

# Ultraviolet leaf pigments as components of autumn colours: a constructive comment on Archetti *et al.*

Aki Sinkkonen

Department of Ecological and Environmental Sciences, University of Helsinki, Niemenkatu 73, 15210 Lahti, Finland

In a recent article in *Trends in Ecology & Evolution* [1], Archetti *et al.* summarise current knowledge of the evolutionary background of autumn leaf colours of deciduous trees. The authors specifically search for appropriate research methodologies to investigate the impact of herbivorous insects on the evolution of autumn leaf colouration, and present the most urgent questions for future research. In the article, autumn leaf colours are classified as red, yellow or brown [1]. Although this classification is currently the prevalent view on autumn leaf pigmentation of deciduous woody plants, it might not be optimal for studies based on insect vision. The reasons are that most herbivorous insects perceive ultraviolet (UV) light [2], and that several taxonomically separate tree species accumulate UV-visible pigments in autumn leaves [3]. For example, Matile [4] documented the increasing UV reflectance of senescing autumn leaves of ginkgo *Ginkgo biloba* at the same time as Hamilton and Brown, and Archetti, formulated the coevolution hypothesis [5,6]. Based on Matile's [4] work, I argue that autumn leaf colouration should have originally been classified as UV, red, yellow and brown instead of the latter three categories.

Although the novel classification should not change the theoretical framework behind the guidelines for research proposed by Archetti *et al.* [1], the colour-specific questions in their article should be reformulated because herbivorous insects usually avoid objects that reflect UV light [2]. In the case of red, the task is simple because aphids prefer green leaves over both red and UV alternatives [2]. However, experimentalists must be aware that an avoidance of red leaves might be a consequence of UV avoidance. If the purpose of a study is to test the potential costs and benefits of autumnal pigment production, the difference is crucial because many UV-visible phenolics and flavonoids are synthesised via the same biochemical pathway as anthocyanins, which are the main red leaf pigments [1]. If UV pigments are not measured, a true null hypothesis might be rejected unless the concentrations of red and UV hues correlate tightly.

One of the major questions asked by Archetti *et al.* [1] is whether coevolution can be applied to the evolution of yellow colour. I propose that the question is crucial only if yellow leaves lack UV pigments. If a yellow-looking canopy is a blend of attractive yellow and unattractive UV hues, insects might respond to differences in the concentrations of UV leaf pigments in the same way as

they respond to differences in the concentrations of red leaf pigments. The same caution should be applied to brown, because many UV-reflecting phytochemicals appear yellowish-brownish to the human eye. Thus, yellow and brown leaves should be divided into two categories. In the coevolutionary context, it might be worth looking for causalities between UV-visible leaves and insect response. European oak *Quercus robur* is an example of a species that synthesises many UV-reflecting compounds, that hosts hundreds of herbivorous insect species and that has a relatively pale yellow-brownish canopy [7,8]. If potential signals at UV wavebands are not thoroughly investigated, the autumn leaf colours of such species might be classified as a result of evolution toward enhanced photoprotection, whereas, in reality, the species might have coevolved with a rich insect fauna, as assumed by Hamilton and Brown [5].

Finally, the UV spectrum is wide and all herbivorous insects do not sense all UV wavelengths. However, the UV receptor of the green peach aphid *Myzus persicae*, the only host-alternating aphid investigated so far, can perceive UV at 270–360 nm [9]. The wavebands of many abundant leaf phenolics and related compounds fall within this range [8,10]. Thus, it is ecologically important to determine the exact behavioural response of aphids and other potentially coevolved insects to autumn leaves containing leaf phenolics.

Currently, only red and yellow leaf colours have been studied in the context of coevolution between deciduous woody plants and insects [1]. Although this has advanced our familiarity with both insect behaviour and tree ecophysiology, such information is not optimal if the goal is to estimate the costs and benefits of autumn leaf pigmentation to host plants. To achieve such comprehensive knowledge, UV hues of autumn leaves must be investigated in parallel with colours that are visible to the human eye. When this is done, it will become possible to estimate the evolutionary background of autumn leaf colouration.

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Corresponding author: Sinkkonen, A. (aki.sinkkonen@helsinki.fi).

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## Letters Response

# Response to Sinkkonen: Ultraviolet reflectance in autumn leaves and the un-naming of colours

Marco Archetti<sup>1</sup>, Thomas F. Döring<sup>2</sup>, Snorre B. Hagen<sup>3</sup>, Nicole M. Hughes<sup>4</sup>, Simon R. Leather<sup>2</sup>, David W. Lee<sup>5</sup>, Simcha Lev-Yadun<sup>6</sup>, Yiannis Manetas<sup>7</sup>, Helen J. Ougham<sup>8</sup>, Paul G. Schaberg<sup>9</sup> and Howard Thomas<sup>8</sup>

<sup>1</sup> Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

<sup>2</sup> Division of Biology, Imperial College London, Silwood Park, Ascot SL5 7PY, UK

<sup>3</sup> Department of Biology, University of Tromsø, 9037 Tromsø, Norway

<sup>4</sup> Department of Biology, Wake Forest University, Box 7325, Reynolda Station, Winston-Salem, NC 27109, USA

<sup>5</sup> The Kampong, National Tropical Botanical Garden, Miami, FL 33155, USA

<sup>6</sup> Department of Science Education–Biology, University of Haifa–Oranim, Tivon 36006, Israel

<sup>7</sup> Department of Biology, University of Patras, Patras 26500, Greece

<sup>8</sup> IBERS, Aberystwyth University, Plas Gogerddan, Aberystwyth SY23 3EB, UK

<sup>9</sup> Northern Research Station, Forest Service, US Department of Agriculture, South Burlington, VT 05403, USA

Ultraviolet (UV) vision, first discovered in ants more than a century ago, is a major area of interest for behavioural ecology. Because, unlike humans, many animal species can see UV light, spectrometry in the UV has revealed fascinating signalling systems that remain hidden to the human eye. In his letter to *Trends in Ecology & Evolution*, Sinkkonen [1] argues that UV should also be considered in investigations on autumn colours, particularly when testing hypotheses that involve insect–tree interactions. Because UV vision is a generic feature of insect vision and has been confirmed for aphids [2], the main taxon of interest in the autumn colour debate, we agree with Sinkkonen that the role of UV needs to be explored in this area. Specifically, we need to know: (i) how much UV is reflected by autumn leaves and how much trees vary in UV reflectance; and (ii) how insects respond to UV leaf reflectance in autumn.

With regard to the first question, it is important to consider spectral reflectance in actual leaves rather than the spectral properties of isolated phytochemicals. The presence of UV-reflecting compounds in a leaf does not mean that the leaf itself will be UV reflecting, given the number of other leaf compounds present that might absorb UV light. In senescent leaves of *Ginkgo biloba* and *Quercus robur*, which Sinkkonen mentions as containing UV-reflecting compounds [1], maximal UV reflectances were found of only 10% and 9%, respectively (unpublished from Ref. [3]). Moreover, the UV-reflective compound in senes-

cent *G. biloba* does not occur widely, especially in woody plants, and it would be misleading to extrapolate to trees as a whole. Indeed, an analysis of 2409 autumnal leaf spectra reveals that 99% have a maximal UV reflectance of <8.6%, whereas at 500–650 nm, half of the spectra exceed 34.4% reflectance (data from Ref. [3]). Thus, all possible UV variability is squeezed into a narrow range of reflectance values.

With regard to the second question, UV is known to be involved in the visual signalling of flowers to pollinators; here, UV reflectance frequently reaches maxima of >30% [4]. By contrast, the low overall UV reflectance in autumn leaves means that the necessarily small differences among leaves would be relatively hard for insects to detect. In fact, a colour choice model developed from trapping migrant aphids in autumn found no effect of UV reflectance, when trap colours, mimicking the situation in leaves, reflected little UV [3]. Further studies are needed to test more thoroughly how aphids respond to UV, but for low UV reflectance (ca. <10%), the blue and green channels have the only significant role in the response of aphids to colours, according to the findings in Ref. [3].

As well as the UV issue, Sinkkonen's comment raises another important question: should leaves be classified by human colour names? Should we just add 'UV' as another category to the range of 'red,' 'brown' and 'yellow' leaves [1], or is there another, more appropriate way of describing leaf colours? Although it has been common practice in plant colour studies to use human colour names, we

Corresponding author: Archetti, M. (marco.archetti@zoo.ox.ac.uk).