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Ecology and Evolutionary Biology of *Arabidopsis*

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Abstract

Arabidopsis thaliana is now widely used as a model system in molecular and developmental biology, as well as in physiology and cell biology. However, ecologists and evolutionary biologists have turned their attention to the mouse ear cress only much more recently and almost reluctantly. The reason for this is the perception that *A. thaliana* is not particularly interesting ecologically and that it represents an oddity from an evolutionary standpoint. While there is some truth in both these attitudes, similar criticisms apply to other model systems such as the fruit fly *Drosophila melanogaster*, which has been extensively studied from an organismal perspective. Furthermore, the shortcomings of *A. thaliana* in terms of its restricted ecological niche are counterbalanced by the wealth of information on the molecular and developmental biology of this species, which makes possible to address evolutionary questions that can rarely be pursued in other species. This chapter reviews the history of the use of *A. thaliana* in organismal biology and discusses some of the recent work and future perspectives of research on a variety of field including life history evolution, phenotypic plasticity, natural selection and quantitative genetics. I suggest that the future of both molecular and especially organismal biology lies into expanding our knowledge from limited and idiosyncratic model systems to their phylogenetic neighborhood, which is bound to be more varied and biologically interesting.

Keywords: Arabidopsis – phenotypic plasticity – evolutionary ecology – quantitative genetics – biogeography – natural selection

What is evolutionary ecology?

Evolutionary ecology is a general term that may mean very different things to different people. The main focus of evolutionary-ecology studies is at the level of population biology (Pianka 2000), with an emphasis on a timescale at the boundary between ecological (i.e., short-term) and evolutionary (i.e., long-term) phenomena. Typically, evolutionary ecologists study a range of phenomena that may include age and size at maturity, phenotypic plasticity, mating/breeding systems and sexual selection, life history, evolution in heterogeneous environments (but which environments are not heterogeneous?), foraging strategies, degrees and patterns of genetic variation, parental effects, and specialist vs. generalist strategies. To this seemingly

endless list, we should add small-scale comparative studies among species or populations informed by phylogenetic analyses (Harvey and Pagel 1991; Martins 2000). This latter category has significantly enlarged the scope of evolutionary ecology to include phenomena above the species level in a quest to understand the link between micro- to macro-evolutionary processes (Hansen and Martins 1996).

In this chapter I will adopt as broad a definition of evolutionary ecology as possible while still retaining some focus. While this may be challenging for the reader, as a variety of questions and sub-fields of ecology and evolutionary theory will be briefly examined, I truly believe that

what makes evolutionary ecology such a fascinating area of inquiry is its expansive reach. Furthermore, one of the greatest open questions of organismal biology is precisely how the gap between ecological-population and evolutionary-species level phenomena is bridged. This question provides formidable challenges for both theoretical and empirical biologists and will likely see increasing attention and efforts over the next decades.

This chapter comprises several sections, ranging from the ecology and biogeography of *Arabidopsis* to the study of its quantitative genetics, from phenotypic plasticity to research conducted on other species comprising *A. thaliana*'s "phylogenetic neighborhood." Within each section I will introduce the reader to the general area of research and the corresponding fundamental questions, moving to brief considerations of several examples of what has been done in the more or less recent past, and ending with a provisional list of questions that I think are likely to be pursued and yield fruitful results over the next few years.

Why ecology and evolution of *Arabidopsis*?

Let us start by answering what might appear at first glance an odd question: why bother studying evolutionary ecology in a plant like *Arabidopsis*? The question is justified by the fact that the mouse ear cress (*A. thaliana*'s common name) was originally selected as a model system for research in genetics (Redei 1992). For geneticists, the main reasons to focus on *A. thaliana* were simply its short life cycle and small size, ideal characteristics to make it the botanical equivalent of *Drosophila melanogaster* (the fact that *A. thaliana* is mostly a selfing species Abbott and Gomes 1989 also simplifies genetic analyses, admittedly at the expense of a difficult handling of the small flowers during pollination). Once that enough knowledge of the genetics and physiology of the plant had accumulated, it naturally became a favorite organism for molecular and then developmental biologists for similar reasons (Dean 1993; Pyke 1994; Anderson and Roberts 1998).

Ecologists and evolutionists have been much slower at capitalizing on the wealth of information available about the mouse-ear cress, despite some interesting early attempts that I will discuss in the next section. Having been on the receiving hand of general criticisms of the use of *A. thaliana* in evolutionary ecology I can testify that the mindset seems to be that this species is both ecologically uninteresting and evolutionarily too peculiar to provide general insights into either plant ecology or evolution. There is a grain of truth in both these accusations.

Ecologically speaking, *A. thaliana* is an opportunistic annual weed, therefore characterized by a rather simple life cycle and a rather narrow ecological valence. Evolutionarily, it probably constitutes a highly derived species with a somewhat unusual mating system. On the other hand, it is easy to push these objections beyond reason. As we shall see, the ecology of this cress is actually more interesting and varied than most people suspected, and annual selfers are by no means unusual beasts among flowering plants. Furthermore, precisely the same objections can be raised to the other major model system in evolutionary biology: the fruit fly *Drosophila melanogaster*, which has not stopped legions of evolutionists from adopting it as their favorite critter.

More importantly, after acknowledging the limitations intrinsic in the use of *Arabidopsis* as a tool for evolutionary ecology research, the advantages should not be underestimated. It is true that if plant ecologists and evolutionists had their pick of a model system they would probably focus on other organisms (though no such species has in fact emerged throughout the 20th century). But it is also true that the astounding and ever increasing database of information about the physiology, molecular biology, genetics, and developmental biology of the mouse ear cress makes it tantalizing for evolutionary ecologists who often find themselves complaining that their inferences about other species are dramatically limited precisely by the lack of such knowledge.

Toward the end of this chapter I will make the case that one of the most important reasons to study *A. thaliana* from an organismal perspective is because it provides a convenient benchmark to extend our investigations into its many relatives within the family Brassicaceae, species that are characterized by much more varied phenotypes, ecologies and evolutionary histories than the mouse ear cress itself.

The classical studies: 1960s and 70s

Early discussions of an ecological, if not evolutionary, flavor about *Arabidopsis thaliana* can be found in the series of short communications collected under the heading of Arabidopsis Information Service (the complete collection from 1964 to 1990 is available at <http://www.arabidopsis.org/ais/>). For example, Ratcliffe (Ratcliffe 1965) discussed the bio-geography of the mouse ear cress, emphasizing the surprisingly wide geographical range in which this species is found and presenting notes on the level of physiological variation necessary to account for the ubiquity of *A. thaliana*'s populations. Figure 1 shows

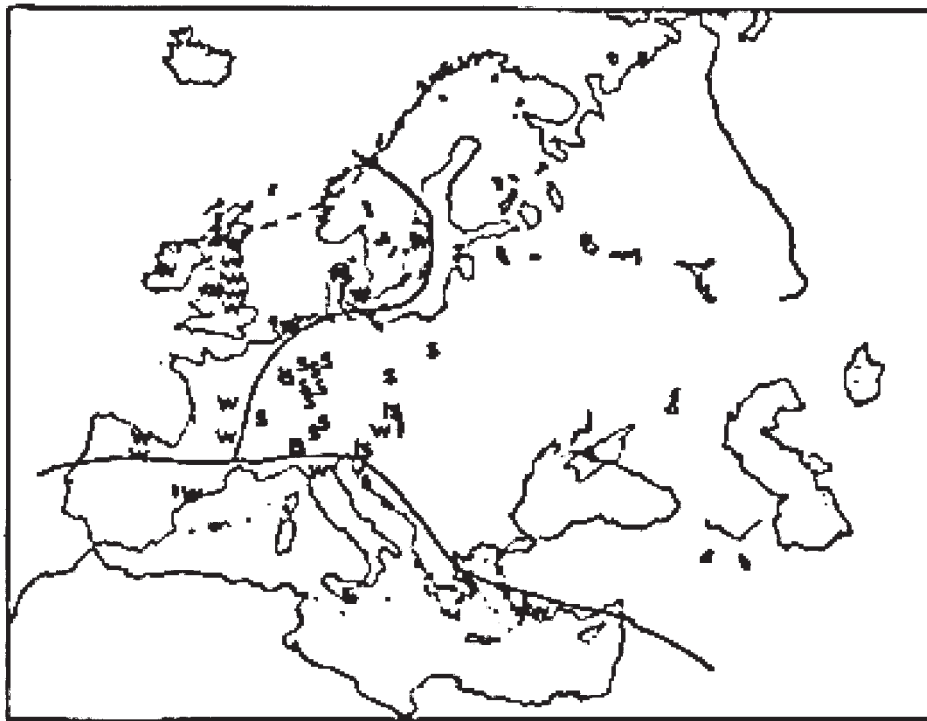


Figure 1. Distribution map of *Arabidopsis thaliana*'s ecotypes according to Radcliffe 1965. (Source <http://www.arabidopsis.org/ais/1965/ratcl-1965-aagli.html>)

a map contained in that article with the approximate European distribution of different ecotypes of *A. thaliana* (termed “races” by Ratcliffe) and how they correspond to different climatic areas. One of the interesting features of the entire collection of documents is that each article comes with the record of a discussion between the author and other researchers attending his talk, in a style that would make any scientific meeting a more valuable experience for everybody.

Perhaps the first study on phenotypic plasticity in *Arabidopsis* was published by Pederson in 1968 (Pederson 1968), where he demonstrated a relationship between genotype-environment interactions (in response to water, nutrients, temperature and light intensity) and heterozygosity (a rare finding in the plasticity literature: Pigliucci in press) by using hybrid lines obtained by crossing ten races of *A. thaliana*. Pederson's study can be considered a landmark in view of the intensive research on phenotypic plasticity that has focused on this plant starting about 30 years after his pioneering work.

Two important series of investigations into the population genetics of the mouse ear cross were published in 1970-71 by Westerman and Lawrence and by Jones. The first series (Westerman 1970a; Westerman 1970b;

Westerman 1970c; Westerman and Lawrence 1970) was devoted to the study of genotype-environment interactions and environmentally-induced variation in developmental regulation. Westerman and Lawrence found that the amount of genotype-environment interaction expressed in response to temperature was higher than the amount of phenotypic variance explained by genetic differences alone and were able to demonstrate a direct relationship between plasticity and fitness in their accessions. Westerman also investigated phenotypic plasticity in response to photoperiod, finding similar results (Westerman 1970b) and her work demonstrated the existence of both additive and non-additive (the latter mostly due to dominance) genetic effects on the phenotype. Additionally, she showed the existence of genetically distinct early and late flowering families within a given population. The second group of papers (Jones 1971a; Jones 1971b; Jones 1971c) also addressed phenotypic plasticity (in response to vernalization, or cold exposure) but focused mostly on the population structure and the breeding system of *A. thaliana*. Contrary to expectations (and to what still seems to be the prevalent opinion among *Arabidopsis* researchers) Jones found evidence of significant outbreeding in five of the seven natural populations

examined, and a detailed investigation of one of these revealed outbreeding progeny in at least seven of 12 families investigated. Jones was also able to associate the degree of phenotypic variation in the mouse ear cress with the habitat of provenance, where populations from highly disturbed habitats such as gardens are much less variable than accessions from less disturbed habitats like abandoned railroads. Furthermore, these populations also differed in their plasticity to vernalization: while the garden population had no cold requirement to flower, the railroad genotypes showed a polymorphism, with five of them needing cold exposure to flower and the remaining seven not. It is interesting that to date we still have relatively scant information about the relationship between plasticity, habitat and life history not only in *Arabidopsis* (Pigliucci 1998) but virtually in any other system.

The last “classical” ecological study of *A. thaliana* I wish to briefly mention before we get into the modern literature is a paper by Myerscough and Marshall (Myerscough and Marshall 1973) who studied the joint effect of density of conspecifics and of nutrient availability on the phenotype and fecundity of the mouse ear cress. Not surprisingly, they found that higher densities cause a significant decrease in fitness (up to 100-fold variation in seed output). What was more interesting was that the highest fecundity occurred for intermediate levels of nutrients and especially the observation of complex interactions between the two environmental parameters, with the maximum seed output altering its dynamics in response to sowing density between lower and higher nutrient availability. This was in fact one of the first multi-factorial studies on phenotypic plasticity, and one of the few that combined a biotic and an abiotic environmental parameter.

It is now time to turn to the more modern literature and to examine current aspects of research on the evolutionary ecology of *Arabidopsis*, starting with what little we know of its life history.

Life history

Life history is defined as the ensemble of characters that determine the timing of crucial events in the existence of an organism, which in plants include germination, the length of the vegetative period, the length and number of reproductive periods, and the timing of senescence. More broadly, life history research includes theoretical as well as empirical investigations of trade-offs between age and size at reproduction (e.g., Stearns and Koella 1986; Yamauchi 1996). In essence, we want to be able to understand variation in life histories among species (or populations of the

same species) and link it to the two major explanatory paradigms in evolutionary ecology: the (functional) ecology of life histories (i.e., how well they match the habitat requirements of the organism) and the (historical) evolutionary trajectory of the species examined (i.e., how much of an organism’s life history is maintained simply because it was inherited by the ancestors of that organism).

The baseline for studies on the life history of *Arabidopsis thaliana* is a chapter by Napp-Zinn in the CRC Handbook of Flowering (Napp-Zinn 1985). It starts with a basic description of the morphology of the inflorescence and flower and goes on to discuss at least three types of life histories in respect to vernalization requirements: 1 – Early summer annuals, which do not respond to vernalization; 2 – Late summer annuals, which delay flowering when exposed to cold; and 3 – Winter annuals, which flower in 4–6 months without vernalization but can be brought to move up the flowering schedule to as little as one month upon cold exposure. Ecologically, the late summer annuals are probably characteristic of areas with harsh winter conditions, which they can withstand as seeds, and flowering is retarded by cold because low temperatures in the natural habitat may indicate a late frost. The opposite situation is likely true for the winter annuals, which overwinter as rosettes in milder climates. Being exposed to cold for them signals the passing of the winter, and therefore the need to switch to the flowering mode. The advantage of overwintering as rosettes (if the temperature does not get so low as to kill the plant) is that it provides a head start on the competition at the beginning of the season, when the plant has already gone through most of the vegetative period and is ready to flower (Silvertown 1988). In fact, *A. thaliana* is a weak competitor and it flowers as early as possible in the spring, presumably to minimize inter-specific competition. What is less clear is what is the ecology of the early summer annuals in Napp-Zinn’s scheme, which do not seem to be responsive to cold treatments one way or the other. At least one of them (and I suspect the others as well) was actually a laboratory line for which it is plausible to hypothesize that it lost plasticity to vernalization under conditions of artificial culture, which select for a fast life cycle under uniform temperature (problems raised by rapid evolution under laboratory conditions have been discussed for the other model system, *Drosophila melanogaster*: Matos et al. 2000; Sgro` and Partridge 2000; Hoffmann et al. 2001). To date we still don’t know if non cold-responsive populations of *A. thaliana* actually exist in nature. However, it is important to note that Napp-Zinn, as Jones before him, reported the existence of genetic polymorphism for the plasticity to cold within a single population, which suggests that some ecological conditions are borderline between the two classes discussed above and may favor some genotypes in cold years and

other genotypes in warmer years. This hypothesis remains to be tested.

A whole sub-area of life history studies in plants deals with seeds and germination, and some research has been done on the mouse ear cress using both natural populations and mutants defective in specific hormonal pathways hypothesized to affect germination (Derks and Karssen 1994). An early work by Baskin and Baskin (Baskin and Baskin 1983) concluded that *A. thaliana* must be a winter annual because seeds can germinate in the field only in the autumn. Seeds are dormant during the spring, and temperatures are too high during the summer and too low during the winter for germination to occur. However, the Baskins used plants collected in Kentucky, USA, where the climate is exactly of the kind (mild winters) that would favor the evolution of winter annual ecotypes. More recent work by Nordborg and Bergelson (Nordborg and Bergelson 1999) has once again turned up evidence of polymorphism within populations, together with information that makes a precise link between life history and habitat less clear than one might hope. For example, these authors found that all Scandinavian ecotypes they studied behaved as “late flowering” and were strongly responsive to cold treatment (flowering earlier with vernalization), but this was true also for collections from the different climates of England and the Netherlands. Similarly, accessions from Kazakhstan, Tajikistan and Libya were “early flowering,” but so was the one from Koln in Germany. Clearly, more effort is needed in this area, and progress will more likely come from the study of fresh collections from the field rather than ecotypes that have been grown under artificial conditions for a long time and that may therefore show atypical or novel responses to the experimental treatments.

An integral component of life history research is the understanding of tradeoffs between different stages of the life cycle, in particular vegetative and reproductive. This is part of a more general quest to evaluate the ecological and evolutionary relationships between allocation to growth and reproduction, both in plants and animals (Roff 2000). The work of Aarssen and Clauss in *Arabidopsis* (Aarssen and Clauss 1992; Clauss and Aarssen 1994b; Clauss and Aarssen 1994a) has provided additional clues to the ecological differentiation of “early” and “late” flowering ecotypes. These authors have found that while there is an overall positive relationship between plant size (as estimated by above ground dry mass) and fecundity, genotypes producing large maximum plant size have relatively low fecundity and suggested that this is representative of an r-K type selection continuum. Indeed, if large plants are allowed to grow throughout a long season they eventually achieve significantly higher reproductive output than they do when their season is cut short. This sort of results has been confirmed by a study exploring the effects of season length and vernalization in 16 populations of *A. thaliana*

(Pigliucci and Marlow 2001) and agrees well with the distinction between disturbed and undisturbed habitats originally drawn by Jones and discussed above.

A concluding note concerning life histories studies in *A. thaliana* is needed to highlight a couple of studies on parental effects on the phenotype of this plant. Parental effects have recently received much attention, together with the realization that they are not just a component of environmental “noise” but can carry cross-generation genotype-environment interactions (Schmitt et al. 1992; Galloway 1995; Weiner et al. 1997; Agrawal et al. 1999). Sills and Nienhuis (Sills and Nienhuis 1995) have demonstrated maternal effects induced in genetically uniform *A. thaliana* by manipulation of the external environment aimed at altering the reproductive sink size. Some of these effects were evident early on during the life cycle of the progeny (14 and 19 days) but not later (24, 29 and 34 days), and maternal effects were clearly determined by seed weight. In an experiment on artificially increased levels of CO₂ (see below), Andalo et al. (Andalo et al. 1998) were able to show that root length and branching were decreased in seeds collected from mother plants exposed to high levels of carbon dioxide and that these effects were genetically variable. Interestingly, there was no direct effect of CO₂ concentration on root growth. For all the effort recently gone into the study of parental effects in a variety of systems it is still not clear what, if any, long-term evolutionary impact these phenomena actually have, but it is clear that they can dramatically affect the ecology and therefore the short term evolution of plant populations.

Open questions: 1) What, if any, is the connection between the ecological setting of a population and its life history in terms of early and late flowering, as well as response to vernalization? 2) How do environmental cues (such as photoperiod and temperature) interact to determine the germination and flowering schedule of natural populations? 3) Do accessions that have been maintained under laboratory conditions undergo significant selection so that they may have lost their original patterns of phenotypic plasticity in response to a variety of environmental stimuli? (This has been demonstrated in the fruit fly, as mentioned above and may have been the case in *A. thaliana* as well: Pigliucci and Byrd 1998). 4) How frequent are polymorphic populations characterized by genotypes that have distinct germination and/or flowering schedules, and in what kinds of habitats do these live? 5) Is there really a differentiation of natural populations of *A. thaliana* along an r-K continuum, and is such continuum determined by the degree of disturbance experienced by the populations under field conditions? 6) What are the consequences of demonstrable parental effects on the ecological dynamics and short-term evolution of the mouse ear cress?

Ecology and selection

Most studies in evolutionary ecology focus on the population level of analysis, leaving questions of community and especially ecosystem ecology largely unaddressed. At the level of interest to evolutionary ecologists natural selection plays an important role in shaping differences among populations, which leads to the prediction that there should be a consistent link between the phenotype expressed by certain organisms and the habitat in which they live. Therefore, barring constraints that preclude the response to selective pressures (see below), it is important to characterize the type and intensity of natural selection acting under field conditions (Kingsolver et al. 2001). However, measuring selection using standard statistical methods (Lande and Arnold 1983; Crespi 1990; Rauscher 1992) is only a first step, since in itself this provides no clue to what environmental factors are actually causing selection to occur. For that, one needs a better understanding of the type and degree of environmental heterogeneity as perceived by the organism under study (Bell 1992; Bell 1997). Measuring selection and uncovering its causal mechanisms are then the crucial objectives of this type of research.

Unfortunately, so far very few studies have addressed the field ecology of *Arabidopsis thaliana*, so that it is difficult to paint a general picture. Thompson (Thompson 1994) has argued for the existence of a complex cycle between alternating (spring-germinating and late-summer germinating) generations in England. In that case the litter from the spring-germinating plants provides nutrients for the summer-germinating generation, which tends to be characterized by many but smaller than normal individuals (due to nutrient limitations). Even after the winter, the now no longer present litter from the summer-germinating plants still has a stimulatory effect on the next round of spring-germinating individuals. The generality of this scenario, however, depends on how frequently natural populations do indeed produce two generations every year, something that might be possible only under unusual climatic circumstances.

A different approach to the study of the effect of environmental heterogeneity has been taken by Bell and Lechowicz (Bell and Lechowicz 1991). These authors used *A. thaliana* (and *Hordeum vulgare*) as bioassays in field trials to determine the spatial scale of variation in the environment as perceived by the plants. They used dry mass as a correlate of reproductive success and showed that it is characterized by modest but significant levels of spatial autocorrelation at different scales. Generally speaking, the within-site variance in dry mass decreased from scales of 10 meters through 0.1 m and the variance among sites

increased with distance. Interestingly, the correlation between sites decreased with increasing separation between sites at the same rate for all scales, which the authors interpreted as indicating that environments are about equally complex (heterogeneous) at all spatial scales.

A variant on the bioassay idea has been implemented by Stratton and Bennington (Stratton and Bennington 1996) who randomly sowed three phenotypically recognizable genotypes of *A. thaliana* over a number of microsites in the field. The assumption was that if there was selection for a particular genotype they should have observed non-random clumps of that genotype. Furthermore, the spatial scale of the clumping would provide indications of the spatial scale of the corresponding selective factor. Indeed, they found that individuals of the same genotype were more likely to be found next to each other than predicted by the random model and that such spatial autocorrelation extended over distances of about 50cm. While the authors did not speculate on the nature of the causal selective factor, such a distance is compatible with observed scales of heterogeneity in fundamental abiotic parameters such as soil pH and abundance of K⁺ and NO₃⁻ ions (Lechowicz and Bell 1991).

To show how difficult it is to connect observed selective forces with the underlying causes let us briefly consider a study by Callahan and Pigliucci (Callahan and Pigliucci in press). In laboratory studies of *A. thaliana*, plants shaded by neighboring vegetation (or subject to treatments mimicking shade) flower at a younger developmental stage (i.e., with fewer leaves), which sometimes corresponds to flowering earlier in chronological time. The authors examined whether this shade-avoidance response (see below) varies among and within natural populations and whether it corresponds to variable selection regimes at shaded and unshaded field sites. They conducted a two-year reciprocal transplant study at sites where *A. thaliana* grows as a naturalized winter-annual weed (in eastern Tennessee, USA). They also conducted a parallel greenhouse study that manipulated the presence and timing of shade. Both studies used seeds derived from two native populations. In the field, shading had limited or inconsistent impacts on survivorship across several phases of the growing season. The date of bolting was earlier at the shadier site compared to the less shady site, but in the greenhouse there was no significant shade-induced plasticity for this trait. In both studies, Callahan and Pigliucci detected directional selection gradients favoring earlier bolting in shade, as expected on the basis of the shade avoidance hypothesis, but gradients favoring earlier bolting were as strong or stronger in non-shaded conditions. The number of rosette leaves at bolting (i.e., the developmental stage of flowering) was significantly reduced by shade in both studies. However, there was either no directional selection on this

trait, or selection to flower with more rather than fewer leaves. Despite the contrast in habitats, there was limited differentiation between populations for survivorship, reproductive fitness, size-related or flowering-time traits, and no differentiation for trait plasticities. The authors concluded that a trade-off between chronological age and developmental stage may limit the response to selection for flowering time, possibly explaining a lack of local adaptation. The adaptive significance of shade-induced flowering-time plasticity remains therefore equivocal, even though shade avoidance plasticity and its molecular basis are among the best known examples of presumably adaptive phenotypic plasticity (Schmitt 1997; Smith 2000).

Open questions: 1) What are the dynamics of natural populations of *A. thaliana* with respect to nutrient cycling and other environmental factors? 2) How frequently does the mouse ear cress go through two reproductive cycles within one year? 3) What environmental factors exercise selection on *A. thaliana* at small and very small spatial scales? 4) Are there significant selective factors acting at larger scales? 5) Is shade avoidance in this species actually an adaptive response, or rather an evolutionary left-over from closely related ancestors characterized by a different ecology?

Quantitative genetics and constraints

Quantitative genetics is a statistical approach to the study of characters affected by multiple loci. In evolutionary ecology, the goals of quantitative genetic studies are to assess the degree and type of genetic variation and covariation for phenotypic traits in natural populations, as well as to assess the potential response of these populations to known selective pressures. Key concepts in quantitative genetics include heritability (the amount of genetic variance for a trait, standardized by the phenotypic variance), the genetic variance-covariance matrix (G , a matrix whose elements are the genetic variances of traits and the genetic covariances among all pairwise combinations of traits), and the selection gradients (the partial regressions of a quantitative trait against an estimate of fitness to determine the kind and intensity of selection on that trait) (Falconer and Mackay 1996; Roff 1997). While quantitative genetics as an approach to the study of the evolution of natural populations is characterized by definite methodological limits (Pigliucci and Schlichting 1997), it is the focus of much empirical and theoretical research. The major issues facing quantitative geneticists encompass the degree of stability of quantitative genetic parameters such as heritabilities and variance-covariance matrices.

These have been demonstrated to be variable not only from population to population—as one would expect by definition, since these quantities depend on allelic frequencies—but also due to the environment (e.g., Mazer and Schick 1991; Ebert et al. 1993) and over relatively short evolutionary time (e.g., Stepan 1997). It is currently problematic to see how these known sources of variation can be accounted for within the framework of available theoretical models of the quantitative genetic evolution of natural populations (e.g., Houle 1991; Gromko 1995).

One of the chief objectives of quantitative genetic studies in *Arabidopsis thaliana* has been the mapping of quantitative trait loci (QTL), especially those affecting key life history traits such as leaf number (a proxy for size at reproduction) and flowering time (age at reproduction). For example, Mitchell-Olds has conducted a QTL experiment using recombinant inbred lines of two standard laboratory accessions, Columbia and Landsberg erecta, grown under rather artificial conditions (growth chambers with continuous illumination). He measured (obviously not “natural”) selection for early flowering and increased leaf number (similar to what has been found under natural conditions by Callahan and Pigliucci, discussed above). He also showed that the two traits in question are positively genetically correlated (an assumption common in many physiological and developmental studies of the same traits in the mouse ear cress; see Figure 2), and that therefore the artificial population would not be able to respond to the observed selective force. Mitchell-Olds found two QTL influencing both leaf number and flowering time, one of which mapped close to the *Gigantea* locus, which codes for a nuclear protein involved in phytochrome signaling and that is known to affect flowering time (Huq et al. 2000).

The observation by Mitchell-Olds of two QTL affecting both traits may readily explain the genetic correlation between them, except for the fact that another study by Stratton found quite different results (Stratton 1998) and complicated the picture considerably. Using the same set of recombinant lines, but different growth conditions (a gradient of light intensity and a more realistic photoperiod of 15 daily hours of light) Stratton found eight QTL affecting leaf number and seven influencing flowering time. But only two of these were involved in variation for both characters. Even though these two were probably the same detected by Mitchell-Olds, the additional, trait-specific and environment-specific loci make it more difficult to understand the strong observed correlation between flowering time and leaf production, since these additional genes should allow for some genetic degrees of freedom between the phenotypic attributes they influence separately. A partial explanation of this apparent incongruity can perhaps be found in Stratton's observation that the QTL with major effects were insensitive to the environmental conditions, while the expression of many minor

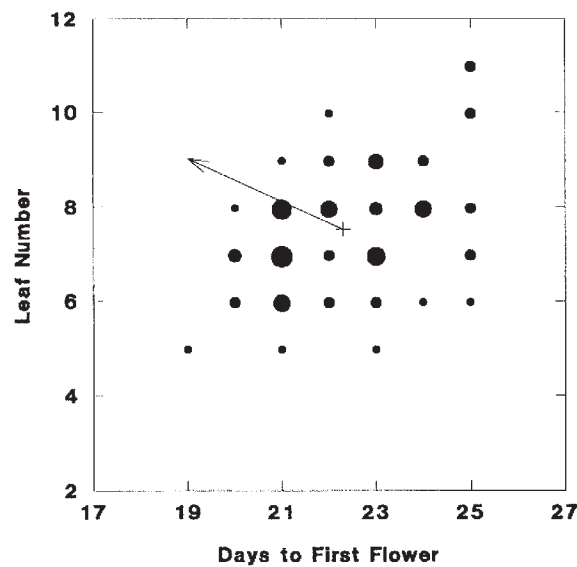


Figure 2. Selection and leaf number and days to flowering in *Arabidopsis* and genetic correlation identified by a scatterplot of different genotypes from 96 recombinant inbred lines. The area of the dots indicates the frequency of lines with a particular combination of the two traits. From Mitchell-Olds 1996.

QTL was affected by the light intensity encountered by the plants.

A very different way to go about the problem of quantitative genetic constraints on phenotypic evolution has been proposed theoretically by Wagner (Wagner and Altenberg 1996) and consists in making a distinction between variation and variability. Variation, in Wagner's terminology, is the actual genotypic variance we observe in natural populations, i.e., the standard target of quantitative genetic studies. Variability, on the other hand, is the set of potential genotypes that can evolve in a short term from the starting point of the currently existing population. Variability, that is, gives us an extended glimpse into what is possible for evolution to do given not just the current state of quantitative genetic parameters, but their likely state in the immediate future. The problem, of course, is how to empirically study variability. My laboratory has taken some steps in that direction (Pigliucci et al. 1998; Camara and Pigliucci 1999; Camara et al. 2000) by using a mutation-selection protocol to study the flexibility of genetic variance-covariance matrices (and therefore of constraints) in *A. thaliana*. We found that some genetic correlations (such as the one discussed so far between flowering time and leaf production) are indeed very resilient and are not altered by mutations or genetic background. Other components of the G matrix, however, are more variable and show some degree of evolvability, the degree of

which varies with different genetic backgrounds. We were also able to demonstrate that it is much easier to change by mutation-selection character means than character plasticities in *A. thaliana*, at least if one uses early flowering ecotypes as a starting point. This finding is consistent with other experimental studies of genetically closely related accessions of this plant (Pigliucci and Byrd 1998).

Open questions: 1) Is the constraint coupling flowering time and leaf production truly universal in *A. thaliana* or is it typical only of the early flowering ecotypes in which it has been repeatedly observed so far? 2) Is this constraint maintained also in other species closely related to *A. thaliana*? 3) To what extent is it possible to build a consensus map of QTL across different accessions and environments, and what can we learn from the QTL that do not maintain their effects across genetic backgrounds and environmental conditions? 4) How far can we extend experimental studies of variability, and how are these results to be incorporated in quantitative genetic theory? 5) How do mechanisms other than mutations (such as recombination) affect the degree of variability for quantitative traits in the cross? 6) Can we extend the concept of variability and its experimental study to other, closely related, species?

Phenotypic plasticity and genotype-environment

interactions

The study of phenotypic plasticity, the characteristic of a genotype to respond differently to different environmental conditions, has seen an explosion of interest in evolutionary ecology over the past two decades (Schlichting 1986; Sultan 1987; West-Eberhard 1989; Scheiner 1993). When different genotypes are characterized by different patterns or degrees of plasticity (i.e., they have a different norm of reaction to the environment) this is conceived of as “genotype-environment interactions.” Plasticity can be studied at many levels, from the molecular to the organismal (Callahan et al. 1997), and the general questions raised by plasticity studies are at the core of much evolutionary biology. Among other things, plasticity researchers are interested in the so-called genotype-to-phenotype mapping function (van-Tienderen and de-Jong 1994), the metabolic or ecological costs of plasticity (DeWitt et al. 1998), the effect of plasticity on life history and breeding systems (e.g., Mendez 1998; Vogler et al. 1998), the role of plasticity in the defense against pathogens and predators (e.g., Schenk et al. 2000; van-Dam et al. 2000), the relationship between plasticity and genetic constraints (Stearns et al. 1991) and several other areas of study (for a comprehensive review and discussion see: Pigliucci in press).

Arabidopsis thaliana has been at the center of a fair number of studies on phenotypic plasticity, mostly but not exclusively, focusing on responses to abiotic environmental factors in early flowering ecotypes. My lab produced a series of papers investigating plasticity of a variety of accessions to light intensity, water, and nutrient availability (Pigliucci and Schlichting 1995; Pigliucci et al. 1995a; Pigliucci et al. 1995b; Pigliucci and Schlichting 1996; Pigliucci 1997). We found that there is usually little genetic variation for plasticity within populations but a significant amount of differentiation among populations, as expected given the life history and breeding system of the mouse ear cress (see below). We demonstrated the lack of a connection between similarities in plastic responses and genetic distances among populations calculated using quasi-neutral molecular markers (Pigliucci and Byrd 1998), which suggests that plasticity does not evolve simply by random genetic drift, a conclusion strengthened by the observation of sets of characters whose plasticities co-vary in a way consistent with functional hypotheses about the ecological role of the plasticities in question. We also found that flowering time—a key aspect of *A. thaliana*’s life history—is in fact a major determinant of the entire phenotypic architecture of the plant and is related in an environment-dependent fashion to other key vegetative and reproductive characters, though in a way that is also influenced to some

extent by the specific genetic background examined (Pigliucci and Schlichting 1998). When we analyzed the response of the mouse ear cress to a series of abiotic stresses (low nutrients, water or light) we found that the plant expresses a higher degree of genetic variance for quantitative traits under stress than under more optimal growth conditions, a result that might shed some light on the ongoing discussion about the effect of stress on the expression of genetic variance and therefore on the potential for future evolution (e.g., Ward 1994; Badyaev and Foresman 2000; Stanton et al. 2000).

A special type of “abiotic” (or, better, indirectly biotic) factor is the partial pressure of carbon dioxide in the atmosphere. This is particularly relevant both from an evolutionary and from an applied standpoint. Evolutionarily speaking, CO₂ concentration in the atmosphere was probably as low as 18Pa during the Pleistocene (Ward and Strain 1997), compared to the current level of 35Pa. On the other hand, human activities and perhaps unknown natural factors are conspiring to increase that level to about 70Pa before the end of the 21st century. Ward and Strain (Ward and Strain 1997) therefore studied the behavior of *A. thaliana* in response to all three levels of carbon dioxide with fascinating results. They found that plants collected at high elevations (naturally exposed to lower levels of CO₂) were better adapted to Pleistocene-like conditions and that in general the mouse ear cress may be able to acclimate and to evolve more readily in response to Pleistocene rather than futuristic levels of carbon dioxide. Interestingly, there was little genetic variation in the response of biomass to CO₂ while there was significant variation in reproductive characters, indicating that different aspects of the phenotype are differentially affected by genotype-environment interactions.

Similar results, but only in the current to future window of carbon dioxide variation, were obtained by two other studies. Van der Kooij and De Kok (Van-der-Kooij and De-Kok 1996) found that increased CO₂ levels cause a transitory increase in vegetative growth rate, which is sufficient to translate into a 51% increase in seed production, despite the fact that the flowering architecture was actually not affected. Zhang and Lechowicz (Zhang and Lechowicz 1995) expanded their research to the consideration of simultaneous variation in CO₂ and nutrients, finding that genotypes responded more strongly to the latter than to the former. Furthermore, there seemed to be a relationship between the plasticity to nutrients and the plasticity to carbon dioxide, with a genotype exhibiting strong response to both and another one little response to either. Given the practical importance of studies on plant’s responses to CO₂ and the amount of knowledge accumulated on the physiology and molecular biology of *A.*

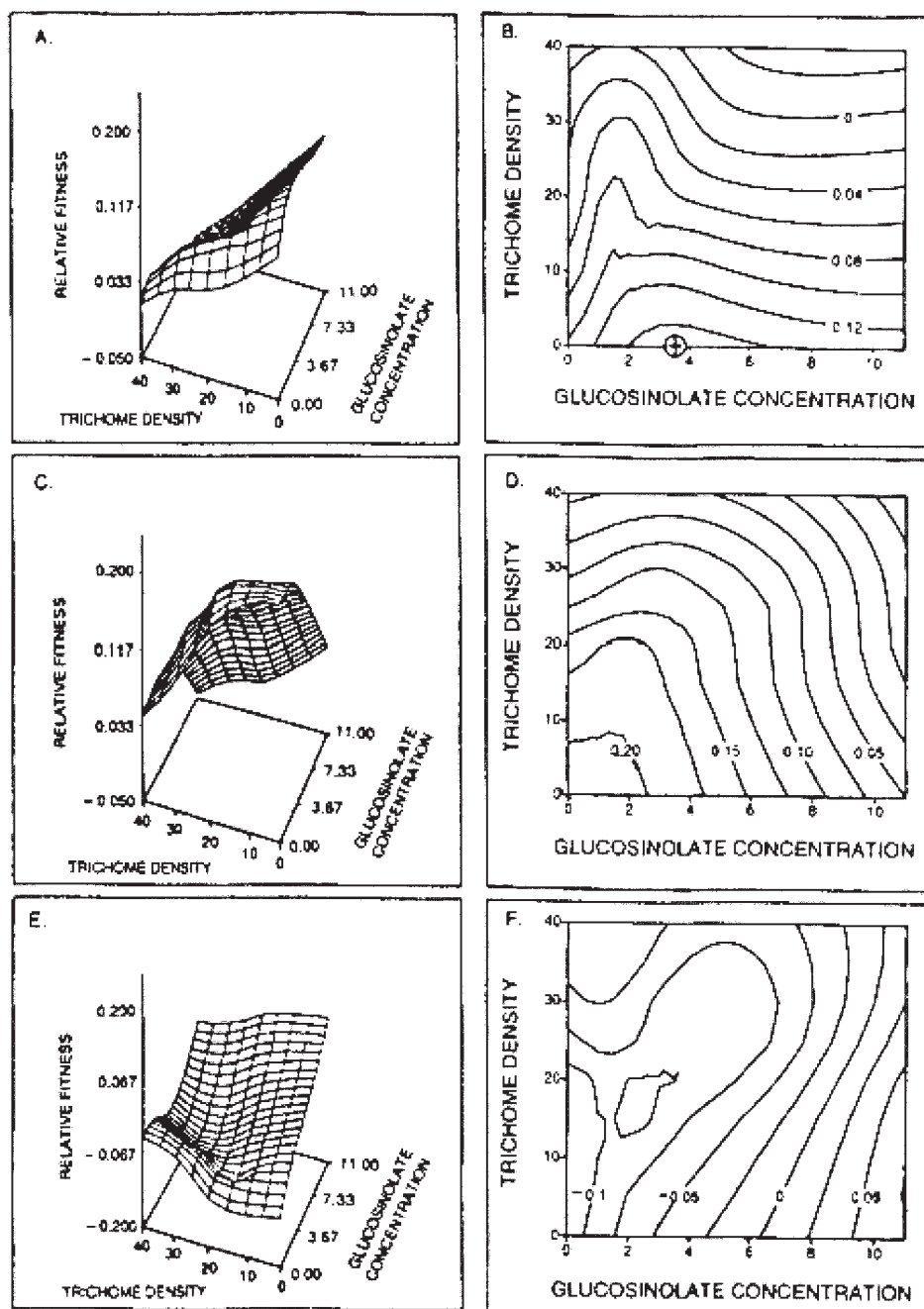


Figure 3. Fitness surfaces for total glucosinolate concentration and trichome density in Arabidopsis: A,B overall pattern of selection (control plants); C,D pattern of selection in absence of natural enemies; E,F difference between fitness surfaces in control and sprayed treatments. From Mauricio and Rauscher 1997.

thaliana, more studies along these lines are surely forthcoming.

Comparatively few studies have focused on the response of *A. thaliana* to biotic factors [other than the classic one by \Myerscough, 1973 #1670 discussed above]. Dorn et al. (Dorn et al. 2000) have investigated the plasticity of 36 inbred lines from four natural populations to light cues and resource availability. They varied both directly the amount of light (an “abiotic” factor) and the ratio of red to far red light (R:FR), which is a biotic cue used by many plants to detect the presence of surrounding vegetation and trigger the so-called “shade avoidance” response (Givnish 1982; Ballare 1999; Weinig 2000). Dorn and colleagues also manipulated plant density directly in an effort to determine the existence of adaptive responses and costs while being able to discern if these were stimulated by a biotic factor, by its correlated abiotic counterpart, or by the cue used by the plants to predict both. They found no evidence of adaptive plasticity to density per se, but they did observe adaptive and maladaptive reactions to shade. Most interestingly, the response to the abiotic factor was maladaptive while the one to the cue was adaptive, highlighting the subtleties embedded in plasticity experiments and the caution one must take before drawing conclusions in favor or against the adaptive plasticity hypothesis.

A special case of biotic interactions is the response of the mouse ear cress to pathogens and herbivores, which has been studied for example by Mauricio and Rauscher (Mauricio and Rauscher 1997). They hypothesized that *A. thaliana* evolved high trichome density and high concentrations of glucosinolate as a response to the presence of natural enemies such as herbivores and fungal pathogens. The pattern and intensity of natural selection on these traits was measured in control plots and in plots that had been sprayed to avoid predatory and pathogenic attacks on the plants. As predicted, the treatment significantly altered the pattern of selection on the two traits, indicating that natural stabilizing selection on anti-predator and anti-pathogen defenses is the result of a balance between the costs and benefits of such defenses and of course depends on the actual presence of pathogens and herbivores under field conditions (Figure 3).

An interesting study by Peters (Peters 1999) combined the study of pathogens, in this case infections of *Pseudomonas syringae* and that of the effect of novel mutations on life history traits, similar to the ones discussed above in the context of variability and constraints. Peters exposed *A. thaliana* to three levels of pathogens and five of ethyl-methane-sulfonate (EMS), a known mutagen. He found that infection with *P. syringae* increased the probability of flowering under short-day conditions, a potentially adaptive response, but ended up in a lower production of flowers nonetheless. The effects of mutations

were linearly related to dose and there were no correlations among the mutational effects on different traits. Interestingly, there was no interaction between mutations and pathogen attack, suggesting that these two phenomena have independent effects on the phenotype and life history of *A. thaliana*.

A very unusual, and so far not follow-through, study of plasticity in the mouse ear cress has investigated the possibility of group selection (Nunney 1989; Stevens et al. 1995; Morell 1996; Wilson and Dugatkin 1997; Getty 1999) on leaf area in *A. thaliana* in response to shade (Goodnight 1985). The author was able to demonstrate the possibility of group selection on “deme” (an ensemble of presumably genetically closely related plants) level leaf area. The biological interest of this lies in the possibility that group leaf area may help plants to suppress competition from other species (or even from other, less genetically related, individuals of the same species) by allowing dominance of the canopy (even though *A. thaliana* is a rosette plant, its “canopy” may be crucial especially during the early stages of development at the beginning of the spring or in late fall, depending on the life cycle of the specific population). Goodnight also observed individual selection on the same trait, and demonstrated that individual and group selection interfered both when acting together and in concert. To date, this remains to my knowledge the only study on group selection in plants, an avenue of research that should be pursued much more vigorously given the resurgence of interest on the issue of multi-level selection in evolutionary biology (Williams 1992; Sober and Wilson 1998).

I would like to conclude this section on plasticity by mentioning a relatively novel approach that attempts to combine investigations at the organismal level with knowledge at the molecular level, arguably one of the chief reasons to use *A. thaliana* as a model system in evolutionary ecology (Pigliucci 1998). van Tienderen and colleagues (van-Tienderen et al. 1996) examined the pleiotropic effects of five one-gene mutants affected in flowering time in response to different levels of nutrient availability. They found that the relationship between flowering time and rosette leaf number (the “constraint” discussed above in the context of quantitative genetic studies) actually varied among mutant lines as well as with nutrient supplies. These authors also demonstrated abundant pleiotropic effects of “flowering time genes” on other characters, including leaf length, number of leaves, and number of axillary inflorescences. Pigliucci and co-workers used mutants affected in key photoreceptors such as phytochromes and blue receptors to study genotype-environment interactions in response to simulated foliar shade (Pigliucci and Schmitt 1999) and combinations of water and light availability (Callahan et al. 1999). The mutations induced significant genotype-environment interactions in

both vegetative and reproductive traits (Figure 4), with the mutants characterized by both broad pleiotropic and epistatic (gene-gene interaction) effects on several characters. It was evident that phytochromes and blue receptors play antagonistic roles in response to simulated canopy shade, as already demonstrated by Mozley and Thomas in

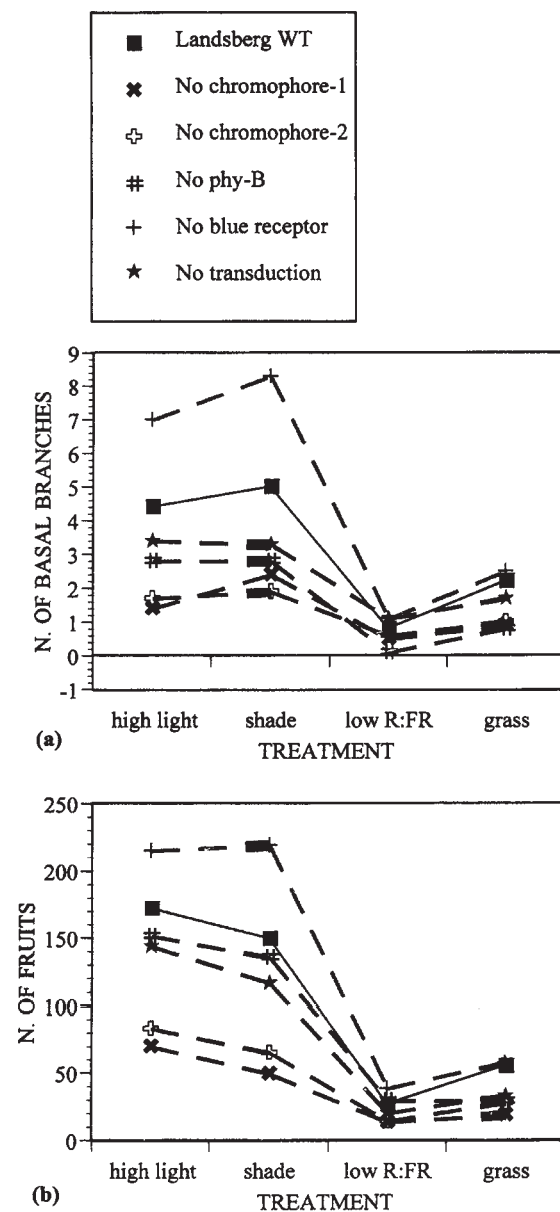


Figure 4. Reaction norms across four treatments of reproductive traits in *Landsberg erecta* and five mutants affected in light perception. From Pigliucci and Schmitt 1999.

the case of photoperiod (Mozley and Thomas 1995; see also: Mas et al. 2000), that phytochrome B's action is partly redundant with other phytochromes (as confirmed by the molecular literature: Whitelam et al. 1998; Ballaré 1999; Smith 2000) and that both classes of mutations are surprisingly responsive to water availability, even though obviously the affected genes do not have anything to do directly with the perception of this environmental factor. Further studies of the behavior of specific single and multiple mutants under ecologically realistic conditions will probably shed light on both the functional meaning (if any) of the object of study of molecular geneticists and on the evolutionary importance of major regulatory genes (Purugganan and Suddith 1998; Purugganan and Suddith 1999).

Open questions: 1) To what extent are studies on plasticity in early flowering ecotypes extendable to a more biologically relevant sampling of *A. thaliana*'s populations? 2) To what extent are the patterns of character covariation observed in the mouse ear cross the result of past selection (functional hypothesis) vs. genetic constraints (historical hypothesis)? 3) What kinds of biotic and abiotic plasticity are adaptive or maladaptive in *A. thaliana*? 4) What are the natural herbivores and pathogens of the cross, and what are their patterns of abundance and impact on natural populations of *A. thaliana*? 5) Does group selection act under natural conditions in *A. thaliana*, and if so on what other traits other than leaf area? 6) To what extent do candidate genes identified by molecular and mutagenic analyses play a role in evolutionary changes in natural populations? 7) What are the usefulness and limitations of studies at the interface between organismal and molecular biology as exemplified by the experience accumulated with a model organism?

Biogeography, phylogeny and the comparative method

In this last section I will examine what we know of the geographical variation of *A. thaliana* and of the genetic and historical relationships among populations. Another chapter in this book will deal more explicitly with systematic problems connected to the inter-specific phylogeny of the *Arabidopsis* clade. The reason historical relationships are important is because they provide a baseline for comparative ecological and evolutionary studies (Harvey and Pagel 1991; Martins 2000). Whatever evolutionary ecological question one is interested in, the possibility that the similarities between populations or species exist because of descent from a common ancestor rather than because

of functional reasons need to be assessed. In fact, in a broad sense the major goal of comparative studies is precisely to disentangle, as much as possible, the relative contributions of history and function to the current features of natural populations.

This research program, however, is fraught with methodological problems springing from the complex intertwining of historical and functional causes in determining biological structures. For example, if a lineage shows phylogenetic niche conservatism (i.e., closely related species tend to occupy similar niches: Westoby et al. 1995) then there will be a history-by-function “interaction” (similar to the genotype-by-environment interaction that makes nature-nurture studies difficult: Pigliucci in press) which will make the question of phylogeny vs. selection somewhat meaningless. To this one should add, as we shall see and as discussed in the chapter by Al-Shehbaz, that the taxonomic relationships among species in the Brassicaceae in general have always been problematic. In addition, there may be strict limits to the possibility of intra-specific phylogenetic studies within *A. thaliana*.

Let us start at the level of the structure of local populations in order to then proceed to large-scale biogeographical patterns within *A. thaliana* and finally to the question of inter-specific comparative studies. A crucial piece of information to understand the patterns of geographical variation of a species is an understanding of its mating system and the consequences it has on population structure. While the agreement seems to be that *A. thaliana* is highly selfing, this is really the result of a single study using allozymes in 16 British populations in which no outcrossing was actually observed and the upper theoretical limit to outcrossing was calculated at 0.3% (Abbott and Gomes 1989). However, the results of an earlier—and admittedly cruder—study by Jones question the general conclusion of high levels of selfing in the mouse ear cress.

A more recent investigation by Bergelson et al. (Bergelson et al. 1998) confirmed a low degree of genetic variation within populations using nucleotide polymorphisms (RFLP), but these authors also found a low degree of genetic differentiation across populations, contrary to both Jones (for quantitative traits) and Abbott and Gomes (for allozymes). Breyne et al. (Breyne et al. 1999) used AFLP analysis on 21 ecotypes and found low but significant levels of genetic variation within populations, which surprised the authors in view of the assumption of high degree of selfing in this species. Furthermore, while Breyne and collaborators admitted that distinguishing closely related populations may be difficult, they emphasized the discovery of at least two and perhaps three subgroups of ecotypes among the accessions they studied. Erschadi et al. (Erschadi et al. 2000) also used AFLP markers on 19 ecotypes and found a few that showed considerable within-population genetic diversity in comparison

with the remaining populations. The diverse ecotypes also clustered significantly apart from the bulk of the accessions based on overall genetic similarity. While the details are still foggy, the general picture that seems to be emerging is along the lines of what Bergelson and coworkers concluded: either *A. thaliana*’s geographical range underwent a recent expansion, or there is significant long distance gene flow (probably mediated by humans) among worldwide accessions. In either case, this explains the consistent lack of a relationship between genetic and geographical distances found by all these studies.

A much larger study of the biogeography of *A. thaliana* has been published by Sharbel et al. (Sharbel et al. 2000), again using AFLP markers, but this time on 142 accessions. They found significant evidence of isolation by distance among accessions from Eurasia and southern Europe, suggesting that the mouse ear cress may have colonized central and northern Europe from Asia and from Mediterranean Pleistocene refugia (Figure 5), a scenario consistent with that of several other species’ movements in the recent past. The authors conclude with a pessimistic evaluation of the possibility of reconstructing ecotype-level phylogenies due to the extreme bush-like shape of dendrograms summarizing genetic distances among populations.

Despite Sharbel et al.’s pessimism about intra-specific comparative studies of *A. thaliana*, Vander Zwan et al. (Vander-Zwan et al. 2000) have used microsatellites and morphological markers to explore intra-specific phylogenetic relationships in this species, and arrived at the conclusion that North American accessions are derived from Europe while the Asia-Europe connection is more ambiguous and requires further study. They also noted that the gross morphology of the plant seems not to have changed much among populations scattered across four continents. Pollard et al. (Pollard et al. 2001) studied the evolution of phenotypic plasticity to daylength in several accessions from Scandinavia for which they had also conducted a study of historical relationships and found that plasticity can evolve rapidly and that the plasticity of a given trait evolves largely independently of the plasticity of other traits. This contrasted with the conclusions obtained from the same dataset when character means (i.e., irrespective of the environment) were considered: in this case the authors clearly identified two sets of covarying traits, one expressed during the vegetative phase, the other during the reproductive one. The two sets also showed evidence of trade-offs with each other so that plants could allocate resources to either but not both sets.

A geographically broad comparison of latitudinal change in *A. thaliana* has been published by Li et al. (Li et al. 1998), who analyzed 40 ecotypes spanning a range from 16°N to 63°N and found that plants from high latitudes tended to be smaller in both vegetative and reproductive characters

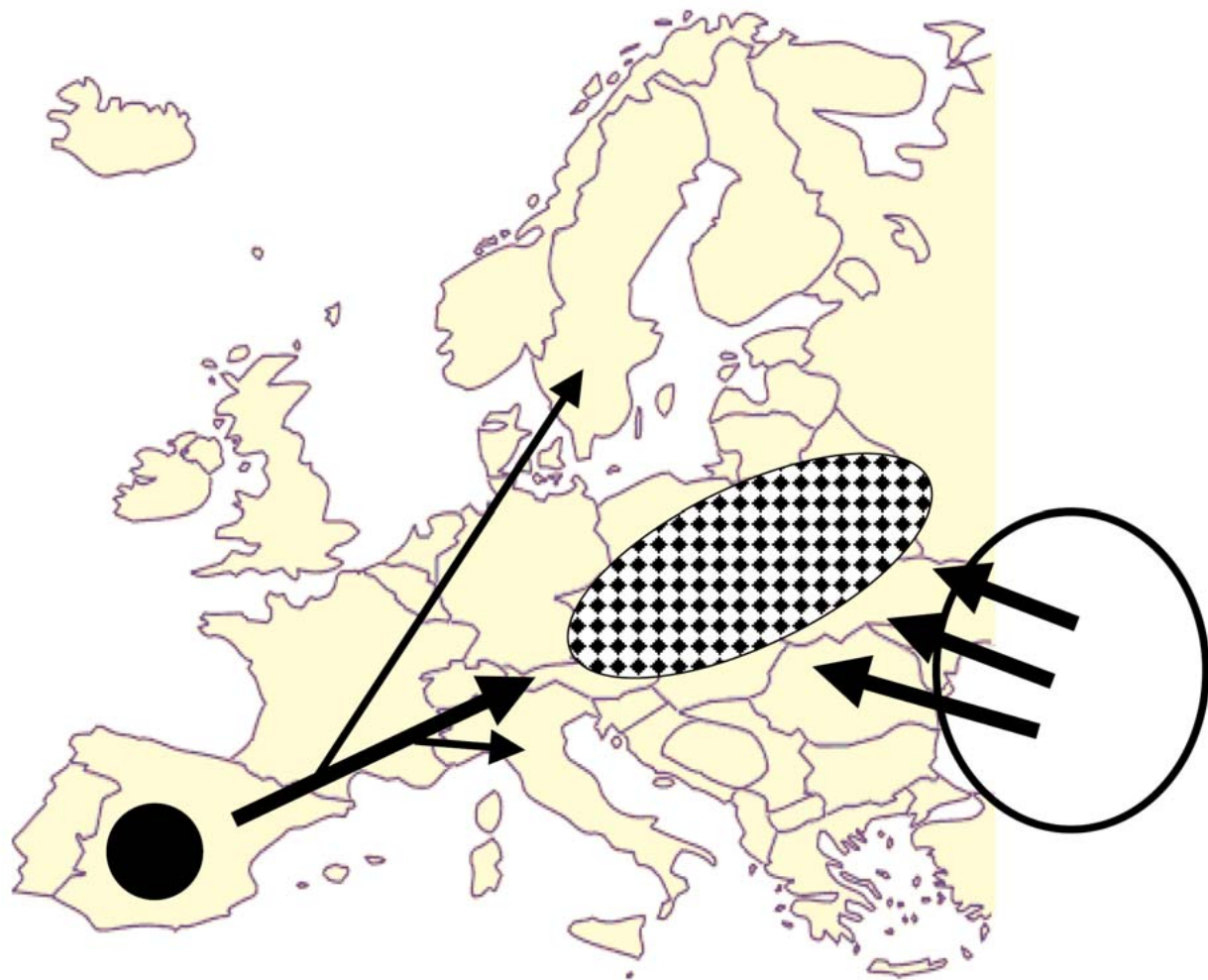


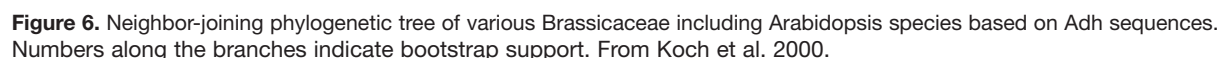
Figure 5. Scenario for *Arabidopsis* post-glacial colonization of Europe from the Iberian peninsula and Asia to a central European contact zone and to Scandinavia. Redrawn from Sharbel et al. 2000.

and that the relative growth rate (RGR) was negatively correlated with latitude. Interestingly, variation in RGR was constrained by variation in its two components: a physiological one (measured by the unit leaf rate) and a morphological one (quantified as leaf area ratio). Unfortunately, no information was available in this case on the possible historical relationships among these populations, so that only the functional side of the equation was explored in this study.

The last issue to be considered here is the possibility of expanding evolutionary ecology studies to species more or less closely related to *A. thaliana*. While there has been little impetus to do so in the molecular/physiological literature (with a few exceptions: Endress 1992; Jonsell et al. 1995; Kamm et al. 1995; Saleeba and Gueriot 1995;

Tsukaya et al. 1997), I think this is eventually the area where research will explode both at the molecular and organismal levels. While it is obvious why ecologists and evolutionists are interested in extending their research to other species, by the very nature of evolutionary and comparative questions, it should also be clear that the future of genomics and proteomics lies in expanding the focus away from the limits of haphazardly chosen and little representative model systems toward a more full understanding of the diversity of life at the molecular level. Until recently, however, the systematics and taxonomy of *Arabidopsis* and of the Brassicaceae at large was rather chaotic. After several recent attempts along classical lines of systematics research (Price et al. 1994; Al-Shehbaz and O’Kane-Jr. 1995; O’Kane-Jr. et al. 1996, see also Al-

One of the few examples so far of inter-specific study addressing organismal questions in *Arabidopsis* is a paper by Pigliucci et al. (Pigliucci et al. 1999) on the evolution of plasticity to foliar shade. The research included early and



late flowering ecotypes of *A. thaliana*, *A. petraea* (a species very closely related to the mouse ear cress), and the clade made of the sister species *A. griffithiana* and *A. pumila* (which according to the latest phylogenies are actually distantly related to *Arabidopsis* and part of a larger clade that includes several *Arabis* species: Koch et al. 2000). The overall results were similar to those reported above for an analogous intra-specific study: 1) plasticities evolve rather rapidly; 2) the plasticities of different species evolve independently of each other (as predicted by ecological theory); and 3) taxa are clearly distinct in early and late flowering, regardless of species or clade association.

Given its importance for both molecular and organismal studies, it is likely that more comprehensive and highly resolved phylogenies will allow for an explosion of inter-specific comparisons of this sort with many more taxa being considered. This will immediately be conducive to a better understanding of the advantages and limitations of using model systems in biological research (Kellogg and Shaffer 1993; Hickok et al. 1995).

Open questions: 1) What is the actual range of outcrossing in natural populations of *A. thaliana*? 2) What pollinators affect the degree of outcrossing, and how do they vary geographically? 3) To what extent can ecotypes be grouped by genetic distance and/or historical relationships given the mating system and population structure of the cress? 4) What are the selective determinants of apparent latitudinal trends in vegetative and reproductive characters observed across the geographical range of *A. thaliana* in Europe? Are similar trends observable in Asia and North America? 5) Is there a consistent difference between the patterns of evolution of trait means and trait plasticities in the mouse ear cress, and is either of these related to the species' biogeography? 6) To what extent can the results obtained with *A. thaliana* be generalized to related species, and when they cannot, what does that tell us about the evolution of life histories and complex phenotypes within the Brassicaceae and, more in general, among flowering plants?

In lieu of a conclusion

I hope to have convinced the reader that evolutionary ecology of *Arabidopsis*, both *A. thaliana* and related species, is a nascent and vibrant field of inquiry which harbors great potential for expansion over the near future. There has been much talk in recent years of "integrative" biology, of finally merging molecular and developmental biology into the unified evolutionary synthesis that emerged in the 1930s and 40s known as neo-Darwinism

(Mayr and Provine 1980; Sultan 1992; Carroll 2000). I doubt such a great "final" synthesis will actually be reached any time soon, especially because of deep philosophical reasons that might actually preclude any sort of "complete" explanatory framework within science (Dupré 1993). Nevertheless, if progress is to be made over the next decades, this will certainly come from the convergence of efforts on model organisms for which a large amount of data is available on a variety of aspects of their biology. Indeed, systems such as *Arabidopsis* may provide a crucial test for the very idea that integrative biology is capable of producing a fruitful research agenda. In either case, we will learn a lot from the process.

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