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COMPARATIVE EVIDENCE FOR THE CORRELATED EVOLUTION OF POLYPLOIDY AND SELF-COMPATIBILITY IN SOLANACEAE

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Breakdown of self-incompatibility occurs repeatedly in flowering plants with important evolutionary consequences. In plant families in which self-incompatibility is mediated by S-RNases, previous evidence suggests that polyploidy may often directly cause self-compatibility through the formation of diploid pollen grains. We use three approaches to examine relationships between self-incompatibility and ploidy. First, we test whether evolution of self-compatibility and polyploidy is correlated in the nightshade family (Solanaceae), and find the expected close association between polyploidy and self-compatibility. Second, we compare the rate of breakdown of self-incompatibility in the absence of polyploidy against the rate of breakdown that arises as a byproduct of polyploidization, and we find the former to be greater. Third, we apply a novel extension to these methods to show that the relative magnitudes of the macroevolutionary pathways leading to self-compatible polyploids are time dependent. Over small time intervals, the direct pathway from self-incompatible diploids is dominant, whereas the pathway through self-compatible diploids prevails over longer time scales. This pathway analysis is broadly applicable to models of character evolution in which sequential combinations of rates are compared. Finally, given the strong evidence for both irreversibility of the loss of self-incompatibility in the family and the significant association between self-compatibility and polyploidy, we argue that ancient polyploidy is highly unlikely to have occurred within the Solanaceae, contrary to previous claims based on genomic analyses.

KEY WORDS: **Angiosperms, breeding systems, comparative methods, polyploidy, self-incompatibility, statistical phylogenetics.**

Self-incompatibility (SI) is the common ability of hermaphrodite plants to recognize and reject their own pollen with a genetically based mechanism. Approximately one-half of all extant angiosperm species prevent self-fertilization by deploying SI (Brewbaker 1959; Igić and Kohn 2006). Although many different mechanisms of SI evolved in flowering plants, a particular system, which uses RNases in the female component of self-rejection, appears to be ancient. It likely originated at least 90 million years ago (mya), and it may cause SI in dozens of extant eudicot families, including some of the most diverse (Igić et al. 2008). A notable property of SI systems is the high rate at which they transition to self-compatibility (SC), considered one of the most common evolutionary transitions in plants (Stebbins 1974). Consequently, many individuals, populations, and species do not express SI. Empirical data on the mechanisms that underlie losses of SI are sparse. Although the genetic causes of transitions from SI to SC vary widely (Stone 2002), a significant proportion of such transitions may involve polyploidization (Livermore and Johnstone 1940; Crane and Lewis 1942; Stout and Chandler 1942; Lewis 1947; Brewbaker 1954; Pandey 1968; Charlesworth 1985; Chawla et al. 1997; Entani et al. 1999; Miller and Venable 2000).

Polyploidy is the duplication of an entire genome, resulting in three or more chromosome sets (Grant 1971). Polyploidy is thought to be common within angiosperms (20–89%; Stebbins 1950; Masterson 1994), although estimates vary widely depending on classification criteria and ability to separate recent from ancient duplication events. Traditionally, estimates of polyploid frequency were calculated using the inferred chromosome number for a particular group (Stebbins 1938) or angiosperms as a whole (Grant 1963; Goldblatt 1980; Masterson 1994). However, polyploids may undergo genetic rearrangements, selective gene loss, and rediploidization over time (Wolfe 2001), precluding cytological diagnoses of polyploid events over deeper evolutionary time scales (Otto and Whitton 2000; Byrne and Blanc 2006). The advent of genomic sequence data has enabled detection of multiple likely ancient polyploidization events in flowering plants (Ku et al. 2000; Blanc et al. 2000, 2003; Paterson et al. 2000; Vision et al. 2000; Simillion et al. 2002; Bowers et al. 2003; Blanc and Wolfe 2004; Schlueter et al. 2004; Barker et al. 2008). In part as a result of these studies, it is widely held that nearly all angiosperms may have undergone a polyploid event in their evolutionary history (Soltis et al. 2009). Sequence-based methods to detect ancient polyploidy generally estimate the ages of paralogous sequences, measured as the number of synonymous substitutions per site. A whole-genome duplication event is expected to produce a detectable peak of sequence similarity approximating the time of the duplication event (Lynch and Conery 2000, 2003). Other methods infer genome duplications from comparative study of microsynteny. Such studies use long sequence reads to seek out duplicated regions with identical or similar gene order (e.g., Vision et al. 2000). The association between polyploidy and the radiation of early angiosperm lineages may suggest a causal positive association between polyploidy and diversification rate (reviewed in Soltis et al. 2009; but see Meyers and Levin 2006). The causes may be related to the number of genotypic and phenotypic changes associated with polyploidy, including changes in morphology, phenology and life-history characteristics (Levin 1983; Ramsey and Schemske 2002), wider ecological tolerances—perhaps leading to an increase in range size (Grant 1971; Levin 1983; Hijmans et al. 2007)—as well as the formation of new gene complexes (Wendel 2000). Because of their far-reaching effects, we are most interested in alterations to the breeding and mating system, specifically, the increased propensity of polyploids to self-fertilize (Lewis 1943, 1947; Brewbaker 1953, 1954, 1958; Pandey 1968; de Nettancourt et al. 1974; Miller and Venable 2000; Barringer 2007; Husband et al. 2008).

The evolutionary link between mating system and ploidy was proposed and empirically investigated at least since Stebbins (1950, 1957) and Grant (1956), who found a strong association between polyploidy and self-fertilization. Phylogenetic comparative studies also find some evidence for the correlated evolution of selfing and ploidy (Barringer 2007; Husband et al. 2008). Theoretical models predict that this association principally depends on the ability of polyploidy to ameliorate the expression of inbreeding depression, as well as the effect of mating system on the rate of polyploid formation and establishment (reviewed in Ramsey and Schemske 1998; Barringer 2007; Husband et al. 2008). A positive correlation may, however, result directly from the genome duplication process itself, at least in families with gametophytic SI (Livermore and Johnstone 1940; Crane and Lewis 1942; Stout and Chandler 1942; Lewis 1947; Brewbaker 1954; Pandey 1968). Evidence from both natural and experimentally induced tetraploids from several families, including Rosaceae, Fabaceae, Onagraceae, and Solanaceae, suggests that polyploidy almost invariably disrupts GSI (reviewed in Ramsey and Schemske 1998; Stone 2002). Lewis (1947) observed that the diploid pollen heterozygous at the S-locus, often termed "heteroallelic," was not degraded, whereas the diploid pollen homozygous at the S-locus was rejected via a normal SI response. A suite of observational and experimental data subsequently led to the modification and generation of several models, which aim to explain the molecular physiological mechanism of RNase-based SI (RSI; reviewed in Hua et al. 2008; McClure 2009). The tendency of polyploidization to break down SI is so well established that the models are constructed specifically around the ability to explain it as a byproduct of the proposed mechanism McClure (2009).

However, a broad comparative study did not find evidence for a correlation between ploidy and SI among all SI systems (Mable 2004). The relationship was significant within groups with gametophytic SI, in which the pollen phenotype is determined by its own haplotype (RSI is one subtype of gametophytic SI systems). It appears that groups with sporophytic SI, in which the pollen phenotype is determined by the maternal genotype, show no such pattern and reduce the power of the combined analysis. In a separate study, Miller and Venable (2000) found strong support for a similar pattern of association within gametophytic SI in a study of the evolution of gender dimorphism. Nevertheless, although they are rare, exceptions exist. In the Rosaceae family, where RSI is common and generally appears associated with diploid species, at least three tetraploid species, *Prunus cerasus, P. spinosa* and *P. fruticosa*, express a functional SI response in heteroallelic pollen (Hauck et al. 2002, 2006; Nunes et al. 2006; Huang et al. 2008; Vieira et al. 2008).

Here, we conduct combined analyses of ploidy and breeding system character evolution, aimed at detecting whether the two characters evolve in a correlated manner. Our study relies on a large comparative dataset to assess the strength of this association within the Solanaceae. We infer the relative rates of breakdown of SI due to polyploidization and other mechanisms, which do not involve genome duplication. Because polyploids can arise on the background of SC or SI, we also compare the magnitudes

of transitions leading to polyploidy. In the process, we propose and use a novel general method to quantify the contributions of pathways of sequential character state changes involved in generating a strong association between polyploidy and SC.

Methods

STUDY SYSTEM

Solanaceae, the nightshade family, contains approximately 2700 species (Olmstead and Bohs 2007), many of which are of considerable agricultural importance (e.g., tomato, potato, eggplant, tobacco, petunia). Partly due to its economic value, the group enjoys a rich tradition in cytogenetic and breeding system studies. There is a wealth of available karyotype data, and the family has long been a model system for study of the genetic basis of SI (East and Mangelsdorf 1925). This group is presently the subject of a large collaborative effort aimed at gaining detailed understanding of phylogenetic relationships among its species (Olmstead and Bohs 2007). In all of the analyses presented below, we rely substantially on such sources of previously generated data.

DATA COLLECTION AND CHARACTER CODING

Self-incompatibility

Taxa were scored as SC or SI based on papers found through extensive searches of the primary literature, and as reported in Igić et al. (2006). We searched the online databases *ISI Web of Knowledge Science Citation Index*^{TM} and the *Google Scholar* (http://www.google.com/schhp) using dozens of search terms related to plant breeding systems and names of taxa. Our search included papers published through 2009. In addition, we used a personal library of reprints (B.I.) with books, monographs, and manuscripts about Solanaceae species, dating from about 1850 through 1995. A vast proportion of designations was made by the authors of the original studies. Occasionally, the authors did not designate a taxon as SC or SI but provided sufficient information for the calculation of the index of self-incompatibility (ISI), a measure of the relative success of manually performed self- and cross-pollinations (Lloyd 1965; Bawa 1974). We employ the relative number of fruits per flower after each pollination treatment as a metric of fertilization success. The ratio of fruit set after self- versus cross-fertilization is subtracted from unity, resulting in a continuous index of values that encompasses all possible strengths of SI. Thus, the metric of ISI is calculated as

$$ISI = 1 - \frac{\text{relative selfed success}}{\text{relative outcrossed success}}.$$

The upper bound is unity (complete SI), but when self-pollinations result in higher fruit set than cross-pollinations, it is possible to obtain negative ISI values. Historically, species with ISI values above 0.8 have been classified as SI (Bawa 1974). Because of the relative dearth of species with intermediate values of ISI, classification is largely insensitive to the exact cut-off value in most angiosperm families studied to date (A. Raduski and B. Igić, unpubl. data).

Ploidy

Taxa were scored as diploid (D) or polyploid (P) based on reports from both haploid and somatic chromosome counts in the Index to Plant Chromosome Number (http://mobot.mobot.org/W3T/Search/ipcn.html) and the Royal Botanical Gardens, Kew (http://www.kew.org) online databases as well as the primary literature (see above). The scoring criterion was based on the inferred basal chromosome number for the taxonomic group in question.

Members of the subfamily Solanoideae, the tribe Anthocercideae, and the genus *Nicotiana* form a monophyletic group with the base chromosome number x = 12 (Olmstead and Palmer 1992; Olmstead and Sweere 1994; Olmstead et al. 2008). Within the Solanoideae, species in *Capsicum, Chamaesaracha, Datura, Dunalia, Dyssochroma, Grabowskia, Iochroma, Jaltomata, Lycianthes, Lycium, Mandragora, Nicandra, Nolana, Nothocestrum, Phrodus, Physalis, Salpichroa, Solandra, Solanum, Vassobia, Withania*, and *Witheringia* were scored as diploid when the somatic chromosome number ranged from $2n = 16$–24, and polyploid when the somatic chromosome numbers ranged from $2n = 34$–96. Also part of the Solanoideae subfamily is the tribe Hyoscyameae, containing the genera *Anisodus, Atropa, Atropanthe, Hyoscyamus, Physochlaina, Przewalskia,* and *Scopolia*. The genera *Anisodus* and *Atropa* are reported as having a base chromosome number of x = 6 (Tu et al. 2005) or x = 12 (Olmstead and Palmer 1992; Badr et al. 1997; Olmstead et al. 1999). We encoded all *Anisodus* and *Atropa* species as polyploid because they had somatic chromosome numbers in excess of $2n = 48$. The genus *Hyoscyamus* has a base chromosome number $x = 14,17$ (Tu et al. 2005). Species with chromosome counts $2n = 28$, 34 were scored as diploid, whereas the species *H. albus* and *H. pusilus* with somatic chromosome counts equal to $2n = 68$ (Goldblatt and Johnson 1979), were scored as polyploid. The remaining genera in the Hyoscyameae, *Atropanthe, Physochlaina, Przewalskia*, and *Scopolia* have somatic chromosome counts ranging from $2n =$ 42–48 (Tu et al. 2005), and were therefore encoded as polyploid. Within the tribe Anthocercideae, species in the genera *Crenidum, Duboisia, Grammosolen*, and *Symonanthus* have somatic chromosome numbers ranging from $2n = 60$–102 (Darlington and Wylie 1956; Goldblatt and Johnson 1979), and were encoded as polyploid. The genus *Nicotiana* forms a dysploid series with basal chromosome numbers ranging from $x = 7$–12. Species in this genus were encoded as diploid or polyploid based on Goodspeed (1954).

In the tribe Petunieae, *Hunzikera* and *Nierembergia* have somatic chromosome numbers $2n = 32$ and $2n = 36$, respectively

(Acosta et al. 2006). We encoded these species as polyploid because other genera in this group have low haploid chromosome numbers; $n = 7$–11 in *Petunia, Bouchetia, Calibrachoa, Fabiana, Leptoglossis*, and *Brunfelsia* (Goldblatt and Johnson 1979).

In the subfamily Cestroideae, species in the genera *Browalia, Cestrum, Salpiglossis, Sesseae, Streptosolen*, and *Vestia* were scored as diploid when somatic chromosome numbers ranged from $2n = 16$–22 (Olmstead et al. 2008). The only species scored as a polyploid in this group, *Browalia speciosa*, has a somatic chromosome number $2n = 44$ (Welsh and Sink 1981). In tribe Benthamiellieae, which is likely sister to the Cestroideae (Olmstead et al. 2008), species in the genera *Benthamiella, Combera*, and *Pantacantha* have somatic chromosome counts $2n = 22$ (Goldblatt and Johnson 1979) and were scored as diploids. No polyploids were found within Benthamiellieae.

The remaining genera with available ploidy information are *Schizanthus* and *Schwenckia*. *Schwenckia* is part of a polytomy with the "$x = 12$" clade (containing the subfamily Solanoideae and the tribe Anthocercideae), the subfamily Cestroideae, and the Petunieae tribe (Olmstead et al. 2008). *Schwenckia browallioides* has a somatic chromosome number $2n = 24$ (Goldblatt and Johnson 1979), and was scored as a diploid. *Schizanthus* forms a sister group to the rest of Solanaceae. *Schizanthus grahamii* and *Schizanthus pinnatus* have somatic chromosome counts of $2n = 20$ (Gaiser 1926; Goldblatt and Johnson 1979), and were both scored as diploids.

Conflicting report

We closely tracked potential errors in reports for the breeding system and ploidy character states. Of hundreds of studies, we found that the information from a single study is consistently in conflict with others. Marks (1965) lists several species as SI in *Solanum* section *Petota*. Specifically, the polyploid *S. agrimoniifolium* Rybd., *S. colombianum* Dun. (syn. *S. moscopanum* Hawkes), *S. oxycarpum* Schiede, *S. stoloniferum* Schltdl. (syn. *S. polytrichon* Rybd), *S. iopetalum* (Bitt.) Hawkes, *S. guerreroense* Corr., and *S. hougasii* Corr. are listed as SI. Instead, these are listed as SC in a minimum of two independent sources (see Table S1 for complete listing of SI-SC and D-P character state data for taxa used in this study). We omitted all data from Marks (1965) because the criterion used for SI determination was failure of fruit set after hand self-pollination, yet these plants autonomously set fruit in the greenhouse with high seed set. Although it is possible, and sometimes observed, that SI species set selfed fruit, it is typically seedless (parthenocarpic), which is inconsistent with the data obtained by Marks. Other reports not included in this study are from the sterile triploids *Solanum commersonii, S. cardiophyllum,* and *S. maglia* (Correll 1962; Hawkes and Hjerting 1969).

Polymorphisms

It is widely held that ploidy and breeding system frequently transition between states, mostly unidirectionally (Stebbins 1974; Meyers and Levin 2006). This is presumably because the mutation rates that generate polyploids and SC, as well as the conditions for fixation of these mutations in plant lineages (evolutionary transitions), are not limiting. The high magnitude and directionality of the two processes are thought to result in the commonly observed pattern of occurrence of rare SC individuals in otherwise SI populations (Rick and Tanksley 1981; Rick 1986; Ando et al. 1998; Bohs 2000), and polyploid individuals in otherwise diploid populations (Lewis and Suda 1976; Halverson et al. 2008). Thus, a major difficulty in determining the correlation of ploidy and SI/SC state is that these traits are rarely measured in the same individual or population. As our analysis is designed to determine the correlation of character state transitions at the species level, not the frequency (and correlation) of the initial mutations, we systematically eliminated polymorphisms for data with phylogenetic information. SI species in which rare SC individuals are found, without strong evidence for local fixation, were encoded as SI (*Capsicum pubescens, Nicotiana glauca, N. langsdorfii, Petunia axillaris, P. reitzii, Solanum arcanum, S. chilense, S. habrochaites, S. pennellii, S. peruvianum, S. sisymbrifolium,* and *Witheringia solanacea*). Diploid species in which rare polyploid individuals are found were encoded as diploid (*Solanum campanulatum, S. cinereum, S. torvum, S. verrucosum* and *S. polyadenium*). *Solanum tuberosum, S. bulbocastanum* and *L. californicum* are polymorphic for both compatibility and ploidy. When the traits are measured in the same individual, SI segregates with the diploid cytotype and SC with the polyploid cytotype [e.g., *S. tuberosum*: SI-D (Kirch et al. 1989) and SC-P (Lewis 1943), *S. bulbocastanum*: SI-D and SC-P (Hermsen and Boer 1971), *L. californicum*: SI-D and SC-P (Yeung et al. 2005)]. We encoded these species as SI-D in our analysis, although the association of SC with the polyploid cytotype is itself suggestive of a causal relationship between SC and polyploidy.

NONPHYLOGENETIC ANALYSES OF CORRELATED CHARACTER EVOLUTION

We used a χ^2-test of association to investigate whether there is a relationship between ploidy and compatibility. We conducted association tests in both a 2×2 table, for which polymorphic species were collapsed into the SI and diploid category as described above, and in a 3×3 table, where they were encoded as a separate category. In the cases where the expected value for any cell was less than five, we applied the Yates' correction for continuity (Yates 1934). An assumption of the χ^2 test is that the data are independent, which is violated when species share ancestry (Felsenstein 1985; Pagel 1994). We use phylogenetic tests (described below) to allow for species relationships.

RECONSTRUCTION OF PHYLOGENETIC RELATIONSHIPS

We constructed a composite phylogenetic hypothesis from a skeletal family phylogeny (Olmstead et al. 2008) augmented by insertion of clades obtained from 18 fine-scale molecular phylogenetic studies (Spooner et al. 1992; Spooner et al. 1993; Mione et al. 1994; Mace et al. 1999; Peralta and Spooner 2001; Walsh and Hoot 2001; Clarkson et al. 2004; Ando et al. 2005; Levin and Miller 2005; Whitson and Manos 2005; Prohens et al. 2006; Levin et al. 2006; Montero-Castro et al. 2006; Perez et al. 2006; Smith and Baum 2006; Bohs 2007; Weese and Bohs 2007; Miller et al. 2008). We imposed the branching order found in strict consensus trees of the individual datasets listed above. Polytomies were randomly resolved to allow analyses that require bifurcating branching events.

Branch lengths proportional to time are not currently available from systematic studies of the family, and we consequently relied on two standard methods for assigning them. First, we set all branch lengths to 1, except for those introduced by resolving polytomies, which were set to 10^{-6}; we refer to this as the "unit" branch length assumption. Second, we used branch lengths computed from node depth with the algorithm described by Grafen (1989), with a root-to-tip time of one and a scaling power of $\rho = 1$. Neither of these methods is an entirely valid substitute for true branch lengths but, when paired, they stand in for a wide range of possibilities. Comparing results from the unit and Grafen assumptions is likely to give a strong indication of how robust our conclusions are to the lack of true branch lengths.

PHYLOGENETIC COMPARATIVE TESTS

Correlated evolution of self-incompatibility and polyploidy

Pagel's (1994) method detects correlated evolution between two discrete characters by comparing the likelihood of a character-dependent model to a model that allows characters to evolve independently. If the characters are evolving independently, the transition rates between states of one character are independent of the state of the other character. For example, the gain of polyploidy would occur at the same rate, irrespective of whether the species is SI or SC ($q_{12} = q_{34}$; Fig. 1). The model of independent evolution will then have four parameters estimated ($q_{12} = q_{34}$, $q_{21} = q_{43}$, $q_{13} = q_{24}$, $q_{31} = q_{42}$), and it is compared to an unconstrained model of correlated or dependent evolution where all eight rate parameters are estimated.

We fit parameter values in these two models using the Markov chain Monte Carlo method implemented in *BayesTraits Discrete*. (The settings detailed here were also used for the *Multistate* analysis described below.) We used an exponential hyperprior that was seeded uniformly between 0 and 100. The rate deviation was set to 0.1–0.3 (unit branch lengths) or 4–8 (Grafen branch lengths)

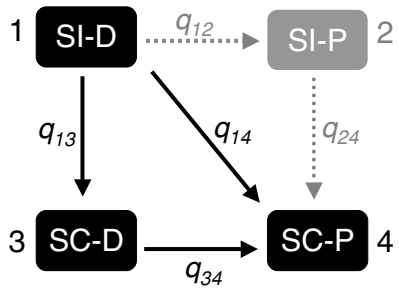

Figure 1. A schematic representation of the model of evolution for breeding system (SI vs. SC) and ploidy (D vs. P). Arrows forming the outer square represent the rates estimated in our *Discrete* model of character evolution (Pagel 1994). A model of correlated evolution estimates all eight rates independently (only the four forward rates q_{12}, q_{13}, q_{34}, and q_{24} are shown) and is compared to a model of independent evolution in which four rates are estimated (only the two forward rates $q_{12} = q_{34}$, $q_{13} = q_{24}$ are shown). The solid black arrows forming the lower left triangle represent the model of character evolution in the *Multistate* framework. SI-D = state *1*, SC-D = state *3*, SC-P = state *4*. SI-P = state *2* is not observed in our dataset and cannot be included in the *Multistate* framework.

to achieve the recommended acceptance rates of 20–40%. The "Pis" option, describing the prior state probabilities at the root, was set to "none" so that the likelihoods of each state at the root were added together. This setting yields the same ratio of likelihoods between different sets of rates as does the "uniform" weighting, and it provides the correct likelihood when only one root state is logically possible in the *Multistate* analysis. After a 50,000 generation burn-in period, the chain was sampled every 1000 generations over a total of 505,000 generations.

The weight of evidence used to evaluate the relative fit of the independent and correlated models was calculated with Bayes factors (*BF*; Kass and Raftery 1995), with the marginal likelihood of each model approximated by the harmonic mean of the likelihoods in the Markov chain, as recommended by the *BayesTraits* manual. For the test statistic 2 ln (*BF*), with the dependent model favored, a value between 2 and 5 provides "positive" evidence for correlated evolution, and a value of more than 10 provides "very strong" evidence (Raftery 1996, p. 165; Pagel and Meade 2006).

Transitions to self-compatibility

The rate parameters describing simultaneous dual transitions (between states 1 and 4, and between 2 and 3) are ordinarily set to zero because the probability of two separate events in a single instant is negligible (Pagel 1994). However, dual transitions are biologically realistic in this system because polyploidy directly breaks down incompatibility through the formation of diploid pollen grains. To allow dual transitions, we modeled the evolution of a single three-state character composed of compatibility

and ploidy: SI-D = state 1, SC-D = state 3, and SC-P = state 4 (see Fig. 1). There were no observations of SI-P (state 2). The *Multistate* model was used to compare the magnitudes of the transition rate parameters to determine the dominant means by which SI is lost and by which polyploidy arises.

We initially prohibited transitions from SC to SI when implementing the model because previous work on the evolution of SI demonstrates that the rates of reversal to SI from SC are negligible and not significantly different than zero (Igić et al. 2006). In Solanaceae, strong negative frequency-dependent selection yields dozens of alleles at the SI locus (S-locus). Every SI species of Solanaceae studied so far exhibits evidence of such ancient S-locus polymorphism, with coalescent times estimated at approximately 40–50 million years old (Ioerger et al. 1990; Igić et al. 2006; Paape et al. 2008). This feature of the S-locus provides powerful evidence for the continuous long-term persistence of SI since the common ancestor of all extant species (Igić et al. 2006). We incorporated these data in our model by setting the reversal transition rates, q_{31} and q_{41} to zero, but we also present results where reversals are allowed, for comparison. We also initially prohibit transitions from polyploidy to diploidy because polyploidy has long been thought to be a character whose evolution is exceptionally asymmetrical (Stebbins 1971, 1980; Bull and Charnov 1985; Meyers and Levin 2006). With the advent of genomic and phylogenetic methods to infer ancient polyploidization, numerous studies have found evidence for polyploid events within angiosperm lineages (reviewed in Soltis et al. 2009). However, within the Solanaceae, genomic evidence indicates there has been no duplication since the family diverged from the Rubiaceae (Lin et al. 2005; Wu et al. 2006) ca. 85 million years ago (Wikstrom et al. 2001). To implement irreversibility of polyploidization, we set the rates q_{43} and q_{41} to zero, but we again present results where reversals are allowed, for comparison.

Loss of SI can occur in diploid or polyploid lineages. To compare the frequencies of these two events, we used the *Multistate* model to compare the rate of SI loss in diploids (q_{13}), presumably occurring by mutations in genes that regulate or encode for components of SI pathway, to the rate of SI loss effected directly by polyploidization (q_{14}). The posterior distribution of the difference between these two rates allows a simple assessment of the magnitude of their difference.

Transitions to polyploidy

Under the assumptions of irreversibility of SC and polyploidy, the root of the tree must have been in state SI-D. Comparing the magnitudes of the different means by which polyploidy can be reached from that ancestral SI-D state is more complicated than directly comparing the transition rates q_{14} and q_{34} from the *Multistate* model because a state 1-to-3 transition must precede a state 3-to-4 transition. We therefore developed a method to compare the transition probabilities of the two routes to self-compatible polyploidy: pathway *14* is polyploidization from self-incompatibility (SI-D directly to SC-P), and pathway *134* is loss of self-incompatibility followed by polyploidization from SC (SI-D to SC-D to SC-P). Let $W_{14}(t)$ and $W_{134}(t)$ be the probabilities of transitions from SI-D to SC-P via pathway *14* and pathway *134*, respectively, after time t has elapsed. Derivation and explicit forms of $W_{14}(t)$ and $W_{134}(t)$ are shown in the Appendix. From the perspective of an extant SC-P species, the values of $W_{14}(t)$ and $W_{134}(t)$ reveal which pathway was more likely as a function of an SI-D ancestor's age, t, which could range from very recent to the age of the tree.

Provided that none of the forward rates are zero, for very small elapsed times, pathway *14* will be more likely than pathway *134* because only a single event is needed. For very large elapsed times and assuming irreversibility, the ratio of pathway *14* to *134* probabilities is q_{14}/q_{13} because it is the first step away from SI-D that determines the pathway taken. At intermediate times, the relative strengths of the two pathways may change with the time available for transitions to take place, depending on the rate values. To compare the relative importance of pathways taken to SC-P, we computed, across the posterior rate distribution, the two pathway probabilities and their differences for time intervals ranging from 0 at the tips to the maximum, root depth of the tree.

An alternative to our pathway analysis might be to use stochastic character mapping to infer the sequence of states traversed as a lineage works its way from SI-D to SC-P. We prefer our approach because the pathway probabilities can be computed analytically and because it is not subject to the additional layer of model uncertainty added by the choice of ancestral state reconstruction method (Pagel 1999).

Results

We collected ploidy information for 917 species, of which 75% are diploid, 20% polyploid, and 5% polymorphic. The distribution of haploid chromosome numbers is given in Fig. 2. The proportion of polyploids observed here is similar to a previous estimate for herbaceous dicots (26.2%; Otto and Whitton 2000). Polyploid species are found in all genera sampled except *Petunia, Jaltomata, Datura,* and *Calibrachoa*. They are especially common in *Solanum* section *Etuberosum* and *Nicotiana* section *Suavolentes*.

We collected breeding system information for 550 species, of which 56% are SC, 35% SI, 4% are polymorphic for SI and SC, and 5% are dioecious. SI is spread throughout the family, including *Solanum, Nicotiana*, and *Physalis*, whereas *Jaltomata, Capsicum*, and *Datura* are primarily SC and *Petunia* and *Calibrachoa*

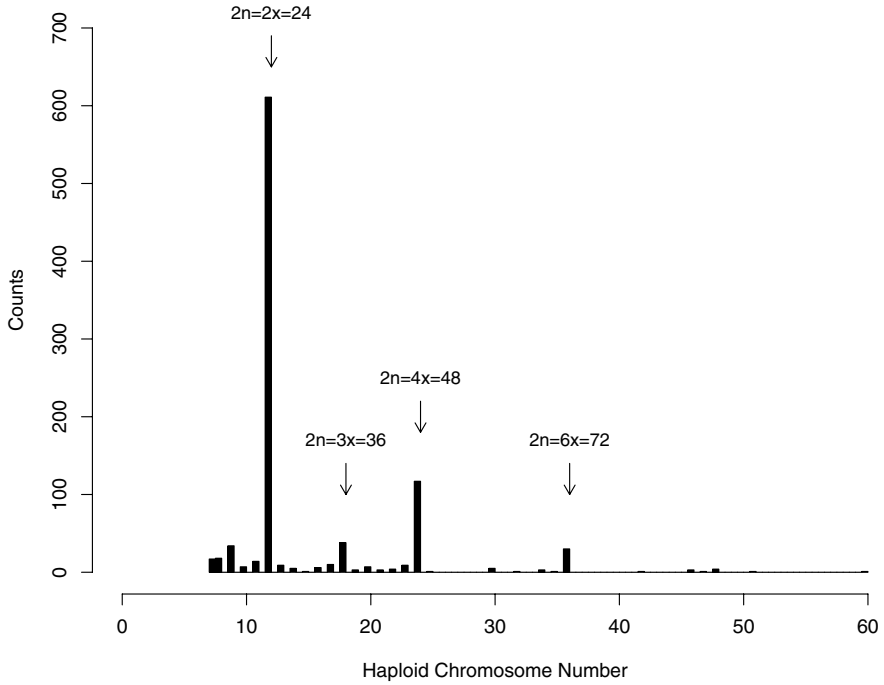

Figure 2. **The distribution of haploid chromosome numbers in the Solanaceae for 917 species. Arrows mark the most frequently observed chromosome counts. Chromosome number found in somatic cells is indicated with "2*n*", and the number preceding "*x*" refers to the inferred ploidy. The marked numbers $2n = 2x = 24$, $2n = 3x = 36$, $2n = 4x = 48$ and $2n = 6x = 72$ refer to the diploid, triploid, tetraploid, and hexaploid cytotypes, respectively.**

are primarily SI. The distribution of ISI for Solanaceae species with sufficient data to calculate ISI is given in Fig. 3. The bimodal distribution suggests that, despite some exceptions, classification of breeding system as binary character appears a reasonable approximation of the continuous empirical distribution of ISI.

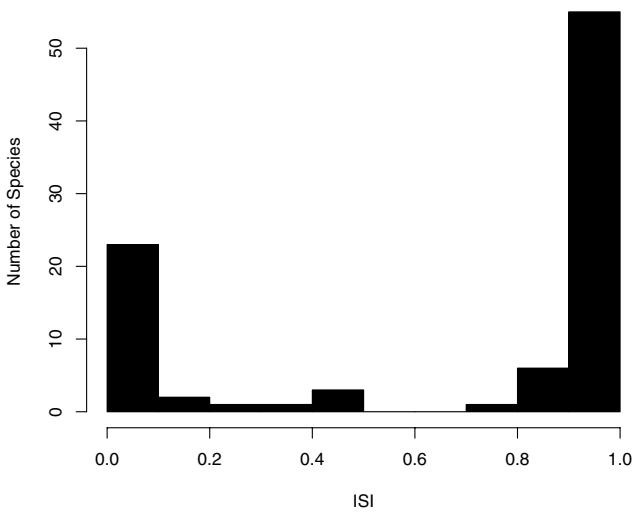

Figure 3. **The distribution of ISI values. Both self- and cross-pollinations were performed manually, and fruit and seed set was scored for 92 species of Solanaceae. Species with ISI values greater than 0.8 are classified SI, whereas species with ISI values less than 0.8 are classified as SC. The ten species with negative ISI values (ranging from −5.5 to −0.03) were set to zero.**

Character data for both self-(in)compatibility and ploidy is known for 408 species; 40.0% are SI-D, 0.3% are SI-P, 44.0% are SC-D, and 15.7% are SC-P (see Table 1). The single instance of SI-P is an allopentaploid hybrid of *Solanum oplocense* Hawkes × *Solanum gourlayii* Hawkes (Camadro and Peloquin 1981). The number of SI-P is significantly under-represented ($\chi^2 = 48.6$, df $= 1$; $P \ll 0.01$). The proportion of SI-P remains significantly underrepresented when polymorphisms are encoded as a separate category ($\chi^2 = 65.9$, df $= 4$; $P \ll 0.01$) in a 3×3 table (not shown).

Table 1. **Table of observed (Obs) and expected (Exp) character state values for species where both ploidy and compatibility states are known. Polymorphic data were collapsed into SI and D categories as described in text. SI-P is significantly under-represented (χ^2=48.6, *df*=1; *p*≪0.01).**

	D		P		Total
	Obs	Exp	Obs	Exp	
SI	164	138.7	1	26.3	165
SC	179	204.3	64	38.7	244
Total	343		65		408

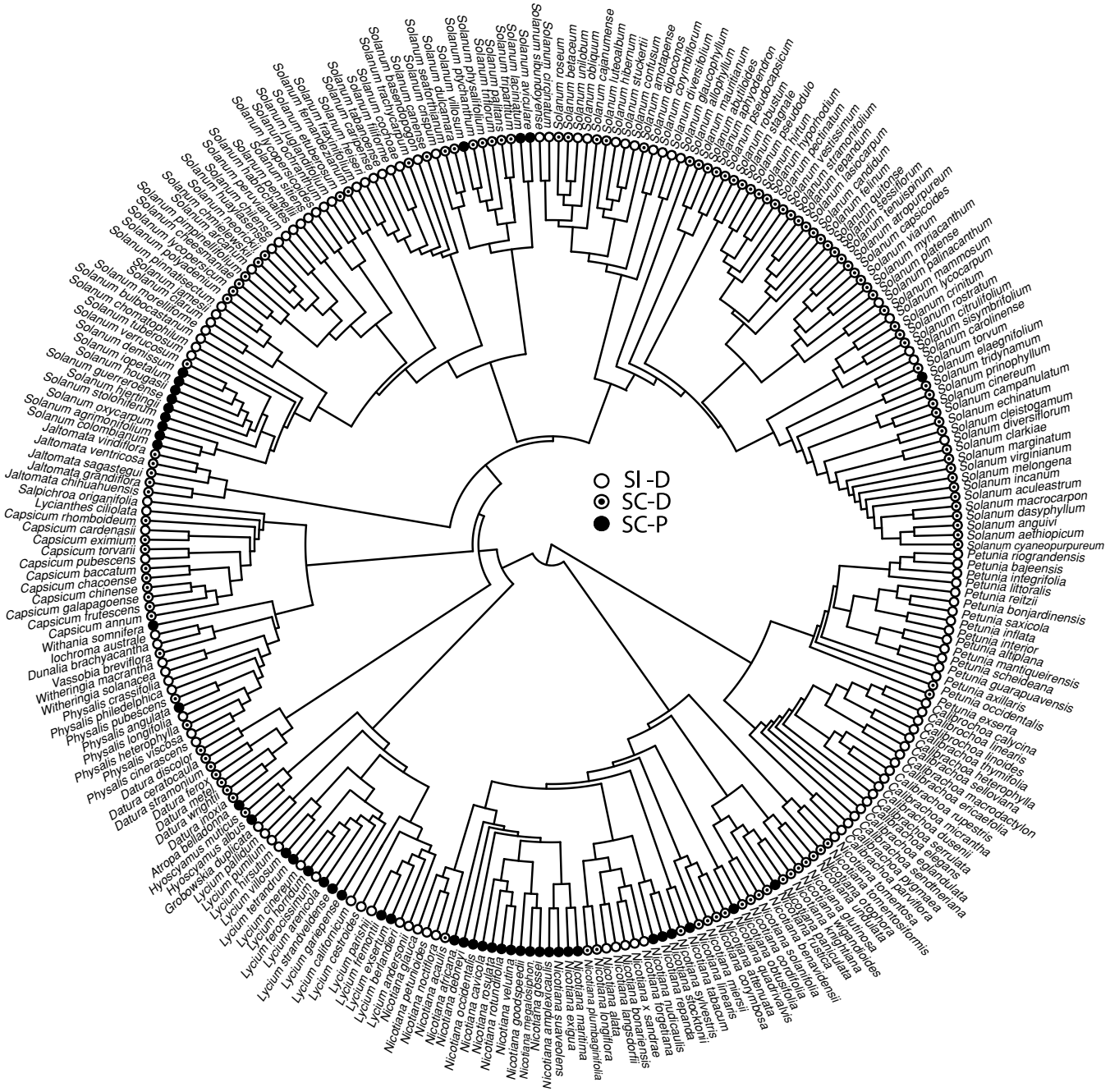

Figure 4. A supertree representing a phylogenetic hypothesis for 266 Solanaceae taxa for which breeding system and ploidy is known. The analyses were performed on a tree with unit and Grafen branch lengths (see text for details). Open circles denote self-incompatible diploids; dotted circles, self-compatible diploids; closed circles, self-compatible polyploids.

PHYLOGENETIC DISTRIBUTION OF CHARACTER STATES

Of approximately 98 genera and 2716 species described in the family (Bohs 2007), our phylogenetic analyses were based on the dataset containing 19 genera and 266 species for which character states and phylogenetic placement were available (Fig. 4). Species in the genera *Solanum* and *Nicotiana* are relatively well sampled (124/1328, 48/108), whereas sampling in the genus *Lycianthes* (1/200) is poor, and *Cestrum* (0/175) is altogether absent. Of the 266 species included in analyses, 38.4% are SI-D, 0% SI-P, 44.7% SC-D, and 16.9% SC-P. These proportions are not significantly different from the larger set of species used in the nonphylogenetic analysis ($\chi^2 = 0.8$; $df = 1$; $p = 0.4$). The association between SC and P remains significant for the subset of species placed on our phylogenetic tree ($\chi^2 = 33.0$; $df = 1$; $p \ll 0.01$).

PHYLOGENETIC COMPARATIVE TESTS

Correlated evolution of SI and polyploidy

For the *Discrete* character analysis on the unit branch length tree, the *log* of the harmonic mean of the likelihoods was −225.4 for the independent model with four estimated rates and −206.2 for the dependent model with eight rates. Comparing the two models therefore gives 2 ln (BF) = 38.4, providing very strong support for correlated evolution between SC and polyploidy within Solanaceae. On the Grafen branch length tree, the log harmonic means were −231.4 and −216.8 for the independent and dependent models, respectively, giving 2 ln(BF) = 29.2 and, again, very strong support for correlated evolution.

Transitions to SC

The *Multistate* analyses performed to reveal how often polyploidy breaks down SI find that the loss of SI occurs more often through mutations in diploids than through polyploidization (Table 2). This conclusion is robust to the branch length assumption and to the irreversibility assumption ($q_{13} > q_{14}$ with posterior probability 1.0 for the restricted model with either type of branch lengths; for the reversible model that probability is 0.994 with unit branch lengths and 0.993 with Grafen branch lengths).

Transitions to polyploidy

Using the unit branch length tree, the probability of the single step pathway to SC polyploids, $W_{14}(t)$, is greater over time intervals $t < 10.5$, and the two-step pathway probability, $W_{134}(t)$, is greater for $t > 10.5$ up to the maximum depth of 17 (Fig. 5A). Both pathways therefore contribute to the evolution of SC polyploids over the time spanned by this tree. To assess the significance of the difference between the two pathway probabilities, we computed $W_{14}(t) - W_{134}(t)$ across the posterior rate distribution for values of time ranging from 0 to 17. Fig. 6A shows probability contours that illustrate the probability associated with pathway *14* or pathway *134* being more likely on the unit branch length tree. For example, at $t = 5.7$ there is a 90% chance (or greater, for $t < 5.7$) that the evolution of SC polyploidy is more likely to occur through pathway *14*. As elapsed time increases, pathway *14* becomes less and less likely until at the maximum node depth of the tree, $t =$ 17, there is a 75% chance that SC polyploidy is more likely to occur through pathway *134*.

Using instead the Grafen branch lengths affects the inference of the relative strength of the pathways leading to the evolution of SC polyploids. In this tree, the single step pathway *14* dominates initially, but only for very short elapsed times ($t < 0.1$; Fig. 5B). Fig. 6B illustrates the probability associated with pathway *14* or pathway *134* being more likely. For example, at $t \leq 0.04$ there is a 90% chance that the evolution of SC polyploidy is more likely to occur through pathway *14*. At an elapsed time of $t = 0.09$, both pathways contribute equally to the evolution of SC polyploidy. However for the majority of time across the Grafen branch length tree ($t = 0.17$ to 1), pathway *134* is the dominant route leading to SC polyploidy.

Table 2. Inferred median rates of character evolution from the *Multistate* analysis. Results are shown for both the restricted model of character evolution, where the evolution of polyploidy and self-compatibility is irreversible, and unrestricted (full) model on the phylogenetic tree with unit or Grafen branch lengths. Under both models and branch length assignment methods, self-incompatibility is inferred to be lost more often through mutations within the diploids than through polyploidization ($q_{13} > q_{14}$ with posterior probability≥0.99 in all cases, as computed from the posterior rate distributions).

Rates	Unit branch lengths		Grafen branch lengths	
	Restricted	Full	Restricted	Full
q_{13}	0.25	0.16	5.6	16.4
q_{31}	0	0.08	0	12.1
q_{14}	0.08	0.05	1.3	3.6
q_{41}	0	0.16	0	11.5
q_{34}	0.05	0.04	6.0	4.3
q_{43}	0	0.11	0	7.8

Discussion

PHYLOGENETIC COMPARATIVE TESTS

A strong association exists between polyploidy and SC in Solanaceae. Although it is perhaps not surprising, given the mechanism of SI breakdown upon polyploidization within RSI systems (Livermore and Johnstone 1940; Stout and Chandler 1942; Pandey 1968; Chawla et al. 1997; Entani et al. 1999), our result provides strong comparative evidence from this family for a causal association, and it therefore predicts similar patterns for all angiosperm groups that share a common genetic basis for SI. In an earlier broad comparative study of the relationship between compatibility and ploidy, Mable (2004) did not find significant evidence for correlated evolution within families with different SI systems, despite recognizing a significant trend within RSI families. The absence of a correlation in Mable's (2004) broader study suggests that a causal relationship between SC and polyploidy may be driving the association within RSI families, but that in general, SC may not be a strict requirement for polyploid establishment. Examining the rate parameters leading to SC and/or polyploidy in other families with non-RSI systems could determine to what extent mate limitation and inbreeding depression contribute to an association between SC and polyploidy. If there is strong selection within newly established polyploids for SC due to mate limitation, the rate from SI-P to SC-P is expected to be larger than the rate from SI-D to SC-D. Conversely, if the alleviation of inbreeding

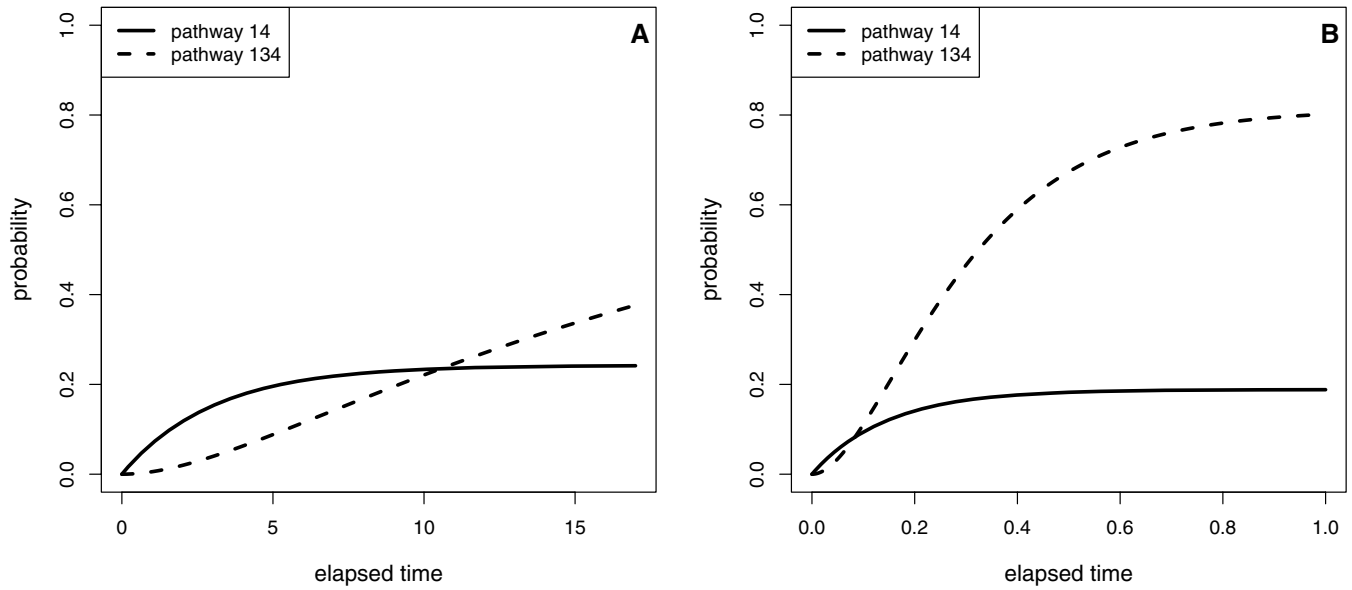

Figure 5. Probabilities of the direct and indirect pathways from self-incompatible diploids (state 1) to self-compatible polyploids (state 4). The pathway probabilities $W_{14}(t)$ (solid lines) and $W_{134}(t)$ (dashed lines) were computed with the median values of the posterior rate distribution under the restricted model (Table 2). Results are shown for the unit branch length tree (A; $q_{13} = 0.25$, $q_{14} = 0.08$, $q_{34} = 0.05$) and for the Grafen branch length tree (B; $q_{13} = 5.6$, $q_{14} = 1.3$, $q_{34} = 6.0$). In each case, the elapsed times plotted cover the full depth of the tree (maximum node depth is 17 for A, root age is 1 for B). With unit branch lengths, the single step pathway *(14)* is more probable over time spans of approximately $t \leq 10.5$ units. Over longer time intervals, the two-step pathway *(134)* becomes dominant. Both pathways therefore may be important contributors in the correlated evolution to self-compatible polyploids in Solanaceae. With Grafen branch lengths, the single step pathway *(14)* is more probable only over time spans of $t \leq 0.1$. Pathway *134* therefore appears to be dominant.

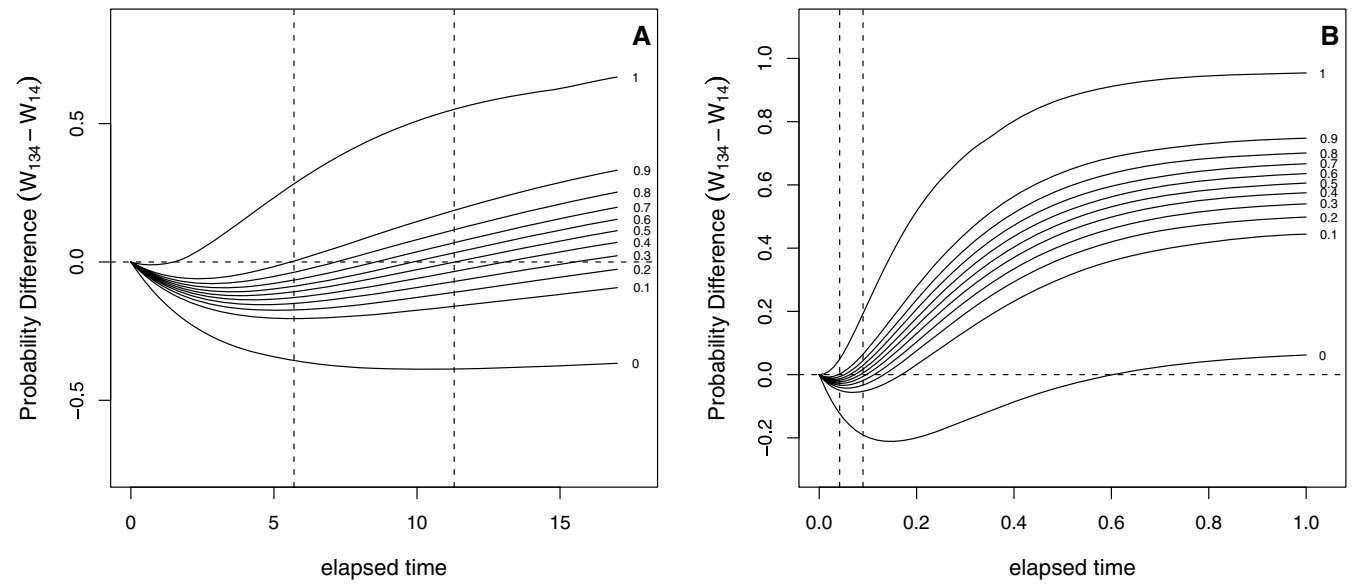

Figure 6. Contour plots of the difference in probability between the two-step pathway *(134)* and the one-step pathway *(14)*. Results are shown for the unit branch length tree (A) and for the Grafen branch length tree (B). The solid contour lines represent the cumulative probability density of $\Delta W(t) = W_{134}(t) - W_{14}(t)$, computed over the posterior rate distribution; their levels are printed on the right. At each time t, there is a 10% chance that $\Delta W(t)$ is less than the value shown by the line marked 0.1, and similarly for the ten other levels shown. The left dashed line (at $t = 5.7$ in A, at $t = 0.04$ in B) marks the time at which there is a 90% probability that pathway *14* is more likely. The right dashed line (at $t = 11.3$ in A, at $t = 0.09$ in B) marks the time at which pathway *134* becomes more likely. Over time spans that are long relative to the tree age (time values near the upper limits plotted), pathway *134* dominates in the Grafen tree but both pathways contribute in the unit tree.

depression is the primary factor leading to a correlation between SC and P, the rate from SC-D to SC-P is expected to be larger than the rate from SI-D to SI-P.

Statistical phylogenetic methods measure lineage transition rates, which depend on the availability of individual transitions (the mutation rate) and selective processes that act to fix these mutations within populations. Our analysis shows that SC lineages arise more often within diploids than as a byproduct of polyploidization ($q_{13} > q_{14}$), which could be a result of differences in the mutational opportunity for character change or selection acting on those mutations. Generally, estimates from mutational studies suggest that the mutation rate of SI breakdown within diploids is approximately equal to or lower than the rate of polyploidization; this suggests that selection, not mutational opportunity, may be the primary factor causing our observed rate difference. Estimates of autopolyploid formation are on the order of the genic mutation rate ($\mu_P = 3 \times 10^{-5}$) (Ramsey and Schemske 1998). The mutation rate to SC has been previously inferred from incompatible pollen tube growth studies (Lewis 1979). These studies often cannot separate the mutations that arise with an increase in ploidy from those that arise without an increase in ploidy (de Nettancourt 1977). We use a conservative assumption, that none of the breakdowns of SI detected in these studies are due to polyploid pollen grains. The estimated rate of breakdown of SI within diploids in *Oenothera organensis, Prunus avium, Trifolium repens, T. pratense, Nicotiana alata*, and *Petunia sp.* ranges from $\mu_{SC} = 0.02 \times 10^{-5}$ to 1×10^{-5} per pollen grain (de Nettancourt 1977; Lewis 1979). Given that an average number of pollen grains per flower is ca. 5×10^5 within an SI diploid, the number of SC diploid gametes is approximately comparable to the number of SC polyploid gametes ($5 \times 10^5 \times \mu_{SC} = 0.1$ to 5 for SC diploid pollen, and $5 \times 10^5 \times \mu_P = 15$ for SC polyploid pollen). Although both measures are associated with a high estimation error, taken together with the transition rate estimates they suggest a remarkably clear result: a more severe selection pressure restricts the ability of newly established polyploids to fix within populations (Ramsey and Schemske 2002; Levin and Miller 2005).

Because polyploidization of diploid GSI individuals almost invariably causes a direct transition to SC in one step (SC-D to SI-P), use of the common statistical phylogenetic models for measuring correlated evolution of discrete characters *(BayesTraits Discrete)* would be inappropriate (Pagel 1994). Consequently, we use a widely employed alternative evolutionary model *(BayesTraits Multistate)*, which allows appropriate single-step transitions (Fig. 1). We also develop a new extension that enables assessment of the relative contribution of multiple rates to the evolution of self-compatible polyploidy. Our results on the unit branch length tree provide considerable support for the direct pathway from SI-D to SC-P, thought to precede the evolution of gender dimorphism in the genus *Lycium*, and many others (Miller and Venable 2000). At the same time, it appears that Brunet and Liston (2001) expressed a valid concern when they highlighted the importance of comparing the relative magnitude of the possible pathways to SC-P, the inferred stepping stone to dioecy. In fact, our results employing the Grafen branch lengths, likely to bear more resemblance to the true tree than the unit branch length assumption, show much greater support for the two-step pathway, from SI-D to SC-D to SC-P, over all but the shortest time intervals. An extension of the approach we use to compare sequential rate pathways could also be employed to directly assess their relative contribution in the evolution of gender dimorphism in *Lycium*, as well as other taxa.

Our *Multistate* model omits SI-P species because they do not occur in the phylogenetic dataset. In the full dataset, including those with no certain placement on the phylogeny, we found the description of one likely occurrence of SI-P. Camadro and Peloquin (1981) describe an allopentaploid hybrid, *S. oplocense* Hawkes × *S. gourlayii* Hawkes, whose expression of self-(in)compatibility depends on which parent was the pollen or ovule donor. Interestingly, it is possible that this exception may not break the genetic rule. If one of the parent species of the allopentaploid hybrid were SI and another SC, with the S-locus sufficiently degraded, the hybrid may have expressed only one functional allele of the S-locus (J. Kohn, pers. comm.). Nonhaploid pollen grains homozygous at the S-locus may be rejected via a normal SI response (Lewis 1947).

Despite the extremely rare occurrence of SI-P in our collection of data from Solanaceae, a few well-studied examples are known from another family with RSI. Self-incompatible Rosaceae express a system that is homologous to the one found in Solanaceae (Igić and Kohn 2001), and members of the family show a strong association between SC and polyploidy (Dickinson et al. 2007). However, the genus *Prunus* presents noted exceptions. Although *Prunus pseudocerasus* (Huang et al. 2008) shows the expected SI breakdown in polyploids, the likely recent allopolyploids *P. cerasus* (Hauck et al. 2002), *P. spinosa* (Nunes et al. 2006) and *P. fruticosa* (Pruski 2007) each retain functioning SI. Alterations in the pollen-S gene of *P. cerasus* are suggested to be responsible for the maintenance of SI in polyploids (Hauck et al. 2006). The source of evidence in support of this hypothesis is the differential SI response to deletion of the pollen-S gene in *Prunus* and the Solanaceae. In *P. avium*, an SI diploid, deletions in the haplotype-specific region of the pollen-S gene result in SC (Sonneveld et al. 2005). However, in Solanaceae, studies of irradiated pollen find instances of pollen-S gene duplications, but no deletions, suggesting that many deletions in the pollen-S gene incapacitate pollen (Golz et al. 1999, 2001). As emphasized in Sonneveld et al. (2005), transgenic pollen-S gene knockouts and gain-of-function mutants could provide more definitive evidence regarding the idiosyncrasy of the S-locus in *Prunus*,

and the exact mechanism responsible for the maintenance of SI in polyploids. Additional evidence stems from sequence diversity differences where the inferred pollen gene of the S-locus in *Prunus* exhibits a higher degree of sequence diversity than the pollen gene in *Antirrhinum* and *Petunia* (Ikeda et al. 2004; Kao and Tsukamoto 2004). Inferences involving the male-expressed gene are made more difficult by the enormous size of the F-box gene family, to which the pollen gene function of RSI belongs. The gene family contains several hundred members, including closely linked paralogous copies at the S-locus (Kuroda et al. 2002). Many questions remain about the exact identity, mode of evolution, and mechanism of action of pollen-expressed genes in RSI, as well as differences in expression between distantly related families (Newbigin et al. 2008). Additional mutational studies, which measure both breeding system and ploidy states within the same individuals, are necessary to determine more precisely the likelihood of occurrence of SI polyploids in Solanaceae and other families.

ANCIENT POLYPLOIDY

Two separate studies, using similar methods, both find an ancient round of polyploidization within the Solanaceae. Schlueter et al. (2004) and Blanc and Wolfe (2004) use expressed sequence tags data to infer paralogous genes and the synonymous distance between them to estimate a distribution of synonymous distances. The expectation that a large-scale duplication event would produce detectable peaks of synonymous distances can be used to estimate the temporal divergence approximating the date of such an event (Lynch and Conery 2000, 2003). Schlueter et al. (2004) report finding two apparent large-scale duplication events, one ca. 52 mya, and another more recent duplication, with an uncertain time due to the large standard deviation around the synonymous distance peak. Using the results from Schlueter et al. (2004), Soltis et al. (2009) argued that the genome duplication could have occurred in the lineage leading to the Solanoideae based on the fact that more "basal" lineages in the Solanaceae have lower chromosome numbers (e.g., Cestroideae $x = 7-12$; Penas et al. 2006) whereas the more "derived" Solanoideae is characterized by a basal chromosome number $x = 12$ (Olmstead et al. 2008). In a separate study, Blanc and Wolfe (2004) infer a large-scale duplication event 18–23 mya. Despite the wide acceptance of these and similar results, it remains unclear how frequently the employed methods falsely infer whole-genome duplications, in part because accurate null models are difficult to construct. Our comparative data, as well as genomic analyses obtained by Doganlar et al. (2002) and Wu et al. (2006), directly contradict the findings of whole-genome duplication events in the recent ancestry of Solanaceae.

Given the strong association between SC and P, and evidence for irreversibility of the transition to SC in the Solanaceae (Ioerger et al. 1990; Miller and Venable 2000; Igić et al. 2004), we argue that ancient polyploidy is, in fact, highly unlikely to have occurred within Solanaceae. First, within Solanaceae, species in a group often termed "$x = 12$" display a remarkably conserved pattern of synteny (Olmstead and Palmer 1992). The highly conserved karyotype evolution in a subset of that group, containing tomato, potato, eggplant, and pepper, requires the inference of only a few dozen rearrangements in karyotype evolution to explain the extant species patterns (Bonierbale et al. 1988; Livingstone et al. 1999; Doganlar et al. 2002). It is therefore extremely unlikely that any large-scale or whole-genome duplications took place in this subset of species (ca. 1500 species, with a 15 my-old common ancestor). Furthermore, Wu et al. (2006) used a set of 2869 conserved gene-based markers, derived from single-copy genes shared by euasterid species, to construct comparative genetic maps of coffee and tomato, with a much older common ancestor (ca. 85 my). They found a strong pattern of conserved synteny between these distantly related species, with absence of "networks of synteny" expected to occur with whole-genome duplication followed by selective gene loss. This finding is inconsistent with a proposed polyploidization event in the Solanaceae, which is supposed to have occurred around 20 mya (Blanc and Wolfe 2004; Schlueter et al. 2004). Consequently, we urge caution in interpreting the ancient duplication events from fitted K_s distributions between paralogous genes. The uncertainty in the null distribution of K_s values may be underestimated in part because the extent to which dysploidy affects the distribution is unclear, and assumptions regarding the operation of the molecular clock may be violated in an unpredictable manner.

LIMITATIONS AND IMPROVEMENTS

Our results should be at least somewhat tempered, however, because of the known weaknesses in our data and models. Promising novel approaches (Smith et al. 2009) allow rapid construction of large-scale datasets with estimates of divergence times, which could allow us to more meaningfully estimate transition rates in units of time, instead of making the branch length assumptions as we did here. Such approaches are likely to yield better tests, especially when combined with our method for assessing relative pathway contributions, which are time dependent. In addition, breeding systems are thought to affect diversification rate, and failure to incorporate differences in diversification rates may lead to incorrect inferences of trait evolution (Maddison 2006; Goldberg and Igić 2008). A multistate version of the model that allows for simultaneous inference of speciation and extinction along with transition rates (Maddison et al. 2007), used in conjunction with a tree with branch lengths proportional to time, will be required to assess this effect. Finally, the models currently in use do not allow for temporal or clade-specific rate heterogeneity, which provide a clear direction for further progress.

It may be that neither polyploidization nor breakdown of SI occurs at a constant family-wide rate, independent of unmeasured traits, for example, and it is unknown how robust these models are to such violations. Nevertheless, we offer what is likely a sound first approximation, which unites a large dataset of breeding system and ploidy, models informed by genetic and genomic data, and improved general methods for evaluation of the relative importance of different pathways in comparative phylogenetic studies.

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Appendix

We wish to compute the transition probabilities of the two pathways from SI-D to SC-P: polyploidization from self-incompatibility (SI-D directly to SC-P, pathway *14*), and loss of SI followed by polyploidization from SC (SI-D to SC-D to SC-P, pathway *134*).

Consider the three states shown in black in Figure 1, but insert an artificial division in the SC-P state so that it can be treated as two different states: state 4*a* contains the members of state 4 that arrived by pathway *14*, and state 4*b* contains those that arrived by pathway *134* (Fig. A1). The implied transition rate matrix (for a row vector of states ordered 1, 3, 4*a*, 4*b*) is

$$\mathsf{Q} = \begin{pmatrix} -q_{13} - q_{14} & q_{13} & q_{14} & 0 \\ q_{31} & -q_{31} - q_{34} & 0 & q_{34} \\ q_{41} & 0 & -q_{41} & 0 \\ 0 & q_{43} & 0 & -q_{43} \end{pmatrix}. \quad \text{(A1)}$$

The probabilities of changing from one state to any other state after time t are given by the elements of the matrix $\mathsf{P} = \exp(\mathsf{Q}t)$. The pathway probabilities of interest are $W_{14}(t) = P_{14a}(t)$ and $W_{134}(t) = P_{14b}(t)$. In the general case in which the reversal rates q_{31}, q_{41}, and q_{43} are nonzero, our interpretation of a pathway is the last route taken to SC-P by time t, but landing in state 4*a* does not preclude having previously been in state 4*b*, and vice versa.

In the special case for this system of no reverse transitions ($q_{31} = q_{41} = q_{43} = 0$), the transition probabilities of interest are:

$$W_{14}(t) = P_{14a}(t) = \frac{q_{14}}{q_{13} + q_{14}} \left(1 - e^{-(q_{13}+q_{14})t}\right) \quad \text{(A2)}$$

and

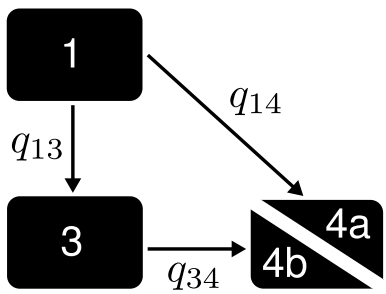

Figure A1. Schematic representation of the states used in the pathway probability derivation. States 1 (SI-D) and 3 (SC-D) are as for the *Multistate* analysis (Fig. 1), but state 4 (SC-P) is divided into two. Transitions to SC-P from SI-D are tracked in state 4a, and transitions to SC-P from SC-D are tracked in state 4b.

$$W_{134}(t) = P_{14b}(t) = \frac{q_{13}}{q_{13}+q_{14}} \left(1 - \frac{1}{q_{13}+q_{14}-q_{34}}\left[(q_{13}+q_{14})e^{-q_{34}t} - q_{34}e^{-(q_{13}+q_{14})t}\right]\right) \tag{A3a}$$

unless $q_{14} = q_{34} - q_{13}$, in which case

$$W_{134}(t) = P_{14b}(t) = \frac{q_{13}}{q_{34}}\left(1 - e^{-q_{34}t}[1+q_{34}t]\right). \tag{A3b}$$

Supporting Information

The following supporting information is available for this article:

Table S1. SI-SC and D-P Character State Table.

Supporting Information may be found in the online version of this article.

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Table S1: SI-SC and D-P Character State Table

Taxon	SI-SC State	D-P State	SI-SC Source	D-P Source
Atropa belladonna	SC	P	[33]	[34]
Calibrochoa calycina	SI	D	[92]	[12]
Calibrachoa dusenii	SI	D	[92]	[12]
Calibrachoa eglandulata	SI	D	[92]	[12]
Calibrachoa elegans	SI	D	[92]	[12]
Calibrachoa ericaefolia	SI	D	[92]	[12]
Calibrachoa heterophylla	SI	D	[92]	[12]
Calibrochoa linearis	SI	D	[92]	[34]
Calibrochoa linoides	SI	D	[92]	[12]
Calibrachoa macrodactylon	SI	D	[92]	[12]
Calibrachoa micrantha	SI	D	[92]	[12]
Calibrachoa parviflora	SC	D	[92]	[12]
Calibrachoa pygmaea	SI	D	[92]	[12]
Calibrachoa rupestris	SI	D	[92]	[12]
Calibrachoa selloviana	SI	D	[92]	[12]
Calibrachoa sendtneriana	SI	D	[92]	[12]
Calibrachoa serrulata	SI	D	[92]	[12]
Calibrachoa thymifolia	SI	D	[92]	[12]
Capsicum annum	SC	D	[70]	[68]
Capsicum baccatum	SC	D	[70]	[68]
Capsicum cardenasii	SI*, SC	D	[70]	[68]
Capsicum chacoense	SC	D	[70]	[68]
Capsicum chinense	SC	D	[70]	[68]
Capsicum eximium	SC	D	[70]	[68]
Capsicum frutescens	SC	D	[70]	[68]
Capsicum galapagoense	SC	D	[70]	[68]
Capsicum pubescens	SI*, SC	D	[70]	[67]
Capsicum rhomboideum	SC	D	[70]	[68]
Capsicum torvarii	SC	D	[70]	[68]
Datura ceratocaula	SC	D	[23]	[23]
Datura discolor	SC	D	[23]	[23]
Datura ferox	SC	D	[23]	[23]
Datura inoxia	SC	D	[23]	[23]
Datura metel	SC	D	[23]	[23]
Datura stramonium	SC	D	[23]	[34]
Datura wrightii	SC	D	[23]	[34]
Dunalia brachyacantha	SI	D	[84]	[34]

* for polymorphic species, the state used in the analysis

† sources listed report SC in conflict with Marks (1965) assignment

Table S1: SI-SC and D-P Character State Table

Taxon	SI-SC State	D-P State	SI-SC Source	D-P Source
Grobowskia duplicata	SI	D	[15]	[34]
Hyoscyamus albus	SC	P	[33]	[34]
Hyoscyamus muticus	SC	D	[77]	[77]
Iochroma australe	SI	D	[84]	[34]
Jaltomata chihuahuensis	SC	D	[63]	[34]
Jaltomata grandiflora	SC	D	[63]	[34]
Jaltomata sagastegui	SC	D	[63]	[34]
Jaltomata ventricosa	SC	D	[63]	[65]
Jaltomata viridiflora	SC	D	[63]	[65]
Lycianthes ciliolata	SI	D	[28]	[28]
Lycium andersonii	SI	D	[62]	[101]
Lycium arenicola	SC	P	[62]	[51]
Lycium berlandieri	SI	D	[62]	[34]
Lycium californicum	SI*, SC	D*, P	[62, 101]	[34, 101]
Lycium cestroides	SI	D	[5]	[34]
Lycium cinereum	SI	D	[60]	[60]
Lycium exsertum	SC	P	[62]	[61]
Lycium ferocissimum	SI	D	[60]	[60]
Lycium fremontii	SC	P	[62]	[61]
Lycium gariepense	SC	P	[62, 58]	[51]
Lycium hirsutum	SI	D	[60]	[60]
Lycium horridum	SC	P	[62]	[94]
Lycium pallidum	SI	D	[62]	[34]
Lycium parishii	SI	D	[62]	[34]
Lycium pumilum	SI	D	[60]	[60]
Lycium strandveldense	SC	P	[62, 95]	[94]
Lycium tetrandrum	SC	P	[62, 51]	[94]
Lycium villosum	SC	P	[62, 51]	[34]
Nicotiana acaulis	SC	D	[36]	[34]
Nicotiana africana	SC	P	[73]	[34]
Nicotiana alata	SI	D	[74]	[34]
Nicotiana amplexicaulis	SC	P	[74]	[34]
Nicotiana attenuata	SC	D	[36]	[34]
Nicotiana benavidensii	SC	D	[36]	[34]
Nicotiana bonariensis	SI	D	[74]	[34]
Nicotiana cavicola	SC	P	[74]	[24]
Nicotiana cordifolia	SC	D	[9]	[34]
Nicotiana corymbosa	SC	D	[74]	[34]
Nicotiana debneyi	SC	P	[74]	[34]

* for polymorphic species, the state used in the analysis

† sources listed report SC in conflict with Marks (1965) assignment

Table S1: SI-SC and D-P Character State Table

Taxon	SI-SC State	D-P State	SI-SC Source	D-P Source
Nicotiana exigua	SC	P	[74]	[34]
Nicotiana forgetiana	SI	D	[74]	[36]
Nicotiana glauca	SI*,SC	D	[74, 35]	[36]
Nicotiana glutinosa	SC	D	[74]	[36]
Nicotiana goodspeedii	SC	P	[74]	[36]
Nicotiana gossei	SC	P	[74]	[36]
Nicotiana knightiana	SC	D	[36]	[36]
Nicotiana langsdorfii	SI*, SC	D	[74]	[36]
Nicotiana linearis	SC	D	[36]	[36]
Nicotiana longiflora	SC	D	[35]	[36]
Nicotiana maritima	SC	P	[74]	[36]
Nicotiana megalosiphon	SC	P	[74]	[36]
Nicotiana miersii	SC	D	[36]	[36]
Nicotiana noctiflora	SI	D	[74]	[36]
Nicotiana nudicaulis	SC	P	[36]	[36]
Nicotiana obtusifolia	SC	D	[36]	[36]
Nicotiana occidentalis	SC	P	[74]	[36]
Nicotiana otophora	SC	D	[36]	[36]
Nicotiana paniculata	SC	D	[74]	[36]
Nicotiana petunioides	SI	D	[30]	[36]
Nicotiana plumbaginifolia	SC	D	[30]	[36]
Nicotiana quadrivalvis	SC	P	[89]	[36]
Nicotiana repanda	SC	P	[74]	[36]
Nicotiana rosulata	SC	P	[74]	[24]
Nicotiana rotundifolia	SC	P	[74]	[36]
Nicotiana rustica	SC	P	[74]	[36]
Nicotiana solanifolia	SC	D	[36]	[36]
Nicotiana stocktonii	SC	P	[36]	[36]
Nicotiana suaveolens	SC	P	[74]	[36]
Nicotiana sylvestris	SC	D	[74]	[36]
Nicotiana tabacum	SC	P	[74]	[36]
Nicotiana tomentosa	SI	D	[74]	[36]
Nicotiana tomentosiformis	SC	D	[35]	[36]
Nicotiana undulata	SC	D	[36]	[36]
Nicotiana velutina	SC	P	[74]	[36]
Nicotiana wigandioides	SC	D	[36]	[36]
Nicotiana sandrae	SI	D	[29]	[34]
Petunia altiplana	SI	D	[91]	[34]
Petunia axillaris	SI*, SC	D	[91]	[34]

* for polymorphic species, the state used in the analysis

† sources listed report SC in conflict with Marks (1965) assignment

Table S1: SI-SC and D-P Character State Table

Taxon	SI-SC State	D-P State	SI-SC Source	D-P Source
Petunia bajeensis	SI	D	[91]	[34]
Petunia bonjardinensis	SI	D	[91]	[34]
Petunia exserta	SC	D	[91]	[12]
Petunia guarapuavensis	SI	D	[91]	[34]
Petunia inflata	SI	D	[91]	[34]
Petunia integrifolia	SI	D	[91]	[34]
Petunia interior	SI	D	[91]	[34]
Petunia littoralis	SI	D	[91]	[34]
Petunia mantiqueirensis	SI	D	[91]	[34]
Petunia occidentalis	SC	D	[91]	[12]
Petunia reitzii	SI*, SC	D	[91]	[34]
Petunia riograndensis	SI	D	[91]	[34]
Petunia saxicola	SI	D	[91]	[34]
Petunia scheideana	SI	D	[91]	[34]
Physalis angulata	SC	P	[57]	[34, 57]
Physalis cinerascens	SI	D	[81]	[81]
Physalis crassifolia	SI	D	[57]	[57]
Physalis heterophylla	SC	D	[57]	[34, 57]
Physalis pubescens	SC	D	[57]	[57]
Physalis longifolia	SI	D	[50, 55]	[34]
Physalis philedelphica	SI	D	[71]	[34]
Physalis viscosa	SI	D	[66]	[34]
Salpichroa origanifolia	SI	D	[66]	[34]
Solanum abutiloides	SC	D	[100]	[3]
Solanum aculeastrum	SC	D	[21]	[1]
Solanum aethiopicum	SC	D	[100]	[78]
Solanum agrimonifolium	SC†	P	[86, 53]	[3]
Solanum allophyllum	SC	D	[16]	[34]
Solanum amotapense	SC	D	[19]	[3]
Solanum anguivi	SC	D	[93]	[34]
Solanum aphyodendron	SC	D	[93]	[3]
Solanum arcanum	SI*, SC	D	[75]	[3]
Solanum atropurpureum	SC	D	[100]	[3]
Solanum aviculare	SC	P	[100]	[34]
Solanum basendopogon	SI	D	[100]	[13]
Solanum betaceum	SC	D	[17]	[3]
Solanum bulbocastanum	SI*, SC	D*, P	[41, 86, 39]	[41, 34]
Solanum cajanumense	SC	D	[17]	[3]
Solanum campanulatum	SC	D*, P	[100]	[78]

* for polymorphic species, the state used in the analysis

† sources listed report SC in conflict with Marks (1965) assignment

Table S1: SI-SC and D-P Character State Table

Taxon	SI-SC State	D-P State	SI-SC Source	D-P Source
Solanum candidum	SC	D	[100]	[14]
Solanum canense	SC	D	[100, 64, 7]	[13, 7]
Solanum capsicoides	SC	D*, P	[96]	[96, 4, 78]
Solanum caripense	SI	D	[100, 64, 7, 6]	[6, 13, 7]
Solanum carolinense	SI	D	[80]	[80]
Solanum cheesmaniae	SC	D	[100]	[75]
Solanum chilense	SI*, SC	D	[100, 44, 75]	[75]
Solanum chmielewskii	SC	D	[75]	[75]
Solanum chomatophilum	SI	D	[53]	[42]
Solanum cinereum	SC	D*, P	[100]	[78]
Solanum circinatum	SI	D	[17]	[34]
Solanum citrulifolium	SC	D	[100]	[54]
Solanum clarkiae	SC	D	[8]	[34]
Solanum clarum	SI	D	[88]	[42]
Solanum cleistogamum	SC	D	[90]	[78]
Solanum cochoae	SI	D	[64]	[34, 13]
Solanum colombianum	SC†	P	[53, 86]	[42]
Solanum confusum	SI	D	[19]	[3]
Solanum corymbiflorum	SI	D	[17]	[34]
Solanum crinitum	SC	D	[100]	[49]
Solanum crispum	SI	D	[10]	[3]
Solanum cyaneopurpureum	SC	D	[21]	[34]
Solanum dasyphyllum	SC	D	[69]	[69]
Solanum demissum	SC	P	[3]	[42, 97]
Solanum diploconos	SI	D	[17]	[3]
Solanum diversiflorum	SI	D	[100]	[34, 78]
Solanum diversifolium	SI	D	[17]	[34]
Solanum dulcamara	SC	D	[22]	[34]
Solanum echinatum	SC	D	[22]	[34, 78]
Solanum elaegnifolium	SC	P	[21]	[34]
Solanum etuberosum	SC	D	[75]	[27]
Solanum felinum	SC	D	[100, 14]	[14]
Solanum fernandezianum	SC	D	[87]	[27]
Solanum filiforme	SI	D	[64]	[13]
Solanum fraxinifolium	SI*, SC	D	[100, 64]	[13]
Solanum glaucophyllum	SI	D	[19]	[34]
Solanum guerreroense	SC	P	[37, 99, 86]	[42]
Solanum habrochaites	SI*, SC	D	[75]	[3]
Solanum heiseri	SI	D	[100, 64]	[13]

* for polymorphic species, the state used in the analysis

† sources listed report SC in conflict with Marks (1965) assignment

Table S1: SI-SC and D-P Character State Table

Taxon	SI-SC State	D-P State	SI-SC Source	D-P Source
Solanum hibernum	SI	D	[19]	[3]
Solanum hirtum	SC	D	[100]	[34, 14]
Solanum hjertingii	SC	P	[3]	[34, 42]
Solanum hougasii	SC	P	[86, 45]	[42]
Solanum huaylasense	SI	D	[44]	[75]
Solanum hyporhodium	SC	D	[100]	[14]
Solanum incanum	SC	D	[79]	[78]
Solanum iopetalum	SC†	P	[99, 86]	[42]
Solanum jamesii	SI	D	[76]	[42]
Solanum juglandifolium	SI	D	[75]	[3]
Solanum laciniatum	SC	P	[100]	[78]
Solanum lasiocarpum	SC	D	[100]	[14]
Solanum luteoalbum	SC	D	[19]	[3]
Solanum lycocarpum	SI	D	[56]	[25]
Solanum lycopersicoides	SI	D	[75]	[3]
Solanum lycopersicum	SC	D	[100]	[75]
Solanum macrocarpon	SC	D	[100]	[69]
Solanum mammosum	SC	D	[100]	[25]
Solanum marginatum	SC	D	[100]	[78, 25]
Solanum mauritianum	SC	D	[82]	[34, 78]
Solanum melongena	SC	D	[100]	[34]
Solanum morelliforme	SC	D	[88]	[42]
Solanum myriacanthum	SC	D	[59]	[34]
Solanum neorickii	SC	D	[75]	[75]
Solanum obliquum	SI	D	[17]	[34]
Solanum ochranthum	SI	D	[75, 43, 76]	[34]
Solanum oxycarpum	SC†	P	[53, 99, 86]	[42]
Solanum palinacanthum	SI	D	[26]	[3]
Solanum palitans	SC	D	[22]	[34]
Solanum pectinatum	SC	D	[100]	[34, 14]
Solanum pennellii	SI*, SC	D	[75]	[34]
Solanum peruvianum	SI*, SC	D	[100, 75]	[75]
Solanum physalifolium	SC	D	[22]	[78]
Solanum pimpinellifolium	SC	D	[100]	[3]
Solanum pinnatisectum	SI	D	[100]	[42]
Solanum platense	SC	D	[75, 43]	[25]
Solanum polyadenium	SC	D*, P	[3]	[72, 86]
Solanum prinophyllum	SC	D	[22]	[78]
Solanum pseudocapsicum	SC	D	[100]	[3]

* for polymorphic species, the state used in the analysis

† sources listed report SC in conflict with Marks (1965) assignment

Table S1: SI-SC and D-P Character State Table

Taxon	SI-SC State	D-P State	SI-SC Source	D-P Source
Solanum pseudodulo	SC	D	[100, 43]	[34, 14]
Solanum ptychanthum	SC	D	[40]	[32]
Solanum quitonse	SC	D	[100, 20]	[34, 14]
Solanum repandum	SC	D	[100, 14]	[14]
Solanum robustum	SC	D	[100]	[46]
Solanum roseum	SC	D	[21]	[34]
Solanum rostratum	SC	D	[100]	[78, 54]
Solanum seaforthianum	SC	D	[2]	[12]
Solanum sessiflorum	SC	D	[100]	[14]
Solanum sibundoyense	SI	D	[17]	[3]
Solanum sisymbrifolium	SI*, SC	D	[100]	[34]
Solanum sitiens	SI	D	[75]	[3]
Solanum stagnale	SC	D	[100]	[14]
Solanum stoloniferum	SC†	P	[76, 98, 38]	[42]
Solanum stramonifolium	SC	D	[100]	[34, 14]
Solanum stuckertii	SI	D	[19, 66]	[34]
Solanum tabanoense	SI	D	[100, 64]	[13]
Solanum tenuispinum	SC	D	[22]	[4]
Solanum torvum	SC	D*, P	[100]	[34, 78]
Solanum trachycarpum	SC	D	[100, 64, 7]	[6, 13]
Solanum tridynamum	SC	D	[79]	[54]
Solanum triflorum	SC	D	[22]	[11, 78]
Solanum tripartitum	SC	D	[22]	[4]
Solanum tuberosum	SI*, SC	D*, P	[52, 48]	[52, 48]
Solanum unilobum	SI	D	[17]	[3]
Solanum verrucosum	SC	D*, P	[100]	[42]
Solanum vestissimum	SC	D	[100]	[34, 14]
Solanum viarum	SC	D	[3]	[34, 25]
Solanum villosum	SC	P	[31]	[32, 78, 83]
Solanum virginianum	SC	D	[100, 79]	[34]
Vassobia breviflora	SC	D	[84]	[34]
Withania somnifera	SC	P	[47]	[34]
Witheringia macrantha	SI	D	[85]	[85]
Witheringia solanacea	SI*, SC	D	[18]	[85]

* for polymorphic species, the state used in the analysis

† sources listed report SC in conflict with Marks (1965) assignment

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