COVARIANCE AND DECOUPLING OF FLORAL AND VEGETATIVE TRAITS IN NINE NEOTROPICAL PLANTS: A RE-EVALUATION OF BERG'S CORRELATION-PLEIADES CONCEPT[1]

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Nearly forty years ago R. L. Berg proposed that plants with specialized pollination ecology evolve genetic and developmental systems that decouple floral morphology from phenotypic variation in vegetative traits. These species evolve separate floral and vegetative trait clusters, or as she termed them, "correlation pleiades." The predictions of this hypothesis have been generally supported, but only a small sample of temperate-zone herb and grass species has been tested. To further evaluate this hypothesis, especially its applicability to plants of other growth forms, we examined the patterns of phenotypic variation and covariation of floral and vegetative traits in nine species of Neotropical plants. We recognized seven specific predictions of Berg's hypothesis. Our results supported some predictions but not others. Species with specialized pollination systems usually had floral traits decoupled (weak correlation; *Canna* and *Eichornia*) or buffered (relationship with shallow proportional slope; *Calathea* and *Canna*) from variation in vegetative traits. However, the same trend was also observed in three species with unspecialized pollination systems (*Echinodorus*, *Muntingia*, and *Wedelia*). One species with unspecialized pollination (*Croton*) and one wind-pollinated species (*Cyperus*) showed no decoupling or buffering, as predicted. While species with specialized pollination usually showed lower coefficients of variation for floral traits than vegetative traits (as predicted), the same was also true of species with unspecialized or wind pollination (unlike our prediction). Species with specialized pollination showed less variation in floral traits than did species with unspecialized or wind pollination, as predicted. However, the same was true of the corresponding vegetative traits, which was unexpected. Also in contrast to our prediction, plants with specialized pollination systems did not exhibit tighter phenotypic integration of floral characters than did species with generalized pollination systems. We conclude that the patterns of morphological integration among floral traits and between floral and vegetative traits tend to be species specific, not easily predicted from pollination ecology, and generally more complicated than R. L. Berg envisaged.

Key words: adaptation; correlated evolution; correlation pleiades; evolution, floral traits; genetic correlation; natural selection; pollination; quantitative genetics.

Relatively few empirical studies have addressed the patterns and causes of the covariation of morphological traits in plants, despite a long history of interest in the topic dating back to Darwin. Such studies are timely because evolutionary biologists are still debating how quantitative traits evolve. There are two divergent views: one holds that the developmental and genetic architecture of organisms (e.g., pleiotropy) constrains morphological evolution, and the other holds that natural selection quickly overwhelms developmental and genetic constraints allowing adaptive evolution to proceed largely unconstrained by these factors (see Lande, 1979, 1980; Clark, 1987; Riska, 1989; Houle, 1991). Thus, multivariate patterns of genetic and phenotypic correlation have been viewed by some as evidence of developmental and genetic constraints on evolution, and by others as reflecting the actions of natural selection generating adaptive patterns of genetic correlation (e.g., Stebbins, 1950; Olsen and Miller, 1958; Lande, 1979, 1982; Cheverud, 1982, 1984, 1996a; Zeng, 1988; Riska, 1989; Diggle, 1992; Wagner, 1996; Wagner and Altenberg, 1996). Interest in, and empirical data on, the evolution of trait covariation have increased markedly in the last decade (see Kingsolver and Wiernasz, 1987, 1991; Zelditch and Carmichael, 1989; Armbruster, 1990, 1991; Bjorklund, 1993; Bjorklund and Merila, 1993; Conner and Via, 1993; Conner and Sterling, 1995, 1996; Armbruster and

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Schwaegerle, 1996; Cheverud, 1996a; Schluter, 1996; Andersson, 1997; Waitt and Levin, 1998), but the issue is far from resolved.

Two of the earliest papers to address the potential influence of natural selection on developmental and genetic architecture of plants were by R. L. Berg (1959, 1960). She provided some of the first insights into how the architecture of phenotypic correlations may be modified by selection. Berg noted that many plants have specialized relationships with pollinators and have evolved precise correspondence between flower and pollinator morphology. She hypothesized that selection against covariation of floral morphology with vegetative traits would be generated by reduced reproduction in plants with flowers (of unusual shape or size) that place pollen in ''improper'' places on pollinators (i.e., places not contacting stigmas) or whose stigmas contact pollinators in places where there is no pollen. Thus the floral morphology of plants with specialized pollination ecology should have evolved to be decoupled from the large phenotypic variation usually exhibited by vegetative traits such as plant stature and leaf size. At the same time, selection should perhaps favor stronger correlations between functionally related floral traits (Stebbins, 1950, 1974; Conner and Via, 1993; Conner and Sterling, 1995; Waitt and Levin, 1998). Thus plants with specialized pollination (i.e., precise and consistent fit between flowers and pollinators) should exhibit floral characters that strongly covary with one another but not with vegetative traits. Or, as Berg, described it, in these species floral and vegetative traits should form at least two distinct ''correlation pleiades.''

In contrast, plants that are pollinated by wind or have ''generalized'' animal pollination systems (i.e., diverse pollinators that move generally about flowers without a precise geometric ''fit'') would not have experienced selection for decoupling. These species should show more phenotypic correlation between vegetative and floral traits and perhaps weaker coupling among floral traits (Berg, 1960; Stebbins, 1974). This dichotomy is based on the concept of specialization of the pollination system as it relates to consistency of flower–pollinator fit (see below). In the absence of detailed information on pollination ecology, Berg (1960) used several floral morphological characters to classify plants as specialized or unspecialized. The most useful were zygomorphic (bilaterally symmetrical) arrangement of floral parts and lateral orientation (facing to one side rather than up) of the flowers so that pollinators contact fertile flower parts in a consistent orientation on each visit. Additional conditions that may be associated with floral–vegetative decoupling included pollination by relatively few species and complex, precise pollen placement mechanisms (Berg, 1960).

Berg (1960) examined 19 temperate Russian herb and grass species exhibiting a variety of pollination systems. She found that plants with zygomorphic or laterally oriented flowers pollinated by relatively few insect species had floral traits phenotypically intercorrelated but decoupled from vegetative traits. She found that wind-pollinated plants and plants with actinomorphic flowers pollinated by a variety of insect species had floral and vegetative traits more fully intercorrelated. These results led her to generalize about the evolution of patterns of phenotypic covariance. In contemporary terminology, Berg

argued that populations of plants with specialized animal-pollination systems have evolved increased phenotypic independence of floral traits from environmentally, developmentally, and genetically generated variation in vegetative traits. This idea has been discussed recently by Andersson (1994), who noted relatively stable flower size and shape in the face of variation in plant size in *Nemophila* (Hydrophyllaceae), and similarly, with regard to pollinator choice, by Møller and Eriksson (1994), who observed apparent buffering of developmental instability (fluctuating asymmetry) in flowers as compared to leaves.

Berg also implied that plants with specialized animal-pollination systems (in which many floral traits are functionally interrelated) should exhibit tighter phenotypic integration among floral traits than plants with wind or unspecialized pollination systems (in which floral traits have fewer functional relationships). This idea has been more fully developed subsequently (e.g., Stebbins, 1974; Conner and Via, 1993; Conner and Sterling, 1995; see also Cheverud, 1996a; Nicotra, Chazdon, and Schlichting, 1997; Waitt and Levin, 1998).

Berg's studies of correlation pleiades has been cited in some of the earliest evolutionary quantitative-genetic literature as a ''benchmark'' study of the evolution of phenotypic (and presumably genetic) covariation in natural populations (e.g., Lande, 1979, 1980, 1982; see also Cheverud, 1996b). Her concept has been developed further in recent discussions of mophological integration and the evolution of modularity (e.g., Wagner, 1996; Wagner and Altenberg, 1996). Her studies have also been widely cited because of the insights they provide on the evolution of floral morphology (e.g., Armbruster, 1991; Diggle, 1992; Conner and Via, 1993; Andersson, 1994, 1997; Conner and Sterling, 1995, 1996; Wilson and Thomson, 1996; see also Sherry and Lord, 1996). Because of the limited sampling of plants, however, it is not clear how generalizable Berg's empirical results really are. For example, all of her insect-pollinated plants were dicots, while all of her wind-pollinated plants were monocots. All plants were temperate herbs or grasses. Five additional species have been tested by Conner and Sterling (1996), but these were also temperate dicots. Does the same pattern hold across plants of other habits (e.g., trees, shrubs, and giant herbs) and regions?

The correlation-pleiades hypothesis reconsidered—To evaluate Berg's ideas in more detail we recognized and tested seven distinct components of the correlation-pleiades hypothesis and attempted to define the concept of specialization more precisely. We also broadened the species sampled to include one tree species, a monoecious shrub, and three insect-pollinated monocots, in addition to wind-pollinated monocots and an insect-pollinated dicot herb, in lowland and montane Costa Rica.

We defined plant–pollinator specialization operationally by considering two features. (1) Is pollen placed and picked up consistently from a specific location on the pollinator, such that there is a consistent, reasonably precise flower–pollinator fit? (2) Is pollination effected primarily by one or a few pollinator species of sufficiently similar morphology and behavior that they likely exert similar, consistent, selective pressures on floral morphology (see Stebbins, 1974; but cf. Waser et al., 1996)? Full

evolutionary "specialization" of the plant–pollinator relationship requires that both conditions be met. A "generalized" flower–pollinator relationship results when neither condition is met. Of course numerous other definitions of specialization have been offered, but this definition operationalizes the concept as it pertains to selection for correlation pleiades (cf. Waser et al., 1996).

In her analysis, Berg (1960) employed the product-moment correlation coefficient as the metric of trait covariance. It is possible, however, that floral traits may be strongly correlated with vegetative traits, yet still developmentally buffered from drastic variation. This would be the situation if there is a strong floral–vegetative correlation, but the proportional slope of the floral–vegetative relationship is very shallow. For example, a twofold increase in plant size might cause a predictable increase in flower size, but by only 10%. Thus the range of floral variation would be buffered and might still permit efficient pollination to occur, even though the vegetative and floral traits are not decoupled in terms of their correlations. We consider this possibility in predictions listed below.

From Berg's pleiades hypothesis we derived (appropriately enough) seven related predictions. (1) Plants with specialized pollination systems have floral traits largely decoupled (reduced phenotypic correlation) from vegetative traits; this preserves the precise flower–pollinator fit in the face of large environmental or genetic variance in plant size, leaf size, etc. (2) Plants with specialized pollination systems have floral traits phenotypically buffered (correlated but with shallow slope) from vegetative traits; this also helps preserve the precise flower–pollinator fit in the face of large variation in vegetative traits. (3) By this argument, phenotypic decoupling and buffering should cause the mean coefficient of variation (CV) of floral traits to be smaller than that of vegetative traits. (4) Plants with wind or generalized animal pollination have flowers that are not phenotypically decoupled from vegetative variation because selection has not broken up default genetic correlations between floral and vegetative traits. (Covariation of these traits is to be expect because floral parts are derived from leaves and still share components of their genetic systems.) (5) Plants with wind pollination or unspecialized pollination systems have flowers that are not phenotypically buffered from vegetative variation, because selection has not favored such buffering, and direct covariation of vegetative and reproductive organs (proportional slopes = 1) is the common condition in angiosperms. (6) If predictions 1 and 4, or 2 and 5 hold, phenotypic variances of floral traits (as measured by their CV's) should be lower in plants with specialized pollination systems than plants with wind or generalized pollination systems. This idea was first explicitly presented by Fenster (1991) and further developed by Herrera (1996). (7) Plants with specialized pollination systems have more tightly intercorrelated floral traits than species with less specialized pollination systems; this maintains adaptive covariation of functionally interacting parts (e.g., lengths of filaments and corolla tubes, sepals and petals, styles and anthers; Stebbins, 1974; Armbruster, 1991; Conner and Via, 1993; Conner and Sterling, 1995).

TABLE 1. Species measured, study locations in Costa Rica, and sample sizes. Meristic structures in column 4 refer to repeated units measured, such as flowers or leaves.

Taxon	Location	No. plants	No. meristic structures per plant	No. traits
Monocots				
1. *Calathea crotalifera* (Marantaceae)	Volcán Cacao	15	1–2	13
2. *Canna glauca* (Cannaceae)	Palo Verde	20	2–3	11
3. *Cyperus* sp. (Cyperaceae)	Palo Verde	11	1	7
4. *Echinodorus* sp. (Alismataceae)	Palo Verde	16	3	9
5. *Eichhornia crassipes* (Pontederiaceae)	Palo Verde	9	3	9
6. Poaceae (genus unknown)	Palo Verde	10	2–3	7
Dicots				
7. *Croton* sp. (Euphorbiaceae)	Palo Verde	15	3	10
8. *Muntingia calabura* (Elaeocarpaceae)	Palo Verde	10	2	9
9. *Wedelia* sp. (Asteraceae)	Palo Verde	10	3	12

MATERIALS AND METHODS

Nine species of angiosperms were sampled and measured during July 1994 in the vicinity of the Organization for Tropical Studies (OTS) stations at Palo Verde (eight species in tropical dry forest or marshland) and Volcán Cacao (one species in premontane wet forest), Guanacaste, Costa Rica (Table 1). These species were chosen for study because no others were reasonably common, accessible, and in bloom at the time of our study. Voucher specimens are deposited at CR, US, and USJ; vouchers are not available for the grass and sedge species. Measurements of flower and vegetative traits were made in the field using calipers and meter tapes, or in the laboratory with a dissecting microscope and calipers (flowers of *Cyperus* and Poaceae). The traits were chosen to be mensurally independent of one another, to have functional interpretations (floral traits), and to be similar to the traits measured by Berg (1960). Nine to 13 traits were measured on 27–60 meristic structures (e.g., flowers, leaves) from nine to 20 individuals of each species (Table 1). The traits measured are listed in Appendices 1–9. Floral visitor and pollinator activity and behavior were observed for each species when possible.

Trait means were calculated for each individual plant and used as independent observations in statistical analyses for each species. Trait values were natural-log transformed prior to statistical analyses to eliminate heteroscedasticity and to allow estimation of proportional variation and covariation of traits. Correlation and regression coefficients were calculated for each species using least-squares analysis. Significance of each correlation (Appendices 1–9) was not corrected for multiple comparisons (e.g., Bonferroni), and the nominal significance level of each should be interpreted with caution. Mean absolute correlation coefficients were calculated for relationships among vegetative traits, among floral traits, and between vegetative and floral traits (interclass) from arcsine square-root transformed correlations. Overall heterogeneity of mean absolute correlations among the three groups was assessed using one-way analysis of variance (ANOVA) using SPSS (SPSS, 1995). Differences between pairs of means were tested post hoc using Tukey's HSD method for correlations passing Levene's test of homogeneity of variances, and using Dunnett's T3 method for correlations not passing

TABLE 2. Mean absolute values of correlation and regression coefficients for relationships between vegetative traits, between floral traits, and between vegetative and floral traits. Overall among-class heterogeneity was tested with ANOVA on arcsine square-root transformed coefficients (correlation) or on untransformed coefficients (regression). Post hoc tests (superscripts) were performed with Tukey's HSD multiple comparison for those taxa passing Levene's test of homogeneity of variances (correlation: *Canna, Echinodorus, Eichhornia,* Poaceae sp., *Croton, Muntingia, Wedelia;* regression: *Canna, Poaceae, Croton*) or Dunnett's T3 test for those not passing Levene's test. Means with different superscripts differ at $P < 0.05$. Probabilities in parentheses in columns 6 and 10 show P values for differences between between-class means and pooled within-class means (vegetative and floral traits pooled when not significantly different according to Tukey's or Dunnett's tests).

Species	Pollination class	Absolute correlation ± SE (N)				Absolute regression coefficient ± SE (N)			
		Vegetative	Floral	Vegetative × floral	P of heterogeneity	Vegetative	Floral	Vegetative × floral	P of heterogeneity
Calathea	specialized	0.86 ± 0.02[1] (15)	0.36 ± 0.05[2] (21)	0.38 ± 0.04[2] (42)	<0.001	0.72 ± 0.03[1] (15)	0.54 ± 0.09[1] (6)	0.14 ± 0.01[2] (17)	<0.001
Canna	specialized	0.46 ± 0.09[1] (10)	0.26 ± 0.05[2] (15)	0.18 ± 0.03[2] (30)	0.001	0.65 ± 0.05[1] (6)	0.40 ± 0.06[2] (5)	0.25 ± 0.05[2] (5)	0.001
Echinodorus	generalized	0.68 ± 0.04[1] (10)	0.41 ± 0.07[1,2] (6)	0.32 ± 0.05[2] (20)	0.001 (0.001)	0.72 ± 0.06[1] (10)	1.11 ± 0.5[1,2] (2)	0.27 ± 0.08[2] (8)	0.001 (0.001)
Eichhornia	specialized	0.52 ± 0.08[1] (10)	0.27 ± 0.08[1,2] (6)	0.30 ± 0.04[2] (20)	0.018 (0.089)	0.76 ± 0.15[1] (5)	0.86[1] (1)	0.50[1] (1)	0.741 (0.438)
Cyperus	wind	0.29 ± 0.27[1] (3)	0.33 ± 0.07[1] (10)	0.22 ± 0.04[1] (15)	0.219 (0.410)	—	—	—	—
Poaceae	wind	0.39 ± 0.10[1] (10)	0.01[1] (1)	0.25 ± 0.06[1] (10)	0.141 (0.367)	1.30 ± 0.23[1] (5)	—	0.18[1] (1)	0.116
Croton	generalized	0.72 ± 0.04[1] (10)	0.42 ± 0.08[2] (15)	0.48 ± 0.04[1,2] (30)	0.012	0.42 ± 0.06[1] (10)	0.72 ± 0.09[2] (8)	0.37 ± 0.04[1] (18)	0.001
Muntingia	generalized	0.31 ± 0.10[1] (10)	0.36 ± 0.06[1] (15)	0.36 ± 0.04[1] (30)	0.925 (0.434)	1.36 ± 0.85[1] (2)	0.74 ± 0.14[1] (4)	0.35 ± 0.7[1] (6)	0.056 (0.054)
Wedelia	generalized	0.69 ± 0.06[1] (10)	0.61 ± 0.05[1] (21)	0.33 ± 0.03[2] (7)	<0.001	0.61 ± 0.12[1] (7)	0.70 ± 0.07[1] (14)	0.16 ± 0.01[2] (4)	0.007

Levene's test. Note that all of these analyses assume independence of observations, when in fact the correlation coefficients are not fully independent because they are sometimes derived from shared variables. It is not clear to what extent violation of this assumption influences our results, but we think the effect is fairly small and unlikely to create apparent differences in correlation strength when they do not exist. The error is instead likely to obscure differences when they actually exist.

Principal components analysis (PCA) and factor analysis were performed on natural-log-transformed data using SYSTAT (Wilkinson, 1988) to explore the correlational structure of the data and search for "unknown factors" influencing trait covariation. Factor analysis was performed by rotating the first four axes obtained in the PCA using varimax rotation. Varimax rotation maintains orthogonality while minimizing variables loading on more than one factor and improving interpretability of multivariate patterns (Manly, 1986).

We tested for phenotypic "buffering" by estimating proportional variation and covariation using the log-transformed data, and then comparing slopes of relationships within and between floral and vegetative traits. Specifically, the mean absolute values of the proportional regression coefficients for within-class analyses (vegetative traits or floral traits) were compared with the mean absolute values of the proportional coefficients for floral traits regressed on vegetative traits, using ANOVA and post hoc tests as described for correlation coefficients. The data were not, however, arcsine square-root transformed. Only significant relationships ($P < 0.10$) were used in order to decrease the redundancy of analyses of correlation and regression coefficients, and because estimates of regression coefficients are notoriously unreliable when relationships are weak. ANOVA P values should be interpreted with caution because the regression coefficients are not all fully independent (as described above). Coefficients of variation (CV's) were calculated by dividing the standard deviations by the means of the untransformed data (Sokal and Rohlf, 1981).

RESULTS

Calathea crotalifera—*Calathea crotalifera* S. Watson (= *C. insignis* Peterson; Marantaceae; voucher Alverson and Di Stilio 2575) is a large-stature terrestrial herb (1–2 m tall) growing in clearings in wet lowland to montane forests. The flowers have "spring-loaded" corollas and special staminodia which act as triggers; pollen presentation is secondary, with deposition and pickup occurring explosively when the flowers are tripped (Kennedy, 1978, 1983; Schemske and Horvitz, 1984; Kunze, 1985: Endress, 1994). The flowers are asymmetrical (but largely bilateral) and oriented laterally in bracteate inflorescences. Nectar is hidden in the base of the narrow floral tube. We observed *C. crotalifera* at the Volcán Cacao site being pollinated by two species of nectar-seeking euglossine bees (*Euglossa* spp.; Hymenoptera: Apidae). These two species were the only visitors observed to trip flowers in two days of observations. *Trigona* cf. *fulviventris* was an occasional visitor but did not trip flowers. Pollinating bees approached only from one direction and always landed in the same position. This tight relationship with only a few species of specialized pollinators (see also Schemske and Horvitz, 1984), consistent orientation of pollinators, and very precise pollen placement/pickup mechanism lead to the expectation, under Berg's pleiades hypothesis, that floral and vegetative traits should be decoupled.

The mean absolute correlations between floral traits and between floral and reproductive traits (interclass) were moderately large and nearly identical (Table 2). This is inconsistent with our expectation for a species with highly specialized pollination. However, interclass correlations (and also floral-trait correlations) were significantly lower than vegetative-trait correlations (Table 2), as predicted.

Principal components analysis helped elucidate the source of the moderately strong correlations between floral and vegetative traits (Table 3). Two floral traits, style

length and floral-tube length, consistently loaded on the first principal axis along with all vegetative traits in analyses with and without axis rotation. A third floral trait, sepal length, loaded on the vegetative axis in the PCA and on an axis with other floral traits when axes were rotated. The other floral traits loaded without vegetative traits on an additional two to three axes in the two multivariate analyses.

Despite moderately strong correlations between vegetative and floral traits in *Calathea*, specialized pollination function might be preserved by buffering floral traits from ''excess'' variation through the evolution of shallower relationships (smaller regression coefficients) between floral and vegetative traits. Data from *Calathea* support this prediction. The mean absolute regression coefficient of interclass relationships was significantly smaller than the means of the absolute vegetative and floral regression coefficients ($P < 0.001$; Table 2).

Both phenotypic decoupling and buffering should lead to lower mean coefficients of variation in floral traits than vegetative traits, at least if they have evolved to maintain pollinator ''fit,'' as described by Berg. *Calathea* supported this prediction: the mean CV was 0.022 for floral traits and 0.064 for vegetative traits, and the difference was significant (one-way ANOVA; $F_{1,12} = 30.04$; $P < 0.001$).

Canna glauca—*Canna glauca* L. (Cannaceae; voucher: Alverson and Di Stilio 2568) is a large-stature monocot (1–2 m tall), which grows in wet soil or shallow water. The flowers are asymmetrical but largely bilateral. Nectar is hidden in a long tube. We observed *Canna glauca* being visited and possibly pollinated by several species of butterflies, moths, and hummingbirds. Nevertheless, pollination appears to be quite specialized, because pollen presentation is secondary and placement involves a trigger and spring system (Kunze, 1985; L. McDade, University of Arizona, personal communication). Berg's pleiades hypothesis therefore predicts decoupling of floral from vegetative traits for this species.

The mean absolute correlation between floral and reproductive traits (interclass) was slightly smaller than that of floral traits and in the direction of our prediction, but the difference was not significant (Table 2). However, interclass correlations (and also floral-trait correlations) were significantly lower than vegetative-trait correlations (Table 2), as predicted.

Principal components analysis of plant traits showed most floral and vegetative traits loading on different axes, generally supporting our prediction (Table 3). However, the length of the style (floral) and the thickness of the stem tip (vegetative) loaded together (with opposite signs) on a single axis both in the PCA and when axes were rotated. This result is consistent with the significant negative correlation between these two traits (Appendix 2). The loading of a vegetative trait and a floral trait involved directly in pollination on the same multivariate axis is contrary to the prediction derived from Berg's hypothesis.

Despite significant correlations between some floral and vegetative traits in *Canna*, specialized pollination function is expected to be preserved by buffering floral traits from ''excess'' variation through the evolution of shallower relationships (smaller regression coefficients)

between floral and vegetative traits. There may be a trend in this direction, although it is not as clear as in *Calathea*. The mean absolute regression coefficient of interclass relationships was significantly smaller than the mean of the absolute vegetative regression coefficient ($P = 0.001$), but not than the floral regression coefficient (Table 2). However, the trend was clearly in the right direction (0.25 vs. 0.40; Table 2) and lack of significance may reflect a power problem due to the small number of significant interclass and floral correlations.

Canna also supported the prediction of a lower mean coefficient of variation for floral traits than vegetative traits. The mean CV was 0.10 for floral traits and 0.205 for vegetative traits, and the difference was significant (one-way ANOVA; $F_{1,10} = 14.99$; $P = 0.004$).

Echinodorus sp.—*Echinodorus* sp. (Alismataceae; voucher: Alverson and Di Stilio 2565) is a large-stature (1–1.5 m tall), herbaceous monocot with open, actinomorphic flowers oriented vertically. The nectar reward is presented openly and is available to a variety of generalist flower-visiting insects. Pollination is clearly by insects, and the system appears to be quite generalized. There are no specific pollen-placement mechanisms or features that precisely orient the pollinators as exhibited by *Calathea* and *Canna*. We observed visitation by a variety of bees and butterflies. Berg's pleiades hypothesis thus predicts strong coupling of floral and vegetative traits.

The mean absolute correlation between floral and reproductive traits (interclass) was slightly smaller than that of floral traits, but the difference was not significant (Table 2). This is reasonably consistent with our expectation for a species with generalized pollination. However, interclass correlations were significantly lower than vegetative-trait correlations (Table 2), as in specialized species and unlike our prediction. Furthermore, when the absolute values of the intraclass correlations are pooled (as is warranted by the lack of significantly difference between the floral- and vegetative-trait means), the mean is significantly larger than the mean of interclass absolute values ($P = 0.001$; Table 2). This result supports a decoupling model but is inconsistent with our prediction.

Principal components analysis of plant traits showed all vegetative and floral traits, except petal and style lengths, loading on the first axis, generally supporting our prediction of lack of decoupling (Table 3). Petal and style lengths loaded together on the second axis. The factor analysis with rotated axes, however, showed all floral traits loading separately from vegetative traits except for stamen length, which loaded on the same axis as plant height and leaf length. These results are somewhat ambivalent, but tend to support the general hypothesis of coupled variation in floral and vegetative traits in a species with generalized pollination.

Because *Echinodorus* has a generalized pollination system, there is no reason to expect buffering of floral traits from environmental or genetic variation reflected in vegetative traits. Thus we did not predict shallow relationships between floral and vegetative traits. However, there was a significant trend in this direction as in specialized species. The mean absolute regression coefficient of interclass relationships was significantly smaller than the mean of the absolute vegetative regression coefficient

TABLE 3. Results of principal components analyses (PCA; axes unrotated) and factor analysis (axes rotated) of the morphological data from the nine study species (see Table 1 for specific epithets). Numbers of the main matrix are trait loadings on each PCA or factor axis. The primary axis loading is indicated in boldface. Trait names are listed in the same order in Appendices 1–9; V refers to vegetative trait, F floral.

Species	Trait		PCA 1	PCA 2	PCA 3	PCA 4	Factor 1	Factor 2	Factor 3	Factor 4
Calathea	% variance explained		55.73	15.90	10.04	5.80	48.06	17.63	12.74	9.04
		V1	**0.90**	0.21	0.25	0.19	**0.97**	0.08	0.01	−0.12
		V2	**0.94**	0.21	0.12	0.08	**0.96**	0.13	0.10	0.02
		V3	**0.91**	0.10	0.21	−0.06	**0.89**	0.30	−0.00	0.03
		V4	**0.93**	0.24	0.07	0.04	**0.95**	0.13	0.12	0.09
		V5	**0.90**	0.27	−0.04	0.10	**0.91**	0.04	0.22	0.11
		V6	**0.86**	0.11	0.19	−0.21	**0.82**	0.35	−0.06	0.16
		F1	**0.66**	−0.56	0.14	−0.16	0.41	**0.76**	0.13	−0.19
		F2	0.16	**0.60**	−0.44	−0.56	0.18	−0.15	0.08	**0.91**
		F3	0.26	−0.30	−**0.83**	0.19	−0.02	0.12	**0.93**	0.07
		F4	0.58	−**0.63**	−0.05	0.13	0.32	**0.60**	0.39	−0.37
		F5	**0.83**	−0.34	−0.24	0.09	**0.60**	0.47	0.53	−0.12
		F6	0.32	−**0.70**	0.07	−0.50	−0.01	**0.92**	0.04	0.02
		F7	**0.80**	0.23	−0.41	0.01	**0.72**	0.05	0.50	0.30
Canna	% variance explained		30.75	21.68	16.32	10.87	29.70	21.01	16.26	12.66
		V1	**0.72**	0.05	0.52	−0.17	**0.81**	0.22	−0.20	−0.26
		V2	**0.78**	−0.08	0.34	0.25	**0.85**	−0.03	−0.21	0.15
		V3	**0.91**	−0.14	0.00	−0.10	**0.89**	−0.05	0.26	−0.03
		V4	**0.91**	−0.02	−0.07	0.03	**0.86**	0.02	0.28	0.14
		V5	−0.35	0.05	**0.65**	0.38	−0.17	0.05	−**0.81**	0.07
		F1	0.52	−**0.62**	−0.27	0.08	0.50	−**0.63**	0.31	0.06
		F2	0.16	**0.87**	0.04	−0.28	0.06	**0.92**	0.16	−0.01
		F3	0.10	**0.78**	0.19	−0.11	0.05	**0.81**	−0.07	0.05
		F4	0.07	0.24	−0.38	**0.83**	−0.03	−0.02	0.01	**0.95**
		F5	0.14	0.16	−**0.82**	−0.24	−0.10	0.08	**0.86**	0.16
		F6	0.38	**0.71**	−0.22	0.31	0.24	**0.60**	0.18	0.59
Echinodorus	% variance explained		52.62	17.91	11.65	7.33	31.33	18.70	26.20	13.28
		V1	**0.89**	0.20	0.33	0.02	0.48	−0.02	**0.82**	0.21
		V2	**0.82**	0.04	−0.39	0.29	**0.90**	0.20	0.20	0.08
		V3	**0.76**	0.34	0.24	0.17	0.53	−0.14	**0.69**	0.03
		V4	**0.89**	0.19	−0.18	0.21	**0.84**	0.05	0.42	0.12
		V5	**0.81**	0.14	−0.47	−0.15	**0.82**	0.00	0.11	0.48
		F1	**0.74**	−0.13	0.02	−0.59	0.28	0.13	0.40	**0.82**
		F2	0.27	−**0.85**	0.16	0.33	−0.01	**0.93**	0.21	−0.11
		F3	**0.71**	−0.21	0.60	−0.08	0.06	0.31	**0.87**	0.26
		F4	0.36	−**0.79**	−0.30	−0.12	0.20	**0.80**	−0.12	0.40
Eichhornia	% variance explained		43.38	20.68	13.95	10.44	34.18	16.90	19.38	17.99
		V1	**0.81**	0.15	−0.20	0.06	**0.74**	0.10	0.30	0.28
		V2	−**0.72**	0.12	−0.00	−0.52	−**0.88**	−0.04	0.18	0.02
		V3	**0.89**	0.10	−0.09	0.20	**0.87**	0.16	0.19	0.19
		V4	**0.96**	0.04	0.10	0.09	**0.85**	0.38	0.12	0.23
		V5	0.36	**0.84**	0.06	−0.30	0.16	0.34	**0.87**	−0.10
		F1	0.40	−**0.66**	−0.59	−0.12	0.32	−0.34	−0.29	**0.80**
		F2	0.63	−0.00	**0.69**	−0.23	0.34	**0.89**	−0.02	0.08
		F3	−0.56	0.37	0.12	**0.68**	−0.13	−0.35	−0.05	−**0.89**
		F4	−0.01	−**0.74**	0.60	0.07	−0.05	0.43	−**0.85**	0.05
Cyperus	% variance explained		32.96	27.75	14.12	12.34	30.46	21.40	14.00	21.32
		V1	0.73	0.50	0.12	−0.04	**0.88**	0.16	0.01	−0.04
		V2	0.03	−0.14	**0.89**	0.38	0.03	−0.05	**0.97**	−0.04
		V3	**0.78**	0.49	0.19	−0.21	**0.96**	0.02	0.01	0.05
		F1	0.12	**0.78**	−0.09	0.45	0.36	**0.84**	0.01	0.02
		F2	−0.41	**0.71**	−0.19	0.42	−0.13	**0.90**	−0.06	0.22
		F3	**0.77**	−0.13	−0.43	0.09	0.50	−0.12	−0.38	−**0.64**
		F4	−**0.82**	0.40	−0.07	−0.14	−0.49	0.39	−0.13	**0.67**
		F5	−0.19	**0.64**	0.23	−0.63	0.30	0.07	−0.10	**0.89**

TABLE 3. Continued.

Species	Trait	PCA 1	PCA 2	PCA 3	PCA 4	Factor 1	Factor 2	Factor 3	Factor 4
Poaceae	% variance explained	41.95	22.00	18.60	10.07	34.99	24.53	16.52	16.58
	V1	**0.96**	0.08	0.14	0.17	**0.77**	0.40	0.17	0.42
	V2	−0.10	0.10	**0.92**	0.33	0.04	−0.05	**0.97**	−0.19
	V3	**0.73**	−0.45	0.03	−0.40	**0.89**	−0.14	−0.26	0.02
	V4	**0.87**	−0.21	0.34	−0.02	**0.91**	−0.09	0.21	0.20
	V5	0.62	**0.67**	−0.06	−0.25	0.38	**0.86**	−0.12	−0.03
	F1	0.55	−0.24	−0.54	**0.58**	0.21	−0.00	−0.22	**0.95**
	F2	0.18	**0.88**	−0.12	0.09	−0.19	**0.89**	0.02	0.06
Croton	% variance explained	59.11	13.66	8.95	6.68	29.34	43.68	23.10	22.27
	V1	**0.90**	0.12	0.16	0.12	0.51	0.06	**0.67**	0.40
	V2	**0.85**	0.10	−0.01	−0.41	0.36	−0.01	0.34	**0.81**
	V3	**0.92**	0.19	0.26	0.18	0.48	0.02	**0.79**	0.35
	V4	**0.64**	0.30	0.59	0.14	0.11	−0.02	**0.85**	0.23
	V5	**0.83**	0.04	0.20	−0.45	0.21	0.11	0.43	**0.83**
	F1	**0.80**	0.08	−0.23	0.45	**0.84**	−0.05	0.45	0.06
	F2	**0.87**	−0.05	−0.32	−0.19	**0.68**	0.03	0.15	0.64
	F3	**0.82**	−0.23	−0.43	−0.06	**0.79**	0.16	0.03	0.50
	F4	**0.87**	−0.20	−0.27	0.22	**0.85**	0.20	0.27	0.29
	F5	−0.05	**−0.89**	0.12	0.01	0.02	**0.86**	−0.24	−0.06
	F6	0.44	**−0.68**	0.40	0.05	0.15	**0.82**	0.30	0.17
Muntingia	% variance explained	40.46	23.41	12.55	10.07	27.19	22.44	19.93	16.95
	V1	0.60	**−0.61**	0.20	0.40	0.08	**0.94**	0.17	0.12
	V2	0.59	**−0.66**	0.26	0.33	0.10	**0.95**	0.10	0.20
	V3	**0.76**	0.54	−0.10	0.10	**0.64**	0.07	0.50	−0.46
	V4	0.22	**0.77**	0.23	0.42	0.32	−0.04	−0.02	**−0.87**
	V5	0.62	0.06	**−0.74**	−0.05	0.20	−0.01	**0.95**	0.07
	F1	**0.68**	0.36	0.34	−0.11	**0.79**	0.18	0.06	−0.24
	F2	**0.82**	0.16	0.37	0.03	**0.76**	0.46	0.11	−0.20
	F3	**0.86**	−0.06	0.06	−0.38	**0.78**	0.28	0.35	0.28
	F4	0.44	0.38	0.11	**−0.50**	**0.73**	−0.24	0.09	0.05
	F5	**0.73**	−0.11	−0.62	0.23	0.12	0.33	**0.92**	−0.03
	F6	0.36	**−0.75**	0.09	−0.42	0.21	0.43	0.04	**0.81**
Wedelia	% variance explained	51.73	24.55	9.78	5.56	31.92	30.70	18.67	10.33
	V1	**−0.81**	0.50	0.07	−0.11	−0.35	**0.86**	0.01	−0.20
	V2	**−0.83**	0.51	0.00	0.12	−0.38	**0.80**	0.10	−0.41
	V3	**−0.62**	0.60	0.35	−0.22	−0.02	**0.95**	−0.09	−0.08
	V4	−0.56	**0.77**	0.09	−0.19	−0.07	**0.94**	0.22	−0.06
	V5	−0.63	0.11	0.19	**0.71**	−0.21	0.29	−0.12	**−0.90**
	F1	**0.79**	0.30	0.33	0.13	**0.87**	−0.19	0.20	0.05
	F2	0.54	**0.69**	−0.46	0.06	0.35	0.01	**0.92**	0.14
	F3	**0.83**	0.34	0.21	−0.01	**0.83**	−0.18	0.29	0.21
	F4	0.27	**0.77**	−0.53	0.13	0.15	0.18	**0.95**	0.00
	F5	**0.89**	0.14	−0.12	−0.04	**0.59**	−0.44	0.42	0.33
	F6	**0.92**	0.24	0.13	0.09	**0.81**	−0.36	0.33	0.17
	F7	**0.69**	0.36	0.57	0.01	**0.96**	0.02	0.01	0.09

($P = 0.001$) and the mean of the pooled absolute values for vegetative and floral traits ($P = 0.001$; Table 2).

Echinodorus had a lower mean coefficient of variation for floral traits than vegetative traits, although this was not expected from our prediction. The mean CV was 0.144 for floral traits and 0.342 for vegetative, and the difference was significant (one-way ANOVA; $F_{1,8} = 33.86$; $P = 0.001$).

Eichhornia crassipes—*Eichhornia crassipes* Solms (Pontederiaceae; voucher: Alverson and Potgieter 2736) is a floating monocot with aerial flowers. The blue flowers are bilateral with lateral orientation. Nectar is contained in a basal tube. The flowers we observed were visited by several species of butterflies. Flowers have been reported as usually tristylous (e.g., Barrett, 1977), although our population appeared to be monomorphic. The pollination system is best interpreted as moderately specialized, with specific orientation of pollinators as a result of the lateral orientation and zygomorphy. The pleiades hypothesis thus predicts decoupling of floral and vegetative characters.

The mean absolute correlation between floral and reproductive traits (interclass) was nearly identical to that of floral traits and the difference was not significant (Table 2). This is inconsistent with our expectation for a species with specialized pollination. However, interclass correlations were significantly lower than vegetative-trait

correlations (Table 2). When the absolute values of the intraclass correlations were pooled (as is warranted by the lack of significantly difference between the floral- and vegetative-trait means), the mean was larger than the mean of interclass absolute values and approached significance ($P = 0.09$; Table 2). These last two results tend to support a decoupling model and our prediction.

Principal components and factor analyses of plant traits showed all vegetative traits, except peduncle length (which we interpreted as arguably nonfloral) loading on the first axis (Table 3). Peduncle length and all floral traits loaded on the second, third, or fourth axes. If we allow peduncle length as a floral trait, these results are strongly consistent with a decoupling model and our prediction for a species with specialized pollination.

Interclass and intraclass slopes were similar and not significantly different (Table 2). This could be an artifact of the small number of significant interclass relationships and instability of slope estimates (Appendix 4).

Eichhornia weakly supported the prediction of lower mean coefficients of variation in floral traits than vegetative traits. The mean CV was 0.079 for floral traits and 0.124 for vegetative, but the difference was not significant (one-way ANOVA; $F_{1,8} = 3.85$; $P = 0.091$).

Cyperus sp.—*Cyperus* spp. (Cyperaceae) are sedges with small, generally wind-pollinated flowers (although there are anecdotal reports of insect pollination in some tropical species with whitish bracts). The species we studied has green bracts and gave no indication of being insect pollinated. Berg's pleiades hypothesis therefore predicts strong coupling between vegetative and floral traits in this species.

The mean absolute correlation between floral and reproductive traits (interclass) was smaller than those of both floral and reproductive traits, but the difference was not significant (Table 2). This is reasonably consistent with our expectation for a species with wind pollination.

Principal components analysis of plant traits showed all vegetative and floral traits loading on different axes, except pistillate glume length, which loaded on the first vegetative axis (Table 3). Rotation of axes broke up this association so that variables loaded primarily on two vegetative axes and two floral axes. These results generally support a decoupling model, at least weakly, in contrast to our prediction of strong coupling of vegetative and floral traits.

The lack of significant interclass correlations among traits precluded analysis of the slopes of regression relationships.

Cyperus had similar mean coefficients of variation for floral and vegetative traits, as was expected from Berg's hypothesis. The mean CV was 0.213 for floral traits and was 0.226 for vegetative (one-way ANOVA; $F_{1,6} = 0.12$; $P = 0.74$)

Poaceae—The grass species we measured also had diminutive, wind-pollinated flowers. The pleiades hypothesis again predicts strong coupling between vegetative and floral traits.

The mean absolute correlation between floral and reproductive traits (interclass) was smaller than those of both floral and reproductive traits, but the difference was not significant (Table 2). This is reasonably consistent with our expectation for a species with wind pollination.

Principal components analysis of plant traits showed vegetative traits all loading on the first axis and floral traits loading on three additional axes (Table 3). Diameter of the stem tip also loaded partially on the second axis with stamen length. Rotation of axes shifted most of the loading of diameter of the stem tip to the second axis with stamen length. All other vegetative traits were on the first axis and the other floral traits on separate axes. These results generally support a partial decoupling model, much like in *Eichhornia*. In both cases floral traits are related only to the thickness of the nearby stem or peduncle, but not apparently influenced by measures of plant stature. Unlike in *Eichhornia*, however, this result is in contrast to our prediction of strong coupling of vegetative and floral traits in this wind-pollinated species.

The slope of the interclass relationship was an order of magnitude smaller than the mean vegetative slope. (There were no significant floral relationships.) However, the small number of significant relationships and low power precluded significance ($P = 0.12$; Table 2). Nevertheless, these results suggest a trend toward buffering of floral traits from vegetative variation, in contrast to our prediction.

This grass did not have a detectably lower mean coefficient of variation for floral traits than vegetative traits, which is consistent with Berg's hypothesis. The mean CV was 0.144 for floral traits and 0.431 for vegetative (one-way ANOVA; $F_{1,6} = 5.48$; $P = 0.18$). However, large difference in means suggests that the nonsignificant difference may be due again to a low power (there were only two floral traits).

Croton sp.—*Croton* sp. (Euphorbiaceae; voucher: Kress and Flores 94–4297) is a short-lived shrub with open, actinomorphic, monoecious, apetalous flowers with vertical orientation. The staminate flowers have moderately showy calyces, while the pistillate flowers are relatively inconspicuous. The flowers are clustered together into fairly tight inflorescences. A nectar reward is presented openly in both staminate and pistillate flowers, and is available to generalist flower-visiting insects. We observed *Croton* flowers being visited by a variety of small bees and flies. The system appears to be fairly generalized, with pollen broadly distributed on the bodies of a variety of pollinator species. There are no systems for restricting or precisely orienting pollinators. Berg's pleiades hypothesis thus predicts coupling of floral and vegetative traits.

The mean absolute correlation between floral and reproductive traits (interclass) was not significantly different from either mean floral or vegetative correlations, although the last two differed significantly from one another (Table 2). This is consistent with our expectation for a species with generalized pollination.

Principal components analysis of plant traits showed all vegetative and pistillate floral traits, loading on the first axis, generally supporting our prediction of lack of decoupling (Table 3). However, all staminate flower traits (sepal and stamen lengths) loaded onto a separate axis, suggesting that the staminate flowers are decoupled from variation in vegetative traits. The analysis with rotated

axes, however, showed floral traits loading onto two axes (staminate vs. pistillate flowers) and vegetative traits loading onto two additional axes. Thus PCA and factor analyses suggest some degree of decoupling of at least staminate floral traits, which is not particularly supportive of our prediction.

Because *Croton* has a generalized pollination system, there is no reason to expect buffering of floral traits from environmental or genetic variation reflected in vegetative traits. Thus we do not predict shallow relationships between floral and vegetative traits. However, the mean absolute regression coefficient of interclass relationships was significantly smaller than the mean of the floral relationships ($P = 0.012$; Table 2), unlike our prediction. Consistent with our prediction, however, the mean interclass and vegetative regression coefficients did not differ significantly (Table 2). Support for coupling and our hypothesis was therefore equivocal.

Croton had a significantly lower mean coefficient of variation for floral traits than vegetative traits in contrast to the prediction of Berg's hypothesis. The mean CV was 0.177 for floral traits and 0.368 for vegetative traits (one-way ANOVA; $F_{1,9} = 6.06$; $P = 0.036$).

Muntingia calabura—*Muntingia calabura* L. (Elaeocarpaceae; voucher: Alverson and Prinzie 2608) is a small secondary tree, which grows in disturbed areas. It has open, actinomorphic flowers, which are oriented more or less vertically and are borne usually singly in leaf axils, scattered along the branches. There appears to be floral dimorphism in this species: about half the flowers on a tree had small pistils and numerous stamens, and half had larger pistils and fewer stamens. We therefore measured pistil characters on "pistillate" flowers and staminal characters on "staminate" flowers. A nectar reward is presented at the base of the style in these open flowers and is available to generalist flower-visiting insects. We observed *Muntingia* flowers being visited by a variety of butterflies and moths. The system appears to be fairly generalized, with no restriction or precise orientation of pollinators. Berg's pleiades hypothesis predicts coupling of floral and vegetative traits.

The mean absolute correlation between floral and reproductive traits (interclass) was not significantly different from either mean floral or vegetative correlations (Table 2). This is consistent with our expectation for a species with generalized pollination.

Principal components analysis of plant traits showed most floral traits loading on the first axis and most vegetative traits loading on the second axis (Table 3). However, leaf length loaded on the floral axis, and ovary width loaded on the vegetative axis. Branch-tip diameter loaded on the third axis and stamen length on the fourth. This indicates decoupling of most floral traits from most vegetative, but it is incomplete. The analysis with rotated axes gave similar results, with only pistil length and ovary width loading with vegetative traits. The other four floral traits loaded together, without vegetative traits, on the first axis. Thus there is decoupling of most floral traits from vegetative, in contrast to our prediction.

Because *Muntingia* has a generalized pollination system, there is no reason to expect buffering of floral traits from environmental or genetic variation reflected in veg-

etative traits. Thus we do not predict shallow relationships between floral and vegetative traits. However, the ANOVA of significant regression coefficients indicated a marginally significant difference ($P = 0.056$; Table 2) among vegetative, floral, and interclass relationships. This is the result of the mean absolute interclass regression being shallower than both the mean absolute vegetative and floral regressions ($P = 0.054$ with intraclass regression coefficients pooled; Table 2).

Muntingia had a significantly lower mean coefficient of variation for floral traits than vegetative traits in contrast to the prediction of Berg's hypothesis. The mean CV was 0.084 for floral traits and 0.216 for vegetative traits (one-way ANOVA; $F_{1,8} = 5.61$; $P = 0.042$).

Wedelia sp.—*Wedelia* sp. (Asteraceae; voucher: Alverson and Prinzie 2612) is a small annual herb growing in weedy sites along roads. This species has radially symmetrical, vertically orientated heads (capitula) with orange ray flowers. Individual florets have radial (disk flowers) or bilateral (ray flowers) symmetry. The flowers were visited by a variety of butterflies, syrphid flies, and probably small bees. It can be categorized as having a generalized pollination system because it does not precisely orient pollinators, and it places pollen broadly on the underside of a variety of pollinator species. Berg studied one Asteraceae herb (*Cosmos*) and also classified it as having a generalized pollination system. Berg's pleiades hypothesis thus predicts strong coupling of floral and vegetative traits (which is what she observed in *Cosmos*).

The mean absolute correlation between floral and reproductive traits (interclass) was significantly smaller than both the floral and vegetative correlations (Table 2). This is in stark contrast with our expectation for a species with generalized pollination.

Principal components analysis of plant traits showed most floral and vegetative traits scattered among the first two axes, with the first being slightly more floral and the second slightly more vegetative (Table 3). However, factor analysis with axis rotation gave very different results. Only floral traits loaded on the first axis, and only vegetative traits loaded on the second axis. The third axis was exclusively floral and the fourth vegetative. Thus the analysis with rotation shows complete decoupling of floral traits from vegetative, in contrast to our prediction. However, because the unrotated analysis gave a very different result, it is difficult to interpret the multivariate analyses on their own (but see below).

Since *Wedelia* has a generalized pollination system, there is no reason to expect buffering of floral traits from environmental or genetic variation reflected in vegetative traits. However, the ANOVA and post hoc analyses of significant regression coefficients indicated that the slope of the interclass relationship was significantly shallower than both vegetative and floral relationships ($P = 0.007$; Table 2).

Wedelia had a significantly lower mean coefficient of variation for floral traits than vegetative traits in contrast to our prediction. The mean CV was 0.130 for floral traits and 0.315 for vegetative (one-way ANOVA; $F_{1,11} = 13.8$; $P = 0.004$).

If our interpretation of this species' pollination system as generalized is correct, these results are strongly incon-

sistent with Berg's pleiades hypothesis. We should have seen coupling of floral and vegetative traits, but instead we find the strongest evidence for decoupling and buffering of any of the species examined. Our observations also differ markedly from Berg's observations of correlation structure for her annual composite *Cosmos* in temperate Russia. The reasons for this discrepancy are not obvious.

Interspecific patterns of variation—The weighted mean coefficient of variation of floral traits was 0.069 for the three species with specific pollination systems, 0.181 for the four species with generalized pollination, and 0.180 for the two wind-pollinated species. These compare with the corresponding values of 0.140, 0.320, and 0.324 for vegetative traits. As predicted, the mean CV for floral traits of species with specialized pollination was significantly smaller than the mean CV of floral traits of species with generalized and wind pollination systems ($F_{1,7} = 7.31$, $P = 0.03$). However, the mean CV for vegetative traits of species with specialized pollination was also significantly smaller than the mean CV of vegetative traits of species with generalized and wind-pollination systems ($F_{1,7} = 10.75$, $P = 0.014$).

The idea that floral traits might often covary adaptively leads to the expectation of tighter intercorrelation of floral traits in species with specialized pollination than in species with unspecialized or wind pollination. The specialists are *Calathea* with an absolute mean floral correlation of 0.36, *Canna* at 0.26, and *Eichhornia* at 0.29. This gives a weighted average of 0.315 and compares with a weighted average of 0.445 for unspecialized and wind-pollinated species. These values are significantly different ($F_{1,8} = 38.9$, $P < 0.001$), but in the wrong direction.

DISCUSSION AND CONCLUSIONS

Of the nine species examined, one showed strong evidence, from correlation statistics, for decoupling of floral and vegetative traits (interclass correlations smaller than both vegetative and floral correlations), four showed significant trends toward decoupling (interclass correlations smaller than vegetative but not floral correlations), and four provided no evidence for decoupling of floral and vegetative traits (Table 2). Developmental "buffering" of floral traits from the variation in vegetative traits was inferred when floral–vegetative relationships had significantly shallower proportional slopes than did intraclass relationships. This pattern was very clear in three species, was reasonably likely (interclass slope significantly shallower than vegetative or floral slopes, but not both) in three species, was supported by a strong trend in one species, and was apparently not the case in only one species. (One species could not be assessed.) Thus even coupled (correlated) floral traits were usually buffered from the level of variation observed in vegetative traits. This observation is further supported by the pattern of variation in floral and vegetative traits. The floral coefficients of variation were smaller than the vegetative CV's in all nine species, and they were significantly different in six.

Several distinctive patterns of covariation were displayed by the plants sampled here. The tree species showed relatively little integration across any organs; most organ systems were decoupled from one another. For example, variation in plant size appeared to have less effect on leaf size in the tree than in the herbs and small shrub. Monocot herbs generally showed strong integration across vegetative organs, e.g., large plants usually had large leaves. In the one monocot (*Eichhornia*) in which we measured it, root length was consistently negatively correlated with shoot traits. This appears to reflect a competitive root–shoot allocation relationship. In the one diminutive dicot annual we measured (*Wedelia*), there was a weak, but consistent, negative relationship between floral size and vegetative size. This also appears to reflect a competitive relationship between reproductive and vegetative allocation. Floral–vegetative correlations were generally positive or near zero in the longer lived plants.

Another interesting pattern in the phenotypic correlations was the striking difference in the degree of phenotypic integration of staminate and pistillate flowers with vegetative traits in *Croton* (the only monoecious species). While 75% of 20 correlations between vegetative traits and pistillate-flower traits were significantly greater than zero, none of the ten vegetative/staminate–flower correlations was significant. The probability of this difference occurring by chance is quite small (Pearson chi-square = 15.0, $P < 0.001$, with and without Yates' correction). Also, staminate floral traits were uncorrelated with pistillate floral traits, even though pistillate floral traits were all tightly correlated with each another. This difference is also unlikely to be the result of chance (Pearson chi-square = 11.4, $P = 0.001$; with Yates' correction, $P = 0.013$). Thus it appears that pistillate flowers are developmentally more integrated with growth rates and vegetative stature, while staminate flower size is fairly independent of growth rates and vegetative stature. This may reflect the greater energy and nutrient investment into pistils, fruits, and seeds than into stamens and pollen. Even pistillate flowers, however, were significantly buffered from variation in vegetative stature in terms of proportional variation; the analysis of coefficients of variation showed pistillate flower size to vary proportionately less than correlated vegetative traits.

Tests of predictions—Our results provide support for some aspects of Berg's correlation-pleiades concept, no support for other aspects, and contradict some aspects. We examine the seven components of Berg's hypothesis below.

Prediction 1 stated that plants with specialized pollination systems will have floral traits uncorrelated with vegetative traits. We established that two species had very precise (specialized) pollination systems (*Canna* and *Calathea*) and one a moderately precise pollination system (*Eichhornia*). These species should all have had floral traits largely uncorrelated with vegetative traits. We did find significantly smaller interclass than vegetative correlations in all three of these species. However in no case was the interclass correlation significantly smaller than the floral correlation, and, in two of the three, the floral correlations were also significantly smaller than the vegetative. Thus there appears to be a trend toward decoupling in these three species, in support for prediction

1, but it is hard to rule out that it is just the result of greater "noise" or error variance in the floral traits

The multivariate analyses showed varying support for the expected decoupling of floral from vegetative traits. Several vegetative and floral traits loaded together on major multivariate axes in *Calathea*, unlike our prediction for this highly specialized species. However, floral and vegetative traits largely loaded on separate axes in *Canna* and *Eichhornia*, supporting prediction 1.

Prediction 2 stated that plants with specialized pollination systems would have relationships between floral and vegetative traits with shallower proportional slopes than the relationships among vegetative traits or among floral traits. This prediction was largely supported. The slopes were significantly shallower in two species (*Calathea*, $P < 0.001$; *Canna*, $P = 0.001$), but were similar (with small sample size) in the third species with specialized pollination (*Eichhornia*).

Prediction 3 stated that the coefficient of variation (CV) would be less for floral than vegetative traits in species with specialized pollination. This would not be expected for species with wind-pollinated or unspecialized flowers. All three species with specialized pollination had lower floral than vegetative CV's, and the differences were significant for two of them. The CV's of floral and vegetative traits were very similar in one wind-pollinated species (*Cyperus*) and not significantly different for the other (Poaceae). However, the floral traits had significantly lower CV's for all four species with generalized pollination systems, in contrast to the expectation from Berg's hypothesis. Thus there was no greater tendency for small floral CV's in species with specialized pollination than in species with generalized pollination.

Prediction 4 predicted the lack of decoupling of floral from vegetative traits in wind-pollinated species and species with unspecialized pollination systems. Consistent with this prediction, *Muntingia* and *Croton*, species with generalized pollination, showed little or no evidence of decoupling of floral from vegetative traits in the analysis of mean absolute correlations and principal components (however, note that in *Croton*, staminate floral traits were consistently decoupled from vegetative and pistillate floral traits in all analyses, and that the factor rotation did place all vegetative and floral traits on separate axes). The two wind-pollinated species, *Cyperus* and the grass, were equivocal, because they showed nonsignificant trends towards decoupling. (Note that there may be reasons to expect wind-pollinated plants to sometimes show decoupling or buffering of floral from vegetative traits: both floral and vegetative traits can have profound effects on the physics of wind pollination, and there may therefore be advantages to phenotypic decoupling of these traits; see Niklas and Buchmann, 1985, 1988; and Niklas, 1987.) *Echinodorus* and *Wedelia*, the two other species with generalized pollination, showed significant decoupling in correlation analyses, in contradiction to our hypothesis. *Wedelia* also showed decoupling in the rotated factor analysis (but not in the PCA), whereas *Echinodorus* was somewhat equivocal. Thus prediction 4 was supported by some species but not others.

Prediction 5 stated that wind-pollinated species and species with unspecialized pollination systems would have inter- and intraclass relationships with similar slopes (but see comment above). This prediction was not supported. All four species with unspecialized pollination systems for which comparisons could be made (*Echinodorus*, *Croton*, *Muntingia*, and *Wedelia*) had highly significantly (three) or marginally significantly (one) shallower slopes for the interclass relationships than for the intraclass relationships. The grass species also had a much shallower interclass slope than interclass, but the difference was not significant due to the small number of traits. *Cyperus* could not be evaluated.

Prediction 6 predicted significantly lower phenotypic variances of floral traits (as measured by their CV's) in plants with specialized pollination systems than plants with wind or generalized pollination systems. This prediction was supported. Our result is consistent with Fenster's (1991) results (but cf. Herrera, 1996). However, the same pattern was also observed for the vegetative traits. This is not predicted by Berg's or Fenster's hypotheses and calls into doubt the significance of the pattern in floral traits. Perhaps by chance the three species with specialized pollination have lower variation in all traits. Note that two of the specialized species (*Calathea* and *Canna*) belong to closely related families (Kunze, 1985) and thus may not be independent (Felsenstein, 1985; Herrera, 1996). Alternatively, selection to reduce variation in floral traits may have indirectly (through pleiotropy) reduced variation in vegetative traits in species with specialized pollination. For the present, however, it seems safer to attribute to chance and phylogenetic structuring the lower CV's for both floral and vegetative traits in species with specialized pollination.

Prediction 7 predicted tighter intercorrelation of floral traits in species with specialized pollination systems than in unspecialized and wind-pollinated species. Instead we saw the opposite trend: specialists had significantly weaker correlations among floral traits than unspecialized and wind-pollinated species, indicating solid rejection of this prediction. Examination of vegetative trait correlations (Table 2) shows that the trend cannot be explained as simply the result of specialist species having generally weaker correlations among traits. It is possible that tighter floral covariation could be selected for by pollination aerodynamics in wind-pollinated species (Niklas and Buchmann, 1985, 1988; Niklas, 1987). However dropping wind-pollinated species failed to reverse the trend (see Table 2). The *Eichhornia* population may not be "behaving" as expected because it is adventive in Costa Rica, does not exhibit the "normal" balanced floral trimorphism, and may be predominantly selfing (see, Barrett, 1977; Barrett, Morgan, and Husband, 1989). However, dropping *Eichhornia* from our analysis did not change the conclusion either.

It is possible that there are weaker correlations among floral traits in species with specialized pollination ecology simply because they have less phenotypic variation in floral traits than species with generalized or wind-pollinated flowers (Falconer, 1981; S. Mazer, University of California, Santa Barbara, personal communication). Species with specialized pollination did have lower floral CV's than species with less generalized pollination (see prediction 6). Thus the failure of our observations to support prediction 7 could be a statistical rather than biolog-

ical effect (but see Conner and Sterling, 1995). This issue requires further study.

General remarks—In short, our Costa Rican data set provided equivocal support for the correlation-pleiades concept. There was moderate support for predictions 1 and 2, weak or questionable support for predictions 4 and 6, some evidence against prediction 3, and solid evidence against predictions 5 and 7.

It appears that the evolution of phenotypic covariance structure in plants is probably more complicated than Berg (1960) originally envisaged. For example, some floral traits (e.g., sepal and pistil size) tend to covary with vegetative traits more than other floral traits (e.g., staminate traits, petals). The selective cost of covariation undoubtedly varies among different floral structures, although it is not immediately apparent why staminate traits might be under more stringent selection for decoupling than pistillate. Strength of correlations may be also influenced by developmental and spatial proximity on the plant (e.g., sepals are the basal floral whorl) as has been documented in vertebrates (Olsen and Miller, 1958). There is a tendency for many floral traits to be decoupled and/or buffered from variation in vegetative traits even in plants with unspecialized pollination systems. This may be because (1) these species have also experienced selection for "consistent" pollen placement, pollen pick-up, or pollinator signaling systems (e.g., Møller and Eriksson, 1994), even though pollinator orientation is imprecise (animal-pollinated species); (2) because measured floral traits are genetically correlated with other reproductive traits under selection for decoupling, such as seed and fruit size (see Primack, 1987); and/or (3) because optimal allocation of resources to reproductive structures imposes limits on sizes of nonphotosynthetic floral structures. It is also possible that some species with generalized pollination systems have evolved from specialized ancestors and not lost the ancestor's phenotypic decoupling and/or buffering. Finally, wind-pollinated plants may also be under selection for decoupling or buffering of floral variation from vegetative traits (see Niklas and Buchmann, 1985, 1988; Niklas, 1987).

The genetic/developmental systems of many species with highly specialized pollination may not accommodate decoupling (eliminating correlation) of floral from vegetative traits. However, reduction of proportional variation by genetic/developmental "buffering" (evolving shallow slopes) may be an equally effective route to achieving successful pollination. *Calathea* may be an example of this evolutionary scenario.

It appears that floral traits do not necessarily covary, inter alia, more tightly in species with more specialized pollination systems, perhaps because the adaptive covariance of traits is not broadly applicable to all floral traits and species. Instead, selection may cause specific pairs of floral traits to be tightly coupled genetically but not others (see Armbruster, 1991; Conner and Via, 1993; Conner and Sterling, 1995).

The variation, covariation, and function of floral and vegetative traits of plants remain a fertile system for the study of multivariate evolution, genetic constraint, and adaptive modification of genetic correlations. This small sample of species indicates how idiosyncratically various species and/or life forms respond to, or because of constraints fail to respond to, selective pressures modifying the genetic/developmental architecture of organisms. The field will be advanced significantly by establishment of well-designed, standard methods of data collection and analysis and their application to many additional species, especially woody plants. Much further work is needed before we can begin to see how generally the various components of Berg's correlation-pleiades concept hold in nature, or whether there are particular patterns across life forms, habitats, or higher taxa.

The evolution of floral integration and independence from vegetative traits may be too complicated to allow generalization across many species or all floral characters. It may prove more profitable to analyze the functional consequences of character variation and covariation and make explicit predictions about which characters should be genetically (and phenotypically) coupled and which decoupled on a species-by-species basis (e.g., Armbruster, 1990, 1991; Conner and Via, 1993; Conner and Sterling, 1995; Armbruster and Schwaegerle, 1996). This will be possible only by combining detailed studies of pollination ecology with phenotypic and genetic studies of morphology.

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APPENDIX 1. Correlation and regression coefficients (in parentheses) for floral and vegetative characters of *Calathea crotalifera*. Numbers in boldface are interclass relationships and the rest are intraclass relationships. Column variables (*y*) were regressed on row variables (*x*). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.1$.

y	Plant height	Inflor. height	Stem girth	Leaf length	Leaf width	Inflor. length	Sepal length	Petal length	Stamen length	Ovary length	Style length	Ovary width
Inflor. height	0.96*** (0.83)	—										
Stem girth	0.91*** (0.65)	0.90*** (0.75)	—									
Leaf length	0.90*** (0.64)	0.91*** (0.75)	0.89*** (0.88)	—								
Leaf width	0.84*** (0.53)	0.87*** (0.64)	0.82*** (0.72)	0.97*** (0.87)	—							
Inflor. length	0.78*** (0.53)	0.87*** (0.70)	0.75*** (0.71)	0.80*** (0.77)	0.78*** (0.84)	—						
Sepal length	**0.51*** **(0.20)**	**0.48†** **(0.11)**	**0.58**** **(0.16)**	**0.46†** **(0.13)**	**0.39**	**0.52*** **(0.15)**	—					
Petal length	**0.08**	**0.14**	**0.17**	**0.23**	**0.24**	**0.15**	−0.12	—				
Stamen length	**0.0**	**0.14**	**0.05**	**0.12**	**0.24**	**0.02**	0.18	0.06	—			
Ovary length	**0.38**	**0.33**	**0.42**	**0.42**	**0.37**	**0.35**	0.74** (0.92)	−0.23	0.27	—		
Style length	**0.68**** **(0.09)**	**0.71**** **(0.11)**	**0.69**** **(0.13)**	**0.64**** **(0.12)**	**0.57*** **(0.12)**	**0.56*** **(0.11)**	0.68** (0.46)	0.02	0.48† (0.26)	0.72** (0.39)	—	
Ovary width	**0.05**	**0.15**	**0.28**	**0.16**	**0.09**	**0.35**	0.56* (0.66)	−0.22	0.21	0.44	0.42	—
Floral tube length	**0.65**** **(0.12)**	**0.74**** **(0.15)**	**0.60*** **(0.15)**	**0.76**** **(0.19)**	**0.78**** **(0.22)**	**0.70**** **(0.18)**	0.31	0.40	0.41	0.39	0.70** (0.52)	0.06

APPENDIX 2. Correlation and regression coefficients (in parentheses) for floral and vegetative characters of *Canna glauca*. Numbers in boldface are interclass relationships and the rest are intraclass relationships. Column variables (*y*) were regressed on row variables (*x*). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.

y	Plant height	Stem girth	Leaf length	Leaf width	Tip girth	Sepal length	Petal length	Stamen length	Ovary length	Style length
Stem girth	0.60** (0.76)	—								
Leaf length	0.67*** (0.80)	0.62*** (0.58)	—							
Leaf width	0.50* (0.50)	0.67*** (0.53)	0.86*** (0.73)	—						
Tip girth	−0.10	0.07	0.30	−0.22	—					
Sepal length	**0.14**	**0.40†** **(0.27)**	**0.45*** **(0.32)**	**0.46*** **(0.39)**	**−0.40†** **(−0.23)**	—				
Petal length	**0.17**	**0.04**	**0.03**	**0.16**	**−0.02**	−0.48* (−0.40)	—			
Stamen length	**0.18**	**0.03**	**−0.03**	**−0.00**	**0.04**	−0.28	0.66*** (0.63)	—		
Ovary length	**−0.20**	**0.05**	**−0.01**	**0.06**	**0.01**	0.05	−0.01	0.06	—	
Style length	**−0.32**	**−0.15**	**0.18**	**0.22**	**−0.45*** **(−0.06)**	0.11	0.24	−0.04	0.14	—
Ovary width	**0.19**	**0.22**	**0.15**	**0.34**	**−0.22**	−0.19	0.50* (0.37)	0.42† (0.33)	0.46* (0.29)	0.19

APPENDIX 3. Correlation and regression coefficients (in parentheses) for floral and vegetative characters of *Echinodorus* sp. Numbers in boldface are interclass relationships and the rest are intraclass relationships. Column variables (*y*) were regressed on row variables (*x*). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.

y	Plant height	Stem girth	Leaf length	Leaf width	Tip girth	Sepal length	Petal length	Stamen length
Stem girth	0.60* (0.91)	—						
Leaf length	0.80*** (0.79)	0.55* (0.36)	—					
Leaf width	0.78*** (0.96)	0.81*** (0.66)	0.67** (0.84)	—				
Tip girth	0.58* (0.73)	0.78* (0.58)	0.50* (0.63)	0.78*** (0.79)	—			
Sepal length	**0.58*** **(0.18)**	**0.46†** **(0.09)**	**0.46†** **(0.14)**	**0.50*** **(0.13)**	**0.63**** **(0.16)**	—		
Petal length	**0.09**	**0.24**	**0.03**	**0.11**	**−0.01**	0.22	—	
Stamen length	**0.80**** **(0.70)**	**0.34**	**0.49*** **(0.44)**	**0.48†** **(0.34)**	**0.31**	0.58* (1.61)	0.42	—
Style length	**0.12**	**0.29**	**−0.00**	**−0.20**	**0.31**	0.37	0.65* (0.61)	0.24

APPENDIX 4. Correlation and regression coefficients (in parentheses) for floral and vegetative characters of *Eichhornia crassipes.* Numbers in boldface are interclass relationships and the rest are intraclass relationships. Column variables (*y*) were regressed on row variables (*x*). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.

y	Bulb thickness	Root length	Leaf length	Leaf width	Peduncle thickness	Flower diameter	Tube length	Stamen length
Root length	−0.48	—						
Leaf length	0.65† (0.57)	−0.69* (−1.31)	—					
Leaf width	0.76* (0.45)	−0.66* (−0.85)	0.93** (0.63)	—				
Peduncle thickness	0.42	−0.08	0.28	0.30	—			
Flower diameter	**0.40**	**0.32**	**0.24**	**0.26**	**−0.38**	—		
Tube length	**0.37**	**−0.34**	**0.40**	**0.65†** **(0.50)**	**0.32**	−0.07	—	
Stamen length	**−0.26**	**0.16**	**−0.40**	**−0.44**	**−0.09**	−0.58† (−0.86)	−0.38	—
Pistil length	**−0.13**	**−0.10**	**−0.15**	**0.01**	**−0.56**	0.12	0.34	−0.14

APPENDIX 5. Correlation and regression coefficients (in parentheses) for floral and vegetative characters of *Cyperus* sp. Numbers in boldface are interclass relationships and the rest are intraclass relationships. Column variables (*y*) were regressed on row variables (*x*). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.

y	Plant height	Stem girth	Leaf length	Staminate glume length	Stamen length	Pistillate glume length	Style length
Stem girth	0.00	—					
Leaf length	0.82** (1.13)	0.04	—				
Staminate glume length	**0.38**	**−0.05**	**0.17**	—			
Stamen length	**−0.01**	**−0.08**	**−0.19**	0.59† (0.78)	—		
Pistillate glume length	**0.37**	**−0.38**	**−0.22**	0.32	−0.23	—	
Style length	**−0.31**	**−0.16**	**−0.41**	0.08	0.58† (0.88)	−0.61* (−0.98)	—
Ovary length	**0.13**	**−0.10**	**0.31**	0.23	0.23	−0.31	0.42

APPENDIX 6. Correlation and regression coefficients (in parentheses) for floral and vegetative characters of an unknown genus of Poaceae. Numbers in boldface are interclass relationships and the rest are intraclass relationships. Column variables (y) were regressed on row variables (x). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.

	x					
y	Plant height	Stem girth	Leaf length	Leaf width	Tip girth	Glume length
Stem girth	0.09	—				
Leaf length	0.56† (0.74)	−0.19	—			
Leaf width	0.83** (1.81)	0.17	0.72* (1.18)	—		
Tip girth	0.65* (1.44)	−0.14	0.17	0.35	—	
Glume length	**0.52**	**−0.38**	**0.28**	**0.32**	**0.07**	—
Stamen length	**0.18**	**0.00**	**−0.19**	**−0.04**	**0.56†** (0.18)	0.01

APPENDIX 7. Correlation and regression coefficients (in parentheses) for floral and vegetative characters of *Croton* sp. Numbers in boldface are interclass relationships and the rest are intraclass relationships. Column variables (y) were regressed on row variables (x). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$.

	x									
y	Plant height	Stem girth	Leaf length	Leaf width	Tip girth	Pistillate sepal length	Style length	Ovary length	Ovary width	Staminate sepal length
Stem girth	0.79*** (0.70)	—								
Leaf length	0.91*** (0.38)	0.73** (0.35)	—							
Leaf width	0.64** (0.20)	0.44† (0.16)	0.78*** (0.58)	—						
Tip girth	0.70** (0.24)	0.85*** (0.33)	0.74** (0.60)	0.57* (0.63)	—					
Pistillate sepal length	**0.74**** (0.18)	**0.56*** (0.16)	**0.78**** (0.45)	**0.47†** (0.37)	**0.44†** (0.32)	—				
Style length	**0.64**** (0.22)	**0.78**** (0.31)	**0.68**** (0.56)	**0.44†** (0.49)	**0.72**** (0.73)	0.67** (0.94)	—			
Ovary length	**0.62*** (0.20)	**0.64**** (0.24)	**0.56*** (0.43)	0.32	**0.60*** (0.57)	0.67** (0.88)	0.88*** (0.82)	—		
Ovary width	**0.75**** (0.22)	**0.59*** (0.20)	**0.74**** (0.53)	0.34	**0.59*** (0.52)	0.80*** (0.97)	0.79*** (0.68)	0.84*** (0.78)	—	
Staminate sepal length	**0.12**	**−0.11**	**0.20**	**−0.11**	**−0.08**	−0.10	−0.01	0.13	0.04	—
Stamen length	**0.38**	**0.28**	**0.41**	**0.16**	**0.40**	0.21	0.25	0.31	0.46† (0.23)	0.44† (0.45)

APPENDIX 8. Correlation and regression coefficients (in parentheses) for floral and vegetative characters of *Muntingia calabura*. Numbers in boldface are interclass relationships and the rest are intraclass relationships. Column variables (y) were regressed on row variables (x). *** P < 0.001, ** P < 0.01, * P < 0.05, † P < 0.10.

					x					
y	Plant height	Stem girth	Leaf length	Leaf width	Tip girth	Flower diameter	Sepal length	Petal length	Stamen length	Pistil length
Stem girth	0.98*** (2.21)	—								
Leaf length	0.14	0.10	—							
Leaf width	−0.14	−0.18	0.66* (0.52)	—						
Tip girth	0.18	0.13	0.51	−0.09	—					
Flower diameter	**0.18**	**0.22**	**0.58†** (**0.30**)	**0.33**	**0.31**	—				
Sepal length	**0.47**	**0.43**	**0.61†** (**0.44**)	**0.33**	**0.26**	0.75* (1.04)	—			
Petal length	**0.34**	**0.40**	**0.60†** (**0.42**)	**0.06**	**0.47**	0.63* (0.85)	0.71* (0.70)	—		
Stamen length	**0.00**	**−0.05**	**0.49**	**0.21**	**0.23**	0.37	0.38	0.38	—	
Pistil length	**0.48**	**0.41**	**0.59†** (**0.35**)	**0.07**	**0.87***** (**0.54**)	0.17	0.36	0.52	0.11	—
Ovary width	**0.48**	**0.58†** (**0.05**)	**−0.10**	**−0.54**	**0.05**	−0.06	0.14	0.60† (0.40)	0.04	0.21

APPENDIX 9. Correlation and regression coefficients (in parentheses) for floral and vegetative characters of *Wedelia* sp. Numbers in boldface are interclass relationships and the rest are intraclass relationships. Column variables (y) were regressed on row variables (x). *** P < 0.001, ** P < 0.01, * P < 0.05, † P < 0.10.

					x					
y	Plant height	Stem girth	Leaf length	Leaf width	Tip girth	Head length	Head width	Phyllary length	Ray length	Tube length	Stamen length
Stem girth	0.91*** (0.96)	—									
Leaf length	0.82** (0.47)	0.75* (0.41)	—								
Leaf width	0.79** (0.58)	0.82** (0.56)	0.90*** (1.13)	—							
Tip girth	0.48	0.64* (0.16)	0.42	0.34	—						
Head length	**−0.44**	**−0.46**	**−0.28**	**−0.2**	**0.31**	—					
Head width	**−0.10**	**−0.10**	**−0.09**	**0.17**	**−0.30**	0.48	—				
Phyllary length	**−0.49**	**−0.50**	**−0.26**	**−0.16**	**−0.44**	0.74* (1.03)	0.59† (0.63)	—			
Ray length	**0.11**	**0.20**	**0.05**	**0.36**	**−0.13**	0.35	0.91*** (1.04)	0.33	—		
Tube length	**−0.69*** (**−0.15**)	**−0.73*** (**−0.15**)	**−0.38**	**−0.36**	**−0.53**	0.60† (0.58)	0.63* (0.46)	0.71* (0.50)	0.38	—	
Stamen length	**−0.63*** (**−0.18**)	**−0.67*** (**−0.18**)	**−0.35**	**−0.31**	**−0.43**	0.79** (1.02)	0.60† (0.59)	0.91*** (0.84)	0.33	0.88*** (1.16)	—
Style length	**−0.33**	**−0.36**	**−0.05**	**−0.09**	**−0.31**	0.88*** (0.66)	0.36	0.76* (0.41)	0.20	0.57† (0.43)	0.72* (0.42)