

REVIEW PAPER

Linking genes with ecological strategies in *Arabidopsis thaliana*

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Abstract

***Arabidopsis thaliana* is the most prominent model system in plant molecular biology and genetics. Although its ecology was initially neglected, collections of various genotypes revealed a complex population structure, with high levels of genetic diversity and substantial levels of phenotypic variation. This helped identify the genes and gene pathways mediating phenotypic change. Population genetics studies further demonstrated that this variation generally contributes to local adaptation. Here, we review evidence showing that traits affecting plant life history, growth rate, and stress reactions are not only locally adapted, they also often co-vary. Co-variation between these traits indicates that they evolve as trait syndromes, and reveals the ecological diversification that took place within *A. thaliana*. We argue that examining traits and the gene that control them within the context of global summary schemes that describe major ecological strategies will contribute to resolve important questions in both molecular biology and ecology.**

Keywords: *Arabidopsis thaliana*, CSR strategy, local adaptation, natural variation, trait syndrome

Local adaptation suggests a diversity of ecological specializations within *A. thaliana*

Arabidopsis thaliana (L.) Heyhn is exceptional within its genus. It is the only annual species, it has adapted to open, dry habitats prone to seasonal drought (Ruppert *et al.*, 2015; Kiefer *et al.*, 2017), and its reproductive success is directly dependent on interannual variation in environmental conditions (Segrestin *et al.*, 2018). It also has the widest geographic range in the *Arabidopsis* genus (Claus and Koch, 2006; Novikova *et al.*, 2016). Natural populations have been found throughout Europe, from the North of Scandinavia to the South of Spain, in the Balkans, in Central Asia, China, and parts of Africa

(Hoffmann, 2005; He *et al.*, 2007; 1001 Genomes Consortium, 2016; Durvasula *et al.*, 2017). It is also naturalized in North America and Argentina (Stock *et al.*, 2015; Kasulin *et al.*, 2017; Exposito-Alonso *et al.*, 2018a). This exceptionally wide distribution range is only limited by very low spring or autumn temperatures or by high temperature in regions of low precipitation (Hoffmann, 2002).

The unrivaled genomic resources available for these populations have helped demonstrate that the last glacial period determined the current distribution of genetic variation (reviewed in Koch, 2019). After the last glacial maximum, populations have spread towards Northern latitudes, experiencing

successive bottlenecks (Durvasula *et al.*, 2017; Svardal *et al.*, 2017). As a result, regional diversity is highest in Africa and lowest in Scandinavia. Genetic variation in Eurasia also follows a longitudinal gradient (1001 Genomes Consortium, 2016; Zou *et al.*, 2017).

The local adaptation of *A. thaliana* populations has been documented throughout its range, despite a history of pervasive gene flow (Fournier-Level *et al.*, 2011; Hancock *et al.*, 2011; Agren and Schemske, 2012; Savolainen *et al.*, 2013; Weigel and Nordborg, 2015; Svardal *et al.*, 2017). Field experiments and correlation analyses with climate parameters identified numerous genomic regions associated with local climatic conditions. Association studies correlating single nucleotide polymorphism (SNP) variants with climatic variation showed that non-synonymous SNPs were enriched among SNPs associating with environmental variance (Hancock *et al.*, 2011; Lasky *et al.*, 2014). Among them, SNPs associating with fitness differences in the field were also over-represented (Hancock *et al.*, 2011). Furthermore, alleles associating with fruit production are more frequent in populations closer to field sites where the selective advantage was expressed (Fournier-Level *et al.*, 2011). Therefore, it is now clear that much of the variation found in this species has played a role in optimizing plant performance to local environmental conditions.

A combination of development traits underpins local adaptation in *A. thaliana*

Flowering time is one of the development traits underpinning adaptation in *A. thaliana*. It has been extensively studied, and elevated levels of variation have been observed in the lab (Koornneef *et al.*, 2004). The adaptive relevance of its genetic variation is supported by multiple independent studies. Variation in flowering time follows climatic clines, at both the regional and species levels (Mendez-Vigo *et al.*, 2011; Montesinos-Navarro *et al.*, 2011; Debieu *et al.*, 2013; Li *et al.*, 2014; Sasaki *et al.*, 2015). Warmer climates appear to favor earlier flowering time, a pattern that has been documented for a great number of species (Austen *et al.*, 2017; Whittaker and Dean, 2017). Strong selection for early flowering was detected in Italy but was weaker in Sweden (Ågren *et al.*, 2017). Population genetics studies also uncovered signatures of natural selection on genes controlling flowering time (Le Corre, 2005; Toomajian *et al.*, 2006). Finally, the analysis of co-variation between environmental and phenotypic variance consolidated evidence for the adaptive distribution of this trait (van Heerwaarden *et al.*, 2015).

Much of the flowering time variation measured in the lab, however, does not manifest as variation in flowering phenology in the field (Wilczek *et al.*, 2009; Brachi *et al.*, 2010; Hu *et al.*, 2017). It is indeed tightly dependent on the environmental conditions prevailing during seedling establishment, and hence on another developmental trait: the timing of germination (Donohue, 2002; Wilczek *et al.*, 2009). Both field experiments and theoretical models integrating seed and flowering phenology have shown that seed dormancy is often decisive for controlling the life cycle across environments

(Chiang *et al.*, 2013; Burghardt *et al.*, 2015). Therefore, the adaptive relevance of variants modulating flowering time control must be examined in the context of variation for the timing of germination.

There is indeed consistent support for the adaptive relevance of traits determining the timing of germination. Seed dormancy has a strong fitness advantage before the hot season, but can impair fitness if it delays plant growth before winter (Donohue, 2002; Donohue *et al.*, 2005; Chiang *et al.*, 2013). Population genetics analysis of seed dormancy and its major quantitative trait locus (QTL) *DOG1* supported the adaptive importance of strong dormancy in Southern regions, to escape dry and hot summers, whereas weaker dormancy was reported in Norway, where the season is shorter (Kronholm *et al.*, 2012; Postma and Ågren, 2016; Kerdaffrec *et al.*, 2016).

Since flowering time determines the maternal environment the seeds experience during their maturation, it also impacts life history traits expressed by the next generation (Chiang *et al.*, 2013; He *et al.*, 2014; Postma and Ågren, 2015). Light, temperature, nutrient availability, and water status have all been identified as significant environmental factors influencing the maternal inheritance of seed dormancy (Footitt *et al.*, 2013; He *et al.*, 2014; Morrison and Linder, 2014; Kerdaffrec *et al.*, 2016). Germination can also be distributed over more than one seasonal window. For example, maintaining a spring germinating cohort is important for the maintenance of populations exposed to low winter temperature (Picó, 2012; Akiyama and Ågren, 2014). Furthermore, later flowering can lead to late seed dispersal, which can result in overwintering at the seed stage (Hu *et al.*, 2017).

Flowering time and seed dormancy are therefore jointly subject to fluctuating seasonal selective forces. They can evolve as a syndrome, defining distinct life history strategies that have diversified across environments (Chiang *et al.*, 2013; Vidigal *et al.*, 2016; Marcer *et al.*, 2018). An analysis of seed dormancy and flowering time co-variation revealed that the optimization of the two traits probably depends on latitudinal differences in climate. Late flowering (i.e. vernalization requirement) and strong dormancy are more frequent in regions where summer drought is typically more severe, whereas late flowering in Northern latitudes co-varies negatively with dormancy (Debieu *et al.*, 2013). Co-variance between flowering time and dormancy is also detected at a much smaller scale, along steep altitudinal gradients (Vidigal *et al.*, 2016). Normally, diverse life history trait combinations can allow comparable population growth rates in field conditions (Taylor *et al.*, 2017). In some years, however, early winter frost can wipe out genotypes expressing inadequate life histories (Hu *et al.*, 2017). Minimum winter temperature and precipitation, in fact, were also the main climatic factors that acted as selective pressures on flowering time and their underpinning genes in a set of Iberian *A. thaliana* genotypes (Méndez-Vigo *et al.*, 2011). This suggests that extreme deviation from seasonal averages may be important drivers of the allelic combination of life history variants adjusting development to the optimal growth season throughout the species range.

Patterns of co-variation between growth rate and developmental traits suggest the existence of trait syndromes

Beyond the combination of life history traits to target the best season for growth, *A. thaliana* also displays considerable genetic variation in its growth rate (Debieu *et al.*, 2013; Marchadier *et al.*, 2018, Preprint). The pattern of co-variation linking growth rate with flowering time and seed dormancy is independent of population structure, and changes from Southern to Northern latitude (Debieu *et al.*, 2013). This suggests that trade-offs between growth rate and life history change across the distribution range of the species (Debieu *et al.*, 2013). It further implies that complex multitrait combinations (i.e. trait syndromes) are necessary to adjust to the changing trade-offs imposed by regional differences in climatic conditions. Co-variation between flowering time, final biomass, and average rate of biomass accumulation before flowering also suggests that genetic adaptation to local climate conditions is mediated by a trait syndrome (Vasseur *et al.*, 2018a).

Genetic variation for tolerance to drought stress, just like that for life history, displays signatures of local adaptation. Many genetic variants have been identified that also affect either root or rosette growth in the face of severe drought stress (El-Soda *et al.*, 2015; Clauw *et al.*, 2016; Davila Olivas *et al.*, 2017). Several studies highlighted the adaptive relevance of variation in the ability to maintain growth and photosynthesis when water is limited. After accounting for the demographic history of the species, stomatal size variation was found to correlate with water-use efficiency (i.e. rate of carbon fixation to water loss) and both air humidity and the local probability of spring drought severity (Dittberner *et al.*, 2018), in agreement with field measurements (Mojica *et al.*, 2016). The molecular evolution of the gene P5CS, which contributes to the synthesis of proline, a potent osmoprotectant in *A. thaliana*, suggests that it contributed to local adaptation (Kesari *et al.*, 2012). Nucleotide variants within genes displaying stress-dependent expression were also shown to be over-represented among variants correlating with climatic parameters (Lasky *et al.*, 2014; Exposito-Alonso *et al.*, 2018c).

In fact, genetic variation for stress tolerance not only is involved in local adaptation, but it also appears to be part of a trait syndrome, because it is often reported to coincide with variation in life history. Early flowering individuals, which sometimes complete their life cycle within a few weeks, can escape conditions causing high pre-reproductive mortality (Franks, 2011; Fournier-Level *et al.*, 2013; Riboni *et al.*, 2013). In addition, the major flowering time QTL *FRIGIDA* controls not only the timing of flowering but also water-use efficiency (Johanson *et al.*, 2000; Lovell *et al.*, 2013). Improved performance in plants exposed to moderate drought stress is correlated with the ability to flower early (Bac-Molenaar *et al.*, 2016), but genotypes with a strong vernalization requirement tend rather to avoid the effect of drought by maintaining their internal water level (McKay *et al.*, 2003; Des Marais *et al.*, 2012; Lovell *et al.*, 2013; Easlon *et al.*, 2014; Davila Olivas *et al.*, 2017). The most stress-tolerant individuals actually appear to be either early flowering or slow growing (Davila Olivas *et al.*, 2017; Vasseur *et al.*, 2018a).

Because of its co-variation with life history, adaptation to drought stress can show counter-intuitive patterns. In *A. thaliana*, local adaptation for increased tolerance to drought stress is not found in the driest regions, because, in these areas, natural selection promoted genotypes with the ability to escape the stress (Kronholm *et al.*, 2012; Vidigal *et al.*, 2016; Mojica *et al.*, 2016; Tabas-Madrid *et al.*, 2018). Genotypes showing smaller stomata, higher water-use efficiency, and longer photosynthetic activity in the face of terminal drought have in fact evolved in Southern Scandinavia, where the growth season is too short to allow an escape from the drier season but dry enough to require improved drought tolerance (Mojica *et al.*, 2016; Dittberner *et al.*, 2018; Exposito-Alonso *et al.*, 2018c). Genotypes with a strong vernalization requirement are in fact more frequent in this region, limiting the possibility to escape drought during the growing season (Li *et al.*, 2014). Non-monotonic patterns of co-variation between flowering time and temperature have also been reported in Spain (Tabas-Madrid *et al.*, 2018), suggesting that the selective advantage of early flowering for persisting in dry regions depends on a broader ecological context, and thus presumably on the possibility to rely on earlier flowering to escape stressful conditions. The evolution of the response to abiotic stress in *A. thaliana* is therefore not independent of the evolution of the timing of life history transitions.

The ability of plants to face biotic stresses is also dependent on life history variation. Alleles accelerating flowering were shown to be often combined with alleles decreasing the expression of plant defense genes throughout natural *A. thaliana* populations (Glander *et al.*, 2018). An indication that this assortment coincides with differential fitness suggests that it has been driven by natural selection. In addition, plant growth in response to the specialist herbivore *Pieris rapae* was enhanced in fast-flowering individuals but showed a trade-off with the drought response (Davila Olivas *et al.*, 2017). Here again, this hints at the evolution of a trait syndrome, where early flowering genotypes may have been selected for their ability to allocate fewer resources into defense, in order to maximize their growth rate or to reshuffle energetic priorities and ensure survival.

Arabidopsis thaliana thus displays significant levels of genetic variation in traits controlling life history, growth rate, or tolerance to diverse stresses, all of which co-vary with each other and with climatic conditions at the location of origin. This suggests that adaptation to novel environments after the last glaciation has allowed the evolution of trait syndromes (i.e. a combination of multiple traits). These combinations probably reflect both adaptive synergies and global trade-offs imposed by resource limitations. Identifying the exact composition of trait syndromes and their variation requires a careful monitoring of life history transitions, growth rates, stress tolerance, and plant fitness in natural conditions. We argue below that interpreting trait variation and co-variation in the global context of plant ecological strategies, within summary schemes developed by ecologists to describe the major dimensions determining variation in form and function within and across habitats, may help resolve the ecological significance of traits and their combinations (Fig. 1).

Interpreting *A. thaliana* trait syndromes in the context of major ecological strategies

Not all possible trait combinations are viable in natural environments: natural selection indeed limits the diversity of forms and functions in plants as a result of trade-offs among the diverse options for resource allocation (Reich, 2014; Díaz *et al.*, 2016). This major constraint has motivated several attempts to classify plants with respect to their ecological strategies (reviewed in Westoby *et al.*, 2002; Díaz *et al.*, 2016). Among them, Grime's CSR theory (Grime, 1974, 1977) is a prominent strategy scheme (Pierce *et al.*, 2017). It distinguishes three primary strategies, namely competitive (C), stress-tolerant (S), and ruderal (R). The first two strategies evolve in rather constant environments, which differ in the severity of resource shortage (light, water, and/or nutrients). The third one prevails in disturbed environments, and involves investment of a large proportion of resources in propagules from which the population can regenerate in the face of repeated biomass destruction events. Distinct strategies may also co-occur within a given environment, enhancing local niche separation between species (Kraft *et al.*, 2008). The multivariate and complex traits that form the basis of ecological strategies are often difficult to

measure. Yet, a small number of plant functional traits related to growth, survival, and reproduction have been shown to summarize efficiently the overall diversity of plant life form and functions (Díaz *et al.*, 2016). Among them, as many as three leaf traits—leaf area, leaf dry matter content, and specific leaf area—can be used as surrogate to describe a species' CSR strategy (Pierce *et al.*, 2017).

Like many other annuals in the Brassicaceae family, these leaf traits position *A. thaliana* as a typical R-strategist (Pierce *et al.*, 2017). It is typically encountered in regularly disturbed habitat patches, such as urban, ruderal, or mountainous habitats, and its seedlings are directly exposed to seasonal climatic fluctuations (Picó *et al.*, 2008; Bomblies *et al.*, 2010; Svardal *et al.*, 2017). However, the past years have shown that plant species are far from having a fixed CSR strategy. On the contrary, strategy classifications at the species level have been more and more challenged by the large spectrum of intraspecific variation (Des Roches *et al.*, 2018; Volaire, 2018). For this reason, it is now increasingly acknowledged that trade-offs in life history and growth strategies can also occur at the level of genotypes and populations, and that more attention should be devoted to interindividual and interpopulation variation of the CSR strategy (Astuti *et al.*, 2018). Intraspecific trade-offs have been

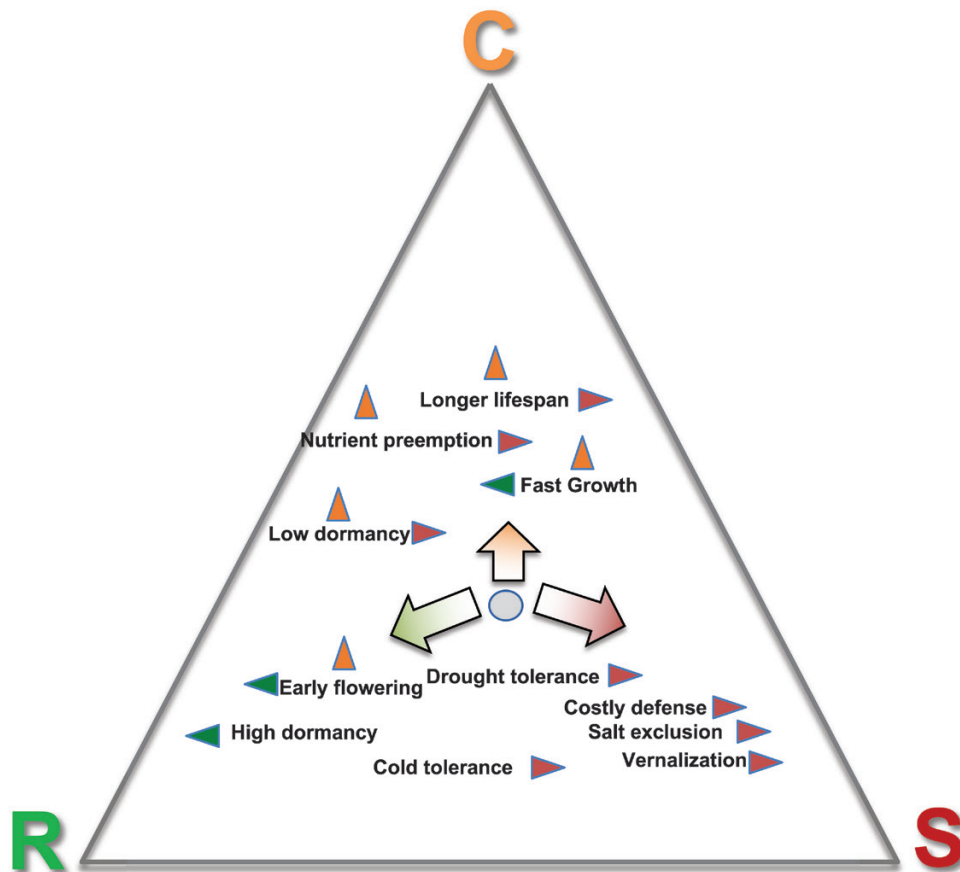


Fig. 1. Hypothetical contribution of adaptive traits to ecological diversification within *Arabidopsis thaliana*. The diversity of ecological strategies can be summarized in Grime's C–S–R strategy triangle which reflects a major trade-off between competitive, stress-tolerant, and ruderal strategies. Large arrows represent the major evolutionary trajectories. Intraspecific variation along the R–S axis has been documented in *A. thaliana*. Fewer studies document intraspecific variation along the R–S and C–S axes. Small arrows represent the contribution of individual traits (green, contribution to increased ruderality; red, contribution to increased stress tolerance; orange, contribution to increased competitive ability). The position of the trait along the vertical axis is dictated by graphical constraints only. The gray dot symbolizes a genotype with a given strategy. Large arrows point to possible ecological shifts that populations can evolve. These shifts can be operated by concomitant trait shifts.

found along the S–R axis of Grime’s CSR strategy scheme (Bilton *et al.*, 2010; May *et al.*, 2017), but also along the C–S axis (Ravenscroft *et al.*, 2014; Astuti *et al.*, 2018). These trade-offs are commonly explained as a mechanism of local adaptation, for example in response to different levels of resource stress. It is thus not surprising that considerable intraspecific variation has also been found for *A. thaliana*. A study with 16 individual accessions sampled along a steep altitudinal gradient revealed that populations from hotter climates clustered towards the stress-tolerant end of the observed strategy spectrum, implying pronounced intraspecific variation along the S–R axis (May *et al.*, 2017). The extent of variation along the S–R axis was recently confirmed by a comprehensive analysis of variation in CSR positioning in some 300 genotypes in *A. thaliana* (Vasseur *et al.*, 2018b). As for other annual plants, we could thus assume that *A. thaliana* populations growing in water- or temperature-limited habitats may be well adapted to high levels of stress and thus characterized as stress tolerant (Volaire, 2018). In contrast, genotypes that grow fast and complete their life cycle within a few weeks may be described as extreme ruderals (Fig. 1). In *A. thaliana*, genotypic variation covers the whole S–R strategy spectrum. The geographical distribution of this variation contrasts with that of genome-wide patterns of variation, suggesting a role in local adaptation (Vasseur *et al.* 2018b).

Intraspecific variation along the S–C or R–C axes involves traits that have not been intensively investigated in *A. thaliana* (Fig. 1). The ability to compete with other species plays a presumably minor role for a pioneer species that only subsists in disturbed environments. Yet, the few studies that investigated this aspect (e.g. Masclaux *et al.*, 2010; Baron *et al.*, 2015; Frachon *et al.*, 2017) suggest that intraspecific variation in C-strategic features will also be significant (Fig. 1). The disturbed environments in which *A. thaliana* can be found are sometimes densely populated (G. Schmitz, personal communication; see also the population studied in Frachon *et al.*, 2017). Interspecific competition has been shown to modify the pattern of natural selection operating on flowering traits in a collection of recombinant inbred lines (Brachi *et al.*, 2012). Some *A. thaliana* genotypes, initially collected in a densely populated habitat patch, displayed the ability to decrease the biomass of some of their interspecific competitors (Baron *et al.*, 2015; Frachon *et al.*, 2017).

Intraspecific competition is also expected to stand under strong selection in the species. The population census size is small in a newly colonized habitat patch but will increase with the age of the habitat patch. Under increasing density of intraspecific competitors, plants differ in their ability to reach the fruiting phase and produce seeds (Masclaux *et al.*, 2010; Muñoz-Parra *et al.*, 2017). Root growth is also negatively impacted by intraspecific competition (Muñoz-Parra *et al.*, 2017). Competitive ability may also modulate the intensity of selection on water-use efficiency variants (Campitelli *et al.*, 2016). Intraspecific variation along the S–C or R–C axes might be less pronounced than along the S–R axis, but is probably not negligible, as indicated by the recent discovery of a gene locus promoting positive interactions between genotypes (Wuest and Niklaus, 2018, Preprint; see also Vasseur *et al.*, 2018b).

The CSR strategy scheme is one of the conceptual frameworks that can help understand the role that specific trait (or gene) combinations have played in the ecological diversification observed within *A. thaliana*. To date, their contribution remains mostly hypothetical (Fig. 1). Late flowering in controlled conditions was reported to associate with increased stress tolerance in the CSR scheme, yet whether this trait mediates an increase in stress tolerance or associates with traits which control stress tolerance has not been elucidated (Vasseur *et al.*, 2018b). Identifying causal links between traits, their underpinning genes, and shifts in CSR strategy could considerably ameliorate knowledge transfer between model and non-model species, because this scheme was designed to facilitate interspecific comparisons (Pierce *et al.*, 2017).

Towards linking molecular biological functions with their role in ecological strategies

Exploring how traits are combined in natural populations to tune the ecological strategy of local genotypes to their local environmental conditions can indeed cast new light on gene function at the molecular level. We illustrate this idea with two points: first we describe how natural variation can help identify genes controlling ecologically important traits and focus on plant nutrition as an exemplary trait. Secondly, we show that the function of the well-known flowering time regulator FLOWERING LOCUS C (FLC) can be revised in the perspective of ecological strategies.

Studies of natural variation have greatly assisted the discovery of the genes controlling functions that cannot be easily dissected in mutant screen approaches (reviewed in Alonso-Blanco *et al.*, 2009). For example, QTL analyses of nutrients unraveled the function of the anion channel AtCLC-c in nitrate transport to vacuoles (Loudet *et al.*, 2003; Harada *et al.*, 2004) or showed that the ATPase subunit G and the multicopper oxidase LPR1 have a major impact on the accumulation of phosphate and phytate (Bentsink *et al.*, 2003; Reymond *et al.*, 2006). They further showed that foliar sulfate accumulation is dependent on sulfate reduction rates (Loudet *et al.*, 2007; Koprivova *et al.*, 2013). The fact that one of the two major QTLs controlling sulfate reduction, the gene *APR2*, has evolved loss-of-function alleles three times independently, in Central Asia, Czech Republic, and Sweden, was also a striking result (Loudet *et al.*, 2007; Chao *et al.*, 2014).

Studies of natural variation can also inform about the genetic architecture and evolutionary potential of specific traits. For example, the major discoveries driven by differences in ionomes between *A. thaliana* populations were not achieved through genome-wide association mapping (Atwell *et al.*, 2010), but through the use of ionomics to screen for genotypes with contrasted nutrient content for analysis (Lahner *et al.*, 2003; Salt *et al.*, 2008). Approximately 20-fold differences in molybdenum concentration were measured in leaves of 98 *A. thaliana* genotypes, and the genetic analysis of the progeny of two of the most contrasted accessions Col-0 and Ler revealed the role of *Molybdenum Transporter-1* (*MOT1*) (Tomatsu *et al.*, 2007;

Baxter *et al.*, 2008). Similarly, tetraploidy was shown to increase potassium content in the progeny of Col-0 and the autotetraploid line Wa-1 (Chao *et al.*, 2013). Such studies demonstrate that heritable variation in nutrient content often results from variants that are (i) large effect mutations since they can be easily dissected in bi-parental progeny and (ii) rare because they do not give a detectable signal in genome-wide association studies (GWAS). This indicates that a plant's ability to pre-empt resources for improved nutrition can be easily manipulated at the genetic level. Such genetic variants in nutrient uptake can be used to understand population maintenance and plant community formation in a context of nutrient depletion or plant-plant competition. In other words, they provide a valuable resource to understand how molecular mechanisms can contribute to ecological diversification.

For most ionic traits, however, a contribution to plant growth rate, competitive ability, or stress tolerance has not been established. Accumulation of sodium is one of the rare examples where the ecological relevance of genetic variation for mineral uptake could be documented. An allele of the sodium transporter gene *AtHKT1* was shown to mediate increased Na^+ concentration in *A. thaliana* genotypes originating from two coastal habitats in Spain and Japan, and was found to co-segregate with salt tolerance (Rus *et al.*, 2006; Baxter *et al.*, 2010). Using distance to sea or to a known saline soil as a quantitative measure, a strong relationship between high leaf Na^+ and origin in potentially saline-impacted soils was confirmed (Baxter *et al.*, 2010). Recently, the mechanism by which the weak allele of *AtHKT1* confers Na^+ tolerance has been elucidated (An *et al.*, 2017). High expression of *AtHKT1* in stems strongly limits the allocation of Na^+ to reproductive tissues and thus confers higher fertility specifically under salt stress (An *et al.*, 2017).

An ecological perspective on functional variation can also allow a more comprehensive description of gene function. For example, the gene *FLC* was named after its typical effect on flowering time: *flc* mutants are considerably earlier flowering in long day-controlled conditions (Michaels and Amasino, 1999). The dissection of natural variation present at this locus in *A. thaliana* uncovered an allelic series conferring a wide range of flowering times and responses to vernalization (Lempe *et al.*, 2005; Shindo *et al.*, 2005; Coustham *et al.*, 2012; Li *et al.*, 2014). Allelic variation at *FLC* orthologs is also responsible for variation in flowering time or duration of flowering in other crucifer species (Albani *et al.*, 2012; Kemi *et al.*, 2013; Baduel *et al.*, 2016). Progressively, however, the specificity of *FLC* action on flowering time has been questioned. *FLC* variation was associated with the timing of germination (Chiang *et al.*, 2009), raising the possibility that *FLC* acts pleiotropically on multiple phenotypes. Indeed, the genome-wide analysis of *FLC*-binding sites uncovered several hundred genes, a large proportion of which were involved in response to cold stress (Deng *et al.*, 2011; Mateos *et al.*, 2015, 2017). Several genes involved in cold stress were strongly deregulated in *flc* mutants compared with the *FLC* wild type when plants were exposed to cold, but not at normal growth temperatures, suggesting that *FLC* has a role in modulating expression of genes conferring tolerance to cold (Mateos *et al.*, 2017). Pleiotropic genes such as *FLC* may respond to the

fundamental requirement for ecological pleiotropy in natural environments that are marked by inevitable fluctuations. Indeed, the monitoring of frequency changes in alleles associated with various reproductive and phenological traits in the field within a single natural *A. thaliana* population showed that variants with intermediate levels of pleiotropy contributed the largest adaptive steps (Frachon *et al.*, 2017). This is because selective forces fluctuate across years and seasons, and they are more likely to act consistently on variants controlling more than one phenotype. Natural selection at this particular site thus appeared to have favored variants contributing to both increased tolerance to local warming and increased competitive ability (Frachon *et al.*, 2017). Although it is beyond the scope of this review to enumerate all molecular functions whose ecological role remains to be fully determined, the examples given by plant nutrition or the pleiotropic effects of *FLC* illustrate how placing molecular functions within the context of ecological strategies helps identify genes and their ultimate role in natural conditions.

Towards resolving ecological questions with a genetically tractable plant system

Conversely, the diverse ecological strategies co-segregating in *A. thaliana* provides a unique system to address, at the genetic and molecular level, those questions that are key to ecologists. We illustrate this idea below with a pressing question in current ecological research: the impact of climate change.

In today's ecological research, discerning the mechanisms behind ecosystem responses to climate change is a central theme (Reed *et al.*, 2012; Ruppert *et al.*, 2015). Extended periods of high temperature and net declines in soil moisture are expected in many regions (IPCC, 2013). Intraspecific variation in functional traits associated with resource-use efficiency and stress tolerance may help understand the determinants of species growth and survival under climate change (Aspinwall *et al.*, 2013).

A first consequence of increased climatic unpredictability is that ecological shifts towards increasingly ruderal strategies will be promoted. The study of flowering time variation in *A. thaliana* has demonstrated that species are not limited in the number of mutations that can promote accelerated flowering (Mendez-Vigo *et al.*, 2011; Sánchez-Bermejo *et al.*, 2012; Hepworth and Dean, 2015; Whittaker and Dean, 2017): species will therefore have ample opportunities to adapt to drought by advancing their transition to flowering (Franks *et al.*, 2007). As a matter of fact, earlier flowering seems to be globally under selection (Munguía-Rosas *et al.*, 2011).

However, adapting the timing of major life history transitions will probably not suffice. As water is a paramount factor in determining both the distribution and the productivity of plant species, drought stress responses will be increasingly critical for species assemblages in most environments (Volaire, 2018). Through manipulative experiments and data fusion approaches, ecologists have learned what they may basically expect for ecosystem dynamics: individual-level responses are followed by species reordering within communities, and finally by species losses and immigration (Smith *et al.*, 2009). These observations lack a generic understanding of individual-level

responses, which are typically initiated at the molecular level, and then cascade upwards to affect plant individuals' physiology and growth (Chaves *et al.*, 2003; Avolio *et al.*, 2018). Unfortunately, detecting and linking cascading stress responses across levels of biological organization is highly challenging (Meyer *et al.*, 2014; Lovell *et al.*, 2016), partly due to the use of different conceptual frameworks and terminologies across the different disciplines and scales (Volaire, 2018). Although ecologists have grown increasingly interested in linking molecular drought responses with physiological data from plant individuals (Lovell *et al.*, 2016; Hoffman and Smith, 2018), very few studies up to now have examined the link between different levels of biological organization in plant water stress responses (Avolio *et al.*, 2018). Besides the research challenges described above, this is partly due to a reluctance of ecologists to include an ecological outlier such as the ruderal *A. thaliana*.

Ecologists nevertheless increasingly acknowledge that an understanding of gene expression is a critical hurdle for dissecting stress response mechanisms (Hoffman and Smith, 2018). Many studies focusing on drought ecology have been conducted in perennial grasses such as *Andropogon gerardii*, *Sorghastrum nutans*, or *Panicum virgatum* (Hoover *et al.*, 2014). Agronomic studies have been mostly conducted on domesticated, annual grasses such as durum wheat (*Triticum turgidum*) or barley (*Hordeum vulgare*). In light of the comparatively high ecological diversification reviewed above, one can argue that the annual forb *A. thaliana* could efficiently complement these studies. Some recent, interdisciplinary attempts have exemplified how such a diverse species could help us understand the mechanisms and ecological trade-offs of stress responses. Combining a characterization of genetic variation in drought stress resistance with current and future climate envelopes revealed the enormous adaptive potential of *A. thaliana* in the face of climate change (Fournier-Level *et al.*, 2016; Exposito-Alonso *et al.*, 2018a). It also documented the genetics of this potential (Exposito-Alonso *et al.* 2018b, c; Fournier-Level *et al.*, 2016). Among European genotypes, it is predicted that those originating from Northern and Southern latitudes will be able to adapt in the new climate, due to their higher drought resistance as well as the genetic variability of the populations (Exposito-Alonso *et al.*, 2018c). In fact, in *A. thaliana*, it is possible to perform experiments quantifying the impact of selection in populations faced with increasingly realistic scenarios of global climate change, where exposure to drought stress, average temperature, or increased frequency of major disturbance set new limits on plant plasticity (Exposito-Alonso *et al.*, 2018b). To enhance the comparability of drought studies across model species and disciplines, drought regimes (e.g. frequency and intensity) should also be characterized with standard methods in the species (Vicca *et al.*, 2012; Ruppert *et al.*, 2015), and diagnostic experimental procedures should be adopted to identify the ecological mechanisms promoting drought resistance (Gilbert and Medina, 2016).

As an undomesticated species, *A. thaliana* has been subject to a complex suite of environmental challenges over the course of its evolutionary history (see Koch, 2019), which promoted a diversification in ecological strategy. Its amenability to genetic approaches (e.g. seed stocks, mapping populations, mutant collections, or GWAS panels) can greatly facilitate trait analysis and

reveal which functional traits or trait combinations are sufficient to promote shifts in ecological strategies. For example, dissecting how the plant combines tolerance to multiple stresses, whilst at the same time fine-tuning the balance between defense, growth, and productivity, is of great importance for interpreting the dynamics of plant communities (Bechtold *et al.*, 2018). Knowing which genes contribute to unobservable traits underpinning key aspects of ecological strategy can also improve the ecological classification of species. Indeed, they provide measurable proxies for traits that are difficult to measure but make important contributions to dimensions of the ecological strategy that leaf traits and the CSR strategy scheme do not fully recapitulate.

Conclusion and outlook

The high natural variation and the unrivaled genomic resources of *A. thaliana* are great assets in understanding pressing questions in contemporary plant ecology but also to dissect gene function comprehensively, from the molecular to the community level. This review has assembled recent conceptual and methodological developments that show how this field is advancing. The advent of new sequencing technologies has increasingly digitalized observations both in the lab and in the field. To enhance our interpretation of these data, links between specific genes and the evolution of novel ecological preferences must be established. The recently published indication that variation in CSR positioning contributes to local adaptation in *A. thaliana* already suggests that variation in global ecological strategy is both heritable and relevant for understanding plant performance in diverse parts of the species range (Vasseur *et al.* 2018b). Yet, variation in CSR positioning also depends on the environment in which CSR-indicative traits are measured (Vasseur *et al.* 2018b). Several key challenges remain to be addressed such as the following: (i) To what extent do intraspecific changes in CSR positioning translate into changes in competitive ability, stress resistance, or tolerance to disturbance? (ii) How many traits in a trait syndrome are sufficient to initiate significant ecological shifts? (iii) What is the importance of plasticity in shifting ecological strategies? (iv) Which gene or gene activity can be used as proxy to quantify ecological dimensions that are not correctly summarized in global strategy schemes? Answering these questions in *A. thaliana* will pave the way for bridging ecology and molecular biology in Plant Sciences.

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