Do autumn leaf colours serve as a reproductive insurance against sucking herbivores?

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Although autumn leaf colours of deciduous trees have been shown to protect against photo-oxidative damage, they are sometimes seen as signals to pests and predators. Here I modify the coevolution hypothesis of autumn leaf colours. I suggest that much of the within-population variation in autumn leaf colours can be explained by differences in the allocation of resources to sexual reproduction. According to the novel hypothesis, reproductively active woody plants produce early and intense autumn leaf colours in order to protect seeds and other reproductive tissues from pests that lay eggs in the autumn. If many seeds mature at times of leaf senescence or during the next summer, a woody plant will reallocate plenty of nitrogen to seeds. If sucking insects reproduce on such hosts, their flightless offspring will suffer poor-quality food after the ripening of seeds. Before this, however, insects will probably concentrate around the ripening seeds to forage on nitrogen-rich veins. This will decline the quality and quantity of developing seeds. If, on the other hand, insects are able to recognize reproductively active plants while laying eggs in the autumn, both the insects and the plants benefit. The flightless offspring of insects feeds on plants that supply sufficiently nitrogen for longer than reproducing plants do, while these optimise their reproduction by avoiding pests, which also contributes to the abundance of specialist pests. Hence, I suppose that while physiological factors are the origin of autumnal colour changes of deciduous leaves, the visible cue utilized by insects has evolved several times to an honest signal that reveals the unsuitability of the potential host in the near future. The reproductive insurance hypothesis may help us to understand why bright autumn leaf colours are rare among herbaceous plants, and why plants at high altitudes and latitudes are often brightly coloured in autumn.

The physiological null hypothesis of autumn leaf colours states that deciduous trees unmask and synthesize autumnal colour pigments in order to avoid photo-oxidative damage at times of intense recovery of nutrients from leaves (Wheldale 1925, Gould et al. 1995, Merzlyak and Gitelson 1995, Hoch et al. 2001, 2003, Wilkinson et al. 2002, Lee and Gould 2003, Ougham et al. 2005). Both anthocyanins that are usually seen as hues of red and carotenoids that humans see as yellowish colours shield leaves from damaging light levels in autumn. Autumn leaves contain also many phenolic compounds that have been associated with similar actions but that are invisible to human eye (Briscoe and Chittka 2001, Mäntylä et al. 2004, Manetas 2006).

Some recent ideas suggest that coevolution between trees and specialist insects, particularly aphids, has been the main reason for the evolution of bright autumn leaf colours (Archetti 2000, Hamilton and Brown 2001, Archetti and Brown 2004). Hamilton and colleagues suggested that autumn leaf colours are an honest signal that facilitates defensively competent trees to avoid insect herbivory. Since substantial evidence contradicts with Hamilton's hypothesis, for example the onset of red colouration correlates with nitrogen deficiency in sugar maple Acer saccharum (Schaberg et al. 2003), Ougham et al. (2005) speculated whether nutrient deficiency is the reason why some trees invest to defend their resources more heavily than other trees that will possibly be able to outgrow their pests. As a result, nutrient-poor trees would reveal the brightest autumn colours (Ougham et al. 2005). The nutrient retranslocation hypothesis by Holopainen and Peltonen (2002) and the defence indication hypothesis by Schaefer and Rolshausen (2006) rely on the physiological explanation of autumn leaf colours, but the authors suggest that insects can utilize the colour cue of the host to maximize their fitness. Holopainen and Peltonen (2002) state that leaf

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colour reveals the availability of nutrients in autumn leaves, while Schaefer and Rolshausen (2006) lean on the fact that anthocyanins and numerous defensively active phenolic compounds are synthesized via the same biochemical pathway (Gould 2004). Derived from this, Schaefer and Rolshausen (2006) hypothesize that stressed plants avoid extra herbivory because insects utilize autumn colour cues to anticipate the level of defence compounds in leaves.

In addition, two novel papers complicate efforts to understand reasons for various autumn leaf colours of deciduous woody plants. Sinkkonen (2006) observed a causal relationship between the amount of female catkins per tree and timing of yellow autumn leaf colour in mountain birch Betula pubescens ssp. czerepanovii. He suggested that trees that are reproducing intensively might benefit from the early cessation of photosynthesis (Hagen et al. 2003). Archetti and Leather (2005) observed a strong preference of the aphid Rhopalosiphum padi for Prunus padus trees with green leaves at times of leaf senescence. They supposed that the ability to fight against sucking insect herbivores depends on tree condition. Based on this, they argued that defensively committed trees produce early or excess leaf colour pigments, despite the costs of the process, in order to reveal their readiness to produce high levels of defence compounds in the near future (Archetti and Leather 2005). Since Ougham et al. (2005) present a lot of evidence that contradicts with the hypotheses used by Archetti and Leather (2005), I postulate a modified version of the coevolution hypothesis, based on the idea by Sinkkonen (2006). According the novel coevolution hypothesis, or the reproductive insurance hypothesis, many woody plant species produce excess leaf colour pigments in order to warn sucking insects about the imminent flow of nutrients to reproductive tissues, e.g. seeds, because this may be followed by low fitness among the progeny of the pests. The honest signal may be costly, or it could be born because a specialist pest and its host have a common interest in ensuring the abundance of the host.

The modified coevolution hypothesis: do trees cover reproduction against sucking insects?

Although it is probable that autumn leaf colours originally evolved for physiological reasons, insects may have been able to utilize the visible cue of autumn colour code for millions of years (Briscoe and Chittka 2001, Ougham et al. 2005, Schaefer and Rolshausen 2006). Because neighbouring woody plants usually differ in their reproductive efforts, and because reproduction affects autumn leaf colours, nearby individuals are expected to be different in their autumnal colouration (Sinkkonen 2006). Based on this, I agree with Hamilton and Brown (2001) that several deciduous woody species may have coevolved with specialist insects, which has led to honest signalling that reveals the upcoming quality of potential host plants in hues, timing, or duration of autumn leaf colours. Due to the fact that autumn colour pigments per se may be virtually costless (Ougham et al. 2005), I suggest that early cessation of assimilation decreases the amount of nitrogen obtained during a growing season (or possibly some other limiting nutrient, Svenby ronnson et al. 1996). Alternatively, the cost may be caused by a prolonged dormancy that exposes plants to attacks by pests and pathogens. The other possibility is that the signal is costless but that the signaler and the receiver share a common interest. While the foraging behaviour of specialist insects, like many aphids, may not have evolved to maximize the reproductive output of host species, the abundance of any specialist pest certainly depends on the abundance of its host, which may facilitate the existence of honest signalling as an evolutionary stable strategy (Maynard Smith 1972, 1989, Maynard Smith and Harper 1995, 2003).

Sucking insects are thought to have more drastic effects than other insect herbivores on seed maturation (Crawley 1985, 1997). Therefore, I suspect that a visible autumn colour cue has evolved several times to an honest signal that reveals the upcoming suitability of a host, and that reduces foraging near seeds. In other words, reproductively active trees produce different autumn colour pigments than other trees do, in order to protect developing seeds. I further assume that seeds do not have to ripen as leaves senesce. Seeds may alternatively develop during summer when aphids or possibly other sucking herbivores reproduce and search for nitrogen-rich veins in tree foliage. Since the flow of nitrogen is likely to be above average in veins that run to reproductive tissues, a relatively small number of insects may cluster around developing seeds and thus decrease the seed lot of the host significantly. Further, herbivores may transmit viruses and other diseases to seeds, which may lower plant fitness (Landis and Van den Werf 1997). The quality and quantity of pollen may be affected for the same reasons (Delph et al. 1997, Aizen and Raffaele 1998, Johnson et al. 2003, Pietarinen and Pasonen 2004), which may enable the evolution of honest signalling in male plants. If, on the other hand, the plant is not going to reproduce intensively, its nutrients will not be concentrated, which may invert the benefits of signalling. Hence, the reproductive insurance hypothesis suggests, that if there is no need to cover ongoing or forthcoming sexual reproduction, mature trees do not discourage sucking insect herbivores with a physiologically needless level of autumn colour pigments. A possible reason for this is that the negative effect of sucking herbivores on the fitness of reproductively inactive plants is often moderate compared to the effects of other herbivores, diseases, and a multitude of abiotic stress factors.
ones (Lee and Gould 2003), which protect against photodamage than undamaged leaves (Shalitin et al. 2005, Schaefer and Rolshausen 2006). Because coevolution cannot occur unless both parties benefit, I argue that it is worthwhile for specialist insect pests to be able to recognize sexually active host plants in autumn. If seeds of these ripen before the latter part of the next growing season, the quality of the hosts will fall drastically as seeds will have ripened. In case of aphids, winged females develop when growing conditions deteriorate and density-dependent competition becomes intense. Because searching for a new host is risky, aphids may have evolved to find trees that will be able to provide a large amount of nutrients for longer than other trees will (Ward et al. 1998, Leather et al. 2005, Schafer and Rolshausen 2006). Hence, natural selection may have favored the ability to recognize pigments and signals that reveal the upcoming nutritive value of the host during the next growing season. Aphids are good candidates for this kind of coevolution for several reasons, but also other sucking insects may benefit from the ability to utilize the autumn color code of deciduous woody plants (Hamilton and Brown 2001).

The reproductive insurance vs the original coevolution hypothesis

Archetti and Leather (2005) feel that the preference of an aphid species for green leaves in autumn supports the original coevolution hypothesis by Hamilton and co-authors (for previous criticism, see Wilkinson et al. 2002, Ougham et al. 2005, Schaefer and Rolshausen 2006). However, the result by Archetti and Leather (2005) can be explained using the physiological null hypothesis: visible differences in the autumn colouration of trees could simply be born because intact leaves can be utilized cost-effectively for longer than leaves damaged by pests, and because damaged leaves need more protection under photo-oxidative stress than undamaged ones (Lee and Gould 2003), which – supposing that damage correlates negatively with the upcoming nutritive value of the tree – might have led to the preference for green observed by Archetti and Leather (2005). Thus, one of the weaknesses of the original coevolution hypothesis is that it relies on intangible terms, i.e. “tree condition” and “defensive commitment of trees”, that are expected to be exactly measurable and dependent on each other (Archetti and Brown 2004). Moreover, Archetti and Brown (2004) suggest that “secondary metabolites or compounds known to be effective against herbivores” could somehow reveal the defensive commitment of trees. Unfortunately, evidence is lacking for a simple, measurable relationship between the growth of plants (i.e. tree condition) and the levels of defence chemicals in leaves (i.e. defensive commitment), and complicated examples are frequent (Northrup et al. 1995, Hartley and Jones 1997, Nitao et al. 2002, Siemssen et al. 2002, Haukioja 2003). Therefore, at least two questions should attract our attention before accepting the hypothesis (Archetti and Brown 2004, Schaefer and Wilkinson 2004, Schaefer and Rolshausen 2006). Because there may not be any costs or tradeoffs connected to the production of defence chemicals (Riipi et al. 2002, Gould 2004, Ougham et al. 2005), we must ask how an honest signal has evolved from the quantitative levels of defence chemicals in trees. Current knowledge supports the view that the levels of defence chemicals in plant tissues have been secondary in the evolutionary race between a short-lived herbivore and its long-lived host, compared to rapid fluctuation in nutritive and qualitative leaf traits (Hartley and Jones 1997, Gardner et al. 1998, Haukioja 2003). For example, the defence of *Betula pubescens* ssp. *czerepanovii* against insects depends largely on rapid temporal changes in leaf quality, instead of the peak levels of defence chemicals in leaves (Riipi et al. 2002, Hagen et al. 2003, 2004, Haukioja 2003, Kozlov 2004). Therefore, the main question to be answered is whether the potential of trees for rapid qualitative changes in leaf biochemistry correlates with leaf colour in autumn. Based on Haukioja (2003), I doubt the phenomenon is so complex and dependent on multiple factors that the next-year (or next-spring) defensive commitment of most tree species cannot be estimated in autumn. Thus, if there has been any co-evolution, or if insects even utilize autumn colour pigments as a cue when selecting the most suitable host plant for their offspring, insects may face severe difficulties when selecting the defensively least competent trees. On the contrary, because allocation of resources to reproduction normally causes a significant fall in plants’ nutritive value (Zackriskson et al. 1999, Rees et al. 2002), insects may well use autumn leaf colours as a cue of the upcoming nutritive value of the host. Since nutrient scarcity correlates with early leaf senescence (Schaberg et al. 2003), several woody plants may have evolved to shield their reproduction using honest signals.

**Evidence of the reproductive insurance hypothesis**

According to the non-coevolutionary hypotheses, all plants that benefit from photoprotection under photo-oxidative stress are expected to reveal hues of yellow or red in autumn (Holopainen and Peltonen 2002, Wilkinson et al. 2002, Schaefer and Rolshausen 2006).
Similarly, the original coevolution hypothesis assumes that all perennial plants benefit from bright autumn colouration, supposing that herbivores are able to recognize the level of current or upcoming defensive commitment of tussocks and other discernible clones. I do not see any reason why this ability should have been restricted to insects foraging on woody plants. Thus, if the physiologically oriented explanations or the original coevolution hypothesis were used to explain the gamut of autumn leaf colouration, we should see brightly coloured herbs and grasses as frequently as we see brightly coloured woody plants. On the contrary, the coloured herbs and grasses as frequently as we see brightly coloured woody plants. On the contrary, the reproductive insurance hypothesis assumes that coevolution is not possible unless a plant has allocated resources to the novel reproductive insurance hypothesis, on the other hand, Larix trees are assumed to show little variation in autumnal colouration, because their seeds develop from spring to early autumn (Mitchell et al. 1997). Although there are differences in the number of ripening seeds per Larix tree (Koski and Tallqvist 1978), sucking insects do not live at the risk of a rapid decline in food quality on Larix. Similarly, Lindens Tilia L. show minor intraspecific differences in autumn colouration, although they are hosts of numerous species of sucking insects. Since species of Tilia flower in midsummer or August (Mitchell et al. 1997), and since the seeds usually ripen before leaves fall, natural selection has probably not led to striking intraspecific differences in their autumn leaf colours. The physiological null hypothesis and differences in environmental conditions, like illumination and wind action, may largely explain the onset and other details of autumn leaf colours in Larix and Tilia.

Testing of the reproductive insurance hypothesis

A causal relationship between tree colour and insect preference does not support the original coevolution hypothesis if insect behaviour and growth rate are expected to remain the same when deciduous trees utilize autumnal colour pigments as a pre-paid insurance against damage to sexual reproduction (Archetti and Leather 2005). Therefore, it is essential to differentiate demonstrations of defensive commitment, or defence indication, from those of reproductive insurance i.e. imminent nutrient loss. The research may be initiated by performing laboratory bioassays where different numbers of specialist pests suck a host species at different temperatures. Reproduction of trees should be manipulated simultaneously, for example by controlling pollination. Field observations could precede and field experiments should follow laboratory tests. Note, however, that if woody plants aim to avoid damage to reproductive tissues, and if specialist insects have coevolved, insect behaviour and leaf senescence are most probably species-specific. For instance, some specialist aphids may always prefer yellow instead of green leaves, and they may continue to lay eggs for weeks after the leaf fall so that the total load of aphids becomes heavier on late-senescing, reproductively inactive trees (Holopainen and Peltonen 2002, Sinkkonen 2006).

Other possible tests of the novel hypothesis include intraspecific comparisons at high and low latitudes (or altitudes). If the only correlation will be observed between timing or intensity of autumnal colouration and insect damage, the reproductive insurance hypothesis is ruled out. If, however, the relationship between autumn colouration and insect damage depends on differences in the reproductive status of tree individuals, the original coevolution hypothesis and the defence
indicating hypothesis may have to be rejected. There are many possibilities how populations may differ from each other. Seeds may mature before or at times of leaf senescence, ripening of seeds may take a different proportion of the growing season, flightless insects may not have to suck trees after the ripening of seeds in all populations, or trees may bloom differently in different parts of the geographical distribution of the species under study. If a study tests a physiologically oriented or the original coevolution hypothesis, it is essential to prove that defensively less committed trees are unable to vary qualitative leaf traits as fast as more committed trees (Archetti and Brown 2004, Kozlov 2004). If the precondition is not found, the reproductive insurance hypothesis may still be valid because it only assumes costs related to early leaf fall, and the sucking of reproductive tissues. Test species should be from the same geographic area since some deciduous trees remain less coloured in areas where they are not native (Hämälä-Ahti et al. 1992, Mitchell et al. 1997, Mäntylä et al. 2004).

Conclusions

While earlier hypotheses on the reasons for autumn colour changes of deciduous woody plants consider physiological necessities and the effect of herbivory on plant growth, the reproductive insurance hypothesis focuses on plants’ need to optimise their reproduction. It suits to situations where prerequisites for coevolution exist; the visible cue utilized by insects may have evolved from the same geographic area since some deciduous trees remain less coloured in areas where they are not native (Hämälä-Ahti et al. 1992, Mitchell et al. 1997, Mäntylä et al. 2004).

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