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Cardamine hirsuta: a comparative view

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Current advances in developmental genetics are increasingly underpinned by comparative approaches as more powerful experimental tools become available in non-model organisms. *Cardamine hirsuta* is related to the model plant *Arabidopsis thaliana* and comparisons between these two experimentally tractable species have advanced our understanding of development and diversity. The power of forward genetics to uncover new biology was evident in the isolation of *REDUCED COMPLEXITY*, a gene which is present in *C. hirsuta* but lost in *A. thaliana*, and shapes crucifer leaf diversity. Transferring two *Knotted1-like homeobox* genes between *C. hirsuta* and *A. thaliana* revealed a constraint imposed by pleiotropy on the evolutionary potential of *cis* regulatory change to modify leaf shape. *FLOWERING LOCUS C* was identified as a heterochronic gene that underlies natural leaf shape variation in *C. hirsuta*.

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Introduction

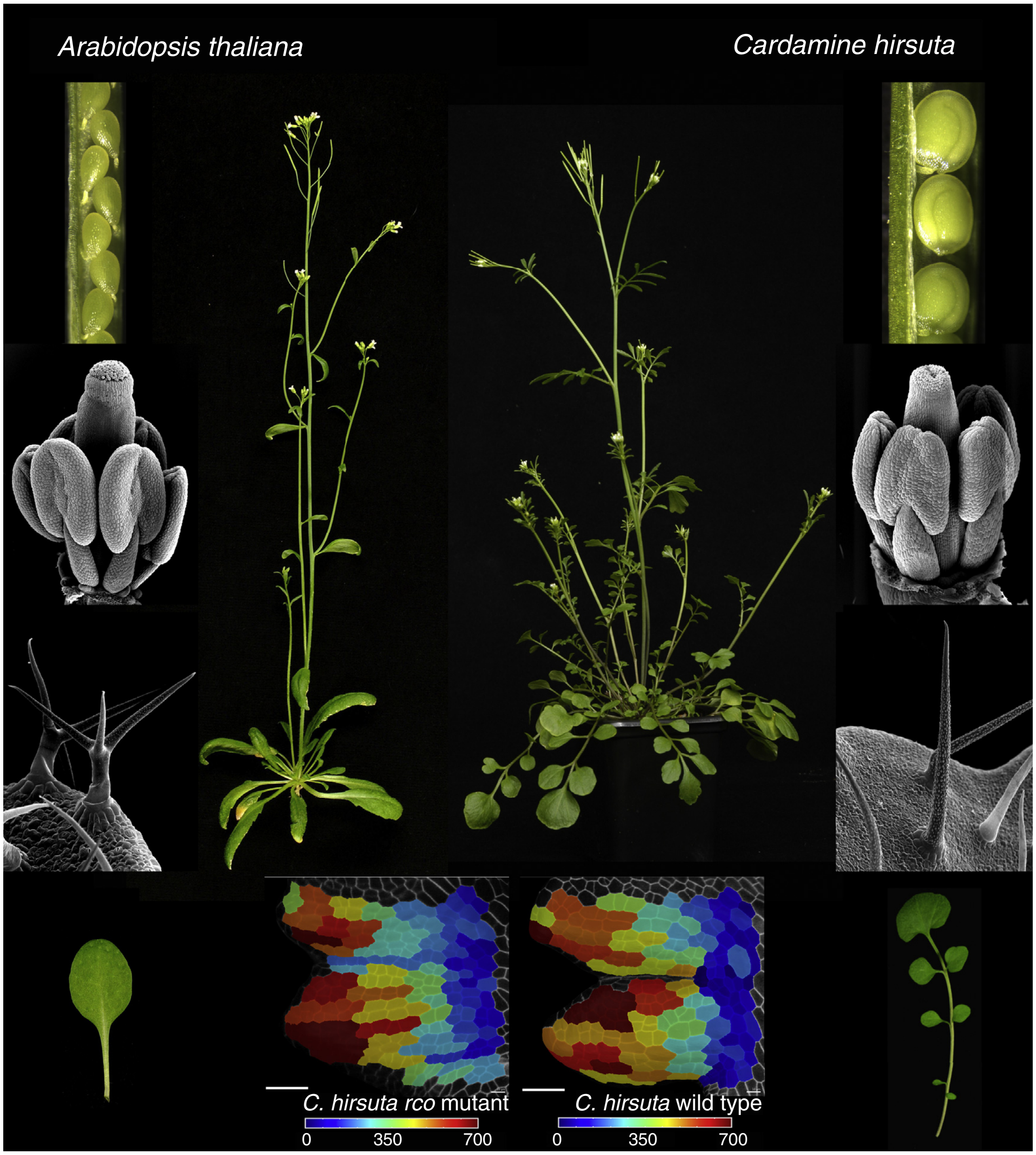
Understanding the genetic basis of phenotypic diversity is a common goal in many areas of research, from evolutionary biology to plant breeding and human genetics. The explosion of high throughput sequencing methods and advances in bioinformatics means that this research is no longer limited by sequence information, but rather by efficient ways to causally connect sequence variation to phenotypic diversity. Comparative genetic studies in the phylogenetic neighbourhood of model organisms have emerged as an important way to address this problem [1]. This approach uses genetic analyses in related taxa to identify molecular changes that underlie phenotypic differences that are of evolutionary significance [2–6]. Key to the success of this comparative approach is that it allows causal genetic differences to be identified and studied within an otherwise broadly comparable genotype to phenotype landscape. Such studies have particularly benefited from the use of interspecific gene transfers to test the evolved functions of sequence variants [7,8]. Other methods that utilize genetic recombination, such as quantitative trait locus analysis (QTL), also provide strong evidence for the genetic basis of morphological diversity and evolutionary change at the species level and between interfertile species [9,10].

Why *Cardamine hirsuta*?

In plants, such comparative studies are particularly attractive in the Brassicaceae family, which includes *Arabidopsis thaliana* — the primary model organism for plant science. This allows the technical and conceptual frameworks established in *A. thaliana* to be exploited in novel contexts to understand the origin of traits or character states not present in the model species, and to provide an evolutionary and ecological perspective [11•,12]. Recent studies have focused on mating system transitions in *Arabidopsis halleri* [13•] and *Capsella* [14,15], alternative life histories in *Arabis alpina* [16] and *Cardamine flexuosa* [17], fruit opening in *Lepidium campestre* [18,19], adaptation to extreme soil conditions in *Arabidopsis lyrata* [20] and *A. halleri* [21,22], and hybridization barriers between *Arabidopsis* species [23]. Within this small group of *A. thaliana* relatives, *Cardamine hirsuta* has emerged as a particularly powerful genetic system for comparative studies of development with *A. thaliana* [24,25•] (Figure 1).

Like *A. thaliana*, *C. hirsuta* was selected as a laboratory subject for its short generation time, small size, inbreeding habit, abundant progeny and ease of large scale cultivation. Importantly, it is a diploid species with a small genome and eight chromosomes, which follows the ancestral genome structure in the Brassicaceae [25•]. Simple, high frequency genetic transformation is routine in *C. hirsuta*, which together with a dense genetic map and chemically mutagenized populations, provide the necessary tools to investigate how genetic changes influence morphogenesis [25•]. The major motivation for studying and developing resources for the *A. thaliana* relative *C. hirsuta* is to understand the genetic basis for morphological evolution. Key to this comparative approach is the abundance of morphological diversity between these reproductively isolated species [25•] (Figure 1). In this review, we will discuss recent work over the past two years that has elucidated how differences in leaf morphology between *A. thaliana* and

Figure 1



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Cardamine hirsuta: a genetic system for comparative studies with *Arabidopsis thaliana.* Whole plant and selected parts are compared between *A. thaliana* (left) and *C. hirsuta* (right). Divergent seed morphology, stamen number, trichome branching and leaf shape are shown from top to bottom. Quantitative image analysis of lateral leaflet growth in *C. hirsuta* is shown in bottom, centre panels for *rco* (left) and wild-type (right). Heat maps show relative surface area increase over 48 h of growth (color bar: percentage increase); scale bars: 30 μm.

C. hirsuta are produced and how these differences evolved. We will also highlight studies of natural variation in *C. hirsuta* leaf shape and petal number that are beginning to show whether the same or different genetic pathways underlie morphological diversity within and between species.

Mutant screen uncovers homeobox gene shaping leaf diversity

Leaves show enormous variation in shape, both within and between species, and differ markedly between *A. thaliana* and *C. 43*. *A. thaliana* leaves are simple with an entire margin while *C. hirsuta* leaves are dissected, also