

Loss of autumn colors under domestication

A byproduct of selection for fruit flavor?

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According to the coevolution hypothesis the red autumn leaves of certain tree species are a warning signal towards insects that lay their eggs on the trees. A recent study has shown that red leaves are common in wild varieties of apple (*Malus pumila*) but not in cultivated varieties. This suggests that autumn colors have been lost during domestication due to relaxed selection against insects. The few varieties with red leaves have small fruits, similar to their wild ancestors, which shows that they have been under less effective artificial selection. As expected by the coevolution hypothesis these red varieties are very susceptible to an insect-borne disease, fire blight. Here I report further data on the loss of autumn colors under domestication. Since red leaf color is correlated with red fruit flesh color, if red fruit flesh has more astringent taste it is possible that loss of autumn colors is not only due to relaxed selection against insect, but also to direct artificial selection against astringent taste. However even varieties with yellow flesh turn out to have astringent taste. Moreover, while red fruit flesh is common in cultivated varieties with red leaves, it is very rare in wild varieties. It is unclear, therefore, whether loss of autumn color under domestication was a byproduct of artificial selection against red fruit flesh.

Autumn Colors

Why the leaves of some species of plants turn red in autumn is still debated.¹⁻³ The coevolution hypothesis⁴⁻⁶ suggests that red leaves are a signal of quality towards the insects that migrate to the trees to

lay their eggs in autumn: red leaves signal better chemical defenses or worst nutritional capacity or any other characteristic that induces a lower fitness in the insects. Insects, therefore, should prefer green trees in autumn, and have higher fitness on these trees in spring. Although the hypothesis has not been disproved so far, it has been difficult to find direct evidence of coevolution between leaf color and insects.

Autumn Colors Lost Under Domestication

A recent study⁷ has used domesticated and wild varieties of apple trees (*Malus pumila*) to test the coevolution hypothesis. The ideal test would be to let populations of the same species evolve with and without insect pests for many generations: if autumn colors are a signal to insects, we would expect red coloration to be lost in the populations evolving without insects. This is what actually happened with the domestication of fruit trees, and apple in particular.

The cultivated apple originated from wild populations (sometimes called *M. sieversii*) in the mountains of Central Asia, and populations of the same species (sometimes called *M. domestica*) evolved under domestication for many centuries.⁸ *M. pumila* is infested by many species of insect pests, including aphids. Insects, however damaging they may be for orchards, are not a selective pressure for trees under domestication, because fruit taste and size, rather than resistance to insects or leaf color, is what the farmers artificially select and reproduce.

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Most species in the genus *Malus* (apple) have red leaves in autumn,⁹ which suggests that red was the ancestral autumn color for *Malus pumila*. If red is a signal towards insects, we would expect autumn colors to be common in wild populations of *M. pumila* but not under domestication. Consistent with this prediction, 62.2% of the trees in wild populations of *M. pumila* in Central Asia change their leaf color to red in autumn, only 2.8% of the 2,170 English cultivated varieties turn red.

Varieties with Red Autumn Colors are More Similar to their Ancestors

Cultivated fruit trees are a good study system because many data are available. The Germplasm Resources Information Network (GRIN) database of the USDA-ARS (http://www.ars-grin.gov/npgs/acc/acc_queries.html), provides information about all the apple varieties present in the USA fruit tree collection, except autumn leaf color, which was determined by the author on the UK fruit tree collection.⁷ These data combined allow an analysis of the correlations between autumn leaf colors and other characters.

Red varieties do not differ from green and yellow varieties in vigor.⁷ If autumn colors are a signal, therefore, signalling theory predicts that red varieties are more in need of signaling.⁷ The need to avoid insects can be quantified by the susceptibility to fire blight, a common and important contagious disease of apple trees induced by *Erwinia amylovora*, a bacterium transmitted by aphids and other insects. Varieties more susceptible to fire blight are the ones more in need of avoiding insects, and therefore more in need of signaling.

The analysis⁷ showed that the red varieties are significantly more susceptible to fire blight than the green ones: only very susceptible varieties have red autumn colors. This suggests that the cultivars that maintain autumn colors are the ones more in need of avoiding insects, as predicted by the coevolution hypothesis.

Moreover, varieties with red autumn leaves have lower fruit size and more astringent taste than varieties with green or yellow autumn leaves, but

similar to the varieties from Central Asia.⁷ Because increasing fruit size and improving taste has been the main selective pressure under domestication, this seems to suggest that red varieties have evolved more slowly and are more similar to their wild ancestors.

Fruit skin color instead does not have any significant correlation with autumn leaf colors; indeed, most cultivars have red or orange fruits.⁷

Loss of Autumn Colors: Relaxed Selection or Direct Artificial Selection?

A recent study¹⁰ shows that there is a single gene, or tight linkage group, for leaf redness in apple and this is also responsible for red flesh in the fruit, although apple skin color is separately determined. This might suggest the following scenario (I owe this suggestion to Helen Ougham and Howard Thomas). Since the red color is due to anthocyanins produced via the phenolic biosynthesis pathway, red flesh may be higher in phenolics generally, making the fruit more astringent and unpleasant for human consumption. As a consequence, there may have been selection against red fruit flesh (for reasons of consumer preference) which would have simultaneously favored non-reddening leaves. In other words, it is possible that loss of autumn colors under domestication was not only due to *relaxed* natural selection against parasites but also to *direct* artificial selection for improved fruit taste, which would have selected against fruits with red flesh (astringent taste) and, as a consequence, against varieties with red leaves.

To test this idea I analysed the correlation between autumn leaf color and fruit flesh color. As expected, the proportion of varieties with red-orange-pink fruit flesh is significantly higher among varieties with red autumn leaves (5 varieties in 30) than among varieties with green autumn leaves (3 in 325) (χ^2 test, $p < 0.0001$) or yellow autumn leaves (3 in 92). However the varieties from Central Asia (autumn leaf color uncertain but most likely red or yellow) have virtually no red fruit flesh colors (2 in 1,722), which suggests that red was not the original fruit flesh color in wild apple trees.

Among the 86 varieties with red-orange-pink fruit flesh, 54 (63%) have astringent taste, whereas only 588 (23%) among the 2,565 varieties with white fruit flesh have astringent taste, which is significantly lower (χ^2 test, $p < 0.0001$). However, there is also a similar correlation (χ^2 test, $p < 0.0001$) between yellow fruit flesh color and fruit flesh taste: 211 varieties (78%) among the 270 with yellow fruit flesh have astringent taste.

Summary

Astringent taste is common in cultivars with red fruit flesh but also in cultivars with yellow fruit flesh. Moreover while the cultivated varieties with red autumn leaves have normally red fruit flesh, the wild trees from Central Asia have no red fruit flesh. This makes the hypothesis of loss of autumn colors as a byproduct of direct selection against red fruit flesh difficult to support with the present data.

It is also possible, on the other hand, that red fruits are not selected against by human taste at all; it has been suggested¹⁰ that consumers might even prefer red fruits because novel or because a better source of antioxidants, with potential health benefits.

It has been shown, however, that red fruit flesh color and red leaf color are genetically linked.¹⁰ This is probably not the case in wild apple trees from Central Asia, which have no red fruit flesh. It should be noted, however, that the link¹⁰ between red fruit flesh and red leaf color was observed in varieties with *constitutive* red leaves, all year round, not in varieties whose leaves turn red in autumn.

In conclusion, at the moment it is difficult to support the idea that the loss of autumn colors under domestication is a byproduct of artificial selection against red fruit flesh for improved taste, although this possibility should be investigated further. Whether loss of autumn colors was due to direct artificial selection against anthocyanins or simply to relaxed selection against insects, this would not affect the observation⁷ that, in domesticated varieties, lower selective pressure against insect allowed autumn colors to disappear, and that autumn colors remain only in varieties with a high need to repel

insects,⁷ as predicted by the coevolution hypothesis.

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