# *The adaptive significance of autumn leaf colours*

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**Recently W.D. Hamilton and colleagues proposed a provocative new theory to explain the adaptive significance of autumnal leaf colours. They suggested that these colours were signals produced by the trees to warn potential insect herbivores of their defensive ability and tested this theory by an analysis of data on aphid species richness on different tree species. Here we argue that the principal assumptions of their theory do not match current knowledge of plant pigment biochemistry and aphid ecology. We therefore present further adaptive explanations for autumn leaf colours and suggest alternative reasons for the reported relationship between tree leaf colour and aphid species richness.**

Over much of the temperate zone autumn is marked by striking colour changes in leaves, prior to abscission. Attenborough (1995) has succinctly described the conventional view of this phenomenon, writing that trees "withdraw the valuable chlorophyll from their leaves. As the green pigment drains away, waste products that have accumulated over the year are revealed and the leaves change colour. In New England, day after day, whole hillsides of maples and aspens flush yellow, orange and red". Two recent papers (Archetti 2000, Hamilton and Brown 2001) have challenged this interpretation by suggesting that these red and yellow leaf colours are an honest signal of a tree's ability to defend itself against potential insect pests. This idea was proposed by the late W.D. Hamilton, one of the major figures in evolutionary theory in the second half of the twentieth century (Nevo 2001, Wilkinson 2000). With such an intellectual pedigree this heterodox idea deserves serious consideration.

The first of these papers (Archetti 2000) presented a game-theoretic model of the evolution of such an honest signalling system, while making it clear that the initial idea was due to Hamilton. The second paper

(Hamilton and Brown 2001) presented a qualitative description of the idea and an analysis of the number of aphid species on tree species with different autumn colours, the results of which appeared consistent with the theory. These papers attracted wide attention from the popular and technical press, being the subject of short reviews in several scientific journals (Atkinson 2001, Whitfield 2001, Lev-Yadum et al. 2002).

## Hamilton's theory

The core of the idea is that "bright autumn coloration serves as an honest signal of defensive commitment against autumn colonising insect pests" (Hamilton and Brown 2001). Better defended trees will have brighter autumn leaf colouration. If this is so then at 'an interspecific level, tree species suffering greater insect attacks should invest more in plant defence and defence signalling. On an intraspecific level within signalling species, the most defensively committed individuals should produce the most intense displays' (Hamilton and Brown 2001). As an evolutionary theory, intraspecific comparisons would make the stronger test of these ideas (compare with the discussion of Hamilton and Zuk (1982) in Wilkinson (2000)). However, Hamilton and Brown chose to address the interspecific test, as it is more amenable to investigation with data that can be assembled from the literature. In support of their theory they found that autumn coloration (particularly yellowness) was more intense in tree species that had high aphid species richness and that the numbers of specialist aphid species correlated most strongly with leaf colour.

One might question how autumn leaf colour acts as a reliable indicator of a plant's defensive ability. Both

Archetti (2000) and Hamilton and Brown (2001) proposed that the handicap theory (Zahavi 1975, Grafen 1990), could help explain the way signal honesty is maintained in such a system. Thus, they proposed that autumn signalling involves a significant cost which only vigorous and therefore well defended plants could afford to incur. It has recently been argued that honest signals do not necessarily have to be costly to ensure their reliability: the only requirement being that the cost of dishonesty is high (Lachmann et al. 2001). However, we feel it appropriate to raise the question of costs in a subsequent section, as this remains an important way of ensuring signal honesty, and it was the only mechanism identified by advocates of the signalling theory.

## Rationale

In this paper, we begin by introducing some of the basic biochemistry underlying autumn leaf colouration. We then point out several key problems we have with Hamilton's theory. Criticisms are rarely satisfactory without alternatives, so in the final sections we put forward other supportable arguments as to why autumn leaves tend to be brightly coloured, and why aphid diversity might correlate with autumn leaf colouration.

## Autumn leaf colouration: the proximate biochemistry

Autumn leaf colours fall into two main groups, those produced by carotenoids (mainly yellow) and those produced by anthocyanins (mainly red). The characteristics of the main pigments involved are summarised in Box 1.

A key point is that seasonal senescence of deciduous tree leaves is a *metabolically active process* (often characterised by high respiration rates), which involves down-regulation of some genes and up regulation of others (Hensel et al. 1993, John et al. 1995). We return to this point later in the context of the sun screen hypothesis where we suggest that the autumn pigments act to protect the necessary photosynthetic apparatus. Of the two main groups of pigments involved, only anthocyanins are synthesised in autumn (from an existing pool of colourless vacuolar flavonols). In contrast the carotonoids are always present in the leaves, their presence being masked by the green chlorophyll pigments prior to the degradation of the latter in the autumn.

## Some problems with Hamilton's theory

In the following sections we outline several facts, principally relating to aphid ecology, that we believe are at odds with Hamilton's theory. While it would be possible to argue that other herbivorous taxa besides aphids may be important in the context of signalling, we have concentrated on aphids because that is the candidate group highlighted by Archetti (2000), and the group for which the supportive correlative evidence has been gathered (Hamilton and Brown 2001).

### a) The timing of the signal does not match its proposed purpose

There are two groups of aphid that feed on trees: host alternating and non-host alternating. Species of the first type typically start returning to trees *before the leaves*

Box 1. The main pigments of leaf senescence

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***Chlorophylls*** (green)
The loss of chlorophyll in senescing leaves is well known and is probably the most visible sign preceding leaf fall. Chlorophyll's *a* and *b* are potent photosensitisers and as such are able to generate reactive oxygen species (ROS). Their mobilisation during the dismantling of pigment–protein complexes in the leaf at senescence could lead to significant damage of cell membranes unless shielded from excess irradiance. Their 'detoxification' to produce a series of colourless catabolites has been well documented (Matile et al. 1999).

***Carotenoids*** (predominately yellow and orange)
The carotenoids are not autumn pigments per se in that they are always present in the leaf, in which they function in both light-capture (as accessory light-harvesting pigments) and photoprotection (e.g. against ROS). During senescence the oxygenated carotenoids (the xanthophylls), which typically represent approximately 70% of the total carotenoid pool, combine with endogenous fatty acids released from cell membranes to produce a series of carotenoid acyl esters. The pattern of carotenoid loss during senescence of leaf tissues has been well documented (Young et al. 1991). Once the chlorophylls have been catabolised, it is this pool of carotenoid acyl esters that is primarily responsible for the yellow colouration of many autumn leaves. There is also the possibility of that flavonids may contribute to yellow autumn colours, although documentation of this is currently lacking.

***Anthocyanins*** (predominately red)
The anthocyanins are red, blue and purple water-soluble pigments derived from flavonoids and are reported to be both developmentally and environmentally transient in plant tissues (Chalker-Scott 1999). As such they can be observed in both juvenile and senescing leaves of many species. Anthocyanins are located in cell vacuoles and are often deposited just below the epidermis (Tevini et al. 1991) and, in contrast to the chlorophylls and carotenoids, they play no direct role in photosynthesis.

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*change colour* and depart from the trees in late spring or early summer (Dixon 1971). The primary reason for the early colonisation is that in most cases their offspring have to complete their development and lay the overwintering eggs *before* leaf fall (Ward et al. 1984, Dixon 1998). The non-host alternating species colonise trees throughout the year, with a high proportion of colonisation of this group occurring in spring and summer (Dixon 1969, Dixon and Kindlmann 1998). Given that most host plants are located well before leaf senescence by both groups of aphids, it is unlikely that the trees would be selected to advertise their defensive capability *after* the key host finding phase has occurred! One might of course argue that even if the advertisement catches only a proportion of the potential population, then it might still be worth signalling. However, this raises an important question, why has there not been selection for a better-timed signal?

### b) The form of the signal does not match its proposed purpose

The extent of anthocyanin accumulation in autumn foliage varies considerably from one tree to another but *also from one leaf to another on the same branch* (Chang et al. 1989). Since individual leaves can give rather different signals, then at the very least this complicates the assessment of the defensive ability of the entire plant. A natural question to ask therefore is why should the signal from a single individual be so variable if it is primarily designed to convey information about a plant's defensive capability?

### c) The inherent preferences of aphids are inconsistent with the proposed meaning of bright leaves

It has long been known that aphids tend to prefer plants with yellow leaves to green plants of the same species (Kennedy et al. 1961), some arboreal species even seek out yellowing leaves within an otherwise green tree canopy (Wratten 1974, Dixon 1979). Indeed it is of interest to note that yellow is recommended as a good colour for insect traps (Southwood and Henderson 2000). These simple facts are in direct contradiction of the signalling theory, which suggests that aphids should prefer to colonise plants with dull coloured autumn leaves rather than yellow leaves!

Hamilton and Brown (2001) cited the work of Furuta (1986, 1990) as supportive of their theory, this time in terms of a far less obvious prediction: a preference of aphids for yellow leaves over red leaves. However, in reporting these results they overlooked the fact that the trees studied by Furuta were not all equally exposed to the sun. Crucially, the autumnal colour of those trees in the shade was yellow–orange, while those in the sun had red leaves. Furthermore, the trees in the shade shed their leaves later and burst their buds earlier than those in the sun. In this case it is therefore likely that the aphids colonised trees with yellow leaves simply to obtain more time to produce overwintering eggs – it was not a consequence of some inherent defensive qualities of trees with red leaves. A further demonstration of this comes when we consider the observed extent of aphid infestation in these trees the following spring (Furuta 1990). At this time the late budding trees (red leaves in the sun the previous autumn) have growing leaves which are attractive to aphids, while the leaves of the earlier budding trees are maturing. As a consequence, aphids tended to move to the trees that had red leaves. Therefore, contrary to the assumption of signalling a fixed level of defensibility, 'red' and 'yellow' trees had varying levels of aphid infestation at different times of the year, suggesting that neither was superior in its anti aphid defences.

### d) Autumn colouration is strongly dependent on environmental factors, such that it is the less well defended trees that are likely to have brightly coloured leaves!

A key element of Hamilton and Brown's (2001) hypothesis is that the insect response is related not to the colour per se but rather to the relative intensity of colour. Therefore, trees are in competition with each other in order to produce the brightest colour in order to avoid insect attack (Archetti 2000). If environmental factors, that are not directly correlated with the likelihood of insect colonisation, influence the intensity of leaf colour, then clearly this weakens the signalling theory.

There is mounting evidence to suggest that the accumulation of anthocyanins in plants is environmentally regulated (Chalker-Scott 1999, Leng and Qi 2002). The photoinduction of anthocyanins in plant tissues is a well-documented process (Mol et al. 1996), particularly when combined with exposure to low temperature (Krol et al. 1995), nutrient deficiency (Bongue-Bartelsman and Phillips 1995, Trull et al. 1997) and drought (Balakumar et al. 1993). Of course one could argue that in these cases the stresses make the need to signal unprofitability to potential herbivores even more important. However here it works in the wrong direction: trees which experience these harsher conditions (and are so likely to be defensively weakened), tend to have more colourful leaves!

### e) Signal honesty

Identifying whether a particular set of metabolic processes carry a net cost is a challenge, particularly when metabolites serve several roles with a number of poten-

tial benefits. However, of the two main groups of pigments involved in leaf colouration, only anthocyanins are synthesised in autumn. Carotenoids, which generate the yellow colouration (and the strongest correlations with aphid species richness in Hamilton and Brown 2001) are simply exposed when the chlorophylls are reabsorbed. In senescent tissues the recovery of nitrogen is of paramount importance; carbon, for instance is generally not limiting. As the presence of carotenoids in fallen leaves does not result in the loss of any key nutrients such as nitrogen (Matile 2000) the potential cost of losing carotenoid pigments on abscission will be very limited. As such it is difficult to make a strong case for any honesty-ensuring costs based on the biochemistry of carotenoids. While there does indeed appear to be a cost to anthocyanin production we believe that there are alternative reasons why a plant may need to produce them (reviewed below).

## Alternatives

As Hamilton's signalling theory does not convince us, it is appropriate to highlight alternative explanations for autumn colouration. We also offer what we believe to be more plausible explanations for the interesting correlation between autumnal leaf colour and aphid diversity observed by Hamilton and Brown (2001).

### a) Why are autumn leaves coloured?

(i ) *A non-adaptive consequence of senescence*. One answer to the above question is to suggest that autumn colours are non-adaptive and just a by-product of the processes of senescence. This common view is implicit in the quotation from Attenborough (1995) cited in our introduction. However these pigments appear to perform several roles both before and during senescence which we now discuss.

(ii ) *A sun screen*. When plants are exposed to levels of irradiance in excess of that which they can utilise in photosynthesis, the absorption of excess excitation energy can bring about photoinhibition. This manifests itself as a decrease in the plant's photosynthetic capacity. This is especially true when plants are exposed to other stresses (especially low temperature, which is more likely in the autumn), which may cause photoinhibition to occur even at relatively low irradiances. Here we concentrate on the potentially important role of anthocyanins as sun screens since these are the pigments that are produced de novo in autumn. However, we note that the carotenoids are also able to act as sun screens (Box 1).

As the recovery of nutrients during senescence is a metabolically active process, protection of photosynthesis will be important for autumn leaves. Hamilton and

Brown (2001) claimed that this light screen hypothesis was ''more relevant to leaf construction'' but others (Krol et al. 1995, Hoch et al. 2001) clearly propose that the sun screen hypothesis is also applicable to autumnal leaf senescence. Clearly any process that serves to regulate the amount of light reaching the vulnerable photosynthetic apparatus would potentially be beneficial to the plant.

Leaf carotenoids (and their esters) absorb light in the blue region of the spectrum ($\sim 400$–$470$ nm). The anthocyanins are also coloured and able to effectively attenuate light in the blue region of the spectrum as well as in the UV (the actual wavelength range is highly dependent upon the structure of these pigments; see Chalker-Scott 1999). Much emphasis has been placed on the relationship of anthocyanins with UV-B but it is interesting that these pigments are themselves produced from colourless flavanoid precursors, which are very effective at absorbing UV-B. Therefore, a natural question is why should a plant invest in the additional metabolic expense of producing anthocyanins? One possibility is that their high solubility may permit higher concentrations to be accumulated within the leaf, as well as allowing them to absorb effectively in the blue region of the spectrum. In an actively growing plant this would reduce the rate of photosynthesis. However, in autumn this could be beneficial because chlorophyll is being mobilised from pigment protein complexes (Box 1) and is therefore particular susceptible to photo-oxidation.

Recent experimental work by Feild et al. (2001), on red-osier dogwood *Cornus stolonifera*, demonstrated that yellow senescent leaves turn red when exposed to light due to anthocyanin accumulation. In another recent study, Havaux and Kloppstech (2001) demonstrated that the *tt* (transparent testa) mutant of *Arabidopsis* is very susceptible to damage from UV radiation due to its inability to produce anthocyanins. Both of these papers provide results that are consistent with the sun screen hypothesis.

(iii ) *Other adaptive explanations*. Alternative theories have been suggested for the function of anthocyanins in plant tissues, especially developing leaves. Chalker-Scott (1999) proposed a role for them as 'osmotic modulators', effectively minimising the damaging effects associated with low temperatures, drought and UV-B. The antioxidant role for these pigments has been largely overlooked but some compelling evidence has been published (Tsuda et al. 1996).

An additional possibility is that some of the deep red leaf colours produced by anthocyanins may lower leaf albedo (surface reflectivity), so increasing the amount of solar energy absorbed and hence increasing leaf temperature. This should allow greater photosynthetic rates under continental climate conditions (i.e. cold air combined with relatively high irradances due to clear skies). There is as yet no direct test of this hypothesis

(Hoch et al. 2001), however we note the apparent correlation between striking red autumn colours and continental climates (described below).

### b) Why did Hamilton and Brown (2001) obtain the correlations?

Here we propose three related reasons for the correlations between leaf colour and aphid species richness.

*i ) Yellowness reflects host suitability due to the relationship between leaf colour and nutrient quality.* Both young and senescing leaves often tend to be yellow–green. As stated earlier, it is well known that aphids tend to prefer plants with yellow leaves to green plants of the same species. The most significant positive correlation reported by Hamilton and Brown (2001) was for yellows. Therefore, one alternative explanation is that tree species with high nutrient quality for aphids happen to be more likely to have yellow leaves in autumn (see our discussion of Furuta's work above).

*ii ) High latitudes have more aphid species and a greater propensity for trees to have coloured leaves in autumn.* It has been widely reported that autumn leaf colour of individual tree species tends to be more intense at high latitude. For instance, recently Hoch et al. (2001) demonstrated that anthocyanin accumulation in deciduous species from nine genera was correlated with geographical origin. Species from the relatively mild climates of Europe failed to display "high anthocyanin production" as seen in those species originating from the continental climate of northern USA and Canada. As such comparisons involve many congeneric trees a phylogenetic explanation appears unlikely. Aphid species richness is greater at high latitudes compared with the equator (Dixon et al. 1987). Hence aphid diversity and leaf colour may be independently correlated.

*iii ) Bright autumn coloration may be associated with increased tree range size, which correlates with insect diversity.* Trees with bright autumnal colouration appear to be able to cope with more extreme climates; probably leading to larger range sizes. Indeed, in general, species that live nearer the poles must be able to cope with a wider range of environmental variation than more tropical species (Janzen 1967) and tend to have larger range sizes (Rapoport's rule; Brown and Lomilino 1998). As tree range size is positively correlated with the number of associated insect species (Southwood 1961, Kelly and Southwood 1999) this provides another mechanism by which aphid species richness and leaf colour may be independently correlated. It is of interest that when Hamilton and Brown (2001) attempted to correct their correlations for tree range size then the significance of their results was greatly reduced.

## Conclusions

Historically relatively little attention has been given to the autumn colouration of leaves, presumably because they are dying and so thought unlikely to show much interesting biology. Hamilton's provocative theory has the merit of causing people to think about this interesting phenomenon. In this paper we have argued that the signalling theory is unlikely to be correct, primarily because the nature of the signal does not match its proposed purpose of repelling aphids. The correlations highlighted in support of the signalling theory are interesting, but we feel that there are more parsimonious explanations for these relationships, based on what is already known.

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