THE ROYAL SOCIETY

Evolution of meiosis timing during floral development

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Meiosis divides the haploid and diploid portions of the life cycle in all sexual organisms. In angiosperms meiosis occurs during flower development, the duration of which varies widely among species and is affected by environmental conditions within species. For 36 species representing 13 angiosperm families, we determined the time at which meiosis ceased in the anthers as a fraction of the total time from floral primordium initiation (beginning of development) to flower opening (end). It was found that this fraction, rather than being continuously distributed among species, occurred in three discrete classes despite wide variations within and among species in absolute developmental durations. Each species was characterized by a single timing class. For all species within a given timing class, therefore, the durations before and after the end of microsporocyte meiosis existed in constant ratio. Each timing class was found in phylogenetically distant species; conversely, a plant family often contained more than one class. Timing class was not related to ploidy level, inflorescence architecture, pollination syndrome or mating system. These findings show that either the durations before and after microsporocyte meiosis are regulated by the same exogenous process, or one duration determines the other. They further imply that the underlying developmental processes have evolved in a limited number of ways among flowering plants.

Keywords: anther; flower development; golden ratio; meiosis timing; microsporocyte; tetrad formation

1. INTRODUCTION

In angiosperms, microsporocyte (pollen-mother-cell) meiosis occurs in the anthers during floral development. The proximate causes of meiotic onset and offset are not yet fully understood for plants or any other organism (Dickinson 1987, 1994; John 1990; Luomajoki 1986; McLeod & Beach 1988; Riggs 1997; Sauter 1971; Stern 1990), although several genes necessary for onset have been identified in a yeast, a lily and maize (Bogdanov 1998; Golubovskaya *et al*. 1993; McLeod & Beach 1988; Riggs 1994, 1997; Sheridan *et al*. 1996; Walters 1985). Although the onset of meiosis has been more intensively studied, there are two respects in which its offset has greater significance. First, in plants, the end of meiosis defines the beginning of the gametophytic generation. Second, pollen tetrad formation corresponds to the end of cell division in the anther and corolla (Hill 1996). After microsporocyte meiosis, all growth, including corolla expansion (flower opening), occurs by cell enlargement.

Events in different whorls of the developing flower are often highly temporally correlated. This is particularly evident between whorls two and three, the corolla and stamens (Erickson 1948; Goldberg *et al*. 1993; Greyson 1994; Kiss & Koning 1989; Koltunow *et al*. 1990; Minter & Lord 1983; Scott *et al*. 1991), where the correlation can result from developmental processes at several levels. For example, some substances produced in the anther are transferred to the corolla and other whorls, where they influence corolla expansion and various other processes (Erickson 1948; Minter & Lord 1983; Mohan Ram & Rao 1984; Raab & Koning 1988). The effects of the stamen on other whorls appear to cease at anther dehiscence (Marre 1946; Mohan Ram & Rao 1984). Other substances, such as homoeotic gene products, are regulated transcriptionally or post-transcriptionally (Coen 1991; Ma 1994; Meyerowitz 1994, 1997). For example, *AGAMOUS* (*AG*) and *FLORAL BINDING PROTEIN1* (*FBP1*) are homeotic genes that code for putative transcription factors (MADS domain proteins) in *Arabidopsis* and *Petunia*, respectively. Transcription of *AG* in the anther and in most ovule-primordium cells ceases when microsporocytes differentiate (Drews *et al*. 1991). In contrast, *FBP1* transcription continues in the anther and corolla throughout development, but the protein becomes undetectable in most anther cells at a specific stage (Canas *et al*. 1994).

Consider a developmental event, for example in the anther, that occurs between initiation of the floral primordium and flower opening. The absolute durations preceding and following the event will clearly vary among species. The absolute durations will also vary among individuals within species according to environmental conditions such as temperature and light intensity. On the other hand, the relative timing of the event (measured as a fraction of total developmental duration) is expected to exhibit less variation within species simply because of the stereotyped and contingent nature of developmental processes. Mathematically, a constant relative timing means that the durations preceding and following the event exist in constant ratio, independent of

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absolute developmental times. Developmentally, a constant relative timing means either that the durations before and after the event are controlled by the same process or that one duration controls the other. All species with the same relative timing of an event also share the same developmental relationships between primordium initiation, the event and flower opening.

Although the absolute timing of tetrad formation in the anther varies among species (Bennett 1977; Bennett *et al*. 1971; Bhandari 1984; Luomajoki 1986), the timing of tetrad formation relative to total floral developmental duration has not previously been studied. The goal of this study was to measure, in flowers of phylogenetically diverse species, the developmental duration preceding tetrad formation as a fraction of total developmental duration. We tested the null hypothesis that species vary continuously in this fraction. A contrary finding of a few discrete timing classes would suggest an evolutionary constraint on the developmental relation between pre- and post-tetrad durations. As defined here, floral development encompasses the period from primordium initiation to flower opening. In species where the flowers are produced sequentially from base to tip (i.e. acropetally) along an inflorescence, the flowers and buds form a chronological sequence. For any developmental event, the time elapsed since primordium initiation can be measured by the number of positions separating the primordium and the event-containing bud. Absolute times can be calculated with knowledge of the plastochron (Erickson 1976; Lamoreaux *et al*. 1978), the time separating consecutive positions (figure 1). Times expressed relative to the total developmental period can be measured only when floral positions representing both the beginning and the end of development exist concurrently on an inflorescence. This study was therefore restricted to species in which floral primordia continued to be initiated while flowers opened at older positions on the inflorescence.

2. MATERIALS AND METHODS

To determine the timing of microspore tetrad formation, the position of each bud on an inflorescence was numbered starting from the newly initiated floral primordium ($P_{\text{primordium}}=0$) and ending with the youngest open flower (P_{opening}, figure 1). Anthers of individual buds pre-stained with safranin-O or acetocarmine were squashed and observed under a compound microscope to determine the position, P_{tetrad}, at which microspore tetrads formed. RAFT, the relative age of a floral bud with tetrads (no units), was calculated as the ratio of the bud position with tetrads to the total number of buds, $P_{\text{tetrad}}/P_{\text{opening}}$. RAFT expresses the time elapsed from primordium initiation to tetrad formation as a proportion of the total time from primordium initiation to flower opening. This method of calculating RAFT assumes that the plastochron remains constant as the inflorescence grows. This has been confirmed for *Amsinckia spectabilis* (M. O. Johnston, personal observations).

The absolute age of a floral bud at tetrad formation (AAFT in days), was calculated when possible (figure 1). To calculate AAFT, the plastochron (days per bud position) was obtained by painting the youngest open flower on inflorescences in the field. D days later (typically five to seven), the inflorescences (one per plant) were collected and fixed in FAA (formalin, acetic acid, ethanol). Plastochron $=D/$(number of flowers opened during D). Fixed inflorescences were dissected as described above to determine P_{tetrad} and P_{opening}. Where more than one bud on an inflorescence contained microspore tetrads, the one adjacent to the bud having microsporocyte meiosis was chosen for calculating the tetrad formation time.

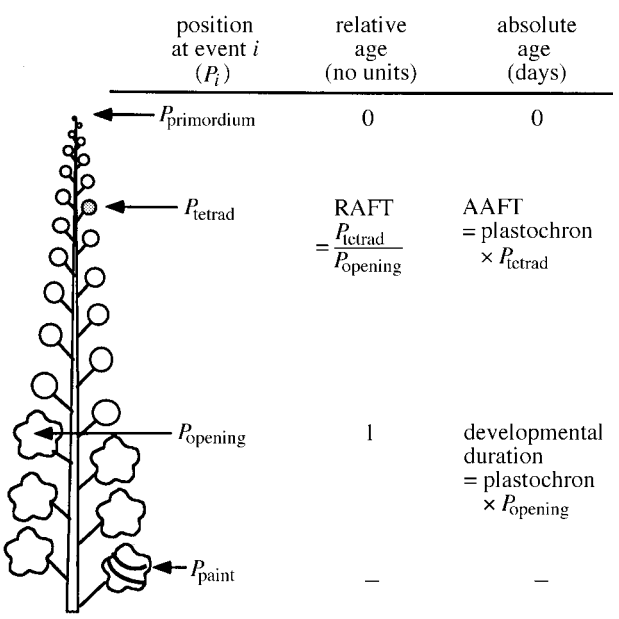
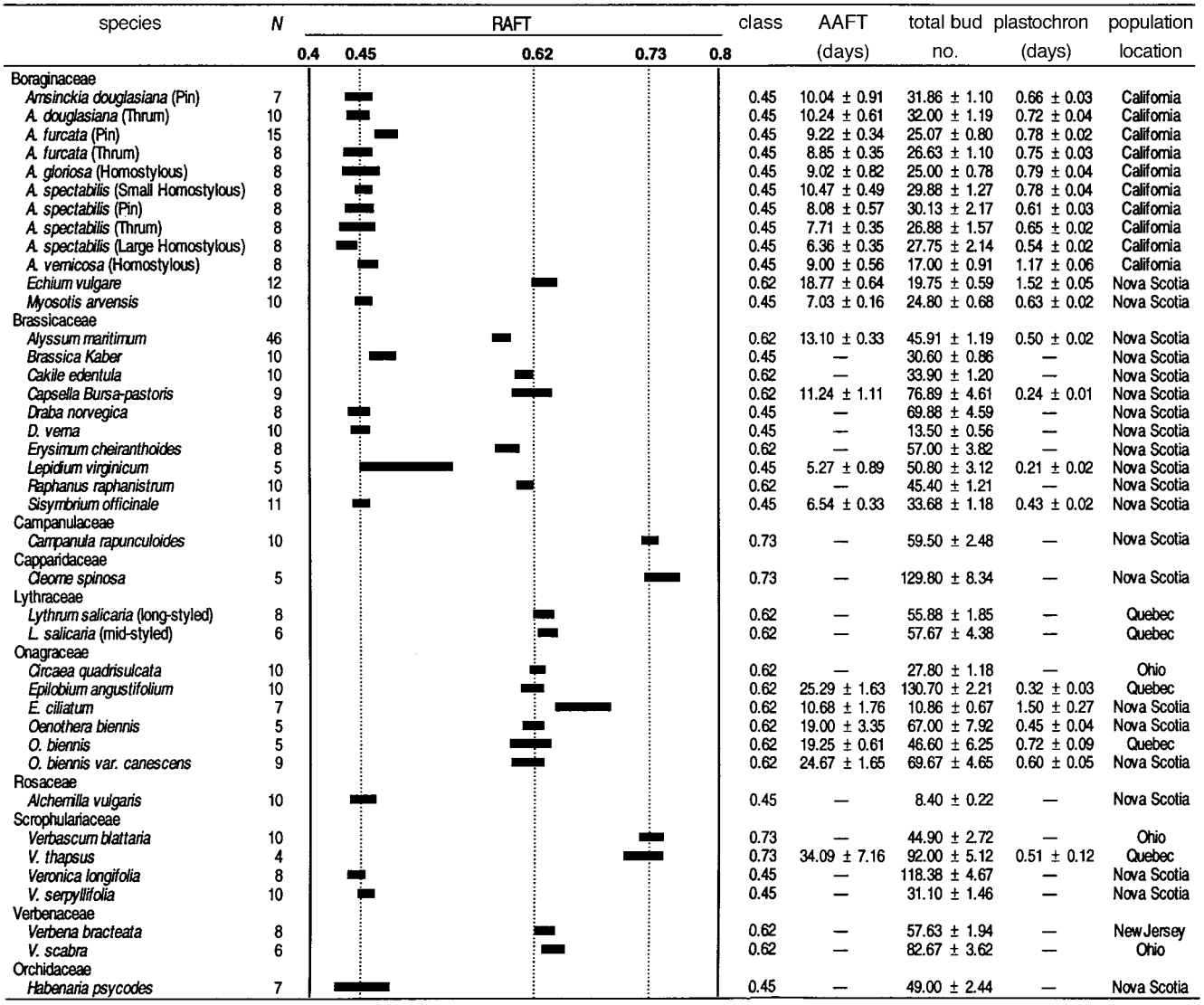


Figure 1. Methods for calculation of RAFT (relative age) and AAFT (absolute age) of a floral bud when its microsporocyte meiosis terminates, indicated by formation of pollen tetrads in the anther. RAFT was calculated for all species; AAFT was calculated for a subset. Floral developmental duration measures the time required for a flower to develop from primordium initiation to corolla opening. Distances between youngest floral buds are greatly exaggerated for clarity.

We examined 32 species representing 23 genera and ten families. Data were analysed by using SYSTAT (1992, Macintosh version 5.2.1). Inflorescence types included racemes (Brassicaceae, Campanulaceae, Capparidaceae, Lythraceae, Onagraceae, Rosaceae), spikes (Orchidaceae, Scrophulariaceae, Verbenaceae) and helicoid cymes (Boraginaceae). Racemes and spikes are indeterminate inflorescences; helicoid cymes are determinate. The literature provided data from which RAFT could be calculated in four additional species: *Arabidopsis thaliana* (Brassicaceae), *Lamium amplexicaule* (Lamiaceae), *Cornus officinalis* (Cornaceae) and *Viola odorata* (Violaceae).

3. RESULTS

RAFT varied significantly among the 32 species analysed (ANOVA $p<10^{-20}$, $n=375$ inflorescences, $F_{31,343}=133$, $r^2=0.92$). Visual inspection of data (figure 2) suggested that mean RAFT fell into three classes. This was confirmed by a three-means cluster analysis using the 32 species means as observations (ANOVA $p<10^{-25}$, $n=32$; $F_{2,29}$, $r^2=0.98$). The mean RAFT for each of these classes (clusters) was 0.45, 0.62 and 0.73, whether determined from all individuals or from species means. A second cluster analysis of all 375 individuals, without regard to species, population or style morph, assigned only five (1.3%) to a class not otherwise representing their species. Only two species differed in mean RAFT from that of the nearest class by more than 0.03: *Lepidium virginicum* (0.04 units from class 0.45) and *Epilobium ciliatum* (0.05 from class 0.62).



species	*N*	RAFT	class	AAFT (days)	total bud no.	plastochron (days)	population location
		0.4 0.45 0.62 0.73 0.8					
Boraginaceae							
Amsinckia douglasiana (Pin)	7		0.45	10.04 ± 0.91	31.86 ± 1.10	0.66 ± 0.03	California
A. douglasiana (Thrum)	10		0.45	10.24 ± 0.61	32.00 ± 1.19	0.72 ± 0.04	California
A. furcata (Pin)	15		0.45	9.22 ± 0.34	25.07 ± 0.80	0.78 ± 0.02	California
A. furcata (Thrum)	8		0.45	8.85 ± 0.35	26.63 ± 1.10	0.75 ± 0.03	California
A. gloriosa (Homostylous)	8		0.45	9.02 ± 0.82	25.00 ± 0.78	0.79 ± 0.04	California
A. spectabilis (Small Homostylous)	8		0.45	10.47 ± 0.49	29.88 ± 1.27	0.78 ± 0.04	California
A. spectabilis (Pin)	8		0.45	8.08 ± 0.57	30.13 ± 2.17	0.61 ± 0.03	California
A. spectabilis (Thrum)	8		0.45	7.71 ± 0.35	26.88 ± 1.57	0.65 ± 0.02	California
A. spectabilis (Large Homostylous)	8		0.45	6.36 ± 0.35	27.75 ± 2.14	0.54 ± 0.02	California
A. vernicosa (Homostylous)	8		0.45	9.00 ± 0.56	17.00 ± 0.91	1.17 ± 0.06	California
Echium vulgare	12		0.62	18.77 ± 0.64	19.75 ± 0.59	1.52 ± 0.05	Nova Scotia
Myosotis arvensis	10		0.45	7.03 ± 0.16	24.80 ± 0.68	0.63 ± 0.02	Nova Scotia
Brassicaceae							
Alyssum maritimum	46		0.62	13.10 ± 0.33	45.91 ± 1.19	0.50 ± 0.02	Nova Scotia
Brassica Kaber	10		0.45	—	30.60 ± 0.86	—	Nova Scotia
Cakile edentula	10		0.62	—	33.90 ± 1.20	—	Nova Scotia
Capsella Bursa-pastoris	9		0.62	11.24 ± 1.11	76.89 ± 4.61	0.24 ± 0.01	Nova Scotia
Draba norvegica	8		0.45	—	69.88 ± 4.59	—	Nova Scotia
D. verna	10		0.45	—	13.50 ± 0.56	—	Nova Scotia
Erysimum cheiranthoides	8		0.62	—	57.00 ± 3.82	—	Nova Scotia
Lepidium virginicum	5		0.45	5.27 ± 0.89	50.80 ± 3.12	0.21 ± 0.02	Nova Scotia
Raphanus raphanistrum	10		0.62	—	45.40 ± 1.21	—	Nova Scotia
Sisymbrium officinale	11		0.45	6.54 ± 0.33	33.68 ± 1.18	0.43 ± 0.02	Nova Scotia
Campanulaceae							
Campanula rapunculoides	10		0.73	—	59.50 ± 2.48	—	Nova Scotia
Capparidaceae							
Cleome spinosa	5		0.73	—	129.80 ± 8.34	—	Nova Scotia
Lythraceae							
Lythrum salicaria (long-styled)	8		0.62	—	55.88 ± 1.85	—	Quebec
L. salicaria (mid-styled)	6		0.62	—	57.67 ± 4.38	—	Quebec
Onagraceae							
Circaea quadrisulcata	10		0.62	—	27.80 ± 1.18	—	Ohio
Epilobium angustifolium	10		0.62	25.29 ± 1.63	130.70 ± 2.21	0.32 ± 0.03	Quebec
E. ciliatum	7		0.62	10.68 ± 1.76	10.86 ± 0.67	1.50 ± 0.27	Nova Scotia
Oenothera biennis	5		0.62	19.00 ± 3.35	67.00 ± 7.92	0.45 ± 0.04	Nova Scotia
O. biennis	5		0.62	19.25 ± 0.61	46.60 ± 6.25	0.72 ± 0.09	Quebec
O. biennis var. canescens	9		0.62	24.67 ± 1.65	69.67 ± 4.65	0.60 ± 0.05	Nova Scotia
Rosaceae							
Alchemilla vulgaris	10		0.45	—	8.40 ± 0.22	—	Nova Scotia
Scrophulariaceae							
Verbascum blattaria	10		0.73	—	44.90 ± 2.72	—	Ohio
V. thapsus	4		0.73	34.09 ± 7.16	92.00 ± 5.12	0.51 ± 0.12	Quebec
Veronica longifolia	8		0.45	—	118.38 ± 4.67	—	Nova Scotia
V. serpyllifolia	10		0.45	—	31.10 ± 1.46	—	Nova Scotia
Verbenaceae							
Verbena bracteata	8		0.62	—	57.63 ± 1.94	—	New Jersey
V. scabra	6		0.62	—	82.67 ± 3.62	—	Ohio
Orchidaceae							
Habenaria psycodes	7		0.45	—	49.00 ± 2.44	—	Nova Scotia

Figure 2. Mean RAFT and associated developmental traits in 32 species of flowering plant. Bar width is ± 1 s.e. Separate analyses are presented for populations within species as well as for floral morphs within populations. RAFT theoretically ranges from zero to unity; for clarity only the region from 0.4 to 0.8 is shown.

Within species, the relative measure RAFT exhibited small standard errors (typically less than 0.01) despite often great variability in the absolute measures of growth, such as total developmental duration, total bud number and plastochron (figure 2; table 1). Within each class, RAFT was generally unrelated to any of these three absolute measures. The sole exception was a correlation between RAFT and plastochron in class 0.62 (Pearson correlation = 0.44, Bonferroni, $p < 0.01$, $n = 103$).

In contrast to the general lack of correlations between RAFT and other variables within classes, higher RAFT classes exhibited statistically greater mean bud number (Tukey test, $p < 10^{-15}$) and floral developmental duration ($p < 10^{-18}$). A positive correlation between AAFT and RAFT therefore also occurred, arising directly as a result of this correlation between RAFT class and developmental duration. Plastochron, the time separating buds, did not differ among classes ($p > 0.6$).

Four previous studies of floral development supply data from which it is possible to calculate RAFT. All support the present results that RAFT falls into a few, narrowly defined classes. RAFT in wild-type *Arabidopsis thaliana* is 0.735 (AAFT = 161 h, floral developmental duration = 219 h) (Crone & Lord 1994); RAFT in chasmogamous flowers of *Lamium amplexicaule* is 0.466 (AAFT = 7 d, floral developmental duration = 15 d) (Lord 1979); RAFT in *Cornus officinalis* is approximately 0.453 (AAFT ≈ 145 d, floral developmental duration *ca.* 320 d) (Li *et al.* 1991); and RAFT in *Viola odorata* is approximately 0.718 (AAFT ≈ 43 d, floral developmental duration *ca.* 59.9 d) for chasmogamous flowers (Mayers & Lord 1983). Inflorescence types for these species are, respectively, racemes, axillary cymes, corymbs and none (flowers solitary).

4. DISCUSSION

(a) *Relation to phylogeny, mating system and ploidy*

Among the 36 species included in this study, RAFT class was highly evolutionarily labile. A particular RAFT class was found in distantly related genera, families and orders (figure 2). Furthermore, class 0.45, common among dicotyledons, was found in the single monocot

Table 1. *Means and coefficients of variation (no. of species in parentheses) of relative and absolute floral developmental traits*

(Values are calculated from the species means and are presented separately for the three RAFT classes. Within each RAFT class, means are presented above coefficients of variation and numbers of species.)

trait				
RAFT	AAFT	total bud number	plastochron	total developmental duration
0.45	8.0	37.2	0.67	16.7
2.8%	20%	73%	42%	30%
(15)	(8)	(15)	(8)	(8)
0.62	16.7	54.3	0.78	26.9
3.2%	36%	57%	75%	37%
(13)	(6)	(13)	(6)	(6)
0.73	34.1	81.6	0.51	45.5
1.1%	—	46%	—	—
(4)	(1)	(4)	(1)	(1)

analysed, the orchid *Habenaria psycodes*. It thus appears that the control of timing of meiosis offset relative to flower opening is similar in monocotyledons and dicotyledons. Although RAFT class often differed among species within a family, there was no evidence of differences in RAFT class at lower taxonomic levels: within the seven genera for which more than one species was analysed (*Amsinckia*, *Draba*, *Epilobium*, *Oenothera*, *Verbascum*, *Verbena*, *Veronica*); among the three populations of *Oenothera* analysed (one population representing a varietal form); or between the two style-length morphs examined in tristylous *Lythrum salicaria*.

Seven of the populations used in this study belong to *Amsinckia*, a genus of yellow- to orange-flowered annuals possessing a variety of mating systems and associated floral traits (Ganders *et al*. 1985; Johnston & Schoen 1995, 1996; Ray & Chisaki 1957; Schoen *et al*. 1997). Distylous species or populations contain two floral morphs, pin (stigma is positioned higher than anthers in flower) and thrum (anthers are higher than stigma). The remaining species or populations were homostylous, bearing stigmas and anthers at similar heights in the flower. Compared with distylous populations, homostylous populations have higher rates of self-fertilization and in most cases smaller flowers. Molecular, morphological and karyological data suggest that *A. vernicosa* is derived from *A. furcata*, *A. gloriosa* (a tetraploid) from *A. douglasiana*, and homostylous *A. spectabilis* (both large- and small-flowered forms) from distylous *A. spectabilis*. If the duration of meiosis was shorter in *A. gloriosa* than in *A. douglasiana*, as has been reported for polyploids compared with related diploids (Bennett 1972, 1977; Bennett *et al*. 1971; John 1990), then there was no consequent effect on RAFT. Within *Amsinckia*, therefore, RAFT class appeared to be unaffected by floral size, floral morph, rate of self-fertilization and ploidy.

(b) *Significance of discrete classes*

The existence of narrowly defined RAFT classes indicates at least two facts concerning the control of floral development. First, within each class, the ratio of time (both absolute and relative) before tetrad formation to time after it is constant and independent of total developmental duration. Second, the end of microsporocyte meiosis is not simply a cue that initiates or potentiates subsequent processes. Instead, one of the following must hold: either the absolute time required for pre-tetrad events determines the time required for post-tetrad events, or the two processes are regulated by an exogenous factor that maintains them in constant temporal ratio.

(c) *Causes of the three RAFT fractions*

The two facts above follow directly from the existence of discrete RAFT classes. The reasons why the classes possess particular numerical values, however, are less certain, because the genetic, cellular and biochemical processes controlling floral development are not sufficiently well known. Furthermore, because $0.45 = 0.62 \times 0.73$, the number of independent RAFT classes is unknown; two developmental processes might act in combination to produce the third class. Despite current ignorance of developmental details, some simple mathematical and developmental possibilities suggest themselves. Below we present two such possibilities and provide evidence against one of them. It is hoped that this brief presentation will stimulate further modelling and testing of the role of microsporocyte meiosis in floral development.

One plausible scenario is that the complementary fractions indicating relative time before and after tetrad formation exist in simple exponential relation, such that $\mathrm{RAFT} = 1 - \mathrm{RAFT}^k$, or $k = \log(1 - \mathrm{RAFT})/\log(\mathrm{RAFT})$. Here, the logarithms, to any base, of the relative durations after versus before tetrad formation exist in constant ratio k. The values $k = 2$ and $k = 4$ correspond to RAFT ≈ 0.618 and 0.724, respectively. In this scenario, RAFT class 0.62 divides total floral development by the golden ratio, $\tau = (1 + \sqrt{5})/2 = 1.618\ldots$, and RAFT class 0.45 can be produced by $k = 3/4$ (if this class is independent of the other two classes, RAFT ≈ 0.450), or by dividing class 0.73 by the golden ratio (if this class is the product of the other two, RAFT ≈ 0.448).

The golden ratio was not explicitly included in the above model, which was based only on simple exponential relations between complementary fractions. Patterns in plant morphology based on the golden ratio are conspicuous and have long been the subject of investigation (Douady & Couder 1996; Green *et al*. 1996; Guerreiro & Rothen 1995; Jean 1994). When an object is divided according to the golden ratio, the ratio of the smaller to the larger part equals the ratio of the larger to the whole. The golden cut of a unit measure results in complementary proportions 0.381 966... and 0.618 034.... It is also the ratio, in the limit, of two successive members of the Fibonacci series (1, 1, 2, 3, 5, 8, 13, ...), the Lucas series (1, 3, 4, 7, 11, 18, ...) and indeed any series constructed by summing the two previous values to obtain the next.

The most conspicuous appearance of the golden ratio in plant morphology concerns phyllotaxis, the spiral or whorled arrangement on an axis bearing structures such as flowers, leaves, branches or scales. A number of clockwise spirals and a different number of anticlockwise

spirals are especially evident on sunflower capitula, pineapple fruits, conifer cones, palm trunks, etc. The number of such spirals winding in each direction is usually a pair of consecutive members of either the Fibonacci or the Lucas series (Jean 1994). The type of phyllotaxis is determined primarily by the divergence angle, d (<0.5 or $<180^\circ$), the angular separation of two successive primordia with respect to the apical centre (Jean 1994; Richards 1951). Fibonacci phyllotaxis arises from divergence angles near $1-\tau^{-1}-\tau^{-2}\approx 0.382\approx 137.5^\circ$, and Lucas phyllotaxis arises from angles near $(3+\tau^{-1})^{-1}=(5-\sqrt{5})/10\approx 0.276\approx 99.5^\circ$. On a given plant specimen, one can readily estimate the divergence angle by locating two nodes on approximately the same line parallel to the axis, determining the number of turns around the axis when proceeding through each successive node and dividing by the number of nodes. Typical fractions in spiral phyllotaxis are 2/5, 3/8, 5/13, etc. (approximating 0.382) for Fibonacci patterns and 2/7, 3/11, 5/18, etc. (approximating 0.276) for Lucas patterns.

A second causal possibility therefore is suggested by the fact that the RAFT classes bear striking relations to the two most common divergence angles causing spiral arrangements of flowers and leaves. The RAFT classes found in this study are related to these two common divergence angles, as follows: $0.45\approx 1-2d_{\mathrm{Lucas}}$, $0.62\approx 1-d_{\mathrm{Fibonacci}}$ and $0.73\approx 1-d_{\mathrm{Lucas}}$. Thus, in this study it was found that the proportion of time that a developing flower spends between meiosis termination and flower opening approximates common divergence angles (or double) between successive primordia. The phyllotactic divergence angle does not refer to processes within individual flowers, but instead to the disposition of separate floral primordia. Therefore, the divergence angle would be able to determine RAFT only as a result of establishing a particular lattice geometry in the inflorescence (Jean 1994). In this scenario RAFT would be determined by the effects of lattice geometry on morphogen diffusion and transport.

At least two empirical facts argue against this hypothesized causal connection between RAFT and divergence angle. First, the explanation applies only to spiral inflorescences, and the present study included two types of non-spiral inflorescence architecture that nevertheless expressed RAFT values in the same three classes as the spiral inflorescences: Boraginaceae and single flowers. In the Boraginaceae primordia are initiated in a zig-zag fashion along one side of the inflorescence. In such cases divergence angles are unrelated to the golden ratio, but classes 0.45 and 0.62 were found in this family. In *Viola odorata* (class 0.73), flowers are borne singly. Because singly borne flowers are not part of an inflorescence lattice, the timing of meiosis termination in such plants cannot be determined by developmental cues from other floral buds. Second, we determined the divergence angles separating floral positions in seven of the species of figure 2 and found that all approximated the Fibonacci angle: *Alyssum maritimum*, *Epilobium angustifolium*, *Verbena scabra*, *Capsella Bursa-pastoris*, *Brassica Kaber*, *Cakile edentula* and *Campanula rapunculoides*. Because these species represented all three RAFT classes, it is clear that RAFT was often related to a floral divergence angle not used by the plant. Therefore, if there is a relation between RAFT and the golden ratio, it is not simply a consequence of developing buds existing in a τ-based cylindrical lattice. This leaves as more probable the scenario of a constant exponential relation between RAFT and 1−RAFT, with very simple exponents.

Other mathematical sequences that approximate the three RAFT classes of course exist, but none is as straightforward as that based on simple exponents. Distinguishing among the possibilities will in general not be achieved by measuring RAFT in a large number of species, because many of the competing mathematical sequences will differ only by a degree of precision greater than that measurable in plants. Instead, the correct mathematical relations among the three classes will be revealed by a mechanistic understanding of the genetic, cellular and biochemical processes of meiosis and floral development. The existence of a small number of discrete RAFT classes suggests that these processes have been highly conserved in angiosperm evolution.

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