

MPG 2010+: Interactions of plants with their environment

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At a glance

Plants form the basis of all food webs on the planet, but we understand very little about the traits that allow plants to survive and reproduce in nature. The majority of our understanding of the molecular basis of plant function comes from laboratory studies with an inbred genotype of *Arabidopsis*., yet it is becoming increasingly clear that the solutions that plants have evolved to environmental challenges vary enormously among plant genotypes, and frequently involve associations with other organisms, such as microbes and insects. Our lack of success in understanding the traits that are important for plant environmental performance is in part a failure to heal the unhappy divorce that split plant biology departments along cellular-molecular and ecological-evolutionary lines. The solution will require training “genome enabled field biologists” who are adept at using the “-omic” tool box and are as well intimate with the art of natural history discovery, developing “-omic” tool boxes for a variety of plant species that span the range of phenotypic solutions to environmental problems and using field stations as natural laboratories for the study of plant gene function.

Definition of topic

Why study the interactions of plants with their environments? Traditionally, plants have been studied in isolation, in the laboratory, where environmental noise can be controlled and eliminated from experimental designs. Here, I lay out why this is no longer sufficient.

Plants form the foundation of the vast majority of food chains on the planet; all members of the complex communities that inhabit the earth rely on them for food, directly or indirectly. In contrast to most of these other community members, plants are largely immobile and must cope with the particular environment in which they find themselves in. They must avoid being consumed by all of the heterotrophs that exploit them as food, cope with abiotic stresses, compete with other autotrophs for the resources (water, light, essential nutrients) that they require for photosynthesis and growth, and find mates. All of these problems must be solved before their genetic representation in future generations, their Darwinian fitness, can be assured. Since environments are ever changing, there’s no one single optimal solution and the remarkable chemical and functional diversity found amongst the quarter of a million described higher plant taxa reflects the millions of different solutions that plants have evolved. Many of the solutions are principally chemical in nature. Plants are known to produce more than 100,000 different described secondary metabolites, a number that will likely double in the next decade as advances in high through-put (HTP) analytical instrumentation facilitates their characterization. While primary metabolites mediate the essential functions of growth under benign conditions, it is the secondary metabolites that allow organisms to solve all of the other challenges they face in the real world. These secondary metabolites represent the planet’s pharmacopeia that has, and remains the basis for most drugs that humans use.

Solving environmental challenges has resulted not only in the astounding chemical and functional diversity found amongst different species of plants, but also in the developmental plasticity of individual plants; an individual plant will reconfigure its phenotype in response to the biotic and abiotic environmental challenges it faces. Thus, a potential phenotype encoded in a plant's genome may only become expressed, when the plant is exposed to the appropriate environment. These environmental cues have provided essential insights into the inner workings of plants. The discovery of the small molecules that function as plant hormones provides an illuminating example. Hormones are the internal signals that all organisms use to adjust their physiologies to the prevailing environment and one might imagine that they would have been discovered through careful analysis of plant metabolomes. Not so. Several major classes of hormones (auxin, jasmonates, gibberellins, salicylates) were first discovered in heterotrophic organisms that had evolved the ability to manipulate their host plant's physiologies with plant hormones or hormone analogues for their own fitness benefit.

While the environment shapes plants, conversely, plants profoundly shape the environment, both in natural and agricultural settings. Not only do they contribute most of the O₂ and hydrocarbons and fundamentally determine the CO₂ concentrations and water vapor of the atmosphere, but their activities also influence the planet's surface energy balance and consequently shape weather patterns at regional and global scales. Plants provide many ecosystem services that are at the heart of human well being: they purify our water, stabilize the composition of the atmosphere, and control floods, to name but a few. However, we are only dimly aware of many of these services, and usually don't appreciate what we have until it is gone. Significant advances in quantifying and modeling the flux of elements through ecosystems and the feedback loops that they have on climate and ecosystem health have been made, but much more information is needed. As public awareness of the risks associated with climate change increases, research is driven by the legal efforts of governments as they wrestle with their country's real or perceived responsibilities in solving the associated problems. More basic research is needed to inform and guide this legislative process. Questions about the amount and duration of carbon storage by plants in different habitats, as well as the flux of nitrogen through wet deposition¹ are some of the key areas that need additional research. The intangible services that intact ecosystems provide -- as a source of solace, inspiration, replenishment and comfort, as well entertainment -- may offer additional political impetus for habitat preservation and should be added to the ever growing list of services that natural habitats provide.

As the activities of the Earth's 6 billion human inhabitants change the chemical composition of the planet, plants will be forced to function under conditions outside their recent evolutionary history. For example, plants are currently living outside the range of CO₂ concentrations they have experienced in the last million years, and it is unclear how their responses to these changes will influence future climatic patterns and the myriad of different effects that they have on the communities that inhabit the planet.

In short, plants can't be understood without the environment in which they have evolved, and the Earth's environment can't be understood without the activities of plants that shape it. Every step in the biological hierarchy from plant genome to planetary climate patterns is influenced by a web of interconnections between plants and their environment.

Status of the field, Key scientific questions research opportunities and needs

Our planet's biological legacy is the result of eons of natural selection. In the innumerable as-yet unmapped genomes of the natural world lie the solutions to the problems that life has faced in the past. This biological legacy is our collective library that we are burning – literally and figuratively -- at an unprecedented rate. Almost all of the books have never been opened, and the vanishingly few that have, have only been lightly browsed. To compound the loss, science is on the verge of discovering the tools our own species needs, so that we can use the information hidden in this treasure. The genomics revolution has fundamentally altered how we can exploit the genetic information in this library; it's as if the once hard-bound lexicons of genetic information of each species have become collections of loose-leaf notebooks within which individual genes can be shuffled from one volume to another, reordered, recollated, recombined, thanks to advances in genetic manipulation. Technology-savvy biologists have so refined the “omic” tools that they can be used with almost any organism. The rapid reduction in sequencing costs is blurring the boundaries between “model” and “non-model” organisms; transcript analyses are commercial commodities; and proteomics and metabolomics are common phrases used to market new analytical instrumentation.

Unfortunately, much of this synopsis has not yet been realized. The urgency is as real as the potential, but the reality of the actual situation is more sobering. The complete sequencing of a single inbred ecotype of *Arabidopsis thaliana* inaugurated the ‘omics’ revolution in plant biology, and while genomes and transcriptomes are now readily and inexpensively sequenced, the other “-omic” analyses (those of proteomes, metabolomes, and the growth and developmental phenotypes) are still in their infancy. The complexity of these analyses stands in stark contrast to the relatively simplicity of analyzing linear sequences of nucleotides. A major gap here is that we do not know how the nucleotides interact in complex ways to finally produce to cornucopia of substances found in plants. Equally as challenging will be the knitting together of these “omic” data bases to understand how the environment shapes the translation of genomes into adaptive phenotypes. To date, most of the discoveries of gene function still come from traditional, narrowly focused approaches that are often claimed to be “hypothesis-driven”, rather than from more open-ended unbiased “omic” approaches. There have, however, been many advances in our understanding of just how little we know, and each discovery points to new opportunities.

We have learned that there's much more “coarse-grained” genetic diversity in the naturally interbreeding populations of plants that we call a biological species than was previously thought. The sequencing of different ecotypes of *Arabidopsis thaliana* has revealed that individuals can differ by hundreds of genes². Previously, population geneticists have focused on the phenotypic consequences of the fine-grained scales of genetic variance, that which occurs within alleles at particular genetic loci. A recent HTP mass spectral analysis of the metabolomes of a population of recombinant inbred lines (RILs) of *Arabidopsis* revealed only 6 major metabolic groupings despite the almost 500,000 single nucleotide polymorphism (SNPs) that the population harbored³. Such admittedly early-stage analyses, suggest that only a small number of the variable genetic loci result in metabolically distinguishable phenotypes and that a better understanding of the more coarse-grained sources of genetic variation will assist our understanding of the genetics of Darwinian adaptation to rapid environmental change. Species hybridizations and the formation of allo- and polyploidy taxa are additional important processes that can extremely rapidly produce coarse-grained genetic variation. In such hybridizations, the environmental signaling systems of the different parental genomes appear to be melded in a “plug and play” fashion to generate tremendous

phenotypic variance ⁴, which likely sets the stage for the longer lasting winnowing of this coarse-grained variance to incorporate the influence of the hundreds of loci responsible for optimizing an organism's Darwinian fitness (see box for definition).

The availability of inexpensive sequencing is fundamentally changing how we address all aspects of the process of adaptation. Progress in genome-wide-association (GWA) mapping, which has produced impressive results for the functional analysis of human genomes, will require the sequencing of thousands of plant genomes ⁵. But for the GWA effort to bear fruit, we need to learn how to conduct HTP phenotyping of plants not only under constant and well-defined laboratory environments, but also the under the panoply of variable stresses that occur in natural habitats. This will require recruiting the expertise of scientists from many different disciplines into plant biology: of engineers for the real-time imaging of plant growth and ontogeny and remote monitoring of growth and spread of populations; of chemists and bioinformaticians to characterize the metabolomes and proteomes of plants and how they change in the face of different environmental stresses; and of mathematicians to create dynamic models with which to interpret the mountains of data, to name just a few.

However, technology alone cannot be our salvation, and making sense of all the data will also require a return to the past. We have lost our ability to train biologists with a “feel for the organism”. The study of natural history lost its clout when the genetic (and later “-omic”) tool box, used to pry open a handful of organisms domesticated for laboratory studies, invalidated “biological intuition”. But this is clearly changing as natural history expertise regains its cache. We need a generation of “molecularly enabled” field biologists, who are adept at using the “-omic” tool box as well as intimate with the art of natural history discovery. Many graduate training programs still reflect the unhappy divorce that split biology departments along cellular-molecular-developmental and ecological-evolutionary lines. As a consequence, students trained to use the powerful tools of molecular biology and chemistry are poorly trained in ecological skills, and vice versa. Graduate training programs that reunify the study of plant biology by focusing on Darwinian fitness as the criteria for understanding gene function will be needed. Field stations that can be used as “natural laboratories” for the phenotyping of genetically defined and manipulated plants in the habitats in which they evolved will also be needed. Along these lines, it is worth noting that “reverse ecology”, that is, establishing the ecological interactions of lab-adapted model organisms for genetic research, is today more difficult than dissecting the genetics of focal species used in ecological studies.

This brings us back to the statement made before, that the full potential of plant genomes is only realized in response to the environmental signals that have shaped these genomes. Among the most important signals are those that emanate from prokaryotic microbes. All plants harbor prokaryotes, some are culturable, but the vast majority are not and unknown. DNA fingerprinting has revealed that most plants are Trojan horses for vast microbial communities feasting on the carbon exuding from leaves and roots. Many of these microbes live endophytically without eliciting disease symptoms, but as many are unculturable, they have been recalcitrant to experimental manipulations that might reveal their exact impact on the plant host, and that would reveal how they function. Many microbial endophytes are known to promote plant growth by altering endogenous hormone responses, functioning probiotically to increase resistance against pathogenic bacteria, and increasing the availability of mineral resources. Understanding the function of this largely hidden community within plants may hold the key to understanding why plant growth is so notoriously environmentally sensitive. Since most members are unculturable, new techniques

will be required for altering their abundance and community composition before their ecological role can fully be appreciated^{6,7}.

Effector molecules from pathogenic microbes, from herbivores, and from mutualists (mycorrhizial, rhizobacteria) are all known to dramatically alter the phenotypes and function of plants. Galling insects create entirely new plant structures and mechanistic analysis of tumor producing *Agrobacterium* gave biologists the ability to genetically transform plants (and a host of other organisms as well). Elicitors in the spit of herbivorous insect larvae are known to increase the production of new direct and indirect defenses, change the phenology of flowers and alter source-sink relationships. Similar elicitors from pathogenic microbes have revealed the logic of elaborate innate immune systems. While the identification of a small number of these signals has greatly simplified the analyses of the mechanisms by which they are perceived, the promise of engineering durable pathogen and herbivore resistance and of harnessing the services of microbial mutualists (mycorrhizae and rhizobia) in crop plants has yet to be realized. There are several reasons for this. First, although we have made great progress in deciphering the general logic of plant-pathogen interactions, precise activities have only been assigned to a very small minority of pathogen receptors encoded in genomes of plants, even those of well-studied model species. Second, we know little about the full spectrum of microbes that plants encounter in their natural environment, let alone about the interactions between these microbes, and how they in turn affect the response to other predators. It is not unlikely that many more partners (and therefore evolving genomes) are involved in this interaction than we commonly imagine.

Plants clearly operate on different time scales than most organisms. They hold the records for the oldest and as well as the largest organisms on the planet and maximizing Darwinian fitness is often a matter of timing: doing the right thing at the right time. How plants time the transition from vegetative to reproductive growth, and how these important transitions are changing in the face of changing climates as seen remarkable progress, but we are still in the dark about how plants tell time, and how they accomplish one of their most remarkable adaptations to environmental stress: that of escaping in time. Most commonly this occurs as the regulation of seed dormancy, but other regenerative organs are also involved. Advances have recently occurred in our understanding of the genetics and phytohormone control of dormancy, very little is known about the environmental cues that plants use to break dormancy, other than the reliable signals of resource availability: light, water and temperature.

An evolutionary context for adaptive mate choice in plants was developed more than two decades ago⁸. Plants have the ability to assess the genetic quality of a potential mate well before committing resources in the production of offspring, due to the large amount of gene expression that occurs in the haploid sporophyte during pollen tube growth. As we make progress in understanding the genetics of adaptive environmental responses we will finally be on a firmer footing to better appreciate the qualities that plants may be seeking when they select their mates.

Expected outcome and benefits

If the Earth is to support 9 billion people by 2050, as has been predicted, crop plants will need to become ever more efficient at fixing carbon and producing nutritious harvestable yields with fewer agricultural inputs from water, fertilizer and pesticides. If we could engineer crops with the carbon- and water-use efficiency of C4 grasses, the N-fertilizer independence of legumes, the P-fertilizer independence of mycorrhizal plants, and the pest and pathogen resistance of many native plants, we would be closer to solving this problem. Nature is still the mother of invention when it comes to improving on plants.

We will also need to consider how construct man-made ecosystems that provide the ecosystem services comparable to those of natural ecosystems.

Metaphors:

A metaphor for Darwinian fitness: Think of Darwinian evolution as a stream of nucleotides flowing forward in time. Organisms move the genetic stream forward; their Darwinian fitness measures the success of this transmission. Organisms are not passive conduits but, rather, the Fed Ex employees of the genetic stream, finding new ways to make their genetic deliveries to the next generation more successful – more timely, more reliable, more economical. Darwinian fitness is the product of genomes, as they are transcribed into ‘transcriptomes’, and further translated into ‘proteomes’ that ultimately produce the organisms that must cope with the challenges of life and pass along their genetic material, lest the stream that is carried forward in time evaporates. These organisms (the Fed Ex employees of the genetic stream) keep trying new ways of garnering resources from the planet (energy, water, minerals) to make their genetic deliveries to the next generation more successful – more timely, more reliable, more economical -- to maximize their Darwinian fitness. Survival in the real world requires complex traits that quantitatively adjust a plant’s metabolism to meet the demands of growth, defense and reproduction required to maximize the production of grandchildren, the currency of Darwinian fitness.

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