EVOLUTION OF DOMINANCE IN SPOROPHYTIC SELF-INCOMPATIBILITY SYSTEMS: I. GENETIC LOAD AND COEVOLUTION OF LEVELS OF DOMINANCE IN POLLEN AND PISTIL

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Recent theoretical advances have suggested that various forms of balancing selection may promote the evolution of dominance through an increase of the proportion of heterozygote genotypes. We test whether dominance can evolve in the sporophytic self-incompatibility (SSI) system in plants. SSI prevents mating between individuals expressing identical SI phenotypes by recognition of pollen by pistils, which avoids selfing and inbreeding depression. SI phenotypes depend on a complex network of dominance relationships between alleles at the self-incompatibility locus (*S*-locus). Empirical studies suggest that these relationships are not random, but the exact evolutionary processes shaping these relationships remain unclear. We investigate the expected patterns of dominance under the hypothesis that dominance is a direct target of natural selection. We follow the fate of a mutant allele at the *S*-locus whose dominance relationships are changed but whose specificity remains unaltered. We show that strict codominance is not evolutionarily stable in SSI, and that inbreeding depression due to deleterious mutations linked or unlinked to the *S*-locus exerts strong constraints on changes in relative levels of dominance in pollen and pistil. Our results provide a general adaptive explanation for most patterns of dominance relationships empirically observed in natural plant populations.

KEY WORDS: Balancing selection, frequency-dependent selection, gene expression, inbreeding depression, multiallelic systems, *S*-locus, sheltered load.

Dominance is a common genetic mechanism whereby the effect of one of the two alleles at a diploid locus is masked at the level of the phenotype. Whether and how dominance evolves has led to one of the most passionate controversies in the history of genetics (for reviews see Bagheri 2006; Cornish-Bowden and Nanjundiah 2006). On the one hand, R. A. Fisher suggested that the dominance level of alleles could evolve through natural selection (Fisher 1928). On the other hand, S. Wright (1929, 1934) contended that dominance is fully determined by the activity of the protein encoded (e.g., enzymatic affinity). Recently, following Haldane (1930) who pointed out that dominance was most likely to evolve in populations in which heterozygotes are frequent,

it was shown that dominance is likely to evolve through modifiers of expression in the case of genes under strong balancing selection (Otto and Bourguet 1999). However, well-described empirical cases consistent with this hypothesis are scarce, and have mostly emphasized balancing selection by migration–selection balance in heterogeneous environments (industrial melanism in *Biston betularia*, Haldane 1956; insecticide resistance in *Culex pipiens*, Bourguet et al. 1997). Other multiallelic genetic systems are subject to strong balancing selection, for instance MHC system genes in vertebrates (Piertney and Oliver 2006), but few studies have addressed the evolution of dominance in such systems, other than for genes involved in host–parasite interactions
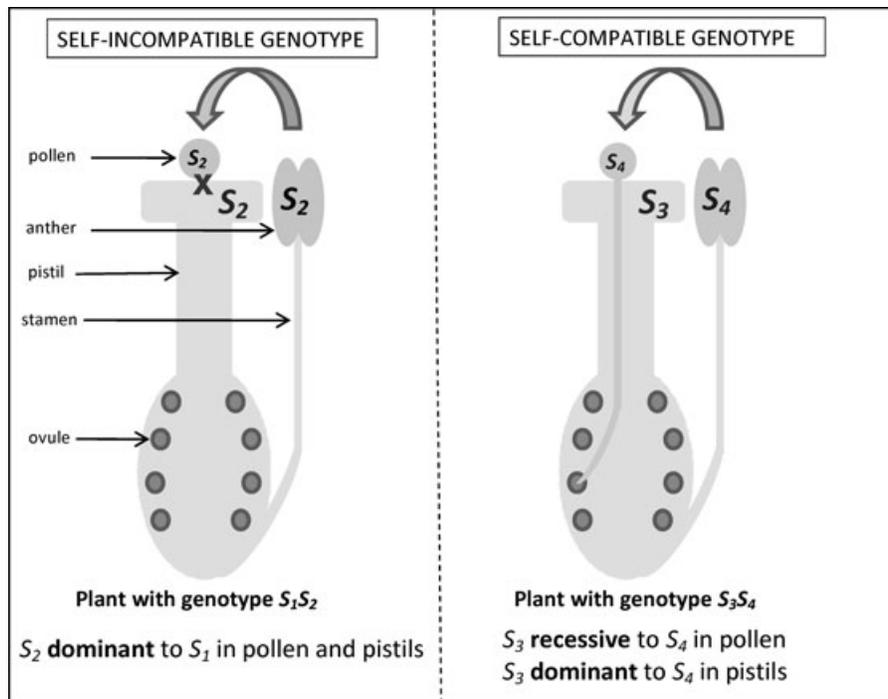
Figure 1. Generation of self-compatible genotypes through inconsistent dominance relationships between pollen and pistils. Results of self-pollination are illustrated for a self-incompatible genotype $S_1 S_2$, and a self-compatible genotype $S_3 S_4$ showing, respectively, consistent and inconsistent dominance relationships in pollen and pistils. Pollen phenotype is determined by proteins produced by sporophytic (diploid) tissues in the anther.

(Nuismer and Otto 2005). In this system, the authors obtained the striking result that codominance is predicted in host-expressed genes, conferring wider surveillance capabilities, while high recessivity is expected in parasite-expressed genes, allowing hiding from the host immune genes.

Here, as well as in a companion paper (Schoen and Busch 2009), the evolution of dominance is studied in a multiallelic genetic system under strong balancing selection: the sporophytic self-incompatibility (SSI) system, a widespread system enforcing outcrossing in hermaphroditic plants. SSI has been extensively studied both theoretically and empirically, so that the evolutionary forces acting on its evolution (reviewed by Castric and Vekemans 2004), and the molecular mechanism involved in one model family (Brassicaceae), are well understood (reviewed by Takayama and Isogai 2005). SSI evolved independently in several families of Angiosperms (de Nettancourt 2001) and is controlled by a single genome region, the so-called S-locus. In Brassicaceae, the S-locus consists of two tightly linked coadapted genes encoding pollen and pistil proteins (named SCR, alternatively SP11, and SRK, respectively) that interact in an allele-specific manner. Molecular interaction between SCR and SRK from the same haplotype initiates a downstream signaling cascade that triggers rejection of the pollen, avoiding self-fertilization and reproduction between mates sharing identical S-locus alleles. In this system, individuals carrying rare S-locus alleles have access to more possible mates

than individuals carrying common S-alleles, which generates negative frequency-dependent selection on the S-locus (Wright 1939).

In SSI, the mating phenotypes of pollen and pistils are determined by the diploid ancestral genotypes at the S-locus and hence dominance interactions are possible among S-alleles (Bateman 1952). The dominance interactions among S-alleles that occur in natural populations may be complex (Castric and Vekemans 2004). Yet S-alleles can often be categorized into hierarchical dominance classes, with codominance interactions among alleles within a class, and dominance between different classes. Dominance is also usually consistent overall between pollen and pistil, although codominance occurs more often in pistil than in pollen (see Schoen and Busch 2009 for a review). In some rare cases, however, dominance interactions among S-alleles are nontransitive, and inconsistencies between dominance levels of a given allele in pollen and pistil have been described (*Sinapis arvensis*, Stevens and Kay 1989; *Brassica campestris*, Hatakeyama et al. 1998). Inconsistent dominance levels between pollen and pistil will allow selfing (Fig. 1). However, the evolutionary processes shaping these complex relationships remain unclear: why is there less codominance in pollen than in pistils? Why are inconsistencies between pistil and pollen rare? Based on their empirical work in *Senecio squalidus*, an invasive species in the British Isles with SSI, Brennan et al. (2002, 2003) suggested that dominance

interactions among S-alleles may evolve within species. Indeed, variation across populations in the relative dominance of *S*-alleles was observed while specificity was conserved (Brennan et al. 2006). They also observed a decrease in number of *S*-alleles in *S. squalidus* across the colonization route. Based on theoretical results showing that dominance interactions increase average compatible mate availability in SSI systems (Byers and Meagher 1992; Vekemans et al. 1998), they suggested that patterns of increasing dominance could have been favored across the colonization route as a result of selection on mate availability (Brennan et al. 2006).

Recent studies showed that the molecular bases of dominance among *S*-alleles for pollen and pistil phenotypes are different. The expression of a recessive *SCR* allele has been found to be suppressed by methylation in the presence of a dominant *SCR* allele (Fujimoto et al. 2006). Moreover, this process occurred even if the dominant *SCR* allele remained untranscribed because of genetic manipulation. This suggests that the dominance of a given *S*-allele in pollen is independent of the specificity encoded by the SCR protein. In pistils, dominance interactions are supposed to be related to the relative capacity of two distinct SRKs to form homodimers versus heterodimers in heterozygotes (Naithani et al. 2007); and homodimers are critical for high-affinity SCR binding (Shimosato et al. 2007). Moreover, SRK dimerization was found to be mediated by a particular subdomain of the SRK protein (Naithani et al. 2007), which suggests that mutations could occur that alter dominance interactions of a given *S*-allele in the pistil without changing its specificity.

Here, we investigated theoretically how evolutionary forces are expected to influence dominance in SSI systems. We explored a deterministic model of SSI, which assumes that the dominance and specificity of a given *S*-allele can be changed independently through mutations occurring within the *S*-locus haplotype. The model includes the two main evolutionary forces acting on the *S*-locus: negative frequency-dependent selection (Wright 1939) and inbreeding depression, a phenomenon assumed to be widespread in species with SI (Glémin et al. 2001). Inbreeding depression in our model could be due either to mildly deleterious mutations distributed across the genome (genomic load), and/or to deleterious mutations linked to specific haplotypes (sheltered load) (Uyenoyama 1997; V. Llaurens et al. unpubl. ms.). We investigated whether dominance of *S*-alleles is selected over codominance, and whether dominance of *S*-alleles could evolve along a dominance hierarchy. We investigated the inbreeding depression level under which haplotypes with inconsistent dominance level in pollen and pistil could occur. Our results complement those of the companion study (Schoen and Busch 2009), which focuses on the effect of recombination between the *S*-locus and a dominance modifier, and on differences in dominance patterns between pollen and pistils.

Materials and Methods

We used a general deterministic model of evolution of allele frequencies at the *S*-locus under SSI (Billiard et al. 2007). We assumed the population to be infinite, initially with *n* S-alleles S_i occurring at their expected equilibrium frequencies determined according to their dominance levels. We assumed that the dominance level of each *S*-allele could evolve through mutations that do not alter the *S*-specificity. In contrast to Schoen and Busch (2009) we assumed modifiers of dominance that are completely linked to the pollen and pistil specificity-determining genes. An individual with genotype $S_i S_j$ produces specificity *i* if S_i is dominant, *j* if S_i is recessive, or *i* and *j* if S_i and S_j are codominant. We introduced a mutant S_k^* at low frequency whose dominance relationships with other *S*-alleles differ from those of ancestral allele S_k. Hence, individuals expressing an *S*-allele, S_k or S_k^*, cannot mate with each other.

We considered two types of frequency-dependent selection acting on the *S*-locus (Vekemans et al. 1998): (1) Wright's model (i.e., selection acting only on paternal success in other words all plants produce the same quantity of seeds) and (2) the fecundity selection model (i.e., selection acting on both male and female success through variation among *S*-locus genotypes in the availability in compatible pollen). The latter case could be realistic in certain ecological situations, including situations when there is pollen limitation. Results under both selection regimes are similar and we show only the results from the fecundity selection model (results obtained by Wright's model are available in Table S2A).

IMPLEMENTATION OF FREQUENCY-DEPENDENT SELECTION

We assumed first that *n* different alleles S_i segregate at the *S*-locus, each with a different specificity when expressed (i.e., when not heterozygous with a more dominant allele). A given individual is characterized by its genotype $S_i S_j$ and its phenotype A_{ij} in anthers and P_{ij} in pistil. The phenotype is defined as a vector of size *n* containing the relative "quantity" of specificity *i* and *j* expressed by a genotype $S_i S_j$: if S_i and S_j are codominant in the anthers, the individual produces one half of specificity *i*, one half of specificity *j* and no other specificity in the pollen. Its phenotype in anthers therefore has 0.5 at positions *i* and *j* only. If allele S_i is dominant over S_j in the pistil, the individual expresses specificity *i* only and therefore its phenotype has 1 at position *i*, and 0 elsewhere. This notation indicates whether pollen from an individual $S_i S_j$ is compatible with the pistil of an individual $S_k S_l$. If the product of the pollen and pistil phenotype vectors is zero, the cross is compatible; all other crosses are incompatible.

We computed the change in frequency of the genotype $S_i S_j$ in one generation, given the frequency of all genotypes in the population f_{kl}, using:

$$\begin{cases} f'_{ij} = \sum_{k=1}^{n} \frac{1}{2} \left(w_{iijk} + w_{jkii} \right) + \sum_{k=1}^{n} \frac{1}{2} \left(w_{ikjj} + w_{jjik} \right) \\ \qquad + \sum_{\substack{k=1 \\ k \neq i}}^{n} \sum_{\substack{l=1 \\ l \neq j}}^{n} \frac{1}{4} \left(w_{ikjl} + w_{jlik} \right) \quad \text{for} \quad i \neq j \\ f'_{ii} = \sum_{\substack{j=1 \\ j \neq i}}^{n} \frac{1}{2} \left(w_{iiij} + w_{ijii} \right) + \sum_{\substack{j=1 \\ j \neq i}}^{n} \frac{1}{4} w_{ijij} \\ \qquad + \sum_{\substack{j=1 \\ j \neq i}}^{n} \sum_{\substack{k>i \\ k \neq j}}^{n} \frac{1}{4} \left(w_{ijik} + w_{ikij} \right), \end{cases} \quad (1)$$

where w_{ijkl} is the fraction of seeds produced by a cross between $S_i S_j$ pollen and $S_k S_l$ ovules among all seeds. The w_{ijkl} values depend on genotype frequencies, compatibility between $S_i S_j$ pollen and $S_k S_l$ pistils and on the selection regime (see eqs. 2–4 in Billiard et al. 2007 for details).

FATE OF THE MUTANT

We first determined the genotype frequencies at deterministic equilibrium of the population without the mutant, using recursions (1). We then introduced the mutant S_k^* at low frequency into a population at deterministic equilibrium. We denoted by S_k^+ and S_k^- mutants derived from S_k, which are respectively dominant or recessive with respect to their ancestral allele. On the appearance of a mutant S-allele in the population, the number of S-alleles increases to $n + 1$, but the number of specificities remains unchanged (n). Hence, the phenotype vectors still have only n elements but the sums in equation (1) now go to $n + 1$ instead of n. For instance, if the mutant allele S_k^* is derived from allele S_k, and is dominant over all other alleles, instead of being codominant in the pollen, its phenotype in anthers has 1 at position k only, whereas the phenotype of its ancestral allele has 0.5 at positions k and j. Finally, we used recursions (1), taking into account the new allele, until the frequency change in one generation of the mutant was lower than 10^{-3}.

PATTERNS OF DOMINANCE

We considered two classical patterns of dominance relationships; the COD and the DOM systems, which have been commonly modeled in theoretical population genetics studies of SSI (Schierup et al. 1997). In the model with codominance in pistils and pollen (COD) system, all S-alleles are fully codominant in both pollen and pistil whereas in the model with dominance in pistils and pollen (DOM) model, dominance relationships among S-alleles are organized in a strict hierarchy (called the dominance ladder). In both the COD and DOM systems we considered dominance evolution in pollen only, in pistil only, or in both simultaneously. For simplification, we chose to use the minimum number of S-alleles necessary for the self-incompatibility to be functional, that

is four alleles in the COD model and three alleles in the DOM model. The increase in the number of S-alleles would lead to difference in the time of invasion of the mutant S-allele and in the rate of invasion in case of finite populations. However, this increase in S-alleles number should not change our results qualitatively.

DOMINANCE AGAINST CODOMINANCE

We first investigated the evolution of a mutant in a population in a COD system with four S-alleles, which is the minimum number of S-alleles for self-incompatibility to function in a COD system (Bateman 1952). We then introduced an S_3 mutant, S_3^+ or S_3^-, that is, respectively, dominant or recessive over all other S-alleles (including S_3, although $S_3 S_3^+$ individuals still express specificity 3).

MOVEMENTS ACROSS A DOMINANCE LADDER

We then investigated whether S-alleles could evolve along a dominance hierarchy. We assumed the simplest case, a DOM model with only three S-alleles with $S_3 > S_2 > S_1$, where $>$ indicates dominance in both pollen and pistils. We checked whether mutants with higher or lower dominance than the ancestral allele in pollen and/or pistil could increase in frequency. The dominance of mutant S-alleles was set to each of the 12 possible levels of a dominance ladder (Fig. 3). The mutant could move (1) between two preexisting dominance levels (e.g., $S_3 > S_k^* > S_2 > S_1$, with $k = 1$, 2, or 3) or (2) to the top ($S_k^* > S_3 > S_2 > S_1$, with $k = 1, 2$, or 3) or bottom ($S_3 > S_2 > S_1 > S_k^*$, with $k = 1, 2$, or 3) of the hierarchy, thus introducing a new dominance level into the hierarchy; or (3) to a preexisting dominance level (e.g., $S_3 > S_k^* = S_2 > S_1$), thus making S_k^* codominant with one of the two other extant alleles.

SHELTERED GENETIC LOAD LINKED TO THE S-LOCUS

We studied the influence of sheltered genetic load linked to the S-locus on the evolution of dominance of S-alleles. Sheltered load is an accumulation of deleterious mutations surrounding the S-locus, due to high heterozygosity and supposed low recombination rate in this genomic region (Uyenoyama 1997; Glémin et al. 2001). Here, we assumed a sheltered genetic load due to recessive deleterious alleles at loci fully linked to the S-locus. We further assumed that each S-allele can have a specific sheltered load, in other words each S-allele can be in linkage with specific deleterious mutations. This sheltered load was assumed to be expressed in homozygotes only. We thus assumed that the sheltered load decreases the survival of homozygotes by a factor $(1 - d)$ with $0 \leq d \leq 1$. The mutant allele S_k^* was assumed to share the same deleterious allele as the ancestral allele S_k so that heterozygotes $S_k^* S_k$ expressed the same decrease in fitness due to the sheltered load as homozygotes $S_k S_k$ and $S_k^* S_k^*$. We simulated the evolution of dominance in the COD model in the presence of sheltered

load with a load identical for all *S*-alleles ($d = 1$). When implementing sheltered load in the DOM model, we set a higher load for *S*-alleles with higher dominance levels ($d_3 > d_2 > d_1$ with $S_3 > S_2 > S_1$) because the sheltered load is predicted to be lower for recessive than dominant alleles (Llaurens et al. 2009). This is because the frequencies of homozygotes at the *S*-locus are expected to be higher for recessive than for dominant *S*-alleles, implying more efficient purging of deleterious alleles linked to recessive *S*-alleles. Several combinations of sheltered load linked to each S-allele were tested and results were qualitatively similar. We show the results for the following values $d_1 = 0.2$, $d_2 = 0.6$, $d_3 = 0.8$.

INBREEDING DEPRESSION

When dominance relationships between S_k^* and S_i are inconsistent (i.e., $S_k^* < S_i$ in pistil and $S_k^* > S_i$ in pollen), $S_k^* S_i$ plants can cross with each other and self-fertilize (Fig. 1). Self-compatibility in itself causes an advantage for the mutant through selfing (Fisher 1941), but also induces a cost through inbreeding depression (Charlesworth and Charlesworth 1987). To disentangle these two effects, we investigated the fate of a mutant with opposite dominance levels in pollen and pistil, starting from a model with all *n* initial *S*-alleles codominant. We assumed a selfing rate *s* in self-compatible genotypes and inbreeding depression (survival of selfed offspring decreased by a factor $1 - \delta$ relative to outcrossed offspring). We recorded the threshold values of parameters *s* and δ below which the mutant increased in frequency for different initial numbers of *S*-alleles ($5 < n < 50$). The computations assumed fecundity selection because the computation times were too long for Wright's selection model, as the number of genotypes to be taken into account increases exponentially with the number of *S*-alleles.

Results

SELECTION FOR DOMINANCE INTERACTIONS

Under the fecundity selection regime (selection through both male and female functions), when a mutant allele S_3^+ with dominance expressed in both pollen and pistil is introduced in a COD system with four *S*-alleles, its frequency increased rapidly, and its ancestral allele S_3 was eliminated (Fig. 2A). A similar result was obtained with a recessive allele mutant S_3^- (Fig. 2B). This occurs because genotype bearing the mutant *S*-allele can cross with a higher number of genotypes than its ancestral *S*-allele (see Discussion). The recessive mutant S_3^- reached a substantially higher frequency than the other alleles, whereas the dominant S_3^+ reached a slightly lower frequency than the other alleles (see Table S1A). This occurs because recessive *S*-alleles in SSI systems reach higher frequencies at equilibrium than dominant ones (Schierup et al. 1997). The results were similar when mutants

S_3^+ or S_3^- affected pollen only or in pistil only, except that the dynamics of invasion of the mutant was slower. This suggests that the male and female components of selection on dominance are additive.

The results under Wright's selection regime (acting on male fitness only) were generally similar, except when the mutation modifying the dominance affected the pistil only (Table S1A). If the mutant allele S_3^+ was dominant in pistil only, the ancestral allele S_3 was maintained and the mutant allele did not invade. This occurs because under Wright's selection regime, the frequency-dependent selection acts on male function only, and all genotypes, including those carrying the dominant mutant allele S_3^+, were assumed to have equal fitness through female function. The dominant mutant allele S_3^+ is thus neutral with respect to the ancestral allele S_3. Surprisingly, a different result was obtained when a recessive mutant allele S_3^- expressed only in the pistil was introduced: this mutant was positively selected. This could be explained by an effect of homozygous genotypes: as the mutant allele S_3^- is recessive in the pistil, S_3^- homozygotes can be formed, which is not possible for the ancestral allele S_3. This produced a selective advantage to the mutant allele S_3^-, although there was no selection on female function.

Overall, these results indicate that mutations either increasing or decreasing dominance are strongly favored by natural selection; in other words dominance is favored relative to codominance. Our results thus suggest that selection on dominance should lead to hierarchical dominance relationships in SSI systems, in both pollen and pistil in case of fecundity selection regime, or in pollen only under Wright's selection regime.

MOVEMENTS ACROSS A DOMINANCE LADDER

We followed the fate of mutants with changed dominance in a DOM system with three *S*-alleles (Fig. 3A,B, see Table S2A for further details). The results are similar for fecundity and Wright's selection regimes. As summarized in Figure 3A, mutants with identical changes of dominance in pollen and pistil never invaded. Codominant mutants were also always eliminated. In contrast, mutants with changed dominance in either the pollen or pistils increased in frequency when a new dominance level was created anywhere in the dominance ladder, that is when it did not lead to codominance among pairs of *S*-alleles (Fig. 3B). Hence, changes in dominance of *S*-alleles occurred only when (1) a strictly hierarchical pattern of dominance was maintained; and (2) the new dominance level was expressed in pollen or pistil only. This is because selfing and mating with individuals sharing the same genotypes are possible for individuals carrying such mutant *S*-alleles: for instance individuals $S_1^* S_2$ with $S_1 < S_2 < S_1^*$ in pollen and $S_1 = S_1^* < S_2$ in pistil express specificity S_1 in pollen and S_2 in pistil can thus self-cross and mate with $S_1^* S_2$ individuals, whereas individuals carrying the ancestral $S_1 S_2$ cannot. This process did
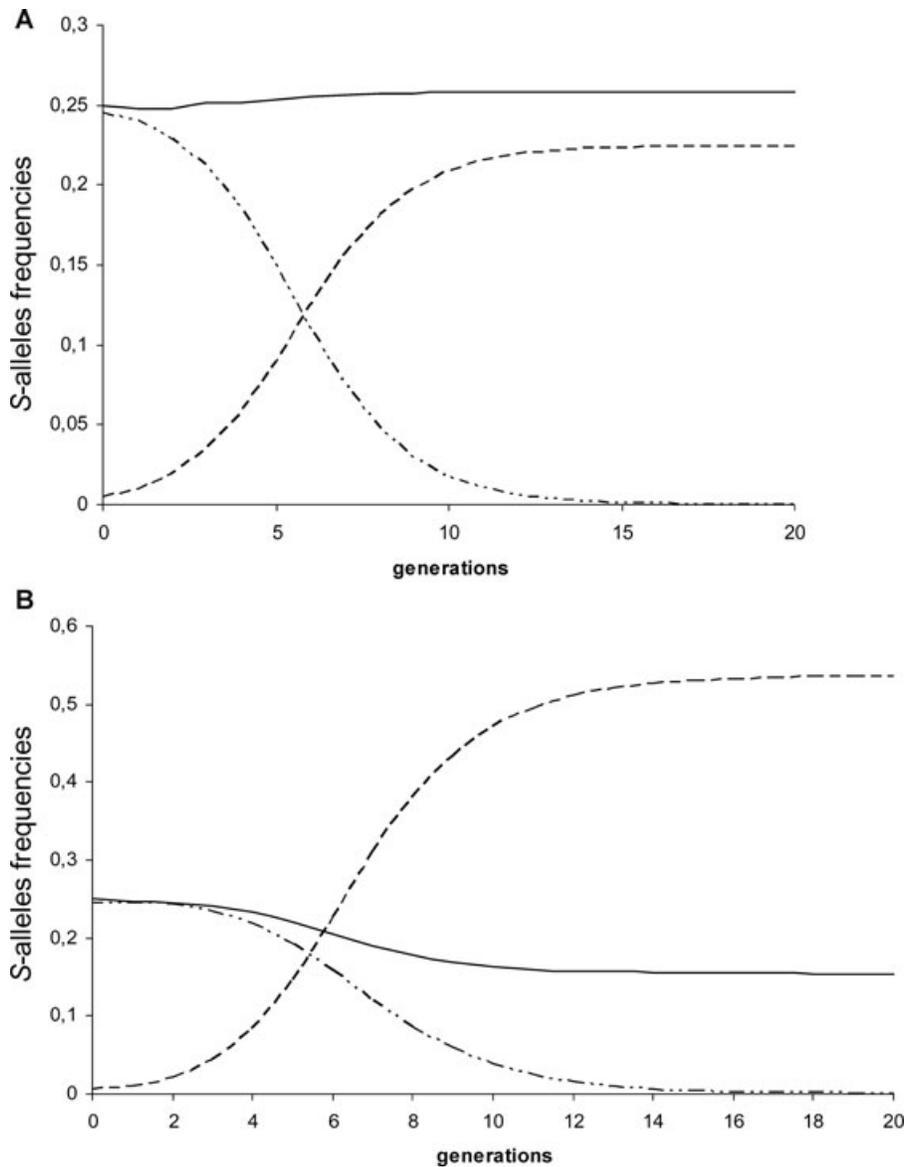
Figure 2. Evolution of S-allele frequencies under fecundity selection, in a COD system with four codominant alleles S_1, S_2, S_3, and S_4 and a mutant allele that is either dominant, S_3^+ (A), or recessive, S_3^- (B) with respect to S_1 to S_4. Solid lines represent evolution of S_1, S_2, or S_4, irregularly dotted lines represent evolution of the ancestral allele (S_3) and regular dotted lines represent the mutant allele (S_3^+ or S_3^-).

not cause the loss of the SI system, because the self-compatibility advantage conferred by the mutant is reduced when its frequency increases. Indeed, only heterozygous genotypes containing the mutant allele were favored. Hence, when there is no inbreeding depression, dominance interactions in pollen are expected to evolve differences from those in pistils.

EFFECT OF A SHELTERED LOAD

A strong sheltered load ($d = 1$) caused S_3^+ and S_3^- mutants introduced into a COD system to increase in frequency under both selection regimes. Hence, such as in the absence of sheltered load, codominance is selected against (Table S1B). The

equilibrium frequency of the mutant allele S_3^+ was higher than those of the codominant S-alleles, the opposite of the result with no sheltered load. A recessive mutant allele S_3^- invaded the population but reached lower frequency than with no sheltered load. In the COD system, sheltered load thus favors mutations increasing dominance levels. The selective advantage of higher dominance levels is due to the fact that the mutant S-allele occurs less frequently in the homozygous state, and consequently the sheltered load associated with the mutant is less frequently expressed than with its ancestral allele. Similar results were obtained in the DOM model. Hence, the sheltered load tends to favor mutations conferring a higher level of dominance, reducing the
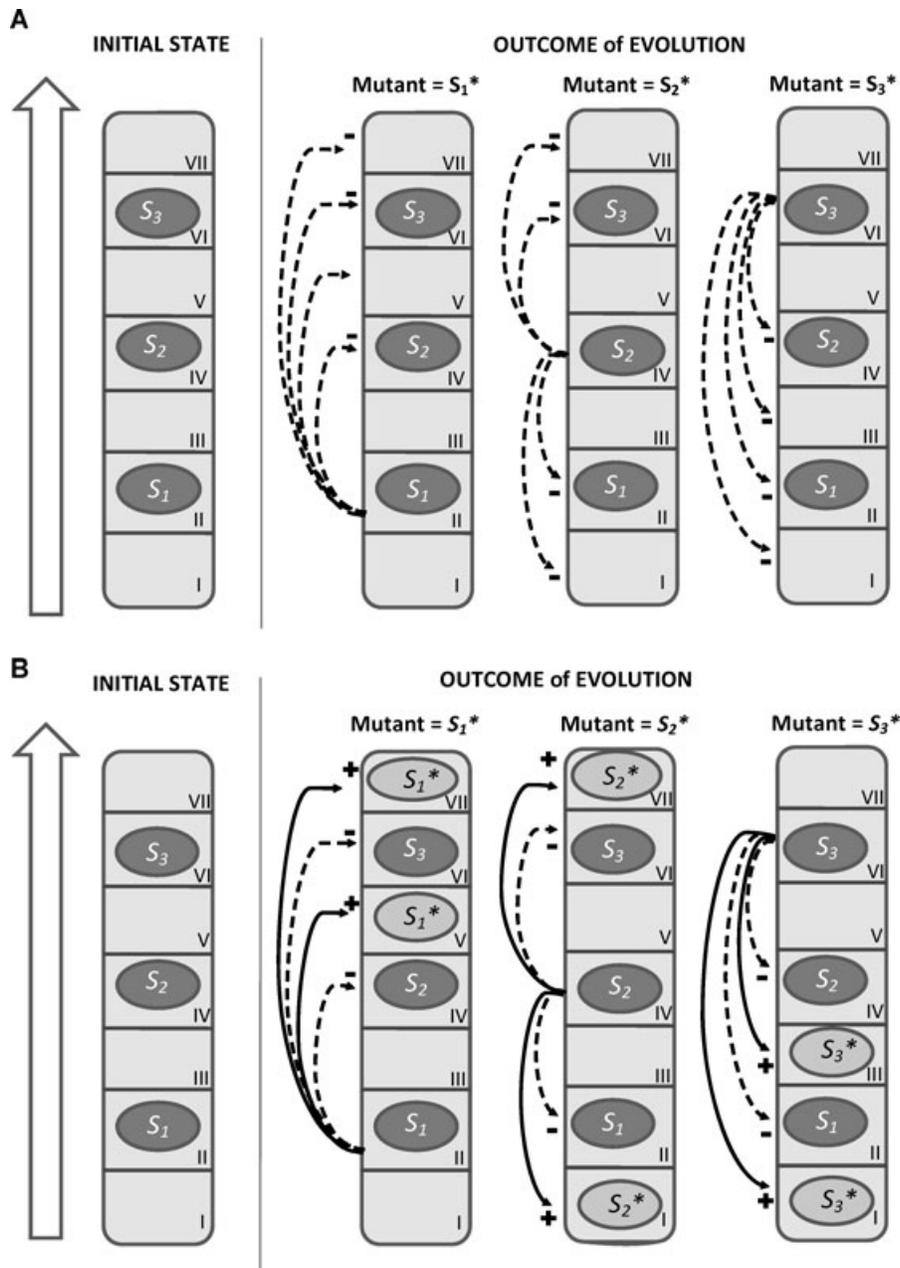
Figure 3. Outcome of evolution of dominance mutants across a dominance ladder in a DOM system with three initial S-alleles ($S_3 > S_2 > S_1$ with > meaning "dominant over"). (A) Simultaneous changes in dominance of the mutant allele S_k^* in pollen and pistils; (B) Change in dominance only in pollen or in pistils.
Continuous arrows: the mutant S-allele increases in frequency.
Dotted arrows: the mutant S-allele does not increase in frequency.
Roman numerals indicated the possible dominance levels of the mutant alleles (I = most recessive; VII = most dominant).

cost of sheltered load by lowering the frequency with which it is expressed.

COEVOLUTION OF DOMINANCE IN POLLEN AND PISTIL

We followed the fate of allele mutants with opposite dominance levels in pollen and pistils. Without inbreeding depression, such mutant alleles always replaced the ancestral alleles (Fig. 4). In the presence of inbreeding depression ($\delta > 0$ and $s > 0$), a mutant with opposite dominance levels in pollen and pistil increased in frequency only if inbreeding depression was not too high, represented by the area below the lines on Figure 4. The success of the mutant also depended on the number of S-alleles (n). When n decreased, the invasion region became larger, that is the
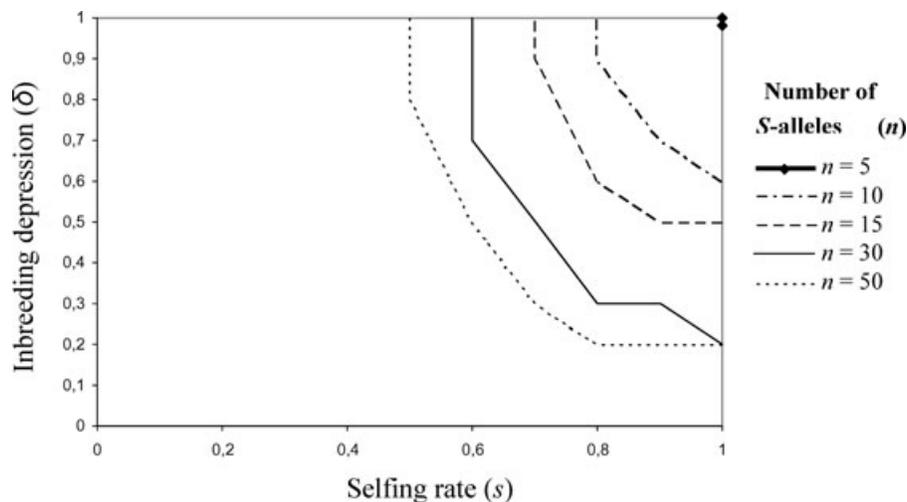
Figure 4. Conditions of inbreeding depression level and selfing rate under which a mutant *S*-allele recessive in pollen and dominant in pistils over all other *S*-alleles could successfully invade. Areas under the lines represent cases in which the mutant S-allele is fixed within the population for different number of *S*-alleles (*n*). We assumed a COD system with ns initial *S*-alleles. *y*-axis = inbreeding depression level (δ); *x*-axis = selfing rate of the self-compatible genotypes (*s*).

mutant was successful in a wider range of inbreeding depression level. The invasion of self-compatible genotypes in SSI is thus possible when the number of *S*-alleles and inbreeding depression δ are low. Similar conclusions were obtained for the occurrence of a self-compatible mutant in GSI (Porcher and Lande 2005). Hence, our results suggest that high levels of inbreeding depression could be the cause of the observed occurrence of consistent dominance hierarchies in pollen and pistil in SSI systems.

Discussion

THE ADVANTAGE OF DOMINANCE OVER CODOMINANCE: THE HIDING EFFECT

Our results show that in SSI systems, mutations either increasing or decreasing the dominance of an *S*-allele relative to other extant alleles are generally favored in populations with codominant alleles, whereas mutations leading to codominance are disfavored when the population contains dominant alleles. This occurs because of a "hiding effect": although strict codominance restricts mating to pairs of genotypes carrying different *S*-alleles (four distinct alleles), a dominant *S*-allele hides its co-occurring allele. Heterozygotes carrying one dominant *S*-allele are therefore expected to have more compatible mates than heterozygotes with codominant alleles, and thus dominance interactions will be favored. Similar results were obtained by Schoen and Busch (2009). The two models differ by the fact that the latter explicitly modeled recombination between the *S*-locus and the modifier locus, and found that tight linkage was required for the evolution of stable associations between *S*-alleles and specific dominance modifier alleles. Because the *S*-locus region in Brassicaceae is highly divergent among *S*-alleles (Tang et al. 2007) and essentially contains nonrecombining allele-specific sequences (Sato et al. 2002;

Kamau et al. 2007), tight linkage between *S*-alleles and modifier alleles may readily occur. In short, this hiding effect creates a selective pressure favoring the evolution of dominance in species with SSI, especially when there is tight linkage between dominance modifier and the *S*-locus. This selective pressure is lowered when the number of S-alleles increases as it is shown in Figure 4, however dominance evolution does not change qualitatively.

This hiding effect is similar to that expected in genes controlling host–parasite interactions (Nuismer and Otto 2005), allowing parasite genes responsible for the infection to minimize the probability of recognition by resistance genes of the host. In Müllerian mimicry in Heliconius butterflies, a high allelic diversity is observed due to selection to mimic phenotypes of other species. In the case of *H. numata*, the mimicry seems to be controlled by a single locus, and hierarchical dominance relationships are observed among alleles (Joron et al. 2006), which suggests that similar selection processes such as in the case of SSI could be acting on dominance at this locus, preventing the appearance of intermediate and nonmimetic phenotypes. Indeed, if alleles at the coloration locus were codominant, individuals would show intermediate coloration phenotype and would not be recognized by predators as unpalatable. Hence, codominant alleles should be disfavored. However, further studies are needed to determine if strong selection is exerted on the dominance of multiallelic loci involved in recognition processes, such as mating-types genes or genes involved in host–parasite interactions.

SHELTERED LOAD MAY FAVOR THE INCREASE OF DOMINANCE

When a sheltered load was added to the model, mutations increasing recessivity were disfavored, because the sheltered load

is expressed in homozygote genotypes only. Indeed, the frequency of homozygote genotypes at the *S*-locus depends largely on the dominance level of the *S*-alleles (Imrie et al. 1972), with a decrease of this frequency when dominance increases. Because the sheltered load is expected to be stronger for dominant *S*-alleles (Llaurens et al. 2009), this suggests that strong selective pressures prevent the decrease in dominance level of a given *S*-allele. In contrast, mutations increasing the dominance level in the hierarchy are favored. Our results thus suggest that sheltered load may produce dominance in an ascending scale, and that a "race" between *S*-alleles could occur to become the most dominant. However, because the accumulation of deleterious mutations in association with specific *S*-alleles follows a mutation—selection–drift dynamic and especially depends on the homozygote frequency in the population, further modeling is necessary to accurately predict the effect of sheltered load on the expected dominance patterns in SSI.

EFFECT OF THE SELECTION REGIME AND INBREEDING DEPRESSION

In agreement with the companion paper by Schoen and Busch (2009), we found that dominance interactions may differ between the two negative frequency-dependent selection regimes: under Wright's selection regime, a dominance hierarchy is expected only in pollen, whereas it is expected in both pollen and pistils under the fecundity selection regime. Dominance hierarchies are indeed more frequent in pollen than in pistils, suggesting that in the majority of the ecological situations encountered by self-incompatible populations, Wright's model is most appropriate, that is there is no pollen limitation. However, we find that, under Wright's selection regime, mutants changing the dominance in pistils are expected to be neutral. Hence, providing that mutations altering the dominance in pistils occur, there is no reason to expect strict codominance in pistils, or consistent dominance relationships between pollen and pistils, rather than random dominance relationships. We thus suggest that the predominant occurrence of consistent patterns of dominance in SI plants is due to the action of an additional evolutionary force, inbreeding depression. Our results show that, if inbreeding depression and the number of co-occurring *S*-alleles are high enough, evolution of dominance should be constrained by selfing avoidance, which occurs in four nonexclusive cases: (1) if the dominance hierarchy is symmetrical in pollen and pistils; (2) if *S*-alleles are codominant only in pistils; (3) if *S*-alleles are codominant only in pollen; and (4) if *S*-alleles are codominant in both pollen and pistils. However, negative frequency-dependent selection should favor a dominance hierarchy in pollen under Wright's selection regime, or in both pollen and pistils under fecundity selection. Hence, case (1) may be expected under pollen limitation, and case (2) with no pollen limitation. The same arguments could also explain the general

maintenance of strict codominance among *S*-alleles in pistils in gametophytic self-incompatibility (GSI) systems. Indeed, in GSI, dominance interactions among *S*-alleles in pistils would lead to a systematic breakdown of self-incompatibility (because pollen phenotypes are determined gametophytically) and this would be counter-selected if inbreeding depression is high. In most species, the number of *S*-alleles is large (Castric and Vekemans 2004), and inbreeding depression levels are high as expected for strictly outcrossing plant species (e.g., Busch 2005, Glémin et al. 2006). In addition to its already recognized role for long-term maintenance of SI (Glémin et al. 2001), inbreeding depression could affect the relative dominance levels of *S*-alleles in pollen and pistils. However, empirical evidence is lacking for mutations altering dominance interactions, in both GSI and SSI systems.

EMPIRICAL EVIDENCE FOR EVOLUTION OF DOMINANCE AT THE *S*-LOCUS

Patterns of dominance relationships among *S*-alleles in SSI systems are usually consistent overall between pollen and pistil (e.g., Kowyama et al. 1994 in *Ipomoea trifida*; Prigoda et al. 2005 in *Arabidopsis lyrata*), but with codominance occurring more often in pistil than in pollen (see Schoen and Busch 2009, for a review). These observations are concordant with expectations from the models of dominance evolution presented here and in the companion paper by Schoen and Busch (2009), if pollen limitation does not often occur within natural populations, and inbreeding depression levels are generally high. However, the observed patterns could alternatively be due to the partial share of dominance interactions between ancestral and derived *S*-alleles. Empirical investigations are needed (1) to identify precisely which molecular mechanisms could be involved in such dominance modifications, (2) to test whether closely related alleles tend to share identical patterns of dominance, and (3) to check the occurrence of spontaneous variation within or between populations in dominance relationships between the same pairs of *S*-alleles. Two examples from the Brassicaceae family seem to indicate a phylogenetic signal of patterns of dominance: the genus Brassica with two phylogenetic clusters of alleles with distinct levels of dominance in pollen phenotype (Nasrallah et al. 1991); and *A. lyrata* with four phylogenetic groups of alleles with hierarchical dominance (Prigoda et al. 2005). This would suggest that dominance properties of a given allele are inherited from its ancestral allele, and do not generally evolve. However, in both cases, detailed analyses have revealed complex dominance interactions among some alleles within these phylogenetic groups (Thompson and Taylor 1966; Hatakeyama et al. 1998; Prigoda et al. 2005), which may indicate subsequent changes in dominance. The occurrence of spontaneous variation in dominance for a given pair of alleles could be tested by assessing dominance patterns in different ranges of a species' distribution, or in closely related species, taking into account the

observation that many pairs of ancestrally derived trans-specific alleles are usually found in such species (e.g., Castric et al. 2008). For example, Llaurens et al. (2008) compared dominance interactions between pairs of *S*-alleles shared trans-specifically between *Arabidopsis halleri* and its sister species *A. lyrata*. The overall dominance ranks of *S*-alleles were similar in both species; however in pollen, the dominance interactions were strictly hierarchical in *A. halleri* whereas there was codominance among some S-alleles in *A. lyrata*. However, this study considered only a small fraction of the trans-specific alleles identified in these taxa (Castric et al. 2008) and the data should be expanded. Within species, variation in patterns of dominance interactions among natural populations has also been documented (in *S. squalidus*, Brennan et al. 2006). Across the distribution range of the species in the British Isles, the authors compared between populations the consistency of dominance relationships between pairs of shared *S*-alleles. Several pairs of *S*-alleles showed dominance in one population, and codominance in another one. This arose either for the pistil or pollen phenotypes. However, they did not observe cases of opposite dominance interactions between pollen and pistil phenotypes, in agreement with the theory presented here. These results, however, should not be taken as conclusive evidence for within-species evolution of dominance as the dominance interactions have been measured in individuals characterized phenotypically only, ignoring the possibility of homozygous genotypes. Experimental validation of variation in dominance patterns would involve, for instance, the production of S_iS_{k*} and S_iS_k heterozygotes and measurement of fertilization success from controlled crosses with S_iS_i individuals.

Some genetic or physiological constraints could limit the occurrence of mutations modifying dominance of *S*-alleles. However, our model clearly shows that the selection pressure acting on dominance is high, especially when the number of *S*-alleles is low, because the elimination of the ancestral allele by the mutant S_k^* occurs rapidly (Fig. 2). This suggests that, even if the mutation rate is low, dominance could evolve. Our theoretical approach thus suggests that sporophytic self-incompatibility systems provide a new example of evolution of dominance through natural selection in a locus under balancing selection. It supports the conjecture by Otto and Bourguet (1999) that evolution of dominance should be investigated in loci under balancing selection.

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Associate Editor: J. Kohn

Supporting Information

The following supporting information is available for this article:

Table S1. Evolution of *S*-alleles frequencies in a COD system with four *S*-alleles, with no inbreeding depression under various conditions: frequency-dependent selection regime (Wright or Fecundity selection) and appearance of the mutant (in pollen only, in the pistils only or simultaneously in the pollen and the pistils).

Table S2. Evolution of allele frequencies in a DOM system with three *S*-alleles ($S_1 < S_2 < S_3$), with no inbreeding depression under various conditions: frequency-dependent selection regime (Wright or Fecundity selection) and appearance of the mutant: the mutation could affect pollen only, in pistil only, or simultaneously in pollen and pistil, with different ancestral *S*-alleles, and confer various positions in the dominance ladder (as described in Fig. 3).

(This link will take you to the article abstract).

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