and at the anterior of the stem, respectively.

Resource budget of new rhizome and fruit

Fruiting rate was 6.1% of the total flowers. And the dry weight of new rhizome per milligram of leaf was 0.397 ± 0.190 mg in fruiting plants and 0.500 ± 0.263 mg in non-fruiting plants. Thus, the low fruiting rate was thought to be a strategy for shade avoidance by allocating resources in the rhizome in a forest gap.

Abbreviation

a.s.l.: Above sea level; CC: Correlation coefficient; L_1: The 1st leaf on a stem (the closest leaf to soil surface); L_2–L_{13}: The 2nd leaf to the 13th leaf; L_R: The leaf which was the closest to the last one and had a reproductive organ; R_0: New (this year) rhizome; R_1: The last year's rhizome; R_2: Two-years-ago rhizome; R_3: Three-years-ago rhizome; SLA: Specific leaf area

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