

Coevolution and the adaptive value of autumn tree colours: colour preference and growth rates of a southern beech aphid

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Abstract

The evolutionary explanation for the change in leaf colour during autumn is still debated. Autumn colours could be a signal of defensive commitment towards insects (coevolution) or an adaptation against physical damage because of light at low temperatures (photoprotection). These two hypotheses have different predictions: (1) under the coevolution hypothesis, insects should not prefer red leaves in autumn and grow better in spring on trees with green autumn leaves; and (2) under the photoprotection hypothesis, insects should prefer and grow better on trees with red leaves because they provide better nutrition. Studying colour preference in autumn and growth rates in spring of a southern beech aphid species (*Neuquenaphis staryi*) on *Nothofagus alessandrii*, we found preference for green leaves in autumn but no differential performance of aphids in spring. We suggest that aphid preference for green might have evolved to exploit better their host during the autumn rather than to improve their performance in spring.

Introduction

The adaptive value of the autumn colours of leaves is still a matter of controversy. Red and yellow autumn colours are produced in all deciduous forests in the temperate regions, although not by all species of deciduous trees. Autumn colours are mainly because of carotenoids (yellow–orange) and anthocyanins (red–blue–brown) (Lee, 2002a). It has been known for at least three decades (Sanger, 1971) that autumn colours are not merely the effect of the breakdown of chlorophyll. Although carotenoids, which are present all year, may become visible because of the degradation of chlorophyll, anthocyanins are actively produced in autumn (Lee, 2002a,b). Their production, however, has a cost for the plant, and the question about the adaptive value of producing pigments in leaves that are about to fall is still unanswered. Two main evolutionary explanations have been proposed: autumn colours could have evolved in plants to protect them against the physical damage induced by intense light at low temperatures (photoprotection hypothesis) or to avoid parasites by signalling the defensive commitment of the tree (coevolution hypothesis).

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Photoprotection

The most likely protective function of anthocyanins against physical agents is protection against photoinhibition (Pringsheim, 1882; Lee, 2002a; Lee & Gould, 2002b). When it is cold, light is intense or phosphorous is limited, the efficiency of photosynthesis often declines, in particular blocks in photosystem II may occur, which may damage chloroplasts and tissues. There is indeed evidence that anthocyanins allow an enhanced photosynthesis under strong light, especially in cold temperatures (Gould *et al.*, 1995; Smillie & Hetherington, 1999; Feild *et al.*, 2001; Hoch *et al.*, 2001), although this does not seem to be always the case (Burger & Edwards, 1996). Protection against oxidative damage also seems to be a function of anthocyanins (Yamasaki, 1997; Gould *et al.*, 2002; Neill *et al.*, 2002), whereas the idea of photoprotection for better starch hydrolysis and sugar translocation (Pick, 1883) seems to have been abandoned. Other hypotheses of protection against physical agents do not seem applicable to autumn leaves and seem to have been abandoned (Lee & Gould, 2002a).

It is important to notice that, because autumn leaves are going to fall in a short time, shielding the photosynthetic apparatus of a falling leaf would add little to the carbon supply of a tree and seem unlikely to justify the metabolic costs of the production of anthocyanins (Lee &

Gould, 2002b). The point, however, is that an efficient photosynthetic apparatus in autumn may allow a better recovery of nutrients from the leaves, most notably of nitrogen, which is mainly present in the leaves and must be recovered before they fall. Therefore, the protection conferred by autumn pigments is not supposed to be useful to the leaves themselves but to the whole tree – because it may recover more nutrients, notably nitrogen (Hoch *et al.*, 2001; Lee, 2002a). Feild *et al.* (2001) failed to detect any difference in resorption of nitrogen and Lee *et al.* (2003) also did not find a better resorption of nitrogen in species with red leaves, although they did find an intraspecific correlation (individuals with a higher anthocyanin concentration had more nitrogen). These results therefore remain open to further investigation (Lee *et al.*, 2003).

Coevolution

Direct evidence for the production of anthocyanins as an immediate consequence of attack by insects, and their effect as unpalatable deterrents against herbivory, is scarce (Lee & Gould, 2002a). The idea that the red colour of young leaves in certain tropical plants warn away potential herbivores by signalling their unpalatability (Kursar & Coley, 1992; Coley & Barone, 1996) or by simply making the leaves less detectable by herbivores that cannot perceive red (Stone, 1979; Juniper, 1993) seems to have scarce application to autumn colours, simply because the leaves are going to fall anyway and avoiding herbivory *per se* does not seem important at this stage.

Coloured pigments may nonetheless protect against herbivores or parasites, not because they are produced as a direct response to damage, but because they reduce future damage. If leaf colour is an indicator of the level of defences of the tree, then it is possible that colour acts as a warning signal towards insects that lay their eggs on the tree in autumn. Archetti (2000) and Hamilton & Brown (2001) put forward the idea that autumn colours are a visual signal of defensive commitment to autumn migrating insects (e.g. aphids). The idea (reviewed in Archetti & Brown, 2004) is that the autumn colours are correlated with the level of defences of the tree, and therefore plants investing more in defences show more autumn colours. If insects adapt to avoid red leaves in autumn, this will lead to a coevolutionary process in which both preference for green in aphids and intensity (or duration) of red in trees increase. If the production of anthocyanins is costly, it is possible that the signal is a handicap *sensu* Zahavi (Archetti, 2000). Note that it is not necessary that the level of the signal is correlated with the vigour of the tree (Archetti & Brown, 2004). It may even be that it is the weakest trees that have more defences (and hence are more coloured). The condition for a signal to be a handicap is that the cost of the signal be,

for weak trees, higher than the cost imposed by parasites (Archetti, 2000). More precisely, the ratio of the fitness cost of the signal and the benefit received (avoiding parasites) must be higher in individuals giving lower signal (green), either because the signal is less costly for a signaller of high quality, or because individuals give stronger signals when in greater need (Maynard-Smith & Harper, 2003). Note also that a signal can also be an *index* (Maynard-Smith & Harper, 2003), which does not need to be costly to be honest, because it cannot be faked (for example, if it is proportional to the level of defences produced by the same biochemical pathway).

The coevolution theory predicts an interspecific association between tree species with autumn colours and insects migrating in autumn to lay their eggs, a prediction that Hamilton & Brown (2001) have shown to be plausible. At the intraspecific level, the coevolution theory predicts a preference of insects for trees with green leaves in autumn, a prediction that has been shown to be plausible by some recent studies (Hagen *et al.*, 2003, 2004; Archetti & Leather, 2005; Karageorgou & Manetas, 2006; see also Furuta, 1986). The coevolution theory also predicts that insects should have a lower growth rate in spring (an indirect measure of the level of defences of the tree) on trees that had red leaves in autumn. This is a crucial prediction that has not been tested so far.

A critical test

It is possible to test whether autumn colours are an adaptation against photooxidation or against parasites because the two hypotheses have different predictions (Archetti, 2007): if aphids prefer green (in autumn) and grow better (in spring) on trees that had green leaves in autumn, then this would support the coevolution theory because performance of aphids in spring is assumed to be negatively correlated with the redness, which is – in the coevolution theory – a signal of defences of the tree. On the contrary, if aphids prefer red (in autumn) and grow better (in spring) on trees that had red autumn leaves, then this would support the photoprotection theory because the correlation of autumn colours with nutrient recovery would be more important than the correlation of colours with the level of defences. There are certainly many factors influencing the performance of aphids on trees in spring, but everything else being equal, the prevalence of defences or of nitrogen content should lead aphid performance in opposite directions, as aphid performance correlate positively with plant nitrogen contents (Sandström & Pettersson, 1994). Estimating the compounds involved in chemical defence would be another option, but measuring growth rates of aphids is a more direct and straightforward method to test the two hypotheses.

A different abundance of aphids on green and red leaves in autumn is not necessarily associated with differential performance of aphids in spring. The tree might exploit the aphid colour vision to reduce its parasite load: as red leaves appear probably more dull and cryptic to aphids (Döring & Chittka, 2007), then being red might confer the tree an advantage by excluding some aphids. If aphids perform equally well in autumn-red and autumn-green trees in spring, then it is possible that the colour is not linked to the level of defences but still confers an advantage to the tree by reducing the number of parasites.

Although there is some evidence for aphid preference for green leaves (Hagen *et al.*, 2003, 2004; Archetti & Leather, 2005; Karageorgou & Manetas, 2006) and that aphids are able to discriminate between trees in the autumn that are better for their offspring in spring (Leather, 1986), growth of aphids in spring, on trees with different autumn colours, has never been measured. Thus, combining tree colour variation and aphid colour preference in autumn with aphid growth in spring would help to elucidate whether or not autumn colours are an evolutionary relevant cue for aphids. Archetti & Leather (2005) did not manage to measure growth rates in spring because of the extremely high mortality of the overwintering eggs.

Study system

The genus *Neuquenaphis* Blanchard (Hemiptera, Aphididae, Neuquenaphidinae) is endemic of the South American temperate forests, grouping 11 'Gondwanan' relic species almost exclusively associated to *Nothofagus* trees (Southern beech forests) (Blackman & Eastop, 1994). Among these species, *Neuquenaphis staryi* Quednau & Remaudière lives exclusively associated to an endangered host, *Nothofagus alessandrii* Esp. (Fuentes-Contreras *et al.*, 1997; Gaete-Eastman *et al.*, 2004; Russell *et al.*, 2004), which has a restricted distribution in the coastal range of Central Chile and whose leaves turn red in autumn. We studied field abundance of *N. staryi* on trees of *N. alessandrii* differing in colours in autumn, and performed a simple choice test of colour preference in the laboratory. We also measured the performance in spring, of aphids born on trees that had different leaf colours in the previous autumn.

Materials and methods

Aphid abundance in autumn (in the field)

Female oviparae (wingless sexual females) and virginoparae (wingless and winged parthenogenetic viviparous females) of *N. staryi* were counted – and some collected for analysis in the lab (see below) – on 16 individual *N. alessandrii* trees on 30 May 2006 at Los Ruiles National Forest Reserve (35°50'1.61"S; 72°30'37.51"W) in Central

Chile. Aphids on 30 leaves per tree were counted for a total of 480 leaves. Trees were marked in order to measure performance of aphids on the same trees during the next spring.

Pictures of each sampled leaf (upper surface) were taken with a digital camera and analysed with the software *ASTRA IMAGE 2.5 MAX* and *ADOBE PHOTOSHOP*. Two kinds of measures were used in the analysis: the ratio between red and green (R/G) calculated from the RGB values and the measure ($a - b$) calculated from the CIE Lab colour space (Commission Internationale d'Eclairage L*a*b). Colour information is contained in the R (red) and G (green) values for the RGB system and in the a and b values for the CIE Lab system, where a denotes a green–red value (with green being negative and red positive) and b denotes a blue–yellow value (with blue being negative and yellow positive). Therefore, the measure ($a - b$) is an approximative measure of how close is a leaf to the red–purple of anthocyanins and how far it is from the green of chlorophyll. These measures, although precise and more accurate than an assessment made by the human vision, quantifies colour according to human trichromatic vision and not according to aphid vision (photoreceptor sensitivities in aphids, at least in the autumn morphs, is still unknown).

This method was chosen instead of measuring spectral reflectance because leaves do not have a uniform colour and may contain different quantities and different hues of green, yellow, brown and red. Because spectrophotometric devices measure only a tiny fraction of a surface, it would be necessary to perform hundreds of measures per leaf in order to have an average reflectance spectrum, and this was not practically possible at the site.

Methods based on spectral reflectance are certainly preferred to get an absolute measure of colour, but what is important for testing preference is the *relative* colour of the leaves, because aphids are expected to select between *relative* colours of neighbouring trees. Absolute measures, therefore, are not essential to our test.

Aphid preference in autumn (in the laboratory)

Winged virginoparae of *N. staryi* collected on *N. alessandrii* on 30 May 2006 at Los Ruiles National Forest Reserve were brought to the laboratory and kept at 4 °C. Individual aphids were placed in a Petri dish (diameter 8 cm) whose top and bottom was covered by two transparent filters of different colours, each occupying half of the dish, thus creating two different light (colour) environments inside the Petri dish. The upper and lower surfaces were illuminated by an artificial white light and the Petri dish was installed in the middle of a white paper cylinder (diameter 20 cm, height 10 cm) to avoid interferences with the external environment. We used three filters (Lee Filters, Andover, UK: green no. 124, yellow no. 767, red no. 25) in three combinations (green–red,

green–yellow, yellow–red) and measured the amount of time each aphid spent in the different halves of the Petri dish during 10 min. The experiment was repeated 12 times for each of the three-colour combinations. A new aphid and a new Petri dish were used for each preference experiment (for a total of 36).

Aphid performance in spring

We looked for aphids on the same 16 trees we had sampled for colour and measured reproduction of the aphids. In order to have more individuals, it would have been better to randomly collect aphids from several different trees, put them on the trees for which we had measured colour in autumn and record their growth rate. The problem, however (common in aphids), is that the current reproduction rate is the consequence of host quality experienced back to three generations (this is due to telescopic generations). Therefore, it would be necessary to put the aphids for three generations on a neutral host and then assess their performance on the trees we intended to measure. This aphid species, however, is a specialist and would not survive on any other host. Therefore, we decided to measure only the growth rates of aphids we already found on the trees for which we had measured colour in autumn.

Performance tests were carried out enclosing one to three adult females in a 2 cm diameter clip-cage using a total of eight cages per tree. The number of offspring was determined 14 days later and the fundamental net reproductive rate (Begon *et al.*, 1990) was calculated from the equation $N_t = N_0 \times R^t$, where N_0 is the initial number of aphids and N_t the number of aphids after t days. Performance of aphids in spring was only measured on 11 of the original 16 trees. Tests were repeated two times at early (October 6, $n = 79$) and late (December 16, $n = 81$) spring. The number of nymphs was expressed as mean nymphs per day and the correlation between the number of nymphs and the mean autumn colour per tree was calculated.

Results

Abundance in autumn in the field

Nothofagus alessandrii leaves turn red in autumn. There was a large variation in colour when we measured aphid abundance in the field, among trees and leaves (Fig. 1). We observed a negative correlation between the number of aphids and autumn colours using the $a - b$ method (Fig. 2) of the 16 individual trees, i.e. higher abundance of aphids on green rather than red or yellow trees (Pearson's correlation for oviparae: $r = -0.422$, $P = 0.10$; for virginoparae $r = -0.502$, $P < 0.05$). The same trend was observed for the 480 individual leaves (Fig. 2; for oviparae: $r = -0.103$, $P < 0.05$; for virginoparae: $r = -0.109$, $P < 0.05$). Similar correlations were observed using R/G as a measure of colour both at individual trees (for oviparae: $r = -0.536$, $P < 0.05$; for virginoparae: $r = -0.487$, $P = 0.056$) and individual leaves (for oviparae: $r = -0.183$, $P < 0.05$; for virginoparae: $r = -0.231$, $P < 0.05$). Aphids abundance, therefore, seem to be higher on green than on red and yellow trees and aphids seem also capable of selecting individual leaves according to their colour.

Preference in autumn in the laboratory

There was also a significant preference for green over red (Student's t -test for dependent samples: $t_{11} = 2.93$, $P < 0.05$; Fig. 3a) and for yellow over red ($t_{11} = -2.42$, $P < 0.05$; Fig. 3b) but no difference between green and yellow ($t_{11} = 0.36$, $P = 0.756$; Fig. 3c) in the laboratory experiment. Our simple laboratory test suggests that red light is less attractive to aphids walking in a Petri dish.

Performance in spring in the field

There was no significant correlation between fundamental net reproductive rate and autumn colours at early (Pearson's correlation, $r = -0.17$; $P = 0.14$; Fig. 4a) and late spring ($r = -0.14$; $P = 0.18$; Fig. 4b). Therefore,

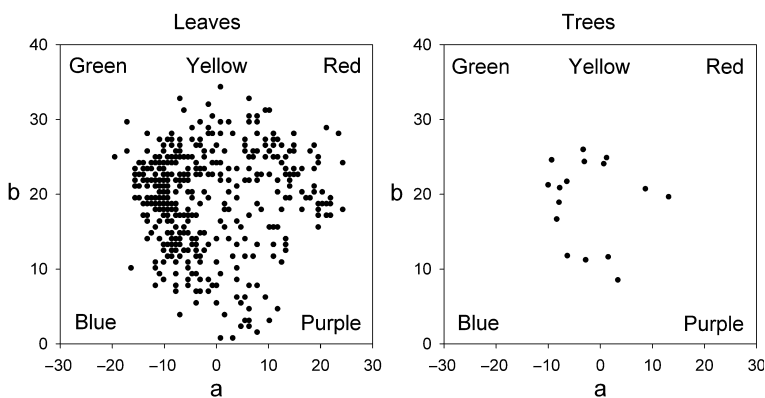


Fig. 1. Colours of the 16 trees and 480 leaves of *N. alessandrii*. Each data point indicates the a and b value of a leaf or a tree.

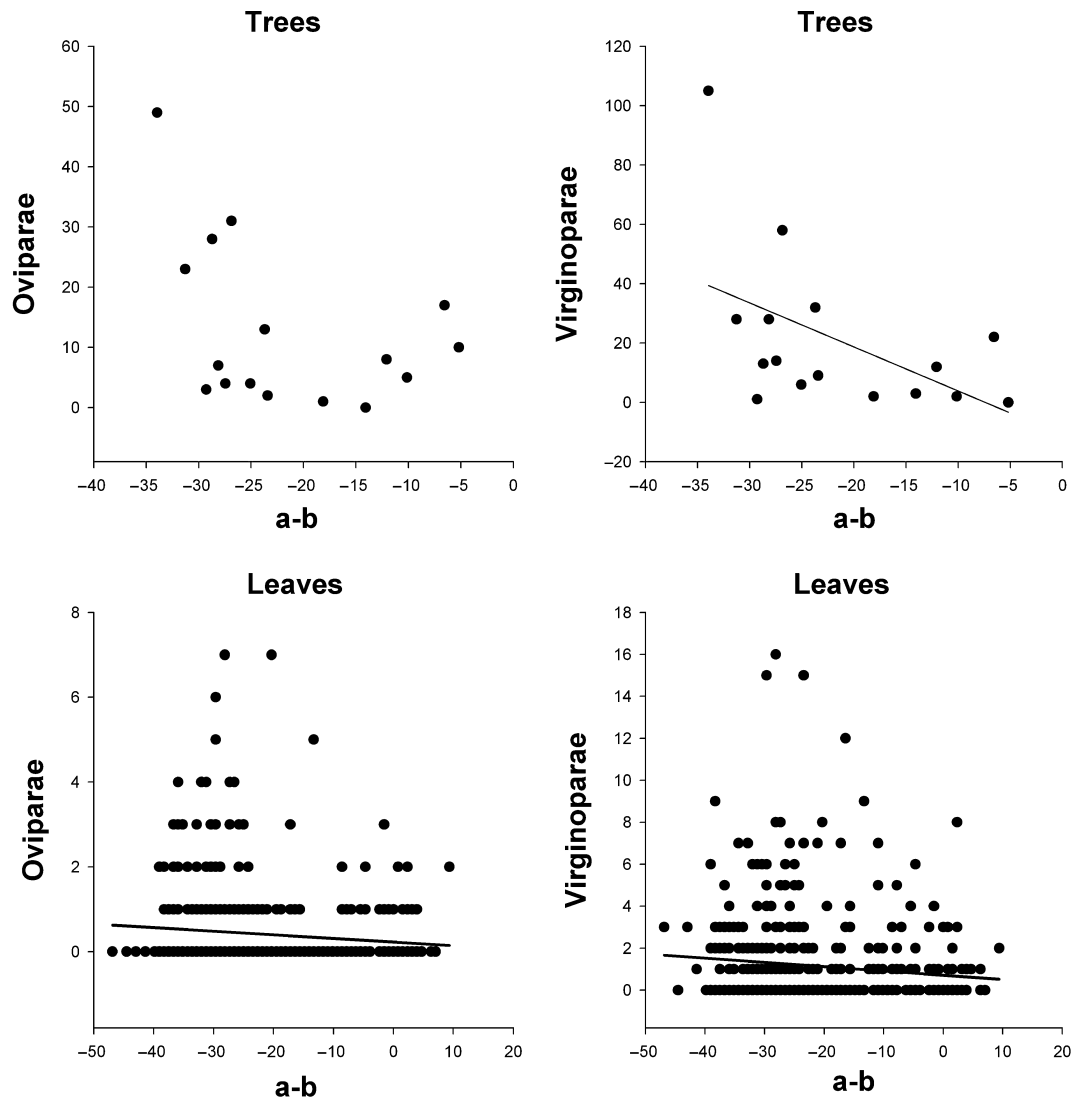


Fig. 2 Aphid abundance on the 16 trees and 480 leaves of *N. alessandrii*. The number of individuals (oviparae or virginoparae) is plotted against the *a-b* values of the individual leaves or the mean value of the individual trees (30 leaves per tree). The linear regression is shown.

there seems to be no differential performance in spring on trees with different autumn colours. Reproductive rate was significantly higher in early than in late spring (1.055 ± 0.03 and 1.007 ± 0.03 , respectively, Student's *t*-test for independent samples $t_{152} = 10.18$, $P < 0.001$).

Discussion

Higher abundance of aphids on green rather than on red or yellow was observed on *N. alessandrii* in autumn. This was the case when the mean leaf colour of the trees was considered but also when abundance per leaf was taken into account. The southern beech aphid *N. staryi*,

therefore, not only seems to prefer green over red and yellow trees but also seems capable of expressing a preference for individual leaves. However, there is some evidence from the bird cherry-oat aphid suggesting that in the field this aphid do not seem to be able or be bothered to distinguish between different coloured leaves on a tree (Leather, 1981). Differently, the sycamore aphid, which normally aestivates over the summer when the leaves are mature and of low nutritional quality, moves from leaf to leaf choosing to feed on senescent leaves when available (Dixon & McKay, 1970). Although there is other evidences of preference for green over yellow and red trees (Furuta, 1986; Hagen *et al.*, 2003, 2004; Archetti & Leather, 2005; Karageorgou & Manetas,

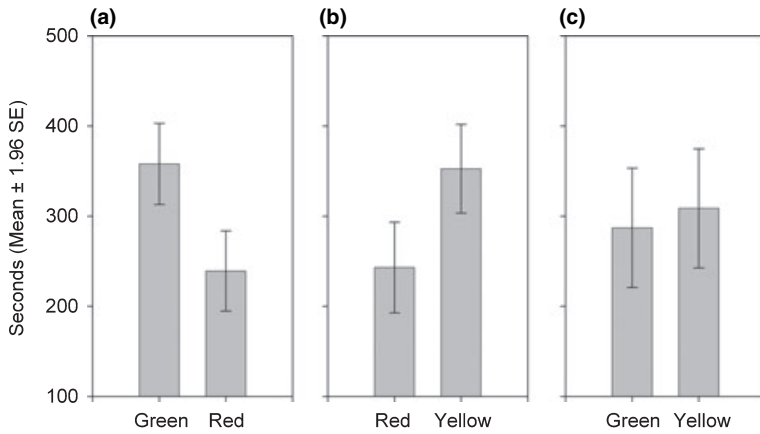


Fig. 3 Colour choice preference of virginoparae individuals of *N. staryi* in the laboratory. Time (mean \pm SE in seconds) spent in each coloured arena is plotted for two-choice colour experiments ($n = 12$ in each case): (a) green vs. red, (b) red vs. yellow and (c) green vs. yellow.

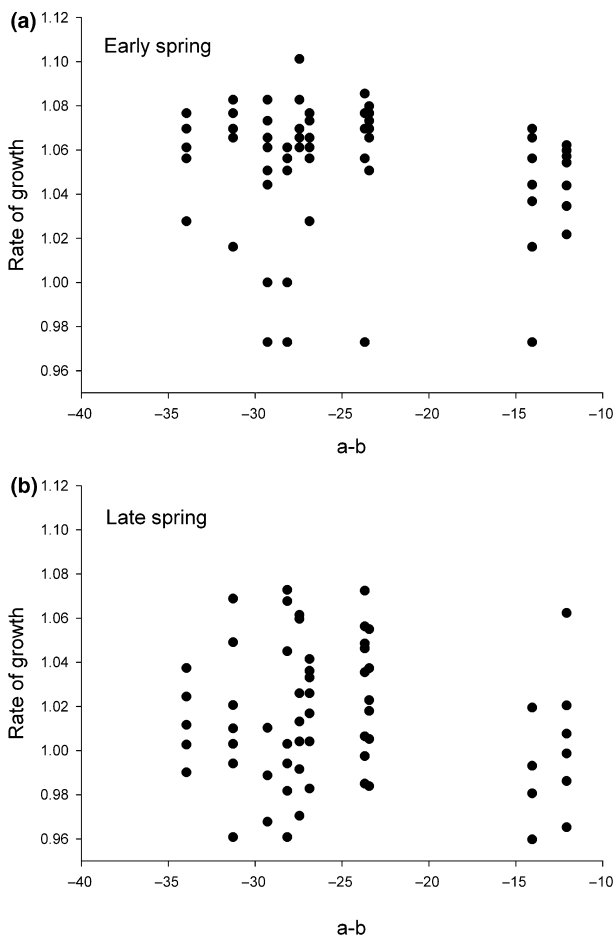


Fig. 4 Performance of *N. staryi* measured as the fundamental rate of growth plotted against the a-b values of the individual aphids during early (a) and late (b) spring.

2006), given the scarce resolution of arthropod vision (Döring & Chittka, 2007) it remain to be tested whether the southern beech aphid could discriminate between individual single leaves.

Our simple laboratory test also suggests that red light is less attractive for aphids walking in a Petri dish. Although it is certainly questionable whether an aphid walking in a Petri dish behaves as an aphid flying towards a tree, this suggests that aphids prefer green or yellow rather than red light (and there is no difference between green and yellow) without any chemical cues involved. These results support the idea that autumn colours are important in host choice by the southern beech aphid, and that aphids are more abundant on green rather than on red leaves. This preference for green might be a colour preference, but it might also be a preference for brighter leaves (red being probably more dull and cryptic for aphids).

No significant correlation was found between the growth rates of aphids in spring and the autumn colours of the trees. Aphid performance in spring was not negatively affected on trees with red leaves in autumn. Therefore, the trees with yellow–red autumn colours seem to have neither higher defences in spring nor better nutrients for the aphids. It seems that aphids such as the specialist *N. staryi* do not prefer red leaves in autumn but this is not related to their performance in spring. As aphids did not prefer red (in autumn) and also did not grow better (in spring) on trees that had red autumn leaves, the photoprotection theory does not seem to be supported in this case.

Moreover, the average rate of growth was significantly higher during early spring as compared with late spring, which could suggest that during early spring *N. alessandrii* trees are less resistance to aphid herbivory. This is a common phenomenon in aphids (Sequeira & Dixon, 1996; Dixon, 1998), also in agreement with the resource-based plant defence theories, such as the carbon/nutrient balance hypothesis (Bryant *et al.*, 1983) and the growth/differentiation balance hypothesis (Lorio, 1986; Herms & Mattson, 1992), which predicts that the growth processes dominate over differentiation or production of carbon-rich secondary compounds. In particular, under the growth/differentiation balance hypothesis, allocation to defensive compounds should be low in early spring

during the rapid growth of the short-shoot leaves which form the vast majority of the trees foliage (Herms & Mattson, 1992; Tuomi, 1992; also see Riipi *et al.*, 2002). Thus, the prediction of differential performance of herbivores in spring of the coevolution theory of autumn colours may not take place because *N. alexandrii* may not spend resources in defence compounds at the beginning of the growing season. Therefore, the importance of avoiding red leaves for aphids seems to be limited to their preference in autumn.

Aphids such as the specialist *N. staryi* could prefer green leaves because they may need to use them as long as possible in autumn and preference for green might have evolved to exploit better their host. It is possible, for example, that high predator densities could modulate resource use and delay oviposition of prey. Parents can protect offspring by actively searching for enemy-free patches (Mappes & Kaitala, 1995; Murphy, 2003; Nomikou *et al.*, 2003; Resetarits *et al.*, 2004). Some evidence of this has been recorded for mites; oviposition was delayed in patches with high predator density as compared with patches with less predators or no predators (Montserrat *et al.*, 2007). If this was true for aphids, females that actively avoid egg predation by searching for low predator pressure patches would therefore need resources to survive longer in the season and search for new patches. Therefore, high egg predation pressures could induce egg retention of oviparous aphids and therefore select for trees with green leaves in order to delay oviposition.

Preference for green in autumn is consistent with the coevolution theory. If the colours are correlated with the levels of defences, however, we would expect a lower growth rate of aphids in spring on trees that had red leaves in the previous autumn. This was not the case. It seems possible, therefore, that the tree is exploiting the aphid colour vision to reduce its parasite load, as red leaves are probably more cryptic to aphids (Döring & Chittka, 2007). Autumn colours, therefore, would still confer an advantage to the tree by reducing the impact of parasites but the advantage for aphids, if any, seems to be restricted to autumn and not related to growth rates in spring. It is possible that aphids simply prefer green because it is an *index* that the leaves are going to stay longer on the tree. This effect must be tested with further experiments showing that aphids actually have a selective advantage in autumn on green leaves. Clearly, in this case, aphids are expected to show an active preference for green over red. As we have discussed, however, the preferential landing of aphids on green leaves might also reflect an inherent bias in their colour vision, with no active preference.

Further data on aphid colour visions will be necessary to understand the effects of hue and brightness on host selection in autumn by aphids, and to understand if the higher abundance of aphids on green rather than on

red leaves is due to an active choice or to an inherent property of aphid vision.

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