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# Notes and records

## Incidence of red leaves in the rainforest of Kibale National Park, Uganda: shade-tolerators and light-demanders compared

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There is often a striking degree of colour variation in young tropical leaves. Although ecologists have long been fascinated by this perplexing feature of tropical plants (Smith, 1909; Coley & Aide, 1989; Juniper, 1993; Gould *et al.*, 1995; Richards, 1996), few studies have quantified the phenomenon (Coley & Kursar, 1996). Prevalent are young leaves that appear red or pink to human observers, being reported in 16% of 154 common tree and shrub species at La Selva, Costa Rica (Opler, Frankie & Baker, 1980) and in 36% of 175 common tree species on Barro Colorado Island, Panama (Kursar & Coley, 1992). In South-East Asia, however, young red leaves may occur in up to 62% of common plant species (Lucas, Dominy & Turner, unpublished data); a proportion that may cause whole forests to appear as a 'blaze of red' during times of leaf flush (Burgess, 1969; Holttum, 1969). Here, in the context of primate feeding observations, I report on the incidence of young red leaves in the shade-tolerant and light-demanding species of an African rainforest. A total of 121 plant species from Kibale National Park, Uganda – from which primates either consumed leaves, flowers, fruits, pith or seeds – formed the data set analysed here (see Appendix 1).

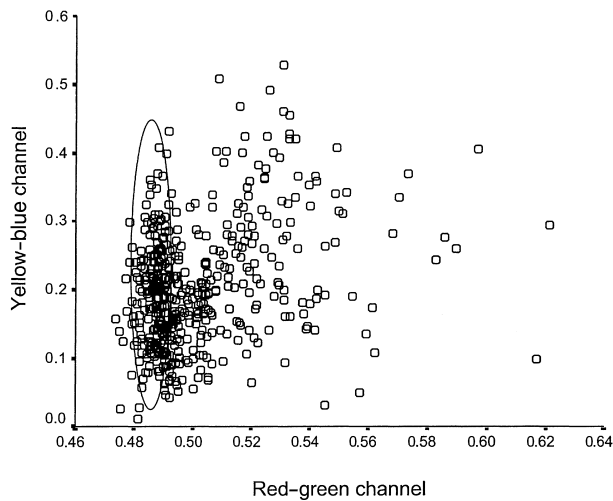
Kibale National Park (0°13'N to 0°41'N and 30°19'E to 30°32'E) is a mosaic of vegetation types ranging from moist evergreen forest (but closely related to moist montane forest) to lowland tropical rainforest (*sensu* Langdale-Brown, Osmaston & Wilson, 1964). Mean annual rainfall at the Kanyawara research station ranges from 1622 mm (1977–1991; Struhsaker, 1997) to 1700 mm

(1990–1996; Chapman & Chapman, unpublished data) and occurs in two distinct rainy seasons: March–May and August–November. The vegetation supports eleven primate species at perhaps the highest density on earth (Struhsaker, 1997). Four of these species: chimpanzees (*Pan troglodytes schweinfurthi* Blumenbach), red-tailed monkeys (*Cercopithecus ascanius schmidtii* Matschie), black-and-white colobus (*Colobus guereza occidentalis* Rochebrune), and red colobus (*Piliocolobus badius tephrosceles* Elliot) were observed for 1177 h from January–October 1999. Whenever possible both the young and mature leaves of primate food species were collected for analysis. Spectra from all specimens were measured fresh with a portable fieldkit described by Lucas *et al.* (2001) and modelled into the opponent colour space of trichromatic primates (Regan *et al.*, 1998; Vorobyev & Osorio, 1998). Taxonomy of trees and climbers follows Hamilton (1991) and Lind & Tallantire (1962), respectively. Further identifications were obtained with the assistance of staff at the Makerere University Herbarium. Classification of light-tolerance follows from P. J. Grubb (unpublished data). Species found in shade at a range of sizes are defined as 'shade-tolerators', while those requiring treefall gaps or edges to establish are considered 'light-demanders' (*sensu* Metcalfe & Grubb, 1995).

Modelling of leaf spectra into the opponent colour channels of trichromatic primates shows that at least 62 (51%) of the 121 species examined exhibit young leaves outside the domain of green (Fig. 1). These young leaves ranged from deep crimson (e.g. *Linociera johnsonii*) to red (e.g. *Saba florida*, Fig. 2) to a subtle shade of pink (e.g. *Balanites wilsoniana*). Overall, there was no significant relationship between shade-tolerance and the probability

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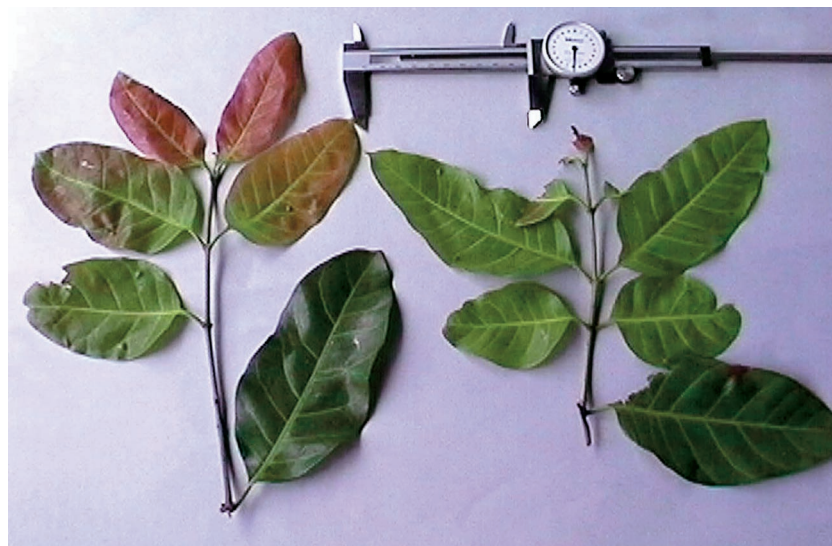


**Fig 1** Leaf specimens ( $n = 522$ ) representing various developmental stages of 107 plant species. Opponent colour channels on each axis represent cone excitation ratios of long- (L) middle- (M) or short-wavelength (S) cones of trichromatic primates, or  $S/(L + M)$  for the Yellow-Blue channel and  $L/(L + M)$  for the Red-Green channel, respectively. Leaves within the vertical ellipse are in the domain of green. Young leaves commonly appear red; with increasing redness moving away from the ellipse to the right

of leaves exhibiting red colouration ( $\chi^2 = 0.18$ , df 1,  $P > 0.5$ ). A separate consideration of trees and shrubs, climbers and herbs shows a similar incidence of young red leaves in the two functional categories (Table 1). Among trees and shrubs, phylogenetically controlled

contrasts (within families) further supports the finding that young red leaves are distributed indifferently among light-demanding and shade-tolerating species. Only the families Oleaceae and Ulmaceae showed differential distribution, i.e. the presence of young red leaves in shade-tolerators but not light-demanders. In other families, where only shade-tolerating species were studied, about half the species exhibited young red leaves (Meliaceae, Rubiaceae, Rutaceae, Sapindaceae, Sapotaceae). Whereas red young leaves were found in all light-demanding and shade-tolerating tree species of Bignoniaceae and Leguminosae, none was found in Apocynaceae, Sterculiaceae and Verbenaceae. The light requirements of species within the Euphorbiaceae, Flacourtiaceae, Loganiaceae and Moraceae are not sufficiently well known to reach a conclusion.

These results are a surprising contradiction to the observation that young red leaves are predominantly found on shade-tolerant plants (Kursar & Coley, 1992). It is also interesting to note a relatively high incidence of red leaves compared to neotropical floras. Indeed, dividing the sum of individual trees  $\text{ha}^{-1}$  exhibiting red leaves by the total number of trees  $\text{ha}^{-1}$ , as reported by Chapman *et al.* (1999), shows that nearly 49% of all individual trees per unit area of forest will exhibit young red leaves at some point during the year (if all re-leaf once). Because catarrhine primates may rely on young red leaves as either a fallback food or staple (Lucas *et al.*, 1998; Dominy & Lucas, 2001), I suggest that the preponderance of young red leaves in palaeotropical floras may have been a key



**Fig 2** The red leaves of *Saba florida* (Apocynaceae), a woody climber consumed by *Colobus guereza*. Note: caliper width is 10 cm

**Table 1** Summary of incidence of young red leaves (omitting introduced species)

	Shade-tolerators	Light demanders	Light-requirement uncertain	Grand total
Trees and shrubs	26/50	13/23	11/19	92
Climbers	1/3	7/11	0/5	19
Herbs	1/3	1/5	0/0	8
Total	28	21	11	119

selective force during the evolution of catarrhine colour vision.

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