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Autumn coloration as a signal of tree condition

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Hamilton and Brown suggested that bright autumn coloration in trees is an energetically expensive and therefore honest (handicap) signal of defensive commitment against insects. If this is so, one should expect that the intensity of the proposed signal should depend strongly on tree health. However, to the best of our knowledge, the link between vigour and autumn colour has never been tested. We explored the relationship between autumn coloration and tree condition (i.e. leaf fluctuating asymmetry) in mountain birch (*Betula pubescens*). Our results indicate that bright autumn birches are in better condition and therefore consequently should be better at combating herbivores.

Keywords: autumn coloration; handicap signal; tree condition; mountain birch; fluctuating asymmetry

1. INTRODUCTION

Autumn colours in deciduous trees have traditionally been viewed as a mere side effect of senescence, rather than as a signal to herbivores. Hamilton & Brown (2001) challenged this view by suggesting that the relative timing and magnitude of autumnal change in colour honestly reveals defensive commitment against herbivorous insects (see Archetti 2000). The evidence consisted of a positive association between aphid diversity and the degree of autumn colour change across 262 tree species, in keeping with the prediction that tree species with an evolutionary history of greater insect attack should invest more in defence and defensive signalling. In addition, they presented evidence that the proposed signal is costly and therefore reliable. First, shedding of strongly pigmented leaves in autumn apparently leads to a loss of lipids in which the pigments are embedded (Archetti 2000; Hamilton & Brown 2001). That is, the greater the magnitude of autumn colour change the greater the loss of energy in the form of lipids and pigments when leaves are shed. Second, since photosynthesis is essential for energy acquisition in trees, the earlier the timing of autumnal coloration the greater is the loss, potentially, of primary production (Hamilton & Brown 2001; Hagen *et al.* 2003). These potentially large costs could contribute to maintain honesty in the proposed signaller receiver system (Archetti 2000; Hamilton & Brown 2001). However, as the authors readily pointed out, only empirical tests will reveal the truth of this autumn signalling hypothesis, which attracted

wide attention (e.g. Atkinson 2001; Whitfield 2001; Holopainen & Peltonen 2002; Wilkinson *et al.* 2002) by being the first handicap signal (Zahavi 1975) to be proposed in plants.

Recently, Hagen *et al.* (2003) explored the autumn signalling hypothesis in mountain birch (*Betula pubescens*). In agreement with the basic within-species prediction of the hypothesis, namely that bright autumn coloration should warn insects not to lay eggs on these plants because they would be detrimental to their larvae (Hamilton & Brown 2001), the authors found that strong September autumn coloration was associated with a reduction in leaf damage from insects in the following season. Moreover, they found that indices of physiological stress and reproductive investment were associated with an increase in insect damage the following season. The challenge, they said, is to determine which of the many potentially correlated traits (tree condition, insect attack, tree reproduction and tree defence) is causal. Hamilton & Brown (2001) were cautious on this point, even suggesting the possibility of a negative relationship between tree condition and investment in defence and defensive signalling. Note, however, that if bright autumn coloration is a handicap signal, which by definition is energetically expensive simply to prevent weak signallers from pretending to be strong (Zahavi 1975), it is reasonable to believe that the intensity of the proposed signal should depend strongly on tree health (Archetti 2000). At the current time, as far as we know the link between vigour and autumn colour has never been tested.

2. METHODS

In the present study, therefore, we investigated the connection between the autumn coloration and tree condition in mountain birch. As an objective measure of condition, or stress as experienced by the birch trees themselves in their environment, we quantified the level of leaf fluctuating asymmetry (FA) (e.g. Møller 1995; Palmer 1996), i.e. random deviation from perfect leaf symmetry (Van Valen 1962). FA is known as a reliable indicator of stress in birch (Kozlov *et al.* 1996; Wilsey *et al.* 1998; Martel *et al.* 1999; Lempa *et al.* 2000) and was the index of tree condition used by Hagen *et al.* (2003). Sampling for FA was carried out in two areas with mature birch forest in northern Norway. One of these areas had an ongoing outbreak of birch defoliating winter moth larvae (*Operophtera brumata*), whereas the other area was virtually empty of larvae (R. A. Ims, N. G. Yoccoz and S. B. Hagen, unpublished data), allowing us to study the connection between FA and autumn coloration both under high and low browsing pressure. In both areas, during two consecutive days in September 2001, we selected 25 pairs of trees of similar size (*ca.* 4 m); each pair contained one early senescing tree, which carried only intensely yellow leaves (strong September autumn coloration), and one late senescing tree, which still carried only green leaves (weak September autumn coloration). The maximum distance between the two trees within a pair was 5 m. By employing a pairwise sampling design, differences in colour could be maximized, while simultaneously minimizing any differences in growth conditions. From each tree, we randomly collected 30 leaves and measured them for FA, at the midpoint between the base and tip, perpendicular to the mid-vein. To separate FA from measurement error (Palmer 1994), two independent repeats were obtained for all leaf measurements. We used the approach derived from the Levene's test (Conover *et al.* 1981) to analyse levels of FA. The difference (L-R) was first analysed using a linear model including the effects of location and colour to remove directional asymmetry, and the absolute value of the residuals was then analysed with a linear mixed model. Tree pairs, trees within tree pairs and leaves within trees were random, nested factors, whereas colour and location were fixed factors (Pinheiro & Bates 2000). In this case, this is a conservative approach, because tree pairs are treated as replicates, while simultaneously controlling for all levels of within-replicate variation (i.e. trees within pairs, leaves within trees and measurements within leaves, i.e. measurement error).

3. RESULTS AND DISCUSSION

The resulting parameter estimates, which represent differences in the mean of the absolute value of the residuals, showed that early senescing trees had a lower level of leaf FA than late senescing trees in both areas ($b = -0.048$, s.e. = 0.023, $t_{48} = 2.05$, $p = 0.046$), indicating that birches with strong September autumn coloration were in better condition than birches with weak September autumn coloration. Moreover, birches growing in the outbreak area of *O. brumata* developed more asymmetric leaves than birches growing in the non-outbreak area independent of coloration ($b = 0.057$, s.e. = 0.024, $t_{47} = 2.34$, $p = 0.024$) consistent with the idea that individuals in stressful environments should be in poor condition compared with individuals in less stressful environments. There was no evidence for an interaction between area and coloration on the level of FA in the trees ($p > 0.5$), i.e. the difference in condition among trees with strong and weak September autumn coloration appeared to be consistent both under high and low browsing pressure.

Our results are the first, to our knowledge, to propose a link between relative autumn coloration and FA in deciduous trees, as bright September autumn birches demonstrated a heightened ability to develop the anticipated optimal phenotype (symmetric leaves) in two very different environments. Such individuals may have experienced favourable growth conditions during development, or they may have a better genetic constitution for the current environment. The use of a pairwise sampling design largely eliminates the former as an explanation of the results observed in this study, since there was no evidence that the FA–colour relationship differed between areas, while at the same time there was a significantly higher level of FA in the outbreak area of *O. brumata* compared with the non-outbreak area. Thus, brightly September coloured birches may be of higher quality (from a tree point of view), which may explain not only why such birches suffer less damage from insects both within and between years (Hagen *et al.* 2003), but may also explain how they can afford the potential handicap of ceasing photosynthesis early. Also, note that there is evidence in the literature of a positive correlation between symmetry and defensive chemistry in leaves. For example, there appears to be a negative correlation between foliar asymmetry and nicotine content in tobacco (*Nicotina tabacum*) (Sakai & Shimamoto 1965). The exact relationship between FA and defensive commitment in mountain birch is less clear (Lempa *et al.* 2000), but it is well known that birch shows tendencies of both direct and delayed defence, and that indices of herbivory in birch and other deciduous trees often correlate positively with FA (e.g. Møller 1995; Martel *et al.* 1999; Lempa *et al.* 2000; Hagen *et al.* 2003).

Finally, note that our present results might also imply that the autumn signalling can be broadened beyond the colour-sensitive insects. This would be possible if insects that are insensitive to colour instead use biochemical cues, which covary with FA, for example odours released under stress, when choosing oviposition sites. Further work is, however, required to sharpen these hypotheses and to improve our knowledge about this fascinating and potentially new branch of signalling theory.

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