

Long-term declines in nutritional quality of tropical leaves

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Abstract. Global change is affecting plant and animal populations and many of the changes are likely subtle and difficult to detect. Based on greenhouse experiments, changes in temperature and rainfall, along with elevated CO₂, are expected to impact the nutritional quality of leaves. Here, we show a decline in the quality of tree leaves 15 and 30 years after two previous studies in an undisturbed area of tropical forest in Kibale National Park, Uganda. After 30 years in a sample of multiple individuals of ten tree species, the mature leaves of all but one species increased in fiber concentrations, with a mean increase of 10%; tagged individuals of one species increased 13% in fiber. After 15 years, in eight tree species the fiber of young leaves increased 15%, and protein decreased 6%. Like many folivores, Kibale colobus monkeys select leaves with a high protein-to-fiber ratio, so for these folivores declining leaf quality could have a major impact. Comparisons among African and Asian forests show a strong correlation between colobine biomass and the protein-to-fiber ratio of the mature leaves from common tree species. Although this model, predicts a 31% decline in monkey abundance for Kibale, we have not yet seen these declines.

Key words: *climate change; folivores; global warming; leaf chemistry; nutritional ecology; primates; tropical foliage.*

INTRODUCTION

The Earth's climate has warmed by approximately 0.6°C over the past 100 years, and some estimates suggest that the climate could warm by a further 0.3° to 6.4°C this century (IPPC 2007). There have been numerous documented shifts in phenology, distribution, population abundance, life history, and species demography in response to climate change (Pounds et al. 1999, Hannah et al. 2002, IPCC 2007, Newman et al. 2011). These impacts are driven partly by direct effects of climate change on species (e.g., responses to temperature), but there is increasing evidence that the indirect effects, mediated via species interactions, could accentuate or buffer these impacts (Angert et al. 2013). An important potential indirect effect on herbivores and

higher trophic levels is the influence of changing climates on the nutritional quality of vegetation (Coley et al. 2002).

Much of what we know about how plant chemistry responds to changes in CO₂ levels and temperature are based on greenhouse and free-air CO₂ enrichment experiments (Zvereva and Kozlov 2006, Stiling and Cornelissen 2007, Robinson et al. 2012). A meta-analysis of grasses, herbs, and trees suggests that elevated atmospheric CO₂ is associated with an average increase in nonstructural carbohydrate concentration of 39%, and decreased protein (–10%) and structural carbohydrates (–13%). However, there was also an increase in toughness across plants under elevated CO₂ in the laboratory (Robinson et al. 2012). Toughness is associated with presence of structural carbohydrates, such as cellulose (Westbrook et al. 2011, Kitajima et al. 2012). The source experiments from the meta-analysis were not uniform, sometimes showing opposite trends, and the variance was often better explained when interacting effects, such as soil nutrient status and

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temperature, were included in the models (Robinson et al. 2012). Although the effects of CO₂ on leaf nitrogen (a primary constituent of protein) are well studied in trees, less is known about how tree leaf fiber is affected by CO₂ and temperature. In a greenhouse study investigating the effects of CO₂ on 27 wild and agricultural herbs and tree seedlings, there was no significant change in fiber (measured as cellulose plus hemicellulose; Poorter et al. 1997). A glasshouse experiment with oak trees found that leaf toughness increased under increasing temperature, but not when exposed to elevated CO₂ (Dury et al. 1998). There is reason to suggest that climate change is affecting the nutritional quality of primary producers, but the causes are complex, and data are needed on how plants in the field respond to changing climatic environmental variables.

Records indicate that both rainfall and temperature have increased substantially over the last century in and around Kibale National Park, Uganda (Chapman et al. 2005, Hartter et al. 2012; C. A. Chapman, *unpublished data*). Kibale National Park is an important conservation refuge for many species that are directly (e.g., herbivores, including primates) or indirectly (predators) reliant on primary production, and it is therefore important to understand how climate change is impacting plant nutritional composition. An important predictor of high primate biomass, and hence a likely indicator of foliage nutritional quality, is a high protein-to-fiber ratio (Chapman et al. 2002, 2004; but see Wallis et al. 2012). Previous studies of tropical trees along a rainfall gradient revealed that nitrogen concentrations and nitrogen-to-fiber ratios decreased with increasing precipitation, and similar effects on foliar chemistry have been found for increasing temperature (Schuur and Matson 2001, Weih and Karlsson 2001, Santiago et al. 2004, Craine et al. 2010). A significant proportion of the nitrogen in the leaf is usually in protein, so this decline could have negative consequences for the nutrition and population dynamics of folivorous animals (Ganzhorn 1992, Chapman et al. 2004).

To test the hypothesis that tropical foliage has declined in nutritional quality in recent decades, perhaps related to climatic changes, we took advantage of two older data sets on nutritional chemistry from Kibale. In the first data set, mature leaf samples were collected from at least two individuals of 10 species in 1976–1982 and assayed for acid detergent fiber (ADF). Within this data set, samples of mature leaves were collected from *Strombosia scheffleri* trees that were individually tagged. The second data set was composed of multiple samples of young leaves eaten by colobus monkeys in 1994–1996. We recollected and reanalyzed mature leaves from the same *S. scheffleri* individuals and the same tree species in the same area of the forest in 2007–2009, and young leaves from the same tree communities in 2007–2010.

MATERIALS AND METHODS

Kibale National Park is a mid-altitude, moist-evergreen forest in western Uganda (0°13'–0°41' N and 30°19'–30°32' E). It was gazetted as a forest reserve in 1932, and named a protected area in 1993. During the time it was a forest reserve, several areas of the forest were logged, but the K-30 area (282 ha) was not, though some stems were removed by pit sawyers before 1970 (Struhsaker 1997).

In 1979–1981, T. T. Struhsaker collected three samples of mature foliage from each of 10 *S. scheffleri* tagged trees, and multiple leaf samples from different individuals in a community in the K-30 compartment of the forest. He collected these leaves using a tree saw from the lower portions of the tree crown, and dried them in the sun. Subsequently, P. G. Waterman analyzed them for their acid detergent fiber (ADF) composition (Van Soest et al. 1991).

In 1979, T. T. Struhsaker created a map of the trees from which he collected samples, and in 2007 joined J. M. Rothman, C. A. Chapman, and D. Twinomugisha in the field to relocate the same area where the trees were sampled, and he provided explicit instructions on how the leaves were sampled. To select tree species for the community comparison, we considered the 20 most abundant tree species and only considered those where T. T. Struhsaker collected foliage from at least two individuals of the same species. Because intraspecific variability in nutrients is expected (Chapman et al. 2003), we did not collect leaf samples where fiber variation exceeded a CV (coefficient of variation) of 0.17, because, after this cutoff, the CV became dramatically larger (i.e., the next CV in the order was 0.33). This sampling regime allowed us to assess differences in tree chemistry more reliably, but might have biased our data set toward trees that are less phenotypically plastic. As in the earlier sample, we collected ~30 g of mature leaves from 10 species over three years, from 2007–2009, at least once in each year. These species were *Trilepsium madagascariense*, *Cassipourea ruwensorenensis*, *Celtis durandii*, *Diospyros abyssinica*, *Dombeya mukole*, *Markhamia lutea*, *Pancovia turbinata*, *Teclea nobilis*, *Uvariopsis congensis*, and *Xymalos monospora*. We followed the same methods of field collections as in the earlier collections, and the leaves were sampled from the same area and trail where T. T. Struhsaker did his original collections in the K-30 area of the forest, from many of the same, now older, marked trees when they were located. For example, we collected the leaves from the lower portion of the tree crown using a tree saw as T. T. Struhsaker did because leaf chemistry may vary within the tree crown according to sun exposure (Rozendaal et al. 2006). We do not know the leaf life spans of the trees in this community, but leaves from other wet tropical forest trees have life spans of 374–679 days (Kitajima et al. 1997), far shorter

than the study period, and at least two of the tree species in our sample are semi-deciduous (*Celtis* spp.). Older leaves do have lower concentrations of protein and possibly higher fiber (Kitajima et al. 1997). When we collected leaves from trees, we sampled them over time and we sampled a mixture of leaves in the lower crown repeatedly, thus we do not believe leaf age could have affected our analyses. In some cases, because the tree had grown in size, and the tree saw could not be extended to reach the leaves, a skilled tree climber collected the leaves from the lower portion of the tree crown. We then dried the leaves in the sun as did T. T. Struhsaker. J. M. Rothman and D. Twinomugisha processed the leaves in the same way that T. T. Struhsaker did earlier by hand crushing the leaves and placing them in paper bags before analysis.

Similarly, we recollected and analyzed the mature leaves from the same *S. scheffleri* individuals for ADF. We collected samples of leaves (~20 g dry mass) three times from each tree over 2007–2009 from eight of the original 10 trees sampled; two trees had died. Collection times for both sample sets were standardized such that each species was collected once a year in the same seasons when T. T. Struhsaker collected them in 1979.

From 1994 to 1997, C. A. Chapman collected young leaves (mean = 18 separate samples of ~20 g dry mass, range = 3–35) from eight tree species *Trilepsium madagascariense*, *Celtis africana*, *Celtis durandii*, *Diospyros abyssinica*, *Dombeya mukole*, *Funtumia latifolia*, *Markhamia lutea*, and *Milletia dura* when he saw the monkeys feeding on them. Young leaves were discerned from mature leaves based on color, size and toughness. More recently (2007–2010), J. M. Rothman, C. A. Chapman, D. Raubenheimer, and D. Twinomugisha collected young leaf samples using the same criteria from this same tree community (mean = 25 samples, range = 4–38 samples for each tree species), and processed them in the same manner that C. A. Chapman did in 1994–1997. Both teams collected the leaves from trees that were eaten by red colobus monkeys in the same tree community.

The sets of samples from the 1990s and 2000s were analyzed for protein (estimated as $N \times 6.25$) via Dumas combustion, and ADF at Hunter College by J. M. Rothman. After confirming the normality of the data sets, we used paired t tests to compare protein and ADF concentrations from earlier sampling to the more recent data set for the same species within a community or the same individuals within a species.

RESULTS

In the mature leaves from the same individual *S. scheffleri* trees, from the 1970s to the 2000s, fiber concentrations increased by $13.1\% \pm 4.5\%$ (mean \pm SD; $n = 8$ trees, paired $t = -6.85$, $P = 0.02$; Fig. 1), indicating that leaf nutritional quality declined over 30

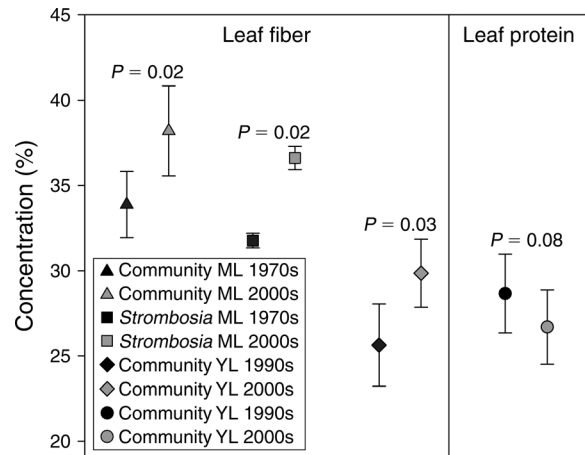


FIG. 1. Long-term changes in leaf acid detergent fiber and crude protein in a tropical forest with climate change (mean \pm SE). Abbreviations are ML, mature leaf; YL, young leaf.

years in these trees. Similarly, across the community of multiple individuals of 10 tree species analyzed in the 1970s and the same tree species again in the 2000s, all but one species (*Dombeya mukole*) declined in quality, with a mean increase in mature leaf fiber of $10.1\% \pm 11.6\%$ ($n = 10$ species, paired $t = -2.89$, $P = 0.02$). Fiber concentrations in young leaves collected from the same species of trees in the same area of the forest increased by $14.5\% \pm 13.2\%$ between 1994–1996 and 2007–2010 ($n = 9$ species, paired $t = -2.68$, $P = 0.03$) and protein concentrations declined by $6.4\% \pm 8.4\%$ ($n = 9$ species, paired $t = 2.03$, $P = 0.08$). The young leaves of one species decreased in fiber by 1.6% (*Markhamia lutea*), and one species (*Milletia dura*) increased in protein by 5.7%. Overall, the protein-to-fiber ratio of young leaves, a predictor of leaf choice and colobus biomass, declined 22.3%, from 1.26 ± 0.57 to 0.98 ± 0.33 ($n = 9$ species, paired $t = 2.77$, $P = 0.03$). The two species whose young leaves were most frequently eaten by red colobus monkeys (Struhsaker 2010), *Celtis africana* and *C. durandii*, declined in their protein-to-fiber ratio by over 30% (*C. africana* $n = 30$ leaf samples for both years, individual sample $t = 4.16$, $P < 0.001$; *C. durandii*, $n = 35$ in 1990s, $n = 38$ in 2000s, individual sample $t = 6.25$, $P < 0.001$; Fig. 2).

DISCUSSION

Our results suggest that nutritional quality of foliage has declined in Kibale National Park, Uganda over the last 15–30 years. In this forest where primate densities are high, fiber concentrations of mature and young foliage increased and protein in young foliage decreased in the tree leaves eaten by colobines. These results are consistent with greenhouse experiments that suggest that leaf nitrogen will decline substantially with global change occurring in the direction we describe (Zvereva

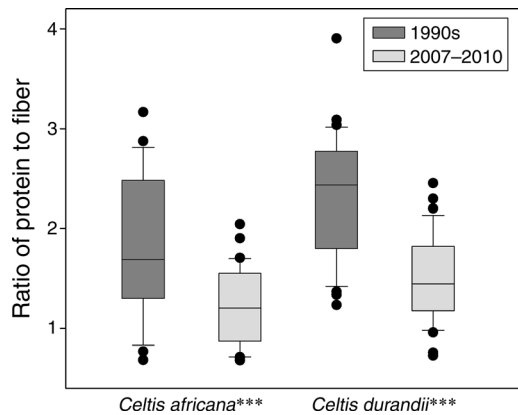


FIG. 2. Variation in the crude protein to acid detergent fiber ratios of young leaves of *Celtis africana* and *C. durandii*, two frequently consumed diet items of colobus monkeys in Kibale in 1996–1999, and 2007–2010.

*** $P < 0.001$.

and Kozlov 2006, Stiling and Cornelissen 2007, Robinson et al. 2012). We do not know what aspect(s) of global change caused our reported patterns. We know little about the role of CO_2 on fiber in tree foliage. Multiple studies demonstrate declines in leaf nitrogen and increases in leaf toughness across different plant species, which is often considered a proxy for fiber, though one study suggests that leaf fiber should decline (Robinson et al. 2012). Less is known about the effects of increasing rainfall and higher temperatures, but a few studies exist. Increasing temperature has been suggested to mitigate the declines in nutritional quality (Robinson et al. 2012), but our data suggest this is not the case. Our documented changing leaf chemistry may impact tropical communities because in addition to providing food for monkeys, a suite of other mammals, insects, reptiles, birds, and detritivores subsist on this foliage.

Milton (1979) proposed that the protein-to-fiber ratio was a good predictor of leaf choice for folivorous primates. Several subsequent studies have found positive correlations between colobine biomass and this index of mature leaf quality at local and regional scales (Waterman et al. 1988, Oates et al. 1990, Ganzhorn 1992, Chapman et al. 2004, Fashing et al. 2007). A meta-analysis that combined published data on protein-to-fiber ratios and colobus biomass from several sites ($n = 5$ sites) and similar data from Kibale ($n = 9$ sites) were used to build a predictive model that accounted for 87% of variation in folivore biomass across these 14 study sites sampled (Chapman et al. 2004). Using this model, if mature leaves respond similarly to young leaves, our data predict there should be a 31% decline in the colobus biomass in Kibale. If this change in nutritional chemistry is generally applicable across rainforests, the model predicts a similar effect for colobines in other habitats.

However, the most recent census of the group densities of colobines suggests that Kibale colobus have been stable over the period covered by this study (Chapman et al. 2010). Why might this be? Monkeys may employ counter-strategies to this change in nutritional quality. For example, though colobine monkeys have a foregut that may limit gut fill, the monkeys could compensate for this decrease in diet quality by eating more food. This effect has been seen in experiments that simulate the effects of climate change on nutrients, whereby insect herbivores consumed more food to obtain adequate quantities of protein, though when faced with higher fiber this is apparently not employed (Buse et al. 1998), possibly because the fiber is too difficult to digest. Monkeys could also switch to other plant species that do not experience severe declines in nutritional quality; *Markhamia lutea* young leaves declined in fiber, as did *Dombeya mukole* mature leaves, thus replacing unprofitable foods in their diets. There is interannual variability in colobine diets, but *Markhamia lutea* increased in the diets of red colobus from 1970 to 1987 (Struhsaker 2010), and despite declines in its abundance (Chapman et al. 2013), it is still a frequently eaten food (Ryan et al. 2013). *Dombeya mukole* mature leaves are not frequently eaten. It is also possible that there is a lag time before we see a population response to this changing leaf chemistry (Struhsaker 1976). Our results highlight the need for ecological and conservation-based models that allow for compensatory responses (Raubenheimer et al. 2012, Seebacher and Franklin 2012). Finally, while the protein-to-fiber model has strong correlative power across study sites in Africa and Asia, the underlying nutritional mechanism for the protein to fiber model predicting colobine biomass is not well understood (Wallis et al. 2012). Leaf nitrogen in Kibale foliage is high compared to other forests (Oates et al. 1990) and is well above the estimated protein requirements for primates. Further studies that incorporate additional nutritional (such as digestible protein, tannins, and metabolizable energy), and nonnutritional measures (such as young leaf abundance) are underway to disentangle the predictors of colobine biomass in Kibale. For example, we found that there are more food trees for red colobus monkeys and these food trees are larger than they were 24 years ago (Gogarten et al. 2015). We are currently conducting a census of the Kibale colobines (the fifth census since 1970) in the old-growth forest to evaluate changes in colobine densities.

In many trees, photosynthetic capacity declines as the tree ages (Ryan et al. 1997). Little is known about the effects of tree age on fiber and protein in its foliage in tropical angiosperms. In a chronosequence of beech stands (*Fagus sylvatica*), leaf nitrogen and carbon contents were unchanged with increasing age (Louis et al. 2012). In gymnosperms, there may be a decline in leaf nitrogen with increasing age (Kull and Koppel 1987,

Niinemets 2002) or leaf nitrogen may not be affected (Mattson et al. 1991). We were unable to control for tree age because Kibale tree ages are not known (diameter at breast height is not a good predictor of tree age; Connell and Green 2000). While we sampled the same trees that increased in age in the 1970 to 2009 comparison, we sampled trees of varying ages that monkeys chose in the 1990 to 2010 comparison. If tree age affected foliar leaf chemistry in the Kibale trees, then we would not expect to see a decline in protein and an increase in fiber in the 1990 to 2010 comparison because some of the trees sampled in 2010 might be younger than those sampled in 1990.

In addition to changes in macronutrients, global environmental changes are predicted to increase secondary compounds, which may exacerbate the effects of reduced nutritional quality. In particular, phenolic compounds like condensed tannins may increase under conditions of high CO₂, temperature, and rainfall (Coley 1998, Dury et al. 1998, Coley et al. 2002, Robinson et al. 2012), although results are variable (Veteli et al. 2007, Robinson et al. 2012). Condensed tannins are prevalent in the diets of colobine monkeys (Chapman and Chapman 2002), and they bind protein and reduce digestibility, so the combined effects could be detrimental for acquisition of adequate nutrition for folivores.

Aside from reducing the anthropogenic consequences of climate change, strictly protecting rainforest habitats provides the most immediate option for conserving folivorous herbivores; however, reforestation of degraded areas may also prove extremely valuable (Millar et al. 2007). Understanding nutritional chemistry could affect selection of trees for restoration. Our results demonstrate that projected climatic shifts in tropical tree communities with concomitant changes in foliar nutrients could affect herbivores, and highlights the need for future studies on the nutritional ecology of wildlife in relation to global change.

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