

## Ontogenetics of QTL: the genetic architecture of trichome density over time in *Arabidopsis thaliana*

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### Abstract

Although much is known about the molecular genetic basis of trichome development in *Arabidopsis thaliana*, less is known about the underlying genetic basis of continuous variation in a trait known to be of adaptive importance: trichome density. The density of leaf trichomes is known to be a major determinant of herbivore damage in natural populations of *A. thaliana* and herbivores are a significant selective force on genetic variation for trichome density. A number of developmental changes occur during ontogeny in *A. thaliana*, including changes in trichome density. I used multiple interval mapping (MIM) analysis to identify QTL responsible for trichome density on both juvenile leaves and adult leaves in replicate, independent trials and asked whether those QTL changed with ontogeny. In both juvenile and adult leaves, I detected a single major QTL on chromosome 2 that explained much of the genetic variance. Although additional QTL were detected, there were no consistent differences in the genetic architecture of trichome density measured on juvenile and adult leaves. The finding of a single QTL of major effect for a trait of known adaptive importance suggests that genes of major effect may play an important role in adaptation.

**Abbreviations:** cM – centiMorgans; LOD – logarithm of the odds; MIM – multiple interval mapping; n – sample size; QTL – quantitative trait locus; RI – recombinant inbred; SE – standard error.

### Introduction

The density of leaf hairs, or trichomes, is a trait of considerable ecological importance for many plants. One of the primary adaptive hypotheses commonly proposed for the presence and density of plant hairs involves their role in defense against herbivores (Levin, 1973; Johnson, 1975; Ågren and Schemske, 1994; Elle et al., 1999). For example, in natural populations of *Arabidopsis thaliana*, genotypes with higher trichome densities suffer significantly less herbivore damage than genotypes with lower trichome densities (Mauricio, 1998). Furthermore, herbivores have been shown to be a

significant selective agent acting on genetic variation for trichome density in *A. thaliana* (Mauricio and Rausher, 1997).

In many plants, trichomes differ on leaves of different age (Poethig, 1997, 2000, 2003). Leaf age has long been recognized as having an important effect on plant resistance to herbivores – herbivores often have strong preferences for tissue of a particular age (Janzen, 1979; Coley 1980; Krischik and Denno, 1983; Karban and Thaler, 1999; Lawrence et al., 2003). Damage to leaves of different ages can have different effects on plant fitness (Stinchcombe, 2002). Therefore, herbivores can impose very different selective pressures on

plants depending on their pattern of feeding (Mauricio et al., 1993). Difference in trichome density on juvenile and adult leaves might mediate such selection.

The vegetative phase change from juvenile to adult rosette leaves in *A. thaliana* is well-described, particularly with respect to trichomes (Telfer et al., 1997). The distribution and density of trichomes varies during vegetative development and has been used in *A. thaliana* to distinguish the juvenile and adult rosette (Lawson and Poethig, 1995; Telfer et al., 1997). Leaves produced early in development have no trichomes on the abaxial (lower) surface and rosette leaves produced later have trichomes on both adaxial (upper) and abaxial surfaces. There are differences in the density of trichomes between juvenile and adult leaves in *A. thaliana*, although the change in trichome density between these vegetative phases occurs gradually through development (Telfer et al., 1997). In particular, total trichome number in *A. thaliana* has been reported to increase with rosette age (Martinez-Zapater et al., 1995; Payne et al., 2000).

Since the magnitude of selection on plants by herbivores may differ depending on the age of the leaves eaten and the density of trichomes on those leaves, the ability to predict the evolutionary response of the plants to that selection will depend on an understanding of the genetic architecture of the traits under selection. Our ability to predict the potential response to selection is directly predicated on knowledge of the number of genes and their effects on the expression of the phenotype (Lande, 1983; Lynch and Walsh, 1998; Barton and Keightley, 2002). Although much is known about the molecular genetics of trichome development in plants (Hülkamp and Schnittger, 1998; Hülkamp and Kirik, 2000; Szymanski et al., 2000; Walker and Marks, 2000), less is known about the genetic basis of trichome density (Larkin et al., 1996) and very little is known about whether the genetic architecture of trichome density changes with ontogeny.

There is a strong genotypic component to variation in trichome density in *A. thaliana*. Considerable among- and within-population variation for trichome density exists in natural populations of *A. thaliana* (Mauricio, 1998, 2001a). The segregation of trichome density in *A. thaliana* strongly suggests that multiple genetic factors and the environment affect the inheritance of this trait

(Larkin et al., 1996; Mauricio, 1998). Trichome density is, therefore, a quantitative trait and the appropriate tool for genetic analysis is QTL (quantitative trait loci) mapping (Mackay, 2001; Mauricio, 2001b).

A QTL mapping approach is likely to be a fruitful one in a completely sequenced model organism, such as *A. thaliana*. Many genetic markers are available, as are several sets of mapping populations. Genome scans for QTL have the potential to identify chromosomal segments containing genes that contribute to variation in a trait of interest (e.g., Doebley et al., 1997; Frary et al., 2000; Johanson et al., 2000).

Despite the fact that QTL mapping has been used extensively in the past decade, some caveats have been raised as to its use (Beavis, 1994, 1998; Mauricio, 2001b). In at least one study, replicate crosses were made from the same parents and QTL analyses were completed on each of the replicates – although the same QTL were detected across studies, some of the QTL detected were unique to each cross (Beavis, 1994, 1998). Environmental conditions have also been shown to play a significant role in the outcome of QTL mapping experiments (Paterson et al., 1991). Obviously, the ability to replicate QTL experiments is of paramount interest, but few studies have specifically addressed this question. In this study, we take advantage of replicate experiments to examine the repeatability of QTL studies.

In addition to providing information about the genetic basis of complex traits, genome scans for quantitative traits provide an empirical basis for testing one of the more enduring controversies in evolutionary biology: the genetic basis of adaptation. Fisher (1930) suggested that mutations of very small effect were responsible for adaptive evolution. Orr and Coyne (1992) reexamined the evidence for this Fisherian view and argued that both the theoretical and empirical basis for it were weak and that adaptive traits may well be controlled by genes of major effect. They encouraged evolutionary biologists to reexamine this research question by the genetic analysis of adaptive differences in natural populations.

In the present study, I investigate three questions addressing the genetic architecture of quantitative variation in trichome density in the plant, *A. thaliana*. First, using QTL analysis, what chromosomal segments in the *A. thaliana* genome