JOURNAL OF
ECOLOGY AND ENVIRONMENT
http://www.jecoenv.org

Research Paper
J. Ecol. Environ. 37(4): 155-163, 2014

The time and duration of flowering in an *Adonis multiflora* (Ranunculaceae) population

Byeong-Mee Min*

Department of Science Education, Dankook University, Yongin 448-701, Korea

Abstract

Adonis multiflora is a spring ephemeral herb growing in temperate deciduous forests. To determine the flowering properties of a natural population of *A. multiflora*, air temperature, flowering time, and flower-falling were monitored from February 2009 to May 2011. The *A. multiflora* population in this study started flowering in early March and ended it in mid-April. The average flowering duration of a flower was 14.4 days in 2009 and 19.6 days in 2011. The average duration of flower-falling was between 3.4 days and 4.2 days for three years. Cumulative flowering rate (CFR) was correlated with year day (YD), year day index (YDI), and Nuttonson's index (Tn), with correlation coefficients (CC) of over 0.9 at the 1% significance level; CC value between CFR and YD was the largest and that between CFR and YDI was the smallest. However, at the 5% significance level, CFR was closely related with Tn more than any other factors. The CCs between flowering times of two years in each plant were high and significant at 1% level. The YD value of flowering time of a flower was inversely related to its flowering duration significantly for three years. In a given plant, when more flowering started early, the flowering duration was longer. The first flower blossomed on 73.4 YD in 2010 and 78.9 YD in 2011, and remained for 16.7 days in 2009 and 27.4 days in 2011, respectively; the fifth flower developed on 92.5 YD in 2010 and 96.6 YD in 2011, and remained for 8.0 days in 2009 and 14.6 days in 2011. The YD differences between the flowering times of two flowers decreased in the order of inflorescence.

Key words: *Adonis multiflora*, air temperature, flowering duration, flowering time, Nuttonson's index, spring ephemeral, year day index

INTRODUCTION

In the deciduous temperate forests of North America, spring ephemerals represent a common component of the herb layer (Schemske et al. 1978, Motten 1986, Lubbers and Lechowicz 1989, Kudo and Maeda 1998). For the spring ephemeral plants, the period of active growth corresponds with high light period, water, and nutrient availability between snow melt and canopy closure in the understory of the deciduous forests in eastern North America (McKenna and Houle 2000). The life of spring ephemerals is characterized by early appearance soon after snowmelt, prompt flowering, and short growing season within the high-irradiance period before canopy closure (Lapointe 2001). However, most spring ephemerals are potentially long-lived herbaceous perennials and the total biomass increases with increasing light intensity (Struik 1965, Tamm 1972, McKenna and Houle 2000, Rothstein and Zak 2001, Whigham 2004, Horibata et al. 2007). They exhibit a typical 'sun-plant' photosynthetic property with high light-saturated rate of photosynthesis and light compensation points (Rothstein and Zak 2001).

http://dx.doi.org/10.5141/ecoenv.2014.019

Received 05 January 2014, **Accepted** 21 August 2014

***Corresponding Author**
E-mail: bmeemin@hanmail.net
Tel: +82-31-8005-3843

pISSN: 2287-8327 eISSN: 2288-1220

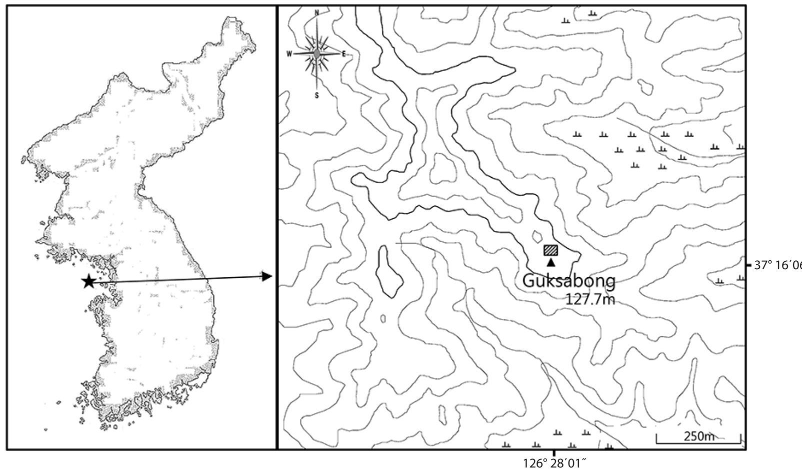

Fig. 1. Map showing the study area. The left map indicates locus of the study area in Korea, and the right map shows the sampling site (▨) in the study area.

Previous studies of the spring ephemerals were focused on energy budget, flowering strategy, and adaptation to low air temperature. The flowering strategy is composed of time and duration of flowering. These parameters can be assessed on four ecological levels: a flower, a plant, a population, and a species. However, much data on the ephemeral plant are required on all levels to understand its strategy comprehensively. Flowering time is important to pollinator limitation, herbivore's activity, and survival in abrupt low temperatures. If a plant flowers in the early spring time, more pollinators can visit and more seeds can be produced by long fruiting period. However, the low air temperatures in early spring slow down the metabolism, restrict cell division and elongation, and thus reduce the growth rate of the plant (Ting 1982). Moreover, cool and unsettled weather conditions in early spring may reduce pollinator availability and cause deterioration in seed-set due to the pollen restriction (Helenurm and Barrett 1987, Nishikawa and Kudo 1995). It was shown that hand pollination produced more seeds than natural one (Schemske et al. 1978). Fortunately, *Anonis ramosa* and *Anemone flaccid* are pollinated by flies and their activity is not affected by low temperature (Kudo et al. 2004). In some spring woodland herbs, the annual differences in flowering times were associated with differences in average temperatures, but cumulative degree-hours or air and soil temperatures were not well correlated with flowering times (Schemske et al. 1978). However, the timing of flowering in plants is temperature-sensitive (Min 2005, Kudo and Hirao 2006).

Flowering duration was responsive to pollinator activity, intensity of competition for pollinator acquisition, and climatic condition (Zimmerman 1988, Helenurm and Barrett 1987). In other words, long flowering duration is beneficial for pollination, but disadvantageous for feeding by herbivorous animal. Moreover, short fruiting periods result in the production of fewer seeds compared to longer fruiting periods. However, strategy for the flowering duration in spring ephemerals is diverse within the plant's microhabitat in a population (Horibata et al. 2007) as a result of their very short life cycle of 40 to 60 days (Lapointe 2001).The spring ephemerals were rich in Korea (Cho 1998). One of the spring ephemerals, *Adonis* L. (Rannunculaceae) that is composed of 30 species is an annual or perennial herb, and grows in temperate region of Europe and Asia (Lee et al. 2003). There is no honey gland in perianth and it is pollinated by the fly (Lee et al. 2003, Kudo et al. 2004). In Korea, *A. amurensis*, *A. pseudoamurensis* and *A. multiflora* are found (Lee et al. 2003). *Adonis multiflora* has several branches and 2 to 6 flowers per plant, and its sepals are longer than petals (Lee et al. 2003). It is typical spring ephemeral, and has a short growing period of a year and several flowers in a plant. Moreover, flowering time of this species is earlier in spring than that of other species. Therefore, this species has several advantages in ecological study. The factors affecting flowering time in several spring ephemerals were studied in Korea (Cho 1998, Min 2003, Lyang and Lee 2010). However, the phenological reports for this species were rare in Korea.

The aim of this study was to examine the factors that influence flowering time in a natural *A. multiflora* population. Specifically, the importance of year day, year day index, and Nuttonson's index for the flowering time of *A. multiflora* were examined.

MATERIALS AND METHODS

The location of the study area was at Nae-ri, Yeongheung-myen, Ongjin-gun, Incheon-city (37°16′14.8″ N, 126°27′49.9″ E) (Fig. 1). The altitude of this study site was 120.7 m above sea level (a. s. l.), with 15° slope and 30° in direction. Vegetation was composed of three layers: tree layer, shrub layer, and herb layer. The tree layer was composed of *Quercus mongolica*, *Q. serrata*, *Platycarya strobilacea*, *Cornus controversa*, and *Betula davurica* and had 90% coverage; *Stephanandra incisa*, *Orixa japonica*, *Rhus trichocarpa*, and *Deutzia parviflora* were in the shrub layer with 30% coverage; *Cardamine leucantha*, *Hepatica asiatica*, *Corydalis turtschaninovii*, *Ainsliaea acerifolia*, *Disporum smilacinum*, *Smilacina japonica*, and *Syneilesis palmate* were in the herb layer with 20% coverage. Litter layer was 10 cm deep and A layer of soil was 40 cm deep. However, rocks or root systems protruded above soil surface and the depth of the two layers was diverse along the microsites.

The permanent quadrat (50 m × 5 m) was located. By using numbered formax bars, 100 plants were individually marked on March 1, 2009. Formax rods were set in the soil near the each plant. Thirty five plants in the quadrat were additionally numbered on February 26, 2010. Reproductive organ of *A. multiflora* was photographed two times a week during the main growth season from February to May in 2009 through 2011. Phenological stages of reproductive organ were analyzed by comparing their photographs and divided into two groups—flowering and flower-falling—based on the criteria described in Table 1: flowering time was when petals opened and when stamens were observed; deflowering time was when petals' color was changed from yellow to dim yellow or white or when a petal fell.

To measure the microclimate, automatic TRIX-8 thermometer (LogTag Recorders, Auckland, New Zealand) was set up at 4 m height from the soil surface on January 1 and collected on May 30 each year from 2009 to 2011. This thermometer was set up to measure air temperature by 0.1°C in a two-hour interval. Daily mean air temperature, daily lowest air temperature, year day index (YDI), and Nuttonson's index (Tn) were calculated from the field data. Tn was calculated by 4°C instead of 5°C (Yim et al. 1983, Min et al. 2007). YDI was the cumulative temperature over 0°C and Tn over 5°C in daily mean air temperature. Year day (YD) refers to the Julian calendar. The fact that was highly correlated with the YD meant nothing to do with daily mean air temperature. Correlation coefficients between phenological events and factors related to temperature were calculated by $y = ax + b$.

RESULTS AND DISCUSSION

Air temperature

In 2009, the daily lowest air temperature (LT) was maintained below 0°C until March 15 (YD 74), except for February 24 (YD 55); LT was also below 0°C from March 24 (YD 83) to March 28 (YD 87). In 2010 and 2011, LT fluctuated above and below 0°C from February 15 (YD 46) to March 28, and thereafter maintained above 0°C. The lowest air temperature was -6.3°C. Thus, plants experienced a sub-zero air temperature in March of each year (Fig. 2a).

In 2009, daily mean air temperature (MT) was maintained above 0°C from February 22 (YD 53) and temporarily above 10°C on March 17 (YD 76); thereafter, MT was maintained below 10°C from March 22 (YD 81) to April 6 (YD 96) (Fig. 2b). In 2010, MT was maintained above 0°C from February 18 (YD 49), except for March 10 (YD 69). In 2011, MT was maintained above 0°C from February 17 (YD 48), except for March 3 (YD 62). The plant growth might have been retarded in mid-March in 2010 as following section.

The values of year day index (YDI, °C·day) were 50 on March 12 (YD 71), 100 on March 20 and 150 on March 29 (YD 88) in 2009. On February 27 (YD 50), March 14 (YD 73), and March 27 (YD 86) in 2010, YDI (°C·day) reached 50, 100, and 150, respectively; and the same pattern re-

Table 1. Phenological stages of sexual organ of *Adonis multiflora*

Stage or Duration	Description
First flowering time (FFT)	When stamen is observed (year day, YD)
First flower-falling time (FFF)	When petal's color is changed or only one petal is fallen (year day, YD)
Flowering duration	Difference between FFT and FFL (day)
Last flower-falling time (LFF)	When there is no petal in blossom (year day, YD)
Flower-falling duration	Difference between FFF and LFF (day)

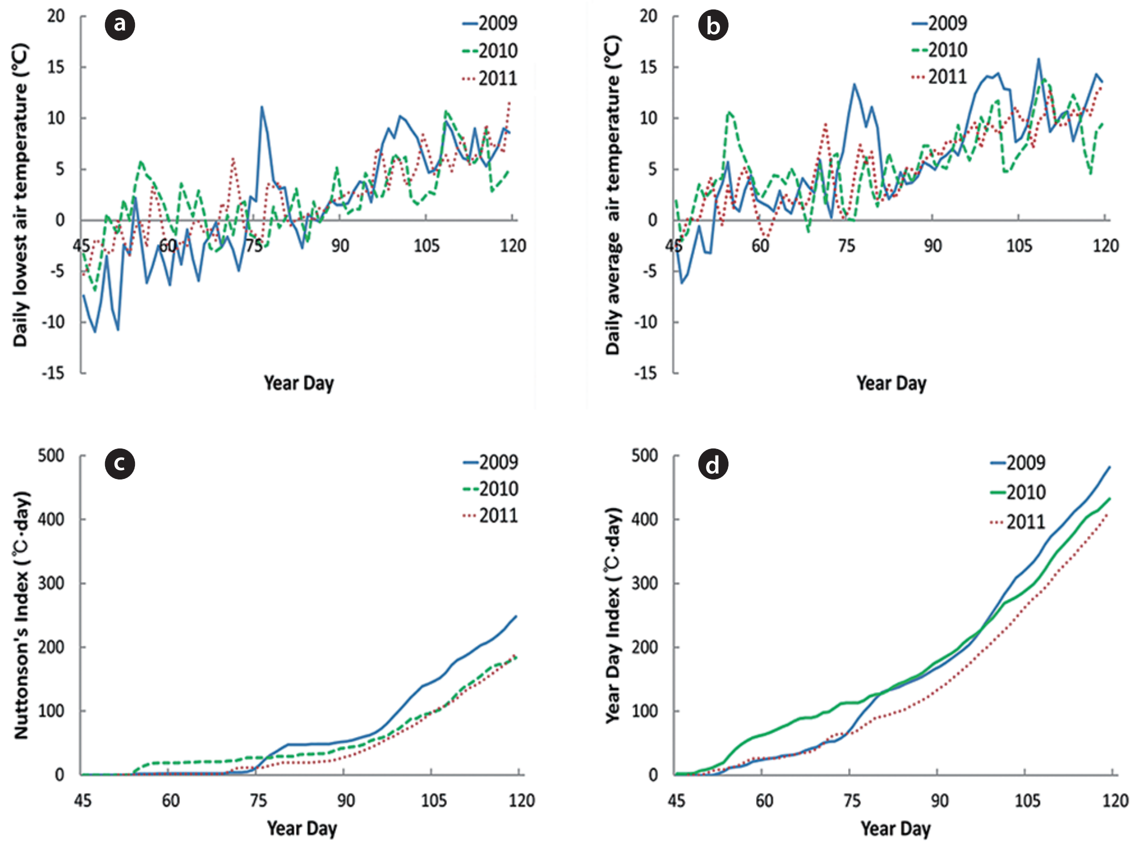

Fig. 2. Minimum (a) and daily mean (b) air temperature, year day index (YDI) (c), and Nuttonson's index (Tn) (d) from February 15 to April 15 in each year of 2009-2011 at the study site.

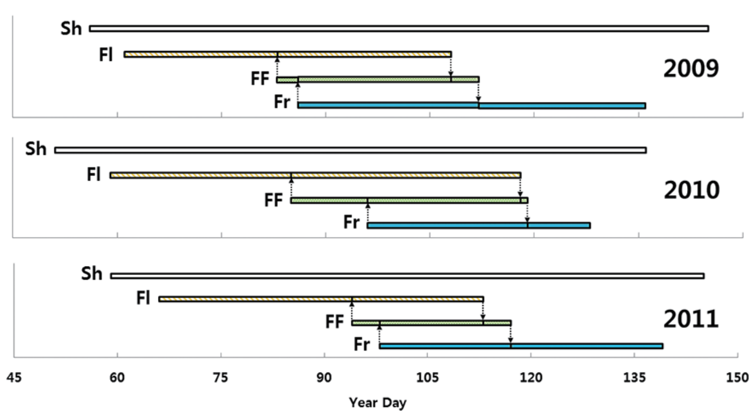

Fig. 3. Life cycle of an *Adonis multiflora* population during growing season in 2009-2011. Sh, shoot duration; Fl, flowering duration; FF, flower falling duration; Fr, fruiting duration.

peated on March 13, March 26, and April 3 in 2011. Thus, cumulative temperature-day of early-March was the highest in 2010. However, the date that YDI reached 150°C·day was similar for all three years.

Nuttonson's index (Tn, °C·day) reached 30 on March 19 (YD 78), 50 on March 30 (YD 89), and 100 on April 10 (YD 100) in 2009. The dates that Tn (°C·day) reached 30, 50, and 100 in 2010 were March 24 (YD 55), April 5 (YD 95), and April 16 (YD 106), and the same pattern repeated on April 2 (YD 92), April 7 (YD 97), and April 17 (YD 107), in 2011. Thus, Tn in March increased faster in 2009 than in 2010 or 2011.

Life cycle of *adonis multiflora* during growth season

A shoot of *A. multiflora* was observed on the soil surface on February 15 in 2009, on February 20 in 2010, and on February 19 in 2011 (Fig. 3). The color of the leaves turned yellow in late-May. Thus, the period of life-cycle was 75 to 85 days. Other spring ephemerals were reported to have the life-cycle of 40 to 60 days (Lapointe 2001). From my results, *A. multiflora*'s life cycle was longer than other ephemerals. The first flower was observed on March 2 in 2009, on February 28 in 2010, and on March 7 in 2011. The last flower-falling started on April 18 in 2009, on April 28 in 2010, and on April 23 in 2011. Thus, the maximum period of flowering in a population was 47 days in 2009, 58 days in 2010, and 47 days in 2011. The last flower-falling completed on April 22 in 2009, on April 29 in 2010, and on April 27 in 2011. In total, the flowering periods were over half of the total growing season each year. Moreover, in regard to the fruiting period, *A. multiflora* had mostly reproductive organs during the life cycle each year. The reproductive period and whole growing season of spring ephemerals are largely overlapping (Lubbers and Lechowicz 1989, McKenna and Houle 2000). That implies that spring ephemerals growing under deciduous forests have characteristic life cycles of emerging and blooming in early spring, setting fruits within a short time period, and with above-ground parts usually dying before or soon after canopy closure (Schemske et al. 1978).

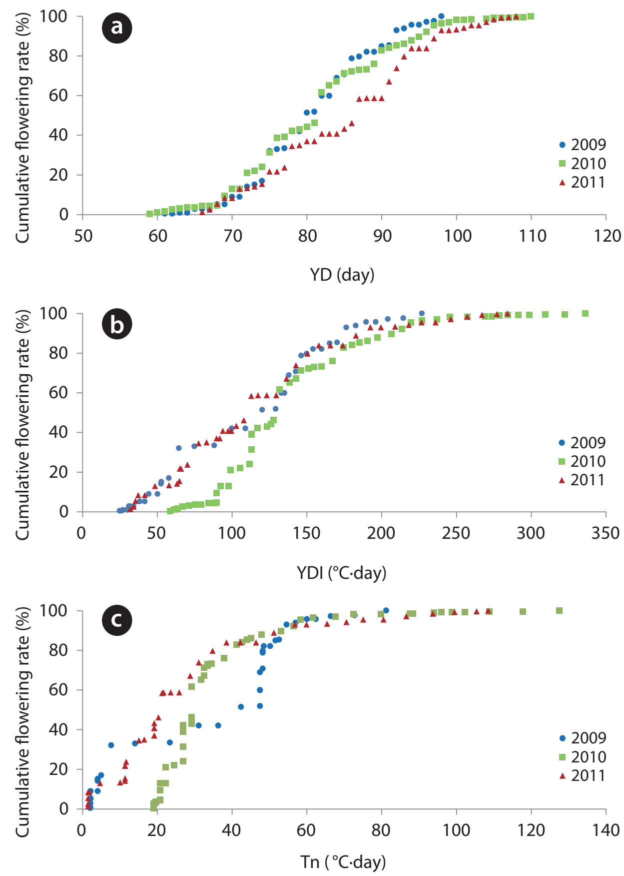

Fig. 4. Relationship between cumulative flowering rate and three parameters: (a) year day (YD), (b) year day index (YDI), and (c) Nuttonson's index (Tn).

Flowering and daily mean air temperature

The YD at which cumulative flowering rate (CFR) reached 25% was 75 in 2009, 75 in 2010, and 79 in 2011; therefore, the difference between the three years was maximum of 3 days (Table 2). YDI (°C·day) and Tn (°C·day) at which CFR reached 25% were from 64.1 to 113.1 and from 7.7 to 27.0, respectively, and the difference between the three years was larger than that of YD. However, YD, YDI, and Tn at which CFR reached 50% during the three years were 80 to 87 of YD, 112.9 to 131.7 of YDI (°C·day), and 21.3 to 42.4 of Tn (°C·day). Thus, the differences between the three years increased in YD and decreased in YDI, and all three years were similar in Tn. YD, YDI, and Tn at which CFR reached 75% during the three years were 86-93 of YD, 146.2 to 167.3 of YDI (°C·day), and 34.8 to 48.2 of Tn (°C·day). Thus, the difference between the three years decreased in Tn only. On the other hand, CFR rates were closely related with YD, YDI, and Tn (Fig. 4) and their correlation coefficients were mostly over 0.9 and significant at 1% level (Table 3). However, their regression curves were sigmoid rather than linear, meaning that anyone of the three factors couldn't be the most important for *A. multiflora* to bloom. Moreover, the plant could abruptly face low air temperature during growing

Table 2. Date, YDI, and Tn at the flowering rate of 25%, 50%, and 75%

Flowering rate (%)	Year	Date*	YDI (°C·day)	Tn (°C·day)
25	2009	03/16	64.1	7.7
	2010	03/16	113.1	27.0
	2011	03/19	77.6	15.1
50	2009	03/21	120.1	42.4
	2010	03/23	131.7	29.2
	2011	03/28	112.9	21.3
75	2009	03/27	146.2	48.2
	2010	03/30	167.3	37.9
	2011	04/03	150.4	34.8

*Date is described as month/day.

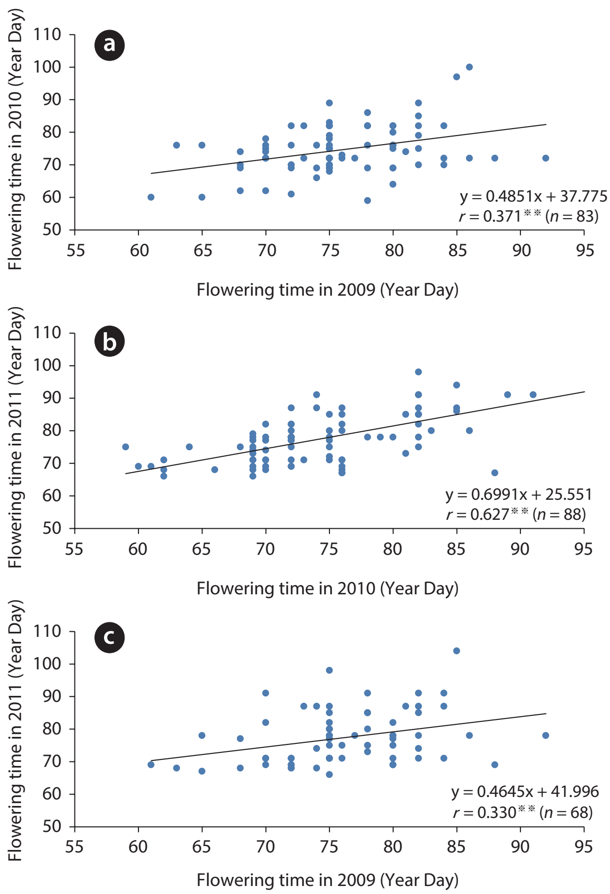

Fig. 5. Relationship of flowering times between the two years in 2009-2011; (a) 2009 and 2010, (b) 2010 and 2011, and (c) 2009 and 2011. *n* is the number of plants that flowered in two years; ** represents significance at an 1% significant level .

Table 3. Correlation coefficients between cumulative flowering rate and YD, YDI, and Tn (*n* = dates from the first flowering time to the last one)

Year	Index		
	YD	YDI	Tn
2009 (*n* = 41)	0.9784*	0.9745*	0.9903*
2010 (*n* = 52)	0.9731*	0.8060*	0.9186*
2011 (*n* = 50)	0.9855*	0.9056*	0.9682*

*significant at 1% level.

season. As described above, the lowest air temperature in March was -6.3°C. At this air temperature, *A. multiflora*'s flower doesn't freeze, but the growth of plants is might be severely retarded. After considering all the temperature factors, CFR might be related to YD in early season, YDI in mid-season, and Tn in the late season. In some spring woodland herbs, annual differences in flowering times were associated with differences in average temperatures, but cumulative degree-hours or air and soil temperatures were not well correlated with flowering times (Schemske et al. 1978). However, many studies revealed that the relationship between flowering time and cumulative temperature was correlated (Rathcke and Lacey 1985, Kudo 1995, Diekmann 1996). Thus, *A. multiflora*'s flowering might be influenced by YDI and Tn, as well as daily mean air temperature. Moreover, increased YD influenced on flowering time, and this might be related to a rise in soil temperature. However, the daily mean air temperature fluctuated extremely, so that it might be impossible to predict flowering time by this temperature datum only. Furthermore, other environmental factors affecting flowering are soil moisture, day length and plant water potential (Flint 1974, Bernier 1988, Wright 1991).

Based on the appearance of the first flower, the relative flowering time of each plant in a population was roughly constant for three years (Fig. 5). The correlation coefficients between two years were 0.371 (in 2009-2010, *n* = 83), 0.330 (in 2009-2011, *n* = 88) and 0.627 (in 2010-2011, *n* = 88). These values were significant at 1% level. Based on these results, the flowering time of the plant appears to be fixed. This phenomenon might be based on the genetic properties, the microhabitat, and the depth of root system of the plants. However, considering the soil temperature, the latest seems to be the most correlated among the three factors, although microhabitat and root systems' depth are intertwined and cannot be critically separated. In general, the more a root system is distributed at the soil surface, the more easily the plant is affected by air temperature. To interpret this fact correctly will need more studies.

Table 4. Average duration (days) or time (YD) of flowering and flower-falling

Year	Flowering time	Beginning time of flower-falling	Finishing time of flower-falling	Flowering Duration	Flower-falling duration
2009	81.1 ± 8.1	95.3 ± 4.7	98.6 ± 4.3	14.4 ± 4.3	3.4 ± 1.2
2010	81.4 ± 9.7	100.4 ± 5.2*	104.6 ± 4.4*	18.9 ± 5.8*	4.2 ± 2.0*‡
2011	86.2 ± 12.5*‡	105.5 ± 4.7*‡	108.9 ± 4.0*‡	19.6 ± 7.4*	3.5 ± 1.0

*1% significant level (between 2009 and 2010 or between 2009 and 2011); ‡1% significant level (between 2010 and 2011); YD is year day (or the Julian calendar).

Flowering time and other properties

Flowering start times (mean ± SD) were 81.1 ± 8.1 YD in 2009, 81.4 ± 9.7 YD in 2010, and 86.2 ± 12.5 YD in 2011 (Table 4). Flowering duration was 14.4 ± 5.8 days in 2010 and 19.6 ± 7.4 days in 2011. Flower-falling duration was 3.4 ± 1.2 days in 2009, 4.2 ± 2.0 days in 2010, and 3.5 ± 1.0 days in 2011. Thus, flowering start time in 2010 was similar to that in 2009. However, flowering duration in 2010 was similar to that in 2011. Consequently, flowering started in early season and was maintained for a relatively long time in 2010. Thus, there was no relationship between the time and the duration of flowering at the population level. Flower-falling durations were similar in the three years. Moreover, the flowering duration was noticeably longer than the flower-falling duration in the three years. It is likely that the long flowering durations in 2010 and 2011 resulted from low air temperatures of mid-March. At the same time, Tn in 2010 and 2011 was lower than that in 2009.

On the other hand, correlation coefficients between time and duration of flowering were below -0.8 and significant at 1% level (Fig. 6). Based on this result, the flowering duration was reversely related to flowering time at a flower level, meaning that the blossoms in early March could be maintained for long time periods. However, when air temperature was low (sub-zero) in mid-March, the flowers were maintained in blossom for a long time. Thus, as the flowering time and duration were considered, the latter does not appear to be related to the former but simply influenced by air temperature. Generally, the timing of flowering in plants is temperature-sensitive (Kudo and Hirao 2006). The life cycle of spring ephemerals inhabiting the deciduous forests is most sensitive to spring climatic conditions in which air temperature and snowmelt timing are major determinants of flowering initiation (Diekmann 1996, Lapointe 2001, Min et al. 2007). To this date, many studies investigated the relationship between the flowering time and air temperature. However, very few looked at the interrelation between flowering duration and air temperature. Hypothetically, low temperatures slow down the metabolism, restrict cell division and elongation, and thus reduce the growth rate of a plant (Ting 1982). Based on this, flower's metabolism might be slowed down by low air temperature.

In this study, *A. multiflora* produced a maximum of seven flowers per plant. When all flowers in a plant were numbered according to blooming order, flowering properties (e.g., the time and duration of flowering) were closely related to inflorescence (i.e., flower order) (Fig. 7).

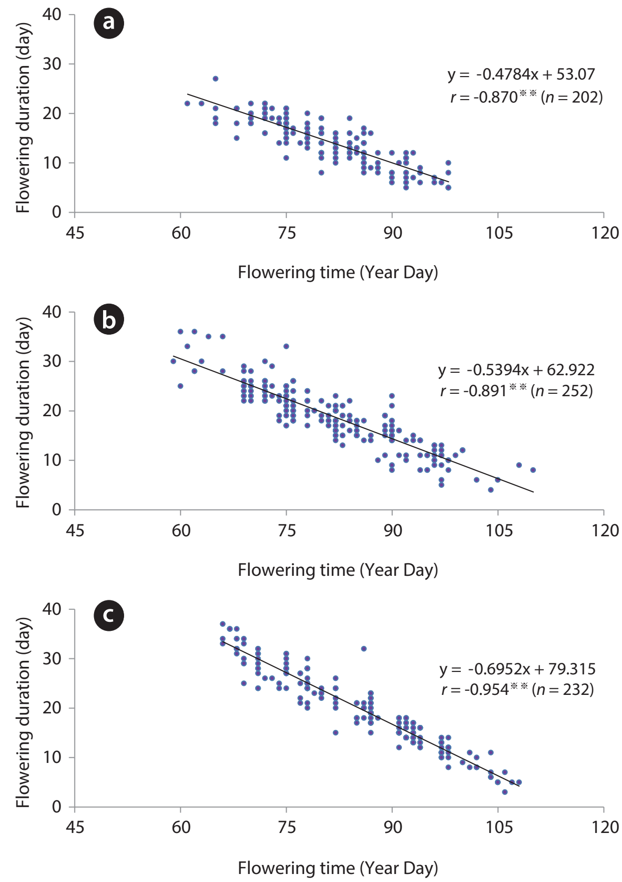

Fig. 6. Relationship between the time (YD) and the duration (day) of flowering in each year; (a) 2009, (b) 2010, and (c) 2011. *n*= number of flowering plants.

The petals opened on 75.07-78.87 YD in the first flower, 82.04-85.96 YD in the second one, 86.92-92.24 YD in the third one, 89.50-95.59 YD in the fourth one, and 92.50-96.57 YD in the fifth one. The differences in flowering time between two successive flowers in the first through third one were significant at 1% level. However, the differences of flowering time between two successive flowers in the third through fifth one were small and not significant. The intervals of flowering time along the inflorescence were shortened step by step. On the other hand, the flowering durations along the inflorescence were 16.68-27.40 days in the first flower, 13.70-19.78 days in the second one, 12.08-15.57 days in the third one, 10.80-14.44 days in the fourth one, and 8.00-14.57 days in the fifth one. Thus, flowering durations were shortened along the inflorescence in all three years. The differences of flowering duration between the first and third flower were significant at 1% level, but the differences between the third and fifth one were not significant. However, the flowers in the same

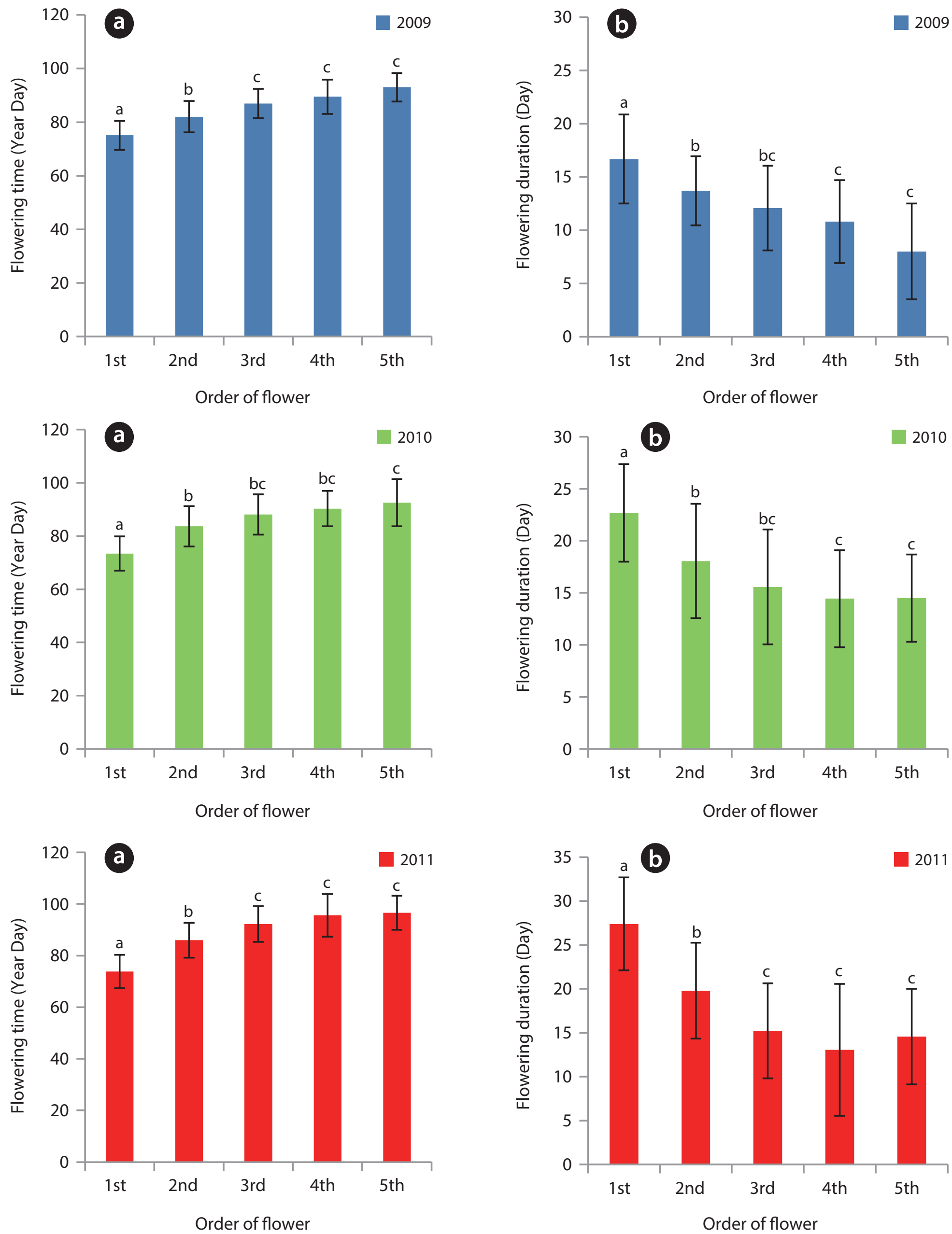

Fig. 7. The duration (day) and the time (YD) of flowering along the inflorescence in a plant; (a) relation between the order of inflorescence and flowering time and (b) relation between the order of inflorescence and flowering duration. Bars indicate the standard deviation and same letters are not significant at 5% level.

order were obviously different in flowering duration year by year. For example, the flowering duration difference of the first flower between 2009 and 2011 was over 10 days.

In summary, my results indicated that the earlier the flower of *A. multiflora* bloomed, the longer its flowering duration was. In addition, we showed that the blossoming state was prolonged to a higher extend in low air temperature than in higher temperatures.

LITERATURE CITED

Bernier G. 1988. The control of floral evocation and morphogenesis. Ann Rev Plant Physiol Plant Mol Biol 39: 175-219.

Cho DS. 1998. A study on the growth and senescence of spring ephemerals. J Nat Sci 19: 199-210.

Diekmann M. 1996. Relationship between flowering phenology of perennial herbs and meteorological data in deciduous forests of Sweden. Can J Bot 74: 528-537.

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

Helenurm K, Barrett SCH. 1987. The reproductive biology of boreal forest herbs. II. Phenology of flowering and fruiting. Can J Bot 65: 2047-2056.

Horibata S, Hasegawa SF, Kudo G. 2007. Cost of reproduction in a spring ephemeral species, *Adonis ramosa* (Ranunculaceae): carbon budget for seed production. Ann Bot 100: 565-571.

Kudo G. 1995. Ecological significance of flower heliotropism in the spring ephemeral *Adonis ramosa* (Ranunculaceae). Oikos 72: 14-20.

Kudo G, Hirao AS. 2006. Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. Popul Ecol 48: 49-58.

Kudo G, Maeda T. 1998. Size-dependent variation of phenotypic gender and functional gender of a spring-ephemeral, *Anemone debill's* Fisch. Plant Species Biol 13: 69-76.

Kudo G, Nishikawa Y, Kasagi T, Kosuge S. 2004. Does seed production of spring ephemerals decrease when spring comes early? Ecol Res 19: 255-259.

Lapointe L. 2001. How phenology influences physiology in deciduous forest spring ephemerals. Physiol Plant 113: 151-157.

Lee JH, Lee ST, Seo YB, Yeo SH, Lee NS. 2003. A morphological reexamination on the genus *Adonis* L. *sensulato* (Ranunculaceae) in Korea. Kor J Plant Tax 33: 435-454.

Lubbers AE, Lechowicz MJ. 1989. Effects of leaf removal on reproduction vs. below-ground storage in *Trillium grandiflorum*. Ecology 70: 85-96.

Lyang DY, Lee KS. 2010. Responses of an herbaceous community to wild boar (*Susscrofacoreanus*Heude) disturbance in a *Quercusmongolica* forest at Mt. Jeombong, Korea. J Ecol Field Biol 33: 205-216.

McKenna MF, Houle G. 2000. Why are annual plants rarely spring ephemerals? New Phytol 148: 295-302.

Min BM. 2003. Seed production of Pes-gallinaceua (*Corydalis*, Fumariaceae) group. Korean J Ecol 26: 189-197.

Min BM. 2005. Ecological characteristics of a *Suaeda japonica* population and the effects of early-season air temperatures on population formation. J Plant Biol 48: 411-421.

Min BM, Yi DH, Jeong SJ. 2007. Relationship between phenonogical stages and cumulative air temperature in spring time at Namsan. J Ecol Field Biol 30: 143-149.

Motten AF. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. Ecol Monogr 56: 21-42.

Nishikawa Y, Kudo G. 1995. Relationship between flower number and reproductive success of a spring ephemeral herb, *Anemone flaccida* (Ranunculaceae). Plant Species Biol 10: 111-118.

Rathcke B, Lacey EP. 1985. Phenological patterns of terrestrial plants. Ann Rev Ecol Syst 16: 179-214.

Rothstein DE, Zak DR. 2001. Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. Funct Ecol 15: 722-731.

Schemske DW, Willson MF, Melampy MN, Miller LJ, Verner L, Schemske KM, Best LB. 1978. Flowering ecology of some spring woodland herbs. Ecology 59: 351-366.

Struik GJ. 1965. Growth patterns of some native annual and perennial herbs in southern Wisconsin. Ecology 46: 401-420.

Tamm CO. 1972. Survival and flowering of some perennial herbs. II. The behaviour of some orchids on permanent plots. Oikos 23: 23-28.

Ting IP. 1982. Plant Physiology. Addison-Wesley Publishing Company, Reading, MA.

Whigham DF. 2004. Ecology of woodland herbs in temperate deciduous forests. Ann Rev Ecol Evol Syst 35: 583-621.

Wright SJ. 1991. Seasonal drought and the phenology of understory shrubs in a tropical moist forest. Ecology 72: 1643-1657.

Yim YJ, Rim MK, Shim JK. 1983. The thermal climate and phenology in Korea. Korean J Bot 26: 101-117.

Zimmerman M. 1988. Nectar production, flowering phenology, and strategies for pollination. In: Plant Reproductive Ecology (Doust JL, Doust LL, eds). Oxford University Press, New York, NY, pp 157-178.