

ORIGINAL ARTICLE

Quantitative genetics of feeding behavior in two ecological races of the pea aphid, *Acyrtosiphon pisum*MC Caillaud¹ and S Via²

Much of the diversity of herbivorous insects stems from the adaptive divergence of populations onto different host plants. This often involves the evolution of specialized patterns of host acceptance that in turn lead to assortative mating for insects that mate exclusively on their hosts. Here, we explore the genetic architecture of feeding behavior in a herbivorous insect that has become a model for the study of incipient speciation, the pea aphid (*Acyrtosiphon pisum*). We use crosses between individuals specialized to either alfalfa or red clover in order to perform both a biometrical analysis and a quantitative trait locus (QTL) analysis of key feeding behaviors. For each character in each environment, Castle–Wright's estimator for the number of effective factors segregating ranged from 0.11 to 2.54. Similarly, between 0 and 3 QTLs were detected. In one case, a single QTL explained over 50% of the variance in the F₂, suggesting that at least one gene (or a complex of tightly linked genes) has a major effect on feeding behavior in the pea aphid. However, the identified QTL explain only 23–73% of the genetic variance for these characters thus additional genes of minor effect are also involved. We found a variety of modes of gene action, including several cases of non-additive gene action. Our results suggest that feeding behavior in pea aphids is neither simple nor highly polygenic. The oligogenetic basis of variation in feeding behavior may facilitate host shifts, providing one explanation for the frequent divergence and speciation of herbivorous insects.

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INTRODUCTION

Behaviors that affect mate choice have an important role in the process of speciation by determining the chances of meeting between potential sexual partners or the recognition of these partners (Slater and Halliday, 1994; Schluter, 1998). These behaviors have been shown to evolve at a relatively rapid rate, and to frequently be the first phenotypes to vary among recently diverged lineages (Foster and Endler, 1999). For organisms that mate within their resource environment, habitat choice behavior is a form of mate choice, because it leads to *de facto* assortative mating (Bush, 1994; Schluter, 1998). The genetic underpinnings of habitat choice behavior may crucially affect the likelihood of speciation driven by selection in different habitats (Gavrilets, 2004; Via, 2009). Thus, the genetic architecture of habitat choice within species is an important aspect of speciation research.

How adaptation to different ecological environments could reduce gene flow has been examined in great detail in host-plant races of phytophagous insects (Itami *et al.*, 1997; Feder, 1998; Funk, 1998; Via, 1999; Nylin *et al.*, 2004; reviewed in Matsubayashi *et al.*, 2010). Research on plant-feeding insects has actually contributed greatly to the development of a general framework for studying a type of speciation known as 'ecological speciation' (Schluter and Conte, 2009; Via, 2009). What do we know about the genetic architecture of habitat choice, or in this case host-plant preference, in host races of phytophagous insects? First, host preference is usually determined by a few (1–5) loci (reviewed in Matsubayashi *et al.*, 2010). Those loci were not characterized further, except for two genes coding for odorant binding proteins in *Drosophila melanogaster* (Matsuo *et al.*, 2007).

Second, preference genes are often located on autosomes, except in two butterfly systems where Z-linked inheritance was reported. Third, dominance of preference for one host over another was found in about half the reviewed studies. Here, we report on the genetic architecture of a suite of behavioral characters that determine host-plant preference in the pea aphid (*Acyrtosiphon pisum* Harris), a phytophagous insect that has become a model system for the study of ecological speciation (Via, 2009; Peccoud and Simon, 2010). Unlike previous studies, we combine biometrical analyses and quantitative trait locus (QTL) mapping analyses. Also unique to this study is the analysis of different steps of the aphid behavior that eventually lead to the acceptance or rejection of the plant as host.

Pea aphids can be found on numerous legume species. However, this broad host range at the species level does not reflect generalized host use at the individual level—instead, reciprocal transplant experiments have revealed genetically differentiated host races in nearly all cases in which individuals collected from different hosts have been tested on alternative plants (Via, 1991; Simon *et al.*, 2003; Ferrari *et al.*, 2008), and these divergent populations span the continuum between populations and species (Peccoud *et al.*, 2009). A large part of this genetic divergence in host use by pea aphids appears to be caused by variation in habitat choice (Via, 1999; Via *et al.*, 2000). Habitat choice is a complex trait as it involves several sequential steps and multiple behavioral components. This trait was dissected by Caillaud and Via (2000). Winged pea aphids from alfalfa and red clover in New York State (USA) land without discrimination on alfalfa and clover. But if a specialist lands on the alternative host, the aphid rapidly abandons the

¹Department of Biology, Ithaca College, Ithaca, NY, USA and ²Department of Entomology, University of Maryland, College Park, MD, USA
Correspondence: Dr MC Caillaud, Department of Biology, Ithaca College, 165 CNS, Ithaca, NY 14850, USA.
E-mail: mcaillaud@ithaca.edu

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