New Phytologist

Research

Correlated evolution of self-incompatibility and clonal reproduction in *Solanum* (Solanaceae)

Mario Vallejo-Marín[1,2] and Heath E. O'Brien[1]

[1]Biology Department, Duke University, Durham, NC 27708, USA; [2]Present address: Department of Ecology & Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada

Author for correspondence:
Mario Vallejo-Marín
Tel: (416) 978 5603
Fax: (416) 978 5878
Email: mvallejo@botany.utoronto.ca

Received: *14 July 2006*
Accepted: *22 September 2006*

Summary

• It has been suggested that clonality provides reproductive assurance in cross-fertilizing species subject to pollen limitation, relieving one of the main selective pressures favoring the evolution of self-fertilization. According to this hypothesis, cross-fertilizing species subject to pollen limitation should often be clonal. Here, we investigated the association between clonality and a genetic mechanism enforcing outcrossing, self-incompatibility, in *Solanum* (Solanaceae).

• We collected self-incompatibility and clonality information on 87 species, and looked for an association between these two traits. To account for the contribution of shared evolutionary history to this association, we incorporated phylogenetic information from chloroplast (NADH dehydrogenase subunit F) sequence data.

• We found that self-incompatibility is strongly associated with clonal reproduction: all self-incompatible species reproduce clonally, while the absence of clonality is widespread among self-compatible taxa. The observed correlation persists after taking into account shared phylogenetic history, assumptions about the evolutionary history of self-incompatibility, uncertainty associated with phylogeny estimation, and associations with life history (annual/perennial).

• Our results are consistent with the hypothesis that clonality provides reproductive assurance, and suggest that the consequences of clonal growth in the evolution of plant reproductive strategies may be more significant than previously thought.

Key words: asexual reproduction, mating system, phylogenetic analysis, reproductive assurance, self-compatibility, Solanaceae, *Solanum*.

New Phytologist (2007) **173**: 415–421

© The Authors (2006). Journal compilation © *New Phytologist* (2006)
doi: 10.1111/j.1469-8137.2006.01924.x

Introduction

Most flowering plants are potentially self-fertilizing hermaphrodites, yet a vast number of species display mechanisms that encourage or enforce cross-fertilization (Darwin, 1876). Cross-fertilization is thought to be advantageous under certain conditions because it reduces inbreeding, which is often associated with the production of offspring of lower genetic quality. However, alleles favoring mechanisms enforcing cross-fertilization may incur high evolutionary costs if low pollinator or mate availability in turn limits reproductive success (Burd, 1994; Larson & Barrett, 2000; Vallejo-Marín & Uyenoyama, 2004; Knight *et al.*, 2005). In fact, the ability to reproduce under conditions unfavorable for cross-fertilization, i.e. reproductive assurance, is considered to be a major selective force driving the evolution of self-fertilization (Darwin, 1876; Baker, 1955; Stebbins, 1957; Schoen *et al.*, 1996; Pannell & Barrett, 1998). Self-fertilization allows individuals to produce offspring even when the availability of compatible mates or pollinators limits the success of cross-fertilization (hereafter 'pollen limitation').

When other mechanisms provide reproductive assurance, the selective advantage of self-fertilization may be reduced. Vegetative (clonal) reproduction, which occurs concurrently with sexual reproduction in a large proportion of flowering plants (Richards, 1986), may provide an alternative way to

achieve reproductive assurance. In this sense, clonality may act as a mechanism of uniparental reproduction comparable to selfing (Nagylaki, 1976; Charlesworth, 1980) that allows a genotype to persist and increase in numbers under conditions of pollen limitation (Baker, 1955; Dole, 1992; Holsinger, 2000). In species that are often subject to pollen limitation, such as colonizing species, clonality may thus relieve the selective pressure favoring the breakdown of outcrossing mechanisms. A simple prediction arising from this hypothesis is that obligate outcrossing should often be associated with the ability to reproduce clonally in colonizing species.

In this study we assessed whether clonal reproduction and self-incompatibility, a genetic mechanism enforcing cross-fertilization, are associated in a plant group that includes many colonizing taxa. We focused on *Solanum* (Solanaceae), which exhibits variation among species in self-incompatibility and clonality (defined here as the ability to spread vegetatively through root- or stem-derived organs) (Whalen & Anderson, 1981). *Solanum* is a widespread genus composed of over 1000 species (D'Arcy, 1972; Nee, 1999) that comprises important crops (e.g. *Solamun tuberosum* (potato) and *Solanum melongena* (eggplant)) as well as noxious weeds (e.g. *Solanum carolinense* (horsenettle) and *Solanum eleagnifolium* (silverleaf nightshade)). Plants in this genus often occur as colonizers of open, disturbed or ephemeral habitats such as old-fields, forest edges or seasonally dried water-pools (Whalen, 1979; Symon, 1981; Nee, 1999), and are thus expected to grow in conditions conducive to pollinator and mate limitation (Wilcock & Neiland, 2002). Indeed, pollen limitation has been shown experimentally for *S. carolinense* (Steven *et al.*, 1999). The mechanism of self-incompatibility in the Solanaceae is gametophytic (de Nettancourt, 1977), which precludes the fertilization of ovules by pollen matching the same (haploid) allele at the self-incompatibility locus (*S*-locus) as either of the two alleles carried by the maternal plant. *Solanum* species have served as a model system for studies of the evolutionary dynamics of self-incompatibility (Igic *et al.*, 2004, 2006; Stone, 2004). Studies suggest that self-incompatible (SI) is the ancestral state in *Solanum*, and that evolutionary transitions to a self-compatibile (SC) state are irreversible (Igic *et al.*, 2004, 2006). Although the extent to which the breakdown of a SI state always increases self-fertilization in natural populations of *Solanum* is not known, this breakdown is a prerequisite for the evolution of self-fertilization, and it has been shown in other species that the frequency of SC variants in SI populations is strongly associated with changes in mating system and genetic diversity (e.g. Mable *et al.*, 2005).

We performed an analysis of the association between clonality and self-incompatibility in a representative subset of species. Species may share traits that evolved in their common ancestor, and therefore may represent nonindependent data, inflating the statistical significance of associations among traits (Felsenstein, 1985; Harvey & Pagel, 1991). We accounted for this by using methods that explicitly incorporate information about the phylogenetic relationships among taxa. In addition, our analyses allowed us to account for the uncertainty inherent in phylogenetic reconstruction, as well as for associations between clonality and life history (annual or perennial). Our results indicate that self-incompatibility and clonality have indeed evolved in a correlated fashion in *Solanum*. We briefly discuss the implication of our results for assessing potential evolutionary scenarios that may help to explain the distribution of clonality and self-incompatibility in flowering plants.

Materials and Methods

Assignment of character states

We collected information on self-incompatibility, clonal reproduction, and life history (annual/perennial) for as many *Solanum* species as possible through extensive bibliographical searches (see References in the supplementary material, Table S1). We scored species as SI or SC as reported in the literature. This scoring generally meant that an author considered a species SI if it failed to set fruit or had extremely low seed set after self-pollination, and SC if it set fruit either autonomously or following artificial self-pollination. Species were considered clonal if they had the ability to spread vegetatively through root- or stem-derived organs. In *Solanum* these are the two only mechanisms of clonal growth reported in the literature. Taxa were assigned to one of two life history groups; strict annuals, and perennials including short-lived species that can occur as annuals. In this genus all reported clonal species are perennial (e.g. Symon, 1981), and thus clonal species for which no data on life history were available were scored as perennials in our survey. We determined the state of missing characters (at least one character missing in $n = 50$ species; see Supplementary Material, Table S1) through direct observations of material grown in pollinator-free glasshouses (Duke University, Durham, NC, USA and Radboud University, Nijmegen, the Netherlands). For these species, a SC state was assumed if abundant autonomous seed set was observed in plants. Species were scored as nonclonal unless there was clear evidence of spontaneous formation of additional shoots or if above-ground stems rooted at the nodes. If the plant was a woody shrub or tree it was scored as a perennial. We obtained information on all three characters for 87 species for which a full list of references is given in the supplementary material (Table S1). Our sample represents ~9% of species in the genus, and includes five *Solanum* subgenera (*sensu* D'Arcy, 1991) (Fig. 1). Because this is admittedly a small sample, the analyses presented here may only detect strong evolutionary associations between characters. Thirty-three species in our sample (38%) were SI, which is close to the estimates for SI taxa in the Solanaceae (39%, Igic *et al.*, 2004). Among all species, 50 were clonal perennials, 26 nonclonal perennials, and 11 strict annuals (Table 1).

 © The Authors (2006). Journal compilation © *New Phytologist* (2006)

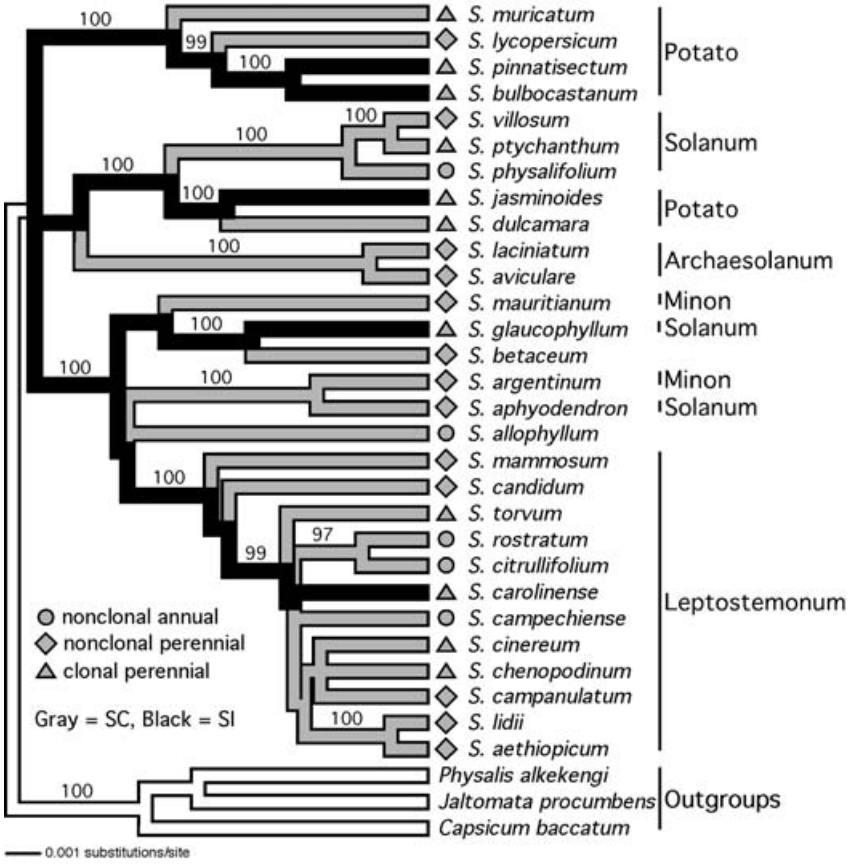


Fig. 1 Phylogenetic distribution of mating system (self-incompatible/self-compatible) and life history in the genus *Solanum*. Shading on branches represents ancestral character reconstruction of mating system, assuming that transitions from self-incompatible (SI, black) to self-compatible (SC, gray) are irreversible starting from a SI ancestor (see Igic *et al*., 2004, 2006). Symbols beside taxon names indicate life history (circles, annual; diamonds, nonclonal perennial; triangles, clonal perennial). Taxa from five subgenera *sensu* D'Arcy (1991) are included, as indicated to the right of the species names.

Table 1 Distribution of self-incompatibility, clonality, and life history in 87 *Solanum* species

	Clonal perennial	Nonclonal perennial	Annual	Total
Self-incompatible (SI)	33	0	0	33
Self-compatible (SC)	17	26	11	54
Total	50	26	11	87

Associations between self-incompatibility and clonality

Using two states for self-incompatibility and three states for life history (SI or SC, and clonal perennials, nonclonal perennials or strict annuals, respectively), we performed a 3×2 χ^2 test of the null hypothesis that self-incompatibility status is independently distributed in relation to the ability to reproduce clonally. Because any observed departure from a random distribution of character states could be a result of the association between annual life history and SC, we excluded strict annuals and performed a 2×2 χ^2 test on the resulting data set. This latter analysis tests the null hypothesis that self-incompatibility and the ability to reproduce clonally are independently distributed in perennial plants, while controlling for associations between SC and annual life history.

Phylogenetic analyses

To correct for shared phylogenetic history among taxa, tests of correlated evolution were performed in a subset of the species for which molecular information (NADH dehydrogenase subunit F (*ndh*F)) was available to infer phylogenetic relationships (Bohs, 2005). Analyses were conducted on all available *Solanum* species and on a subset including only perennial taxa.

Data assembly and phylogenetic tree sampling Partial chloroplast *ndh*F sequences from Bohs (2005) were obtained from GenBank and manually aligned. We performed heuristic searches using maximum likelihood (ML) with 10 random sequence addition replicates using PAUP* 4.0b10 (Swoford, 2003). To assess branch support and to determine the effect of topological uncertainty, we also conducted Bayesian Markov chain Monte Carlo (MCMC) analyses (1.5 million generations plus 0.5 million generations burn in; sampling every 500 generations) using MRBAYES 3.0 (Huelsenback & Ronquist, 2001). We pruned outgroup taxa from the phylogenies and recalculated branch lengths using ML with the molecular clock enforced using PAUP*.

Correlated evolution analysis We used Pagel's phylogenetic methods (Pagel, 1994; Pagel & Meade, 2006) for detecting correlated evolution between two binary characters. To test for a correlation between self-incompatibility and life history (annual/perennial) we grouped clonal and nonclonal perennials, and compared them against annuals. To test for correlated evolution between self-incompatibility and clonality, we compared nonclonal perennials and annuals with clonal perennials, and compared nonclonal perennials with clonal perennials to account for the contribution of annual life history.

Tests of correlated evolution were performed with the programs DISCRETE and BAYES MULTISTATE AND DISCRETE (Pagel, 1994; Pagel & Meade, 2006), using the ML option. Statistical significance was assessed by comparing the likelihood ratio (LR) test statistic of the independent and dependent models (i.e. −2LR) to a χ^2 distribution with 3 degrees of freedom (d.f.), as recommended for data sets with a small number of taxa (Pagel, 1994). Empirical *P*-values obtained through 1000 Monte Carlo simulations (Pagel, 1994) indicated that a χ^2 distribution with 3 d.f. was a slightly conservative criterion for the present analyses (data not shown). The effect of topological uncertainty was assessed by repeating the correlation analysis on the 2000 topologies obtained from the MCMC tree samples. The consequences of assigning SI as the ancestral state, and restricting back transitions to SC to zero (Igic *et al.*, 2004, 2006), were evaluated in DISCRETE. These two restrictions were also used to calculate transition rates among character states (q_{ij}) in the correlated evolution model.

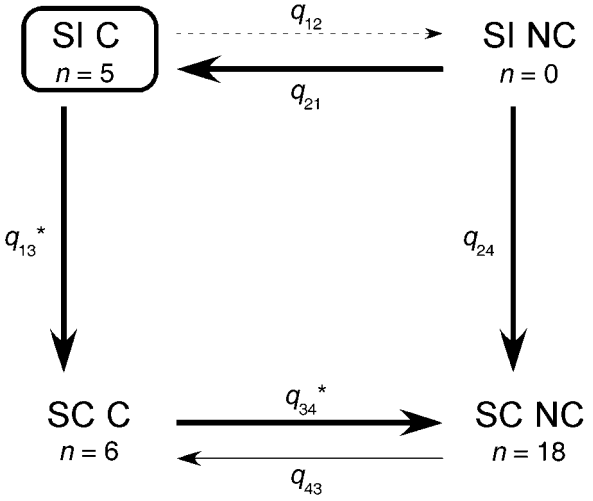


Fig. 2 Transition rates between the four possible character-state combinations for two binary characters (self-incompatibility and clonality) among sampled *Solanum* species. The parameter q_{ij} represents transitions from state *i* to state *j*. 1, self-incompatible, clonal (SI C); 2, self-incompatible, nonclonal (SI NC); 3, self-compatible, clonal (SC C); 4, self-compatible, nonclonal (SC NC). The model used to calculate the transition rates assumes that self-incompatibility is the ancestral state in the group (circled), and that transitions from self-incompatibility to self-conpatibility are irreversible (Igic *et al*., 2004, 2006) ($q_{31} = q_{42} = 0.00001$; lines not shown). Line types indicate the magnitude of the transition rates: $q_{ij} < 1$, dashed line; $q_{ij} < 10$, thin line; $q_{ij} < 100$, thick line. *, transition rates significantly greater than zero. Values and significance of individual transition rates are provided in Table 2. *n*, number of taxa in each character state combination.

Results

We detected a strong departure from random association between the ability to reproduce clonally and the presence/absence of self-incompatibility ($\chi^2 = 39.343$, $P < 0.0001$, $n = 87$). This nonrandom distribution remained highly significant when annual plants were excluded from the analysis ($\chi^2 = 32.621$, $P < 0.0001$, $n = 76$). In the sample analyzed here, all SI species were clonal, and all strict annuals were SC (Table 1). Perenniality by itself was not a good predictor of self-incompatibility as perennials were equally likely to be SI or SC (40 and 60%, respectively; $\chi^2 = 1.883$, $P = 0.169$, $n = 43$; Table 1).

Our phylogenetic analyses indicate that the observed association between clonality and self-incompatibility cannot be explained exclusively by shared phylogenetic history. We detected a correlation between self-incompatibility and clonality based on the results of our correlated character analysis using the phylogenetic relationships suggested by the ML tree (LR = 10.53, $P = 0.014$, $n = 29$ species; Fig. 1). To control for the contribution of annual life history to the observed correlation, we conducted a further analysis excluding annual species. When annual species were excluded, the correlation between SI/SC and clonality was significant on the ML tree (LR = 8.13, $P = 0.043$, $n = 24$ species) as well as on all of the 2000 topologies of our Bayesian tree sample (LR range = 8.09–8.24). By contrast, we failed to reject the model of independent evolution between mating system and life history when comparing perennials (both clonal and nonclonal) and annuals (LR = 2.13, $P = 0.543$, $n = 29$ species), and this correlation was not significant in any of the 2000 topologies in our Bayesian tree sample (LR range = 1.30–3.80). The correlation between self-incompatibility and clonality was not affected by restricting the ancestral state of mating system to SI and setting back transitions from SC to SI to zero (LR = 10.80, $P = 0.012$, $n = 29$ species). Transition rates among character states are graphically shown in Fig. 2, and their numerical values are presented in Table 2. Only the transitions from SI/clonal to SC/clonal (q_{13}), and from SC/clonal to SC/nonclonal (q_{34}) were statistically different from zero (Fig. 2, Table 2).

Discussion

Our results demonstrate a strong correlation between self-incompatibility and clonality. This correlation persisted after incorporation of phylogenetic relationships among taxa,

 © The Authors (2006). Journal compilation © *New Phytologist* (2006)

Table 2 Likelihood ratios (LRs) of models excluding one of the transition rates (q_{ij}) compared with a model in which this particular rate is freely estimated

Parameter	Maximum likelihood estimate	−2LR	*P*-value
q_{12}	0.000562	−0.00034	0.9852
q_{13}	23.29191	3.823523	0.050
q_{21}	22.303968	0.000226	0.988
q_{24}	45.553848	−0.00018	0.989
q_{34}	50.004586	5.790648	0.016
q_{43}	6.7496	0.430665	0.511

The parameter q_{ij} represents transitions from state *i* to state *j*. 1, self-incompatible (SI), clonal; 2, SI, nonclonal; 3, self-compatible (SC), clonal; 4, SC, nonclonal. All models assume that SI/clonal is the ancestral state, and that transitions from SI to SC are irreversible (i.e. $q_{31} = q_{42} \sim 0$; Fig. 2) (Igic *et al*., 2004, 2006; see Discussion section).

different assumptions about the evolutionary history of self-incompatibility, and uncertainty associated with phylogeny estimation, and after exclusion of annual species from the analysis. All SI species in our data set were recorded as clonal, consistent with the hypothesis that clonality provides reproductive assurance in species subject to pollen-limited conditions. However, like all correlations, this relationship does not necessarily imply causation. It is possible that both traits have evolved as a correlated response to the same environmental variable, or as a by-product of genetic correlations with an unmeasured character. Furthermore, clonal reproduction may alter other important mating components in addition to providing reproductive assurance, which may result in correlated evolution between self-incompatibility and clonality. Below we briefly outline two additional mechanisms that have the potential to affect the evolution of reproductive systems including self-incompatibility.

First, clonal growth alters the spatial arrangement of flowers and inflorescences, affecting patterns of pollen transfer and changing the rate of self-pollination through geitonogamy (i.e. pollen transfer among flowers of the same plant) (Cook, 1983; Handel, 1983, 1985; Charpentier, 2002). Clonality can increase geitonogamy between flowers of the same genetic individual or genet by increasing both the size of floral displays and the distance between different genets (Handel, 1985; Charpentier, 2002). Because geitonogamy requires pollen vectors regularly involved in outcrossing, an increase in geitonogamy may in turn reduce the numbers of both ovules and pollen grains available for cross-fertilization (Lloyd, 1992). Empirical evidence suggests that clonality may indeed increase the production of selfed offspring because of geitonogamy (Handel, 1985; Eckert, 2000) and reduce pollen export to other genets (Handel, 1985; Reusch, 2001). Changes in mating patterns as a result of clonal reproduction may result in correlated evolution of self-incompatibility and clonality. For instance, it has been proposed that the avoidance of self-fertilization promotes SI expression in animal-pollinated species (Arroyo, 1976). Unfortunately, we are not aware of any studies providing quantitative estimates of the extent to which clonal propagation influences self-fertilization in natural populations of *Solanum* species.

Secondly, theoretical studies suggest that clonality has the potential to change the degree of inbreeding depression through its effects on life-span and (somatic) mutation rates (Morgan *et al*., 1997; Muirhead & Lande, 1997; Morgan, 2001; see also Scofield & Schultz, 2006). The specific effects of clonality on inbreeding depression (fitness of selfed/outcrossed offspring) depend on the assumptions of the different models and parameter values, but clonality has been found to increase (Morgan *et al*., 1997; Muirhead & Lande, 1997) as well as decrease (Morgan, 2001) inbreeding depression relative to nonclonal taxa. Changes in inbreeding depression associated with clonality may either facilitate the maintenance of self-incompatibility (high inbreeding depression) or promote its breakdown (low inbreeding depression) (Charlesworth & Charlesworth, 1979; Uyenoyama, 1988; Steinbachs & Holsinger, 1999). To the extent that clonality does increase inbreeding depression in *Solanum*, the higher genetic cost of producing inbred offspring may favor the maintenance of self-incompatibility (Morgan *et al*., 1997; Muirhead & Lande, 1997). Empirical surveys of inbreeding depression in clonal and nonclonal species in *Solanum* and other taxa are needed to evaluate the specific effect of clonality on the degree of inbreeding depression.

The hypothesis of clonality conferring reproductive assurance provides a scenario for the evolutionary sequence of character states. Self-incompatibility is thought to be ancestral in *Solanum* because polymorphisms at the *S*-locus are shared with SI species in other genera of the Solanaceae (Igic *et al*., 2004, 2006). As all extant SI species examined are clonal (supplementary material, Table S1), we assume that the ancestor was SI/clonal (SI/C; Fig. 2). Under this scenario, clonality in SI/C taxa is maintained though selection favoring reproductive assurance, and thus transitions towards SI/nonclonal (SI/NC) should be rare. By contrast, the transition away from the SI/C state should occur more often when SI breaks down first, yielding SC/clonal taxa (SC/C). Consistent with this sequence of events, the magnitude of the transition rate from SI/C to SI/NC (q_{12}) is low and undistinguishable from zero, while the transition rate from SI/C to SC/C (q_{13}) is larger and statistically different from zero (Fig. 2, Table 2). Subsequently, in SC/C taxa, clonality may be maintained or lost according to the ecological pressures acting on each species, although our analysis suggests that the transition from SC/C to SC/NC is relatively frequent (Fig. 2). Although further studies are required to establish why clonality may be disfavored in SC taxa, some possibilities include selection to reduce self-fertilization among plants of the same genetic

individual, or a reduced selective advantage of clonality in taxa in which selfing already provides a mechanism of uniparental reproduction (cf. Charlesworth, 1980).

Perhaps because of the wide occurrence of joint sexual and asexual reproduction in a large number of angiosperms (Richards, 1986), the consequences of clonality for mating system evolution have increasingly attracted the attention of evolutionary biologists (e.g. Stebbins, 1950; Handel, 1985; Eckert, 2000; Reusch, 2001; Charpentier, 2002; Dorken & Barrett, 2003). Our results demonstrate that, in *Solanum*, self-incompatibility and clonality do not evolve independently. Although further studies are required to test whether mating system and the ability to reproduce clonally, as well as the type of clonal growth (e.g. phalanx vs guerrilla strategies), evolve in a correlated manner in other taxa (cf. grasses, Stebbins, 1950; see also Ruggiero *et al.*, 2005), our results suggest that the consequences of clonal growth in the evolution of reproductive strategies may prove wider than previously acknowledged.

Acknowledgements

We thank M. Uyenoyama, M. Rausher, W. Morris, A. Case, S. Barrett, and the Rausher Laboratory for comments and discussion, and B. Calhoun and M. Smith-DeCoster for assistance. M. Nee generously provided his expertise in *Solanum*, and M. Cipollini kindly contributed seed material. J. Stuefer facilitated research at Radboud University, and offered stimulating discussions on clonality and mating systems. Sonia Sultan and three reviewers provided valuable suggestions on a previous version of the manuscript. This study was partially supported by a CONACyT (Mexico) fellowship and an OTS research award to M.V.M., and an A. W. Mellon Foundation Graduate Training Grant to H.E.O.

References

Arroyo MTK. 1976. Geitonogamy in animal pollinated tropical angiosperms. A stimulus for the evolution of self-incompatibility. *Taxon* **25**: 543–548.

Baker HG. 1955. Self-compatibility and establishment after 'long distance' dispersal. *Evolution* **9**: 347–349.

Bohs L. 2005. Major clades in *Solanum* based on *ndh*F sequence data. In: Croat TB, ed. *A Fetschrift for William G. D'Arcy*. St Louis, MO, USA: Missouri Botanical Garden, 27–49.

Burd M. 1994. Bateman's principle and plant reproduction: The role of pollen limitation in fruit and seed set. *Botanical Review* **60**: 83–139.

Charlesworth B. 1980. The cost of sex in relation to mating system. *Journal of Theoretical Biology* **84**: 655–671.

Charlesworth D, Charlesworth B. 1979. The evolution and breakdown of *S*-allele systems. *Heredity* **43**: 41–55.

Charpentier A. 2002. Consequences of clonal growth for plant mating. *Evolutionary Ecology* **15**: 521–530.

Cook RE. 1983. Clonal plant-populations. *American Scientist* **71**: 244–253.

D'Arcy WG. 1972. Solanaceae studies II: Typification of subdivisions of *Solanum*. *Annals of the Missouri Botanical Garden* **59**: 262–278.

D'Arcy WG. 1991. The Solanaceae since 1976, with a review of its biogeography. In: Hawkes JG, Lester RN, Nee M, Estrada RN, eds. *Solanaceae III: taxonomy, chemistry, evolution*. London, UK: Kew Royal Botanical Gardens, 75–137.

Darwin C. 1876. *The effects of cross- and self-fertilization in the vegetable kingdom*. London, UK: John Murray.

Dole JA. 1992. Reproductive assurance mechanisms in 3 taxa of the *Mimulus guttatus* complex (Schrophularaceae). *American Journal of Botany* **79**: 650–659.

Dorken ME, Barrett SCH. 2003. Life-history differentiation and the maintenance of monoecy and dioecy in *Sagittaria latifolia* (Alismataceae). *Evolution* **57**: 1973–1988.

Eckert CG. 2000. Contributions of autogamy and geitonogamy to self-fertilization in a mass-flowering, clonal plant. *Ecology* **81**: 532–542.

Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**: 1–15.

Handel SN. 1983. Pollination ecology, plant population structure, and gene flow. In: Real L, ed. *Pollination Biology*. New York, NY, USA: Academic Press, 163–211.

Handel SN. 1985. The intrusion of clonal growth patterns on plant breeding systems. *American Naturalist* **125**: 367–383.

Harvey PH, Pagel MD. 1991. *The comparative method in evolutionary biology*. New York, NY, USA: Oxford University Press.

Holsinger KE. 2000. Reproductive systems and evolution in vascular plants. *Proceedings of the National Academy of Sciences, USA* **97**: 7037–7042.

Huelsenback JP, Ronquist F. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.

Igic B, Bohs L, Kohn JR. 2004. Historical inferences from the self-incompatibility locus. *New Phytologist* **161**: 97–105.

Igic B, Bohs L, Kohn JR. 2006. Ancient polymorphism reveals unidirectional breeding system shifts. *Proceedings of the National Academy of Sciences, USA* **103**: 1359–1363.

Knight TM, Steets JA, Vamosi JC, Mazer SJ, Burd M, Campbell DR, Dudash MR, Johnston MO, Mitchell RJ, Ashman TL. 2005. Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology Evolution and Systematics* **36**: 467–497.

Larson BMH, Barrett SCH. 2000. A comparative analysis of pollen limitation in flowering plants. *Biological Journal of the Linnean Society* **69**: 503–520.

Lloyd DG. 1992. Self-fertilization and cross-fertilization in plants. II. The selection of self-fertilization. *International Journal of Plant Sciences* **153**: 370–380.

Mable BK, Robertson AV, Dart S, Di Berardo C, Witham L. 2005. Breakdown of self-incompatibility in the perennial *Arabidopsis lyrata* (Brassicaceae) and its genetic consequences. *Evolution* **59**: 1437–1448.

Morgan MT. 2001. Consequences of life history for inbreeding depression and mating system evolution in plants. *Proceedings of the Royal Society of London Series B* **268**: 1817–1824.

Morgan MT, Schoen DJ, Bataillon TM. 1997. The evolution of self-fertilization in perennials. *American Naturalist* **150**: 618–638.

Muirhead CA, Lande R. 1997. Inbreeding depression under joint selfing, outcrossing, and asexuality. *Evolution* **51**: 1409–1415.

Nagylaki T. 1976. A model for the evolution of self-fertilization and vegetative reproduction. *Journal of Theoretical Biology* **58**: 55–58.

Nee M. 1999. Synopsis of *Solanum* in the New World. In: Nee M, Symon DE, Lester RNJ, eds. *Solanaceae IV*. London, UK: Kew Royal Botanical Gardens, 285–333.

de Nettancourt D. 1977. *Incompatibility in Angiosperms*. Berlin, Germany: Springer.

Pagel MD. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Academy of Science London B* **255**: 37–45.

Pagel M, Meade A. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *American Naturalist* **167**: 808–825.

Pannell JR, Barrett SCH. 1998. Baker's law revisited: reproductive assurance in a metapopulation. *Evolution* **52**: 657–668.

 © The Authors (2006). Journal compilation © *New Phytologist* (2006)

Reusch TBH. 2001. Fitness-consequences of geitonogamous selfing in a clonal marine angiosperm (*Zostera marina*). *Journal of Evolutionary Biology* **14**: 129–138.

Richards AJ. 1986. *Plant breeding systems*. London, UK: Chapman & Hall.

Ruggiero MV, Capone S, Pirozzi P, Reusch TBH, Procaccini G. 2005. Mating system and clonal architecture: a comparative study in two marine angiosperms. *Evolutionary Ecology* **19**: 487–499.

Schoen DJ, Morgan MT, Bataillon T. 1996. How does self-pollination evolve? Inferences from floral ecology and molecular genetic variation. *Philosophical Transactions of the Royal Society of London Series B* **351**: 1281–1290.

Scofield DG, Schultz ST. 2006. Mitosis, stature and evolution of plant mating systems: low-Phi and high-Phi plants. *Proceedings of the Royal Society of London B* **273**: 275–282.

Stebbins GL. 1950. *Variation and evolution in plants*. New York, NY, USA: Columbia University Press.

Stebbins GL. 1957. Self fertilization and population variability in higher plants. *American Naturalist* **91**: 337–354.

Steinbachs JE, Holsinger KE. 1999. Pollen transfer dynamics and the evolution of gametophytic self-incompatibility. *Journal of Evolutionary Biology* **12**: 770–778.

Steven JC, Peroni PA, Rowell E. 1999. The effects of pollen addition on fruit set and sex expression in the andromonoecious herb Horsenettle (*Solanum carolinense*). *American Midland Naturalist* **141**: 247–252.

Stone JL. 2004. Sheltered load associated with *S*-alleles in *Solanum carolinense*. *Heredity* **92**: 335–342.

Swoford DL. 2003. PAUP*. *Phylogenetic analysis using parsimony (and other methods) (version 4.0b10 ed.)*. Sunderland, MA, USA: Sinauer Associates Inc.

Symon DE. 1981. A revision of the genus *Solanum* in Australia. *Journal of the Adelaide Botanical Gardens* **4**: 1–367.

Uyenoyama MK. 1988. On the evolution of genetic incompatibility systems IV. Modification of response to an existing antigen polymorphism under partial selfing. *Theoretical Population Biology* **34**: 347–377.

Vallejo-Marín M, Uyenoyama MK. 2004. On the evolutionary costs of self-incompatibility: incomplete reproductive compensation due to pollen limitation. *Evolution* **58**: 1924–1935.

Whalen MD. 1979. Taxonomy of *Solanum* section *Androceras*. *Gentes Herbarum* **11**: 359–426.

Whalen MD, Anderson GJ. 1981. Distribution of gametophytic self-incompatibility and infrageneric classification in *Solanum*. *Taxon* **30**: 761–767.

Wilcock C, Neiland R. 2002. Pollination failure in plants: why it happens and when it matters. *Trends in Plant Science* **7**: 270–277.

Supplementary Material

The following supplementary material is available for this article online:

Table S1 Data on self-incompatibility, clonality, and life-history for 87 species of *Solanum* included in this study

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-8137.2006.01924.x
(This link will take you to the article abstract.)

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than about missing material) should be directed to the corresponding author for the article.



About *New Phytologist*

- *New Phytologist* is owned by a non-profit-making **charitable trust** dedicated to the promotion of plant science, facilitating projects from symposia to open access for our Tansley reviews. Complete information is available at **www.newphytologist.org**.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as-ready' via *OnlineEarly* – our average submission to decision time is just 30 days. Online-only colour is **free**, and essential print colour costs will be met if necessary. We also provide 25 offprints as well as a PDF for each article.
- For online summaries and ToC alerts, go to the website and click on 'Journal online'. You can take out a **personal subscription** to the journal for a fraction of the institutional price. Rates start at £131 in Europe/$244 in the USA & Canada for the online edition (click on 'Subscribe' at the website).
- If you have any questions, do get in touch with Central Office (**newphytol@lancaster.ac.uk**; tel +44 1524 594691) or, for a local contact in North America, the US Office (**newphytol@ornl.gov**; tel +1 865 576 5261).