

LETTER

Autumn colouration and herbivore resistance in mountain birch (*Betula pubescens*)

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Abstract

We explored Hamilton and Brown's autumn signalling hypothesis in mountain birch (*Betula pubescens*). As predicted by the hypothesis, early autumn colour change (i.e. high degree of autumn colouration in September) was negatively correlated with insect damage the following season. Furthermore, as expected, indices of physiological stress (i.e. leaf fluctuating asymmetry) and reproductive investment (i.e. catkin production) were positively correlated with insect damage the following season. Indirectly, we also found support for the idea that the proposed handicap signal (i.e. early autumn senescence) might be associated with an honesty ensuring cost in terms of lost primary production. Further work is, however, required to determine whether the link between autumn colours and insect damage observed in this study is causal.

Keywords

Autumn colouration, fluctuating asymmetry, handicap signal, herbivore resistance, reproductive investment.

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INTRODUCTION

Most deciduous trees change colour in autumn. However, within and between species, there is considerable variation both in the timing and magnitude of autumn colour change. Hamilton & Brown (2001) recently launched a hypothesis to explain this phenomenon (see also Archetti 2000). Their idea was that the relative degree of autumn colouration in trees is an honest (handicap) signal (Zahavi 1975) to insects about investment in defence. As support for this signalling hypothesis, they analysed published data and found that autumn colouration is more intense in tree species suffering greater attack from specialist aphids. In addition, they presented evidence that the conditions for a handicap signalling system between trees and their insect pests are met. Although highly controversial (Holopainen & Peltonen 2002; Wilkinson *et al.* 2002), the signalling hypothesis remains largely unexplored.

From an empirical perspective, the basic prediction of the signalling hypothesis is the expected association between signal intensity and insect attack within tree species (Hamilton & Brown 2001; Wilkinson *et al.* 2002). The prediction is that defensively committed individuals should produce intense displays, compelling insects to lay eggs on another individual of the same species (Hamilton & Brown 2001). If this is so, one should expect a negative correlation

between the degree of autumn colouration and the degree of insect damage the following season. Although the colour *per se* may also differ, the timing of autumnal colouration is both the key source of variation in degree of autumn colouration and of potential handicap costs among individuals of a tree species at a single site. Trees that express autumn colouration early will not only be conspicuous, but they will also potentially lose primary production following an early cessation of photosynthesis (Hamilton & Brown 2001). Consequently, the signalling hypothesis predicts an association between exposure to egg-laying insects and timing of colour change in autumn, with defensively committed trees expressing autumn colouration earlier.

However, the sources of intraspecific variation in insect attack are likely to be diverse. For example, reproduction may be traded against defence, yielding increased attack in reproductively committed individuals (Karlson *et al.* 1996). Stress from browsing may in turn affect the ability of the tree to grow, reproduce and defend itself in future. A commonly used index of stress is fluctuating asymmetry (FA) (Martel *et al.* 1999), i.e. random deviation from anticipated symmetry in morphological traits (Van Valen 1962). The basis of this inference is that, because the same genes regulate the development of both halves of a bilaterally symmetrical character, differences between halves is a measure of developmental noise (Palmer 1996). In

deciduous trees, FA in leaves has been shown to increase with pollution, altitude and hybridization (Kozlov *et al.* 1996; Wilsey *et al.* 1998). Yet, of particular interest to the signalling hypothesis, FA in leaves of trees often correlates positively with indices of herbivory (Møller 1995; Zvereva *et al.* 1997), suggesting a close connection between FA, nutrient value and defensive chemistry in leaves (Lempa *et al.* 2000). Thus, in addition to indicate stress, FA in leaves of trees might indicate susceptibility to attacking herbivores.

We assessed the relative role of timing of autumn colour change (i.e. degree of autumn colouration in September), physiological stress (i.e. leaf FA) and reproductive investment (i.e. catkin production) in predicting insect damage in mountain birch (*Betula pubescens*). The main aim was to explore the signalling hypothesis, which was carried out by examining the link between timing of autumn colour change and insect damage the following season. Furthermore, we wanted to explore the possibility that the proposed handicap signal (i.e. early leaf senescence) might be energetically expensive. This was carried out by examining the relationship between insect damage and timing of colour change within years, i.e. by looking for evidence that trees suffering greater damage extended their photosynthetic season, which would indicate an association between potential primary production and timing of autumn colour change. As stressed and/or reproductively committed trees may be more susceptible to insect attack, variation among trees both in the level of leaf FA and level of catkin production was controlled for in the analyses, which enabled us to explore the signalling hypothesis within the framework of established ecological theory.

METHODS

The study was carried out from 1999 to 2001 in northern Norway (69°16'N, 17°59'E). Twelve mountain birch trees of similar size (*c.* 4 m), standing within an area of *c.* 10 m × 10 m, were selected for the study. Each year, we recorded four variables for each tree (details below) (i) autumn colouration, (ii) insect damage, (iii) physiological stress (i.e. leaf FA), and (iv) reproductive investment (i.e. catkin production). Thus, the design of this observational study allowed us to (1) estimate the strength of both direct and delayed effects of the selected variables on level of insect attack, (2) examine whether other specific conditions in time (i.e. year) affected the response of insects, and (3) test whether the insects responded in a consistent way to the variables of interest in different years (i.e. test for interactions).

Autumn colouration was estimated in mid-September. The trees were photographed with a 25–80 mm lens. To standardize background and light conditions, all pictures were taken against a portable black background within

c. 20 min on a clear day. From these pictures, two persons independently scored degree of autumn colouration as percentage yellow vs. green leaves. The repeatability of this method was high ($R^2 = 0.80$, $P < 0.0001$, $n = 12$; between persons), showing that within-tree variation had little effect on colour perception at the tree level. Measuring colouration visually was preferred because the signalling hypothesis predicts that defensive investment should be readily observable.

Insect damage was estimated as percentage grazed vs. intact leaves in a random sample of 100 leaves collected from each tree in mid-August ($R^2 = 0.96$, $P < 0.0001$, $n = 12$; between persons). We focused on damage caused by leaf chewing insects, because it is easily detected and therefore also easily quantified with high accuracy. Moreover, leaf chewers represent a very diverse group of insects, not only taxonomically, but also in their degree of host plant specialization and activity period. The test of the signalling hypothesis presented here should therefore be conservative, because of the potentially large variation in the response of different insect species.

Reproductive investment was estimated by counting the total number of catkins on each tree in mid-August ($R^2 = 0.97$, $P < 0.0001$, $n = 12$; between persons). Fluctuating asymmetry was estimated from 30 (1999) and 60 (2000–2001) leaves collected randomly from each tree in mid-August. The leaf dimensions measured were the length of the left and right halves at mid-point between the base and the tip, perpendicular to the midvein. Phenodeviants, i.e. leaves with FA values >2 SD from the mean, were removed. Measurement error of FA was estimated by letting another person re-measure 30 randomly selected leaves. Measurement error was small relative to differences in asymmetry between leaves ($F_{29, 60} = 28.18$, $P < 0.0001$). Moreover, right minus left dimensions did not deviate from zero ($b = 0.062$, $SE = 0.043$, $P = 0.15$), showing that the leaves demonstrated FA (Palmer 1994). As FA increased with leaf size ($b = 0.016$, $SE = 0.0046$, $P = 0.0004$), we used relative FA values (Palmer 1994) in the subsequent analyses.

The relationship between insect damage and the predictor variables (year, FA, catkins, autumn colour) was studied using linear mixed model analysis with tree as random factor to control for repeated measurement (Pinheiro & Bates 2000). Two separate but interrelated analyses were carried out. In the first analysis, in which the aim was to investigate the signalling hypothesis, we looked for delayed effects of the various variables on level of insect attack. This was carried out using a reduced data set consisting of predictor variable values for the years 1999 and 2000 and insect attack values for the years 2000 and 2001. In the second analysis, in which the aim was to explore whether the proposed signal might carry a cost, we used the full data set to look for

patterns in insect attack within years. In both analyses, we used model selection based on the Akaike information criterion (AIC) and the maximum likelihood (ML) method to find the model that best explained the variation in insect attack (Pinheiro & Bates 2000). As this paper tests clear hypotheses, that FA and reproduction should be positively associated with insect attack, whereas the degree of autumn colouration should be negatively associated with insect attack, one-tailed significance levels are appropriate. All analyses were carried out in S-Plus (Insightful, Seattle, WA, USA).

RESULTS

The first analysis showed that the increasing degree of autumn colouration in September was associated with a reduction in leaf damage the following season ($b = -0.29$, $SE = 0.15$, $d.f. = 8$, $t = -1.89$, $P = 0.048$, one-tailed; Fig. 1), indicating that the most autumn coloured/early senescing trees might have been less exposed to egg-laying insects. In contrast, both increasing FA ($b = 5.89$, $SE = 3.08$, $d.f. = 8$, $t = 1.91$, $P = 0.046$, one-tailed) and increasing catkin production ($b = 0.082$, $SE = 0.054$, $P = 0.086$, one-tailed) were associated with an increase in leaf damage the following season, suggesting that stressed and reproductively committed trees, respectively, might have been less exposed to egg-laying insects. There was also

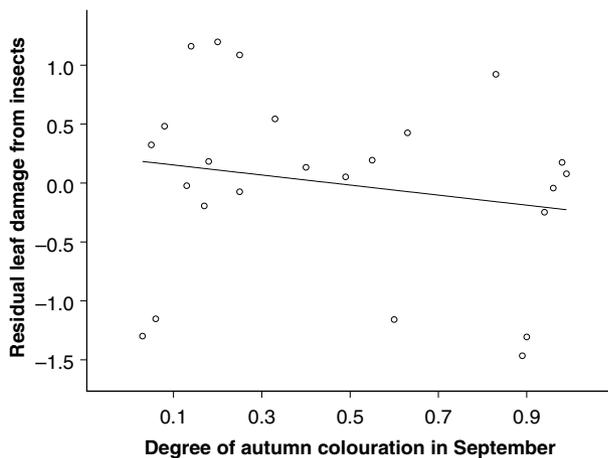


Figure 1 The estimated linear relationship between relative degree of autumn colouration in September and leaf damage from insects the following year in mountain birch. The figure is based on 2 years of data from 12 trees and represents the most parsimonious way to present the data according to the Akaike information criterion. Residual leaf damage from insects is the remaining variance in leaf damage after having removed the effects of all other significant variables (year, fluctuating asymmetry, catkin production) than that of interest (autumn colouration).

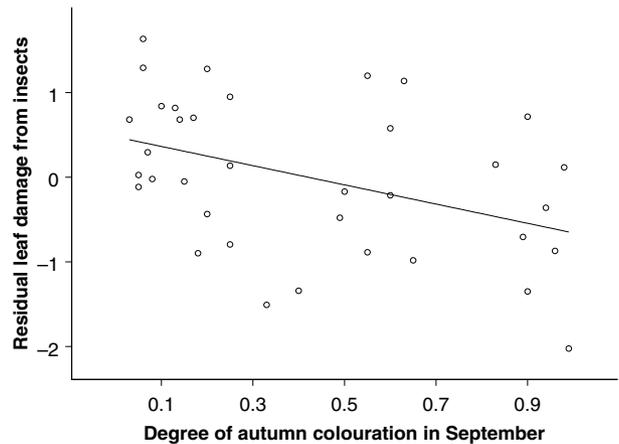


Figure 2 The estimated linear relationship between relative degree of autumn colouration in September and leaf damage from insects the same year in mountain birch. The figure is based on 3 years of data from 12 trees and represents the most parsimonious way to present the data according to the Akaike information criterion. Residual leaf damage from insects is the remaining variance in leaf damage after having removed the effects of all other significant variables (fluctuating asymmetry, catkin production) than that of interest (autumn colouration).

a significant effect of year ($b = 0.089$, $SE = 0.036$, $d.f. = 8$, $t = 2.48$, $P = 0.038$), because of a higher level of insect damage in 2002 compared with 2001. No interaction effects were selected according to AIC, suggesting that the observed effects were consistent between years.

The second analysis showed that leaf damage was also less frequent among trees expressing a high degree of autumn colouration in September the same season ($b = -0.27$, $SE = 0.078$, $d.f. = 21$, $t = -3.43$, $P < 0.0013$, one-tailed; Fig. 2). This indicates that heavily attacked trees might have extended the photosynthetic season to recoup resources, which in turn indicates a possible association between potential primary production and timing of autumn colour change. Moreover, leaf damage was greater both in trees with high levels of leaf FA ($b = 3.59$, $SE = 1.59$, $d.f. = 21$, $t = 2.25$, $P < 0.018$, one-tailed; Fig. 3) and in trees with high catkin production ($b = 0.10$, $SE = 0.044$, $d.f. = 21$, $t = 2.28$, $P = 0.017$, one-tailed; Fig. 4), supporting the idea of a link between insect attack, stress and reproduction in trees. No year effect or interaction effects were selected according to AIC, suggesting that the observed effects were consistent between years.

DISCUSSION

We explored the autumn signalling hypothesis using a phenology-based approach. The potential role of phenology-based variation in degree of autumn colouration in

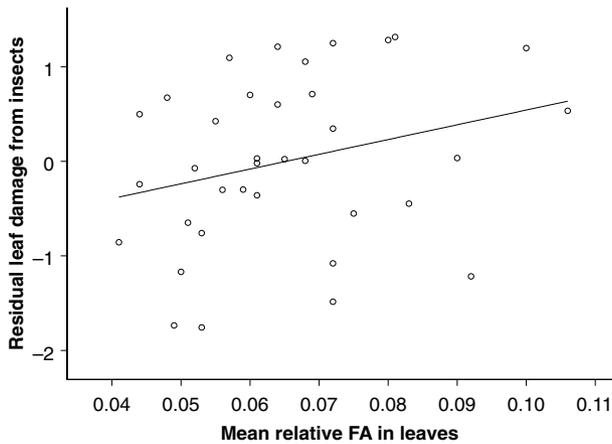


Figure 3 The estimated linear relationship between mean relative fluctuating asymmetry (FA) in leaves and leaf damage from insects the same year in mountain birch. The figure is based on 3 years of data from 12 trees and represents the most parsimonious way to present the data according to the Akaike information criterion. Residual leaf damage from insects is the remaining variance in leaf damage after having removed the effects of all other significant variables (catkin production, autumn colouration) than that of interest (FA).

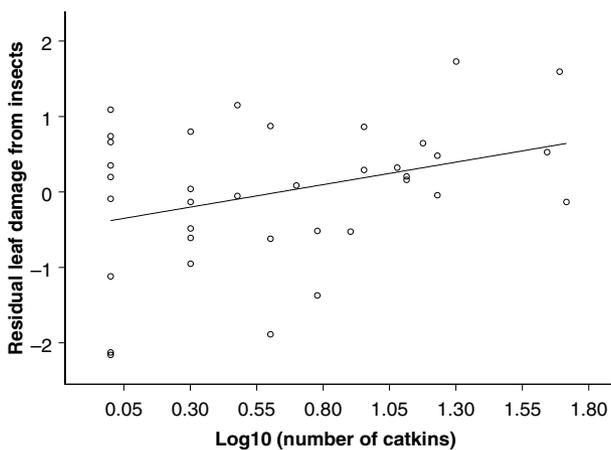


Figure 4 Relationship between reproductive investment (\log_{10} total number of catkins) and leaf damage from insects the same year. The figure is based on 3 years of data from 12 trees and represents the most parsimonious way to present the data according to the Akaike information criterion. Residual leaf damage from insects is the remaining variance in leaf damage after having removed the effects of all other significant variables (FA, autumn colouration) than that of interest (catkin production).

insect host selection was pointed out by Hamilton & Brown (2001), who noted that a strong signal (i.e. early autumn colour change/relatively strong autumn colouration at a given time) might lead to loss of primary production. Our results supported the prediction of a delayed negative

association between insect damage and the strength of this proposed warning signal, and indirectly, we also found a certain support for the idea that a strong signal might be energetically expensive. The positive correlation observed between insect damage and the various covariates (FA, catkins) seem to be biologically sound and as such strengthen the results found for autumn colouration.

What is it that makes early senescing mountain birches less troubled by insects is unclear. This is partly because it is unknown whether the insects causing the damage in this study colonize the trees at the time of year when they are in autumn colour, whether they are more likely to use visual cues during host selection, or whether they stay on the trees they use for over-wintering. Furthermore, correlative measurements are always open to alternative interpretations. For example, FA could correlate both with autumn colour and insect attack but colour might have no involvement in host selection as the insects are using other measures of tree quality (perhaps biochemical), which allow them to avoid unstressed (low FA) trees. Our study cannot rule out this kind of alternative explanations to the observed patterns. The challenge is to determine which of the many (probably) correlated traits (tree condition, insect attack, tree defence, tree reproduction) is causal. Hence, experiments are needed, including data on leaf chemical composition and tests with key herbivores known to be autumn ovipositors and sensitive to colour. A potentially fruitful approach could be to manipulate tree resource holding, e.g. by adding fertilizer, as this might give important insight into the link between tree condition, tree defence and autumn colouration (Hamilton & Brown 2001). Interestingly, we have observed a link between early autumn senescence and reduced leaf FA in mountain birch in our study area (manuscript in preparation).

The most common leaf chewers in our study area are the geometrid moth species *Epirrita autumnata* and *Operophtera brumata*. Both these species lay eggs around the timing of autumn colour change in birch (Tenow 1972). As such, they are potential candidates for a future experimental test of the signalling hypothesis in this system. Note, however, that Hamilton & Brown (2001) believed that specialist pests might be more suitable for such a test, and that both *Epirrita* and *Operophtera* are generalists (Tenow 1972). To design a better test of the signalling hypothesis, it is also important to consider the dispersal ecology of insects. We believe that host selection based on autumn colouration is most likely to have evolved in insects with low larval/nymphal dispersal, and both *E. autumnata* and *O. brumata* larvae can disperse through ballooning (Tenow 1972). Insects that disperse mainly in the adult stage will potentially face large losses in fitness by selecting a host plant with poor food quality for their progeny. Consequently, they would also potentially

face strong selection pressure to develop abilities for recognizing good-quality hosts during the egg-laying process. Autumn colonizing species with limited larval/nymphal dispersal probably exist in most groups of insects. Both aphids and cicada are examples of entire groups of insects with this type of dispersal ecology. Particularly certain species of cicada may occur at high densities in northern birch forests (personal observation), although their impact on the trees is yet to be studied.

In conclusion, we have shown that early autumn senescing mountain birches suffer less leaf damage from insects, which is consistent with the basic within-species prediction of the autumn signalling hypothesis. Further investigation is, however, needed in order to determine whether the link between insect damage and autumn colours observed in this study is causal.

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