Evolution of inbreeding depression in species combining self-incompatibility and partial asexual reproduction

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EVOLUTION OF INBREEDING DEPRESSION IN SPECIES COMBINING SELF-INCOMPATIBILITY AND ASEXUAL REPRODUCTION

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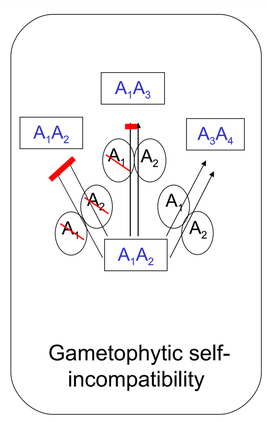
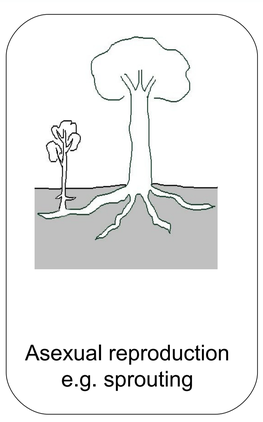
INTRODUCTION

The origin and maintaining of self-incompatibility systems in angiosperms are still debated questions. The level of inbreeding depression in species that show a self-incompatibility system is a key parameter for the maintenance of the system. Several studies were developed to predict when the system can breakdown. A decrease of inbreeding depression, but also a reduction in the number of alleles at the self-incompatibility locus and outcross polenn limitation, are generally associated with that breakdown. Two studies (Chen *et al*., 1997; Vallejo-Marín & O'Brien, 2007) have suggested that clonality could relieve the main selective pressures favouring the breakdown of self-incompatibility. In this study, we developed a model to simulate the evolution of inbreeding depression in a diploid species that reproduce both asexually and sexually with a self-incompatibility system. Our aim was to answer the following question:



Gametophytic self-incompatibility


Asexual reproduction e.g. sprouting

➡ **Does clonality allow maintaining self-incompatibility in plants?**

DESCRIPTION OF THE MODEL

N diploid hermaphroditic plants

Reproduction system
Clonal with probability *c*
Sexual with probability (1-*c*)
Gametophytic self-incompatibility controlled by a *S* locus

Modelled locus
2 neutral loci
S locus
Viability locus causing inbreeding depression

Random sample of one individual

Asexual reproduction
New individual that undergoes selection
Or sexual reproduction
Random sample of a second individual
Sample of a pollen grain
Iteration until a compatible cross is found
Zygote that undergoes selection
Until *N* individuals are formed

Mutation
μ_S for the *S* locus
μ_N for the neutral locus
μ_1 if the allele is *A*
μ_2 if the allele is *a*
for the viability locus

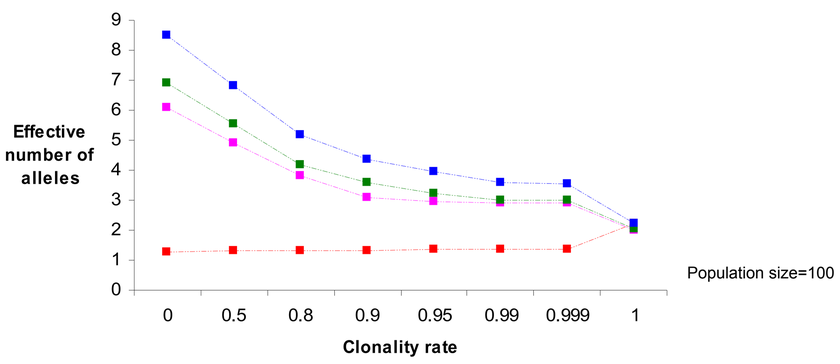
Principal monitored variables

For each locus
Observed heterozygosity
Expected heterozygosity
Allelic richness
Effective number of alleles
Within population fixation index
Linkage disequilibrium between each pair of loci

Viability locus
Inbreeding depression
Mutation load
Frequency of the deleterious allele

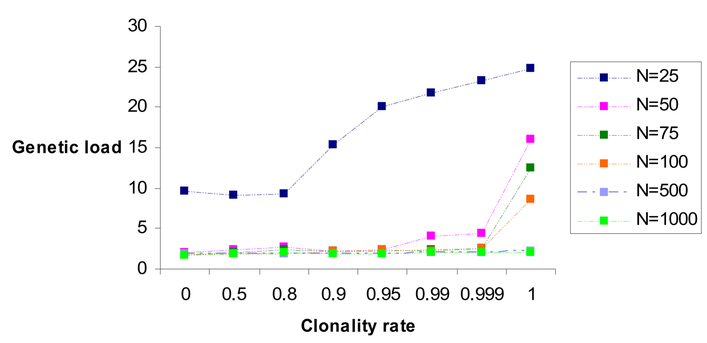
RESULTS

1. Effective number of alleles as a function of clonality



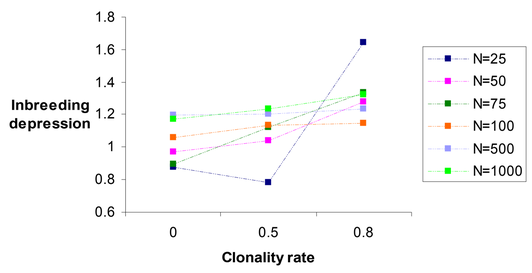
The effective number of alleles at neutral loci ($\mu_N=10^{-3}$) increases with clonality. Our results show that the effective number of S alleles decreases with mutation rate ($\mu_S=10^{-3}$, $\mu_S=10^{-4}$, $\mu_S=10^{-5}$) at the S locus but also with clonality.

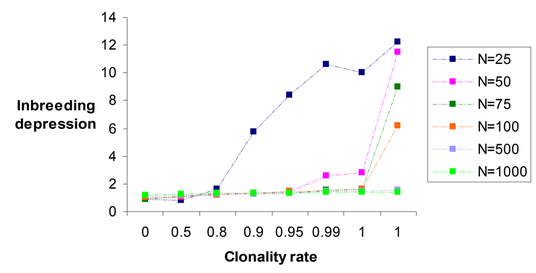
2. Mutation load as a function of population size and clonality



For a fixed clonality rate, the mean mutation load (selection coefficient=0.1 and dominance coefficient=0.2) increases as population size decreases. For a fixed initial population size, it increases as clonality rate increases (except for *N*=25 for which it slightly decreases between *c*=0 and *c*=0.5).

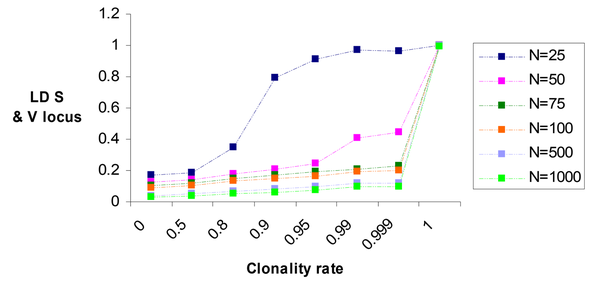
3. Inbreeding depression as a function of population size and clonality





For low clonality rates (*c*<0.8), inbreeding depression decreases when population size decreases. For *c*<0.8, inbreeding depression is higher in small populations than in large ones. Inbreeding depression increases with clonality rate (except for *N*=25 for which it slightly decreases between *c*=0 and *c*=0.5).

4. Linkage disequilibrium between the *S* locus and the viability locus as a function of population size and clonality



Linkage disequilibrium between all pairs of loci increases when clonality increases. The linkage between the S locus and any other locus was higher than the linkage between the other locus (data not shown).

CONCLUSIONS & PERSPECTIVES

Clonality favours heterozygosity at all loci (Balloux *et al*. 2003), homozygotes at the viability locus cannot be produced, and thus eliminated. As a result, the frequency of deleterious alleles (data not shown), mutation load and inbreeding depression increase with clonality. This effect is reinforced in small populations. At the same time, our results showed that a strong linkage disequilibrium is created between the *S* locus and the viability locus while increasing clonality, this can theoretically also reinforces polymorphism at the viability locus (Glémin *et al*. 2001). Simulations without self-incompatibility are necessary to disentangle the effect of clonality alone and the effect of self-incompatibility on the viability locus.

As a consequence, clonality can theoretically favours maintaining self-incompatibility in populations. However, since our results also showed that the effective number of *S* alleles decreased with clonality, this may create cases for which self-incompatibility can breakdown.

Balloux F, Lehmann L, De Meeûs T. 2003. The population genetics of clonal and partially clonal diploids. *Genetics* 164: 1635-1644.
Chen L, James SH, Stace HM. 1997. Self-incompatibility, seed abortion and clonality in the breeding systems of several western Australian *Drosera* species (Droseraceae). *Autralian Journal of Botany* **45**: 191-201.
Glémin S, Bataillon T, Ronfort J, Mignot A, Olivieri I. 2001. Inbreeding depression in small populations of self-incompatible plants. *Genetics* **159**: 1217-1229.
Vallejo-Marín M, O'Brien HE. 2007. Correlated evolution of self-incompatibility and clonal reproduction in *Solanum* (Solanaceae). *New Phytologist* **173**: 415-421.