

# Current Biology

## Whole-Genome Hitchhiking on an Organelle Mutation

### Highlights

- Selection on organelles can effect nuclear genetic diversity via genetic hitchhiking
- Organelle-mediated genetic draft is an underappreciated evolutionary phenomena

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### In Brief

Flood et al. discover that strong selection on a chloroplast gene has extended to the nuclear genome, which has hitched a ride along with the selected chloroplast. This is the first description of organelle-mediated genetic draft and shows that selection on organelles can directly impact nuclear genetic diversity.



# Whole-Genome Hitchhiking on an Organelle Mutation

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## SUMMARY

Strong selection on a beneficial mutation can cause a selective sweep, which fixes the mutation in the population and reduces the genetic variation in the region flanking the mutation [1–3]. These flanking regions have increased in frequency due to their physical association with the selected loci, a phenomenon called “genetic hitchhiking” [4]. Theoretically, selection could extend the hitchhiking to unlinked parts of the genome, to the point that selection on organelles affects nuclear genome diversity. Such indirect selective sweeps have never been observed in nature. Here we show that strong selection on a chloroplast gene in the wild plant species *Arabidopsis thaliana* has caused widespread and lasting hitchhiking of the whole nuclear genome. The selected allele spread more than 400 km along the British railway network, reshaping the genetic composition of local populations. This demonstrates that selection on organelle genomes can significantly reduce nuclear genetic diversity in natural populations. We expect that organelle-mediated genetic draft is a more common occurrence than previously realized and needs to be considered when studying genome evolution.

## RESULTS AND DISCUSSION

In outcrossing species, the extent to which selection on a locus in the nuclear genome can distort neighboring gene frequencies is restricted by recombination [1, 2]. In non-recombining genomes, such as those of mitochondria, chloroplasts, and bacteria, selection at a single locus can, however, result in genome-wide selective sweeps [5]. Although the potential consequences of selection on organellar genomes have been frequently discussed [6], there has been little recognition that the effect of selection on organelles may extend to the nuclear genome as well [7, 8].

Here we make use of the natural distribution of an easily detectable chloroplast mutation to study the impact of selection on organelles in a wild plant population. The chloroplast mutation

confers resistance to triazine herbicides, which were widely used along British railways from 1957 until their discontinuation in 1992 due to environmental concerns. Triazines inhibit photosynthesis by competing with plastoquinone for the Q<sub>B</sub> binding site of the D1 protein of photosystem II (PSII), thereby inhibiting photosynthetic electron flow [9]. The D1 protein is common to all photosynthetic eukaryotes and is encoded by the chloroplastic *psbA* gene. A conserved Ser-264-Gly amino acid substitution confers resistance via the removal of a hydrogen bonding site, which prevents triazines from binding to D1 [9]. This particular amino acid substitution has evolved at least 73 times across multiple plant species [10]. In addition to conferring resistance to triazine herbicides, this substitution also reduces the affinity of the Q<sub>B</sub> site for plastoquinone, thereby reducing the efficiency of PSII [9] (Figure 1). This reduction in PSII efficiency limits carbon assimilation under most environmental conditions [11] and consequently results in a fitness cost [12, 13]. Resistant genotypes are therefore expected to be strongly selected for by triazine application but gradually removed from the population in its absence [12, 13].

Triazine resistance in the wild plant species *Arabidopsis thaliana* was first detected in 1988 at Ely railway station, Cambridgeshire, UK, after which the resistant genotype is named [14]. From an existing dataset of 149 nuclear SNPs [15], we identified four genotypes from Liskeard, Cornwall, over 400 km from Ely (Figure 2; Table S1), that were identical to the Ely genotype for all SNPs. Progeny of all four genotypes tested positive for the *psbA* mutation and exhibited atrazine resistance (Table S2), suggesting that resistance may be associated with a single nuclear haplotype. To estimate the frequency of triazine-resistant genotypes and detect the occurrence of organelle-mediated nuclear genetic hitchhiking, we sampled a total of 60 populations of *A. thaliana* at 47 distinct locations along British railways in the east and southwest of England and tested for the presence of triazine resistance and the nuclear genetic diversity of resistant and non-resistant plants. A subset of 36 populations was specifically sampled alongside railway tracks, where selection for chloroplast-mediated triazine resistance was known to occur, whereas the remaining populations were sampled at least 500 m from the nearest railway track, where no record of triazine application was noted and thus strong selection on the organelle mutation was unlikely.

Of the 573 plants assayed, 51 carried the *psbA* mutation (Figure 2; Table S1). These resistant plants were found at 12 of the 47 sampled locations and were all located on or next to railway

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