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Population Dynamics of *Heloniopsis orientalis* C. Tanaka (Liliaceae) in Natural Forests - Sexual Reproduction

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This study investigated the effects of climate on reproduction, consecutive flowering, and the level of energy investment toward sexual reproduction, as well as the relationships between flowering rates and plant size, and between seed production and plant size. The target species was *Heloniopsis orientalis* C. Tanaka (Liliaceae), an evergreen perennial herbaceous plant. Natural populations were monitored in permanent quadrats for seven years in a low-elevation area (Namhansanseong) and for five years in an area with a high elevation (Maranggol). The Tn indices required for flowering were relatively similar each year, but those for seed dispersal fluctuated. The period for seed production was proportional to the total length of the growing season. Rates of flowering varied annually, and depended on conditions in each study area. Flowering was discontinuous (i.e., not consecutive) at Namhansanseong, but was continuous (i.e., consecutive) at Maranggol. The rates were proportional to plant size; the minimum size class that supported flowering was 60~90 cm^2, and almost all plants with >210 cm^2 leaf area flowered. The overlapping range in plant size between flowering and non-flowering plants was relatively broad. Numbers of fruit per plant ranged from 1~12, with an average of 6.0 fruits at Namhansanseong and 5.0 fruits at Maranggol. In the latter area, the range in the number of seeds produced and their weight per plant varied drastically, being 1700~1867 seeds and 133.2~177.5 mg, respectively. Almost all correlation coefficients between plant size and fruit number, plant size and seed number, or plant size and seed weight were significant at the 1% level. Lastly, energy investment rates for sexual reproduction were about 30~50% of the net productivity, varying over the years. These rates were proportional to growth rates.

Keywords: Energy investment, Flowering rate, Fruit, *Heloniopsis orientalis*, Leaf area, Mortality, Plant size, Seed production, Tn index

In temperate forests, various aspects of reproduction patterns in perennials have been studied. These include the effects of environmental factors on floral development, flowering times and frequencies during a life cycle, the minimum plant size or age necessary for onset of flowering, the energy budget designated for reproduction, as well as seed size and dispersal mechanisms (Silvertown, 1982). Flowering depends on intrinsic and extrinsic factors in temperate forests. Extrinsic factors generally include climatic effects such as day length, air temperature or precipitation, plus soil factors such as moisture or temperature. Because air temperature is the most important influence on flowering (Brown, 1953), many studies and theories have been developed for clarifying this relationship (Kira, 1945; Lindsey and Newman, 1956; Yim, 1987). In Korea, many of these theories have proven useful for predicting the onset of flowering time (Yim and Cho, 1977; Yim et al., 1983, Yim, 1986, 1987; Min and Choi, 1993; Min, 2000a).

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Although the biological characteristics of sexual reproduction and seed development may vary by species, all have two aspects in common (Silvertown, 1982). One is the energy budget, i.e., the energy investment toward sexual reproduction. The limited energy that is produced through photosynthesis is effectively distributed between vegetative growth and sexual reproduction. One group of species may invest more energy for maintenance (vegetative growth more than sexual reproduction), while the opposite would be true for the other species group. The former group comprises the *K*-strategy species; the latter, the *r*-strategy species.

When a large quantity of energy is invested in sexual reproduction, the amount of vegetative growth, or clonal propagations, will diminish. Therefore, the two strategies are antipodal (Reznick, 1985; Young, 1985; Snow and Whigham, 1989; Primack and Hall, 1990; Reznick et al., 1990; Reekie, 1991; Primack et al., 1994). Generally, because herb species invest more energy in sexual reproduction compared with woody species, they increase in size relatively slowly (Sohn and Policansky, 1977; Law, 1979; Meagher and Antonovics, 1982). However, their germination rates are also very low under natural conditions, so the energy used in seed production cannot adequately contribute toward increasing the population to the extent that might, otherwise, be expected (Putwain et al., 1968).

The other aspect of reproduction is the timing of the onset of sexual reproduction during a life cycle. Except in annuals, sexual maturity depends upon the age or size of a plant. This has been demonstrated in numerous studies of iteroparous species. However, plant size, rather than age, is the controlling factor in sexual reproduction in semelparous species (Sarukhan, 1974; Law, 1979, 1983; Kawano, 1985; Kozlowski, 1992; Wesselingh et al., 1993, 1997; Worley and Harder, 1996). For example, *Dipsacus fullonum,* a biennial, must achieve a certain size before reproduction is possible, generally at least three years after germination (Werner, 1975). Although flowering potential or fecundity may be proportional to size (Lee and Hamrick, 1983; Augspurger, 1985; Roff, 1992), the requisite plant size is not constant throughout a population, but varies with environment (Wesselingh et al., 1997) and past history (Geber et al., 1997; Wijesinghe and Whigham, 1997). Because the process of sexual reproduction is pliable and adaptable to the environment, the minimum plant size also is not exact. Wesselingh et al. (1993) describes this phenomenon as "threshold size", in which an iteroparous species maintains an equilibrium between the benefits derived and the loss of energy that is invested in reproduction (Stearns and Koella, 1986; Wesselingh et al., 1997).

Much data have been accumulated for systematizing reproduction ecology in many countries (Silvertown, 1982). Studies on flowering and seed production are important in population ecology, so long-term research is required (Silvertown et al., 1993, 1996). In Korea, studies on plant populations have been carried out with regard to vegetative growth (Choung and Kim, 1989; Choung, 1991, 1993, 1996; Kang and Min, 1994; Min 1997), but few have investigated reproduction (Min and Kang, 1994; Min and You, 1998). Therefore, a focus on population ecology and species conservation is urgently needed.

The aim of the current research was to clarify reproductive characteristics and their effects on population dynamics by examining flowering and seed production in natural *Heloniopsis orientalis* populations. In particular, the study examined the long-term effects of air temperature on reproduction, flowering rates, and seed production in relation to plant size, as well as the rate of energy invested toward reproduction in two areas of South Korea, Namhansanseong and Maranggol.

MATERIALS AND METHODS

The study areas, plant species, survey period, and methods have been previously described by Min (2000b, 2000c). Permanent quadrats were set up in the Namhansanseong and Maranggol areas, the areas comprising 69 and 160 plants, respectively. The field survey was conducted weekly from March 1991 to June 1997 (June) at Namhansanseong, and from July 1993 to June 1997 at Maranggol. By following the growth rate estimation method previously used by Min (2000b, 2000c), plant sizes (as estimated by total leaf area) were classified in 30-cm^2 intervals. Dates for flowering, deflowering, and seed dispersal were recorded when half of all the plants were in those particular stages. Seeds from each plant were collected when the ventral suture was about half open. They were counted and weighed to the nearest 0.1 mg on a chemical balance (Mettler) after air-drying in the shade for 15 d. The seeds were then dispersed at their respective sampling sites.

Fruiting rates were calculated for each study area by determining the number of fruits in proportion to the number of flowers at the time of seed dispersal. For flowering plants, correlation coefficients between the two properties of seed production (i.e., energy budget and annual flowering patterns) were determined with the formula $y = ax + b$. The energy investment rate toward sexual reproduction was estimated, according to size class, as the difference between the growth rate of a non-flowering plant and that of a flowering plant, following the Model conceived by Lochle (1987). Here, it was assumed that V was zero, and that the belowground biomass was proportional to the aboveground biomass:

T (Total biomass) = S (Sexual biomass) + V (Vegetative reproductive biomass) + NR (Non-reproductive biomass)

The estimation method for determining growth rates used climatic data adopted from the Korean Meteorological Administration. The Tn indices were calculated as in previous studies by Min (2000a, 2000b).

RESULTS

Tn Index and Phenophases of Sex Organs

The phenophases of the sex organs from plants in the Namhansanseong and Maranggol areas are shown in Table 1. At Namhansanseong, except in 1996, flowering began in late March, with 6 d being the maximum difference between earliest and latest dates of onset over the years. The average annual Tn index required for flowering was 36°C·d (with a range of 17~49°C·d). Annual dates for deflowering (i.e., petal drop-off) were April 7 to April 20 (average, April 10). The mean and the range of Tn indices were 86°C·d, and 52~130°C·d, respectively. Peduncles matured, on average, by May 18 (from May 8 to May 28), with the mean and the range for Tn indices being 462°C·d, and 361~653°C·d, respectively. The average date for seed dispersal was May 26, ranging from May 17 to June 4 over the years. The mean and the range of the Tn indices for these dates were 568°C·d, and 438~756°C·d, respectively. As demonstrated here, the annual dates of onset as well as the period for seed dispersal (and corresponding Tn indices) varied over the seven-year study.

At Maranggol, annual flowering times ranged over a nine-day period, from April 11 to April 20, with an average date of April 15. The average Tn index required for flowering was 48°C·d, with a range of 20~86°C·d. Deflowering occurred from April 19 to April 28, depending on the year (average, April 23). During that period, the mean value and the range of Tn indices were 99°C·d, and 85~116°C·d, respectively. Peduncles matured, on average, by May 25 (May 21 to May 30), with a mean and range of Tn indices of 381°C·d, and 311~428°C·d, respectively. The average date of seed dispersal was June 2 (May 28 to June 6, for a difference of 9 d). For this event, the mean and the range of Tn indices were 490°C·d, and 422~553°C·d, respectively. The comparison of Tn indices showed that the times for flowering and deflowering were consistent over the four years.

Compared with Maranggol, the timing for floral events was earlier at Namhansanseong for flowering, by 16 d; deflowering, by 12 d; peduncle maturation, by 6 d; and seed dispersal, by 7 d. However, the starting times and Tn indices for each phenophase varied continuously over the years at Namhansanseong. Furthermore, the annual period for flowering varied widely, even though the timing of seed dispersal was fairly uniform. Thus, the Tn index for flowering was lower at Namhansanseong, but that of seed dispersal was higher. The average time between flowering and seed dispersal was 58 d at Namhansanseong, 10 d longer than in the Maranggol area.

Sexual Reproduction

Flowering rates are shown in Figure 1. The average flowering rate over seven years at Namhansanseong

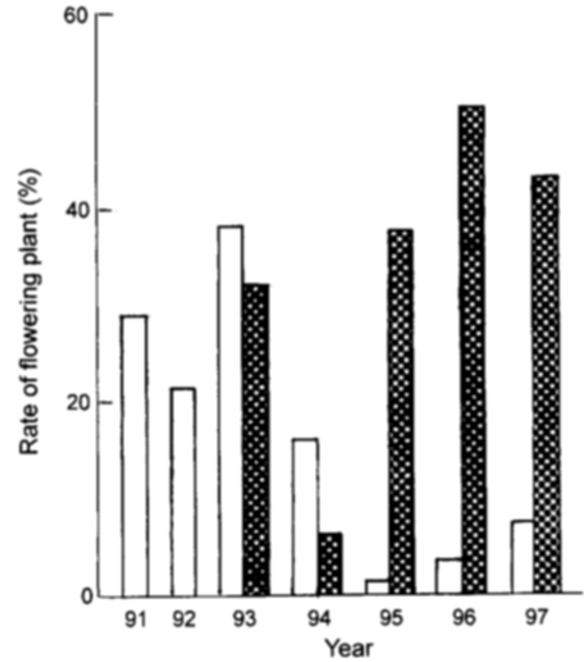

Figure 1. Flowering rate of *H. orientalis* in the Namhansanseong area (over 7 years) and in the Maranggol area (over 4 years). ☐, Namhansanseong; ▩, Maranggol.

Table 1. The phenological dates (month/date) for reproductive organs of *H. orientalis* in the Namhansanseong and Maranggol areas, from 1991 to 1997. Parentheses indicate Tn Index (°C·d).

Year	Area							
	Namhansanseong				Maranggol			
	Flower	Deflower	Mature	Disperse	Flower	Deflower	Mature	Disperse
1991	3/27(26)	4/08(61)	5/20(448)	5/28(564)	–	–	–	–
1992	3/25(41)	4/07(124)	5/10(364)	5/17(438)	–	–	–	–
1993	3/28(27)	4/07(52)	5/25(477)	6/02(598)	–	–	–	–
1994	3/30(17)	4/15(130)	5/28(653)	6/04(756)	4/11(57)	4/19(101)	5/25(428)	6/03(535)
1995	3/29(46)	4/05(55)	5/12(448)	5/18(514)	4/12(20)	4/22(85)	5/30(390)	6/02(422)
1996	4/12(49)	4/20(78)	5/26(481)	6/03(615)	4/20(30)	4/28(95)	5/23(311)	6/06(553)
1997	3/24(45)	4/10(105)	5/08(361)	5/19(492)	4/15(86)	4/21(116)	5/21(396)	5/28(451)
Mean	3/29(36)	4/10(86)	5/18(462)	5/26(568)	4/15(48)	4/23(99)	5/25(381)	6/02(490)

Table 2. The number of flowering plants over a four-year-period in the Namhansanseong (1991~1994) and Maranggol (1994~1997) areas.

Frequency	Status	Area	
		Namhansanseong	Maranggol
1		28	47
2	discontinuous	9	22
	continuous	2	22
3	discontinuous	5	1
	continuous	0	21
4		1	1

was 16.7%, ranging from 1.5% (1995) to 37.7% (1993). The flowering rate at Maranggol over five years averaged 33.8%, ranging from 6.4% (1994) to 50.3% (1996). Therefore, the flowering rate in the Maranggol area was about twice as high.

The amounts of consecutive flowering in both areas are shown in Table 2. At Namhansanseong, 45 of the 69 plants flowered; 29 plants only once in the four-year period. Of those flowering twice (11), nine flowered every other year (discontinuously), while two plants flowered continuously. Those that flowered three times (9), did so in alternating years. Only one plant flowered each year over the four-year period.

In the Maranggol area, 160 plants flowered. Of these, 47 flowered once. Half (22) of those that flowered twice, did so every other year; the other half, every year. Of those that flowered three times (22), all except one flowered each year; the remaining one

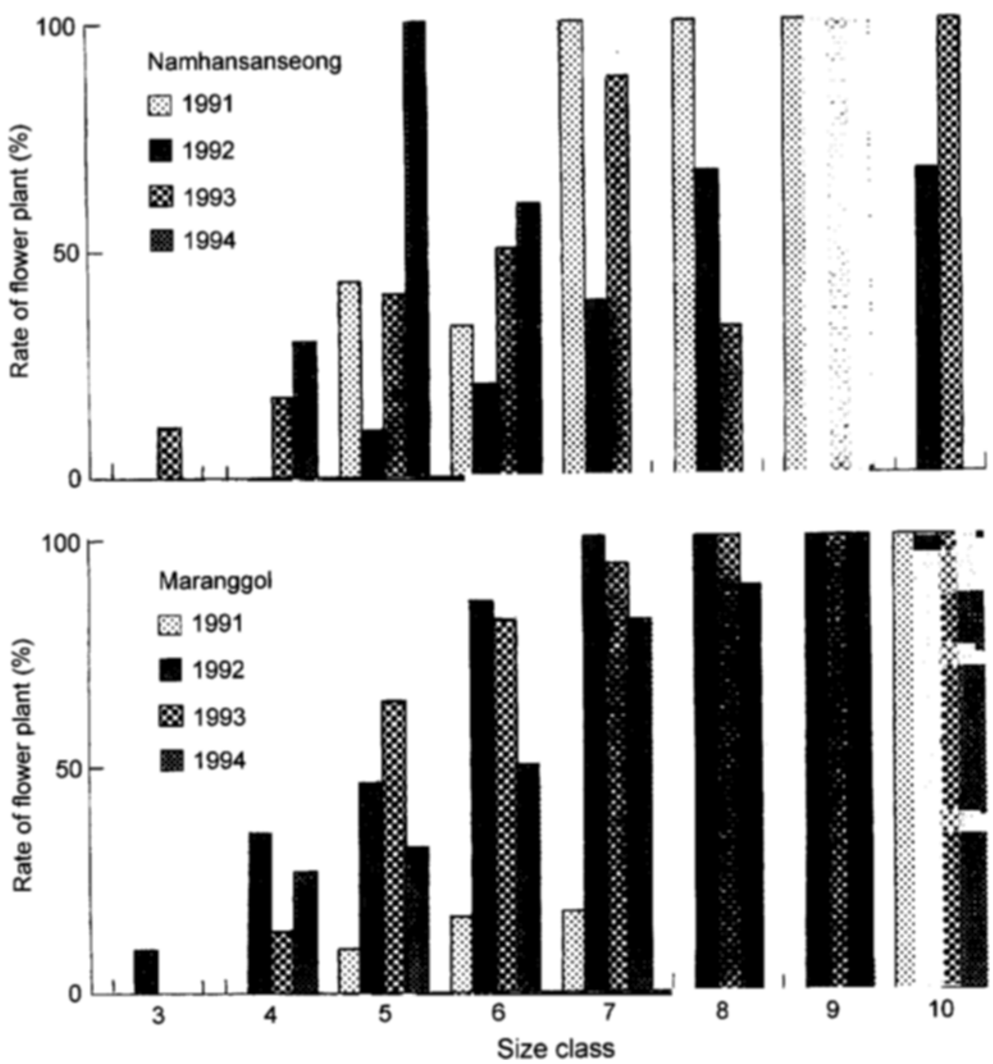

Figure 2. Flowering rate by plant size class in the Namhansanseong area (for 7 years) and in the Maranggol area (for 4 years). Size classes: 3, 60.0~89.9 cm^2; 4, 90.0~119.9 cm^2; 5, 120.0~149.9 cm^2; 6, 150.0~179.9 cm^2; 7, 180.0~209.9 cm^2; 8, 210.0~239.9 cm^2; 9, 240.0~269.9 cm^2; 10, 270 cm^2 ~.

flowered in alternating years. Overall, the flowering patterns were dissimilar between the two areas, with a discontinuous pattern predominating at Namhansanseong, and a continuous pattern being more common at Maranggol.

The rates for flowering, by plant size, are shown in Figure 2. At Namhansanseong, the rates varied from year to year; plants that were larger than medium-sized did not always flower. The minimum size for flowering was in the 60- ~90-cm^2 class, with rates being largely proportional to size. The 120- ~150-cm^2 class had 100% flowering. At Maranggol, the minimum size also was 60~90 cm^2, with flowering rates highly proportional to size. All plants with >210 cm^2 in total leaf area showed 100% flowering, except in 1994.

Figure 3 illustrates fruiting rates, i.e., the number of fruits per plant in relation to the number of flowers. The Namhansanseong area had rates between 46.5% (1996) and 100% (1995). If years with rates <10% were excluded, the range was 65.4~87.7%. In the Maranggol area, fruiting rates were between 78.2% and 90.3%, a higher but not broader range compared with the Namhansanseong area.

Reproductive attributes for the flowering plants are summarized in Table 3. In general, the average yearly number of fruits per plant varied somewhat more at Namhansanseong. The number of seeds produced at Maranggol was extremely variable (349~3950 per plant). However, the average number of seeds produced per plant per year was relatively constant. The total weight of the seed per plant also was extremely variable, but the annual mean values were similar, as were the average number of seeds. The data for seed weight and numbers are missing for the Namhan-

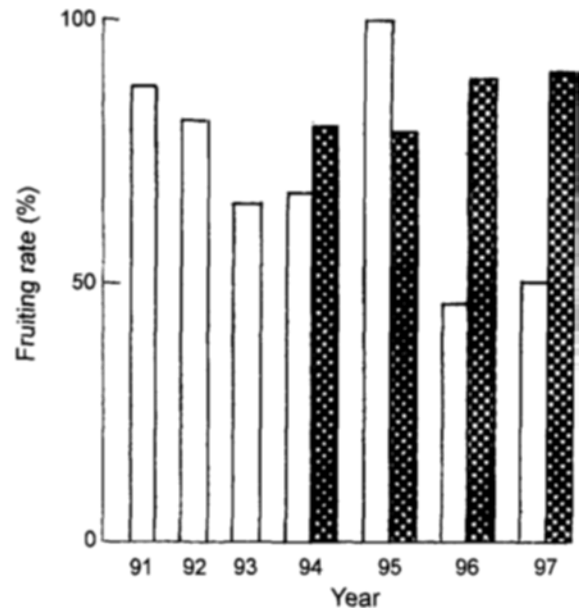

Figure 3. Fruiting rates of *H. orientalis* in the Namhansanseong area (□) and the Maranggol area (▩).

Table 3. Summary of plant properties in flowering plants of *H. orientalis* in the Namhansanseong (1991~1994) and Maranggol (1994~1997) areas. Parentheses indicate ranges.

Area/Year	Properties			
	Plant size (cm^2)	No. of fruit per plant	No. of seed per plant	Weight of seeds per plant (mg)*
Namhansanseong				
1991	179.34±49.51 (124.2~268.9)	7.1±3.1 (3~12)	– –	– –
1992	220.37±43.91 (145.7~285.9)	4.2±2.5 (1~10)	– –	– –
1993	161.27±29.21 (73.1 ~ 299.9)	5.6±2.3 (1~10)	1923.2±992.8 (336~4011)	162.3±145.9 (23~515)
1994	146.61±41.92 (93.0~247.0)	6.9±2.7 (1~9)	– –	– –
Maranggol				
1994	190.41±84.91 (128~199.8)	4.9±1.6 (3~8)	1727.6±882.2 (889~3727)	177.5±111.4 (78~425)
1995	174.97±57.43 (67.2~284.8)	4.9±1.2 (2~8)	1867.0±657.0 (349~3353)	142.7±54.7 (70~333)
1996	184.71±51.60 (103.0~347.5)	4.9±1.7 (1~9)	1834.2±942.2 (332~3950)	133.2±60.0 (29~304)
1997	180.13±44.23 (104.6~337.2)	5.3±1.4 (3~9)	1699.4±557.3 (696~3196)	163.5±99.4 (59~401)

Table 4. Correlation coefficient among reproductive properties, for one year (1993) in the Namhansanseong area and for three years (1994~1996) in the Maranggol area. Except for * (significant at the 5% level), all CC values are significant at the 1% level.

	Plant size	No. of fruit per plant	No. of seed per plant
No. of fruit per plant	a: 0.633 b: 0.805* c: 0.372 d: 0.544		
No. of seed per plant	a: 0.845 b: 0.913 c: 0.653 d: 0.782	a: 0.892 b: 0.934 c: 0.894 d: 0.901	
Seed weight per plant	a: 0.661 b: 0.861 c: 0.452 d: 0.651	a: 0.911 b: 0.931 c: 0.524 d: 0.898	a: 0.934 b: 0.981 c: 0.591 d: 0.887

a, Namhansanseong 1993 (v = 20); b, Maranggol 1994 (v = 6); c, Maranggol 1995 (v = 47); d, Maranggol 1996 (v = 71).

sanseong area.

Correlation coefficients (CC) between plant size and fruit number, plant size and seed number, and plant size and seed weight, for years in which the flowering rate was >30%, are shown in Table 4. Except for the correlation between plant size and fruit number at Maranggol in 1994, all values were significant at the 1% level. CC values between plant size and fruit number were roughly lower than the others.

Energy Investment Rate to Reproductive Organs

The energy investment rate to reproductive organs was estimated as the difference between annual growth rates of flowering and non-flowering plants, for each year in which the flowering rate was >30%. Rates for each size class were compared at individual study areas.

For Namhansanseong, the energy investment rates are shown in Table 5. Rates ranged from 14.7% (1993) to 45.2% (1992). In a certain size class in 1993, the growth rate for flowering plants was higher than that for non-flowering plants, and there was extreme variation with size class. In 1992, however, the rate was generally uniform in the size class, 35.8 ~53.2%. The energy investment rates normally were inversely proportional to the size of the plant or its growth rate.

Table 5. Differences between non-flowering and flowering plants, based on rates of increase in plant size, in the Namhansanseong area.

Plant size (leaf area, cm^2)	Year					
	1992		1993		1994	
	D*(%)	M**(%)	D(%)	M(%)	D(%)	M(%)
90.0~119.9	–	–	15.3	57.2	71.6	147.2
120.0~149.9	46.6	104.0	26.1	66.0	–	–
150.0~179.9	35.8	106.7	21.2	64.1	16.4	121.4
180.0~209.9	53.2	86.3	−3.8	52.1	–	–
Mean	45.2	99.0	14.7	59.9	44.0	134.3

*D, difference, growth rate of non-flowering plants minus that of flowering plants.
**M, mean growth rate [data from Min (2000b)].

Table 6. Differences between non-flowering and flowering plants, based on rate of increase in plant size, in the Maranggol area.

Plant size	Year							
	1994		1995		1996		1997	
	D*(%)	M**(%)	D(%)	M(%)	D(%)	M(%)	D(%)	M(%)
90.0~119.9	–	–	37.1	135.8	36.2	133.8	39.1	116.4
120.0~149.9	10.3	97.5	16.7	114.9	45.2	106.3	36.5	110.8
150.0~179.9	39.2	108.4	–	–	28.0	98.5	43.7	107.6
180.0~209.9	49.6	108.4	–	–	–	–	51.5	97.5
Mean	33.0	104.8	26.9	125.4	36.5	112.9	42.7	108.1

*D, difference, growth rate of non-flowering plants minus that of flowering plants.
** M, mean growth rate [data from Min (2000b)].

The energy investment rates for Maranggol are shown in Table 6, and range from 33.0% (1994) to 53.8% (1995). Rates were proportional to plant size in 1994 and 1997, but inversely proportional in 1995 and 1996.

In most cases, as the absolute growth rates decreased, the relative difference in growth rates between flowering and non-flowering plants also decreased. Although mean values were similar in the two study areas, the variation was greater at Namhansanseong. Generally, the range in energy investment rates was 30% to 50% of net productivity, regardless of plant size or study area, while plant growth rates were inversely proportional to investment rates.

DISCUSSION

Because both study areas had similar latitudes, their day lengths were also quite parallel. However, annual flowering times averaged 16 d earlier at Namhansanseong. This may have been a result of the difference in mean annual air temperatures: 11.8°C at Namhansanseong vs 8.2°C at Maranggol. The Tn indices at flowering time were similar in these two areas −17~49°C·d in the former, 20~86°C·d in the latter. Therefore, it was difficult to estimate precise flowering times using the Tn index, but a rough date was possible.

In temperate forests, flowering times could be predicted using the Tn index (Yim, 1987), with smaller-sized species being more sensitive to that index (Min, 2000a). This observation was also supported by the results of the current study. The fact that Tn indices and flowering times did not coincide precisely in the two areas, nor from year to year, may have been due either to microclimatic differences or to the peculiarities of *H. orientalis*. This evergreen herb species is inherently tolerant of low air temperatures, so that its reproductive organs can grow at <5°C. Therefore, it was not possible that a Tn index based on air temperatures >5°C could coincide precisely with the flowering times recorded here.

The period from flowering to seed dispersal and the corresponding Tn indices at seed dispersal were 58 d, and 568°C·d (438~756°C·d), respectively, for Namhansanseong; 48 d, and 490°C·d (422~553°C·d), respectively, for Maranggol. Two conclusions about ecological properties can be drawn from this. First, the total period for seed production was inversely proportional to the annual mean air temperature. That is, under relatively low temperatures, the onset for growth of reproductive organs was later, but seed dispersal was still completed at the normal time. Conditions of lower air temperature usually mean that each stage in the life cycle is truncated because of the overall shorter growing season (Harper and White, 1974; Silvertown, 1982). This strategy is well-adopted by plants growing in varying climates, a phenomenon demonstrated in this study of *H. orientalis* populations. Second, Tn indices had some effect, perhaps significantly, on the process of seed maturation in *H. orientalis*. However, this aspect must be further explored.

Flowering rates were 1.5~37.7% at Namhansanseong, and 6.3~50.3% at Maranggol, with annual variations. Flowering depends on intrinsic and extrinsic factors, such as plant size, the growth rate in the previous year, physiological properties, climate, and soil moisture (Silvertown, 1982; Augspurger, 1985; Wesselingh et al., 1997). In the current study, growth rates in the previous year affected flowering rates the following year. For example, when flowering rates were highest, at 37.7% in 1993 for Namhansanseong, and at 50.3% in 1996 at Maranggol, the growth rates in the previous year also were relatively high, at 97% and 135%, respectively. The field survey showed that the flowering buds of *H. orientalis* developed on the shoots late in the growing season of the previous year.

At Maranggol, relatively more plants flowered consecutively (i.e., year after year). In contrast, relatively more plants flowered in alternating years at Namhanasanseong. This suggests that *H. orientalis* adapts its pattern of reproduction to the specific area or environment, as has been shown in other studies (Wesselingh et al., 1997).More precisely, *H. orientalis* maintained a balance of energy expenditures between vegetative growth and reproduction when it is growing in a suitable environment.

In the years when the flowering rate was >30%, those rates conspicuously increased according to plant size. This indicates that flowering was determined by size, as has been seen in other studies (Werner and Caswell, 1977; Baskin and Baskin, 1979; Silvertown, 1982; Roff, 1992). Total leaf area per plant ranged from 20 to 300 cm^2. Plants with <60 cm^2 leaf area did not flower at all; some of those with leaf areas of 60~210 cm^2 flowered; while all the plants with >210 cm^2 total leaf area flowered. Therefore, the frequencies of non-flowering and flowering plants overlapped in the mid-sized range. Although size can determine a particular reproduction mechanism, in general, it does not seem to be a critical factor in influencing *whether* a plant will flower or not (Tamm, 1972; Young, 1985; Worley and Harder, 1996). The concept of a threshold size (Wesselingh et al., 1993) describes a loosely defined, minimum size, required for the onset of flowering, that fits into a balance the plant maintains for the most cost-effective use of energy.

The numbers of fruit and seed produced per plant differed between the two areas. Although yearly averages fluctuated at Namhansanseong, they were relatively constant at Maranggol. Based on these observations, one could infer that the environment at Maranggol was more suitable for growth of the *H. orientalis* population. In general, shade-tolerant herb species produce a maximum of $3\text{-}4\times10^2$ seeds per plant per year (Harper and White, 1974). At Maranggol, however, seed numbers for *H. orientalis* ranged from 1700 to 1867. Therefore, this species produced five-fold more seeds compared with other herbs. This was an excessive, though variable, level of seed production per plant for this particular species (Harper and White, 1974).

The field survey showed that no new plants were being introduced as seedlings into the permanent quadrats. Therefore, it is likely that *H. orientalis* produced a large amount of seeds but only a small number were able to germinate. Most of the correlation coefficients between plant size and fruit number, plant size and seed number, or plant size and total seed weight per plant were significant at the 1% level. This suggests that the fecundity of *H. orientalis* may be dependent upon plant size, as is the case for other species (Silvertown, 1982; Roff, 1992).

The energy investment rate to reproductive organs (or sexual reproduction) varied with plant size and by year but, in general, was proportional to the annual growth rate. Annual investments toward reproduction were 30~50% of the net productivity. It appears that this species invests more energy for vegetative growth than for reproduction, but the energy needed for reproduction seems to fit within the limits for maintaining adequate plant growth.

In contrast to annuals or biennials, perennials generally are iteroparous, a strategy that can be advantageous for the plant (Silvertown, 1982). The current size of a flowering plant was largely decreased from the previous year, especially at Namhansanseong, a phenomenon that may have been due to an excessive investment in reproduction during that previous year (Harper and White, 1974). The source of energy for reproductive organs varies among perennial herb species but, generally, originates from either the taproots (Glier and Caruso, 1973) or the bulb (Fortainier, 1973). In *H. orientalis*, sources were the taproots and old leaves during the early stages of reproductive organ growth. In the later stages, energy was derived from new, rather than old, leaves (Min, 2000b).

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