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PATTERNS OF PHENOTYPIC AND GENETIC CORRELATIONS AMONG MORPHOLOGICAL AND LIFE-HISTORY TRAITS IN WILD RADISH, *RAPHANUS RAPHANISTRUM*

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Genetic correlations can have profound effects on evolutionary change (Lande and Arnold, 1983; Mitchell-Olds and Rutledge, 1986). Present patterns of genetic correlations in an organism may be caused by pre-existing pleiotropic and developmental relationships among traits and may produce constraints on evolution by natural selection (Cheverud, 1984; Maynard Smith et al., 1985; Via and Lande, 1985; Futuyma, 1986; Mitchell-Olds and Rutledge, 1986; Barker and Thomas, 1987; Clark, 1987*a*; Zeng, 1988). Alternatively, selection may directly alter the patterns of genetic correlations, especially in cases in which two or more traits interact to perform a given function (Cheverud, 1984; Lande, 1984; Clark, 1987*a*, 1987*b*). In this paper we examine the patterns of phenotypic and additive genetic correlations among 10 morphological and life-history traits in wild radish plants. We hypothesized that some of these correlations have been influenced by selection. We predicted that floral and vegetative traits would be uncorrelated and that correlations among the lengths of the corolla tube, pistil and stamens would be higher than the rest of the floral correlations. The results were consistent with most of these predictions.

Wild radish, *Raphanus raphanistrum* (Brassicaceae), is an annual weed of disturbed areas. The hermaphroditic flowers of wild radish are almost entirely self-incompatible (Sampson, 1964; Stanton et al., 1989) and this species does not propagate vegetatively, so virtually all reproduction depends on successful insect pollination. Wild radish is pollinated by a variety of insects, mainly bees, butterflies, and flies (Kay, 1976; Stanton et al., 1989; Conner and Jennetten, unpubl. data). Pollination success is affected by floral morphology in the closely related *R. sativus* (Stanton et al., 1991).

Therefore, patterns of correlations among floral and vegetative morphological traits may reflect past selection on these traits caused by differential pollination success. Selection can theoretically increase or decrease correlations, and our results suggest that both may have occurred in wild radish. First, selection could increase the correlation between functionally related traits, that is, traits that interact to perform a given function. Therefore, positive correlations may evolve under selection to increase the functional integration of trait groups. Our results show that the correlations among the lengths of the filaments and corolla tube (which together determine anther placement) are much higher than the correlations among the rest of the floral traits; this higher correlation could be due to selection for effective pollination.

Alternatively, selection could reduce pre-existing correlations if functional independence between traits or groups of traits increases fitness. Berg (1960) found that the phenotypic correlations between floral and vegetative parts were reduced in insect-pollinated plants relative to wind-pollinated plants. Berg hypothesized that selection to maintain a proper fit between the flower and its pollinators reduces the correlation between the flower and the rest of the plant. Our results show that wild radish also fits the Berg pattern.

MATERIALS AND METHODS

Experimental Procedures

Seeds were collected from a population of *R. raphanistrum* in an alfalfa field near Binghamton, NY,

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in August 1988. A narrow central strip of this field (approximately 6 m by 400 m) had been left unmowed. Five transects, 1 m from each other, were laid out along the long axis of this strip. Fruits were collected from one plant each meter along these transects. If no plant with fruits was located within 0.5 m of a sampling point, then that point was skipped. Fruits were collected from a total of 1,550 plants. Fruits were dried at room temperature and stored at 5°C until used.

To estimate additive genetic variances and correlations among the 10 phenotypic traits, a quantitative genetic half-sibling analysis was performed. For the parental generation of the sib analysis, 500 of the field plants were randomly selected from the entire 1,550. Since the seeds are difficult to remove from their fruits and the fruit segments probably do not split open until germination in nature, nine fruit segments were randomly selected from each of the 500 parental plants. In June 1989, the nine fruit segments from each field plant were sown at a depth of 1 cm in a single 2 liter pot using a three × three grid pattern. Since the fruit segments sometimes contain aborted or inviable seeds (pers. obs.), the actual number of viable seeds planted per pot was unknown. The potting medium consisted of mainly peat and vermiculite, with smaller amounts of bark ash and sand (MetroMix 360, Grace Horticultural Products).

The plants were grown in a greenhouse under natural light plus an array of 1,000 W Metal Halide light fixtures on a 16L:8D photoperiod. Temperatures were maintained at 25 to 30°C during the day and 20 to 25°C at night. Plants were watered as needed using a solution of Peters Peat-Lite Special 15-16-17 fertilizer to provide 100 ppm nitrogen. Plants were placed in a randomized array, and for the first month the entire array was shifted every two or three days in a systematic way to reduce the effects of microenvironmental variation.

Most (81%) of the seeds that germinated did so in the first nine days after planting. In those pots where more than one seed sprouted, a single seedling was chosen randomly and the rest were removed. Twenty-two days after planting, 350 seedlings were established and the remaining 150 pots that had no germination were discarded. While this selected against very late germination, most of the remaining seeds probably would not have sprouted because the germination rate by this time was very low. Discarding these plants is unlikely to affect the distributions of traits other than emergence time, because there were no strong correlations between seedling emergence time and the other traits (at least among the 350 plants that were measured; Tables 2 and 3).

Two life-history traits were recorded on each parental plant: the number of days from planting to seedling emergence and the number of days from emergence to first flowering. In addition, eight morphological traits were measured. All morphological measurements were made with digital calipers (Fowler Ultra-Cal II). Measurement errors were estimated by first taking the variance of 6 to 10 repeated measurements of the same plant part, and then calculating the average of the variances from four sets of these repeated measurements on different plants. This average variance was divided by the variance among individual plants for each trait (calculated from the mean values of two measurements on each parental plant, see below) to give percent error. Measurement errors calculated in this way were less than one percent for all traits.

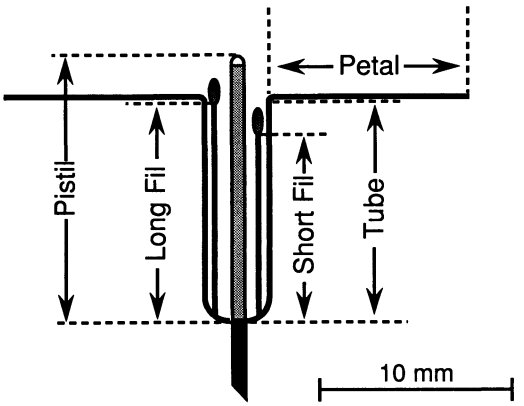

FIG. 1. Schematic diagram of a wild radish flower, depicted in lateral cross-section, showing the five floral length traits measured (the width of the petal was also measured). All Brassicaceae have four long and two short filaments. Only one of the short and one of the long stamens are shown for clarity; Long Fil and Short Fil denote the lengths of the filaments on these stamens. The scale is approximate and based on average dimensions.

For leaves, the overall length (including any lobes but excluding the petiole) and width (at widest point) of the leaf blade were measured on both of the first pair of true leaves. Leaves were measured on the 17th day after emergence. Although the exponential growth phase for these leaves is, in general, complete at this time and many leaves are starting to senesce (Conner, unpubl. data), some leaves do grow after the 17th day in slow-growing plants. Therefore, the leaf traits measured are not necessarily final length and width but also include a small component of growth rate.

Flower traits were measured on the second and third flowers of each plant on the day after they opened. Flowers open sequentially moving up each raceme, starting with the central raceme. In some cases (5.4%), one or both of the flowers were wilted or did not open properly, so another flower (the first, fourth, or fifth) was measured. Flower traits vary much less within plants than between plants, and adjacent flowers on a raceme are extremely similar to each other (Conner, unpubl. data).

The flower of *R. raphanistrum* is shown schematically in Figure 1. The six flower traits measured were: the length and width of the distal part of the petal (outside the corolla tube), the length of the corolla tube (the proximal part of the petal), the length of the pistil, and the lengths of one of the long filaments and one of the short filaments. Note that what we refer to as the corolla tube is not a true tube since the petals are not fused. However, it functions like a true tube during pollination by controlling the access of insects to the nectaries, which are at the base of the tube.

After the measurements of the parents were completed, a half-sib mating design was performed. Fifty of the parental plants were randomly chosen to be sires

(pollen donors); each sire was used to pollinate six different randomly selected dams (females). Single anthers were removed from the sires with forceps and applied to the stigmas of the dams. Groups of 3 to 10 flowers on individual racemes were pollinated, with a central flower of each group left as a control for accidental pollination. If any ovule of the control flower produced seeds, all seeds from that raceme were discarded and the dam was pollinated again. The self-incompatibility system of wild radish also causes some cross-pollinations to be incompatible, particularly matings between close relatives (Sampson, 1964). When an incompatible mating occurred, the incompatible dam was switched with a dam assigned to a different sire. When the fruits matured they were collected and stored as described above.

Four offspring from each dam were grown and measured, with two offspring from each dam in individual pots in each of two blocks planted in January and March 1990. Thus the experimental design was 50 sires × six dams/sire × four offspring/dam = 1,200 offspring total. The actual number of offspring in the analyses was 1,133, however, because four dams were not successfully pollinated and not all offspring germinated. All planting and growing techniques were the same for the offspring as for the parental generation, except that two to nine seeds were initially planted per pot because female parents produced different numbers of seeds. As before, one seedling per pot was chosen randomly and the rest were thinned. Measurements also were done the same way, except that only one flower (the third) and only one of the first pair of true leaves (chosen randomly) were measured. The third flower could not be measured in 3.5% of the offspring; in these cases one of the first 10 flowers was measured (88% of these were the 2nd, 4th, or 5th flower). The leaf was measured on the 18th day after emergence instead on the 17th (as in the parental generation) to allow for more complete leaf growth.

Data Analysis

All phenotypic analyses (means, standard deviations, correlations) were done on the measurements on the parental generation, using only the 340 individuals for which all 10 traits were successfully measured. Because morphological measurements were made on two leaves and two flowers for most individuals in the parental generation, the analyses were performed on the average of the two measurements. For comparison, phenotypic correlations were also calculated using variance components from the offspring analysis; the two sets of correlations were very similar so only the parental correlations are presented.

All analyses of additive genetic variances and correlations were done using the offspring generation only. Since many of these traits are positively genetically correlated (see below), a multivariate analysis of variance was performed to test for significant additive genetic variance over all traits simultaneously (PROC GLM, SAS, 1985). Univariate analyses of variance also were conducted for each trait individually, but these tests are not independent due to the correlations among the traits. Most of the traits were normally distributed, and residual plots did not indicate heteroscedasticity. Normality of some of the traits was improved by transformation, but these transformations made no difference in any of the analyses so untransformed traits were used for ease of interpretation. The sire variance and covariance components were estimated by equating observed and expected mean squares after the block effect was removed (by using the residuals of a model in which the only independent variable was block), and the additive genetic correlations were calculated as the sire variance component correlations (PROC NESTED, SAS, 1985). These least-squares estimates should be very accurate given that the data are nearly balanced. In fact, variance components estimated using restricted maximum likelihood methods (PROC VARCOMP, SAS, 1985) were very similar to the least-squares estimates (within 2% except for emergence time which was 12% different). The formulae in Becker (1984) and Grossman and Norton (1974) were used to calculate standard errors of the variance components and genetic correlations respectively. Narrow-sense heritabilities were calculated as four times the sire variance component divided by the total phenotypic variance.

Results

Patterns of Variability

The multivariate analysis of variance showed a highly significant overall sire effect on the set of traits (Wilks' criterion = 0.0056, $F = 3.35_{490,2,355}$, $P < 0.0001$). In addition, the univariate analyses of variance revealed significant additive genetic variances for all traits (Table 1).

The three traits that are the most phenotypically variable, as measured by their phenotypic coefficients of variation [leaf length and width, emergence time (Table 1)], have the lowest narrow-sense heritabilities; this suggests that these traits are strongly affected by the environment. The lower heritabilities occur in spite of the finding that the additive genetic coefficients of variation (CV_A; Houle, 1992) are the highest for these three traits, indicating substantial additive genetic variation. This supports Houle's (1992) view that heritability may not always be a good measure of genetic variation. Although flowering time was also quite phenotypically variable, most of this variability was additive genetic (63%). The floral morphological traits had moderate to very high narrow-sense heritabilities (0.52–1.16) but generally had less phenotypic and additive genetic variation (as measured by the CVs) than the leaf and life-history traits. This suggests that the floral traits were less affected by the environment than the other traits in our study.

The sire and dam variance components were generally similar, with overlapping 95% confidence intervals for all traits except emergence time (Table 1). This suggests that dominance and maternal effects had little influence on the phenotypic variability of these traits (Falconer, 1989). In contrast, the dam variance component was almost five times the sire component for emergence time, suggesting strong dominance variance and/or maternal effects on this trait.

Phenotypic and Genetic Correlations

The phenotypic correlations among the traits are given in Table 2. The phenotypic correlations among the floral parts were all positive, and most were moderate in magnitude (0.3–0.6). However, the phenotypic correlations among three of the traits, the lengths of the

TABLE 1. Descriptive statistics, variance components and heritabilities for the 10 traits. Means and phenotypic coefficients of variation (CV_P) were calculated from the parental generation ($N = 340$); all other statistics calculated from the offspring generation ($N = 1{,}133$). Morphological traits are in mm, times in days. CV_A = additive genetic coefficient of variation (Houle, 1992). h^2_N = narrow sense heritability; the "sire" effects in the univariate ANOVAs for these traits were all significantly different from zero at $P < 0.0001$ except emergence time where $P = 0.001$.

Trait	Mean (SD)	CV_P	Variance components			CV_A	h^2_N
			Sire (*SE*)	Dam (*SE*)	Error		
Petal length	9.98 (1.19)	11.9	0.21 (0.06)	0.23 (0.04)	0.91	8.6	0.63
Petal width	8.43 (1.18)	14.0	0.41 (0.09)	0.21 (0.04)	0.79	14.6	1.16
Tube length	11.96 (1.04)	8.7	0.14 (0.04)	0.12 (0.03)	0.59	6.6	0.68
Short filament	9.74 (1.00)	10.3	0.09 (0.03)	0.09 (0.02)	0.52	6.3	0.52
Long filament	11.70 (1.06)	9.1	0.13 (0.04)	0.16 (0.03)	0.60	6.1	0.58
Pistil length	14.56 (1.77)	12.2	0.73 (0.18)	0.52 (0.09)	1.92	11.5	0.92
Leaf length	92.93 (20.72)	22.3	36.81 (12.79)	40.21 (15.23)	448.43	15.1	0.28
Leaf width	60.60 (13.31)	22.0	20.56 (5.96)	8.55 (5.42)	177.17	17.4	0.40
Emergence time	7.88 (4.14)	52.5	6.40 (3.00)	31.57 (4.44)	65.32	37.2	0.25
Flowering time	24.96 (4.49)	18.0	2.02 (0.57)	2.98 (0.46)	7.83	11.4	0.63

short and long filaments and the corolla tube, were much higher than the rest of the floral correlations (0.75–0.9). None of the 95% confidence intervals for these three phenotypic correlations (calculated using the *z*-transformation; Snedecor and Cochran, 1989) overlapped the confidence intervals of any of the other correlations. The confidence intervals of the rest of the floral phenotypic correlations were broadly overlapping.

The phenotypic correlation between the two leaf traits was strongly positive (0.86), but the phenotypic correlations between the leaf traits and the floral traits were small and generally not significant. The phenotypic correlations between the morphological traits and the life-history traits (emergence and flowering time) were generally negative in sign, but they were small in magnitude ($\leq |0.22|$) and most were not significant.

Overall, the additive genetic correlations among the traits (Table 3) were very similar to the phenotypic correlations. This was expected for the floral traits due to their high heritabilities, which cause phenotypic correlations to resemble the underlying genetic correlations (Falconer, 1989). Most of the floral genetic correlations were slightly lower than the corresponding phenotypic correlations, but overall they were still moderately positive (0.13–0.53). As with the phenotypic correlations, the exceptions to this pattern were the genetic correlations among the filaments and the corolla tube, which were much higher (0.8–0.9) than the rest of the floral genetic correlations. The additive genetic correlation between leaf length and width was very similar to the phenotypic correlation (0.84 genetic versus 0.86 phenotypic).

The additive genetic correlations between the leaf and floral traits were lower than the additive genetic correlations within either the leaf or the flower, but this pattern was not as strong as for the phenotypic correlations. In particular, the genetic correlations between the leaf traits and pistil were similar in magnitude to most of the intrafloral genetic correlations, in contrast to the phenotypic correlations between the leaf and pistil which were lower. The additive genetic correlations between the morphological and the life-history traits were generally similar to the phenotypic correlations (i.e., small and mostly negative). The exceptions to this similarity were the correlations between the leaf traits and flowering time, which changed sign.

DISCUSSION

Correlation Patterns

On the whole, the additive genetic and phenotypic correlation matrices are very similar; the average absolute difference between pairs of corresponding elements of the two matrices (Willis et al., 1991) is 0.12. This is in contrast to the average difference of 0.366 between genetic and phenotypic correlations for 54 pairs of traits in *Drosophila* (Willis et al., 1991). The small difference here is not surprising given the high narrow-sense heritabilities for these traits.

There have been few studies of correlations among floral morphological traits, especially genetic correlations. Berg (1960), Armbruster (1991) and Schlichting (1989) reported phenotypic correlations among floral traits, while Meagher (1992), Schwaegerle and Levin (1991), and Shore and Barrett (1990) reported both phenotypic and genetic correlations. The latter three papers found generally similar results to ours for analogous floral traits, that is, mostly moderately positive phenotypic and genetic correlations.

Correlations among floral morphological traits have not been reported previously for *R. raphanistrum,* but Mazer (1987, 1989) found weakly positive additive genetic and phenotypic correlations between emergence time and flowering time for this species in a garden experiment. The lack of strong correlation between these traits was confirmed by our study, in which neither the additive genetic nor the phenotypic correlations between emergence time and flowering time were significantly different from zero.

Evolutionary Interpretations of Correlation Patterns

Before discussing possible evolutionary interpretations of the correlation patterns in wild radish, it should

TABLE 2. Phenotypic correlations in wild radish, calculated as the Pearson product-moment correlations among the traits measured in the parental generation ($N = 340$). Significance levels are from a sequential Bonferroni technique (Rice, 1989); using a table-wide significance level of 0.05, individual P-values less than 0.002 are judged significant. The traits are the same as those in Table 1. Standard errors (in parentheses) were calculated using the z-transformation (Snedecor and Cochran, 1989). Lines separate the correlations within and among the three groups of traits: floral, leaf, and life history.

	PetalL	PetalW	TubeL	ShrtFil	LongFil	Pistil	LeafL	LeafW	EmergeT
Petal W	0.59**								
	(0.04)								
TubeL	0.38**	0.32**							
	(0.05)	(0.05)							
ShrtFil	0.45**	0.37**	0.76**						
	(0.04)	(0.05)	(0.02)						
LongFil	0.46**	0.35**	0.84**	0.89**					
	(0.04)	(0.05)	(0.02)	(0.01)					
Pistil	0.42**	0.28**	0.41**	0.42**	0.44**				
	(0.05)	(0.05)	(0.05)	(0.05)	(0.04)				
LeafL	0.11	0.10	0.12	0.10	0.13	0.18*			
	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)			
LeafW	0.09	0.16	0.12	0.12	0.13	0.15	0.86**		
	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.01)		
EmergeT	−0.12	−0.17*	−0.22**	−0.15	−0.17*	−0.13	0.10	0.01	
	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	
FlowerT	−0.02	−0.10	−0.15	−0.12	−0.11	−0.04	−0.20*	−0.21**	−0.03
	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)	(0.05)

* $P < 0.002$, ** $P < 0.0001$.

TABLE 3. Genetic correlations in wild radish with standard errors in parentheses. Correlations that differ from zero by more than two times their standard deviation are shown in bold. Note that this is not a true significance test as the sampling distribution of genetic correlations is unknown, and no correction for multiple comparisons was used.

	PetalL	PetalW	TubeL	ShrtFil	LongFil	Pistil	LeafL	LeafW	EmergeT
PetalW	**0.53** (0.13)								
TubeL	0.25 (0.18)	0.23 (0.17)							
ShrtFil	0.31 (0.18)	0.13 (0.18)	**0.80** (0.08)						
LongFil	**0.39** (0.17)	0.17 (0.18)	**0.85** (0.06)	**0.91** (0.04)					
Pistil	**0.35** (0.16)	0.31 (0.16)	0.32 (0.16)	0.26 (0.18)	**0.34** (0.17)				
LeafL	0.29 (0.21)	0.15 (0.20)	0.03 (0.22)	0.16 (0.22)	0.14 (0.22)	**0.50** (0.18)			
LeafW	0.26 (0.19)	0.22 (0.18)	0.09 (0.20)	0.16 (0.20)	0.08 (0.21)	**0.42** (0.17)	**0.84** (0.06)		
EmergeT	−0.18 (0.25)	−0.08 (0.23)	−0.17 (0.25)	−0.22 (0.26)	−0.12 (0.26)	−0.13 (0.24)	−0.01 (0.29)	−0.04 (0.26)	
FlowerT	0.18 (0.20)	0.21 (0.18)	**−0.46** (0.17)	−0.14 (0.20)	−0.15 (0.20)	0.13 (0.19)	0.34 (0.21)	**0.43** (0.18)	−0.11 (0.26)

be noted that the correlations presented here were estimated in the greenhouse and therefore may not reflect accurately the correlations in the field. Preliminary results, however, suggest that the pattern of phenotypic correlations among *R. raphanistrum* floral traits in an experimental field population is very similar to that reported here (Conner and Jennetten, unpubl. data).

Floral–Vegetative Correlations.—The phenotypic correlations among morphological traits presented here fit the pattern noted by Berg (1960), in which flower traits were positively correlated with each other, as were vegetative traits, but the two groups were generally uncorrelated (Table 2). Since we measured only two vegetative traits (leaf length and width), it is difficult to assess the overall level of correlation among vegetative traits in our population of wild radish. However, Mazer (1987) found positive phenotypic correlations among several other vegetative traits in *R. raphanistrum,* so it is reasonable to conclude that wild radish does fit the Berg pattern. This is consistent with the hypothesis that selection has reduced the correlations between floral and vegetative traits.

Intrafloral Correlations.—Both the additive genetic and phenotypic correlations among most of the floral traits (excluding the correlations between corolla tube and filaments) were low to moderate in magnitude, ranging between 0.13 and 0.59. The moderate genetic correlations among floral traits may be caused by pleiotropic effects of genes affecting overall flower size. However, because floral size seems to be uncorrelated with the overall size of the plant (see above), the correlations among the floral traits are probably not due to pleiotropic effects of genes affecting overall plant size.

The exceptions to this general low to moderate level of correlation among flower traits are the highly positive genetic and phenotypic correlations between the filaments and the corolla tube. There are at least two possible explanations for this result. The first is that the filaments and corolla tube may be much more closely related developmentally than are the rest of the floral traits measured, so that the high genetic correlation may be due to a high degree of pleiotropy in the genes affecting these traits. There is evidence in other plant species that the stamens and petals (of which the filaments and corolla tube are parts) are more closely related in development than are the rest of the floral parts (Hill and Lord, 1989 and references therein). However, phenotypic correlations among these same floral traits in several other plant species do not always show a higher correlation between filament and tube length (Conner and Sterling, unpubl. data), so either the developmental relationships cited above are not found in all angiosperms or they do not always lead to increased phenotypic correlations.

The second possibility for the particularly high genetic correlations that we observed between the filaments and corolla tube is that selection has acted to increase the correlations for effective pollination. The major pollinators of *R. raphanistrum* land on the petals and insert a proboscis into the corolla tube to obtain nectar from the base of the tube. The pollinators are too large to crawl into the narrow tube, so they receive pollen from the anthers while perched at the top of the tube (pers. obs.). The placement of the anthers at the top of the corolla tube is determined by the relative lengths of the corolla tube and the filaments (see Fig. 1). If the filaments are too short relative to the tube length, the anthers might be too far down the corolla tube to contact the pollinator's body. If the filaments are too long, the anthers might be too high for effective pollen placement. Therefore, there may be selection to increase the correlation between filament and corolla tube length, maintaining proper placement of the an-

thers for effective pollination. We are currently testing this hypothesis.

A similar hypothesis of selection for effective pollination could be advanced for the correlation between the pistil and the corolla tube, because the relationship between the pistil and tube lengths determines the placement of the stigma, where pollen is received. However, this correlation (0.41 phenotypic, 0.32 additive genetic) is not greater than the general level of correlation among the flower traits. The lack of an increased correlation between the pistil and tube could mean either that the adaptive correlation hypothesis for the filaments and corolla tube is wrong or that selection is stronger on the male function of the flower than it is on the female function. There is evidence for stronger selection on male function for a different trait (petal color) in *R. raphanistrum* (Stanton et al., 1986).

Effects of Correlations on Future Evolution.—In addition to suggesting how selection might have acted in the past, patterns of genetic correlations can suggest the most likely paths of future evolution. For example, if there was selection for a new floral shape, this new shape should evolve fairly rapidly given the high heritabilities and moderate genetic correlations among most of the floral traits. However, the high genetic correlations between the corolla tube and the filaments would be expected to slow the evolution of different spatial relationships among them, unless the high correlations are due to linkage disequilibrium.

The only other strong evolutionary constraint suggested by our results would be in the evolution of a new leaf shape, which would be constrained by the high genetic correlation between leaf length and width (assuming pleiotropy). Interestingly, a change in the pattern of selection on either of the life-history traits (emergence and flowering time) would not have a strong effect either on the other life-history trait or on any of the morphological traits.

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