Tansley review

The occurrence of red and yellow autumn leaves explained by regional differences in insolation and temperature

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Summary

Red or yellow autumn leaves have long fascinated biologists, but their geographical concentration in trees in Eastern North America (ENA) has defied evolutionary explanations. In this review, anthocyanins and xanthophylls are discussed in relation to their occurrence in different regions of the Northern Hemisphere, phylogenetic distribution and photoprotective function during the breakdown of chlorophylls. Pigments in senescing leaves that intercept incident light and dissipate the absorbed energy extend the time available for nutrient resorption. Experiments with Arabidopsis have revealed greatest anthocyanin photoprotective function at low temperatures and high light intensities, and high-resolution solar irradiation maps reveal that ENA and Asia receive higher irradiation than does Europe. In addition, ENA experiences higher temperature fluctuations in autumn, resulting in cold snaps during leaf senescence. Under common garden conditions, chlorophyll degradation occurs earlier in ENA species than in their European and East Asian relatives. In combination, strong solar irradiation, temperature fluctuations and, on average, 3-wk shorter vegetation periods of ENA species favour investment in pigments to extend the time for nutrient resorption before abscission, explaining the higher frequency of coloured species in ENA compared to Europe. We end by outlining research that could test this new explanation of bright New England autumns.

I. Introduction

In the temperate zone, decreasing day length and cold temperatures induce the breakdown of leaf chlorophyll (Chl) during senescence, followed by the eventual shedding of most leaves. During this process, plastid-located carotenoid pigments (xanthophylls), present throughout the year but initially masked by Chl, become visible. These pigments play a major role in deactivating the Chl

triplet state (^{3}Chl*) and singlet oxygen (^{1}O$_2$*) formed during light excitation and help dissipate excess light energy (Ruban *et al.*, 2002). The Chl breakdown process often is accompanied by the synthesis of vacuole-located anthocyanin pigments that also have a protective function against excess light and reactive oxygen species (ROS) (Chalker-Scott, 1999; Close & Beadle, 2003; Lee *et al.*, 2003; Gould *et al.*, 2018; Xu & Rothstein, 2018). During the past 20 yr, the possible adaptive value of yellow- or red-coloured autumn leaves has attracted the interest of both physiologist and evolutionary biologists. Indeed, Lev-Yadun & Holopainen (2009) mention that over 80 papers have discussed the adaptive value of autumn colouration.

A review of autumn colour change published 10 yr ago, based on a meeting, ended on 'the uncomfortable fact that there seem to be more hypotheses, and more published reviews and opinion pieces, on the subject of red leaf colouration than sources of good experimental data' (Ougham *et al.*, 2008, p. 13). Over the past decade, better data have become available on the phylogenetic and geographical distribution of the phenomenon of autumn coloura-tion, the pathway of Chl degradation and the protection of senescing cells from oxidative damage (Archetti, 2009; Lev-Yadun & Holopainen, 2009; Landi *et al.*, 2015; Viola *et al.*, 2016; Gould *et al.*, 2018). These data prompted us to revisit the function and evolution of autumn colouration.

A key aspect of Chl breakdown is the recycling of nutrients, especially the nitrogen (N)-rich proteins in the organellar cell walls (Matile *et al.*, 1999; Keskitalo *et al.*, 2005). Nutrient resorption needs a functioning metabolism, which in turn requires that cells be protected from oxidative damage when photons are no longer fully used in photosynthesis. This sets up the expectation that autumn colouration should be especially important under environmental conditions of high light intensities and low temperatures, damaging senescing leaves (Fig. 1). This expectation can now be tested against 'big data' temperature and irradiation maps that provide high-resolution measurements on the long-term monthly averages of temperatures and solar irradiation in North America, Europe and Asia, the continental regions most relevant to the topic of autumn colouration in arborescent species. In combination, the new climate and irradiation data, experiments on the environmental conditions under which anthocyanins are most beneficial for senescing leaves (Gould *et al.*, 2018), the relative frequencies of red, yellow and noncoloured leaves in different regions of the World, and common garden experiments on Chl breakdown in Northern Hemisphere species (Zohner & Renner, 2017; Zohner *et al.*, 2017) have led to a new framework for an adaptive understanding of autumn colouration.

In this review, we begin with the geographical and phylogenetic distribution of autumn colour change, summarize current phys-iological understanding of the function of anthocyanins and xanthophylls in senescing leaves, and present the arguments in support of the photoprotection hypothesis (Gould *et al.*, 1995, 2018; Feild *et al.*, 2001; Hoch *et al.*, 2001; Wilkinson *et al.*, 2002) and those for bright 'signalling' colours as resulting from coevo-lution with herbivorous insects (Archetti, 2000; Hamilton & Brown, 2001; Archetti & Brown, 2004; Archetti *et al.*, 2009), including extinct herbivore–plant interactions (Lev-Yadun &

Fig. 1 Autumn leaves of the Asian species *Cornus kousa* (a) and the North-American *Vaccinium corymbosum* (b) showing that anthocyanin production is sun-induced. Shaded parts of leaves remained yellow due to the lack of anthocyanin, whereas sun-exposed parts turned red. Feild *et al*. (2001) observed a similar pattern in *Cornus stolonifera*. Photos: E. I. Arndt.

Holopainen, 2009). We end by laying out a new explanation for why leaf colouration is more critical for North American and Asian woody species than for European species. We also outline further research that could clarify the adaptive value of red and yellow leaves, and the role played by regional temperature and irradiation differences that affect the phenological behaviour of long-lived woody plants.

II. Phylogenetic and geographical occurrence of autumn colour change

Transplantation experiments have shown that individuals maintain their autumn colour change when grown in different places (Archetti *et al.*, 2009), and many predictably colour-changing cultivars are available commercially, implying a strong genetic basis for patterns of autumn colour change. Even so, before 2009, there were no data on the phylogenetic distribution of autumn leaf colours. In that year, Archetti (2009) compiled the autumn leaf colours of 2368 tree species from 400 temperate zone genera, including both deciduous and evergreen groups, and then recon-structed the evolutionary origin of red and yellow autumn leaves using the 567-taxon phylogeny of Soltis *et al.* (2007) and standard parsimony reconstruction. Archetti categorized species as having (or not) green, yellow or red autumn leaves, and for a few also distinguished yellow-orange, brown-yellow-orange, yellow-red and other combinations. He found red autumn leaves in 290 (12%) species from 70 (17.5%) genera and yellow (independent from red) in 378 (16%) species from 97 genera (24%). The list includes hundreds of nondeciduous species (e.g. 125 species of *Rhododendron*, 53 of *Pinus*, numerous *Cupressus*, *Cotoneaster*) as well as arctic, temperate and subtropical species.

An analysis of autumn colour change in 1308 individuals from 711 deciduous woody species in a common garden in Munich (48°09′N, 11°30′E; 501 m asl) by a team of three observers from September to November 2017, found pure red autumn leaves in 5% (32) of the species, yellow and red leaves in 32% (228), and pure yellow leaves in 63% (451). There were no deciduous noncolour-changing species. In combination these data show that – as pointed

out by Archetti (2009, p. 707) – coloured senescing leaves are rare in flowering plants and gymnosperms overall, and it 'should not be taken for granted that they are a normal side-effect of leaf senescence'. However, in deciduous temperate-zone trees and shrubs of the Northern Hemisphere they are common. This point is highlighted by comparing a phylogeny of 1369 temperate species including deciduous and evergreen species (Fig. 2a) and one of 501 deciduous-only species (Fig. 2b), with the autumn colours of their leaves colour-coded.

It has long been noticed that anthocyanin-coloured red autumn leaves are commoner in Eastern North America (ENA) than in Europe or Asia, either because more species there turn red or (also) because red-leaved species are especially abundant (Lee *et al.*, 2003; Lev-Yadun & Holopainen, 2009). To quantify the phenomenon, Lev-Yadun & Holopainen (2009) examined the geographical distribution of all of the species with red autumn leaves listed by Archetti (2009) and found that ENA has 89 such species, whereas the whole of Europe has only 24, a number that agrees with our own compilation (Fig. 3). In Asia, at least 152 species have yellow or red leaves (Lev-Yadun & Holopainen, 2009). This needs to be seen in the context of the different tree species richness of these regions (Fine & Ree, 2006): The ENA temperate biome has 300 tree species (at least 30% of them with red leaves), the European temperate biome 124 (at least 19% of them with red leaves), and the East Asian temperate biome 729 (at least 21% with red or yellow leaves).

Of 711 species studied in the common garden in Munich, 119 came from Europe (i.e. 96% of Europe's native tree species), 148 from North America (49% of the region's tree species) and 444 from Asia (61% of the region's tree species), and in this sample, North America has a significantly higher proportion of species with red autumnal colouration than do Europe or Asia (*P* < 0.05; Fig. 3). Of the North American species, about equal numbers turn red (47%) or yellow (53%). Europe again has the lowest proportion of species with red-coloured autumn leaves (20%), followed by Asia (38%). The colour change in all these deciduous species was documented with photographs taken, on average, every 10 d per individual, and the observer team agreed on the categorization of colours. Following Archetti (2009), orange was grouped with yellow because both colours are caused by xanthophylls. The phylogenetic distribution of the species with red- or yellow-coloured senescing leaves shows that red-coloured leaves occur in 77 of 179 genera and are relatively evenly spread among temperate zone clades (Fig. 2b).

In St Louis, MO, USA, colour-change in marked red maple (*Acer rubrum*) individuals has been monitored by the first author (2007–2018), confirming that cold sunny days intensify anthocyanin production (Lee *et al.*, 2003; Fig. 4). This is supported by experimental cooling of autumnal maple branches, which led to increased foliar sucrose, glucose and fructose concentrations (two- to nearly 10-fold) and intensified anthocyanin production (Schaberg *et al.*, 2017). In *Arabidopsis*, cold conditions activate the transcription of arogenate deshy-dratase, the enzyme that transforms arogenate into L-pheny-lalanine, which also increases anthocyanin accumulation (Chen *et al.*, 2016).

III. Physiological functions of autumnal leaf xanthophylls and anthocyanins

Both young leaves and senescing leaves are at risk of photo-oxidation damage because their photosynthetic apparatuses are incomplete and unable to deal with high irradiance (Juvany *et al.*, 2013). In young growing leaves, damage can occur because of the intense generation of ROS due to low ascorbate peroxidase activity. In old leaves, it occurs because the first step in senescence is a rapid increase of ROS following the degradation of Chl, which leads to the oxidation of pigments, proteins and lipids. These oxidation processes are needed for nutrient remobilization, but they are necessarily accompanied by a risk of oxidative damage (Introduction). This is where autumnal pigments appear to play a role.

Xanthophylls are the pigments responsible for the yellow-orange colours of autumn leaves (Figs 1, 4). They are accessory light-harvesting pigments and present year-round in the photosynthetic membrane or in the hydrophobic environment of plastoglobules (Matile *et al.*, 1999). During leaf senescence and Chl breakdown, xanthophyll concentration steadily declines in both yellow- and red-senescing leaves (Lee *et al.*, 2003), and their role may be limited to protecting chloroplasts from short-term exposure to light stress (Ruban *et al.*, 2002; Gould *et al.*, 2018). Anthocyanins are the pigments responsible for colours ranging from blue to purple and red, and sometimes also yellow (Figs 1, 4). They are highly water-soluble and are a cationic sub-class of flavonoids, with their precise colour depending on vacuole pH and co-pigmentation processes with other flavonoids, hydroxycinnamic acids or metallic cations. Different from the xanthophylls, the anthocyanins' role in photoprotection is becoming well-understood, at least mechanistically as we describe in the following sections.

In the photo-oxidative context, anthocyanins in vacuoles (and other phenolic compounds in apoplast compartments) may have an important role in scavenging ROS (Zhang *et al.*, 2012; Xu & Rothstein, 2018), and in some cases anthocyanin biosynthesis is under redox control (Page *et al.*, 2012; Awad *et al.*, 2015; Viola *et al.*, 2016). Oxidative conditions induce anthocyanin synthesis via redox-sensitive-transcription factors (Viola *et al.*, 2016). Particularly important is TCP15, a transcription factor that negatively regulates anthocyanin accumulation. It is inactivated by oxidation under high-light conditions, and it always precedes anthocyanin accumulation. In TCP15-overexpressing plants, the transcription of PAP1, TT8 and DFR is lowered compared to wild-type (WT) plants. Furthermore, ascorbate peroxidase-deficient mutants (*apx1/tapx*) and catalase-deficient mutants (*Cat2HP1*, Vander-auwera *et al.*, 2005) accumulate more anthocyanin in response to low temperatures (*apx1* mutant; Asai *et al.*, 2004) and to high light (Awad *et al.*, 2015). Put differently, anthocyanin biosynthesis genes are impaired by high light in peroxisomal catalase-deficient plants (Vanderauwera *et al.*, 2005), and inhibition of catalase transcription after a cold night leads to increased photo-oxidation and favours anthocyanin accumulation (Macrae & Ferguson, 2006).

Comparative physiological experiments on the function of anthocyanins were first carried out in two unrelated species of tropical understorey herbs (*Begonia* and *Triolena*) that each have green and red leaves: Anthocyanins intercepted quanta otherwise
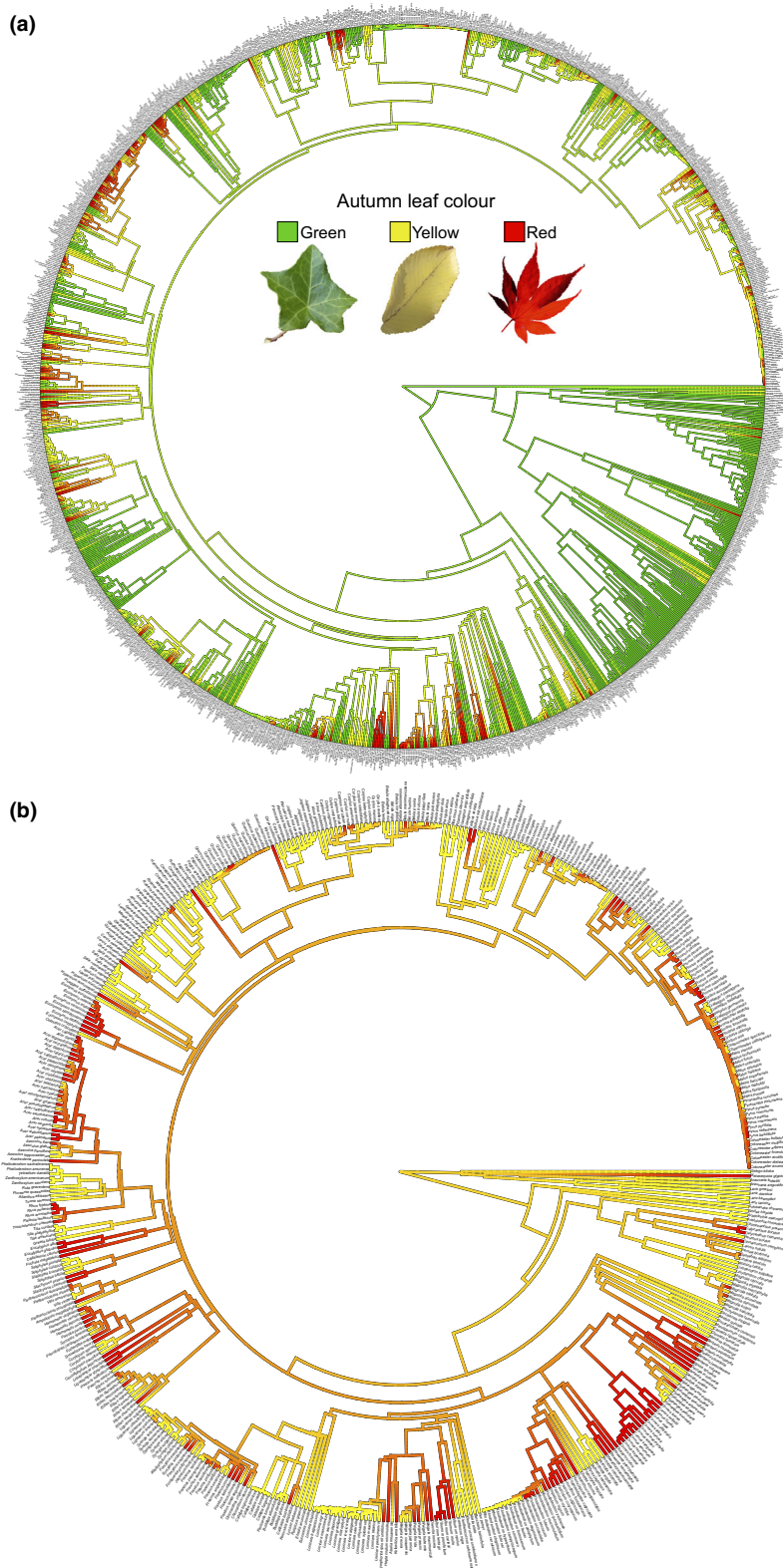
(a)

Autumn leaf colour

Green   Yellow   Red

(b)

Fig. 2 Phylogenies of 1369 temperate species (a) or 501 deciduous-only species (b) with autumn colours of leaves indicated by colours. Pagel's $\lambda = 0.6$ for both phylogenies. Phylogenetic data from Zanne *et al*. (2014). Leaf colouration data from own observations. For (a), data from Archetti (2009) were added to include evergreen species.

absorbed by Chl *b*, thereby protecting leaves from photoinhibition (Gould *et al.*, 1995). Experiments in a North American dogwood species further supported the hypothesis that optical masking of Chl by anthocyanins could reduce the risk of photo-oxidative damage to leaf cells as they senesce, which otherwise might lower

the efficiency of nutrient retrieval from senescing autumn leaves (Feild *et al.*, 2001). Over the past two decades > 50 studies have explicitly tested for photoprotection in a wide variety of systems to explain seasonal, developmental, and inter- and intraspecific differences in leaf pigmentation (Gould *et al.*, 2018, table 1). In
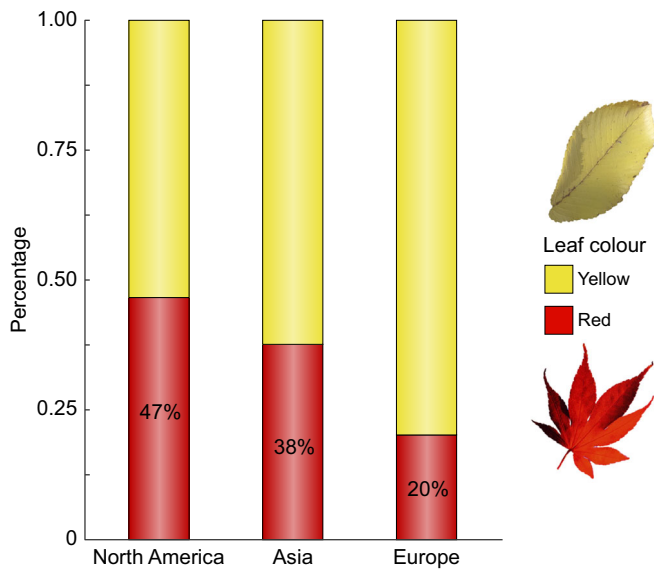
Fig. 3 Percentages of yellow and red species per continent for 711 species monitored in the Munich Botanical Garden. North America, Asia and Europe are significantly different in their occurrence of anthocyanin (chi-squared test: $P < 0.001$).

Fig. 4 Colour change in *Acer rubrum* and *Liriodendron tulipifera* individuals monitored in St Louis, MO, USA, 2007–2018. The timing of colour change in both species is highly consistent among years, with the intensity of the anthocyanin colour in the maple trees depending on the preceding night frost; no such intensity difference could be seen in the carotenoid colour of the tulip tree. Photo: P. Renner, 11 November 2013.

c. 30% of these studies, however, the physiological responses of red and green leaves to light were comparable or else, the anthocyanin-red foliage appeared to perform worse than green foliage. The explanation for this probably lies in the context-dependence of anthocyanin benefits.

In order to test for such context-dependence, Gould *et al.* (2018) compared the stress responses of WT (Col-0) *Arabidopsis thaliana*, which had only trace amounts of foliar anthocyanins, with stress responses in the anthocyanin-rich pap1-D mutant, and, in some experiments, the anthocyanin-deficient ttg1-1. They recorded effects of light quality, light intensity, air temperature and duration of exposure on quantum yield of photosystem II (ΦPSII) in leaves of different ages and compared pigment profiles before and after treatment. Although similar in anatomy, Chl content and xantho-phyll cycle activity, the anthocyanin-rich pap1-D mutants were less photoprotected than WT Col-0 (with only trace amounts of anthocyanin), but only when given at least 2 h exposure to saturating light at 10°C. Differences between the responses of red and green leaves were greatest in older plants that were given protracted exposures to high fluxes of cool-white light (5600 K) at chilling temperatures. This shows that anthocyanins' photopro-tective function is greater at lower temperatures and under higher light intensities (Gould *et al.*, 2018, figs 2–4).

Based on these findings, Gould *et al.* (2018) suggested that photoprotection by anthocyanins should be of greatest adaptive value for plants receiving prolonged exposure to intense cool-white light or natural sunlight at low temperatures, when the capacities of other photoprotective mechanisms are insufficient. Anthocyanins may, in addition, serve as useful sinks for excess photosynthates produced under saturating light; the close association between anthocyanin accumulation and sucrose content suggests that this could be their other important role (Gould *et al.*, 2018).

IV. The adaptive value of colour-changing leaves

Two main adaptive explanations for red or yellow autumn colouration have been put forward: the coevolution hypothesis and the photoprotection hypothesis. According to the coevolution hypothesis, bright autumn colours are warning signals to insects, especially aphids, that lay their eggs on the trees in that season. 'If the colour is linked to the level of defensive commitment of the tree and the insects learn to avoid bright colours, this may lead to a coevolutionary process in which bright trees reduce their parasite load and choosy insects locate the most profitable hosts for the winter' (Archetti & Brown, 2004, p. 1219). This explanation was first proposed by William Hamilton (Archetti, 2000; Hamilton & Brown, 2001; Archetti & Brown, 2004; Archetti *et al.*, 2009).

The two fundamental predictions of Hamilton's signalling hypothesis are that (1) trees use leaf colouration as an honest signal to communicate their defensive capacities to insects and (2) differences in leaf colours change the behaviour of insects. Over the past 18 yr, neither of these predictions has been supported by experimental or comparative data. On the contrary, there is evidence that the defensive commitment of a tree or a tree branch is negatively correlated with anthocyanin production. This is because phenylalanine precursors used in anthocyanin synthesis cannot

instead be used to produce other flavonoids of higher defence value (e.g. tannins, lignin, flavonols or flavones) or in the synthesis of hydroxycinnamic acids esterified to cell walls for reinforcing mechanical barriers against herbivores (see Meyer *et al.*, 2006, for the broader context of these trade-offs). Indeed, a study on Norway maple (*Acer platanoides*) found that anthocyanin production was highest in trees with the lowest defensive commitment, such as partially dead trees with low leaf N content (Sinkkonen, 2008). Autumn pigmentation is thus not an honest signal of defence commitment.

The largest study designed to test the second prediction (that colour affects herbivore behaviour) used *Betula pendula* genotypes with green or yellow autumn colouration and *Euceraphis betulae*, one of the most widespread tree aphids in Western Eurasia (Sinkkonen *et al.*, 2012). The study failed to find a significant relationship between genotypic variation in leaf colour reflectance or leaf attractiveness and the numbers of nymphs, males, or winged females on the respective trees. It appears that autumn-migrating aphids do not automatically concentrate on trees with the most attractive (yellow) leaves, but also use other cues for their orientation, such as female pheromones in the case of male aphids.

In a permutation of Hamilton's hypothesis, Lev-Yadun & Holopainen (2009) proposed that the solution to the problem of the origin of red autumn leaves in general, and their limited distribution in Northern Europe in particular, is the difference in the extinction histories of trees in ENA and East Asia (lower extinction rate) and those in Northern Europe (higher extinction rate). 'Not only did trees with red leaves mainly become extinct in Europe, but when many of their herbivores became extinct, the driving selective agents for red autumn colouration also declined. [. . .] Thus, the anti-herbivory component of the character of red autumn leaves partly reflects anachronistic adaptations to past faunas, many of which became extinct' (Lev-Yadun & Holopainen, 2009, p. 510). This strikes us as circular-sounding or, to paraphrase Olson & Arroyo-Santos (2015, p. 167), 'this trait was shaped by selection in unseen ancestral populations and this selection must have occurred because the trait is present'.

Under the photoprotection hypothesis, the yellow carotenoids and the red anthocyanins both function in photoprotection (Section III), which is beneficial because it helps extend the period of nutrient resorption, especially N and phosphorus (Feild *et al.*, 2001; Hoch *et al.*, 2001). Resorption from senescing leaves requires synthesizing numerous enzymes and regulatory elements involved in the degradation and remobilization of leaf nutrients (Hoch *et al.*, 2001; Landi *et al.*, 2015). Reflecting this, leaf respiration continues unchanged or at an increased rate during senescence (Hoch *et al.*, 2001) because as chloroplasts are getting impaired, the remaining organelles acquire novel functions, particularly the mitochondria (Keskitalo *et al.*, 2005). In essence, senescing leaves need to retain, at least in part, their defence potential against both ROS and toxic lipid peroxidation products to successfully dismantle their photosynthetic apparatus during senescence in a relatively safe manner.

Although the photoprotection hypothesis has solid experimental support (Section III) it fails to explain why red and yellow leaves should be more common in ENA and Asia than in Europe (Fig. 3). This is where Gould *et al.*'s (2018) experimental evidence from Arabidopsis comes in. Their data show that anthocyanins' photoprotective function is greatest at lower temperatures and under higher light intensities when the need to quench excess light exceeds the cells' capacity for thermal energy dissipation (further relevant experiments are cited in Section III). One would therefore expect that red and yellow autumn leaves should be most common in species exposed to sudden cold spells and high light intensities.

This expectation can be tested against climate and solar irradiation high-resolution data on the long-term monthly averages of temperatures and incoming radiation in North America, Europe and Asia, the regions that are most relevant to the question of the adaptive value of autumn colouration in arborescent species. The temperate deciduous forests of North America and Asia receive higher solar irradiation during autumn than does Europe (Fig. 5). In North American deciduous forests, the average daily short-wave radiation in September is $168\,W\,m^{-2}$. In Asian forests, it is $165\,W\,m^{-2}$. By contrast, with only $114\,W\,m^{-2}$, European forests receive 32% less irradiation during autumn than North America (Fig. 5b). Also, for shrub-/grasslands, autumn irradiation is highest in North America ($190\,W\,m^{-2}$) and lowest in Europe ($141\,W\,m^{-2}$), with Asia intermediate ($162\,W\,m^{-2}$; Fig. 5c).

Intercontinental differences in both leaf-out and Chl breakdown times between the arborescent species of ENA, Asia and Europe have been found in studies that compared species from the three regions grown under identical conditions (Zohner & Renner, 2017; Zohner *et al.*, 2017). Experiments on 396 species from East Asia, Europe and ENA revealed that the length of the vegetation period, which is the time between leaf-out and leaf senescence (measured as 50% colour change and/or leaf abscission), of ENA species is 3 wk shorter than the vegetation periods of their European and East Asian relatives, because their leaves flushed 9 ± 4 and 13 ± 4 d later and senesced 9 ± 4 and 11 ± 4 d earlier (Zohner & Renner, 2017). The authors attributed these regional differences to higher interannual temperature fluctuations in North America compared to Asia and Europe (see fig. 1a in Zohner *et al.*, 2017). Less predictable springs and autumns apparently have favoured more conservative (safer) phenological strategies in North America compared to Asia and Europe.

Given these regional differences in the leaf-out and Chl breakdown strategies of Northern Hemisphere trees and shrubs, we believe that the higher frequency of red leaves in North America compared to Europe reflects the combined effects of higher average autumn irradiation and earlier initiation of senescence when intensities of solar irradiation are higher (Fig. 5). Additionally, North American species likely experience more cold days during the senescence process than do Asian and European species because of greater temperature fluctuations (above). Because the environmental conditions under which the photoprotective benefit of leaf pigments is greatest are precisely conditions of low temperatures and higher light intensities (Gould *et al.*, 2018), the higher frequency of colour-changing species in North America and Asia (and their rarity in Europe) exactly match theoretical expectations. In addition, the on-average 3-wk shorter vegetation periods of ENA species (Zohner & Renner, 2017) may place an additional burden on American species of extending the period during which their
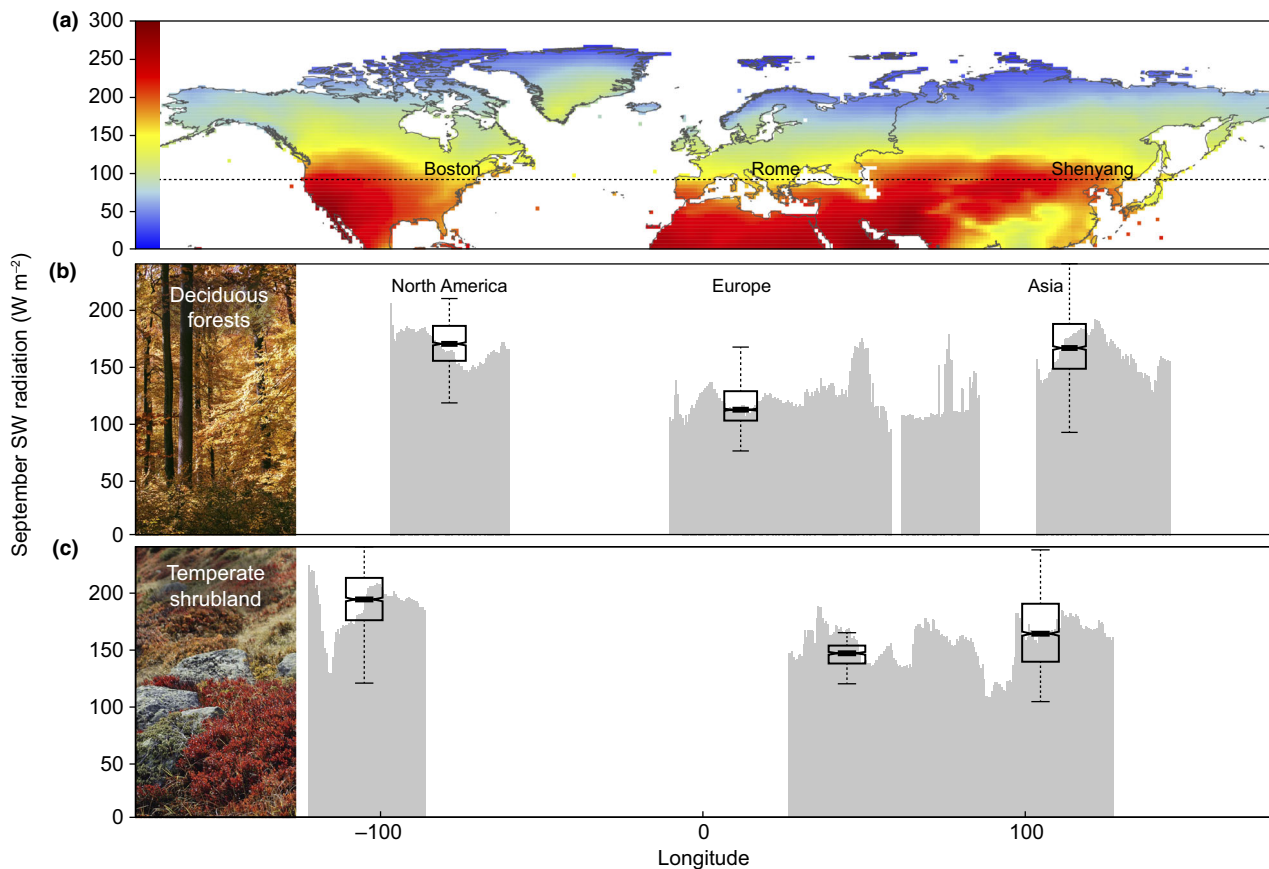
Fig. 5 Longitudinal differences in autumn solar irradiation. (a) Average (from 1901 to 2010) daily short-wave (SW) irradiation for the month of September. Data on SW radiation from Beer *et al.* (2014). (b, c) Continental differences in autumn SW radiation for deciduous forests (b) and temperate shrub-/grasslands (c). Error bars refer to 95% confidence intervals. Information on spatial distribution of biome types from Olson *et al.* (2001).

photosynthetic tissues are protected from ROS by anthocyanins so that nutrients can be resorbed.

V. Outlook

This review sets up a new framework for an evolutionary understanding of autumn colouration. To test whether our photoprotection-cum-regional-climate hypothesis explains spatial patterns of autumn colouration, species-level colouration data need to be linked to species distribution data. Databases are available (e.g. GBIF for species occurrence points or GFBI for abundance-weighted plot-level data) that would allow such analyses. Also, a global map of solar insolation for the relevant autumnal period is needed. The relevant period needs to be defined based on regional leaf-senescence times obtained from remote sensing data. Having data on the relevant autumn period will also allow testing for the effects of cold days during leaf senescence.

Another possibility to test the photoprotection-cum-regional-climate hypothesis would be to compare nutrient resorption strategies. In species (or populations) strongly limited by N, one would expect higher selection for efficient nitrogen resorption in autumn than in species less limited by N and thus higher investment in anthocyanins. Conversely, the active production of

anthocyanin should be less beneficial in nutrient-rich sites. This theoretically expected trade-off between investment in anthocyanin production and benefits from recycled nutrients receives some support from the observation that plants living in symbiosis with N-fixing bacteria, such as alders (*Alnus*), do not produce autumn colours (Archetti, 2009). A global test of this hypothesis is still missing.

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