



Time – size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora

Kjell Bolmgren and Peter D. Cowan

K. Bolmgren (bolmgren@berkeley.edu) and P. D. Cowan, Dept of Integrative Biology, 3060 Valley Life Sciences Building, Univ. of California, Berkeley, CA 94720-3140, USA.

Parents face a timing problem as to when they should begin devoting resources from their own growth and survival to mating and offspring development. Seed mass and number, as well as maternal survival via plant size, are dependent on time for development. The time available in the favorable season will also affect the size of the developing juveniles and their survival through the unfavorable season. Flowering time may thus represent the outcome of such a time partitioning problem. We analyzed correlations between flowering onset time, seed mass, and plant height in a north-temperate flora, using both cross-species comparisons and phylogenetic comparative methods. Among perennial herbs, flowering onset time was negatively correlated with seed mass (i.e. plants with larger seeds started flowering earlier) while flowering onset time was positively correlated with plant height. Neither of these correlations was found among woody plants. Among annual plants, flowering onset time was positively correlated with seed mass. Cross-species and phylogenetically informed analyses largely agreed, except that flowering onset time was also positively correlated with plant height among annuals in the cross-species analysis. The different signs of the correlations between flowering onset time and seed mass (compar. gee regression coefficient = -7.8) and flowering onset time and plant height (compar. gee regression coefficient = $+30.5$) for perennial herbs, indicate that the duration of the growth season may underlie a tradeoff between maternal size and offspring size in perennial herbs, and we discuss how the partitioning of the season between parents and offspring may explain the association between early flowering and larger seed mass among these plants.

The seasonality of favorable conditions has generated some of the most conspicuous adaptations in nature: long-distance bird migration, hibernation in mammals, and autumn leaf shedding. The limited length of the favorable season adds to this seasonality-driven evolution, illustrated by expected shifts in phenology along gradients in seasonal length. For example, plants flower earlier and at a smaller size at higher latitudes and altitudes, and insects reduce the length of the larval development period, the number of instars, and the number of broods per year as the growth season becomes shorter (Clausen et al. 1948, Masaki 1967, Karlsson 1976, Mousseau and Roff 1989, Nylin and Svård 1991, Berner and Blanckenhorn 2006). Many resources and hazards are also seasonally distributed within the favorable season, generating further selection pressures on the timing of different phases in the annual growth and reproductive cycle (Augspurger 1981, Galen and Stanton 1991, Albon and Langvatn 1992, Verhulst et al. 1995, Bradshaw et al. 2004, Dickerson et al. 2005, Tikkanen et al. 2006, Sola and Ehrlén 2007). Because the different phases of growth and reproduction are often temporally linked, these selection pressures will involve tradeoffs and the evolutionary outcome may be difficult to understand from studies of singular phases (Ollerton and Lack 1992, Verhulst et al. 1995). For example, in plants, vegetative growth, flowering,

seed development, dispersal, and germination typically follow in sequence with more or less overlap between the phases, which means that the timing of any of these phases must be considered the integrated outcome of selection on the timing of all phases linked to it (Oberrath and Böhning-Gaese 2002, Pico et al. 2002, Bolmgren et al. 2003, Freeman et al. 2003, Bolmgren and Lönnberg 2005, Sola and Ehrlén 2007).

Parents face a timing problem as to when they should begin devoting resources from their own growth and survival to mating and offspring development (Cohen 1976, Kozłowski 1992, Roff 2002). Earlier reproduction (in this paper approximated as earlier flowering onset time) implies fewer resources allocated for maternal plant growth, smaller size at time of reproduction, and thus fewer resources available for seed production. On the other hand, earlier flowering will allow for a longer development time of seeds, larger seeds, and a longer period available for germination and juvenile growth. Few comparative studies have asked whether such time–size tradeoffs are manifested at the inter-specific level, and none have included highly resolved data on both phenology and phylogenetic relations (Primack 1985, Mazer 1989, 1990, Eriksson and Ehrlén 1991, Kolb et al. 2006, Vile et al. 2006). It is not obvious that the time–size relations often found in intra-specific

comparisons (Clausen et al. 1948) will translate to the interspecific level, because resource allocation strategies differ between lineages. For example, in perennial plants, stored resources may be more important for reproduction than resources acquired during the current season. The vegetative and reproductive phases may even be separated by a dormant phase such that flowers appear on leafless plants, which, for example, is found in temperate, early-flowering, wind-pollinated trees and Mediterranean, late-flowering, bulbiferous herbs (Johnson 1993, Bolmgren et al. 2003, Debussche et al. 2004). However, previous comparative studies have found a positive correlation between flowering onset time and plant size (Dahlgren et al. 2006, Kolb et al. 2006, Vile et al. 2006) and a positive correlation between fruit development time and seed size (Eriksson and Ehrlén 1991, Moles and Westoby 2003), while flowering onset time was negatively correlated with both fruit size (Primack 1985) and seed mass (Mazer 1990, Vile et al. 2006; but see Eriksson and Ehrlén 1991, Kolb et al. 2006). Flowering onset time may thus represent the outcome of the parent vs offspring development time partitioning problem also at the inter-specific comparative level (cf. Shitaka and Hirose 1998).

Two seemingly contradictory views of flowering time evolution persist in the literature. On the one hand, the phylogenetic signal found for flowering time (Kochmer and Handel 1986, Smith-Ramírez and Armesto 1994, Wright and Calderon 1995) is often interpreted as evidence for constrained evolution of flowering time (Ollerton and Lack 1992, Fenner 1998). On the other hand, there are many classical examples of adaptive variation in flowering time (Clausen et al. 1948), and sometimes these adaptive responses have been very rapid (Franks et al. 2007). Here, we try to bridge these perspectives by including information on phylogenetic relations in analyses of life history correlates. This approach will promote more mechanistic interpretations of phylogenetically conserved patterns of flowering time. Convergent evolution of flowering times have previously been documented in relation to pollination and dispersal modes, as well as growth forms (Johnson 1993, Bolmgren et al. 2003, Oberrath and Böhning-Gaese 2002). The present study tests for evidence of time–size tradeoffs by analyzing interspecific correlations between flowering onset time, seed mass, and plant height in a north-temperate flora. This is the first phylogenetic comparative analyses to use a resolved phylogeny and detailed flowering time data, applying both independent contrasts and generalized estimating equations approaches. We asked whether flowering times differ between life/growth forms and dispersal modes, then controlled for these effects when further analyzing correlations between flowering time, seed mass, and plant height.

Methods

Data set

A phenological survey was performed between 1873–1917 in the provinces of Uppland and Södermanland (59°–60°N) in southeastern Sweden (Arnell 1923). This data set consists of 572 species and 133 000 data points (mainly

flowering onset) compiled by laymen and professionals according to a specified procedure and reported to the Swedish National Meteorological-Hydrographical Institute. From this data set, Arnell (1923) derived mean flowering onset dates for the city of Uppsala (59°51′36″N, 17°38′24″E). We used these mean flowering onset dates as our measure of flowering time. Data for all other traits (seed mass, plant height, dispersal mode, and life/growth form) were compiled from the literature (see References in Online Appendix 1). Dispersal mode was coded as anemochorous, autochorous (including ballistic), or zoochorous (endozoochorous, ectozoochorous and myrmecochorous), while growth/life form was coded as woody perennials, perennial herbs and annual herbs. For the 126 species for which data on all traits was available, a supertree was constructed (Appendix 1, Fig. A1). The ‘backbone’ of the supertree was generated using Phylomatic (Webb and Donoghue 2005), and the phylogenetic hypothesis generated by Phylomatic was checked against the APG II hypothesis (Bremer et al. 2003) and the Angiosperm Phylogeny Website (Stevens 2001 onwards). Increased resolution at lower level nodes was accomplished by grafting phylogenetic hypotheses from more focused studies published as of 20 February 2007 (see References in Online Appendix 1).

Analyses

All analyses were performed in R (R Development Core Team 2006. R code is available upon request from the corresponding author). We used Pearson product moment correlation analyses (the `cor.test` function) to test for cross-species correlations between flowering time, seed mass (log-transformed) and plant height (log-transformed), and analysis of variance (‘`aov`’ and Bonferroni corrected ‘paired t-test’ functions) to test for differences in flowering time between modes of dispersal and life/growth forms.

Phylogenetic relations were considered in two different ways using the analyses of phylogenetics and evolution (APE) package (ver. 1.9) in R (Paradis et al. 2004). First, we analyzed a general linear model based on phylogenetically independent contrasts (PIC Felsenstein 1985): $\text{flowering time} = \beta_{C1} \text{PIC}[\log(\text{plant height})] + \beta_{C2} \text{PIC}[\log(\text{seed mass})]$. Phylogenetically independent contrasts were calculated using the default settings of the ‘`pic`’ function in APE. Branch lengths were set to 1 (Ackerly 2000) and linear model regressions were forced through the origin (Garland et al. 1992). Polytomies were resolved randomly with the ‘`multi2di`’ function in APE prior to linear model regressions. Thus, we generated 999 completely and randomly dichotomized trees and analyzed the linear models for each one of them. When the model itself was significantly different from the null in all analyses (p -values < 0.05), we present the mean statistics. In the case of marginally rejected null models, i.e. when the mean of p -values < 0.05 , but some of the randomly resolved phylogenies yielded a p -value > 0.05 , both the mean and range of the statistics are presented.

We also applied a second phylogenetic comparative method, the implementation of generalized estimating equations (GEE) in the ‘`compar gee`’ function of APE

(Paradis and Claude 2002). GEE allows the dependences of the observations to be quantified by a correlation matrix, and in the ‘compar.gee’ function this correlation matrix is based on the phylogenetic relationships among the observed taxa. Using the unresolved phylogeny (Appendix 1, Fig. A1), we analyzed the model (flowering time = $\beta_{G1}[\log(\text{plant height})] + \beta_{G2}[\log(\text{seed mass})] + \text{factor}(\text{dispersal mode}) + \text{factor}(\text{life/growth form})$).

Results

Flowering onset times in the sample (126 species) ranged from 12 April to 8 August (Julian dates 103–220) as compared to 2 April to 16 August in the larger phenological survey (572 species). 21 woody plants (trees, shrubs, and shrublets), 93 perennial herbs and 12 annuals were sampled, 40 of which were zoochorous (endozoo-, ectozoo- and myrmocochorous), 76 autochorous (including ballistic), and 10 anemochorous (Fig. 1).

Both life/growth forms (Fig. 1A; ANOVA: $F = 3.7_{2,123}$, $p = 0.027$) and dispersal modes (Fig. 1B; ANOVA: $F = 12.0_{2,123}$, $p = 0.00002$) differed in flowering time. However, Bonferroni-corrected pairwise comparisons only found significant differences between dispersal modes (Fig. 1B: anemochory vs autochory, $p = 0.008$; anemochory vs zoochory, $p = 0.00003$; autochory vs zoochory, $p = 0.007$), and not between life/growth forms (annual herbs vs perennial herbs, $p = 0.16$; annual herbs vs woody perennials, $p = 1.0$; perennial herbs vs woody perennials, $p = 0.1$). The association between late flowering time and anemochorous dispersal must be treated with caution, as all anemochorous species in this data set were herbs while in larger data sets early flowering, anemochorous trees are common.

Correlations between flowering time, plant height and seed mass (Table 1 and 2) differed between growth forms. In the cross-species analyses, seed mass was correlated with plant height in all samples except perennial herbs. The perennial herbs also differed from the other groups in the relations between flowering time and both plant height and seed mass. While no relationship was found between flowering time and the size measures in the full sample and the woody perennials sub-sample (Table 1), both plant height and seed mass were positively correlated with flowering time in the annual herbs sub-sample. Whereas in the perennial herbs sub-sample, plant height was positively correlated and seed mass negatively correlated with flowering time (Table 1).

The general linear models based on phylogenetically independent contrasts (Table 2) confirmed several of the patterns found in the cross-species analyses. Among perennial herbs, shifts in flowering time were positively correlated to shifts in plant height and negatively correlated to shifts in seed mass. Shifts in seed mass and plant height had no effect on flowering time shifts in the subset of woody plants. Among annual plants, the general linear model based on plant height and seed mass contrasts differed marginally from the null. Neither of the predictors was found to have a significant effect, though the relationship between seed mass and flowering time exhibited the same positive trend as in the cross-species analysis (Table 2).

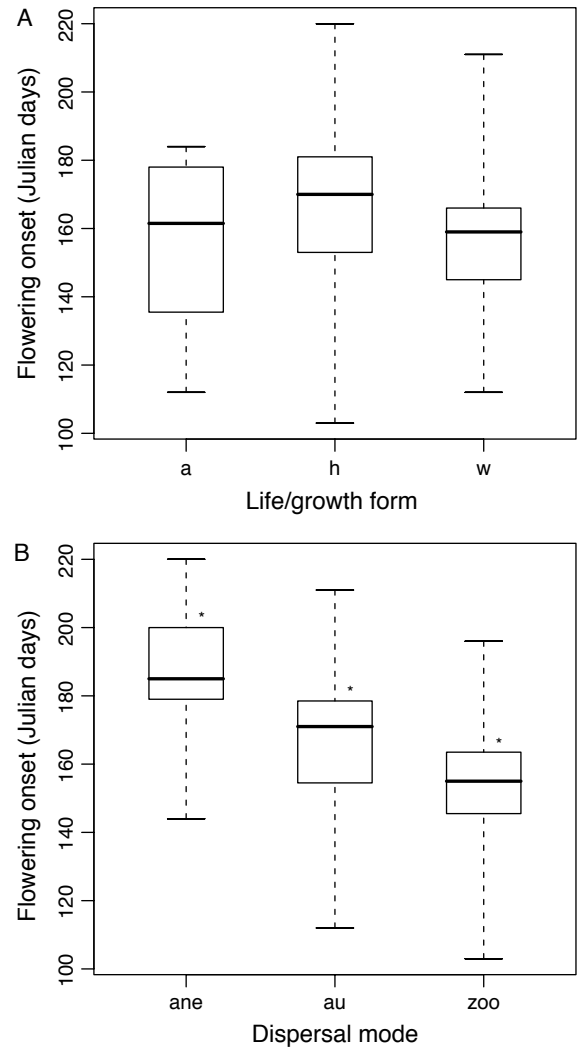


Fig. 1. Variation in flowering time in relation to (A) life/growth form (w = woody perennials, h = perennial herbs, a = annual herbs) and (B) dispersal mode (ane = anemochory, au = autochory, zoo = zoochory). Boxplots show the median, 1st and 3rd quartiles, and the full range of the sample. * All groups differed from each other based on a Bonferroni corrected pairwise comparisons. The result that later flowering time is associated with anemochory in this study must be treated with caution, as all anemochorous species were herbaceous in this study while it is common to find early-flowering, anemochorous trees in more complete data sets.

After a model simplification, when plant height contrasts were excluded from the general linear model, seed mass contrasts were a significant predictor of flowering time contrasts among annuals (lm: $\beta_{c2} = 23.6$, $R^2 = 0.49$, $p = 0.01$).

The analyses using the GEE approach (Table 3) were congruent with the ANOVA analyses (Fig. 1) and with all analyses based on the ‘perennial herbs’ subsample (Table 2). Plant height, seed mass, dispersal mode and growth form were all significant in predicting variation in flowering time. The different dispersal modes predicted different flowering times, while no difference was found in the estimated coefficients for the different life/growth forms. The regression coefficients estimated for plant height and seed mass

Table 1. Pearson product moment correlation coefficients without considering phylogenetic relations. Plant height and seed mass were log-transformed.

	n	Flowering time over Plant height	Flowering time over Seed mass	Seed mass over Plant height
Full sample	126	ns	ns	0.52***
Subsamples				
Woody perennials	21	ns	ns	0.73***
Perennial herbs	93	0.34***	-0.26*	ns
Annual herbs	12	0.62*	0.73**	0.67*

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns $p > 0.05$.

are similar to the ones estimated in the PIC analyses of perennial herbs, suggesting that the heavy bias towards perennial herbs in the data set is skewing the coefficients. This suspicion is supported by GEE analyses on the different life/growth form subsets (results not shown), which are fully congruent with the PIC analyses (cf. Table 2 with the following): no correlations were found between flowering time and plant height and seed mass in the woody subsample; a weak, positive relationship ($p = 0.09$) was found between flowering time and seed mass in the subset of annual herbs; the estimated regression coefficients in the GEE analyses based on perennial herbs only were $\beta_{G1} = +30.5$ for $\log(\text{plant height})$ and $\beta_{G2} = -7.8$ for $\log(\text{seed mass})$.

Discussion

The obvious dependencies on other organisms (pollinators, seed dispersers, herbivores, seed predators) and on external and internal cues (photoperiod, temperature, soil water content, plant size) suggest that it is necessary to have a complex life cycle perspective when interpreting the evolution of a single phenological trait like flowering time (Lacey et al. 2003). Flowering time must fit with the conditions for pollination, but that does not mean that it evolves independently of other traits (Rathcke and Lacey 1985, Oberrath and Böhning-Gaese 2002, Bolmgren and Lönnberg 2005, Sola and Ehrlén 2007). A classic example of this interdependence, and relevant to this study, is the parallel evolution of plant size and flowering time often found along latitudinal gradients (Clausen et al. 1948).

Here, we found that correlations among flowering time, seed mass, and plant height differed between plant life and growth forms. This lack of congruence supports the idea that different ways of partitioning and storing resources between annual, perennial, herbaceous, and woody plants

constrain reproductive phenology (Rathcke and Lacey 1985, Johnson 1993, Debussche et al. 2004, Sola and Ehrlén 2007). In woody plants, flowering time was not correlated with plant height nor seed mass, suggesting that the amount of stored resources allows for a complete decoupling of reproductive and vegetative phenology. The decoupling hypothesis is supported for shrubs and trees by the well-known phenomena of flowering on leafless twigs (e.g. *Betula*, *Corylus*, *Daphne*, *Magnolia*, *Salix*, *Ulmus*). A basic assumption in many life history models is that delayed reproduction is associated with larger maternal size and thereby larger reproductive output. This pattern was confirmed in the cross-species comparison of annuals here; the larger annuals flowered later and produced heavier seeds. However, only a weak correlation between seed mass and flowering time persisted in the phylogenetically informed analyses. Considering the small sample of annuals and the inconsistency between the statistical methods, we refrain from drawing general conclusions and call for further comparative studies of this question. Life history models also predict that annuals should reproduce earlier than their perennate equals to counteract the greater cost of mortality before reproduction in annuals, but we found no such difference between perennials and annuals here.

Among perennial herbs, flowering time was negatively correlated with seed mass and positively correlated with plant height. This pattern was consistent in all analyses. That increased maternal size is associated with later flowering is in accordance with theory, but why should larger seeds be associated with earlier flowering? In life history models, the question about the optimal time of reproduction is most often presented as the question about maximizing fecundity and survival of the maternal plant. In its trivial sense, fecundity is measured as the number of offspring times their mean size, but as Ydenberg (1989) discussed an essential part of this equation is what happens to the offspring. Survival, growth and fecundity of the

Table 2. General linear model analyses of the effects of plant height and seed mass on flowering time based on phylogenetically independent contrasts. Regression coefficients and R^2 -values are given as means from the 999 runs based on randomly dichotomized phylogenetic hypotheses (Methods) and are only presented when the mean p -value < 0.10 . Statistics in parantheses represent the range of values for the 999 runs when some runs resulted in p -value > 0.05 .

	Plant height (log) β_{C1}	Seed mass (log) β_{C2}	DF	R^2
Full sample	20.6***	-7.9**	2, 123	0.12***
Subsamples				
Woody perennials	ns	ns	2, 18	ns
Perennial herbs	25.1***	-6.3*	2, 90	0.16***
... annual herbs	ns	20.6 ^m (18.7, 21.8)	2, 9	0.51* (0.45, 0.56)

^m $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns $p > 0.10$.

Table 3. Generalized estimating equations (GEE) analyses, as implemented in the phylogenetic comparative methods package APE (Paradis and Claude 2002), of the effects of plant height, seed mass, dispersal mode, and life/growth form on flowering time ($n = 126$). The degrees of freedom (DF_p) were recalculated as part of the analysis.

Effect	DF_p	F	p	
Plant height (log)	1, 28	70.6	<10 ⁻⁷	
Seed mass (log)	1, 28	8.6	0.008	
Dispersal mode	2, 28	44.9	<10 ⁻⁷	
Life/growth form	2, 28	8.2	0.002	

Estimation of coefficients:				
Variable	Estimate	SE	t	p
Intercept	135.4	9.5	14.2	<10 ⁻¹¹
Plant height (β_{G1})	24.9	3.0	8.4	<10 ⁻⁷
Seed mass (β_{G2})	-4.4	1.5	-2.9	0.008
Dispersal mode:				
Zoochory	-28.2	4.6	-6.2	<10 ⁻⁵
Autochory	-12.7	4.0	-3.2	<10 ⁻²
Anemochory	40.9			
Life/growth form:				
Woody plants	-4.7	5.4	-0.9	0.397
Perennial herbs	4.6	2.6	1.7	0.095
Annual herbs	-0.1			

offspring are the non-trivial part of fecundity, which must be included to understand the evolution of flowering time. For example, early flowering time may imply early dispersal, germination, and emergence and thus a longer period of growth available to the juvenile. But a long juvenile period, including the unfavorable season, increases the risk of mortality before reproduction.

Recent meta-analyses suggest that higher seed mass only reduces juvenile mortality in the very early stage. Once seed cohorts reach the stage where seed resources are depleted, the number of surviving individuals does not differ depending on seed mass (Moles and Westoby 2004, Verdu and Traveset 2005). However, if seed mass evolved as a response to evolution of earlier flowering and emergence time in perennial herbs, it may have outweighed the increased mortality risks due to the longer juvenile season. Or, vice versa, if seed mass evolved first, earlier flowering time could evolve as mortality per time was reduced allowing the surviving juveniles to become larger when the first favorable, reproductive season is entered. Mazer (1990), who also found a negative correlation between flowering time and seed mass in a comparative study of the Indiana dunes flora (Vile et al. 2006), pointed out two other possible explanations. Firstly, larger seeds require a longer development time (Eriksson and Ehrlén 1991, Moles and Westoby 2003), which may lead to earlier flowering time when the growth period is limiting. A similar effect, i.e. earlier flowering, has been found for zoochorous plants (Oberrath and Böhning-Gaese 2002, Bolmgren and Lönnberg 2005), which are known to have larger seeds (Moles et al. 2005). Secondly, Mazer (1990) suggested that the seed mass-flowering time correlation may have come about due to a third factor linking these traits. In the present case a plausible such factor could be habitat. Plants growing in deciduous forests often flower early before the canopy closes (Schemske et al. 1978), thus they do not have time to grow large before they flower. At the same time these plants need

to be able to germinate and survive under a closed canopy with a lot of falling debris, which is the typical habitat where larger seeds have been found to improve survival (Leishman et al. 2000). An association between larger seed mass and earlier flowering as part of an adaptation to this habitat should then be coupled with the evolution of more post-mating maternal growth (Kozłowski 1992).

To conclude: In this north-temperate sample, perennial herbs show a positive correlation between flowering time and plant height and a negative correlation between flowering time and seed mass. This indicates that the duration of the growth season may underlie a tradeoff between maternal size and offspring size in perennial herbs, and several testable hypotheses emerge. Is the negative correlation between seed mass and flowering time habitat dependent? Do early-dispersed seeds have a lower survival rate? Is the early flowering and heavier seeds in perennial herbs coupled with a comparably longer period of post-mating maternal growth? At the mechanistic level, these questions will be best approached at the intra-specific level. However, it will also be interesting to see if these correlations hold up at the inter-specific level, both within clades and communities. If they do, it suggests that time-size tradeoffs are constraining evolution within clades and affecting the assembly of communities.

Acknowledgements – During this work KB was supported by a post doc grant from the Swedish Research Council.

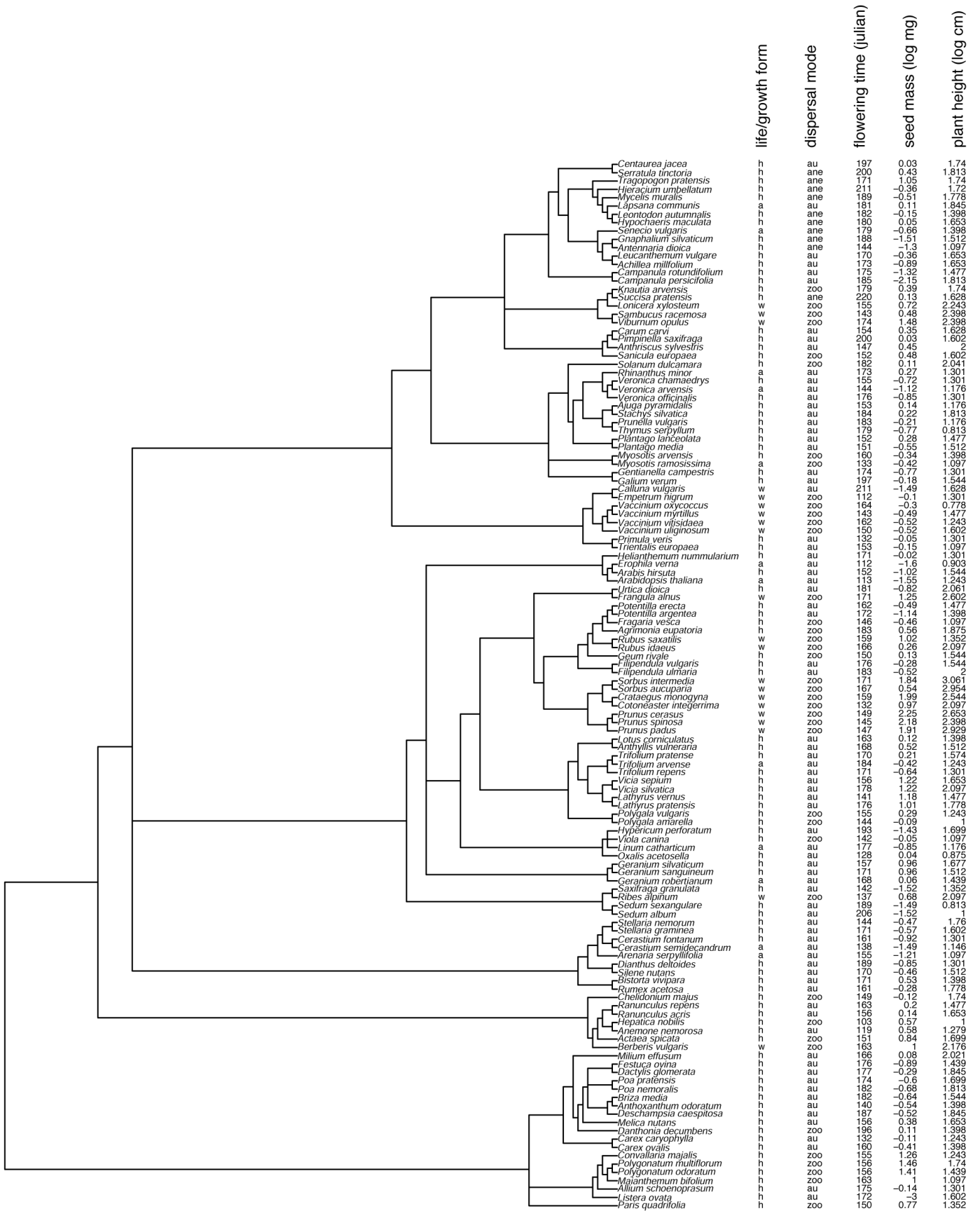
References

- Ackerly, D. D. 2000. Taxon sampling, correlated evolution, and independent contrasts. – *Evolution* 54: 1480–1492.
- Albon, S. D. and Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. – *Oikos* 65: 502–513.
- Bremer, B. et al. 2003. An update of the Angiosperm phylogeny group classification for the orders and families of flowering plants: APG II. – *Bot. J. Linn. Soc.* 141: 399–436.
- Arnell, H. A. 1923. Vegetationens årliga utvecklingsgång i Svealand. – *Medd. för Statens meteorologisk-hydrografiska anstalt.*
- Augspurger, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). – *Ecology* 62: 775–788.
- Berner, D. and Blanckenhorn, W. U. 2006. Grasshopper ontogeny in relation to time constraints: adaptive divergence and stasis. – *J. Anim. Ecol.* 75: 130–139.
- Bolmgren, K. and Lönnberg, K. 2005. Herbarium data reveal an association between fleshy fruit type and earlier flowering time. – *Int. J. Plant Sci.* 166: 663–670.
- Bolmgren, K. et al. 2003. Contrasting flowering phenology and species richness in abiotically and biotically pollinated angiosperms. – *Evolution* 57: 2001–2011.
- Bradshaw, W. E. et al. 2004. Adaptation to temperate climates. – *Evolution* 58: 1748–1762.
- Clausen, J. et al. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. – *Carnegie Inst. Washington.*
- Cohen, D. 1976. Optimal timing of reproduction. – *Am. Nat.* 110: 801–807.
- Dahlgren, J. P. et al. 2006. Specific leaf area as a superior predictor of changes in field layer abundance during forest succession. – *J. Veg. Sci.* 17: 577–582.

- Debusche, M. et al. 2004. Exploring the causes of variation in phenology and morphology in Mediterranean geophytes: a genus-wide study of *Cyclamen*. – *Bot. J. Linn. Soc.* 145: 469–484.
- Dickerson, B. R. et al. 2005. Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. – *Ecology* 86: 347–352.
- Eriksson, O. and Ehrlén, J. 1991. Phenological variation in fruit characteristics in vertebrate-dispersed plants. – *Oecologia* 86: 463–470.
- Felsenstein, J. 1985. Phylogenies and the comparative method. – *Am. Nat.* 125: 1–15.
- Fenner, M. 1998. The phenology of growth and reproduction in plants. – *Persp. Plant Ecol. Evol. Syst.* 1: 78–91.
- Franks, S. J. et al. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. – *Proc. Natl Acad. Sci. USA* 104: 1278–1282.
- Freeman, R. S. et al. 2003. Flowering phenology and compensation for herbivory in *Ipomopsis aggregata*. – *Oecologia* 136: 394–401.
- Galen, C. and Stanton, M. L. 1991. Consequences of emergence phenology for reproductive success in *Ranunculus-Adoneus* (Ranunculaceae). – *Am. J. Bot.* 78: 978–988.
- Garland, T. et al. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. – *Syst. Biol.* 41: 18–32.
- Johnson, S. D. 1993. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. – *J. Ecol.* 81: 567–572.
- Karlsson, T. 1976. *Euphrasia* in Sweden: hybridization, parallelism and species concept. – *Bot. Notiser* 129: 49–60.
- Kochmer, J. P. and Handel, S. N. 1986. Constraints and competition in the evolution of flowering phenology. – *Ecol. Monogr.* 56: 303–325.
- Kolb, A. et al. 2006. Determinants of local abundance and range size in forest vascular plants. – *Global Ecol. Biogeogr.* 15: 237–247.
- Kozłowski, J. 1992. Optimal allocation of resources to growth and reproduction implications for age and size at maturity. – *Trends Ecol. Evol.* 7: 15–19.
- Lacey, E. P. et al. 2003. Multigenerational effects of flowering and fruiting phenology in *Plantago lanceolata*. – *Ecology* 84: 2462–2475.
- Leishman, M. R. et al. 2000. The evolutionary ecology of seed size. – In: Fenner, M. (ed.), *Seeds: the ecology of regeneration in plant communities*. CABI, pp. 31–57.
- Masaki, S. 1967. Geographic variation and climatic adaptation in a field cricket (Orthoptera -Gryllidae). – *Evolution* 21: 725–741.
- Mazer, S. J. 1989. Ecological, taxonomic, and life-history correlates of seed mass among Indiana dune Angiosperms. – *Ecol. Monogr.* 59: 153–175.
- Mazer, S. J. 1990. Seed mass of Indiana dune genera and families-taxonomic and ecological correlates. – *Evol. Ecol.* 4: 326–357.
- Moles, A. T. and Westoby, M. 2003. Latitude, seed predation and seed mass. – *J. Biogeogr.* 30: 105–128.
- Moles, A. T. and Westoby, M. 2004. Seedling survival and seed size: a synthesis of the literature. – *J. Ecol.* 92: 372–383.
- Moles, A. T. et al. 2005. Factors that shape seed mass evolution. – *Proc. Natl Acad. Sci. USA* 102: 10540–10544.
- Mousseau, T. A. and Roff, D. A. 1989. Adaptation to seasonality in a cricket-patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. – *Evolution* 43: 1483–1496.
- Nylin, S. and Svård, L. 1991. Latitudinal patterns in the size of European butterflies. – *Holarct. Ecol.* 14: 192–202.
- Oberrath, R. and Böhning-Gaese, K. 2002. Phenological adaptation of ant-dispersed plants to seasonal variation in ant activity. – *Ecology* 83: 1412–1420.
- Ollerton, J. and Lack, A. J. 1992. Flowering phenology -an example of relaxation of natural selection. – *Trends Ecol. Evol.* 7: 274–276.
- Paradis, E. and Claude, J. 2002. Analysis of comparative data using generalized estimating equations. – *J. Theor. Biol.* 218: 175–185.
- Paradis, E. et al. 2004. APE: analyses of phylogenetics and evolution in R language. – *Bioinformatics* 20: 289–290.
- Pico, F. X. et al. 2002. An extended flowering and fruiting season has few demographic effects in a Mediterranean perennial herb. – *Ecology* 83: 1991–2004.
- Primack, R. B. 1985. Patterns of flowering phenology in communities, populations, individuals and single flowers. – In: White, J. E. (ed.), *The population structure of vegetation*. Junk, pp. 571–593.
- Rathcke, B. J. and Lacey, E. P. 1985. Phenological patterns of terrestrial plants. – *Annu. Rev. Ecol. Syst.* 16: 179–214.
- Roff, D. A. 2002. *Life history evolution*. – Sinauer.
- Schemske, D. W. et al. 1978. Flowering ecology of some woodland herbs. – *Ecology* 59: 351–366.
- Shitaka, Y. and Hirose, T. 1998. Effects of shift in flowering time on the reproductive output of *Xanthium canadense* in a seasonal environment. – *Oecologia* 114: 361–367.
- Smith-Ramírez, C. and Armesto, J. J. 1994. Flowering and fruiting patterns in the temperate rain-forest of Chiloe, Chile-ecologies and climatic constraints. – *J. Ecol.* 82: 353–365.
- Sola, A. J. and Ehrlén, J. 2007. Vegetative phenology constrains the onset of flowering in the perennial herb *Lathyrus vernus*. – *J. Ecol.* 95: 208–216.
- Stevens, P. F. 2001 onwards. Angiosperm phylogeny website. Ver. 7, May 2006 [and more or less continuously updated since].
- Tikkanen, O. P. et al. 2006. Are polyphagous geometrid moths with flightless females adapted to budburst phenology of local host species? – *Oikos* 112: 83–90.
- Webb, C. O. and Donoghue, M. J. 2005. Phylomatic: tree assembly for applied phylogenetics. – *Mol. Ecol. Notes* 5: 181–183.
- Verdu, M. and Traveset, A. 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. – *Ecology* 86: 1385–1394.
- Verhulst, S. et al. 1995. Seasonal decline in reproductive success of the great tit-variation in time or quality. – *Ecology* 76: 2392–2403.
- Vile, D. et al. 2006. A structural equation model to integrate changes in functional strategies during old-field succession. – *Ecology* 87: 504–517.
- Wright, S. J. and Calderon, O. 1995. Phylogenetic patterns among tropical flowering phenologies. – *J. Ecol.* 83: 937–948.
- Ydenberg, R. C. 1989. Growth mortality tradeoffs and the evolution of juvenile life histories in the Alcidae. – *Ecology* 70: 1494–1506.

Appendix 1 is available online as Appendix O16142 at www.oikos.ekol.lu.se/appendix

Bolmgren, K. and Cowan, P. D. 2007. Time – size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. – *Oikos* 000: 000–000.



Appendix 1

Fig. A1. Phylogenetic hypothesis used in the independent contrast and GEE analyses. Life/Growth form (w=woody perennials, h=perennial herbs, a=annual herbs), dispersal mode (ane=anemochory, au=autochory, zoo=zoochory), flowering onset day, seed mass, and plant height are indicated to the right of each terminal taxon. Seed mass (mg) data was compiled from recent studies performed in the same provinces as the phenology study (Eriksson and Ehrlén 1991, Eriksson and Eriksson 1997, Fröberg and Eriksson 1997, Kiviniemi and Eriksson 1999, Fröberg 2001, Kiviniemi 2001, Jakobsson and Eriksson 2003), while plant height (cm), dispersal mode, and growth/life form were found in Mossberg and Stenberg (2003). The 'backbone' of the supertree was generated using Phylomatic (Webb and Donoghue 2005), and the phylogenetic hypothesis generated by Phylomatic was checked against the APG II hypothesis (Bremer et al. 2003) and the Angiosperm Phylogeny Website (Stevens 2001 onwards). Increased resolution at lower level nodes was accomplished by grafting phylogenetic hypotheses from more focused studies published as of 20 February 2007 (Asteraceae (Funk et al. 2005, B. Gemeinholzer unpubl. and M. Englund, Dept of Botany, Stockholm, pers.comm); Dipsacales (Bell and Donoghue 2005); Apiaceae (Downie et al. 2000); *Veronica* (Taskova et al. 2004); Lamiaceae (Wink 2003); Ericales/Ericaceae (Kron et al. 2002, Schönenberger et al. 2005); Rosaceae (Eriksson et al. 2003, Potter et al. 2002); *Prunus* (Shaw and Small 2004, Bortiri et al. 2006); Fabaceae (Wojciechowski et al. 2004); *Trifolium* (Ellison et al. 2006); *Geranium* (Zoubir 2006); Saxifragales (Fishbein and Soltis 2004); Caprifoliales (Cuénoud et al. 2002); Caprifoliaceae (Fior et al. 2006); Ranunculaceae (Johansson 1995); Poaceae (Barker et al. 2001, Catalán et al. 1997, 2004)).

References

- Barker, N. P. et al. 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). – *Ann. Miss. Bot. Gard.* 88: 373–457.
- Bell, C. D. and Donoghue, M. J. 2005. Dating the dipsacales: comparing models, genes and evolutionary implications. – *Am. J. Bot.* 92: 284–296.
- Bortiri, E. et al. 2006. Phylogenetic analysis of morphology in *Prunus* reveals extensive homoplasy. – *Plant Syst. Evol.* 259: 53–71.
- Catalán, P. et al. 1997. Phylogeny of Poaceae subfamily Pooideae based on chloroplast *ndhF* gene sequences. – *Mol. Phylogenet. Evol.* 8: 150–166.
- Catalán P. et al. 2004. Phylogeny of the festucoid grasses of subtribe Lolinae and allies (Poaceae, Pooideae) inferred from ITS and *trnL-F* sequences. – *Mol. Phylogenet. Evol.* 31: 517–541.
- Cuénoud, P. et al. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbcl*, *atpB*, and *matK* DNA sequences. – *Am. J. Bot.* 89: 132–144.
- Downie, S. R. et al. 2000. A phylogeny of the flowering plant family Apiaceae based on chloroplast DNA *rpl16* and *rpoC1* intron sequences: towards a suprageneric classification of subfamily apioidae. – *Am. J. Bot.* 87: 273–292.
- Ellison, N. W. et al. 2006. Molecular phylogenetics of the clover genus (*Trifolium* -Leguminosae). – *Mol. Phylogenet. Evol.* 39: 688–705.
- Eriksson, Å. and Eriksson, O. 1997. Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. – *Nord. J. Bot.* 17: 469–482.
- Eriksson, O. and Ehrlén, J. 1991. Phenological variation in fruit characteristics in vertebrate-dispersed plants. – *Oecologia* 86: 463–470.
- Eriksson, T. et al. 2003. The phylogeny of Rosoideae (Rosaceae) based on sequences of the internal transcribed spacers (ITS) of nuclear ribosomal DNA and the *trnL/F* region of chloroplast DNA. – *Int. J. Plant Sci.* 164: 197–211.
- Fior, S. et al. 2006. Molecular phylogeny of the Caryophyllaceae (Caryophyllales) inferred from chloroplast *matK* and nuclear rDNA *its* sequences. – *Am. J. Bot.* 93: 399–411.
- Fishbein, M. and Soltis, D. E. 2004. Further resolution of the rapid radiation of saxifragales (angiosperms, eudicots) supported by mixed-model Bayesian analysis. – *Syst. Bot.* 29: 883–891.
- Fröberg, H. 2001. Seed size and seedling emergence in 16 temperate forest herbs and one dwarf-shrub. – *Nord. J. Bot.* 21: 373–384.
- Fröberg, H. and Eriksson, O. 1997. Local colonization and extinction of field layer plants in a deciduous forest and their dependence upon life history features. – *J. Veg. Sci.* 8: 395–400.
- Funk, V. et al. 2005. Everywhere but Antarctica: using a supertree to understand the diversity and distribution of the Compositae. – *Biologische Skrifter* 55: 343–373.
- Jakobsson, A. and Eriksson, O. 2003. Tradeoffs between dispersal and competitive ability: a comparative study of wind-dispersed Asteraceae forbs. – *Evol. Ecol.* 17: 233–246.
- Johansson, J. T. 1995. A revised chloroplast DNA phylogeny of the Ranunculaceae. – *Plant Syst. Evol.* 253–261.
- Kiviniemi, K. 2001. Evolution of recruitment features in plants: a comparative study of species in the Rosaceae. – *Oikos* 94: 250–262.
- Kiviniemi, K. and Eriksson, O. 1999. Dispersal, recruitment and site occupancy of grassland plants in fragmented habitats. – *Oikos* 86: 241–253.
- Kron, K. A. et al. 2002. Phylogenetic classification of Ericaceae: molecular and morphological evidence. – *Bot. Rev.* 68: 335–423.
- Mossberg, B. and Stenberg, L. 2003. Den nya nordiska floran. – Wahlström & Widstrand.
- Potter, D. et al. 2002. Phylogenetic relationships in Rosaceae inferred from chloroplast *matK* and *trnL-trnF* nucleotide sequence data. – *Plant Syst. Evol.* 231: 77–89.
- Schönenberger, J. et al. 2005. Molecular phylogenetics and patterns of floral evolution in the Ericales. – *Int. J. Plant Sci.* 166: 265–288.
- Shaw, J. and Small, R. L. 2004. Addressing the “hardest puzzle in American pomology”: phylogeny of *Prunus* sect. *Prunocerasus* (Rosaceae) based on seven noncoding chloroplast DNA regions. – *Am. J. Bot.* 91: 985–996.
- Taskova, R. M. et al. 2004. Phylogeny of *Veronica* – a combination of molecular and chemical evidence. – *Plant Biol.* 6: 673–682.
- Wink, M. 2003. Evolution of secondary metabolites from an ecological and molecular phylogenetic perspective. – *Phytochemistry* 64: 3–19.
- Wojciechowski, M. F. et al. 2004. A phylogeny of legumes (Leguminosae) based on analyses of the plastid *matK* gene resolves many well-supported subclades within the family. – *Am. J. Bot.* 91: 1846–1862.
- Zoubir, M. 2006. A *trnL*- and ITS based phylogeny of 22 *Geranium* species compared to the current classification based on seed dispersal mechanisms. – Dept of Botany, Stockholm Univ.