

HERBARIUM DATA REVEAL AN ASSOCIATION BETWEEN FLESHY FRUIT TYPE AND EARLIER FLOWERING TIME

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Herbarium phenology data were evaluated and then applied in a phylogenetically independent contrast study in which flowering times were compared between fleshy and nonfleshy-fruited plants growing in the north-temperate provinces of Uppland and Södermanland, southeastern Sweden (59°–60°N). To evaluate herbarium phenology data, flowering-time information taken from herbarium specimens in the Swedish Natural History Museum (S) was compared with two independent field phenology data sets. Herbarium collections and the field studies were restricted to the province of Uppland. Flowering times derived from herbarium specimens correlated equally well with each of the two field-phenology data sets as the field phenology data sets did to each other. Differences between flowering times derived from field and herbarium collections were not affected by the number of herbarium specimens used. However, these differences in flowering times were affected by flowering season such that herbarium-derived flowering times were later for early spring-flowering species and earlier for late summer-flowering species when compared with flowering times derived from field data. In the phylogenetically independent contrast study of mean flowering times in fleshy- compared with nonfleshy-fruited plants, herbarium data were compiled for 77 species in 17 phylogenetically independent contrasts. Flowering time was found to be earlier for fleshy-fruited taxa, illustrating the evolutionary interdependence between flowering and fruiting phases and the constraining effects of a north-temperate climate on phenology evolution. This study shows that herbaria are reliable and time-saving data sources for comparative phenology studies and allow for studies at large phylogenetic and geographic scales that would otherwise be impossible.

Keywords: fleshy fruits, flowering phenology, fruiting phenology, frugivory, herbaria, phylogenetic comparative methods, reproductive phenology, temperate biome.

Introduction

Seasonal change is one of the most striking phenomena in nature, and phenological knowledge is of great economic importance in agriculture, silviculture, and hunter cultures. Accordingly, the literature holds numerous phenological data sets, and phenology may even be the most widely documented quantitative character in ecology, considering the amount of flowering-time data found in the floristic literature. Numerous laymen and professionals have documented phenological events during the last centuries (Schnelle 1955), and some long-term data sets have become biological indicators of the globally changing climate (Walther et al. 2002; Root et al. 2003).

Despite this long-standing tradition of field observations, plant phenological traits are lacking from general ecological and evolutionary theories. Seed size, leaf type, plant height, dispersal syndrome, pollination syndrome, age at reproduction, growth form, and position of buds or regenerating parts have all been examined in relation to general theories on plant strategy, distribution, and diversity, but never plant phe-

nology (Raunkiaer 1934; Grime 1977; Regal 1982; Eriksson and Bremer 1992; Westoby 1998; Dodd et al. 1999; Verdu 2002; Wright et al. 2004). Most empirical work on plant phenology has analyzed phenological variation within local populations in relation to plant-animal interactions and abiotic cues (Primack 1985; Rathcke and Lacey 1985; Primack 1987; Fenner 1998). Only rarely has interspecific variation in phenology been examined at wider geographic and phylogenetic scales (Bell and Stephens 1984; Kochmer and Handel 1986; Johnson 1993; Wright and Calderon 1995), and little more than a handful of studies have controlled for phylogenetic relatedness when analyzing phenology in relation to other plant characteristics (Eriksson and Ehrlén 1991; Johnson 1993; Eriksson and Ehrlén 1998; Oberrath and Böhning-Gaese 2002; Bolmgren et al. 2003; Debussche et al. 2004). Understanding variation in phenology in relation to variation in climate, life history, and phylogeny would be an important contribution to the understanding of plant ecology and evolution and would advance the science of predictive modeling by a better understanding of differential phenological response to changing conditions, e.g., global change.

The lack of general theories on the ecology and evolution of plant phenology, we believe, is the result of two main problems. First, phenology observations are expressed in calendar days, and because of the strong correlation between local climate and phenological events, calendar days are not

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homologous between distant localities; April in Paris is not homologous to April in Moscow from a phenological point of view. Thus, phenological information from distant localities is difficult to compare, which is probably one reason for phenology to be excluded from systematic literature with a worldwide coverage (Engler and Prantl 1887–1915; Kubitzki 1990). Second, the compilation of phenological data with sufficient resolution for most comparative studies is labor intensive. The inclusion of plant phenology within theories on plant strategies, distribution, and diversity that are valid across climate regions, vegetation types, latitudes, altitudes, and across phylogenies is therefore in need of phenological measures comparable between sites/climates and accessible phenological data that is resolved at a finer scale than in the existing literature. Herbarium specimens include information on date and locality of collection and phenological phase and may therefore be an alternative source of data for comparative phenology studies solving one of the two main problems for comparative phenology. Herbarium phenology data have previously been used in comparative studies to analyze flower initiation in relation to photoperiod (Rivera and Borchert 2001) and seasonal drought (Borchert 1996) and to quantify effects of climate change (Primack et al. 2004). However, its reliability has never been evaluated. In this study, we set out to do such an evaluation, by comparing flowering times derived from herbarium specimens with flowering-time data collected by two independent field studies (Arnell 1923; Diekmann 1996).

As an illustration of the usefulness of herbarium phenology data, the second part of this study uses herbarium phenology data in a comparative study of flowering time for fleshy-versus nonfleshy-fruited angiosperms. Previous examinations of phenological patterns in fleshy-fruited plants have focused on fruiting phenology, examining whether seasonal shifts in frugivore behavior and abundance are associated with shifts in ripening phenologies (Stiles 1977; Thompson and Willson 1979; Stapanian 1982; Skeate 1987; Debussche and Isenmann 1992; French 1992; Fuentes 1992; Noma and Yumoto 1997; Guitián 1998). The morphological continuity between flowers and fruits underline the phenological interdependence expected between the flowering and fruiting phenophases (Primack 1987), and evolution of flowering and fruiting phenologies are generally assumed to be constrained by each other (Rathcke and Lacey 1985; but see Primack 1987; Gorchoy 1990; Eriksson and Ehrlén 1991; Lechowicz 1995; Fenner 1998; Oberrath and Böhning-Gaese 2002; Bolmgren 2004; Debussche et al. 2004). A short vegetative and reproductive season, which is the case for the north-temperate plants sampled in this study, may also constrain the evolution of flowering and fruiting phenologies. These constraints may be further accentuated for fleshy-fruited plants, as fleshy fruits in general have larger seeds (K. Bolmgren et al., unpublished data; Hughes et al. 1994), larger seed size is correlated with longer fruit development time (Eriksson and Ehrlén 1991), and fleshy fruits need to ripen before autumn-migrating frugivores leave and/or before autumn frosts.

The objective of this study is twofold. First, we evaluate flowering-time data derived from herbarium collections by posing three questions: (1) do herbarium-derived flowering-time data correlate as well to field-derived data as indepen-

dent field data do to each other? Are differences between herbarium-derived and field-derived flowering-time data affected by (2) flowering season and/or (3) the available number of herbarium specimens? The second objective of the study is to use herbarium-derived flowering times in a phylogenetically independent contrast study in which we test for a difference in flowering time between fleshy- and nonfleshy-fruited taxa.

Material and Methods

For both the evaluation of herbarium phenology data and the independent-contrasts study of flowering times in fleshy-versus nonfleshy-fruited taxa, herbarium flowering times were derived from specimens in the Nordic Herbarium of the Swedish Natural History Museum (S). In total, this study was based on ca. 5500 specimens collected from 1813 to 2000.

Herbarium Phenology Evaluation

Two independent field phenology studies (Arnell 1923; Diekmann 1996) were used to evaluate the reliability of herbarium-derived flowering-time data. Arnell (1923) was based on a 45-yr-long phenological survey in the provinces of Södermanland and Uppland (59°–60°N), southeastern Sweden. The Arnell (1923) data set consists of 133,000 data points, mainly on flowering onset, compiled by laymen and professionals according to a specified procedure and reported to the Swedish National Meteorological-Hydrographical Institute. Arnell (1923) derived mean flowering onset dates for the provinces as a whole and, which is more relevant for this study, a calendar for the province of Uppland, stating which species start to flower on a specific date. This calendar was derived from a subsample of the larger survey and additional studies by Arnell in the vicinity of the city of Uppsala. Diekmann (1996) performed a 2-yr phenology study in a deciduous forest close to the city of Uppsala (59°49'N) on 29 understory species. Twenty-six species overlapped between the Arnell and Diekmann data set, and for these we compiled flowering times based on herbarium specimens collected in the province of Uppland. The herbarium data set thus consisted of collection dates for all specimens that were in flower. For each species, three different flowering-time measures were derived: (1) mean flowering date based on all flowering specimens (MFD); (2) mean flowering date based on 90% of the specimens, that is, the 5% tails of early- and late-opening tails were excluded (MFD-10%); and (3) first flowering date derived by taking the collection date of the first flowering specimen after excluding the first flowering 10% (FFD-10%). All measures are expressed in day number of the year (Julian day). The reason for excluding the “tails” in measures (2) and (3) was a suspicion that collectors overestimate extreme events.

To evaluate herbarium flowering-time data, we (1) compared correlations between flowering times for the 26 species in the two field data sets and the herbarium data set. We also analyzed whether the differences between herbarium-derived and field-derived flowering times were affected by (2) the number of herbarium specimens used per species or (3) flowering season. In (2) and (3), we used a larger subsample of 77 species from the Arnell data set, overlapping with the

sample used in the independent-contrasts study (see below). All analyses were performed as product-moment correlations in STATISTICA (StatSoft 1999). In (1), α values were Bonferroni adjusted by dividing them with the number of tests performed.

Independent Contrast Study

Mean flowering times were compared for fleshy- and nonfleshy-fruited taxa in a phylogenetically independent contrasts study. We derived 17 phylogenetically independent contrasts based on the provincial floras of Uppland and Södermanland and recently published phylogenetic hypotheses. Contrasted taxa and references to phylogenies are given in the appendix. In total, the sample consisted of 77 species. Collection dates for flowering specimens were compiled from herbarium specimens collected in the provinces of Södermanland and Uppland, southeastern Sweden (59°–60°N). Mean flowering times were derived for each sister clade (Møller and Birkhead 1992; Wickman 1992), and we used the Wilcoxon matched-pair test in STATISTICA (StatSoft 1999) to analyze the phylogenetically independent flowering-time contrasts.

Results

Flowering times derived from herbarium specimens correlated equally well with field data as the field data sets did with each other, irrespective of which flowering-time measure that was derived from the herbarium collections (table 1). No effect was found for the number of herbarium specimens used on the differences in flowering time between herbarium and field data (fig. 1A; $N = 77$, $P = 0.17$), while flowering time was negatively correlated to this difference between herbarium and field data (fig. 1B; $N = 77$, $P = 0.025$, $R = -0.25$). This negative correlation may be an effect of the earliest and latest flowering species, as the effect disappeared when the first and last flowering month of the sample (seven out of 77 species) were excluded from the analysis.

In 13 out of 17 phylogenetically independent contrasts, the fleshy-fruited plants flowered earlier than their nonfleshy-fruited sister plants (fig. 2), which indicates that there is a significant effect of fruit type on flowering time (Wilcoxon matched-pair test; $N = 17$, $P = 0.04$).

Discussion

Herbarium Phenology Data

In addition to the traditional use for morphological, systematic, and biogeographic work, herbaria have to some extent been used in applied ecology studying effects of climate change (Primack et al. 2004), plant invasions (Catling and Porebski 1994; Stadler et al. 1998; Weber 1998; Heise and Merenlender 2002; Saltonstall 2002; Delisle et al. 2003), and temporal variation in abundance (Burgman et al. 1995; McCarthy 1998; Ponder et al. 2001; Hedenäs et al. 2002; Skarpaas 2003). However, herbarium-based studies in comparative phenology are scarce (Karlsson 1976; Borchert 1996; Rivera and Borchert 2001; Primack et al. 2004). Based on the experience from this study, herbaria are time-saving and reliable data sources for studies in comparative phenology. Herbarium flowering-time data may be given on a much finer scale compared to most data in the floristic literature, and herbaria are available independent of season. For future herbarium studies, we estimate that flowering time may be derived for at least 10 species per day. Previous examinations of herbaria as a phenology data source have found that herbarium data yield longer flowering-time duration than field studies, because herbarium specimens are collected from a larger geographic area (Borchert 1996), and that herbarium data yield shorter flowering-time durations than is given in floras (Bolmgren et al. 2003).

A word of caution is warranted because this study of north-temperate data found a negative correlation between flowering time and the differences between herbarium and field data. A plausible explanation for this pattern may be that field collectors aim at collecting many species on each trip and therefore avoid early and late seasons when few species are flowering. Thus, early-flowering species are mainly collected late in their flowering period and late-flowering species early in their flowering period. Acknowledging such problems with herbarium data, we believe that the tremendous amount of phenology data stored in herbaria will make an outstanding contribution for studies in comparative phenology. For many studies, the resolution of flowering-time data given in floras will be sufficient, but when a higher resolution is needed, herbaria will be most interesting to consider. Herbarium data can, of course, never replace transplantations and experimental treatments, and herbarium data will not be very useful when examining details of the phenological

Table 1

Product-Moment Correlation Coefficients between Different Flowering-Time Measures Derived from Herbarium Collection (This Study) and Field Observations

$N = 26$	MFD (this study)	MFD-10% (this study)	FFD-10% (this study)	FFD (Diekmann 1996)
MFD-10% (this study)	0.998***
FFD-10% (this study)	0.983***	0.988***
FFD (Diekmann 1996)	0.969***	0.967***	0.958***	...
FFD (Arnell 1923)	0.963***	0.968***	0.972***	0.937***

Note. MFD, mean flowering date; FFD, first flowering date; MFD-10%, mean flowering date derived after excluding the earliest and latest 5% of the sample; FFD-10%, first flowering date derived after excluding the earliest 10% of the sample. All analyses were based on the same sample of 26 species, and α values were Bonferroni adjusted.

*** $P < 0.001$.

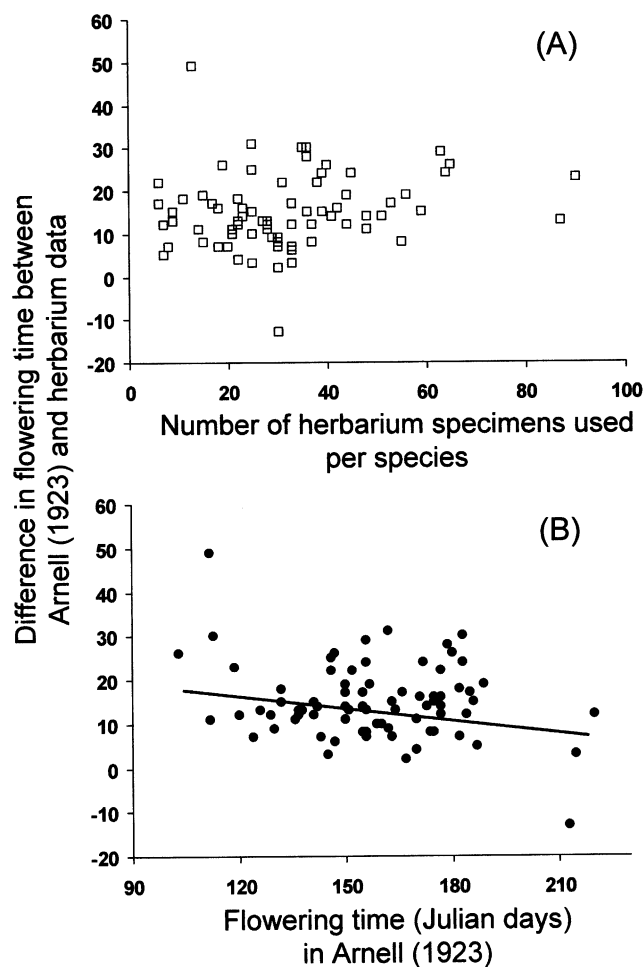


Fig. 1 Differences in flowering time between mean flowering date derived from the herbarium data set and first flowering date from the Arnell (1923) data set in relation to (A) the number of herbarium specimens used per species and (B) flowering time.

curve, e.g., the shape of the temporal distribution of flowering opening or fruit ripening (Malo 2002). But for more coarse studies in comparative phenology, herbarium data will be most suitable and time saving. The between-year variation in climate (and other phenological cues) may not be as big a problem for herbarium data as one may first suspect. Field phenology data collected in a few consecutive years in a restricted number of populations and in a restricted area suffers from being dependent from the conditions prevailing during years in a similar way as herbarium phenology data suffer from being collected in a large number of years and in larger areas.

Phenological observations are among the best indicators of global change (Walther et al. 2002; Root et al. 2003), and recently Primack et al. (2004) showed that herbaria may be used in such studies. We believe a word of caution is warranted when considering herbarium data for studies in relation to climate change, as variation in collectors' efforts over time may create important biases in herbarium data sets. Our data set covered the last two centuries and would thus

be most interesting to examine in relation to climate change. However, the collections are unequally distributed over time, with many fewer collections per year in the post-World War period, and thus mean values are expected to decrease over time. Therefore, any variation in flowering time over time may be an effect of variation in collectors' efforts rather than of raising temperatures.

Flowering-Time Contrasts

This study underlines the evolutionary interdependence between flowering and fruiting phases (Primack 1987; Johnson 1993; Fenner 1998). Similar to Oberrath and Böhning-Gaese (2002), our results indicate that the fruiting and dispersal ecology affect the evolution of flowering phenologies. However, assigning the whole difference in flowering time only to fruit type differences is premature. For example, several of the contrasts also differ in growth form. From previous studies, we know that fleshy fruits are associated with higher species richness in woody lineages and that the evolution of fleshy fruits is associated with a shift to more closed habitats (Bolmgren and Eriksson 2005). The stored resources in woody plants may allow for a fast development from winter dormancy to flowering, while the light conditions in closed habitats are expected to delay flowering. In deciduous vegetation such as in the study area, wind-pollinated woody species typically flower in spring before the plants leaf out (Bolmgren et al. 2003), while insect-pollinated species flower in close connection to leafing. Still, spring flowering in southeastern Sweden is characterized by a number of phylogenetically independent herbaceous lineages. So, even if other traits associated with fleshy fruits may explain flowering-time evolution

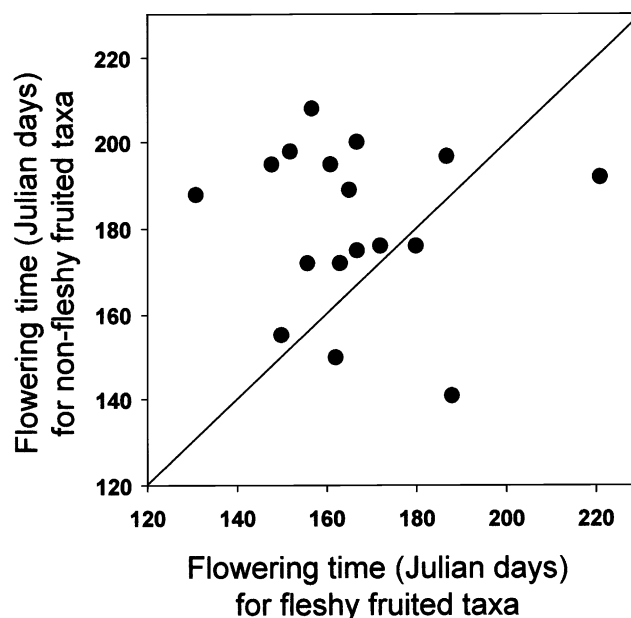


Fig. 2 Phylogenetically independent flowering-time contrasts. Each data point represents mean flowering dates derived from herbarium collections for a sister-pair comparison of fleshy- versus nonfleshy-fruited taxa.

better than fruit type itself, it is out of the scope of this study to disentangle such relations.

Earlier flowering, as an effect of fruit ecology, may be the result of earlier fruiting and/or longer fruit development times, but no studies exist in which fruiting phenologies or fruit development times have been compared between fleshy- and nonfleshy-fruited plants using phylogenetically independent contrasts. Guitián (1998) and Fuentes (1992) examined intraspecific variation in fruiting phenologies along a European latitudinal transect and did not find earlier fruiting phenologies at higher latitudes. Thus, it is likely that earlier flowering in fleshy-fruited plants at higher latitudes is a result of longer fruit development time for fleshy fruits. Fleshy fruits, in general, have larger seeds (Hughes et al. 1994), larger seed size is correlated to longer fruit development time in fleshy-fruited plants (Eriksson and Ehrlén 1991), and fruit size and seed size are negatively correlated to flowering time (Primack 1985; Mazer 1990).

Lönnberg (2004) compared flowering times of fleshy- versus nonfleshy-fruited plants in the Mediterranean flora of Andalusia, southern Spain, without finding any effect of fruit type on flowering time. One reason for the different outcomes in Mediterranean and north-temperate samples may be the different lengths of the reproductive season. That seasonal length is an important factor in phenology evolution is supported by several studies (Perry and Wu 1960; Ray and Alexander 1966; Smithberg and Weiser 1968; Karlsson 1976; Bannister 1978; Somers and Grant 1981; Reader 1983), and assuming that the species in the fleshy-fruited sister clades in this study have larger seeds and fruits, and longer fruit de-

velopment times than the nonfleshy-fruited taxa, the shorter reproductive season at higher latitudes may constitute a phenological constraint generating a comparatively stronger selection pressure on phenology evolution in fleshy-fruited plants. The realized length of the reproductive season may be further reduced by recurring spring and autumn frosts, lower temperatures during the fruit development period, and autumn migration of seed-disseminating birds. Several authors have examined the “adaptive delay” hypothesis, i.e., that fruiting time is delayed at lower latitudes as a result of adaptation to variation in frugivore abundance during autumn bird migration (Thompson and Willson 1979; Stiles 1980; Skeate 1987; Debussche and Isenmann 1992; Fuentes 1992; Guitián 1998). At the intraspecific level, the “adaptive delay” hypothesis has been rejected (Fuentes 1992; Guitián 1998), while patterns at the community level are congruent with the hypothesis. This has been interpreted as if demographic (Janzen 1985) and not evolutionary processes are responsible for the present geographic distribution of fruiting phenologies. So, even if local adaptation is a plausible explanation for the earlier flowering times in north-temperate fleshy-fruited plants found in this study, environmental filtering processes may have been equally important.

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Appendix

Table A1

17 Phylogenetically Independent Contrasts Examined in the Comparative Study of Flowering Times in Fleshy- versus Nonfleshy-Fruited Sister Taxa

Contrast no.	Fleshy-fruited clades	Nonfleshy-fruited clades	References
1	<i>Actaea spicata</i>	<i>Anemone nemorosa</i> , <i>Ranunculus acris</i> , <i>Ranunculus bulbosus</i> , <i>Ranunculus flammula</i> , <i>Ranunculus repens</i>	Ro et al. 1997
2	<i>Ribes alpinum</i> , <i>Ribes nigrum</i> , <i>Ribes spicatum</i> , <i>Ribes uva-crispa</i>	<i>Saxifraga granulata</i> , <i>Saxifraga tridactylites</i>	Fishbein et al. 2001
3	<i>Rubus chamaemorus</i> , <i>Rubus saxatilis</i>	<i>Geum rivale</i> , <i>Geum urbanum</i>	Morgan et al. 1994; Campbell et al. 1995; Eriksson et al. 1998; Eriksson et al. 2003
4	<i>Rosa dumalis</i>	<i>Potentilla argentea</i> , <i>Potentilla erecta</i> , <i>Potentilla reptans</i>	Morgan et al. 1994; Campbell et al. 1995; Eriksson et al. 1998; Eriksson et al. 2003
5	<i>Prunus avium</i> , <i>Prunus padus</i> , <i>Prunus spinosa</i>	<i>Agrimonia eupatoria</i> , <i>Filipendula vulgaris</i> , <i>Filipendula ulmaria</i> , <i>Geum rivale</i> , <i>Geum urbanum</i> , <i>Potentilla argentea</i> , <i>Potentilla erecta</i> , <i>Potentilla reptans</i>	Morgan et al. 1994; Campbell et al. 1995; Eriksson et al. 1998; Eriksson et al. 2003
6	<i>Fragaria moschata</i> , <i>Fragaria vesca</i> , <i>Fragaria viridis</i>	<i>Comarum palustre</i>	Morgan et al. 1994; Campbell et al. 1995; Eriksson et al. 1998; Eriksson et al. 2003
7	<i>Amelanchier spicata</i> , <i>Cotoneaster scandinavicus</i> , <i>Crataegus laevigata</i> , <i>Crataegus monogyna</i> , <i>Malus sylvestris</i> , <i>Sorbus aucuparia</i> , <i>Sorbus intermedia</i>	<i>Agrimonia eupatoria</i> , <i>Filipendula vulgaris</i> , <i>Filipendula ulmaria</i> , <i>Geum rivale</i> , <i>Geum urbanum</i> , <i>Potentilla argentea</i> , <i>Potentilla erecta</i> , <i>Potentilla reptans</i>	Morgan et al. 1994; Campbell et al. 1995; Eriksson et al. 1998; Eriksson et al. 2003
8	<i>Frangula alnus</i> , <i>Rhamnus catharticus</i>	<i>Humulus lupulus</i> , <i>Ulmus glabra</i>	Sytsma et al. 2002
9	<i>Daphne mezereum</i>	<i>Helianthemum nummularium</i>	Alverson et al. 1998; Soltis et al. 2000

Table A1

(Continued)

Contrast no.	Fleshy-fruited clades	Nonfleshy-fruited clades	References
10	<i>Vaccinium myrtillus</i> , <i>Vaccinium oxycoccus</i> , <i>Vaccinium uliginosum</i> , <i>Vaccinium vitis-idaea</i>	<i>Andromeda polifolia</i>	Kron et al. 2002
11	<i>Empetrum nigrum</i>	<i>Rhododendron tomentosum</i>	Kron et al. 2002
12	<i>Arctostaphylos uva-ursi</i>	<i>Orthilia secunda</i> , <i>Pyrola chlorantha</i> , <i>Pyrola rotundifolia</i>	Kron et al. 2002
13	<i>Solanum dulcamara</i> , <i>Solanum nigrum</i>	<i>Hyoscyamus niger</i>	Olmstead and Palmer 1992
14	<i>Sambucus nigra</i> , <i>Viburnum opulus</i>	<i>Adoxa moschatellina</i>	Zhang et al. 2003; Bremer et al. 2002
15	<i>Lonicera xylosteum</i>	<i>Knautia arvensis</i> , <i>Linnaea borealis</i> , <i>Succisa pratensis</i> , <i>Valeriana officinalis</i>	Bremer et al. 2001, 2002
16	<i>Convallaria majalis</i> , <i>Maianthemum bifolium</i> , <i>Polygonatum multiflorum</i> , <i>Polygonatum odoratum</i>	<i>Allium oleraceum</i> , <i>Allium schoenoprasum</i> , <i>Allium scorodoprasum</i>	Judd et al. 2002
17	<i>Paris quadrifolia</i>	<i>Fritillaria meleagris</i> , <i>Gagea minima</i> , <i>Gagea pratensis</i> , <i>Lilium martagon</i>	Judd et al. 2002

Note. Contrasted clades were represented by a subsample of 77 species.

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