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Population Dynamics of *Heloniopsis orientalis* C. Tanaka (Liliaceae) in Natural Forests - Plant Growth and Population Structure

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Natural populations of *Heloniopsis orientalis* C. Tanaka, a perennial herb, were examined at two sites from 1991 to 1997. This study addressed the effects of climate on leaf growth early in the growing season, as well as the rate of increase in plant biomass per year, changes in size-class structure, and mortality. Permanent quadrats were located in the Namhansanseong area of Kyonggi-do and at Maranggol in the Kangwon-do area. All correlation coefficients were significant at the 1% level, and were >0.9 for all interactions between leaf length and other properties, i.e., leaf area, leaf weight, and total weight per plant. Plant size was correlated with leaf length. Early leaf growth was closely related to the Tn Index (Nuttonson's Index), with the correlation coefficient being significant at the 1% level. At the stages of 20% and 90% of maximum leaf growth, the Tn indices were 80 and 314°C·d, respectively, at Namhansanseong;128 and 456, respectively, at Maranggol. The annual Tn indices at 20% leaf growth did not vary much when individual locations were compared. However, the indices at 90% growth fluctuated over time. The Tn index at 10% maximum peduncle growth was around 60°C·d for both areas; at 50% growth, the indices were 170°C·day at Namhansanseong and 160°C·d at Maranggol. However, the two areas had dissimilar Tn indices at 100% peduncle growth. Rates of mean annual increase were 101% over the seven-year period at Namhansanseong, varying year by year. At Maranggol, the mean growth rate was 123% during the four years, with little annual fluctuation. Mean annual growth rates were high for small leaves and low for large leaves. Without recruitment by seedlings, population structures based on plant size were constant in the Namhansanseong area during the seven years, but they changed at Maranggol over the four-year-period. There, the mode shifted from smaller to large size classes over time, and the population structure changed to a normal distribution. At Namhansanseong and Maranggol, mean annual mortalities were 4.1% and 2.8%, respectively. The sizes of the dead plants varied in the former area, but generally were small in the latter. These results show that, for *H. orientalis*, the Maranggol environment was more suitable for sustaining the population than that in the Namhansanseong area.

Keywords: Air temperature, Growing season, Growth rate, *Heloniopsis orientalis*, Leaf growth, Peduncle, Population structure, Precipitation, Size class, Tn index

The leaf-growth process, general plant development, and changes in population structure are serial elements in the study of plant dynamics. The structure of a population can be modified through mortality, natality, and changes in plant size. Energy used in plant growth is derived from photosynthesis occurring in leaves.

The study of plant population ecology includes three emphases. First, leaves have a characteristic growth pattern that is unique to a particular species. In temperate forests, the early-season growth of leaves on perennial plants is affected by several abiotic factors, including air temperature, light intensity, and soil moisture (Flint, 1974; Bierzychudek, 1982; Lucier and Hinckley, 1982; Jackson and Bliss, 1984; Hicks and Chabot, 1985; Kawano, 1985). Of these, air temperature is the most critical factor for plant growth and flowering. Its effects on timing of leaf growth and its pattern have been designated by Tn index, warmth index, and year day index (Kira, 1945; Brown, 1953; Lindsey and Newman, 1956; Yim et al., 1983). Of these, the Tn index has been used frequently to estimate the onset of leaf growth and flowering in Korea (Yim et al., 1983; Yim, 1987; Min and Choi, 1993; Min, 2000a). Susceptibility to air temperature varies with species. Shrubs are more sensitive than trees (Min, 2000a), and herbaceous species may be more sensitive than woody species. In temperate forests, evergreen herbs differ from deciduous herbs in their response pattern to temperatures below 5°C (i.e., a Tn index of zero). *Heloniopsis orientalis* C. Tanaka (Liliaceae) perhaps begins growing earlier than deciduous species.

Second, the effects of intrinsic factors, such as physiology and energy budget, and extrinsic factors, such

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as herbivory, can influence the increase in plant size over time. Of those intrinsic factors, energy allocation among plant organs varies with its particular survival strategy and the plant's use of photosynthetic substances in vegetative growth and reproduction. Plants must produce sufficient photosynthates and/or decrease their investment to reproduction in order to increase their size. Yet, it is leaf area that determines the amounts of photosynthetic substances that are produced (Evance, 1972).

Third, population dynamics depend on the population structure, which is determined by the age of the plants, growth stage, and changes in size over time. Although a model of population dynamics, based on age, has been used to predict mortality, it is difficult to estimate the ages of individual plants at any given time. Furthermore, because the stage of growth, rather than age, is more closely related to life span, growth rate, and reproduction in individual plants, it is used more often in describing and distinguishing individual plants (Harper and White, 1974; Werner and Caswell, 1977; Silvertown, 1982; Law, 1983; Hughes, 1984; Huenneke and Marks, 1987; Harvell et al., 1990; Manly, 1990). For a simple description of structure at a given time, populations are sometimes classified by size. By grouping the members of the population into several stages, the structure can be determined accurately. Because reproduction in perennial plants depends mainly on plant size, these classifications are necessary for predicting the status of the future population (Solbrig, 1981). Structure and changes are dependent on the population itself and on the surrounding environments.

H. orientalis is an evergreen, perennial herbaceous plant that is rosette in form. Leaves persist for 15 months, with active leaf growth occurring primarily from March to May (Min, 2000b). During this period, the general pattern of leaf growth for such an evergreen herb species may be understood by analyzing the relationship between the Tn index and leaf growth. Because this particular species has simple leaves, rarely reproduces by clonal propagation, and has a ramet that is separated from the others, the dynamics of its growth can be easily understood. Due to its simplicity, the life cycle of *H. orientalis* can provide a basic model for understanding population dynamics.

This paper presents three themes for investigating the *H. orientalis* population: 1) the relationship between air temperature and leaf growth early in the growing season; 2) the estimation of growth rates, and 3) interpretation of the population structure in terms of the first two themes. The two study areas chosen in South Korea, Namhansanseong and Maranggol, have similar latitudes but different elevations. Early-season leaf growth, Tn index, plant growth per year, and changes in population structure (according to size class) were surveyed for seven years in the Namhansanseong area and for four years at Maranggol.

MATERIALS AND METHODS

The study areas and *H. orientalis* populations have been described by Min (2000b). Three permanent 5-m × 5-m quadrats were set up in the Namhansanseong area and one in the Maranggol area. The Namhansanseong study included 69 plants over a period of seven years (from 1991 to 1997); Maranggol covered 160 individuals over four years (from 1994 to 1997). *H. orientalis* was randomly distributed and the leaves from one plant did not overlap the leaves of another. Field surveys started in late March at Namhansanseong and in mid-April at Maranggol, when the leaves and peduncles began to grow. Weekly surveys were carried out in both locations until seeds were dispersed in early June. The lengths of the leaves and peduncles were measured to the nearest cm. Plant heights, however, were recorded only once, before leaf-out.

About 50 plants (20~30 flowering plants and 20~30 non-flowering plants) were sampled eight times at Namhansanseong, from March to July of 1991. The harvested plants were measured for total weight as well as length, width, area, and weight of individual leaves.

Relative sizes of leaves and peduncles were calculated as percentages, using maximum size as the base value. These maximum sizes were determined for leaves the following year, while those for peduncles were established at the time of seed dispersal. The rate of increase in plant size, or growth rate per year, was based on total area of leaves per plant, as follows:

$$[1]\ \text{Growth rate} = \frac{A_{t+1}}{A_t} \times 100$$

where A = total area of leaves per plant and t = year.

The relationships between climate and growth were calculated according to $y = ax + b$. The determination of the Tn index (Nuttonson's Index) was modified from that of Yim (1987) so as to include minus 5°C, rather than 43°F

$$[2]\ \text{Tn} = \Sigma(\text{mean daily air temperature-5}),\ \text{in d of } 5^{\circ}\text{C} \leq$$

Tn index and precipitation amounts were cumulative from January 1 and March 1, respectively. Significant differences between the two dates were then decided with a *t*-test. Classification of plants by total leaf area was done in intervals of 30-cm^2 units, which resulted in a total of ten classes. The frequencies of each class were converted into relative values.

Climatological data for the Namhansanseong area were obtained from the Suwon Meteorological Station (1991-1997); those for Maranggol were collected from the nearby Hongchon and Taegwallyong Weather Observation Station (1994-1997) (Korean Meteorological Administration, 1991-1997).

RESULTS

Relation between Leaf Length and Other Properties

Table 1 shows plant sizes as estimated by leaf length before the start of the growing season and after seed dispersal, as well as correlation coefficients (CC) between property pairings (total weight, and length, area, and weight of individual leaves). The CC values between leaf length and leaf area were 0.929 (n = 325) in late March and 0.946 in late July; both were significant at the 0.1% level. Therefore, leaf area could be estimated by leaf length alone. Leaf area generally is estimated from its length and width (Šesták et al., 1971) but in this study, estimations by leaf length only were sufficient because *H. orientalis* possesses a simple leaf shape. The relationship between leaf length (x) and leaf area (y) was:

[3] $y = 0.569x + 7.351$

Before the growing season began, CC values between leaf area and leaf weight, and between leaf weight and total plant weight, were 0.927 and 0.978, respectively. After seed dispersal, they were 0.989 and 0.977, respectively, for flowering plants and 0.986 and 0.936, respectively, for non-flowering plants. Because an *H. orientalis* plant can have 2 to 21 leaves, its total weight cannot be estimated directly by summing each leaf length; leaf-length estimates are only an indirect means for determining plant size.

Table 1. Correlation coefficient values among properties of each plant part for *H. orientalis* in the Namhansanseong area, before growing season and after seed dispersal.

Leaf Properties	Before growing season (March 29)			After seed dispersal (July 31)					
				Seed-producing plant			Nonseed-producing plant		
	Length	Area	Weight	Length	Area	Weight	Length	Area	Weight
Leaf area	0.929* n = 99			0.946* n = 111			0.485* n = 175		
Leaf weight	0.956* n = 99	0.927* n = 20		0.773* n = 111	0.989* n = 20		0.933* n = 175	0.986* n = 30	
Total weight	–	0.961* n = 20	0.978* n = 20	–	0.977* n = 20	0.988* n = 20	–	0.936* n = 30	0.963* n = 30

*; significant at 1% level.

Table 2. Tn Index (Nuttonson's Index) for the two study areas from 1991 to 1997 (month/day).

Tn Value	1991	1992	1993	1994		1995		1996		1997	
	N	N	N	N	M	N	M	N	M	N	M
50°C·day	4/07	3/27	4/05	4/05	4/11	4/01	4/18	4/13	4/25	3/29	4/08
100°C·day	4/12	4/04	4/20	4/11	4/19	4/15	4/28	4/24	4/29	4/09	4/19
150°C·day	4/20	4/10	4/25	4/18	4/25	4/22	5/03	4/28	5/05	4/17	4/27
200°C·day	4/26	4/22	5/02	4/22	5/01	4/28	5/09	5/03	5/12	4/23	5/02
250°C·day	5/03	4/29	5/06	4/26	5/08	5/03	5/17	5/08	5/17	4/29	5/05
300°C·day	5/08	5/04	5/11	4/30	5/13	5/08	5/22	5/13	5/22	5/04	5/12
350°C·day	5/13	5/09	5/15	5/04	5/18	5/13	5/27	5/17	5/26	5/07	5/15
400°C·day	5/17	5/14	5/19	5/09	5/23	5/18	5/31	5/21	5/29	5/12	5/22
450°C·day	5/21	5/19	5/23	5/13	5/27	5/21	6/06	5/24	6/02	5/16	5/28
500°C·day	5/24	5/23	5/27	5/17	6/01	5/25	6/10	5/28	6/06	5/20	6/02
550°C·day	5/27	5/28	5/30	5/22	6/05	5/29	6/14	5/31	6/09	5/25	6/06
600°C·day	5/31	6/01	6/03	5/25	6/09	6/02	6/18	6/03	6/13	5/29	6/10

N, Namhansanseong area; M, Maranggol area.

Achieving such high CC values suggests that Equation [3] might be applicable for estimates in any *H. orientalis* population.

Climate

The data for determining Tn indices between 1991 and 1997 are shown in Table 2. At Namhansanseong, the earliest date that a Tn value reached 50°C·d was on March 27 (1992), the latest was on April 13 (1996), a real difference of 17 d. The earliest that an accumulated Tn value was 600°C·d was on May 25 (1994), the latest, June 3 (1996), a difference of 9 d. At Maranggol, the difference in earliest and latest dates for achieving a Tn value of 50°C·d was also 17 d (earliest: April 8, in 1997; latest: April 25, in 1996). A Tn value of 600°C·d was earliest on June 9 (1994); latest on June 18 (1995), also a difference of 9 d. When the two areas were compared for earliest dates on which Tn values accumulated to 50°C·d and 600°C·d, the differences were 12 and 15 d, respectively.

Precipitation records for the two areas are shown in Table 3. At Namhansanseong, the lowest monthly average occurred in March (46.3 mm); the highest, in May (117.1 mm). Lowest and highest monthly averages at Maranggol also were in March (47.4 mm) and May (114.8 mm), respectively.

Changes in Plant Size during the Growing Season

Relative leaf growth of *H. orientalis* during the early growing season is shown in Table 4. The current-year shoots had developed in the previous year and were about 1 cm long when they began their overwintering period (Min 2000b).

In the Namhansanseong area, leaves reached approximately 20% maximum growth by April 9th and 90% of maximum by May 7th. Therefore, the main leaf-growth period, defined as the time elapsed between 20% and 90% growth, lasted 28.4 d. In other words, leaves grew approximately 10% every 4 d. The earliest date for achieving 20% growth was March 29 (1992); the latest, April 19 (1993), a difference of 21 d. The corresponding Tn indices for those dates were 64.5°C·d and 94.2°C·d, respectively. Mean Tn indices associated with 20% and 90% growth were 80°C·d and 314°C·d, respectively.

At Maranggol, 20% growth was achieved, on average, by April 27; 90% growth by May 31. Here, the main leaf-growth period lasted 34.5 d, with 10% of maximum growth occurring every 4.9 d. The difference in dates for achieving 20% growth was, at most, 7 d, but Tn indices were similar between those dates; mean indices for 20% and 90% leaf growth were 128°C·d and 456°C·d, respectively.

Cumulative precipitation recorded during those periods of 20% and 100% leaf growth were 11.6~96.8 mm and 75.2~166.2 mm at Namhansanseong and 42.5~101.8 mm and 133.5~344.5 mm at Maranggol. Annual fluctuations in precipitation meant that no direct relationship could be found between actual amounts and those required for a particular growth rate.

CC values between leaf growth and Tn index were >0.96, and were significant at the 1% level (Table 5). In contrast, CC values between leaf growth and precipitation were not significant at the 1% level, and were lower than those between leaf growth and Tn values.

Table 3. Precipitation (mm) in study areas from 1991 to 1997.

Month	Year										
	1991	1992	1993	1994		1995		1996		1997	
	N	N	N	N	M	N	M	N	M	N	M
Jan	17.2	14.2	2.2	4.4	10.4	13.4	10.4	20.4	21.4	14.4	14.2
Feb	42.1	25.5	56.0	10.8	4.2	11.2	5.3	4.1	3.6	41.4	29.3
Mar	51.7	11.6	27.1	50.9	18.5	46.2	57.3	100.8	69.8	30.4	16.5
Apr	52.6	78.6	63.5	25.3	24.0	33.7	44.5	51.1	49.0	60.7	38.5
May	123.0	122.0	84.0	141.4	126.5	59.0	48.0	26.5	23.5	260.3	289.5
Jun	89.8	51.3	151.9	94.0	124.5	67.7	64.0	286.4	251.0	150.4	141.5
Jul	567.6	169.2	458.1	81.3	123.0	372.9	394.0	241.1	385.0	331.7	319.5
Aug	82.4	334.4	208.0	327.2	297.5	967.9	822.5	77.5	130.5	299.2	119.5
Sep	185.2	168.6	84.0	68.1	71.0	24.2	80.5	9.2	7.5	25.0	118.0
Oct	30.8	37.7	21.8	191.0	183.5	29.2	20.0	70.0	67.5	52.3	23.5
Nov	25.2	62.8	62.3	31.2	35.5	24.8	49.1	49.0	29.8	82.0	93.0
Dec	52.8	53.5	19.1	20.0	13.8	3.1	2.4	16.0	18.2	46.5	32.2
Total	1,320.4	1,129.4	1,238	1,045.6	1,032.4	1,653.3	1,598.0	952.1	1,056.8	1,394.3	1,235.2

N, Namhansanseong area; M, Maranggol area.

Table 4. Date and Tn index at each growth stage *H. orientalis* during the growing season, over seven years.

Level (%)	1991	1992	1993	1994		1995		1996		1997	
	N	N	N	N	M	N	M	N	M	N	M
Date											
20	4/09	3/29	4/19	4/10	4/28	4/06	5/01	4/10	4/30	4/14	4/24
30	4/11	4/03	4/21	4/12	5/02	4/12	5/05	4/20	5/12	4/18	4/27
40	4/13	4/09	4/23	4/15	5/05	4/16	5/09	4/24	5/14	4/22	4/30
50	4/15	4/13	4/26	4/17	5/08	4/23	5/15	4/27	5/18	4/26	5/02
60	4/21	4/16	4/30	4/20	5/12	4/26	5/23	4/30	5/21	4/28	5/05
70	4/26	4/22	5/04	4/24	5/15	4/29	5/30	5/04	5/25	5/01	5/12
80	4/30	4/28	5/06	4/28	5/18	5/03	6/06	5/07	5/28	5/07	5/18
90	5/08	5/02	5/10	5/02	5/22	5/07	6/11	5/15	6/07	5/11	5/30
Tn index											
20	70.0	64.5	94.2	96.9	179.4	55.2	134.7	45.4	111.8	132.4	130.6
30	94.8	94.2	114.1	113.3	215.3	80.9	163.1	77.8	205.9	157.7	158.1
40	113.4	141.6	136.4	129.8	230.4	114.0	204.8	104.5	222.1	192.6	185.9
50	124.0	155.7	156.2	147.6	257.4	160.6	235.5	139.1	261.6	224.1	210.7
60	158.2	162.2	186.8	182.7	299.4	182.7	314.2	173.2	293.6	243.4	251.2
70	202.7	202.0	224.4	230.9	326.2	211.0	390.0	213.5	338.7	272.1	308.7
80	237.1	247.2	250.7	271.0	350.4	253.5	448.7	243.7	380.3	353.5	376.4
90	300.8	280.7	296.9	331.2	388.9	291.1	520.0	329.0	523.8	393.1	472.4

N, Namhansanseong area; M, Maranggol area.

Changes in Peduncle Size during the Growing Season

The relative growth of peduncles during the growing season is shown in Table 6. Over the seven-year period at Namhansanseong, most of the peduncles had grown to 10% of full size by April 5 of each year, with the final size reached by May 24. The respective Tn indices for those two dates were 59.7°C·d and 511.7°C·d. The mean Tn index for dates representing 10% growth was 64.5°C·d. For 50% maximum growth, the difference in dates between earliest and latest was 12 d. Tn indices for these dates were similar. The earliest by which 100% growth was achieved was on May 10 (1995), with a Tn index of 326.3°C·d; the latest date, June 7 (1996), with a Tn index of 683.8°C·day. From 40 to 58 d elapsed between the times of 10% and 100% peduncle growth. The main growing period (20~90% growth) of the peduncle covered 49 d.

In the Maranggol area, the peduncles grew to an

Table 5. Correlation coefficients between leaf growth and Tn index, leaf growth and precipitation (v = 6, 1% level = 0.834).

Year	Tn Index		Precipitation	
	Namhansanseong	Maranggol	Namhansanseong	Maranggol
1991	0.9742		0.9656	
1992	0.9870		0.9747	
1993	0.9911		0.9344	
1994	0.9727	0.9969	0.5852	0.9424
1995	0.9977	0.9875	0.8555	0.9614
1996	0.9861	0.9651	0.9583	0.8839
1997	0.9815	0.9687	0.7943	0.8720

Table 6. The relative growth of *H. orientalis* peduncles during each growing season.

Level (%)	1991	1992	1993	1994		1995		1996		1997	
	N	N	N	N	M	N	M	N	M	N	M
10	4/05	3/29	4/08	4/06	4/13	3/30	4/19	4/10	4/24	4/04	4/14
20	4/11	4/02	4/17	4/09	4/17	4/11	4/24	4/20	4/28	4/11	4/20
30	4/14	4/06	4/20	4/12	4/25	4/14	4/27	4/23	4/30	4/16	4/24
40	4/17	4/10	4/22	4/15	4/28	4/19	4/30	4/28	5/02	4/21	4/26
50	4/20	4/18	4/27	4/18	5/01	4/23	5/03	4/30	5/06	4/23	4/28
60	4/22	4/23	5/01	4/21	5/04	4/27	5/07	5/02	5/09	4/27	5/01
70	4/27	4/28	5/06	4/26	5/08	4/30	5/10	5/05	5/13	5/01	5/03
80	5/01	5/05	5/10	5/01	5/11	5/03	5/15	5/07	5/19	5/07	5/09
90	5/08	5/11	5/14	5/05	5/21	5/06	5/23	5/15	5/24	5/12	5/15
100	5/15	5/16	5/28	5/18	5/29	5/10	6/01	6/07	6/05	5/16	5/25

N, Namhansanseong area; M, Maranggol area.

average of 10% maximum size by April 18, and were fully grown by about May 31. The main growing period of the peduncles lasted about 43 d, with beginning and ending Tn indices of 63.2°C·d and 451.6°C·d, respectively. The earliest date for achieving 10% maximum growth was April 14 (1994; Tn index, 68.2°C·d); the latest, April 24 (1996; Tn index, 49.7°C·d), for a difference of 10 d. April 28 (in 1997) was the earliest in the year by which time 50% maximum growth was attained; the latest date for achieving half-sized peduncles was May 6 (1996), a difference of 8 d. Corresponding Tn indices were 157.0°C·d and 160.0°C·d, respectively. Maximum (100%) growth was reached as early in the growing season as May 25 (1997), with a Tn index of 423.2°C·d; the latest date was June 5 (1996), with a Tn index, 496.6°C·d. The length of the main growth period for peduncles ranged from 41 d (1997) to 46 d (1994).

The average starting date for peduncle development was 12 d earlier at Namhansanseong than at Maranggol; growth was completed 7 d earlier in the former area as well. The average annual dates by which certain levels of growth were achieved varied widely at Namhansanseong, but only slightly at Maranggol. In contrast, the Tn indices for 10% growth were similar for both areas, at around 60°C·d. Moreover, Tn indices for Namhansanseong and Maranggol were 166°C·d and 159°C·d, respectively, for 50% growth; 505°C·d and 460°C·d, respectively, for 100% growth.

Table 7. Correlation coefficients between peduncle growth and Tn index (v = 8, 1% level = 0.765).

Year	Area	
	Namhansanseong	Maranggol
1991	0.9677	
1992	0.9843	
1993	0.9518	
1994	0.9477	0.9691
1995	0.9982	0.9606
1996	0.8498	0.9318
1997	0.9857	0.9605

N, Namhansanseong area; M, Maranggol area.

Therefore, the Tn indices required for achieving particular growth rates were similar for both areas.

Almost all the CC values between Tn index and peduncle growth were >0.93 and significant at the 1% level (Table 7).

The Annual Rate of Change in Plant Size

Plant growth rates, i.e., the rates of increase in leaf surface area, are shown in Figure 1. In the Namhansanseong area, the seven-year mean was 101.6%. However, the annual growth rates were extremely variable, being highest (152.4 ± 43.0%) in 1994, and lowest (61.3 ± 18.6%) in 1993, when the plants actually decreased in size. These differences were significant at the 1% level (Table 8). In the Maranggol area, the mean growth rate over four years was 123.7%. The rate was highest (135.2 ± 41.4%) in 1995, and lowest (115.2 ± 53.8%) in 1994. However, these annual fluctuations were not significantly different.

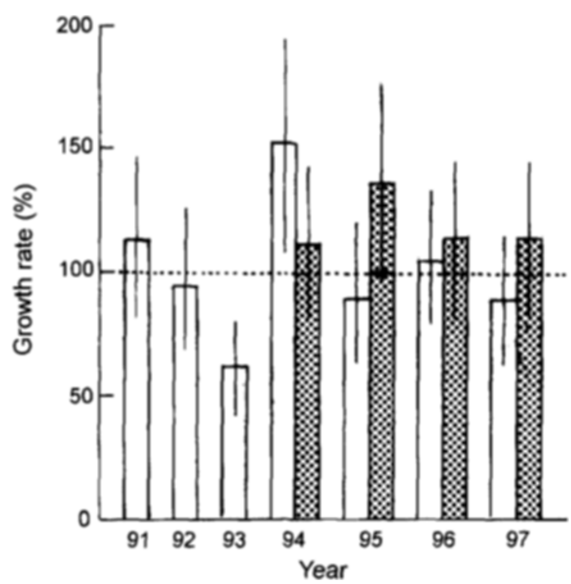

Figure 1. Mean annual growth rate of *H. orientalis* population. □, Namhansanseong area; ▩, Maranggol area.

Table 8. The level of significance, by t-testing, between pairs of years. The parentheses indicates the Maranggol area.

Year	1991	1992	1993	1994	1995	1996
1992	2.727**					
1993	10.210***	2.206*				
1994	4.357***	9.048***	16.242***			
1995	3.508***	1.195	7.123***	9.356***(3.607***)		
1996	1.252	1.826	10.841***	6.899***(0.532)	2.883**(2.129*)	
1997	3.558***	1.346	6.751***	8.581***(1.767)	0.210 (2.044*)	2.974**(0.782)

*, 5% level; **, 1% level; ***, 0.1% level.

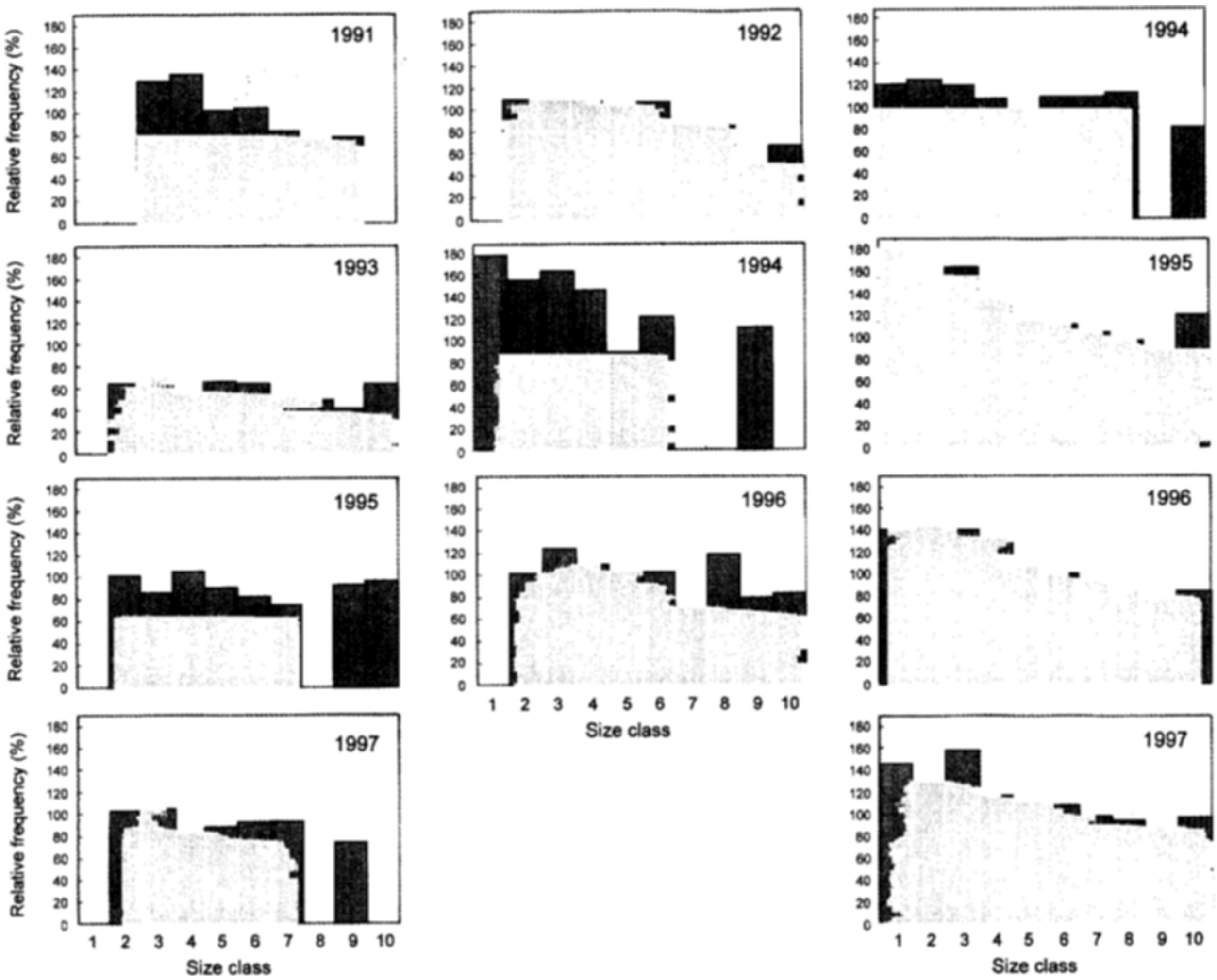

Figure 2. Annual growth rate of *H. orientalis* population; size class based on total leaf area (cm^2): 1, 0.0~29.9; 2, 30.0~59.9; 3, 60.0~89.9; 4, 90.0~119.9; 5, 120.0~149.9; 6, 150.0~179.9; 7, 180.0~209.9; 8, 210.0~239.9; 9, 240.0~269.9; 10, 270.0~.

As plant size increased, its growth rate decreased (Fig. 2). This was especially true in the Namhansanseong area, where a plant with a total leaf area of >180 cm^2 for one year decreased in leaf size the following year.

Changes in Population Structure

In a distributional mode over the seven-year growth period at Namhansanseong, the 90~120-cm^2 size class had the highest frequencies (Fig. 3). Although this was the general pattern, the frequencies of plants with smaller leaf areas were high in 1994 and 1998, while those of larger-leafed plants were relatively high in 1992. Likewise, the frequency distribution patterns were similar at Maranggol, but the mode shifted upward yearly, to higher leaf area classes (Fig. 4).

Mortality

Annual mortality rates for *H. orientalis* populations in the two study areas are shown in Figure 5. For Namhansanseong, the cumulative rate over seven years was 29.0% (4.1% per year). The highest rate of mortality was recorded in 1995, at 13.6%; the lowest (0.0%) was in 1991 and 1993. In the Maranggol area, the four-year rate was 11.3% (2.8% per year), ranging from 0.7% (1996) to 6.4% (1995).

The relationship between mortality and plant size is shown in Figure 6. In general, the mortality rates for smaller plants were high in both study areas. Although

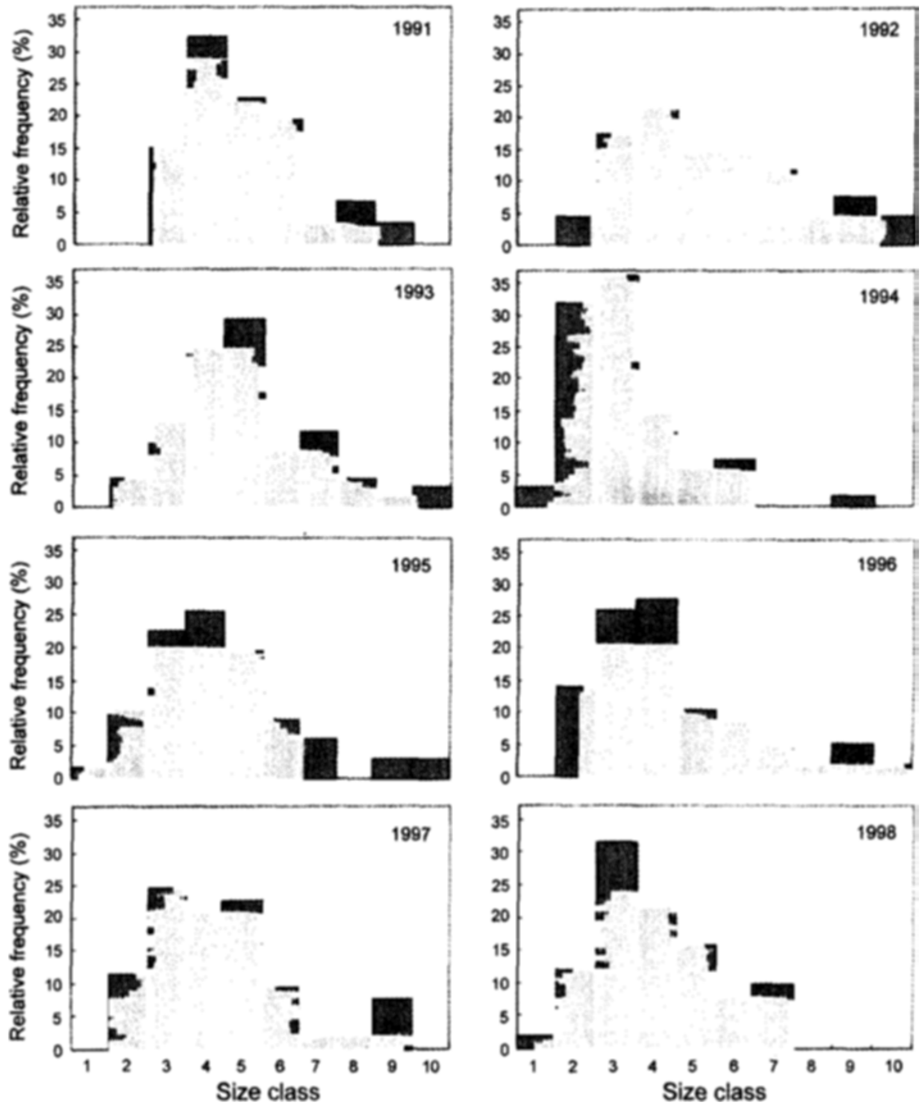

Figure 3. The changes of frequency with size class of the *H. orientalis* population in the Namhansanseong area. The size classes are described in Figure 2.

the size of the dead plants varied at Namhansanseong, most of those at Maranggol were relatively small (e.g., 72.2% of the dead Maranggol plants were <30 cm^2).

DISCUSSION

Leaf Growth and Tn Index

The Tn index for 20% maximum leaf growth was lower at Namhansanseong than at Maranggol, which demonstrates that *H. orientalis* can grow at temperatures <5°C. Furthermore, the higher Tn index for 90% of maximum growth at Maranggol indicates that variations above a certain temperature do not affect leaf growth. The period spanning 20% to 90% growth was 6 d longer at Namhansanseong than at Maranggol (28.4 vs 34.5 d). This month-long period during which 70% of the entire growth took place is rather short, especially when one considers that each 10% increment in growth required, on average, only 4~5 d, which is very important for leaf development.

The period between achieving 20 and 90% maximum growth was longer at Namhansanseong, an area with a longer growing period and, thus, more total growth. This is further demonstrated by noting that the highest increase in growth at Maranggol took place over 40 d (in 1995); the least amount of growth occurred over a 24-d period (in 1994). Therefore, a

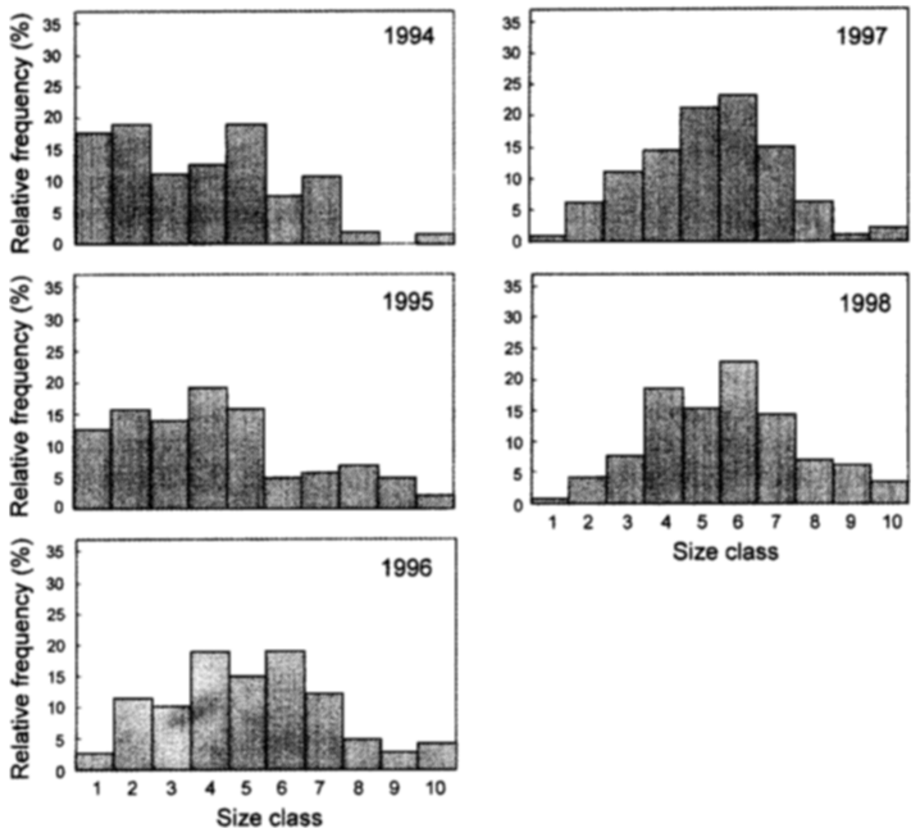

Figure 4. The changes of frequency with size class of the *H. orientalis* population in the Maranggol area. The size classes are described in Figure 2.

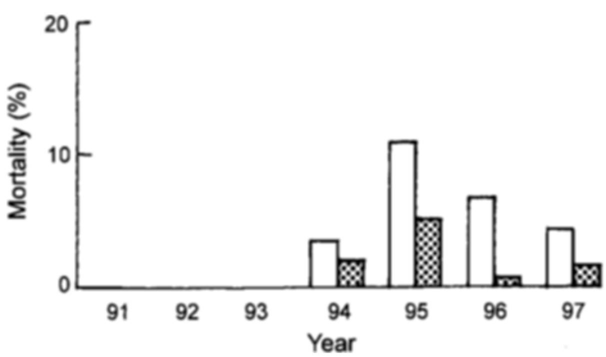

Figure 5. Change in mortality of *H. orientalis* over seven years in the Namhansanseong area (□) and over four years in the Maranggol area (▩).

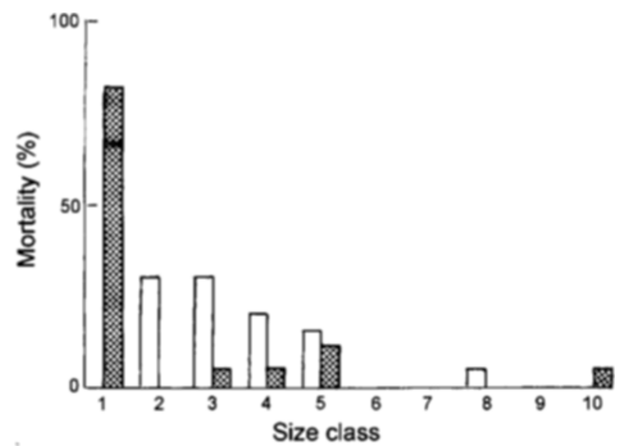

Figure 6. The relationship between mortality and plant size at Namhansanseong (□) and Maranggol (▩). The size classes are described in Figure 2.

longer leaf-growth period means more growth and, consequently, an increase in the annual growth rate of the plant.

However, Min (2000a) has shown that leaf growth in woody plants is related to the Tn index during the early growing season, and that shrubs are more sensitive to temperature than are trees. Therefore, one could reason that herbs might be temperature-sensitive early in the growing season, with growth being directly related to temperature. Later in the growing season, other factors, such as precipitation, would more likely affect plant growth. Although several variables may interact in the relationship between precipitation and plant growth, field studies have shown that the taproots of *H. orientalis* are distributed primarily in the litter layer or topsoil. This suggests that this species may be sensitive to topsoil moisture.

Tn Index and Peduncle Growth

Although the Tn index affected peduncle growth (Table 5), its influence varied according to the stage of growth. First, regardless of study area, the Tn index was extremely highly relative to growth during the first half of peduncle development. (Tn indices for 10%, 30%, and 50% levels of growth were 60°C·d, 110°C·d, and 165°C·d, respectively). Second, the Tn indices for 50~100% growth varied by year and by study area, which suggests that, peduncle growth was not related to air temperatures above a certain point.

Annual Rates of Increase in Plant Size

The annual growth rate at Namhansanseong varied over the seven-year period, with a mean rate of 101.6%. At Maranggol, the four-year mean growth rate was 123.7%, with little fluctuation among individual years. At Namhansanseong, plant sizes actually decreased in the fourth year, but plants continued to increase in size at Maranggol over four years. Therefore, the Maranggol area might be a more suitable habitat for *H. orientalis*.

These two areas have similar latitudes (thereby affecting day length), but dissimilar elevations (influencing mean air temperature) as well as levels of precipitation (Min and Choi, 1993). This suggests that *H. orientalis* may prefer relatively lower air temperatures and higher precipitation. In general, higher net productivity can be achieved with the same amount of sunlight, even at lower air temperatures. Although photosynthesis is directly related to air temperature, respiration has a much greater effect on the net productivity of the leaf (Larcher, 1980). Likewise, the current study demonstrated that, based on the 50% growth rate, longer growth periods meant increased rates of growth.

Changes in Population Structure by Size Class

Discounting the effect of new seedling growth, the frequency for each size class was normally distributed at Namhansanseong during the seven-year study. However, during the four years at Maranggol, smaller plants had the highest frequencies, with frequencies decreasing as plant size increased. This indicates a decrease in the population at Namhansanseong, but a stable population at Maranggol. In the latter area, the mode of the distribution curve shifted annually to larger sizes, a result of increasing plant size.

Another factor that may have affected the population structure in the two areas was the difference in mean growth rates among the size classes. That is, growth rates for small classes were high, but those of the large size classes were low, with plant size even decreasing in some cases. In a marginal population, the long-term structure generally is constant, regardless of member turnover (Grant and Antonovics, 1978). The size classes had stabilized at Maranggol, despite mortality and no new input by seedlings. However, the *H. orientalis* population in the Maranggol area may eventually decrease, so this unique situation should be researched further.

Mortality

Average annual rates of mortality were 4.1% in the Namhansanseong area and 2.8% in the Maranggol area. Mortalities were irregular among the different plant sizes in the former but high in the small size classes in the latter.

When climate, growth rate, population structure, and mortality all are compared, the Namhansanseong area appears to be a less suitable environment for growth of *H. orientalis* than does the Maranggol area. For example, Namhansanseong had a higher average air temperature and less precipitation. Lower growth rates could have been related to higher, irregular patterns of mortality as well. Therefore, the population structure of *H. orientalis* at Namhansanseong, with its yearly fluctuations, can be considered a particularly unique case.

Depending on the site and the time period, even populations of the same species can vary in their survival rates, growth patterns, and production of seed (Barkham, 1980; Svensson and Callaghan, 1988; Menges, 1991; Oostermeijer et al., 1996; Damman and Cain, 1998). To precisely interpret these diverse phenomena, population dynamics must be studied long-term and at many different sites (Usher, 1979; Silvertown et al., 1996). Because only two areas were surveyed in the current study, errors may have arisen through a lack of data from these diverse study locations.

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LITERATURE CITED

Barkham JP (1980) Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). 1. Clonal growth, seed reproduction, mortality and the effects of density. J Ecol 68: 607-633

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

Brown DS (1953) Climate in relation to deciduous fruit production in California. VI. The apparent efficiencies of different temperatures for the development of apricot fruit. Proc Amer Soc Hort Sci 62: 173-183

Damman H, Cain ML (1998) Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*. J Ecol 86:13-26

Evance (1972) Quantitative Analysis of Plant Growth. Stud Ecol Vol 1. Blackwell, Oxford

Flint HL (1974) Phenology and genecology of woody plants, *In* H Lieth, ed, Phenology and Seasonality Modeling, Springer-Verlag, New York, pp 83-97

Grant MC, Antonovics J (1978) Biology of ecologically marginal populations of *Anthoxanthum odoratum*: I. Phenetics and dynamics. Evolution 32: 822-838

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

Harvell CD, Caswell H, Simpson P (1990) Density effects in a colonial monoculture: experimental studies with a marine bryozoan (*Membranipora membranacea* L.). Oecologia 82: 227-237

Hicks DJ, Chabot BF (1985) Deciduous forest, *In* BF Chabot, HA Mooney, eds, Physiological Ecology of North American Plant Communities, Chapman and Hall, New York, pp 257-277

Huenneke LF, Marks PL (1987) Stem dynamics of the shrub *Alnus incana* ssp. *rugosa*: transition matrix models. Ecology 58: 1234-1242

Hughes TP (1984) Population dynamics based on individual size rather than age: a general model with a reef coral example. Amer Natur 123: 778-795

Jackson LE, Bliss LC (1984) Phenology and water relation of three plant forms in a dry tree-line meadow. Ecology 65: 1302-1314

Kawano S (1985) Life history characteristics of temperate woodland plants in Japan, *In* J White, ed, The Population Structure of Vegetation, Dr. W Junk Publishers, Dordrecht, The Netherlands, pp 515-549

Kira T (1945) A new classification of climate in eastern Asia as the basis for agricultural geography. Hort Inst Kyoto Univ, Kyoto

Korean Meteorological Administration (1991-1997) Monthly weather report. Seoul

Larcher W (1980) Physiological Plant Ecology. 2nd ed, Springer-Verlag, New York

Law R (1983) A model for the dynamics of a plant population containing individuals classified by age and size. Ecology 64: 224-230

Lindsey AA, Newman JE (1956) Use of official weather data in springtime temperature analysis of an Indiana phenological record. Ecology 37: 812-823

Lucier AA, Hinckley TM (1982) Phenology growth and water relations of irrigated and non-irrigated black walnut. Forest Ecol Manage 4: 127-142

Manly BFJ (1990) Stage-structured Populations. Chapman and Hall, New York

Menges ES (1991) The application of minimum viable population theory to plants. *In* DA Falk, KE Holsinger, eds, Genetics and Conservation of Rare Plants, Oxford University Press, New York, pp 45-61

Min BM (2000a) Phenological characteristics of several woody plants in urban climate. J Plant Biol 23: 10-17

Min BM (2000b) Population dynamics of *Heloniopsis orientalis* C. Tanaka (Liliaceae) in natural forests - Annual life cycle. J Plant Biol 23: in press

Min BM, Choi JK (1993) A phenological study of several woody plants. Korean J Ecol **16:** 477-483

Oostermeijer JGB, Brugman ML, de Boer ER, den Nijs HCM (1996) Temporal and spatial variation in the demography of *Gentiana pneumonanathe*, a rare perennial herb. J Ecol 84:153-166

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

Silvertown J (1982) Introduction to Plant Population Ecology. Longman Group Limited, Burnt Mill

Silvertown J, Franco M, Menges E (1996) Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conser Biol 10: 591-597

Solbrig OT (1981) Studies on the population biology of the genus *Viola*. II. The effect of plant size on fitness in *Viola sororia*. Evolution 35: 1080-1093

Svensson BM, Callaghan TV (1988) Small-scale vegetation pattern related to the growth of *Lycopodium annotium* and variations in its microclimate. Vegetatio 76: 167-177

Usher MB (1979) Markovian approaches to ecological succession. J Animal Ecol 48: 413-426

Werner PA, Caswell H (1977) Population growth rates and age vs. stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). Ecology 58: 1103-1111

Yim Y-J (1987) The effects of thermal climate on flowering dates of plants in South Korea. -For the exploitation of honey and pollen resources plants- Korean J Apiculture 2: 9-28

Yim Y-J, Rim M-K, Shim J-K (1983) The thermal climate and phenology in Korea. J Plant Biol 26: 101-117