

Bright autumn colours of deciduous trees attract aphids: nutrient retranslocation hypothesis

Jarmo K. Holopainen and Petri Peltonen, Dept of Ecology and Environmental Science, Univ. of Kuopio, P.O. Box 1627, FIN-70211 Kuopio, Finland (jarmo.holopainen@uku.fi), (J. K. H, Agrifood Research Finland, Plant protection, FIN-31600 Jokioinen, Finland) (P. P., Finnish Forest Research Institute, Suonenjoki Research Station, Juntantie 40, FIN-77600 Suonenjoki, Finland).

We propose an alternative hypothesis to the handicap-signalling hypothesis, to explain the high number of specialist aphids on tree species having bright autumn colour. Since birch aphids actively seek the first yellowing leaves for breeding in autumn, it is obvious that autumn colour of foliage does not repel migrating aphids. We suggest that aphids use bright colours as a cue to detect individual trees and leaves that are good sources of nitrogen in the form of amino acids in autumn. The active formation of bright-coloured pigments in leaves is needed to protect them from photo inhibition during energy consuming nutrient retranslocation under cold autumn conditions. During nutrient export from leaves, nitrogen is in the form of amino acids in the sieve elements and easily available for aphids. Therefore, bright colours may act as a signal of easily available high-quality food for viviparous aphid migrants that are selecting suitable trees for their sexual offspring reproduction. The females of sexual generation grown on the better quality food probably can oviposit the over-wintering eggs to the twigs in higher numbers, which may have an adaptive advantage in competition with conspecific females.

Several hypotheses concerning the evolutionary significance of autumn colours of trees have been presented (Hoch et al. 2001). These include e.g. attraction of fruit dispersing birds, antiherbivory, antimicrobial effects and drought and freezing tolerance. One of the latest hypotheses (Hamilton and Brown 2001) explains that bright colour of autumn foliage acts as a signal for aphids to indicate that the tree species or individuals have invested heavily in chemical defence, and consequently not suitable for aphids. According to this handicap-signalling hypothesis, individuals within a signalling species show the variation in the expression of autumn coloration. Individuals committed to high defence can produce a more intense display of colours. Hamilton and Brown (2001) predicted that tree species which suffer greater insect damage could invest more in autumn-colour signalling than less troubled species.

The hypothesis is based on the analysis of the literature indicating that there is a higher number of specialist aphids on tree species which show stronger hues of yellow and red autumn colours. Therefore, Hamilton and Brown (2001) suggested that these species could invest more in autumn-colour signalling than less troubled species. This coevolution hypothesis of autumn colours of trees is largely based on the assumption that synthesis of new pigments in the leaves, just before abscission, is considered to be unnecessary for the physiology of trees and needs an adaptive explanation (Archetti 2000). However, if we assume that investment in the production of leaf pigments in the autumn is important for the sake of tree physiology, handicap-signalling theory of Hamilton and Brown (2001) might not be the only explanation for the higher numbers of specialist aphid species on trees that have bright-coloured leaves in the autumn.

What happens during autumnal colour change in senescing leaves?

Hoch et al. (2001) suggested that apparently worthless production of antocyanins and other flavonoid pigments in senescing leaves provides an effective photoprotection for photosynthetic machinery during the critical period of foliar nutrient resorption. Thus, the stunning autumn colours of leaves are a crucial part of investment to shield against photoinhibition during the leaf senescence process, which takes place at relatively low temperatures in the autumn. Accumulation of anthocyanins begins shortly after the onset of chlorophyll decline, usually before any visible change in leaf colour (Collier and Thibodeau 1995). On the other hand,

nitrogen export from the leaves takes place after chlorophyll content has been reduced by 70% (Proietti 1998), which means that leaves have already lost most of the green colour when nutrient transportation from the leaves is most active.

The accumulation of antocyanins and other flavonoids is maximum in the leaves exposed to direct sunlight (Tattini et al. 2000), whereas shaded leaves or cloudy autumn weather produce less pigments. Higher investment for shield against photoinhibition in sunny leaves explain this variation. Nutrient resorption from senescing leaves requires an investment in resources to synthesise the numerous enzymes and regulatory elements involved in the degradation and remobilisation of leaf nutrients. These investments should be non-costly for the trees and energy for that should be produced in senescing leaves. Besides the need for energy to support the metabolic processes, resorption probably requires a constant supply of photosynthate to drive the translocation stream in which the nutrients are suspended (Feild et al. 2001, Hoch et al. 2001).

The turnover of nutrients in senescing leaves is considerable in the autumn and it is indicated by elevated concentrations of free amino acids in the phloem sap compared to the concentrations in summer (Sandström 2000). The needles of evergreen conifers lose 60% of their total nitrogen content during senescence (Kainulainen and Holopainen 2002), while in the leaves of deciduous trees the reduction of nitrogen content can be even 75% during senescing process (Scherzer et al. 1998.). It appears that alders, *Alnus* spp., which usually do not have change in the colour of leaves in autumn, do not strongly translocate the nitrogen in the autumn, and the shed leaves have higher nitrogen concentrations than other deciduous trees in the northern forests (Taylor 1998).

If the production of anthocyanins and other flavonoid pigments in senescing leaves in the autumn has a plant physiological explanation, should we reject the handicap-signalling hypothesis? Possibly not, but the empirical testing to reveal the truth of this hypothesis will be a hard work (Atkinson 2001).

How autumn colours of trees affect the behaviour of aphids?

The data of Hamilton and Brown (2001) indicate that the numbers of aphid species are higher in tree species with higher autumn coloration index, and the correlation is stronger with yellow-leaved trees than with red-leaved species. Unfortunately, there are no data to support the prediction of handicap-signalling hypothesis that aphids in autumn avoid colonisation of trees with most intense colour. The results of Wratten (1974) and Moran and Whitham (1990) suggested even the

opposite. The authors found higher densities of migrant aphids when the leaf senescence had proceeded further. This might indicate the higher migration rate to leaves with higher flavonoid concentrations and more intense coloration. Furthermore, our observations on densities of deposited birch aphid (*Euceraaphis betulae*) eggs in autumn and phenolic defence compound concentrations in the leaves of the same trees in the following spring, indicated that aphids can lay more eggs on the trees that have a noticeably higher level of defence compounds (Peltonen et al., unpubl.).

Nitrogen concentrations, or levels of free amino acids, (Holopainen et al. 1997) in tree foliage typically explains better aphid performance than concentration of total phenolics including anthocyanins (Kainulainen et al. 2000). The fact is that the flavonoid pigments in senescing leaves accumulate only in the upper palisade of leaves (Hoch et al. 2001) suggests that pigments cannot be directly feeding deterrents for phloem feeders. Possibly aphids can even detoxify phenolics in their host plants (Urbanska et al. 1998). However, the effects of antocyanins and other flavonoids in autumn leaves on the aphid performance and behaviour should be investigated.

Against the predictions of handicapped-signalling hypothesis, our observations on the behaviour of the birch aphid on cloned *Betula pendula* trees, described earlier by Mutikainen et al. (2000), suggest that trees with bright colour may even attract aphids in the autumn. In September, when we were collecting aphid nymphs for feeding trials in ozone and CO₂ experiments (Holopainen 2002), we observed that alate viviparous females of *E. betulae* had selected the first senescing yellow leaves for the production of nymphs of sexual morphs. Newly-born nymphs with migrant viviparous females were visible on the same leaves indicating that nymphs were deposited already on yellow leaves (Fig. 1). The frequent occurrence of migrant viviparous aphids with nymphs on yellow leaves, and lower number of aphids on green leaves at the same time, suggest that migrating aphids prefer the branches of trees that have the first yellowing leaves. This might be an indication that bright yellow colour of the leaves act as a signal for the last winged aphid generation indicating high-quality food value for its oviparous offspring.

Are autumn colours of tree leaves affecting number of aphid species in boreal forests?

Aphids differ from most other groups of herbivorous insects by being in inverse relationship to the number of plant species in different parts of the world resulting in a higher density in the temperate regions than in the tropics (Dixon et al. 1987). High diversity in the tem-

perate and boreal areas is also considered to indicate the adaptation of aphids to climates with cold winter. The best evidence of this adaptation is over-wintering diapause eggs which aphid usually lay on tree branches (Heie 1994). Minimum winter temperatures are critical for survival of over-wintering insect eggs (Virtanen and Neuvonen 1999), and therefore maximising the number of eggs produced will increase the offspring survival.

To evaluate if the trend observed by Hamilton and Brown (2001) is apparent in the boreal environments, we analysed the data of the number of specialist aphids on the nine tree species having natural distribution up to the Polar Circle (66.6°N) in Finland (Alanko 2001). Two of these trees (*Alnus incana* and *A. glutinosa*) do not have yellow or red autumn colour, and the leaves are shed green (Table 1). The data on the number of specialist aphid species in Finland on these tree species are from Heie (1995). There appeared to be less specialist aphid species on *Alnus* species (3.5 ± 0.7 , SD) than on other deciduous trees (8.9 ± 3.7), but the difference

was not significant (Mann-Whitney $U = 0.50$, $p > 0.05$). Since there was only one species having frequently reddish autumn colour, *Sorbus aucuparia*, we omitted aphid data from this species. *S. aucuparia* also has exceptionally few specialist aphid species (six) among the woody plants within the family Rosacea in the whole northern Europe (Heie 1995). After omission there was a significant difference in the number of aphid species (3.5 in *Alnus* vs 9.7 ± 3.3 on other species, $p = 0.046$). Aphid species feeding on trees of the family Betulaceae are not host alternating. The number of specialist aphid species within this family on *Alnus* (five) differed significantly ($\chi^2 = 4.26$, $p = 0.039$) from the number of aphid species on *Betula* (14). Although these results are only indicative from one geographical area, there was support for the observations of Hamilton and Brown (2001) that the tree species with yellow and red autumn colours have higher number of the specialist aphid species than tree species with green autumn colour.



Fig. 1. A group of young nymphs and a migrant viviparous female of *Euceraphis betulae* on a yellow birch leaf in early September.

Table 1. The number of specialist aphid species reported from Finland (Heie 1995) on green and autumn-coloured indigenous tree species able to grow to the height of 15 m, and which have distribution in Finland up to Polar Circle in the north (Alanko 2001).

Tree species	Total number of aphid species	Number of host alternating aphid species
Trees with green autumn colour		
<i>Alnus glutinosa</i>	4	0
<i>Alnus incana</i>	3	0
Trees with typical red or yellow autumn colours		
<i>Betula pubescens</i> , yellow	10	0
<i>Betula pendula</i> , yellow	13	0
<i>Populus tremula</i> , yellow	6	4
<i>Prunus padus</i> , yellow	7	7
<i>Salix caprea</i> , yellow	14	4
<i>Salix pentandra</i> , yellow	8	4
<i>Sorbus aucuparia</i> , red, yellow	4	2

Why aphids prefer trees with bright autumn colours?

The analyses of aphid numbers and diversity on tree species with bright autumn colours (Hamilton and Brown 2001) and our circumstantial evidence of aphid migration on yellow leaves suggest that aphids might have adapted to use colour signals of tree leaves for host selection in the autumn. Comparison of migratory aphid densities on tree clones and provenances with different leaf yellowing time, and grown alongside might offer the best experimental set up to test in intraspecies level; how attractive trees with different leaf colours are to aphids?

Moran and Whitham (1990) showed that migrants of *Pemphigus betae* deposited all progeny within 48 h after arriving at their primary host plant *Populus* sp. *P. betae* migrants do not feed when leaving their secondary host and therefore rapid detection of a suitable host plant is crucial. More migratory aphids went on trees that had a higher retention score which indicated partial abscission of leaves, and thus higher senescence rate in tree foliage. This observation obviously gives a support for the idea that migratory aphids use the rate of senescence and higher rate of autumn coloration, for orientation to the host plant, although Moran and Whitham (1990) did not report the coloration of the leaves. However, pemphigid aphids do not follow the other premise of our nutrient translocation hypothesis. Better food quality for the sexual offspring of migrants in autumn is not needed, since oviparous females do not feed and the female lays only one egg (Heie 1980).

According to our observations the aphids in the family Drepanosiphidae continue to oviposit on twigs few weeks after the abscission of the leaves until frost kills the aphids. Development of females on high-quality food may increase their capacity to lay eggs and thus increase their reproductive potential. It is possible that for some migratory aphid species the coloured leaves only have flag-like value to locate suitable host plant species. For other species, senescing leaves may serve food for egg-laying females for several weeks, since leaf abscission

does not take place in the whole tree at the same time. This source of energy and food for oviparous aphids in late autumn could be one of the key factors explaining the success of aphids in the temperate region, and their high diversity in northern latitudes (Dixon et al. 1987, Heie 1994). Especially host-alternating aphid species exploit complementary growth patterns of woody and herbaceous plants and migrate from herbaceous plants back to woody plants when nutrient translocation in senescent of tree leaves takes place. However, factors that trigger the attraction to certain tree individual are poorly known (Dixon 1971, Moran 1992).

Direct experimental investigations are required to test the idea that aphids have 'learnt' to select tree species and tree individuals that have bright autumn colours to indicate easily available nutrient. So far, our observations on the behavioural response of non-host-altering drepanosid *E. betulae* in the autumn as well as observation by Wratten (1974) of similar behaviour of *E. punctipennis* on *B. pubescens*, supports this hypothesis. To validate this hypothesis as an indicator of coevolutionary adaptation of aphids to bright coloured tree species for better autumn survival might be difficult to demonstrate as handicap signalling of autumn colours for aphids (Atkinson 2001). Experimental work with oviparous sexual forms of the aphids may confirm the basic assumptions of the suitability of coloured autumn leaves as food source for sexual generation of aphids. If early leaf coloration is a major factor increasing migration pressure of aphids in early autumn, premature senescence of the leaves in ozone sensitive trees (Saleem et al. 2001) may as a consequence increase aphid damage on these trees. These interactions should be considered when the effects of global climate change on herbivore and tree interactions are estimated.

Conclusions

There seems to be evidence that higher numbers of aphids are related to the trees with bright autumn leaf

colours. The autumn colour of tree foliage both at the intraspecific and interspecific level may affect aphid behaviour. We suggest that mostly this is a result of adaptation of migrant aphids to detect the start of nutrient retranslocation process in the tree leaves in autumn. During nutrient retranslocation nitrogen is in the form of amino acids in the sieve elements and easily available for aphids. For migratory aphids early detection of nutrient export from the leaves means higher reproduction rate and more oviparous sexual offspring. For the oviparous aphids high nutritive quality of food may offer higher potential to produce eggs and thus have an adaptive advantage in competition with conspecific females. Direct experimental investigations are needed to test these hypotheses.

Acknowledgements – We thank Dr. Elina Oksanen and for stimulating discussions and comments on the manuscript. Comments by Dr. G. V. P. Reddy improved the manuscript. The work was funded by the Research Council for Biosciences and Environment, the Academy of Finland (project no. 48605).

References

- Alanko, P. 2001. Finnish indigenous trees. – *Sorbifolia* 32: 125–133.
- Archetti, M. 2000. The origin of autumn colours by coevolution. – *J. Theor. Biol.* 205: 625–630.
- Atkinson, N. 2001. Out on a limb, or a new branch of signalling theory? – *Trends Ecol. Evol.* 16: 603.
- Collier, D. E. and Thibodeau, B. A. 1995. Changes in respiration and chemical content during autumnal senescence of *Populus tremuloides* and *Quercus rubra* leaves. – *Tree Physiol.* 15: 759–764.
- Dixon, A. F. G. 1971. The life-cycle and host preferences of the bird cherry-oat aphid, *Rhopalosiphum padi* L., and their bearing on the theories of host alternation in aphids. – *Ann. Appl. Biol.* 68: 135–147.
- Dixon, A. F. G., Kindlmann, P., Leps, J. and Holman, J. 1987. Why there are so few species of aphids, especially in the tropics. – *Am. Nat.* 129: 580–592.
- Feild, T. S., Lee, D. W. and Holbrook, N. M. 2001. Why leaves turn red in autumn. The role of anthocyanins in senescing leaves of red-osier dogwood. – *Plant Physiol.* 127: 566–574.
- Hamilton, W. D. and Brown, S. P. 2001. Autumns tree colours as a handicap signal. – *Proc. R. Soc. Lond. B Biol. Sci.* 268: 1489–1493.
- Heie, O. 1980. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. I. – *Fauna Ent. Scand.* 9: 1–236.
- Heie, O. E. 1994. Why are there so few aphid species in the temperate areas of the southern hemisphere? – *Eur. J. Entomol.* 9: 127–133.
- Heie, O. 1995. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. VI. – *Fauna Ent. Scand.* 31: 1–222.
- Hoch, W. A., Zeldin, E. L. and McCown, B. H. 2001. Physiological significance of anthocyanins during autumnal leaf senescence. – *Tree Physiol.* 21: 1–8.
- Holopainen, J. K. 2002. Aphid response to elevated ozone and CO₂. – *Ent. Exp. Appl.* (in press).
- Holopainen, J. K., Kainulainen, P. and Oksanen, J. 1997. Growth and reproduction of aphids and levels of free amino acids in Scots pine and Norway spruce in an open-air fumigation with ozone. – *Global Change-Biol.* 3: 139–147.
- Kainulainen, P. and Holopainen, J. K. 2002. Concentrations of secondary compounds on Scots pine needles at different stages of decomposition. – *Soil Biol. Biochem.* 34: 37–42.
- Kainulainen, P., Holopainen, J. K. and Holopainen, T. 2000. Combined effects of ozone and nitrogen on secondary compounds, amino acids and aphid performance in Scots pine seedlings. – *J. Environ. Qual.* 29: 334–342.
- Moran, N. A. 1992. The evolution of aphid life cycles. – *Annu. Rev. Entomol.* 37: 321–348.
- Moran, N. A. and Whitham, T. G. 1990. Different colonisation of resistant and susceptible host plants *Pemphigus* and *Populus*. – *Ecology* 71: 1059–1067.
- Mutikainen, P., Walls, M., Ovaska, J. et al. 2000. Herbivore resistance in *Betula pendula*: effect of fertilisation, defoliation and plant genotype. – *Ecology* 81: 49–65.
- Proietti, P. 1998. Gas exchange in senescing leaves of *Olea europaea* L. – *Photosynthetica* 35: 579–587.
- Saleem, A., Loponen, J., Pihlaja, K. and Oksanen, E. 2001. Effects of long-term open-field ozone exposure on leaf phenolics of European silver birch (*Betula pendula* Roth). – *J. Chem. Ecol.* 27: 1049–1062.
- Sandström, J. 2000. Nutritional quality of phloem sap in relation to host plant-alternation in the bird cherry-oat aphid. – *Chemoecology* 10: 17–24.
- Scherzer, A. J., Rebbeck, J. and Boerner, R. E. J. 1998. Foliar nitrogen dynamics and decomposition of yellow-poplar and eastern white pine during four seasons of exposure to elevated ozone and carbon dioxide. – *For. Ecol. Manag.* 109: 355–366.
- Tattini, M., Gravano, E., Pinelli, P. et al. 2000. Flavonoids accumulate in leaves and glandular trichomes of *Phillyrea latifolia* exposed to excess solar radiation. – *New Phytol.* 148: 69–77.
- Taylor, B. R. 1998. Air-drying depresses rates of leaf litter decomposition. – *Soil Biol. Biochem.* 30: 403–412.
- Urbanska, A., Tjallingii, W. F., Dixon, A. F. G. and Leszczynski, B. 1998. Phenol oxidising enzymes in the grain aphid's saliva. – *Ent. Exp. Appl.* 1998: 197–203.
- Virtanen, T. and Neuvonen, S. 1999. Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. – *Oecologia* 120: 92–101.
- Wratten, S. D. 1974. Aggregation in the birch aphid *Eucercaphis punctipennis* (Zett.) in relation to food quality. – *J. Anim. Ecol.* 43: 191–198.