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Ecological Correlates of Flowering Seasons in Korean Angiosperms

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ABSTRACT: Ecological correlates of flowering times often are examined to infer evolutionary mechanisms for flowering time diversities. We examined ecological characteristic associations such as growth habits and pollination modes with flowering times among 3,037 Korean angiosperms experiencing strong climatic seasonalities. We first examined taxonomic membership effects on flowering times across diverse taxonomic levels. Phylogeny constrained flowering times at all levels down to the genus level. We then analyzed the effects of ecological characteristics using subset data consisting of species randomly selected from each genus to control phylogenetic effects. The commonly observed patterns of early flowering of woody species in temperate regions existed. Spring flowering shrubs and trees, however, both being woody, were involved with biotic and abiotic vectors, respectively. In two herbaceous groups of annuals and perennials, annuals flowered later in the growing season than perennials although both herbs tended to be associated with abiotic vectors when flowering in autumn. These results support our hypothesis that species able to decouple vegetative and reproductive growth flower in spring's dry season, but species with different habits, even when they flower within the same season, are subjected to different selective pressures for efficient pollination.

Key words: Decoupling of growth, Flowering, Growth habit, Korean angiosperms, Pollen vector, Phylogeny

INTRODUCTION

Diverse factors are associated with flowering times, e.g., habitats (Jackson 1966, Pojar 1974), pollination modes (Whitehead 1983), dispersal systems (Rathcke and Lacey 1985), growth habits (Wright and Calderon 1995) and fruit predators (Brody 1997). Since flowering time is one of several major fitness components, selection may have driven such associations of flowering times and ecological traits. Korean flowers are most active in summer, like many other flora in temperate areas. For instance, about two thirds of species flower in summer (63.8%), while the rest flower, almost in similar proportion, in spring and autumn (19.5% vs. 16.5%) (Kang and Jang 2004). Although comparative studies have been conducted (Lee 1969, Oh 1982, Yim 1986) on flowering phenology of Korean angiosperms, ecological correlates and evolutionary mechanisms for flowering time diversities in Korean angiosperm species remain unidentified.

Perhaps the most frequently observed ecological correlates of flowering times in temperate flora are growth habits and pollination modes, e.g., early season flowering of woody species (e.g. Whitehead 1969, 1983, Kochmer and Handel 1986). Although Korea maintains strong rainfall and temperature seasonalities, rainfall and temperature vary almost concordantly, with both peaking in August and troughing in January (Kang and Jang 2004). Analogous to Mediterranean and tropical species (Janzen 1967, Johnson 1992, Bawa et al. 2003), Korean plants may undergo allocation trade-offs to reproductive and vegetative growth in stressful environmental conditions such as drought. If so, plants flowering in a spring that followed a cold and dry winter would involve decoupling of vegetative growth and reproductive activity, while those flowering in a summer with sufficient rainfall might experience a coupled vegetative growth. Since woody species tend to have more reserves and relatively deeper roots than herbaceous species (Canadell et al. 1996), we propose that woody species flower earlier in the season, i.e., spring, as opposed to herbs. Furthermore, if stored reserves play a critical role in the early flowering of woody species, perennial herbs with storage organs such as corms or rhizomes also may flower earlier than annuals. Only a few studies (e.g. Kochmer and Handel 1986) have examined this possibility.

A number of studies have attempted to relate the role of pollinators to flowering times at community or population levels, but coevolutionary changes in flowering times and pollen vectors have been inferred (e.g. Stiles 1978) or unsupported (e.g. Murray et al. 1987, Bosch et al. 1997). In temperate regions, the abundance of animal pollen vectors change with the seasons, e.g., relatively low levels in spring due to low temperatures (Primack 1985). Should the majority of Korean angiosperms be involved with animal vectors,

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and pollinator competition be the major driving force causing flowering time variations, the most active flowering occurring during summer (Kang and Jang 2004) might reflect selective outcome, taking advantage of abundant pollen vectors during a favorable season. The association of wind-pollinated trees in spring, however (Whitehead 1969, 1983), implies correlations between habits and pollen vectors regarding flowering times. Thus, pollen vector effects on flowering times should be examined after controlling species habit distributions.

Phylogeny often confounds evolutionary patterns among related species as these related species share common ecological and life history traits through their shared ancestries (e.g. Peat and Fitter 1994, Harvey et al. 1995, Vamosi et al. 2003, Gross 2005). Because angiosperm phylogeny is not yet firmly established, we examined the phylogenetic effects on flowering parameters by analyzing taxonomic effects with the assumption that taxonomic classifications reflect plant phylogenies to some degree. This study specifically addresses the following questions: 1) Does taxonomic membership affect flowering parameters? 2) Do woody species flower earlier than herbaceous species? and, 3) Do abiotically pollinated species flower earlier in the growing season than biotically pollinated ones?

MATERIALS AND METHODS

Data Collection

Data on flowering parameters were collected from a recent monograph treating 3,037 Korean angiosperm species (Lee 1998). Starting and ending months of flowering were noted for each species, with flowering midpoints also calculated. In this analysis, four flowering seasons were categorized based on flowering midpoints: spring (March ~ May); summer (June ~ August); autumn (September ~ November); and winter (December ~ February). Winter flowering was combined with autumn flowering in all analyses since only a few species flowered in winter. Detailed descriptions on flowering times are available in a previous study on flowering phenology (Kang and Jang 2004). For each species, taxonomic memberships at the higher levels – genus, family, order, and class – also were noted. Among Lee's (1998) listing of angiosperm species, species primarily cultivated in greenhouses, e.g., *Gloxinia speciosa*, *Hippeastrum hybridum*, and *Musa paradisiaca,* were omitted from the data.

For the hierarchical analysis of taxonomic effects, only species groups characterized by well-defined phylogeny based on DNA sequences (Chase et al. 1993, referred in Judd et al. 2002) were included. We selected two large clades within the dicots (Rosids and Asterids) and two large monocot groups (Petaloids and Commelinoids), often referred to as the superorder level (Judd et al. 2002), but noted as clade for convenience in this study. Within each clade, orders consisting of large families with >= 10 species, in which flowering dispersed across all three seasons – spring through autumn – were selected. The data set to test taxonomic effects thus comprised 1,313 species of 19 families, 9 orders, 4 clades, and 2 classes (Table 1).

Growth habit information primarily was obtained from Lee (1998) and supplemented from several monographs (Lee 1985, Lee et al. 2000, Oh 2000). Growth habits were diverse, ranging from annuals, biennials, perennial herbs, shrubs, small trees, trees, herbaceous and woody vines, and parasites. For some species with growth habits not concordant among authors, we used growth habits with longer life spans because longer life spans are assumed to represent those species' genetic capacities. For example, species described as either annual or biennial were noted as biennial herbs; those described as either biennial or perennial were treated as perennial herbs. Finally, growth habits were categorized into three groups, i.e., herbs, shrubs, and trees. Parasites were distinguished into either herbaceous or woody species. Woody vines were not included in the growth habits' three categories. Since pollen vector information is nearly nonexistent in Korea, we thus referred to Mabberley (1997) and Phillips and Rix (2002), which contain genus level pollen vector information. Further, species level information was obtained from the web (http://www.pfaf.org/). These references primarily treat European or American species or genera. We assumed any vector differences between regions, should this be the case, would occur within biotic vectors, e.g., between bees and birds, but not between biotic and abiotic vectors, e.g., between bees and wind. Pollen vectors were categorized into three groups: biotic vector; abiotic vector, such as selfing, water, and wind; and mixed vector, involving both animal and non-animal vectors.

Analysis

We first comprehensively analyzed phylogenetic effects on flowering times across a range of taxonomic levels. Associations between hierarchical taxonomic levels and flowering times were tested with nested categorical analyses. Due to extremely unbalanced distributions of genera within families and species within genera across flowering times, genus and flowering time associations were examined separately, using each of the nine largest genera within the Rosaceae and Asteraceae. Rosaceous species with autumn flowerings or composite species with spring flowerings proved rare; thus the analyses included only two categories of spring and summer flowerings for the Rosaceae, and of summer and autumn flowerings for the Asteraceae.

In evaluating overall patterns of flowering times and ecological characteristic associations, two-way contingency table analyses (time × habit, time × pollen vector, and habit × pollen vector) were employed

Table 1. Distribution of flowering times among species within families. Only families with >= 10 species of which flowering are dispersed across the three seasons are included

Class	Clade	Order	Family	Flowering time		
				Spring	Summer	Autumn
Monocots	Petaloids	Liliales	Liliaceae	15	69	4
Monocots	Petaloids	Asparagales	Amaryllidaceae	1	6	5
Monocots	Petaloids	Asparagales	Iridaceae	5	8	2
Monocots	Petaloids	Asparagales	Orchidaceae	7	67	4
Monocots	Petaloids	Asparagales	Alliaceae	1	7	5
Monocots	Commelinoids	Poales	Juncaceae	4	12	1
Monocots	Commelinoids	Poales	Poaceae	10	121	49
Monocots	Commelinoids	Poales	Cyperaceae	31	91	36
Dicots	Rosids	Saxifragales	Saxifragaceae	24	26	3
Dicots	Rosids	Malpighiales	Euphorbiaceae	5	17	3
Dicots	Rosids	Rosales	Moraceae	4	11	2
Dicots	Rosids	Rosales	Urticaceae	2	17	4
Dicots	Rosids	Rosales	Rosaceae	69	79	5
Dicots	Rosids	Rosales	Rhamnaceae	1	15	1
Dicots	Asterids	Solanales	Solanaceae	2	15	2
Dicots	Asterids	Laminales	Oleaceae	19	11	3
Dicots	Asterids	Laminales	Lamiaceae	5	55	15
Dicots	Asterids	Laminales	Scrophulariaceae	2	52	17
Dicots	Asterids	Asterales	Asteraceae	7	140	119

using the overall data. Since flowering times differed significantly even among genera within families, and congeneric species were more or less similar in growth habits and pollen vectors, growth habit and pollen vector contributions to heterogeneity of flowering times were re-examined with subset data consisting of species randomly selected from each genus. Two-way contingency table analyses of subset data were conducted to test associations of three habit groups (herb vs. shrub vs. tree and annual vs. perennial) × two vector groups (biotic vs. abiotic), and then of two habit groups (annual vs. perennial) × vector groups (biotic vs. abiotic). Habit and vector contributions on flowering times were examined simultaneously using log-linear analyses on subset data. Only two vector groups (biotic vs. abiotic) were compared due to a few empty cells involving mixed vectors. Flowering time also was categorized into early season (spring) vs. late season (summer and autumn) when comparing three habits (herb, shrub, and tree) because shrubby species visited by abiotic vectors in autumn were not found. All analyses were conducted with SAS 9.1 (2002).

RESULTS

Associations of Flowering Times and Taxonomies

In nested categorical analyses simultaneously testing taxonomic effects across all levels, flowering times differed among the taxonomic groups at all levels except among orders within the Rosids (Table 2A). Higher taxonomic levels thus tended to constrain variations in flowering seasons, but effects of order within clades proved inconsistent depending upon the taxa. Flowering times also differed among Rosaceae and Asteraceae genera (Table 2B). In the Rosaceae, all *Prunus* species flowered in spring, while most *Potentilla* species flowered in summer. In the Asteraceae, most *Senecio* species flowered in summer, contrasting to the *Aster* and *Chrysan-*

Table 2. The contribution of higher taxonomic groups to heterogeneity in flowering time distributions. A. The phylogenetic effects across taxonomic levels from class to family level. B. The phylogenetic effects at family and genus levels

Source	G	df	P
A.			
Monocots vs Dicots	13.25	2	0.0013
Petaloids vs Commelinoids (Monocots)	12.73	2	0.0017
Rosids vs Asterids (Dicots)	131.28	2	< 0.0001
Orders (Rosids)	8.87	4	0.0656
Orders (Asterids)	51.61	4	< 0.0001
Families (Poales)	54.57	6	< 0.0001
Families (Rosales)	53.07	6	< 0.0001
Families (Laminales)	25.15	6	0.0001
B.			
Genera (Rosaceae)	45.73	8	< 0.0001
Genera (Asteraceae)	23.22	8	0.0031

The significance of each effect was tested at alpha = 0.00625 after Bonferonni correction in A. Chi-square scores, instead of G scores, are reported in B.

themum species, which flowered in autumn. Thus, to summarize, phylogenetic effects on flowering times were evident at all taxonomic levels examined except among the Rosid orders.

Associations of Flowering Times and Ecological Characteristics

In overall data involving 3,007 Korean angiosperm species with habit data, slightly more than half the species were herbaceous perennials (N=1676, 55.7%), followed by shrubs (N=375, 12.5%)> annuals (N=322, 10.7%) > trees (N=290, 9.6%) > biennials (N=174, 5.8%) > herbaceous vines (N=79, 2.6%) > woody vines (N=65, 2.2%) > parasites (N=26, 0.9%). Herbaceous species thus were 3.4 times more abundant than woody species, including both shrubs and trees (77.3% vs. 22.7%). Among 2,987 species with pollen vector data, biotic vectors (N=2,173, 72.3%) visited about two thirds of species, followed by abiotic vectors (N=674, 22.6%) and mixed vectors (N=140, 4.7%).

Associations of flowering times and growth habits proved highly significant in the overall data (Table 3). Only 60% of the expected distribution of herbaceous species flowered in spring, whereas shrub and tree species flowered in spring 2.0 and 2.7 times more than

Table 3. Distribution of Korean angiosperm species in a two-way contingency table of flowering times and ecological characteristics. Analyses were conducted based on overall data pooled across all higher taxonomic levels. Observed/expected values are provided for each cell. +/− sign indicates observed values are greater or less than the expected values at alpha = 0.05 level

	Flowering time			χ^2	P
	Spring	Summer	Autumn		
Habit					
Herb	255/424	1439/1350+	443/362+		
Shrub	149/73+	198/234	23/63		
Tree	148/54+	119/172	6/46	413.50	<0.0001
Pollen vector					
Biotic	396/416	1381/1349	342/354		
Abiotic	118/113	337/365	118/96+		
Mixed	41/26+	80/85	12/22	23.14	0.0001
	Pollen vector			χ^2	P
	Biotic	Abiotic	Mixed		
Habit					
Herb	1568/1619	558/508+	107/106		
Shrub	364/273+	12/86	1/18		
Tree	169/209	89/65+	30/14+	151.44	<0.0001

expected, respectively. Flowering times also were associated significantly with pollen vectors, but proved rather weak relative to growth habits (Table 3). Data revealed that biotic vectors did not show any particular seasonal patterns: 65.2% of species visited by biotic vectors flowered in summer, while the remaining species flowered in spring and autumn in almost similar proportions. Species involved with abiotic vectors, however, flowered in autumn 1.2 times more than expected. Additionally, among spring flowering species, the proportion of species visited by mixed vectors was 1.6 times higher than expected. Woody species such as shrubs and trees differed in vector associations (Table 3). For example, almost all shrubs (96.6%) showed involvement with biotic vectors, whereas abiotic vector proportions were relatively high only in trees (30.9%) and herbs (25.0%).

Associations of Flowering Times and Ecological Characteristics after Considering Taxonomic Memberships

After disregarding vector types in the subset data, flowering times differed among habits (Table 4A). In spring, for example, more than one third of both shrub and tree species flowered as opposed to less than one tenth of the herb species (39.8%, 37.1%, and 7.8%, respectively), while in autumn, one fifth of the herb species flowered in contrast to less than one tenth of the shrub and tree species (21.0%, 7.8%, and 4.5%, respectively). Herbs, then, were far less likely than woody species to flower in the spring. Habit and flowering season associations, however, varied somewhat, depending upon pollen vectors (Table 4A). In spring, for example, both shrubs and trees flowered disproportionately, relative to herbs and regardless of vectors. Summer and autumn flowering, however, was characterized by different habits depending on vectors: in biotically pollinated species, shrub flowerings were rare in both summer and autumn, while in abiotically pollinated species, tree flowerings were rare only in autumn. The significant interactions of habits and vectors in log-linear analyses revealed that habit effects on flowering seasons varied with pollen vector types (Table 5A). When disregarding pollen vectors, annuals and perennials also tended to flower in somewhat different seasons (Table 4B). For example, a higher proportion of annuals flowered in autumn than did perennials (28.2% vs. 17.1%), whereas spring flowering reversed this pattern (6.4% vs. 8.4%). Data showed that despite an overall tendency of autumn flowering of annuals, this autumnal flowering pattern was conspicuous only for annuals pollinated by biotic vectors (Table 4B). In log-linear analyses showing the effects of habits(annual vs. perennial) and vectors, however, flowering seasons were affected by both, although habit contributions were only marginal (Table 5B).

DISCUSSION

Taxonomic Effects on Flowering Times

Strong taxonomic effects on flowering times of Korean angiosperms were found at all taxonomic levels examined from class to the genus, the single exception among orders of Rosids. According to Peat and Fitter (1994), such strong taxonomic effects indicate variations in flowering times of angiosperms occurred at the time of divergence of classes, clades, orders, families, and genera. Analogous, strong taxonomic effects also have been found in tropical plants on Barro Colorado Island (Wright and Calderon 1995), emphasizing the importance of considering phylogeny at higher levels in revealing evolutionary patterns of flowering phenologies. In other words, an overall pattern of confamilial species may not reveal evolutionary factors if those species consisted of genera with diverse ecologies and flowering parameters, although previous studies largely have focused on species patterns of large families (e.g. Kochmer and Handel 1986, Smith-Ramírez and Armesto 1994, Kang and Jang 2004).

This study evaluated only flowering time patterns using the assumption that the midpoint of flowering months was the time of maximum flowering intensity. On the other hand, Wright and Calderon (1995) employed different parameters of flowering times, finding that different parameters were subject to phylogenetic effects at different taxonomic levels. For example, confamilial species exhibited similar patterns of flowering synchrony, while congeneric

Table 4. Distribution of Korean angiosperm species in a two-way contingency table of flowering times and ecological characteristics for each vector group. Analyses were conducted twice, using subset data that included all three habit groups (A: herb vs. shrub vs. tree) and only herb groups (B: annual vs. perennial). Observed/expected values are provided for each cell. +/− sign indicates that observed values are greater or less than the expected values at alpha = 0.05 level

	A.	Habit			χ^2	P		B.	Habit		χ^2	P
		Herb	Shrub	Tree					Annual	Perennial		
Biotic vector	Spring	41/72	39/14+	15/9+			Biotic vector	Spring	8/11	33/30		
	Summer	360/343	50/66	42/42				Summer	88/96	263/255		
	Autumn	95/81	7/16	4/10	78.29	<0.0001		Autumn	35/24+	52/63	9.45	0.0089
Abiotic vector	Spring	5/18	2/0+	15/3+			Abiotic vector	Spring	2/2	3/3		
	Summer	79/72	1/2	6/12				Summer	23/25	56/54		
	Autumn	37/31	0/1	0/5	70.52	<0.0001		Autumn	14/12	23/25	1.02	0.5999
Mixed vector	Spring	3/5	0/0	3/1			Mixed vector	Spring	1/1	1/1		
	Summer	15/14	0/1	3/4				Summer	7/8	8/8		
	Autumn	3/3	1/0+	0/1	10.00	0.0404		Autumn	2/2	1/2	0.40	0.8187

Table 5. The contributions of habit and pollen vector to the heterogeneity in flowering times in subset data. The first log-linear analysis (A) was conducted to test the effects of habit (herb vs. shrub vs. tree) and vector on flowering times (early vs. late season), and the second (B) evaluated the effects of habit (annual vs. perennial) and vector on flowering times (spring vs. summer vs. autumn). If a habit × pollen vector interaction occurred, the effect of habit subsequently was tested for each vector. Analyses were based on subset data in both A and B

Source	df	G	P	Total N	Source	df	G	P	Total N
A. Herb vs. Shrub vs. Tree					B. Annual vs. Perennial				
1) Habit × Vector					1) Habit × Vector				
Intercept	1	14.10	0.0002		Intercept	2	135.41	<0.0001	
Habit	2	59.07	<0.0001		Habit	2	5.02	0.0802	
Vector	1	2.68	0.1017		Vector	1	7.13	0.0283	
Habit × Vector	2	14.06	0.0009	798	Habit × Vector	2	1.18	0.5553	600
2) Biotic vector									
Intercept	1	96.49	<0.0001						
Habit	2	61.42	<0.0001	653					
3) Abiotic vector									
Intercept	1	1.21	0.2708						
Habit	2	39.60	<0.0001	145					

species possessed similarity in flowering midpoints. If both flowering synchrony and intensity contribute to fitness (Bawa 1983, Kang and Bawa 2003), one necessarily must consider not only the midpoint of flowering months but also flowering pattern concentrations, as Wright and Calderon (1995) did.

Despite employing subset data to control taxonomic effects, we admit that taxonomic effects still might confound the patterns observed in subset data due to skewed taxonomic distribution, e.g., a few families containing a large number of genera. Until phylogeny is clearly defined, however, using subset data to control taxonomic effects may be compromised.

Effects of Growth Habits and Pollen Vectors

The earlier flowering of woody species than herb species noted in temperate and Mediterranean regions (Grainger 1939, Whitehead 1983, Kochmer and Handel 1986, Petanidou 1995) also was evident among the Korean angiosperms. These results correspond as well to Yim's (1986) report of trees in a Seoul arboretum reaching peak flowering in April. Although Kochmer and Handel (1986) suggested the possibility of developmental patterns as responsible for flowering time differences among habits, they did not provide any clear mechanism for how determinate or indeterminate growth controls flowering times. In this study, we propose that species flowering early in the season do so through decoupling of vegetative and reproductive growth. This is possible for the woody species as they have reserved resources and, in addition, tend to tap roots deeply. Across diverse ecosystems, trees have roots deeper than shrubs, with shrubs deeper than herbs among 253 species from various biomes (Canadell et al. 1996). On Barro Colorado Island, species using abundantly more water in the deep soil maintain better leaf water status (Jackson et al. 1995). These results support our argument that woody species flower earlier than herbaceous species because they use reserved resources or they find quick relief from water stress in the spring. Flowering seasons correlated poorly with tropical species habits (Wright and Calderon 1995), however, and the causes for such disparate results are not obvious. Because Wright and Calderon (1995) did not control species taxonomies in habit groups, direct comparisons of results may be inappropriate.

We also compared flowering times between annual and perennial herbs in Korean angiosperms, and found that annuals tended to flower later than perennials. Seven spring flowering 'ephemeral' species in woodlands in Illinois were also all perennials (Schemske et al. 1978). In the Cape flora, monocot species flowering in leafless conditions at the end of the dry season was ascribed to storage organs (Johnson 1992). Thus, relatively earlier flowering of perennials than annuals may reflect the influence of stored resources. However, annual, biennial, and perennial herbs in the Carolinas showed no difference in flowering times (Kochmer and Handel

1986). Analyses restricted to related species in the same habit, e.g., congeneric herbs or trees but with contrasting leafing and flowering phenologies, would allow us to determine the precise effects of habit on flowering times.

Habit effects on flowering peaks disappeared after considering family memberships and other ecological characteristics, such as pollen vectors (Smith-Ramírez and Armesto 1994, Kang and Bawa 2003). We found that early flowering of woody species continued as other authors (e.g. Kochmer and Handel 1986, Mazer 1989) already had noted. Interestingly, however, species of different habits were associated with different vectors. For example, in the spring, shrubs proved three times more likely than expected to be visited by biotic vectors whereas trees proved five times more likely than expected to be involved with abiotic vectors. In our subset data, species pollinated only by wind comprised 92% of abiotic pollination. Thus, disproportionate springtime flowering of abiotically pollinated trees may reflect selective advantage of wind- pollination before plant leafings cause canopy closure (e.g. Whitehead 1983). Leafless conditions also may confer advantages upon biotically pollinated woody species by attracting animal vectors (Robertson 1895 cited in Kochmer and Handel 1986). Of particular note, specialist pollen vectors are relatively rare in temperate regions (Waser et al. 1996). Shrubs flowering early in the growing season in leafless conditions would be conducive to attracting generalist vectors. The difference in flowering times between shrubs and trees, and potentially between annual and perennial herbs, with each being involved with different vectors, thus gives ample warnings concerning pooling data regarding habits without clear justification.

CONCLUSION

Our study differs from previous studies on flowering times in temperate flora because we simultaneously tested the contributions of taxonomic memberships, growth habits, and pollen vectors. Despite widespread phylogenetic effects, both habits and pollen vectors exerted influence over species flowering times. The early flowering patterns of woody species relative to herbaceous species were consistent with our proposition. Interactions of habits and pollen vectors, however, proved more complex than expected. Recent studies demonstrating strong correlations among diverse ecological characteristics (e.g. Vamosi et al. 2003, Gross 2005) suggest the possibility of a multitude of factors affecting species flowering times. For example, spring flowering of woody species also may be derived from selection pressures to produce fleshy fruits, which require a longer time to mature than dry fruits (e.g. Primack 1985, Rathcke and Lacey 1985). A subsequent study will examine the diversities of fruiting phenologies in relation to flowering parameters.

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