POLYPLOIDY AND DIVERSIFICATION: A PHYLOGENETIC INVESTIGATION IN ROSACEAE

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Polyploidy has been described both as an evolutionary dead end and as a major engine of diversification for angiosperms. Two recent studies have found that genera with higher proportions of polyploid species are more species rich. Here, we investigate patterns of diversification and polyploidy by performing traditional and phylogenetically corrected analyses within the Rosaceae. We find that polyploidy is associated with increased species richness and then differentiate between three alternative hypotheses for this pattern: (1) that polyploidy is associated with herbaceous growth habit, a trait that is in turn associated with increased species richness; (2) that polyploid clades are more evolutionarily successful (i.e., experience increased speciation and/or fewer extinction events) than diploid clades, perhaps because of the increase in genomic content or the increase in plant/flower size that often accompanies polyploidization; and (3) that the polyploidization events themselves, along with the reproductive isolation from the parental clade(s) that follows polyploidization, are responsible for the increased species richness observed in clades with a high proportion of polyploids. There is no evidence that polyploidy and herbaceous growth habit were correlated or that polyploid clades are more species rich than their diploid sister groups. We posit that the third hypothesis has the greatest potential for explaining the pattern of higher species richness of polyploid clades.

Keywords: diversification, extinction, phylogenetic analysis, Rosaceae, speciation.

Introduction

Polyploidy is the inheritance of more than two basic genome copies. It has been estimated that up to 70% of land plants and 95% of ferns have some polyploidy in their evolutionary history (Leitch and Bennett 1997; Otto and Whitton 2000). These high proportions indicate that changes in ploidy level have undoubtedly played some role in the evolution of plants. Polyploidization is thought to arise more often in certain clades, such as those containing perennial herbs (Stebbins 1938), and/or species in colder climates (e.g., at high latitudes or high altitudes; Brochmann et al. 2004). Furthermore, the resulting polyploid clades are thought to be different from their diploid progenitors in important traits such as breeding system (Campbell et al. 1991; Miller and Venable 2000; Mable 2004), ecological tolerances, growth rates, pollinators and herbivores (Thompson et al. 1997; Segraves and Thompson 1999), and rates of adaptation (Otto and Whitton 2000). The observations that (1) polyploidy is not evenly distributed among clades and (2) newly formed polyploid clades are markedly different from their diploid progenitors in their genetics and ecology indicate that polyploidy may influence the pattern of nonuniformity in the

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diversification (speciation minus extinction) rates of lineages of angiosperms (Sanderson and Donoghue 1994, 1996).

Whether polyploidy has been a major factor in the diversification of angiosperms has been somewhat controversial (Stebbins 1950; Petit and Thompson 1999). Stebbins (1950), for example, described polyploid species as evolutionary dead ends because of the decreased rates of adaptive evolution that accompany (1) having extraneous genomes that mask both deleterious and beneficial mutations and (2) self-fertilization that decreases the formation of new gene combinations. More recently, it has been suggested that polyploid clades may be larger than diploid clades, a finding that indicates that polyploidization may allow species to radiate into unoccupied niches (Tate and Simpson 2003) and/or outcompete their diploid counterparts (Soltis et al. 1995). By plotting species richness against the proportion of polyploid species in a genus, a positive relationship has been observed for herbaceous dicots (Otto and Whitton 2000) and 50 angiosperm genera of the Pyrenees (Petit and Thompson 1999). Interestingly, both of these studies found the relationship between species richness and the proportion of polyploidy to be nonlinear, with the greatest species richness being found in genera characterized by having 50%–75% of their species polyploid.

A positive relationship between species richness and percent polyploidy, however, need not automatically rule out Stebbins's (1950) theory. The intriguing results found by Petit and Thompson (1999) and Otto and Whitton (2000) could be caused by a number of factors. (1) Polyploidization is one accepted form in which sympatric speciation might occur, as

polyploids can become genetically isolated from their diploid predecessors in one generation because matings with diploids result in sterile progeny (Ramsey and Schemske 1998). With the knowledge that doubling the genome in both odd- and even-numbered chromosome counts would result in an even-numbered chromosome count, Otto and Whitton (2000) developed a method of estimating the rate of polyploidization using the ratios of even- to odd-numbered chromosome counts within the major angiosperm groups and estimated that 2%–4% of speciation events in angiosperms involve polyploidization (Otto and Whitton 2000). There will most certainly be variation in this rate between lineages of angiosperms (Ellstrand et al. 1996). Clades that undergo polyploidization events more frequently may be more species rich because of this increase in sympatric speciation (fig. 1A). (2) Polyploid clades may be more evolutionarily successful, experiencing higher speciation rates or lower extinction rates once they are established, because of novel physiological and life-history characteristics (Levin 1983; Thompson and Lumaret 1992) or increased visitation from pollinators (Segraves and Thompson 1999; Thompson et al. 2004) (fig. 1B). (3) Polyploidy may arise more often in clades with traits that are correlated with high species richness. To illustrate by one example, it has been suggested that cambium formation may inhibit the creation of polyploid races in woody lineages, which may result in a correlation between perennial herbaceous growth habit and polyploidy (Stebbins 1938; Otto and Whitton 2000). Having a herbaceous growth habit may in turn have a positive effect on the speciation rate of a lineage for a number of reasons, such as high fecundity or lower age at maturity (Ricklefs and Renner 1994; Dodd et al. 1999; Verdú 2002; Verdú and Traveset 2004). If both the former (herbaceous ⟶ polyploidy) and latter (herbaceous ⟶ high species richness) patterns are strong and widespread, a third pattern of highly polyploid clades with high species richness may appear when in fact no causative pathway exists between the two (fig. 1C).

One limitation of previous studies examining the link between diversification and polyploidy is that they have treated genera as independent units. Without accounting for phylogenetic relationships between genera, one cannot rule out the possibility that species-rich genera (with many polyploid species) are large simply because they are older than smaller genera with fewer polyploid species (Felsenstein 1985; Garland et al. 1992). There is also the possibility that species richness values are dependent on taxonomic treatment, with the assignment of the designation of "species" being less conservative in some lineages than in others depending on the presence of certain traits (Campbell and Dickinson 1990; Dickinson and Campbell 1991). If these artificially species-rich genera also have more polyploid species (as may be the case in the genera of Maloideae, for example), correlations between polyploidy and species richness may not be real. A phylogenetic comparative approach largely circumvents the problem of nonuniformity in taxonomic treatment because genera that are subject to similar taxonomic treatments are compared only to each other and therefore should not have undue influence on the results (Felsenstein 1985).

The Rosaceae represent a family for which phylogenetic data are becoming increasingly available and for which
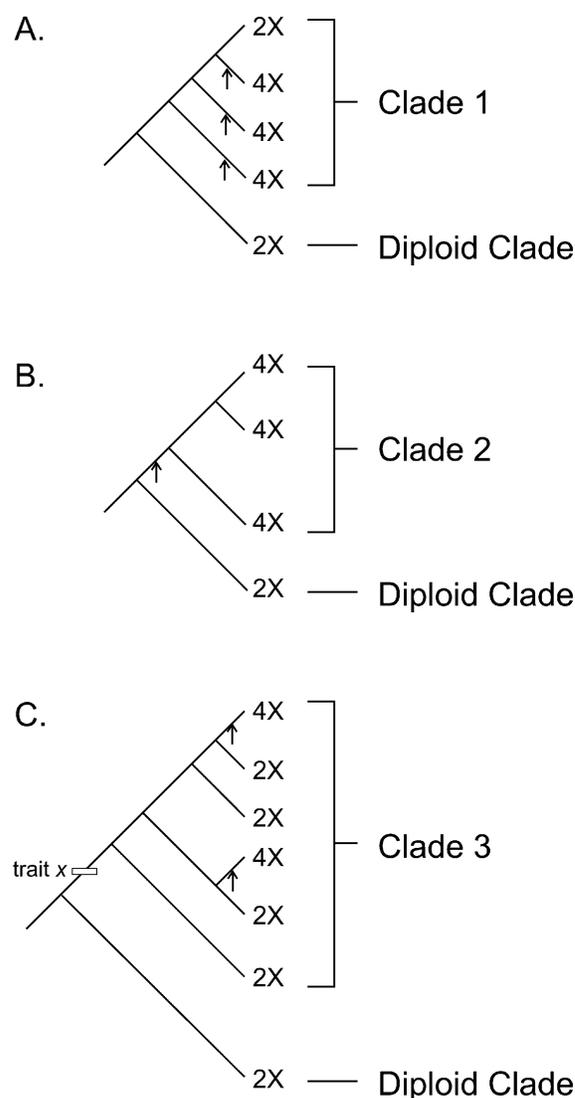

Fig. 1 Three hypotheses, not mutually exclusive, for the cause of a correlation between polyploidy and species richness tested in this article. Arrows indicate the hypothesized origin(s) of polyploidy. *A*, Polyploidization events result in the creation of species. *B*, Polyploid lineages diversify at higher rates (i.e., experience more speciation or less extinction) than diploid lineages. *C*, Polyploidization events occur more often in lineages that are already diversifying at greater rates.

there are relatively abundant data on chromosome number (Kalkman 2004) and nuclear DNA content (Dickson et al. 1992). Depending on the source, there are 85–95 genera and 2000–2825 species in the family (Mabberley 1997; Kalkman 2004). Polyploidy has evolved numerous times within Rosaceae; indeed, the subfamily Maloideae likely arose following a polyploidization event (Evans and Campbell 2002). In this study, we use the substantial knowledge of Rosaceae phylogeny and ploidy level variation to examine the association between polyploidy and species richness with both traditional and comparative phylogenetic approaches. We investigate the following questions: (1) Is there a relationship between the proportion of polyploid species and the species richness of

clades? (2) In instances where there is an exclusively polyploid clade with an exclusively diploid sister group, are the polyploid clades larger on average than their sister diploid clades? (3) Is polyploidy associated with clades that have a large number of diploid species; i.e., do some clades experience increased rates of polyploidization that are independent of and/or in addition to already elevated rates of diversification? (4) Specifically, is there a relationship between herbaceous growth habit and polyploidy that could result in the appearance of an association between polyploidy and high species richness?

Material and Methods

Data Set

We estimated the percentage of polyploid species for every genus, using Robertson (1974), Campbell et al. (1991), the Index to Plant Chromosome Numbers Web site (Goldblatt and Johnson 2003), and Kalkman (2004). Percentages of polyploid taxa in an entire genus were estimated from the percentage of polyploid taxa in the sampled species within genera (e.g., if only three species within a genus having 12 species had ploidy estimates and all three have been found to be polyploid, then the entire genus was assumed to be polyploid). Our estimates of polyploidy of the genera were based on known ploidy counts from between 5% and 100% (mean = 63.8%) of the species in the genera. A complicating factor with regard to species richness values is that polyploidy is associated with gametophytic apomixis, the production of unreduced female gametes together with their parthenogenetic development into embryos. Apomixis could artificially inflate the estimated species richness of polyploid clades if individual apomictic genotypes are mistaken for species because of their frequency and local abundance. We corrected for the inclusion of apomictic taxa by subtracting the number of reported apomictic species (from Campbell et al. 1991, 1997; Mabberley 1997; Alice and Campbell 1999; Werlemark 2000; Nelson-Jones et al. 2002; Hovalm et al. 2004) from the total number of species and the total number of polyploid species. This is not to assume that all apomictic taxa truly belong to one species but instead to generate conservative species richness counts for the polyploid genera included in the analysis. Woodiness and species richness (SR) data were obtained from Kalkman (2004).

Diversification in Polyploid Clades

We first employed a traditional approach to document the relationship between SR and percent polyploidy, in order to see whether the same patterns observed by Petit and Thompson (1999) and Otto and Whitton (2000) emerge from an examination of within-family variation in ploidy. Following Petit and Thompson (1999) and Otto and Whitton (2000), we divided genera into four groups based on their proportion of polyploid species—$\leq 25\%$, 25%–50%, 50.1%–75%, >75%—in order to determine the generality of a nonlinear relationship between SR and percent polyploidy. The effect of percent polyploidy on log-transformed SR was assessed with a one-way ANOVA. We also tested whether "100% polyploid" genera had significantly more species than did "0% polyploid" genera with a t-test.

We created a composite tree of Rosaceae (Sanderson et al. 1998) consisting of a skeletal family phylogeny (Potter et al. 2002) augmented by the insertion of clades from more detailed phylogenetic studies (Amygdaloideae: Bortiri et al. 2001; Maloideae: Morgan et al. 1994, Campbell et al. 1995, Evans 1999; Potentilleae: Eriksson et al. 2003; Sanguisorbeae: Helfgott et al. 2000, Eriksson et al. 2003, Kurtto and Eriksson 2003; Rosoideae: Smedmark and Eriksson 2002). In three groups (*Bencomia* alliance [Helfgott et al. 2000], *Rubus*-Colurieae-Roperculina within Rosoideae [Eriksson et al. 2003], and *Geum* plus relatives [Smedmark and Eriksson 2002]), the relationships between clades (genera) are poorly resolved, and the clades were analyzed as polytomies. This procedure generated a phylogeny for 83 genera within Rosaceae, for 79 of which we were able to estimate the frequency of polyploidy. Although we realize that generic delimitations are in a state of constant flux, the MacroCAIC program (Isaac and Purvis 2004) assumes that each genus is a monophyletic clade at a tip in the tree. The program then calculates the difference in SR at each node in the tree and examines whether the clades with the higher proportion of polyploidy also have higher SR more often than expected by chance, using the highly conservative statistical approach provided by the sign test. MacroCAIC does not compute SR contrasts within polytomies, which, in our data set, reduces the number of potential contrasts in the phylogeny from 78 (number of genera $-$ 1) to 64. Tests were performed counting only polyploidization events within Maloideae and also interpreting all of Maloideae ($n = 17$) as a large allopolyploid clade sister to diploid ($n = 9$) *Gillenia* (Evans and Campbell 2002).

Nonnested Sister-Group Comparisons

To test whether polyploid clades experience increased diversification rates over their diploid counterparts (i.e., fig. 1B), we used nonnested sister-group comparisons. In this analysis, contrasts between SR were performed on only the subset of rosaceous clades where we either knew (in the case of monotypic clades) or estimated (see above) that one clade consisted entirely of polyploid species and its sister group consisted entirely of diploid species (table 1). Nonnested sister-group comparisons represent a far more direct test of whether clades with a certain trait (e.g., polyploid genome) experience heightened evolutionary success (Heilbuth 2000). If polyploidy does result in increased cladogenesis, the signature of this process should be apparent, notwithstanding the inevitably incomplete sampling of taxa for phylogenetic analysis (Ree 2005), because more polyploid species than diploid species will be sampled for phylogenetic analysis and these polyploid species will appear clustered together in large clades on the resulting tree. We tested whether the ratio of species numbers in sister-group pairs of polyploid and diploid clades departs significantly from 1 : 1, using a Wilcoxon signed-rank test (Barraclough et al. 1995; Vamosi and Vamosi 2005).

Correlations of Polyploidy

To address whether polyploidy is associated with clades that have high SR (removing the contribution of polyploidization), we calculated the number of diploid species in each

Table 1

Results of a Sister-Group Comparison of Completely Polyploid Clades and Completely Diploid Clades

Polyploid clade	No. of species	Diploid clade	No. of species	References[a]	Proportion
Amelanchier arborea + *A. canadensis* +					
A. lucida + *A. nantucketensis* + *A. stolonifera*	5	*Amelanchier bartramiana*	1	1	0.83
Dasiphora	26	*Chamaerhodos* + *Drymocallis*	35	2	0.43
Maloideae	≥558	*Gillenia*	2	3	0.99
Prinsepia	3	*Exochorda*	4	4	0.43
Prunus serotina	1	*Prunus mahaleb*	1	4	0.50
Rubus saxatilis	1	*Rubus idaeus*	1	5	0.50
Potentilla tridentata (syn. *Sibbaldiopsis*					
tridentata)	1	*Sibbaldia*	17	2	0.06
Sorbaria	4	*Chamaebatiaria*	1	6	0.80

Note. Comparison uses a Wilcoxon signed-rank test (Barraclough et al. 1995). The proportion of the species in the polyploid clade, listed in the last column, is not significantly different from 0.5 (the null distribution of diploid and polyploid clades diversifying at a 1 : 1 ratio; $P = 0.66$), indicating that, in general, polyploid and diploid clades diversify at equivalent rates.

[a] 1 = Campbell et al. 1997; 2 = Eriksson et al. 2003; 3 = Evans and Campbell 2002; 4 = Bortiri et al. 2001; 5 = Alice and Campbell 1999; 6 = Potter et al. 2002.

genus by subtracting the estimated number of polyploid species from the total SR of the genus. Then we determined whether an association exists between the percentage of polyploid species and the diploid SR, using traditional (nonphylogenetic) analysis by least squares regression of the proportions of polyploid species on the log-transformed number of estimated diploid species. To examine whether herbaceous growth habit, in particular, could influence the SR of highly polyploid clades, we tested whether an association exists between herbaceous growth habit and (1) diversification rate (using MacroCAIC, ver. 1.0.1) and (2) percent polyploidy (using CAIC, ver. 2.6.9; Purvis and Rambaut 1995).

Results

Species Richness and Polyploidy

Traditional (i.e., nonphylogenetic) and phylogenetic analyses revealed similar relationships between percent polyploidy and SR. In agreement with previous studies, the nonphylogenetic analysis demonstrated that SR does indeed increase with the proportion of polyploid species in Rosaceae ($F_{3,75} = 17.75$, $P < 0.0001$; fig. 2). Peak SR, however, appears to be associated with genera possessing intermediate levels of polyploidy (i.e., percent of polyploid species between 25% and 75%) rather than those with greater degrees of polyploidy (fig. 2). After removing polytomies, our analysis of a large-scale phylogeny (fig. 3; appendix) for Rosaceae using MacroCAIC examined the potential contrasts at 64 nodes in the tree. When sister groups have identical degrees of polyploidy, the contrast is, of course, zero, and the sister groups are treated as a single clade in comparisons deeper in the tree. Using the 50 nonzero contrasts in the tree, this analysis reveals that clades with higher proportion of polyploidy do have, on average, greater SR than their sister groups (36 positive vs. 14 negative contrasts; two-tailed sign test, $P = 0.003$). Qualitatively similar though nonsignificant results are obtained if we assume that all species of the genera within Maloideae are allopolyploid (21 positive vs. 11 negative contrasts; $P = 0.11$). This effect on diversification was obtained despite efforts to

rule out the possible influences of apomixis and estimate the SR of polyploid clades conservatively.

Nonnested Sister-Group Comparisons

There were 59 genera in our data set that were estimated to be either entirely diploid or entirely polyploid. In a comparison using only these genera, polyploid genera appear to have marginally greater SR ($F_{1,57} = 3.52$, $P = 0.06$). However, despite the indications from this nonphylogenetic analysis, increased diversification of polyploid clades does not appear to be a large factor contributing to the larger size of clades with high proportions of polyploid species. Our comprehensive search of phylogenies for Rosaceae turned up very few instances where an entirely polyploid clade was sister to an entirely diploid clade. The strong phylogenetic signal of polyploidy can be seen in figure 3 (i.e., polyploid genera tend
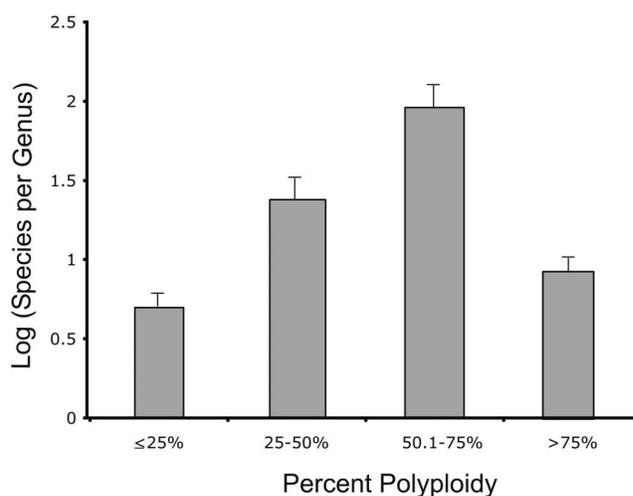
Fig. 2 Nonphylogenetic analysis of the means and standard errors of species richness (measured in log (species per genus)) of broad-scale groupings (based on estimates of the percent of species in the genus that are polyploid) of Rosaceae genera.
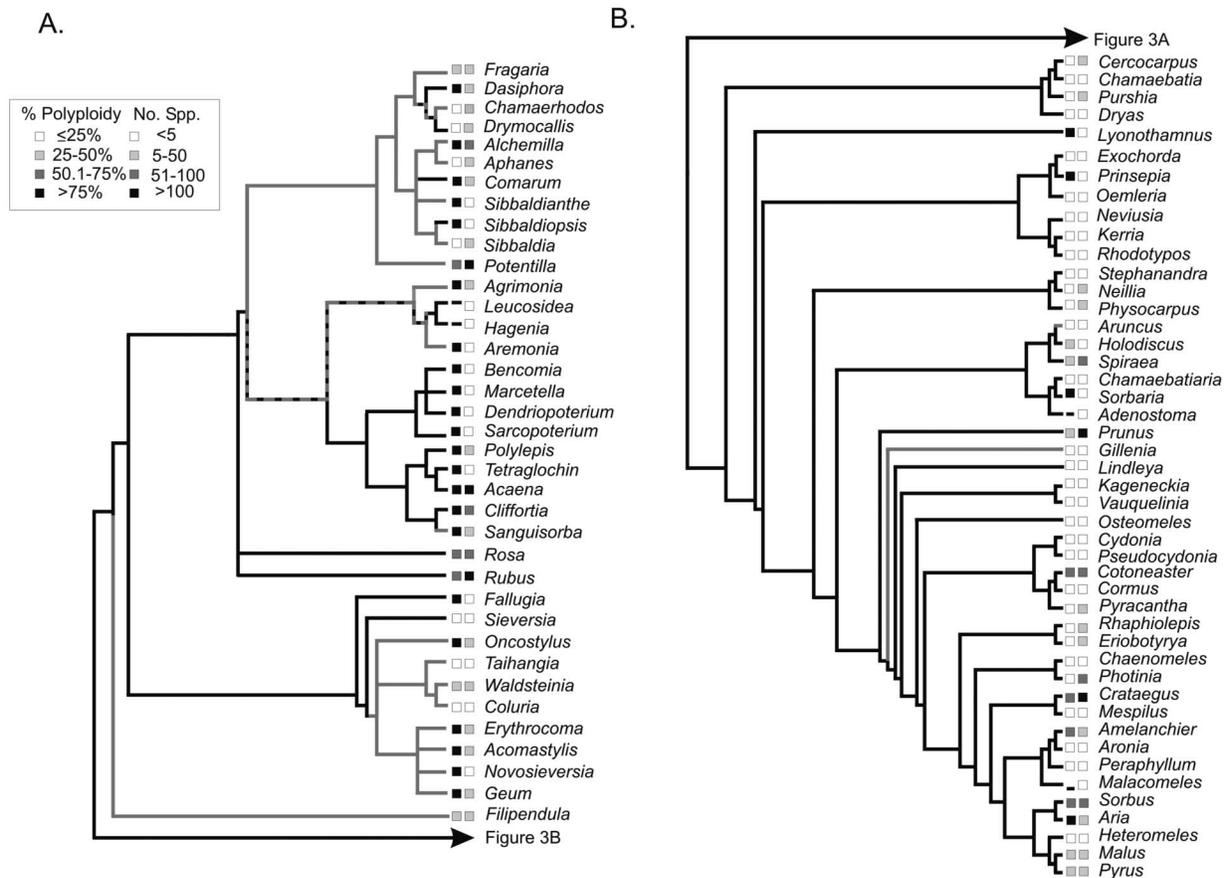
Fig. 3 Composite tree of Rosaceae. Black branches depict woody lineages, and gray branches depict herbaceous lineages (parsimoniously equivocal ancestral reconstructions are represented by dashed branches). Boxes to the right of the genus names indicate the following: first column, the proportion of polyploid species within the genus (dashes indicate genera for which no information on ploidy is available); second column, the number of species in the genus. See appendix for exact values for each genus.

to group together to form clades). Furthermore, within phylogenies of genera that have both polyploid and diploid members (e.g., *Amelanchier*, *Prunus*, and *Rubus*), the majority of polyploid lineages consisted of one to a few species that are sister to a similar number of diploid species. However, even when we interpret Maloideae as a large allopolyploid clade sister to diploid *Gillenia*, a sister-group comparison of exclusively polyploid clades and their exclusively diploid sister groups did not detect significantly greater SR in polyploid clades (Wilcoxon signed-rank test, $P = 0.66$; table 1). Caution must be exercised in interpreting the results because sample size was low ($n = 8$ sister-group comparisons), and incomplete sampling of phylogenies may not place polyploid clades with their true sister groups. Nevertheless, we posit that there is little evidence to suggest that polyploid clades generally experience higher rates of speciation or lower rates of extinction (fig. 1*B*).

Correlations of Polyploidy

Using the subset of genera that have at least one diploid species, we found a positive relationship between percent polyploidy and the number of diploid species in a nonphylogenetic analysis ($F_{1,54} = 12.73$, $P = 0.001$). This relationship indicates that polyploidization may occur more often in clades that are larger for unrelated reasons (fig. 1*C*). A herbaceous habit is unlikely to be the causative factor, however, because polyploidy was not found to be significantly associated with this trait in Rosaceae (clades with more herbaceous representatives had less polyploidy in 18 out of 26 contrasts; two-tailed sign test, $P = 0.08$; fig. 3). Furthermore, it is unlikely that an association with growth habit would cause an apparent correlation between polyploidy and SR, because growth habit showed no significant relationship with SR (in only 16 out of 28 contrasts were the more herbaceous clades also more species rich than their sister groups; two-tailed sign test, $P = 0.57$).

Discussion

This study represents the first formal comparative phylogenetic analysis of the association between polyploidy and SR. This study gathers further evidence that polyploidy is associated with increased SR, agreeing with the results of Petit and Thompson (1999) and Otto and Whitton (2000). Clades with higher degrees of polyploidy were larger than their sister groups even when phylogenetic relationships and apomixis

(agamospermy) were taken into account. Using a large phylogeny of Rosaceae and methods for phylogenetically controlled comparisons, we find that diversification is indeed higher in clades with more polyploid species. The question of why clades with more polyploid species are more species rich appears to have little to do with polyploid clades experiencing increased evolutionary success. We found no evidence to support the prediction that completely polyploid taxa are species rich compared with their diploid sister groups. Finally, the percentage of polyploid species in a genus shows a positive relationship with the number of diploid species in a genus, indicating that the pattern may be caused by other unknown traits that may concurrently encourage polyploidization and spur diversification. One such trait that could potentially encourage both SR and polyploidy is herbaceous growth habit, but we found no evidence for a correlation between growth habit and either polyploidy or SR within Rosaceae.

We posit that the greater SR in predominantly polyploid clades occurs because (1) some clades experience polyploidization events more frequently, and these events lead to speciation events, and (2) these polyploidization events may occur more frequently in clades that are already diversifying at high rates (i.e., fig. 1A, 1C). Analysis of species-level phylogenies indicates that many speciation events are associated with a change in ploidy levels. For example, ploidy was determined to change seven times in a phylogeny of 20 species of the *Geum* complex (Smedmark and Eriksson 2002), eight times in a phylogeny of 40 species of *Rubus* (Alice and Campbell 1999), and even more than once within a single species of *Heuchera* (Segraves et al. 1999). It is likely that, as more complete phylogenies are created, estimates of the number of polyploidization events within angiosperms will increase.

For the first time, we report that a correlation exists between polyploidy and an already elevated diversification rate (i.e., lineages with a high number of diploid species have disproportionately more polyploid species). Although woodiness was not shown to affect the proportion of polyploid species in our analysis, other traits are likely to play a role in this heterogeneity in polyploidization events. Polyploidy is more prevalent at high altitudes and high latitudes and in areas of recent glaciation (Otto and Whitton 2000; Brochmann et al. 2004). Polyploidy is associated with self-compatibility and with the ability to enter into interspecific crosses (Grant 1971; Ramsey and Schemske 1998). Neither high latitude (e.g., Martin and McKay 2004) nor self-compatibility (Heilbuth 2000; Igic et al. 2004) has been correlated with increased diversification in angiosperms, making it unlikely that the connection between high SR and polyploidy could be entirely due to these two traits. The correlation between altitude and polyploidy, on the other hand, may contribute to a perceived correlation of polyploidy and SR, as mountainous regions have higher SR than flatlands (Stohlgren et al. 2005), potentially because of speciation events caused by the migration of populations to isolated peaks (Schluter and Ricklefs 1993). There may thus be complex interactions between environmental heterogeneity in space (Stohlgren et al. 2005) and time (e.g., deglaciation; Kadereit et al. 2004), high SR, and polyploidy within angiosperm lineages.

Our sister-group comparison of exclusively polyploid clades and exclusively diploid clades found no trend for increased speciation of polyploid clades, although, admittedly, sample size was low. To some degree, the dearth of comparisons found may be due to the very nature of polyploidization. When allopolyploidization occurs through the hybridization of two species, the resulting clade is sister to both ancestral species (Smedmark et al. 2003), and no clear comparison in SR can be made. Although there is no evidence that polyploid clades diversify more than their diploid sister groups, there is also no evidence that they diversify less. In other words, polyploidy may be neither the evolutionary dead end imagined by Stebbins (1950) nor a key innovation. Our results are consistent with previous work on the ecological interactions of polyploid and diploid sister taxa indicating that, although interactions with pollinators and herbivores differ between these two ploidy levels, there is no directional superiority of one ploidy level over the other (Thompson et al. 1997; Segraves and Thompson 1999). Because polyploid species do not appear to experience heightened extinction rates, the creation of species via polyploidization is magnified through time because clades that undergo polyploidization will later experience allopatric speciation at the same rate as their diploid sister clades. Finally, we were not able to distinguish between allopolyploid and autopolyploid lineages in this analysis. Allopolyploidy (originating from the hybridization of two species) and autopolyploidy (duplication of a single species' genome) both increase the number of chromosomes, but the potential for further evolution after the polyploidization may differ significantly. A newly formed allopolyploid species, for instance, has a much larger potential variation than an autopolyploid, and this may affect whether polyploidization increases diversification.

Polyploidy was not associated with growth form, and growth form does not appear to be responsible for differences in SR heterogeneity in Rosaceae. Our findings of herbaceous and woody rosaceous clades experiencing equivalent diversification are in stark contrast to that found by Dodd et al. (1999). Admittedly, our comparisons did not take into account the presence of woody underground structures (e.g., caudices, rhizomes) that are often present in perennial herbs in Rosaceae. The presence of many long-lived perennial herbs in our study compared with previous studies (Verdú 2002) may have resulted in comparisons between woody and herbaceous clades with similar ages to maturity. Our data certainly seem to indicate that the presence of a vascular cambium (either in above- or belowground woody structures) does not impede the establishment of polyploidy, as Stebbins (1938) suggested, because large proportions of polyploidy are often observed in predominantly woody clades (e.g., *Rubus*, *Rosa*; fig. 3). Whether polyploidy is most common among perennial herbs has been refuted by other recent studies that take phylogeny into account as well (Tate and Simpson 2003). Further broad-scale comparative studies may reveal that polyploidy is equally prevalent among lineages with diverse life histories and ecological traits.

In summary, phylogenetic analysis confirms previous assertions that polyploidy is associated with heightened SR (Petit and Thompson 1999; Otto and Whitton 2000). However, our investigation into the cause of this association indicates that polyploid clades appear to experience diversification rates equivalent to those of diploid clades. Thus, the simplest

explanation for the observation that clades with high proportions of polyploid species tend to be species rich is that each polyploidization event produces an additional species. Another potential cause of the correlation between SR and polyploidy revealed by our study is that polyploidization events may occur disproportionately more often in clades that already have a higher number of species, because of underlying traits that encourage polyploidy and diversification. Growth form was ruled out by our analysis as the cause of this pattern in Rosaceae, although many other traits could be potentially responsible. Further work investigating range size and temperature tolerance may reveal patterns of concurrent increases in polyploidization and diversification rates.

Acknowledgments

Appendix

Table A1

Percent Polyploidy, Species Richness, and Growth Form in the Genera Used in This Study

Genus	Percent polyploid	Species richness	Herbaceous?
Acaena	100	110	N
Acomastylis	100	12	Y
Adenostoma	?	3	N
Agrimonia	100	13	Y
Alchemilla	100	60 (190)	Y
Amelanchier	60	15 (5)	N
Aphanes	0	20 (1)	Y
Aremonia	100	1	Y
Aria[a]	50	49 (1)	Y
Aronia[b]	0	2	N
Aruncus	0	1	Y
Bencomia[c]	100	4	N
Cercocarpus	0	5	N
Chaenomeles	0	3	N
Chamaebatia	0	1	N
Chamaebatiaria	0	1	N
Chamaerhodos	0	5	Y
Cliffortia	100	100	N
Coluria[d]	0	4	Y
Comarum[e]	1	5	N
Cormus	0	1	N
Cotoneaster	72	60 (23)	N
Crataegus	65	168 (19)	N
Cydonia	0	1	N
Dasiphora[e]	100	26	N
Dendriopoterium[c]	100	1	N
Dryas	0	2	N
Drymocallis[e]	0	30	N
Eriobotyrya	0	18	N
Erythrocoma[d]	100	6	Y
Exochorda	0	4	N
Fallugia	100	1	N
Filipendula	43	15	Y
Fragaria	47	10 (1)	Y
Geum	94	30	Y
Gillenia	0	2	Y
Hagenia	?	1	N
Heteromeles	0	1	N
Holodiscus	50	2	N
Kageneckia	0	3	N
Kerria	0	1	N
Leucosidea	?	1	N
Lindleya	0	1	N
Lyonothamnus	100	1	N
Malacomeles	?	2	N

Table A1

(*Continued*)

Genus	Percent polyploid	Species richness	Herbaceous?
Malus	46	31 (9)	N
Marcetella[c]	100	2	N
Mespilus	0	1	N
Neillia	0	12	N
Neviusia	0	2	N
Novosieversia[d]	100	1	Y
Oemleria	0	1	N
Oncostylus[d]	100	5	Y
Osteomeles	0	1	N
Peraphyllum	0	1	N
Photinia	0	60	N
Physocarpus	17	6	N
Polylepis[c]	100	20	N
Potentilla	55	117 (83)	Y
Prinsepia	100	3	N
Prunus	34	200	N
Pseudocydonia	0	1	N
Purshia (includes *Cowania*)	0	8	N
Pyracantha	0	3	N
Pyrus	20	15	N
Rhaphiolepis	0	5	N
Rhodotypos	0	1	N
Rosa	58	95 (4)	N
Rubus	60	232 (132)	N
Sanguisorba	93	15	Y
Sarcopoterium	100	1	N
Sibbaldia[e]	0	17	Y
Sibbaldianthe	100	3	Y
Sibbaldiopsis[e]	100	1	N
Sieversia[d]	0	2	Y
Sorbaria	100	4	N
Sorbus	59	80 (38)	N
Spiraea	50	80	N
Stephanandra	0	3	N
Taihangia	0	1	Y
Tetraglochin	100	4	N
Vauquelinia	0	3	N
Waldsteinia	40	5	Y

Note. Numbers in parentheses reflect the number of estimated apomictic species in the genus (where there is evidence available), which has been subtracted from the number for species richness reported by Kalkman (2004). Species that are polymorphic for ploidy were interpreted to be diploid, and genera with unknown ploidy are indicated by question marks. In cases where information on species richness and/or ploidy could not be found in Kalkman (2004) or Goldblatt and Johnson (2003), the source is given in a footnote.

[a] Nelson-Jones et al. (2002).
[b] Hovalm et al. (2004).
[c] Helfgott et al. (2000).
[d] Smedmark and Eriksson (2002).
[e] Eriksson et al. (1998).

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