

# Life-history strategies affect aphid preference for yellowing leaves

Jarmo K. Holopainen<sup>1,\*</sup>, Gürkan Semiz<sup>2</sup> and James D. Blande<sup>1</sup>

<sup>1</sup>Department of Environmental Science, University of Kuopio, PO Box 1627, 70211 Kuopio, Finland

<sup>2</sup>Department of Biology, Faculty of Arts and Sciences, Akdeniz University, 07058 Antalya, Turkey

\*Author for correspondence (jarmo.holopainen@uku.fi).

**According to the nutrient-translocation hypothesis, yellowing tree leaves are colonized by aphids at the end of the growing season owing to improved availability of nutrients in the phloem sap after chlorophyll degradation. We measured aphid densities on potted *Betula pendula* seedlings in a field site where a small proportion of foliage rapidly turned yellow before normal autumn coloration as a consequence of root anoxia. The number of adults and nymphs of the birch-feeding specialist aphids *Euceraphis betulae*, *Betulaphis brevipilosa* and *Callipterinella tuberculata* were counted from leaves on each of the 222 plants. Aphids were detected on 19 per cent of green leaves and on 41 per cent of yellow leaves. There was no indication of aphid avoidance of yellow leaves, and the number of winged (alate) viviparous *E. betulae* adults and their nymphs were significantly higher on yellow leaves than on green leaves, while the numbers of apterous *B. brevipilosa* and *C. tuberculata* did not differ between the leaf colour types. Our result suggests that only aphid species with alate generation during colour change can take advantage of yellowing leaves. This may explain the exceptional abundance of *E. betulae* compared with other aphid species on birches.**

**Keywords:** *Betula pendula*; leaf colour; visual signals; food selection; insect behaviour

## 1. INTRODUCTION

Why do trees displaying brighter yellow and red colours in autumn host an increased diversity of host-alternating aphids? Hamilton & Brown (2001) analysed the diversity of aphid species on trees with green, yellow or red autumn coloration. Their analysis revealed significant correlation between the intensity of yellow coloration in autumn leaves and the number of aphid species, and the correlation was strengthened when focused on specialist aphids. The correlation between intensity of red leaf coloration and aphid diversity was less significant. This dataset was used to formulate the coevolution hypothesis (Archetti 2000; Hamilton & Brown 2001; Archetti & Brown 2004); that trees with bright yellow and red autumn leaves will advertize that they are better defended against herbivores. Archetti (2009a,b) and Archetti *et al.* (2009) have

indicated that only red autumn colour is repellent for aphids.

The original coevolution hypothesis has been criticized primarily because there was earlier evidence that yellow leaves could attract aphids (Holopainen & Peltonen 2002; Wilkinson *et al.* 2002). Yellow foliage could be an indicator of poorer food quality for chewing insects (Hagen *et al.* 2003) when nitrogen bound in chloroplasts is degraded and mobilized, but aphids can take advantage of this increase of soluble nitrogen (amino acids) in phloem during leaf senescence, when the concentration can be at the same level as during leaf flush (Sandström 2000). There is ample evidence that aphids prefer yellow foliage (Wratten 1974; Holopainen & Peltonen 2002; Johnson *et al.* 2003). Recent observations from a catch experiment with artificial traps (Döring *et al.* 2009) combined with evidence from the first experiment measuring carry-over effects of green, yellow and red autumn leaf colour on aphid fitness in spring (Archetti 2009b), have given evidence that only red autumn leaf colour signals in accordance with the original coevolution hypothesis.

There is still need for an adaptive explanation for the high aphid diversity on tree species with yellow autumn leaf coloration. The nitrogen translocation hypothesis (Holopainen & Peltonen 2002), a refinement of the earlier senescence-feeding hypothesis (White 1993, 2003), states that senescing yellow leaves are good sources of nitrogen in the form of amino acids for phloem-feeding aphids. *Betula pendula* Roth has yellow coloration in autumn and is known to host 13 specialist aphid species, none of which host-alternate (Holopainen & Peltonen 2002). The current study was aimed at evaluating whether aphids with different life-history strategies show different rates of preference for yellow leaves in late summer. We did this by evaluating aphid densities on *B. pendula* saplings, which had flood-induced acceleration of leaf yellowing in certain parts of the foliage.

## 2. MATERIAL AND METHODS

Two-year-old micro-propagated silver birch (*B. pendula*) saplings were grown in pots at the Ruohoniemi Free Air Concentration Enrichment (FACE) facility used for elevated ozone and temperature exposure in the field at the University of Kuopio (62°53' N, 27°37' E, 80 m above sea level) in central Finland. Saplings were grown in four plots with ambient ozone and four with enhanced ozone (1.3–1.4 times ambient, e.g. Blande *et al.* 2007). The saplings selected for monitoring were protective boundary plants from various genotypes grown at the edges of experimental subplots, half of which had infrared heaters to enhance the temperature of foliage. After heavy rain in late July, part of the foliage of the selected 222 birch saplings had premature senescence as a result of anoxia. This was caused by rain water flooding the depression where the pots were located.

To analyse aphid densities on the seedlings, we used random numbers to choose one branch per tree for aphid counting. On selected branches, we counted aphids on two yellow leaves (at least 50% of leaf area affected) and two green leaves. The yellow leaves were normally older and closer to the base of the branch. Therefore, we selected the two yellow leaves closest to the middle of the branch, and the two closest fully green leaves. Often there were few or no yellow leaves, mostly because of leaf fall.

The three aphid species recorded differ in life-history strategy, with apterous (wingless) or alate (winged) viviparae. *Euceraphis betulae* Koch is a relatively large aphid species (body length 3.0–4.2 mm), it walks actively, and all viviparae in summer are alate and able to fly. *Betulaphis brevipilosa* Börner has smaller (1.5–2.0 mm) apterous viviparae until autumn while *Callipterinella tuberculata* von Heyden (1.7–2.2 mm) has both apterous and alate viviparae during the whole summer (Heie 1982). We assessed density and

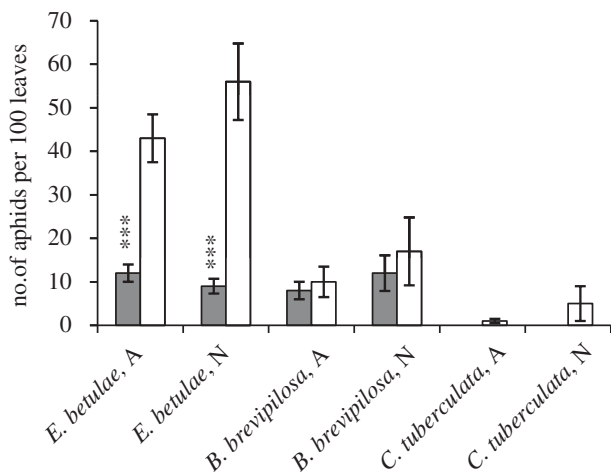


Figure 1. Density of adults (A) and nymphs (N) of *Euceraphis betulae*, *Betulaphis brevipedilosa* and *Callipterinella tuberculata* aphids on green and yellowing silver birch leaves on 31 July 2008. Only trees with yellow leaves were analysed. Filled bars represent green leaves and open bars represent yellow leaves. \*\*\*indicates statistical significance at  $p < 0.001$  level.

distribution of adult and nymphal aphids of each species on green and yellowing leaves. The aphid numbers in both categories were compared by a paired-sample  $t$ -test using  $\log(x+1)$  transformed data. The results are shown as number of aphids per 100 leaves.

### 3. RESULTS

Aphids did not avoid yellow leaves. The proportion of aphid-infested leaves was actually higher for yellow (172 out of 418; 41%) than green (85 out of 440; 19%) leaves ( $\chi^2 = 48.69$ ;  $p < 0.0001$ ). Of the evaluated saplings, 209 had yellowing leaves. Only these saplings were selected for further analyses of aphid densities. Total number of aphids per leaf was significantly ( $t_{417} = 7.721$ ,  $p < 0.001$ ) higher on yellow ( $1.31 \pm 0.16$ , s.e.) than green leaves ( $0.41 \pm 0.06$ ). Mean density of *E. betulae* adults ( $t_{417} = 6.079$ ,  $p < 0.001$ ) and nymphs ( $t_{417} = 6.756$ ,  $p < 0.001$ ) was significantly higher on yellow than green leaves, while densities of the other aphid species did not significantly differ (figure 1). Density of *B. brevipedilosa* was not affected by leaf colour and *C. tuberculata* density was too low for proper statistical analysis, although aphids were mostly found on yellow leaves.

### 4. DISCUSSION

Our observation of nearly fivefold greater *E. betulae* density on yellow leaves compared with green leaves gives numerical evidence of aphid preference for yellowing leaves. This confirms the earlier anecdotal evidence that aphids prefer yellow over green leaves in late-season birch (Wratten 1974; Holopainen & Peltonen 2002; Johnson *et al.* 2003) and apple trees (Archetti 2009b), strongly suggesting that yellow is not a warning signal for aphids. The results with *E. betulae* indicate that it is not only host-alternating aphid species that respond to yellow leaves as predicted by Archetti & Brown (2004). A specialist aphid species that is able to colonize leaves rapidly during the yellowing process, can take advantage of the improved amino-acid composition in leaf phloem sap (White

1993), leading to improved fitness. Manipulation of host plant quality with phytotoxic saliva to promote host plant senescence is typical to some aphid species (White 1993). Earlier observations (J. Holopainen 1995, field notes) during outbreak of *E. betulae* have indicated that more than 50 alate viviparae can colonize one birch leaf, but feeding by this species does not cause leaf yellowing.

*Euceraphis betulae* is known to undergo long-distance (more than 1000 km) mass migrations in densities detectable by radar (Nieminen *et al.* 2000). Mobile alate viviparae can easily change host plant individuals when a high-quality host is available in the neighbourhood. This life-history strategy will take advantage of rapidly mobilized nitrogen in yellowing leaves under stress conditions and this behavioural adaptation can probably explain the enormous success of *E. betulae* compared with less abundant species like *B. brevipedilosa* and *C. tuberculata*. Equal population density of apterous summer generations of *B. brevipedilosa* on yellowing and green leaves probably indicates that apterous females are not able to colonize yellowing leaves, but that the aphids were on the leaf before the colour changed.

It has been suggested that aphid preference for yellow is only a sensory bias, where yellow simply becomes a super-normal green (Chittka & Döring 2007). However, if we accept that yellow is an unavoidable signal of chlorophyll degradation in leaves (Keskitalo *et al.* 2005) and an indication of mobilized nitrogen as amino acids in phloem, then most sucking insects may be interested in yellow foliage (White 1993). Stronger shades of yellow may even increase the attraction, while red colour does not have this function, as the data by Hamilton & Brown (2001) suggested. The options for a deciduous tree to deal with the sucking herbivore load are to mask yellow pigment by staying green and lose nitrogen during leaf fall (Holopainen 2008), become yellow and be exposed to sucking herbivores (Archetti 2009b; Holopainen & Peltonen 2002), or mask yellow with red pigments (Archetti 2009b) to avoid aphid load.

Archetti (2009b) has shown with one woody species (*Malus pumila*), that being red in autumn really could signal greater commitment to defence in the host plant, which will lead to reduced aphid fitness the following year. Being yellow in autumn does not affect fitness of the second aphid generation on *M. pumila* (Archetti 2009b), but a higher density of aphids on yellow foliage in autumn could harm the overwintering physiology of the host plant. Therefore, developing red pigment in otherwise yellow leaves in autumn may mask the yellow, reduce the pressure of migrating aphids, and improve the fitness of the host plant. This conclusion is supported by the fact that *Betula nana*, the only *Betula* species in northern Europe that, like many other subarctic shrubs (Lev-Yadun & Holopainen in press), has distinctively red autumn coloration, has only two specialist aphid species (Heie 1995), while *B. pendula* has 13 and *B. pubescens* 10 specialist aphid species (Holopainen & Peltonen 2002).

To conclude, we observed that specialist aphid species with a life-history strategy of alate females

late in the season are more successful than solely apterous species at rapidly colonizing yellowing leaves. Our results also suggest that the large diversity of aphids at northern latitudes (Dixon *et al.* 1987; Hamilton & Brown 2001) can be partly explained by the high preference of certain aphid species to use the best-quality food using yellow leaf colour as an indicator. The ability of *E. betulae* to colonize yellowing leaves rapidly could be an explanation for the extreme abundance of this species on birches.

The work was supported by the Academy of Finland (decision no. 111543).

- Archetti, M. 2000 The origin of autumn colours by coevolution. *J. Theor. Biol.* **205**, 625–630. (doi:10.1006/jtbi.2000.2089)
- Archetti, M. 2009a Classification of hypotheses for the evolution of autumn colours. *Oikos* **118**, 328–333. (doi:10.1111/j.1600-0706.2008.17164.x)
- Archetti, M. 2009b Evidence from the domestication of apple for the maintenance of autumn colours by coevolution. *Proc. R. Soc. B.* (doi:10.1098/rspb.2009.0355)
- Archetti, M. & Brown, S. P. 2004 The coevolution theory of autumn colours. *Proc. R. Soc. Lond. B* **271**, 1219–1223. (doi:10.1098/rspb.2004.2728)
- Archetti, M. *et al.* 2009 Unravelling the evolution of autumn colours: an interdisciplinary approach. *Trends Ecol. Evol.* **24**, 166–173. (doi:10.1016/j.tree.2008.10.006)
- Blande, J. D., Tiiva, P., Oksanen, E. & Holopainen, J. K. 2007 The emission of herbivore induced volatile terpenoids from two hybrid aspen (*Populus tremula* × *tremuloides*) clones under ambient and elevated ozone concentrations in the field. *Glob. Change Biol.* **13**, 2538–2550. (doi:10.1111/j.1365-2486.2007.01453.x)
- Chittka, L. & Döring, T. F. 2007 Are autumn foliage colours red signals to aphids? *PLoS Biol.* **5**, 1640–1644. (doi:10.1371/journal.pbio.0050187)
- Dixon, A. F. G., Kindlmann, P., Leps, J. & Holman, J. 1987 Why there are so few species of aphids, especially in the tropics? *Am. Nat.* **129**, 580–592. (doi: 10.1086/284659)
- Döring, T. F., Archetti, M. & Hardie, J. 2009 Autumn leaves seen through herbivore eyes. *Proc. R. Soc. B* **276**, 121–127. (doi:10.1098/rspb.2008.0858)
- Hagen, S. B., Folstad, I. & Jakobsen, S. W. 2003 Autumn coloration and herbivore resistance in mountain birch (*Betula pubescens*). *Ecol. Lett.* **6**, 807–811. (doi:10.1046/j.1461-0248.2003.00496.x)
- Hamilton, W. D. & Brown, S. P. 2001 Autumn tree colours as a handicap signal. *Proc. R. Soc. Lond. B* **268**, 1489–1493. (doi:10.1098/rspb.2001.1672)
- Heie, O. E. 1982 The aphidoidea (Hemiptera) of Fennoscandia and Denmark. II. *Fauna Ent. Scand.* **11**, 1–176.
- Heie, O. E. 1995 The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. VI. *Fauna Ent. Scand.* **31**, 1–222.
- Holopainen, J. K. 2008 Importance of olfactory and visual signals of autumn leaves in the coevolution of aphids and trees. *BioEssays* **30**, 889–896. (doi:10.1002/bies.20796)
- Holopainen, J. K. & Peltonen, P. 2002 Bright autumn colours of deciduous trees attract aphids: nutrient retranslocation hypothesis. *Oikos* **99**, 184–188. (doi:10.1034/j.1600-0706.2002.990119.x)
- Johnson, S. N., Elston, D. A. & Hartley, S. E. 2003 Influence of host plant heterogeneity on the distribution of a birch aphid. *Ecol. Ent.* **28**, 533–541. (doi:10.1046/j.1365-2311.2003.00547.x)
- Keskitalo, J., Bergquist, G., Gardeström, P. & Jansson, S. 2005 A cellular timetable of autumn senescence. *Plant Physiol.* **139**, 1635–1648. (doi:10.1104/pp.105.066845)
- Lev-Yadun, S. & Holopainen, J. K. In press. Why red-dominated autumn leaves in America and yellow-dominated autumn leaves in Northern Europe? *New Phytol.* (doi:10.1111/j.1469-8137.2009.02904.x)
- Nieminen, M., Leskinen, M. & Helenius, J. 2000 Doppler radar detection of exceptional mass-migration of aphids into Finland. *Int. J. Biometeorol.* **44**, 172–181. (doi:10.1007/s004840000064)
- Sandström, J. 2000 Nutritional quality of phloem sap in relation to host plant-alternation in the bird cherry-oat aphid. *Chemoeology* **10**, 17–24. (doi: 10.1007/s000490050003)
- White, T. C. R. 1993 *The inadequate environment. Nitrogen and the abundance of animals*. Berlin, Germany: Springer-Verlag.
- White, T. C. R. 2003 Nutrient retranslocation hypothesis, a subset of the flush feeding/senescence feeding hypothesis. *Oikos* **103**, 217. (doi:10.1034/j.1600-0706.2003.12674.x)
- Wilkinson, D. M., Sherratt, T. N., Phillip, D. M., Wratten, S. D., Dixon, A. F. G. & Young, A. J. 2002 The adaptive significance of autumn leaf colours. *Oikos* **99**, 402–407. (doi:10.1034/j.1600-0706.2002.990223.x)
- Wratten, S. D. 1974 Aggregation in the birch aphid *Eucera-phus punctipennis* (Zett.) in relation to food quality. *J. Anim. Ecol.* **43**, 191–198. (doi:10.2307/3166)