

Feeding site location in birch aphids (Sternorrhyncha: Aphididae): The simplicity and reliability of cues

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Abstract. To establish the importance of different cues for feeding site location in aphids, two birch-feeding species were given access to leaves that were either orientated normally or inverted. *Euceraphis betulae* used gravity and/or light as the main cue, and settled on the surface that was orientated down. *Monaphis antennata* additionally used leaf surface features to locate its feeding site, and approximately half of the individuals settled on the correct feeding surface whatever its orientation. This is one of the few examples of positive stimuli being used by aphids during feeding site location.

INTRODUCTION

Aphid species have characteristic feeding sites on their host plants, which they can locate by responding to gravity, light or features of the plant itself (Klingauf, 1970). Some aphids use gravity and/or light as the dominant cues (Dixon, 1976) but other aphids may initially respond to gravity, to move upwards towards the growing shoots, only to be repulsed by plant surface features, such that they ultimately settle elsewhere (Holtfreter, 1977). On many hosts, however, clones (Müller et al., 1974) and species (Jackson & Dixon, 1996) utilise different feeding sites. In such instances different aphids must either differ in the cues that they utilise or they must respond differently to the same cues. This study examines this hypothesis, to identify the factors that aphids use to select their feeding sites.

MATERIALS AND METHODS

Natural history

Two species of birch-feeding aphids were used. *Euceraphis betulae* (Koch) is specific to *Betula pendula* Roth and feeds on the growing shoots and the undersides of leaves, presumably in response to their proximate quality (Hopkins, 1996). *Monaphis antennata* (Kaltenbach) utilises a number of birch species and the nymphs have very specific feeding sites, on the adaxial (upper) surfaces of leaves and petioles. It is thought that these feeding sites are enemy-free space (Hopkins & Dixon, 1997). The nymphs of both species often disperse over a plant, and since they have long mouthparts they are thought to be physically capable of feeding from all parts of a leaf (Hopkins, 1996).

Feeding-site location

Nymphs of each species were introduced to cut-stems of *B. pendula*, with the leaves either orientated normally or inverted. To invert the leaves, the stems were held at an angle of 45° with the shoot tip pointing up and rotated, such that the leaves were then inverted with the abaxial (lower-) surface uppermost. All but four leaves were removed, as were the growing tips, and the stems were 20 cm long. The leaves that remained on the stems were not a random selection of those originally present, but, apart from orientation, they appeared superficially similar to those removed.

A single fourth instar nymph was introduced to each stem, below the leaves, with twenty replicates of each species. The experiment was performed in a constant temperature room with

long-day conditions ($20 \pm 1^\circ\text{C}$, 16L : 8D), illuminated from above. In the original stock cultures, which were on *B. pendula* in an unheated outdoor insectary, the *E. betulae* nymphs were feeding on the lower surfaces of leaves and the *M. antennata* were on the adaxial surfaces of petioles.

RESULTS

On the leaves that were orientated normally all of the *E. betulae* settled on the down-facing abaxial surface of a leaf, and all the *M. antennata* settled on the upwards-facing, or adaxial surface of a petiole (Fig. 1). On inverted leaves the majority of

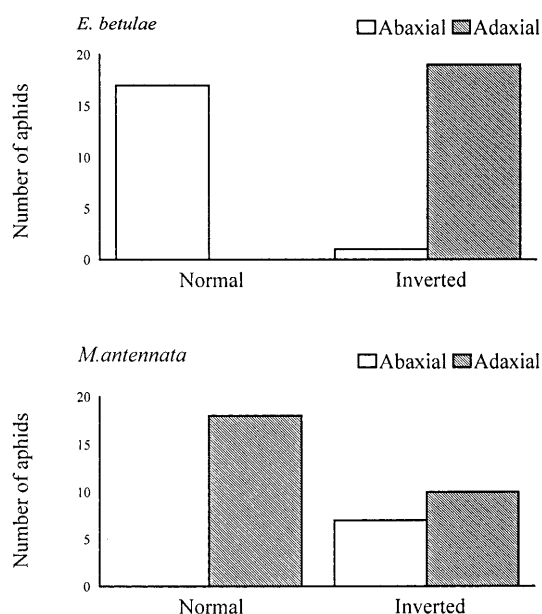


Fig. 1. The feeding positions of aphids after 14 h on normal and inverted leaves.

E. betulae settled on the surface which was then facing down, the adaxial surface. In contrast, approximately half of the *M. antennata* settled on the adaxial surface, which was now facing down, and half on the upwards-facing abaxial surface of the petioles of the inverted leaves.

The behavioural response of the two species to leaf inversion differed (Fisher's exact test: $P < 0.001$). *E. betulae* maintained its feeding orientation rather than re-locate its normal feeding surface (1 re-located the abaxial surface and 19 did not), but *M. antennata* showed a mixture of the two responses (10 re-located the adaxial surface and 7 did not).

DISCUSSION

The problem that aphids must overcome is how to utilise the available cues to identify reliably the feeding sites that maximise their fitness. The two species differ in the cues they predominantly respond to. *E. betulae* responds mainly to gravity and/or light, but *M. antennata* uses features of the plant itself, in addition to gravity and/or light.

The behaviour of *M. antennata* is notable because there are few examples of aphids responding positively to plant features during feeding site location (Müller et al., 1974), although positive stimuli are known to be important during the process of host plant selection (Dixon, 1997). In contrast, there are numerous examples of plant features having a negative impact on feeding site selection (e.g. Holtfreter, 1977; Bergman et al., 1991; Jackson & Dixon, 1996). It is not known what features of the petiole that *M. antennata* is responding to, although it occupies the same feeding site on at least eight species of *Betula* (Blackman & Eastop, 1994) and therefore the character is probably widespread within this plant genus.

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