

# Do aphids paint the tree red (or yellow)—can herbivore resistance or photoprotection explain colourful leaves in autumn?

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**Abstract** We explored two mutually nonexclusive hypotheses on autumnal leaf colouration. The co-evolutionary hypothesis states that autumnal leaf colouration functions as a handicap signal to herbivorous insects, whereas the photoprotection hypothesis posits that plant pigments primarily protect the plant against cold-induced photoinhibition and enhance nutrient transfer. To contrast both hypotheses, we compared yellow and red leaf colouration in three groups of mountain ash (*Sorbus aucuparia* L.). Two montane groups of different age were characterised by low aphid numbers and low temperature, and a lowland group by high aphid numbers and high temperature. There were no consistent altitudinal differences in leaf colouration. Compared to young trees, adult trees developed fewer red but more yellow leaves at high altitude. In the lowland population, the development of red leaf colour was related to decreasing daytime temperature, whereas the appearance of yellow leaf colouration corresponded to the decreasing photoperiod. This is consistent with the photoprotection hypothesis. Individual differences in red and yellow leaf colouration were inversely correlated to the number of fruits, which might be

interpreted as a trade-off between reproductive and protective commitment. Temperature effects explained variation in aphid numbers over time and leaf colouration explained aphid distribution on a given day. As predicted by the co-evolutionary hypothesis, strongly coloured individuals harboured fewer aphids than green or dull-coloured ones. Since decreasing temperature reduced the number of migrating aphids but induced red leaf colouration, these processes are not mutually fine-tuned, which likely restricts the potential for co-evolution between mountain ash and aphids.

**Keywords** *Sorbus aucuparia* · Autumnal senescence · Pigments · Co-evolution · Photoinhibition · Handicap signal

## Introduction

The conceptual framework of plant–animal communication has mainly been developed in the context of pollination and seed dispersal (Schaefer et al. 2004). A new hypothesis is that plants communicate their defensive strength to herbivores visually. Accordingly, brightly coloured yellow and red leaves in autumn are proposed to be costly and thus classical handicap signals indicating the fitness of individual plants (Archetti 2000; Hamilton and Brown 2001). The fundamental conjecture of this hypothesis is that

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signalling defensive strength enables well defended plant individuals with strong yellow and red colouration to reduce their herbivorous load and, at the same time, allows insects to locate suitable (less defended) dull-coloured hosts more efficiently. Proponents of this view argue that such a signalling system is maintained by a co-evolutionary process between plants and insects e.g. aphids that migrate to their hosts in autumn (Archetti 2000).

The co-evolutionary hypothesis is remarkable because it is the first to propose that plants communicate their defensive strength visually, it ascribes signalling as a new function to leaves, and it focuses on autumnal leaf colouration, a phenomenon that evolutionists and ecologists had previously regarded as a mere by-product of senescence. Tests of the hypothesis support its main prediction i.e. that individuals with brightly coloured leaves suffered less damage by herbivorous aphids (Archetti and Leather 2005; Hagen et al. 2003, 2004).

However, there are various alternative hypotheses on leaf colouration e.g. that it serves to undermine crypsis (Lev-Yadun et al. 2004). The co-evolutionary hypothesis in particular was questioned based on theoretical considerations of the physiological role that plant pigments serve in senescent leaves (Holopainen and Peltonen 2002; Schaefer and Wilkinson 2004; Wilkinson et al. 2002). There is growing evidence from a large number of plant species that carotenoids and anthocyanins, the pigments imparting yellow, orange and red hues to leaves, influence the elemental processes of photosynthesis and nutrient recovery during autumnal senescence. In autumn, decreasing temperatures often inhibit photosynthesis, a process called cold-induced photoinhibition (Egerton et al. 2000; Dungan et al. 2004). In such conditions, anthocyanins provide a sunscreen to intercept excess light quanta, thereby reducing damage caused by photoinhibition and extending the period of photosynthesis (Adams et al. 2004; Pietrini et al. 2002). Moreover, the autumnal leaf pigments are important scavengers of reactive oxygen species (Adams et al. 2004; Gould et al. 2002) that might develop during photoinhibition or during the controlled breakdown of leaf tissue during

senescence (Close and Beadle 2003; Hoch et al. 2003). During this breakdown nutrients are transferred from leaves to perennial tissue and comparisons between anthocyanin-deficient mutants and wild-type individuals demonstrated that anthocyanins facilitate this recovery of nutrients (Hoch et al. 2003).

As emphasised by Gould (2004) and Lev-Yadun (2006) pigments serve multiple roles in communication and protection. It is therefore surprising that, until now, tests of the co-evolutionary hypothesis and of the protective physiological effects of plant pigments (termed hereafter the photoprotection hypothesis) are published concomitantly, but with minimal impact on each other. To examine both hypotheses, we compared leaf colouration in three groups of European mountain ash (*Sorbus aucuparia* L.) growing at two different altitudes. At the montane site, young and adult trees were characterised by relative low temperature and low numbers of parasitising aphids, whereas adult trees in the lowland were characterised by higher temperature and higher aphid numbers. While the photoprotection hypothesis expects a higher degree of leaf colouration in the montane population, the co-evolutionary hypothesis predicts a higher degree of red and yellow colouration in the lowland population. Measuring the variation in leaf colouration within a population, we asked which factors explain the onset and progression of yellow and red leaf colouration. Finally, we investigate which biotic or abiotic factors explain variation in the number of aphids in mountain ash individuals.

## Methods

The mountain ash is distributed over a wide altitudinal range from approximately 200–2000 m a.s.l. (Raspe et al. 2000). The species sports red and yellow leaf colouration in autumn and hosts over ten aphid species (Blackmann and Eastop 1994). Since it adapts to adverse climates at higher altitudes, the species is particularly suited to contrast the protective physiological and the co-evolutionary hypotheses on autumnal leaf colouration. Our study is focused on aphids

because of their importance as tree pests and their migratory behaviour in autumn (Dixon 1969, 1976; Blackman and Eastop 1994).

We recorded leaf colouration and the number of aphids in two populations of mountain ash near Freiburg (south-west Germany, 48°N; 8°O) from end of September to mid-November 2004. The population located at an altitude of 1100 m a.s.l. (termed the montane group) included 30 mature individuals (3.5–5 m high) and 25 young individuals (<1.5 m high) on an area of 2.5 ha, the other population (termed the lowland group) included 25 individuals (2–4 m high) growing at 360 m a.s.l. on an area of 0.15 ha. The populations were 5 km apart.

At each location, air temperature was measured continuously every 30 min with a Testo® Logger (Lenzkirch, Germany), positioned in a tree 2 m above the ground. The data were pooled to obtain a mean day (8<sup>00</sup>–20<sup>00</sup>) and night time (20<sup>00</sup>–8<sup>00</sup>) temperature, respectively. The montane group was permanently exposed to lower ambient temperatures (mean SE = 7.48 0.85°C) than the lowland group (mean ± SE = 11.99 ± 0.80°C; Wilcoxon:  $n = 46$ ,  $z = -5.905$ ,  $P < 0.001$ ). The time of direct sunshine did not differ between both locations (Wilcoxon-test:  $z = -0.57$ ,  $P > 0.5$  data from Deutscher Wetterdienst, Offenbach). The photoperiod was calculated as the time between sunrise and sunset as obtained from a local weather station. The same observer monitored leaf colour change (prior to abscission) of each individual in both locations every 2–4 days in the period from 28th September 2004 to 21st November 2004. We assessed colour changes by determining the percentage of red, yellow, green, and brown leaves of each tree to the nearest 5%, using a prepared colour chart as reference as well as spectrometric reflectance measurements. Several modes of leaf colour progression occurred in the observed populations. Mountain ashes changed from green to yellow and then red, but also from green to yellow and finally brown or from green directly to red or brown. Abscission occurred when leaves were yellow, red or brown.

To assess the density of aphids in both locations, we installed 15 traps, consisting of laminated, brown coloured paper sheets with a

size of 10 × 10 cm, covered with a thin layer of Temmen® insect-glue (Hattersheim, Germany). In both locations we put one trap in each of 15 randomly chosen *Sorbus* trees and counted the insects on the glue in intervals of 2–4 days. The trap was located approximately 2.5 m above the ground in the middle of the plant. Since a large aphid population was only present in the lowland population, we restricted our analyses of a possible deterrent function of leaf colours to this site. In order to determine variation in the number of aphids landing on *Sorbus* individuals within this population, we covered four branches of each tree with insect-glue on an area of 200 cm<sup>2</sup>. Every 2–4 days, all insects were removed from the glue and all winged aphids were counted on each individual. To assess individual parameters that might relate to fitness, we counted the number of ripe fruits in mid-October and the degree of fluctuating asymmetry (FA) in leaves for each plant individual. To investigate the possible link between leaf colouration and reproduction in the following year (see Hagen et al. 2003; Sinkkonen 2006a, b), we counted the number of unripe fruits in the following year. To measure FA, we randomly selected eight leaves from each tree and measured the distance from the midpoint of the leaf midvein to the left and right leaf margin in mm (Lempa et al. 2000). Individual FA was defined as the mean difference between the left and right side of the leaves. Since right minus left dimensions did not deviate from zero (one-tailed  $t$ -test:  $n = 25$ ;  $t = -1.65$ ;  $P > 0.05$ ), the leaves demonstrated FA (Palmer 1996).

### Statistical analyses

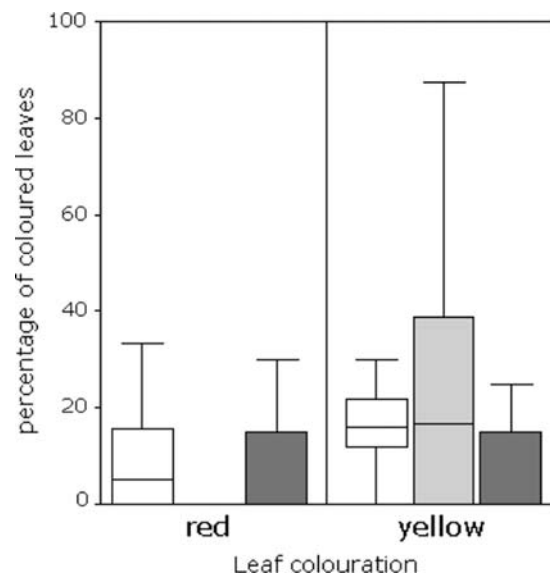
To analyse which factors explain the onset and progression of leaf colour changes in the lowland population of mountain ash, we constructed Generalised Linear Models with the daily individual percentage of coloured leaves for each tree as the dependent variable. We tested the influence of abiotic parameters (temperature and photoperiod) and individual variables (FA and number of fruits). Since abiotic parameters change over time, they were included in the model as covariates, whereas individual parameters were included as factors. For the analyses we

used the mean temperature of 3 days, including the observation day (of leaf colouration and aphid numbers) plus the two preceding days because we assumed that plants and insects react to changes in the temperature over the course of several days rather than instantaneously to the temperature at any given day. The full model was reduced by sequentially excluding variables that did not explain a significant part of the deviation. The model was run with the same factors and covariates for red and yellow leaf colour, respectively. In a second model we tested which factors determine the within-population variability of aphids caught on trees. We entered red and yellow leaf colouration, abiotic factors and individual parameters as independent variables in the model. It was our aim to test the basic assumption of the co-evolutionary hypothesis that the proportion of individual colouration is, relative to the mean colouration of the population, the important signal to herbivores. Each census date, we therefore categorised individuals as pale (0–5%), medium (6–16%), or strongly (>16%) coloured according to the proportion of yellow or rather red leaves. Since individual leaf colouration changes over time, trees were allowed to change categories in this model. Thus, the model tests whether the extent of leaf colouration, relative to the mean of the population on a given day, influences individual parasitism rate. We assessed the effects of leaf colouration with Scheffé post-hoc tests, and therefore repeated the analysis with all variables entered as factors, which increased the  $r^2$  value from 0.44 to 0.56. All Generalised Linear Models are based on linear regressions. Since the models did not fulfil the criteria of homogeneity in variance (Levene-test), the level of significance for exclusion was set from  $P < 0.05$  to  $P < 0.01$  (see RRZN 2000). We used Mann–Whitney  $U$  test for unpaired data and Wilcoxon signed rank test for paired data. Statistical analyses were performed with SPSS 10.5.

## Results

Mountain ash individuals of the lowland population and two different age groups of the montane population showed different leaf colour changes

during autumnal senescence. At the montane site, adult individuals showed a lesser percentage of red leaves (mean  $\pm$  SE =  $0.25 \pm 0.25$ ) than young trees ( $10.4 \pm 2.9$ ) (one-way ANOVA:  $F = 7.80$ ,  $P > 0.01$ , Post-hoc Bonferroni correction  $P < 0.01$ ). Over the entire study period trees of the lowland population with higher ambient temperature had a higher proportion of red leaves ( $8.13 \pm 2.07$ ) than same-sized montane individuals (Post-hoc Bonferroni correction  $P < 0.05$ ), while there was no difference between lowland and young montane trees (Post-hoc Bonferroni correction  $P > 0.05$ ; Fig. 1). However, young trees started to develop red leaves earlier (peak of mean colouration 4th October) than individuals in the lowland (peak of mean colouration 11th November) resulting in a higher mean of red colouration in the beginning of October (Mann–Whitney test,  $z = -1.95$ ,  $P < 0.05$ ). Young trees had fewer yellow leaves than adult trees at the same site (one-way ANOVA:  $F = 5.43$ ,  $P < 0.01$ , Post-hoc Bonferroni correction:  $P < 0.01$ ), while there was no difference between



**Fig. 1** Comparison of red and yellow leaf colouration in a lowland (white bars) and montane population (grey bars: adult group, dark grey bars: young group) of mountain ash. Displayed are the means for each population, 2nd and 3rd quartiles and 5th and 95th percentiles. Note the lack of red colouration in the adult montane group

yellow leaf colouration in the lowland population and the two montane groups (Post-hoc Bonferroni both  $P > 0.05$ ). The numbers of aphids caught at both sites differed greatly over the entire season with consistently higher aphid numbers (mean  $\pm$  SE =  $26.10 \pm 5.49$ ) on lowland individuals than on montane ones ( $0.74 \pm 0.21$ ; Wilcoxon:  $z = -2.20$ ;  $P < 0.05$ ).

Due to the scarcity of aphids in the montane population, we restricted the further analysis to the lowland group. Here, individual colour changes in yellow leaf colouration were strongly related to the photoperiod (Table 1). The number of fruits and the FA of the leaves also contributed to changes in yellow leaf colouration. However, there was no linear relationship between the extent or onset of yellow leaves and FA (both  $P > 0.05$ ). Changes in red leaf colouration were strongly related to daytime temperatures, but also to the number of fruits (Table 1). The onset of the development of red leaves correlated positively with the extent of red leaves ( $r^2 = 0.53$ ,  $P < 0.05$ ). Consequently, early senescing trees had a higher proportion of red leaves during the entire study period. There were no correlations between the extent or onset of red leaves and FA (both  $P > 0.05$ ). The number of fruits in the same year was negatively correlated with the extent of red leaf colouration ( $r^2 = 0.29$ ,  $P < 0.05$ ); there was no such relationship for yellow leaf colouration or between red leaf colouration and the number of fruits in the following year.

Abiotic factors and leaf colouration influenced aphid parasitism rates ( $r^2 = 0.44$ ) with a strong positive influence of day and night temperatures on aphid numbers (Table 2). While temperature

is important in explaining variation in aphid numbers over time, it cannot explain the differences in individual aphid numbers on a given day that the co-evolutionary hypothesis aims to address. As predicted by the co-evolutionary hypothesis, there was a negative relationship between the proportion of both yellow and red leaf colouration and aphid numbers (Table 2). Post-hoc Scheffé-procedures showed that strongly coloured red or yellow individuals hosted fewer aphids than medium or pale-coloured ones, which did not differ in parasite load (Fig. 2).

## Discussion

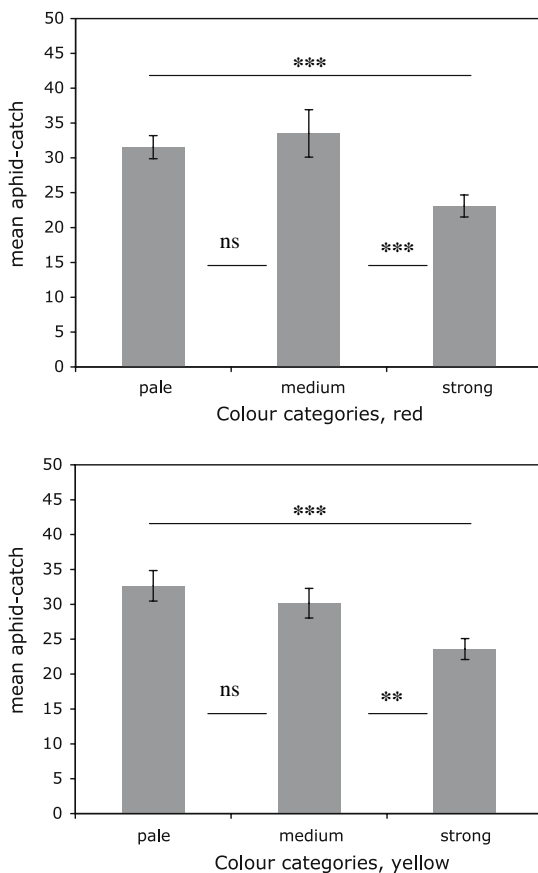
Young and adult mountain ash individuals growing at the montane location differed in the onset and development of autumnal leaf colour. Likewise, similar-aged individuals growing at different altitudes showed distinct colour changes. Consistent with the photoprotective hypothesis, our study shows that leaf colour changes in the intensively studied mountain ash population were strongly related to abiotic factors. Differences between individuals in the extent of red and yellow leaf colouration were linked to reproductive investment in fruits, suggesting a trade-off between reproductive and protective or defensive commitment. Finally, the inverse relationship between aphid numbers and the proportion of yellow and red autumnal leaf colouration in the lowland population suggests that aphids react to tree colouration and therefore supports the co-evolutionary hypothesis. To disentangle the causes and effects of autumnal leaf colour

**Table 1** Generalised linear models on yellow ( $r^2 = 0.253$ ) and red ( $r^2 = 0.301$ ) leaf colouration revealed that abiotic and individual factors contributed to colour changes in mountain ash

	Yellow leaf colour			Red leaf colour		
	<i>F</i>	<i>P</i>	<i>T</i>	<i>F</i>	<i>P</i>	<i>T</i>
Model factors	4.715	0.000		6.715	0.000	
FA	10.798	0.000			ns	
Number of fruits	3.311	0.000		6.423	0.000	
Covariates						
Photoperiod	16.409	0.000	-4.051		ns	
Temperature (day)		ns		11.682	0.001	-3.418
Temperature (night)		ns			ns	

**Table 2** Temperature and leaf colouration influenced the number and distribution of aphids on mountain ash trees, Generalised Linear Model ( $r^2 = 0.442$ )

	<i>F</i>	<i>P</i>	<i>T</i>
Model factors	25.378	0.000	
Red colouration	11.605	0.000	
Yellow colouration	7.263	0.001	
FA		ns	
Number of fruits		ns	
Covariates			
Photoperiod		ns	
Temperature (day)	107.388	0.001	3.521
Temperature (night)	7.144	0.008	2.673



**Fig. 2** Results of post-hoc Scheffé tests on the distribution of aphids according to colour categories of mountain ash individuals in the lowland group. Strongly coloured red (**a**) and yellow (**b**) individuals harboured fewer aphids (mean  $\pm$  SE) compared to medium or pale-colour ones (\*\*\* $P < 0.001$ ; \*\* $P < 0.01$ )

changes for an evaluation of both hypotheses, we consider first the factors related to colour changes and second the implication of these changes.

## Leaf colouration

Different mechanisms are responsible for the development of yellow and red leaf colouration. The degradation of chlorophyll in the leaf leads to the gradual appearance of yellow carotenoids that function as accessory pigments in the photosynthetic apparatus, whereas anthocyanins imparting red colours are synthesised *de novo* in senescent leaves (Ougham et al. 2005). Consistent with the photoprotection hypothesis, our GL-models revealed that abiotic factors are associated with yellow and red leaf colouration. The appearance and proportion of yellow leaves in mountain ashes were inversely correlated with the decreasing photoperiod in autumn as well as with individual factors of tree quality such as FA of the leaves and the number of fruits. Previous studies found similar correlations between yellow leaves and the photoperiod (Schaberg et al. 2003) or FA (Hagen et al. 2003). In contrast to Hagen et al. (2003), we did not find that early senescing yellow or red trees had lower FA values than later senescing ones.

The development and extent of red leaf colouration in the lowland population of mountain ash did not depend on the photoperiod but on daytime temperatures. The overall effects of temperature on anthocyanin synthesis are well known (e.g. Pietrini et al. 2002; Schaberg et al. 2003). However, our model distinguishes between temperatures during the day and night, and revealed that mainly daytime temperatures are related to the extent of red leaf colour. Since the photoprotection hypothesis assumes that anthocyanins function to protect the photosynthetic apparatus against excess light (see Pietrini et al. 2002; Schaefer and Wilkinson 2004), it predicts that daytime temperatures are most relevant. Our results are therefore consistent with the photoprotection hypothesis. In contrast to our predictions based on this hypothesis, red leaf colouration was lower in adult trees growing at the colder montane location than in similar-aged trees at the lowland site. The lack of red leaves in adult montane individuals is not only attributable to site-specific conditions such as soil quality, nitrogen availability or shading because young individuals at that site developed red leaves. This

difference may be due to age-dependent strategies of photoprotection (see below) or nutrient utilisation (see Harper 1989; Karageorgou and Manetas 2006). Further research is clearly needed to assess the effects of leaf pigments on physiological processes like differing levels of nitrogen resorption (e.g. via fluorescent measurements).

The inverse relationship between red leaf colouration and fruit numbers suggests a trade-off between reproduction and investment in bright colours (for photoprotection or as defence against insects) similar to that found between catkin production and leaf colouration in mountain birch (*Betula pubescens*) (Hagen et al. 2003, but see Sinkkonen 2006a). There was no relationship between autumnal leaf colouration and fruit production in the following year. We suggest that nutrient restricted mountain ash individuals produce less fruits and invest more in anthocyanin production to enhance nutrient recovery from autumnal leaves (see Hoch et al. 2003). This conjecture is consistent with the observation that young trees developed more red leaves than adult trees. Young trees are characterised by a lower shoot:root ratio, the importance of transferring nutrients from leaves to perennial tissue is therefore probably more pronounced at this age class than in adult trees. We suggest that future studies should test whether age-dependent differences in the autumnal leaf colouration of other species are consistent with this conjecture. Note that in contrast to the co-evolutionary hypothesis, this prediction of the photoprotection hypothesis expects individuals of lower fitness to show a higher degree of leaf colouration.

### Aphids and leaf colouration

The GL-Model on the aphid catch on *Sorbus* trees yielded a strong positive influence of day and night time temperature and a negative influence of leaf colouration on aphid numbers. On a given day, temperature effects mainly determined the overall number of aphids present in the population, whereas leaf colouration probably explains individual differences in the distribution of aphids on trees. Since the co-evolutionary hypothesis aims to explain the latter, our results that fewer aphids were caught on strongly coloured mountain ashes

than on medium or pale-coloured ones support this hypothesis. This inverse relationship between leaf colour and aphid numbers is consistent with previous studies showing lower insect damage (Hagen et al. 2003, 2004) or aphid numbers on strongly coloured trees (Archetti and Leather 2005). Ougham et al. (2005) pointed out that insects might not have reacted to plant colouration in these studies, but landed initially in equal numbers on all trees and vacated strongly coloured plants only after sampling. Since we caught the aphids landing on a tree with glue, our data directly reflect winged aphids' choice of host trees. We can, however, not exclude that cues other than colours (e.g. olfactory cues) might have contributed to host choice.

An important implication of our study is that decreasing temperatures reduced the number of migrating aphids but induced leaf colouration. We therefore suggest that both processes are not mutually fine-tuned, which probably reduces the likelihood for a co-evolutionary origin of leaf colouration in mountain ash. In this scenario, aphids might react to leaf colouration because pigments are often correlated with defensive compounds (Nozzolillo et al. 1990; Syvacy and Münevver 2004) or with the production of anti-feedants (Huang et al. 2001). A parsimonious explanation for such correlations is the common biosynthetic pathway of anthocyanins and various defensive compounds (see Schaefer and Rolshausen 2006). In conclusion, more knowledge is required on leaf colouration as the interface between the biochemistry of defensive compounds and feeding preferences in insects.

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