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AGE AT MATURITY AND DIVERSIFICATION IN WOODY ANGIOSPERMS

MIGUEL VERDÚ
Centro de Investigaciones sobre Desertificación (CSIC-UV), Camí de la Marjal s/n Apartado Oficial, 46470 Albal, Valencia, Spain E-mail: Miguel.Verdu@uv.es

Abstract.—Angiosperm diversification has been associated with plant-animal interactions such as seed dispersal and pollination and life-history characters such as rapid growth and fast reproduction. This paper relates a life-history character (age at maturity) to woody angiosperm diversification. Here I present a comparative analysis of data drawn from the literature, indicating that time to first reproduction is shorter in woody angiosperms than in gymnosperms. In addition, age at maturity is negatively correlated with the rate of diversification (measured as the number of species per genus) at all the taxonomic levels analyzed and also when phylogenetically independent contrasts were conducted. This correlation suggests that early reproduction promotes diversification in woody angiosperms. Furthermore, this correlation is not a confounding effect of the association between age at maturity and other ecological factors that promote angiosperm diversification, such as pollination and seed dispersal systems.

Key words.—Dispersal, early reproduction, phylogenetically independent contrasts, pollination, species diversity.

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The well-known dramatic rate of diversification of angiosperms and the concomitant loss of gymnosperm lineages is reflected today in the high relative diversity of angiosperms in most terrestrial habitats (Bond 1989). This difference between angiosperm and gymnosperm diversities continues to puzzle evolutionary biologists. One popular explanation, the reproductive coevolution hypothesis, focuses on plant-animal interactions, such as seed dispersal and pollination (Raven 1977; Regal 1977, 1982; Crepet 1983, 1984). Here, the role of animals in angiosperm diversification has been attributed to increased speciation rates and/or decreased extinction rates as a result of animal-mediated isolating mechanisms (Midgley and Bond 1991a,b).

Several studies have been carried out to test the association between angiosperm diversification and seed dispersal and pollination by animals, with different conclusions reached. Herrera (1989), Fleming (1991), and Eriksson and Bremer (1992) were unable to find any significant association between seed dispersal mode (biotic vs. abiotic) and rates of angiosperm diversification. In contrast, an analysis of separate groups of woody and herbaceous families of angiosperms by Tiffney and Mazer (1995) found evidence for an association between dispersal by vertebrates and high levels of diversification in woody angiosperms only, with the same mode of dispersal associated with low levels of diversification in herbaceous angiosperms. (Similar conclusions were found by Eriksson and Bremer [1991] within the Rubiaceae.) A significant role of animal pollinators in angiosperm diversification was found by Eriksson and Bremer (1991) at the family level, an association that has been confirmed by a phylogenetic analysis conducted by Dodd et al. (1999).

The other major explanation offered for the relative rates of angiosperm and gymnosperm diversification, the regeneration niche hypothesis, focuses on physiological and life-history characters that allow angiosperms to colonize a wide range of habitats, excluding gymnosperms by competition (Stebbins 1974; Bond 1989; Midgley and Bond 1991a,b). These physiological and life-history characters, such as rapid growth and fast reproduction, allow angiosperms to increase their reproductive rate through a shortening of their age at maturity relative to gymnosperms (Stebbins 1974; Bond 1989). It is well known, for example, that whereas many angiosperm species are able to reach reproductive maturity within weeks (e.g., *Arabidopsis thaliana* reaches maturity within 24 days), ‘‘even the most rapidly growing gymnosperms, like *Ephedra*, typically take years to reach sexual maturity’’ (Niklas 1997, p. 205). Evidence on association between these life-history characters and angiosperm success has been inferred from biogeographical and forestry studies designed to understand the current competitive dominance of angiosperms over gymnosperms (Bond 1989). However, to date no studies have been carried out across taxa to test statistically the association between those life-history characters and angiosperm diversification. This is despite clear evolutionary explanations for the association, namely increased rates of evolution (anagenesis) as a result of shorter generation times (Kimura 1983; Barraclough et al. 1996; Eyre-Walker and Gaut 1997; Barraclough and Savolainen 2001).

Here I provide the first phylogenetic evidence for a correlation between rates of diversification (cladogenesis) and shorter generation times. In particular, I present analyses of data drawn from the literature that show that age at maturity is indeed lower in angiosperms than in gymnosperms and that diversification rates correlate negatively with age at maturity. Age at maturity was considered together with pollination and dispersal modes to examine whether all these variables provide independent explanation of the intergeneric variation of the diversification rates.

METHODS

Data from age at maturity, measured as the minimum age when the first reproduction occurs, were obtained from U.S. Department of Agriculture websites at http://www.fs.fed.us/database/feis/plants (Forest Service Intermountain Research Station’s Fire Sciences Laboratory [IFSL] in Missoula, MT) and http://willow.ncfes.umn.edu (Forest Service, St. Paul [MN] Field Office), from Bingelli’s webpage on the ecology of invasive tropical trees (http://members.lycos.co.uk/WoodyPlantEcology/), Niembro (1988), Pausas (1999), and field observations (see Appendix 1). Most of the species were

North American temperate trees and shrubs, although tropical and Mediterranean trees and shrubs were also included. In total, 174 woody angiosperm species corresponding to 95 genera within 46 families were included in the analysis. In addition, data from 68 species corresponding to 21 genera of gymnosperms were obtained from the same sources, from the cycad page at http://plantnet.rbgsyd.gov.au/PlantNet/cycad/cycsour.html, and from K. J. Niklas (pers. comm.) for further analyses. Data from congeneric species were averaged to obtain a single value for each genus.

Data on angiosperm diversification, measured as the number of species per genus, were obtained from Mabberley (1997). Because the ages of genera will not be the same, the number of species per genus may reflect age as well as the rate of diversification, and therefore, the use of the species-per-genus ratio as a proxy for angiosperm diversification should be validated. I did this by testing the correlation between this ratio (log[species/genus]) and the net diversification rate estimated for the clade the genus comes from. Net diversification rates of the clades were obtained from Magallón and Sanderson (2001), who calculated the age of the taxa based on the paleobotanical record and modeled diversification as a stochastic, time-homogeneous birth-and-death process that depends on the diversification and extinction rates. I used the species to genus ratio instead of Magallón's net diversification rates because the former provides one diversification value per genus, whereas the latter only provide diversification values for families or higher taxonomic groups.

All data were log-transformed to obtain a normal distribution. The ordinal classification for the families of flowering plants published by the Angiosperm Phylogeny Group (1998) was used as a reference framework of the phylogenetic relationships among taxa.

The relationship between the age at maturity and the number of species per genus was examined by fitting major axis regression (MAR) between both variables across genera, families, orders, and higher monophyletic groups as defined by the Angiosperm Phylogeny Group (1998). In this way, the regression was directionally conducted from lower to higher nodes to evaluate the taxonomic levels in which the relationship was significant. Data at the family level were obtained by averaging the values of all the sampled genera within the families. Data at the higher taxonomic levels were obtained in a similar way (i.e., averaging values of families within orders and orders within higher monophyletic groups). MAR is more appropriate than the traditional least squares regression because the x variable (age at maturity) has not been fixed by the researcher and therefore has a measurement error associated with it.

To take into account the effect of taxonomic relatedness on the covariation of the variables, phylogenetically independent contrasts (PICs) were run in the program COMPARE version 4.4 (Martins 2001) using the phylogeny published in Soltis et al. (2000). A cladogram was drawn by using the TREEVIEW program (Page 1996a). When possible, I grafted clades resolving phylogeny at the genus level (Fig. 1). These clades were Fabaceae (Doyle et al. 1997); Betulaceae (Chen et al. 1999); Ericaceae, Empetraceae, and Caprifoliaceae (TreeBASE Console at http://herbaria.harvard.edu/treebase/console.html); Rhamnaceae (Richardson et al. 2000); and Rosaceae (Dickinson lab homepage at http://www.botany.utoronto.ca/faculty/dickinson/DickinsonLab.html). When the phylogeny was unknown (i.e., Fagaceae, Cistaceae), I averaged the values of all genera within the family. By combining information from all these sources, it is possible to construct a supertree without polytomies (Fig. 1) but the cost is that it makes it impossible to obtain consistent branch lengths representing the evolutionary time (Ackerly and Reich 1999). For this reason, equal branch lengths were assumed in the analysis of PICs between age at maturity and diversification. Equal branch lengths may be appropriate under the punctuational evolutionary model, but may inflate the Type I error rates (Ackerly 2000). To ensure that the results were not statistically flawed by the assumption of equal branch lengths, I reran PICs in a tree with branch lengths. To do this, I pruned the Soltis et al. (2000) tree and calculated the branch lengths for the taxa included in my database. The correct branch lengths in the pruned tree were calculated by summing the branch lengths in the Soltis et al. phylogeny. Because this pruned tree did not have grafted clades, the number of taxa was reduced to 51.

PICs were normally distributed (Kolmogorov-Smirnov $P > 0.05$ for both variables). Phylogenetic independence of contrasts was checked, as suggested by Garland et al. (1992) and Freckleton (2000), by correlating the contrast values against the mean values of the variables on each node (Spearman's rho $= 0.01$, $P > 0.05$ for age at maturity, $n = 84$; Spearman's rho $= -0.05$, $P > 0.05$, $n = 84$ for diversification). PICs were arbitrarily positivized, and the statistical significance was tested by means of a MAR fitted through the origin (for an explanation about this procedure see Harvey and Pagel 1991; Garland et al. 1992).

PICS assume homogeneity in the evolutionary process and calculate contrasts over the full phylogeny by averaging the values of age at maturity and diversification at higher nodes (Ackerly 2000). To test for a different evolutionary scenario where correlated changes represent a recent divergence, I used paired comparisons by running independent contrasts only between pairs of taxa for which the age at maturity is actually known (i.e., contrasts at the tips of the tree). The statistical significance of the paired comparisons between age at maturity and the species-to-genus ratio was estimated by means of the sign test because this method does not allow one to estimate the magnitude of the correlation (Ackerly 2000).

To test for the association of age at maturity with other variables that may also be related to angiosperm diversification, each genus was classified regarding its pollination and seed dispersal types. This information was obtained from the same databases consulted for data on age at maturity. In the few cases in which all the species within a genus did not have the same pollination or dispersal system, the genus was classified according to the system of the greatest number of the congeneric species.

A two-way ANOVA with age at maturity (log-transformed) as dependent variable and pollination and dispersal systems as fixed factors was conducted. The significance of the non-orthogonal contrasts for studying the interaction between the levels of the factors was corrected by the Bonferroni pro-

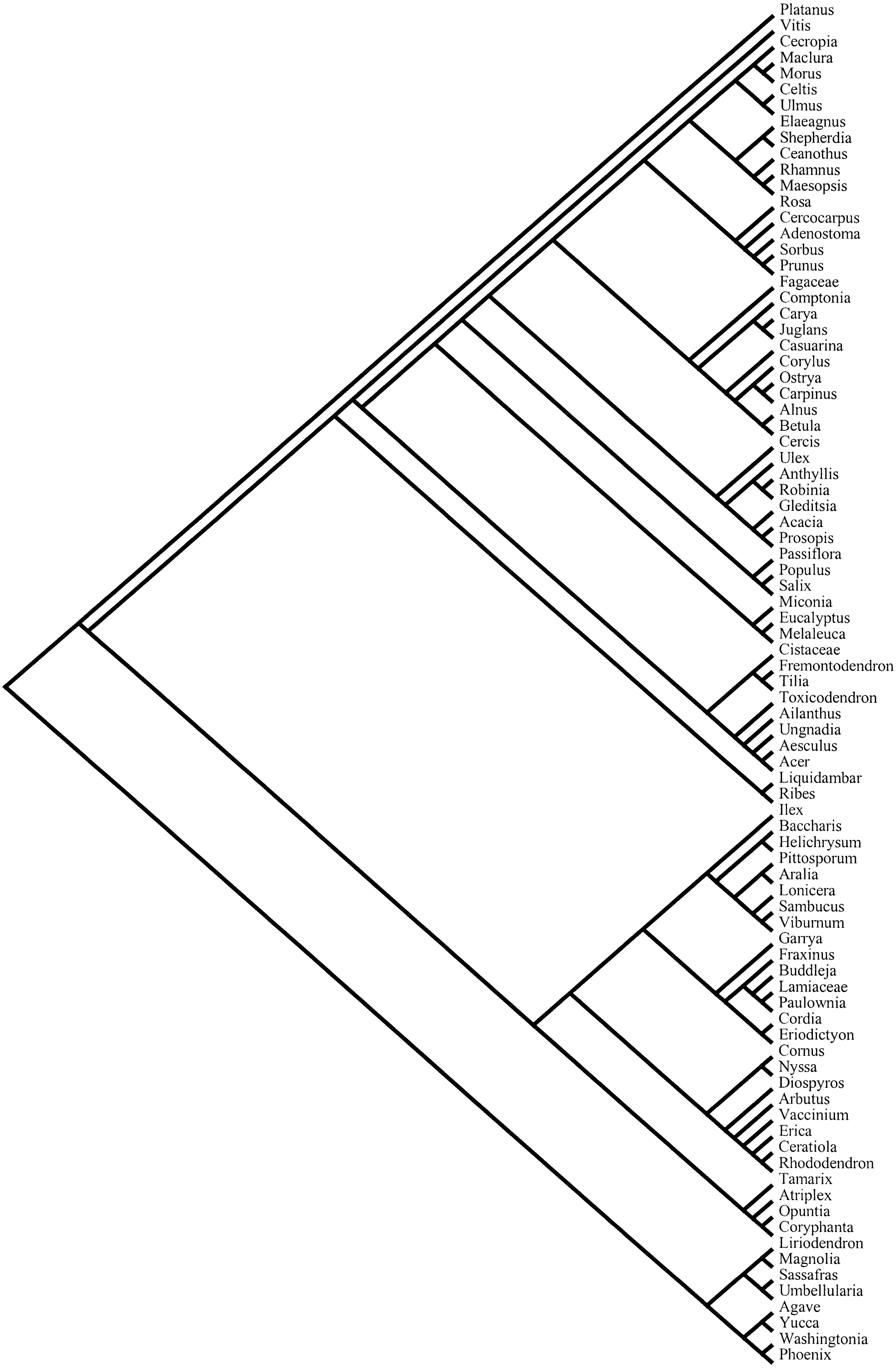

FIG. 1. Phylogeny used to test the relationship between age at maturity and diversification throughout phylogenetically independent contrasts.

cedure by adjusting the alpha-value as a function of the number of contrasts performed.

After study of statistical associations between age at maturity and pollination and dispersal types, I constructed a statistical model including all the variables to detect if angiosperm diversification is explained by all or some combination of these variables. I computed an ANCOVA model with the number of species per genus (log-transformed) as dependent variable, pollination type and dispersal type as fixed factors, and age at maturity (log-transformed) as the covariate. The covariate was nested within the interaction of the factors due to the lack of homogeneity among slopes for the different combinations of factor levels.

To statistically control the phylogenetic relationships and the effect of both pollination and dispersal types on the relationship between age at maturity and angiosperm diversification, both PICs and paired comparisons were rerun on the residuals extracted from the two-way ANOVA of age at maturity on pollination × dispersal types and the two-way ANOVA of angiosperm diversification on pollination × dispersal types.

RESULTS

The frequency distribution of the ages at maturity in the woody angiosperms is biased toward early reproduction, the modal class being that of 1–5 years (Fig. 2 [top] and Appendix 1). In contrast, the modal class of age at maturity in gymnosperms is much later, at 6–20 years (Fig. 2 [bottom] and Appendix 2). Mean age at maturity of woody angiosperms is significantly shorter than that of gymnosperms ($t = -5.2$, df = 37.6, $P < 0.001$; separate estimation of variances due to heteroscedasticity).

The species-to-genus ratio was significantly correlated with the net diversification rate under the two scenarios analyzed by Magallón et al. (2001): in the absence of extinction ($r = 0.24$, $P = 0.036$, $n = 77$) and under a high relative extinction rate ($r = 0.27$, $P = 0.016$, $n = 77$). This means that the species-to-genus ratio may be used as a proxy for diversification rate. In woody angiosperms, there is a negative significant relationship between the age at maturity and the number of species per genus at all the taxonomic levels studied from genus to higher monophyletic groups. This correlation is consistent with the causal model of early reproduction promoting diversification (Fig. 3). A negative relationship remains significant when phylogeny is controlled by means of standardized independent contrasts assuming equal branch lengths (Fig. 4). This relationship is not a statistical flaw due to the assumption of equal branch lengths because the same result is also found in the pruned tree with the original branch lengths from Soltis et al. (2000; $y = -0.26x$; 95% CI = −0.50, −0.02; MAR). Similarly, the negative relationship between age at maturity and diversification occurs under the evolutionary scenario where correlated changes represent a recent divergence, because paired comparison test between pairs of taxa at the tips of the tree was significant (19 of 27 contrasts were negative; $P = 0.027$; sign test).

The ANOVA performed on age at maturity at the genus level showed a significant interaction between pollination and dispersal types (Table 1). This interaction, as shown in Figure 5, is explained because biotic pollination is associated with lower ages at maturity in abiotically dispersed genera (contrast value = 0.37 ± 0.11, $P < 0.01$ after Bonferroni correction) but not in those biotically dispersed (contrast value = −0.01 ± 0.15, $P > 0.05$).

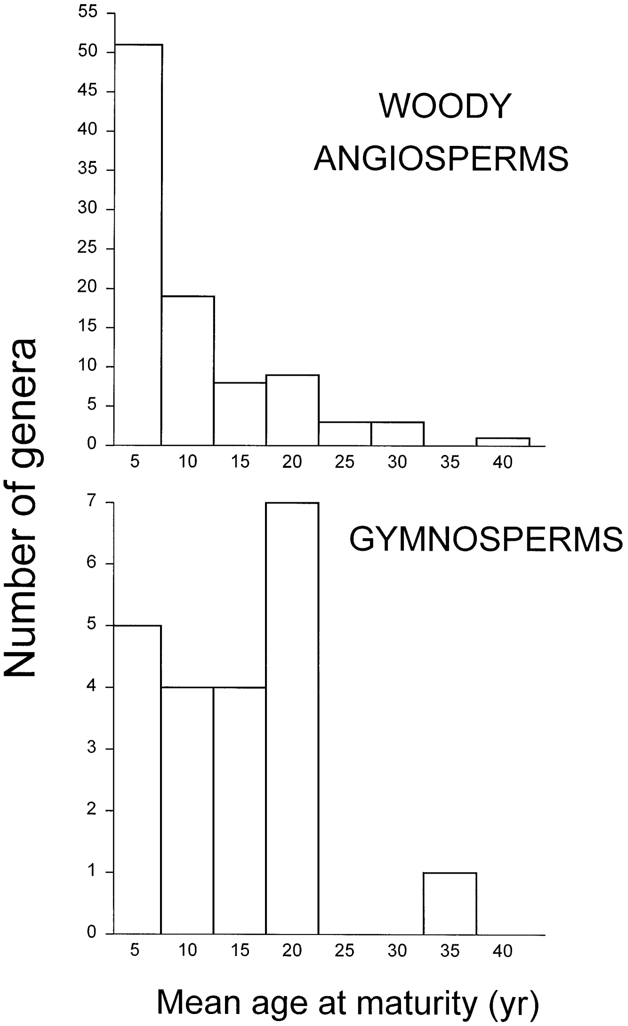

FIG. 2. Frequency distribution of age at maturity among (top) woody angiosperm genera and (bottom) gymnosperm genera. Data from congeneric species were averaged to obtain a single value for each genus.

Even though age at maturity is associated with modes of pollination and seed dispersal, these variables provide independent explanation of the intergeneric variation of the number of species per genus. As shown in the ANCOVA model (Table 2), both age at maturity and pollination type are statistically significant. When age at maturity is included in the analysis, biotically pollinated genera are richer in species than those abiotically pollinated (1.57 ± 0.11 vs. 1.28 ± 0.19, respectively; estimated marginal means of the log-transformed variable). Similarly, the statistical association between age at maturity and angiosperm diversification remains significant after controlling for pollination and dispersal types and for phylogenetic relationships over the full phylogeny (Fig. 6). The relationship is marginally significant when only pairs of taxa at the tips of the tree were considered

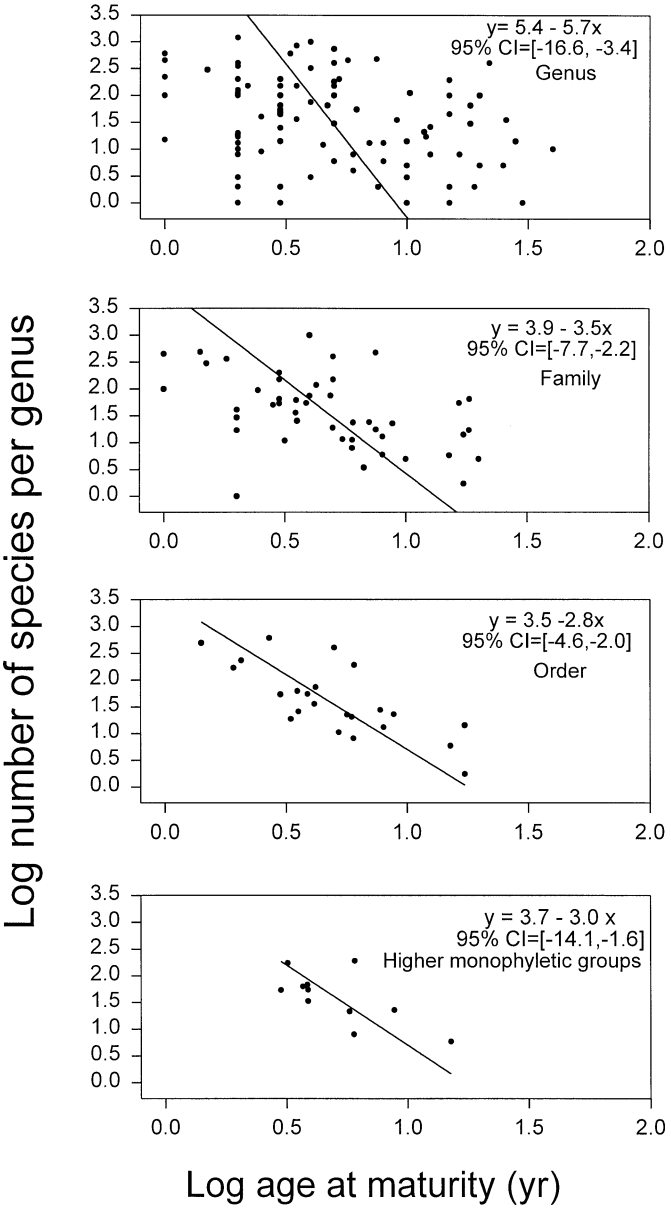

FIG. 3. Relationship between age at maturity and the number of species per genus in woody angiosperms across genera, families, orders, and higher monophyletic groups. Data from congeneric species were averaged to obtain a single value for each genus. Data at the family level were obtained by averaging the values of all the genera within the families. Data at the higher taxonomic levels were obtained in a similar way (i.e., averaging values of families within orders and orders within higher phylogenetic groups). The major axis regression lines and their 95% confidence intervals are also shown.

because 18 of 27 contrasts were negative ($P = 0.06$, sign test).

DISCUSSION

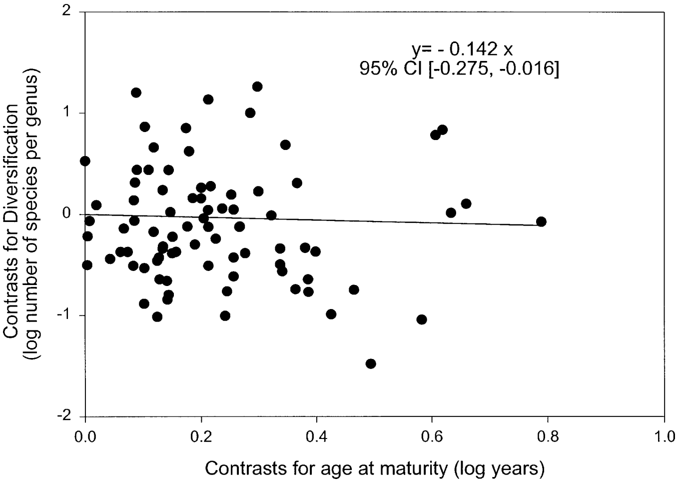

FIG. 4. Scatterplot of standardized independent contrasts of age at maturity versus diversification (measured as the number of species per genus) of woody angiosperms. The major axis regression line forced through the origin and its 95% confidence interval is also shown.

The main results of this paper show that woody angiosperms reproduce sooner than gymnosperms, and that age at maturity is negatively correlated with genus size in woody angiosperms.

Plant age at maturity is rarely reported in the scientific literature but it is a common datum provided in the forestry databases, where only economically important species are considered. Because the main sources used in this study were U.S. forestry databases, the taxa analyzed here are principally temperate trees and shrubs. This bias indicates that biological generalizations of the results of this study should be done with caution (for the implications of a similar taxonomic sampling bias see Herrera et al. 1998). Nevertheless, the bias is not expected to affect the correlation between age at maturity and diversification provided that both traits evolved independently of the sampling character (economic importance; for an explanation of the statistical consequences of sampling bias see Ackerly 2000).

Genus size (number of species per genus) is correlated with the net diversification rates estimated by Magallón and Sanderson (2001), indicating that the former is a good proxy for diversification. The main advantage of the ratio of number of species per genus as a measure of diversification rate is that it provides one measure per genus. To estimate net diversification rates for each genus, we would need to know their evolutionary ages, and ages are unknown for most of the genera.

Age at maturity is one of the life-history characters that may have driven the ecological and evolutionary rise of an-

TABLE 1. Effects of pollination type (biotic vs. abiotic) and dispersal type (biotic vs. abiotic) on age at maturity of angiosperm genera.

Source	df	MS	*F*
Pollination type	1	0.55	3.84
Dispersal type	1	0.01	0.32
Pollination × dispersal	1	0.61	4.29*
Error	91	0.14	

* $P < 0.05$, $R^2 = 0.11$.

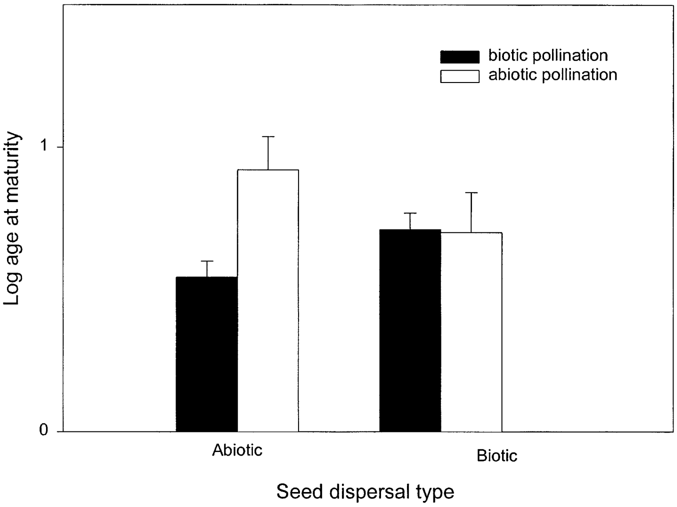

FIG. 5. Mean ± SE values of age at maturity (log-transformed) of genera with different systems of seed dispersal and pollination.

TABLE 2. Effects of pollination type (biotic vs. abiotic), dispersal type (biotic vs. abiotic), and age at maturity on the rate of diversification of angiosperm genera, measured as the number of species/genus.

Source	df	MS	*F*
Pollination type	1	3.86	6.31*
Dispersal type	1	0.06	0.10
Pollination × dispersal	1	1.48	2.41
Age at maturity (pollination × dispersal)	4	2.09	3.42*
Error	87	0.61	

* $P < 0.05$, $R^2 = 0.19$.

giosperms (Bond 1989). Early reproduction represents ecological and evolutionary benefits across different types of life history (Sibly and Calow 1986; Stearns 1992). In plants, the age at maturity can have an enormous effect on fitness when generations overlap (Willson 1983). A relatively small decrease in age at maturity may produce effects equivalent to a large increase in offspring number (Willson 1983). The results of this study show that age at maturity of woody angiosperms is significantly lower than that of gymnosperms. Early reproduction is usually linked to high fecundity, short life spans, limited parental care, rapid development, and a greater proportion of available resources committed to reproduction (Gould 1977). These characters provide the organisms with the ability of rapid reproduction and early colonization (*r* strategy; Harper 1977; Chasan and Hart 1996; Rejmánek and Richardson 1996). Because angiosperms can be considered as *r* strategists, or colonizing species, in comparison to gymnosperms (Stebbins 1974; Krassilov 1991), the high colonization ability is a feature considered by many authors to explain angiosperm dominance in the Cretaceous (Bond 1989; Midgley and Bond 1991a,b). For example, Bond (1989) suggested that gymnosperms are restricted to stressful environments because fast-growing angiosperms eliminated slow-maturing gymnosperms from nonstressful habitats. Precocious sexual maturation revealed here may support the hypothesis of some authors who have invoked the role of progenesis in the rise of angiosperms (Takhtajan 1969, 1976; Doyle 1978).

Doyle and Donogue (1986) suggested that the dominance of angiosperms is an indirect cause of the increment in the diversification rates. A second result of this study shows that age at maturity is negatively correlated with diversification (measured as the number of species per genus) in woody angiosperms. This correlation is consistent across all the taxonomic levels from genus to higher monophyletic groups and when phylogeny is controlled by means of PICs. This relationship suggests that early reproduction promotes diversification by decreasing the probability of extinction and/or by increasing the probability of speciation of taxa. A similar argument has been proposed to explain why herbs are more diverse than woody plants. Herbaceous growth form is associated with lower generation times, which could increase speciation rates (Eriksson and Bremer 1992; Dodd et al. 1999). A theoretical possibility of direct association between age at maturity and diversification is that shorter reproductive cycles will produce higher per year mutation rates, thus increasing the genetic divergence and therefore the probability of speciation per unit time.

The generation-time effect hypothesis predicts that organisms with shorter generation times have a higher mutation rate (Gaut et al. 1996). This prediction is most pertinent for organisms with germline replication, and therefore it appears to hold true in animals (Gaut et al. 1997). For example, differences between rates of molecular evolution between pocket gopher lice and their mammalian hosts are attributed to differences in generation time between both taxa (Hafner et al. 1994; Page 1996b). Bromham et al. (1996) supports the negative relationship between generation time and substitution rate in mammals by means of PICs. Evidence on the association between generation time and the rate of molecular evolution has been also found in birds (Mooers and Harvey 1994), but not in insects (Crozier and Crozier 1992). Plants do not undergo determinate germline replication, and therefore the basis for the correlation is not so clear. Gaut et al. (1997) tested the generation-time effect hypothesis within the

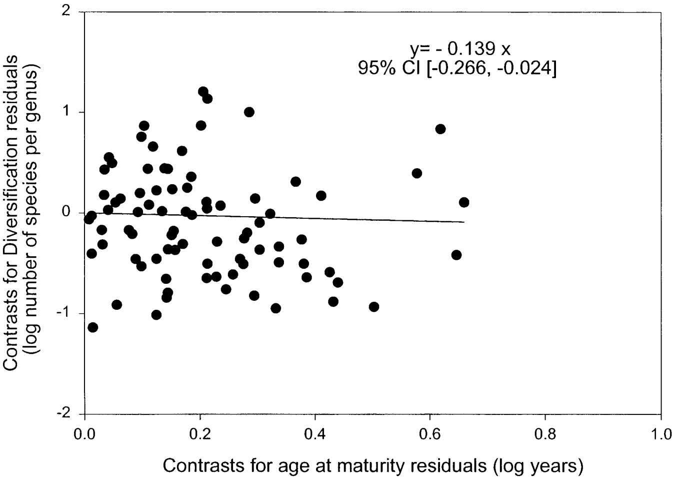

FIG. 6. Scatterplot of standardized independent contrasts of age at maturity and diversification (measured as the number of species per genus) of woody angiosperms after controlling for pollination and dispersal types. The major axis regression line forced through the origin and its 95% confidence interval is also shown.

family Poaceae by comparing the substitution rates between species with long versus short generation times (woody bamboos, with first reproduction at 10–60 years vs. other grasses, including herbaceous bamboos, with first reproduction at one to two years) and found, as predicted, that woody bamboos had slower rates of synonymous substitutions. Other authors have invoked the generation-time effects to explain the differences in molecular evolution rates among plant taxa. For example, Wilson et al. (1990) suggested that the great difference in base substitution rates between palms and grasses may be an indication of an effect of generation time on cpDNA evolutionary rates.

Nevertheless, we need to ask whether higher substitution rates are related to plant speciation. The theory predicts that acceleration in rates of sequence divergence may be associated with the formation of new species (Carson and Templeton 1984). Comparative evidence has been recently provided by Barraclough and Savolainen (2001), who described a significant, although weak, positive relationship between angiosperm diversification and the rate of molecular evolution. The first hypothesis that these authors invoke to explain the observed pattern is that generation times may vary among angiosperms, thus speeding up both the rates of phyletic changes and speciation. The present study provides the first comparative evidence for a relationship between rates of diversification and generation times.

Other selective pressures are also acting in the diversification rates of woody angiosperms, as the large scatter around the regression line between diversification and age at maturity indicates (Fig. 4). It is well known that many ecological factors may promote species divergence (Schluter 2001), such as pollination and seed dispersal types, the two factors most studied in the literature regarding angiosperm diversification. Although age at maturity varies among pollination and dispersal systems, the relationship between age at maturity and diversification remains significant after controlling for them. For this reason, age at maturity is not spuriously correlated with diversification throughout the confounding effects of the pollination and dispersal systems. All the three variables provide complementary explanation of the variance in angiosperm diversification. However, other confounding effects on the relationship between age at maturity and diversification cannot be discarded. Factors such as biogeographical distribution (Ricklefs and Renner 1994), life span and net reproductive rates (Franco and Silvertown 1996), ploidy (Petit and Thompson 1999), plant defenses (Farrell et al. 1991), and breeding system (Heilbuth 2000) are associated with angiosperm diversification and, perhaps, to age at maturity. Consequently, future analyses on angiosperm diversification should include as many factors as possible to account for the multivariate nature of this evolutionary process.

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Appendix 1

Values of age at maturity, diversification (number of species per genus), pollination, and seed dispersal systems of woody angiosperms across the taxonomic classification used in the analysis. The number of species used to average the values of age at maturity is indicated in parentheses after each genus. A and B in both the pollination and dispersal columns mean abiotic and biotic, respectively.

Higher group	Order	Family	Genus	Age of maturity (years)	Number species/genus	Polli-nation	Dispersal
Commelinoids	Arecales	Arecacae	*Washingtonia* (1)	19.0	2	B	B
			Phoenix (1)	12.0	17	B	B
Euasterids II	Apiales	Araliaceae	*Aralia* (1)	3.5	36	B	B
		Pittosporaceae	*Pittosporum* (1)	5.0	150	B	B
	Aquifoliales	Aquifoliaceae	*Ilex* (2)	5.0	400	B	B
	Asterales	Asteraceae	*Baccharis* (1)	2.0	400	A	A
			Helichrysum (1)	1.0	600	B	A
	Dypsacales	Caprifoliaceae	*Lonicera* (1)	5.0	180	B	B
			Sambucus (2)	2.5	9	B	B
			Viburnum (2)	3.5	150	B	B
Euasterids I		Boraginaceae	*Cordia* (1)	4.0	320	B	A
			Eriodictyon (1)	2.0	8	B	A
	Garryales	Garryaceae	*Garrya* (1)	8.0	13	A	B
	Lamiales	Lamiaceae	*Teucrium* (1)	2.0	100	B	A
			Thymus (1)	2.0	350	B	A
			Rosmarinus (1)	2.0	2	B	A
		Buddlejaceae	*Buddleja* (1)	1.0	100	B	A
		Oleaceae	*Fraxinus* (4)	183	65	A	A
		Pawlonioaceae	*Paulownia* (1)	8.0	6	B	A
Core eudicots	Cariophyllales	Amaranthaceae	*Atriplex* (2)	1.5	300	A	A
		Cactaceae	*Coryphanta* (1)	3.0	45	B	B
			Opuntia (1)	2.0	200	B	B
		Tamariacaceae	*Tamarix* (1)	3.0	54	B	A
	Saxifragales	Hammamelidaceae	*Liquidambar* (1)	20.0	5	A	A
		Grossulariaceae	*Ribes* (1)	30	150	B	B
		Vitaceae	*Vitis* (1)	3.0	65	B	B
Asterids	Cornales	Cornaceae	*Cornus* (4)	4.7	65	B	B
			Nyssa (1)	16.5	8	B	B
	Ericales	Ebenaceae	*Diospyros* (2)	7.5	475	B	B
		Ericaceae	*Arbutus* (1)	3.0	14	B	B
			Ceratiola (1)	15.0	1	B	B
			Erica (1)	5.0	735	B	A
			Gaylussacia (1)	3.0	48	B	B
			Rhododendron (2)	3.5	850	B	A
			Vaccinium (4)	5.7	450	B	B
Eurosids I	Rosales	Elaegnaceae	*Eleagnus* (2)	2.5	40	B	B
			Shepherdia (2)	4.0	3	B	B
		Rhamnaceae	*Ceanothus* (5)	6.2	55	B	A
			Maesopsis (1)	10.0	1	A	B
			Rhamnus (1)	2.0	125	B	B
		Rosaceae	*Adenostoma* (1)	3.0	2	B	A
			Cercocarpus (2)	12.5	8	B	A
			Prunus (3)	5.3	200	B	B
			Purshia (3)	7.6	2	B	B
			Rosa (4)	2.2	150	B	B
			Sorbus (2)	15.0	193	B	B
		Moraceae	*Maclura* (1)	10.0	1	A	B
			Morus (2)	4.5	12	A	B
		Ulmaceae	*Celtis* (1)	15.0	100	A	B
			Ulmus (1)	18.3	30	A	A
		Urticaceae	*Cecropia* (1)	4.0	75	A	B
	Fabales	Fabaceae	*Anthyllis* (1)	2.0	20	B	A
			Robinia (1)	60	4	B	A
			Ulex (1)	2.0	20	B	A
			Acacia (2)	2.0	1200	B	A
			Prosopis (1)	3.0	44	B	A
			Cercis (1)	5.0	6	B	B
			Gleditsia (1)	10.0	14	B	B
	Malphigiales	Saliaceae	*Populus* (6)	9.1	35	A	A
			Salix (1)	2.0	400	B	A
		Passifloraceae	*Passiflora* (1)	1.0	450	B	B
	Fagales	Betulaceae	*Alnus* (2)	3.0	25	A	A
			Betula (3)	25.7	35	A	A
			Carpinus (2)	12.5	26	A	A
			Corylus (1)	1.0	15	A	B
			Ostrya (1)	25.0	5	A	A

Appendix 1. Continued.

Higher group	Order	Family	Genus	Age of maturity (years)	Number species/genus	Polli- nation	Dispersal
		Casuarinaceae	*Casuarina* (1)	2.0	17	A	A
		Fagaceae	*Castanea* (1)	2.0	10	A	A
			Chrysolepis (1)	2.0	2	A	A
			Fagus (2)	40.0	10	A	A
			Lithocarpus (1)	5.0	100	A	A
			Quercus (20)	21.1	400	A	A
		Jungladaceae	*Carya* (6)	28.1	14	A	A
			Juglans (6)	11.8	21	B	A
		Myricaceae	*Comptonia* (1)	2.0	1	A	B
Eudicots	Proteales	Platanaceae	*Platanus* (1)	6.0	8	A	A
Monocots	Asparagales	Agavaceae	*Agave* (1)	3.0	100	B	A
			Yucca (1)	5.0	30	B	A
	Laurales	Lauraceae	*Sassafras* (1)	10.0	3	B	B
			Umbellularia (1)	30.0	1	B	B
		Magnoliaceae	*Liriodendron* (1)	15.0	2	B	A
			Magnolia (1)	20.0	100	B	B
Eurosids II	Malvales	Malvaceae	*Fremontodendron* (1)	2.0	3	B	A
			Tilia (1)	15.0	45	B	A
		Cistaceae	*Cistus* (1)	2.0	18	B	A
			Fumana (1)	2.0	13	B	A
			Helianthenum (1)	2.0	110	B	A
		Melastomataceae	*Miconia* (1)	4.0	1000	B	B
		Myrtaceae	*Eucalyptus* (1)	3.3	600	B	A
			Melaleuca (1)	1.0	220	B	A
	Sapindales	Anacardiaceae	*Toxicodendron* (1)	3.0	200	B	B
		Sapindaceae	*Acer* (8)	10.3	111	B	A
			Aesculus (2)	7.0	13	B	A
			Ungnadia (1)	3.0	1	B	A
		Simaroubaceae	*Ailanthus* (1)	10.0	5	B	A

Appendix 2

Values of age at maturity of gymnosperms. After each genus the number of species used to average the values of age at maturity is shown in parentheses.

Genus	Age at maturity (years)
Abies (3)	18.3
Ceratozamia (1)	5.0
Cupressus (7)	7.1
Cycas (2)	10.0
Dioon (1)	10.0
Encephalartos (1)	10.0
Ephedra (2)	5.0
Gnetum (1)	30.0
Ginkgo (1)	20.0
Juniperus (6)	16.6
Larix (4)	33.2
Lepidozamia (1)	15.0
Macrozamia (1)	15.0
Picea (8)	14.5
Pinus (20)	15.5
Sequoia (1)	5.0
Sequoiadendrum (1)	20.0
Thuja (1)	13.0
Torreya (1)	20.0
Tsuga (4)	20.0
Zamia (1)	2.0