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Vegetative morphology and trait correlations in 54 species of Commelinaceae

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The morphospace of 54 species of Commelinaceae from nine genera was examined with simultaneous attention to constraints, adaptive hypotheses and relatedness. Eleven morphological traits, including leaf length and width, angle between the leaves and internode distances, were measured for each species and analysed by principal components analysis and nested analysis of variance. The results revealed a significant signal of relatedness in vegetative morphology; genus explained 20–50% of the variance in a single trait. The relationships between some traits are consistent with adaptive explanations. The findings are consistent with the prediction that evolution for optimal phyllotaxis should be relaxed as self-shading decreases, and that light availability governs leaf size and branching patterns. Constraints potentially explain some trait correlations, and support was found for the hypothesis that structural constraints govern leaf size and internode size correlations. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, **158**, 257–268.

ADDITIONAL KEYWORDS: comparative study – constraint – leaf size – morphospace – phyllotaxis – phylogeny – plant architecture – shape.

INTRODUCTION

Because shape can affect the interactions of organisms with their environment and determine individual fitness, inferences about, for example, phylogeny, evolutionary diversification and character displacement (see, for example, Evans *et al.*, 2000; Adams, 2004; Holliday & Steppan, 2004; respectively) can be drawn from comparative studies of shape differences amongst organisms (see, for example, Raup & Michelson, 1965; Karr & James, 1975). The quantification of shape in plants can be especially difficult because of their modular body plan, but plant shape has important implications for plant fitness (Berg, 1960; Givnish, 1987).

The factors controlling plant shape can be separated into three groups. First, the similar physiology and resource requirements of all plants lead to specific shapes related to the acquisition of water, light, nutrients and CO_2 (see, for example, Wright *et al.*, 2004). It is well known that light availability affects plant architecture, especially features related to the surface area that intercepts light and the branching pattern (see, for example, Poorter, Bongers & Bongers, 2006). Plants growing in shady environments should experience strong selection to avoid self-shading (Niklas, 1988) and should have more constrained phyllotaxis than do plants experiencing a high-light environment. Plants grown in shade should also be selected for decreased branching, which increases height and may, in turn, increase the ability to compete for light (for example, Faden, 1988; Faden & Evans, 1999).

Second, certain structural constraints apply to any upright form. For example, heavier leaves and reproductive structures on upper branches require stronger, generally thicker, lower support structures (Niklas, 1993, 1994). Trade-offs governed by structural or physiological constraints should govern the covariation amongst traits (see, for example, Wright *et al.*, 2004; Reich *et al.*, 2006). We predict that mechanical support, like internode thickness, should

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be positively correlated with leaf size, as dictated by structural constraints (Corner's rules; Westoby *et al.*, 2002).

These first two factors have been investigated in several earlier studies (for example, Bragg & Westoby, 2002), but the third, evolutionary constraints, has been studied rarely in plant vegetative morphology. The morphology of any given species must, in part, be the result of a shared evolutionary history, which may place constraints on the shapes of related plants. Givnish (1987) noted that phylogeny may contribute significantly to the evolution of particular morphologies by certain lineages, but few studies have interpreted plant shape within a group of plants in a phylogenetic context (but see Ackerly & Donoghue, 1998; Cavender-Bares *et al.*, 2004), perhaps, in part, because plant shape is difficult to quantify and relatedness is usually unknown. The morphology of resource-garnering organs, such as stems, roots and leaves, can be quite complex and difficult to describe mathematically. Previous modelling of plants, in which a modular approach has been used to describe branching lengths and angles (Niklas, 2004; see also Givnish & Vermeij, 1976), provides some guidance in determining appropriate shape measures.

Several mechanisms may result in phylogenetic constraints. Phylogenetic history may constrain morphological evolution if evolution occurs in the direction of greatest genetic variance (Schluter, 1996). Preadaptations may also constrain the likely direction of evolution, such that different taxa evolve different traits under the same selective regime (see, for example, Bock, 1959). In addition, closely related species may share selective regimes, so that phylogeny and morphological evolution may be correlated (Martins, 2000). Any of these mechanisms, and probably others as well, could lead to a signal of relatedness in morphological diversification.

The goals of our study were to describe the vegetative morphology/shape of 54 species of Commelinaceae, to determine the ability of evolutionary history and selection or drift to explain the morphological diversity in this family and to evaluate hypotheses with respect to the influence of constraints or selection on the coevolution of particular traits (or combinations of traits). We predicted that: (1) most of the variance in vegetative traits should occur at the species level (Givnish, 1987), as variation in many vegetative traits in Commelinaceae appears to be evolutionarily labile (for example, Faden & Evans, 1999); (2) phyllotaxis should be constrained more heavily in plants with short internode lengths, as a result of selection to decrease self-shading (Niklas, 1988); (3) branching degree and leaf size should be subject to the same selection pressures (light environment) and should be positively correlated if less branching, greater height and larger leaves are favoured in shady environments (for example, Ackerly & Donoghue, 1998); and (4) constraints should govern the internode diameter, such that the diameter should be positively correlated with leaf size, as larger leaves require greater support (Niklas, 1994; Westoby *et al.*, 2002).

MATERIAL AND METHODS

Commelinaceae include about 630 species in 40 genera (Faden, 2000). Fiftyfour of these species from nine genera were sampled for our study (Appendix, Table A1; see Figs 1–6 for some examples), including two genotypes of *Murdannia simplex* and three of *Cyanotis repens* with different ploidy levels. Both major tribes of the family were well represented: 24 members of Commelineae and 30 members of Tradescantieae were included.

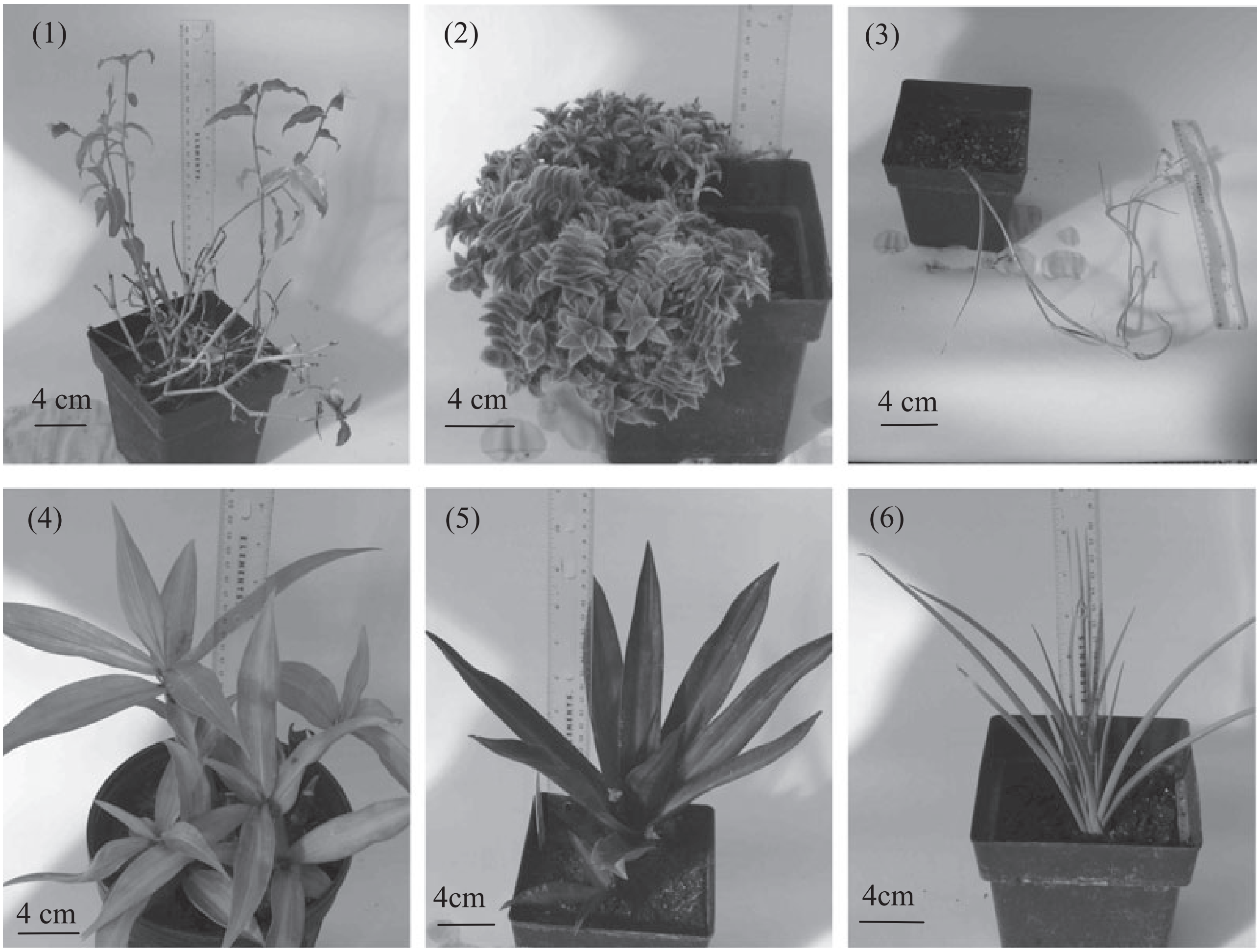
The taxonomy of Hunt (1980), Faden & Hunt (1991) and Faden (2000) was followed. Molecular phylogenies were used when available to verify the taxonomic classifications (tribes and subtribes within Commelinaceae: Evans *et al.*, 2003; sections and groups within *Callisia*: Bergamo, University of Georgia, Athens, unpubl. data).

The status of each of the chosen morphological traits as a good 'species-level trait' was determined from a quantification of all of the traits for five clones of each of the three species for which sufficient genotypes were available (*Commelina benghalensis*, *Tradescantia fluminensis* and *Commelina erecta*). Species-level traits are those in which most of the variance occurs at the species level or higher and much less occurs amongst clones within species.

MORPHOLOGICAL TRAITS

Before the study began, the plants were all grown in a common glasshouse environment at Florida State University under similar soil, water and nutrient regimes for at least 1 year. Temperatures were maintained at about 22 °C with approximately 50% relative humidity. Plants were grown in a 2 : 1 mixture of sterilized fine sand and potting mix, with moisture levels maintained to prevent wilting and nutrients applied as an aqueous solution of 20 : 20 : 20 of N : P : K monthly ($2.4\ \mathrm{g\ L^{-1}}$ to soil saturation monthly of Peter's fertilizer; W. R. Grace, Fogelsville, PA, USA). All plants were exposed to full light under glasshouse conditions. Measurements of morphological traits were made between March 7 and 11, 2005.

Whole-plant morphology was described as the scores, for each individual, of branching degree (0, basal rosette; 1, primary branching; 2, secondary branching; etc.) and orientation (vertical, horizontal



Figures 1–6. Growth forms of several Commelinaceae, chosen to illustrate the broad variation in the family. Fig. 1. *Commelina mascarenica*. Fig. 2. *Cyanotis somaliensis*. Fig. 3. *Commelina welwitschii*. Fig. 4. *Dichorisandra thyrsiflora*. Fig. 5. *Tradescantia spathacae*. Fig. 6. *Tradescantia ohiensis*.

or polymorphic). A single individual per species was scored, with the exception of the three species used to determine whether the traits were species-level traits ($N = 54$, see data analysis below). Phyllotaxis and leaf shape were determined from a single branch, chosen because it appeared to be representative of that individual and, where possible, had at least four fully expanded leaves. Four of these leaves, including the most distal (youngest) and most proximal (oldest), were chosen to represent a developmental series. The internode length and diameter were measured to the nearest 1 mm for the internodes basal to the three most distal leaves. The angle between a leaf and the leaf above it (leaf angle) was measured to the nearest degree with a protractor for each of the bottom three leaves, as a measure of phyllotaxis. The four focal leaves were then harvested, photographed and digitally imaged (Rasband, 1997–2005). From the images, the distance from the base to the point of maximum width (L_1), the distance from the point of maximum width to the tip (L_2), maximum leaf width, width at the base (leaf basal width), leaf perimeter and leaf area were measured. Averages of the internode length, internode diameter ($N = 3$), leaf angle, L_1, L_2, maximum leaf width, leaf basal width, leaf perimeter and leaf area ($N = 4$) were taken on an individual basis for multiple individuals (sample sizes above), and all analyses were conducted on averages.

DATA ANALYSIS

Testing for trait redundancy

A principal components analysis (PCA) with L_1, L_2, total leaf length, maximum leaf width, leaf basal width, leaf perimeter, leaf area, internode length, internode diameter, branching degree, leaf angle and variance in leaf angle for 54 species revealed which morphological variables were redundant in the characterization of plant shape. A single trait was chosen when two or more traits were highly redundant. Ratio traits (such as L_1/L_2) describe plant shape, and these were considered in the preliminary analysis. However, ratio traits are difficult to interpret, as it is unclear which portion of the ratio drives any relationship. No results with such shape metrics were found that were not apparent in analyses without shape metrics, and the raw variables are presented here for ease of interpretation.

Verification that traits were species-level traits

A separate analysis of variance (ANOVA) with genotype nested within species and species nested within genus for the three species with multiple genotypes ($N = 5$) (Gittleman & Luh, 1992) tested the 'species-level' nature of each trait.

Effects of relatedness on these traits

Additional nested ANOVAs were conducted for all traits at the species level and higher for all 54 species (57 genotypes) sampled. These nested ANOVAs were used to determine whether relatedness (here taxonomy) could explain a significant proportion of the variance in species traits (Harvey & Pagel, 1991; Gittleman & Luh, 1992). Only species, genus and tribe were known for all species in the study, so that the ANOVA model included species nested within genus and genus nested within tribe. The internode length, internode diameter, total leaf length, leaf area and variance in leaf angle were natural logarithmically transformed to meet the assumptions of ANOVA.

Partitioning the relative importance of relatedness and trait covariation

Hypotheses about the relationships between morphological traits, with partial correction for taxonomic relatedness, were tested by analysis of covariance (ANCOVA) in which genus was nested within tribe as a covariate (see, for example, Harvey & Pagel, 1991). This analysis effectively assumes that all of the variance that can be attributed to phylogeny is the result of phylogenetic constraints and removes it from consideration in testing further hypotheses (see the discussion by Harvey & Pagel, 1991). The internode length, internode diameter, total leaf length, leaf area and variance in leaf angle were natural logarithmically transformed to meet the assumptions of ANCOVA. A covariate-by-predictor variable interaction was tested for, and violations of the assumption of the parallelism of slopes are reported. All analyses were conducted in SAS (SAS Institute, 1999–2000).

RESULTS

GENERAL DESCRIPTION OF MORPHOLOGY

Figures 1–6 shows the range of plant shape amongst the species sampled. Species differed widely in phyllotaxis; the mean between-leaf angle was 140° [standard deviation (SD), ± 30°], close to the theoretical optimum of 135° (Niklas, 1988), and leaf angles were in the range 57–180°. The SD of within-plant variance in leaf angle varied from zero (mostly for strictly distichous species, e.g. *Tradescantia ohiensis*; Fig. 6) to 3.0. Plant growth form varied from true rosette (internode length of zero) to internode lengths up to 100 mm. Species also varied in orientation, from sprawling to upright (Figs 1–6).

Leaves were all entire and linear, lanceolate or ovate, but varied in size and narrowness. The leaf area ranged from 0.5 to 18 cm^2; the among-species average was 7 cm^2 (± 6.6 cm^2). The total leaf length divided by the leaf width (a unitless measure of leaf narrowness) varied from 1.3 to 33 (mean, 6.7 ± 8.6).

TRAIT REDUNDANCY

The first three axes of PCA on 12 morphological traits explained 74% of the variance in among-species vegetative morphology (Fig. 7). Because L_1, L_2, the total leaf length and leaf perimeter were tightly correlated on PC1, they were considered to be redundant, and only the total leaf length was used in further analyses. L_2 explained only 63% of the variance on PC1 and was eliminated from consideration. L_1, the total leaf length and leaf perimeter explained 81%, 85% and 88% of the variance on PC1, respectively, and the total leaf length was chosen arbitrarily from the three traits. The basal leaf width and maximum leaf width were also correlated. The latter was most strongly correlated with PC2 (91% of the variance versus 46% for the basal width), and so only the maximum leaf width was used in further analyses.

The first principal component axis explained 41% of the variance in vegetative morphology amongst species and was primarily correlated with measures of leaf size. The second axis explained 19% of the variance and was correlated with the maximum leaf width and internode diameter. The third axis explained 14% of the variance and was associated with the internode length, variance in angle between the leaves and angle.

SPECIES-LEVEL NATURE OF THE TRAITS

The results of the nested ANOVA for each individual trait showed that the amount of variance at the genotype-nested-within-species level was always approximately one to two orders of magnitude less than that at the species-nested-within-genus or genus level (results not shown). These results support our use of these as species-level traits.

EFFECTS OF RELATEDNESS ON TRAITS

Vegetative morphology was evolutionarily labile, but some of the variance amongst species can be

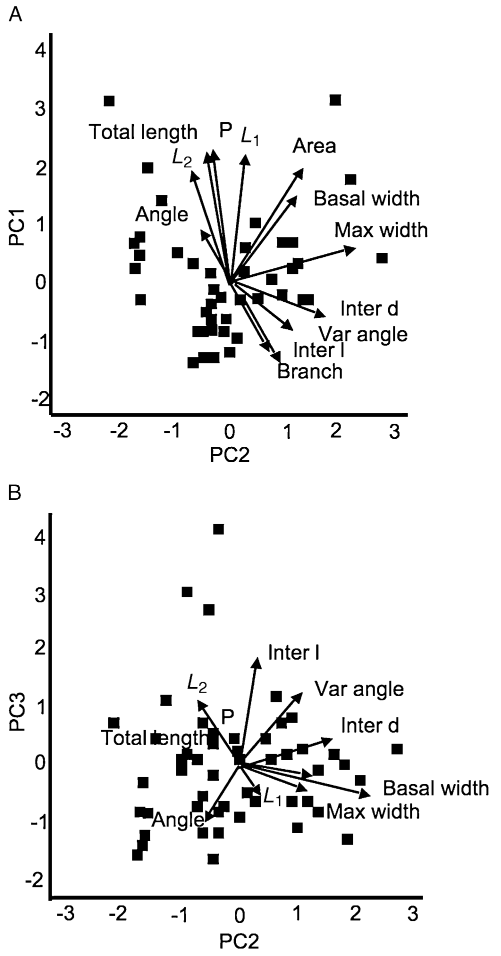


Figure 7. Principal components analysis of morphological traits of 54 species of Commelinaceae: A, principal component 1 (PC1) plotted against PC2; B, PC3 plotted against PC2. A vector represents the contribution of each variable to the variance in that PC: longer vectors indicate stronger correlations; vectors in the same direction are positively correlated. Points are species centroids. Names are sometimes offset to improve readability. Angle, angle between a leaf and the leaf above it; Area, leaf area; Basal width, leaf width at the base; Branch, branching degree (0, basal rosette; 1, primary branching; 2, secondary branching; etc.); Inter d, internode diameter; Inter l, internode length; L_1, distance from the base of the leaf to the point of maximum width; L_2, distance from the point of maximum width to the tip; Max width, maximum leaf width; P, leaf perimeter; Total length, total length of the leaf; Var angle, variance in angle.

explained by genus nested within tribe in the nested ANOVA (Table 2). A significant proportion was explained by phylogeny for leaf length, area and perimeter, internode length and diameter and angle between the leaves. For these traits, genus explained 26–40% of the variance. The maximum leaf width and variance in angle exhibited no detectable phylogenetic signal, perhaps because they are plastic or relatively rapidly evolving traits.

RELATEDNESS AND TRAIT COVARIATION

ANCOVA confirmed that some of the variance in plant morphology can be explained by phylogeny, suggesting that relatedness influences plant shape (Table 1). Phyllotaxis, the variance in leaf size traits (leaf perimeter, length and area), internode diameter and branching degree all showed phylogenetic components, consistent with the nested ANOVA.

The associations between many morphological traits were significant, even after the variance caused by relatedness had been partially accounted for. The variance in angle between the leaves increased as the internode length increased, and this relationship was not affected by plant orientation (Table 1). The internode length and diameter were positively correlated (Table 1). The angle and variance in angle were negatively correlated (Table 1). Most morphological associations remained the same after phylogenetic correction, but the angle between the leaves did not increase with increasing leaf size (as suggested by correlations that were not corrected for phylogeny; Table 1; Appendix, Table A2).

The results of three of the ANCOVAs were more ambiguous. Genus nested within tribe interacted significantly with the predictor variable for the relationship between internode length and diameter and analyses involving branching degree, suggesting that genera differ in these relationships (Table 1).

DISCUSSION

A shared evolutionary history significantly affects the morphology of species within Commelinaceae, especially the vegetative traits leaf size, angle between the leaves and internode size. In addition, a number of vegetative traits were associated with one another in a manner consistent with similar selection histories or morphological constraints. Most of the variance in vegetative traits occurred at the species level. Phyllotaxis appeared to be constrained more heavily in plants with short internode lengths (Niklas, 1988). Branching degree and leaf size were positively correlated, so both may be subject to the same selection pressures (for example, light environment). Finally, the internode diameter was positively correlated with leaf size, consistent with Corner's rule (Westoby *et al.*, 2002).

Once redundant traits had been eliminated, much of the variance in the data could be explained by the leaf length and perimeter and branching degree (PC1) and by the leaf maximum width and internode

Table 1. Analysis of covariance (ANCOVA) at the species level testing hypotheses about constraints and selection. The internode length, internode diameter, leaf length, leaf area and variance in leaf angle were natural logarithmically transformed

Source	d.f.	Type III SS	*F* value	*P* value	Effect size*
Variance in angle increases as internode length increases					
Genus (tribe)	8	56	1.54	0.1681	0.21
Internode length	1	50	4.12	0.0018	0.19
Error	47	210			
Plant orientation affects the relationship between variance in angle and internode length					
Genus (tribe)	8	53	1.42	0.2159	0.20
Orientation	2	3.1	0.33	0.7177	0.013
Internode length	1	26	5.67	0.0215	0.11
Error	45	210			
Angle increases with leaf perimeter					
Genus (tribe)	8	17 000	3.10	0.0068	0.35
Leaf perimeter	1	1 500	2.19	0.1459	0.045
Error	47	32 000			
Angle increases with leaf length					
Genus (tribe)	8	17 000	3.10	0.0068	0.35
Leaf length	1	1 800	2.63	0.1118	0.053
Error	47	32 000			
Internode diameter is positively correlated with leaf size					
Leaf perimeter					
Genus (tribe)	8	210	3.26	0.0049	0.36
Leaf perimeter	1	80	9.83	0.0030	0.17
Error	47	380			
Leaf length					
Genus (tribe)	8	220	3.42	0.0035	0.37
Leaf length	1	89	11.19	0.0016	0.19
Error	47	370			
Leaf area					
Genus (tribe)	8	240	3.08	0.0072	0.34
Leaf area	1	4.4	0.45	0.5054	0.0095
Error	47	460			
Internode length and diameter are positively correlated†					
Genus (tribe)	4	1.7	2.8	0.36	0.20
Internode length	1	0.46	3.0	0.090	0.065
Genus (tribe) × internode length	4	3.7	6.0	0.0006	0.36
Error	43	6.6			
Plants that branch more have smaller (shorter) leaves†					
Genus (tribe)	6	5.4	2.9	0.018	0.29
Branching degree	1	2.9	9.4	0.0038	0.18
Genus (tribe) × branching degree	4	2.9	2.3	0.070	0.18
Error	43	13			
Branching degree is positively correlated with internode length†					
Genus (tribe)	6	370	7.0	< 0.0001	0.49
Branching degree	1	58	6.6	0.014	0.13
Genus (tribe) × branching degree	4	180	5.2	0.0018	0.32
Error	43	380			
Angle and variance in angle are negatively correlated					
Genus (tribe)	8	20 000	6.13	< 0.0001	0.50
Variance in angle	1	14 000	32.98	< 0.0001	0.41
Error	47	20 000			

*Effect size was measured as partial eta squared [$\eta_p^2 = \text{SS effect}/(\text{SS effect} + \text{SS error})$], and measures the relative explanatory power of the effect of the independent variable on the dependent variable, excluding an effect of the covariate.
†Interactions were not significant ($P < 0.10$), with these three exceptions. SS = sum of squares.

diameter (PC2). Leaf length and maximum width were nearly orthogonal to one another, suggesting that leaf shape (narrowness) is free to vary independent of leaf size.

Role of phylogenetic constraints in vegetative morphology

Taxonomy was used as an approximation of evolutionary history to determine the relative influence of tribe, genus and species on the variance in morphological traits. Botanists (for example, Faden, 2000) have generally preferred floral traits to vegetative traits for the identification of species, presumably because vegetative traits are highly evolutionarily labile (see, for example, Meade & Parnell, 2003). In other words, most of the variance was predicted to occur at the species level for vegetative traits. The influence of relatedness was expected to be smaller at the genus level or higher. However, Givnish (1987) predicted that leaf shape would be relatively consistent within genera (within a single habitat), suggesting that an influence of genus on leaf shape would not be surprising. Givnish's (1987) prediction, based on observations of herbaceous species in the Virginia Piedmont, was that congeners would have similar leaf morphology, but that, amongst genera, leaf morphology would be evolutionarily labile. Thus, the similarity within genera may indicate the role of constraints in determining which lineages evolve particular traits.

All the traits measured in the present study were, to some degree, evolutionarily labile, but relatedness also constrained some trait variability. Vegetative traits seemed to fall into one of two categories: either 30–40% of the variance could be explained by genus nested within tribe (for example, angle between the leaves; Table 2) or none of the variance could be explained by genus and perhaps a very small amount could be explained by tribe (for example, maximum leaf width; Table 2). In all cases, a majority of the variance in vegetative traits occurred at the species level, consistent with the prediction that vegetative morphology should be evolutionarily labile (see, for example, Cavender-Bares *et al.*, 2004).

The variance pattern for vegetative traits was consistent with a recent morphological phylogenetic study in Commelinaceae on mostly floral traits (Evans *et al.*, 2000), which, when compared with molecular phylogenetic studies (Evans *et al.*, 2003), suggested a high degree of homoplasy amongst floral morphological traits (that is, suggested that these traits were not informative with respect to phylogeny). Natural selection or drift must therefore have played a role in the morphological evolution of this group, at least with respect to floral traits. This conclusion is consistent with the observation that much of the variance in vegetative traits occurs at the species level, especially for leaf width, leaf area and variance in leaf angle, suggesting that vegetative traits also respond readily to natural selection or drift.

Hypotheses about evolution and constraints

Our data also provided the opportunity to address several constraints in plant growth that have been proposed previously, generally on the basis of the trade-off between the maximization of resource uptake and maintenance of adequate structural support (see, for example, Niklas, 2004). For example, variance in phyllotaxis has been predicted to increase with increasing internode length (Niklas, 1988). Upright plants with large leaves should be selected for an optimal leaf angle of 137.5°, which would maximize light interception (Niklas, 1988). Selection for the optimal leaf angle should be relaxed as the probability of self-shading decreases. Therefore, as the internode length increases or plant growth becomes more prostrate, selection for an optimal leaf angle should be relaxed, and the variance in leaf angle should increase.

Consistent with this prediction, the relationship between internode length and variance in leaf angle was positive in the present study, but plant orientation (vertical or horizontal) had no influence on the variance in leaf angle. The positive relationship between internode length and variance in leaf angle is consistent with the observation that self-shading influences carbon gain (Falster & Westoby, 2003), and should therefore be a strong selective force. It is also consistent with a study in *Psychotria*, which demonstrated that shade-tolerant species have lower levels of self-shading than do light-demanding species, possibly resulting in a greater efficiency in light absorption (Pearcy *et al.*, 2004), and the observation that forest-dwelling Commelinaceae often have large leaves, upright growth forms and spiral phyllotaxis, all presumably adaptations to increase light capture (Faden, 1988; Faden & Evans, 1999).

Species that showed more branching also had smaller, shorter leaves. This pattern has at least two plausible explanations. Plants that have evolved in environments with high light availability may produce both small leaves and high degrees of branching. There is ample evidence that species in high-light environments evolve small leaves, presumably for water conservation (see, for example, Bragg & Westoby, 2002; McDonald *et al.*, 2003). We found that species from shady habitats produced wider leaves and branched less than species from sunny habitats (analysis not shown). Branching may also respond to

Table 2. Nested analysis of variance (ANOVA) on traits at the species level. The internode length, internode diameter, leaf length, leaf area and variance in leaf angle were natural logarithmically transformed. Variance component analysis is from a separate nested ANOVA

Source	d.f.	Type III SS	*F* value	*P* value	Variance component
Angle					
Tribe	1	970	1.40	0.2426	0
Genus (tribe)	7	20 000	4.12	0.0013	40
Species (genus)	48	33 000			60
Internode length					
Tribe	1	5.2	0.40	0.5283	0
Genus (tribe)	7	350	3.85	0.0021	38
Species (genus)	48	620			62
Internode diameter					
Tribe	1	3.5	0.36	0.5504	0
Genus (tribe)	7	220	3.28	0.0062	33
Species (genus)	48	460			67
Leaf length					
Tribe	1	1.6	4.0	0.0519	0
Genus (tribe)	7	9.2	3.3	0.0056	42
Species (genus)	48	19			58
Maximum leaf width					
Tribe	1	0.81	1.55	0.2187	12
Genus (tribe)	7	5.2	1.43	0.2138	0
Species (genus)	48	25			88
Leaf area					
Tribe	1	2.8	3.99	0.0515	42
Genus (tribe)	7	14	2.85	0.0143	0
Species (genus)	48	34			58
Leaf perimeter					
Tribe	1	1.2	3.81	0.0568	0
Genus (tribe)	7	7.6	3.36	0.0054	41
Species (genus)	48	16			59
Variance in leaf angle					
Tribe	1	0.59	0.11	0.7446	0
Genus (tribe)	7	30	0.79	0.5955	14
Species (genus)	48	260			86

high-light environments. First, if high-light environments are also disturbed environments, a high degree of branching may be adaptive, increasing the ability of the plant to colonize by vegetative spread. Consistent with this explanation, the branching degree was also positively correlated with the internode length, a potential measure of vegetative spread in prostrate plants. Second, branching degree may be lower for plants selected in low-light environments, because they are selected to increase height at the expense of spread. This selective regime would also result in a negative correlation between leaf size and branching degree.

Structural constraints have been predicted to govern the relationships between the variables involved in support. Consistent with these predictions, the internode diameter was positively correlated with the total leaf length, leaf perimeter and internode length. Other studies have also found a positive association between stem thickness and leaf area (for example, Ackerly & Donoghue, 1998), consistent with a structural constraint hypothesis (Niklas, 1993, 1994) or a xylem supply hypothesis (Shinozaki *et al.*, 1964).

Finally, the leaf angle and variance in leaf angle were strongly negatively correlated. This relationship was probably driven (at least in part) by the many species that were strictly distichous, having a leaf angle of 180°, upright growth forms and little to no variance in leaf angle (for example, *Tradescantia ohiensis*; Fig. 6). Distichous species may be well adapted to high-light environments, where light is not limiting, and other factors, such as herbivory, may have a greater influence on plant morphology than does light availability in these species. In contrast, forest-dwelling Commelinaceae tend to have spiral phyllotaxis (Faden & Evans, 1999), a presumed adaptation to low light availability. A distichous leaf arrangement may also be the result of constraints, such as those that occur between leaf size and leaf thickness (Ackerly & Reich, 1999).

CAVEATS

The present study is relatively novel in attempting to quantify the evolutionary constraints on plant vegetative morphology, and we recognize that the adaptive and constraint interpretations described here are plausible but speculative. The presence of multiple optima in the selective landscape may contribute to the diversity of morphological forms amongst taxa, and may complicate our ability to detect signals of selection (Marks & Lechowicz, 2006).

Furthermore, taxonomy is not equal to true evolutionary history. The explanatory power of taxonomy may be interpreted as a conservative estimate of the influence of phylogeny, because additional information about relatedness not incorporated in the taxonomy may also explain some of the variance in these traits. The explanation of 30–40% of the variance in some traits by genus alone therefore suggests a strong influence of relatedness, but genus is not independent of environment, and species within genera may, in many cases, share aspects of their selective regime.

In addition, taxonomy may not accurately reflect evolutionary relationships if the genera are not monophyletic. Analyses based on *rbcL* suggest that *Gibasis* may have arisen within *Tradescantia*, and *Callisia* may be polyphyletic with respect to *Tripogandra* (Evans *et al.*, 2003). Preliminary phylogenies suggest that the genera used here are monophyletic (*trnL-trnF*, plastid DNA; J. H. Burns, unpubl. data), with the exception of *Callisia*, which appears to be polyphyletic. The relative importance of the evolutionary history and trait correlations reported here should be considered as approximate, especially for *Gibasis*, *Callisia* and *Tradescantia*.

A final caveat is that these plants were all grown in a common glasshouse environment. This procedure corrects for any confounding effects of environment – a necessary control and especially important for potentially plastic traits, such as plant growth form – but if the morphological traits used are very plastic, they may not have been measured as they occur in the native habitat of the plant. Adaptive explanations should therefore be considered as speculative.

CONCLUSIONS

The vegetative morphospace for species in Commelinaceae is described here for the first time, and the potential of phylogeny, evolution and structural constraints to explain the diversity of vegetative shape in the family was also explored. A number of traits exhibited strong influences of phylogeny, despite their presumed evolutionary lability. In addition, the relationships amongst some traits were consistent with adaptive explanations. For example, the variance in leaf angle increased with increasing internode length, consistent with Niklas' (1988) prediction that evolution for optimal phyllotaxis should be relaxed as self-shading decreases. To our knowledge, this is the first test of this hypothesis.

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APPENDIX

Table A1. Species of Commelinaceae used in the study and measures of vegetative morphology

Species	Mean angle (deg)	Internode length (mm)	Standard deviation of angle (deg)
Callisia cordifolia (Sw.) E.S.Anderson & Woodson	130	5.8	2.15
Callisia elegans Alexander ex H.E.Moore	150	10.4	2.15
Callisia fragrans (Lindl.) Woodson	133	0.0	2.17
Callisia gracilis (Kunth) D.R.Hunt	117	7.9	2.62
Callisia graminea (Small) G.C.Tucker	167	0.0	2.21
Callisia guerrerense Matuda	107	5.9	2.62
Callisia macdougallii Miranda	150	22.0	2.56
Callisia micrantha (Torr.) D.R.Hunt	120	7.2	2.54
Callisia multiflora (M.Martens & Galeotti) Standl.	123	14.8	2.35
Callisia navicularis (Ortgies) D.R.Hunt	170	0.0	2.39
Callisia repens (Jacq.) L.	114	5.8	2.46
Callisia rosea (Vent.) D.R.Hunt	180	0.0	0.00
*Callisia soconuscensis** Matuda	150	8.0	2.15
Commelina africana L. var. *villosior* (C.B.Clarke) Brenan	123	12.6	2.84
Commelina benghalensis L.	155	8.1	2.13
Commelina bracteosa Hassk.	112	13.2	2.17
Commelina coelestis Willd.	117	18.8	2.21
Commelina congesta C.B.Clarke	138	10.8	2.58
Commelina eckloniana Kunth	128	18.2	2.02
Commelina erecta L.	151	21.2	2.56
Commelina fluviatilis Brenan	157	42.0	2.72
Commelina foliaceae Chiov. subsp. *amplexicaulis*	160	20.8	2.15
Commelina imberbis Ehrenb. ex Hassk.	180	32.7	0.00
Commelina lukei?	167	18.2	2.34
Commelina mascarenica C.B.Clarke in DC.	165	26.1	2.27
Commelina nairobiensis Faden	122	19.9	2.96
Commelina purpurea C.B.Clarke	103	67.1	2.62
Commelina schliebenii Mildbraed	167	33.9	2.17
Commelina sp.	165	13.3	2.08
Commelina welwitschii C.B.Clarke	87	68.1	2.81
Cyanotis repens Faden & D.M.Cameron subsp. *repens* (cyarep1)	57	11.8	1.88
Cyanotis repens subsp. *robusta* Faden & D.M.Cameron (cyarep2)	107	10.2	2.21
Cyanotis repens subsp. *robusta* Faden & D.M.Cameron (cyarep3)	60	16.8	2.61
Cyanotis somaliensis C.B.Clarke	127	0.0	1.88
Cyanotis speciosa (L.f.) Hassk.	73	0.0	1.88
Dichorisandra hexandra (Aubl.) Standl.	147	5.4	2.46
Dichorisandra thyrsiflora J.C.Mikan	147	6.0	2.21
Gibasis pellucida (Mart. & Gal.) D.R.Hunt	132	7.0	1.88
Murdannia acutifolia 'variegata'?	167	0.0	2.21
Murdannia bracteata (C.B. Clarke) J.K.Morton ex D.Y.Hong	85	0.0	2.90
Murdannia simplex (Vahl) Brenan (mursim1)	147	0.0	2.67
Murdannia simplex (Vahl) Brenan (mursim2)	177	0.0	1.88
Pollia japonica Thunberg	127	6.7	1.88
Tinantia pringeli (S.Wats.) Rohw.	153	15.2	1.49
Tradescantia virginiana L. × *Tradescantia ohiensis* Raf. × *Tradescantia subaspera* Ker-Gawl.	180	0.0	0.00
Tradescantia bermudensis?	140	0.0	2.87
Tradescantia blossfeldiana Mildbraed	170	7.6	2.15
Tradescantia bracteata Small	180	0.0	0.00
Tradescantia brevifolia (Torr. ex Emory) Rose	142	18.6	2.58
Tradescantia fluminensis Vell.	114	16.0	2.31
Tradescantia occidentalis (Britt.) Smyth	180	0.0	0.00
Tradescantia ohiensis Raf.	180	0.0	0.00
Tradescantia pallida (Rose) D.R.Hunt	145	11.6	2.78
Tradescantia sillamontana Matuda	180	4.9	0.00
Tradescantia spathacea Sw.	160	0.0	1.81
Tradescantia zanonia (L.) Sw.	158	8.2	2.17
Tradescantia zebrina Bosse	127	13.9	2.76

*Identification subject to verification; specimen not in flower.

Table A2. Nonparametric Spearman's rho correlations amongst morphological traits for the 54 species of Commelinaceae used in the study

Trait	Angle	Internode length	Internode diameter	Leaf length	Maximum leaf width	Leaf area	Leaf perimeter
Angle							
Internode length	–0.233*						
Internode diameter	–0.0113	0.609‡					
Leaf length	0.363‡	–0.163	–0.139				
Maximum leaf width	–0.049	0.161	0.546‡	0.109			
Leaf area	0.221*	–0.093	0.168	0.168	0.656‡		
Leaf perimeter	0.340†	–0.176	–0.111	0.993‡	0.161	0.811‡	
Variance in leaf angle	–0.512‡	0.305†	0.169	–0.127	0.019	–0.094	–0.133

*$P < 0.10$.
†$P < 0.05$.
‡$P < 0.01$.