

CONTRASTING FLOWERING PHENOLOGY AND SPECIES RICHNESS IN ABIOTICALLY AND BIOTICALLY POLLINATED ANGIOSPERMS

KJELL BOLMGREN,¹ OVE ERIKSSON, AND H. PETER LINDER²
Department of Botany, Stockholm University, SE-106 91 Stockholm, Sweden
¹*E-mail: bolmgren@botan.su.se*

²*Institute of Systematic Botany, University of Zurich, Zollikerstrasse 107, Zurich CH 8007, Switzerland*

Abstract.—Biotic pollination is thought to correlate with increased interspecific competition for pollination among plants and a higher speciation rate. In this study we compared patterns of flowering phenology and species richness between abiotically (wind) and biotically pollinated plants, using phylogenetically independent contrasts. We compiled phenological data from eight local seasonal floras, in which we found geographically overlapping sister clades. Of 65 documented origins of wind pollination, we were able to use up to 17 independent contrasts. In contrast to previous studies we found no difference in global species richness between wind- and biotically pollinated sister clades. Regarding phenology, we found wider phenological spread in biotically pollinated clades, earlier flowering onset in wind-pollinated trees, but no difference in duration of flowering between pollination modes. These results corroborate previous views that niche space is more constrained for wind-pollinated species, and that niche partitioning is less important between wind-pollinated plants compared to plants pollinated by animals.

Key words.—Anemophily, diversity, flowering time, phenological spread, phylogenetically independent contrasts, pollination syndrome.

Received July, 30, 2002. Accepted March 20, 2003.

Flowering phenology is one of the plant traits most studied in relation to plant pollination systems and considered potentially important for their ecology and evolution (Primack 1985; Rathcke and Lacey 1985; Gotelli and Graves 1996; Fenner 1998). Assuming pollinators to be a limiting resource, two main hypotheses for phenology of biotic pollination have been developed. Levin and Anderson (1970) suggested that coexistence would be promoted by phenological character displacement, that is, a staggered phenological community structure. This hypothesis is based on the assumption that pollinator competition could lead to competitive exclusion. Mosquin (1971) and Heinrich (1976) restricted the generality of the hypothesis suggesting that pollinator limitation is less probable during large parts of the flowering season and in plant assemblages dominated by strong disturbance regimes. As an alternative hypothesis, Thomson (1978) and Rathcke (1983) proposed facilitation to be more important than competition. By aggregating flowering times, coexisting species could generate a net gain of fertilizations for each other.

For abiotic (wind) pollination, previous evolutionary hypotheses on phenology have focused on the time of flowering within the season and the duration of flowering. To reduce the area of inert surfaces, it has been suggested that release of pollen in wind-pollinated plants (especially trees and shrubs) should be advantageous in early parts of the growing season before leafing has occurred (Whitehead 1969; Heinrich 1976; Faegri and van der Pijl 1979). Heinrich (1976) pointed out, though, that early flowering can be important for biotically pollinated plants too, as for the ground flora in deciduous communities to track the phenological niche when pollinators and insolation are more abundant. To overcome the particular problems correlated to anemophily, it has also been suggested that wind-pollinated plants are favored by mass release of pollen on specific environmental cues (Whitehead 1969; Faegri and van der Pijl 1979). Therefore, flowering phenology in wind-pollinated plants has been expected to show intrapopulation synchronization and thus shorter du-

ration of flowering (Whitehead 1969; Rabinowitz et al. 1981). Further, wind-pollinated plants do not compete for pollinators and have been shown to be able to select conspecific pollen from the air (Linder and Midgley 1996). Thus, we expect interspecific overlap in flowering time to be more common in wind-pollinated plants compared to biotically pollinated plants that potentially compete for pollinators. Interspecific flowering overlap is also motivated by the need for wind-pollinated plants to track environmental conditions (dry, windy) favoring pollen dispersal, conditions which are common to wind-pollinated species in general (Culley et al. 2002a,b).

The question of phenological community structure is still unresolved. The results of Stiles (1977) and Ashton et al. (1988) on interspecific division of the phenological niche, and Carpenter (1976) and Waser (1983) on character displacement, provide limited evidence for nonrandom structuring of phenological patterns (Gotelli and Graves 1996; Fenner 1998). A lack of support for phenological structure in plant communities has been used as a justification for advocating that selection on phenology is weak or nonexistent (Ollerton and Lack 1992). In contrast, there are many reasons why existing competition for pollinators is difficult to detect in phenological community structure. Several studies of community structure have used a null model approach and the biological soundness of these models has been questioned (Gotelli and Graves 1996). Moreover, Brody (1997) pointed out that selection on other traits might offset or constrain the evolution of flowering phenology. For example, Pico and Retana (2000) found counterbalancing effects between different reproductive phases over an extended flowering season. Finally, Kochmer and Handel (1986), Bell and Stephens (1984), and Johnson (1993) have shown strong lineage-specific effects, often called constraints, on flowering phenology (but see Petanidou et al. 1995). Based on these findings Kochmer and Handel (1986) did not exclude effects of interspecific interactions on phenological community pat-

terns, but suggested that they probably only have a role in fine-tuning these patterns.

In concordance with the hypothesis on pollinators as a limited resource, competition for pollinators would not only generate phenological character displacement and/or divergence in other character traits related to the pollinator interaction (Grant 1994), but also be expected to enhance speciation. Biotic pollination is regarded as one of the most important determinants for angiosperm speciation, both at the overall level (Stebbins 1981; Crepet 1984) and, as suggested by the positive correlations found between pollination mode and species richness (Eriksson and Bremer 1992; Ricklefs and Renner 1994; Dodd et al. 1999), compared to other interactions and pollination modes. Central to the hypothesis of pollinator-assisted speciation is the idea of faithful pollinators (Crepet 1984). Such constancy would promote reproductive isolation between species and evolutionary change within lineages, forming the basis for gradual development of ‘‘pollination races’’ and later allopatric speciation (Ricklefs and Renner 1994; Waser 1998). Therefore, clades characterized by biotic pollination would be associated with higher species richness compared to clades consisting of abiotically pollinated plants.

In this study we use a phylogenetically independent contrast approach (Felsenstein 1985; Harvey and Pagel 1991; Møller and Birkhead 1992; Wickman 1992) to compare phenology evolution and species richness in abiotically (wind) and biotically pollinated sister clades. Basically, we have addressed the same phenological issues as Rabinowitz et al. (1981) in their detailed study of the wind- and insect-pollinated subsets of a prairie plant community, although our study is based on monophyletic clades, not communities (Grandcolas 1998). We have compiled literature data on flowering onset and duration of flowering from geographic areas where sister clades overlap. For each sister clade we have calculated phylogenetically uncorrected means of onset and duration, and standard deviations of flowering onset (SD_{onset}). The SD_{onset} , which we will call phenological spread, is adopted as our measure of niche structure.

We test four different hypotheses: (1) wind-pollinated plants flower earlier in the season; (2) biotically pollinated plants have a longer duration of flowering; (3) phenological spread is wider in biotically pollinated clades; and (4) biotic pollination enhances species richness.

To our knowledge, this is the first study on comparative plant phenology using phylogenetically independent replicates. Because plant phenology, pollination mode, and species richness are all correlated to latitude, we have used floristic information from areas where sister clades overlap geographically.

MATERIALS AND METHODS

Dataset

The dataset was delimited by two main criteria. First, we needed phylogenies resolved at a level making it possible to locate the node of change from biotic to wind pollination mode. Second, phenology information had to be comparable for the contrasted clades. As phenology is correlated to latitude, we looked for geographic regions where distribution

areas of the sister clades overlapped, and for which reliable floras including flowering phenology existed. Of 65 listed origins of wind pollination (Ricklefs and Renner 1994; Dodd et al. 1999; H. P. Linder, unpubl. manuscript), 17 phylogenetically independent contrasts (PIC) that satisfied the criteria above could be constructed (See Table 1 for references to phylogenies and floras, and Table 2 for an overview of derived data).

Traits

Phenology information on flowering onset and duration of flowering was taken from eight local floras from Japan, Australia, North America, and Europe (Table 1). For each species belonging to a sister clade used, and found in the local flora, flowering onset was denoted as the first day of the time period given for flowering in the local flora. The flowering time was expressed by month or part of month in the floras used. Duration of flowering was denoted as the sum of days of the flowering period given in the floras. Mean flowering onset, mean duration of flowering, standard deviation of flowering onset (SD_{onset}), and flowering overlap (eq. 1; developed from Augspurger 1983) were then derived for each sister clade in all 17 phylogenetically independent replicates, using all species belonging to each sister clade once. These clade quantities were derived without considering internal phylogenies (Møller and Birkhead 1992; Wickman 1992); that is, at this level each species was used as an independent unit. Not considering internal phylogeny may affect values of both means and standard deviations. The particular effect, though, is intimately correlated to the topology and we have no reason to believe that the topological patterns are biased between the matched pairs, that is, the biotic and wind-pollinated clades.

$$O_A = \left(\frac{1}{n-1} \right) \times \left(\frac{1}{f_i} \right) \times \sum_{j=1}^n e_{i \neq j}. \quad (1)$$

Flowering overlap (O_A) of species i in a local flora is a function of the number of species in the local flora (n), the number of days species i is flowering (f_i), and the number of days both species i and j ($i \neq j$) are flowering simultaneously ($e_{i \neq j}$).

SD_{onset} and flowering overlap are two measures of phenological spread. There are several other closely related concepts to these phenological community characteristics, for example, phenological overlap, dispersion, divergence, character displacement, phenological displacement, and staggering. Here, we will use phenological spread in a general sense simply because we believe it is sound to have a common biological term for the phenomenon, that is, interspecific phenological dispersion, even if different studies use different quantitative measures suitable for their study system and approach.

Data on species richness were collected from Mabberley (1997) except for PIC numbers, 3 and 14 (Table 1), which were from Ackerly and Donoghue (1998) and Wallander (2001), respectively. Bremer et al. (1998) and Soltis et al. (2000) were consulted for updated delimitations of families and higher taxonomic levels.

Pre-analyses

To check for any bias between pollination modes regarding phenology information in flora publications, we performed a paired *t*-test on phenology information from a flora of southernmost Sweden (Weimarck 1963) and conspecific herbarium specimens from the same area. The sample was chosen to match the dataset in Table 1 as much as possible. As expected, the recorded onset of flowering is earlier in the flora than was evident from herbarium specimens, whereas the recorded duration of flowering in the flora was longer than evident from herbarium material, but no bias between pollination modes existed (*t*-test: $N_{\text{paired}} = 13$, $P_{\text{onset}} = 0.72$, $P_{\text{duration}} = 0.54$).

We also checked for correlations between the two measures of phenological spread (SD_{onset} and flowering overlap) and between flowering onset and the rest of the phenology measures respectively, using a subset from Table 1. No correlation was found except between flowering overlap (eq. 1) and SD_{onset} , which were negatively correlated (Pearson correlation: $N_{\text{wind}} = 12$, $P < 0.01$, $R^2 = 0.53$; $N_{\text{biotic}} = 12$, $P = 0.08$). Thus, we have excluded flowering overlap from the rest of the study, and SD_{onset} alone represents phenological spread. All tests in the preanalyses were performed in Statistica version 5.5 (StatSoft 1999).

Tests

All tests of hypotheses 1–4 were performed as one-tailed sign tests, and we calculated cumulative *P*-values according to Sokal and Rohlf (1995, p. 78). In the test of hypothesis 4 (species richness) each sign value (+, supporting the hypothesis; –, opposing the hypothesis; 0, draw) was based on a single global calculation of species richness for each PIC (Table 2, species richness).

When testing the phenological hypotheses 1–3, the sign value (+, –, 0) for each PIC was equal to the dominating sign among all the local contrasts nested within each PIC. This dominating sign was derived by summing up the sign values for all local contrasts nested within a PIC. For example, for PIC 1 (Table 2) the dominating sign for phenological spread was [$\text{sign}(17.3 - 60) + \text{sign}(54.5 - 45) + \text{sign}(35.5 - 24.5) + \text{sign}(45.8 - 25.3)$] = (–) + (+) + (+) + (+) = (+). If no sign dominated, the PIC was given sign value 0. Because such zero contrasts are noninformative in sign tests, sample sizes (*N* in Table 3) were sometimes lower than expected from the available number of PICs (*n* in Table 3).

The sample size in the tests of hypothesis 3 (phenological spread) was further diminished as calculations of standard deviation of flowering onset requires data from more than one species per clade (see missing data in Table 2). When analyzing phenological spread, we both derived the dominating sign to use each phylogenetically independent replicate only once ($n = 12$, test 3a, Table 3), and used the sign value of each local contrast as an independent replicate ($n = 33$, test 3b, Table 3). The decision to use both levels of replication is further elaborated in the Discussion.

RESULTS

Mean onset of flowering ranged from late winter to late autumn, and mean onset date differed as much as three

months between sister clades (Fig. 1). We believe such data on phenology evolution, as presented in Figure 1, are important to consider in relation to conceptions of phylogenetic constraints, and we will discuss this further below.

No difference in flowering onset dates was found (Fig. 2) in the PIC study contrasting wind- versus biotically pollinated clades (test 1a, Table 3): five contrasts were in favor of the hypothesis and five were against; that is, there was no consistent directional difference between wind- and biotically pollinated sister clades. However, a closer analysis of the dataset revealed that all clades consisting of wind-pollinated trees (PICs 2, 3, 5, 7, and 14 in Tables 1 and 2) flowered earlier than their biotically pollinated sister clades (test 1b, Table 3).

As phenological information in floras most often is denoted by months only, the duration of flowering is undoubtedly overestimated. Mean duration of flowering per clade was normally distributed and varied from less than a month to more than seven months. We found no difference in duration of flowering between pollination modes (test 2, Table 3): five contrasts were against and five were in favor of the hypothesis.

Phenological spread (Fig. 3), that is, standard deviation of onset of flowering of species within a clade, was analyzed using two different levels of replication (see Discussion). In both analyses we found significant differences between pollination modes (tests 3a and 3b, Table 3). These results indicate that biotically pollinated plant species separate their flowering more than abiotically pollinated plant species. Using all local contrasts, 22 contrasts were in favor and 10 were against the hypothesis, whereas, using the dominating sign within each PIC, nine were in favour and two were against the hypothesis.

Finally, we compared species richness between the different pollination modes in geographically overlapping sister clades. In biotically pollinated clades species richness ranged between five and almost 4000 species, whereas the species richness in wind-pollinated clades varied from two to more than 16,000 species (Table 2). In contrast to previous studies, we found no difference in species richness (test 4, Table 3) between pollination modes. Nine contrasts were in favor and six were against the hypothesis that biotic pollination enhances species richness.

DISCUSSION

Based on studies in temperate communities, it has been suggested that wind-pollinated species flower earlier than biotically pollinated species (Clarke 1893; Robertson 1895; Faegri and van der Pijl 1979; Proctor et al. 1996), and it has been described both at the intrageneric level (Wallander 2001) and at the community level (Heinrich 1976) focusing on tree species. This is presumably the result of selection for spreading pollen before the canopy closes (Whitehead 1969; Heinrich 1976), and as such applies primarily to trees. Since all clades consisting entirely of wind-pollinated trees, that is, *Platanus*, *Acer* sp., Fagales, *Populus*, and *Fraxinus* sp., flowered earlier than their biotically pollinated sister clades, this hypothesis was corroborated in the present study. However, if all life-forms of plants were included, there was no

TABLE 2. Derived phenology values and species richness data for phylogenetically independent contrasts (PIC) of pollination modes. Phenology data were compiled from local floras (see Table 1) but species richness is given at the global level. All phenological clade measures (means for flowering onset and duration of flowering, and standard deviations for phenological spread) were derived for each local flora, using each species in the local flora once. Flowering onset is expressed in Julian day number, and duration of flowering and phenological spread in days. *m* is the total number of local samples for each variable.

PIC no.	Region	Local flora†	Sample size		Flowering onset‡		Duration of flowering		Phenological spread		Species richness	
			Biotic	Wind	Biotic	Wind	Biotic	Wind	Biotic	Wind	Biotic	Wind
1	North America	California	3	3	141	121	90	100	17.3	60		
1	North America	Texas	5	4	109	83.5	162	105	54.5	45		
1	North America	Illinois	2	4	116	121	85	60	35.4	24.5		
1	East Asia	Honshu	3	10	101	163	80	84	45.8	25.3		
1	global										89	331
2	North America	Carolinas	2	1	151	91	120	60	0	*		
2	North America	Texas	1	1	121	61	90	90	*	*		
2	North America	Illinois	1	1	181	121	60	30	*	*		
2	global										1600	8
3	North America	Illinois	3	4	91	76	60	60	0	17.3		
3	North America	Texas	5	3	61	41	80	90	0	17.3		
3	North America	California	3	1	121	61	60	60	*	*		
3	North America	Carolinas	4	5	97.7	61	46.7	84	11.5	47.4		
3	global										5	5
4	North America	Illinois	4	1	151	151	67.5	90	42.4	*		
4	North America	Carolinas	9	7	137.7	138.1	66.7	128.6	60.2	34		
4	Europe	The Netherlands	12	4	156	151	80	97.5	25	24.5		
4	East Asia	Honshu	20	5	169	175	70.5	102	48.1	74.7		
4	Australia	South Australia	15	29	119	80.7	106	146.9	111.9	57.4		
4	global										1100	145
5	North America	Illinois	3	17	161	108.6	110	47.6	34.6	26.1		
5	East Asia	Honshu	7	32	211	115.4	68.6	44.1	0	38.4		
5	global										1717	1025
6	North America	Texas	11	1	121	61	98.2	120	48.4	*		
6	Europe	The Netherlands	18	2	132.7	136	98.3	105	29.4	21.2		
6	East Asia	Honshu	24	5	133.5	205	86.3	78	35.3	13.4		
6	global										854	10
7	North America	Illinois	15	5	103	85	46	48	15.2	13.4		
7	Europe	The Netherlands	12	6	81	81	57.5	40	19.5	15.5		
7	East Asia	Honshu	2	2	151	91	45	75	42.4	0		
7	global										400	35
8	North America	Illinois	6	17	126	136.9	55	65.3	12.2	43.9		
8	Europe	The Netherlands	2	10	121	121	105	108	0	46.9		
8	East Asia	Honshu	14	46	163.9	173.2	47.1	73.7	52.2	64.6		
8	Australia	South Australia	27	5	29.7	78.8	158.9	162	48.4	81.4		
8	global										945	2329
9	North America	Illinois	28	27	124.2	181	79.3	92.2	27.5	22		
9	Europe	The Netherlands	63	44	130.4	180.3	106.8	96.8	30.9	17.7		
9	East Asia	Honshu	50	28	141.4	199.2	93.6	91.1	42.6	30.9		
9	global										2300	2050
10	North America	Texas	10	4	76	143.5	225	142.5	73.8	56.8		
10	East Asia	Honshu	3	3	151	151	140	140	52	0		
10	global										1850	65
11	North America	Illinois	1	10	181	199	90	81	*	15.5		
11	North America	California	1	13	181	183.3	60	99.2	*	46.6		
11	Europe	The Netherlands	2	5	166	199	105	72	21.2	16.4		
11	East Asia	Honshu	10	22	256	215.1	69	72.3	40.6	21.3		
11	Australia	South Australia	2	1	136	91	135	120	21.2	*		
11	global										41	503
12	North America	Illinois	2	5	196	193	90	102	21.2	16.4		
12	North America	Texas	5	19	157	196.8	102	69.5	32.9	32.2		
12	global										16	70
13	global										300	18
14	North America	Carolinas	4	4	143.5	98.5	52.5	45	15	15		
14	Europe	Hungary	2	2	106	91	60	60	21.2	0		
14	East Asia	Honshu	7	1	146.7	91	47.1	60	11.3	*		
15	global										3982	2
16	global										475	3006
17	global										2400	16,189
<i>m</i>					43	43	43	43	38	35	16	16

† See Table 1 for references.

‡ Julian day number (denoting flowering onset) in the flora of South Australia were transformed to Northern Hemisphere values by subtracting 180 days.

* Denotes missing data.

TABLE 3. Results of one-tailed sign tests using N phylogenetically independent contrasts. N is the number of informative (non-zero) PICs; n is the total number of PICs including draws, which are uninformative in sign tests. P is the cumulative P -value (Sokal and Rohlf 1995, p. 78). Test 1b was based on a subset in which all wind-pollinated clades consisted entirely of trees. In test 3a the analysis was based on the dominating sign among the local contrasts nested within each PIC, and thus only one contrast for each phylogenetically independent replicate. In test 3b all local contrasts within each PIC were used as independent replicates.

Test	Trait	Prediction	N (n)	P
1a	Flowering onset	biotic > wind	10 (13)	0.38
1b	Flowering onset (trees)	biotic > wind	5 (5)	0.03
2	Duration of flowering	biotic > wind	10 (13)	0.62
3a	Phenological spread	biotic > wind	11 (12)	0.03
3b	Phenological spread	biotic > wind	32 (33)	0.03
4	Species richness	biotic > wind	15 (16)	0.3

consistent directional difference in onset time of flowering. To what extent the other wind-pollinated life-forms have evolved to track or avoid any other biotic or abiotic conditions in a comparable way to wind-pollinated trees remains to be studied. For herbaceous wind-pollinated plants, Kochmer and Handel (1986) suggested an alternative strategy to early flowering, and that is to overtop the surrounding plants, or at least grow high enough to accomplish adequate pollen dispersal. As for early flowering, such a strategy seeks to avoid physical obstacles for pollen dispersal created by the surrounding vegetation. Because of lineage-specific (inherent) differences in growth rate and pollen dispersal efficacy, different species would then reach the necessary height at different times of the season, and subsequently different flowering times. Thus, if the overtopping strategy is true, it could be one explanation for the lack of consistent directional differences in flowering onset between wind- and biotically pollinated clades of other life-forms than trees.

It has been suggested that biotically pollinated plants flower longer than abiotically pollinated plants, and Rabinowitz et al. (1981) actually found narrower (smaller standard deviations) flowering curves for wind-pollinated populations. Longer duration of flowering in biotically pollinated plants is related to the ‘erratic and capricious behaviour of insects’ (Proctor et al. 1996, p. 265), and is considered a bet-hedging strategy. By flowering for a long time, the biotically pollinated plants can track the unpredictable peaks of visitation from pollinators. In contrast, wind-pollinated plants can gain from a shorter duration of flowering. Whitehead (1969) argued that a close coordination of flowering and thus a coincidental release of pollen would be a strategy to overcome the physical obstacles (distance, leaves, interspecific neighbors) for wind pollination. In our study such synchronization of flowering should be reflected by a shorter duration of flowering. However, these hypotheses were not supported here, as we found no difference in duration of flowering between wind- and biotically pollinated plants. It is obvious, though, that Whitehead (1969) focused on the male behavior (pollen dispersal) of the wind-pollinated plant. Our experience from studies within Restionaceae (P. Linder, unpubl. data) is that pollen is released during very short periods of time creating clouds of pollen. But these episodes of pollen release may

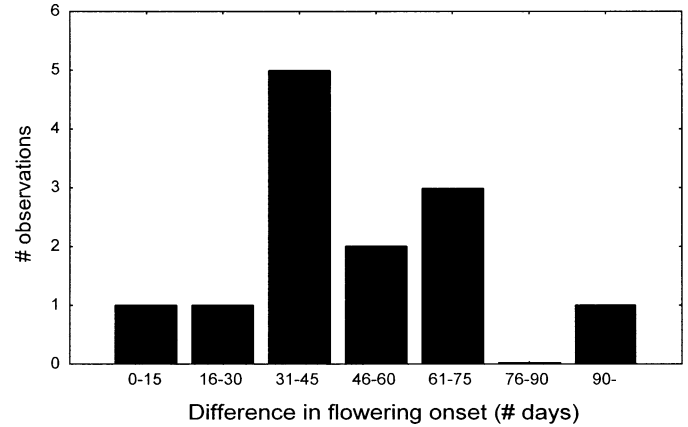


FIG. 1. Differences in flowering onset between contrasted sister clades of wind- versus biotically-pollinated plants. The sample is based on a subset of Table 1, comprising the most species rich local samples of each phylogenetically independent contrast.

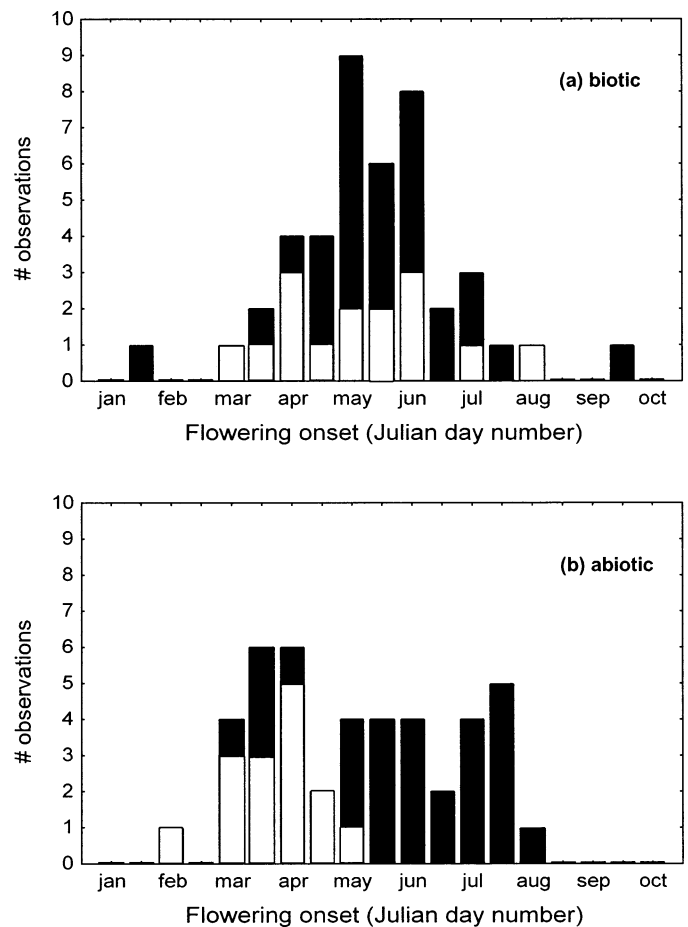


FIG. 2. The distribution of flowering onset for (a) biotically pollinated clades, and (b) abiotically pollinated clades, based on all local samples of each sister clade ($N_{\text{biotic}} = N_{\text{abiotic}} = 43$). White columns represent PICs in which the wind-pollinated clade consists entirely of trees. Flowering onset dates from the flora of South Australia were transformed to Northern Hemisphere values by subtracting 180 days.

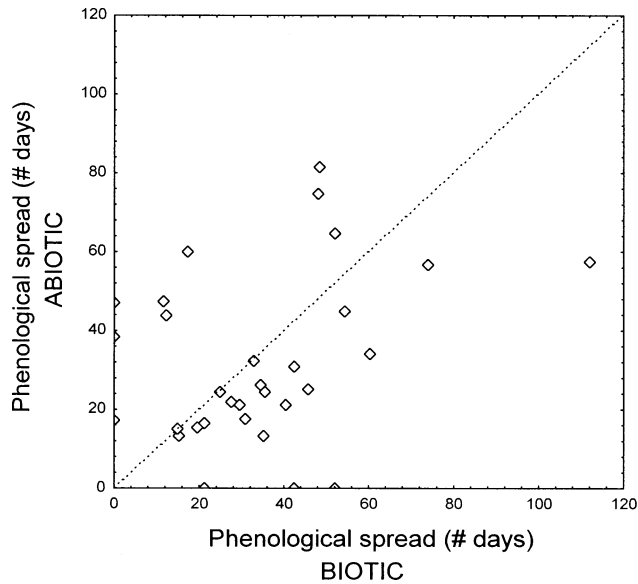


FIG. 3. Independent contrasts of phenological spread for biotically versus abiotically pollinated sister clades, based on all local contrasts of each phylogenetically independent replicate (listed in Table 2). Phenological spread was measured as the standard deviation of flowering onset.

be dependent on unpredictable environmental cues, implying that the female flowering would gain from being extended in time. That stigmas are receptive for a much longer time than the pollen release we also know for Restionaceae. Such an extended duration of female flowering could explain the unpredicted indifference in duration of flowering between wind- and biotically pollinated plants.

Our study supports the idea that biotically pollinated plants separate their flowering times more than abiotically pollinated plants. The main proposed process behind phenological spread among related species has been competition for pollinators (Fenner 1998), but the only previous comparative study on this issue did not find such a difference in phenological spread (Rabinowitz et al. 1981). Because we have only compared patterns, it is of course important to note that any selective process behind these patterns could have been working to aggregate wind-pollinated species as well as separating biotically pollinated species. The advantage for synchronized flowering in wind-pollinated populations is easy to understand (see above). But aggregation of several closely related species, as we have found here, would indicate that pollen clogging is a less important problem in wind-pollinated plants compared to the advantages of environmental cueing. Linder and Midgley (1996) were able to show that wind-pollinated plants can select conspecific pollen from the air, thus avoiding pollen clogging. This is also consistent with the results of Honig et al. (1992).

In contrast, the hypothesis of enhanced pollinator attraction by synchronized flowering, that is, facilitation (Thomson 1978; Rathcke 1983), does not gain any support from this study, even though facilitation as a concept has been developed for species growing together and sharing pollinators (receptor guild), and may not be found among phylogenetically related species.

When analyzing the community-related parameter phenological spread we used both the dominating sign among local contrasts of each PIC, and each local contrast as an independent replicate (tests 3a and 3b respectively, Table 3). The decision to treat each local contrast as an independent replicate was based upon two considerations. First, in their paper on flowering phenology, Kochmer and Handel (1986) found phylogenetic effects (which they called “constraints”). Kochmer and Handel’s (1986) main finding, in this context, was that families flowered in a common order between continents, and not a restriction of the variability of flowering phenologies within families. This family “flowering time mean”, we argue, is proof of lineage-specific effects in a Darwinian unity-of-type sense (Darwin 1859, p. 233), not of constraints, and such lineage-specific effects do not necessarily constrain the possibility of local adaptation. Moreover, sister clades in the present study differed by up to three months in mean flowering onset (Fig. 1). We believe such quantitative information does not help us at all in deciding whether the local adaptability is constrained or not. Therefore, we think it is too early to advocate any statistical decision (cf. Mazer 1998). Second, our study is not a phylogenetically informed community study (Brooks and McLennan 1993; Grandcolas 1998), but a comparison of the evolution in monophyletic clades. Still, the species in each local sample of a clade share a common local ecological history different from samples in other localities. It is difficult to assess to what extent this common ecological history can be responsible for evolved patterns overriding effects based on the common phylogenetic history. Petanidou et al. (1995) argued that local ecological history could be important for phenological community assembly after finding varying patterns of family flowering order on different continents. The argument by Petanidou et al. (1995) is strengthened by the fact that very few species in our study were shared between different local floras.

Based on these two considerations, we believe that phenology studies are improved by incorporating separate analyses of local contrasts. We argue that it is too early to omit local contrasts on assumptions of phylogenetic constraints. Also, the ongoing discussion of “true” replication or “pseudoreplication” resulting in inflated degrees of freedom in comparative ecology (e.g., Harvey et al. 1995; Westoby et al. 1995; Mazer 1998) calls for the incorporation of both levels of replication.

The idea of pollinator-assisted radiation of species has strong proponents in the history of evolutionary botany (Grant 1949; Stebbins 1981; Crepet 1984). But during the last decades the mechanisms behind this positive correlation between biotic pollination and speciation have been questioned, mainly due to growing evidence that many plant-pollinator interactions are generalized (Waser et al. 1996; Ollerton and Cranmer 2002). At the same time, support for an association between biotic pollination and species richness has come from phylogenetically informed studies (Eriksson and Bremer 1992; Ricklefs and Renner 1994; Dodd et al. 1999). In fact, our study is the first considering phylogenetic information that finds no support for higher species richness in biotically pollinated clades. We would like to think that this finding is a result of two improvements in the approach

we have used. First, using more detailed phylogenies, we located nodes of change in which wind pollination evolved, and used the descending clades for our comparisons rather than using a certain taxonomic level, for example family, as has been common previously. Furthermore, we had to omit a large proportion of the nodes used in Dodd et al. (1999) as they are not supported by recent phylogenies (e.g. Soltis et al. 2000). Apart from the exception Poaceae, mentioned by Dodd et al. (1999), we have also found comparatively high species richness in the wind-pollinated clades of *Thalictrum*, Urticales, Artemisiinae, Ambrosiinae, and Sauraceae/Piperaceae. Second, and probably more interesting, we included in our dataset only sister clades that have overlapping global distributions. Because wind pollination increases as a function of latitude (Whitehead 1969; Regal 1982) and diversity decreases with latitude (Brown and Lomolino 1998, p. 450), there is a biogeographic autocorrelation between pollination mode and diversity. We tried to reduce this effect by restricting our dataset to geographically overlapping sister clades.

A potential problem when correlating a character state to species richness and diversification rates, is that the clade characterized by the novel trait is by definition entering a new niche space. Of the two sister clades contrasted, one is thus being retained in an existing occupied niche space and the other is entering an unoccupied niche space, and their potential radiation may therefore not be comparable. From this perspective, the prediction would be that change in itself enhances species richness. The present study, in which we have contrasted species richness between biotic versus wind-pollinated clades, wind pollination is consistently the derived state, and thus we can not know if it is the change per se or wind pollination that is responsible for the pattern found. Preferably, to test for effects of pollination mode on species richness, we would need independent contrasts of both gains and losses of the contrasted modes. Secondary origins of biotic pollination are extremely rare, though, and neither we nor any of the previous students of these issues (Eriksson and Bremer 1992; Ricklefs and Renner 1994; Dodd et al. 1999) have been able to incorporate any of them in their studies.

A shortcoming in our study, which is common to studies using phylogenetically independent contrasts, is the small sample size. In the current study the dataset was reduced even further by the requirement of geographically overlapping sister clades. In spite of these weaknesses, we conclude that wind pollination does not generally imply “a lowering of net speciation rate” as Dodd et al. (1999, p. 737) suggested, and believe it is still an open question to what extent, and under which conditions, biotic pollination has been important for angiosperm radiation. Temporal and spatial variation in plant-pollinator interactions needs to be investigated to quantify whether local or ephemeral periods of specialization (Thompson 1994) might be a mechanism behind pollinator-assisted speciation. Because most plant-pollinator assemblages are compiled from flower visitation data, there is a need to quantify pollinator efficacy. From such information we can judge whether apparently generalized plant-pollinator interactions are in fact specialized, or at least exert directional selection, due to certain particularly efficient pollinators

(Schemske and Horvitz 1984; Ollerton 1996; Waser et al. 1996). Furthermore, we hope our approach will be used both in local field studies of phenological community structure and with better-resolved phylogenetic hypotheses. The primary advantage of better-resolved data would of course be to challenge not only the evidence from this study of wider phenological spread in biotically pollinated plants, but also the lack of differences in the other phenological variables. Detailed field phenology data for wind-pollinated plants are extremely rare in the literature. Field studies are also needed to evaluate the relative selective importance of phylogenetically related versus functionally related species. In addition, internal phylogenies and higher resolution of phenological data would admit a deepened discussion about which evolutionary processes have been responsible for the differing phenological patterns, both in particular clades and in communities with varying conditions.

ACKNOWLEDGMENTS

We are grateful to C. Fenster, D. Ackerly, and two anonymous reviewers who made valuable comments on the manuscript. The Swedish Natural History Museum kindly gave access to their herbarium and library, and the Swedish Research Council supported the study financially.

LITERATURE CITED

- Ackerly, D. D., and M. J. Donoghue. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). *Am. Nat.* 152:767–791.
- Ashton, P. S., T. J. Givnish, and S. Appanah. 1988. Staggered flowering in the Dipterocarpaceae—new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* 132:44–66.
- Augsburger, C. K. 1983. Phenology, flowering synchrony, and fruit set of six Neotropical shrubs. *Biotropica* 15:257–267.
- Bell, D. T., and L. J. Stephens. 1984. Seasonality and phenology of kwongan species. Pp. 205–226 in J. S. Pate and J. S. Beard, eds. *Kwongan: plant life of the sandplain*. Univ. of Australia Press, Nedlands, Australia.
- Bremer, K., A. Anderberg, P. O. Karis, B. Nordenstam, J. Lundberg, and O. Ryding. 1994. Tribe Anthemideae. Pp. 438–478 in K. Bremer, ed. *Asteraceae. Cladistics and classification*. Timber Press, Portland, OR.
- Bremer, K., M. W. Chase, P. F. Stevens, A. A. Anderberg, A. Backlund, B. Bremer, B. G. Briggs, P. K. Endress, M. F. Fay, P. Goldblatt, M. H. G. Gustafsson, S. B. Hoot, W. S. Judd, M. Kallersjö, E. A. Kellogg, K. A. Kron, D. H. Les, C. M. Morton, D. L. Nickrent, R. G. Olmstead, R. A. Price, C. J. Quinn, J. E. Rodman, P. J. Rudall, V. Savolainen, D. E. Soltis, P. S. Soltis, K. J. Sytsma, and M. Thulin. 1998. An ordinal classification for the families of flowering plants. *Ann. Mo. Bot. Gard.* 85: 531–553.
- Brody, A. K. 1997. Effects of pollinators, herbivores, and seed predators on flowering phenology. *Ecology* 78:1624–1631.
- Brooks, D. M., and D. A. McLennan. 1993. Historical ecology: examining phylogenetic components of community evolution. Pp. 267–280 in R. E. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities. Historical and geographical perspectives*. Univ. of Chicago Press, Chicago, IL.
- Brown, J. H., and M. V. Lomolino. 1998. *Biogeography*. Sinauer Associates, Sunderland, MA.
- Carpenter, F. L. 1976. Plant-pollinator interactions in Hawaii: pollination energetics of *Metrosideros collina* (Myrtaceae). *Ecology* 57:1125–1144.
- Chase, M. W., D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y. L. Qiu,

- K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedren, B. S. Gaut, R. K. Jansen, K. J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. H. Strauss, Q. Y. Xiang, G. M. Plunkett, P. S. Soltis, S. M. Swensen, S. E. Williams, P. A. Gadek, C. J. Quinn, L. E. Eguarte, E. Golenberg, G. H. Learn, S. W. Graham, S. C. H. Barrett, S. Dayanandan, and V. A. Albert. 1993. Phylogenetics of seed plants—an analysis of nucleotide-sequences from the plastid gene *rbcL*. *Ann. Mo. Bot. Gard.* 80: 528–580.
- Clarke, H. L. 1893. The philosophy of flower seasons. *Am. Nat.* 27:769–781.
- Correll, D. S., and M. C. Johnston. 1970. *Manual of the vascular plants of Texas*. Texas Research Foundation, Renner, TX.
- Crepet, W. L. 1984. Advanced (constant) insect pollination mechanisms: patterns of evolution and implication vis-a-vis angiosperm diversity. *Ann. Mo. Bot. Gard.* 71:607–630.
- Culley, T. M., S. G. Weller, and A. K. Sakai. 2002a. The evolution of wind pollination in angiosperms. *Trends Ecol. Evol.* 17: 361–369.
- Culley, T. M., 2002b. Evolution of wind pollination in angiosperms. *Trends Ecol. Evol.* 17:491.
- Darwin, C. 1859. *On the origin of species by means of natural selection*. Penguin Books, London.
- Dodd, M. E., J. Silvertown, and M. W. Chase. 1999. Phylogenetic analysis of trait evolution and species diversity variation among angiosperm families. *Evolution* 53:732–744.
- Eriksson, O., and B. Bremer. 1992. Pollination systems, dispersal modes, life forms, and diversification rates in angiosperm families. *Evolution* 46:258–266.
- Eriksson, T., M. J. Donoghue, and M. S. Hibbs. 1998. Phylogenetic analysis of *Potentilla* using DNA sequences of nuclear ribosomal internal transcribed spacers (ITS), and implications for the classification of Rosoideae (Rosaceae). *Plant Syst. Evol.* 211: 155–179.
- Faegri, K., and L. van der Pijl. 1979. *The principles of pollination ecology*. Pergamon Press, Oxford, U.K.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- Fenner, M. 1998. The phenology of growth and reproduction in plants. *Perspect. Plant Ecol. Evol. Syst.* 1:78–91.
- Giannasi, D. E., G. Zurawski, G. Learn, and M. T. Clegg. 1992. Evolutionary relationships of the Caryophyllidae based on comparative *rbcL* sequences. *Syst. Bot.* 17:1–15.
- Gotelli, N. J., and G. R. Graves. 1996. The temporal niche. Pp. 95–111 in N. J. Gotelli and G. R. Graves, eds. *Null models in ecology*. Smithsonian Institution, Washington, D.C.
- Grandcolas, P. 1998. Phylogenetic analysis and the study of community structure. *Oikos* 82:397–400.
- Grant, V. 1949. Pollination systems as isolating mechanisms in angiosperms. *Evolution* 3:82–97.
- . 1994. Modes and origins of mechanical and ethological isolation in angiosperms. *Proc. Natl. Acad. Sci. USA* 91:3–10.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford Univ. Press, Oxford, U.K.
- Harvey, P. H., A. F. Read, and S. Nee. 1995. Why ecologists need to be phylogenetically challenged. *J. Ecol.* 83:535–536.
- Heinrich, B. 1976. Flowering phenologies: bog, woodland, and disturbed habitats. *Ecology* 57:890–899.
- Honig, M. A., H. P. Linder, and W. J. Bond. 1992. Efficacy of wind pollination: pollen load size and natural microgametophyte populations in wind-pollinated *Staber banksii* (Restionaceae). *Am. J. Bot.* 79:443–448.
- Jessop, J. P., and H. R. Toelken. 1986. *Flora of South Australia*. South Australia Government Printing Division, Adelaide, Australia.
- Johansson, J. T. 1995. A revised chloroplast DNA phylogeny of the Ranunculaceae. *Plant Syst. Evol.* 9(supp.):253–261.
- Johnson, S. D. 1993. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. *J. Ecol.* 81:567–572.
- Jones, G. N., and G. D. Fuller. 1955. *Vascular plants of Illinois*. Univ. of Illinois Press, Urbana, IL.
- Kochmer, J. P., and S. N. Handel. 1986. Constraints and competition in the evolution of flowering phenology. *Ecol. Monogr.* 56: 303–325.
- Leskinen, E., and C. Alstrom-Rapaport. 1999. Molecular phylogeny of Salicaceae and closely related Flacourtiaceae: evidence from 5.8 S, ITS 1 and ITS 2 of the rDNA. *Plant Syst. Evol.* 215: 209–227.
- Levin, D. A., and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. *Am. Nat.* 104: 455–467.
- Linder, H. P., and J. M. Midgley. 1996. Anemophilous plants select pollen from their own species from the air. *Oecologia* 108:85–87.
- Mabberley, D. J. 1997. *The plant-book*. Cambridge Univ. Press, Bath, U.K.
- Mazer, S. J. 1998. Alternative approaches to the analysis of comparative data: compare and contrast. *Am. J. Bot.* 85:1194–1199.
- Miao, B. M., B. L. Turner, and T. J. Mabry. 1995. Systematic implications of chloroplast DNA variation in the subtribe Ambrosiinae (Asteraceae, Heliantheae). *Am. J. Bot.* 82:924–932.
- Møller, A. P., and T. R. Birkhead. 1992. A pairwise comparative method as illustrated by copulation frequency in birds. *Am. Nat.* 139:644–656.
- Mosquin, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* 22:398–402.
- Munz, P. A. 1974. *A flora of southern California*. Univ. of California Press, Berkeley, CA.
- Ohwi, J. I. E. 1965. *Flora of Japan*. Smithsonian Institution, Washington, D.C.
- Ollerton, J. 1996. Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant-pollinator systems. *J. Ecol.* 84:767–769.
- Ollerton, J., and L. Cranmer. 2002. Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? *Oikos* 98:340–350.
- Ollerton, J., and A. J. Lack. 1992. Flowering phenology—an example of relaxation of natural selection. *Trends Ecol. Evol.* 7: 274–276.
- Petanidou, T., W. N. Ellis, N. S. Margaritis, and D. Vokou. 1995. Constraints on flowering phenology in a phryganic (east Mediterranean shrub) community. *Am. J. Bot.* 82:607–620.
- Pico, F. X., and J. Retana. 2000. Temporal variation in the female components of reproductive success over the extended flowering season of a Mediterranean perennial herb. *Oikos* 89:485–492.
- Primack, R. B. 1985. Patterns of flowering phenology in communities, populations, individuals and single flowers. Pp. 571–593 in J. E. White, ed. *The population structure of vegetation*. Junk, Dordrecht, The Netherlands.
- Proctor, M., P. Yeo, and A. Lack. 1996. *The natural history of pollination*. Harper Collins, London.
- Qiu, Y. L., M. W. Chase, S. B. Hoot, E. Conti, P. R. Crane, K. J. Sytsma, and C. R. Parks. 1998. Phylogenetics of the Hamamelidae and their allies: Parsimony analyses of nucleotide sequences of the plastid gene *rbcL*. *Int. J. Plant Sci.* 159:891–905.
- Rabinowitz, D., J. K. Rapp, V. L. Sork, B. J. Rathcke, G. A. Reese, and J. C. Weaver. 1981. Phenological properties of wind and insect pollinated prairie plants. *Ecology* 62:49–56.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. *Manual of the vascular flora of the Carolinas*. Univ. of North Carolina Press, Chapel Hill, NC.
- Rathcke, B. J. 1983. Competition and facilitation among plants for pollination. Pp. 305–338 in L. A. Real, ed. *Pollination biology*. Academic Press, New York.
- Rathcke, B. J., and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.* 16:179–214.
- Regal, P. J. 1982. Pollination by wind and animals: Ecology of geographic patterns. *Annu. Rev. Ecol. Syst.* 13:497–524.
- Rezső, S. 1966. *A Magyar Flóra és Vegetáció Rendszertani-Növényföldrajzi Kézikönyve II*. Akadémiai Kiadó, Budapest.
- Richardson, J. E., M. F. Fay, Q. C. B. Cronk, D. Bowman, and M. W. Chase. 2000. A phylogenetic analysis of Rhamnaceae using *rbcL* and trnL-F plastid DNA sequences. *Am. J. Bot.* 87: 1309–1324.
- Ricklefs, R. E., and S. S. Renner. 1994. Species richness within families of flowering plants. *Evolution* 48:1619–1636.

- Robertson, C. 1895. The philosophy of flower seasons, and the phaenological relations of the entomophilous flora and the anthophilous insect fauna. *Am. Nat.* 29:97–117.
- Schemske, D. W., and C. C. Horvitz. 1984. Variation among floral visitors in pollination ability: a precondition for mutualism specialization. *Science* 225:519–521.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. 3rd ed. W. H. Freeman, New York.
- Soltis, D. E., P. S. Soltis, D. R. Morgan, S. M. Swensen, B. C. Mullin, J. M. Dowd, and P. G. Martin. 1995. Chloroplast gene sequence data suggest a single origin of the predisposition for symbiotic nitrogen-fixation in angiosperms. *Proc. Natl. Acad. Sci. USA* 92:2647–2651.
- Soltis, D. E., P. S. Soltis, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Sweere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, S. M. Chaw, L. J. Gillespie, W. J. Kress, and K. J. Sytsma. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Ann. Mo. Bot. Gard.* 84:1–49.
- Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, L. M. Prince, W. J. Kress, K. C. Nixon, and J. S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, rbcL, and atpB sequences. *Bot. J. Linn. Soc.* 133:381–461.
- StatSoft 1999. *Statistica for Windows*. StatSoft, Inc., Tulsa, OK.
- Stebbins, G. L. 1981. Why are there so many species of flowering plants? *Bioscience* 31:573–577.
- Stiles, F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* 198:1177–1178.
- Thomson, J. D. 1978. Effect of stand composition on insect visitation in two species mixtures of *Hieracium*. *Am. Midl. Nat.* 100:431–440.
- Thompson, J. N. 1994. *The coevolutionary process*. Univ. of Chicago Press, Chicago, IL.
- Ueda, K., T. Hanyuda, A. Nakano, T. Shiuchi, A. Seo, H. Okubo, and M. Hotta. 1997. Molecular phylogenetic position of Podostemaceae, a marvelous aquatic flowering plant family. *J. Plant Res.* 110:87–92.
- van der Meijden, R. 1996. *Heukels' Flora van Nederland*. Wolters-Noordhoff, Groningen, The Netherlands.
- Wallander, E. 2001. Evolution of wind-pollination in *Fraxinus* (Oleaceae)—an ecophylogenetic approach. Ph.D. diss. Göteborg University, Göteborg.
- Wallander, E., and V. A. Albert. 2000. Phylogeny and classification of Oleaceae based on rps16 and trnL-F sequence data. *Am. J. Bot.* 87:1827–1841.
- Waser, N. 1983. Competition for pollination and floral character differences among sympatric plant species: a review of evidence. Pp. 277–293 in C. S. Jones and R. J. Little, eds. *Handbook of experimental pollination biology*. Van Nostrand-Reinhold, New York.
- . 1998. Pollination, angiosperm speciation, and the nature of species boundaries. *Oikos* 82:198–201.
- Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77:1043–1060.
- Watson, L. E., T. M. Evans, and T. Boluarte. 2000. Molecular phylogeny and biogeography of tribe Anthemideae (Asteraceae), based on chloroplast gene ndhF. *Mol. Phylogenet. Evol.* 15: 59–69.
- Weimarck, H. 1963. *Skånes flora*. Bokförlaget Corona AB, Malmö, Sweden.
- Westoby, M., M. R. Leishman, and J. M. Lord. 1995. On misinterpreting the phylogenetic correction. *J. Ecol.* 83:531–534.
- Whitehead, D. R. 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. *Evolution* 23: 28–35.
- Wickman, P.-O. 1992. Sexual selection and butterfly design—a comparative study. *Evolution* 46:1525–1536.

Corresponding Editor: C. Fenster