Can plants evolve to meet a changing climate? The potential of field experimental evolution studies

Nora Mitchell[1,2] (iD) and Kenneth D. Whitney[1] (iD)

WHY AND HOW TO UNDERSTAND CONTEMPORARY MICROEVOLUTION IN PLANTS

Human impacts are rapidly influencing the biotic and abiotic environments that plants inhabit. Climate change, habitat destruction and fragmentation, the movement of invasive species, and agriculture are all factors impacting plants on rapid time scales. It is unclear how plant species will respond to these multiple and simultaneous pressures. In the face of rapidly changing environments, there are three main mechanisms to avoid extinction: plasticity, migration, or evolution (Anderson et al., 2012). The speed and magnitude of these predicted global changes may mean migration will be too slow (Aitken et al., 2008) and plasticity insufficient (Franks et al., 2014) for many plant species, leaving evolution as a key process to understand. Because both current evolutionary rates and selective forces differ from those in the recent geological past, explicitly experimental studies of evolution are needed to predict whether plant populations will persist and how they will adapt under these novel conditions.

Classic evolutionary studies in plants have assessed the speed and extent of evolution, identified selective pressures, quantified responses in key traits, and detected loci under selection (Bone and Farres, 2001). Such observational studies provide important baseline information for understanding plant evolution, as do studies of local adaptation across a species range, which can guide expectations for the range of ecological conditions to which species can adapt. However, experimental work is needed to predict responses under current rates of environmental change and combinations of stressors. While experimental evolution is often associated with bacteria, yeast, or *Drosophila* (Kawecki et al., 2012; Lenski, 2017), studies of longer-lived plants and animals are needed, given that patterns and processes may vary between micro- and macroorganisms, which differ in reproductive systems, sources of genetic variation (de novo mutations versus standing genetic variation), and for which questions regarding sexual selection and speciation may be lineage-specific (reviewed by Kawecki et al., 2012). Further, plants have unique interspecific interactions (e.g., with pollinators, mycorrhizae) and uncommon biological attributes (e.g., indeterminate growth), which mean both the relevant questions and evolutionary outcomes may differ from nonplant model systems. As an example of plant-specific selective pressures via pollinators, Roels and Kelly (2011) found that *Mimulus guttatus* grown in a greenhouse with or without pollinators diverged drastically in several phenotypic traits in just five generations, with those deprived of pollinators evolving an enhanced ability to self-fertilize. Such inferences are not possible from studies of nonplant model organisms that lack such reproductive modes.

Controlled laboratory experiments are useful in identifying potential evolutionary rates and trajectories, but field experiments can be used to assess changes under more realistic conditions, including the presence of multi-dimensional selective pressures. Under field conditions, pleiotropic effects and trade-offs may be

expressed differently. Accordingly, dramatically different conclusions may be drawn from field versus lab experiments. For instance, in Trinidadian guppies (*Poecilia*), laboratory experiments demonstrated that populations experiencing predation evolved delayed senescence relative to populations that did not, but in field experiments high-predation populations evolved earlier senescence (Reznick and Ghalambor, 2005).

Our definition of "field experimental evolution" requires that a study (1) take place in an outdoor or otherwise natural setting, (2) measure an evolutionary response across generations (not just selection), and (3) involve manipulation at the individual or population level to isolate specific factors and disentangle correlation from causation. Here, we briefly review two major themes in past studies of field experimental evolution in plants before proposing several areas of focus for future work.

HOW QUICKLY DO POPULATIONS EVOLVE IN THE "REAL-WORLD"

Previous field experimental evolution studies in plants have established that evolution can occur on time scales that humans can witness. In 12 years, experimental populations of the wheat *Triticum aestivum* evolved later flowering time in northern European populations and advanced flowering time in southern populations (Rhoné et al., 2010). Two 3-yr field studies on *Oenothera biennis* found evolutionary responses in life history (shorter life span and delayed flowering time) (Agrawal et al., 2013), decreased herbivore resistance, and increased competitive ability in response to experimental reduction of insect herbivores (Agrawal et al., 2012). These studies demonstrate that evolution of key plant traits can occur within just a few generations.
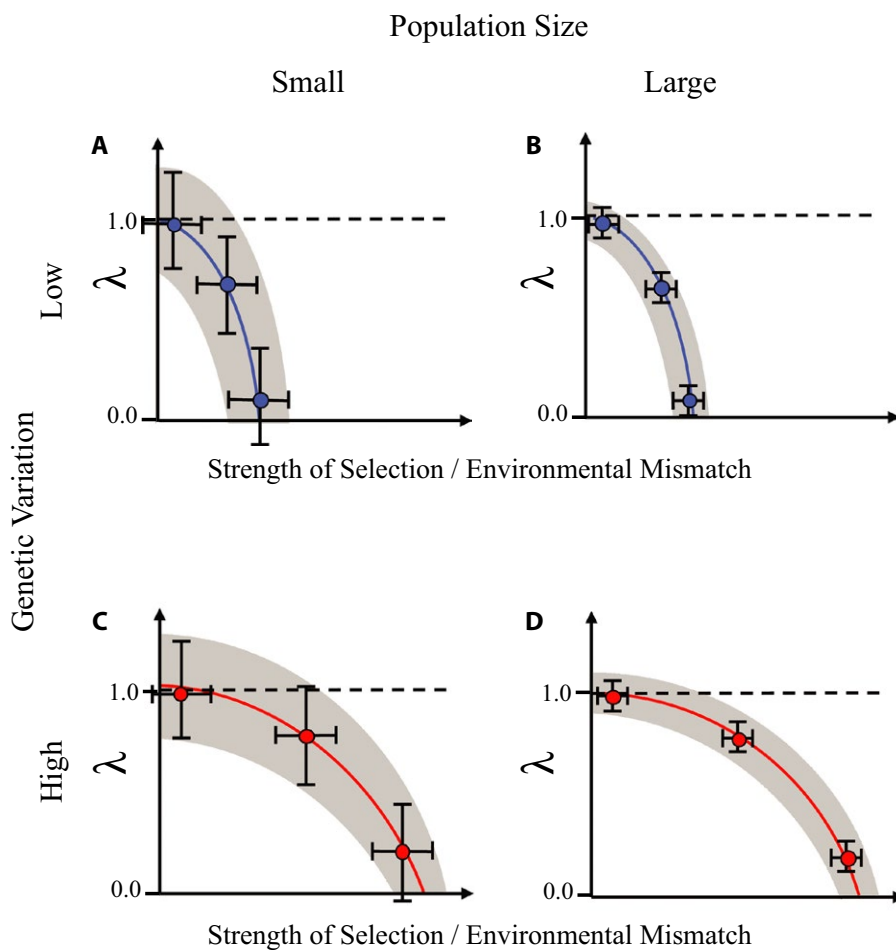
CAN WE DETECT GENETIC CHANGES IN PLANT POPULATIONS EXPERIENCING HUMAN-INDUCED CHANGE?

On the basis of predictions under various climate change scenarios, previous experimenters have manipulated conditions that are likely to have consequences for plant functioning and assessed genetic changes. For instance, in a long-term grassland experiment, plant communities were grown under simulated warming, drought, and precipitation treatments. After 15 years, AFLP analyses revealed significant genetic divergence between control and experimental treatments in sheep fescue (*Festuca ovina*) and common plantain (*Plantago major*) (Ravenscroft et al., 2015). Similar genetic divergence was found after 7 yr of drought and warming treatments on the Mediterranean shrub *Fumana thymifolia* (Jump et al., 2008). Under a 10-yr manipulation of precipitation variability, the dominant grass species *Andropogon gerardii* had reduced genetic diversity under the more variable treatment and a genomic signature of niche differentiation between treatments (Avolio et al., 2013). These studies demonstrate genetic evolution in direct response to climatic conditions, but more work is needed to understand the associated phenotypic changes, direction of responses, how specific factors interact, and their effects on population persistence.

FIGURE 1. Field evolutionary experiments are needed to parameterize hypothesized relationships between strength of selection (generated by environmental mismatch between current and future climates) and population growth λ. Gray bands represent confidence intervals. Expectations differ for small vs. large populations (A, C vs. B, D) and low vs. high within-population genetic variation (A, B vs. C, D). In small populations, we expect demographic stochasticity to result in larger variation in λ, which could result in increased risk of local extinction, while larger populations are buffered. Low levels of genetic variation will result in a rapid decline in λ with increasing strength of selection, due to paucity of individuals with nonzero fitness under stressful conditions. High levels of genetic variation provide a substrate on which selection can act and are expected to result in a shallower reduction in λ with increasing degree of environmental mismatch.

HARNESSING THE POWER OF PLANT FIELD EXPERIMENTAL EVOLUTION

Here, we focus on unstudied or under-studied areas amenable to field experimental evolution approaches that are critical for predicting and managing plant responses to global change.

Phenotypic plasticity may not be sufficient to allow plants to adjust to novel or less predictable climates (Franks et al., 2014), but evolving increased plasticity is a potential adaptive solution (Matesanz et al., 2010). Greenhouse studies have documented the evolution of increased plasticity. For instance, in "resurrection studies" (where stored ancestor seeds are grown with descendants in a common setting) on the North American invasive plant *Polygonum cespitosum*, phenotypic plasticity increased in 11 years (Sultan et al., 2013). Similar experiments in the field are necessary to account for potential differences in trade-offs and pleiotropic effects under additional selective pressures and to understand the extent to which plasticity can evolve: Will increased plasticity allow plants to tolerate climatic conditions that they have not historically experienced and to respond to increased inter- and intra-annual variation?

Experimental manipulation of population-level parameters and subsequent evolution in plants is also an understudied area. Human impacts are likely to result in changes to population size, density, age structure, genetic diversity, and other population-level characteristics, with poorly understood consequences for evolutionary rates and responses (Jump and Peñuelas, 2005). A few field studies have addressed these issues; e.g., Cook-Patton et al. (2017) manipulated both genotypic diversity and population density of *Oenothera biennis* and found significant interactions: Higher genetic diversity was associated with the evolution of increased germination and establishment at low densities, while the opposite was true at high densities. Follow-up evolutionary experiments that measure responses across multiple generations could elucidate the interactions between genetic diversity and other factors. Gene flow is another population-level parameter that will affect the rate and direction of evolution in plant populations, as it can either provide additional genetic variation to rescue a population or, conversely, can prevent local adaptation (migration load) (Lenormand, 2002). Rates of gene flow both within and between species may increase, given predicted distributional shifts. Experiments varying levels and sources of gene flow are needed to understand its potential role in climate change adaptation. Overall, field experiments on the interactions between climate and these population parameters in plants will help to inform conservation strategies, especially in terms of reserve design, assisted migration, and target population sizes.

Much more information is also needed on the interactions between strength of selection and these key population parameters. Assuming hard selection via global shifts in the trait thresholds allowing reproduction, if selection is too strong and standing genetic and phenotypic variation (including plasticity) is insufficient, extinction will be a more likely outcome than adaptation. Multigeneration experiments are needed to estimate the strength of selection and how it interacts with population-level parameters (such as population size and within-population genetic variation), as well as stochasticity, to lead to different outcomes. For instance, populations with high enough levels of genetic diversity will provide sufficient substrate for selection and result in a less-shallow drop in population growth rates with increasing environmental mismatch (Fig. 1), but we generally have little information about what levels of diversity should be considered "low" or "high". Large populations may be able to buffer against demographic stochasticity, resulting in less local extinction (Fig. 1). The interaction between these parameters is also important: populations with high levels of genetic variation may still be more at risk for extinction if they are small, due to demographic stochasticity (Fig. 1C vs. D). Field experiments that measure these interactions will provide critical information on

which natural populations are capable of effective evolutionary responses to climate change and can point to specific parameters for conservation and management attention.

Experimental evolution studies in the above-described areas will benefit from tests in a diversity of systems. Although annual plant species are the obvious choice for experimental subjects given their fast generation time, studies of plants with slightly longer generation times, such as short-lived shrub species, will broaden the field's taxonomic and growth habit breadth and allow predictions for different plant groups. Additionally, experiments need to target plants along different axes of variation, for instance, species differing in mating systems (selfing to outcrossing), life history strategies (e.g., ruderals, competitors, tolerators), and position along the leaf economics spectrum (fast to slow), since climate change's effects may vary.

FINAL POINTS

We believe that there is a historical legacy of thinking that field evolutionary experiments in plants are not worthwhile because evolutionary change takes too long. Extensive work contradicts this paradigm, supporting the idea that evolution happens rapidly in natural plant systems. However, most experimental studies of evolution in plants have utilized a small number of species and manipulated a limited set of factors in a limited region of parameter space. An expansion of all these aspects is needed to give a more complete picture of the conditions under which evolution will stave off plant extinctions in the face of global change.

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AUTHOR CONTRIBUTIONS

N. Mitchell and K. D. Whitney contributed to the concept behind this work, the background research, writing, and revision.

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