

Human impacts on leaf economics in heterogeneous landscapes: the effect of harvesting non-timber forest products from African mahogany across habitats and climates

Orou G. Gaoue^{1,2,3*}, Lawren Sack⁴ and Tamara Ticktin²

¹Department of Biology, Institute of Theoretical and Mathematical Ecology, University of Miami, Coral Gables, FL 33146, USA; ²Department of Botany, University of Hawaii at Manoa, Honolulu, HI 96822, USA; ³Université de Parakou, BP 123, Parakou, Benin; and ⁴Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA 90095, USA

Summary

1. Non-timber forest products (NTFP) are harvested by millions of people for their livelihood. To define sustainable harvest limits it is critical to understand the biological impacts of harvest. In the last decade we have improved our understanding of the demographic mechanisms driving population level responses to harvest. Our understanding of the ecophysiological underpinnings for these processes is still limited.

2. We tested the effect of foliage harvest by indigenous *Fulani* people on leaf stoichiometry and economics in *Khaya senegalensis* (Meliaceae) in two vegetation types (fallows vs. forest) and in two ecological regions (dry vs. moist) in Benin, West Africa.

3. Leaf mass per area (LMA) increased with aridity. Across sites and treatments, LMA correlated negatively with nitrogen and phosphorus per mass (N_{mass} and P_{mass} respectively), more strongly than with concentrations per area (N_{area} and P_{area} respectively) consistent with world-wide trends in leaf economics. The effect of foliage harvest on foliar nutrient concentrations was dependent on plant size and habitat. Harvesting increased N_{mass} and P_{mass} in larger trees, and altered the LMA – N_{mass} relationship between vegetation types and the LMA – P_{area} relationship between ecological regions, but it did not affect stoichiometry (N:P or C:N ratios).

4. *Synthesis and applications.* The context-dependent effect of harvest on leaf economics emphasizes the importance of considering plant size and climate in predicting the biological consequences of NTFP harvest, and explains some of the ecophysiological mechanisms underlying demographic responses to harvest. The plant size- and climate-dependent effects of harvest on leaf composition suggest a different approach for assessing the impact of NTFP harvest on population dynamics. NTFP harvest should be modelled explicitly as a size dependent factor and integral projection models provide the framework for this. Our findings suggest that to reduce harvesting pressure on wild populations, it is important to encourage Fulani owned *K. senegalensis* plantations, especially in the dry region where harvest had greater effects.

Key-words: ecological differences, *Khaya senegalensis*, leaf functional traits, NTFP harvest impact, stoichiometry, tropical trees, West Africa

Introduction

Wild plants are harvested world-wide by local people for their livelihood and serve as important sources of medicine, food and income for millions of people (Bawa *et al.* 2004; Ticktin

2004). Long-term harvesting of non-timber forest product (NTFP) may have severe ecological and evolutionary consequences. For example, heavy harvest of plant organs over the long term can reduce mean individual plant size (Law & Salick 2005), water uptake (Snyder & Williams 2003), and induce a shift in allocation of limited resources to leaf production at the expense of reproductive structures (Anten, Martinez-Ramos

*Correspondence author. E-mail: ogaoue@bio.miami.edu

& Ackerly 2003) thereby affecting overall population fitness (Ghimire *et al.* 2008; Gaoue & Ticktin 2010). Harvesting a NTFP such as bark can damage the phloem, disrupt nutrient transport and create an imbalance in the proportion of nutrients in different parts of the plant. Studying leaf stoichiometry, that is the study of the balance of nutrients (particularly C:N and N:P ratios) in organisms, can provide insights on potential nutrient limitation in plants (Tessier & Raynal 2003; Gusewell 2004), leaf palatability (Fornara & du Toit 2007) and it can clarify the physiological underpinnings for demographic bottlenecks (Moe *et al.* 2005). Moreover, an improved understanding of how NTFP harvest affects plant carbon capture, growth strategy and response to stress can elucidate the mechanisms responsible for harvest-induced changes in demographic rates and the impact on population fitness, as well as the degree that plants can shift their allocational patterns in response to human harvesting pressure. To develop sound management guidelines for sustainable harvest, this information on the ecophysiological mechanisms driving the demographic responses to harvest is critical for targeted management actions.

The global theory of the coordination of leaf economics traits (Wright, Reich & Westoby 2001; Ackerly *et al.* 2002; Wright *et al.* 2004) holds that leaf mass per area (LMA) correlates positively with leaf life span and negatively with leaf nitrogen and phosphorus concentrations per dry mass (N_{mass} and P_{mass}), and photosynthetic capacity. World-wide, plants vary along a leaf economics spectrum between the extremes of species with short leaf life span that favour quick return on investments (low LMA, high nutrient concentrations and high net photosynthesis rates per mass) and species that favour slow return on investments over a longer leaf life span (Wright *et al.* 2004). Shifts along this leaf economics continuum can reveal plant adaptation to maximize carbon capture over the leaf lifetime, and scale up to demographic performances (Poorter & Bongers 2006). Leaf economics relationships may shift across species in different vegetation types (e.g., Hoffmann *et al.* 2005) and across rainfall, soil fertility gradients (Wright, Reich & Westoby 2001), growth form or life-history (Santiago & Wright 2007). However there has been little study of shifts in leaf economics relationships or leaf stoichiometry for species with wide distributions, and subject to human impacts under variable ecological conditions. It is reasonable to hypothesize that the physiological responses of plants to human activities such as NTFP harvest will vary with changes in climate and between habitats for a given species. Moreover, given that LMA and leaf nutrient concentration depend on leaf age and plant size (Anten *et al.* 1998; Kitajima *et al.* 2002; Sack, Marañón & Grubb 2002; Reich *et al.* 2006), these responses are likely to change with the size of individual plant. In this study, we investigated how NTFP harvest may alter leaf economics relationships and stoichiometry, if the effects vary with individual plant size, and how variation in ecological conditions may influence these effects.

We studied the impact of foliage harvest by *Fulani* people on the leaf stoichiometry and economics relationships of *Khaya senegalensis* (Meliaceae) in two ecological regions (dry vs.

moist) and two vegetation types (forest vs. fallow) in Benin. *Khaya senegalensis* is a timber species distributed across Africa and has been heavily logged since the 19th century (Parren 2003). Remnant populations of *K. senegalensis* are heavily pruned by the Fulani people to feed their cattle during the dry season (Gaoue & Ticktin 2007). Previous studies on *K. senegalensis* have illustrated that foliage harvest reduces reproductive output (Gaoue & Ticktin 2008) and alters population size structure (Gaoue & Ticktin 2007) and dynamics (Gaoue & Ticktin 2010). These effects were stronger in the dry than in the moist region. However, it has been unclear if such effects were associated with specific changes in plant nutrient concentration, carbon capture and growth, or with modification of leaf functional trait correlations or stoichiometry.

From a plant–herbivore interaction perspective, understanding whether repeated foliage harvest by Fulani improves fodder nutrient concentration and palatability to their cattle has practical implications and may improve our understanding of some of the complex relationships between the Fulani, their environment and their herds. Harvesting *K. senegalensis* foliage is culturally and economically important to the Fulani (Petit 2003), and an improvement in foliage nutritional quality and quantity can lead to increased milk production and herd size. The milk produced by the cows is consumed by the Fulani and sold in local markets (Gaoue & Ticktin 2009). The Fulani rely on these products as a source of income. Their movement across the landscape, and decisions about the location and the timing of harvest, are influenced by the quality and quantity of fodder trees as well as the availability of water, which is disproportionately distributed between ecological regions (Gaoue & Ticktin 2007, 2009). Future climate projections in West Africa suggest a gradual shift with the moist region becoming drier (Paeth & Thamm 2007). Therefore, comparing the effects of harvest on leaf economics and stoichiometry across the aridity gradient can provide insight into factors that may affect population responses under future climate regimes, at least in the moist region, as well as indicate potential changes in Fulani harvesting practices across regions.

We tested if foliage harvest by Fulani increases *K. senegalensis* leaf nutrient concentration and alters leaf structure, and how such effects may vary with tree size and across a gradient of aridity from the dry to the moist region. Based on leaf economics theory (Small 1972; Ackerly *et al.* 2002; Wright *et al.* 2004) and stoichiometric theory (Reich & Oleksyn 2004; Elser *et al.* 2010), we hypothesized that leaf traits would shift along an aridity gradient for *K. senegalensis* and that (i) foliar mass-based nutrient concentrations (N_{mass} and P_{mass}) will correlate negatively with LMA while area-based nutrient concentrations (N_{area} and P_{area}) and carbon isotope ratio ($\delta^{13}\text{C}$; an index of long-term integrated water use efficiency) will correlate positively with LMA, and (ii) foliar nutrient concentrations will correlate positively with each other. We also predicted that (iii) foliage harvest, by rejuvenating the canopy and increasing light penetration, will reduce LMA and increase leaf mass-based nutrient concentrations but will not change the stoichiometric ratios (C:N and N:P) or the relationships of nutrients to leaf structure. We predicted that (iv) any effect of harvest on leaf

economics relationships and stoichiometry will be stronger in the nutrient poor environment (forest) in the dry region than in the nutrient-rich environment (fallow) in the moist region. We consider the implications for management and for modelling the effect of harvest on population dynamics.

Materials and methods

STUDY DESIGN

Khaya senegalensis grows in the wild throughout a wide range of habitats (gallery forests, dry forest and savanna woodland) in Africa, from 8° to 14°N (Normand & Sallenave 1958; CTFT 1988). It is a semi-deciduous, shade intolerant and slow growing tree that may reach up to 30 m in height and 3 m in girth, with a short bole, dense crown and leaves composed of 3–4 pairs of elliptic leaflets, 5–10 cm long by 2.3–5 cm wide (CTFT 1988).

This study was conducted in the Republic of Benin (6°–12°50N; 1°–3°40E) in West Africa. Annual rainfall increases gradually from the dry Sudanian region (9°30′–12°N) with annual rainfall of 900–1000 mm to the moist Sudano-Guinean region (7°30′–9°30N) with 1000–1100 mm year⁻¹. We selected 16 *K. senegalensis* populations distributed in the two regions (see Table S1, Supporting information). In each region, we selected trees in two vegetation types: fallows (abandoned fields previously used for agriculture) and forest (gallery and dry dense forests). Water availability and tree density (all species included) is greater in fallows (331 ± 148 stems ha⁻¹) than in forests (576 ± 98 stems ha⁻¹). In each region and for each vegetation type, we selected two independent populations with low foliage harvest intensity (< 5% trees pruned) and two populations heavily harvested (> 50% trees pruned) for their foliage by the Fulani people.

LEAF TRAIT MEASUREMENTS

Five mature trees of diameter at breast height (d.b.h.) > 20 cm were randomly selected per population. For each of the 80 trees, we recorded d.b.h., height, neighbour tree density within a 5 m radius, and we collected two fully expanded mature leaves from the northern facing side of the tree and from the highest possible branch (13.4–25.4 m above-ground). Leaves were scanned on a flatbed scanner and images were analysed (using IMAGEJ; available online: <http://rsb.info.nih.gov/ij/>) to determine leaf area, and as a shape index, the leaf perimeter²/area (P²/A), a size-independent measure of relative edge per leaf area (Sack *et al.* 2003). Leaf samples were oven-dried at 60 °C for 48 h before measuring dry mass. We determined leaf dry mass per area (LMA) and the proportion of leaf mass allocated to support (midrib and rachis). Leaf samples were analysed for nitrogen concentration per mass (N_{mass}) and carbon isotope composition (δ¹³C) using high temperature combustion in an elemental analyzer (Costech ECS 160 4010; Valencia, CA, USA), with effluent passed into a continuous flow isotope ratio mass spectrometer (CF-IRMS; ThermoFinnigan Delta V Advantage with a ConFlo III interface; ThermoFisher Scientific; Waltham, MA, USA; Fry *et al.* 1996). Samples were dried and ashed in glass vials (Miller 1998), dissolved in 1 N HCL and analysed for phosphorus per mass (P_{mass}) using inductively coupled plasma-optical emission spectrometry (ICP-OES; Varian Vista MPX Instrument, Varian Inc., Palo Alto, CA, USA; Porder, Paytan & Vitousek 2005). Concentrations of nitrogen and phosphorus per area (N_{area} and P_{area} respectively) were determined by multiplying N_{mass} and P_{mass} by LMA.

DATA ANALYSIS

We log₁₀-transformed leaf trait variables (except δ¹³C) to meet the normality and homogeneity of variance assumptions. We tested the main effects and interactions of harvest, vegetation type and ecological region on each variable. We fitted four different types of models (with or without covariate): an analysis of variance and analysis of covariance with tree height, d.b.h. or neighbouring tree density as covariate. To select the best fitting models (models with or without covariate; see Table S2, Supporting information) for each variable, we used an information-theoretic approach (Burnham & Anderson 2004). For each response variable, we estimated the Akaike Information Criterion (AIC) for each model, the difference in AIC between each model, *i*, and the model with the lowest AIC value: ΔAIC (= AIC_{*i*} – AIC_{min}). We selected models with ΔAIC < 2 as the best supported models. For each variable, we tested the significance of the effect of each predictor using the simplest best fitting model. We used the 'effect' package (Fox 2003) in R 2.6.1 (R Development Core Team 2007) for the graphical illustrations of the analysis of (co)variance.

To test if the pairwise relationships among leaf traits were altered by foliage harvest and ecological conditions, we determined standard major axes (SMA; Warton *et al.* 2006) for the log-transformed variables using the SMATR package in R 2.6.1. For each trait pair, we determined the intercept *a* and slope *b* for the SMA log *y* = *a* + *b* log *x* (where *y* and *x* are leaf functional traits) and we tested if *a* and *b* differed significantly between dry and moist regions, low and high harvest levels, fallow and forest and the combinations of different ecological region, harvest intensity and vegetation type. When there were significant differences in slope *b* between groups, we estimated group-specific slopes and tested for significant difference in their intercepts (Wright, Reich & Westoby 2001).

Results

MODEL FITTING

The three-way ANCOVA with tree height as covariate was the best fitting model for N_{mass}, P_{mass}, P_{area} and δ¹³C (Table S2, Supporting information); the three-way ANCOVA with neighbouring tree density as covariate was the best fitting model for leaf mass, area and C:N ratio; and the three-way ANOVA was the best model for leaf (perimeter)²/area, LMA, N_{area}, N:P ratio and the proportion of leaf mass allocated to support. The three-way ANCOVA with d.b.h. as covariate was not selected as the best model for any of the variables.

LEAF FUNCTIONAL TRAIT VARIATION

For *Khaya senegalensis*, leaf traits varied significantly between ecological regions and vegetation types (Table 1). Leaves in the dry region had lower nutrient concentrations (P_{mass}: ANCOVA, $F_{(1, 64)} = 5.18, P = 0.026$; Fig. 1a) but were greater in mass [ANCOVA, $F_{(1, 64)} = 19.9, P < 0.0001$; Fig. 1b], with higher LMA [ANOVA, $F_{(1, 72)} = 22.0, P < 0.0001$; Fig. 1d] and with more dissection, i.e. higher P²/A [ANOVA, $F_{(1, 72)} = 9.62, P = 0.0027$; Fig. 1c] than those in the moist region. The larger the leaves, the greater N_{mass} and P_{mass} they tended to have although the correlation was weak ($r = 0.22$ for both, $P \leq 0.05$). Leaf N:P ratio [ANOVA, $F_{(1, 72)} = 9.03, P = 0.0036$; Fig. 1e] and N_{mass} [ANCOVA, $F_{(1, 64)} = 9.61, P <$

Table 1. Analysis of (co)variance (with tree height as covariate for N_{mass} , P_{mass} , P_{area} , $\delta^{13}\text{C}$ and $^{\text{a}}$ tree density as covariate for leaf mass, leaf areas) testing the effect of ecological region, harvest intensity and vegetation type on leaf traits. Values are mean square and degree of freedom (d.f.) for main effects and interactions. $^{\text{b}}$ The residual d.f. for ANOVA for N:P, C:N, N_{area} and Leaf mass per area (LMA) is in parenthesis

	d.f.	N_{mass}	P_{mass}	P_{area}	$\delta^{13}\text{C}$	Leaf mass	Leaf area	N:P	C:N	N_{area}	LMA
Region	1	0.133	0.622*	0.129	0.081	2.67***	0.173	0.198	0.119	0.631**	1.483***
Harvest	1	0.003	0.023	0.014	2.142	0.564*	0.589*	0.046	0.003	0.0047	0.00026
Vegetation	1	0.400**	0.030	0.056	1.721	2.024***	2.067***	0.629**	0.349**	0.354**	0.00023
Height ^a	1	0.008	0.099	0.069	18.94**	0.078	0.213	–	–	–	–
Region × harvest	1	0.035	0.294	0.008	11.01*	0	0.213	0.133	0.013	0.064	0.148
Region × vegetation	1	0.040	0.319	0.045	3.118	0.098	0.004	0.125	0.033	0.018	0.079
Harvest × vegetation	1	0.052	0.00092	0.027	5.208	0.565*	0.416*	0.033	0.019	0.0026	0.021
Region × height ^a	1	0.0008	0.00022	0.047	6.464	1.130**	0.133	–	–	–	–
Harvest × height ^a	1	0.246*	0.487*	0.265*	0.754	0.052	0.014	–	–	–	–
Vegetation height ^a	1	0.029	0.227	0.008	11.43*	1.307**	1.196***	–	–	–	–
Region × harvest × vegetation	1	0.014	0.004	0.100	0.943	0.00003	0.045	0.051	0.0012	0.237*	0.139
Region × harvest × height ^a	1	0.00002	0.03	0.068	0.693	0.309	0.052	–	–	–	–
Region × vegetation × height ^a	1	0.111	0.571*	0.135	2.632	1.541**	0.804**	–	–	–	–
Harvest × vegetation × height ^a	1	0.00031	0.164	0.266*	3.436	0.004	0.035	–	–	–	–
Region × harvest × vegetation × height ^a	1	0.112	0.285	0.042	17.10**	0.037	0.012	–	–	–	–
Residuals	64 (72) ^b	0.042	0.120	0.062	1.681	0.134	0.098	0.069	0.041	0.036	0.067

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$ and other values are not significant.

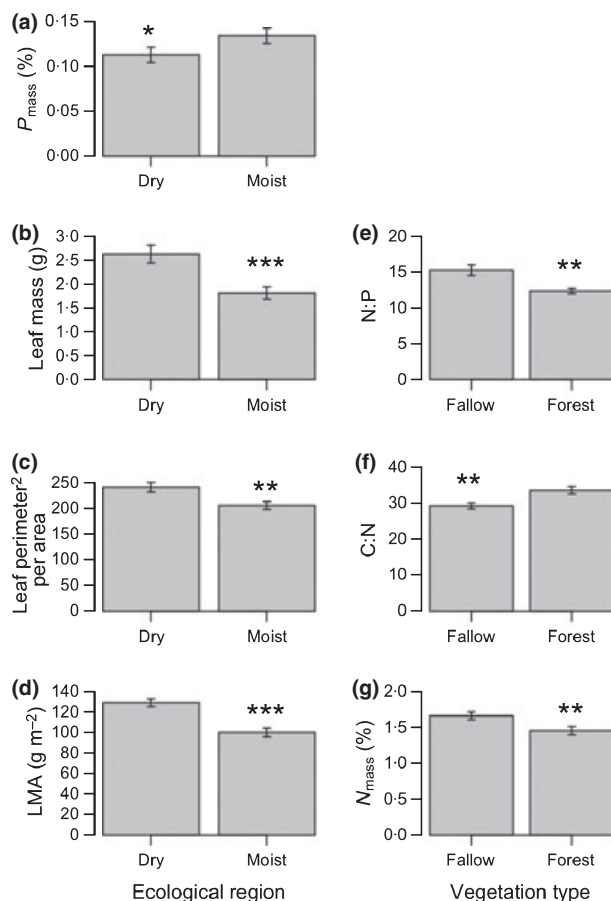


Fig. 1. Main effects of ecological differences on mean leaf (a) phosphorus per mass (P_{mass}), (b) leaf mass, (c) leaf perimeter²/area, (d) leaf mass per area (LMA), and of vegetation type on leaf (e) N:P, (f) C:N and (g) N_{mass} . Error bars are 1 standard error of means. *** $P < 0.001$, ** $P < 0.01$; * $P < 0.05$.

0.0028; Fig. 1g], were higher in fallows than in forests but C:N ratio showed the opposite trend [ANCOVA, $F_{(1, 72)} = 0.35$, $P = 0.0032$; Fig. 1f].

The effect of foliage harvest on leaf nutrient concentration was size dependent. In both ecological regions and vegetation types, heavy foliage harvest reduced leaf nutrient concentrations for smaller trees (height < 18 m), but increased nutrient concentrations in larger trees [ANCOVA, $F_{(1, 64)} = 5.89$, $P = 0.0180$; Fig. 2a, P_{mass} : ANCOVA, $F_{(1, 64)} = 4.05$, $P = 0.048$; Fig. 2b and P_{area} : ANCOVA, $F_{(1, 64)} = 4.31$, $P = 0.042$; Fig. 2c]. The leaves in the dry region tended to have higher N_{mass} and P_{mass} in high-harvest trees but the contrary was true for low-harvest trees. Heavy harvest increased carbon isotope ratio ($\delta^{13}\text{C}$) in the dry region (in fallows) but reduced $\delta^{13}\text{C}$ in the moist region both in fallow and forest [ANCOVA, $F_{(1, 64)} = 10.2$, $P = 0.0022$; Fig. 2d]. The increase in water use efficiency (higher $\delta^{13}\text{C}$) also corresponded with higher leaf nutrient concentrations (Fig. 3a, b). Regardless of ecological region, leaves with greater water use efficiency tended to have higher nutrient concentrations per mass (N_{mass} : $r = 0.41$, $P < 0.001$; Fig. 3a and P_{mass} : $r = 0.48$, $P < 0.001$; Fig. 3b), and to a lesser extent, per area (P_{area} : $r = 0.26$, $P = 0.017$; N_{area} : $r = -0.085$, $P = 0.45$). Within each vegetation type, and at a given $\delta^{13}\text{C}$ value, high-harvest trees tended to acquire more P per unit of mass than low harvest trees (Fig. 3b). Moreover, higher LMA leaves in the moist region tended to have the least water use efficiency (lower $\delta^{13}\text{C}$) ($r = -0.35$, $P = 0.001$; Fig. 3c) regardless of their size ($\delta^{13}\text{C}$ vs. leaf area: $r = -0.005$, $P = 0.96$) or shape ($\delta^{13}\text{C}$ vs. leaf shape index: $r = -0.18$, $P = 0.11$).

In both ecological regions, leaves in harvested trees in forest were heavier [leaf dry mass ANCOVA, $F_{(1, 64)} = 4.21$, $P = 0.044$; Fig. 2e] and larger [leaf area ANCOVA, $F_{(1, 64)} = 4.26$, $P = 0.043$; Fig. 2f] than in non-harvested trees, but the difference was moderate in fallows. Leaf mass increased with leaf

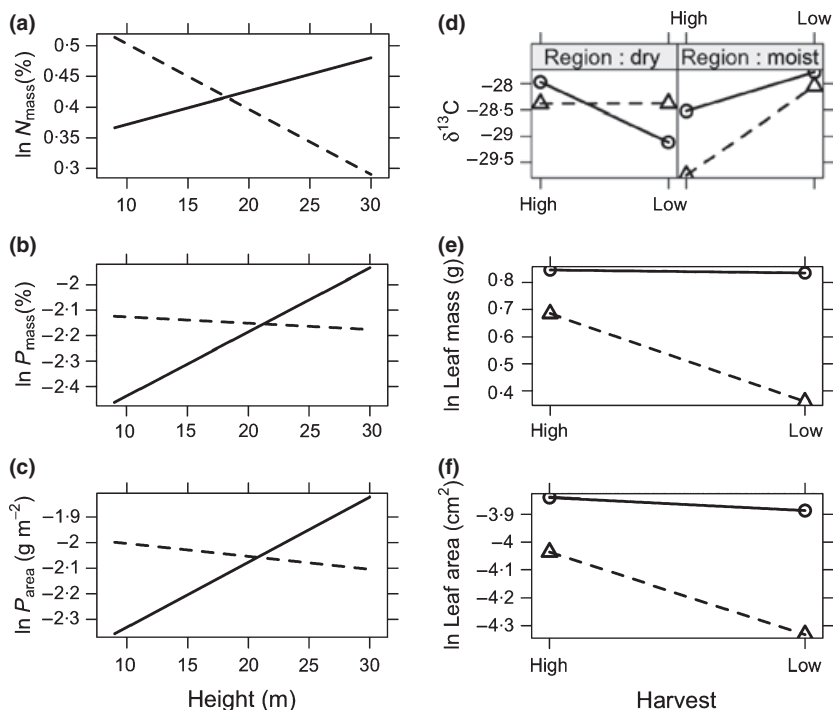


Fig. 2. The effect of foliage harvest on leaf nutrient concentration (a) N_{mass} , (b) P_{mass} , (c) P_{area} is size (height) dependent (regression fit lines) but region or habitat-dependent for (d) carbon isotope discrimination ($\delta^{13}\text{C}$), (e) leaf mass and (f) area. Solid lines represent high-harvest populations for (a), (b), (c) and fallows for (d), (e), (f); dashed lines represent low-harvest populations for (a), (b), (c) and forests for (d), (e), (f).

area with a log-log slope of 1.14 (95% CI = 1.01; 1.30; Fig. 3e) independent of harvest intensity, region or vegetation type.

LEAF ECONOMICS RELATIONSHIPS

Leaf functional traits were strongly inter-correlated. Nutrient concentrations per unit mass (N_{mass} and P_{mass}) decreased with increasing LMA ($r = -0.65$ to -0.72 , $P < 0.001$, Fig. 4a, b). Leaf P_{mass} and N_{mass} were positively correlated ($r = 0.65$, $P < 0.001$, Fig. 4c). The effect of harvest on the leaf economics relationships varied significantly between ecological regions and vegetation types (Table 2; Fig. 4). Foliage harvest did not affect the rate of decrease in P_{mass} with increasing LMA ($P = 0.28$; common SMA slope = -1.38 ; 95% CI = -1.63 ; -1.18 ; Fig. 4b). By contrast, the rate of decrease of N_{mass} with increasing LMA was faster in trees in high-harvest populations than it was in low harvest populations in forest (significant difference in SMA slope: $P = 0.0088$; Table 2) but the opposite pattern was observed in fallows (Fig. 4a). Foliar P_{area} correlated significantly with LMA only in low-harvest populations in the dry region (Fig. 4c). The rate of increase of P_{mass} with increasing N_{mass} differed between vegetation types. At a given P_{mass} ($< 0.20\%$), N_{mass} was higher in fallows than in forest (SMA slope: $P = 0.048$; Fig. 4d).

Discussion

Consistent with the global trends in the coordination of leaf economics traits (Wright *et al.* 2004), LMA in *K. senegalensis* was higher in the dry region and drove a positive relationship between N_{mass} and P_{mass} as both decreased with increasing LMA. Foliar nutrient concentrations are constrained by the investment of dry mass in cell walls. High LMA leaves can be

thicker, with greater number of cell layers, and thus tend to have higher N_{area} , but because of internal self-shading, ultimately have lower photosynthetic nitrogen-use efficiency at a given N_{area} ; high LMA leaves can additionally be denser, and the dilution of cell contents with greater amount of dry mass in the cell walls can also lead to lower nitrogen-use efficiency at a given N_{mass} (Poorter & Evans 1998; Wright *et al.* 2004). Thus, by increasing light availability and yielding foliage renewal, foliage harvest may increase leaf N acquisition and photosynthetic capacity, although this increase may not always compensate for the carbon loss caused by heavy and frequent defoliation (Anten & Ackerly 2001). This mechanism may explain the increase in *K. senegalensis* N_{mass} and P_{mass} observed in larger trees after foliage harvest, even though harvest had an opposite effect on N_{mass} in smaller trees. In younger actively growing trees, the loss of carbohydrates and nutrients through repeated foliage harvest may affect the trees' ability to deploy carbon to roots and thus to access water (e.g. Snyder & Williams 2003), as well as depleting nutrients necessary to construct new leaves.

Harvest increased *K. senegalensis* leaf nutrient concentration in large trees and water use efficiency in dry areas, as indicated by $\delta^{13}\text{C}$. The increase in N_{mass} with increasing leaf area suggested that the increase in leaf nutrient concentrations after harvest was coordinated with an increase in leaf size as a response to harvest. However, this increase may not benefit harvested trees in the long term for few reasons. First, LMA reflects the dry mass cost of deploying new leaves and positively correlates with leaf life span (Wright *et al.* 2004). The high LMA in the dry region probably makes it more difficult for *K. senegalensis* to regenerate leaves after heavy foliage harvest. Ultimately, even though foliage harvest may improve photosynthetic capacity in the dry region, the frequent and

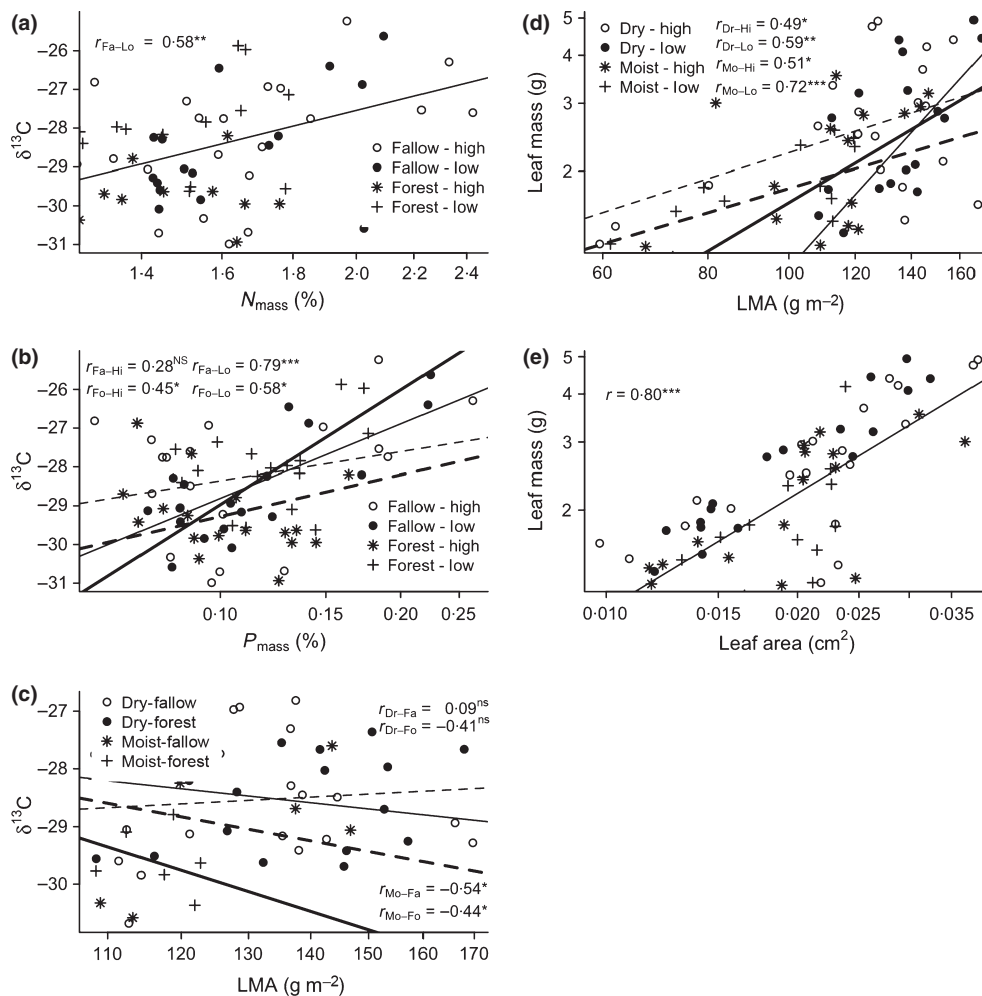


Fig. 3. Bivariate relationships between carbon isotope discrimination $\delta^{13}\text{C}$ and leaf nutrient concentration per unit of mass (a) N_{mass} (for vegetation \times harvest), (b) P_{mass} (for vegetation \times harvest) and (c) leaf mass per area (LMA; for region \times vegetation); and between leaf mass and (d) LMA (region \times harvest) or (e) leaf area; x and y (except for $\delta^{13}\text{C}$) axes are \log_{10} scaled. Solid fit lines represent low-harvest (lo) populations for (b), (d) or forest (fo) for (c) and dashed lines represent high-harvest (hi) populations for (b), (d), or fallow (fa) for (c). Thick lines represent regression fits for forest (fo) for (b) or moist (mo) region for (c), (d) and thin fit lines for fallows (fa) for (b) or dry (dr) region for (c), (d). r values are Pearson correlation coefficients and subscripts indicate different combinations of factors (region, vegetation, harvest) and are consistent with the associated legends; P -values test if r is significantly different from zero: $***P < 0.001$; $**P < 0.01$; $*P < 0.05$; NS, not significant.

heavy foliage harvest that is currently taking place (Gaoue & Ticktin 2007) has led to fewer leaves. Secondly, since plant water-use efficiency is negatively correlated with photosynthetic nitrogen use efficiency (Warren & Adams 2006), the cost of harvest on leaf economics may override the benefits associated with increased water-use efficiency. Thirdly, defoliation in other species causes a shift in the allocation of mass to leaf construction, at the expense of reproductive structures (e.g. Anten, Martinez-Ramos & Ackerly 2003; Fornara & du Toit 2007). Such a shift in resource allocation may be responsible for the lowered reproductive output found for harvested *K. senegalensis* populations in the dry region (Gaoue & Ticktin 2008). Given that the reduction in fruit production was only found in the dry region, the shift in resource allocation may be stronger when the tree is experiencing additional stress. This may ultimately affect the long-term persistence of *K. senegalensis* populations in the dry region, it is important to develop strategies to

limit the pressure of harvest on wild populations of *K. senegalensis*. One approach would be to encourage the establishment of Fulani owned plantations of *K. senegalensis* and other fodder tree species such as *Azelia africana* and *Pterocarpus erinaceus*. In addition, local management programmes for wild populations of *K. senegalensis* should encourage harvest of larger trees instead of smaller trees, given that the former seem more resilient to harvest than the latter.

Trees in the dry region and in forest had low leaf nutrient concentrations, consistent with the dynamics of nutrients across regions and vegetation types, as soil N decreases from the moist to dry region in our study area (Assogbadjo *et al.* 2005). Our finding that leaves in the dry region tended to have higher LMA and lower nutrient concentrations than in the moist region is consistent with Fulani herders migrating southward to the moist region in quest of water and perhaps also better *K. senegalensis* fodder (Gaoue & Ticktin 2007). However, *K. senegalensis* leaf N:P and C:N ratios did not vary

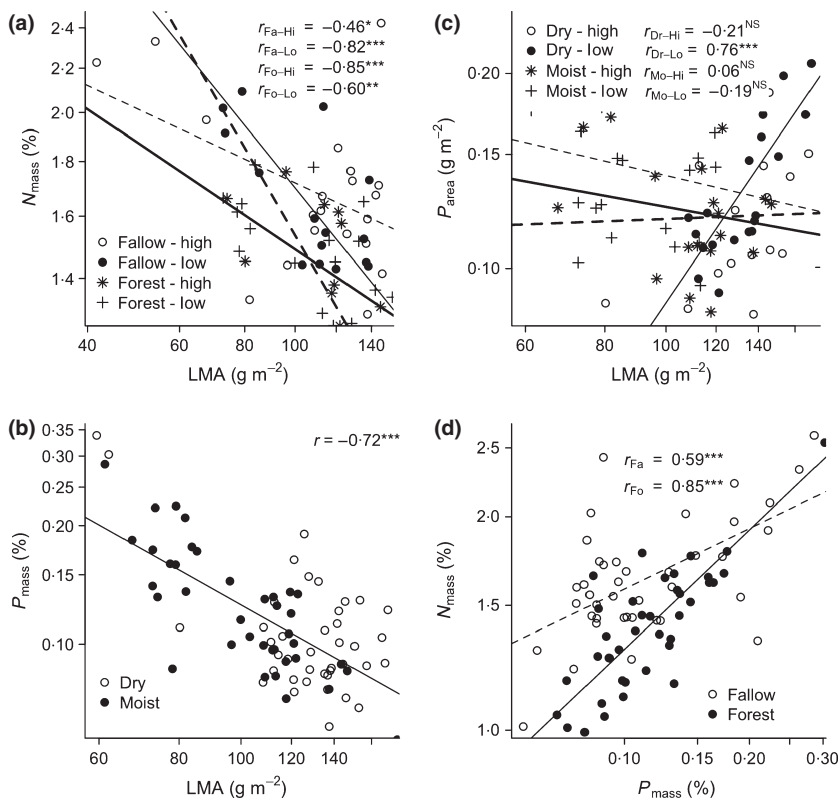


Fig. 4. Leaf mass per area (LMA) negatively correlated with (a) N_{mass} (for vegetation \times harvest), (b) P_{mass} and (c) P_{area} (for region \times harvest); (d) leaf nitrogen N_{mass} and phosphorus P_{mass} correlated positively but more strongly in forest (fo) than in fallows (fa). x and y axes are \log_{10} scaled. Solid fit lines represent low-harvest (lo) populations and dashed lines represent high-harvest (hi) populations for (a), and (c). Thick lines represent regression fits for forest (fo) for (a) or moist (mo) region populations for (c) and thin fit lines for fallows (fa) for (a) or dry (dr) region for (c); r values are Pearson correlation coefficients and subscripts indicate different combinations of factors (region, vegetation, harvest) and are consistent with the associated legends; P -values test if r is significantly different from zero. $^{***}P < 0.001$; $^{**}P < 0.01$; $^*P < 0.05$; NS, not significant.

between regions. This finding confirms recent work that showed that N:P ratio does not always vary with increasing annual rainfall in the tropics (Townsend *et al.* 2007).

The C:N ratio is an index of leaf palatability for browsers (see Fornara & du Toit 2007). Contrary to findings elsewhere, where browsing improved leaf palatability (Fornara & du Toit 2007), our results suggest that even though harvest may improve leaf nutrient concentration in selected cases, it did not affect P limitation or improve the palatability of *K. senegalensis* foliage. However, leaves in the fallows had a lower C:N, indicating a higher leaf palatability. Although one would expect that Fulani would prefer to harvest in fallows, that seems not to be the case (Gaoue & Ticktin 2007, 2009). However, we did observe that long unharvested trees that had old dark-green leaves – probably alkaloid-rich and N poor – were disliked by cattle (Gaoue & Ticktin 2009). Previous work also indicated that leaf N decreases with leaf age (Anten *et al.* 1998; Kitajima *et al.* 2002) but increases with plant size (Reich *et al.* 2006). Since foliage harvest rejuvenates the canopy and increases leaf N, as found in this study and others (see du Toit, Bryant & Frisby 1990), trees that escape foliage harvest for two or three consecutive years develop alkaloid rich and nutrient poor foliage. Therefore, those trees probably then escape harvest for an even longer time.

Our study of the leaf economics of *K. senegalensis* in Benin is one of the few on tropical African species outside of South Africa (e.g. Meir *et al.* 2007) and the first to our knowledge to assess the effects of traditional plant harvesting practices on leaf economics and stoichiometry. We found that foliage

harvest increases leaf nutrient concentrations and improves water use efficiency in fallows in dry regions. However, the high cost of leaf construction in dry regions and the low photosynthetic capacity in the thick leaves produced in that region coupled with the net loss of leaves are probably responsible for the documented negative impacts of foliage harvest on *K. senegalensis* reproduction and long-term demographic persistence (Gaoue & Ticktin 2008, 2010). Therefore given that what matters most to Fulani herders is the amount of foliage and its nutrient content, the benefits of pruning are mixed. Repeated foliage harvest at current levels may improve foliage nutrient concentrations but will be likely to decrease foliage quantity and quality in the long term, both at the individual and population levels. We also found that the effect of foliage harvest on leaf economics relationships was dependent on vegetation type and ecological region. This finding suggested that harvest has a complex impact on plant carbon and nutrient allocation. To detect a significant effect of harvest on plant nutrient composition it is therefore important to consider the additive or interactive effects of other compounding factors. This finding has implications for the study of the response of plants to NTFP harvest, suggesting that demographic studies that test the effect of NTFP harvest on population dynamics but do not account for ecological variation at individual and/or population levels may yield misleading conclusions.

What are the implications of our results for the study of the effects of NTFP harvest on plant population dynamics? The effects of NTFP harvest on population dynamics are assessed using matrix models (Caswell 2001; Ticktin 2004). The size

Table 2. Standard major axis regression analysis testing the interactive effects of ecological regions, harvest intensity and vegetation type on *Khaya senegalensis* leaf economics relationships: leaf mass per area (LMA), carbon isotope discrimination $\delta^{13}\text{C}$, nitrogen and phosphorus per mass (N_{mass} , P_{mass}) and per area (N_{area} , P_{area}). For each pair of leaf traits, we tested for significant differences in slopes and intercepts between interaction levels and reported associated *P*-values

Trait pairs (X and Y)	Interactions	Slope	Intercept	<i>r</i>	<i>P</i> -values	
					Slope	Intercept
LMA – N_{mass}	Fallow-High	–0.493 ^a	1.742	–0.65***	0.008	0.005
	Fallow-Low	–0.733 ^b	1.726			
	Forest-High	–1.040 ^b	1.668			
	Forest-Low	–0.558 ^a	1.681			
LMA – P_{mass}	–	–1.369	1.636	–0.72***	0.293	0.076
LMA – P_{area}	Dry-High	–1.078 ^a	–3.355	0.06 NS	0.002	0.009
	Dry-Low	1.895 ^b	–3.396			
	Moist-High	0.641 ^c	–3.316			
	Moist-Low	–0.971 ^a	–3.237			
LMA – Leaf mass	Dry-High	1.446 ^a	–3.442	0.60***	< 0.0001	0.107
	Dry-Low	4.053 ^b	–3.579			
	Moist-High	1.277 ^a	–3.443			
	Moist-Low	1.796 ^a	–3.458			
N_{mass} – P_{mass}	Fallow	2.060 ^a		0.65***	0.048	< 0.0001
	Forest	1.499 ^b				
$\delta^{13}\text{C}$ – LMA	Dry-Fallow	–3.306 ^a	–4.368	–0.36**	0.0046	0.0002
	Dry-Forest	7.302 ^b	–4.384			
	Moist-Fallow	5.653 ^b	–4.485			
	Moist-Forest	2.593 ^c	–4.501			
$\delta^{13}\text{C}$ – P_{mass}	Fallow-High	–7.393 ^a	9.067	0.48***	0.034	0.582
	Fallow-Low	–7.917 ^a	9.100			
	Forest-High	–8.295 ^a	9.154			
	Forest-Low	–3.857 ^b	9.100			
$\delta^{13}\text{C}$ – N_{mass}	Fallow-High	–3.109 ^a	5.557	0.41***	0.032	0.173
	Fallow-Low	–4.202 ^a	5.541			
	Forest-High	–5.710 ^b	5.511			
	Forest-Low	–2.220 ^c	5.492			

Slopes with the same letter are not significantly different.

r is Pearson correlation coefficient for each pair.

****P* < 0.001; ***P* < 0.01; **P* < 0.05 and other values are not significant.

dependent effect of harvest on plant nutrient concentration found in our study suggests that a different approach is needed to more accurately model the impact of NTFP harvest on plant population dynamics. Harvest intensity should be evaluated at the individual level rather than at the population level as it is unclear if the fitness of an individual in a harvested population is different from that of one in an unharvested population. The effect of harvest should therefore be modelled explicitly, at the individual level, as a size dependent factor. For this purpose, integral projection models, for which demographic rates are modelled as size-dependent functions (Ellner & Rees 2006), rather than matrix projection models (Caswell 2001), would provide the appropriate framework.

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References

- Ackerly, D.D., Knight, C.A., Weiss, S.B., Barton, K. & Starmer, K.P. (2002) Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia*, **130**, 449–457.
- Anten, N.P.R. & Ackerly, D.D. (2001) Canopy-level photosynthetic compensation after defoliation in a tropical understory palm. *Functional Ecology*, **15**, 252–262.
- Anten, N.P.R., Martinez-Ramos, M. & Ackerly, D.D. (2003) Defoliation and growth in an understory palm: quantifying the contribution of compensatory responses. *Ecology*, **84**, 2905–2918.
- Anten, N.P.R., Miyazawa, K., Hikosaka, K., Nagashima, H. & Hirose, T. (1998) Leaf nitrogen distribution in relation to leaf age and photon flux density in dominant and subordinate plants in dense stands of a dicotyledonous herb. *Oecologia*, **113**, 314–324.
- Assogbadjo, A.E., Sinsin, B., Codjia, J.T.C. & Van Damme, P. (2005) Ecological diversity and pulp, seed and kernel production of the Baobab (*Adansonia digitata*) in Benin. *Belgian Journal of Botany*, **138**, 47–56.

- Bawa, K.S., Kress, J.W., Nadkarni, M.N. & Lele, S. (2004) Beyond paradise: meeting the challenges in Tropical biology in the 21st century. *Biotropica*, **36**, 437–446.
- Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods Research*, **33**, 261–304.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis and Interpretation*, 2nd edn. Sunderland, Massachusetts, USA.
- CTFT (1988) *Khaya senegalensis* (Desr.) A. Juss. *Bois et Forêts des Tropiques*, **218**, 43–56.
- Ellner, S.P. & Rees, M. (2006) Integral projection models for species with complex demography. *American Naturalist*, **167**, 410–428.
- Elser, J.J., Fagan, W.F., Kerkhoff, A.J., Swenson, N.G. & Enquist, B.J. (2010) Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. *New Phytologist*, **186**, 593–608.
- Fornara, D.A. & du Toit, J.T. (2007) Browsing laws? Response of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology*, **88**, 200–209.
- Fox, J. (2003) Effect displays in R for generalised linear models. *Journal of Statistical Software*, **8**, 1–18.
- Fry, B.R., Thoulke, K., Neill, C., Michner, R.H., Mersch, F.J. & Brand, W. (1996) Cryoflow: cryofocusing nanomole amounts to CO₂, N₂ and SO₂ from an elemental analyzer for stable isotopic analysis. *Rapid Communications in Mass Spectrometry*, **10**, 953–958.
- Gaoue, O.G. & Ticktin, T. (2007) Patterns of harvesting foliage and bark from the multipurpose tree *Khaya senegalensis* in Benin: variation across ecological regions and its impacts on population structure. *Biological Conservation*, **137**, 424–436.
- Gaoue, O.G. & Ticktin, T. (2008) Impacts of bark and foliage harvest on *Khaya senegalensis* (Meliaceae) reproductive performance in Benin. *Journal of Applied Ecology*, **45**, 34–40.
- Gaoue, O.G. & Ticktin, T. (2009) Fulani knowledge of the ecological impacts of *Khaya senegalensis* (Meliaceae) foliage harvest in Benin and its implications for sustainable harvest. *Economic Botany*, **63**, 256–270.
- Gaoue, O.G. & Ticktin, T. (2010) Effects of harvest of nontimber forest products and ecological differences between sites on the demography of African mahogany. *Conservation Biology*, **24**, 605–614.
- Ghimire, S.K., Gimenez, O., Pradel, R., McKey, D. & Aumeeruddy-Thomas, Y. (2008) Demographic variation and population viability in a threatened Himalayan medicinal and aromatic herb *Nardostachys grandiflora*: matrix modelling of harvesting effects in two contrasting habitats. *Journal of Applied Ecology*, **45**, 41–51.
- Gusewell, S. (2004) N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, **164**, 243–266.
- Hoffmann, W.A., Franco, A.C., Moreira, M.Z. & Haridasan, M. (2005) Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. *Functional Ecology*, **19**, 932–940.
- Kitajima, K., Mulkey, S.S., Samaniego, M. & Wright, S.J. (2002) Decline of photosynthetic capacity with leaf age and position in two tropical pioneer tree species. *American Journal of Botany*, **89**, 1925–1932.
- Law, W. & Salick, J. (2005) Human-induced dwarfing of Himalayan snow lotus, *Saussurea laniceps* (Asteraceae). *Proceedings of the National Academy of Science, USA*, **102**, 10218–10220.
- Meir, P., Levy, P.E., Grace, J. & Jarvis, P.G. (2007) Photosynthetic parameters from two contrasting woody vegetation types in West Africa. *Plant Ecology*, **192**, 277–287.
- Miller, R.O. (1998) High temperature oxidation: dry ashing. *Handbook of Reference Methods for Plant Analysis* (ed. Y.P. Kalra). CRC Press, Boca Raton, FL, 53–56.
- Moe, S.J., Stelzer, R.S., Forman, M.R., Harpole, W.S., Daufresne, T. & Yoshida, T. (2005) Recent advances in ecological stoichiometry: insights for population and community ecology. *Oikos*, **109**, 29–39.
- Normand, D. & Sallenave, P. (1958) Caractéristiques et propriétés des acadjous (*Swietenia* et *Khaya*). *Bois et Forêts des Tropiques*, **59**, 43–52.
- Paeth, H. & Thamm, H.-P. (2007) Regional modeling of future African climate north of 15°S including greenhouse warming and land degradation. *Climatic Change*, **83**, 401–427.
- Parren, M.P.E. (2003) *Liana and logging in West Africa*. PhD dissertation, Wageningen University, Wageningen.
- Petit, S. (2003) Parklands with fodder trees: a Fulbe response to environmental and social changes. *Applied Geography*, **23**, 205–225.
- Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, **87**, 1733–1743.
- Poorter, H. & Evans, J.R. (1998) Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia*, **116**, 26–37.
- Porder, S., Paytan, A. & Vitousek, P.M. (2005) Erosion and landscape development affect plant nutrient status in the Hawaiian Islands. *Oecologia*, **142**, 440–449.
- R Development Core Team (2007) *R: A Language and Environment for Statistical Computing*. R Foundation for statistical computing, Vienna, Austria.
- Reich, P.B. & Oleksyn, J. (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Science, USA*, **101**, 11001–11006.
- Reich, P.B., Tjoelker, M.G., Machado, J.L. & Oleksyn, J. (2006) Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature*, **439**, 457–461.
- Sack, L., Marañón, T. & Grubb, P.J. (2002) Global allocation rules for patterns of biomass partitioning. *Science*, **296**, 1923a.
- Sack, L., Cowan, P.D., Jaikumar, N. & Holbrook, N.M. (2003) The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant, Cell and Environment*, **26**, 1343–1356.
- Santiago, L.S. & Wright, I.J. (2007) Leaf functional traits of tropical forest plants in relation to growth form. *Functional Ecology*, **21**, 19–27.
- Small, E. (1972) Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Canadian Journal of Botany*, **50**, 2227–2233.
- Snyder, K.A. & Williams, D.G. (2003) Defoliation alters water uptake by deep and shallow roots of *Prosopis velutina* (Velvet Mesquite). *Functional Ecology*, **17**, 363–374.
- Tessier, J.T. & Raynal, D.J. (2003) Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. *Journal of Applied Ecology*, **40**, 523–534.
- Ticktin, T. (2004) The ecological implications of harvesting non-timber forest products. *Journal of Applied Ecology*, **41**, 11–21.
- du Toit, J.T., Bryant, J.P. & Frisby, K. (1990) Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. *Ecology*, **71**, 149–154.
- Townsend, A.R., Cleveland, C.C., Asner, G.P. & Bustamante, M.M.C. (2007) Control over foliar N:P ratios in tropical rain forests. *Ecology*, **88**, 107–118.
- Warren, C.R. & Adams, M.A. (2006) Internal conductance does not scale with photosynthetic capacity: implications for carbon isotope discrimination and the economics of water and nitrogen use in photosynthesis. *Plant, Cell and Environment*, **29**, 192–201.
- Warton, D.I., Wright, I.J., Falster, D.S. & Westoby, M. (2006) Bivariate line-fitting methods for allometry. *Biological Reviews*, **81**, 259–291.
- Wright, I.J., Reich, P.B. & Westoby, M. (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, **15**, 423–434.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, W., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklass, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Populations of *Khaya senegalensis* surveyed and sampled.

Table S2. Model selection for the effect of harvest, regions, and habitat.

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