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Population Dynamics of *Heloniopsis orientalis* C. Tanaka (Liliaceae) in Natural Forests - Annual Life Cycle

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Annual changes in the leaves and reproductive organs of *Heloniopsis orientalis* C. Tanaka (Liliaceae), a perennial evergreen herb, were studied from 1991 to 1997 in two areas of South Korea, Namhansanseong and Maranggol. The period for active growth in the leaves was from mid-March to early June. Average leaf angle was 70° in early June, decreasing to 50° in late October. From December until June of each following year, leaf angle was maintained a 0° to horizontal. The specific leaf area (SLA) value was 185 $cm^2 \cdot g^{-1}$ early in the growing season, increasing to 332 $cm^2 \cdot g^{-1}$ in early June. By the end of October, SLA had decreased to 159 $cm^2 \cdot g^{-1}$, after which it increased again from March to June. Because the SLA curve had two peaks, it was inferred that *H. orientalis* possesses two means for survival: 1) an anti-freezing mechanism by which its leaves thicken during the winter, and 2) a reallocation of energy from old leaves to new leaves or to reproductive organs. *H. orientalis* flowered in a semi-enclosed state in late March. Blooming out of the bract, the front of the flower faced the ground. Growth of the peduncle ended in early June, at which point it was 60 cm long. At that time, the fruit was oriented so that the seeds were dispersed upward. Therefore one can see that *H. orientalis* has two physiological features that enhance long-distance seed dispersal - a rather long peduncle relative to overall plant size and an upward seed-dispersal mechanism. In the Namhansanseong area, energy from the roots and old leaves was translocated to new leaves early in the growing season (from late March to early May). However, after mid-May, energy was re-translocated from new leaves to the roots. Moreover, the leaves on flowering plants grew more slowly than on non-flowering plants because energy was translocation to the reproductive organs. Therefore, new leaf growth depended on energy stores of the roots and the biomass of old leaves early in the growing season.

Keywords: Growing season, *Heloniopsis orientalis*, Leaf growth, Leaf length, Life cycle, Peduncle, Seed dispersion, Specific leaf area

Population ecology is a specialized branch dealing with the numerical impact of interactions between species and their environment on the specific set of individuals that occur within a defined geographical area (Silvertown, 1982). A population has both biological and group attributes (Odum, 1983). Life history, natality, and mortality for a population must be examined when studying its dynamics (Harper and White, 1974). Because of their diverse mechanisms for reproduction, the study of plant demography differs from that of animal populations. In particular, the reproduction mechanisms are peculiar to each species (Harper, 1980; Silvertown, 1982; White, 1985). Therefore, information on factors that govern long-term dynamics of a plant population is essential in many areas of both fundamental and applied ecology (Harper, 1977; Falk and Holsinger, 1991; Stearns, 1992; Cain et al., 1997). Despite such importance, studies of long-term demographic patterns are relatively few (Inghe and Tamm, 1985; Kawano et al., 1987; Svensson et al., 1993; Horvitz and Schemske, 1995).

Heloniopsis orientalis C. Tanaka (Liliaceae) is an evergreen, herbaceous perennial that grows under undisturbed temperate forests (Lee, 1982). Its rosette form is composed of apetiolated leaves and adventitious roots. This species is mainly reproduced by seed. Occasionally, a decaying leaf may establish roots from its basal portion and spread new adventitious roots. Few if any studies have been made of the Liliaceae population (Choung, 1991, 1996), especially on the population dynamics for this species in Korea. Demographic data are urgently needed for all of these evergreen herbaceous plants.

The purpose of this study was to describe the life history, growth patterns, relationship between plant and climate, energy budget, and seed production of *H. orientalis* in its natural environment. The particular focus was on estimating plant size from its leaf length, as well as determining the life stages of the plant, annual changes in leaf properties, and energy budget early in the growing season.

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STUDY AREAS

As shown in Figure 1, this study was conducted in two temperate deciduous forests: 1) Namhansanseong, located in the Sanseong Township (Jungbu-Myeon, Gwangju County) within the Kyonggi Province (37° 28′ 00″ N, 127° 11′ 30″ E); and 2) Maranggol, located in the Whaeui Township (Jinbu-Myeon, Pyeongchang County) within the Kangwon Province (37° 33′ 00″ N, 128° 32′ 30″ E). The two areas are similar in latitude but not in elevation. Populations of *H. orientalis* in the Namhansanseong area were found on a 5% declining slope that faced east, at an elevation of 280 m. The Maranggol population was located on a 10% northerly sloping hill, at an elevation of 650 m. The litter layer was 8 cm deep in the Namhansanseong area and 3 cm deep at Maranggol. Both areas had a loamy soil texture. The climates of the two areas have been described previously (Min and Choi, 1993). Annual mean air temperature and precipitation in the Namhansanseong area are 11.8°C and 1,370 mm, respectively; in the Maranggol area, 8.2°C and 1,423 mm, respectively. Although the mean air temperature at Namhansanseong is higher, the Maranggol area receives more precipitation.

The Namhansanseong study site is second-growth forest, comprising trees that average 30 years old, with a mean dbh of about 23 cm. The tree layer is 10 m in height, with 90% coverage. This layer is composed mainly of *Quercus mongolica, Quercus serrata, Castanea crenata, Alnus hirsuta, Carpinus tschonoskii, Betula davurica, Maackia amurensis, Prunus sargentii,* and *Sorbus alnifolia*. In the sub-tree layer, height and coverage are 3 m and 10%, respectively; in the shrub layer, 1.8 m and 5%, respectively. The dominant sub-tree species are *Acer pseudo-sieboldianum* and *Rhus trichocarpa*, with *Rhododendron yedoense* var. *poukhanense* and *Stephanandra incisa* predominating in the shrub layer. The herb layer is 30 cm tall, with 10% coverage. It is composed of *Carex lanceolata, Arisaema robustum, Disporum smilacinum, Convallaria keiskei, Asarum sieboldii, Pyrola japonica*, and *Ainsliacea acerifolia*.

The Maranggol study site also is second-growth forest, but without either a tree or a shrub layer. The sub-tree layer averages 15 years old, with a mean dbh of about 11 cm. This layer is 5 m tall, with 90% coverage, and is composed of *Q. mongolica, Q. serrata, Corylus heterophylla* var. *thunbergii*, and *B. davurica*. The herb layer is 40 cm in height, with 50% coverage. It is composed of *Woodsia manchurica, Athyrium nipponicum, Melica onoei, A. sieboldii, Hepatica asiatica, Anemone reflexa, P. japonica, Viola collina, Torilis japonica, Pimpinella brachycarpa*, and *Angelica gigas*.

MATERIALS AND METHODS

For this study, *H. orientalis* was located in perma-

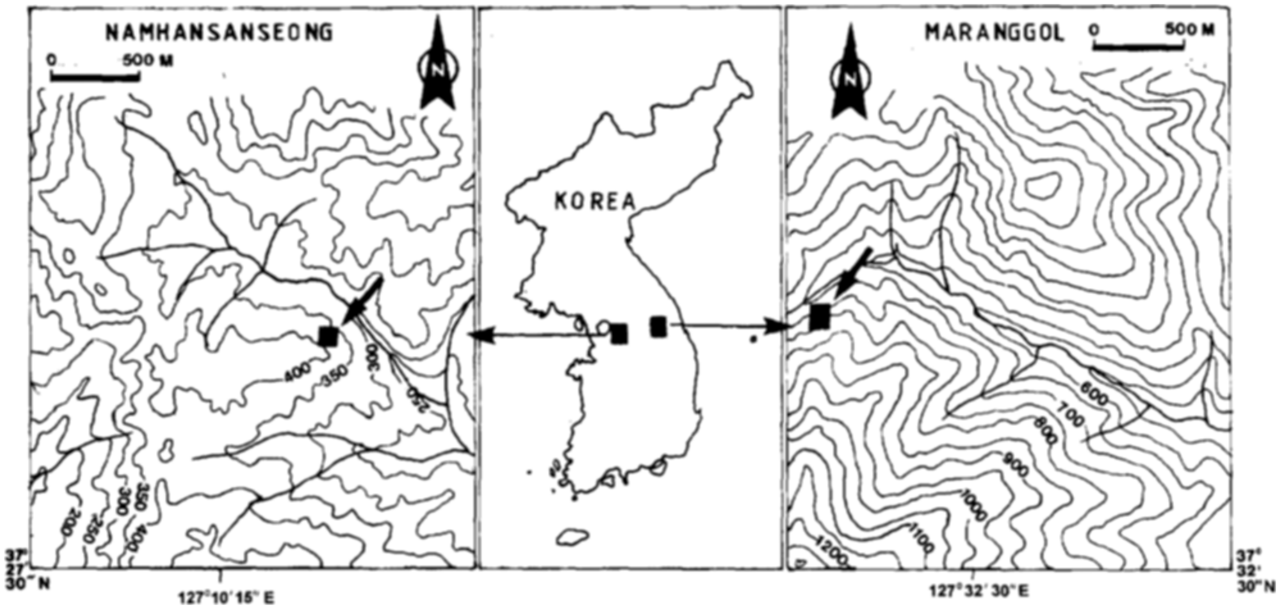

Figure 1. Map of study areas.

nent 5-×5-m quadrats (three at Namhansanseong; one at Maranggol) that were surveyed at fixed intervals, then harvested and analyzed nearby. By using numbered bamboo rods, 69 plants were marked in March 1991 in the Namhansanseong area, and 160 plants were marked in March 1994 in the Maranggol area. From the onset of flowering in March until fruiting time in June, the leaf length, number of leaves, angle between a leaf and the ground (i.e., leaf angle), peduncle length, and the angle between flower and peduncle were measured weekly. From July to October, the leaf angle was measured monthly.

To estimate the Specific Leaf Area (SLA), five non-flowering plants were sampled each month in the two areas from March to October in 1995. After the old leaves were separated from the new ones, the reproductive organs as well as root and leaf samples were pressed under paper. The length and breadth of the leaf were measured in mm. Leaf area was measured in units of 0.1 cm^2, using a leaf area-measuring device (Delta-T Device, UK). The pressed tissue samples were weighed to the nearest 0.1-mg on an analytical balance (Mettler Toledo, Switzerland) after they had been oven-dried at 80°C for 48 h.

The SLA value was calculated as [leaf area (cm^2)] divided by [leaf weight (g)]. Correlation coefficient (CC) values were calculated according to $y = ax + b$. Values of CC between leaf length and other properties were calculated on a per-leaf basis; those between total weight and other properties were determined for individual plants.

RESULTS AND DISCUSSION

Leaf Life Cycle

Though leaf growth of *H. orientalis* began later in the Maranggol area, the annual changes in patterns of leaf properties were similar in the two study areas. Therefore, data mainly from the Namhansanseong area will be discussed here.

The relative leaf-growth curve is shown in Figure 2. At the beginning of the annual cycle, buds (leaf and flower) sprouted no more than 0.5 cm during the fall and did not grow further throughout the winter. In the following year, leaves of non-flowering plants began growing vigorously for 2.5 months, from mid-March to late May. In contrast, flowering plants continued to grow an additional month, until the end of June. This extended growing period may have been prompted by the amount of energy from the peduncle that was partially translocated to new leaves.

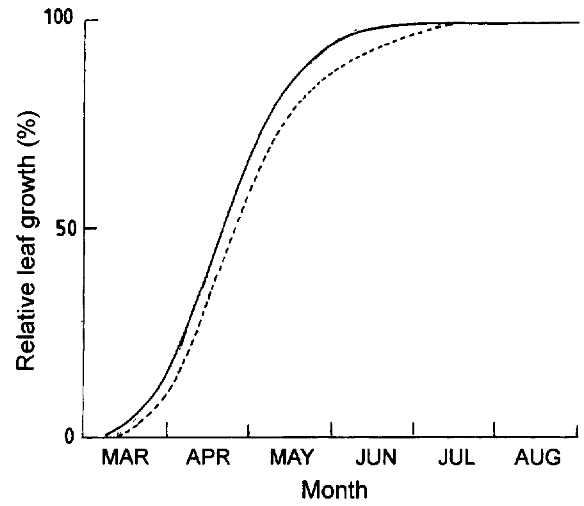

Figure 2. Relative growth curve of *H. orientalis* leaf in the Namhansanseong area. Solid and dotted lines indicate the non-flowering plant and the flowering plant, respectively.

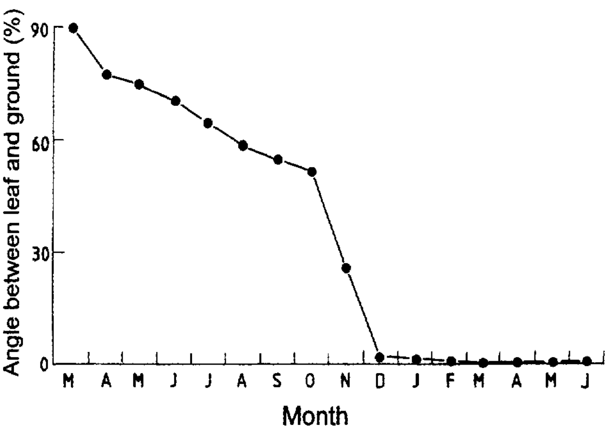

Figure 3. Annual change in angle between leaf and the ground in the Namhansanseong area.

Changes in leaf angle are shown in Figure 3. In mid-March, the new leaves, still in an unfolded state, grew 5~6 cm long, with a leaf angle of 90°. Except for a couple of small leaves in the interior part of the plant, almost all the leaves unfolded at the same time. The angle gradually decreased as the leaves unfolded. By mid-June, the leaves were nearly full-sized, 15~18 cm long. Leaf angle had by now gradually decreased to 70°. By the end of October, the angle had again slowly decreased to 50°, but it sharply decreased to 0° thereafter. This drastic decrease may have resulted from the leaves being pressed to the ground under the weight of defoliated material from woody plants above, or it may have been an adaptation to cold

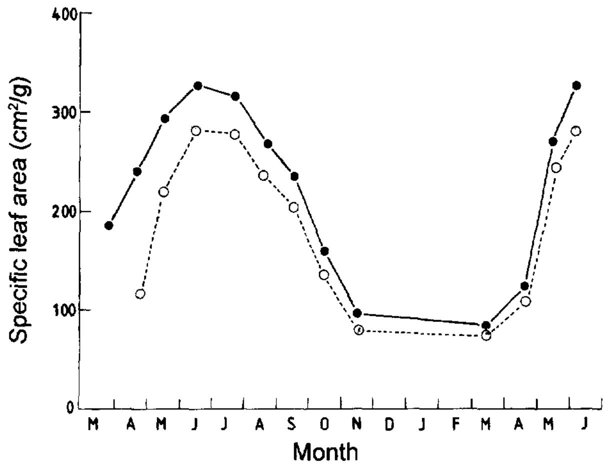

Figure 4. Annual change in SLA of *H. orientalis* in the Namhansanseong area (closed circle) and the Maranggol area (open circle).

temperatures. In the winter, intermittent snowfall increased the pressure on the *H. orientalis* foliage. Leaves remained parallel to the ground until mid-June of the following year, when the old leaves died. Total life of a leaf covered 15 months, of which 6 months was spent in active growth and 9 months as a mature leaf.

The annual curves of specific leaf area are shown in Figure 4. In the Namhansanseong area, the SLA value of the new leaves was 185 $\text{cm}^2\cdot\text{g}^{-1}$ at the end of March, increasing to 332 $\text{cm}^2\cdot\text{g}^{-1}$ by the end of June. At the end of October, the SLA again decreased, to 159 $\text{cm}^2\cdot\text{g}^{-1}$. In mid-March of the following year, the value was 190 $\text{cm}^2\cdot\text{g}^{-1}$, after which it increased to 352 $\text{cm}^2\cdot\text{g}^{-1}$ by the end of June. Therefore, the SLA curve had two peaks. The annual pattern of change in SLA values was similar for plants in the Maranggol area, although absolute values were 20~30 $\text{cm}^2\cdot\text{g}^{-1}$ lower than those at Namhansanseong. In both study areas the SLA values fluctuated with the growing stages. Although seasonal changes in both total leaf area and size of individual leaves hardly influence the constancy of SLA (Robinson and Massengale, 1967), the adaptability of their SLA in relation to environmental conditions differs among species (Šesták et al., 1971).

In the early stage of a growing season, the SLA value increases for herbaceous species or woody plants in temperate forests (Viragh and Precsenyi, 1985; Sharma and Osunkoya, 1989). This is because the rate at which leaves unfold outpaces the photosynthetic process (Evance, 1972; Viragh and Precsenyi, 1985). In addition, the SLA reaches a maximum value in summer when production of thinner leaves is more economical than that of thick leaves. By increasing the SLA, a plant could increase the amount of light harvested in photosynthesis without a concomitant increase in the biomass of the leaf tissue (Poorter and Remkes, 1990; Shipley, 1995). This also reduces "maintenance" costs because thinner leaves have fewer mesophyll cells than do thicker leaves (Chabot et al., 1979).

Likewise, the sharp decrease in the SLA value from autumn to winter could be a seasonal adaptation, in which the leaf's anti-freezing ability is increased through deposits of organic matter into the leaf tissue. Within the Namhansanseong area, the SLA values for deciduous plants during autumn were higher than those for the evergreen *H. orientalis*. For example, SLA values were estimated at 418~526 $\text{cm}^2\cdot\text{g}^{-1}$ in *A. robustum* (Min, 1997) and 301~499 $\text{cm}^2\cdot\text{g}^{-1}$ in *Symplocarpus renifolius* (Min and Kang, 1994), compared with only 159 $\text{cm}^2\cdot\text{g}^{-1}$ for *H. orientalis* in October. The fact that the SLAs for *H. orientalis* were lower in the Maranggol area probably indicates that those values varied in proportion to air temperature. The anti-freezing mechanism might first be a response to the change in morphological properties of the leaves.

Finally, the SLA value for old leaves in *H. orientalis* gradually increased during the growth season in the following year. This may have been a result of organic matter from old leaves being reallocated to other plant tissues, such as new leaves or reproductive organs.

Changes of Reproductive Organs

The change in the angle between the flower (fruit)

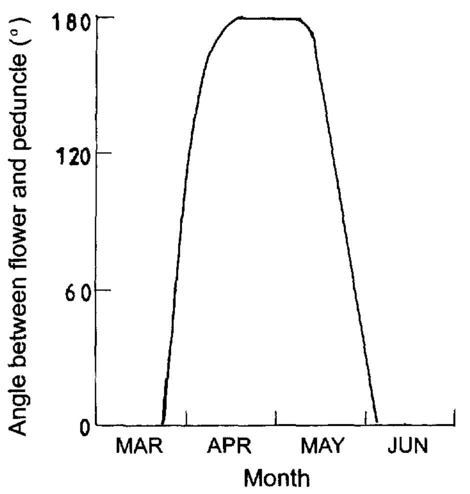

Figure 5. Change in angle between flower and peduncle.

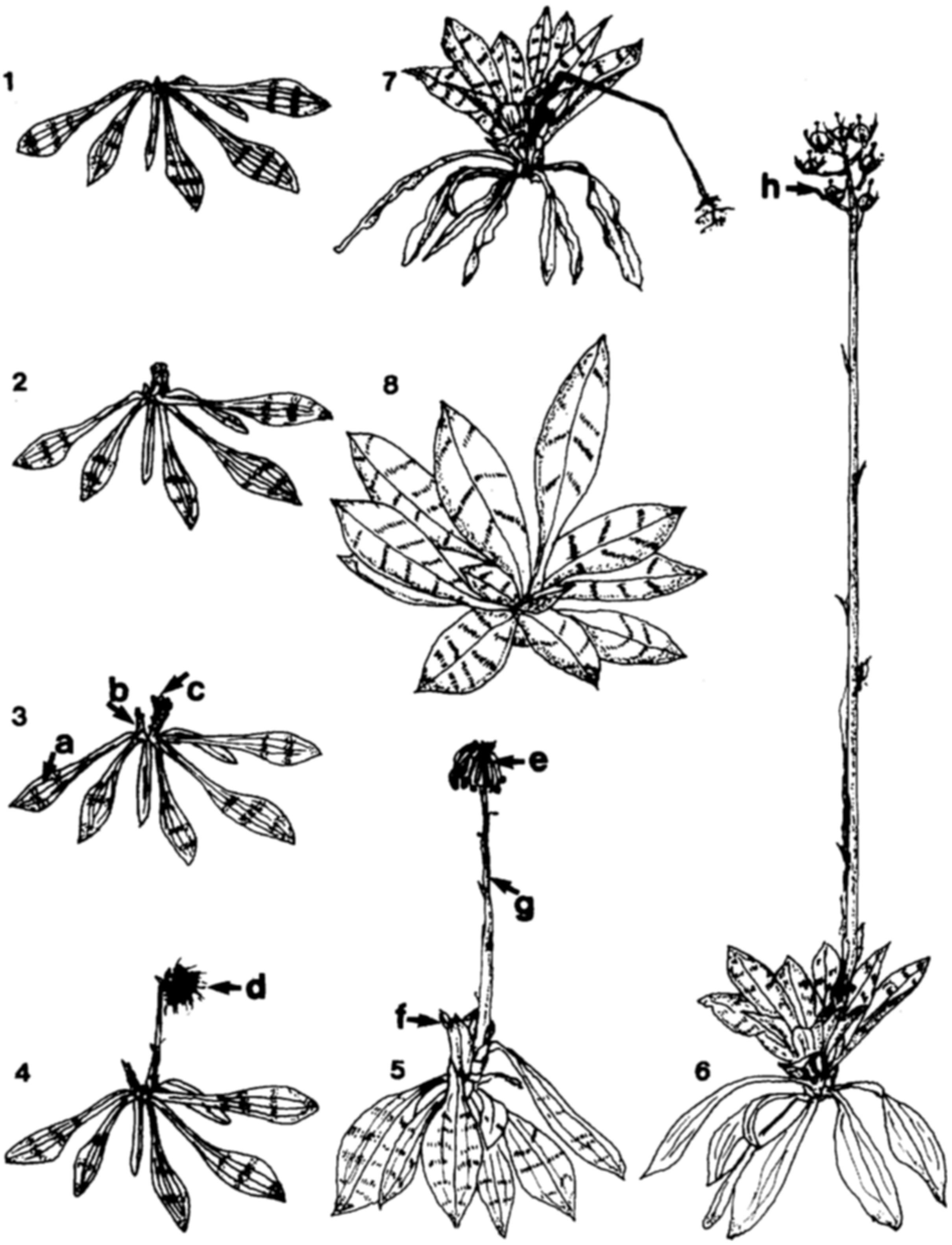

Figure 6. Schematic diagram of the annual life cycle of *H. orientalis* in the Namhansanseong area. **1,** before growth season (mid-March); **2 and 3,** beginning of flowering (late March); **4,** fully flowering; **5,** deflowering (early April); **6,** seed dispersal (late May); **7,** after seed dispersal; **8,** late growth season (after early June); **a,** old leaf; **b,** leaf bud; **c,** flower bud; **d,** flower; **e,** fruit; **f,** new leaf; **g,** peduncle; **h,** calyx.

and the peduncle is shown in Figure 5. Transformation of the leaves and the sexual organs over time is illustrated in Figure 6. *H. orientalis* flowered in late March, when the peduncle was 4~5 cm long. Plants had 3~10 flowers each. The corollas that had been semi-enclosed in the bracts began to grow upward , parallel to the peduncle. When the flower protruded from the bract, the corolla completely opened, so that the angle between the flower and peduncle was 90°. All the flowers at Namhansanseong were violet, but 1/3 of the plants in the Maranggol area had white flowers. The flowers of the other 2/3 plants were the same color as in previous years. These colors were genetically fixed for individual plants (Lee, 1996).

The flowering period lasted 15 days. Afterward, the corolla closed and the flower oriented toward the ground. The dry corolla and the green bracts protected the tiny fruit. The peduncle was now 15~20 cm long. In mid-April, the corolla broke away from the reproductive organ and the flower turned into fruit, although the dry pistil and stamen persisted. Three 1-cm-long calyces covered the fruit, which were trifurcated with each section being 5 mm long. In mid-May, the length of the peduncle was about 55 cm, and the end point of the fruit, the pistil, changed its orientation from downward to sideways.

In late May, the fruit was parallel to the ground and the suture faced upward. The mean length of the peduncle was now about 60 cm (52.9 cm at Namhansanseong, 68.0 cm at Maranggol), as shown in Table 1. The fruit opened into three forks from the middle, with the dry stamen still attached. When the seeds were completely dispersed from the capsule, the peduncle became thin and broke away from the plant. The period from flowering to seed dispersal covered about 60 days. Because the peduncle was relatively long, and the orientation of the fruit suture was upward, *H. orientalis* could effectively disperse its seeds long distances. In comparison, the great majority of herbaceous plants can dispersed their seed over only short distances, i.e., just a few meters (Bierzychudek, 1982; Levin et al., 1984; Cain et al., 1997; Cheplick, 1998). Because the regeneration of *H. orientalis* depends mostly on sexual reproduction by seeds, this particular mechanism is most favorable for this species.

Table 1. Length of peduncles on *H. orientalis* during 7 years in the Namhansanseong area and during 4 years in the Maranggol area.

Year	Namhansanseong Mean±SD (cm)	Namhansanseong Range (cm)	Maranggol Mean±SD (cm)	Maranggol Range (cm)
1991	46.7±13.2	36.5~54.6		
1992	58.9± 5.5	52.5~66.0		
1993	46.3±16.8	5.0~69.5		
1994	51.6±15.8	16.0~60.0	72.9±11.9	59.0~99.0
1995	51.0		67.4± 8.3	52.0~84.0
1996	53.0		65.4± 9.2	42.0~85.0
1997	63.0± 1.0	62.0~64.0	66.2± 9.4	48.0~84.0
Mean	52.9± 5.7		68.0± 2.9	

Energy Budget during the Growing Season

Relative changes in the tissues of *H. orientalis*, from March 20 to July 17 in the Namhansanseong area, are shown in Table 2. The amount of "energy" described here is based on the percent dry weight for a particular plant tissue. In non-flowering plants, root masses had decreased from 48% on March 20 to 32% on May 9, then increased to 44% by July 17. This percentage increased again to 48% at the beginning of the growing season the following year. The percentage of old leaves decreased from 51% on March 20 to 0% by June 6. In contrast, new leaves increased from 1% of the total on March 20 to 59% by June 6. Therefore, from early in the growing season until May 9, energy that had been stored below ground probably was translocated up to the new leaves. Energy from the old leaves might be continuously translocated to other parts, e.g., roots or new leaves (Chabot and Hicks, 1982). New leaves were formed late in the growing season of the previous year; translocation of energy from new leaves to roots may have started after June 6, when leaf growth was mostly completed.

In flowering plants, the percentage of roots decreased from 47% on March 20 to 38% by April 9, then increased to 45% by July 17. The amount of energy supplied by old leaves continuously decreased from 51% in late March to 0% by mid-July. During this period, the percentage of new leaves also continuously increased from 1% to 55%. In particular, new leaf biomass increased noticeably after the reproduc-

Table 2. Energy budget for each organ of *H. orientalis* during the growing season in the Namhansanseong area.

Date	Flowering plant RO:OL:NL:SO	Non-flowering plant RO:OL:NL
20 Mar	47:51: 1: 1	48:51: 1
9 Apr	38:48: 8: 6	41:50: 9
26 Apr	39:33:21: 7	37:38:25
9 May	40:24:26:10	32:33:35
6 Jun	43:15:42: 0	41: 0:59
17 Jul	45: 0:55: 0	44: 0:56

RO, roots; OL, old leaves; NL, new leaves; SO, sex organ.

Table 3. Correlation coefficient values among the properties of each plant part in the Namhansanseong area. DW=dry weight.

	Root		Old leaf		
	DW	%DW	Area	DW	%DW
Old leaf					
Area	a : –0.803** b : 0.867** c : 0.415				
DW	a : 0.821** b : 0.859** c : 0.471		a : 0.953** b : 0.990** c : 0.958**		
%DW		a : –0.914** b : –0.882** c : –0.515			
New leaf					
Area	a : – b : 0.882** c : 0.100		a : – b : 0.952** c : 0.608*	a : – b : 0.932** c : 0.474	
DW	a : 0.845** b : 0.840** c : 0.291		a : 0.703** b : 0.943** c : 0.580*	a : 0.785** b : 0.957** c : 0.500	
%DW		a : 0.013 b : –0.550 c : –0.787**			a : –0.410 b : 0.060 c : –0.123

a, April 9, 1991; b, April 26, 1991; c, May 9, 1991.
*, significant at 5% level; **, significant at 1% level.

tive organs had disappeared. Earlier, the percentage for reproductive organs had increased from 1% in late March to 10% by early May. These results indicated that patterns of energy translocation in flowering plants were similar to those of the non-flowering plants. However, in plants with reproductive organs, less energy was translocated from the roots and old leaves to the new leaves compared with that in non-flowering plants. Furthermore, the old leaves of a flowering plant persisted longer than those of a non-flowering plant. Additionally, the timing of energy translocation to or from the roots was earlier in flowering plants (see also Bell, 1980; Kozlowski, 1992; Worley and Harder, 1996). Therefore, in flowering plants, because the energy was being translocated not only to new leaves but also to reproductive organs and to the roots, growth of new leaves might have been retarded and restricted. After seed dispersal, the photosynthetic substances produced in the new leaves may have been transported mostly to the roots.

CC values between various organs early in the growing season (April 9 to May 9) are shown in Table 3. In April, CC values between roots and old leaves, roots and new leaves, and between old and new leaves were high and significant at 1% level. By May, however, CC values between the same pairings of tissues were lower, but not significantly. One could assume that, before late April, growth of new leaves depended on the biomass of the roots and old leaves. Likewise, plant sizes during both the previous year and the current year could have been strongly related. After early May, energy may have been reallocated to various organs - new or old leaves, reproductive organs, and roots.

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LITERATURE CITED

Bell G (1980) The costs of reproduction and their consequences. Amer Natur 116: 45-76

Bierzychudek P (1982) Life histories and demography of shade-tolerant temperate forest herbs: a review. New Phytol 90: 757-776

Cain ML, Damman H, Muir A (1997) Seed dispersal and the Holocene migration of woodland herbs. Ecol Monogr 68: 325-347

Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. Ann Rev Ecol Syst 13: 229-259

Chabot BF, Jurik TW, Chabot JF (1979) Influences of instantaneous and integrated light-flux density on leaf anatomy and photosynthesis. Amer J Bot 66: 940-945

Cheplick GP (1998) Seed dispersal and seedling establishment in grass populations, *In* GP Cheplick, ed, Population Ecology of Grass, Cambridge University Press, UK

Choung Y (1991) Growth characteristics and demography of *Polygonatum involucratum* and *Polygonatum humile* ramet population. Korean J Ecol 14: 305-316

Choung Y (1996) Clonal strategy and physiological integration of a rhizomatous perennial, *Convallaria keiskei*. I. Ramet growth and clonal structure. Korean J Ecol 19: 507-517

Evance GC (1972) The Quantitative Analysis of Plant Growth. University of California Press, Berkeley and Los Angeles

Falk DA, Holsinger KE (1991) Genetics and Conservation of Rare Plants. Oxford University Press, London

Harper JL (1977) Population Biology of Plants. Academic Press, New York

Harper JL (1980) Plant demography and ecological theory. Oikos 35: 244-253

Harper JL, White J (1974) The demography of plants. Ann Rev Ecol Syst 5: 419-463

Horvitz CC, Schemske DW (1995) Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecol Monogr 65: 155-192

Inghe O, Tamm CO (1985) Survival and flowering of perennial herbs. IV. The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943-1981. Oikos 45: 400-420

Kawano S, Takata T, Nakayama S, Hiratsuka A (1987) Demographic differentiation and life-history evolution in temperate woodland plants, *In* M Urbanska, ed, Differentiation Patterns in Higher Plants, Academic Press, New York, pp 152-181

Kozlowski J (1992) Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. Trends Ecol Evol 7: 15-19

Lee TB (1982) Illustrated Flora of Korea. Hyangmunsa, Seoul

Lee YN (1996) Flora of Korea. Kyo-Hak Publishing Co, Ltd, Seoul

Levin SA, Cohen D, Hastings A (1984) Dispersal strategies in patchy environments. Theor Pop Biol 26: 923-936

Min BM (1997) Patterns of leaf and leaf growth in *Arisaema robustum* population. Korean J Ecol 20: 339-345

Min BM, Choi JK (1993) A phenological study of several woody plants. Korean J Ecol 16: 477-487

Min BM, Kang HJ (1994) Population dynamics of *Symplocarpus renifolius* 1. Population structure and vegetative growth. Korean J Ecol 17: 453-461

Odum EP (1983) Basic Ecology. Saunders College Publishing, Philadelphia, USA

Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia 83: 553-559

Robinson GD, Massengale MA (1967) Use an area-weight relationship to estimate leaf area in alfalfa (*Medicago sativa* L. cultivar Moapa). Crop Sci 7: 394-395

Šesták Z, Čatský J, Jarvis PG (1971) Plant photosynthetic production manual and methods. Dr. W Junk NV Publishers, The Hague, pp 517-565

Sharma BM, Osunkoya OO (1989) Growth analysis of *Lycopersicon esculentum* Mill. in south-west Nigeria. Ekol Pol 36: 545-560

Shipley B (1995) Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms. Funct Ecol 9: 312-319

Silvertown JW (1982) Introduction to Plant Population Ecology. Longman, London, p 209

Stearns SC (1992) The Evolution of Life Histories. Oxford University Press, New York

Svensson BM, Carlsson BA, Karlsson PS, Nordell KO (1993) Comparative long-term demography of three species of *Pinguicula*. J Ecol **81:** 635-645

Viragh K, Precsenyi I (1985) Leaf growth investigations on tree, *In* P Jakucs, ed, Ecology of an Oak Forest in Hungary, Akademiai Kiado, Budapest, pp 232-260

White J (1985) Studies on Plant Demography. Academic Press, London

Worley AC, Harder LD (1996) Size-dependent resource allocation and costs of reproduction in *Pinguicula vulgaris* (Lentibulariaceae). J Ecol 84: 195-206