



# Classification of hypotheses on the evolution of autumn colours

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I review the hypotheses that have been proposed to explain the adaptive value of autumn leaf colours. The available adaptive hypotheses can be reduced to the following. Photoprotection: pigments protect against photoinhibition or photooxidation allowing a more efficient recovery of nutrients. Drought resistance: pigments decrease osmotic potential allowing leaves to tolerate water stress. Leaf warming: pigments convert light into heat and warm leaves. Fruit flag: colour attracts animals that help disperse seeds. Coevolution: colour signals that the tree is not a suitable host for insects. Camouflage: colour makes leaves less detectable to herbivores. Anticamouflage: colour enhances conspicuousness of parasites dwelling on leaves to predators or parasitoids. Unpalatability: pigments act as direct anti-feedants against herbivores. Reduced nutrient loss: yellow leaves have less to lose against herbivory. Tritrophic mutualism: colour attracts aphids which attract ants that defend the trees from other insects. For each hypothesis I mention the original references, I define assumptions and predictions, and I discuss briefly conceptual problems and available evidence.

## Autumn colours

Why do leaves change their colour in autumn? Autumn colours are one of the most striking natural phenomena, and their physiology and biochemistry are well known. Their adaptive value, however, is still a matter of controversy (Ougham et al. 2008). We have all learnt at school that autumn colours are a by-product of leaf senescence, and until about ten years ago it seemed common wisdom that no adaptive explanation was necessary for autumn colours. The simple fact that anthocyanins are produced *de novo* in autumn, however – a fact that has been known at least since the seminal paper by Sanger (1971) – suggests that autumn colours are not simply a by-product of senescence. What use is the production of a pigment in leaves that are about to be shed? Moreover, an adaptive explanation seems necessary to explain the intra-specific variation (some individuals drop their leaves when they are still green, others change colour before falling) and the inter-specific variation (only some species have autumn colours). In fact, adaptive hypotheses had been proposed in the nineteenth century (Pringsheim 1879, Pick 1883, Stahl 1896) but were largely ignored until recently.

Interest in the adaptive significance of autumn colour was revived by the rediscovery and elaboration of the photoprotection hypothesis (Gould et al. 1995, Feild et al. 2001, Hoch et al. 2001, Lee et al. 2003) and by the publication of the coevolution hypothesis (Archetti 2000, Hamilton and Brown 2001). These two lines of research, which have been pursued by plant physiologists and evolutionary biologists, respectively, have proceeded more

or less unaware of each other for some years, but there are now signs that the two schools are merging their efforts (Ougham et al. 2008). This renewed interest in autumn colours has produced a proliferation of new and allegedly new hypotheses, which is generating some confusion.

My purpose here is to classify, in the most simple and schematic way, all of these hypotheses to help reduce the confusion. For each case I will mention what the hypothesis states, the original references, and predictions for possible tests. My aim is not to discuss extensively the available evidence, but I will mention recent tests and conceptual problems to point out where further work is required.

## Non adaptive explanation

### By-product of other functions

*Hypothesis.* Autumn colours are not adaptive. They are the by-product of leaf senescence, of the detoxification of secondary metabolites or of other biochemical pathways, but they did not evolve for any specific purpose – they do not confer any selective advantage.

*References.* This idea is implicitly assumed as the standard explanation in most textbooks and it has been recently reviewed by Ougham et al. (2005).

*Predictions.* All the adaptive hypotheses proposed (below) should be disproved.

*Available evidence.* All of the tests that manage to disprove adaptive explanations (below) are consistent (but not sufficient) for the non-adaptive explanation.

## Adaptation against abiotic factors

### Photoprotection

*Hypothesis.* Autumn colours protect against photoinhibition or photooxidation, by acting directly as a sun-screen or indirectly as an anti-oxidant, thus allowing a more efficient resorption of nutrients – especially nitrogen – before leaf fall. According to an older version of the hypothesis, photoprotection allows for more efficient starch hydrolysis and sugar translocation.

*References.* The original idea that anthocyanins may protect the leaves in stress conditions dates back to Pringsheim (1879–1882); Pick (1883) proposed the importance of starch hydrolysis. The photoprotection theory was revived and proposed in its present form more recently by Gould et al. (1995), Hoch et al. (2001), Feild et al. (2001), Lee et al. (2003) and others (reviewed by Lee and Gould 2002).

*Predictions.* Individuals and species more in need to reabsorb nutrients (nitrogen) should display more autumn colours. Red phenotypes should be more resistant against photoinhibition or photooxidation and reabsorb nutrients more efficiently.

*Available evidence.* Evidence for a photoprotective role of anthocyanins is contradictory (in favour: Gould et al. 2002, Lee et al. 2003, Hoch et al. 2003; against: Hormaetxe et al. 2005, Kyparissis et al. 2007, Esteban et al. 2008; previous studies are reviewed by Lee and Gould 2002). Differences in resorption of nitrogen was not found by Feild et al. (2001) but was found by Hoch et al. (2003) and Lee et al. (2003), although photoprotection, could not explain the greater leaf mass/area and the lower nitrogen contents of the leaves of autumn-red species found by Lee et al. (2003). Protection against oxidative damage has been reported in some cases (Neill et al. 2002a, Gould et al. 2002, Neill and Gould 2003) but not in others (Neill et al. 2002b). The importance of starch hydrolysis does not seem to have had much credit (Lee 2002).

*Conceptual problems.* Manetas (2006) and others (Lee et al. 1987, Woodall and Stewart 1998, Lee and Collins 2001) suggest that anthocyanins, and especially red anthocyanins, are not the optimal, nor optimally located for photoprotection, and other colorless flavonoids (indeed even precursors of anthocyanins) are more abundant and more efficient for photoprotection. An antioxidant function is likely to be important only for leaves having anthocyanins located in mesophyll cells (Kytridis and Manetas 2006). The hypothesis is not relevant for yellow.

### Drought resistance

*Hypothesis.* Anthocyanins decrease leaf osmotic potential and allow leaves to tolerate water stress.

*References.* Chalker-Scott (1999, 2002).

*Predictions.* Individuals and species more in danger of water stress should display more autumn colours. Anthocyanic phenotypes should be more resistant against drought. Colour is not important.

*Available evidence.* A number of environmental conditions can induce water stress in plant tissues and the production of anthocyanins in response (Do and Cormier 1991,

Tholalakabavi et al. 1997) but there is no evidence that plant species more in danger of drought display more autumn colours or that red phenotypes are more resistant against water stress.

*Conceptual problems.* It is not clear why drought resistance should be especially important in autumn. In New England, drought causes premature leaf drop without color production (D. W. Lee, pers. comm.). The concentration of anthocyanins is not enough to affect significantly the leaf water potential (Manetas 2006). The hypothesis is not relevant for yellow.

### Leaf warming

*Hypothesis.* Anthocyanins convert light into heat in order to warm leaves and increase rates of transpiration and metabolism, or protect against cold temperatures.

*References.* Stahl (1896), Oberbauer and Starr (2002).

*Predictions.* Individuals and species more in danger of frost should display more autumn colours. Red phenotypes should be more resistant against cold temperatures.

*Available evidence.* There is anecdotal evidence that anthocyanins are more common at high latitudes, but red young leaves are also common in the tropics. The evidence that leaf temperature is influenced by colour is contradictory (Lee et al. 1987, Lee and Gould 2002).

*Conceptual problems.* It is not clear why leaf warming should be important for the autumn leaves of trees. It may be more important for evergreen species that turn transiently red in winter. Keeble (1895) suggested that, on the contrary, leaf temperature is moderated by anthocyanins (in tropical plants). The hypothesis is not relevant for yellow.

## Adaptation against biological factors

### Fruit flag

*Hypothesis.* Colour attracts birds and other dispersal agents to its non-conspicuous associated fruits and allow a better dispersal of the seeds.

*References.* Stiles (1982).

*Predictions.* Species with autumn colours should be the ones with animal-dispersed seeds and whose fruits ripe in autumn. Trees with more autumn colours should attract more dispersal agents.

*Available evidence.* Not supported by the only available study, performed on the genus that seemed the most obvious possible example (Li et al. 1999).

*Conceptual problems.* Only relevant for animal-dispersed species whose fruits ripe in autumn.

### Coevolution

*Hypothesis.* Autumn colours are a signal towards insects (for example aphids) that migrate to the tree in autumn and use the tree as a host until spring. Colour reveals better chemical defenses or worst nutritional capacity or any other characteristic that may induce a lower fitness in the insects. Insects will develop a preference for green.

*References.* Archetti (2000) and Hamilton and Brown (2001).

*Predictions.* Tree species with autumn colours should be the ones that coevolved with insects migrating to trees in autumn. Within each tree species, insects should avoid trees with red leaves in autumn, and should grow better in spring on trees with green autumn leaves.

*Available evidence.* Hamilton and Brown (2001) support the inter-specific prediction. There is empirical evidence of preference for green versus red in autumn (Furuta 1986, Archetti and Leather 2005, Rolshausen and Schaefer 2007, Ramirez et al. 2008) and for green versus yellow (Hagen et al. 2003, 2004). Aphids are about 70% less attracted by the red colour of leaves, an effect not due to brightness differences but based on a true colour difference between red and green (Döring et al. 2009). Yellow, however, is more attractive to aphids than green (Döring et al. 2009). Ramirez et al. (2008) show no differential growth in spring but they tested individual red leaves rather than whole trees. Karageorgou et al. (2008) show a correlation between anthocyanins and chemical defenses as expected by the coevolution hypothesis.

*Conceptual problems.* Many insects, including aphids, lack a 'red' photoreceptor, and it has been argued that they may not be attracted or repelled by the colour but by chemicals or volatiles, or that red and green leaves might only differ in brightness rather than colour (Döring and Chittka 2007). It is now known, however, that aphids can distinguish red from green using the green/blue ratio (Döring et al. 2009). Evidence that aphids prefer green over red, however, is only necessary and not sufficient to prove that red is a signal (it is also consistent with a cryptic function – below).

## Camouflage

*Hypothesis.* Autumn colours make the leaves less detectable to insects that migrate to the trees in autumn. Red does not reveal any quality of the tree but is only used as camouflage.

*References.* Karageorgou and Manetas (2006), Döring et al. (2009). A similar idea has been suggested by Stone (1979) and Juniper (1993) for the young leaves of tropical trees.

*Predictions.* Same as the coevolution hypothesis, but insect are not expected to have different performance on trees with different autumn colours.

*Available evidence.* The evidence that insects are more abundant on green than on red leaves cited for the coevolution hypothesis (above) is also consistent with a cryptic role. The lack of differential performance on different colours in spring (Ramirez et al. 2008, above) is consistent with a cryptic role, but the correlation of anthocyanins with chemical defenses (Karageorgou et al. 2008, above) is against.

*Conceptual problems.* Red leaves are clearly not invisible to animals lacking a 'red' receptor. Crypsis implies that the trees exploit insect colour vision to conceal its leaves, but there will be selective pressure on the insects to develop counteradaptations.

## Anticamouflage

*Hypothesis.* Autumn colours enhance conspicuousness of parasites dwelling on the leaves to predators and parasitoids.

*References.* Proposed by Lev-Yadun et al. (2004) as a general explanation for colours in plants; also used by Archetti (2000) as a solution to the problem of the origin of the signal in the coevolution theory.

*Predictions.* Tree species with autumn colours should be the ones with an evolutionary history of interaction with parasite insects and their predators or parasitoids in autumn. Insects should be conspicuous on autumn leaves. No differential growth of insects is expected on different leaf colours.

*Available evidence.* None.

*Conceptual problems.* It requires a further level of interaction compared to the coevolution hypothesis, therefore it is perhaps not so widely applicable to autumn colours (but it might be applied to other cases of colours in plants).

## Unpalatability

*Hypothesis.* Colour does not play any role, but anthocyanins act as direct anti-feedants against herbivores or fungal growth.

*References.* The idea was proposed only with reference to the young leaves of tropical plants (it seems to be common knowledge in tropical biology, see for example Rosenthal and Janzen 1979). Coley and Aide (1989) suggest a role as antifungal defense in tropical plants. Application to autumn colours has not been proposed so far, but the idea can be clearly applied to autumn colours as well.

*Predictions.* Individuals and species more in danger of herbivory or fungal attack should display more autumn colours. Anthocyanic phenotypes should be more resistant to fungal attack or repel herbivores more efficiently.

*Available evidence.* There is some evidence of induced production of anthocyanins following lesions or fungal attack, but no evidence that they serve to inhibit herbivory or fungal growth (Lee and Gould 2002). Indeed it is quite well known that anthocyanic tissues are well-tolerated in the diet of many animals.

*Conceptual problems.* Not relevant for yellow.

## Reduction of damage

*Hypothesis.* Autumn leaves have lower levels of nutrients and therefore lose fewer resources for a given amount of herbivory.

*References.* Originally proposed for the delayed greening of tropical plants (Kursar and Coley 1992), but it could be applied to autumn leaves as well (yellow only).

*Predictions.* Autumn colours (yellow) are expected only in species that suffer great herbivory in autumn.

*Available evidence.* None.

*Conceptual problems.* Only relevant for yellow.

## Tritrophic mutualism

*Hypothesis.* Autumn colours signal tree quality to myrmecophilous specialist aphids, which attract aphid-tending ants that defend the trees from other herbivores.

*References.* Yamazaki (2008).

*Predictions.* Species with autumn colours must have coevolved with beneficial aphids; these aphids must also be ant-tended, and attacked by other insects against which defence by ants is effective. Red and yellow leaves should attract more beneficial aphids and their ants, and should suffer less herbivory from other insects due to defense by ants.

*Available evidence.* None.

*Conceptual problems.* It requires very specific interactions that seem unlikely to apply in many cases.

## Other hypotheses

The following ideas have been presented as new hypotheses for the evolution of autumn colours but they are either the same hypotheses described above or particular cases of these hypotheses (photoprotection or coevolution), or they are hypotheses about something else.

### **Nutrient retranslocation**

The function of autumn colours is photoprotection, but insects look actively for yellow and red leaves because these have more nutrients available (Holopainen and Peltonen 2002). This is simply a prediction about insect behaviour (Archetti 2007a).

### **Defence indication**

The function of autumn colours is photoprotection, but insects avoid red leaves because autumn colours are correlated with the chemical defenses of the tree (Schaefer and Rolshausen 2006). This is not a new hypothesis but simply a mix of the photoprotection hypothesis and the coevolution hypothesis (Archetti and Brown 2006, Archetti 2007b).

### **Reproductive insurance**

Autumn colors are a signal of scarce availability of nutrients in the leaves for herbivorous insects, as more nutrients are allocated to reproduction (Sinkkonen 2006). This is a specific version of the coevolution hypothesis, specifying why the trees with red leaves are less suitable for the insects.

### **Signal of fall approaching**

Autumn colors are a signal that leaves are going to fall in a short time (Lev-Yadun and Gould 2007). This is also a specific version of the coevolution hypothesis specifying why the trees with red leaves are less suitable for the insects (because they drop their leaves early).

### **Aposematism**

Autumn colours are warning signals against parasites (Lev-Yadun and Gould 2007). This is equivalent to the coevolution hypothesis. The authors acknowledge this, but point out that Archetti (2000) did not call autumn

colours ‘aposematic’ in the original model of the coevolution hypothesis; the distinction is rather semantic, and it might be argued that handicap signals are not aposematic (Dawkins and Guilford 1993), but as it has been pointed out before (Archetti and Brown 2004) autumn colours are not necessarily handicaps.

## Summary

I have listed 16 different hypotheses that have been put forward to answer the question ‘What is the adaptive advantage of leaf colour change in autumn?’ The actual number depends on how these hypotheses are grouped. I used the relevant advantage for the plant as a criterion for the definition of a hypothesis. For example I classified protection against photoinhibition and photooxidation under a common name (photoprotection) because the relevant advantage is efficient resorption of nutrients, even though the relevant damages are, respectively, photoinhibition and photooxidation. For the same reason it would not make much sense to have two separate coevolution theories for protection against aphids or lepidoptera, because the signal would work for both and the relevant advantage for the tree would be the same – less parasite load. The ultimate advantage from the point of view of the plant, however, is the maximization of fitness, and pushing this argument to the extreme, it could be argued that there is no classification at all but just a common hypotheses of ‘protection against loss of fitness’. Any classification of this kind must be arbitrary to a certain extent. My purpose is not an exercise in logic but just to provide a clear idea of the possibilities. I have therefore defined a hypothesis as an idea with assumptions and predictions sufficiently different from other ideas to be distinguished and tested as described.

For all these hypotheses (Table 1) I have tried to list assumptions and prediction, but this is meant to be a clarification of the ideas rather than a complete list of available evidence or possible experimental tests. Other experiments must be performed. In all cases it is not enough

Table 1. A summary of the hypotheses for the evolution of autumn colours.

Hypothesis	Summary
Photoprotection	Pigments protect against photoinhibition or photooxidation allowing a more efficient recovery of nutrients
Drought resistance	Pigments decrease osmotic potential allowing the leaves to tolerate water stress
Leaf warming	Pigments convert light into heat and warm the leaves
Fruit flag	Colour attracts animals that help disperse the seeds
Coevolution	Colour signals that the tree is not a suitable host for insects
Camouflage	Colour makes the tree less detectable by insects
Anticamouflage	Colour enhances conspicuousness of parasites dwelling on the leaves to predators or parasitoids
Unpalatability	Pigments act as direct anti-feedants against herbivores
Reduction of damage	Yellow leaves have less nutrients to lose against herbivory
Tritrophic mutualism	Colour attracts aphids which attract ants that defend the trees from other insects

to show that the proposed advantage exists, but also that it is the very reason for the evolution of autumn colours. We have no such evidence for any of the hypotheses.

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