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Article Addendum

The Paradox of Clonality and the Evolution of Self-Incompatibility

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Addendum to:

Correlated Evolution of Self-Incompatibility and Clonal Reproduction in Solanum (Solanaceae)

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ABSTRACT

In the January issue of *New Phytologist* Vallejo-Marín and O'Brien[1] documented that in the genus *Solanum* (Solanaceae) clonality and self-incompatibility, a common genetic mechanism enforcing cross-fertilization, co-occur more often than expected by chance. Using a phylogenetic approach the authors showed that the statistical association between clonality and self-incompatibility persists even after taking into account phylogenetic relationships among species, uncertainty in the phylogenetic reconstruction, and associations between clonality and life history (annual/perennial). Vallejo-Marín and O'Brien[1] suggest that clonality and self-incompatibility tend to co-occur because clonality, by allowing the persistence and propagation of a genotype in environments with limited pollinator or mate availability, reduces the selective pressure favoring the breakdown of self-incompatibility. In addition to promoting the maintenance of self-incompatibility, when clonality results in the spatial aggregation of genetically identical individuals, clonality may promote its breakdown by restricting pollen transfer between different genotypes. Here I call attention to these contradictory predictions of the effects of clonality on the evolution of self-incompatibility, and suggest that the outcome of this paradox depend on both the extent to which clonal propagation compensates for limited seed production, and on the extent to which clonality reduces pollen transfer between genotypes.

Flowering plants display a variety of mechanisms preventing self-fertilization, among which self-incompatibility is one of the best studied.[2,3] In the genus *Solanum* (Solanaceae) ancestrally present self-incompatibility has broken down multiple independent times through out the evolutionary history of this group to give rise to self-compatible lineages.[4,5] The breakdown of outcrossing mechanisms, including self-incompatibility, is one of the most common and best studied evolutionary transitions in flowering plants.[6]

Self-incompatibility is a genetic mechanism by which the maternal plant can recognize and reject pollen grains expressing alleles in common with the maternal genotype.[7] The reproductive advantages of self-incompatibility can be understood as a balance between two forces. On one hand the rejection of pollen grains is a mechanism for the preferential support of outbred progeny which, generally, is of higher genetic quality. On the other hand, if pollen or pollinator availability is low, pollen grains that are rejected by the self-incompatibility mechanism may not be substituted, and thus some ovules would go unfertilized. The evolutionary maintenance of self-incompatibility depends on the relative benefit of producing higher quality offspring and the relative costs incurred by potential reduction in offspring number[8]

Plant clonality can affect the relative benefits and costs of self-incompatibility through its effects on the persistence and spatial distribution of genotypes. For instance, Vallejo-Marín and O'Brien[1] suggest that clonality provides reproductive assurance in colonizing taxa by allowing genotypes to persist and propagate even in the absence of conditions conducive to seed production. The reproductive assurance conferred by clonality would then relief the evolutionary costs of self-incompatibility incurred through reduced seed number, favoring the *maintenance* of self-incompatibility (Fig. 1).[1,9,10] In contrast, clonality may increase the evolutionary costs of self-incompatibility, by restricting pollen transfer between genotypes.[11,12] In some forms of clonal growth, dispersal of asexual propagules is very localized, resulting in an aggregation or clumping of genotypes. If spatial clumping restricts pollen flow between distinct genetic individuals, plants may not receive enough compatible pollen to fertilize all ovules (incomplete reproductive compensation) thus resulting in reduced seed set, which may favor the *breakdown* of self-incompatibility (Fig. 1).[8,12,13] It is important to note that both the maintenance and the breakdown effects mentioned

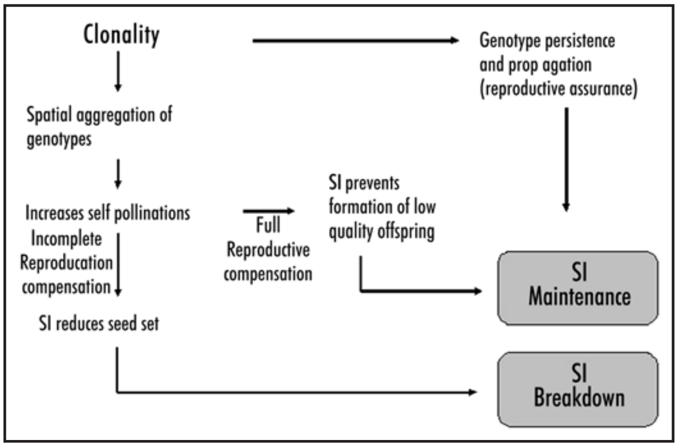

Figure 1. Potential consequences of clonality for the evolutionary maintenance of self-incompatibility (SI). Full reproductive compensation occurs when pollen grains rejected by the SI system can be replaced with other compatible pollen grains. Under full reproductive compensation, seed set is independent of the level of SI expression.[8] When pollen receipt is limited, rejected pollen grains cannot be always substituted (incomplete reproductive compensation) and consequently seed set is negatively related to the level of SI expression.[8] Notice that under similar ecological conditions, e.g., when pollen receipt is limited (outside arrows), clonality may both favor the maintenance of SI through reproductive assurance, and facilitate its breakdown through increasing within-genotype pollen transfer and reducing seed set.

above are expected to occur in the same ecological conditions, namely when the availability of pollen, pollinators, or compatible mates limit seed set (collectively known as pollen limitation).

A contrasting ecological scenario, may in turn favor the maintenance of self-incompatibility in clonal taxa. When pollen is abundant, and pollinators transport pollen through larger distances, enough pollen might still be received to fertilize all ovules even after accounting for pollen rejected by the self-incompatibility system (full reproductive compensation; Fig. 1). In this case, seed number will not be affected by the expression of self-incompatibility, but seed quality may be increased through the rejection of inbred pollen.[14] In other words, when pollen receipt does not limit seed number, the presence of clonality is expected to favor self-incompatibility as a mechanism to successfully screen inbred pollen originated from different individuals of the same genotype or clone.

To summarize, under the same ecological conditions (i.e., pollen limitation) the co-occurrence of clonality and self-incompatibility may have contrasting effects (Fig. 1). On one hand clonality favors the maintenance of self-incompatibility by providing reproductive assurance. On the other hand clonality may favor the breakdown of self-incompatibility, because rejected pollen cannot be compensated for, ensuing in a reduction in seed number. The resolution of the paradox of clonality for the evolution of self-incompatibility is likely to depend on the degree to which clonal propagation compensates for limited reproduction through seeds (e.g., during population establishment), as well as on the extent to which clonality reduces pollen flow between established genotypes, which in turn is affected by characteristics such as clonal architecture, plant density, and pollinator type and availability.[12,15,16]

Vallejo-Marín and O'Brien's data[1] suggest that in the colonizing genus *Solanum*, which is expected to experience pollen limiting conditions, clonality reduces the costs of self-incompatibility through reproductive assurance (maintenance effect) more than it increases the costs of self-incompatibility due to pollen flow within spatially clumped genotypes (breakdown effect). Future comparative studies of the association between self-incompatibility and clonality in other groups could help us determine the general conditions in which the maintenance effect outweighs the breakdown effect.

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