

Commentary

Plants as epigenetic mosaics: harnessing variability to thrive in a variable world

A central question in biology is how life persists in the face of environmental variability. Fundamental biological processes are efficient over a surprisingly narrow range of environmental conditions, but organisms rarely experience their optimal conditions because spatial and temporal variability is ubiquitous. Plant biologists have appreciated the importance of biological optima at least since Gabrielle Howard's (née Matthaei) pioneering experiments on photosynthesis in the early 1900s. Howard, best known as a co-founder of organic agriculture, rigorously demonstrated that photosynthesis has an optimal temperature, wedged between the rate limitation and 'injurious effect' of lower and higher temperatures (Matthaei, 1905) (Fig. 1). How then do plants survive when temperature and other crucial factors vary manyfold at every scale?

One way plants thrive in the face of variability is by being variable themselves. Indeed, much of plant biology examines plasticity – how plants vary their phenotype to match their environment. Most plasticity research has examined how plants optimize their whole or average phenotypes, but environmental factors also vary significantly within plants – light and herbivore attack, for example, often vary among leaves within plants. Our understanding of how plants cope with external variability by developing trait variability within themselves – known as subindividual variability – has advanced dramatically over the last decade, thanks in large part to work by Carlos Herrera and colleagues, including the recent article published in this issue of *New Phytologist*, Herrera *et al.* (2021; pp. 2065–2076).

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Variability in traits among reiterated organs (e.g. leaves) within plants – surprisingly often greater than average variability across plants within populations (Herrera, 2009) – has long been

hypothesized to be an adaptation to environmental variability (Whitham, 1983; Orians & Jones, 2001). For example, subindividual variability could optimize the phenotype of each plant unit to its specific microenvironment, thereby enhancing total resource collection. It could also hedge against temporal variability by expanding the range of conditions over which at least some tissue performs well, reduce the amount of tissue susceptible to any one herbivore species, inhibit herbivore acclimation to plant defenses (Wetzel & Thaler, 2016), or increase pollinator effort and fidelity (Herrera, 2009). Crucially for the evolutionary importance of subindividual variability, evidence has emerged that plant species and genotypes have distinctive levels and patterns of subindividual variability that differ among populations with different evolutionary histories (Harder *et al.*, 2019; Robinson *et al.*, 2020). A key lesson from this research is that plants are more than the sum – or mean – of their parts. As a field, we need to expand beyond our focus on trait means to include the role of trait variability.

Whereas many studies have documented subindividual trait variability and explored its ecological consequences, fewer have revealed the mechanistic causes. This is a major knowledge gap because how subindividual variability arises, changes through time and space, and whether it is or is not transmitted between generations will determine its ecological and evolutionary roles. Certainly, much subindividual variability is related to organ ontogeny – leaves change as they age – but trait variability among leaves of the same age is also high (Wetzel & Meek, 2019). One of the oldest hypotheses for subindividual variability is somatic mutation (Whitham & Slobodchikoff, 1981; Gill, 1986). Genetic mutations in meristematic cells would be passed to derivative cells and could cause plants to become genotypic chimeras containing multiple phenotypes. Since plants are an amalgamation of reiterated units that compete among themselves, somatic mutations were proposed to be an important way plants could adapt to changing environments within their lifetimes and pass those changes to their offspring (Whitham & Slobodchikoff, 1981). Subindividual genotypic diversity could also slow adaptation by insect herbivores, which often have faster generation times than their hosts. The genetic mosaicism hypothesis was an elegantly simple and provocative explanation for subindividual plant variability – indeed, it inspired decades of work.

Alas, reality is unconcerned with our perception of elegance. Despite decades of searching, there are very few examples of natural plants with somatic mutation rates high enough to create meaningful genetic mosaicism (Schmid-Siegert *et al.*, 2017), indicating somatic mutations are not a major source of subindividual variability. When Whitham & Slobodchikoff (1981) first proposed the genetic mosaicism hypothesis, they also proposed 'epigenetic factors' as an alternative, nonadaptive, hypothesis for subindividual plant variability. By epigenetics, however, they

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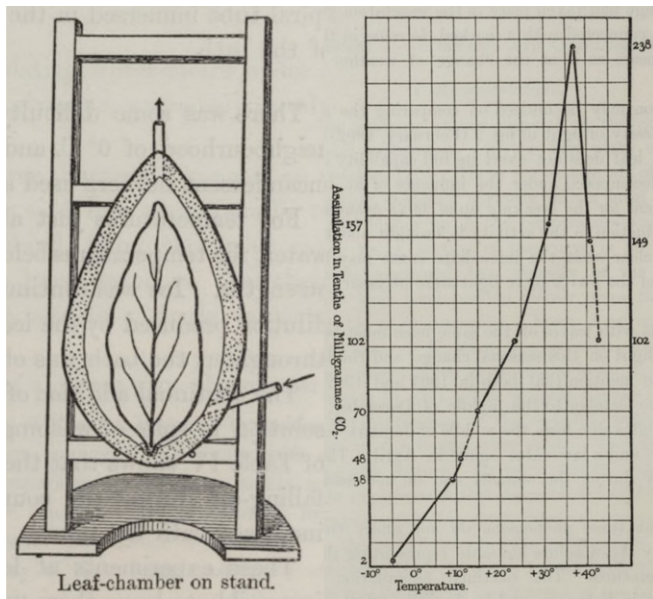


Fig. 1 The chamber Gabrielle Howard (née Matthaei) used in the early 1900s in her pioneering work on factors limiting the rate of carbon assimilation in photosynthesis. Her data (right) showed photosynthesis has a clear and narrow optimal temperature (modified from Matthaei, 1905). These results directly inspired early, influential thinking on optima and limiting factors in plant biology – and may have helped guide plant biology towards its focus on understanding how plants cope with environmental variability.

meant any environmental factor that influences phenotype during development, the term's contemporaneous definition. They explained that microscale environmental variation could interact with the sectorial nature of plant vascular systems to cause phenotypic variation within plants, a view further developed by Orians & Jones (2001) after the weak support for genetic mosaicism became apparent. This view has to be correct. Variation in environmental factors causes variation within plants. But at the time, lacking an understanding of modern epigenetics, no one imagined that environmentally-induced phenotypic variation

could have a persistent, heritable basis that transmits across dividing cell and generations. Without a heritable basis, subindividual variability seemed a passive response and unlikely to have an important role in evolutionary dynamics, and to some extent the field lost interest – that is, until Herrera and colleagues returned to these ideas armed with modern epigenetics.

In a beautiful example of science circling around to old ideas but spiraling upwards in terms of understanding, Herrera and colleagues have shown that plants are indeed epigenetic mosaics – in the modern sense of epigenetics. Multiple distantly related plant species possess within-plant variation in methylation related to subindividual phenotypic variability (Herrera & Bazaga, 2013; Alonso *et al.*, 2018). Epimutations therefore occur quickly enough and with enough spatial variation to lead to epigenetic mosaicism, but for this mosaicism to persist in an ecologically and evolutionarily meaningful way, the epimutation rates cannot be so fast that the patterns change before they influence phenotypes. Herrera *et al.* tackle this question in their article in *New Phytologist* by examining the temporal occurrence of epimutations through the growth of a wild lavender (*Lavandula latifolia* Lamiaceae, Fig. 2). They mapped the substantial epigenetic heterogeneity they found within each plant onto genealogies representing each plant's branching history and used phylogenetic methods to estimate the within-plant trajectory of epigenetic modification. Crucially, epimutations were not distributed randomly within the architecture of *L. latifolia*. Instead, they occurred steadily through time and were transmitted spatially in new tissue through growing branches, representing an internal information transfer that could enhance fitness in variable environments. This major advance in our understanding of subindividual variability led the authors to propose the epigenetic mosaicism hypothesis, which mirrors the genetic mosaicism hypothesis except that the mechanism is epigenetic rather than genetic.

Epigenetic mosaicism as a mechanism for coping with variability is so elegant it makes genetic mosaicism look clumsy in comparison. Whereas genetic mutations are essentially random with respect to the environment, epimutations are often adaptive responses to environmental cues. This difference means epigenetic mosaicism



Fig. 2 Mid-aged (left) and older individuals (right) of the lavender *Lavandula latifolia* (Lamiaceae). These plants accumulate epigenetic mutations in their somatic tissues continuously as they grow and age, and those epimutations are passed onwards within plants via the growth of new tissue and branches. This process of epimutation and internal propagation leads to epigenetic mosaicism, which likely structures subindividual trait variability. This discovery represents a potentially important and previously underappreciated mechanism that could help plants thrive in the face of environmental variability. Photographs courtesy of Carlos M. Herrera.

can benefit plants by matching the phenotype of each module to its specific microenvironment (e.g. light level), optimizing the overall phenotype of the plant. By contrast, genetic mosaicism would benefit plants only by increasing variability in general, which epimutations also achieve. Moreover, epimutation rates are much higher than genetic mutation rates, making epigenetics a faster mechanism for exploring the phenotypic landscape. Additionally, epimutations are reversible, whereas genetic mutations are essentially permanent and are passed to offspring (when mutant tissue undergoes reproduction). Because epimutations can be cleared in the soma, in gametogenesis, or not at all, plants potentially have three options for matching the persistence of epigenetic mosaicism to the timing of environmental variability. These features make epigenetic mosaicism a powerful and flexible solution for coping with variability – fast and responsive to cues but with a multiscale spatial and temporal memory that allows the perpetuation of successful epimutations.

An untested hypothesis for how plants might time epimutations is that epimutations that help plants match each branch to its spatial microenvironment should be cleared at gametogenesis because offspring will have to match new microenvironmental spatial patterns. By contrast, epimutations that enhance the whole phenotype of the plant in response to temporally autocorrelated environmental factors should be passed to offspring because parents and offspring are likely to experience similar values of temporally autocorrelated factors. Finally, epimutations that benefit plants by presenting herbivores with defensive mosaics – moving targets – that inhibit acclimation or adaptation should occur stochastically (Adler & Karban, 1994). Testing this hypothesis and advancing our understanding of epigenetic mosaicism will require functional research that links epimutations with their phenotypic and ecological effects.

There are two schools of thought about how subindividual variability benefits plants. The first sees plants as carefully optimizing their phenotypes in response to external cues. The second sees plants as neophiliacs or moving targets that benefit from stochastic change that stymies enemies and explores phenotypic space. While both views probably apply, it has been unclear how much or when. The discovery by Herrera *et al.* that epimutations accumulate steadily through time and are passed through branches suggests plants may use epimutations for microenvironmental matching. However, not all markers had genealogical signatures, and none deviated from Brownian motion, suggesting epimutations may also simply promote variability *per se*. The ecological role of epigenetic mosaicism and its position within this fundamental dichotomy are therefore open and tantalizing questions.

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