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# Flowering Patterns among Angiosperm Species in Korea: Diversity and Constraints

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**Because of the complexities of their flowering parameters, it is difficult to make generalizations about flowering phenology among temperate angiosperms. We examined patterns of flowering time and duration among 2867 Korean angiosperm species, and these patterns were associated with climatic factors. The effect of taxonomic membership was also tested. Overall data pooled over species from 165 families showed that 63.8% of these angiosperms flowered in summer, 19.5% in spring, 16.5% in autumn, and 0.2% in winter. Summer and autumn flowering periods were significantly longer than springtime events. Both mean monthly temperature and precipitation were strongly positively correlated with the number of species in flower, but not with flowering duration. The seven largest families differed in their flowering season and duration; both parameters were also segregated among genera within large families. In a two-way analysis, both flowering season and family membership exerted significant effects on flowering duration. These results demonstrate that the evolutionary influence on flowering time and duration can be observed at the community level when two factors are considered, i.e., the interaction of flowering parameters and the taxonomic composition of species within those communities.**

*Keywords:* flowering duration, flowering time, Korean angiosperms, taxonomic membership

Temperate and Mediterranean regions demonstrate drastic changes in the number of plants flowering across seasons, which is generally in accordance with strong seasonal changes in temperature and/or precipitation (Jackson, 1966; Johnson, 1992; Smith-Ramirez and Armesto, 1994). In many temperate regions with four distinct seasons, plants are more likely to flower in the summer or between spring and summer. For example, in Portugal and Italy the number of flowering species is at a maximum in June; for Greenland, Denmark, Switzerland, and Florida, July is the peak month (Lee, 1970). However, flowering activity is often bimodal in those temperate areas, with two peaks in the spring (Apr - May) and the autumn (Sep - Aug), and a low point in July (Jackson, 1966; Kochmer and Handel, 1986; Rathcke, 1988; Abe and Kamo, 2003). Thus, it is difficult to make generalizations regarding the pattern of flowering time even in regions with similar climatic conditions.

Although not examined as extensively, duration is another component that defines flowering phenology, with several hypotheses to explain its variations while assuming that it is independent of flowering time (Bawa, 1983; de Jong et al., 1992). However, in diverse climatic regions, duration varies with time. For example, in both wet and dry tropical forests, species that flower in the dry season do so only briefly compared with those that flower in the wet season (Stiles, 1978; Bawa et al., 2003). Similarly, the flowering period during hot, dry seasons is shorter than in rather cool, wet seasons in the temperate and Mediterranean regions (Johnson, 1992; Smith-Ramirez and Armesto, 1994). Likewise, flowering in the spring is brief among flora in the temperate areas of the Northern Hemisphere (Schemske et al., 1978; Kochmer and Handel, 1986). Therefore, because quantitative information on the seasonality of flowering duration among temperate flora is rare, it is necessary to examine these phenomena in diverse regions.

Related species exhibit the same or similar life histories through a common descent (Harvey et al., 1995; Westoby et al., 1995). Various methodologies have recently been employed to test the effects of phylogeny on flowering parameters (Kochmer and Handel, 1986; Peat and Fitter, 1994; Wright and Calderon, 1995; Bawa et al., 2003), in contrast to earlier studies that did not consider those influences (Lee, 1969, 1970; Pojar, 1974; Heinrich, 1976). Most of these recent studies revealed strong phylogenetic effects on flowering parameters, with the assumption that taxonomic membership reflects phylogeny at least to some extent. For example, flowering time is quite concordant within taxonomic groups, e.g., gen-

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era (Johnson, 1992), families (Kochmer and Handel, 1986), or groups at higher taxonomic levels (Wright and Calderon, 1995). Studies of flowering duration are quite limited and provide conflicting results: either describing (Petanidou et al., 1995) or failing to identify the effect of phylogeny (Smith-Ramirez and Armesto, 1994). Therefore, if flowering parameters are correlated with each other and phylogeny constrains their variations, selective factors affecting variation in flowering time should be examined only after considering the potential effects of phylogeny and duration, or vice versa.

Here, we examined the pattern of flowering among angiosperms of Korea. The Korean peninsula covers 222,209 km$^2$ (33° 07′ N - 43° 0′ N, 124° 11′ E - 131° 53′ E), and is characterized by strong seasonality in its precipitation and temperatures. This country is also known for its relatively high number of species, e.g., >3600 angiosperms (MOE, 2003). So far, only a couple of descriptive studies have been conducted that regard their flowering time but do not consider the taxonomic skewness of species or flowering duration (Lee, 1969, 1970; Yim, 1986). Therefore, our objectives in this study were to determine: 1) the overall pattern of flowering among Korean angiosperms, 2) the relationship between flowering time and duration, and 3) the extent to which taxonomic membership affects variations in flowering.

## MATERIALS AND METHODS

### Data Sets

Data on flowering parameters were collected primarily from a recent monograph treating 3037 Korean angiosperm species (Lee, 1998) since this monograph provided detailed information on flowering parameters for most of the species. This information was supplemented, if any, from two other monographs (Lee, 1985; Oh, 2000) about species for which phenology data were lacking from our primary source. Thus, the final data set included 2867 angiosperms. Following Kochmer and Handel (1986), we selected a midpoint between the starting and ending months of flowering as the presumptive peak flowering month for each species. For example, for a species flowering from April to June, May represented a midpoint of flowering: for a species flowering from April to May, May was also treated as a midpoint of flowering. The four flowering seasons were defined as: spring (Mar - May), summer (Jun - Aug), autumn (Sep - Nov), and winter (Dec - Feb). Thus, flowering time was described by two variables, i.e., flowering month and flowering season.

Because only a few species bloom in the winter, in most analyses they were combined with those showing activity in the autumn. Duration was estimated as the total number of months spent in flowering; frequency was not a factor here because Korean angiosperms, like other temperate plants, by and large flower only once per year.

Information on taxonomic membership of species - genus and family - was obtained from Lee (1998), resulting in a data set of 165 families and 902 genera. Species were not evenly distributed among taxonomic groups, with, for example, some families comprising a large number of species and genera, such as the 275 species in 76 genera of Asteraceae, 232 species / 90 genera in Poaceae, 133 species / 39 genera in Fabaceae, and 113 species / 32 genera in Liliaceae. In contrast, about 70 families, including Symplocaceae and Sabiaceae, contained only a single genus, and 33 families, such as Capparidaceae and Zygophyllaceae, consisted of just one species.

The mean annual precipitation and temperature were obtained from 30 years of compiled data (1970 - 2000) from 26 weather stations each in North and South Korea

(http://www.kma.go.kr/weather/climate/normal/nor_year.jsp, http://www.kma.go.kr/weather/climate/climate_pok.jsp). Mean annual precipitation is 1126 mm, with 50 to 60% of the rain falling in summer (Fig. 1). Because the mean temperature ranges from –5°C (Jan) to 26°C (Aug), the frost-free period is about 180 d in the central region. Overall, oaks and pines are the two dominant forest species, but toward the north, transitions occur from broadleaf evergreen and deciduous trees to those bearing needles.

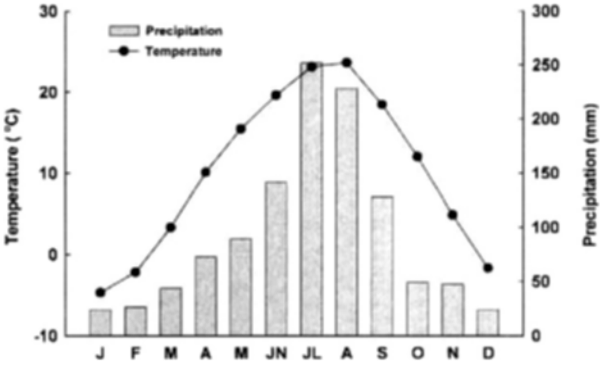

**Figure 1.** Monthly mean temperature and precipitation in Korea.

## Data Analysis

We first analyzed the pattern of flowering time and duration using data including 2867 angiosperms. The pattern of flowering month was descriptively presented, while flowering season was used as a variable representing flowering time in all ANOVAs and categorical analyses. The relationship between flowering time and duration was examined with a one-way ANOVA with flowering season as an independent variable and duration as a dependent variable. Spearmen rank correlations were employed to test the association of climate factors (mean monthly temperature and precipitation) with the number of species reaching their flowering peak in each month as well as with their mean flowering duration.

We also analyzed the effects of family membership on flowering time and duration for > 100 species in each of the seven largest families, i.e., Asteraceae, Cyperaceae, Fabaceae, Poaceae, Liliaceae, Ranunculaceae, and Rosaceae. The 1095 species in those families represented 38.2% of all Korean angiosperms examined. In addition, the association between genus and flowering season was examined separately, using the nine largest genera each within Rosaceae and Asteraceae. Aster species that flower in spring or rosaceous species that bloom in autumn are rare; only two categories - summer and autumn (Asteraceae) and spring and summer (Rosaceae) - were included in the analyses. Data on the nine largest genera in Asteraceae, Poaceae, and Rosaceae were used to simultaneously separate the effects of family and genus on flowering duration. Two-way contingency table analyses were employed to test the association between categorical variables such as flowering season and family membership. The relationship between flowering season, duration, and family membership was assessed via two-way ANOVAs with flowering duration as a dependant variable and both flowering season and family membership as independent variables. Because information was lacking for flowering parameters in some species, the sample size was reduced slightly in those analyses. Flowering duration was log-transformed to improve normality. All means were provided with 1 SD, and all analyses were conducted with SAS 8.1 (1999).

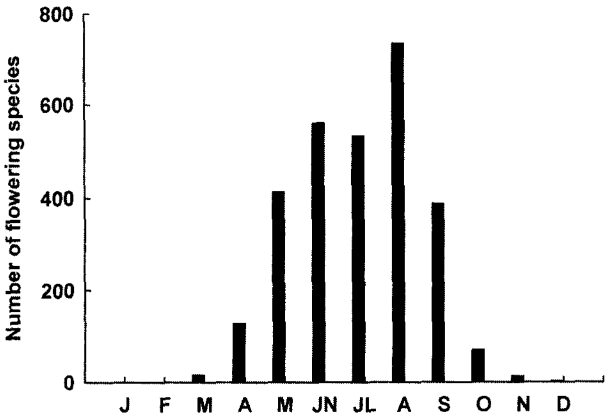

**Figure 2.** Number of Korean angiosperm species in flower by month.

# RESULTS

## Overall Pattern of Flowering

*Flowering time* -- Overall data showed that the largest proportion (25.6%) of Korean angiosperms flowered in August, followed by June (19.6%), July (18.6%), May (14.5%), September (13.6%), April (4.5%), October (2.5%), March (0.6%), November (0.5%), and December (0.1%) (Fig. 2). In January and February, only *Osmanthus insularis* and *Narcissus tazetta*, respectively, reached their flowering peaks. Therefore, about two-thirds (63.8%) of angiosperm species flowered in summer, while nearly one-fifth (19.5%) bloomed in spring. Slightly fewer flowered in autumn than in spring (16.5%), but the number of species in flower declined drastically in winter (0.2%). Thus, the proportion of species flowering across seasons was not homogeneous ($X^2 = 1200.66$, df = 2, $P < 0.0001$).

*Flowering duration* -- Flowering lasted for 1 to 9 months among 2867 Korean angiosperms. Species such as *Actinidia arguta* and *Petasites japonicus*, flowered briefly for one month, while others, e.g., *Malva verticillata*, bloomed for nine months, from spring to autumn (Fig. 3). With 52.7% of all species flowering for two months, the overall average was 2.03 ± 1.53 mo.

*Climatic influence* -- The number of species in flower during a given month was strongly positively correlated with both mean monthly temperature and precipitation ($r = 0.97$ and 0.94, respectively, $P < 0.0001$ for both). However, mean monthly temperature and precipitation were not correlated with mean flowering duration ($r = -0.004$ and $-0.09$, respectively, $P >> 0.05$ for both). When January and February were deleted from the analysis (each having only a single species in peak bloom), this pattern changed, so that mean monthly temperature and precipitation were then positively correlated with duration, although not significantly ($r = 0.54$ and

0.57, $P = 0.11$ and 0.08, respectively). Nevertheless, it should be noted that the monthly patterns of temperature and precipitation were extremely concordant ($r = 0.97$, $P < 0.0001$).

*Relationship between flowering time and duration* -- Flowering duration tended to become prolonged as the seasons progressed, and species flowering in different seasons varied in their durations (Table 1). Pair-wise comparisons of these means showed that plants flowering in autumn bloomed significantly longer than those in either summer or spring; likewise, species flowered for significantly longer periods in summer than in spring.

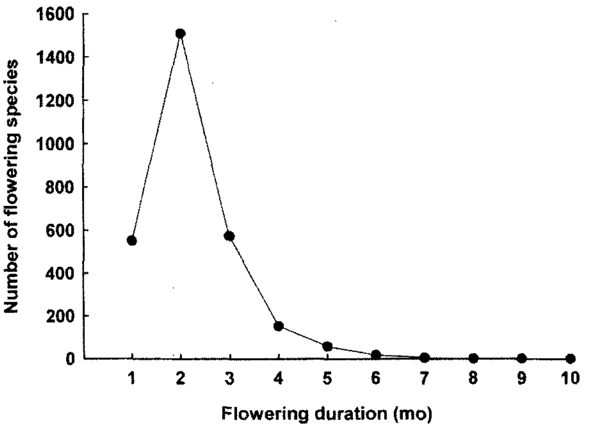

**Figure 3.** Frequency distribution of flowering duration among Korean angiosperm species.

**Table 1.** Means and standard deviations for flowering duration (months) of Korean angiosperms in different season. Means with different letters are significantly different at alpha = 0.05 level.

| Season | X | SD | N |
|---|---|---|---|
| Spring | $1.55^{a}$ | 1.53 | 560 |
| Summer | $2.13^{b}$ | 1.50 | 1829 |
| Autumn | $2.28^{c}$ | 1.41 | 478 |
| | $F_{2,2864} = 161.92$, $P < 0.0001$ | | |

## Patterns for the Largest Families and Genera

*Flowering season* -- Patterns of flowering season varied among families (Table 2). For example, both Ranunculaceae and Rosaceae were more likely to flower in the spring, less likely in the autumn. Within Rosaceae, the probability of springtime flowering was 14 times higher than in autumn, whereas, within Asteraceae, autumnal flowering was 17 times more likely. The Poaceae was less likely to flower in spring, while Fabaceae and Liliaceae were less likely to flower in autumn. Flowering season also differed among the nine genera within Rosaceae and Asteraceae ($X^2 = 45.73$, df = 8, $P < 0.0001$, and $X^2 = 23.22$, df = 8, $P = 0.0031$, respectively). In the former, all 23 species of *Prunus* flowered in the spring, while 18 of 22 *Potentilla* bloomed in the summer. For Asteraceae, most species of *Senecio* (8 of 9) flowered in summer, in contrast to the autumn flowering observed in *Aster* and *Chrysanthemum* (each having 13 of 16 species).

*Flowering duration* -- Mean flowering duration was significantly different among families ($F_{6,1088} = 30.10$, $P < 0.0001$). In pair-wise comparisons of means, Asteraceae ($X = 2.56 \pm 1.55$ mo) and Cyperaceae ($X = 2.52 \pm 1.44$ mo) flowered significantly longer. In contrast, Ranunculaceae ($X = 1.70 \pm 1.47$ mo) bore flowers for significantly shorter periods than did any of the Asteraceae, Cyperaceae, or Liliaceae. A nested ANOVA that included nine large genera from each of Asteraceae, Poaceae, and Rosaceae revealed that dura-

**Table 2.** Frequency distribution for Korean angiosperms in a two-way contingency table of flowering season and family membership.

| Family | Flowering season | | |
|---|---|---|---|
| | Spring | Summer | Autumn |
| Asteraceae | 7 - | 140 - | 119 + |
| Cyperaceae | 31 | 91 | 36 |
| Fabaceae | 14 | 95 | 18 - |
| Liliaceae | 16 | 85 | 10 - |
| Poaceae | 10 - | 121 | 49 |
| Ranunculaceae | 27 + | 77 | 17 - |
| Rosaceae | 69 + | 79 | 5 - |
| | | $X^2 = 251.68$, df = 12, $P < 0.0001$ | |

+/- sign indicates observed values are greater or less than the expected values at alpha = 0.05 level.

tion differed among families as well as among genera (Family $F_{2,32.29} = 6.98$, $P = 0.0030$; Genus $F_{24,270} = 1.90$, $P = 0.0078$), even though family level accounted for a greater proportion of the variance than did the genus level (12.8% vs. 6.8%).

*Relationship among flowering time, duration, and family membership* -- The two-way interaction effect of flowering season and family membership was marginally significant (Table 3A). In separate one-way ANOVAs for each family, the effect of flowering season on duration was significant in all families except Asteraceae and Liliaceae (Asteraceae $F_{2,263} = 1.48$, $P = 0.2289$; Cyperaceae $F_{2,155} = 11.29$, $P < 0.0001$; Fabaceae $F_{2,126} = 6.45$, $P = 0.0022$; Liliaceae $F_{2,85} = 0.82$, $P = 0.4456$; Poaceae $F_{2,177} = 9.81$, $P < 0.0001$; Ranunculaceae $F_{2,118} = 3.52$, $P = 0.0327$; Rosaceae $F_{2,150} = 18.72$, $P < 0.0001$). Pair-wise comparisons of means showed that both summer and autumn flowering (Cyperaceae, Fabaceae, and Poaceae) or only summer flowering (Ranunculaceae and Rosaceae) was significantly longer than spring flowering; autumn flowering was significantly longer than summer flowering only for Cyperaceae. Two patterns were generated with these data (Fig. 4). First, Cyperaceae contributed to the interaction of flowering season and family membership on duration by possessing species that flowered significantly longer in autumn than in summer. Second, the seasonal difference in duration, in particular for autumn vs. spring flowering, was minor in Liliaceae. Excluding Cyperaceae, both season and family membership exerted strongly significant effects on duration without a two-way interaction effect (Table 3B). Therefore, our results indicate that spring flowering was brief compared with either summer or autumn flowering across large families, and that certain families flowered either more extendedly or briefly than other families that bloomed in the same season.

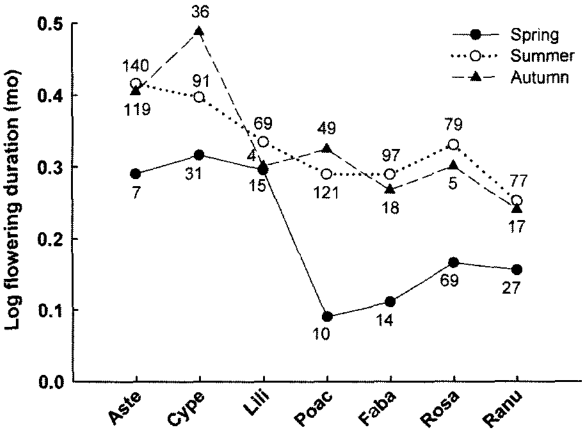

**Figure 4.** Mean (± SE) log of flowering duration for each of seven largest families (Comp = Compositae; Cype = Cyperaceae; Lili = Liliaceae; Poac = Poaceae; Faba = Fabaceae; Rosa = Rosaceae; and Ranu = Ranunculaceae), according to flowering season. Values next to symbols indicate number of species flowering in each season for each family. Families are listed in decreasing order of mean flowering duration. Lines connecting symbols are included to illustrate relatively consistent pattern of seasonal differences in mean flowering durations across families.

## DISCUSSION

### Overall Pattern of Flowering

In our data, the number of species in flower increased rapidly from spring through summer, then decreased during autumn. However, the bimodality of the flowering month, which has been demonstrated in several temperate regions (Jackson, 1966; Kochmer and Handel, 1986; Rathcke, 1988; Abe and Kamo, 2003) did not seem to exist among Korean angiosperms. For example, the number of species blooming in July declined by only 1% compared with those active in June. Thus, we conclude that the monthly pattern of flowering among Korean angiosperms is unimodal, rather than bimodal, with a peak occurring in August.

In a previous study of 2856 Korean angiosperm

**Table 3.** Two-way ANOVA for effects of flowering season and family membership on flowering duration of Korean angiosperms. Analyses were conducted twice, first by using species in the seven largest families (A), and then by excluding species belonging to Cyperaceae (B).

| Source of variation | A | | | B | | |
|---|---|---|---|---|---|---|
| | df | F | P | df | F | P |
| Flowering season (Season) | 2 | 27.16 | < 0.0001 | 2 | 23.20 | < 0.0001 |
| Family membership (Family) | 6 | 17.69 | < 0.0001 | 5 | 7.56 | < 0.0001 |
| Season x Family | 12 | 1.63 | 0.0776 | 10 | 1.16 | 0.3124 |
| Model | 20, 1074 | 14.65 | < 0.0001 | 17,919 | 13.26 | < 0.0001 |

species (Lee, 1969), flowering was most abundant in July, rather than in August. Such a disparity may have resulted from a difference in the methodology used for the previous study. Species that bloomed for more than one consecutive months were counted in each month in Lee (1969), while in our study each species was counted only once with the use of a midpoint of flowering. Nonetheless, both studies confirm that summer is the most favorable season for flowering among Korean angiosperms.

Although climate has, for many years, been assumed to be a proximate factor that triggers flowering, the relative importance of climate factors tends to vary by climate. For example, flowering in the Tropics may be induced by rainfall (Opler et al., 1976; Reich and Borchert, 1984) or high light intensity (Wright and Schaik, 1994), while in the temperate flowering activity appears to be largely controlled by temperature parameters, such as mean monthly air temperature (Sparks et al., 2000), ocean temperature (Beaubien and Freeland, 2000), and temperature sums (Jackson, 1966; Yim, 1986). In Korea, the number of species in flower, by month, corresponds well with annual patterns of temperature and precipitation. However, those nearly concordant seasonal patterns of temperature and precipitation make it difficult to conclude that active flowering in summer is primarily a response to high temperatures during that season.

Flowering lasts an average of 75 d among 30 shrubby species in Doñana, Spain (Herrera, 1986), and 55 d for 133 species in Athens, Greece (Petanidou et al., 1995). Considering the number of species examined, the flowering duration for our Korean angiosperms is relatively brief, averaging two months. However, duration varies here by season. Although quantitative studies on climatic effects are quite rare, the flowering period tends to be longer in the wet season in various regions (Stiles, 1978; Smith-Ramirez and Armesto, 1994; Petanidou et al., 1995). Korean-angiosperm flowering is prolonged in the wettest summers, but remain extended until winters with low precipitation. Thus, mean monthly temperature and precipitation could not directly account for the interaction of season and duration found here. This result may reflect the fact that the national mean climatic data employed in this study do not take into account variations within local areas, e.g., along latitudinal, longitudinal, or altitudinal gradients. Information on the geographic ranges of those species, as well as long-term climatic data, are necessary if one is to evaluate the proximate role of such factors on flowering.

## Effects of Taxonomy

Flowering time has reportedly diverged among families in temperate regions (Jackson, 1966; Lee, 1969; Kochmer and Handel, 1986; Smith-Ramirez and Armesto, 1994) and in the Mediterranean region (Johnson, 1992), and also differ among genera and families on Barro Colorado Island, Panama (Wright and Calderon, 1995). However, timing does not always segregate among families in either the Tropics (Gentry, 1974; Opler et al., 1980; Appanah, 1985; Bawa et al., 2003) or the Mediterranean area (Petanidou et al., 1995). In addition, taxonomic effects on duration are not always obvious (Smith-Ramirez and Armesto, 1994). Families in the current study are characterized by their specific flowering time and duration. For example, Ranunculaceae and Rosaceae are families that typically flower in the spring for a brief period. Season and duration are segregated again among genera within families. One example was the genera within Rosaceae, where flowering times differed by more than four months and duration varied 3.5 times. Therefore, these results suggest that community-level studies on flowering phenology or other evolutionary patterns should consider the taxonomic composition of the species involved.

Strong taxonomic constraints on flowering season may imply that developmental pathways tightly control that parameter. In particular, if flowering time is associated with other life-history traits, e.g., times for leafing and fruiting (Primack, 1987; Lechowicz, 1995) or the dispersal and predation of seed (Janzen, 1967; Brody, 1997), then changes in such pathways may be quite difficult. In contrast, despite the statistical significance of family and genus membership on flowering duration, 80.4% of the variance in duration occurred among species within genera. The major portion of the variance among related species within genera suggests that closely affiliated species have relatively recently diverged in their flowering duration in response to selection pressures. Duration may then have been shortened or extended relatively easily because such variation would likely have involved only minor changes in developmental pathways once plants flowered in a certain season.

## Relationship between Flowering Time and Duration

The patterns of flowering briefly in spring and for an extended duration in summer existed in our data pooled over all families as well as that pooled for only the largest families. For example, brief flowering in Ranunculaceae and Rosaceae was a function of both family membership and spring flowering for the majority of species. This interaction between season and duration, even after taxonomic effects are excluded, suggests that flowering parameters cannot be treated as isolated traits in studies on flowering phenology.

We hypothesize that the low level of brief flowering in the spring and the high level of extended flowering in the summer may be a response to the level of soil moisture, which varies across seasons. Janzen (1967) has argued that active flowering in the dry season and vigorous growth in the wet season in dry tropical forests reflects strong selection for rapid growth in the wet season. Decoupling of vegetative and reproductive growth is frequently reported on sites subjected to seasonal water stress, such as the Mediterranean area (Johnson, 1992; Petanidou et al., 1995) and dry tropical forests (Opler et al., 1980; Reich and Borchert, 1984; Murali and Sukumar, 1994). Disassociating these two activities limits the opportunity for flowering (Johnson, 1992; Bawa et al., 2003). In Korea, plants begin to grow in spring after a long cold, dry winter. Mean monthly precipitation is > 60 mm from April to September, and substantial rains of > 100 mm occur for only four months, from June to September. Plants that flower early in spring may be under water stress due to the previous drought, thereby decoupling reproductive and vegetative activity. This then leads to a lower probability of flowering and a shorter duration for the species involved. In contrast, the summer that follows the monsoon rains is the optimal season for plant growth in Korea, in terms of both temperature and soil moisture. Thus most plants that emerge and flower somewhat later, i.e., in summer, may bloom for an extended period because they are not required to decouple vegetative and reproductive growth. This hypothesis must still be tested by a comparing species with different patterns of flowering and leafing phenologies.

Alternatively, seasonal variations in flowering duration may have been selected through pollinator activity. To avoid or reduce competition, plants may flower en masse, but for only a brief period, due to metabolic energy costs (Bawa, 1983). However, pollinator competition may not effectively segregate flowering times when visitation by pollinators is tenuous. Indeed, flowering is most extended into the wettest season when pollinator activity is low and unpredictable in the Tropics (Frankie et al., 1974; Stiles, 1978; Bawa et al., 2003) and in the Mediterranean region (Johnson, 1992; Petanidou et al., 1995). Rainfall is heavy and stochastic through the summer and until September which is classified as autumn in this study. Thus, the capriciousness of pollinator activity may possibly have extended flowering duration in the summer and autumn. However, further testing is required concerning seasonal pollinator patterns and their roles regarding brief, springtime flowering and extended blooming later in the year.

In conclusion, Korean angiosperms tend to exhibit a unimodal pattern of flowering activity that peaked in summer. Flowering duration, which historically has received much less attention, varies with the season, being shorter in spring than in summer and autumn. Because we used data pooled over species, without regard to geographic distribution, this current study is necessarily limited to elucidating the evolutionary mechanisms responsible for variations in flowering parameters among 2867 Korean angiosperm species. We are currently examining the pattern of flowering phenology among species within communities, data which will provide clues to the interactions and evolutionary factor(s) that affect flowering parameters.

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