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Selective herbivory on mosaic leaves of variegated *Acer pseudoplatanus*

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Summary. The color mosaicism was observed to correlate with selective herbivory on different leaf areas of individual leaves of the variegated sycamore *Acer pseudoplatanus*. The mosaicism affected the content of nutrients and of phenolic compounds and also the mechanical properties of the different leaf areas; this offers an explanation for the observed selective feeding by insect herbivores.
Key words. Somatic mutation; color mosaicism; leaf chemistry; herbivory.

The variation in both plant nutrients and secondary metabolites can affect the feeding behavior of insect herbivores, which are expected to favor resource patches with high levels of nutrients, and low levels of those plant allelochemicals that have adverse effects on their growth, reproduction and survival[2,3]. The heterogeneity of food resources for herbivorous insects includes variation among host plant species[4], among individual plants of the same host species[5], and even among leaves of the same individual plant[6]. Selective feeding by insect herbivores on leaves of variegated *Acer pseudoplatanus* was studied in order to test the hypotheses that 1) genetic mosaicism in plants can affect the quality of food resources for insect herbivores and 2) this variation can lead to selective feeding on the foliage of individual plants[7]. The color mosaicism of sycamore provides a special case in which individual leaves can represent mosaics as a resource for herbivores.

Material and methods. Three variegated trees of *Acer pseudoplatanus* (var. 'brilliantissima') were sampled on 27 July 1983 in a garden in Cambridge, England. The lower branches of the trees were studied and leaves partially damaged by three insect herbivore groups, lepidopterans, coleopterans and sawflies, were removed and dry material was later analyzed in the laboratory. Because the leaves were collected in late July, the material contained the consumption that had taken place during the first half of the growing season which is generally the most intensive feeding period of lepidopterans[2]. Leaves with evidence of extensive feeding were omitted from the analysis because it was impossible to estimate the proportion of different color areas in the damaged parts of these leaves. The amount of grazing damage, consumed leaf area and biomass were estimated in the total sample of 83 leaves in order to analyze the feeding preference between different leaf areas in natural conditions. The expected values for these parameters were calculated from the proportional distribution of leaf area and biomass among the different color areas of the leaves. The differences between the observed and expected values were tested by means of the χ^2-test. The phenolic and nutrient contents in the different color areas were analyzed by combining samples from the investigated leaves where these areas were available. The Folin-Denis method was used to analyze phenolics and standard methods for nutrients.

Results and discussion. The normal green leaves contain plastids both in spongy and palisade parenchyma, whereas white mutant leaves and leaf areas contain colorless plastids in all the layers of mesophyll. Mixed, mosaic-like, leaf areas contain colorless mutant plastids either in the palisade or spongy parenchyma[8,9]. Because the mosaicism of sycamore varied considerably in the variegated leaves of the investigated trees, we divided the area of each leaf into three major classes: 1) white areas with no or few green chloroplasts, 2) mixed areas consisting of an irregular mixture of white and green cells, and 3) green areas consisting of a more or less uniform population of cells with green plastids. On average, about a half of the leaf area consisted of a mixture of white and green cells and the other half was divided between white and green areas (fig. 1A). The proportional distribution of leaf biomass was slightly more skewed towards mixed and green areas (fig. 1B) because leaf biomass per unit leaf area was lower for white than for

Chemical composition of different leaf areas of variegated *Acer pseudoplatanus*. All values on a dry weight basis

	White	Mixed	Green
Biomass (mg/cm^2)	0.93	1.09	1.59
Nutrients (g/kg)			
N	34	31	33
P	5.2	2.9	2.7
K	30	19	18
Ca	23	26	28
Mg	3.2	3.0	3.2
Phenolics (%)	4.55	6.47	10.95

mixed and green areas (table). The reduced biomass per unit leaf area in white areas can probably be explained, at least partially, by the lack of photosynthetic products. The lower dry matter content of white areas also indicates that white areas were thinner and less tough than mixed and green areas. The photosynthetic activity of leaves and leaf areas can be a crucial factor in the maintenance of secondary metabolite production. Because plant carbon-based chemical resistance is supported by carbohydrate surplus[10, 11], photosynthesis leading to a build-up of carbohydrates can affect the level of secondary metabolites. The present study shows that leaf areas with lower photosynthetic activity are able to maintain lower levels of carbon-based allelochemicals than those with higher carbohydrate reserves because phenolic content was lower in white than in mixed and green areas (table). Leaf nutrient content may also be affected by color mosaicism. In *Acer negundo,* leaf areas with low photosynthetic activity have a higher content of nitrogen, phosphorus and potassium and a lower content of calcium and magnesium than normal green leaf areas[12]. We found similar differences in P, K and Ca levels in leaves of *Acer pseudoplatanus* (table). However, no differences were found in leaf nitrogen and magnesium content. A possible explanation of these differences in mineral nutrients is that the ratio cytoplasm/cell walls is higher in white areas than in mixed and green areas[12].

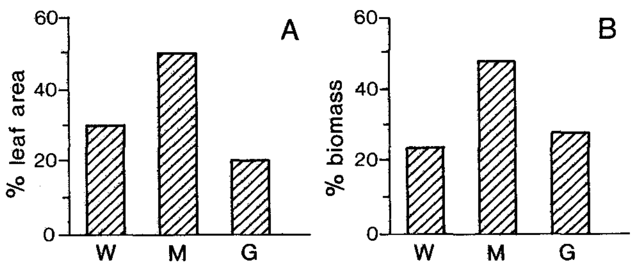

Figure 1. The distribution of total leaf area (A) and biomass (B) between white W, mixed M and green G areas of the leaves.

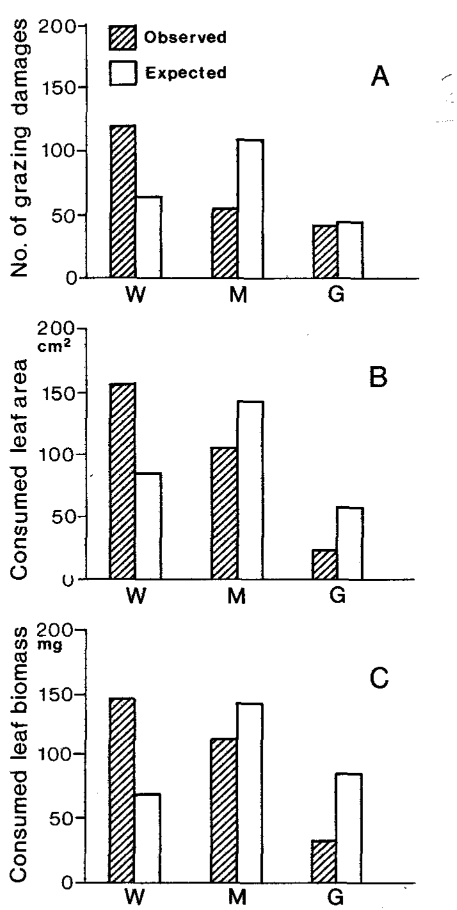

Figure 2. Seletive herbivory on the mosaic leaves of *Acer pseudoplatanus.* A, total grazing damage on the investigated leaves ($\chi^2 = 71.9$, $p < 0.01$); B, total consumed leaf area ($\chi = 92.1$, $p < 0.01$); C, total consumed leaf biomass ($\chi^2 = 111.1$, $p < 0.01$). The expectations were calculated for the two upper comparisons (A and B) from the values given in figure 1A, and for the lowest comparison (C) from figure 1B.

The above results support the first hypothesis[7] that genetic mosaicism in plants can led to the variation of leaf quality within the foliage of individual plants. The potential sources of heterogeneity include, at least, the availability of various resource patches (leaves and leaf areas) in the foliage (fig. 1) and the mechanical properties, nutrient content and secondary metabolites of leaves and leaf areas (table). We tested a null hypothesis that insect herbivores had randomly fed on white, mixed and green areas in the same proportions as these areas were available to them as indicated by leaf area (fig. 1A) and leaf biomass (fig. 1B). However, the observed frequency distributions of the amount of grazing damage (fig. 2A) and that of the total leaf area removed by insect herbivores (fig. 2B) deviated from the expectations of this null hypothesis. The result was similar with the total leaf biomass removed by herbivores (fig. 2C). The difference between the observed and expected frequency distributions were statistically significant in all three comparisons, indicating that insect herbivores had favored white areas over mixed and green areas. This preference correlates well with the chemical and mechanical properties of white areas which contain more nutrients (especially phosphorus) and less digestibility-reducing phenolics (table). Furthermore, white areas are softer and therefore easier to consume. Consequently, the present study also supports the second hypothesis[7] that genetic mosaicism can lead to selective feeding by herbivores on the foliage of individual plants. Obviously the variation in the quality of food resources within individual plants is an element of heterogeneity in the environment of insect herbivores. This can be best detected in cases where the variation of leaf quality correlates with observable differences in the color or morphology of leaves. However – and this is important – this element of heterogeneity can also be present in cases where there are no visible differences in plant tissue, but chemical differences nevertheless exist.

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