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Digest: Plants adapt under attack: genotypic selection and phenotypic plasticity under herbivore pressure*

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Plant species adapt to changing environmental conditions through phenotypic plasticity and natural selection. Agrawal et al. (2018) found that dandelions responded to the presence of insect pests by producing higher levels of defensive compounds. This defensive response resulted both from phenotypic plasticity, with individual plants' defenses triggered by insect attack, and from evolution by natural selection acting on genetic variation in the plant population.

Most plants spend their lives rooted to the spot in often challenging and changing conditions, and so they must adapt to their environment to survive. Explaining the nature of this adaptability is important for understanding the natural evolutionary dynamics between hosts and pathogens (Kraemer and Boynton 2017) and predators and prey (Ohgushi 2016), and for predicting responses to anthropogenic environmental change, such as species' adaptive resilience to cope with climate change (Williams et al. 2008) or the unwanted resurgence of weeds upon developing resistance to herbicides (Neve et al. 2009). In all of these cases, a key question is whether plants adapt to the stress at an individual level, through inducible responses that comprise phenotypic plasticity; at a population level, through genetic variation that provides adaptive potential under natural selection; or through a combination of the two.

In this issue, Agrawal et al. (2018) studied anti-herbivore defenses in experimentally evolving populations of dandelion (*Taraxacum officinale*), with insect herbivores either present at naturally occurring levels or suppressed by insecticide treatment as the dandelions colonized cleared plots. The level of herbivory was sufficient to slow dandelion colonization on the untreated plots in earlier years, but competition from later-successional plant species then took over as the main factor limiting dandelion abundance across all plots.

The authors measured the concentrations of six defense compounds in plant material and used microsatellite markers to assess genotypic diversity and abundance. Levels of di-phenolic inositol ester (di-PIE) defense compounds varied both between genotypes and between treatments. Treatment effects produced 72% higher di-PIE levels due to phenotypic plasticity, and genotypic effects contributed at least a 10% increase. The authors thereby separate the contributions of plasticity and evolution to the increased defense compound levels in the plots with more insect pests.

The authors note that the early years of their experiment represented an early-successional site, with initial plant colonization limited by predation in the untreated plots. In the insecticide-treated plots, faster growth and higher fecundity were more advantageous, and in more established plant communities, competitiveness against other plants becomes more important (Fig. 1). This results in the maintenance of variation in defense levels if there are tradeoffs in growth or competitiveness against resource allocation to defense compounds (Strauss et al. 2002). There may also be indirect costs due to genetic linkage, or ecological tradeoffs such as subversion of defense pathways by specialist herbivores.

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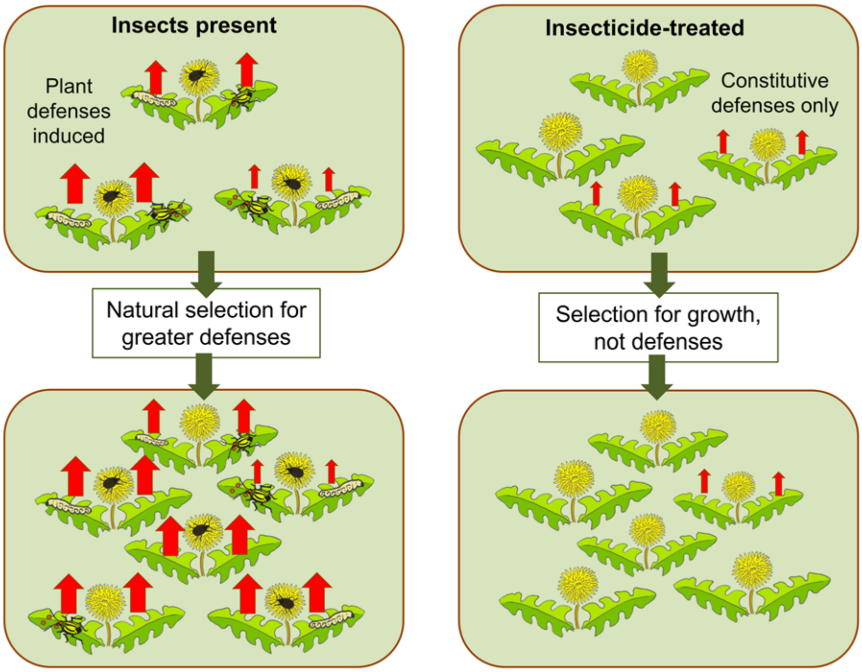

Figure 1. **Induction and selection of plant defenses in the presence of insect herbivores, compared to insecticide-treated populations.**

Interestingly, the most dominant genotype in insect-exposed plots, with lower frequency in the insecticide-treated plots, showed higher constitutive expression of di-PIE compounds. Continuous production of defense compounds may carry a higher cost than inducible defenses, leading to greater fitness penalties in the absence of insect selection. However, phenotypic plasticity can carry its own costs. An interesting avenue for further study could be to investigate whether fluctuating selection within plots would retain more genotypic diversity, or select for more plastic adaptations.

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