Many Facets of Dynamic Plasticity in Plants

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The evolutionary processes that transitioned plants to land-based habitats also incorporated a multiplicity of strategies to enhance resilience to the greater environmental variation encountered on land. The sensing of light, its quality, quantity, and duration, is central to plant survival and, as such, serves as a central network hub. Similarly, plants as sessile organisms that can encounter isolation must continually assess their reproductive options, requiring plasticity in propagation by self- and cross-pollination or asexual strategies. Irregular fluctuations and intermittent extremes in temperature, soil fertility, and moisture conditions have given impetus to genetic specializations for network resiliency, protein neofunctionalization, and internal mechanisms to accelerate their evolution. We review some of the current advancements made in understanding plant resiliency and phenotypic plasticity mechanisms. These mechanisms incorporate unusual nuclear–cytoplasmic interactions, various transposable element (TE) activities, and epigenetic plasticity of central gene networks that are broadly pleiotropic to influence resiliency phenotypes.

Crop improvement strategies to address food security demands have relied on a diversity of germplasm as a resource from which to derive plant stress tolerance in breeding. However, with increasing environmental challenges, rising soil salinity and encroaching desertification, annual climate instability, and drought and flooding threats of increasing frequencies, additional knowledge is needed to interpret plant environmental sensing and response behaviors and their amenability to direct manipulation. Toward these ends, emerging data, and a careful rereading of past research, provide valuable insight into the multiplicity and interconnections of adaptive strategies in plants that serve to enhance their environmental resiliency. Here, we review four of the areas in which epigenetic and

environmental sensing mechanisms have integrated with genetic plasticity to broaden intra-specific adaptation in plants.

REPRODUCTIVE PLASTICITY

In an agricultural context, plant fruit and seed production can define crop yield. Consequently, factors associated with optimizing yield have been subjected to intense selection. Plant reproductive behavior within a high-density, intensive agricultural system is often modified relative to a species' natural habitat (in situ) reproductive strategies to accommodate breeding schemes (discussed in Altieri and Merrick 1987). This is particularly the case for crops that display predominantly or exclusively self-pollination

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X. Yang and S.A. Mackenzie

under agricultural (ex situ) cultivation (Zuellig et al. 2014). In native ecosystems, capacity for self-pollination safeguards a lineage during plant isolation, but this system of reproduction results in significant inbreeding, so is generally accompanied by incidence of male (pollen) sterility or other mechanisms to facilitate outcrossing and/or genetic recombination. Nuclear male sterility mutations can arise, but generally at sufficiently low frequency to make them minimally influential on gene flow (Willis 1999). Rather, many species display a facultative, reversible system for male sterility that capitalizes on pliancy of the mitochondrial genome, a feature that is distinctive to plants.

“Facultative gynodioecy” is a reproductive system that produces both hermaphrodite and females in a population. The phenomenon arises with the propensity of plant mitochondrial genomes to undergo rearrangement and non-homologous recombination (Gualberto and Newton 2017). Unlike animal systems, in which mitochondrial genomes are conserved in size and structure, plant mitochondrial genomes are unusually variable in organization and recombinogenic. In *Arabidopsis*, large (>1000 bp) repeats participate in high-frequency, reciprocal recombination, whereas smaller repeats, from 50 to 500 bp in size, engage in asymmetric DNA exchange events that produce rearrangement of the genome (Davila et al. 2011), as well as substoichiometric shifting events that alter the relative copy number of subgenomic DNA molecules (Arrieta-Montiel et al. 2009). Aberrant recombination activity within plant mitochondria has resulted in introgression of foreign DNA as well as intragenic DNA exchange events that can, collectively, produce dominant mutations (Gualberto and Newton 2017). Many of these aberrant gene configurations, at least those that are retained within plant lineages, condition male sterility. Pollen disruption conditioned by a mitochondrial mutation is termed cytoplasmic male sterility (CMS), a trait that has been used since the 1950s for agricultural purposes to reduce costs in hybrid seed production for numerous crops (Chen and Liu 2014).

Within natural plant populations, CMS mutations can be countermanded by nuclear fertil-

ity restorer genes. Modeling the frequency and longevity of population genetic impact attributable to a CMS mutation is a function of the frequency and fitness of male fertility restorer alleles within a given population (Case and Caruso 2010; Caruso et al. 2012; Caruso and Case 2013). What generally goes unnoticed in the development of these nuclear–cytoplasmic models, however, is the influence of environment. The recombinogenic behavior of the mitochondrial genome can be controlled by nuclear genes that are environmentally responsive. In the case of plant-specific nuclear gene *MutS HOMOLOG 1 (MSH1)*, for example, mutation or suppression of the gene activates recombination at ~50 mitochondrial repeats and leads to genomic substoichiometric shifting in *Arabidopsis* (Davila et al. 2011) as well as *Brassica juncea* (Zhao et al. 2016) and other species (Sandhu et al. 2007). In a wild-type plant, suppression of *MSH1* can lead to male sterility (Sandhu et al. 2007; Zhao et al. 2016); however, altered expression of *MSH1* in a cytoplasmic male sterile line can cause reversion to fertility (Zhao et al. 2016; N Zhao, L Zhang, X Yang, et al., unpubl.), reflecting a reversible dynamic inherent to mitochondrial genomic rearrangement. Steady-state transcript levels for *MSH1* in reproductive tissues are suppressed under abiotic stress conditions that include heat, cold, salt, drought, and high light (Shedge et al. 2010; Xu et al. 2011; Virdi et al. 2016; Kenchanmane Raju et al. 2018), but markedly amplified by changes in sucrose levels (Hruz et al. 2008; N Zhao and X Yang, pers. comm.). Thus, the mitochondrial genome is conditioned for greater recombination during stress conditions and stabilized by enhanced sucrose availability. The flowering and fertilization process involves changes in sugar transport to accommodate the energy-intensive process of seed development following successful pollination. During conditions of plant isolation and cross-pollination failure, the absence of these sugar signals can serve as a sufficient cue to alter *MSH1* expression, leading to low-frequency reversion to pollen fertility and successful self-pollination. Alternatively, successful early pollination by a maintainer genotype and enhanced sucrose transport stabilize the mito-

chondrial genome and permit transmission of the male sterility trait (Zhao et al. 2016; N Zhao, X Yang, and S Mackenzie, unpubl.).

“Apomixis” is a second reproductive strategy that shows unusual plasticity in plants, representing a series of inherited mechanisms for asexual reproduction by clonal seeds that bypass meiosis and egg cell fertilization. In the apomict, meiotic mother cells or ovule somatic cells produce unreduced products that divide mitotically to form the embryo sac (Carman 1997). The phenomenon of apomixis is relatively widespread, occurring naturally in more than 120 genera of angiosperms in nearly 40 families, with ~75% of apomicts identified in Asteraceae, Rosaceae, and Poaceae (Carman 1997; Asker and Jerling 2017). Agriculturally, the apomictic trait permits genetic fixation of a desirable genotype, and so has been the subject of intensive investigation.

In most cases, species with this trait are facultatively apomictic but also undergo sexual reproduction to some extent (Koltunow and Grossniklaus 2003). Apomixis is most often observed in polyploid species, but is also observed in some diploids, so that polyploidy is not required for the phenomenon. The apomictic abnormalities associated with gametogenesis are thought to arise by ectopic expression of developmental pathways caused by multiple genome asynchrony in polyploids (Carman 1997). Variable alterations in reproductive development can result in apomixis. During early ovule ontogeny, it is possible for sexual and apomictic development to occur together within the same ovule or in multiple ovules of a single plant. These observations suggest that apomixis arises by dysregulation of various developmental steps of sexual reproduction (Koltunow and Grossniklaus 2003). For example, unfertilized ovules produce somatic cells that can form embryos in the case of adventitious embryony. Alternatively, gametophytic apomixis occurs from an unreduced egg cell that forms an embryo by variously altered processes (Rodriguez-Leal and Vienne-Calzada 2012).

Aposporous apomixis in *Hieracium praelatum*, producing 2n gametophytes from vegetative cells, is shown by deletion studies to involve

at least two genetic loci, *LOSS OF APOMEIOSIS* (*LOA*) and *LOSS OF PARTHENOGENESIS* (*LOP*). *LOA* is thought to participate in apospory and suppression of sexual megaspore development, whereas *LOP* may function in the separate development of embryo and endosperm (Koltunow et al. 2011). Loss of the two loci restores sexual development, indicating that sexual reproduction is a default pathway that can be interrupted by apomictic processes.

There is increasingly compelling evidence that apomixis is an environmentally responsive function that is epigenetically controlled (Grimanelli 2012). In species that undergo both sexual and apomictic reproduction, the balance between these two pathways can be influenced by oxidative stress conditions (Nedelcu et al. 2004). Numerous species have shown apomixis frequency to be responsive to changes in photoperiod (Knox 1967; Evans and Knox 1969; Klatt et al. 2016), and to abiotic stress conditions (Gounaris et al. 1991; Rodrigo et al. 2017).

Female gametogenesis appears to be regulated by epigenetic mechanisms that participate in sexual versus apomictic development. In *Arabidopsis*, female gametophyte development from sporophytic cells in the absence of meiosis can occur in *AGO9* dominant mutants (Olmedo-Monfil et al. 2010), implying a role for the small RNA and RNA-dependent DNA methylation pathways in distinguishing sexual from aposporous development. Similarly, the *AGO104* gene, another component of the small RNA pathway that influences centromeric chromatin, participates in the production of functional unreduced gametes and apomixis-like behaviors in maize (Singh et al. 2011). In dandelions, interploidy crosses that produce diplosporous progeny undergo changes in genome-wide methylation patterning (Verhoeven et al. 2010) and appear able to confer epigenetic abiotic stress signaling transgenerationally (Morgado et al. 2017). Coupled with earlier evidence of epigenomic reprogramming during gametogenesis in plants (Wang and Köhler 2017), these observations suggest that epigenetic programming of gamete “specification” occurs as well, representing an underrecognized plant developmental decision point in response to environmental change.

X. Yang and S.A. Mackenzie

**ORGANELLAR GENE
NEOFUNCTIONALIZATION**

Protein multifunctionalization is an evolutionary process that serves to enhance phenotypic plasticity as plants expand their growth range in variable environments (Fig. 1). Two examples of this phenomenon share similarities in features and in their unexpected functional versatilities.

The plastid is a subcellular compartment that is unique to the plant kingdom and shows a range of behaviors important to adaptation, including photosynthesis, carbohydrate storage in stems and roots, phytohormone biosynthesis, pigment synthesis in flowers and fruits, and abiotic and biotic stress response. Evolution of novel plastid types and functions relies on the amenability of nuclear-encoded proteins to multitargeting and spatiotemporal regulation of expression. An example of this adaptability is the recent discovery of the “sensory” plastid, a plastid type that is localized to vascular parenchyma and epidermal cells, is ~30% the size of a

mesophyll chloroplast, and displays distinctive proteome enrichment in stress-response proteins (Virdi et al. 2016; Beltrán et al. 2018). Genes that encode sensory plastid-specific proteins appear to contain promoters under spatiotemporal regulation (Virdi et al. 2016). Circumstances like this provide an ideal opportunity for protein multifunctionalization.

Plastids contain a nucleoid subcompartment that harbors the plastid genome and DNA replication, transcription, and RNA-processing functions (Sato et al. 2003; Melonek et al. 2016). Consequently, the plastid nucleoid has the capability of responding to environmental cues that include nuclear signals to alter photosynthesis, ROS-mediated cellular stress signals, and developmental cues for plastid redifferentiation. Protein composition of the nucleoid is variable across plant lineages, providing evidence of its repatterning over evolution (Pfalz and Pfannschmidt 2015; Kobayashi et al. 2016). Whirly proteins comprise a small family (Desveaux et al. 2005) of nucleoid-localizing proteins that

Figure 1. Diagrammatic overview of nuclear epigenetic and organellar components of phenotypic plasticity in plants. CMS, Cytoplasmic male sterility.

have adapted through multifunctionalization in plants. The proteins localize not only to plastids, but to the nucleus and/or mitochondria (Desveaux et al. 2005; Isemer et al. 2012).

Whirly proteins in *Arabidopsis* bind single-stranded DNA/RNA and may have originated, early in their evolution, to provide organellar genome stability by suppressing illegitimate recombination at small DNA regions of microhomology (Marechal et al. 2009; Cappadocia et al. 2010). Consistent with this hypothesis, analysis of *WHY*-GFP fusions show that the WHIRLY1 protein localizes to the plastid nucleoid, and the Whirly family of proteins target both mitochondria and plastids (Krause et al. 2005). Yet, Melonek et al. (2010) provide evidence that only a portion of *WHY1* is nucleoid-bound, and the protein can also be found associated with intron-containing transcripts (Melonek et al. 2010). Moreover, in maize, *WHY1* appears to participate in splicing of the *atpF* group II intron and may be essential for assembly of the large ribosomal subunit (Prikryl et al. 2008), underscoring the importance of these proteins in organelle biogenesis.

Remarkably, recombinant *WHY1* protein has the capacity to translocate from chloroplasts to the nucleus (Isemer et al. 2012), and *WHY1* appears to function as a nuclear transcription factor in salicylic acid signaling (Desveaux et al. 2004, 2005). Additionally, the protein appears to function in the nucleus to influence telomere length homeostasis (Yoo et al. 2007). It has been suggested that *WHY1* participates in environmental sensing, functioning in chloroplast-to-nucleus retrograde cross talk to facilitate abiotic-biotic stress tolerance following changes in redox state of the photosynthetic electron transport chain (Foyer et al. 2014).

A second multifunctional organellar protein has been identified that similarly appears to enhance phenotypic plasticity in response to environmental change. *MUTS HOMOLOG 1* (*MSH1*) was initially identified in *Arabidopsis* to be a plant-specific, mitochondrially targeted protein that suppresses illegitimate recombination (Abdelnoor et al. 2003, 2006). More extensive study of its mitochondrial association showed that *MSH1* functions in the induction/

suppression of CMS, as described earlier. However, the *MSH1* protein also targets to plastids, and its transcription is regulated to permit specific accumulation in epidermal, vascular parenchyma, and reproductive tissues that contain sensory plastids (Virdi et al. 2016).

Whereas suppression of mitochondrial *MSH1* influences mitochondrial genome configuration, disruption of the plastid form results in epigenomic reprogramming of the plant (Xu et al. 2012; Virdi et al. 2015). The *msh1* phenotype includes genome-wide methylome repatterning (Virdi et al. 2015) and altered expression of numerous abiotic, biotic, phytohormone, and circadian clock networks (Shao et al. 2017), resulting in enhanced tolerance to high light (Xu et al. 2011), heat (Shedge et al. 2010), cold (Kenchamane Raju et al. 2018), drought (Virdi et al. 2016), and salt (Kenchamane Raju et al. 2018). Within sensory plastid-containing cells, the *msh1* phenotype includes changes in expression of DNA methylation and histone-modifying genes, as well as calcium and mitogen-activated protein kinase (MAPK) signaling pathways (Beltrán et al. 2018).

RNAi suppression of *MSH1* is followed by segregation of the RNAi transgene to produce transgene-null segregants that retain *msh1* “memory” (Xu et al. 2012; Virdi et al. 2015). The memory phenotype, involving delayed flowering, delayed maturity transition, reduced growth rate, altered circadian clock, and enhanced stress responsiveness, is heritable indefinitely (Xu et al. 2012; Virdi et al. 2015). Reciprocal crossing of the “memory” lines with wild-type produces plant lineages with measurable growth and yield enhancement and reduced genotype x environment interaction effects, a phenomenon recapitulated in both monocot and dicot crop species (De La Rosa Santamaria et al. 2014; Virdi et al. 2015; Yang et al. 2015; Raju et al. 2018). These *MSH1* features are epigenetic, reproducible, and conserved within a range of plants to influence phenotypic resiliency to environmental stress.

What is striking about the *MSH1* and *WHY1* examples of protein multifunctionalization are their seemingly similar evolutionary features. Both represent nuclear genes encoding

X. Yang and S.A. Mackenzie

organellar proteins that display DNA-binding and regulatory functions. Both proteins show evidence of multitargeting, nucleoid and thylakoid localization, redox influence, and participation in plant environmental adaptation. These similarities imply that there may be additional multifunctional proteins emerging from future sensory plastid and nucleoid proteome studies. Similarly, these parallels imply that plant mitochondria and plastids, as highly versatile organelles in plants, serve central roles in phenotypic plasticity for rapid adaptation functions of the plant.

TRANSPOSABLE ELEMENT DYNAMICS

Transposable elements (TEs), or transposons, are mobile genetic elements found in virtually all genomes sequenced to date. Together with genome polyploidization events during plant evolution, TEs serve to greatly enlarge plant genomes in size (Wendel et al. 2016). Although TE families are numerous and highly varied, expansion within a plant lineage is often attributable to a single or small number of TE families (El Baidouri and Panaud 2013; Vicent and Casacuberta 2017). In *Arabidopsis*, ~18% of the genome is comprised of TEs, whereas 85% of the maize genome displays homology with TEs, with most other plant species falling somewhere between (Kaul et al. 2000; Oliver et al. 2013). Among closely related species, such as *Sorghum bicolor* versus *Zea mays*, the difference in TE composition is significant, with TEs accounting for ~65% of the sorghum genome (Kaul et al. 2000; Oliver et al. 2013; Hirsch and Springer 2017). The vast disparities in TE numbers per genome is, in part, caused by an equilibrium between TE gain and loss processes. TE loss from a genome occurs through unequal homologous and illegitimate recombination activity, which appears to be fairly efficient because, in most plant genomes, the majority of long terminal repeat (LTR) retrotransposons comprise relatively recent insertions (Bennetzen and Wang 2014).

A significant proportion of TEs are associated with genes; 36% of *Arabidopsis* genes contain a TE within a 1 kb distance, whereas this number goes to 86% in maize (Li et al. 2015).

Recent studies show evidence that TEs play beneficial roles for plant genome evolution and chromatin behavior. Remarkably, TE presence or insertion within genes is often tolerated and does not necessarily disrupt gene function (Bera et al. 1995; Weiss 2013; West et al. 2014; Sahebi et al. 2018). Evidence suggests that TEs factor prominently in plant–environment interaction, phenotypic plasticity, and as a driving force of evolution. These functions play out in three primary ways.

TEs as Mobile Elements

The traditional role attributed to TEs is as important sources of accelerated mutation frequency. Their activity in high-frequency mutation occurs most often under stress conditions, generating genetic diversity that is subject to natural selection. As with any type of mutation, TE-associated activity can be harmful, causing genome instability, inversions, and deletions (Mieczkowski et al. 2006; Zamudio and Bourc'His 2010; Lee et al. 2015). However, a significant number of plant genes have been derived from TEs through exaptation, in which TE regulatory or coding sequences that previously functioned in transposition activities now provide adaptive advantage to the host (Feschotte and Pritham 2007; Hoen and Bureau 2012). TEs also participate in the evolution of promoter and intron sequences (Zhao et al. 2016).

Exapted TEs are thought to benefit plants in the process of environmental adaptation. New traits may emerge via element transposition under stress conditions, with beneficial traits retained during directional selection. Some proportion of TE mutations will become fixed in a population, participating as potential networks of coordinate DNA-binding sites to comprise stress adaptive features, and finally undergoing immobilization and full co-opting by the host genome (Joly-Lopez and Bureau 2018). Evidence in support of this hypothesis by reverse genetics and phenomics shows that mutations within exapted TEs in *Arabidopsis* produce novel plant phenotypes under stress conditions, and affirm participation of exapted TEs in plant responses to phosphate limitation, high salt con-

centration, freezing temperatures, and arsenic toxicity (Joly-Lopez et al. 2017).

TEs in Gene Regulation

Beyond promotion of accelerated genome mutation, TEs are a rich resource of regulatory activities, including *cis* regulation mediated by regulatory elements containing TEs and *trans* regulation mediated by TE-produced noncoding RNAs and proteins at both transcriptional and posttranscriptional levels (Chuong et al. 2017). TEs often contain tissue-specific promoter activity or stress-responsive elements, affording the ability to adjust transcription in different tissues or under different environmental conditions, activities that can pass through to nearby genes (Naito et al. 2009; Guio et al. 2014; Bouttier et al. 2016; Chuong et al. 2016). In a genome-wide study of transcriptional response during heat stress, conducted in ten ecotypes of *Arabidopsis*, 203 of 3822 tested TEs showed significant differential expression in response to heat stress (Barah et al. 2013). Studies of the stress-induced transcriptome and transposon proximity to genes in maize showed evidence of strong correlation between TE insertions and stress-responsive gene up-regulation, suggesting that TEs can provide local enhancer activities that stimulate stress-responsive gene activity (Makarevitch et al. 2015). In rice, insertions of a high-copy-number TE, mPing can enhance responsiveness to cold stress in nearby genes (Naito et al. 2009). Agriculture-based selection has been an important contributor to the identification of TE-associated trait acquisition. For example, the LTR retrotransposon Hopscotch is responsible for an insertion in the maize domestication gene *teosinte branched1* (*tb1*) that acts as an enhancer of *tb1* expression and partially explains the increased apical dominance phenotype of domesticated maize (Studer et al. 2011). Similarly, research on Sicilian blood oranges (*Citrus sinensis*) identified a Copia-like retrotransposon insertion in a region adjacent to the MYB transcriptional factor named Ruby, controlling its expression in a cold-dependent manner to modulate anthocyanin production and fruit color (Butelli et al. 2012).

TEs in Epigenetic Regulation

In plants, cytosine methylation is found in three contexts, CG, CHG, and CHH, in which H is A, T, or C. The distribution of these three methylation contexts is uneven, with the majority of CHG and CHH associated with silencing and found in repetitive and heterochromatic regions that are highly populated by TEs. Genic regions show higher levels of CG methylation, with CHG methylation localized primarily within introns that contain TEs, supporting a relationship between CHG methylation and TE presence within gene regions. This trend holds true in *Arabidopsis* (Le et al. 2015), soybean (Kim et al. 2015), maize (West et al. 2014), and several other species in which genome-wide methylome data are available. In maize, 10% of genes have intragenic CHG methylation associated with TEs and use H3K9me2 chromatin marks (West et al. 2014).

In *Arabidopsis*, the heterochromatic state of intronic TEs is critical for proper transcription of associated genes (Le et al. 2015). TEs are subjected to tight regulation imposed by DNA-modifying machinery. Their presence is associated with high-density, localized DNA methylation, small RNA activity, and histone-modification changes that lead to chromatin structure changes, alternative splicing, and gene expression changes that can influence neighboring gene regions as well and alter phenotype (Lisch and Slotkin 2011; Lisch 2013; Oberlin et al. 2017; Sahebi et al. 2018).

Local methylation changes and histone modifications induced by intragenic TEs influence gene splicing or expression patterns. In oil palm, sporadic demethylation of the Karma TE located within an intron of the *MANTLED* gene results in unmasking of a cryptic splice acceptor site and premature termination signal, causing a mantled fruit phenotype that emerges sporadically in this crop to diminish agricultural value (Ong-Abdullah et al. 2015). In winter wheat, an intragenic TE located in an intron of the *VPN1-A1* gene shows increased non-CG DNA methylation in response to cold treatment, altering *VPN1-A1* expression. Data suggest that the intragenic TE plays a role in vernalization (Khan

X. Yang and S.A. Mackenzie

et al. 2013). Similarly, the large CACTA transposon located within an intron of an MYB transcription factor in soybean is subjected to methylation to impact anthocyanin synthase gene expression and seed coat color (Zabala and Vodkin 2014). The TE COPIA-R7 element of *Arabidopsis* inserted into an intron of disease-resistance gene *RPP7* recruits the histone mark H3K9me2 to this locus. H3K9me2 levels at COPIA-R7 affect the choice between two alternative *RPP7* polyadenylation sites in the pre-mRNA and, thereby, influence the critical balance between a functional *RPP7*-coding and a nonfunctional transcript isoform. This outcome decides capacity for response to a specific pathogen (Tsuchiya and Eulgem 2013). In melon, sexual forms are controlled by a balance between andromonoecious locus *CmACS-7* and gynoeceous locus *CmWIP1*. Expression of *CmWIP1* leads to repression of *CmACS-7* and carpel abortion, resulting in the development of unisexual male flowers. Interestingly, the activation of *CmWIP1* expression requires DNA methylation changes at its promoter region, which are introduced by insertion of a transposon under natural conditions (Martin et al. 2009).

TE-associated DNA methylation and chromatin alterations often spread to neighboring genes, providing additional regulation of local gene expression (Ahmed et al. 2011; Eichten et al. 2012). One particularly intriguing example of this is *ROS1*. RNA-dependent DNA methylation and demethylation activities occur within a TE proximal to this DNA demethylating gene to regulate its expression in a feedback loop that serves as an epigenetic rheostat (Williams et al. 2015). In rice, methylome analysis of plants under low-phosphate stress suggests a correlation between low-phosphate stress-induced gene expression and nearby TE methylation status. A model of this process suggests that TEs are a part of phosphate stress-induced gene regulation. Low-phosphate stress-induced genes often colocalize with TEs, and during short-term phosphate stress, low-phosphate stress-induced genes up-regulate. This high expression state is released once the stress is removed, but if the stress is maintained for a longer duration, nearby TEs will activate and attract the methylation machin-

ery. Hypermethylation serves to repress highly expressed phosphate stress-induced genes, restoring homeostasis. This phenomenon may represent a species-specific mechanism, because similar phenomena are not observed in parallel analysis of *Arabidopsis* (Secco et al. 2015).

GENE NETWORK RESILIENCE

Epigenetically induced resilience in plants has long been known to contribute to phenotypic plasticity, but only in the past few years has the underlying basis for these environmentally responsive processes begun to be understood. Recombinant inbred lines of *Arabidopsis* that derive from crossing a *ddm1* mutant, deficient in cytosine methylation, with an isogenic wild-type line provide a system for investigating the phenotypic implications of epigenomic disruption. Derived *DDM1* progeny lineages are altered in cytosine methylation patterning and display transgenerational phenotypic variation (Kooke et al. 2015). These observations provide some of the most compelling evidence of association between DNA methylation patterning and heritable quantitative phenotypic variation, as well as a viable hypothesis for environmental responsiveness of the plant genome. Some proportion of plant phenotypes derived by methylome repatterning are transgenerationally heritable, implying that epigenetic phenomena may participate in preadapting progeny to environmental conditions (Weinhold 2018; Friedrich et al. 2019).

Environmentally responsive gene networks in plants comprise an elegant and sophisticated synthesis of multiple reaction pathways to singular, centralized hubs (Cramer et al. 2011). One central network hub that is integral to the coordination of phenotypic plasticity is the circadian clock (Filichkin et al. 2011). In plants, the clock is comprised of three components, a central oscillator that generates rhythmic output signal, input pathways that entrain the central oscillator to the timing of environmental cues, and output signals that regulate physiological events within the plant (Harmer 2009). The circadian oscillator includes morning and evening peak-expressing components in a coalesced series of

repressive feedback loops controlled by at least one key activator (Fogelmark and Troein 2014). For example, reciprocal expression occurs between *CCA1* (*CIRCADIAN CLOCK-ASSOCIATED 1*) and *TOC1* (*TIMING OF CAB EXPRESSION 1*), which display morning and evening expression peaks, respectively (Alabadi et al. 2001). *CCA1*, a myb-type transcription factor, represses *TOC1* expression by binding to an evening regulatory element (CCRE) in the *TOC1* promoter. Numerous similar feedback interactions have been mapped within clock functions (Harmer 2009).

In a core oscillator network of tightly controlled, repressive transcription factors, *REV-EILLE8* (*RVE8*), a homolog of *CCA1* (and *LHY*) serves as a primary activator (Fogelmark and Troein 2014). Similar to morning-phased factors, *RVE8* binds to evening-phased genes but functions to activate rather than repress expression (Rawat et al. 2011). Whereas mutations of *CCA1* and *LHY* shorten clock period, mutations of *RVE*-clade genes lengthen clock pace (Rawat et al. 2011; Gray et al. 2017), reflecting rhythmic robustness of the system (Shalit-Kaneh et al. 2018).

Linked to the oscillation core are environmental sensing networks, with the most prominent entrainment stimuli being light and temperature. Light qualitative and quantitative input signals are conveyed by phytochrome red/far-red light sensors (*phyA*, *phyB*) and cryptochrome (*cry*) blue light photoreceptors (Somers et al. 1998), which are regulated in both their transcription and photosensitivity by clock functions (Toth et al. 2001). Components also integrate temperature information to the clock, with *phyB* serving a thermosensory role (Jung et al. 2016; Legris et al. 2016), and clock gene mutation data showing temperature as a clock entrainment stimulus (Heintzen et al. 1994; Thines and Harmon 2010). An important regulatory influence of temperature on clock functions occurs through changes in alternative splicing of several of the clock genes (James et al. 2012; Gil and Park 2019).

Clock output pathways show significant alignment with plant environmental adaptation (Covington et al. 2008). Clock regulation is

documented in plant growth, flower induction, photosynthesis, sugar metabolism, nutrient homeostasis, phytohormone signaling, and abiotic and biotic stress responses (Dodd et al. 2005; Covington and Harmer 2007; Greenham and McClung 2015; Sanchez and Kay 2016). Timing of vegetative to reproductive growth transition is influenced by regulators of flowering that show circadian control (Song et al. 2013). Biotic stress-response networks are also integrated to the clock (Goodspeed et al. 2013), as is the cellular regulation of ROS and oxidative stress factors (Lai et al. 2012). Although the details of multinetwork regulation during development and in response to environmental cues are not yet well understood, as much as one-third of the plant transcriptome shows evidence of potential circadian control (Covington et al. 2008). Modulation of *RVE8*-related loci, interacting with *PHYTOCHROME INTERACTING FACTOR4* (*PIF4*) and *PIF5*, influence plant growth rate and cell size to increase overall plant biomass and fitness (Gray et al. 2017). These studies, of increasing interest for their agricultural potential, underline the integral role of circadian networks in natural plant adaptation and environmental signal perception (Green et al. 2002).

Plant environmental responsiveness shows a direct, but not yet well detailed, relationship with epigenetic changes in chromatin features (Richards et al. 2017). DNA methylation is a highly dynamic and heterogeneous process across plant cell types, and coordinates with active demethylation activity and transcriptional regulators to effect cell-type differential gene expression and its subsequent cellular and transgenerational memory (Schübeler 2015). In circadian clock-related pathways, DNA methylation and chromatin modifications are associated with alternative splicing of clock-related genes (Sanchez et al. 2011). Whether gene-associated methylation is a cause or consequence of the splicing behavior is not yet clear. *PIF4*, an integral component of clock-associated thermomorphogenesis in plants, also shows evidence of epigenetic regulation (Quint et al. 2016). Histone H3 acetylation and H3K4 trimethylation (H3K4me3) serve as key regulators of the clock oscillator in plants (Malapeira et al.

X. Yang and S.A. Mackenzie

2012; Malapeira and Mas 2013). These chromatin modifications can work coordinately to regulate rhythmic changes in transcriptional activity, but also to influence transgenerational behaviors. The salicylic acid induction pathway, for example, is subject to transgenerational priming, such that progeny plants display more rapid and effective response to pathogen attack (Slaughter et al. 2012). In mammals as well, machinery controlling epigenetic behaviors show rhythmic expression, a likely consequence of epigenetic circuitry coevolution with daily and seasonal cycling patterns across life forms (Stevenson 2018).

POTENTIAL FOR AGRICULTURAL ADVANCEMENTS

The plant kingdom has evolved innumerable strategies for environmental adaptation, many of which become fixed within a species or result in the emergence of new species (Vicent and Casacuberta 2017). However, intraspecific phenotypic plasticity mechanisms that facilitate accelerated evolution following environmental change can offer valuable insights of agricultural value. For example, epigenetic breeding efforts have begun to emerge, exploiting both the epirIL (Johannes et al. 2009) and *MSH1* reprogramming systems (De La Rosa Santamaria et al. 2014; Virdi et al. 2015; Yang et al. 2015; Raju et al. 2018). *MSH1*-based breeding efforts have produced yield increases of 20%–40% together with enhanced resilience. Genome-wide methylome studies in crop plants offer insight into available epiallelic variation (Rodríguez López and Wilkinson 2015) as well as agronomic traits that are influenced by TE-target gene proximity (Butelli et al. 2012; Khan et al. 2013; Ong-Abdullah et al. 2015; Hirsch and Springer 2017). Elaboration of the genetic regulation of embryogenesis has permitted successful engineering of asexual, apomictic propagation in rice (Khanday et al. 2019), likely to represent a significant agricultural advancement. Greater resolution of the circadian clock and related gene networks provide strategies for enhancing plant growth and productivity (Gray et al. 2017), as well as stress tolerance (Grundt et al. 2015). The future of

plant breeding may very well emerge as an integration process that incorporates high-resolution genomic data with epigenetic, environmental sensory, and growth phenotyping data into a multicomponent selection scheme (Furbank and Tester 2011; Tardieu et al. 2017). As resolution of these mechanisms improves, selection can be adjusted to exploit the many and varied mechanisms employed by each plant species to enhance resilience and maintain energy balance.

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X. Yang and S.A. Mackenzie

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