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# Autumn leaf colours as indicators of decomposition rate in sycamore (*Acer pseudoplatanus* L.)

J.H.C. Cornelissen[1,2,5], N. Pérez-Harguindeguy[3], D. Gwynn-Jones[1,4], S. Díaz[3], T.V. Callaghan[1] and R. Aerts[2]

[1]*Sheffield Centre for Arctic Ecology and Unit of Comparative Plant Ecology Department of Animal and Plant Sciences, Sheffield University, 26 Taptonville Road, S10 5BR Sheffield, UK.* [2]*(Current address): Institute of Ecological Science, Department of Systems Ecology, Vrije Universiteit, De Boelelaan 1087, 1081 HV Amsterdam, The Netherlands.* [3]*Instituto Multidisciplinario de Biología Vegetal, Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina.* [4]*Institute of Biological Sciences, University of Wales, Edward Llwyd Building, Aberystwyth, Ceredigion, Wales SY23 3DA, UK.* [5]*Corresponding author**

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**Abstract**

We tested the hypothesis that there is a causal connection between autumn colour, nutrient concentration and decomposibility of fresh leaf litter. Samples from patches of different autumn colours within the leaves of the deciduous tree sycamore (*Acer pseudoplatanus*) were sealed into litter bags and incubated for one winter in an outdoor leaf mould bed. Green leaf patches were decomposed faster than yellow or brown patches and this corresponded with the higher N and P concentrations in the former. Black patches, indicating colonisation by the tar spot fungus *Rhytisma acerinum*, were particularly high in P, but were decomposed very slowly, owing probably to resource immobilisation by the fungus. The results supported the hypothesis and were consistent with a previous study reporting an interspecific link between autumn coloration and decomposition rate. Autumn leaf colour of deciduous woody plants may serve as a useful predictor of litter decomposibility in ecosystem or biome scale studies where extensive direct measurements of litter chemistry and decomposition are not feasible.

## Introduction

It is now widely accepted that mass loss rates of leaf litter are under strong control of its physico-chemical quality before decomposition, particularly within biomes that do not experience severe climate stress (Aerts, 1997; Anderson, 1991; Cadisch and Giller, 1997; Couteaux et al., 1995; Swift et al., 1979). This control has major implications for carbon and nutrient turnover of ecosystems differing or changing in plant species composition or in leaf quality of given species (Aerts, 1995; Berendse, 1994; Hobbie, 1992; Pastor et al., 1984). Important biochemical indicators of litter resistance to decomposition are lignin concentration, lignin:N ratio and C:N ratio (Berg and Ekbohm, 1991; Cadisch and Giller, 1997; Cotrufo et al., 1984; Meentemeyer, 1978; Melillo et al., 1982; Swift et al., 1979; Taylor et al., 1989, 1991; Upadyayh et al., 1989). Litter N concentration itself tends to be a reasonable predictor of mass loss rate at least during the earlier phase of decomposition (Aerts and De Caluwe, 1997; Broadfoot and Pierre, 1939; Cotrufo et al., 1994; Ohlson, 1987; Taylor et al., 1989), but not necessarily during the latter phase (Berg et al., 1996). Quantifying such biochemistry is often labour intensive and expensive and not always feasible for studies at the ecosystem or biome scale. The search for leaf or litter traits that can be used as easy and inexpensive substitutes for litter biochemistry and mass loss has yielded some promising candidates. Leaf or litter toughness (tensile strength) or toughness:N ratio have revealed close correspondence with resistance

* FAX No: 031 20 4447123. E-mail: hansco@bio.vu.nl

to decomposition (Cornelissen and Thompson, 1997; Cornelissen et al., 1999; Gallardo and Merino, 1993), as explained by the correspondence of toughness with proportional amount of lignin deposition in cell walls, particularly in fibres (Choong et al., 1992; Wright and Illius, 1995). Near-infrared reflectance spectroscopy (NIRS) is another useful, quick and non-destructive method to quantify lignin concentration and predict litter mass loss rate (Gillon et al., 1999; Wessman et al. 1988). Generally applicable cheap and easy substitutes for litter nutrient concentration have not been found yet. However, Cornelissen (1996) showed for a deciduous woody flora in Britain that shrub and tree species which shed their leaves (partially) green had faster potential decomposition than those which shed them mostly yellow, red or brown or combinations thereof, and this difference was independent of the taxonomic relatedness of the many species involved. It was presumed that the green litter, representing high chlorophyll concentrations (Sanger, 1971), would still contain high concentrations of photosynthesis-related nutrients, but this was not tested. Thus, these results could not confirm whether the connection between autumn colour and decomposition rate was causal or an accidental by-product of other traits that happened to vary between green and non-green leaf litter. Here, we test the causality of this relationship by comparing nutrient concentrations and mass loss rates of differently coloured patches within the same autumn leaves. We selected the common temperate deciduous tree sycamore *Acer pseudoplatanus* L. because of the striking colour patterns within its individual autumn leaves. These patterns not only include mosaics of green and yellow (or brown), but also black spots indicating localised fungal infection. We anticipate that these patches will vary in nutrient concentration and decomposibility.

## Methods

### *Experimental procedures*

We collected freshly fallen, undamaged *Acer pseudoplatanus* leaves from below four different trees within a 1 km radius around the main campus of Sheffield University, Sheffield, Central England in October 1997. Most leaves, generally 5-lobed, showed both green and yellow parts, in varying proportions and usually 3–10 black spots of approx. 100 $mm^2$ area, indicating colonisation by the coelomycete anamorph of the tar-spot fungus *Rhytisma acerinum* (Pers.) Fries (Ascomycota), the nomenclature and life cycle of which were described by Stevens (1925), Hawksworth et al. (1995) and Ellis and Ellis (1997). This fungus is very common on otherwise healthy leaves of *Acer pseudoplatanus* in most parts of Great Britain except certain urban areas (Jones, 1944; Leith and Fowler, 1988; authors' observations). A minority of the leaves also had brown or yellowish-brown sections. None of the colours appeared to be consistently localised in particular sections of the leaves, so the different colours most likely did not represent leaf parts of different structural properties.

For each colour in each leaf we cut one or two pieces of approx. $10 \times 10$ mm from central parts of the leaf lobes, away from the primary veins. We avoided intermediate colours and fine-scale colour mixtures. We bulked all squares of the same leaf population (tree) of each colour (green, yellow, brown, black) to obtain 16 samples representing four leaf populations times four colours. For each sample, we took at random 1–4 (average 2.5) lots (pseudoreplicates) of squares adding up to 1 g each, then sealed these into nylon litter bags of 0.3 mm mesh (details in Cornelissen, 1996). One additional random subsample for each colour was weighed, oven-dried (48 h at 80 °C) and reweighed. The ratio between air-dry and oven-dry mass was used to calculate initial true dry mass of each sample. Another additional random subsample from each sample was analysed for mass-based N and P concentration at Analytical Services, Department of Animal and Plant Sciences, Sheffield University, using a Kjeldahl method. Leaf samples (plus marker samples of standard hay powder, CRM 129 from the Laboratory of the Government's Chemist, The Office for Reference Materials, Teddington, UK) were ground and digested at 370 °C using a mixture of sulphuric acid, salicylic acid, and the catalysing agents copper sulphate and lithium sulphate. The diluted digests were analysed colorimetrically using a Tecator FIA Star 5012 flow injection analysis system (Tecator AB, Sweden).

In order to crudely characterise green versus non-green parts more objectively, we quantified absorbance by chlorophyll spectrophotometrically. We took a third set of 10 air-dry (pseudoreplicated) subsamples (5–20 mg each) from the lumped leaf populations for each colour. We ground these with sand and 5 ml of methanol, then centrifuged them for 15 min at 50 rotations per second and scanned them for absorbance in the area around 650 (representing chlorophyll *b*) and

665 nm (chlorophyll *a*), using a spectrophotometer. Relative absorbance in this range was measured as maximum peak height.

On 22 January 1998, we remoistened all litter bags with rain water (cf. Cornelissen, 1996) and buried them in random positions at 40 mm depth in a 100 mm thick leaf mould layer in a purpose-built outdoor decomposition bed at Tapton Garden, Sheffield University, UK (details in Cornelissen, 1996). This procedure should be seen as an outdoor laboratory test of decomposibility rather than a simulation of natural decomposition conditions. The leaf mould, collected from a pile consisting of a mixture of recent and previous years' litter from diverse woodland trees and shrubs representing a broad range of litter qualities (see Cornelissen, 1996), had been thoroughly mixed and put onto the decomposition bed a month before incubation of the litter bags. On 25 March (day 62), we retrieved the litter bags, removed extraneous particles, oven-dried the incubated leaf samples (48 h at 80 °C) and reweighed them. Mass loss is defined here as a percentage of initial mass.

Data from the Weston Park Meteorological Office, Sheffield, at 800 m NNE of the experimental site, indicated that the total rainfall during the first 3 weeks in January 1998, up to incubation day, was 86 mm, which was one third above the long-term average (1961–1990) for that period and enough to start the experiment with the decomposition bed presumably close to field capacity. The period 22 January–28 February (precipitation 7 mm, mean temp. 6.7 °C) was 85 mm drier and 3 °C warmer than the long-term average for that period (1961–1990), while the period 1 to 25 March (precipitation 90 mm, mean temp. 7 °C) was 27 mm wetter and 2 °C warmer than the long-term average. The decomposition bed appeared moist throughout the experimental period and mild air frost was measured on 9 nights.

### *Data analysis*

We employed one-way analyses of variance (on untransformed data) and subsequent Tukey's tests (SPSS release 6.0, SPSS Inc.) to compare mean values between colours. We used the average value of 1–4 subsamples of the same sample as one statistical observation.

## Results

Green parts of autumn *Acer* leaves showed the highest mean peak height (100%) in the chlorophyll absorbance range, followed by yellow (43%), brown (16 %) and black (4%). One-way ANOVAs revealed that initial autumn colours differed in chemistry, with green parts being significantly higher in N concentration than any other colour (Figure 1 A) and P concentrations decreasing in the order black (tar spot) > green > yellow > brown, although yellow parts did not differ significantly from brown or green ones (Figure 1B). Litter mass loss was greatest in green parts (Figure 1C), as corresponding with N and, in comparison with other non-fungal parts, with P. The tar spots combined the highest P concentration with the lowest mass loss.

## Discussion

Our results have provided clear support for the hypothesis that litter mass loss can be predicted from autumn leaf colour in *Acer pseudoplatanus* and that this relationship can be explained from the nutrient concentrations and fungal presence or absence in the tissues of the different colours. If we first focus only on the leaf parts uncolonised by the tar spot fungus, green sections combined high concentrations of N (and probably of chlorophyll) and, to a lesser degree, high P with fast decomposition. In contrast, yellow and brown sections combined (40%) lower N and (22; 28%) lower P concentrations with (13; 18%) slower decomposition. It is most likely that the differently coloured sections in *Acer* leaves did not vary importantly in structure-providing (lignin-based) chemistry, given that the different colours were taken from similar leaf parts. We attribute the differences in litter mass loss within *Acer* leaves principally to variation in the amounts of chlorophyll broken down to retranslocate N before leaf abscission. Indeed, it is well established that the great majority of foliar N is locked up in photosynthetic enzymes that are associated with (green) chlorophyll (Evans, 1983; Field and Mooney, 1986; Huffaker, 1982) and recycled during foliar senescence (Yamashita and Fujino, 1987). P in other organic compounds linked with photosynthesis may play an additional role in the link between green autumn colour and mass loss in the soil.

The black tar spot patches in *Acer* leaves are indicative of very slow litter decomposition. In this

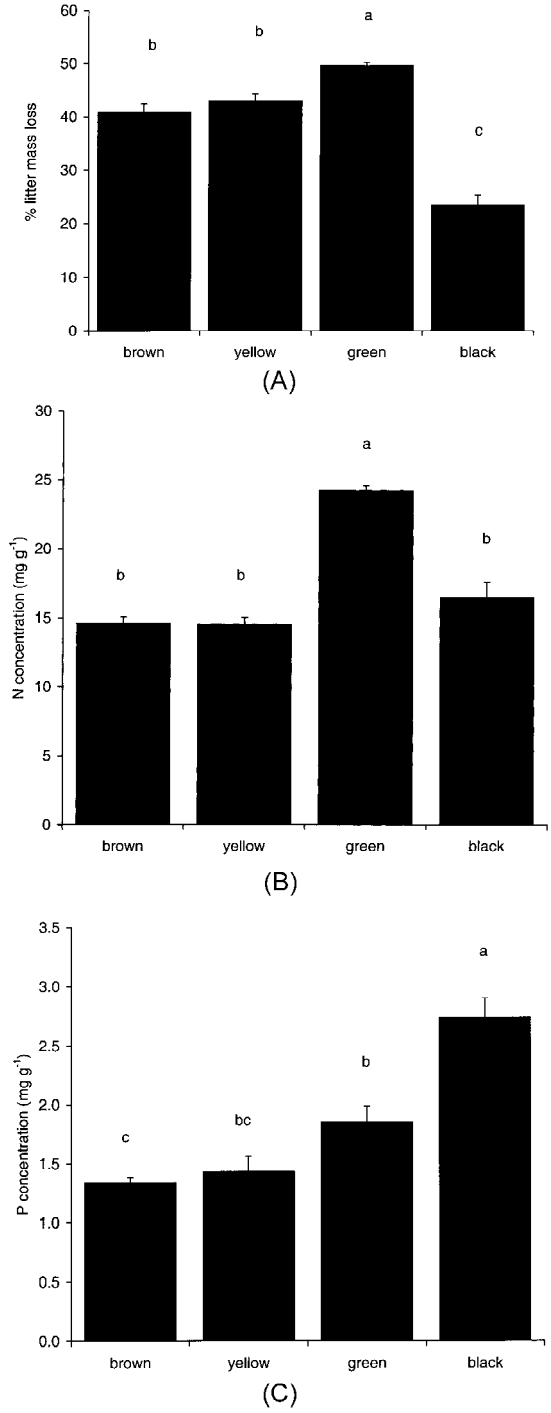


*Figure 1.* Leaf litter mass loss and leaf litter nutrient concentrations in *Acer pseudoplatanus* tissues of different colours, with results from one-way ANOVAs (F values) and subsequent Tukey's tests (letters in figures). The black colour relates to tar spot patches. Means (+ standard error) which share the same letter are not significantly different at the $P<0.05$ level. (A) Percentage litter mass loss, F 57.3, $P<0.001$. (B) N concentration, F 44.4, $P<0.001$. (C) P concentration, F 25.5, $P<0.001$.

respect, our results confirm our own observations in English woodlands, where tar spot patches remain on the soil surface, apparently unchanged, until well into the following spring, with very little remaining of the surrounding parts that were yellow or green at abscission. This is not surprising, given that the winter is an essential period in the normal life cycle of the fungus *Rhytisma acerinum*, with the production of apothecia usually at the end of it (Ellis and Ellis, 1997; Stevens, 1925). The fungus appears to immobilise nutrients in *Acer* leaf patches already before leaf senescence by monopolising the resources in the substrate; the same rust is believed to suppress subsequent decomposition by inhibiting colonisation by other heterotrophic organisms such as saprotrophic fungi (cf. Dighton and Boddy, 1989). The remarkable accumulation of P in the tar spot patches agrees with the high P concentrations associated with other parasitic fungi in leaves, such as rusts and powdery mildew (Walters, 1989). Accumulation of N in connection with fungal leaf infection has also been reported (Gange, 1996; Gunnarsson, 1987; Walters, 1989), but is not apparent from our results. Much of the 'surplus' P in infected parts probably originates from fungus-induced enhanced host root uptake and xylem supply rather than from the leaves themselves and is stored mostly as polyphosphates (Walters, 1989). The surplus P has been thought to serve as a backup for 'leaching' from the fungus to the photosynthetic tissues during leaf senescence, which would prolong photosynthesis by the host leaf and carbohydrate extraction by the fungus (Ahmad et al., 1984). Thus, the association between black colour, high P and slow decomposition represents a specific phenomenon linked with fungal colonisation and is in a different league from the association between green autumn colour, high N and P and fast decomposition in non-colonised leaf parts.

In conclusion, not only interspecific (Cornelissen, 1996), but also intraspecific variation in autumn leaf colour (this paper) can serve as easy and inexpensive predictors of litter mass loss rates of deciduous woody plants. Study on additional species with multicoloured autumn leaves should reveal the generality of the intraspecific patterns reported here. Given the prominent role of decomposition in ecosystem function, the predictive power of autumn colour may well lead to useful applications in ecosystem or biome studies where large scale or other constraints do not allow direct analyses of litter chemistry and decomposition. Future studies could focus particularly on the role of different types of non-green coloration in leaf litter as

potential indicators of slow decomposition. We hypothesise that brown and green autumn leaf colours of deciduous plants represent the two sides of a trade-off (*sensu* Coley, 1988; Herms and Mattson, 1992) between investments in leaf defence (lignin, tannins; high C:N ratio) and leaf photosynthetic production (low C:N ratio).

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