

ESTIMATING PHYLOGENETIC INERTIA IN *TITHONIA* (ASTERACEAE): A COMPARATIVE APPROACH

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Abstract.—Phylogenetic inertia is a difficult issue in evolutionary biology because we have yet to reach a consensus about how to measure it. In this study a comparative approach is used to evaluate phylogenetic inertia in 14 demographic and morphological characters in 10 species and one subspecies of the genus *Tithonia* (Asteraceae). Three different methods, autocorrelational analysis, phylogenetic correlograms, and ancestor-state reconstruction, were used to evaluate phylogenetic inertia in these traits. Results were highly dependent on the method applied. Autoregression and phylogenetic eigenvector regression (PVR) methods found more inertia in morphological traits. In contrast, phylogenetic correlograms and ancestor-state reconstruction suggest that morphological characters exhibit less phylogenetic inertia than demographic ones. The differences between results are discussed and methods are compared in an effort to understand phylogenetic inertia more thoroughly.

Key words.—Ancestor-state reconstruction, autoregression model, comparative method, phylogenetic inertia, *Tithonia*.

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An important issue in comparative studies is the degree of “phylogenetic inertia,” or “phylogenetic effect.” How much are traits affected by the phylogenetic history of the species that exhibit them? Phylogenetic inertia is the tendency for traits to resist evolutionary change despite environmental perturbations (Edwards and Naeem 1993), but there has been much disagreement about how this should be measured. The comparative method offers an interesting mechanism to evaluate the phylogenetic inertia of a trait (Brooks and McLennan 1991; Harvey and Pagel 1991; Martins and Hansen 1997). In this study, I investigate ways of using the phylogenetic comparative method to estimate phylogenetic inertia and concentrate on the evolution of demographic and morphological characters in the plant genus *Tithonia* (Asteraceae).

Phenotypic values of traits are influenced by their evolutionary history and evolutionary forces in their actual environment. “Phylogenetic inertia,” “phylogenetic effects,” and “phylogenetic constraint” are all terms used to describe the effects of history in character evolution. Some authors describe phylogenetic inertia as the amount of character variation explained by the phylogeny. Traits that evolve slowly are said to have more phylogenetic inertia than quickly evolving traits. Others estimate ancestor-states and argue that traits evolving fewer times have more phylogenetic inertia (Maddison and Slatkin 1990).

Jordano (1995) has pointed out that a comparative approach (Harvey and Pagel 1991) is indispensable for distinguishing similarity that is attributable to common ancestry (phylogenetic inertia) from similarity to parallel and convergent evolutionary change. He expected the latter “among plants sharing the major seeds dispersers if evolutionary change in fruit traits is attributable to coevolved selective pressures by frugivores” (Jordano 1995, p. 164). Lord et al. (1995) consider that an increasingly common approach in the comparative literature is to regard phylogenetic explanations

for variation as alternatives to adaptive explanations. In studies taking this approach, phylogenetic constraints have been described as taxon-specific limitations that force a taxon into certain combinations of characters regardless of where that taxon occurs. Phylogenetic constraint is thus an explicitly nonadaptive interpretation of phylogenetic correlated patterns of variation.

Stebbins (1974) argues that phylogenetic effects are greater in complex anatomical structures or physiological processes that evolve as integrated suites of traits. In this case, traits subject to strong stabilizing selection are said to exhibit high levels of phylogenetic inertia.

Few studies have considered the degree of phylogenetic inertia on evolutionary potential of plant life-history traits. Franco and Silvertown (1996) analyzed demographic characters with a hierarchical analysis of variance (HAV) to identify taxonomic levels at which most of the variation occurs. They demonstrate that traits that can be described as age-dependent: Total life span, age at sexual maturity, generation time, and life expectancy had their variation concentrated at the division level and the fraction of total variance explained at this level varies between 40% and 75%. In contrast, traits that can be described as time dependent, such as the population intrinsic rate of natural increase and net reproductive rate, had their variation (44% and 58%, respectively) concentrated at the species level. Age-dependent traits have more phylogenetic inertia.

Several types of traits might be expected to have lower levels of phylogenetic inertia than others. For example, the available evidence suggests that there is a greater environmental contribution to life-history traits than to morphological ones (Campbell 1977). Thus, I expect to observe more phylogenetic inertia in morphological traits than in demographic ones.

Several comparative methods have been proposed to estimate phylogenetic inertia, and it is not clear which is the

most effective or how these methods are similar. First there are three statistical methods that have been proposed explicitly to estimate phylogenetic inertia from comparative data. All three partition phenotypic variation into phylogenetic and specific components and then calculate phylogenetic inertia as the proportion of variation explained by phylogenetic similarity (e.g., Cheverud et al. 1985; Lynch 1991; Diniz-Filho et al. 1998). Although the methods evaluate inertia in the same way, their theoretical and statistical approaches are different.

Cheverud et al.'s (1985) method extends spatial autocorrelation statistics to the phylogenetic case by formally partitioning trait variation into phylogenetic values, which are inherited from an ancestral species, and specific values, which are the result of independent evolution. The method allows a quantitative assessment of the strength of inertia, so its relative importance in evolution can be assessed.

Diniz-Filho et al.'s (1998) phylogenetic eigenvector regression (PVR) method also partitions phenotypic variation into phylogenetic and specific components, but it starts with a principal coordinate analysis of the phylogenetic distance matrix that extracts eigenvalues and eigenvectors of this matrix. A multiple regression of trait data variation on those vectors can then be used to partition the total phenotypic variation into phylogenetic and nonphylogenetic components.

Finally, Lynch's (1991) mixed model partitions the observed species mean phenotype into a phylogenetic heritable component and a residual component due to nonadditive phylogenetic effects, environmental effects, and measurement error. Unfortunately, implementation of Lynch's (1991) method is not yet possible due to complications in the estimation algorithm (M. Lynch, pers. comm.). Therefore, I do not consider it further.

Another approach that can be used to estimate phylogenetic inertia has been proposed by Gittleman et al. (1996). Gittleman and Kot (1990) showed that Moran's I , a measure of spatial autocorrelation, can be used to gauge the importance of phylogeny in explaining trait variation. A trait has greater evolutionary lability (i.e., less phylogenetic inertia) if it is not correlated or has a low correlation with phylogenetic distance. Thus, Gittleman et al. (1996) construct phylogenetic correlograms to assess the relationships between phylogeny and character variation at different levels of phylogenetic relatedness. They predicted and found that behavioral traits (home-range size, population group size) show either no phylogenetic pattern or less phylogenetic correlation than morphological and life-history traits. Note that this approach is very different from application of the Cheverud et al. (1985) estimation for phylogenetic inertia (above).

A third way to estimate phylogenetic inertia is to reconstruct attributes of hypothetical ancestors and the number and the magnitude of evolutionary changes occurring in the clade. As proposed by Maddison and Slatkin (1990), a small number of changes implies greater phylogenetic inertia.

In this study, I use these three approaches to test the hypothesis that demographic characters have less phylogenetic inertia than morphological ones, using data collected for 11 taxa of the genus *Tithonia* (Asteraceae). First, I applied two forms of autocorrelation analyses to estimate phylogenetic

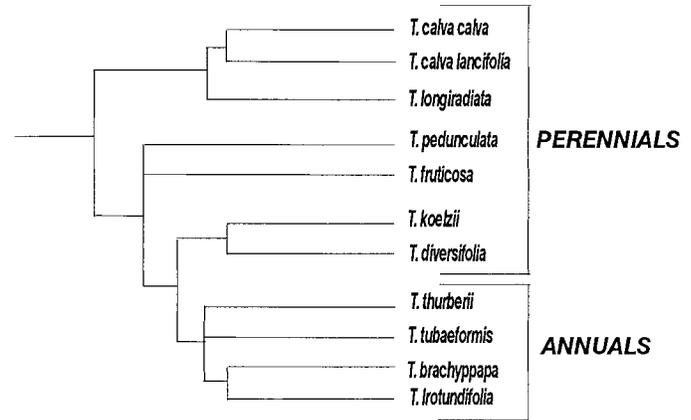


FIG. 1. Phylogenetic relationships for the genus *Tithonia* (Asteraceae) based on morphological characters as proposed by La Duke (1982). Branch lengths are arbitrary.

inertia in the traits. Second, I calculated Moran's I correlograms to detect whether patterns of phylogenetic prediction were similar for the two types of traits. Finally, I used Schluter et al. (1997) method to reconstruct ancestor-states and consider the number and magnitude of changes occurring in different types of traits. I then compared the results from using these different methods to gain greater insight into available measures of phylogenetic inertia.

There are other methods that can assess the influence of phylogeny (i.e., Legendre et al. 1994). This method applies multiple regression methods to describe variation of interspecific data using phylogenetic distance matrices. In this analysis, a correlation coefficient provides a measure of phylogenetic correlation or "inertia." I do not apply this method, because it has not been formally developed and the evolutionary implications of the model are as yet unknown.

The genus *Tithonia* (Asteraceae) represents an interesting system in which to evaluate phylogenetic inertia in demographic and morphological characters due to its variation in life span (annuals and perennials) and patterns of distribution (wide distribution and endemic). Life forms also vary from herbs to shrubs. This variation provides a good model to understand general trends and patterns of evolution and diversification in a genus of the largest family of plants in the world. Ecological theory (Harper and White 1974) predicts that annuals tend to diverge more and faster due to environmental pressures. Annuals living in constantly perturbed environments tend to modify their demographic responses to fit the environment. Thus, I expect to find more evolutionary changes, presented in this study as less inertia, in demographic traits and in annual species than in morphological traits and perennial species.

METHODS

The Phylogeny and Species Data

The genus *Tithonia* consists of 11 species of coarse annual or perennial herbs or shrubs found from the southwestern United States to Costa Rica (La Duke 1982; Bremer 1994). The only available phylogeny is one proposed by La Duke (1982), which is based on morphological characters (Fig. 1).

Although it may not be entirely correct, it is the only available estimate, and for the purpose of this study, is assumed to be a true description of the evolutionary relationships of the genus.

I obtained life-history data from natural populations and a demographic experiment. Seeds for 10 species and one subspecies were obtained from individual heads and demographic experiments were also conducted. One species and one subspecies (*T. hondurensis* and *T. calva auriculata*) are not included in this study due to my inability to obtain material. Life-history traits surveyed were seed size, number of flowers per head, number of seeds per head, flower size, leaf size, head size, germination, establishment, viability, germination time, growth rate, resource allocation, and dormancy.

To measure viability, I collected seeds and put them in petri dishes filled with water for 24 h. After that period, I exposed the achenes to a 1% tetrazolium clohoxide solution. Between 12 h and 15 h later, I counted the number of embryos that were receptive to the solution and used this as an estimate of viability for each species. Dormancy was measured using the same procedure, but prior to the tetrazolium test, seeds were put in nylon bags and buried for two-month periods. The procedure was repeated every two months for one year, and values were averaged to obtain species means.

Seeds from different individuals were measured and weighed to assess seed size. Fifty of those seeds in each of six replicate experiments were sown in a controlled environment chamber. For all species and populations, I analyzed germination time and germination by exposing them to similar conditions as in the field. When plants developed their first leaf pair, I considered them to be established and evaluated establishment for each population and species. Also in this stage, an individual sample was taken to estimate resource allocation, the proportion of aerial mass devoted to leaves and stems with respect to subterranean mass assigned to roots. This comparison also was performed also for the adult stage. Growth rate was measured from when plants were established to reproduction for annual plants or from establishment to just before reproduction for perennial plants.

Data Analysis

First, the autocorrelational analysis (Cheverud et al. 1985) and the PVR (Diniz-Filho et al. 1998) were used to estimate phylogenetic inertia. These methods assume that within-species phenotypic variation does not exist, the phylogenetic relationships are known, total trait values are composed of phylogenetic and nonphylogenetic values, and the residuals of the linear model can be used in further analyses (Martins 1996). The phylogenetic autoregressive model (Cheverud et al. 1985) analysis, was performed with the computer program MRHO3 (Miles and Dunham 1992), whereas PVR analysis was conducted with NTSYS (Rohlf 1989) and SYSTAT (Wilkinson 1989).

Second, I constructed phylogenetic correlograms (Gittleman and Kot 1990), calculating Moran's *I* coefficient at three distance classes. The *Z*-scores associated with each Moran's *I* can be used to assess the significance of the correlograms. These correlograms were used to assess the pattern of cor-

relation between the traits and phylogenetic distance among species and to determine where this variation lies on the phylogeny (Gittleman et al. 1996). Correlograms were constructed with the program AUTOPHY (Diniz-Filho 1996).

Third, I applied the Schluter et al. (1997) method for reconstructing ancestor states to determine the number and magnitude of evolutionary changes in each trait. The method assumes that each trait evolves according to a Brownian motion process governed by a parameter (β). Under this model, the expected squared difference (variance) between any two species (β) is multiplied by the time since the species last shared a common ancestor. The Brownian motion model assumes that the evolutionary process includes no trends, because trends cannot be estimated from data solely on contemporary species (Schluter et al. 1997). Reconstruction of the ancestor-states was performed with the program ANCML (<http://www.zoology.ubc.ca/~schluter/ancml.html>).

RESULTS

The average phenotypic values and their estimated standard errors for the morphological and demographic traits analyzed in this work are presented in Table 1. Variation between species is observed and demographic traits tend to be more dissimilar than morphological ones.

Explicit Estimators of Phylogenetic Inertia

For the Cheverud et al. (1985) analysis, the autocorrelation coefficient (ρ) was significantly greater than zero for five morphological traits (seed size, flowers per head, seeds per head, leaf size, and head size) and two demographic traits (viability and resource allocation; Table 2). These results suggest that variation in these characters has an important phylogenetic component. The proportion of the variance explained by phylogeny (R^2) was also high: 30–80%. However, some demographic traits (i.e., seedling height, establishment, and adult height) present autocorrelation coefficients (ρ) very close to significance and variance explained by phylogeny varying between 21% and 23%.

Using the Diniz-Filho et al. (1998) analysis, only five of the 14 characters (seed size, viability, flowers per head, seeds per head, and resource allocation) had R^2 -values significantly greater than zero (Table 2). Three of the characters are morphological and two are demographic. Note that these traits also had large ρ -values with the Cheverud et al. (1985) method. For the demographic characters the variance associated with phylogeny varies between 10% and 67% and for the morphological ones between 1% and 69%. From the different eigenvectors extracted, only the first two were considered important according to the broken-stick method. These two eigenvalues explain 74.23% of the variability in phylogenetic distances.

Correlograms

In the phylogenetic correlograms (Figs. 2, 3), Moran's *I* steadily decreased with phylogenetic distance for seven (seed size, flowers per head, seeds per head, seedling height, resource allocation, viability, and growth rate) of the 14 traits analyzed. Moran's *I* coefficients were significantly different

TABLE 1. Average values (± 2 SE) for 14 life-history and morphological traits in the genus *Tithonia* (Asteraceae).

Species	Morphological traits										Demographic traits						
	Seed size (mm)	Flower size (mm)	Leaf size (cm)	Head size	Flowers per head	Seeds per head	Seedling height (cm)	Growth rate (cm/day)	Germination time ¹	Establishment (%)	Viability (%)	Germination (%)	Resource allocation ²	Adult height (m)			
<i>T. calva calva</i>	4.10 (0.30)	5.98 (1.21)	10.62 (3.27)	2.72 (0.63)	140 (17.14)	90 (17.21)	2.63 (1.12)	0.09 (0.06)	15.5 (0.43)	5.00 (1.78)	7.00 (1.23)	6.00 (3.46)	15 (6.01)	4.4 (0.42)			
<i>T. lancifolia</i>	3.77 (0.007)	5.59 (1.03)	7.84 (0.53)	2.35 (0.18)	120 (22.9)	75 (15.89)	3.36 (1.36)	0.11 (0.02)	11.83 (0.58)	4.00 (2.82)	14.00 (2.37)	9.20 (2.24)	11 (3.23)	4.0 (2.10)			
<i>T. longiradiata</i>	3.73 (0.20)	5.97 (0.39)	45.68 (10.94)	2.22 (0.02)	140 (7.43)	125 (9.45)	4.24 (0.38)	0.09 (0.06)	17.10 (0.42)	4.10 (1.41)	21.00 (1.61)	11.50 (0.70)	16 (9.41)	4.5 (3.61)			
<i>T. pedunculata</i>	6.10 (0.75)	7.10 (1.01)	21.52 (14.35)	3.01 (0.73)	100 (18.21)	90 (17.46)	2.79 (0.09)	0.14 (0.18)	15.30 (1.62)	1.50 (0.03)	28.05 (3.53)	11.00 (1.41)	51 (12.28)	2.7 (0.85)			
<i>T. fruticosa</i>	4.57 (0.60)	11.25 (1.71)	46.71 (9.70)	2.49 (0.48)	120 (3.40)	100 (21.22)	3.71 (0.06)	0.48 (0.16)	25.16 (1.51)	1.00 (0.25)	14.50 (12.03)	4.00 (2.82)	46 (9.73)	7.0 (1.2)			
<i>T. koeltzii</i>	5.52 (0.30)	4.50 (1.16)	62.16 (3.45)	4.5 (1.16)	100 (17.28)	60 (7.61)	4.15 (1.72)	0.06 (0.21)	19.20 (0.62)	2.00 (3.21)	5.00 (4.62)	2.00 (3.13)	18 (4.21)	3.5 (1.4)			
<i>T. diversifolia</i>	6.24 (0.62)	6.12 (0.02)	35.55 (18.7)	2.28 (0.82)	130 (22.9)	90 (16.89)	3.21 (0.07)	0.16 (0.02)	8.99 (0.43)	27.00 (11.63)	66.00 (13.82)	59.00 (4.24)	17 (3.26)	5.0 (2.1)			
<i>T. thurberii</i>	6.54 (0.25)	6.99 (1.06)	141.8 (51.00)	2.55 (0.60)	92 (9.6)	71 (12.41)	9.85 (0.45)	0.33 (0.12)	16.66 (1.53)	1.50 (0.03)	70.50 (4.94)	5.50 (3.53)	89 (6.61)	3.5 (0.73)			
<i>T. tubaeformis</i>	5.45 (0.57)	6.37 (0.67)	33.23 (7.07)	2.57 (0.06)	120 (10.35)	90 (11.68)	15.90 (2.20)	0.44 (0.06)	6.19 (0.14)	59.50 (4.23)	81.50 (4.04)	73.00 (23.9)	95 (4.77)	3.0 (0.19)			
<i>T. brachypappa</i>	5.59 (0.63)	5.71 (0.65)	8.49 (1.70)	1.67 (0.11)	85 (15.55)	71 (21.13)	7.11 (0.21)	0.27 (0.04)	13.28 (1.77)	4.00 (1.41)	63.50 (7.07)	12.00 (2.82)	89 (3.49)	2.5 (0.36)			
<i>T. rotundifolia</i>	7.71 (0.49)	7.81 (1.31)	56.80 (46.06)	2.52 (0.05)	60 (7.46)	56 (4.84)	6.69 (0.08)	0.22 (0.03)	7.23 (0.34)	26.50 (6.36)	74.20 (6.17)	36.00 (8.48)	93 (5.22)	3.5 (0.79)			

¹ Represents the number of days elapsed since seeds were sown until the 50% of the final germination percentage is obtained, that is, the maximum rate of germination.

² Represents the proportion of aerial mass devoted to leaves and stems relative to subterranean mass devoted to roots.

TABLE 2. Phylogenetic autocorrelation coefficients (ρ), variance due to phylogenetic relationships (R^2) for the phylogenetic autocorrelation model (Cheverud et al. 1985) and for the phylogenetic regression (PVR; Diniz-Filho et al. 1998).

	Trait	Phylogenetic autocorrelation		PVR
		ρ	R^2	R^2
Morphology	Seed size	0.75*	0.62	0.69*
	Flower size	0.39	0.37	0.01
	Leaf size	0.46*	0.30	0.16
	Head size	0.52*	0.38	0.01
	Flowers per head	0.71*	0.58	0.51*
	Seeds per head	0.83*	0.67	0.57*
Demography	Seedling height	0.42	0.23	0.26
	Growth rate	0.04	0.03	0.21
	Germination time	0.36	0.15	0.67
	Establishment	0.44	0.23	0.13
	Viability	0.43*	0.24	0.53*
	Germination	0.36	0.25	0.16
	Resource allocation	0.81*	0.80	0.53**
	Adult height	0.43	0.21	0.10

* $P < 0.05$; ** $P < 0.01$.

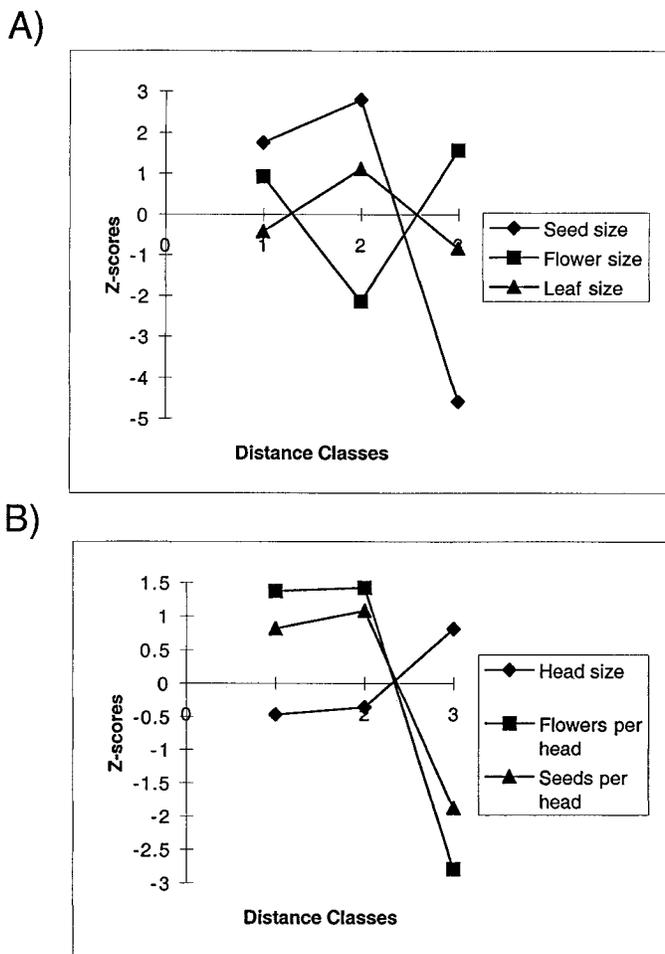


FIG. 2. Phylogenetic correlograms for six morphological characters in the genus *Tithonia* (Asteraceae) using Z-scores derived from Moran's I coefficient. Z-values $> |1.96|$ are significant. (A) Seed size, flower size, leaf size. (B) Head size, flowers per head, seeds per head.

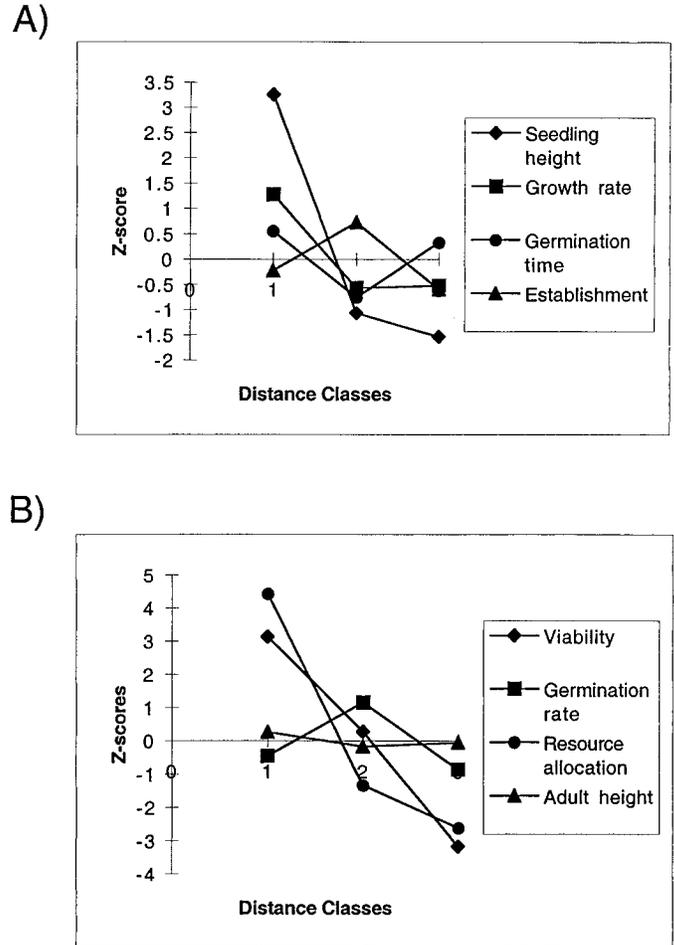


FIG. 3. Phylogenetic correlograms for eight demographic characters in the genus *Tithonia* (Asteraceae) using Z-scores derived from Moran's I coefficient. Z-values $> |1.96|$ are significant. (A) Seedling height, relative growth rate, germination time, and establishment (%). (B) Viability, germination (%), resource allocation, adult height.

from zero mainly in the first distance class (at the species level), but I also found significant values in the second and third classes (genus and family level). The seven traits with a clear relationship between Moran's I and phylogenetic distance consisted of three morphological traits (seed size, flowers per head, and seeds per head) and four demographic characters (viability, seedling height, resource allocation, and growth rate). These correlograms demonstrate that closer taxonomic levels are more phenotypically similar, a pattern expected for phenotypes evolving if by a simple Brownian motion (i.e. pure random genetic drift), (Gittleman et al. 1996).

Ancestor-State Reconstruction

For the 14 characters analyzed I found only a few large evolutionary changes between the estimated ancestor state and the phenotypic observed value (Figs. 4–7). Demographic traits had 14 changes in eight traits, whereas morphological traits had 14 changes in six traits. When considering the differences between annuals and perennials, I found that more of these changes were found in annual clade than in the

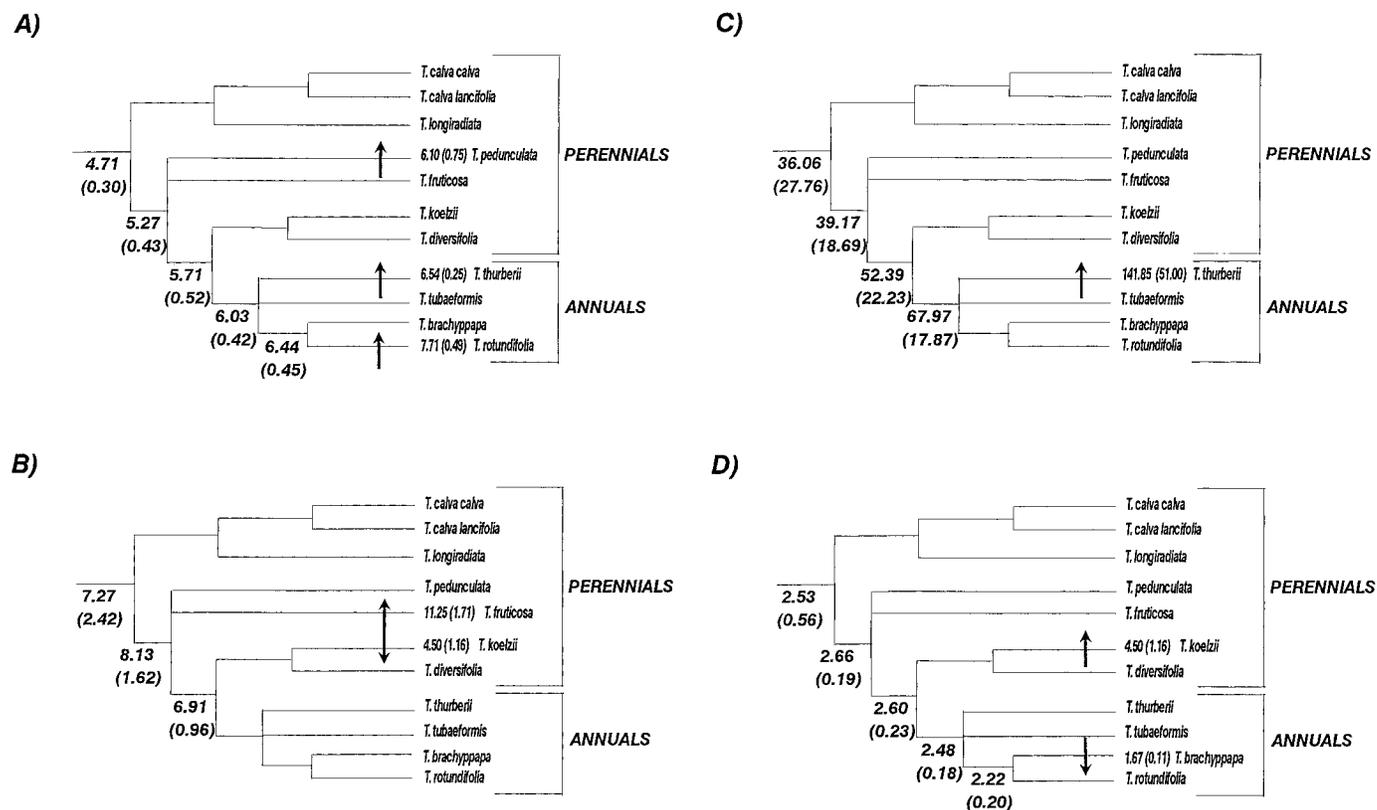


FIG. 4. Ancestor-state reconstruction (Schluter et al.1997) four morphological characters in the genus *Tithonia* (Asteraceae). (A) Seed size; (B) flower size; (C) leaf size; (D) head size. Arrows up and down represent differences from the ancestor greater or less than two standard errors of the estimate. Only taxa that differ from the ancestor are illustrated.

perennial clade. Also the square sum of changes in the phylogeny was obtained and was standardized by the branch length for annuals and perennials (Table 3). When these values are compared, the greatest amount of change is related with annuals.

DISCUSSION

The results of this study show that several traits have significant levels of phylogenetic inertia, but which traits these are depends on the statistical method of estimation. The hy-

TABLE 3. Sum of squares of changes (SSC) for morphological and demographic traits in the genus *Tithonia* (Asteraceae).

Trait	SSC	SSC/ branch length	Perennials		Annuals	
			SSC	SSC/ branch length	SSC	SSC/ branch length
Morphology						
Seed size	5.742	0.318	2.540	0.211	3.201	0.266
Flower size	19.766	1.098	17.333	1.444	2.432	0.202
Leaf size	10,372.235	576.171	1465.943	122.151	8906.291	742.129
Head size	1.1299	0.0627	0.641	0.053	0.487	0.040
Flowers per head	2547.238	141.497	1165.946	97.154	1381.292	115.098
Seeds per head	1954.090	108.548	1571.957	130.985	382.133	31.841
Demography						
Seedling height	67.622	3.756	12.100	1.008	55.522	4.626
Growth rate	0.115	0.006	0.091	0.007	0.024	0.002
Germination rate	218.207	12.121	134.176	11.180	84.031	7.002
Viability	3269.892	181.640	2458.334	204.844	811.558	67.624
Resource allocation	2416.164	134.216	1229.911	102.484	1186.253	98.846
Establishment	2591.192	143.939	1165.946	97.154	1381.292	115.098
Germination	4649.736	258.290	1882.283	156.843	2767.453	230.601
Adult height	12.150	0.674	10.943	0.911	1.206	1.100

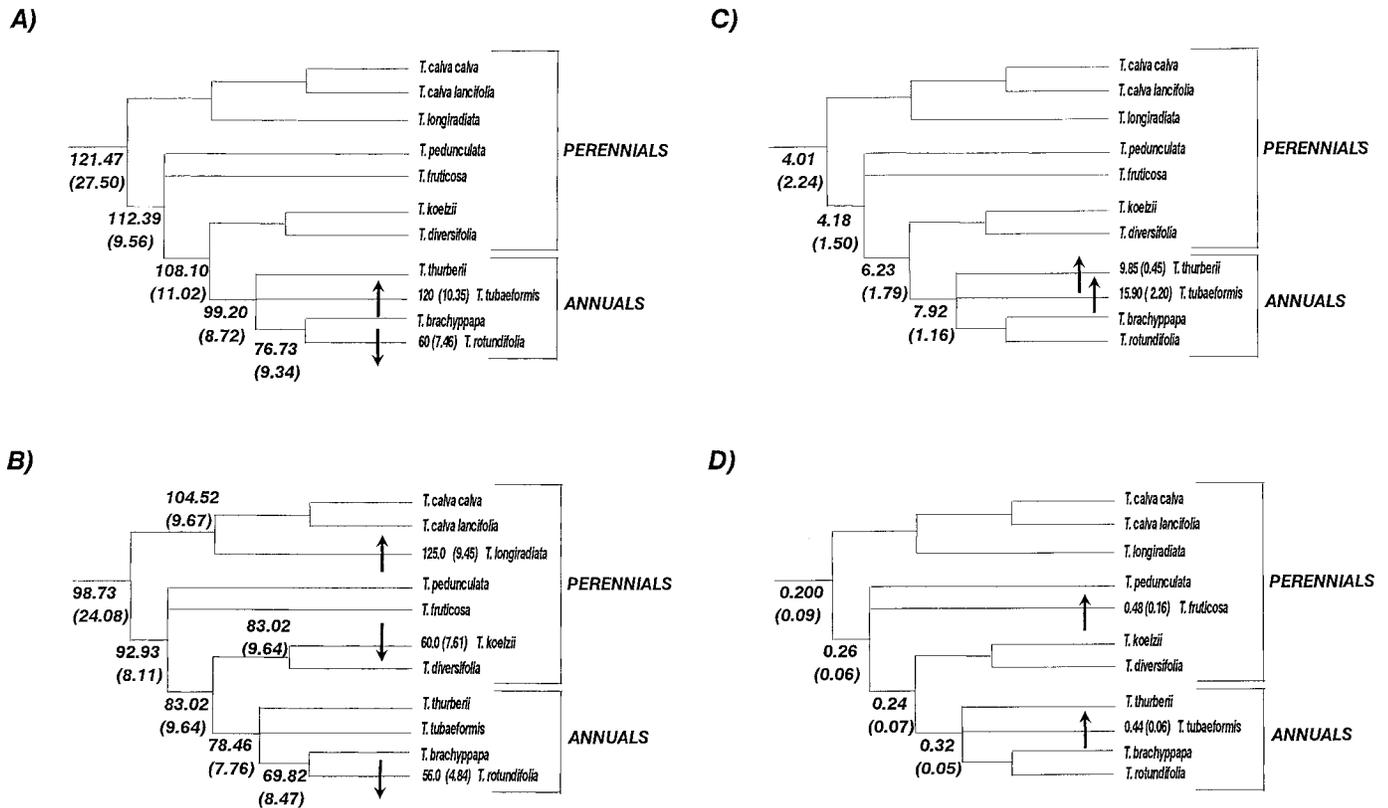


FIG. 5. Ancestor-state reconstruction (Schluter et al 1997) for two morphological characters, flowers per head (A) and seeds per head (B) and two demographic characters, seedling height (C) and relative growth rate in the genus *Tithonia* (Asteraceae). Arrows up and down represent differences from the ancestor greater or less than two standard errors of the estimate. Only taxa that differ from the ancestor are illustrated.

pothesis that morphological traits exhibit more inertia was not conclusively confirmed. Using the Cheverud et al. (1985) and Diniz-Filho et al. (1998) autocorrelation model, I found similar levels of phylogenetic inertia for morphological traits and demographic ones. Using phylogenetic correlograms (Gittleman et al. 1996) and estimation of ancestor-states (Schluter et al. 1997), however, there was evidence for more inertia in demographic traits.

Comparison of Methods

Autoregressive methods

Using the Cheverud et al. (1985) autocorrelation analyses, I found that morphological traits had a larger phylogenetic component than did demographic traits, suggesting that life-history traits are more evolutionarily flexible than morphological traits. This difference was not so evident using the PVR (Diniz-Filho et al. 1998) method, with five traits showing estimates of phylogenetic inertia significantly greater than zero, and two of these (viability and resource allocation) being demographic ones. Both methods, however, exhibited the same trend, with more phylogenetic inertia associated with morphological traits, as expected.

Martins (1996) suggested that the spatial autoregressive method (Cheverud et al. 1985) can perform very poorly with sample sizes of less than 40 species. Diniz-Filho et al. (1998) showed that PVR performs better than the autoregressive

method with low sample size and low levels of phylogenetic inertia. Thus, given the small sample size in the current study, it would be wise to conclude that morphological and demographic traits show similar levels of inertia

Phylogenetic correlograms

About half of the traits evaluated for the genus *Tithonia* exhibited correlogram patterns, with closely related taxa exhibiting greater phenotypic similarity and increased dissimilarity with greater phylogenetic distances. Thus, they seem to have substantial levels of phylogenetic inertia. Three of these traits were morphological, whereas four were demographic.

Ancestor-state reconstruction

I predicted that demographic characters and annual species would exhibit more evolutionary changes along the phylogenetic tree than morphological traits and perennial species. However, the results only partially support the hypothesis. I detected more phylogenetic inertia for demographic traits.

Annual species exhibited more and greater evolutionary changes than perennials in both demographic and morphological traits. For seven traits, there was more differentiation from the ancestor for annuals, in six cases the change was equal, and only in one case were there more changes from the ancestor in perennials. Given the relative numbers of

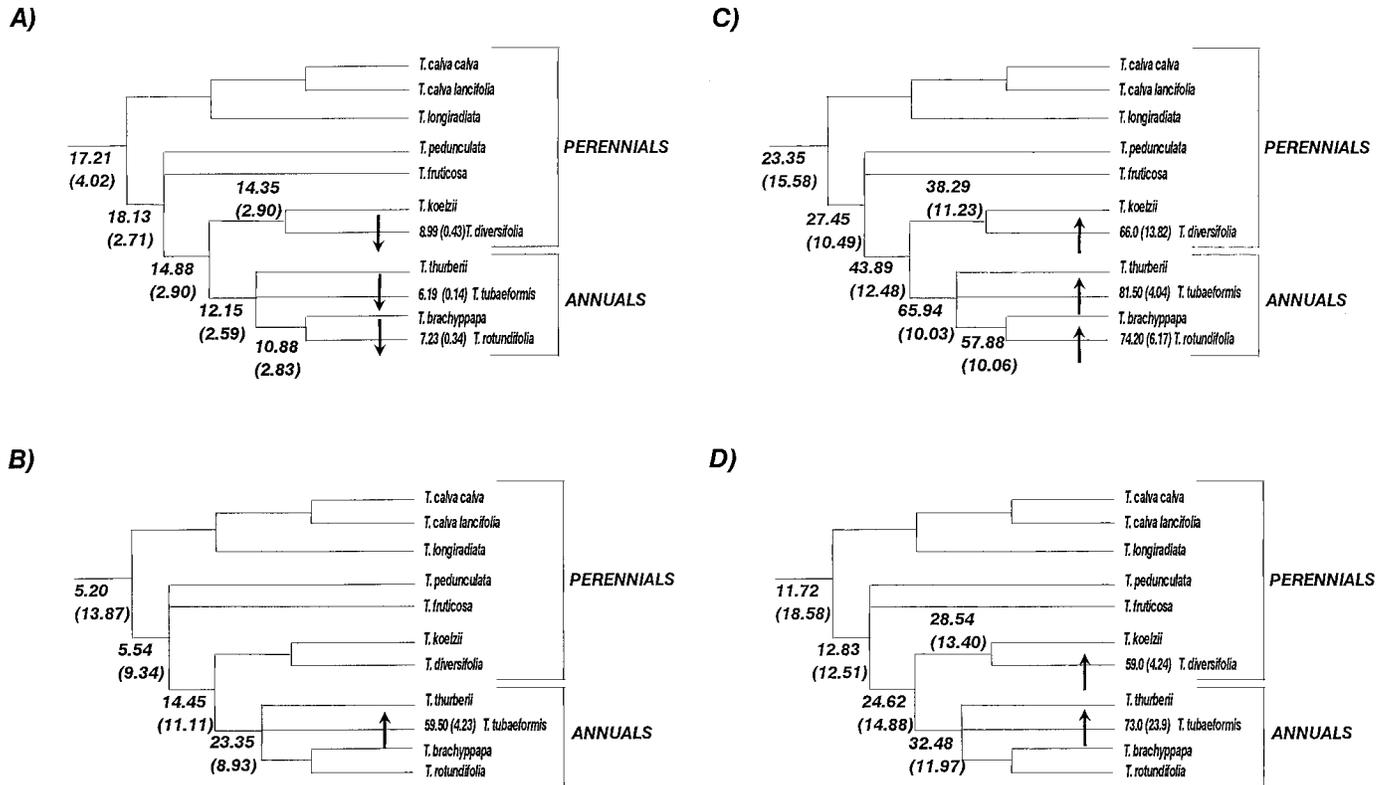


FIG. 6. Ancestral state reconstruction (Schluter et al 1997) for four demographic characters in the genus *Tithonia* (Asteraceae). (A) Germination time; (B) establishment (%); (C) viability; (D) germination (%). Arrows up and down represent differences from the ancestor greater or less than two standard errors of the estimate. Only taxa that differ from the ancestor are illustrated.

annuals (four) and perennial (seven) taxa, we would expect roughly one annual change for every two evolutionary changes in perennials. The reverse was true. Nearly twice as many evolutionary changes occurred in the annual clade. The amount of diversification from the estimated ancestor for each trait, expressed here as the square sum of change in relation with branch length, also demonstrates that annual species tend to diverge more than perennials.

It is thus not easy to choose among these methods, which can give very different results. In terms of choosing between autoregressive models, PVR is probably the best option, due to its best performance with a small sample size. In relation to phylogenetic correlograms and autocorrelation, however, one difficulty with these approaches is that both ignore the evolutionary mechanisms leading to the observed pattern. Those characters that exhibited larger autocorrelation coefficients did not exhibit more or less evolutionary changes in trait value across the phylogeny. One alternative explanation for the observed patterns is that species of the genus *Tithonia* exhibit similar phenotypic responses to selection. All together, my results show that phylogenetic inertia depends on which method you use and suggest that a more explicit definition of phylogenetic inertia needs to be adopted.

Estimates of Phylogenetic Inertia in Plants

Jordano (1995) conducted a comparative analysis to estimate phylogenetic effects in phenotypic traits of angiosperm fleshy fruit. Strong phylogenetic effects were obtained for 11

of 16 traits. (R^2 from Cheverud et al. [1985] method varies from 21% to 31%). All form and design fruit traits ($n = 7$) and four of nine nutrient content traits exhibited highly significant autocorrelation coefficients.

Other studies examining correlations with seed and fruit attributes have found that fruit and seed traits are strongly correlated with taxonomic level. Mazer (1989) reports that genus accounted for 71% of the variance in seed mass in some species of Indiana dunes angiosperms and Herrera (1992) found that family, genus, and species accounted for 20%, 49%, and 27% of total variation in fruit width and length. From these studies, phylogenetic effects seem clearly evident in morphological attributes of fruits and seeds.

Alternatively, Lord et al. (1995) demonstrated that a large proportion of between-species variation in seed mass is correlated with taxon membership (i.e., lineage history), but they argued that phylogenetic niche conservatism (sensu Harvey and Pagel 1991) rather than phylogenetic constraint is responsible for much if not all of this patterns.

Fewer data are available on demographic or life-history traits. Franco and Silvertown (1996) reported that some demographic characters related to reproductive output or time dependence had the major variance explanation at the species level and age-dependent characters had it at the division level. This could be indirect evidence of phylogenetic inertia in life-history traits, but the authors did not make any statement about it.

Thus, my results that demographic traits tend to have more

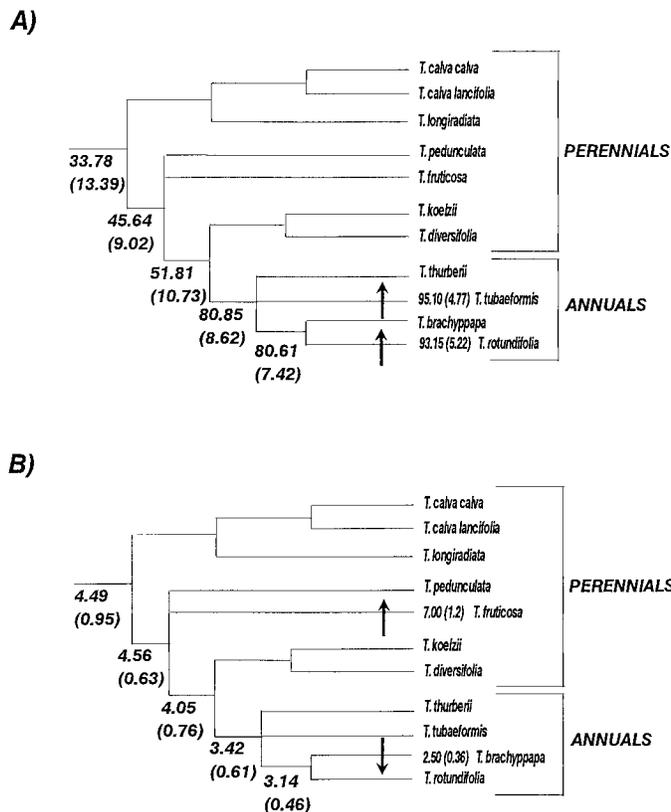


FIG. 7. Ancestor-state reconstruction (Schluter et al 1997) for two demographic characters in the genus *Tithonia* (Asteraceae). (A) Resource allocation; (B) adult height. Arrows up and down represent differences from the ancestor greater or less than two standard errors of the estimate. Only taxa that differ from the ancestor are illustrated.

phylogenetic inertia than morphological ones may not be as unexpected as they at first appear. Lord et al. (1995) addressed the question of how to interpret taxonomic patterns when phylogenetic inertia is detected. The main discussion around this issue is to understand the adaptive value or lack of adaptive value of this inertia. The conclusions for the analyses presented here may vary in regards of the applied method, although not the actual presence or absence of inertia. Here I have demonstrated the relevance and the need to understand the historic component in plant demography and morphology by combining experimental evidence for demographic effects and statistically developed phylogenetic comparative methods.

My results demonstrate that phylogenetic inertia is present in morphological and demographic traits; however, my results are based on a common variable, phylogeny. It would be very restrictive to invoke a single cause to explain morphological and demographic evolution. It is also important to consider genetic and environmental pressures when analyzing trait evolution and diversification. The present and other recent studies (i.e., Jordano 1995; Franco and Silvertown 1996) demonstrate the need to address the historic component by using both phylogenetic comparative methods and experimental ecological approaches. However, a formal recommendation of which comparative approach to apply is not

yet possible. It seems that an integrative approach to recognize processes (i.e., phylogenetic inertia, actual selection, environmental variation) and understanding their significance could give us some key aspects to understand the mechanisms of trait evolution.

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